Arctoa (2020) **29:** *135–178*
doi: 10.15298/arctoa.29.11

THE GENUS *PYLAISIA* (PYLAISIACEAE, BRYOPHYTA) IN RUSSIA

РОД *PYLAISIA* (PYLAISIACEAE, BRYOPHYTA) В РОССИИ

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Abstract

The genus *Pylaisia* is revised for the Russian moss flora basing on morphological and molecular phylogenetic studies of nuclear ITS and IGS markers and plastid *trn*L-F. The main subdivision of the genus in the obtained phylogeny splits it into two clades. The first clade includes species with the endostome totally adherent to exostome; it is represented in Russia only by *P. stereodontoides* that is related to North American *P. intricata* and more southern East Asian *P. cristata*. The second clade includes a rather well supported clade composed of species with endostomes rather strongly adherent to exostome (*P. brotheri, P. condensata, P. obtusa, P. subcircinata*), that is nested in a polytomy of species with endostomes either free or only a little adherent to exostomes. The latter polytomy includes *P. polyantha, P. curviramea, P. steerei, P. coreana, P. bezgodovii* sp. nov., and *P. camurifolia* (= 'Asiatic *P. falcata*'). Asian *P. condensata* differs from the North American *P. selwynii*, thus they may not be considered as synonymous, as it was usually assumed. A complicated diversity is found within *P. polyantha* s.l. in TCS network of ITS haplotypes: a group of European and North American haplotypes is the most isolated; mainly Siberian group of haplotypes is moderately delimited whereas the Far Eastern haplotypes form a reticulation with *P. steerei* and *P. curviramea*, and also a small-sized plants with free endostomes of *P. polyantha*-group. The latter form a moderately supported clade in IGS based trees and has morphological distinctions, allowing its resurrection as a separate East Asian species, *P. coreana.* One Genbank accession from Alaska referred to *P. selwynii* is deeply nested in *P. obtusa*, thus we presume that the latter species occurs in North America.

Резюме

На основании морфологических и молекулярно-филогенетических данных (ядерные маркеры ITS и IGS и хлоропластный маркер *trn*L-F) проведена ревизия рода *Pylaisia* во флоре России. Таксоны, включенные в анализ, распадаются на две клады. Первая из них включает виды, эндостом которых полностью срастается с экзостомом; в России она представлена только *P. stereodontoides,* которая близка к североамериканской *P. intricata* и более южной восточноазиатской *P. cristata*. Вторая клада включает умеренно поддержанную кладу, образованную видами, эндостом которых частично прирастает к экзостому (*P. brotheri, P. condensata, P. obtusa, P. subcircinata*), которая вложена в политомическую кладу, образованную видами со свободным или лишь слегка прирастающим к экзостому эндостомом – *P. polyantha, P. curviramea, P. steerei, P. coreana, P. bezgodovii* sp. nov. и *P. camurifolia* ('азиатская *P. falcata*'). Азиатская *P. condensata* отличается от североамериканской *P. selwynii*, что позволяет не рассматривать второе название как синоним первого. В *P. polyantha* s.l. сеть гаплотипов ITS показала сложное разнообразие: группа европейских и американских гаплотипов наиболее отграничена, тогда как сибирская группа гаплотипов не полностью отграничена и вместе с *P. steerei*, *P. curviramea* и наиболее восточными гаплотипами группы *P. polyantha* s.l. образует комплекс с сетчатыми взаимоотношениями его элементов. Обособленность группы, включающей мелкие растения с наиболее восточным распространением, позволяет восстановить *P. coreana* в качестве самостоятельного вида; ранее его обычно рассматривали в качестве синонима *P. polyantha.* Последовательность ДНК, депонированная в генбанке под названием *P. selwynii* для растения с Аляски, оказывается в кладе *P. obtusa*, так что мы предполагаем произрастание этого вида в Северной Америке.

KEYWORDS: mosses, taxonomy, haplotype network, biodiversity, biogeography

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INTRODUCTION

The genus *Pylaisia* was segregated by Bruch *et al*. (1851) partly from *Leskea* and partly from *Pterigynandrum*, the earlier established genera of pleurocarpous mosses with erect capsules. The family Pylaisaeaceae was also established at the same time, but unlike the genus that was universally accepted and widely used since its description, the family Pylaisiaceae was submerged in Hypnaceae and remained in oblivion until Gardiner *et al*. (2005) resurrected it.

Ignatov *et al*. (2006) listed in Russia eight species of *Pylaisia*, with one species, *P. polyantha,* being widespread almost throughout Russia, also rather widespread *P. selwynii*, with interesting distribution (Ignatov, 1999), and six species occurring in the eastern regions of Russia: *P. brotheri, P. curviramea, P. obtusa, P. steerei, P. stereodontoides*, and *P. subcircinata*. Their distribution and relative abundance in the Far Eastern region were reported by different authors in a somewhat different ways (Bardunov & Cherdantseva, 1982, 1984; Bakalin *et al*., 2009; Czernyadjeva, 2012; Cherdantseva *et al*., 2018).

The recent molecular phylogenetic studies (Arikawa & Higuchi, 2003) and taxonomic treatment of Arikawa (2004) provided a careful revision of the genus. The results of the molecular phylogenetic analysis based on plastid *rbc*L marker found the genus *Pylaisia* homogeneous, although not monophyletic because of insufficient resolution of that marker. Among others, Arikawa (2004) found that specimens of *P. polyantha* from the Russian Far East are phylogenetically delimited from European ones, thus he referred eastern Russian plants to *P. curviramea* (described from Central China).

Identification of many specimens of the genus however remains difficult, especially when capsules are not fully developed, which is a common case, as many East Asian species start spore release very late in autumn (or in winter?), when the time of field work is already over. Thus, we undertake the present revision of *Pylaisia* specimens from Russia, attempting also to find a useful DNA barcoding markers for identification of specimens without sporophytes and for plants with ambiguous morphology.

MATERIALS AND METHODS

This study was based on the herbarium specimens from MW and MHA with several additional collection from IRK, VLA, SASY, and LE. All species reported from Russia were included, and some specimens from neighboring countries were used as well.

In addition to standard microscopic observations, peristomes were studied by SEM Jeol 6380, coated by gold without any additional preparation. Light microscope observations were made under a stereomicroscope (Olympus SZX16) equipped with an Infinity 4 digital camera, and compound light microscope Olympus CX-41 with an Infinity 2 digital camera. Stacked micrographs using several optical sections were composed using the software package HeliconFocus 4.50 (Kozub *et al*., 2008).

DNA study

We included ITS, the most commonly used and informative DNA region in pleurocarpous mosses (Huttunen *et al.,* 2012), *trn*L-F, a traditionally used region which showed however insufficient variation, and IGS, a rarely used region, which provided a higher resolution than ITS in our previous studies of the genus *Fabronia* (Ignatova *et al*., 2017).

DNA extraction and amplification

Total genomic DNA was extracted from dry plants using the Nucleospin Plant Extraction Kit (Macherey-Nagel, Germany). For ITS region the laboratory protocol was essentially the same as in previous moss studies, described in detail by, *e.g.*, Gardiner *et al.* (2005).

The nuclear IGS region was amplified with primers complementary to 3' end of 26S rRNA gene - 26dR2 (forward) 5’-GAGATGAATCCTTTGCAGACG -3’and 5S rRNA gene - 5S(r)R2 (reverse) 5'-GAGTTCTGATGGGATCYGGTG -3', the latter following Wicke *et al.* (2011).

Amplification was conducted under the following conditions: 94°C – 3' (initial denaturation); 30 cycles: 94°C – 20", 62°C –20", 72°C – 40"; 72– 5' (final extension step). Amplification products were separated on a 1% agarose gel in 1xTAE with ethidium bromide staining and purified using MinElute © Gel Extraction Kit (Qiagen, Germany). The length of IGS region varied from 453 to 582 bp in PCR product from different specimens.

PCR products were sequenced using the ABI PRISM © BigDye™ Terminator v. 3.1 and further analyzed on an automated sequencer (Applied Biosystems) 3730 DNA Analyzer in common use facility “Genom”. The specimen vouchers and GenBank accession numbers are given in Table 1.

Phylogenetic analyses

Sequences were aligned manually in Bioedit (Hall, 1999). Three datasets were used for phylogenetic inferences; first and second datasets correspond to nr ITS (105 terminals including 95 representing *Pylaisia* and 10 *Homomallium*, 743 positions) and IGS (87 terminals, 83 represent *Pylaisia*, 610 positions). The third dataset (82 terminals, 1775 positions) represents a combined ITS plus IGS dataset, supplemented by 26 originally obtained *trn*L-F sequences after checking topologies inferred from single gene analyses for lack of supported conflict. Indel data in all analyses were scored using simple indel coding approach (Simmons & Ochoterena, 2000) using SeqState 1.4.1. (Müller, 2005). In the single gene analyses ITS was divided into three partitions, which corresponded to ITS1, 5.8S rRNA gene and ITS2; IGS and *trn*L-F were treated as single partitions. In the combined dataset all nuclear data were combined in a single partition as was suggested by Partitionfinder 2.1.1 (Lanfear *et al.*, 2017). Phylogenetic analysis was performed using Bayesian Inference (BI) and Maximum likelihood (ML). Bayesian inferences were performed by running two parallel analyses in MrBayes 3.2.7a (Ronquist *et al.*, 2012) with each run consisted of six Markov chains and 10,000,000 generations. The sampling frequency was one tree each 2 000 generations, and the chain temperature was set at 0.02 in all analyses. The convergence between runs (i.e. split deviation frequency lower than 0.01) was reached after 0.5 – 5 million generations. Consensus trees were calculated after omitting the first 25% trees as burn-in. Maximum likelihood analyses were performed using RAxML 8.2.12 (Stamatakis, 2014), robustness of the nodes was assessed using the thorough bootstrapping algorithm (Felsenstein, 1985) with 1000 iterations. All ML and BI analyses were performed on the Cipres Science Gateway (Miller *et al.*, 2010).

The haplotype network was built using the TCS program (Clement *et al.*, 2000) with a cut-off level of 0.95. Gaps in the data matrix were manually coded simple indel coding approach. Thus in the analysis parameter, gaps were considered as missing data.

RESULTS

The preliminary studies of the *trn*L-F sequences of 40 specimens of *Pylaisia* and 6 of *Homomallium* found *Pylaisia* monophyletic, but in a polytomy almost without further resolution (thus it is not shown). Two clades of two specimens each were found for specimens discussed below as *P. camurifolia* (=Asian '*P. falcata*'), and *P. stereodontoides* + *P. intricata*, whereas other accessions were either unresolved or showed stochastic gropping, joining samples of obviously unrelated species.

