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PHILONOTIS (BARTRAMIACEAE, BRYOPHYTA) IN RUSSIA

PHILONOTIS (BARTRAMIACEAE, BRYOPHYTA) В РОССИИ

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Abstract

The genus *Philonotis* in Russia includes two species with a subcontinuous holarctic distribution, *P. fontana* (Hedw.) Brid. and *P. tomentella* Molendo, one holarctic highly disjunctive species, *P. marchica* (Hedw.) Brid., three mainly European and western Asian species, *P. calcarea* (Bruch et al.) Schimp., *P. rigida* Brid. and *P. seriata* Mitt., and one mainly SE Asiatic and African species, *P. falcata* (Hook.) Mitt. *Philonotis capillaris* Lindb. has a disjunct distribution from western Europe to the Caucasus area, and in western North America through the Aleutian Islands to Russian Far East. *P. yezoana* Besch. & Cardot is known in addition to Japan and Korea from North and South Far East regions of Russia, and *P. americana* Dism. ranges from the Kuril Islands and Kamchatka to Western North America. Only a few specimens from European Russia can be referred to *P. caespitosa* Jur. A key to the species is given, they are illustrated and their taxonomy is discussed. The total ranges of taxa based on specimens studied, previous revisions and checklists and floras are given. Some erroneous reports are corrected and correct reports are confirmed. DNA studies (nrITS1-2 and cp *trn*L-F) show distiction of sect. *Philonotis* and sect. *Philonotula,* however *P. capillaris* is resolved within the former one. ITS analysis supports the distinction of *P. caespitosa* and *P. tomentella* from *P. fontana*, but the latter species appears to be paraphyletic.

Резюме

Род *Philonotis* в России представлен двумя видами с панголарктическим распространением (*P. fontana* (Hedw.) Brid. и *P. tomentella* Mol.), одним видом с дизъюнктивным распространением в Голарктике (*P. marchica* Brid.), тремя европейскими видами, встречающимися в Азии только на западе (*P. calcarea* (Bruch et al.) Schimp., *P. rigida* Brid. и *P. seriata* Mitt.) и одним видом с восточноазиатско-африканским ареалом (*P. falcata* (Hook.) Mitt). *Philonotis capillaris* Lindb. имеет дизъюнктивное распостранение в Западной Европе, на Кавказе и далее на Российском Дальнем Востоке, Алеутских островах и на западе Северной Америки. *P. yezoana* Besch. & Cardot известен из Японии и на Российском Дальнем Востоке от Камчатки до юга Приморья; *P. americana* Dism. встречается на Курильских островах, Камчатке и на западе Северной Америки. К *P. caespitosa* Jur. могут быть отнесены лишь немногочисленные образцы из центра европейской России; этот таксон остается проблематичным. Приводятся ключ для определения видов, иллюстрации и карты распространения в России, обсуждаются проблемы таксономии и общее распространение видов. Некоторые ошибочные указания исправлены. Данные анализа последовательностей ДНК (nrITS1-2 и cp *trn*L-F) подтверждают отличия секций *Philonotis* и *Philonotula,* однако *P. capillaris* оказывается в первой из них. Анализ ITS показывает отличия P. caespitosa и *P. tomentella* от *P. fontana*, при этом последний вид оказывается парафилетичным.

KEYWORDS: Bryophyta, Bartramiaceae, *Philonotis*, molecular phylogenetic, Russia

INTRODUCTION

This study began as a part of “The moss flora of Altai” project. The Altai Mts are located within the Southern Siberian regional division of Siberia (Ignatov *et al*., 2006). Six species of *Philonotis* are listed from that area: *P. caespitosa* Jur., *P. calcarea* (Bruch et al.) Schimp., *P. falcata* (Hook.) Mitt., *P. fontana* (Hedw.) Brid., *P. seriata* Mitt. and *P. tomentella* Molendo.

The *Philonotis* flora of Siberian Russia is actually rather similar to that of Western Europe. The only European taxa not occurring in Siberia are *P. cernua* (Wilson) D.G. Griffin & W.R. Buck, *P. marchica* (Hedw.) Brid. and *P. rigida* Brid. However, *P. rigida* occurs in the Caucasus and, as the DNA research has shown, *P. marchica* occurs in the Russian Far East. The presence of *P. hastata* (Duby) Wijk & Margad. in Europe (Hill *et al*.,

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2006) should be confirmed (Koponen, 2009a).

We enlarged the area covered by this revision to the whole territory of Russia. Therefore, we include in the key and give descriptions of, in addition *to P. marchica* and *P. rigida*, three other *Philonotis* taxa occurring within the present study area: *P. capillaris* Lindb., *P. yezoana* Besch. & Cardot and *P. americana* Dism.

The previous revision of the genus for the Soviet Union was published by Savich-Lyubitskaya & Smirnova (1970), but it does not include several recently found species, and provides only general distribution data. Since Ignatov & Ignatova (2003) dealt with the *Philonotis* flora of Middle European Russia, the Russian part of Eastern Fennoscandia was covered by Brotherus (1923), and arctic areas of European Russia by Abramova *et al*. (1961), we pay special attention to the areas east and southeast of the Ural Mountains and the Caucasus. We list some specimens from neighboring countries, such as Kazakhstan, Kirgizia, Georgia, and Azerbaijan, as well as China, Japan, and Turkey. Preliminary revisions for Japan, China and SE Asia were published by Koponen & Norris (1996) and Koponen (1998, 2009b, 2010a, b).

MATERIAL AND METHODS

Morphology. The investigation began by studies of the *Philonotis* collections by the junior authors from the Altai Mts and was extended with the collections preserved in MHA, MW, LE, H, H-BR and H-SOL. Very useful for this study were the specimens in H-BR, studied and annotated by earlier bryologists and specialists on *Philonotis,* such as M.G. Dismier, L. Loeske and W.M. Zales. The revision of H-BR material revealed many misidentifications and misunderstandings of species concepts, which resulted in range extension for several taxa, such as *P. capillaris* and *P. falcata*.

For studies with the dissecting microscope the specimens were first dipped in alcohol and then soaked in ca. 7 % KOH solution and finally rinsed in water. This method destroys the internal contents of the cells such as chloroplasts, colours the cell walls in brownish, so that papillae and mammillae become more easily visible (Koponen, 1970). For the key, the vegetative leaves from fertile, female stems of the previous growing season were used (for details see Koponen, 2009a).

We cite only a few specimens from outside Russia. The detailed distribution areas of the taxa in SE Asia from Pakistan to Japan in the East and New Guinea in the South will be published later (Koponen, in prep.) The total distribution ranges we give are based mainly on standard floras and the latest checklists. However, if we have studied previously unreported specimens from SW Asiatic countries, such as Iran or Afghanistan, we add an exclamation mark (!) after the country name.

DNA study. The sampling strategy addresses mostly the possibility of differentiating *P. fontana* from *P. tomentella* and understanding the delimitation between these two species, which was a point of continuous disagreement among bryologists. Besides this we focused on *P. caespitosa*, which is also a problematic taxon. Additionally, all other species occurring in Russia were sampled, although less extensively. Specimen data and GenBank voucher numbers are provided in Appendix 1.

Protocols of DNA extraction, amplification and sequencing were the same used in previous moss studies, described in detail by, *e.g.,* Gardiner *et al.* (2005).

Sequences were aligned manually in BioEdit (Hall, 1999), and analyzed by Nona under the Winclada shell (Goloboff, 1994). The overall alignment of ITS includes 940 positions, 226 variable, and 140 parsimony informative. The chloroplast *trn*L-F region is less variable: 448 positions, 37 variable, and 24 parsimony informative.

Maximum parsimony trees for ITS (Fig. 1A) and for *trn*L-F (Fig. 1B) were rooted on *P. hastata* (tests revealed no principal difference in topology in most parts of the tree if *P. calcarea* or *P. rigida* were chosen as outgroups). Members of other genera of the family, *Anacolia* and *Bartramia*, have ITS that is very different from *Philonotis*, and cannot be unequivocally aligned.

Jackknife support was calculated in Nona for 1000 replications (number of search reps 10, hold 10, max tree 100, do max). Obtained values for nodes in tree are shown in Fig. 1A,B and given below as ITS/*trn*L-F support.

RESULTS AND DISCUSSION OF THE MOLECULAR STUDY

General topology. The topology of ITS and *trn*L-F trees were found to be principlly similar, although the latter has poorer resolution, especially in *P. fontana* complex. All the clades outside the *P. fontana* complex in the *trn*L-F tree were found in ITS tree as well, with a slightly better resolution.

The ITS phylogenetic tree includes a basal clade of *Philonotis calcarea* (jackknife support 100) and a terminal clade (jackknife support 74) with two subclades. The first subclade (I) includes species without proximal or central papillae on the laminal cells (jackknife support 67), while the second one (II) is formed by species with proximal or central papillae of the *P. fontana* complex, *P. yezoana* and *P. capillaris* (jackknife support 100). The latter species has only distal papillae on its laminal cells, except for the proximal leaf lamina in some specimens, and it has so far been classified together with the species of group I. However, both nuclear and chloroplast markers indicate its position within group II. Considering this exception, and to simplify the discussion, we refer to Clade I as including species with distal papillae on the laminal cells, and to Clade II as *P. fontana* complex, or species with proximal papillae on the laminal cells [*i.e.*, including the exceptional of *P. capillaris*, and including *P. yezoana*, a species with central position of papillae on the laminal cells].

The clade of *Philonotis calcarea*

Interestingly, *P. calcarea*, traditionally classified in sect. *Philonotis*, was found not to be closely related to the *P. fontana* complex at all, despite sharing the proxi-

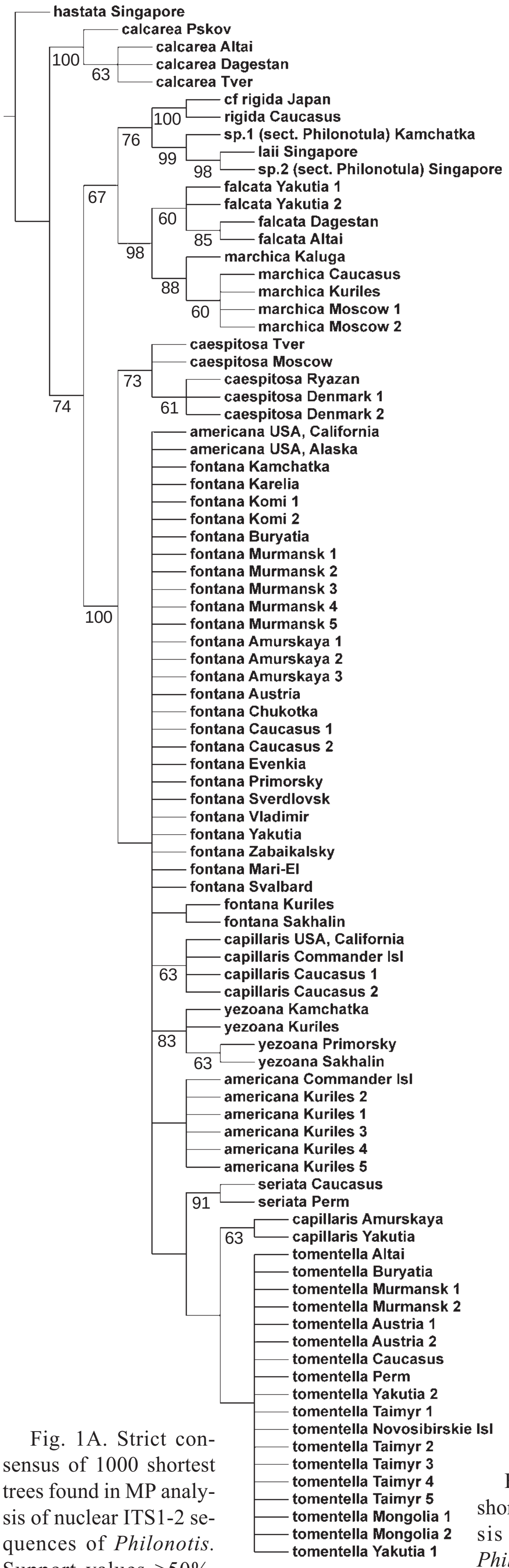


Fig. 1A. Strict consensus of 1000 shortest trees found in MP analysis of nuclear ITS1-2 sequences of *Philonotis*. Support values >50%, calculated by 1000 iterations in Nona, are indicated below branches.

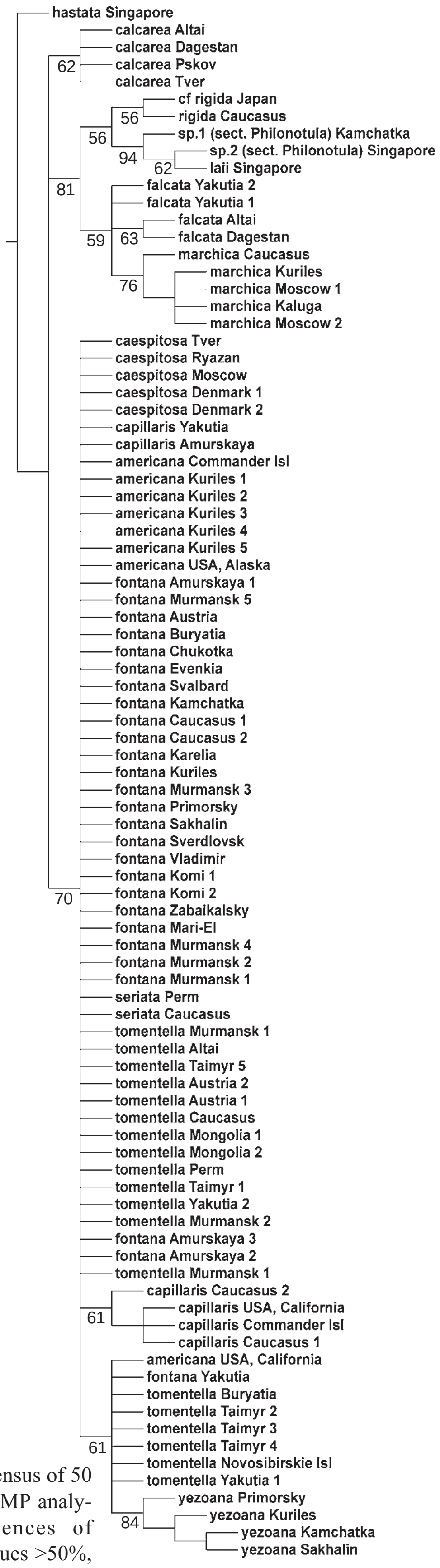


Fig. 1B. Strict consensus of 50 shortest trees found in MP analysis of trnL-F sequences of *Philonotis*. Support values >50%, calculated by 1000 iterations in Nona, are indicated below branches.

mal papillae on the laminal cells with the latter. Specimens from NW and Central European Russia, Caucasus and the Altai in South Siberia were found to be subidentical. Some motifs in the alignment correspond to those of species with distal papillae on the laminal cells.

The clade of species with distal papillae on the laminal cells (I)

Within the clade of species with distal papillae, two subclades were found. One includes *P. marchica* and *P. falcata* (ITS/*trn*L-F support 98/59); another one is formed by *P. rigida*, *P. laii* T.J. Kop., *P.* sp. 2*,* and *P.* sp. 1 (ITS/*trn*L-F support 76/56). The latter is represented by one specimen from Kamchatka, morphologically most similar to poorly developed *P. falcata,* but the genetic differences preclude that it belongs to this species.

Philonotis marchica and *P. falcata* have never been the focus of special morphological comparisons, largely because *P. marchica* was reported mostly from Europe and North America, while *P. falcata* occurs mostly in Asia. Although *Philonotis marchica* was reported, from time to time, from Asia, *e.g.* from the Russian Far East (Lazarenko, 1941), this raised the suspicion that it is just a misidentification of *P. falcata*. Moreover, the specimen could not be checked in KW and LVS. However, the molecular data revealed a population of *P. marchica* in the Russian Far East that is subidentical in ITS to those occurring in Middle European Russia and Caucasus. The clade of *P. marchica* is moderately supported both in ITS *trn*L-F analyses (88/76), while *P. falcata* has lower support in the ITS tree (60) and form a polytomy in the *trn*L-F tree.

Philonotis falcata shows a high variation in both ITS and *trn*L-F sequences, which is caused by two specimens from Yakutia. These were collected only a few kilometers from each other. They differ considerably from specimens from Altai and Caucasus, which are subidentical. There are 12 substitutions in ITS and 4 in *trn*L-F that differentiate two latter specimens of “typical” *P. falcata* from *P. marchica*. At the same time, the Yakutian specimens have eight ITS substitutions in common with other specimens of *P. falcata* and four in common with *P. marchica*, while in *trn*L-F two substitutions are in common with other specimens of *P. falcata* and two with *P. marchica*. This situation can be interpreted as a hybridization event between the two species, unless they are not considered as just one species with a number of haplotypes. However, the latter conclusion disagrees with a rather great difference in DNA sequences between the species of Clade I (much bigger than between species in *P. fontana* group, on average).

One specimen, *Philonotis* sp. 1, from Kamchatka that is morphologically similar to *P. falcata,* appeared, in both the ITS and *trn*L-F trees, in another clade together with *P. rigida* and two South-East Asiatic species, *P. laii* and *P.* sp. 2 from Singapore*,* which were included in the analysis as outgroup. The close relationship of the Kamchatkan specimen with the two latter species received very high support (ITS/*trn*L-F: 99/94). Interestingly, the Kamchatkan plant was collected in a thermal field, and this type of habitat in Kamchatka and the Kuril Islands is peculiar for the occurrence of species with generally tropical distributions, *e.g. Campylopus umbellatus* (Arn.) Paris and *C. atrovirens* De Not. (Ignatova & Samkova, 2006), *Trematodon longicollis* Michx. (Bakalin *et al*., 2009). At the moment, the identity of the Kamchatkan specimen remains open, because more comprehensive material is required for a well-founded decision.

Philoniotis rigida from Caucasus also brought a surprise by unexpectedly grouping with one specimen from Japan, previously referred to *P. mollis* (ITS/*trn*L-F support 100/56). The correctness of the DNA data was in this case confirmed by an additional morphological study: the Japanese specimen was proved to be autoicous.

The clade of species with proximal papillae on the laminal cells (II)

This clade includes mainly species of the *Philonotis fontana* complex. In the ITS tree it contains two subclades, a smaller one formed by *P. caespitosa* (with support 73), and a bigger one that includes all other species, but without support. In the *trn*L-F analysis *P. caespitosa* is not resolved, and appears within a polytomy.

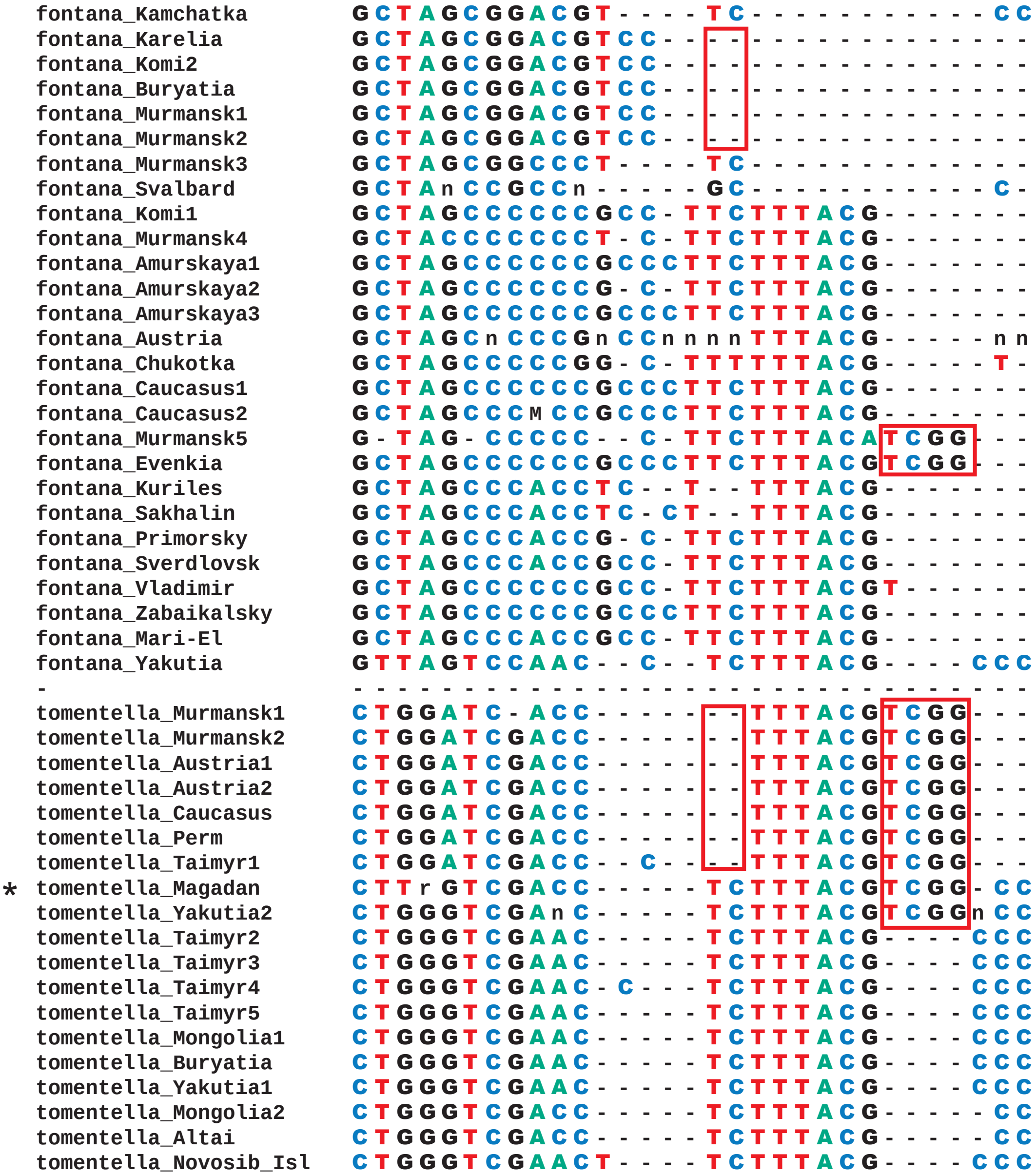
In the ITS analysis, the bigger subclade is formed by a polytomy of *Philonotis fontana* (and two *P. americana* specimens) with several nested clades consisting of *P. capillaris* (in two separate clades)*, P. americana* (in part), *P. yezoana*, *P. seriata,* and *P. tomentella*.

In the *trn*L-F tree, only the two most distinct species, *P. capillaris* and *P. yezoana*, form two clades among the polytomy of all other species of the *P. fontana* group.

Smaller clades nested in the ITS tree within the polytomy of *P. fontana* (and *P. americana,* two American specimens) have rather poor support; only two species have support above 80: ***P. seriata*** (91), and ***P. yezoana*** (83). These species are also the morphologically most distinctive ones in this complex. *Philonotis yezoana* is the only species with high support in the *trn*L-F tree (84). The only other clade with support >50 in the *trn*L-F tree is formed by an oceanic group of samples of ***P. capillaris*** (61), which got about the same support in the ITS tree (63). The continental group of samples of *P. capillaris* is equally poorly supported in the ITS tree (63), and they are found in a polytomy by *trn*L-F analysis. ***P. americana*** (East Asian specimens) is resolved as a separate clade only in the ITS tree, although with support <50.

One of the main motivations for this study was the issue of separating ***P. fontana*** and ***P. tomentella***, which has been discontinuously discussed by bryologists, without obvious progress. It was caused by a situation when characters being distinctive for a species in one region did not work with specimens collected in another one, resulting in a kaleidoscope of opinions on species differentiation and distribution.

The strict consensus tree in Fig. 1A illustrates a clear separation of these two species. However, this topology



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  fontana_Kamchatka       GCTAGCGGACGT----TC-----------CC
  fontana_Karelia         GCTAGCGGACGTCC-----------------
  fontana_Komi2           GCTAGCGGACGTCC-----------------
  fontana_Buryatia        GCTAGCGGACGTCC-----------------
  fontana_Murmansk1       GCTAGCGGACGTCC-----------------
  fontana_Murmansk2       GCTAGCGGACGTCC-----------------
  fontana_Murmansk3       GCTAGCGGCCCT----TC-------------
  fontana_Svalbard        GCTAnCCGCCn-----GC-----------C-
  fontana_Komi1           GCTAGCCCCCCGCC-TTCTTTACG-------
  fontana_Murmansk4       GCTACCCCCCCT-C-TTCTTTACG-------
  fontana_Amurskaya1      GCTAGCCCCCCGCCCTTCTTTACG-------
  fontana_Amurskaya2      GCTAGCCCCCCG-C-TTCTTTACG-------
  fontana_Amurskaya3      GCTAGCCCCCCGCCCTTCTTTACG-------
  fontana_Austria         GCTAGCnCCCGnCCnnnnTTTACG-----nn
  fontana_Chukotka        GCTAGCCCCCGG-C-TTTTTTACG-----T-
  fontana_Caucasus1       GCTAGCCCCCCGCCCTTCTTTACG-------
  fontana_Caucasus2       GCTAGCCCMCCGCCCTTCTTTACG-------
  fontana_Murmansk5       G-TAG-CCCCC--C-TTCTTTACATCGG---
  fontana_Evenkia         GCTAGCCCCCCGCCCTTCTTTACGTCGG---
  fontana_Kuriles         GCTAGCCCACCTC--T--TTTACG-------
  fontana_Sakhalin        GCTAGCCCACCTC-CT--TTTACG-------
  fontana_Primorsky       GCTAGCCCACCG-C-TTCTTTACG-------
  fontana_Sverdlovsk      GCTAGCCCACCGCC-TTCTTTACG-------
  fontana_Vladimir        GCTAGCCCCCCGCC-TTCTTTACGT------
  fontana_Zabaikalsky     GCTAGCCCCCCGCCCTTCTTTACG-------
  fontana_Mari-El         GCTAGCCCACCGCC-TTCTTTACG-------
  fontana_Yakutia         GTTAGTCCAAC--C--TCTTTACG----CCC
  -                       -------------------------------
  tomentella_Murmansk1    CTGGATC-ACC-------TTTACGTCGG---
  tomentella_Murmansk2    CTGGATCGACC-------TTTACGTCGG---
  tomentella_Austria1     CTGGATCGACC-------TTTACGTCGG---
  tomentella_Austria2     CTGGATCGACC-------TTTACGTCGG---
  tomentella_Caucasus     CTGGATCGACC-------TTTACGTCGG---
  tomentella_Perm         CTGGATCGACC-------TTTACGTCGG---
  tomentella_Taimyr1      CTGGATCGACC--C----TTTACGTCGG---
* tomentella_Magadan      CTTrGTCGACC-----TCTTTACGTCGG-CC
  tomentella_Yakutia2     CTGGGTCGAnC-----TCTTTACGTCGGnCC
  tomentella_Taimyr2      CTGGGTCGAAC-----TCTTTACG----CCC
  tomentella_Taimyr3      CTGGGTCGAAC-----TCTTTACG----CCC
  tomentella_Taimyr4      CTGGGTCGAAC-C---TCTTTACG----CCC
  tomentella_Taimyr5      CTGGGTCGAAC-----TCTTTACG----CCC
  tomentella_Mongolia1    CTGGGTCGAAC-----TCTTTACG----CCC
  tomentella_Buryatia     CTGGGTCGAAC-----TCTTTACG----CCC
  tomentella_Yakutia1     CTGGGTCGAAC-----TCTTTACG----CCC
  tomentella_Mongolia2    CTGGGTCGACC-----TCTTTACG-----CC
  tomentella_Altai        CTGGGTCGACC-----TCTTTACG-----CC
  tomentella_Novosib_Isl  CTGGGTCGAACT----TCTTTACG----CCC
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Fig. 2. Thirty one parsimony informative positions of *Philonotis fontana* and *P. tomentella*, arranged from right to left by decrease of their impact into differentiation of *Philonotis fontana* from *P. tomentella* (*i.e.* the order is not as in alignment itself).

was achieved only after omission of one specimen of *P. tomentella* from the Magadan Province (marked by asterisk in Fig. 2). Inclusion of this specimen collapsed the topology of the terminal subclade of the ITS tree, so that the *P. fontana*-complex appeared as an almost totally unresolved polytomy (not shown). The polytomy had a few nested clades composed of *P. seriata* and *P. yezoana*, but *P. fontana* and *P. tomentella* remained unresolved.

A visual analysis of variable ITS positions (Fig. 2) might explain this situation. There is only one position in the alignment which separates all specimens referred by morphology to *P. tomentella* or *P. fontana.* A number of additional positions delimit them with 1-2 exceptions. However, in a number of positions, common substitutions and indels are shared by some specimens of *P. tomentella* and some of *P. fontana* (some of them are framed in Fig. 2). This pattern in ITS sequences may indicate rather frequent recombination events.

There is no difference between *P. tomentella* and *P. fontana* in *trn*L-F. Although a few specimens of *P. tomentella* form a clade within a polytomy of *P. fontana* plus other *P. tomentella* specimens and other species of the group, the specimens of *P. tomentella* segregated in the ITS and *trn*L-F analyses are mostly different. In the latter analysis they are grouped with one specimen of *P. americana* and one of *P. fontana*, and *P. yezoana* shares the same substitutions.

The molecular data indicate incomplete genetic separation of *P. fontana* and *P. tomentella*. The taxonomic conclusions from this situation may differ. Considering the presence of areas in the Arctic and permafrost zone of Siberia, where both species occur and intergrade, the status of subspecies would be the most appropriate. Arguments in favor of the separate species status include: (1) there are extensive areas in the mountains of Central Europe and Caucasus where no intermediates exist, and (2) the total absence of *P. tomentella* in lowland regions of the southern portion of the boreal and hemiboreal zones. In addition, there is a practical reason, since infraspecific taxa are often ignored during collection identification, and this leads to a loss of information.

Both nuclear and chloroplast markers resolve *P. fontana* as paraphyletic. It is problematic and questionable to separate ***P. americana***, which has usually been treated as a subspecies of *P. fontana* (Griffin, 2003). According to our molecular data, it is not separated from *P. fontana* by *trn*L-F, while ITS reveals two haplotypes of *P. americana*, one of which (from North America) is not separable from *P. fontana*, whereas the other one (from Russian Far East) forms a clade nested in a *P. fontana* polytomy. Plants of both haplotypes are identical in morphological characters and quite distinct from *P. fontana* in their leaf arrangement. The haplotype from the Russian Far East differs in a common insertion of five nucleotides, which can be treated as one character. Therefore, we place all specimens in the same taxon, taking into consideration its apparently young age and morphological distinctiveness.