The tree based solely on ITS resolves *Pylaisia* species in two clades, one composed of the species with the endostome totally adherent to exostome (*P. stereodontoides* + *P. intricata* + *P. cristata*), while another clade includes the rest of the studied species of this genus (Fig. 1). The variation in ITS is relatively low and several groups of species in the second clade are not or weakly resolved. In particular, East Asian accessions referred to *P. curviramea*, *P. coreana* (= 'East Asian *P. polyantha*') and parly of *P. steerei* form a polytomy, where several weakly to well supported clades are nested. Among these nested clades, (1) two Mexican specimens of *P. falcata* (PP=1, BS=99), (2) two Asian specimens, previously referred to *P. falcata* and shown in Fig. 1 as *P. camurifolia* (PP=1, BS=94), (3) three specimens, which superficially resemble small plants of *P. steerei* and are shown on tree as *P. bezgodovii* (PP=1, BS=99), (4) not supported clade (PP=0.99, BS<50) of five small east Asian specimens of *P. polyantha*, shown in Fig. 1 as *P. coreana*, (5) European, American and Siberian accessions of *P. polyantha* (PP=0.99, BS=61) + three specimens of *P. steerei*, within which north Asian *P. polyantha*+*P steerei* p.p. form polytomy where weakly supported clade of European and North American specimens is nested, and (6) well resolved clade with remaining included species (PP=1, BS=87). The latter splits into two clades: the first (PP=1, BS=87) comprises a single accession of *P. subcircinata* in sister position to not supported clade of accessions of *P. obtusa* and single GenBank accession of *P. selwynii* AY009797; the second clade represents not supported tritomy of single accession of *P. brotheri*, two American accessions of *P. selwynii* (PP=1, BS=99) and a suite of Russian accessions of *P. condensata* (PP=1, BS=60).

IGS based tree (Fig. 2) is largely congruent with the ITS based one and better resolved. Accessions of *Pylaisia* form a clade, though not supported, within which not supported *P. cristata* + *P. intricata* + *P. stereodontoides* clade occupies the basalmost position; remaining clade is moderately supported (PP=1, BS=86). Accessions, which in the ITS based tree were found in not resolved polytomy, in IGS based tree form a clade sister to the maximally supported one formed by species with endostome adherent to exostome (*P. brotheri*, *P. subcircinata*, *P. obtusa*, *P. selwynii*, and *P. condensata*); topology of the latter clade is nearly identical to that in the ITS based tree excepting the shift of *P. brotheri* in a basalmost position sister to well supported clade with remaining accessions. The clade formed by accessions with free or nearly free endostome represents a tritomy that includes: (1) maximally supported *P. camurifolia* clade; (2) moderately supported (PP=1, BS=78) *P. falcata* plus *P. coreana* clade, where terminals of *P. coreana* form a not supported clade, which, however, consists of two well supported ones; and (3) *P. polyantha*, *P. steerei*, *P. bezgodovii* and *P. curviramea* clade. Within the latter, accessions of *P. bezgodovii* and *P. steerei* p.p.+ *P. curviramea* form two maximally supported clades, while the clade corresponding to *P. polyantha* + *P. steerei* p.p. is not supported.

The tree based on concatenated ITS+IGS+*trn*L-F dataset in topology is nearly identical to IGS based one, since this marker bears the strongest phylogenetic signal, but has a better resolution and support for most of clades, partly reached by excluding problematic specimens from the analysis. *Pylaisia* was resolved monophyletic, although weakly supported (PP=1, BS=67). At the earliest divergence moderately supported main *Pylaisia* clade (PP=1, BS=90) and the clade of *P. cristata* + *P. intricata* + *P. stereodontoides*, which got high support (PP=1, BS=99) split. Within "the main *Pylaisia* clade" composition of the major clades remained the same, but support for grouping of species with nearly free endostome slightly increased. Within it not supported *P. falcata* + *P. coreana* clade occupies the sister position to the major clade, where maximally supported *P. camurifolia* clade splits first. Even concatenated dataset failed to separate accessions referred to *P. curviramea* and *P. steerei*, which are found in a polytomic, maximally supported clade splitting on the next node. It is followed by a grade of maximally supported *P. bezgodovii* clade, sister to not supported *P. polyantha* clade, which splits into well supported (PP=1, BS=99) clade composed of European and North American accessions and not supported clade composed of plants from Asian Russia and some specimens of *P. steerei* from Altai and NW China (its support decreased comparing the IGS based reconstruction). To-

Fig. 1. Bayesian molecular phylogenetic tree inferred from nrITS sequences of *Pylaisia* species. Posterior probabilities from Bayesian analysis and ML bootstrap support are shown at branches.

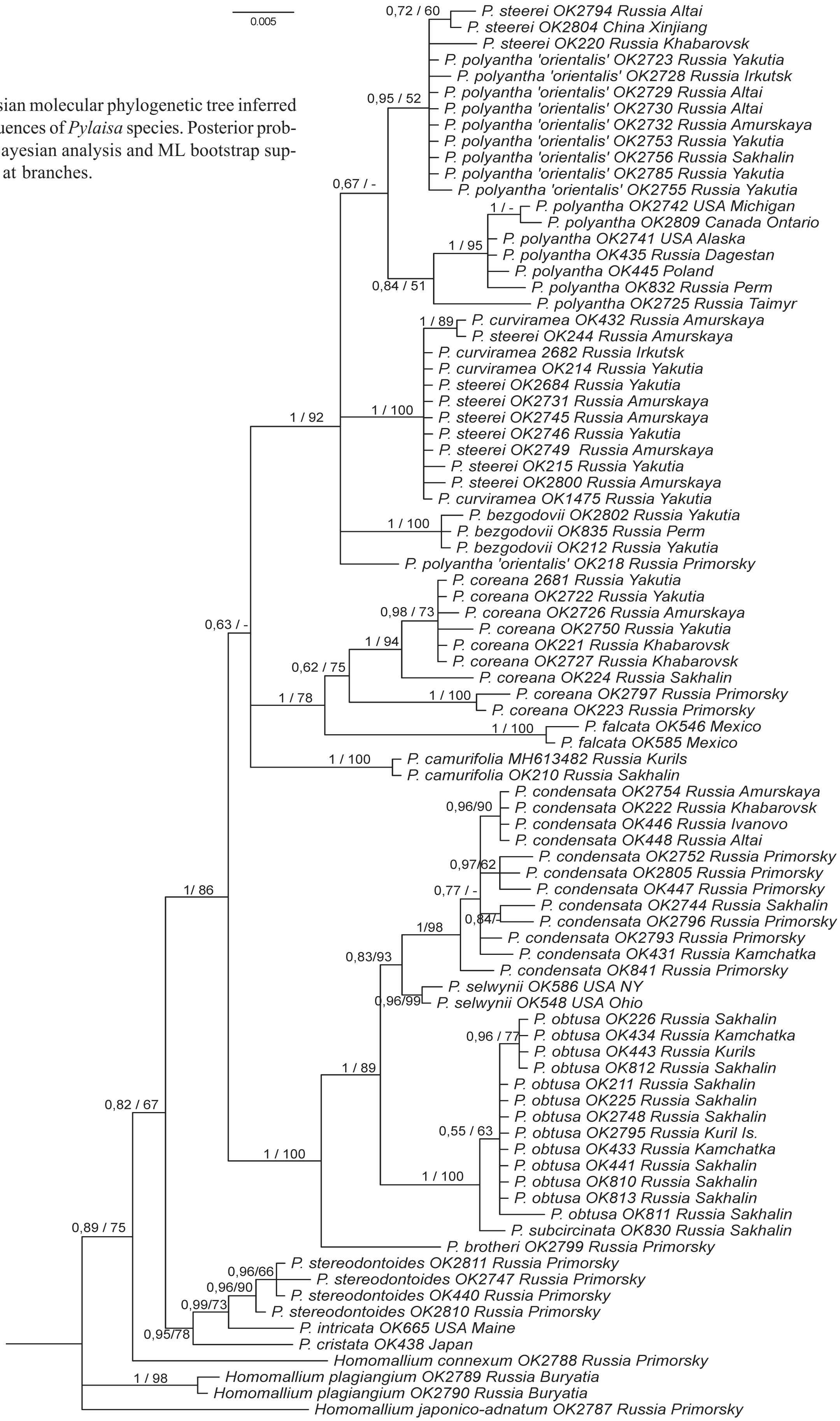

Fig. 2. Bayesian molecular phylogenetic tree inferred from nrIGS sequences of *Pylaisa* species. Posterior probabilities from Bayesian analysis and ML bootstrap support are shown at branches.

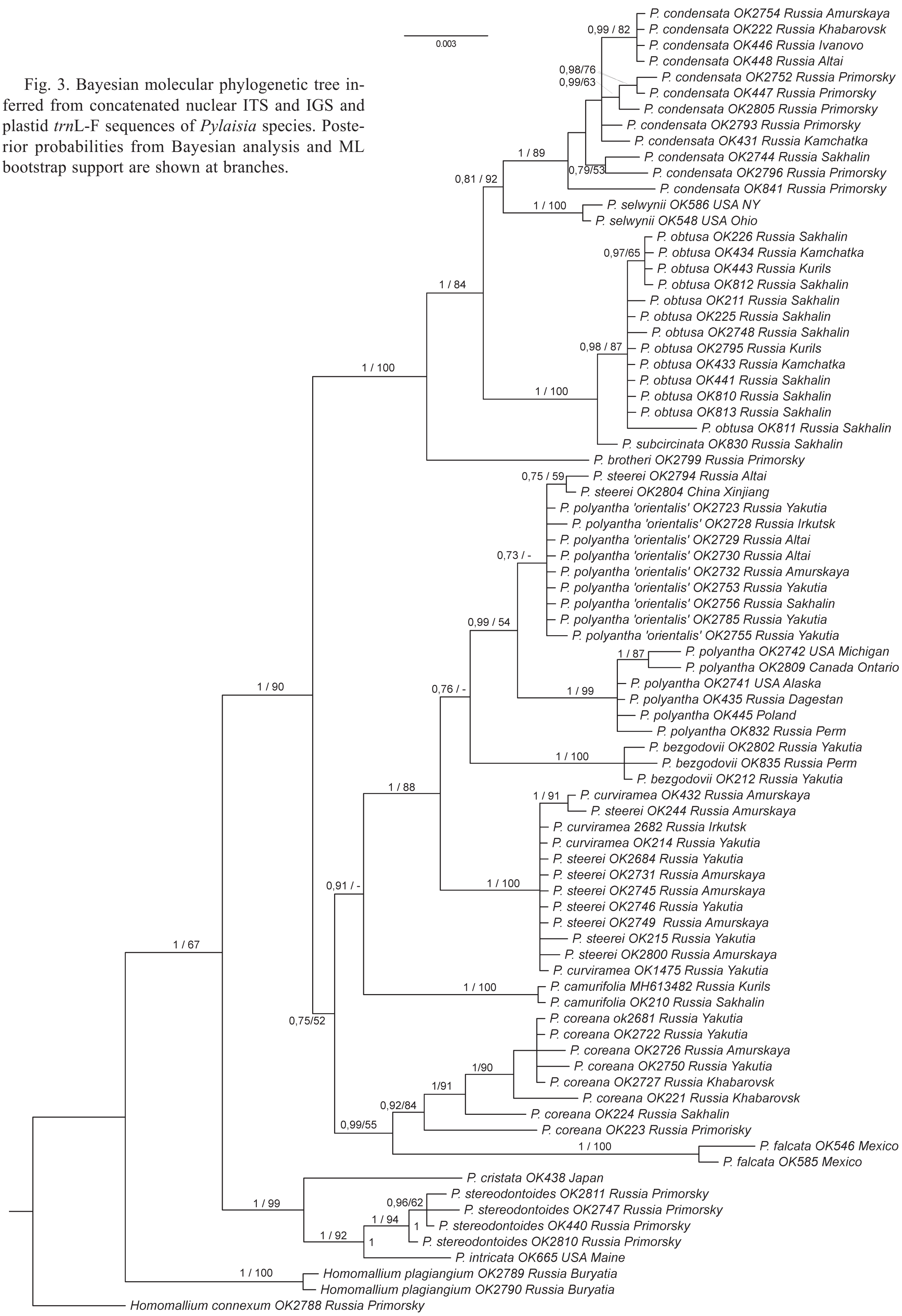

Fig. 3. Bayesian molecular phylogenetic tree inferred from concatenated nuclear ITS and IGS and plastid *trn*L-F sequences of *Pylaisia* species. Posterior probabilities from Bayesian analysis and ML bootstrap support are shown at branches.

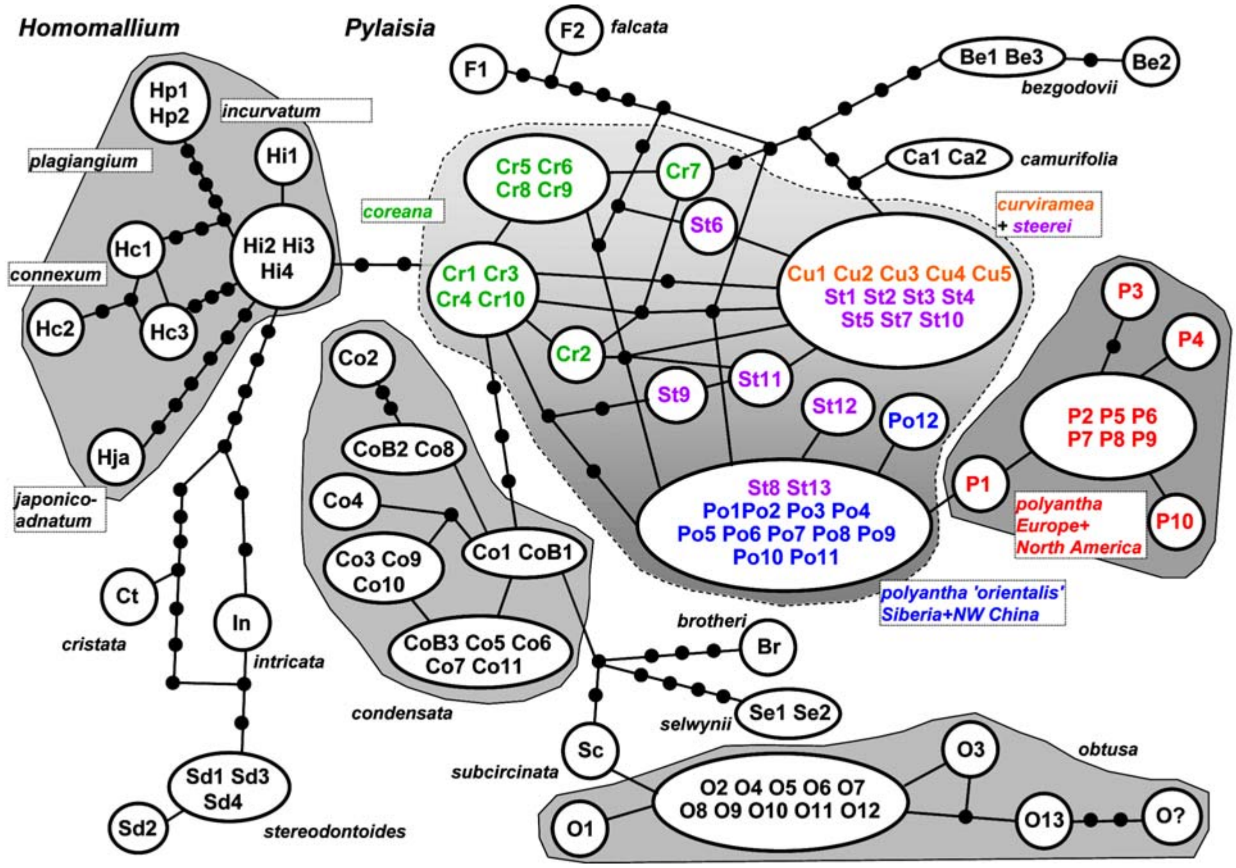

Fig. 4. TCS haplotype network based on ITS dataset (105 accessions) for *Homomallium* and *Pylaisia*. Missing haplotypes are shown as small black circles upon haplotype interlinks. Abbreviations and specimen details are in Table 1, the distribution of *P. polyantha, P. coreana, P. steerei*, and *P. curviramea* is shown in Fig. 5.

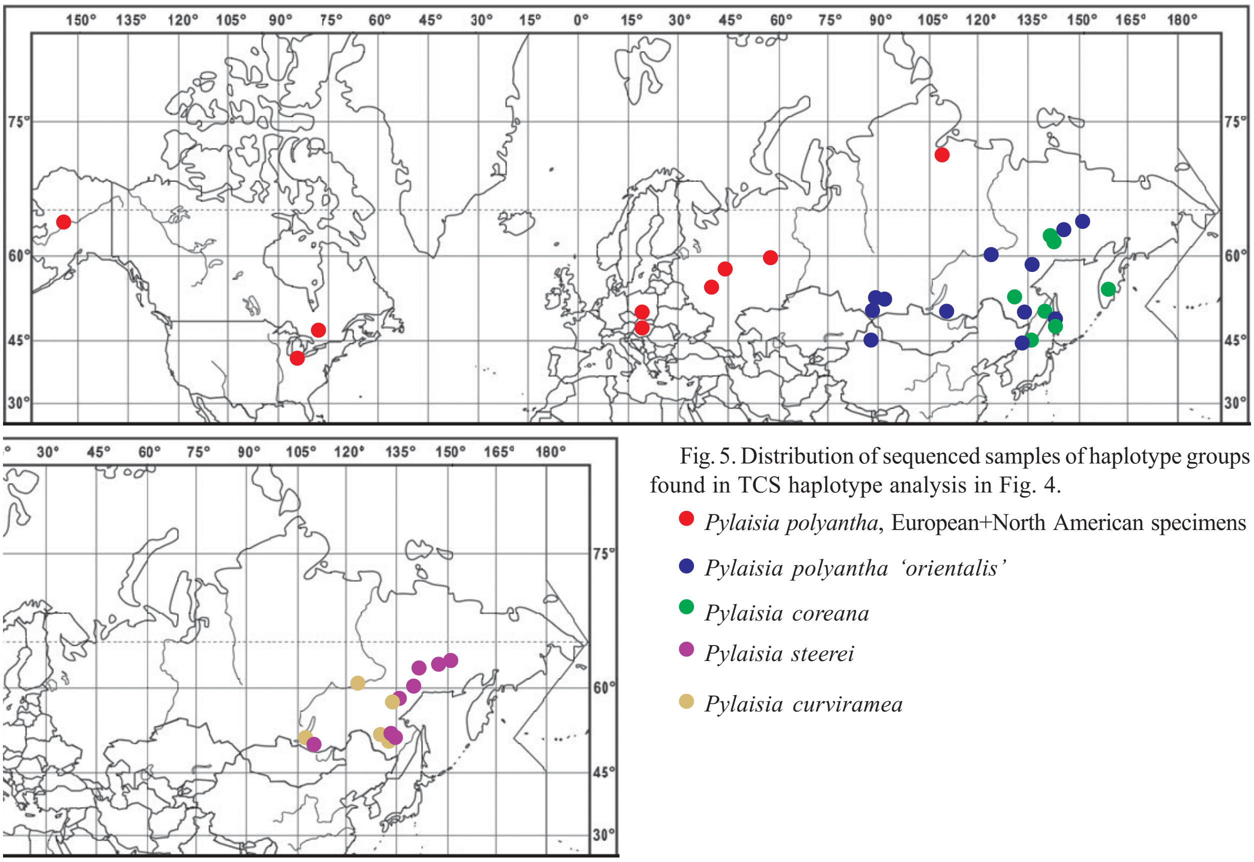

Fig. 5. Distribution of sequenced samples of haplotype groups found in TCS haplotype analysis in Fig. 4.

● *Pylaisia polyantha*, European+North American specimens

● *Pylaisia polyantha ‘orientalis’*

● *Pylaisia coreana*

● *Pylaisia steerei*

● *Pylaisia curviramea*

Table 1. Specimens used for molecular phylogenetic analysis with GenBank accession numbers and codes for TCS analysis (Fig. 4).