Unexpectedly plants identified by morphology as ***P. capillaris*** appeared to be heterogeneous. It seemed to be easily identified due to slender habit, not pentastichous and relatively flat leaves, as well as by a frequent presence of axillary gemmae. Most studied specimens were found in a consistent clade, resolved both in the ITS and *trn*L-F trees and equally moderately supported (63/61); they exhibit a wide distribution range: Europe (Caucasus), North America (California),and the Russian Far East (Commander Islands). However, two specimens, from Eastern Yakutia and the Amurskaya Province in Russia, which display almost no morphological differences from other specimens of *P. capillaris*, were found to be (1) fully identical to each other by morphology and sequences; (2) more similar by ITS to *P. tomentella*, than to *P. capillaris* and not resolved by *trn*L-F. The present poor material does not allow making a decision if they represent a cryptic undescribed species, or a putative hybrid between *P. capillaris* and *P. tomentella*.

Another problem is ***P. caespitosa***, hardly separable from *P. fontana* by morphology, especially from the underdeveloped male plants of the latter species, with similar habit and lamina areolation. These species can be easily separated if male plants are at hand, because they have different inner perigonial leaves (acuminate in *P. caespitosa* vs. mostly obtuse or shortly acute in *P. fontana*). Unfortunately male plants are rarely found in *P. caespitosa*. Two specimens with perigonia (from Denmark and the Tver Province of Russia) were included in the molecular analysis. They formed a separate clade together with three sterile specimens (from Denmark and Central European Russia) in ITS tree. At the same time, a number of other specimens previously identified as *P. caespitosa* (from Caucasus, the Murmansk Province and Asiatic Russia) were found within the *P. fontana* grade, and after careful morphological studies they were re-identified as slender forms of *P. fontana*. Summing up, our molecular data support the species status for *P. caespitosa*, which is apparently restricted to North America and Europe, including European Russia.

TAXONOMY

Philonotis Brid., Bryol. Univ. 2: 15. 1827.

Plants in moist persistent or ephemeral habitats, small to robust, growing in dense or loose tufts; stems erect, branching irregularly and with subfloral innovations; one or several innovations may continue as main stems; young stems green, old stems brown to reddish, with hyalodermis and one layer of substereid cortical cells, many layers of parenchymatous medullar cells and distinct central strand. Old stem parts tomentose by rhizoids born from rows of initials on imaginary line decurrent from lateral margin of leaf (lateral macronematal apparatus) or on line at side of lateral margin of leaf. Micronemata not seen. Axillary hairs very short, 2(-3)-celled, with dark-colored basal cell and pale terminal cell(s). Leaves linear, linear-lanceolate or lanceolate, rarely ovate; costa mostly percurrent or excurrent, in cross section with weakly differentiated epidermis, and filled by stereidal cells, guide cells and conducting cells hardly differentiated; basal costa mostly smooth and distal costa papillose or prorulate; leaf cells usually with distinct mammillae/papillae. Most species are dioicous; perichaetia terminal and perigonia terminal or on branches; perigonia disk-like or bud-like; seta elongate; capsule ovoid, gibbous or globose, furrowed to smooth when old; neck short, stomata cryptopore; annulus lacking, dehiscence of operculum by breaking cells; calyptra cucullate.

In the description above those characters are given which are in common to all or most of the species of *Philonotis* studied so far. In the specific descriptions these characters are not repeated.

The characters useful in the classification and identification of *Philonotis*, such as the transparency of the leaf cell areolation, leaf shape, mammillosity/papillosity of leaf cells, capsule shape, and structure of exothecium, were reviewed in previous papers (Koponen, 1996a, 1999, 2009b, 2010a, b; Koponen & Virtanen, 1998). These are discussed and described under each species dealt with in this paper. Special attention is drawn to the sectional characters which separate the species of the section *Philonotis* from the species of the section *Philonotula*, the only sections present in Russia. The kinds of macronematal apparatus are explained in Norris & Koponen (1996, fig. 1). Koponen (2009c) discovered the lateral macronematal apparatus in *Philonotis*, but the placement of macronemata (or initials) in *Philonotis americana* situating laterally on line at side of lateral margin of leaf should be studied further.

The mammillae are either totally over the lumen or bulging and overlapping at the lower or distal ends of the cells, and could in some cases better be called scindulae.

Sectional taxonomy. On the basis of its distal leaf cells with mammillae/papillae at distal cell end, *Philonotis capillaris* was previously thought to be a member of the section *Philonotula*. The section *Yezoanae* was separated based on central mammillae/papillae of the distal leaf cells (Koponen 2010b). On the basis of DNA results, it is possible to include *P. capillaris* and *P. yezoana* in the section *Philonotis*.

KEY TO *PHILONOTIS* IN RUSSIA

The key is based on fully grown specimens of female plants. Fully grown vegetative leaves from below the modified leaves under the perichaetium were used for the key. For identification, use the leaves of previous growing season. In the key the term “mammillae/papillae” refers to structures of the cells that are most clearly seen under a compound microscope. *Philonotis cernua* has not been recorded from the study area and is marked in the key by brackets.

1\. Distal leaf cells with central papillae… *P. yezoana*
– Mammillae/papillae either on lower or distal cell end; central papillae rare 2

2\. Distal leaf cells with mammillae/papillae at lower cell end; lower leaf border with double-crenulate teeth (two adjoining cells form a tooth) 3
– Distal leaf cells with mammillae/papillae at distal cell end; lower leaf border entire, serrate or serrulate ... 10

3\. Leaves in five vertical rows along the stem….. 4
– Leaves not in rows 5

4\. Leaves falcate to one direction, ovate, tapering gradually to acute point; costa usually coarsely mammillose at back ± from base .... *P. seriata*
– Leaves spirally twisted, abruptly acuminate from broadly ovate base; costa rarely coarsely mammillose .... *P. americana*

5\. Leaf cell areolation translucent; leaf cells smooth or lowly mammillose; leaf border plain or revolute; distal cells narrow or wide 6
– Leaf cell areolation dim or only basal leaf ± translucent; cells distinctly mammillose/papillose; leaf border recurved or revolute; distal leaf cells clearly narrower (–1/3) than proximal cells 7

6\. Leaves erect, triangular, ovate or from broadly ovate base tapering to short acute or obtuse apex; leaves plicate or smooth, leaf border plain or recurved; costa strong; leaf cells quadrate, rectangular or rhomboidal, smooth or lowly mammilose, usually thin-walled, cells at apiculus narrow elongate or vermicular and thick-walled; inner perigonial leaves short acute or obtuse .... *P. fontana*, male plants
– Leaves usually one-sidedly secund, with ovate base and rather short apex, not plicate, leaf border plane or narrowly recurved; costa narrow; leaf cells regular, rectangular or rhomboidal, smooth or lowly mammilose, cells at apiculus ± rectangular, all laminal cells thin-walled; inner perigonial leaves acuminate .... *P. caespitosa*

7\. Leaves twisted when dry, forming spiraling stem tip, diverging from the stem at a wide angle; often in vertical rows .... *P. americana*
– Leaves not twisted, at stem apex straight or falcate-secund, leaf base erect or spreading; leaves not in rows 8

8\. Plants robust, leaves (1.5-)1.8-3.0 mm long; costa 60-125(-200) µm wide near base; cells near costa at widest part of leaf mostly 48-100 µm long, narrow rectangular, thin-walled and translucent; perigonial leaves acute .... *P. calcarea*
– Plants smaller, slender or tiny to moderately robust, leaves (0.5-)1-2 mm long; costa 25-80 µm wide near base; cells near costa at widest part of leaf 24-40 µm long, quadrate, rectangular or rhomboidal, thin- to firm-walled; perigonial leaves obtuse or acute 9

9\. Stems matted together into solid tufts; leaf tapering from ovate base to acuminate or cuspidate, straight or slightly flexuose apex; leaf acumens bending to different directions; costa excurrent to longly excurrent; leaf cell areolation in basal leaf dim and leaf cell walls firm, cells ± rectangular; inner perigonial leaves acute to acuminate .... *P. tomentella*
– Stems in loose tufts; leaf tapering from broadly ovate base to acute or acuminate apex, leaf acumens one-sidedly secund, especially in the apical part of stems; costa not or scarcely excurrent, rarely longly excurrent; leaf cell areolation in ovate basal leaf ± translucent and cells thin-walled, quadrate, rectangular or rhomboidal; inner perigonial leaves obtuse to short-acute .... *P. fontana*

10(2). Synoicous or autoicous; often with sporophytes 11
– Dioicous; sporophytes rare 12

11\. Autoicous; perigonia bud-like below perichaetia; costa strong, excurrent; capsule asymmetrical; peristome present .... *P. rigida*
– Synoicous; costa usually percurrent; capsule symmetrical; peristome lacking .... [*P. cernua*]

12\. Tiny, 0.5-2.0 cm tall, thread-like plant; leaves straight, linear-lanceolate, slightly concave, not in rows; all leaf cells mammillose/papillose at distal cell end or leaf cells bulging at proximal cell end in basal leaf and mammillose/papillose in distal cell end in apical part of leaf .... *P. capillaris*
– Larger, 1-5(-9) cm tall, plants; leaves falcate-secund, from ovate or triangular base gradually tapered to acute or acuminate apex, concave to carinate, often

distinctly pentastichous, all leaf cells mammillose/papillose at distal cell end 13

13\. Leaves distantly situated, slightly carinate to concave; marginal teeth single; costa 50-75 µm wide at base; brood branches with long stalk and acuminate leaflets .... *P. marchica*

– Leaves imbricate, strongly carinate; marginal teeth single or in long leaves geminate; costa 75-100 µm wide at base; brood branches with short stalk and acute leaflets .... *P. falcata*

Philonotis section ***Philonotula*** (Bruch et al.) Jaeger Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1873-74: 78 (Gen. Sp. Musc. 1: 540). 1875. – *Bartramia* sect. *Philonotula* Bruch et al., Bryol. Eur. 4: 1. 1851. – *Philonotis* subgen. *Philonotula* (Bruch et al.) Schimp., Syn. Musc. Eur. (ed. 2). 424. 1876.

Type: *Philonotis rigida* Brid.

Plants small to medium-sized; inhabiting moist or mesic habitats in temperate to tropical areas; leaf dimorphism not or weakly present; marginal teeth single-crenulate, serrulate or serrate, turned towards apex, or teeth partially geminate; leaf cells often narrow and mammillose/papillose to leaf base; single papillae or more pronounced mammillae/papillae at distal ends of leaf cells, either over lumen or on end walls of cells. Capsule horizontal or inclined, ellipsoid or gibboid; peristome complete.

Philonotis falcata (Hook.) Mitt., J. Linn. Soc. Bot. Suppl. 1: 62. 1859. – *Bartramia falcata* Hook., Trans. Linn. Soc. London 9: 317, *27 f. 4.* 1808. – *Philonotis fontana* var. *falcata* (Hook.) Brid., Bryol. Univ. 2: 21. 1827. – Lectotype (designated by Koponen, 2012a): Nepal, coll. Dr. *Buchanan* (BM!, ex herb. Hooker, ex herb. Kew, "Dr. Smith 1808, No. H/2359"; isolectotypes in BM!, ex herb. Dawson Turner, ex herb. Hooker; FH!, ex herb. Mitten, ex herb. Hooker).

P. carinata Mitt., Trans. Linn. Soc. London, Bot., ser. 2, 3: 164. 1891. – *P. falcata* var. *carinata* (Mitt.) Ochi, Nova Hedwigia 4: 100. 1962. – Holotype: Japan. Ishikawa Pref., Kaga Prov., Miyanoshita, V.1887 *Bisset* (NY-Mitten!; isotype: *J. Bisset 67* in H-BR!). – Synonymized by Dismier (1912). Figs. 3, 5.

Historical review. Koponen (2010b) discussed lengthily on the previous misunderstandings in the taxonomy of *Philonotis falcata*, *P. turneriana* (Schwägr.) Mitt. and *P. nitida* Mitt.

Plants slender to medium sized, 1-3(-5) cm, often pale in colour; leaves 1-1.8 mm long and 0.5-0.6 mm wide, on short innovations narrower, imbricate, erect when dry, falcate, carinate, in five rows (best seen on innovations of wet specimen), from broadly ovate or triangular base gradually tapering to an acute or acuminate apex; margin plane, basal marginal leaf cells smooth, with thin bulging outer walls, middle margin uniserrulate or irregularly geminate by protruding cell corners, distal margin uniserrate; costa 75-100 µm broad at leaf base, percurrent or excurrent, on dorsal side smooth at base, with minute papillae or protruding cell corners at apical part; leaf areolation translucent, lowest basal cells low mammillose but not distinctly differentiated from upper cells which have distinct mammilla/papilla at distal cell end, no distinct mammilla/papilla visible at proximal cell end; basal leaf cells thin-walled, 20-55×10-20 µm, quadrate to short rectangular, mid-leaf cells with thicker walls, elongate, ± rectangular, 20-50×5-7µm, narrower than basal cells, distal leaf cells still narrower, rectangular or vermicular, 25-37×2-5 µm. Short-stalked bulbils with acute leaflets are commonly present along stem.

Dioicous. Sporophytes not seen in specimens from Russia. [Perichaetia terminal; perichaetial leaves ca. 1.7 mm long, from broad triangular base long acuminate, costa long excurrent, areolation translucent, cells slightly mammillose; perigonia terminal or on specialized branches; leaves below perigonium slightly smaller than the vegetative leaves of female or sterile shoots; perigonial leaves 2.0-2.3 mm long, with broad concave uncoloured or brownish base, lax and translucent; inner perigonial leaves acute or acuminate. Dry capsule horizontal, short ellipsoid or gibbous, 2-3 mm long. Spores ca. 25 µm, minutely papillose.]

Illustrations: Ochi, 1962: pl. 4, figs. A-D, drawn from the type of *P. falcata*; Ochi, 1962: pl. 5, figs. A-F, drawn from the type of *P. carinata*; Noguchi, 1989: 569, fig. 252; Koponen, 1996b: 115, fig. 1; Kürschner & Ochyra 1999: 272, fig. 2; Eddy 1996: 234, fig. 489; 235, fig. 490, as *P. turneriana*.

Differentiation. The safest diagnostic characters of *Philonotis falcata* are the strongly carinate leaves, which are often clearly inserted in rows on the stem, and mammillae/papillae at the distal end of the leaf cells. The costa is often bending both dorsally, ventrally and sideways, which gives a very characteristic shape to the leaves. Most *Philonotis* species have flat leaves, or the leaves are concave at most. The five rows of leaves are best seen in plants with short and imbricate leaves. If the leaves are distant, the rows are not as easily visible, but even in such plants the innovations, where the leaves are not yet fully grown, show this character (best seen when wet). The leaf shape itself, and connected with it, the shape of the leaf cells is rather variable. Ochi (1962) separated the variety *carinata* which has acute leaves with shortly excurrent or percurrent costa. In these plants the leaf cells are shorter and wider than in plants with longer leaves. This possibly gives these plants their characteristic pale colour. The leaves of *P. falcata* tend to have a uniserrate, plane border, and this is a regular character of its short-leaved forms. However, the leaf margin may be geminate or partly geminate in plants with long leaves and a long acuminate apex (var. *falcata*). The total variation of leaf shape is wider than in *P. marchica.* Other characters separating *P. marchica* and *P. falcata* are discussed under *P. marchica*.

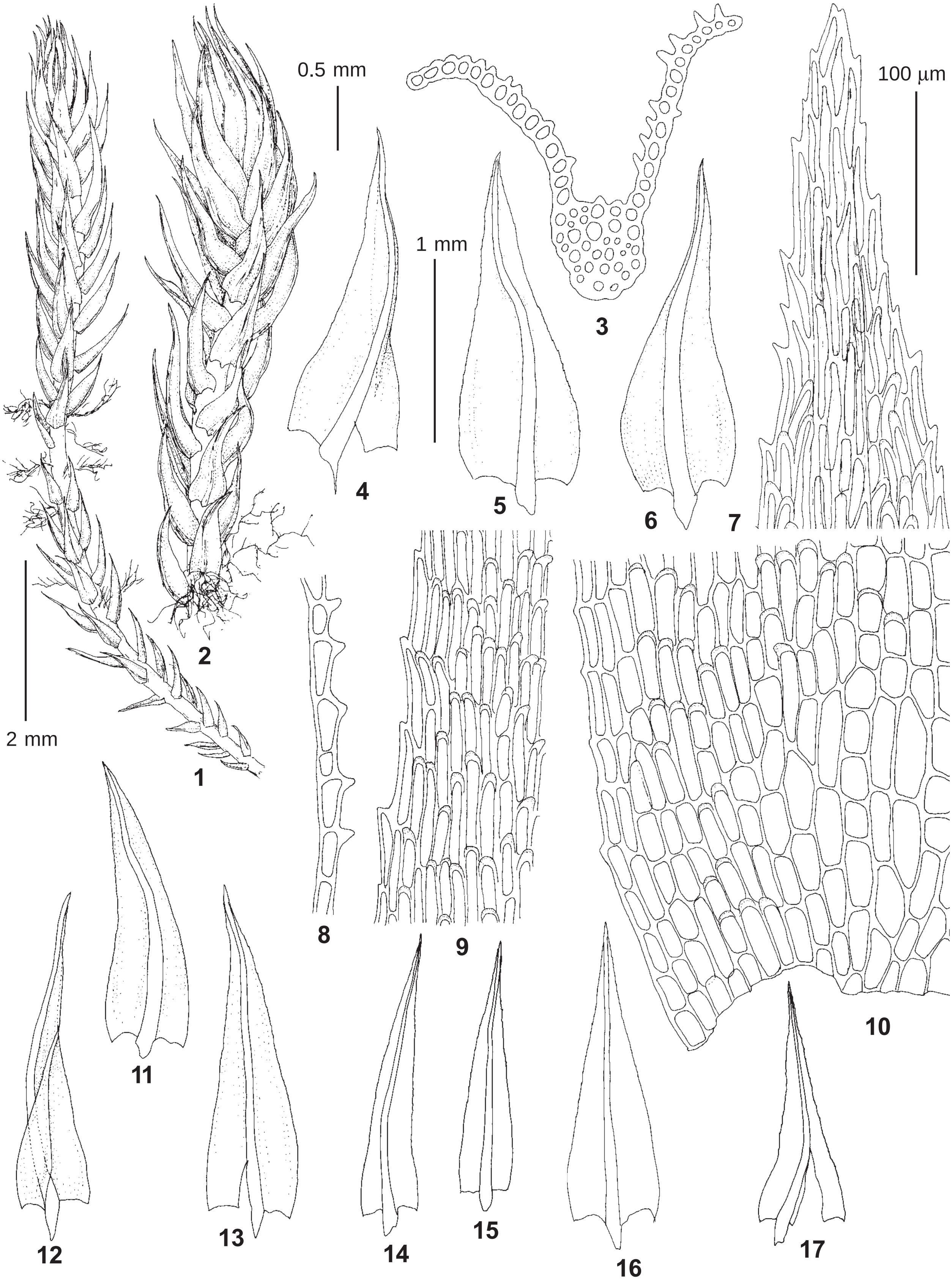

Fig. 3. *Philonotis falcata* (Hook.) Mitt. (1-10 – from Dagestan, Gunib, 23.V.2009, *Ukrainskaya s.n.*, MW; 11-13 – from Yakutia, Teplyj Klyuch, *Ignatov & Ignatova #11-2107*, MHA; 14-17 from Altai, Chemal, 2.VIII.2000, *Ignatova s.n.*, MW): 1 – habit, wet; 2 – habit, dry; 3 – leaf transverse section; 4-6, 11-17 – leaves; 7 – cells of leaf apical part; 8 – leaf longitudinal section; 9 – upper laminal cells; 10 – basal laminal cells. Scale bars: 2 mm for 1; 1 mm for 4-6, 11-17; 0.5 mm for 2; 100 µm for 3, 7-10.

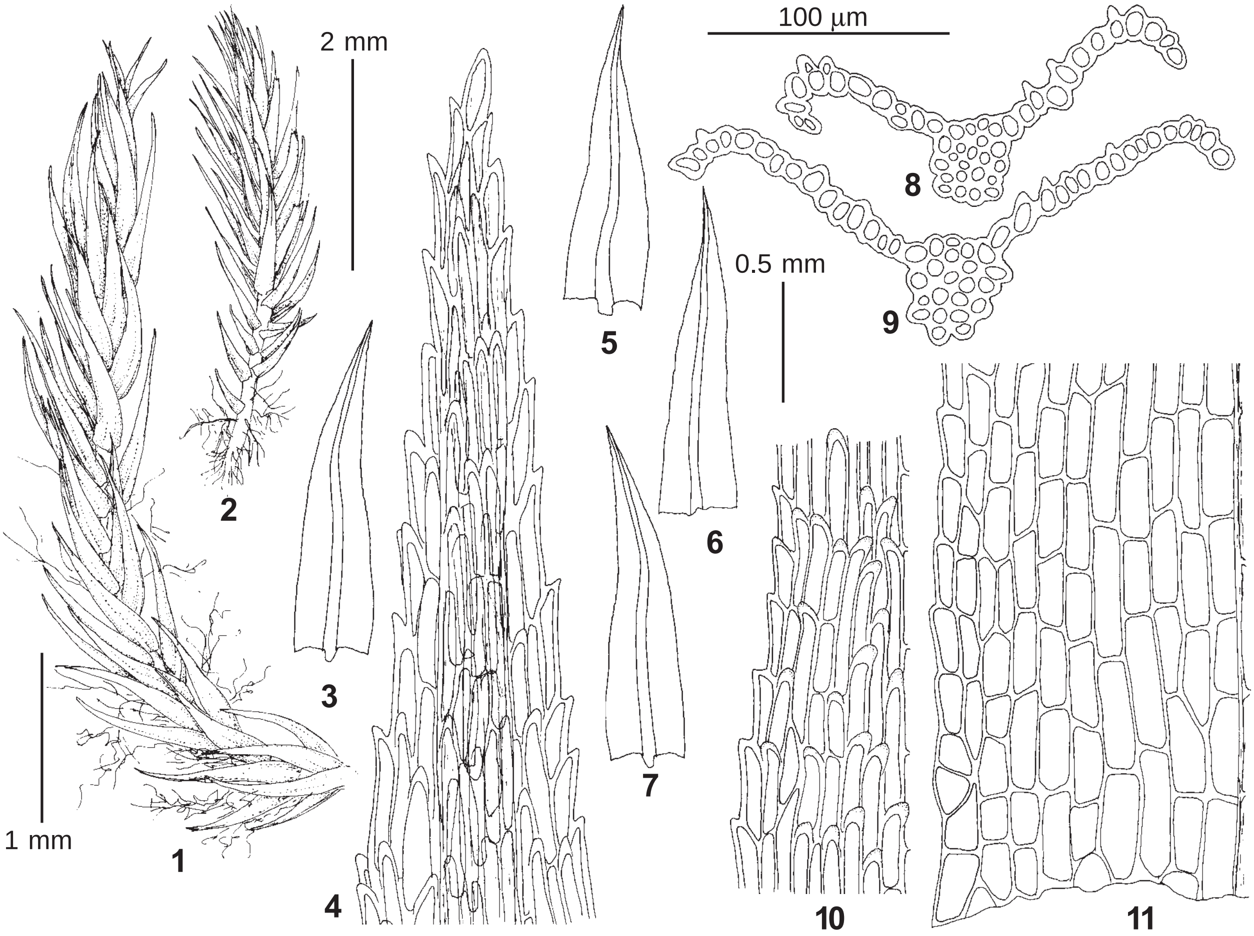

Fig. 4. *Philonotis* sp. 1 (sect. *Philonotula*) (from: Kamchatsky Territory, Karymskoe Lake, 17.VII.2006, *Samkova s.n.*, MW): 1 – habit, dry; 2 – habit, wet; 3, 5-7 – leaves; 4, 10 – upper laminal cells; 8-9 – leaf transverse sections; 11 – basal laminal cells. Scale bars: 2 mm for 2; 1 mm for 1; 0.5 mm for 3, 5-7; 100 μm for 4, 8-11.

Philonotis falcata has commonly been misidentified as *P. seriata*, another species having leaves in five rows. The latter is easily separated from *P. falcata* by the leaf cells having mammillae/papillae at the proximal ends of the leaf cells.

A specimen from Kamchatka, *P.* sp. 1 (sect. *Philonotula*), which was previously identified as *P. falcata,* was resolved by molecular data apart from *P. falcata* and together with *P. laii* and *P.* sp. 2 from Singapore. It is illustrated in Fig. 4. The plants are rather slender, with narrow, gradually tapering leaves, most similar to those in specimens of *P. falcata* from the Altai Mts. The clearly 5-ranked, imbricate and strongly carinate leaves separate this specimen from *P. laii* and *P.* sp. 2 from Singapore and suggest its placement in *P. falcata*. Poor sampling of *P. falcata* and other members of section *Philonotula* in the molecular study does not allow a reliable understanding of their genetic variability and relationships; this is beyond the scope of the present study. Thus the exact identity of Kamchatkan specimen remains unclear.

Habitat ecology. *Philonotis falcata* grows on wet substrates such as cliffs and stones along creek beds and on rocks with trickling water.

Range in Russia. *Philonotis falcata* was first recorded outside its previously known Himalayan-Japanese range from Kirgizia by Koponen (1996b) and from the Altai area (Ignatov *et al*., 2006). The present records from the Caucasus (Ignatov *et al*., 2010) were surprising finds; several specimens we also found among misidentified herbarium specimens. The specimens H-BR 3133 002, H-BR 3125 018, and H-SOL 1551 003, with propagules, are quite typical *P. falcata*, with strongly carinate, falcate leaves. Four other specimens (H-BR 3123 009, 3123 001, 3125 020 and 3125 034) are very slender, but the three listed last have short-stalked propagules, which confirm their identification.

Recent records of the species in Buryatia and especially in Yakutia expand its known area far to the north.

Specimens examined: **RUSSIA**: CAUCASUS: **Ossetia**: Lars, ad fl. Terek, 24.V.1881, *A.H. & V.F. Brotherus s.n.* (LE, H-BR 3125 018); **Dagestan**: Dargi District, in valle pr. pagum Balkar, 19.VII.1898, *Alexeenko s.n.* (LE); Gunib District, Gunib, 23.V.2009, *Ukrainskaya s.n.* (LE, MW). ASIATIC RUSSIA: **Altai Republic**: Shebalino District, Chemal, 2.VIII.2000, *Ignatova s.n* (MW); same place, 5.VIII.1991, *Ignatov* #29/33 (MHA); **Republic Sakha/Yakutia**: Tomponsky District, Teplyj Klyuch, *Ignatov & Ignatova #11-2102, 11-2107* (MW, MHA);

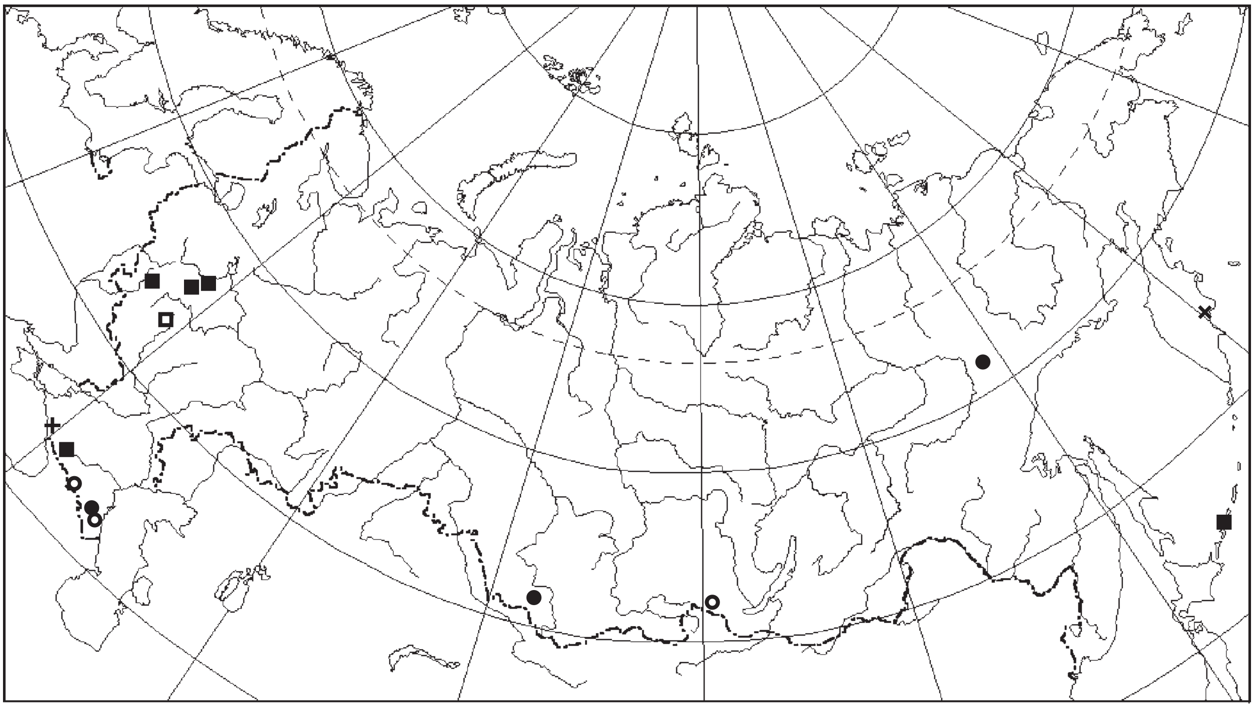

Fig. 5. Distribution of *Philonotis falcata* (Hook.) Mitt. (circles), *P.* sp. 1 (oblique cross), *P. marchica* (Hedw.) Brid. (squares) and *P. rigida* Brid. (cross) in Russia. Solid figures show specimens used in DNA studies.

Buryatia: Eastern Sayan Mts, Oka River basin, Sorok River, *Afonina #02808, 04108* (LE).

Specimen of P. sp. 1**: Kamchatsky Territory**, Elizovo District, Karymskoe Lake, 17.VII.2006, *Samkova s.n.* (MW).