Species	Code	Isolate	Country and voucher	ITS	IGS	Trnl–F
Homomallium						
H. connexum	**Hc1**	OK2788	Russia, Primorsky Terr., Ignatov et al. 13-1863 (MHA9130361)	MW396476	MW392650	
H. connexum	**Hc3**		Russia, Primorsky Terr.	JN896316		
H. connexum	**Hc2**		Russia, Primorsky Terr.	MH613384 (as *plagiangium*)		
H. incurvatum	**Hi1**		Russia, Altai	JQ247725		
H. incurvatum	**Hi2**		Russia, Dagestan	MH613382		
H. incurvatum	**Hi3**		Czech Republic	MH613383		
H. incurvatum	**Hi4**			MK211840		
H. japonico-adnatum	**Hja**	OK2787	Russia, Primorsky,Ignatov 08-260 (MHA9130363)	MW396473	MW392647	
H. plagiangium	**Hp1**	OK2789	Russia, Buryatia, Tunka, Afonina 0919 (MHA9130358)	MW396474	MW392648	
H. plagiangium	**Hp2**	OK2790	Russia, Buryatia, Baikal, Afonina 1414 (MHA9130357)	MW396475	MW392649	
Pylaisia						
P. bezgodovii	**Be1**	OK2802	Russia, Yakutia, Ignatov 00-711 (MHA9130416)	MW396550	MW392724	
P. bezgodovii	**Be2**	OK835	Russia, Perm Terr., Bezgodov 21 Aug 2014 #548a (MHA)	MW396551	MW392725	
P. bezgodovii	**Be3**	OK212	Russia, Yakutia, Ignatov 00-711 (MHA)	MW396552	MW392726	MW394386
P. brotheri	**Br**	OK2799	Russia, Primorsky Terr., Ignatov & Ignatova 06-3413 (MHA9130414)	MW396480	MW392654	
P. camurifolia	**Ca2**	OK210	Russia, Sakhalin, Ignatov&Teleganova 06-861 (MHA)	MW396496	MW392670	MW394368
P. camurifolia	**Ca1**	OK209	Russia, Kurils	MH613482 (as *falcata*)		
P. condensata	**Co1**	OK2744	Russia, Sakhalin, Cherdantseva s.n. 17 Jul 2001 (MHA)	MW396477	MW392651	
P. condensata	**Co5**	OK2752	Russia, Primorsky Territory, Ignatov, Ignatova & Malashkina 13-1768 (MHA)	MW396485	MW392659	
P. condensata	**CoB1**	OK2793	Russia, Primorsky Territory, Ignatov, Ignatova & Malashkina 13-1768 (MW9061947)	MW396478	MW392652	
P. condensata	**CoB2**	OK2796	Russia, Primorsky Territory, Ignatov & Ignatova 13-1942 (MW9061948)	MW396479	MW392653	
P. condensata	**CoB3**	OK431	Russia, Kamchatka, Fedosov, 12-201 (MHA)	MW396484	MW392658	MW394362
P. condensata	**Co2**	OK841	Russia, Primorsky, Ignatov & Ignatova 06-2401 (MHA)	MW396494	MW392668	
P. condensata	**Co3**	OK448	Russia, Altai, Ignatov & Ignatova 35/16 (MHA)	MW396493	MW392667	MW394366
P. condensata	**Co4**	OK221	Russia, Khabarovsk, Bureya, Ignatov 97-424 (MHA)	MW396526	MW392700	MW394384
P. condensata	**Co6**	OK2754	Russia, Amurskaya Prov., Bezgodov 1 July 2010 #55 (MHA)	MW396486	MW392660	
P. condensata	**Co7**	OK2805	Russia, Primorsky Terr., Ignatov & Ignatova 13-1942 (MHA9130405)	MW396487	MW392661	
P. condensata	**Co8**		Russia, Irkutsk	MK327358		
P. condensata	**Co9**	OK222	Russia, Khabarovsk,Bureya, Ignatov 97-424a (MHA)	MW396489	MW392663	MW394364
P. condensata	**Co10**	OK446	Russia, Ivanovo, Sorokin 2008 #236 (MHA)	MW396491	MW392665	MW394365
P. condensata	**Co11**	OK447	Russia, Primorsky, Ignatov & Ignatova 06-3406 (MHA)	MW396492	MW392666	MW394363
P. coreana	**Cr1**	OK2722	Russia, Yakutia, Sette-Daban, Ignatov & Ignatova 17-895 (MHA9029883)	MW396523	MW392697	
P. coreana	**Cr2**	OK2726	Russia, Amurskaya Prov.,Dudov 2016_Br_0573 (MW9079141)	MW396524	MW392698	
P. coreana	**Cr3**	OK2750	Russia, Yakutia, Sette-Daban, Ignatov & Ignatova 17-895 (MW9090300)	MW396525	MW392699	
P. coreana	**Cr4**	OK2727	Russia, Khabarovsk Territory, Botchi Ignatov & Ignatova 13-237 (MW9061891)	MW396556	MW392727	
P. coreana	**Cr5**	OK2797	Russia, Primorsky Territory, Vladivostok Ignatov, Ignatova & Cherdantseva 06-3351 (MHA9130415)	MW396521	MW392695	
P. coreana	**Cr6**	OK223	Russia, Primorie, Pidan, Ignatov&Ignatova 06-2401 (MHA)	MW396522	MW392696	MW394380
P. coreana	**Cr7**	OK2801	Russia, Amurskaya Province, Tukuringra Ridge Dudov 2016_Br_0735 (MW9079150)	MW396558		
P. coreana	**Cr8**	OK224	Russia, Sakhalin Ignatov&Teleganova 06-832 (MHA)	MW396536	MW392710	MW394379
P. coreana	**Cr9**	OK217	Russia, Kamchatka Chernyadjeva 17 July 2001 #12 (LE, MHA)	MW396555		
P. coreana	**Cr10**	OK2681	Russia, Yakutia, Sakkyryr, Ivanov 17-595 (MHA)	MW396495	MW392669	
P. cristata	**Ct**	OK438	Japan, Shikoku, Deguchi #185 (MHA)	MW396499	MW392673	MW394369
P. curviramea	**Cu1**	OK219	Russia, Khabarovsk , Bureya, Ignatov #5 (MHA)	MW396553		
P. curviramea	**Cu2**	OK2682	Russia, Irkutsk Province, Listvyanka Ignatov et al. 18-4742 (MHA)	MW396539	MW392713	
P. curviramea	**Cu3**	OK214	Russia, Yakutia, Ignatov 00-704 (MHA)	MW396540	MW392714	MW394382
P. curviramea	**Cu4**	OK432	Russia, Amurskaya, Norsky Reserve Bezgodov 1 July 2010 #41 (MHA)	MW396483	MW392657	MW394381
P. curviramea	**Cu5**	OK1475	Russia, Yakutia, Ignatov & Ignatova 16-263 (MHA)	MW396549	MW392723	
P. falcata	**F1**	OK546	Mexico, Buck 21483 (NY00831097)	MW396497	MW392671	
P. falcata	**F2**	OK585	Mexico, Delgadillo 3 October 2004 (NY01243709)	MW396498	MW392672	
P. intricata	**In**	OK665	USA, Maine, Town of Allagash, Allen 27718 (MW)	MW396500	MW392674	MW394370
P. obtusa	**O1**	OK211	Russia, Sakhalin, Ignatov&Teleganova 06-245 (MHA)	MW396488	MW392662	MW394371
P. obtusa	**O10**	OK810	Russia, Sakhalin, Cherdantseva 15 Aug 2001 (MHA ex VLA)	MW396508	MW392682	
P. obtusa	**O11**	OK812	Russia, Sakhalin, Cherdantseva 23 July 2001 (MHA ex VLA)	MW396509	MW392683	
P. obtusa	**O12**	OK813	Russia, Sakhalin, Cherdantseva 17 July 2001 (MHA ex VLA)	MW396510	MW392684	
P. obtusa	**O13**	OK811	Russia, Sakhalin, Cherdantseva 15 Aug 2001 (MHA ex VLA)	MW396560	MW392728	
P. obtusa	**O2**	OK225	Russia, Sakhalin, Ignatov&Teleganova 06-293 (MHA)	MW396490	MW392664	MW394372
P. obtusa	**O3**	OK2748	Russia, Sakhalin, Ignatov & Teleganova 06-263 (MHA)	MW396501	MW392675	
P. obtusa	**O4**	OK226	Russia, Sakhalin, Ignatov&Teleganova 06-268 (MHA)	MW396502	MW392676	MW394373
P. obtusa	**O5**	OK2795	Russia, Kunashir Island, Tubanova et al. K14035/33 (MHA9130413)	MW396503	MW392677	

Species	**Code**	**Isolate**	**Country and voucher**	**ITS**	**IGS**	**Trnl–F**
P. obtusa	**O6**	OK433	Russia, Kamchatka, Chernyadjeva 8 August 2002 (MHA ex LE)	MW396504	MW392678	MW394374
P. obtusa	**O7**	OK434	Russia, Kamchatka, Chernyadjeva 16 August 2002 (MHA ex LE)	MW396505	MW392679	
P. obtusa	**O8**	OK441	Russia, Sakhalin, Ignatov & Teleganova, 06-598 (MHA)	MW396506	MW392680	MW394375
P. obtusa	**O9**	OK443	Russia, Kurils Islands, Shikotan Island, Bakalin, K-37-48-07 (MHA)	MW396507	MW392681	MW394376
P. obtusa?	**O?**		USA, Alaska	AY009797 (as *selwynii*)		
P. polyantha	**P2**	OK2741	U.S.A., Alaska, Afonina 21 July 1993 (LE931001536)	MW396515	MW392689	
P. polyantha	**P1**	OK2725	Russia, Taimyr, Fedosov 11-464 (MW9061845)	MW396514	MW392688	
P. polyantha	**P3**	OK2742	U.S.A., Michigan, Si He 38059 (LE)	MW396516	MW392690	
P. polyantha	**P4**	OK2809	Canada, Ontario, Buck 56621 27 Sept 2010 (NY01206488)	MW396517	MW392691	
P. polyantha	**P5**	OK435	Russia, Dagestan,Ignatov & Abakarova 11-127 (MHA)	MW396518	MW392692	MW394377
P. polyantha	**P6**	OK445	Poland, Seregin *et al.*, M-3106 (MW)	MW396519	MW392693	MW394378
P. polyantha	**P7**	OK832	Russia, Perm Territory, Cherdynsky District, Kolva River, 21/VIII/2014, Bezgodov 548a (MHA)	MW396520	MW392694	
P. polyantha	**P8**		Russia, Kostroma	MH613483		
P. polyantha	**P9**		Czech Republic	MH613484		
P. polyantha	**P10**		Russia, Moscow	AY528881		
P. polyantha *'orientalis'*	**Po1**	OK2808	Russia, Altai, Chulyshman River, Ignatov 0/1695 (MHA9130409)	MW396559		
P. polyantha *'orientalis'*	**Po2**	OK2794	Russia, Altai, Ignatov & Ignatova 24/160 29 Jul 1991 (MHA)	MW396527	MW392701	
P. polyantha *'orientalis'*	**Po3**	OK2723	Russia, Yakutia, Vostochnaya Khandyga River, Ignatov & Ignatova 17-786 (MHA9029882)	MW396528	MW392702	
P. polyantha *'orientalis'*	**Po4**	OK2728	Russia, Irkutsk Province, Seregin, Seregina & Khokhlov 8 Aug 2007 M-1991	MW396529	MW392703	
P. polyantha *'orientalis'*	**Po5**	OK2729	Russia, Altai Republic, Ignatov & Ignatova 12-814 (MW9061821)	MW396530	MW392704	
P. polyantha *'orientalis'*	**Po6**	OK2730	Russia, Altai Republic, Ignatov & Ignatova 12-321 (MW9061823)	MW396531	MW392705	
P. polyantha *'orientalis'*	**Po7**	OK2732	Russia, Amurskaya Province, Dudov & Kotelnikova 2013_Br_0032 (MW9061886)	MW396532	MW392706	
P. polyantha *'orientalis'*	**Po8**	OK2753	Russia, Yakutia, Suntar-Khayata, Ignatov & Ignatova 15-881 (MHA)	MW396533	MW392707	
P. polyantha *'orientalis'*	**Po9**	OK2756	Russia, Sakhalin, Ignatov & Teleganova 06-418 (MHA)	MW396534	MW392708	
P. polyantha *'orientalis'*	**Po10**	OK2785	Russia, Yakutia, Ulakhan-Chistai Range, Ignatov & Ignatova 18-1986 (MHA9130362)	MW396535	MW392709	
P. polyantha *'orientalis'*	**Po11**	OK218	Russia, Primorsky, Ignatov et al., 06-3349 (MHA)	MW396481	MW392655	
P. polyantha *'orientalis'*	**Po12**	OK2755	Russia, Yakutia, Orulgan, Ignatov 11-3987 (MHA)	MW396538	MW392712	
P. selwynii	**Se2**	OK548	USA, Ohio , Buck 50412 (NY00829715)	MW396513	MW392687	
P. selwynii	**Se1**	OK586	USA, New York State, Buck 52101 (NY00928468)	MW396512	MW392686	
P. steerei	**St1**	OK2684	Russia, Yakutia, Khandyga settl., Ignatov 17-40 (MHA)	MW396541	MW392715	
P. steerei	**St2**	OK2731	Russia, Amurskaya Province, Bezgodov 23 June 2011 #411 (MHA)	MW396542	MW392716	
P. steerei	**St3**	OK2745	Russia, Amurskaya Province, Norsky Reserve, Bezgodov 12 June 2011 #190 (MHA)	MW396543	MW392717	
P. steerei	**St4**	OK2746	Russia, Yakutia, Ust-Maya Distr., Ignatov 00-981 (MHA)	MW396544	MW392718	
P. steerei	**St5**	OK2749	Russia, Amurskaya Province, Norsky Reserve, Bezgodov 15 Jul 2010 #439 (MHA)	MW396545	MW392719	
P. steerei	**St6**	OK215	Russia, Yakutia, Ignatov 00-703 (MHA)	MW396546	MW392720	MW394385
P. steerei	**St7**	OK2800	Russia, Amurskaya Province, Selemdzhinsky Distr., Bezgodov 17 Jun 2011 #246 (MHA9130411)	MW396548	MW392722	
P. steerei	**St8**	OK2804	China, Xinjiang, Tan 93-926 (MHA)	MW396537	MW392711	
P. steerei	**St9**	OK244	Russia, Amurskaya Province, 23 June 2011 Bezgodov #411 (MHA)	MW396547	MW392721	MW394383
P. steerei	**St10**		Russia, Buryatia	MK327359		
P. steerei	**St11**	OK243	Russia, Amurskaya Province, Norsky Reserve, Bezgodov 19 June 2011 #318 (MHA)	MW396554		
P. steerei	**St12**	OK437	Russia, Altai, Ignatov & Ignatova 24/60 (MHA)	MW396557		
P. steerei	**St13**	OK220	Russia, Khabarovsk, Bureya, Ignatov 97-428 (MHA)	MW396482	MW392656	
P. stereodontoides	**Sd1**	OK2810	Russia, Primorsky Territory, Ussuriisky Reserve, Ignatov 08-217 (MHA9130412)	MW396561	MW392729	
P. stereodontoides	**Sd2**	OK2811	Russia, Primorsky Territory, Isakov Klyuch, Ignatov, Ignatova & Malashkina 13-1701 (MHA9047657)	MW396562	MW392730	
P. stereodontoides	**Sd3**	OK2747	Russia, Primorsky Territory, Terney Distr., Ignatov, Ignatova & Malashkina 13-1779 (MHA)	MW396563	MW392731	
P. stereodontoides	**Sd4**	OK440	Russia, Primorsky Territory, Ussurijsky State Reserve, Ignatov & Ignatova 06-3522 (MHA)	MW396564	MW392732	MW394387
P. subcircinata	**Sc**	OK830	Russia, Sakhalin,Nevel District, Nevelsky Pass, 17/IX/2009, Pisarenko op03714 (MHA)	MW396511	MW392685	

pology of the clade where remaining species with endostome adherent to exostome are captured does not differ from IGS driven one. Three of five species within it are represented by more than one specimen, which are combined in well- to maximally supported clades. Low support of *P. obtusa* clade likely originates from insufficient representation of *P. subcircinata*. Surprisingly, support for common clade of *P. condensata* and *P. selwynii* is absent, that may indicate need of considering *P. selwynii* as a separate North American species.

TCS haplotype network from ITS sequences (Fig. 4) shows the overall grouping of taxa consistent with that obtained from the Bayesian analysis (Fig. 1). However, the reticulation among species with free endostome, i.e. *P. polyantha* and closely related species available from haplotype network is particularly interesting. In general likewise Bayesian results, *Pylaisia* species with the endostome totally adherent to exostome were found in a separate group linked to most common haplotype of *Homomallium incurvatum*, which also links to the rest of *Pylaisia* species. The closest to this *Homomallium* species is one of haplotypes of *P. coreana* that was referred by Arikawa (2004) to synonymy of *P. polyantha*, but is resurrected here as will be discussed below.

One of *Pylaisia coreana* haplotypes keeps the central position in the network, being linked to (1) *Homomallium* + *Pylaisia* species with totally adherent endostomes; (2) *Pylasia* species with free endostomes, *P. polyantha*-group, and those with endostome only slightly adherent to teeth at base, i.e. *P. falcata*-group s.l.; and (3) *Pylaisia* species with endostomes more or less strongly adherent to exostome teeth, so the only upper parts of segments are free. The latter group includes species that form a well supported clade in all variants of Bayesian analysis. It includes, expectedly, *P. condensata, P. obtusa, P. brotheri*, and *P. subcircinata*; however, North American specimens referred to *P. selwynii* appeared unrelated to Eurasian *P. condensata*: western North American *P. selwynii* forms its own group, as in Bayesian analysis. One Alaskan plant deposited in Genbank as *P. selwynii* represents a marginal haplotype of *P. obtusa*-group.

Among the species with free exostomes, the situation is especially complicated in plants previously referred to *P. polyantha, P. steerei* and *P. curviramea*. European and North American plants of *P. polyantha* (and one sample from Arctic Siberia) appeared to be maximally isolated from others. At the same time, most samples from Asian Russia usually referred to *P. polyantha, P. curviramea* and *P. steerei* form a reticulum (Fig. 4).

In this reticulum the 'Asian *P. polyantha*', called here as *P. polyantha* '*orientalis*', is most compact, with most samples in one haplotype, although this haplotype has also few specimens of *P. steerei*. *Pylaisia coreana* is represented by four haplotypes and interconnected by nine links through one to five missing haplotypes with other entities of this reticulum. Seven out of eleven samples of *P. steerei* belong to one 'main' haplotype of this species, which also includes five samples of *P. curviramea;* other five haplotypes of *P. steerei* are scattered, and it is notable that two its samples belong to the core haplotype of *P. polyantha* '*orientalis*'. Further discussion on how to apply these highly ambiguous data to taxa delimitation is given under each species. Each of several possible decisions has its own pro and contra.

Besides this reticulation, there are three entities that are distinctly separated from the group of *P. coreana+P. curviramea+P. steerei+P. polyantha* '*orientale*'. These are: (1) two Mexican samples of *P. falcata*; (2) two samples of 'Asian *P. falcata*', called here *P. camurifolia*, as discussed below; (3) two samples shown as three due to separate extractions of one of collection, which is described here as a species new for science, *P. bezgodovii*.

DISCUSSION

Pylaisia is a small genus with about 15 species worldwide, and its infrageneric classification was never properly developed formally, or its subdivisions appeared to be not related to this genus. The erroneously applied names also preclude acceptance of subdivisions suggested by some authors, as discussed by Arikawa (2004). Brotherus (1925) subdivided the genus into four groups: (1) with totally adherent endostome (e.g. *P. intricata*); (2) with partly adherent endostome (e.g. *P. brotheri*); (3) with free endostome (e.g. *P. polyantha*); and (4) with free endostome and also totally smooth teeth (e.g. *P. extensa*). A similar and somewhat more detailed grouping of taxa into five entities was suggested by Arikawa (2004). He subdivided plants with free peristomes into two groups, with the unperforated endostome segments along keels (*P. polyantha* and *P. steerei*), and those with the perforated ones (*P. curviramea, P. falcata*, *etc.*).

The present study does not include Himalayan taxa with smooth teeth, while the obtained three groups appear to be in good correspondence with groups outlined by Brotherus and Arikawa:

(1) *P. polyantha, P. coreana, P. steerei,* and *P. curviramea* are plants with free endostome; *P. falcata, P. camurifolia*, and *P. bezgodowii* are somewhat apart from the core species, which correspond to the Arikawa's segregation of *P. falcata* in a separate group (with Himalayan *P. extensa*);

(2) *P. selwynii* s.l.*, P. brotheri, P. subcircinata,* and *P. obtusa*, species with endostome in its basal part strongly adherent to exostome but with upper parts of segments free;

(3) *P. stereodontoides*, *P. intricata,* and *P. cristata,* species with endostome strongly adherent to exostome, and seen only on the inner surface of exostome teeth.

A somewhat unexpected is the arrangement of these groups in phylogenetic trees: one might expect that more 'Hypnoid' or 'perfect' peristomes with free endostome should be present in a basal group, immediately linked to saxicolous species of *Homomallium* that have curved capsules, fully developed peristome with long ciliae and transversely striolate teeth at their base from dorsal side. Also, *Homomallium* species gametophytically are especially similar to *Pylaisia* species of the *P. polyantha*-group.