Total range. *Philonotis falcata* is widely distributed and common in southeast Asia from western Himalaya to Japan in the east and Indonesia in the south. It is known from many central and South African localities (distribution maps in Koponen, 1996b, 2003). The African specimens seen, as well as the specimens from Caucasus area and Altai have ± triangular leaves with a short acute apex and represent *P. falcata* var. *carinata*. According to Ochi (1962, 1963) both varieties are common in Japan. – Europe (Ignatov *et al*., 2010). – SW Asia: Afghanistan, Yemen (Kürschner & Frey, 2011). The record of *P. falcata* from Iran (Koponen, 2012a) joins its ranges in Caucasus area and in the Himalayas. – *Philonotis falcata* and *P. turneriana* have been included in the flora of Hawaii (Bartram, 1933; Crosby, 1965; Staples *et al*., 2004) but the specimens so named represent other taxa (Koponen, in prep.).

Selected specimens examined: **GEORGIA**: **Imeretia:** Oprtsheti ad. fl. Rion, 31.V.1877 *Brotherus* (H-BR 3123 009, as *P. capillaris*); ad ripam dextr. fluminis Tschorek, prope Batum, 20.VI.1890 *S. Sommier & E. Levier* – Iter Caucasicum 24 (H-BR 3133 002, as *P. marchica*).

AZERBAIJAN: Lenkoran, Alaschinsk, 13.V.1916 *Voronichin* (H-BR 3123 001, as *P. arnellii*).

KAZAKHSTAN: Terskei Alatau, in trajectu Barskom, reg. alp. super., 1896 *Brotherus* (H-BR 3118 013, as *P. seriata*); jugum Tianschan Septentrionalis, Montes Transilienses, vallis Bolschoje Almaatinskoje Uschtschelje, supra lacum Bolschoje Almaatinskoje, 5.IX.1958, *S. Lisowski* (H 3106933, as *P. seriata*).

Philonotis marchica (Hedw.) Brid., Bryol. Univ. 2: 23, 735. 1827. – *Mnium marchicum* Hedw., Spec Musc. 196. 1801. 2– Type: Europe, not seen. Figs. 5-6.

Plants slender to medium sized, 1-3(-5) cm, often pale in colour; leaves 1.5-2 mm long and 0.4-0.5 mm wide, loosely arranged, ± erect when dry, slightly falcate and carinate or concave, sometimes in five rows, from ovate or triangular base gradually tapering to an acuminate apex; margin plane, basal marginal leaf cells smooth, with thin bulging outer walls or basal leaf margin weakly serrulate, middle margin uniserrulate by protruding cell corners, distal margin uniserrate; costa 50-75 µm wide at leaf base, excurrent, on dorsal side smooth at base, with minute papillae or protruding cell corners at apical part; leaf areolation translucent, leaf cells papillose with papilla at distal cell end, no distinct mammilla/papilla visible at proximal cell end; leaf cells thin-walled, at base 22-47×7.5-10 µm, rectangular, distal leaf cells narrower, rectangular or narrow elongated, 20-50×5 µm. Long-stalked propagules with acuminate leaves are known for the species.

Dioicous. Perichaetia terminal; perichaetial leaves as in *P. falcata*. Perigonia terminal, perigonial leaves as in *P. falcata*. Dry capsule horizontal, short ellipsoid, ca. 2 mm long. Spores ca. 25 µm, minutely papillose.

Illustrations: Ignatov & Ignatova, 2003: 582, fig. 416; Crum & Anderson, 1981: 652, figs. 309 D-F; Guerra & Gallego, 2010: 262, figs. a-d.

Differentiation. The leaves of *P. marchica* known from Europe, the Near East and North America are not as carinate as the leaves in *P. falcata*, more distantly situated on the stem, have a narrower costa, have always

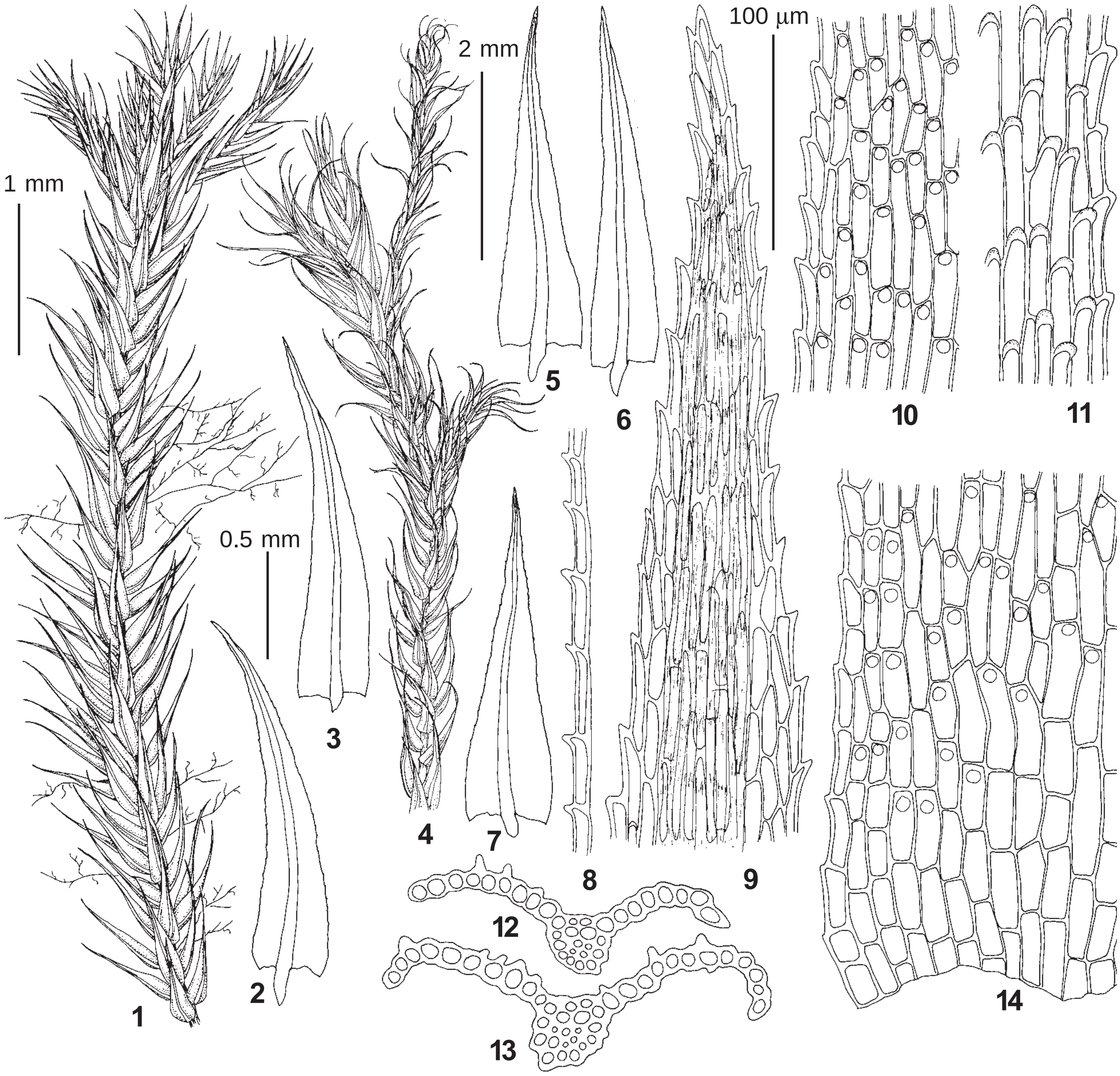

Fig. 6. *Philonotis marchica* (Hedw.) Brid. (from: Kuril Islands, Iturup, *Nyushko #H-28.2-08b*, MHA): 1 – habit, wet; 2-3, 5-7 – leaves; 4 – habit, dry; 8 – leaf longitudinal section; 9 – cells of leaf apical part; 10-11 – upper laminal cells; 12-13 – leaf transverse sections; 14 – basal laminal cells. Scale bars: 2 mm for 4; 1 mm for 1; 0.5 mm for 2-3, 5-7; 100 µm for 8-14.

single, not geminate marginal teeth; it also has long-stalked propagules with acuminate leaves (Petit, 1976). The leaves are sometimes inserted in rows on the stem. The papillae of the leaf cells seem to be taller than in *P. falcata* in the basal leaf portion, and the cells are narrower, which makes the cell areolation more dim in appearance than in the translucent basal leaf in *P. falcata*. According to Ochi (1962, 1963) *P. falcata* differs from *P. marchica* in having more triangular and more strongly carinate leaves that are arranged in regular rows on the stem. The cells of the leaf-blade are more conspicuously broader toward the base, which is hardly narrowed.

Sterile specimens of *P. marchica* and *P. rigida* can be separated by the shorter stems and more rigid habit of the latter, its leaves being straight and not arcuate and having narrower leaf cells throughout the leaf (compare Fig. 6: *9-14* and Fig. 7: *3,6,11*). The leaf margin of leaves of *P. rigida* from below the perichaetium is regularly recurved and irregularly geminate, contrary to plane and uniserrulate margin of *P. marchica*.

Habitat ecology. In central European Russia and in Caucasus, *P. marchica* was collected in spring mires, mesotrophic bogs, and wet meadows with peat deposits. In Iturup Island (Northern Kuril Islands) it grew on wet cliffs near a hot waterfall.

Range in Russia. Until recently, *P. marchica* was known from Russia by a few, mostly old records from the Moscow Province. In many cases the habitats have been destroyed

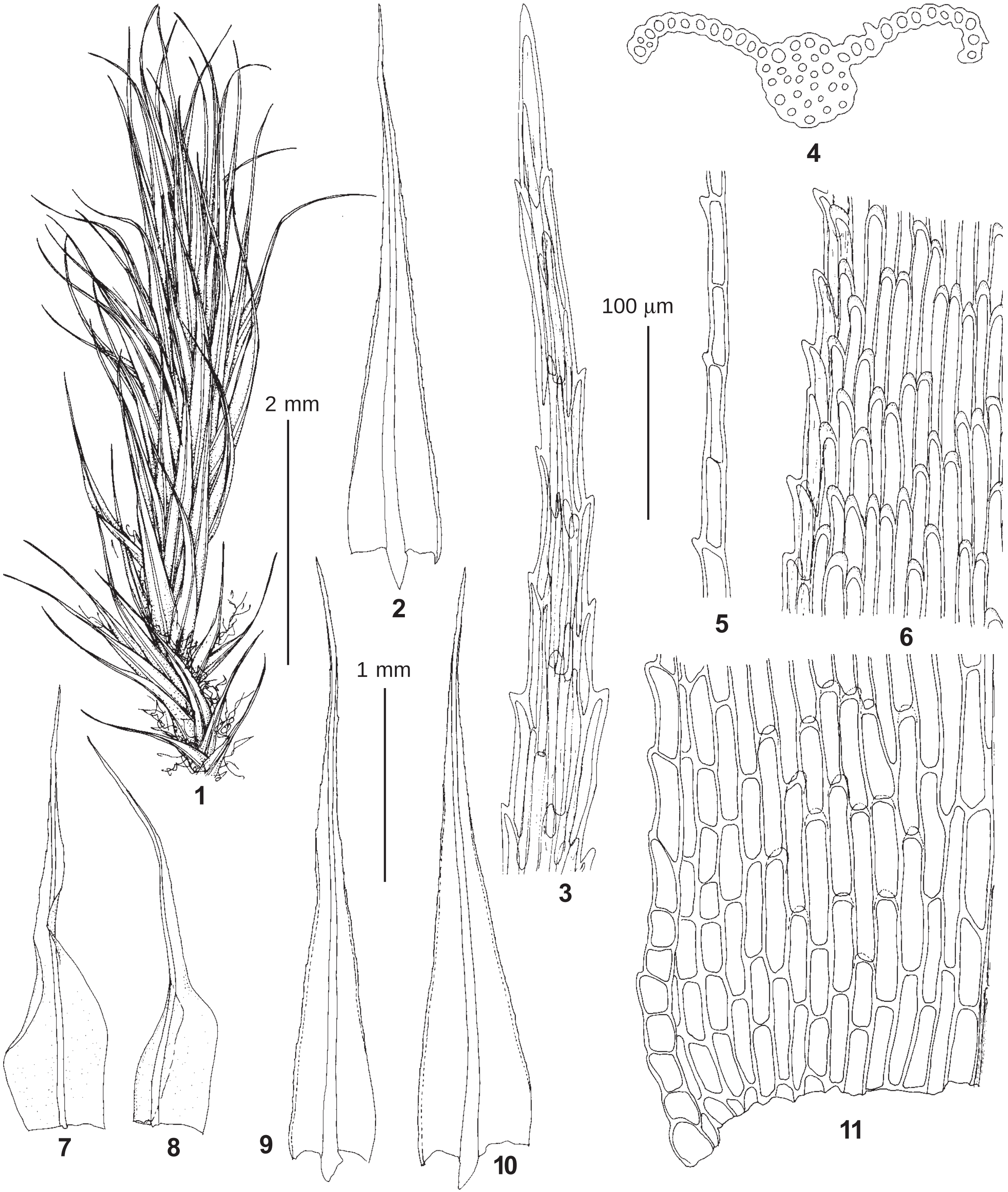

Fig. 7. *Philonotis rigida* Brid. (from: Caucasus, Krasnodar Territory, Shakhe River, 23.VIII.1999, *Ignatov s.n.*, MHA): 1 – habit, dry; 2, 9-10 – leaves; 3 – cells of leaf apical part; 4 – leaf transverse section; 5 – leaf longitudinal section; 6 – upper laminal cells; 7-8 – inner perigonial leaves; 11 – basal laminal cells. Scale bars: 2 mm for 1; 1 mm for 2, 7-10; 100 µm for 3-6, 11.

by drainage of wetlands. It was also recorded from Caucasus (Ignatova *et al.*, 2008) and recently found in new localities in central European Russia. Its area was considerably expanded by a locality in Northern Kuril Islands, where its occurrence was confirmed by the molecular data.

Specimens examined: **RUSSIA**: EUROPEAN RUSSIA: **Moscow Province**: Krasnogorsk District, Petrovo-Dal'nee, 18.VI.1985, *Ignatov s.n.* (MHA, MW); Dmitrov District: Konchinino, 27.VIII.1909, *Petrov #53* (MW); Ochevo, 24.IV.2011, *Teplov s.n.* (MHA); **Kaluga Province**: Spas-Demensky District, Pustovsky Mokh, 6.VI.2012, *Teleganova s.n.* (MHA); **Orel Province**: Dolzhansky District, between Novyj Tim & Lebedki, 16.VIII.1989, *Zolotukhin s.n.* (MHA). CAUCASUS: **Karachaevo-Cherkessia**, Teberda Reserve, *Ignatov & Ignatova #05-3275* (MW). ASIATIC RUSSIA: **Sakhalinskaya Prov-**

ince, Kuril Islands, Iturup, *Nyushko #It-28.2-08b* (MHA).

Total range. – North America (Zales, 1973, map fig. 67). – Europe (Düll, 1985; Sabovljević *et al*., 2008). – SW Asia: Afghanistan, Israel (Frey & Kürschner, 1991), Iran (Akhani & Kürschner, 2004), Lebanon (Kürschner & Frey, 2011), Turkey! (Uyar & Çetin, 2004). – Africa: Algeria, Egypt and Mali (Ros *et al*., 1999). Russian Far East: Present report. – Nyholm (1998) listed *P. marchica* from China and Korea, but the specimens so named that were seen represent other taxa (see Koponen, 2009b).

Brotherus (1892) cited a specimen from "Cauc. minor occ." probably the same as *S. Sommier & E. Levier* – Iter Caucasicum 24 = *P. falcata.*

Selected specimens examined: **GEORGIA**: **Adzharia**, Batumi, Botanical garden, 27.VI.1961, *A.L. Abramova & I.I Abramov s.n.* (LE).

TURKEY: Kurdistania occidentalis: Taurus Armenius. Prope vicum Göldschik ad lacum subsalsum oedem nomine (fonets Tigridis occid.), c. 1350 m, 28.VII.1910, *H. Handel-Mazzetti #2551* (H-BR 3133 007).

U.S.A.: New Brunswick, Bass River, 1871 *J. Fowler* (H-BR 3133 005); Massachusetts, Wellesley 1881 *Cl. E. Cummings* (H-BR 3133 006); USA, Arkansas, *Redfearn #29083* (MHA).

Philonotis rigida Brid., Bryol. Univ. 2: 17. 1827. – Holotype: In Calabriae humidis caespitosa habitat, *Reynier* (B, not seen). – See Raeymaekers (1983).

P. rigida var. *longipedunculata* Müll. Hal., Acta Horti Petropolitani 10(1): 257. 1887, nom. nud. This taxon was not described by Brotherus either, in Acta Soc. Sci. Fenn. 19(12): 15. 1892; see Rayemaekers in Lindbergia 9: 30. 1983. Figs.5, 7.

Historical review. Since the species is very distinct from other European species of *Philonotis*, *P. rigida* has been accepted in all standard European handbooks.

Plants slender, 1-2 cm, densely tufted, pale to brownish in colour; leaves 1.5-2.8 mm long and 0.2-0.6 mm wide, densely arranged, ± erect when dry, straight and slightly concave, not in rows, from narrow base lanceolate, gradually tapering to an acuminate apex; margin recurved on strong leaves of female plants, plane on leaves from sterile shoots, basal marginal leaf cells smooth or crenulate, middle margin uniserrate or in places distinctly geminate, distal margin uniserrate; costa 32-65 µm wide at leaf base, longly excurrent, dorsally papillose at base and serrate at apical part; leaf areolation translucent or apically dim, leaf cells papillose with papilla at distal cell end, lowest basal cells with bulging proximal cell end; leaf cells thin-walled and narrow throughout the leaf, at base 25-87×5-7.5 µm, narrow rectangular, distal leaf cells narrower, rectangular or narrow elongated, 20-45×2.5-5 µm. Long-stalked propagules with acuminate leaves are known for the species (Petit, 1976; Raeymaekers, 1983).

Monoicous. Perichaetia terminal; perichaetial leaves from translucent ovate and concave base long acuminate, with excurrent costa. Male gametangia on short branches below perichaetial leaves. Perigonial leaves similar to perichaetial leaves. Spores 25-30 µm, minutely papillose. Dry capsule horizontal, short ellipsoid, ca. 2 mm long.

Differentiation. The distinction of *Philonotis rigida* from *P. marchica* is discussed under the latter. Sterile specimens of *P. falcata* are readily separated from *P. rigida* by clearly pentastichous and strongly carinate leaves with a curved costa and flat margins. Raeymaekers (1983) stated that the marginal teeth of *P. rigida* are single from near the base up to the apex. This is true for leaves from sterile shoots and innovations, but the margin of well-developed leaves from fertile stems have geminate teeth.

In the single collection from Russia, only plants with gametangia occur. Both perichaetia (with unfertilized archegonia) and bud-like perigonia are situated side by side terminally. It is apparent that after sporophyte formation perigonia would be found in lateral position below perichaetia.

Specimen examined: **RUSSIA**: CAUCASUS: **Krasnodar Territory**: Sochi District, Shakhe River, 23.VIII.1999, *Ignatov s.n.* (MHA).

Total range. Raemaekers (1983) mapped the distribution of *Philonotis rigida* in Europe and additionally reported it from Algeria, Azores and Madeira. He also studied a specimen from Lebanon. Kürschner and Frey (2011) recorded it from Iran, Lebanon and Turkey. Dixon in Potier de la Varde (1923) reported "without doubt", *P. rigida* specimens from Kodaikanal, S. India. According to Koponen (2010b) the plant in India is the specifically distinct, *Philonotis subrigida* Cardot & P. de la Varde.

Selected specimens examined: **GEORGIA**: **Adzharia**: Batumi District, Mtirala Mt., 21.VI.1961, *A.L. Abramova & I.I. Abramov s.n.* (LE); **Imeretia**: Oprtsheti, in en gvarnränna (in a mill course), 1.VI.1877, *Brotherus* (H-SOL 1551 003 as *P. seriata* + *P. rigida*); Oprtsheti ad fl. Rion, 29.V.1877, *V. F. Brotherus* (H-BR 3102 010), Oprtsheti ad fl. Rion, 1.VI.1877, *V. F. Brotherus* (H-BR 3102 003 3102 013), Oprtsheti pr. fl. Rion, ad rupes humidas schistosas, 1.VI.1877, *V. F. Brotherus 292* (H-SOL 1549 004), pr. fl. Rion, ad rupes schist. humo obtectas, 1.VI.1877, *A. H. & V. F. Brotherus* (H 3106786).

Philonotis Brid. section **Philonotis**

Type: *Philonotis fontana* (Hedw.) Brid.

Philonotis Brid. sect. *Yezoanae* T.J. Kop. ("Yezoana"), Acta Bryolich. Asiatica 3: 88. 2010, syn nov.

Type: *Philonotis yezoana* Besch. & Cardot.

Plants slender to rather large; inhabiting wet habitats in the arctic, boreal and temperate zones of the northern hemisphere and corresponding zones in southern mountainous areas. Perichaetial leaves from ovate base long acuminate, erect to spreading. Perigonia discoid. Leaves dimorphous; female and sterile plants have ordinary vegetative leaves, male plants may have modified leaves below perigonia and female plants below perichaetia; lower leaf margin with perpendicular double-crenulate teeth, middle leaf margin often ± geminate and margin near apex serrate; basal leaf cells wide and mammillose; upper leaf cells narrower, mostly linear or vermicular, mammillose/

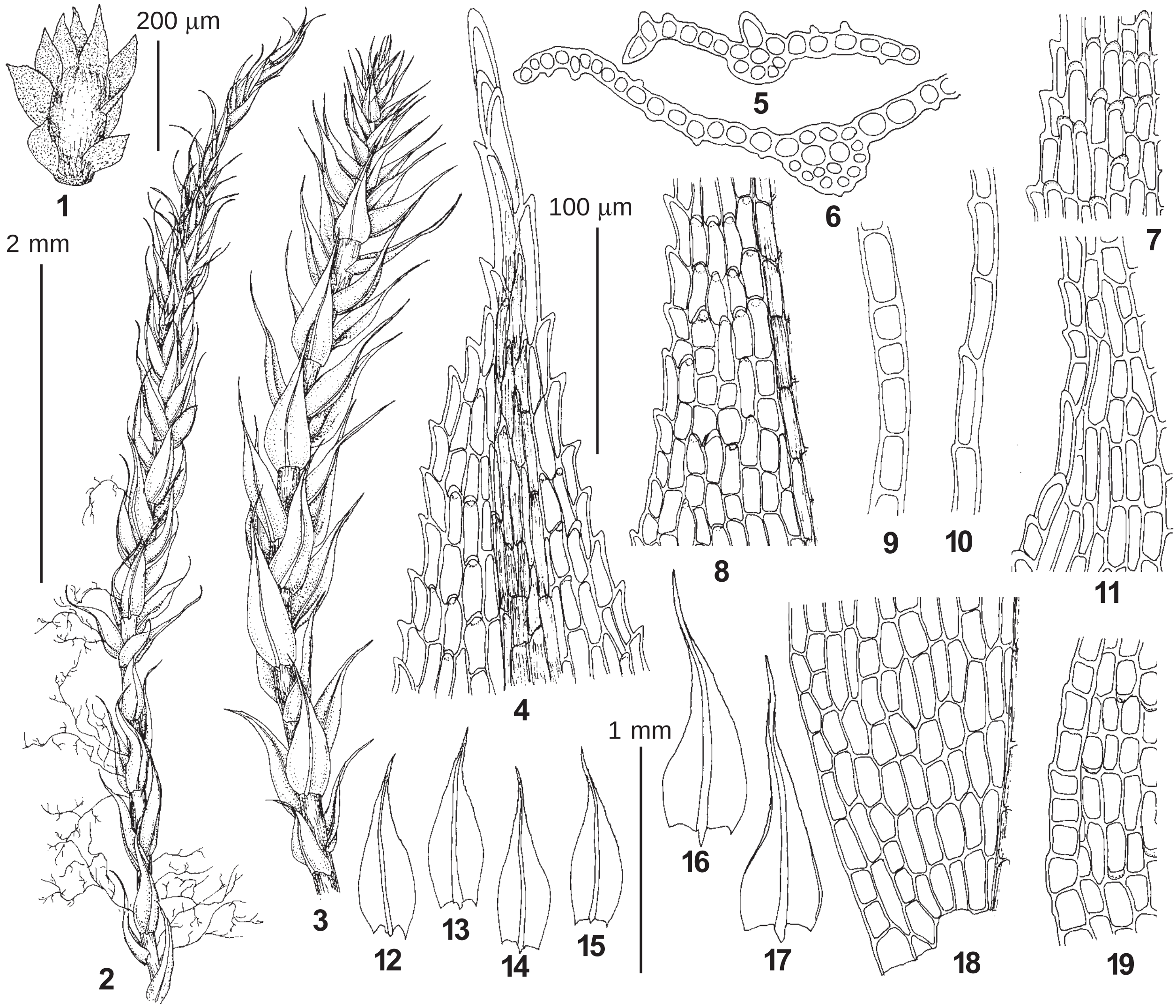

Fig. 8. *Philonotis capillaris* Lindb. (1-4, 8-10, 12-15, 18 – from: Russia, Krasnodar Territory, Adler Distr., Mzymta River, *Seregin et al. #M-2278*, MW; 5-7, 11, 16-17, 19 – from: Russia, Krasnodar Territory, Shakhe River, 23.VIII.1999 *Ignatov s.n.*, MHA): 1 – propagule; 2 – habit, dry; 3 – habit, wet; 4 – cells of leaf apical part; 5-6 – leaf transverse sections; 7 – upper laminal cells; 8, 11 – median laminal cells; 9-10 – leaf longitudinal sections; 12-17 – leaves; 18-19 – basal laminal cells. Scale bars: 2 mm for 2-3; 1 mm for 12-17; 200 µm for 1; 100 µm for 4-11, 18-19.

papillose. Mammillae/papillae are at the proximal end of the leaf cells, or rarely at the middle of basal leaf cells, or regularly at the middle of distal leaf cells (*P. yezoana*). Papillae on distal cell end of narrow apical cells are present in *P. capillaris* and have been observed in *P. fontana*. Capsule horizontal, gibbous; peristome complete.

The stem leaves are dimorphic on male plants and dimorphy has been observed in female plants. In most specimens studied the sterile shoots and female plants have similar vegetative leaves, but on fertile male plants the leaves below the perigonium at a distance downwards are appressed and shorter than vegetative leaves lower down on the same stem. The cells of these leaves are usually larger than the cells of vegetative leaves and thin-walled. This character is most pronounced in *Philonotis fontana*, in which also some female plants may have short-acute leaves below the perichaetium This difference between female and male plants has not been generally understood, although it is described in some floras, such as Flowers (1935), Lawton (1971), Smith (1978, 2004), and Nyholm (1998). It may even happen that a male plant produces these modified leaves year after year without developing a perigonium. Such plants have been misidentified and described as different species or varieties.

The double-crenulate teeth are formed by the cell ends of two adjoining marginal cells so that the lower cell has the crenula at the distal cell end and the adjoining cell has proximal crenula. This character was known 100 years ago but was then forgotten. Rancken (1914) used the character “double-mammillate” as a key character, as did Brotherus (1923): “Blätter wenigstens am Rande mit einfachen und Doppelmamillen”. On depauperate shoots of *Philonotis caespitosa* and *P. tomentella* the double-crenulate teeth may be few, but such teeth can always be found on some of the leaves of the shoot. This character is weakly developed in *P. capillaris* and *P. yezoana*, while in *Philonotis* plants belonging to the section *Philonotula*, or the other sections of *Philonotis*, it has not been observed.

Accordingly, the section *Philonotis* is well defined by three unique character states: (1) The leaf cells mostly with proximal mammillae/papillae, (2) the dimorphy of leaves, and (3) a double-crenulate lower leaf border (especially if *P. capillaris* and *P. yezoana* are considered as belonging to this section and not to sections *Philonotula* and *Yezoanae*). The most reliable differentiating characteristic of the species in the section *Philonotula* is the major mammilla/papilla situated at the distal cell end. Additional species of section *Philonotula* were dealt with by Koponen & Norris (1996) and Koponen (2010b).

Philonotis capillaris Lindb., Hedwigia 6: 40. 1867. – *Bartramia capillaris* (Lindb.) Lindb. ex T. Jensen, Bot. Tidsskr. 2: 272. 1868. – *Philonotis marchica* var. *capillaris* (Lindb.) Limpr. in Cohn, Krypt. Fl. Schlesien 1: 117. 1875. – *P. fontana* var. *capillaris* (Lindb.) Lindb., Musci Skand. 15. 1879. – *P. fontana* subsp. *capillaris* (Lindb.) Hèrib., Mem. Ac. Sci. Clermont-Ferrand ser. 2, 14: 284. 1899. – Lectotype (designated by Koponen & Isoviita, 2010): "359. *Bartramia*, flos masc? et foem." Denmark. "Mellem Björnsholm og Lindgerd i vejgröft, skjult under lyng og pors, i skygge. Logstor, IV.1863" *T. Jensen* ("*Philonotis capillaris* Lindb. n. sp.", H-SOL).

Philonotis arnellii Husn., Rev. Bryol. 17: 45. Apr-Mai 1890; Muscol. Gallica 268. Jun-Jul 1890. – Lectotype (designated by Koponen & Isoviita, 2010): Sweden. Smeland, Barkeryd, Boarp, ad radices rupium, 2.VII.1884 *H. Wilh. Arnell* (GB, male, isolectotype in S, male, "vid skuggade bergsrötter").

P. capillaris Lindb. *sensu* Husnot, Muscol. Gallica 269. 1890. – Based on: Pyrenees, Lesperou, *Spruce* (H-SOL, H; S, ex herb. S. O. Lindberg). – Synonymized by Dismier (1908). Figs. 8-10.

Historical review. For the nomenclature and synonymous names, see Koponen & Isoviita (2010).

Plants pale green to brownish, very slender and thread-like, shoots 0,5-2 cm; stem reddish; leaves 1-1,5 mm long, distantly situated, not arranged in rows, erect to erecto-patent when dry, slightly concave, from narrow lanceolate base gradually tapering to slender, filiform, serrate apex; margin plane, basal border entire, apical border crenulate to serrulate; costa weak, 12-25 µm broad near leaf base, apical dorsal side mammillose by protruding cell corners as large as serration at apex, percurrent or excurrent; areolation translucent, in lower part of leaf cells quadrate to rectangular, 15-70×10-20 µm, gradually narrower toward apex, 17-50×5-12 µm, ca. 1/2 of the width of basal leaf cells; basal leaf cells with bulging proximal cell end, cells in apical part of leaf with mammilla/papilla at distal cell end, or all leaf cells with mammilla/papilla at distal end of cells. Short branch-like propagules at leaf axils sometimes present.

Dioicous. Sporophytes not seen in specimens from Russia. [Perichaetial leaves acuminate. Perigonia bud-shaped, perigonial leaves from concave base gradually tapering to acuminate apex; capsule ca. 2 mm long.]

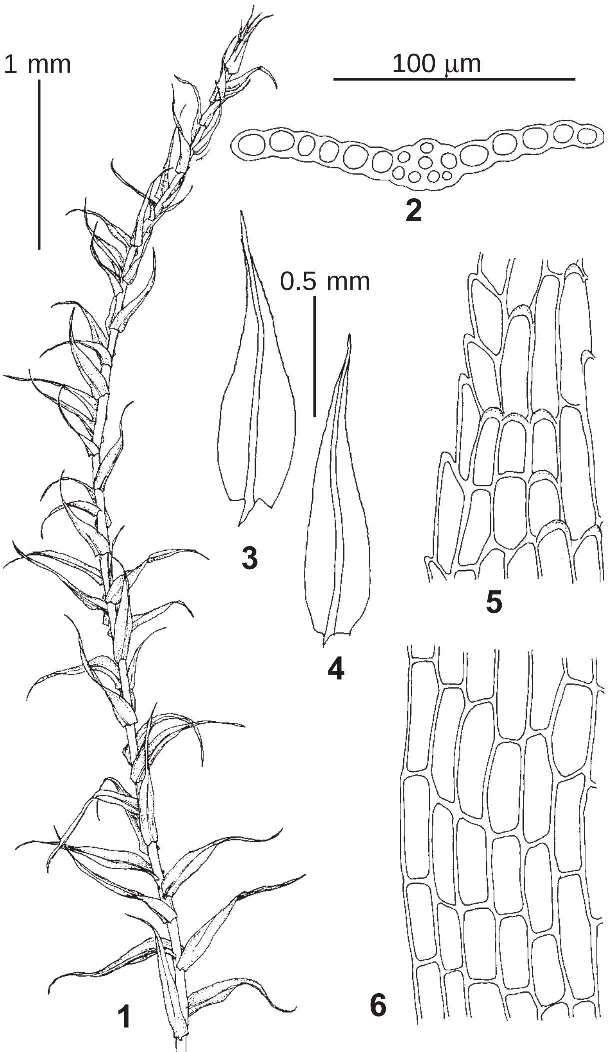

Fig. 9. *Philonotis capillaris* Lindb. (from: Yakutia, Allakh-Yun, *Ignatov #00-978*, MHA): 1 – habit, dry; 2 – leaf transverse section; 3-4 – leaves; 5 – upper laminal cells; 6 – basal laminal cells. Scale bars: 1 mm for 1; 0.5 mm for 3-4; 100 µm for 2, 5-6.

Illustrations: Brotherus, 1923: 358, fig. 63, A, B, perigonial leaves; Möller, 1925: figs. 1-8, as *P. arnellii*; Lawton, 1971: pl. 115, 12-16; Smith, 1978: 460, fig. 222, 10-13, as *P. arnellii*; Crum & Anderson, 1981: 652, fig. 309, A-C; Nyholm, 1998: 259, fig. 217 B, as *P. arnellii*; Hallingbäck, 2008: 288, 289, as *P. arnellii*; Guerra & Gallego, 2010: 260, fig. 92, g-l.

Differentiation. The diagnostic characteristics of *Philonotis capillaris* are the very slender thread-like habit, lax and translucent leaf areolation and the leaf cells with mammillae bulging over the proximal end of the basal leaf cells and the distal end of upper leaf cells mammillose/papillose. The translucent leaves are due to that the mammillae/papillae are low and the leaf cells thin-walled and that the leaf cells in the distal part of leaf are not much narrower than the cells in the proximal part of leaves. In this respect *P. capillaris* resembles *P. caespitosa*, which

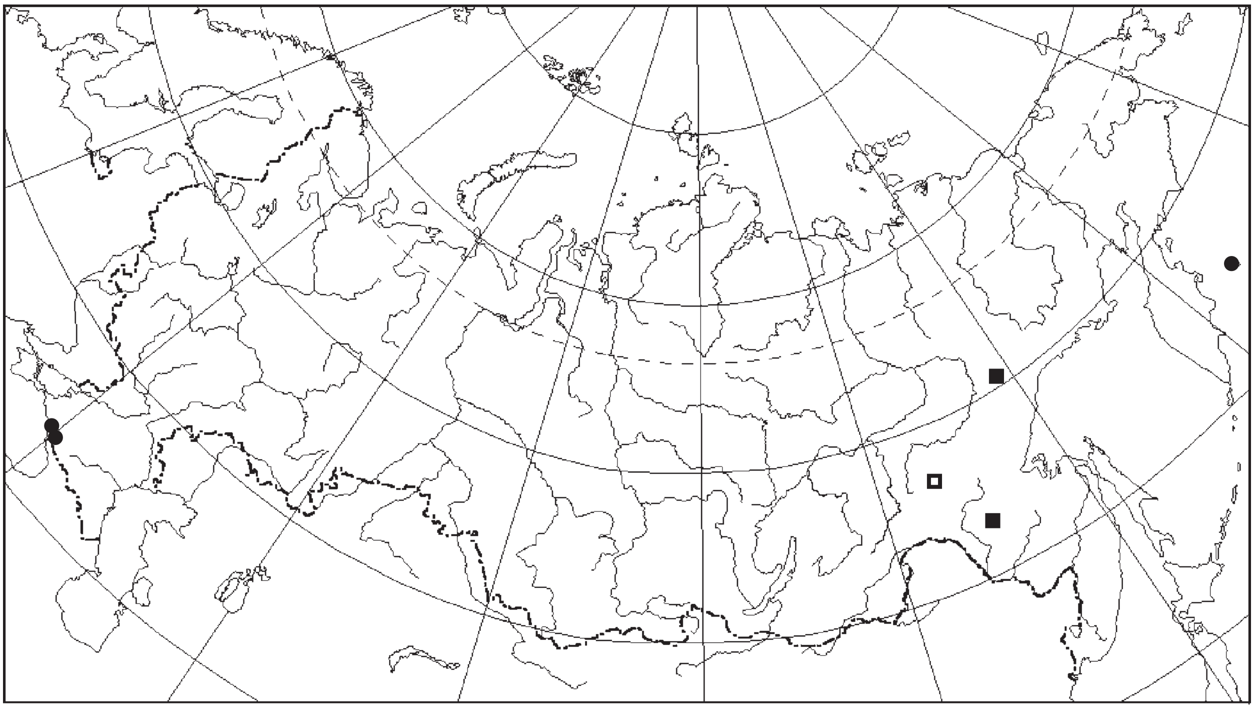

Fig. 10. Distribution of *Philonotis capillaris* Lindb. in Russia. Solid figures show specimens used in DNA studies. Circles – main haplotype; squares – second haplotype revealed in Siberia.

is a larger plant, has all mammillae at the proximal cell end and a double-crenulate leaf border at the leaf base. Some herbarium specimens were misidentified as *P. calcarea*, which is much larger plant, has a wider costa and mammillae/papillae at the lower end of the leaf cells, and much longer juxtacostal cells near the leaf base. The specimen H-BR 3130 005 has propagules resembling the flagelliform shoots reported for the species by Petit (1976).

Our molecular study revealed that *P. capillaris* is polyphyletic, represented by two haplotypes (Figs. 1-2). There is no evident difference in morphology between these plants, and we refer all of them to *P. capillaris*. However, their distribution is shown separately in Fig. 10.

Habitat ecology. *Philonotis capillaris* grows on moist soil along creeks, at bases of cliffs and on banks in meadow ground.

Range in Russia (Fig. 10). The species is known from the Caucasus and the Commander Islands in Russian Far East; the second haplotype was revealed from Yakutia and Amurskaya Province. There is a report of *Philonotis capillaris* from Chukotka (Afonina, 2004); however, it was based on misidentified specimens.

Specimens examined: **RUSSIA**: CAUCASUS: **Krasnodar Territory**: Adler District, Mzymta River valley, *Seregin # M-2278* (MW); Sochi District, Babuk-Aul, Shakhe River, 23.VIII. 1999, *Ignatov s.n.* (MHA). ASIATIC RUSSIA: **Republic Sakha/Yakutia**: Ust-Maya District, Allakh-Yun, *Ignatov #00-978* (MHA); Neryungri District, Zolotinka, 01.VII.1987, *Filonenko s.n.* (MHA); **Amurskaya Province**: Norsky Reserve, 16.VII.2010, *Bezgodov #472* (MHA); **Kamchatsky Territory**: Aleutsky District, Commander Islands, Bering Island, *Fedosov #10-3-492* (MW).

Total range (recorded as *P. capillaris* or *P. arnellii*). – Central America (Allen, 2002). – North America (Zales, 1973, map fig. 69; Crum & Anderson, 1981). – Europe: (Düll, 1985; Saboljević *et al.,* 2008; Koponen & Isoviita, 2010). – SW Asia: Iran (Akhani & Kürschner, 2004), Israel (Nyholm, 1998), Turkey (Uyar & Çetin, 2004). Kürschner & Frey (2011) repeated the same information for SW Asian countries. – Russian Far East (present report). – Africa: Algeria and Tunisia (Ros *et al.*, 1999).

Selected specimens examined: **GEORGIA**: Oprtsheti ad fl. Rion, 1.VI.1877, *Brotherus* (H-BR 3130 005 as *P. fontana* fo. *gracilis*).

U.S.A.: California, *Norris #72095* (MHA).

Philonotis fontana (Hedw.) Brid., Bryol. Univ. 2: 18. 1827. – *Mnium fontanum* Hedw., Spec. Musc. 195. 1801. – Type: “Locis paludosis apertis spongiosis” (G, not seen). Figs. 11-14.

Historical review. The extreme variation of *Philonotis fontana* has led to a situation where many varieties and forms have been described and listed in floras and revisions, such as Loeske (1905a, 1906), Dismier (1908, 1910) and Flowers (1935). According to Crum and Anderson (1981), Flowers later came to the conclusion “that he would no longer recognize any of the sterile varieties included there”, and Crum and Anderson agreed: “In view of its extreme variability, we are glad to follow Flowers in regarding as synonyms the numerous “sterile varieties” of *P. fontana* (see also discussion under *P. tomentella*).

Plants green to brownish, loosely tufted, small to tall, shoots 1-10 cm; leaves 1-2 mm long and 0.5 mm wide, not arranged in rows, leaf bases erect when dry, covering

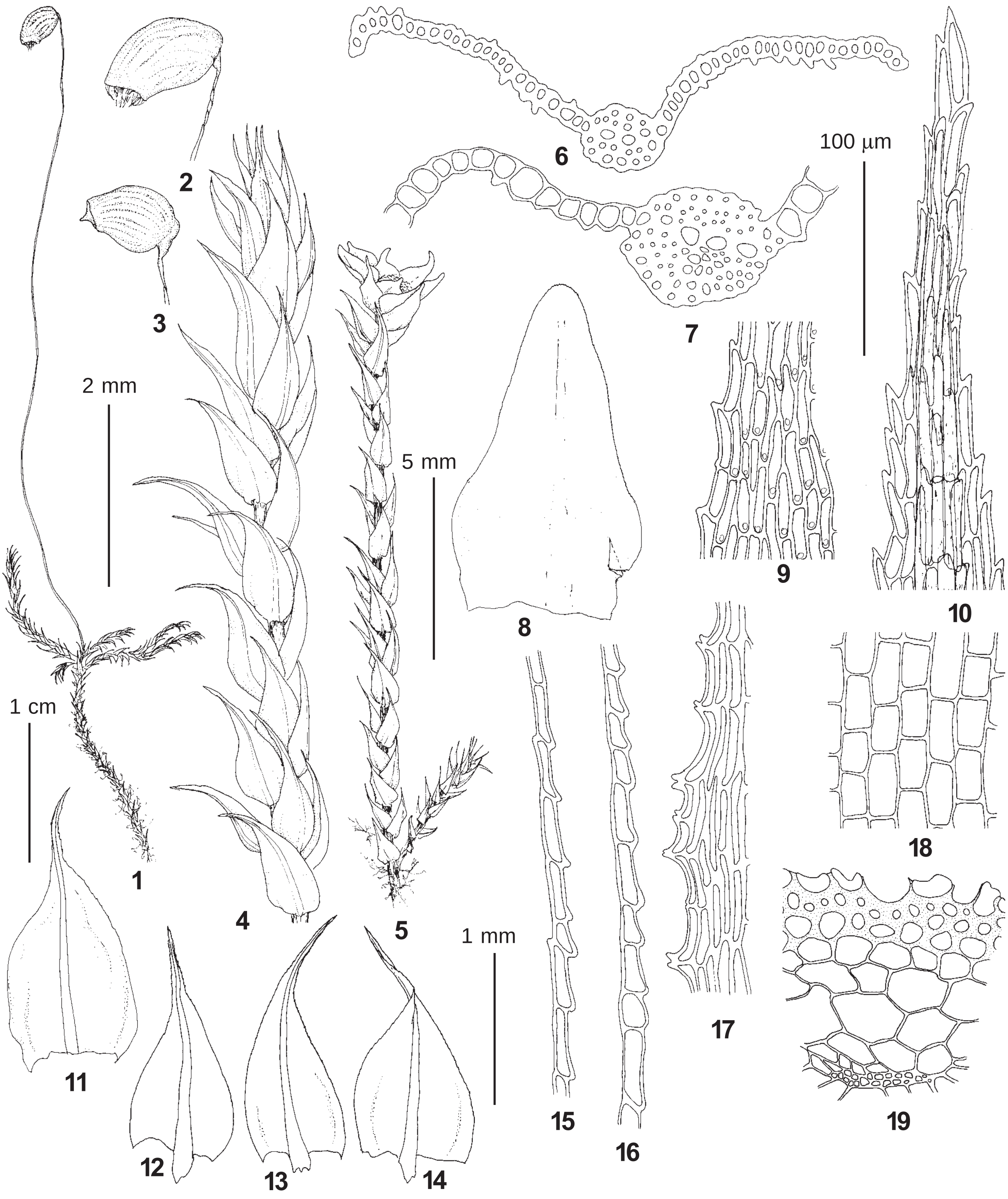

Fig. 11. *Philonotis fontana* (Hedw.) Brid. (from: Ivanovo Province, Zavolzhsk Distr., Nodoga Creek, 9.VIII.2001, *Ignatov s.n.,* MW): 1, 4-5 – habit, dry; 2-3 – capsules; 6-7 – leaf transverse sections; 8 – inner perigonial leaf; 9 – upper laminal cells; 10 – cells of leaf apical part; 11-14 – leaves; 15-16 – leaf longitudinal sections; 17 – marginal cells in middle part of leaf; 18 – basal laminal cells; 19 – stem transverse section. Scale bars: 1 cm for 1; 5 mm for 2-3, 5; 2 mm for 4; 1 mm for 8, 11-14; 100 µm for 6-7, 9-10, 15-19.

the stem completely, leaves concave, plicate, from broadly ovate base ± abruptly tapering to acuminate apex, narrow distal part of leaf 1/4–1/3 of leaf length, distal parts usually spreading or secund to same direction especially at apical stem; margin recurved, crenulate and double-crenulate below, serrate near apex; costa 50-80 µm wide near leaf base, dorsal side mammillose by protruding cell corners, ending below apex or excurrent; leaf areolation ± translucent in lower ovate part of leaf, apical part dim; in lower part of leaf cells quadrate, short rectangular or rhomboi-

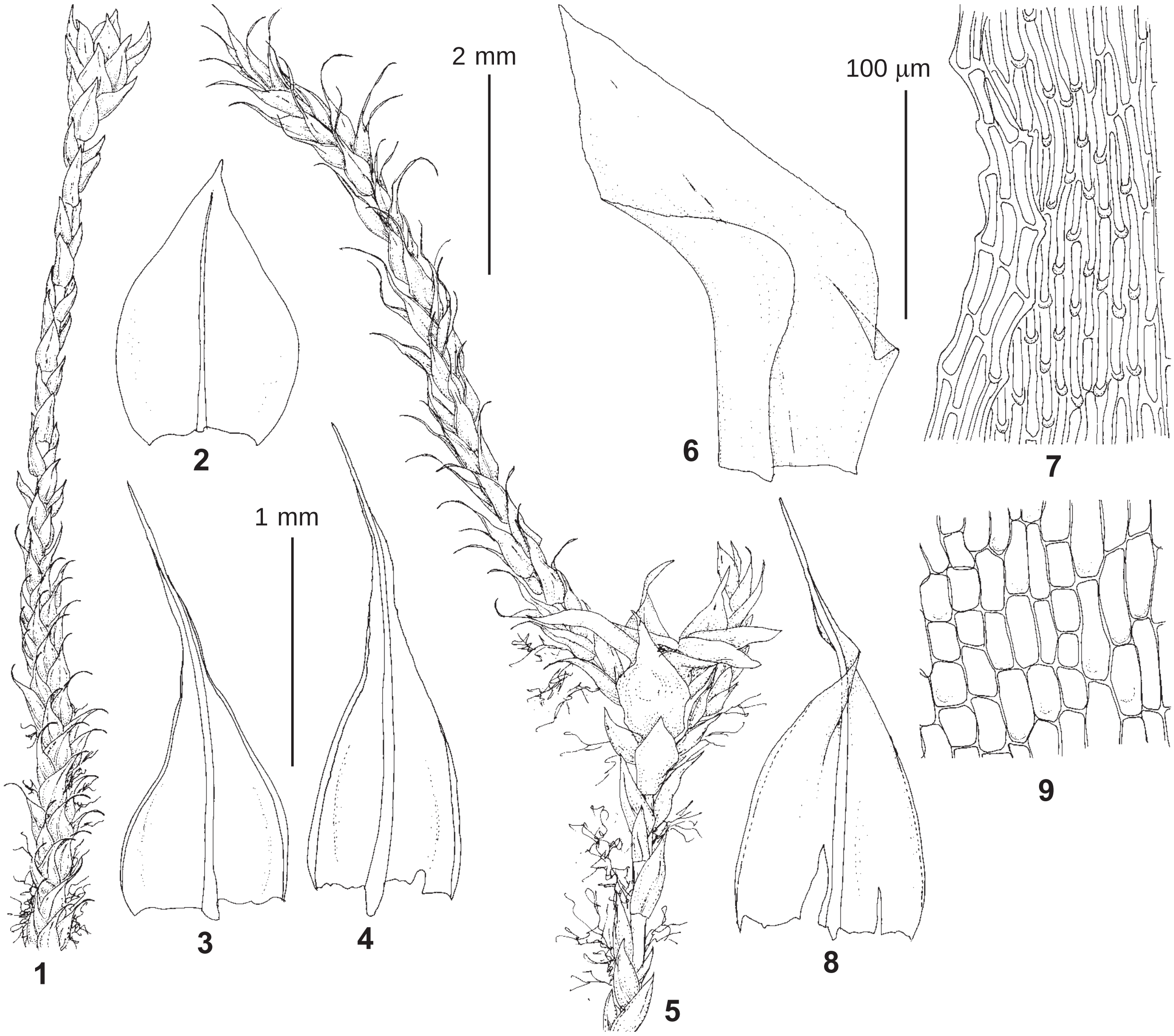

Fig. 12. *Philonotis fontana* (Hedw.) Brid. (from: Karelia, Loukhi District, *Maksimov & Maksimova #125-34*, MW): 1, 5 – habit, dry; 2 – leaf below perigonium; 3-4 – leaves from innovation; 6 – inner perigonial leaf; 7 – upper laminal cells; 8 – leaf from lower part of fertile male stem; 9 – basal laminal cells. Scale bars: 2 mm for 1, 5; 1 mm for 2-4, 6, 8; 100 µm for 7, 9.

dal, 15-40×5-15 µm, thin-walled, juxtacostal cells near base 25-75×7.5-20 µm, gradually narrower toward apex, distal leaf cells linear or vermicular, 22-50×5-7 µm, mammilla/papilla proximal on leaf cells, rarely central on broad and short cells near leaf base; narrow linear or vermicular cells at leaf apex may have papilla on distal cell end.

Dioicous. Perichaetial leaves erect or spreading, from ovate base long acuminate, stem leaves below perichaetium sometimes shorter than ordinary leaves, appressed or erect. Base of perigonial leaves erect and concave, apex wide-spreading, outer leaves tapering to acute and inner leaves to ± obtuse apex; leaves below perigonia erect, appressed and shorter than vegetative leaves on sterile and female shoots. Seta 2-3 cm, capsule ca. 2 mm long. Spores ca. 25 µm, minutely papillose.

Illustrations: Brotherus, 1923: 358, fig. 63, F, G, perigonial leaves; Möller, 1925: figs. 26-29; Lawton, 1971: pl. 116, 1-6, as *P. fontana* var. *fontana*; Smith, 1978: 463, fig. 223, 1-6; Crum & Anderson, 1981: 654, fig. 310; Noguchi, 1989: 571, fig, 253 A, as *P. fontana* var. *fontana*; Nyholm, 1998: 263, fig. 222; Ignatov & Ignatova, 2003: 584, fig. 418; Hallingbäck, 2008: 295, 296; Guerra & Gallego, 2010: 268, fig. 95, a-f.

Differentiation. The leaf shape, from a broadly ovate base ± abruptly tapering to a falcate-secund acumen is usually sufficient to distinguish *P. fontana* from *P. calcarea*, *P. caespitosa* and *P. seriata*, and these taxa, and *P. americana*, are discussed in more detail below. It is most difficult to distinguish *P. fontana* from *P. tomentella*. The following observations may help in their identification.

Habit. Philonotis tomentella is always slender while *P. fontana* is more variable; slender plants similar to *P. tomentella* occur, but usually the size alone is sufficient to distinguish these taxa. Under the dissecting microscope well-developed plants of *Philonotis tomentella* are easily

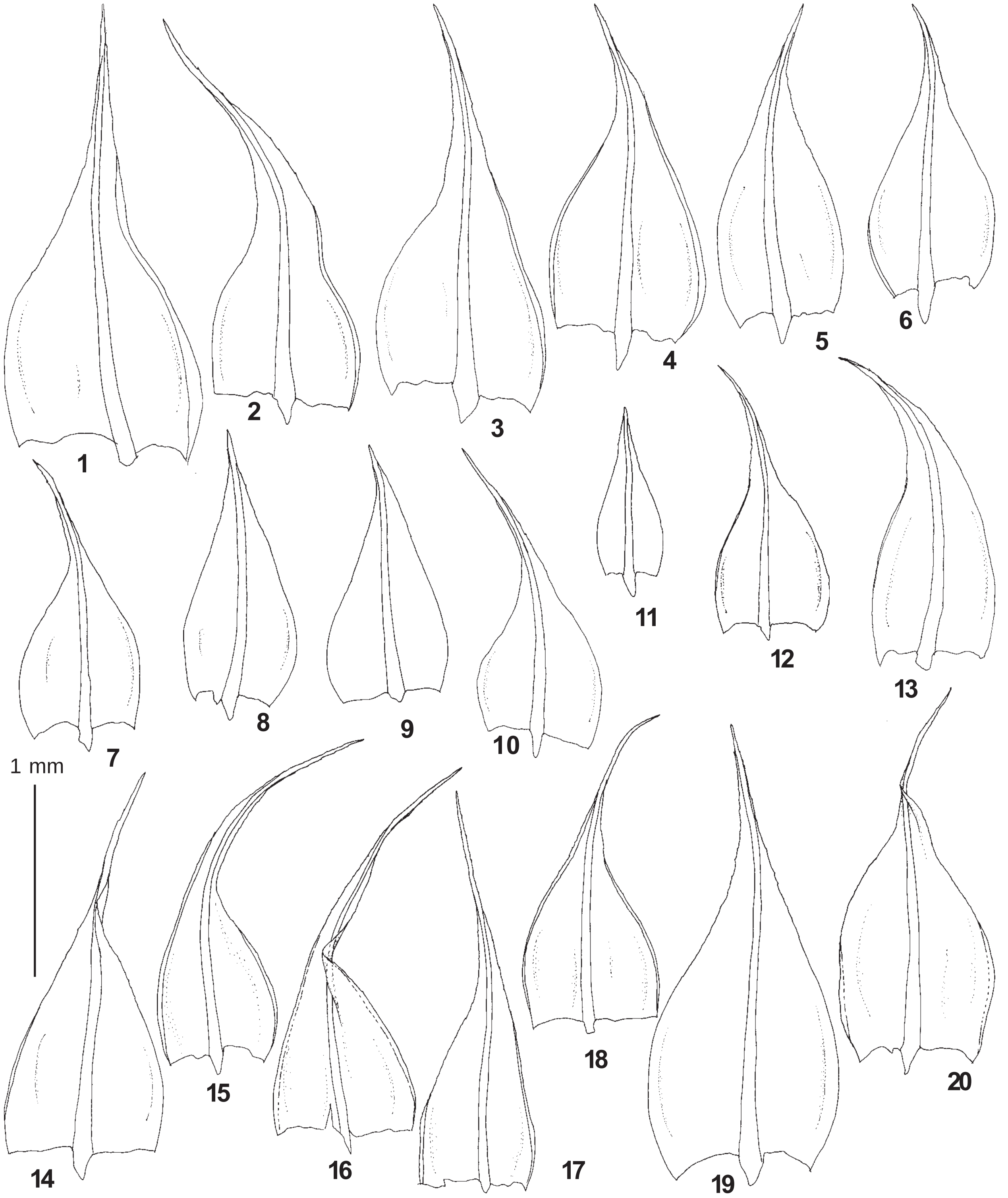

Fig. 13. Stem leaves from female or sterile shoots of *Philonotis fontana* (Hedw.) Brid. (from: 1 – Austria, *Kockinger #14907*, MW; 2 – Vladimir Province, *Seregin #M-2654*, MW; 3 – Sverdlovsk Province, 21.VII.1995, *Marina s.n.*, MW; 4 – Sakhalin, *Ignatov & Teleganova #06-875*, MHA; 5 – Chukotka, 24.VIII.2001, *Afonina s.n.*, MW; 6 – Evenkia, 21.VII.1992, *Shcherbina s.n.*, MW; 7 – Kuril Islands, Iturup, *Bakalin# K-17-13-07*, MW; 8 – Amurskaya Province, 9.VII.2010, *Bezgodov #370*, MHA; 9 – Caucaus, *Ignatov & Ignatova #05-3496*, MW; 10 – Komi Republic, *Ivanov & Donskov #09-428*, MW; 11 – Primorsky Territory, *Ignatov # 07-353*, MHA; 12 – Yakutia, *Ignatov & Ignatova #11-3471*, MW; 13 – Zabaikal'sky Territory, *Afonina #A5210*, LE; 14 – Karelia, *Maksimov & Maksimova #125-34*, MW; 15 – Buryatia, 23.VIII.2008, *Krivobokov s.n.*, MW; 16 – Murmansk Province, 30.VI.2012a, *Ignatov s.n.*, MHA; 17 – Murmansk Province, 4.IX.2001, *Ignatov s.n.*, MW; 18 – Murmansk Province, 30.VI.2012b, *Ignatov s.n.*, MHA; 19 – Komi Republic, *Ivanov & Donskov #09-423*, MHA; 20 – Kamchatka, 5.VIII.2007, *Czernyadjeva #9-07*, MW). Scale bar: 1 mm for 1-20. All specimens were used in the molecular study.

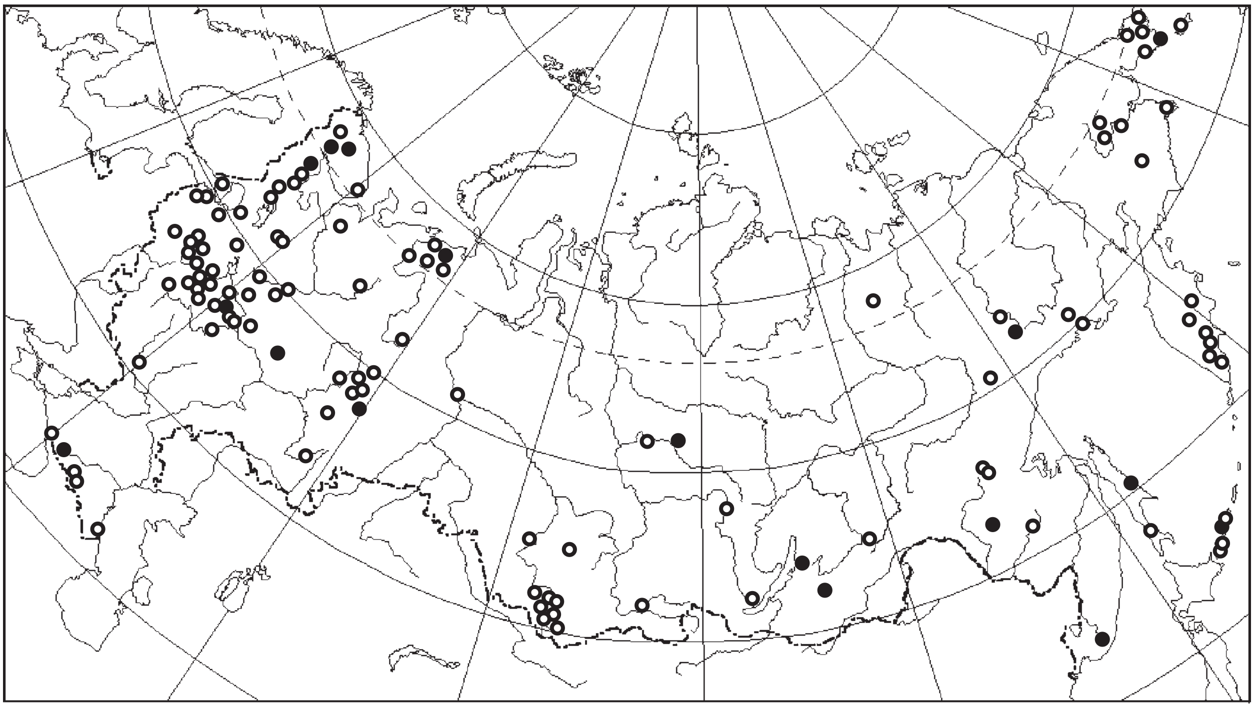

Fig. 14. Distribution of *Philonotis fontana* (Hedw.) Brid. (circles) in Russia. Solid figures show specimens used in DNA studies.

separated from *P. fontana* by the size and different position and shape of the leaves. The leaves in *P. fontana* are densely situated and falcate-secund in one direction especially at the stem apex, while the leaves of *P. tomentella* are more distant, so that the brownish stem is visible between the leaves. The leaves are straight or the long acuminate apices are slightly bending in different directions.