Unexpectedly, the clade with the maximally modified peristome (*P. stereodontoides*, *P. intricata* and *P. cristata*) appeared in the most basal position, sister to all other species of *Pylaisia* or, in ITS tree, even independently nested among *Homomallium*. However, the most ancient age of these species is consistent with their (1) good morphological differentiation, as they unlikely can be confused with species of other groups; and (2) greatest genetic difference: even in ITS haplotype network all of them are far one from another. At the same time, the specialized epiphytes with moderately modified peristomes provide difficulties in species morphological delimitations, causing confusions, as will be discussed for pairs of *P. brotheri / P. condensata, P. condensata / P. selwynii, P. obtusa / P. subcircinata, P. obtusa / P. selwynii*. However, DNA markers draw in general a clear picture of species delimination.

The group of *Pylaisia* species with endostomes either free or only a little adherent to exostomes is the most difficult and need further studies. However, we believe that suggestions from the present analysis might help as a stepping stone towards the better understanding of the genus, especially in the Asian part of Russia.

TAXONOMY

In the present paper we omit a detailed taxonomic accounts of species, with type designations and lectotypifications provided by Arikawa (2004). Instead, we expand a discussion of molecular delimitation, differentiation, variation and distribution of taxa in Russia.

Pylaisia Bruch, Schimp. & W. Gümbel, Bryologia Europaea 5: 87 (fasc. 46–47. Monogr. 1). 1851, nom. cons.

Plants small to medium-sized, light-, yellowish- or dark-green, silk-glossy, in flat, rather dense tufts or creeping by individual shoots upon thin twigs. Stems regularly pinnately to fasciculately branched, terete or complanate, in transverse section round to ovoid, with central strand, without hyalodermis; axillary hais 3-5 celled; first proximal branch leaf in lateral position to branch bud, entire to incised, and occasionally split to base, margin coarsely toothed to irregularly incised. Stem leaves straight to homomallous, erect to falcate-secund or even circinate, ovate-lanceolate to broadly ovate, gradually or abruptly tapered to long or short acumen, slightly to strongly and abruptly tapered to leaf insertion, more or less concave; margins plane, recurved at base or incurved at places, subentire to serrulate below the apex; costa short and double; median laminal cells rhomboidal to linear; alar cells subquadrate to rectangular, forming more or less well-defined group which is elongate along the margins or triangular, or sometimes wider than long. Branch leaves smaller and relatively narrower, sometimes lanceolate. Autoicous. Inner perichaetial leaves erect, oblong-lanceolate, more or less plicate. Setae long. Capsules erect, symmetric, cylindrical to broadly ovoid and sometimes subglobose. Operculum conic to rostrate. Annulus separated by fragments, composed of thick-walled quadrate cells. Peristome perfect, with exostome and endostome free, to strongly modified, with endostome partly or totally adherent to exostome teeth; all peristomes xerocastique, reflexing after wetting. Exostome teeth smooth below, papillose above. Endostome segments entire or perforated along keel or split by keel into halves, occasionally split at basal membrane level and entire above. Spores 10–35 μm, mature in winter. Calyptra cucullate.

KEY TO SPECIES IDENTIFICATION OF *PYLAISIA* IN RUSSIA

1. Endostome free; segments keeled, solid at apex, entire or perforated along the keel 2
— Endostome adherent to exostome, at least at base; segments usually split or perforated along the keel, rarely entire, or totally adherent to exostome teeth and fragmentary 6

2. Branches julaceous; stem leaves broadly ovate, acute to shortly acuminate, shorter than 1.1 mm, strongly concave; median laminal cells 20–45 μm long .... 4. *P. curviramea*
— Branches non-julaceous; stem leaves ovate-lanceolate, short to long acuminate, (0.6–)0.9–1.5(–1.7) long, slightly or moderately concave; median laminal cells 30–75(–90) μm long 3

3. Foliage non-complanate; stem and branch leaves straight to homomallous and turned outwards substrate 4
— Foliage complanate; stem and branch leaves more or less falcate, turned towards substrate 5

4. Stem leaves 1.1–1.5(–1.7)×0.5–0.6(–0.7) mm; laminal cells 35–70(–90)×5–6(–7) μm; spores (10–)11–16(–18) μm; widespread .... 1. *P. polyantha*
— Stem leaves 0.6–1.1×0.3–0.4 mm; laminal cells 35–75×4–5 μm; spores 9–12(–13) μm; eastern part of Russia .... 2. *P. coreana*

5. Plants small to medium-sized; stem leaves 1.1–1.6 mm long; alar group triangular, to 10–15 cells long and 5–10 cells wide; spores 12–18 μm; endostome densely papillose .... 3. *P. steerei*
— Plants small; stem leaves 0.9–1.2 mm long; alar group elongate along leaf margin, 12–22 cells long and 5–6 cells wide; spores 10–12 μm; endostome moderately papillose .... 5. *P. bezgodovii*

6(1). Endostome totally adherent to exostome teeth, fragmentary; alar group triangular, 10–14 cells along leaf margin .... 11. *P. stereodontoides*
— Endostome partially adherent to exostome teeth, not fragmentary; alar group comparatively small, subquadrate or transversely rectangular, 7–15(–20) cells

along leaf margin, or elongate, extensive, 20–35 cell along leaf margin 7

7. Alar group subquadrate or transversely rectangular, 7–15(–20) cells along the leaf margin 8

— Alar group elongate, 20–35 cell along the leaf margin 10

8. Endostome segments free, broad, keeled, but at the level of basal membrane endostome is partly adherent to exostome, and split along the continuation of the keel; leaves falcate; spores 19–22 µm .... 6. *P. camurifolia*

— Endostome adherent to exostome teeth to the base of segments or higher; leaves falcate or straight; spores 15–35 µm 9

9. Operculum obtuse or with stump-like truncate beak; endostome adherent to exostome at a level of basal membrane, segments bifid, with free broad branches; leaves homomallous or looking falcate on stems, but in microscope slides more or less straight .... 10. *P. obtusa*

— Operculum shortly rostrate; endostome segments partially adherent to exostome teeth, their ends are entire or bifid with narrow branches; leaves falcate on stems and strongly curved in microscope slides .... 9. *P. subcircinata*

10(7). Leaves rather abruptly narrowed to a short acumen; alar group 20–25 cells long and 6–10 cells wide; median laminal cells 25–40(–50)×6–9 µm; inner perichaetial leaves comparatively short, ca. 1.5 mm long; capsules oblong-ovoid; spores 16–30 µm .... 7. *P. condensata*

— Leaves gradually, rarer more or less abruptly narrowed into a long acumen; alar group 25–35 cells long and 10–12 cells wide; median laminal cells 40–55×4–5 µm; inner perichaetial leaves comparatively long, ca. 2.0 mm long; capsules ovoid to subglobose; spores 20–30 µm .... 8. *P. brotheri*

1. **Pylaisia polyantha** (Hedw.) Bruch, Schimp. & W. Gümbel, Bryol. Eur. 5: 89 (fasc. 46-47. Monogr. 3). — *Leskea polyantha* Hedw., Sp. Musc. Frond. 229. 1801.

Figs. 6–9, 14B-F, 15A-D, 34D,E.

Note on taxonomy. *Pylaisia polyantha* is usually considered to be a most widespread species of the genus in more northern part of temperate zone of the Holarctic, including North America (Arikawa, 2014), Europe (Hodgetts & Lockhart, 2020), East Europe and North Asia (Ignatov *et al.*, 2006), whereas in Mexico, China and Japan it is rarer than other species. Molecular phylogengetic analysis based on *rbc*L showed a genetic differentiation between Asian and European populations of *P. polyantha* (Arikawa & Higuchi, 2003), and we confirmed this based on nuclear ITS and IGS markers (Figs. 1–4). For plants from Asian Russia with julaceous habit Arikawa (2004) suggested the name *P. curviramea* Dixon, applied to a species described from Central China which remained little known for its morphology and distribution before this study of Arikawa.

The present study confirmed this in general. Plants from Europe, Arctic Siberia and North America belong to one group of haplotypes, and in this region *P. polyantha* is less polymorphic comparatively with South Siberia and Russian Far East. Asian plants differ from European ones, but they were found to be not homogeneous (Fig. 4). The outstanding morphological variation in Asian *P. polyantha* was noted as early as by Lindberg (1872), who described from Bureya River (Amur River tributary) var. *homomalla* Lindb. (later synonymized by Arikawa (2004) with *P. steerei*), and subsequently Lindberg & Arnell (1890) added, also from Yenissey River, var. *brevifolia* Lindb. & Arnell and var. *julacea* Lindb. & Arnell, which descriptions fit well *P. curviramea.*

Morphological differentiation of *P. steerei* and *P. curviramea* from *P. polyantha* is supported in general by IGS nuclear molecular marker (Figs. 2–3), although ITS haplotype network illustrates an imperfect segregation and three samples with *P. steerei* morphotype were found having core ITS haplotype of *P. polyantha* '*orientalis*' (Fig. 4).

Siberian plants of *P. polyantha* are very variable and can not be differentiated morphologically from European plants, and therefore they are treated here within *P. polyantha*, excluding morphologically different *P. steerei* and *P. curviramea.* Also, *P. polyantha* is treated here excluding haplotypes from the eastern regions of Russia that were (1) resolved monophyletic in molecular phylogenetic analyses; (2) have small but stable distinctions in leaf and spore sizes. They are accepted as a separate species, *Pylaisia coreana*.

Description. Plants small to medium-sized, yellowish- to dark-green, sometimes brownish. Stem and branches straight or only indistinctly curved, densely foliate; leaves straight to indistinctly homomallous and turned outwards substrate. Stem leaves 1.1–1.5(–1.7) ×0.5–0.6(–0.7) mm, ovate to ovate-lanceolate, gradually narrowed into a long acumen, slightly rounded to insertion; margins entire or serrulate above; median laminal cells 35–70(–90)×5–6(–7) µm, alar cells subquadrate, forming slightly elongate triangular or subquadrate group 10–15 cells long and 5–6 cells wide. Branch leaves somewhat smaller. Capsules cylindrical, 1.5–1.8 mm long without operculum. Operculum high conic to conic-rostrate. Peristome forming high conus when dry. Exostome teeth 250–300 µm long above the mouth, dorsal plates smooth below, papillose above; endostome 300–350 µm above the mouth, not adherent to exostome, segments narrow or broad, not or slightly perforated along keel, slightly papillose. Spores (10–)11–16(–18) µm.