Steere (1978) emphasized the difference in growth habit of *P. fontana* and *P. tomentella*: "The most common species, by far, is the smaller and more compact *P. tomentella* Mol. (*P. fontana* var. *pumila* [Turn.] Brid.), in which the individual plants are so matted together into solid tufts by the brownish-red tomentum on the stems that they are nearly impossible to separate".

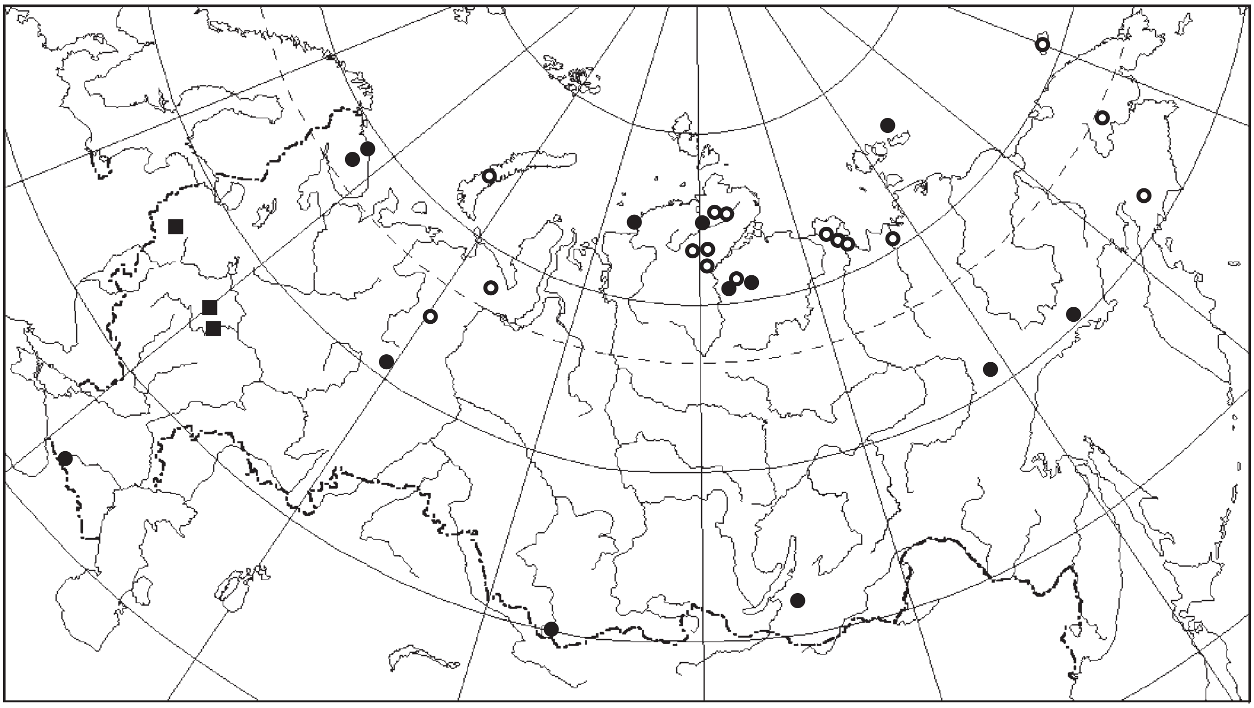

Fig. 15. Distribution of *Philonotis tomentella* Molendo (circles) and *P. caespitosa* Jur. (squares) in Russia. Solid figures show specimens used in DNA studies.

Cellular details. The cell areolation at the leaf base of *Philonotis fontana* and *P. tomentella* differ. The leaf cells in the basal leaf in *P. fontana* are larger, thin-walled, quadrate, rectangular and rhomboidal, and in most specimens the cells are only mammillose, not papillose. Therefore, the basal areolation in *P. fontana* is more translucent than in the leaves of *P. tomentella*. This may be due to more regularly rectangular cells, thicker cell walls, and more pronounced papillae in *P. tomentella* making its basal leaf areolation more dim than in *P. fontana*.

Male plants. The habit of slender male plants of *P. fontana* resembles *P. tomentella.* The brownish stem is visible between erect and short leaves just like in typical plants of *P. tomentella*. The obtuse inner perigonial leaves have been used as the separating character of *Philonotis fontana* from *P. tomentella,* which has acute to acuminate such leaves. This difference has been emphasized in many floras, but a more reliable distinction seems to be that the stem leaves below the perigonium in *P. fontana* are often straight and with a short acute or even obtuse apex (cf. Fig. 12: 1) while the stem leaves on male stems of *P. tomentella* do not differ as much from the vegetative leaves on female and sterile shoots (Fig. 17: 4). The cells in the basal part of the leaf are larger and their cell walls thinner in *P. fontana*.

In the NW and NE European Russia plants of *P. fontana* with longly acuminate leaves that are strongly reflexed in all directions, with a longly excurrent costa occasionally occur (Fig. 12). They are even weakly differentiated molecularly and form a subclade in some analyses (not shown). Such plants are also similar to the northern phenotype of *P. tomentella* to some extent. However, usually the larger size of such plants and the thin-walled basal laminal cells help to separate them from the latter species.

Leaf shape and size are not always enough to differentiate *P. fontana* from *P. tomentella*, because they are rather variable, especially in *P. fontana*, and overlapping (see Figs. 13 and 18 showing leaves of specimens used in the molecular analysis). However a combination of these characters and lamina areolation of the proximal part of leaf is usually more suggestive.

Male plants of *P. fontana* that only have modified leaves are most difficult to identify. Such leaves are erect and adpressed against the stem, have larger, thin-walled leaf cells in the basal leaf than in vegetative leaves and a short acute apex with linear to vermicular leaf cells. Such stems should finally develop a perigonium, but in some populations the perigonia are not produced and the innovations continue as modified male stems year after year. Such specimens have been given taxonomic status as "var. *adpressa*" or "var. *laxa*" or are misidentified as *P. caespitosa*, *P. calcarea*, or *P. tomentella*.

Juvenile plants of *P. fontana* may be difficult or impossible to identify. They have erect, ovate and ± imbricate leaves and the leaf apex is straight and short, not secund as in the leaves of fully grown plant. The leaf border may be plane, not recurved. The cell areolation is lax even at the apex. Such plants are easily misidentified as *P. caespitosa*.

Habitat ecology. *Philonotis fontana* grows in many kinds of wet habitats such as springs, sometimes partially submerged, spring-fed brooks, on shore meadows and marshes, and on rocks with trickling water.

Range in Russia. *Philonotis fontana* is the most common species of *Philonotis* in hemiarctic, boreal and temperate forested areas and occurs in more open continuously wet habitats outside the forest belt (map in Fig. 14). Its occurrence in the Siberian Arctic and Subarctic (Taimyr, Lower Lena River, *etc*.) was not confirmed by the molecular study; it is more common in oceanic regions, such as NW European Russia, Chukotka, and Kamchatka.

Selected specimens examined: **RUSSIA**: EUROPEAN RUSSIA: **Murmansk Province**: Khibiny Mts, Takhtarvumchorr, 4.IX.2001, *Ignatov s.n.* (MW); **Karelia**, Loukhi District, *Maksimov & Maksimova #125-34* (MW); **Leningrad Province**: Volosovo District, Shugovitsy, 14.V.1985, *Ignatov s.n.* (MHA); **Arkhangelsk Province**: Kargopol District, Nokola, 4.VII.2001, *Churakova #1268* (MW); Onega District, Lyampa, 5.VII.2000, *Churakova #464* (MW); **Komi Republic**: Nenetzky Autonomous District, Ad'zva River, *Ivanov & Donskov #09-423* (MHA); Bolshezemel'skaya Tundra, Pechora River mouth, Varandej, 13.IX.1999, *E.Yu. Kuz'mina s.n.* (LE); Polar Urals, 106 km railway station, 17.VIII.1964, *Filin s.n.* (MW); **Vologda Province**: Belozersk District, Palkino, 5.VIII.2005, *Chemeris s.n.* (MW); Nyuksensky District, Sukhona River opposite Nyuksenitsy, 13.VIII.2001, *Ignatov & Ignatova s.n.* (MHA); **Perm Province**: Krasnovishersk District, Bolshoj Shchugor River, 6.VIII.1995, *Bezgodov #634* (MW); **Sverdlovsk Province**: Visimsky Nature Reserve, 21.VII.1995, *Marina s.n.* (MW); **Bashkortostan Republic**: Ishimbaj District, Kulgunino, *Ignatova #15/64* (MHA); Zilair District, Dmitreevka, Suren' River, 06.VIII.1989, *Grigoriev #713* (MHA); **Kirov Province**: Slobodskoj District, Lipovka, 25.V.1925, *Fokin s.n.* (MW); **Chelyabinsk Province**: Asha (former Minjyar) District, Kazamash-Atya Hill, 5.IX.1940, *Sokolova s.n.* (LE)**; Udmurtia**: Kez District, Gulejshur, 17.VII.2004, *Rubtsova s.n.* (MHA); **Kostroma Province**: Vokhma District, Penomskoe Forestry, 12.VII.2003, *Braslavskaya s.n.* (MW); **Tver Province**: Nelidovo District, Tsentral'no-Lesnoj Nature Reserve, 28.VII.2003, *Andreeva s.n.* (MW); Staritsa District, between Kuchkovo & Voevodino, 3.VII.1993, *Notov s.n.* (MW); **Moscow Province**: Taldom District, Dubna River, 04.VII./1985, *Ignatov s.n.* (MHA); Moscow, Losiny Ostrov, 21.IX.1996, *Ignatov s.n.* (MHA); **Vladimir Province**: Sudogda District, 8 km S of Vladimir, *Seregin #M-2654* (MW); **Ivanovo Province**: Zavolzhsky District, Nodoga Creek, 9.VIII.2001, *Ignatov s.n.* (MW); **Ryazan Province**: Klepikovsky District, 1955, *Barabanova & Shevyreva s.n. (*MW); **Mari-El Republic**: Bolshaya Kokshaga Nature Reserve, 26.VI.1998, *Czernyadjeva s.n.* (LE); **Chuvashia**: Prisursky Nature Reserve, 01.V.1999, *Moshkovsky s.n.* (MHA); **Voronezh Province**: Voronezhsky Nature Reserve, 10.IX.1983, *Popova #4594* (MW). CAUCASUS: **Karachaevo-Cherkessia**: Teberda Nature Reserve, *Ignatova #07-108* (MW); **Kabardino-Balkaria**: Cherek-Bezengijsky River Gorge near Mizhirgi River mouth, 2.VIII.2004, *Ignatov & Ignatova s.n.* (MW); **North Ossetia/Alania**: North Ossetian Nature Reserve, Tsei River, 31.VII.1976, *L.I. Abramova #114* (MW); **Dagestan**:

Agul'sky District, Samursky Mt. Range, Chiragchaj River, 17.V.1988, *Bochkin s.n.* (MHA); **Krasnodar Territory**: Adler District, Krasnaya Polyana, Aishkha My. Range, 11.IX.2004, *Portenier #899* (MHA); **Adygeya**: Majkop District, Caucasian Nature Reserve, upper course of Belaya River, 18.VIII.1999, *Ignatov s.n.* (MHA). ASIATIC RUSSIA: **Khanty-Mansijsk Autonomous District**: Samarovo, 8.VIII.1957, *Tyuremnov s.n.* (MW); **Altai Republc**: Ulagan District, Chulyshmanskoe Upland, Kayakkatuyaryksy Creek, *Ignatov #8/175* (MHA); Chemal District, Chemal, *Ignatov #34/208* (MHA); **Tyva Republic**: 3 km NW of Cherbi, 1.VII.1946, Shreter s.n. (MW); **Krasnoyarsk Territory**: Turukhansk District, Bakhta River basin, Kaetaeollo Lake, 13.VIII.1992, *Shcherbina #81* (MW); Evenkia, Baikit District, Kochumdek River, 21.VII.1992, *Shcherbina s.n.* (MW); **Republic Sakha/ Yakutia**: Neryungri District, Tokinsky Stanovik Mt. Range, Maloe Toko Lake, 23.VII.1987, Volotovsky s.n. (MW); Ust-Maya District, Allakh-Yun, Tarbagannakh Creek, *Ignatov #00-509* (MHA); Oimyakon District, Mus-Khaya Mt., Kongor Creek, *Ignatov & Ignatova #11-3471* (MW); **Magadan Province:** Severo-Evensky District, Kedon meteostation, Tik Creek valley, 1.VII.1957, *Nikolaev s.n.* (MW); **Irkutsk Province**: Ust-Ilimsk District, 12 km NNE of Nevon, Angara River bank, *Seregin #M-2033* (MW); Irkutsk District, Baikal Lake, Bol'shie Koty, 21.VII.1986, *Kosovich #96-2* (LE); **Buryatia**: Barguzinsky Nature Reserve, 23.VIII.2008, *Krivobokov s.n.* (MW); Eastern Sayan Mts, upper course of Oka River, Dodo-Zhakhna, 6.VII.2008, Afonina s.n. (LE); **Zabaikal'sky Territory**: Kalarsky District, Udokan Mt. Range, Myortvoe Lake (sources of Nirungnakan River), 16.VIII.1987, *Filin s.n.* (MW); Sokhondinsky Nature Reserve, *Afonina #A5210* (MW); **Khabarovsk Territory**: Verkhnebureinsky District, upper course of Bureya River, Dusse-Alin Range, Medvezh'e Lake, *Ignatov #97-689* (MHA); **Amurskaya Province**: Norsky Nature Reserve, 9.VII.2010, *Bezgodov #370* (MHA); **Chukotsky Autonomous District**: Providensky District, Provideniya Bay, 24.VIII.2001, *Afonina s.n.* (LE); Anadyrsky District, Malaya Vesnovannaya River, 12.VIII.1980, Afonina s.n. (LE); **Kamchatsky Territory**: Icha Volcano, 5.VIII.2007, *Chernyadjeva #9-07* (MW); Mutnovsky Volcano, foothills of Skalistaya Mt., 23.VIII.2002 *Czernyadjeva #86* (LE); Karaginsky District, Pereval'naya River, 31.VIII.2006, *Samkova s.n.* (MW); **Sakhalinskaya Province**: Sakhalin, Tymovsky District, Nabil'sky Mt. Range, *Ignatov & Teleganova #06-875* (MHA); Kuril'sky District, Iturup Island, Bogatyr' Mt. Range, Burevestnik Mt., *Bakalin #K-15-29-07* (MW); Yuzhno-Kuril'sky District, Kunashir Island, Ruruj Mt., Dal'nij Creek, Ignatov #06-1914 (MW); **Primorsky Territory**: Ol'ga District, Milogradovsky Waterfall, *Ignatov #07-353* (MHA).

See also a list of specimens in Koponen *et al*. (1978).

Total range. *Philonotis fontana* is widely distributed in the boreal and temperate areas of the northern hemisphere, and is the most common species of *Philonotis* section *Philonotis*. – North America: Widely distributed (Zales, 1973, map fig. 69), Mexico (Sharp *et al*., 1994). – Central America: Guatemala and Panama (Allen, 2002). – South America: Bolivia (Koponen, 2012b). – Azores, Lameiro, com. J. Henrigues 661 (H-BR 3130 020). – Canaries, Cape Verde Islands (Nyholm, 1998). – Europe (Düll, 1985; Saboljević *et al.,* 2008). – SW Asia: Afghanistan (Frey & Kürschner, 1991), Iran! (Akhani & Küschner, 2004), Iraq (Kürschner & Frey, 2011), Turkey! (Uyar & Çetin, 2004). Kürschner & Frey (2011) repeated the same information for SW Asian countries. – Africa: Algeria, Morocco and Tunisia (Ros *et al*., 1999). – Ethiopia. "Demerki, 9.VIII.1842 Schimperi iter Abyssinicum. Sectio secunda 453. *Bartramia fontana* Brid." (H-BR 3131 002).

The range in central African high mountains in Kenia and Tanzania needs to be confirmed. Some of the specimens seen that were named *P. fontana* or *P. tomentella* seem to represent other taxa (Koponen, in prep.). Some specimens misidentified as *P. calcarea* from the Himalayan area are given below.

Selected specimens examined: **INDIA:** Kashmir, Kaylee-ban, Gurais Valley, 10 500 p., 1.VII.1901 *Inayal Khan 2933*, Bryotheca E. Levier. Musci Indiae orientalis, curante cl. W. Gollan lecti, det. V.F.B. (H-BR 3125 007, as *P. calcarea*); Vallis Surú, Surú-Purkutte, 3200-3400 m, 11.VI.1913 *L. Borelli* (B-BR 3125 004, as *P. calcarea*); Vallis Brahma in jugo Nun–Kun, ca. 3800 m. VII.1913 *L. Borelli* (H-BR 3125 001, as *P. calcarea*).

Philonotis caespitosa Jur., Verh. Zool. Bot. Ges. Wien 11: 234. 1862. – *Philonotis fontana* var. *caespitosa* (Jur.) Limpr., Krypt.-Fl. Schlesien 1: 116. 1875.– Type: Europe (not seen). Figs. 15-16.

Historical review. After its description by Jurazka (1862), *P. caespitosa* has been accepted in Europe by the specialists of *Philonotis*, such as Loeske (1905a, 1906) and Dismier (1908, 1910), and the major European moss floras followed their lead. In North America it has been accepted as a variety of *P. fontana* (Flowers, 1935; Zales, 1973; Crum & Anderson, 1981).

The senior author has no field experience of *P. caespitosa*. The key characters given above and the description below are based mainly on opinions of previous authors such as Loeske (1905a, 1906), Dismier (1908, 1910), Brotherus (1923), Möller (1925), and on Central European specimens, which have both male plants and sporophytes (in H). In addition, one specimen with male plants from European Russia (Tver Province) was studied by the junior authors and included in the molecular analysis. Specimens revealed in the molecular trees as *P. caespitosa* were also taken into consideration.

Plants green, slender, shoots 1-4 cm; leaves 1-1.8 mm long and 0.5-0.8 mm wide, not arranged in rows, mostly distant, not covering the stem completely, leaves patent to flexuose when dry, concave, apical part falcate-secund; leaves from ovate base gradually tapering to acuminate apex; margin plane or narrowly recurved, entire below, crenulate and double-crenulate at midleaf, serrulate near apex; costa weak, ca. 30-55 µm near leaf base, dorsal side slightly mammillose, percurrent or excurrent; leaf areolation translucent also near apex, leaf cells at leaf base near costa rectangular, in rows parallel to costa, 30-62×10-17 µm, cells near leaf margin and upper on leaf shorter, rhomboidal to quadrate, upper cells rectangular to rhomboidal, narrower, 22-37×2.5-7.5 µm at apex, proximal mammilla at basal leaf inconspicuous, low or more pronounced near apex.

Dioicous. Perichaetial leaves erect, from ovate base

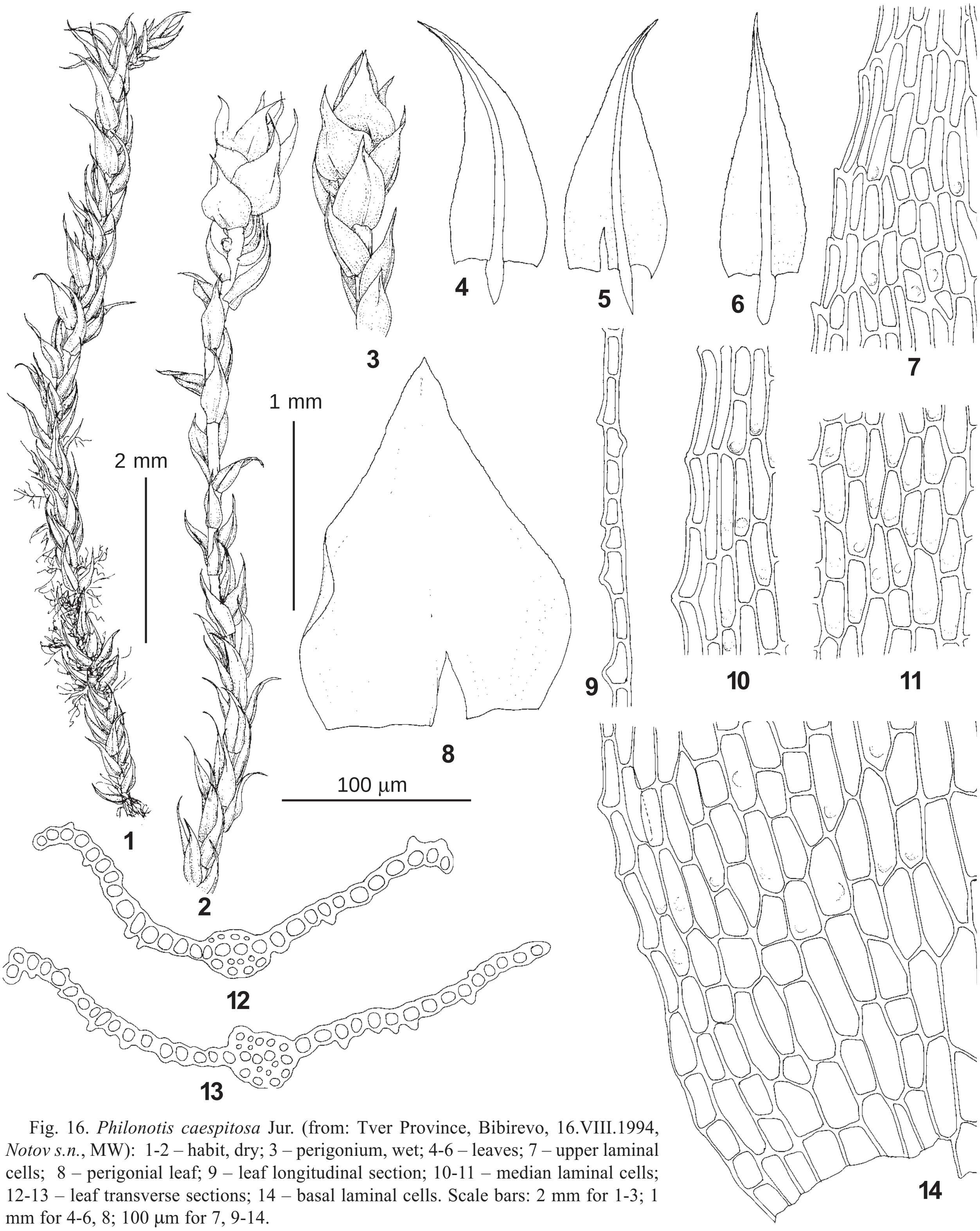

Fig. 16. *Philonotis caespitosa* Jur. (from: Tver Province, Bibirevo, 16.VIII.1994, *Notov s.n.*, MW): 1-2 – habit, dry; 3 – perigonium, wet; 4-6 – leaves; 7 – upper laminal cells; 8 – perigonial leaf; 9 – leaf longitudinal section; 10-11 – median laminal cells; 12-13 – leaf transverse sections; 14 – basal laminal cells. Scale bars: 2 mm for 1-3; 1 mm for 4-6, 8; 100 µm for 7, 9-14.

long acuminate. Vegetative leaves below perichaetia ± erect and smaller than leaves of strong sterile shoots. Perigonia disk-shaped, inner perigonial leaves from concave base tapering to acuminate apex; leaves below perigonia erect, appressed and shorter than vegetative leaves on sterile shoots. Capsule 2-2.5 mm long, spores ca. 25 µm, minutely papillose.

Illustrations: Brotherus, 1923: 358, fig. 63, C, D, perigonial leaves; Möller, 1925: figs. 9-12; Smith, 1978: 460, fig. 222, 14-17; Crum & Anderson, 1981: 655, fig. 311, A-C, as *P. fontana* var. *caespitosa*; Nyholm, 1998: 262, fig. 220; Ignatov & Ignatova, 2003: 583, fig. 417; Hallingbäck, 2008: 293; Guerra & Gallego, 2010: 262, fig. 93e-j.

Differentiation. Slender shoots and green colour are the habit characters of *Philonotis caespitosa*. Dried specimens remain pale green while the herbarium specimens of the other species of section *Philonotis* turn yellowish to brownish. Microscopic characters include its much less serrate leaf margins, not plicate leaves and lax leaf areolation. The leaves look much more translucent than the leaves of related species, in which the cells of apical part of the leaf are linear or vermicular. Altogether, the basal leaf cell areolation resembles that of *P. calcarea* and specimens misidentified as *P. caespitosa* but belonging to *P. calcarea* were found in herbaria. However, the much narrower costa of *P. caespitosa*, shorter juxtacostal cells, and not similarly narrow or vermicular cells near leaf apex provide a clear distinction.

When identifying *Philonotis fontana* and *P. caespitosa*, only fully grown old stems of the previous growing season should be used. The broadly ovate, erect leaf base ± abruptly narrowing to a slender acumen, strongly recurved leaf margins and plicate leaves separate *P. fontana* from *P. caespitosa*, which has more spreading to flexuose, ovate, gradually tapering and not plicate leaves. The leaf margins are plane, or only one margin is slightly recurved in *P. caespitosa*. At the leaf base the cell rows closest to the costa seem to be more regularly rectangular and longer than the corresponding rectangular, rhomboidal or quadrate cells in *P. fontana*. Sterile male plants of *P. fontana* may have a similar ovate leaf shape and lax areolation than fully grown *P. caespitosa*. At least in most cases such plants of *P. fontana* have the most apical leaf cells narrowly linear or vermicular. Even many male specimens of *P. fontana* having slender fully developed perigonia with obtuse inner perigonial leaves were found misidentified as *P. caespitosa* (in H). Juvenile plants of *P. fontana* with narrow leaves and translucent areolation may not be possible to separate from juvenile plants of *P. caespitosa*.

Habitat ecology. *Philonotis caespitosa* is reported to grow on swampy meadows, banks, pastures, forest paths, at creeks and lake shores, in springs, on moist cliffs and heaths, and on rocks with trickling water.

Specimens examined: **RUSSIA**: EUROPEAN RUSSIA: **Tver Province**: Andreapol District, Bibirevo, 16.VIII.1994, *Notov s.n.* (MW); **Moscow Province**: Shatura District, Beloe Bordukovskoe Lake, 9.IX.2010, *Teplov s.n.* (MHA); **Ryazan Province**: Spassk District, Oksky Nature Reserve, 1.VIII.2002, *Volosnova s.n.* (MW).

Philonotis caespitosa has been reported from several northern Asiatic regions (Ignatov *et al.*, 2006) and in some recent publications from Russian Far East (Czernyadjeva & Ignatova, 2008, Bakalin *et al.*, 2009). However, the specimens seen from North Asia are not fully developed and are all sterile or juvenile. Some recent collections from Kamchatka and Kuril Islands that were preliminarily named *P. caespitosa* cannot be identified for certain. No specimen from Asiatic Russia previously identified as *P. caespitosa* was resolved in the same clade as the specimens from the central part of European Russia and Western Europe by molecular data; all studied Asiatic specimens turned out to be slender forms of *P. fontana*. Furthermore, all fertile specimens (with sporophytes) in H-BR from Asia belong to *P. fontana*. Only the specimen *S. Ganeschin 1742* (see below) although not fully grown and lacking gametangia, has the habit and cellular details of *P. caespitosa*.

Total range. Brotherus (1923) had a cautious opinion regarding the range of *P. caespitosa*: “Europa. Überall nur von wenigen Fundorten bekannt”. – North America (Dismier, 1910; Zales, 1973 and Crum & Anderson, 1981, as *P. fontana* var. *caespitosa*). – Azores (Nyholm, 1998). – Europe (Düll, 1985; Saboljević *et al.,* 2008). – North Africa: Morocco (Ros *et al*., 1999). – South Africa (Koponen, 2003). – SW Asia: Caucasus (Nyholm, 1998), Iran (Akhani & Kürschner, 2004), Turkey (Uyar & Çetin, 2004). Kürschner & Frey (2011) added Afghanistan, Iraq, and Saudi Arabia. – North and Central Asia (Smith, 1978; Nyholm, 1998).

Selected specimens examined: **DENMARK**: Jylland, Åtte Bjerge east of Føvling, 11.IV.2012, *Goldberg s.n.* (MW).

GREAT BRITAIN: England. Pr. Warrington – Lane, *Wilson* (H-SOL 1544 013, male plants)

KAZAKHSTAN: Sibiria. region Akmolinsk, distr. Atbasarskij, Ulu-Tau, 2.VII.1914 *S. Ganeschin*, Inst. cr. no. 1742 (H-BR 3126 001).

Philonotis tomentella Molendo in Lorentz, Moosstudien 170. 1864.

Philonotis fontana var. *pumila* (Turner) Brid., Bryol. Univ. 2: 20-21. 1827. – *Bartramia fontana* var. *pumila* Turner, Muscol. Hibern. Spic. 107, pl. 10, f. 1. 1804. – Type: Europe (not seen). Figs. 15, 17-18.

Historical review. The delimitation of *Philonotis tomentella* was not always clear. In North American floras (Flowers, 1935; Lawton, 1971; Crum & Anderson, 1981) *P. tomentella* was treated as a variety of *P. fontana* (as *P. fontana* var. *pumila*). Zales (1973), in his revision of North American *Philonotis,* came to the conclusion that “*P. fontana* var. *pumila* is a distinct arctic-alpine variety recognized by its small size, strict, erect and closely packed stems clothed with abundant tomentum and small sporophyte”. “Fertile plants are easily placed in either var. *fontana* or var. *pumila* depending on their size and ± erect habit, while sterile specimens beyond the distributional limits of var. *pumila* should be included in the species”.

Dismier (1908) presented clear differences between *Philonotis fontana* and *P. tomentella* in his key and since then many European floras (Brotherus, 1923; Smith, 1978, 2004; Nyholm, 1960, 1998) accepted *P. tomentella* at the specific level, although difficulties in their recognition have occurred from time to time. This may be partly due to the highly confusing subspecific taxonomy (see e.g. Mönkemeyer, 1927; Podpera, 1954; Geissler, 1976). Loeske (1905a, b, 1906, 1908) tried to solve the problem by studying *Philonotis* in the field using only a hand lens to identify the taxa. He found that *P. tomentella* grows at higher altitudes than *P. fontana*, but found plants, which he thought to be intermediate forms. Dismier's (1908) paper was perhaps a surprise to him; Loeske (1909) agreed with most of Dismier's taxonomic solutions but wrote: "Meine ursprünliche Absicht, eine Monographie der Philonoten zu schreiben, werde ich nicht ausführen…" Mårtensson (1956) was another field bryologist who became fed up with the extreme variability of *P. tomentella* and its tangled varietal nomenclature: "Because the intricate problem will not be solved by mere classification of the material in main species and several more or less dubious varieties…." Later Mårtensson (in Arnell & Mårtensson, 1959) stated that the narrow-leaved populations dominate in Spitsbergen and their variation in the Spitsbergen type appears to be very limited compared with that of the *fontana-tomentella* complex of the Scandes. Mårtensson's explanation for this observation is: "There is therefore reason to believe that most or perhaps all earlier records of *Ph. fontana* refer to the type that we in Fennoscandia – perhaps mainly by convention – treat or try to treat as a separate species, *Ph. tomentella."*

Plants brownish, small-sized, in tight tufts, shoots 1-10 cm; leaves 1.2-1.8 mm long and 0.3-0.6(-0.7) mm broad, not arranged in rows, leaf bases erect when dry, concave, imbricate to erecto-patent; leaves not or slightly plicate, from ovate or broadly ovate or triangular base gradually tapering to acuminate apex, narrow distal part of leaf 1/4–1/3 of leaf length, straight or slightly bending to different directions; leaf margin strongly recurved, crenulate and double-crenulate below, double-crenulate, serrulate or geminate at mid leaf, serrate near apex; costa narrow, 25-50 µm near leaf base, dorsal side mammillose by protruding cell corners, percurrent or excurrent to longly excurrent; leaf areolation dim, in lower part of leaf cells short rectangular to rhomboidal, 12-37×7-12 µm, in rows parallel to costa, cell walls thickened, upper leaf cells gradually narrower and linear, 12-30×5-10 µm at apex, mammilla/papilla at proximal end of cells.

Dioicous. Perichaetial leaves from ovate base long acuminate. Perigonia disk-shaped, perigonial leaves concave at base, acute to acuminate; leaves below perigonia erect, appressed or spreading and not much different from vegetative leaves on sterile and female shoots. Seta 1.8-3 cm. Capsule ca. 2 mm long. Spores 15-25 µm.

Illustrations: Brotherus, 1923: 358, fig. 63, E, perigonial leaf; Möller, 1925: figs. 19-23; Lawton, 1971: pl. 116, 7-9, as *P. fontana* var. *pumila*; Smith, 1978: 463, fig. 223, 7, 8; Nyholm, 1998: 262, fig. 221; Guerra & Gallego, 2010: 268, fig. 95, g-l.

Differentiation. The characteristics separating *P. tomentella* from *P. fontana* are discussed above under *P. fontana*. Growth in tight tufts, small size and leaf shape separate it from the larger *P. calcarea* and *P. seriata*. It differs from *P. caespitosa* also in dim lamina areolation, narrow and thick-walled distal laminal cells and high papillae.

Habitat ecology. Brotherus (1923) stated that *Philonotis tomentella* grows in "Sümpfen, an Quellen, Bachufern und an trockenen bis nassen, besonders kalkhaltigen Felsen". According to Loeske (1906) it may be more common in calcareous habitats than *P. fontana* and the same was observed by Mårtensson (1956) in the northern Scandes. Holmen (1955) described, from North Greenland, the *Philonotis tomentella* community, which "is found first of all in springs, often along rivers. It is always poor in flowering plants, and often occurs with *Philonotis* as the only species". Later Holmen (1960) stated: "*Philonotis tomentella* is found in most parts of Greenland, but it is especially common north of 70° lat. N., where calcareous soils are present". Steere (1978) reported it as growing "on moist to wet soil, usually in percolation flushes on slopes in arctic Alaska".

In Arctic and Subarctic regions of Asiatic and European Russia, *P. tomentella* grows in various types of wet tundra, both in mountainous areas and in the lowland, and occasionally on wet cliff ledges, swampy slopes, damp willow stands, *etc.* In the mountains of Caucasus and southern Siberia it was collected from rock outcrops and cliffs with percolating water and in wet mountain tundra.

Range in Russia. *Philonotis tomentella* was previously reported from the northern part of European Russia, Ural and Caucasus, and from nearly all regions of Russian Asia (Ignatov *et al*., 2006). It is common in the Siberian Arctic and Subarctic, being more rare in NW European Russia and Chukotka, and known from few confirmed records in the mountain areas of south Siberia and Caucasus.

Selected specimens examined: **RUSSIA**: EUROPEAN RUSSIA: **Murmansk Province**: Dalnie Zenentsy, 29.VII.2001, *Belkina #34-21-01* (KPABG); **Arkhangel'sk Province**: Novaya Zemlya, Matochkin Shar, 1904, *R. Pohle s.n.* (LE); **Perm Province**: Krasnovishersk District, Vishersky Nature Reserve, 24.VI.1995, *Bezgodov & Selivanov #347* (MW); CAUCASUS: **Karachaevo-Cherkessia**: Teberda Nature Reserve, *Onipchenko #100/94* (MW). ASIATIC RUSSIA: **Khanty-Mansijsky Autonomous District**: Berezovo District, Nyaruo-yu Creek (Mokva River right tributary), 6.IX.1950, *Kil'dyushevsky #100/29* (LE); **Yamalo-Nenetsky Autonomous District**: Yunto Lake, 17.VII.1994, *Czernyadjeva #29* (LE); **Altai Republic**: Kosh-Agach District, Kurajsky Mt. Range, Tabozhok Mt., *Ignatov #31/185* (MHA); **Krasnoyarsk Territory**: Taimyrsky Municipal District: Maimecha River, *Fedosov #09-335* (MW); Byrranga Mt. Range, Bootonkaga River, Krutoj Creek, 12.VII.1991, *Kuvaev #1765-1* (MW); Taimyrskoe Lake, Ledyanaya Bay, *Fedosov #Phil3* (MW); Anabar Plateau, Afanas'evskie Lakes, *Fedosov #06-52* (MW); Jenisej River, Noven'koe, 15.VIII.1914, *Kuznetsov & Reverdatto #2175* (LE); **Republic Sakha/ Yakutia**: Ust-Maya District, Allakh-Yun, *Ignatov #00-613* (MHA); Bulunsky District, Lena River delta, Tiksi, Kharaulakh Mt. Range, 2.IX.1979, *Filin s.n.* (MW); Ust-Yansky District, Yana River 15 km downstream of Kular, 25.VII.1971, Filin s.n. (MW); Novosibirskie Islands, De Long Arkhipelago, Zhokhov Island, 1989, *Samarsky s.n.* (LE); **Buryatia**: Eravninsky District, *Tubanova #EpT-20/08* (MW); **Magadan Province**: Ola District, Ola River, *Malashkina #Mg-30-07-11* (MW); **Chukotsky Autonomous District**: Ioni Lake, Ioniveem River,

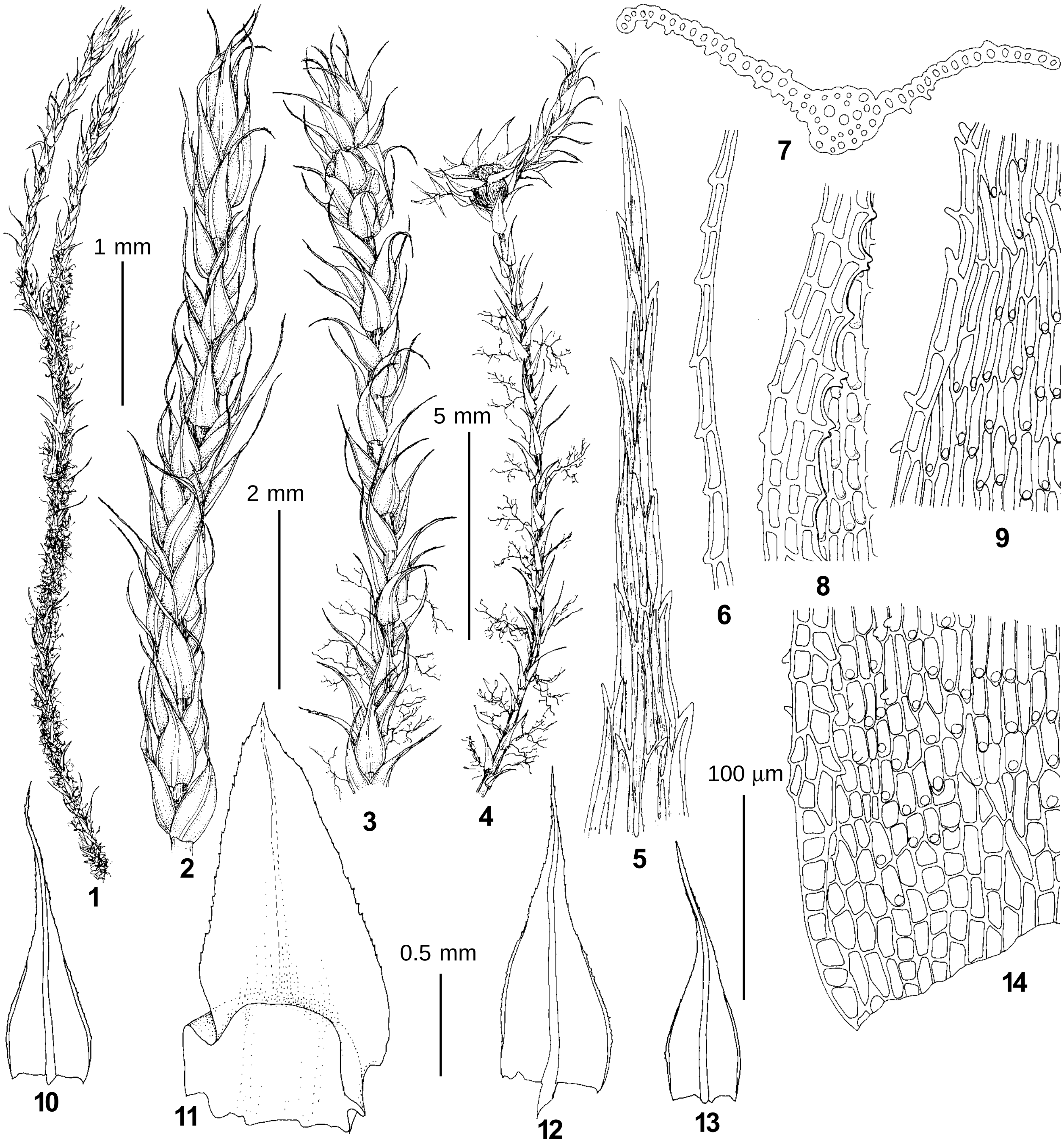

Fig. 17. *Philonotis tomentella* Molendo (from: Taimyr, Fomich River, 19.VIII.2003, *Pospelov s.n.*, MW): 1, 2 – habit, dry; 3-4 – habit, wet; 5 – cells of leaf apical part; 6 – leaf longitudinal section; 7 – leaf transverse section; 8 – median laminal cells; 9 – upper laminal cells; 10, 12-13 – leaves; 11 – inner perigonial leaf; 14 – basal laminal cells. Scale bars: 5 mm – for 1, 4; 2 mm for 3; 1 mm for 2; 0.5 mm for 10-13; 100 µm for 5-9, 14.

Ioni Mt., 3.VIII.1977, *Afonina s.n.* (LE); Anadyrsky District, Koryakskoe Upland, Pekul'nejskoe Lake, 15.VIII.1986, *E.Yu. Kuz'mina s.n.* (LE); Vrangel Island, Somnitel'naya Bay, 15.VIII.1985, *Afonina s.n.* (LE).

Total range (as *P. tomentella* or *P. fontana* var. *pumila*). According to standard floras (Smith, 1978, 2004; Crum & Anderson, 1981; Nyholm, 1998; Casas *et al.*, 2006) and floristic reports (Loeske, 1906; Steere, 1978) *P. tomentella* is more common in arctic areas and in the corresponding zones of southern mountainous areas. – North America (Zales, 1973, map fig. 71). – Europe (Düll, 1985; Saboljević *et al.,* 2008). – SW Asia: Caucasus (Nyholm, 1998), Iran (Akhani & Kürschner, 2004), Iraq (Frey & Kürschner, 1991), Turkey (Uyar & Çetin, 2004). Kürschner & Frey (2011) repeated the same information for SW Asian countries. – Koponen (2010 a) recorded *P. tomentella* from China (Xizang, E Tibet, Upper Mekong basin). – Africa: Algeria and Morocco (Ros *et al.*, 1999). – Specimens seen from high Kenyan and Tanzanian mountains that

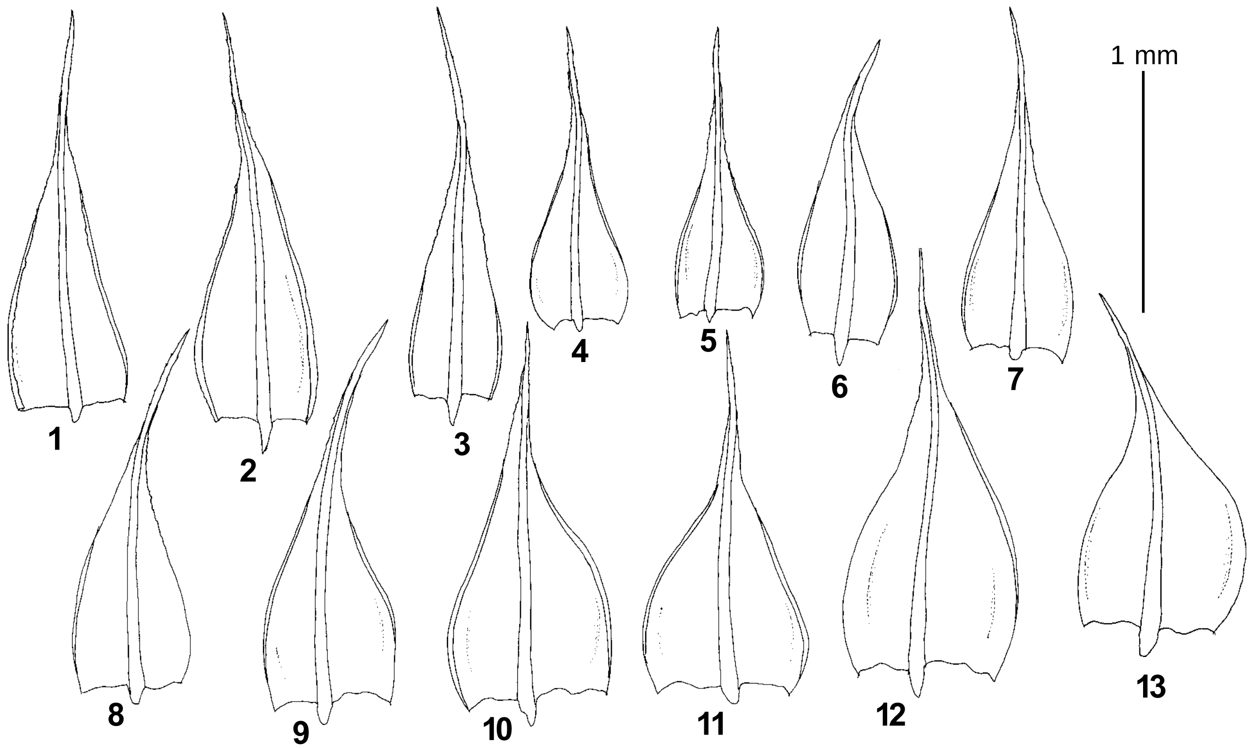

Fig. 18. Stem leaves from female or sterile shoots of *Philonotis tomentella* Molendo (from: 1 – Austria, *Köckinger #14908*, MW; 2 – Austria, *Köckinger #14906*, MW; 3 – Caucasus, Teberda Reserve, *Onipchenko #100/94*, MW; 4 – Buryatia, Eravninsky District, *Tubanova #EpT-20/08*, MW; 5 – Taimyr, Maimecha River, *Fedosov #09-335*, MW; 6 – Mongolia, Govi-Altai Province, *Ignatov #01-405*, MHA; 7 – Altai, Tabozhok, *Ignatov #31/185*, MHA; 8 – Yakutia, Allakh-Yun, *Ignatov #00-613*, MHA; 9 – Mongolia, Bayan-Hongor Province, *Ignatov #01-406*, MHA; 10 – Taimyr, Ledyanaya Bay, *Fedosov #Phil3*, MW; 11 – Anabar Plateau, Afanas'evskie Lakes, *Fedosov #06-52*, MW; 12 – Taimyr, Medusa Bay, 10.VII.2002, *Varlygina s.n.*, MW; 13 – Magadan Province, Ola River, *Malashkina #Mg-30-07-11*, MW. Scale bar: 1 mm for 1-13. All specimens were used in the molecular study.

were named *P. fontana* or *P. tomentella* seem to represent other taxa (Koponen, in prep.).

Selected specimens examined: **AUSTRIA**: Vorarlberg, Lechquellen-Gebrige, E Lech, Rüfikopf, *Köckinger #14908* (MW).

MONGOLIA: Bayan-Hongor Province, Bogd Somon, Ikh-Bogd Mt., *Ignatov #01-406* (MHA).

INDIA: Kashmir, above Gulmarg, 10-11.000’, 31.V.1892 *J. F. Duthie 11316* (H-BR 3130 028, as *P. fontana*).

CHINA: Yunnan, Lijiang, Yulong snow Mts, under *Rhododendron* shrubbery, 3800 m, 1980 *X.-J. Li 80-217* (H, HKAS 43151).

Philonotis americana Dism., Mem. Soc. Bot. France 17: 35. 1910. – *P. fontana* var. *americana* (Dism.) Crum, Bryologist 72: 244, 1969. – Type: North America (see below).

P. seriata subsp. *americana* Dism., Mem. Soc. Bot. France 17: 22. 1910. – Homotypic with *P. americana* Dism.

Figs. 19-20.

Historical review. Dismier (1910: 22) first described *Philonotis americana* as a subspecies of *P. seriata*, but in the same paper (1910: 35) accepted it as a new species and gave a Latin description due to “aux recommendations du Congrès de Vienne”. Britton (1911) reviewed Dismier’s (1910) paper, and it was translated into English (Dismier, 1911). Britton (1911) treated *Philonotis americana* as a subspecies, but Flowers (1935) accepted it at the specific level. However, Flowers (1935) erroneously cited Dismier’s (1908) European monograph for the basionym (but cited also Dismier, 1911) and gave the type locality to be British Columbia, but did not list a type specimen. Flowers (1935) cited several exsiccate specimens, and as the first one “Holz. Musci Acro. Bor. Amer. 70b”. Zales (1973) cited the same specimen as the “lectotype”, without citing where the typification was published, or whether it was a new designation. In the latter case Zales’ lectotypification is illegal, since his thesis is not effectively published (The Code, Art. 29-31). Lawton (1965, 1971) and Malcolm *et al.* (2009) accepted *P. americana* as a species (“treated by some authors as a variety of *Philonotis fontana*”). Crum (1969) and Zales (1973) used the name *P. fontana* var. *americana*.

Persson (1954) compared *Philonotis americana* with *P. seriata*, and came to the conclusion that *P. americana* is extremely closely related to *P. seriata* and cannot be given a higher rank than a subspecies. According to Persson, “*P. seriata* subsp. *americana* is smaller plant than *seriata*. The leaves are less dense and less regularly disposed in spiral rows, they are broadly ovate, abruptly acuminate and broader than those of *seriata*. The other distinctions that are given regarding the form of leaf apex, the papillosity of the back of the costa, the excurrence of the latter, *etc.*, are erroneous.” Later, Persson (1963) dealt with *P. americana* at the specific level. Zales (1973), following Crum (1969), had *P. americana* as a variety of *P. fontana*, stating that Persson's opinion that ssp. *americana* is closely related to extra-North American *P. seriata* in erroneous.

Lawton (1965, 1971) separated *P. americana* from *P. fontana* on the basis of habit characters: "Leaves twisted when dry, diverging from the stem at a wide angle, often in vertical rows" in *P. americana* and "Leaves not twisted, sometimes falcate, not diverging at a wide angle" in *P. fontana*. Lawton (1971) recognized two varieties, *P. americana* var. *americana* and var. *torquata* (Renauld & Geh.) Flowers. The latter differs from var. *americana* in having a percurrent or shortly excurrent costa and strongly twisted leaves. She also recognized the difference between female and male plants: "Dioicous, the leaves of male plants often imbricate and scarcely twisted when dry". Zales (1973) synonymized var. *torquata* with var. *americana*, which "can be recognized by its large size (5-10 cm) which is the largest of the genus in North America, the widely spaced erect spreading leaves with several plications on each side of the costa, and the very broadly ovate-lanceolate leaves that form a spiralling stem tip". Malcolm *et al.* (2009) described the leaves as ovate to ovate-lanceolate with short to long-acuminate apex, percurrent or excurrent costa and ± spirally twisted around the stem. They also stated that the leaves are in five rows along the stem.

The description below is based on specimens from America and the Russian Far East.

Plants pale green to brownish, loosely tufted, small to tall, shoots 5-10 cm, leaves ca. 1,5 mm long and 0,6-1 mm wide, diverging from the stem at a wide angle so that the stem is visible between the leaves, leaves often in vertical rows, concave, plicate, from broadly ovate base tapering to acuminate apex, apex twisted when dry, narrow distal part of leaf 1/2–1/3 of leaf length; margin recurved at leaf base, crenulate and double-crenulate below, serrate near apex; costa 50-75 μm wide near leaf base, dorsal side mammillose by protruding cell corners, percurrent or long excurrent; leaf areolation ± translucent in lower ovate part of leaf, in apical part dim, in lower part of leaf cells quadrate, rectangular or rhomboidal, 12-55×5-17 μm, thin-walled, gradually narrower and linear or vermicular toward apex, 30-45×12-17 μm, mammilla/papilla proximal at leaf cells and commonly central even in elongate cells near leaf base.

Dioicous. Perichaetial leaves from ovate base gradually tapering to a long stiff apex with excurrent costa; vegetative leaves below perichaetium ± erect and shorter and narrower than the vegetative leaves of the previous year. Base of perigonial leaves erect and concave, apex wide-spreading, acute or ± obtuse in inner perigonial leaves; leaves below perigonia erect, appressed and shorter than vegetative leaves on sterile and female shoots. Sporophytes unknown in Russia, the description is based on specimens from North America. [Seta ca. 4 cm long. Capsule ca. 3 mm long, old capsule striate on all sides. Spores ca. 25 μm, minutely papillose].

Illustrations. Flowers, 1935: pl. 70 F; Lawton, 1971: pl. 115, 1-6, as *P. americana* var. *americana*, 7-8, as *P. americana* var. *torquata*; Malcolm *et al.*, 2009: 199.

Differentiation. The habit characters of *P. fontana* discussed above in connection with *P. tomentella* separate it from *P. americana*. Especially the attachment of twisted leaves gives a characteristic habit to *P. americana*: the leaves are not imbricate so that brownish stem is visible between leaves. The leaves in *P. fontana* are more imbricate, and the stem is covered by basal parts of the leaves (except in male plants with appressed erect leaves). *P. fontana* leaves taper more abruptly than the leaves of *P. americana* and are secund in one direction. A cellular difference seems to be that even narrow cells in the basal leaf of *P. americana* have commonly a central papilla, whereas only quadrate cells may have central papilla in *P. fontana*.

P. americana differs from *P. seriata* in having leaves tapering from a broadly ovate base to rather short straight or slightly secund apex. The leaves of *P. seriata* have a narrower proximal part. The costa of *P. seriata* is much broader at the leaf base, flexuose and bulging strongly on the dorsal leaf side. This causes the leaves to be and remain falcate when wetted. The moist leaves of *P. americana* are straight or slightly secund.

The well developed Japanese specimen (*Koponen 21183*) was compared with the specimen "M. Holzinger, Musci Acrocarpi Boreali-Americani 70b", which may later be selected as the lectotype (see above and below), and they are identical.

Habitat ecology. The label information of the specimens from Kamchatka and Kunashir (Kunashiri) Island gives the habitats as follows: spring mire at lake shore; springs in valley, near springs with rather cold water; hot springs, thermal field; bank of stream, river or lake (4 specimens); on soil on riverside; on rock at stream bank; river bank, in water; in wet place; sedge bog (2 specimens), on wet soil. The habitats and substrates of the Japanese localities are described below.

Range in Russia (Fig. 20). Bakalin *et al.* (2009) were the first to report *Philonotis americana* from Asia. The new material showed that it has a wide range in Kamchatka and the Kuril Islands. *P. americana* is here reported as new to Japan. The Japanese localities in the Rausu District are close to the Kuril Islands.

Specimens examined: **RUSSIA**: ASIATIC RUSSIA: **Kamchatsky Territory**: Kamchatka, Sredinny Range, Kirevna River valley, Verkhnekireunskie hot springs, 22.IX.1989, *Chernyagina s.n.* (LE); Aleutsky District, Commander Islands, Bering Island, *Fedosov #10-3-601* (MW); **Sakhaliskaya Province**: Sakhalin: Okha District, Lagurinka River mouth, 25.VIII.2009, *Pisarenko s.n.* (MHA); Yuzhno-Kuril'sky District: Kuril Islands, Kunashir: Golovnin Volcano, *Ignatov #06-1043, 06-3026* (MHA); 08.IX.1988, *Zolotukhin s.n.* (MHA) Shikotan, Voloshin Bay, *Bakalin #K-39-3-07* (MW); Ins. Kurilenses, *J. Matsumura 11* (H-BR 3131 001, as *P. fontana*).

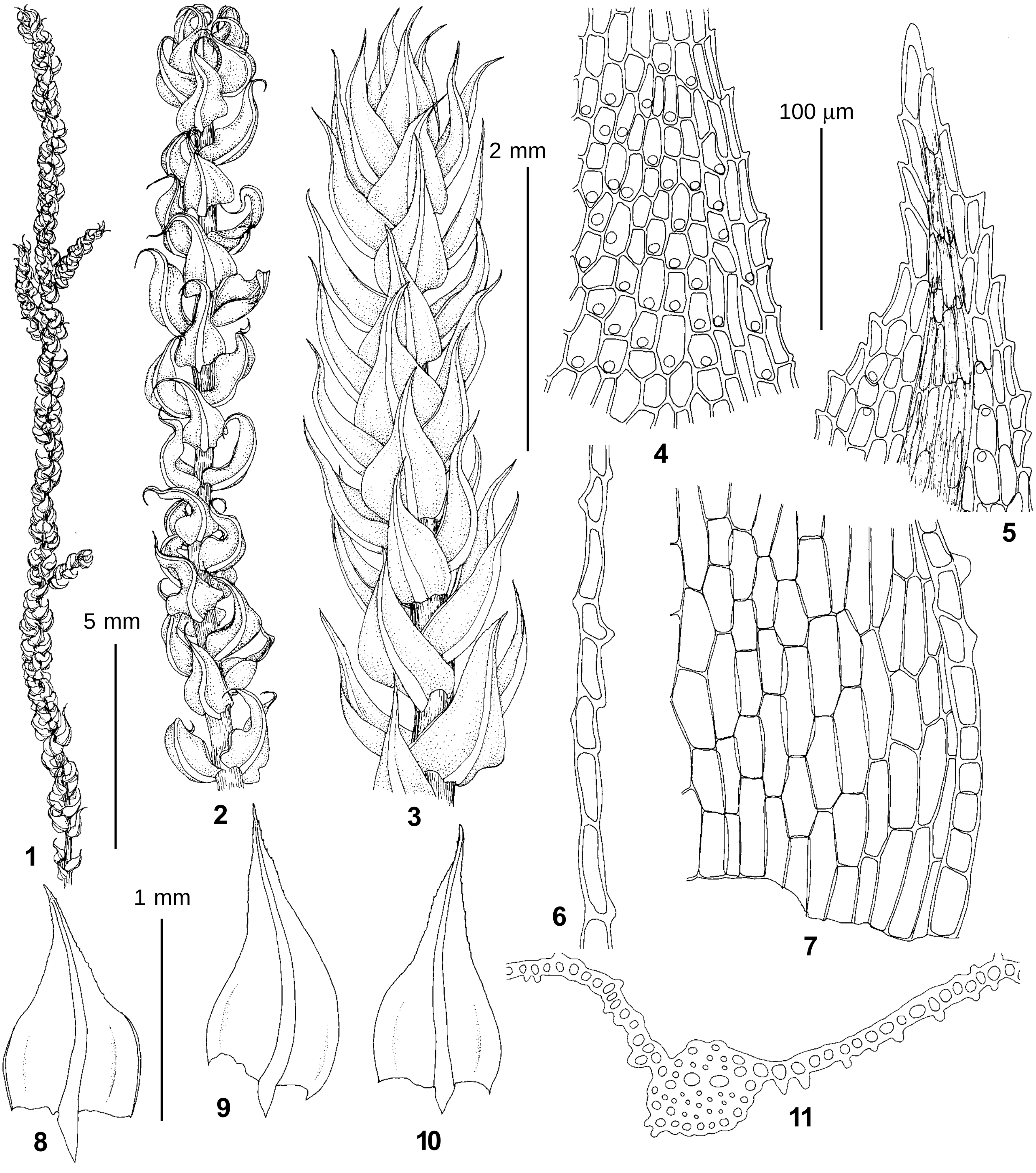

Fig. 19. *Philonotis americana* Dism. (from: Kuril Islands, Kunashir, *Ignatov #06-1043*, MHA): 1, 2 – habit, dry; 3 – habit, wet; 4 – upper laminal cells; 5 – cells of leaf apical part; 6 – leaf longitudinal section; 7 – basal laminal cells; 8-10 – leaves; 11 – leaf transverse section. Scale bars: 5 mm – for 1; 2 mm for 2-3; 1 mm for 8-10; 100 µm for 4-7, 11.