Variation and differentiation. The morphological differences between two main genetic entities of *P. polyantha*, i.e. between mainly European and Asian '*orientalis*' group of haplotypes is difficult to present without

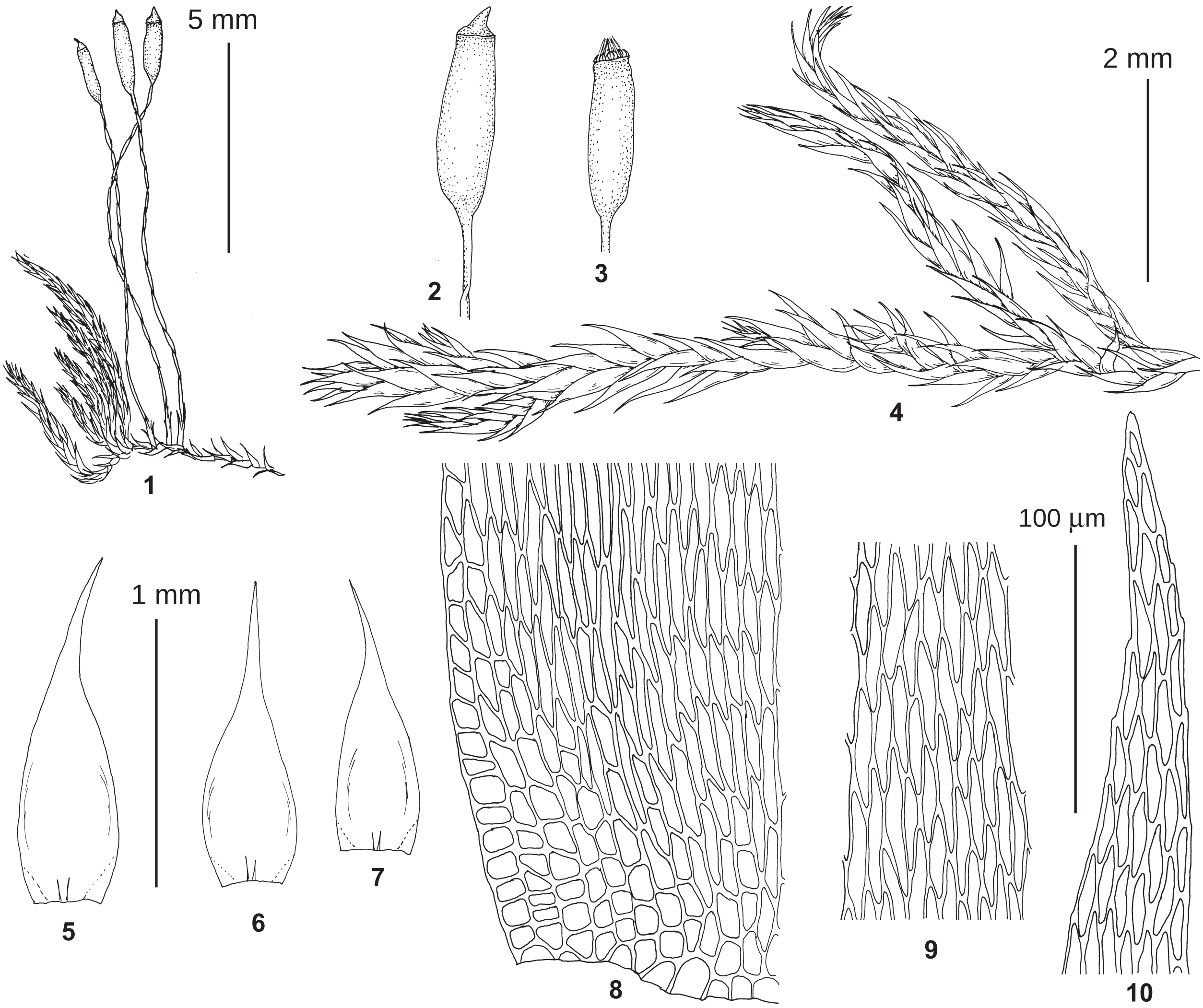

Fig. 6. *Pylaisia polyantha*, from most common European haplotype (**P8**, OK216, Russia, Kostroma Province). 1–4: habit, dry; 2–3: capsules; 5–6: stem leaves; 7: branch leaf; 8: basal laminal cells; 9: median laminal cells; 10: upper laminal cells. Scale bars: 5 mm for 1; 2 mm for 2–4; 1 mm for 5–7; 100 µm for 8–10.

special extensive morphometric study, as both are very widespread and very variable. In Figs. 7–8 we can only show a relatively higher variation in Asian population by comparison of leaf shape of sequenced plants. In each collection one of the best developed shoot was used for illustration of two stem leaves taken below stem apex and above part where branches already elongate, and one branch leaf. This comparison shows that Asian plants are somewhat larger, have leaves more abruptly tapered to acumen and with a larger difference between stem and branch leaves. Of course, this illustration cannot pretend to any completeness: e.g., Arikawa (2004) illustrated stem leaves from the type of *P. polyantha* of 2.0 mm long, whereas in Russia we never saw stem leaves longer than 1.7 mm. However, with some hesitation we present this comparison, which generally agree with our observations on numerous other collections from Russia, showing at the same time differentiation that unlikely may be interpreted as a basis for taxa delimitation.

The differentiation in peristome structure between these two groups of haplotypes is discussed below separately, with comparison with other species of *Pylaisia polyantha*-complex (Figs. 14–16).

The distinction between *P. polyantha* and *P. coreana* is discussed under that species.

Distribution: In European Russia *P. polyantha* occurs almost throughout its territory, except islands of Arctic Ocean and tundra areas. It is rare in Kola Peninsula, xeric areas near Caspian Sea, otherwise it is ubiquitous species, growing on various trees. Due to the fact that *Populus* is widely used in cultivation in cities and along roads, *Pylaisia polyantha*, which is especially common of *Salix* and *Populus* trunks, is an abundant species in almost all climatic zones.

Besides Salicaceae, *Pylaisia polyantha* is not rare in boreal forests on *Betula* trunks, while in broad-leaved forest zone it may grow on hardwood trees (*Tilia, Quercus, Acer, etc*.), growing on them sporadically in Central

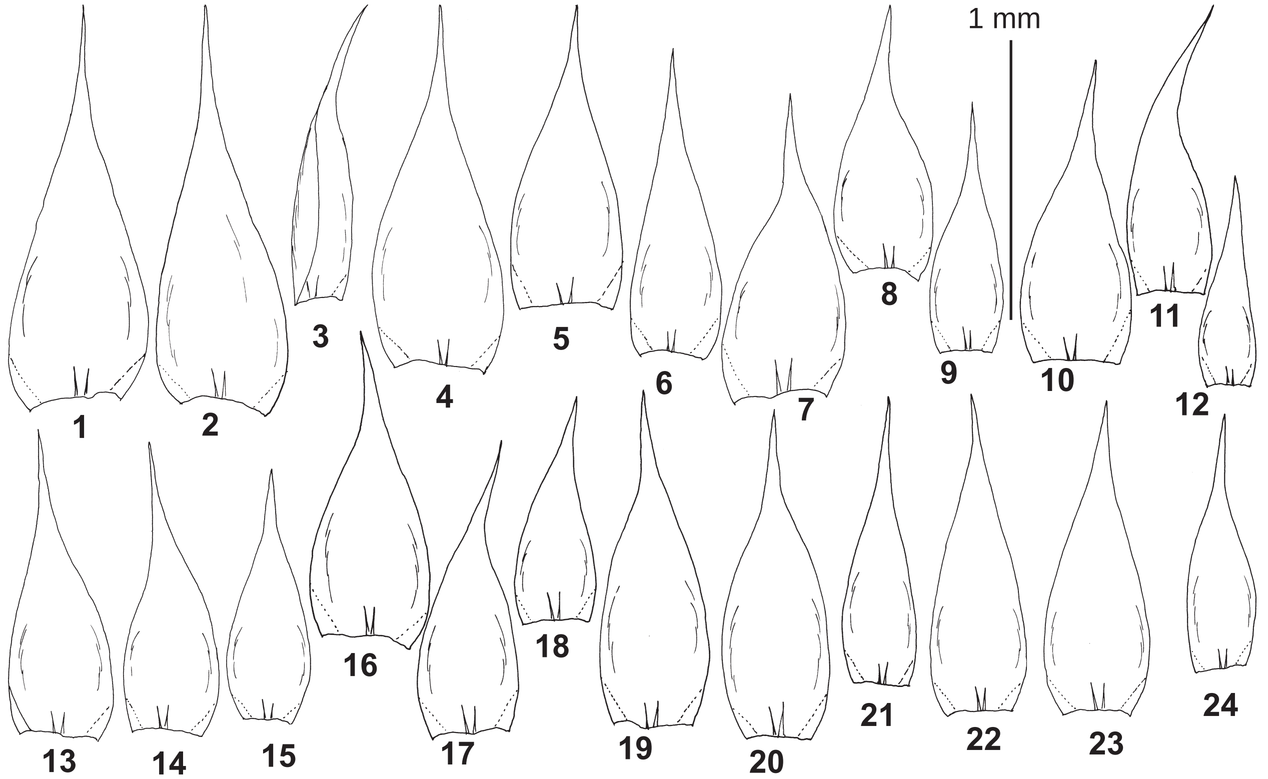

Fig. 7. *Pylaisia polyantha* s. str.: 1–3: **P6**, OK445, Poland; 4–6: **P10**, AY528881, Russia, Moscow; 7–9: **P5**, OK435, Russia, Dagestan; 10–12: **P7**, OK832, Russia, Perm Territory; 13–15: **P1**, OK2725, Russia, Taimyr; 16–19: **P2**, OK2741, U.S.A., Alaska; 19–21: **P4**, OK2809, Canada, Ontario; 22–24: **P3**, OK2742, U.S.A., Michigan. 1–2, 4–5, 7–8, 10–11, 13–14, 16–17, 19–20, 22–23: stem leaves; 3, 6, 9, 12, 15, 18, 21, 24: branch leaves. Scale bar: 1 mm for all.