Total range. Crum (1969) saw specimens of *P. americana* only from the Aleutians, Alaska, British Columbia and California. Crum wrote further: "The only specimens I have seen from eastern North America…are various expressions of *P. fontana*, none worthy of distinction, although some indeed resemble *P. americana* somewhat in aspect." Lawton (1971) added Washington, Oregon, Idaho, Wyoming and Utah to the range of *P. americana*. Zales' (1973, fig. 70) thesis has a distribution map of *Philonotis fontana* var. *americana* and he reported it as an endemic to North America and restricted to the Coastal and Rocky Mountains, from California to the Aleutian Islands. According to Malcolm *et al.* (2009) it grows "throughout montane regions of California; often grows in extensive pure stands". Based on these statements, *Philonotis americana* has a western range in North America, similar to a number of other moss taxa (Schofield, 1969). The present records from East Asia add *P. americana* on the list of bryophytes ranging from western North America to East Asia, the North Pacific element (Scho-

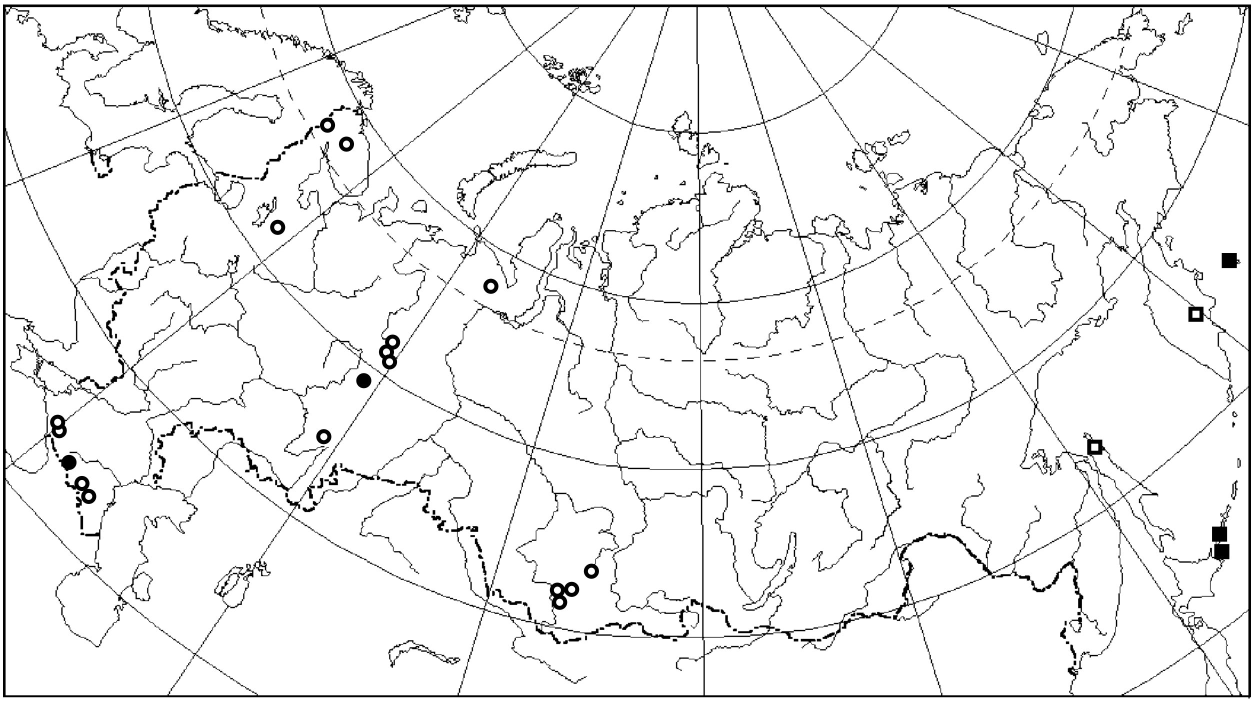

Fig. 20. Distribution of *Philonotis seriata* Mitt. (circles) and *P. americana* Dism. (squares) in Russia. Solid figures show specimens used in DNA studies.

field, 1965; Iwatsuki, 1972). – Russian Far East: Bakalin *et al.* (2009), and present report.

Selected specimens examined: **JAPAN**: Hokkaido. Nemuro Distr., Rausu-cho, valley of R. Sashiruisawa (5 km NE of Rausu village). Deep river valley with cliffy walls and northern temperate *Acer – Alnus – Ulmus* woodland, 20 m, on open moist boulder, 5.VII.1971 *T. Koponen #21300* (H); Mt Rausu, *Betula ermanii* wood on slope, 600–700 m, lower oroboreal zone, on open moist humus, 4.VII.1971 *T. Koponen #21178, 21183* male and female plants, and sporophytes (H); Mt. Rausu, main branch of Rausu River, deep river valley with hot springs, 700–800 m, lower oroboreal zone, on wet soil, submerged, 4.VII.1971 *T. Koponen #21209* (H).

U.S.A.: California, 26.VIII.1989, *Ignatov s.n.* (MHA); Alaska, 30.VIII.1992, *H. Dupree #94* (MHA). Wyoming, Yellowstone National Park, 2.IX.1888 *J. Röll 1496* (H-BR 3130 046, as *P. fontana* var. *falcata*).

CANADA: British Columbia, High up on the Selkirk Mts, near Armstrong, 19.VII.1904 *E. Wilson* = M. Holzinger, Musci Acrocarpi Boreali-Americani 70b (H-BR 3130 062, PC!).

Philonotis seriata Mitt., J. Linn. Soc. Bot. Suppl. 1: 63. 1859. – *P. fontana* var. *seriata* (Mitt.) Kindb., Bih. Kongl. Svenska Vetensk.-Akad. Handl. 7(9): 255. 1883. – *P. fontana* subsp. *seriata* (Mitt.) Dixon, Stud. Handb. Brit. Mosses 294. 1896. – Lectotype (designated by Ochi, 1962): [Scotland]. In Britannia boreali in monte Benna-Bourd, *W. Gardiner* (NY, not seen). Figs. 20-21.

For the typification, see Koponen (2009b, 2010a).

Historical review. *Philonotis seriata* (Mitten, 1859) remained unnoticed in Europe for several decades. The reasons are probably that: (1) it was published in a paper dealing with East Indian mosses (see Koponen, 2009b), although the specimens cited were from Europe, and (2) the species is rare in Central Europe. Lindberg (1877) reported *P. seriata* from Finland and accepted it at the specific level in his "Musci Scandinavici" (1879). Lindberg and Arnell (1890) repeated Mitten's (1859) Latin description and reported the species from Siberia at the river Jenisei (however, see below). Kindberg (1883) and Dixon & Jameson (1896) accepted *P. fontana* var. *seriata,* while Braithwaite (1888-1895) and Limpricht (1895) accepted the taxon at the specific level. Loeske (1906) discussed lengthy on the *Philonotis* taxa of Europe and accepted *P. seriata* at the specific level, and Dismier (1908) followed him, writing "*Ph. seriata* (Mitt.) emend. Lske". Since then *P. seriata* has been treated at the specific level in the major European floras (Brotherus, 1923; Mönkemeyr, 1927; Nyholm, 1960, 1998; Smith, 1978, 2004).

Mitten's (1859) publication misled Ochi (1962, 1963) to cite the type locality to be in India and to state that *P. fontana* var. *seriata* is widely distributed in Japan. However, the Japanese specimens are another species, *P. yezoana* (Koponen, 2009b, and below).

Plants brownish, usually tall, shoots 2-10 cm, leaves 1-2 mm long and 0.5-0.9 mm wide, arranged in five spiral rows, falcate-secund when dry, carinate with dorsally bulging costa; leaves plicate at basal part, broadly lanceolate, from base gradually tapering to acute apex, margin plane or narrowly recurved, crenulate and double-crenulate below, serrate near apex; costa strong, 75-140 μm or wider near leaf base, dorsal side usually densely mammillose throughout, ending below apex or shortly excurrent; lower leaf cells short rectangular to rhomboidal, 15-30×5-12 μm, gradually narrower and linear or vermicular toward apex, 22-37×2.5-7.5 μm at apex, mam-

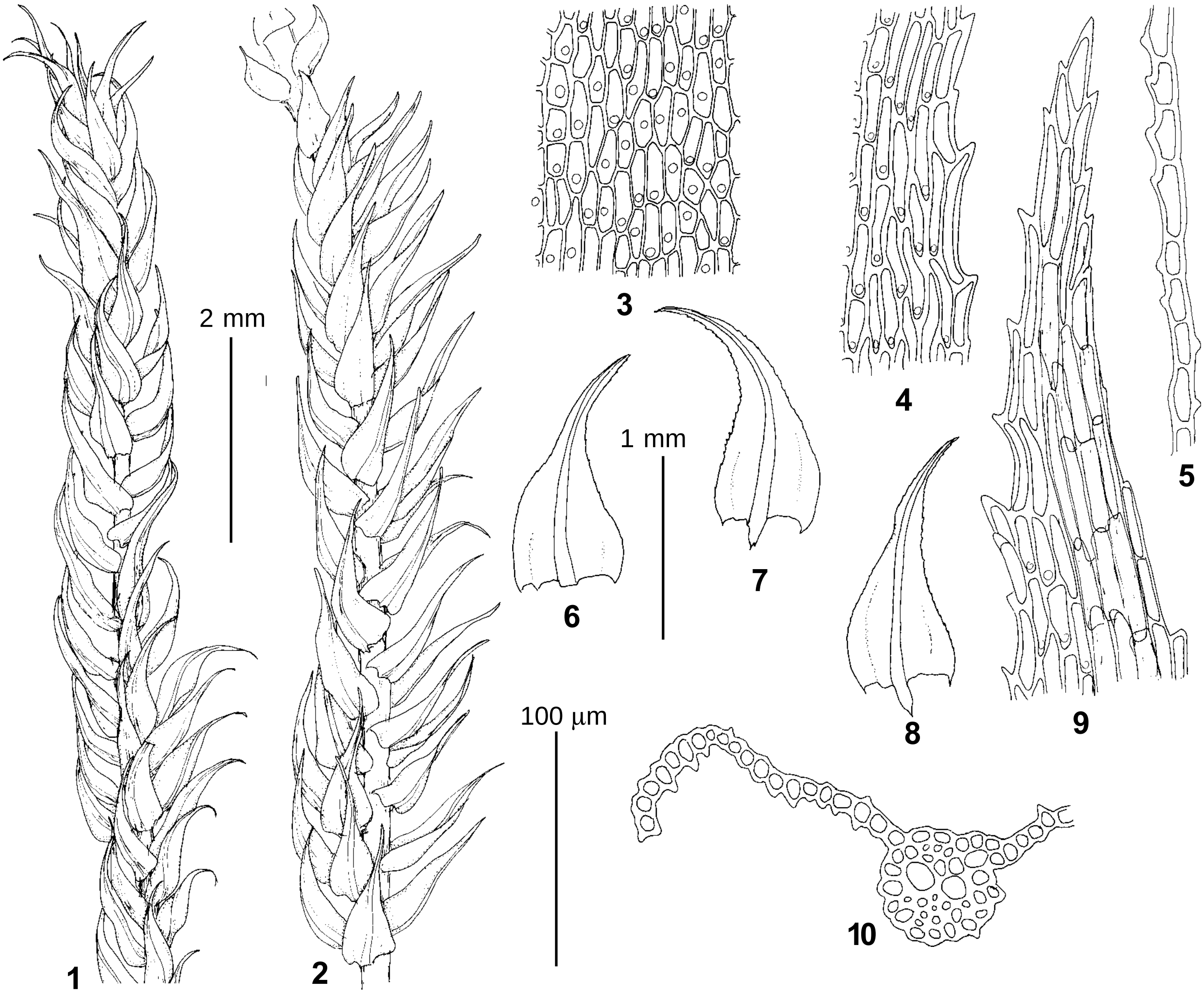

Fig. 21. *Philonotis seriata* Mitt. (from: Perm Province, Vishersky Nature Reserve, 28.VII.1994, *Bezgodov #605* (MW): 1 – habit, dry; 2 – habit, wet; 3 – basal laminal cells; 4 – upper laminal cells; 5 – leaf longitudinal section; 6-8 – leaves; 9 – cells of leaf apical part; 10 – leaf transverse section. Scale bars: 2 mm for 1-2; 1 mm for 6-8; 100 µm for 3-5, 9-10.

milla mostly proximal in linear cells, but commonly central in quadrate cells near leaf base; leaf areolation ± dim throughout.

Dioicous. Perigonial leaves erect, from concave translucent base shortly tapering to acute or obtuse apex; leaves below perigonia erect, appressed and shorter than vegetative leaves on sterile and female shoots and may have short acute or obtuse apex. Sporophyte not seen in specimens from Russia, but it is similar to that in *Philonotis fontana*.

Illustrations: Brotherus, 1923: 358, fig. 63, H, perigonial leaf; Möller, 1925: figs. 32-35; Nyholm, 1998: 261, fig. 219; Ignatov & Ignatova, 2003: 586, fig. 420; Hallingbäck, 2008: 292; Guerra & Gallego, 2010: 264, fig. 94, h-n.

Differentiation. The spiral rows of leaves in *Philonotis seriata* are best seen on fresh specimens in the field. Its bulging costa is much stronger than that of *P. fontana* and has large colourless mammillae on its dorsal side (best seen in side view). The costa of related species has small papillae or scindulae only. The leaves of *P. calcarea* are not arranged in rows and are relatively longer with longer excurrent costa, and have long and uncoloured juxtacostal cells. The basal leaf cells of *P. seriata* are smaller than in *P. fontana* and *P. calcarea*, and have the mammillae/papillae central on the cell more commonly than in the other species of section *Philonotis*. Short-leaved male plants can be recognized by the strong arcuate costa with wide mammillae on the dorsal surface and smaller basal leaf cells than in *P. fontana* and *P. calcarea*.

Habitat ecology. In Altai, *Philonotis seriata* was collected in a spring mire in a subalpine meadow. According to the field experience from northeastern Europe (T. K.) and Ural Mts (M. I.) it is strictly limited to springs or spring-fed brooks in areas with siliceous bedrock. It is common in similar habitats in Caucasus, mostly in the subalpine and alpine belts, and grows in brooks and spring mires in the Kola Peninsula. Many literature reports and floras report similar habitats. Möller (1925) states that it has not been found on calcium rich soil, and Mårtensson (1956) confirms that in the northern Scandes *P. seriata* has mostly been collected in the non-calcareous areas, but occurs also in places where the vegetation is fairly rich. Smith (1978, 2004) states that it grows in acidic springs and flushes and on wet ground at high altitudes. Loeske (1909: 45) described it as "kalkfeindlich" in the Alps, and according to Geissler (1976) *P. seriata* is character species of Cratoneureto-Philonotidetum and Marsupello-Scapanion associations in acid spring brooks occurring often as wide stands, and frequent also in Hygrohypnion association.

Range in Russia. In European Russia, *P. seriata* is known from montane areas – in the Murmansk Province, the Urals, and Caucasus and is totally absent in the central planes. Lindberg & Arnell (1890) reported the species from Siberia at the river Jenisei. However, the vouchers seen by us (H-SOL) are *P. fontana*. Bardunov (1974) reported *P. seriata* from Altai, and from there we can list specimens, as well as from Khakassia.

Specimens examined: **RUSSIA**: EUROPEAN RUSSIA: **Murmansk Province**: Kirovsk District, Kibiny Mts, Vudjavrchorr Mt., 31.VIII.2001, *Ignatov & Ignatova* (MW); Kandalaksha District, Alakurtti, Akhkijoki River, 30.VII.1971, *Konstantinova #147* (MW); **Karelia:** Pudozh District, 13.VII.1977, Volkova s.n. (LE); **Komi Republic**: Kozhva District, Malyj Patek River (Pechora River basin), southern foothills of Sylova Mt., 19.IX.1948, *Kuvaev s.n.* (LE); Troitsko-Pechorsky District, Pechoro-Ilychsky Nature Reserve, Medvezh'ya Mt., 22.VII.2005, *Smirnova #65* (MW); **Perm Province**: Gremyachinsk District, Basegi Nature Reserve, 9.VI.1994, *Ignatov s.n.* (MW); **Bashkortostan**: Beloretzk District, Yuzhno-Ural'sky Nature Reserve, NW slope of Nara Mt. Range, 11.VII.2004, *Martynenko #196* (MW); CAUCASUS: **North Ossetia/Alania**: Urikh River gorge, Dzinga, 13.VIII.1947, *Tarnogradsky s.n.* (LE); **Karachaevo-Cherkessia**: Teberda Nature Reserve, *Ignatova #07-5* (MW); Kuban, in silvis ad flumen Tieborda, 14–1500 m, 1.IX.1890 *S. Sommier & E. Levier* – Iter Caucasicum *559* (H-BR 3125 042, as *P. calcarea*); **Kabardino-Balkaria**: upper course of Adyl-su River, Dzhankuat glacier, X.1994, *Pospelov #49* (MW); **Krasnodar Territory**: Caucasian Nature Reserve, Urushtein Mt., upper course of Urushtein River, 10.VII.1935, *Vasil'eva s.n* (MW); **Adygeya**: Caucasian Nature Reserve, Abago Mt., 20.VII.1960, *Artamonov s.n.* (MW); ASIATIC RUSSIA: **Yamalo-Nenetsky Autonomous District**: Polar Urals, 106 km railway station of Seida – Labytnangi Railway, 5.VIII.1977, *Filin s.n.* (MW); **Altai Republic**: Katru River (left tributary of Bolshoj Abakan), watershed of Odulu & Edy-kol Creeks, 12.VII.1935, *Goncharova s.n.* (MW); **Khakassia**: Ordzhonikidzevsky District, Zolotogorsky, Sarala River, 14.VII.1970, *Vasiljev s.n.* (LE).

Total range. Dismier (1910) thought that *P. seriata* is rare in North America. Zales (1973) and Persson (1954) excluded *P. seriata* from North America and cited it in Asia from Kashmir, Siberia and Himalaya. Dismier (1907) cited a specimen from Greenland, later (1910) doubted the record, but confirmed it in 1912. Koponen (2012c) listed specimens from Greenland and mapped the range there. – Europe: (Düll, 1985, Saboljević *et al.*, 2008). – SW Asia: Afghanistan (Frey & Kürschner, 1991), Iran (Akhani & Kürschner, 2004), Iraq, Israel (Nyholm, 1998), Turkey! (Uyar & Çetin 2004). Kürschner and Frey (2011) repeated the same information for the SW Asian countries. – Africa: Morocco (Ros *et al.*, 1999).

Dismier (1912) and Kabiersch (1937) cited specimens from NW Himalayas and Kashmir. Koponen (2009b) confirmed them to be *P. seriata. P. seriata* occurs at high elevations in Tibet (Koponen, 2010a) and Yunnan (see below) in China, but specimens cited from southern Chinese provinces (Zang & He, 2007) must be based on miss-identifications (Koponen, 2010a). Koponen (2009b) excluded *P. seriata* from Japan and Korea.

Selected specimens examined: **SOUTH OSSETIA**: Ermani ad fl. Didi Liachva, 23.VII.1881, *Brotherus* (H-BR 3125 036, as *P. calcarea*); Gudshevi ad fonets fl. Aragva, 23.VII.1877, *Brotherus* (H-BR 3118 012).

ABKHASIA: In summon jugo Kluckor, juxta moles glaciales, 25-2700 m, 28.VIII.1890, *S. Sommier & E. Levier* – Iter Caucasicum 482 (H-BR 3118 029).

GEORGIA: Svania libera occid. In jugo alpino inter flumina Neuskra et Seku; lat. orient., 2000-2200 m, 21.VIII.1890 *S. Sommier & E. Levier* – Iter Caucasicum 332 (H-BR 3118 026).

CHINA: Yunnan. Lijiang, Yulong snow Mts, under *Rhododendron* shrubbery, 3800 m, 26.VIII.1980, *X.-J. Li 80-217* (H, HKAS 43151), new to Yunnan.

Philonotis calcarea (Bruch et al.) Schimp., Coroll. Bryol. Eur. 86. 1856. – *Bartramia calcarea* Bruch et al., Bryol. Eur. 4: 49. 325. 1842. – *Philonotis fontana* ssp. *calcarea* (Bruch et al.) Boulay, Musc. France 214. 1884. – Type: Europe (not seen). Figs. 22, 24.

Plants pale green, medium-sized to tall, shoots 2-10(-15) cm, leaves 1.5-3×0.7-1 mm, not arranged in rows, leaf bases erect when dry, plane or concave, apical part falcate-secund, erect spreading when wet; leaves plicate, from ovate or triangular base gradually tapering to acute or acuminate apex, margins plane or narrowly recurved, basal border cells smooth, thin-walled, lowest bulging, crenulate and double-crenulate at midleaf, serrate near apex; costa strong, 60-125 μm or wider near leaf base, bending, dorsal side mammillose by protruding cell corners, percurrent or excurrent; in lower part of leaf cells low mammillose, rectangular to rhomboidal, 25-75×10-27 μm, juxtacostal cells near leaf base 65-100×10-25 μm, gradually narrower and linear to vermicular toward apex, 32-55×2.5-10 μm in distal part of leaf; mammilla proximal on cells; central mammilla occur in quadrate basal leaf cells.

Dioicous. Perichaetial leaves from concave base long acuminate. Perigonia disk-shaped, perigonial leaves from concave base tapering to acuminate apex; leaves below perigonium erect, shorter than vegetative leaves on sterile and female shoots, ± triangular, costa excurrent. Seta ca. 4 cm long, capsule ca. 3-4 mm, gibbous and horizontal to nutant when dry. Spores ca. 25 μm, slightly papillose.

Illustrations: Brotherus, 1923: 358, fig. 63, I, K, perigonial leaves; Möller, 1925: figs. 37-40; Smith, 1978: 224, fig. 224, 4-8; Nyholm, 1998: 260, fig. 218; Ignatov

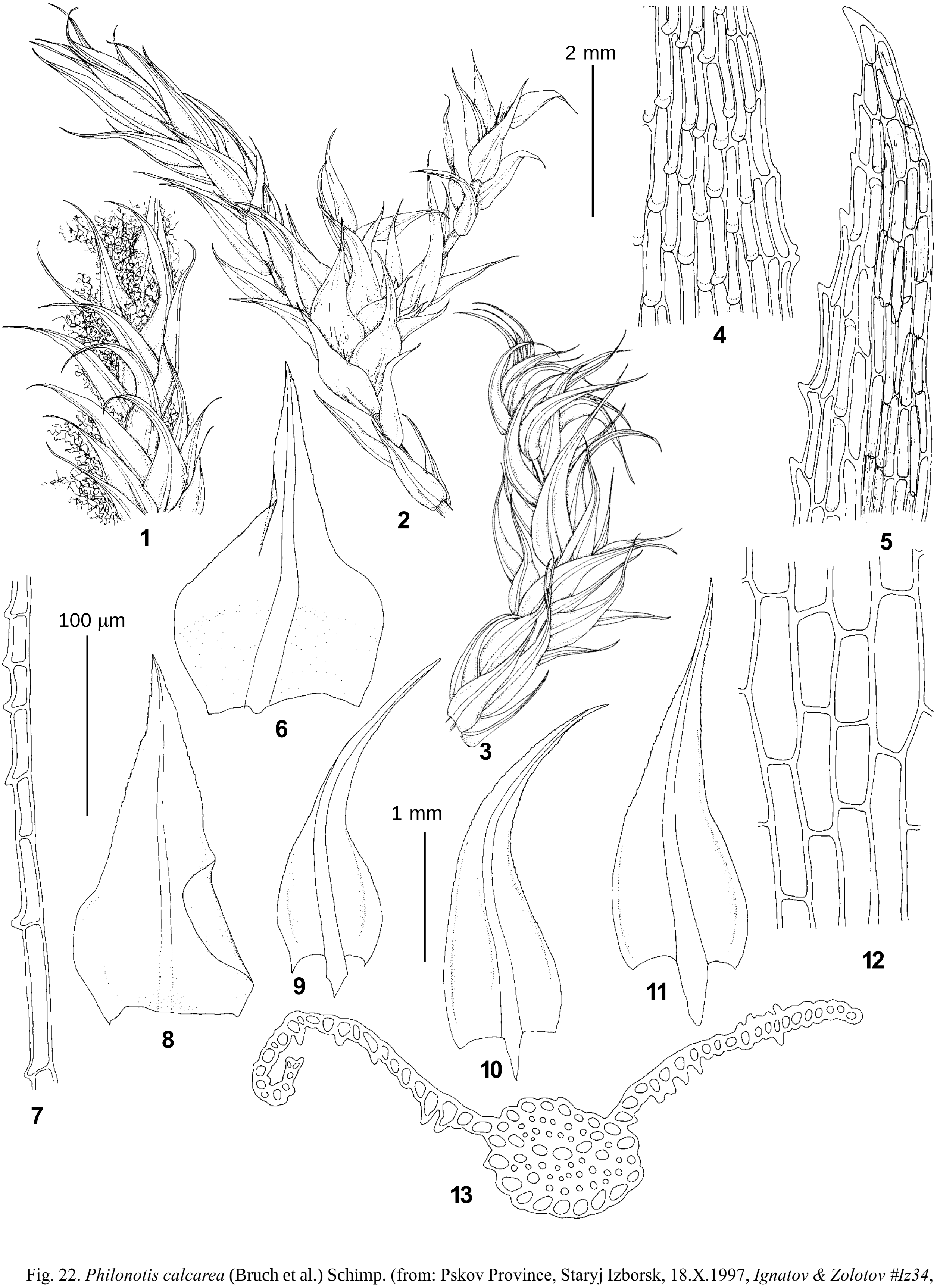

Fig. 22. *Philonotis calcarea* (Bruch et al.) Schimp. (from: Pskov Province, Staryj Izborsk, 18.X.1997, *Ignatov & Zolotov #Iz34*, MHA): 1-3 – habit, dry; 4 – upper laminal cells; 5 – cells of leaf apical part; 6, 8 – inner perigonial leaves; 7 – leaf longitudinal section; 9-11 – leaves; 12 – basal laminal cells; 13 – leaf transverse section. Scale bars: 2 mm for 1-3; 1 mm for 6, 8-11; 100 µm for 4-5, 7, 12-13.

& Ignatova, 2003: 585, fig. 419; Hallingbäck 2008: 290, 291; Guerra & Gallego 2010: 264, fig. 94, a-g.

Differentiation. *Philonotis calcarea* has a rather stiff habit, large plants, gradually tapering leaves, and long and narrowly elongate cells of the basal leaf. The leaves look much more translucent than the leaves of *P. seriata* and *P. fontana*. The long, rectangular and colourless juxtacostal cells are a good diagnostic character. The costa is nearly as strong as in *P. seriata*. *P. caespitosa* has smaller leaf cells, a narrower costa and a more slender and flexuose leaf acumen. The male plants of *P. fontana* may resemble male plants of *P. calcarea*. If a perigonium is not present they can be separated on the basis of the longer juctacostal cells and stronger costa in *P. calcarea*. Male plants of *P. calcarea* without perigonia, sometimes marked as "forma *tenuis*" on herbarium labels, and plants floating or growing under water can be separated from male plants of *P. fontana* by longer and narrower basal leaf cells.

Habitat ecology. The epithet "*calcarea*" was selected by the describing authors since they knew the plant only from calcareous districts. The citations below from floras and floristic field studies unanimously describe *Philonotis calcarea* as a calcicole. Brotherus (1923): "In kalkhaltigen Quellen und Sümpfen." Smith (1978, 2004): "…in fens, basic springs and flushes and dune slacks, calcicole..." Nyholm (1998): "… wet calcareous soils, fens, beside springs…". Geissler (1976) described Cratoneuro-Philonotidetum calcaerae from the Alps, which occurs in "Quellfluren (Rheokrenen) in basischen Gebieten." In Russia, it also grows in areas with calcareous bedrock, in springs, fens and on wet rock outcrops.

Range in Russia (Fig. 24). *P. calcarea* is known in European Russia from its northern part (from the Pskov and Arkhangelsk Provinces to the Kola Peninsula), South Urals and East Caucasus. There are also several localities in the Tver Province, where spring mires and springs at river banks occur. Ignatov (1994) reported *Philonotis calcarea* from the Altai Mts.

Specimens examined: **RUSSIA**: EUROPEAN RUSSIA: **Murmansk Province**: Kirovsk District, Khibiny Mts, Vud'yavrchorr Mt., 3.VIII.1946, *Kuvaev #71* (MW); **Karelia**: Karelia ladogensis, Suistamo, Saariselkä, near Väisänen, 6.X.1936, *Huuskonen* (LE); **Leningrad Province**: between Ropsha & Glyadino, 14.VII.1976, *Vjyunova s.n.* (LE); **Arkhangel'sk Province**: Val'tevo, Pinega River, 15.VIII.1985, *Vjyunova s.n.* (LE); **Pskov Province**: Pechory District, Novyj Izborsk, *Ignatov & Zolotov #Jz34* (MHA); **Tver Province**: Staritsa District, between Kultino & Koshevo, 18.VI.1990, *Notov s.n.* (TVBG, MW); **Bashkortostan**: Sterlitamak District, Abzanovo, Inzer River, Susak Mt., 20.VII.1924, *Lipshitz s.n.* (MW); CAUCASUS: **Dagestan**: Gunib District, Gunib, *Ukrainskaya #13992* (LE, MHA); Tlyarata District, Kolorosl' Pass, 19.VIII.1940, *Elenevskyj s.n.* (MW); ASIATIC RUSSIA: **Altai Republic**: Turochak District, Teletzkoe Lake, Yailyu, 21.VII.1991, *Ignatov s.n.* (MW).

Total range. Dismier (1910) and Zales (1973) excluded *P. calcarea* from North America, and it is not included in most North American floras (Lawton, 1971; Crum & Anderson, 1981). Malcolm *et al.* (2009) record it from California, but the voucher specimens have been renamed as *P. fontana* and *P. americana* (D.H. Norris, personal information). – Azores, Cape Verde Islands (Nyholm, 1998). – Europe (Düll, 1985, Saboljević *et al.*, 2008). – SW Asia: Afghanistan! (Frey & Kürschner, 1991), Iran! (Akhani & Kürschner, 2004), Iraq, Israel, Lebanon!, Syria, Turkey! (Uyar & Çetin 2004). Kürschner and Frey (2011) repeated the same information for the SW Asian countries. Tibet (Nyholm 1998). – Africa: Algeria, Morocco and Tunisia (Ros *et al.* 1999).

Zang & He (2007) listed several specimens from China. These records, and older records from Tibet (Xizang in Chinese terminology) and the Himalayas need confirmation (see Koponen, 2010a). Kabiersch (1937) did not report *P. calcarea* from China or the Himalayas and Gangulee (1974) does not report it from the Himalayas. Ochi (1963) excluded *P. calcarea* "from the Regions". Of four specimens named as *P. calcarea* from Himalayan area in H-BR, three specimens are *P. fontana* (see above) and one specimen is *P. calcarea*.

Selected specimens examined: **SPAIN:** Gran Canaria, Arûcas, 24.IV.1897, *O. Gelert* (H-BR 3125 047).

Pamir, in montibus Alai, ad Sufi Kurgau, submers. in rivulo frigido, 2100 m, 18.VI.1898, *O. Paulson* (H-BR 3125 003).

Philonotis yezoana Besch. & Cardot, Bull. Soc. Bot. Genève, sér. 2, 1: 123. 1909. – Lectotype (designated by Koponen, 2009b): Japan. Sur de lac e Mori (Yezo), 5.V.1889, *Faurie 3505* (BM!; isolectotypes in PC!, KYO, not seen). Figs. 23-24.

Plants slender, 1-4 cm tall, pale, rhizoids brown, smooth; leaves 0.7-1.2 mm long and 0.3-0.6 mm wide, distant, appressed against stem, straight or slightly falcate, concave, from broadly ovate base shortly triangular to acute or shortly acuminate, leaves on innovations narrower than stem leaves below perichaetium; margin plane, basal marginal cells smooth or bulging, middle marginal cells entire, rectangular or margin uniserrate or irregularly geminate by small protruding cell corners, near apex uniserrate; costa short excurrent, on dorsal side smooth at leaf base, with minute papillae or protruding cell corners at apical part; basal leaf cells 25-50×10-20 µm, thin-walled, elongated hexagonal to rhomboidal, smooth or slightly bulging, much larger than upper leaf cells, which are hexagonal, rectangular or quadrate, 12-30×7-15 µm and with central mammilla/papilla.

Dioicous. Perichaetial leaves ca 1.7 mm long, from concave narrow ovate base long acuminate; perigonia bud-like, perigonial leaves 1.2-1.5 mm, with broad concave base and short acute or obtuse apex. Leaves on male plants below perigonia similar to leaves on female stems. Seta 3-4 cm long. Dry capsule 2.5-3 mm long, horizontal, short ovoid, smooth, or smooth below and lowly furcate dorsally. Peristome complete, endostome segments nearly as long as peristome teeth, minutely papillose; spores 17-25 µm, papillose.

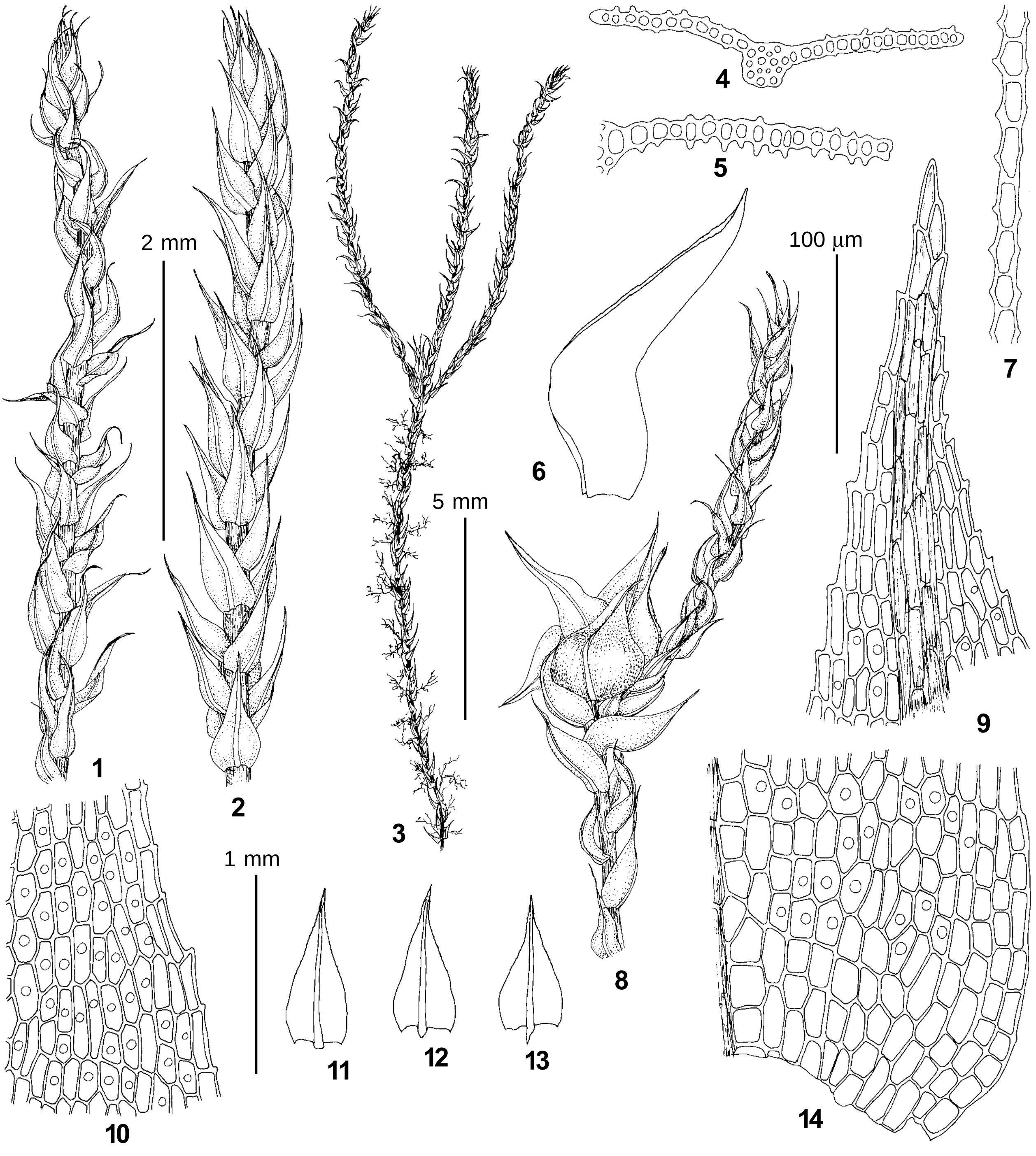

Fig. 23. *Philonotis yezoana* Besch. & Cardot (from: Kamchatka, 23.VIII.2002, *Czernyadjeva #86*, LE): 1, 3, 8 – habit, dry; 2 – habit, wet; 4-5 – leaf transverse sections; 6 – inner perigonial leaf; 7 – leaf longitudinal section; 9 – cells of leaf apical part; 10 – upper laminal cells; 11-13 – leaves; 14 – basal laminal cells. Scale bars: 5 mm – for 3; 2 mm for 1-2, 8; 1 mm for 6, 11-13; 100 µm for 4-5, 7, 9-10, 14.

Illustrations: Noguchi, 1989: 571 B, as *P. fontana* var. *seriata*; C, as *P. fontana* var. *tenuicuspes*; Czernyadjeva, 1995: 16, fig. 1; Kekes, 2006: 42, fig. 2; Malcolm *et al.*, 2009: 200.

Philonotis yezoana is always easily distinguished by its very slender habit, and the upper leaf cells with a central papilla. Also some species of *Philonotis* sect. *Philonotis* may have single cells with central papillae, but the majority of their cells, especially in the distal, narrow leaf portion have the mamillae/papillae at proximal end of the cells (except in *P. fontana* which may have papillae on the distal cell end close th the leaf apex).

Habitat ecology. According to Ochi (1962, as *Philonotis fontana* var. *seriata*) *P. yezoana* grows on moist or wet soil, humus, or moist to wet rocks. The habitats of the species in Russia are similar. Examples of the habitats and substrates are given in the list of specimens from Japan.

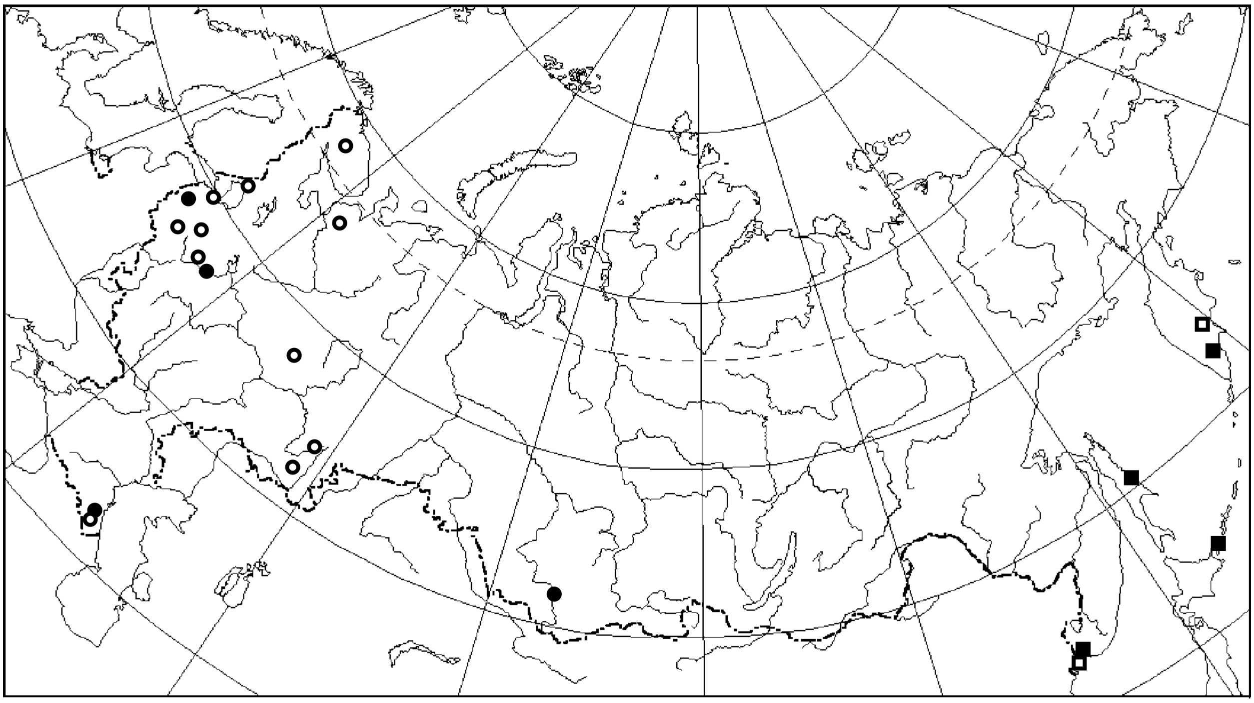

Fig. 24. Distribution of *Philonotis calcarea* (Bruch et al.) Schimp. (circles) and *P. yezoana* Besch. & Cardot (squares) in Russia. Solid figures show specimens used in DNA studies.

Range in Russia (Fig. 24). Czernyadjeva (1995) reported *Philonotis yezoana* for Russia, although it was known from the Kuril Islands already previously (see below). Koponen (2009a) gave it in addition to Japan from Korea.

Specimens examined: **RUSSIA**: ASIATIC RUSSIA: **Kamchatsky Territory**, Elizovo District, Mutnovsky Volcano, 23.VIII.2002, *Czernyadjeva #86* (LE); **Primorsky Territory**: Vladivostok, Okeansky Range, Shamorsky Pass, *Ignatov et al. # 06-2076* (MHA); Khasansky District, L'va Bay; 14.IX.1985, *Ignatov s.n.* (LE); **Sakhalinskaya Province**: Sakhalin, 17.IX.2009, *Pisarenko #op04027* (MW); Yuzhno-Kuril'sky District, Kunashir: Veslo Peninsula, *Ignatov # 06-3096* (MHA); Tyatya Volcano, 14.IX.2006, *Ignatov #06-1844* (MHA).

Total range. North America: (Zales, 1973, map fig. 72; Crum & Anderson, 1981; Kekes, 2006), Greenland (Koponen, 2009a). – Crum and Anderson (1981) reported *P. yezoana* from Europe, but Geissler (1984) identified the specimen in question as *P. seriata*. The recent checklist of European bryophytes (Hill *et al.*, 2006) does not list *P. yezoana*.

Philonotis yezoana is rather common in Japan (Ochi, 1962, most Japanese specimens listed as *P. fontana* var. *seriata*). Koponen (2010a) recorded it from Korea. *Philonotis yezoana* was first recorded for the Russian Far East by Czernyadjeva (1995). However, Ochi (1962) reported a specimen under *P. fontana* var. *seriata* from the Kuriles (see above). Zang & He (2007) reported it from China but we have not seen the voucher specimens. The illustration in Li (2006, Pl. 77, figs. 8-11, Heilongjiang, from *C. Gao 13633*) cannot illustrate *P. yezoana* since the papillae are at the proximal cell end.

Selected specimens examined: **JAPAN**: Honshu: Tottori Pref., Mt. Daisen, mountain top, 1600-1650 m, submerged in pond, 1971 *T. Koponen 21791* (H). Hokkaido: Sôya Distr., Rebun Island, in valley with small creek and sloping fen, 180 m, on wet bank, 1971, *T. Koponen 20589* (H); shore bank of Lake Kushuko, 10 m, open wet soil, 1971, *T. Koponen 20682* (H), on moist peat, *T. Koponen 20673* (H). Rishiri Island, Mt. Rishiri, valley with ever-lasting snow-bed, low *Alnus* wood, 500 m, open mesic boulder, 1971, *T. Koponen 20477* (H); Nemuro Distr., Mt. Rausu, deep river valley with hot springs, 700-800 m, wet open soil, 1971 *T. Koponen 21212* (H); Rausu spa, valley surrounded by northern temperate woodland, 130 m, open moist boulder, 1971 *T. Koponen 20965* (H). Kamikawa Distr.: Mt. Daisetsu Nature Park, Sounkyo Spa, canyon of small river with *Picea – Abies – Acer – Cercidiphyllum – Tilia* wood, 700–800 m, on boulder at river, 1970 *A. & T. Koponen 15565* (H). Hidaka Distr., Urakawa Nat. Forest, valley of small stream in *Acer – Cercidiphyllum – Quercus – Tilia – Ulmus* wood, 250 m, on cliff at stream, 1970, *T. Koponen 13372*, *13394* (H). Oshima Distr., Hakodate-shi, Ayudomari Fall, river valley in deciduous *Acer – Fagus – Fraxinus – Populus – Quercus – Ulmus* woodland, 200 m, cliff at stream, 1970, *T. Koponen 11384*, *11386* (H).

DISCUSSION

Morphology, habitats and ranges

The morphological concept of species is based on three facts: a species is a taxon which has (1) characters separating it definitely from its closest relatives; it has its own (2) habitat ecology and (3) geographical range, which can be explained by climatic or ecological parameters or by the geological history of the earth. Moreover, complete plants, which in mosses would mean plants with sporophytes, should be known. If this concept is accepted, most of the taxa dealt with here can be accepted at the specific level. They have the habitat ecology in common, they grow in constantly wet habitats, either in places with running water or in areas with regular precipitation and high humidity. This means that they thrive best in boreal to temperate areas in lowlands, and on corresponding altitudes in southern mountainous areas and are lacking from areas with a definite dry season or irregular pattern of precipitation. It may be emphasized in this connection that most of them have been classified in the section *Philonotis*. Many of the species of the other sections of *Philonotis* (mainly *Philonotula*) are warm-temperate to tropical areas, and they may have habitat requirements different from the habitats of the species of the section *Philonotis*.

Two of the taxa of the section *Philonotis*, *Philonotis calcarea* and *P. seriata*, are distinct both morphologically and ecologically, and have their own ranges. Both of them are mainly European species, the easternmost occurrences being in the Altai Mountains and western Himalaya. *P. calcarea* grows only in calcareous habitats in springs and brooks from the lowlands to mountains in boreal to temperate zones. On the contrary, *P. seriata* thrives only in acid water and grows mainly in boreal or oroboreal zones. Hájkova *et al.* (2007: 784) stated: "Our study revealed well-differentiated ecological niches for *P. seriata* and *P. calcarea*. The two morphoplogically similar species, *P. fontana* and *P. caespitosa*, had only slightly differentiated ecological niches."

Philonotis fontana seems to have no other habitat requirements except a constantly wet substrate, such as mires, springs and other damp habitats. Therefore, *P. fontana* is most common of the species under discussion and has a typical circumpolar range similar to many other bryophytes of constantly wet habitats. The wide range is one of the reasons for its phenotypic plasticity (see Buryová & Shaw, 2005), and the sexual dimorphism and the difficulty to identify juvenile plants and stunted modifications have caused the description of numerous unnecessary varieties. Fully developed plants can always be separated from its close relatives.

If we include in *Philonotis tomentella* only plants with narrow proximal leaf cells with distinct papillae, nearly straight leaves with a longly excurrent costa, and which occur on calcareous rocks or soil and form tight tufts, we have a rather good taxon which can be accepted as species (see also discussion on p. 25-26). It also has its own high arctic circumpolar distribution and the southern disjunct localities are from high, alpine elevations.

Philonotis capillaris is a rather variable plant. Populations exist which have mammillae/papillae both on the proximal and distal cell ends, or the proximal cell end is bulging. The small size and the fact that the leaf margin does not have geminate teeth are other character states. It has a characteristic range in North America in the western oceanic portion, now extended from there to the North Pacific Commander Islands. Its exact range in Europe is not well known. If it is similarly oceanic in Europe as in North America, it has a typical range similar to some other mosses (*e.g. Plagiothecium undulatum* (Hedw.) Schimp.). Some records from Siberia and Chukotka are probably incorrect; however we can confirm its occurrence in Yakutia and the Amurskaya Province, where it is represented by another haplotype (see p. 26). Due to its small size it is a weak competitor, which explains its habitats at moist cliff bases (and banks in meadow ground), different from the habitats of the species of the section *Philonotis*.

Philonotis yezoana is morphologically distinct. It has a characteristic East Asiatic range extending via the Kuril Islands and Alaska to the west coast of North America. It has not been found from the inland of North America and the disjunct finds in eastern North America (Vermont, New York, Greenland) are in the oceanic east. It is not found in Europe or continental Asia, except in Korea and the Russian Far East. The habitat is similar to that of the species of the section *Philonotis*, on wet cliffs and brook shores.

Philonotis caespitosa is least well-known of the taxa of the section *Philonotis*. As discussed above, both old and modern European bryologists have accepted it at the specific level, but in North America it has been treated as *P. fontana* var. *caespitosa*. More recent studies retain its specific value. For instance, Buryová (2004) stated that "…the two taxa are genetically distinct although closely related." She also claims to have studied or seen mixed populations of *P. fontana* and *P. caespitosa* (as did Loeske, 1905b), and gives only North America and Europe as the range of *P. caespitosa*. The habitats of *P. caespitosa* are described to be similar to those of *P. fontana* (*e.g.* Möller, 1925) but they are perhaps not quite as wet and eutrophic. Hájkova *et al.* (2007) also mention ecological similarity of these species (see above).

In the course of this research, a number of Central European specimens, some of them with sporophytes, were used for comparison. We re-checked Asiatic specimens similar to and named as *P. caespitosa*, but found that they were all young plants or could otherwise not be identified for certain. Zales (1973) had a similar experience with North American specimens: "*Philonotis caespitosa* and several lesser varieties of *P. caespitosa* have been described from small plants that usually have flat leaves with plane margins. These plants are almost always sterile and represent small plants of *P. fontana*". Accordingly, whether the range of *P. caespitosa* extends beyond Europe to the Asiatic side of North Asia remains uncertain. Our molecular study confirms its occurence only in central part of European Russia, while all sequenced specimens from Asiatic Russia, Caucasus, and the Kola Peninsula turned to be slender forms of *P. fontana*.

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Appendix 1. GenBank accession numbers and voucher specimen data.

Species	Locality	Voucher data	ITS	trnL-F
P. americana	Commander Isl	Russia, Commander Islands, Fedosov #10-3-601 (MW)	KC111019	KC111108
P. americana	Kuriles 1	Russia, Kuril Islands, Kunashir, 08.IX.1988, Zolotukhin s.n. (MHA)	KC111020	KC111109
P. americana	Kuriles 2	Russia, Kuril Islands, Kunashir, Ignatov #06-3026 (MHA)	KC111021	KC111110
P. americana	Kuriles 3	Russia, Kuril Islands, Shikotan, Bakalin #K-39-3-07 (MW)	KC111022	KC111111
P. americana	Kuriles 4	Russia, Kuril Islands, Kunashir, Ignatov #06-1043 (MHA)	KC111023	KC111112
P. americana	Kuriles 5	Russia, Kuril Islands, Shikotan, Bakalin #K-58-6-07 (MW)	KC111024	KC111113
P. americana	USA, Alaska	U.S.A., Alaska, 30.VIII.1992, H.Dupree #94 (MHA)	KC111025	KC111114
P. americana	USA, California	U.S.A., California, 26.VIII.1989, Ignatov s.n. (MHA)	KC111026	KC111115
P. caespitosa	Denmark 1	Denmark, 11.IV.2012, Goldberg s.n. (MW)	KC111027	KC111116
P. caespitosa	Denmark 2	Denmark, 26.04.2012, Goldberg s.n. (MW)	KC111028	KC111117
P. caespitosa	Moscow	Russia, Moscow Province, 9.IX.2010, Teplov s.n. (MHA)	KC111029	KC111118
P. caespitosa	Ryazan	Russia, Ryazan Province, 1.VIII.2002, Volosnova s.n. (MW)	KC111030	KC111119
P. caespitosa	Tver	Russia, Tver Province, 16.VIII.1994, Notov s.n. (MW)	KC111031	KC111120
P. calcarea	Altai	Russia, Altai Republic, 21.07.1991, Ignatov s.n. (MW)	KC111032	KC111121
P. calcarea	Dagestan	Russia, Dagestan, Ukrainskaya #13992 (MHA)	KC111033	KC111122
P. calcarea	Pskov	Russia, Pskov Province, Ignatov & Zolotov #Iz34 (MHA)	KC111034	KC111123
P. calcarea	Tver	Russia, Tver Province, 10.VII.2001, Notov & Spirina (MW)	KC111035	KC111124
P. capillaris	Amurskaya	Russia, Amurskaya Province,16.VII.2010, Bezgodov #472 (MHA)	KC111036	KC111125
P. capillaris	Caucasus 1	Russia, Krasnodar Territory, Seregin #M-2278 (MW)	KC111037	KC111126
P. capillaris	Caucasus 2	Russia, Krasnodar Territory, 23.VIII.1999, Ignatov (MHA)	KC111038	KC111127
P. capillaris	Commander Isl	Russia, Commander Islands, Fedosov #10-3-492 (MW)	KC111039	KC111128
P. capillaris	USA, California	U.S.A., California, Norris #72095 (MHA)	KC111040	KC111129
P. capillaris	Yakutia	Russia, Yakutia, Ust-Maya Distr., Ignatov # 00-978 (MHA)	KC111041	KC111130
P. falcata	Altai	Russia, Altai Republic, 2.VIII.2000, Ignatova s.n. (MW)	KC111044	KC111133
P. falcata	Dagestan	Russia, Dagestan, 23.V.2009, Ukrainskaya s.n. (MW)	KC111045	KC111134
P. falcata	Yakutia 1	Russia, Yakutia, Tomponsky Distr., Ignatov & Ignatova #11-2107 (MHA)	KC111046	KC111135
P. falcata	Yakutia 2	Russia, Yakutia, Tomponsky Distr., Ignatov & Ignatova #11-2102 (MW)	KC111047	KC111136

P. fontana	Amurskaya 1	Russia, Amurskaya Province, 9.VII.2010, Bezgodov #370 (MHA)	KC111048	KC111137
P. fontana	Amurskaya 2	Russia, Amurskaya Province, 19.06.2011-Bezgodov #347 (MHA)	KC111049	KC111138
P. fontana	Amurskaya 3	Russia, Amurskaya Province, 10-06-2011, Bezgodov #82 (MHA)	KC111050	KC111139
P. fontana	Austria	Austria, Köckinger #14907 (MW)	KC111051	KC111140
P. fontana	Buryatia	Russia, Buryatia, 23.VIII.2008, Krivobokov s.n. (MW)	KC111052	KC111141
P. fontana	Caucasus 1	Russia, Karachaevo-Cherkessia, Ignatova #07-108 (MW)	KC111053	KC111142
P. fontana	Caucasus 2	Russia, Karachaevo-Cherkessia, Ignatov & Ignatova #05-3496 (MW)	KC111054	KC111143
P. fontana	Chukotka	Russia, Chukotka, 24.VIII.2001, Afonina s.n. (MW)	KC111055	KC111144
P. fontana	Evenkia	Russia, Evenkia, 21.VII.1992, Shcherbina s.n. (MW)	KC111056	KC111145
P. fontana	Kamchatka	Russia, Kamchatka, 5.VIII.2007, Chernyadjeva #9-07 (MW)	KC111057	KC111146
P. fontana	Karelia	Russia, Karelia, Maksimov & Maksimova #125-34 (MW)	KC111058	KC111147
P. fontana	Komi 1	Russia, Komi Republic, Ivanov & Donskov # 09-428 (MW)	KC111059	KC111148
P. fontana	Komi 2	Russia, Komi Republic, Nenetzky Autonomous District, Ad'zva River, Ivanov & Donskov 09-423 (MHA)	KC111060	KC111149
P. fontana	Kuriles	Russia, Kuril Islands, Iturup, Bakalin #Ę-17-13-07 (MW)	KC111061	KC111150
P. fontana	Mari-El	Russia, Mari-El, 26.VI.1998, Czernyadjeva s.n. (LE)	KC111062	KC111151
P. fontana	Murmansk 1	Russia, Murmansk Province, 30.VI.2012, Ignatov s.n. (MHA)	KC111063	KC111152
P. fontana	Murmansk 3	Russia, Murmansk Province, 4.IX.2001, Ignatov s.n. (MW)	KC111064	KC111153
P. fontana	Murmansk 4	Russia, Murmansk Province, 28.VI.2012, Ignatov s.n. (MHA)	KC111065	KC111154
P. fontana	Murmansk 5	Russia, Murmansk Province, 29.VII.1988 Belkina & Lichachev #301/8 (KPABG)	KC111066	KC111155
P. fontana	Primorsky	Russia, Primorsky Territory, Ignatov # 07-353 (MHA)	KC111067	KC111156
P. fontana	Sakhalin	Russia, Sakhalin, Ignatov & Teleganova #06-875 (MHA)	KC111068	KC111157
P. fontana	Svalbard	Norway, Svalbard, Belkina #106-16-05 (KPABG)	KC111069	KC111158
P. fontana	Sverdlovsk	Russia, Sverdlovsk Province, 21.VII.1995, Marina s.n. (MW)	KC111070	KC111159
P. fontana	Vladimir	Russia, Vladimir Province, Seregin #M-2654 (MW)	KC111071	KC111160
P. fontana	Yakutia	Russia, Yakutia, Oimyakon Distr., Ignatov & Ignatova #11-3471 (MW)	KC111072	KC111161
P. fontana	Zabaikalsky	Russia, Zabaikal'sky Territory, Afonina #A5210 (MW)	KC111073	KC111162
P. hastata	Singapore	Singapore, 26.XI.1999, Ignatov s.n. (MHA)	KC111106	KC111195
P. laii	Singapore	Singapore, 28.XI.1999, Ignatov & Tan s.n. (MHA)	KC111081	KC111170
P. marchica	Caucasus	Russia, Karachaevo-Cherkessia, Ignatov & Ignatova #05-3275 (MW)	KC111075	KC111164
P. marchica	Kaluga	Russia, Kaluga province, 6.VI.2012, Teleganova s.n. (MHA)	KC111076	KC111165
P. marchica	Kuriles	Russia, Kuril Islands, Iturup, Nyushko #It-28.2-08b (MHA)	KC111077	KC111166
P. marchica	Moscow 1	Russia, Moscow Province, 18.VI.1985, Ignatov s.n. (MW)	KC111078	KC111167
P. marchica	Moscow 2	Russia, Moscow Province, 24.IV.2011, Teplov s.n. (MHA)	KC111079	KC111168
P. rigida	Caucasus	Russia, Krasnodar Territory, 23.VIII.1999, Ignatov s.n. (MHA)	KC111080	KC111169
P. cf. rigida	Japan	Japan, Honshu, 16.4.1986, Higuchi (MHA)	KC111043	KC111132
P. seriata	Caucasus	Russia, Karachaevo-Cherkessia, Ignatova #07-5 (MW)	KC111082	KC111171
P. seriata	Perm	Russia, Perm Province, 9.VI.1994, Ignatov & Bezgodov s.n. (MW)	KC111083	KC111172
P. sp. 1	Kamchatka	Russia, Kamchatka, 17.VII.2006, Samkova s.n. (MW)	KC111042	KC111131
P. sp. 2	Singapore	Singapore, 26.11.1999, Ignatov s.n. (MHA)	KC111074	KC111163
P. tomentella	Altai	Russia, Altai Republic, Ignatov #31/185 (MHA)	KC111084	KC111173
P. tomentella	Austria 1	Austria, Köckinger #14908	KC111085	KC111174
P. tomentella	Austria 2	Austria, Köckinger #14906	KC111086	KC111175
P. tomentella	Buryatia	Russia, Buryatia, Tubanova #EpT-20/08 (MW)	KC111087	KC111176
P. tomentella	Caucasus	Russia, Karachaevo-Cherkessia, Onipchenko #100/94 (MW)	KC111088	KC111177
P. tomentella	Mongolia 1	Mongolia, Ignatov #01-405 (MHA)	KC111089	KC111178
P. tomentella	Mongolia 2	Mongolia, Ignatov #01-406 (MHA)	KC111090	KC111179
P. tomentella	Murmansk 1	Russia, Murmansk Province, Belkina #88-22-84 (KPABG)	KC111091	KC111180
P. tomentella	Murmansk 2	Russia, Murmansk Province, Belkina #34-21-01 (KPABG)	KC111092	KC111181
P. tomentella	Novosibirskie Isl	Russia, Novosibirskie Islands, 1989, Samarsky s.n. (LE)	KC111093	KC111182
P. tomentella	Perm	Russia, Perm Province, 24.VI.1995, Bezgodov & Selivanov #347 (MW)	KC111094	KC111183
P. tomentella	Taimyr 1	Russia, Taimyr, Fedosov #09-335 (MW)	KC111095	KC111184
P. tomentella	Taimyr 2	Russia, Taimyr, Fedosov #11-1260 (MW)	KC111096	KC111185
P. tomentella	Taimyr 3	Russia, Taimyr, 10.VII.2002, Varlygina s.n. (MW)	KC111097	KC111186
P. tomentella	Taimyr 4	Russia, Taimyr, Fedosov #Phil3 (MW)	KC111098	KC111187
P. tomentella	Taimyr 5	Russia, Taimyr, Fedosov #06-52 (MW)	KC111099	KC111188
P. tomentella	Yakutia 1	Russia, Yakutia, Ust-Maya Distr., Ignatov #00-613 (MHA)	KC111100	KC111189
P. tomentella	Yakutia 2	Russia, Yakutia, Ust-Maya Distr., Ignatov #00-434 (MHA)	KC111101	KC111190
P. yezoana	Kamchatka	Russia, Kamchatka, 23.VIII.2002, Chernyadjeva #86 (LE)	KC111102	KC111191
P. yezoana	Kuriles	Russia, Kuril Islands, Kunashir, Ignatov # 06-3096 (MHA)	KC111103	KC111192
P. yezoana	Primorsky	Russia, Primorsky Territory, Ignatov et al. # 06-2076 (MHA)	KC111104	KC111193
P. yezoana	Sakhalin	Russia, Sakhalin, 17.IX.2009, Pisarenko #op 04027	KC111105	KC111194