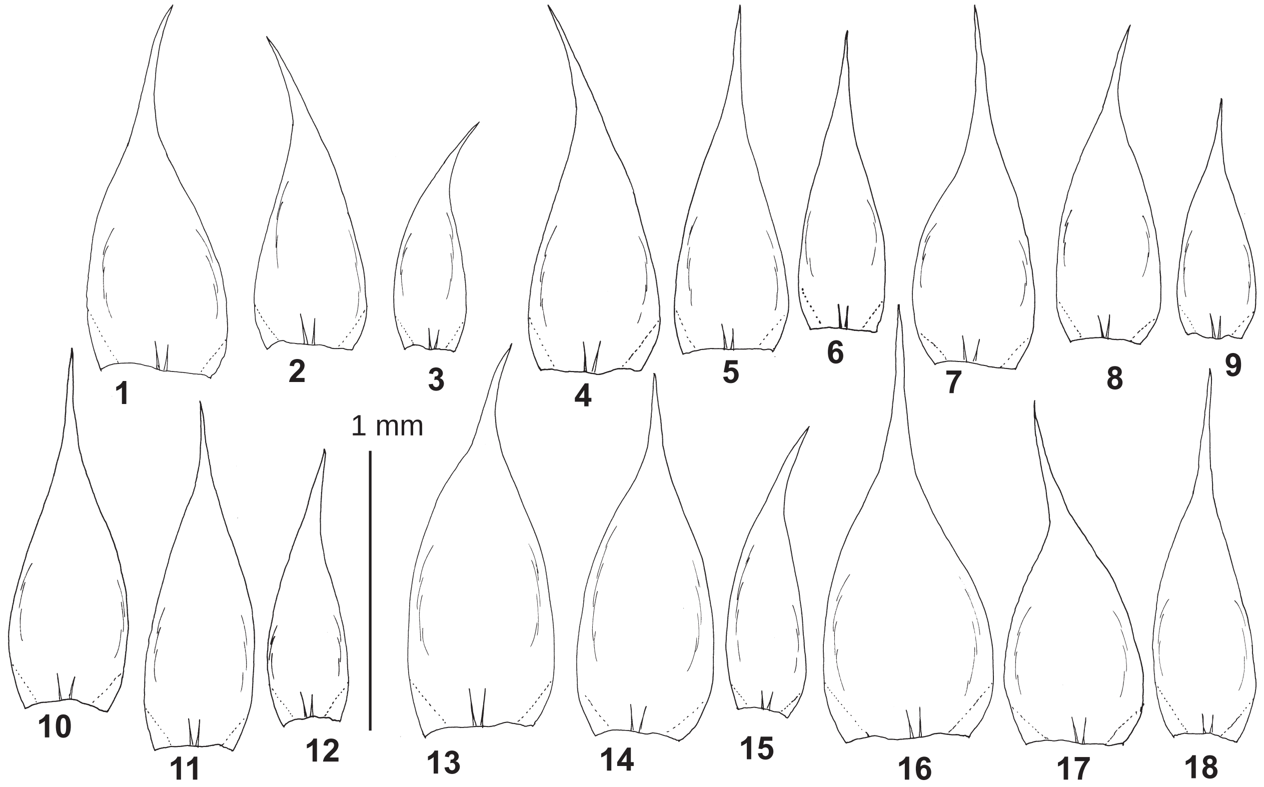

Fig. 8. *Pylaisia polyantha,* '*orientalis*' haplotype group (all specimens from Russia): 1–3: **Ps7**, OK2730, Altai Mts, Ust-Sema; 4–6: B, OK2732, Amurskaya Province, Zeisky Reserve; 7–9: **Ps14**, OK2755, Yakutia, Orulgan Range; 10–12: **Ps16**, OK218, Primorsky Territory, Vladivostok; 13–15: **Ps11**, OK2785, Yakutia, Ulakhan-Chistai Range; 16–18: **Ps6**, OK2729, Altai Mts., Kaitanak. 1–2, 4–5, 7–8, 10–11, 13–14, 16–17: stem leaves; 3, 6, 9, 12, 15, 18: branch leaves. Scale bar: 1 mm for all.

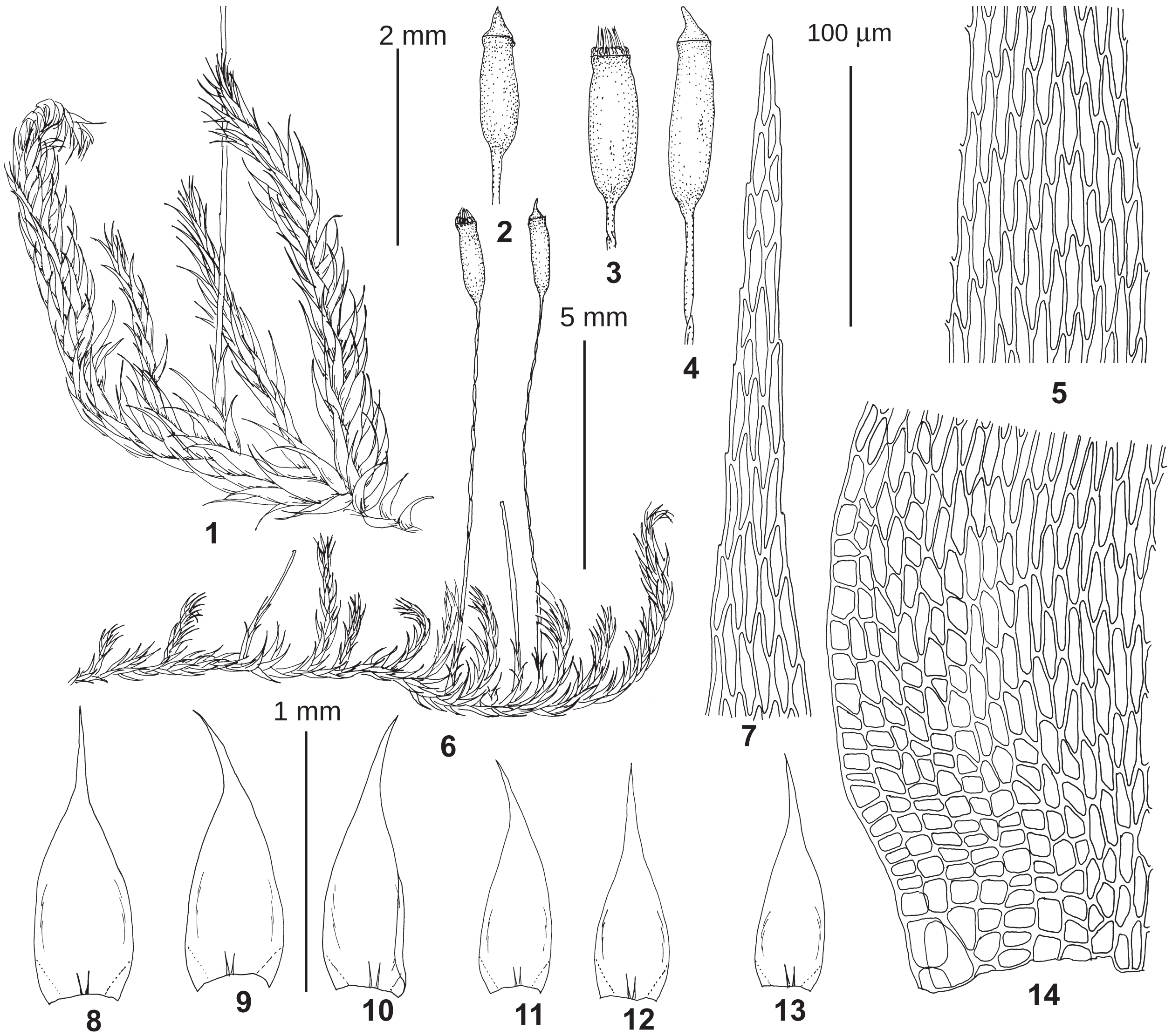

Fig. 9. *Pylaisia polyantha,* '*orientalis*' haplotype (**Po9**, OK 2753, Russia, Yakutia, Suntar–Khayata Mts). 1, 6: habit, dry; 2–4: capsules; 5: median laminal cells; 7: upper laminal cells; 8–10: stem leaves; 11–13: branch leaves; 14: basal laminal cells. Scale bars: 5 mm for 6; 2 mm for 1–4; 1 mm for 8–13; 100 µm for 5, 7, 14.

European Russia, but rarely in the Caucasus, where it is more strictly associated with Salicaceae. Also throughout its range it occasionally grows on fresh logs (including decorticated wood of *Picea*) and on rocky susbstrates, both natural (e.g. granites, schists and other metamorphic rosks) and man-made (concrete, various roof materials, old woody walls and fences in more or less wet places, *etc*.).

The above characteristics of habitats and overall distribution of *Pylaisia polyantha* s.l. pertains the Asiatic Russia as well. The northernmost localities are in Arctic in Taimyr Region and at the mouth of Lena River.

Selected specimens examined: (in addition to Table 1): WEST EUROPE: FINLAND: Lieto, Aurajoki River, *Ignatov & Ignatova 10-1018* (MW9078580). POLAND: Warmian-Masurian Voivodeship, Nature reserve "Springs" on the Lyna river, *Seregin et al. M-3109* (MW9061553). BULGARIA: Western Stara-Planina, Vidin Province, Nature Park "Belogradchik Cliffs", *Seregin M-1135* (MW9061554). EUROPEAN RUSSIA: **Kaluga Province**, Borovsk Distr., Satino, 26 Jul. 1998 Maksimova s.n. (MW9061610); **Ryazan Province**: Oksky State Reserve, Lakash sttl., 25 Oct. 1995 *Volosnova s.n.* (MW9061598); **Vladimir Province**: Gus-Khrustalny Distr., Nikulino Village, *Seregin M-2582* (MW9061577); Suzdal Distr., Smolino Village, 29 Apr. 2006 *Seregin M-1493* (MW9061584); **Tver Province**: Nelidivo Distr., Tsentralno-Lesnoy Nature reserve, 26 Jul.1994 *Kuraeva s.n.* (MW9061592); **Kostroma Province**, Kologriv Distr., Varzengskoe forestry, 6 Jul. 2005 *Tikhonova D12m* (MW9061595); **Moscow Province**, Odintsovo Distr., Zvenigorod biostation, 4 Jul. 2009 *Obukhova s.n.* (MW9061653); **Arkhangelsk Province**, Primorsky Distr., Onezhsky peninsula, Bolshoe Paranino Lake, 16 Aug. 2015 *Korotkov 11* (MW9061706); **Komi Republic**, North Urals, Pechoro-Ilychsky Reserve, *Seregin M-3678* (MW9061705); **Vologda Province**, Kirillov Distr., National Park "Russian North", Vognema settl., *Karmazina 207-04* (MW9061704); **Kirov Province**, Nagorsky Distr., Nurgush Nature Reserve, 25 May 2017 *Bakka 162* (MW9114694); **Perm Province**: Krasnovishersk Distr., Vishersky Nature Reserve, 9

Jul. 1995 *Bezgodov 524* (MW9061733); Basegi Nature Reserve, Vilva River, 8 Jun. 1994 *Ignatov & Bezgodov 223* (MW9061737); **Chelyabinsk Province**, Troitsky Forestry, 14 Jul. 1989 *Bezgodov 47* (MW9061809); **Orenburg Province**, Buzuluksky Distr., Buzukuksky Forest, 4 Jul. 2000 *Kalmykova s.n.* (9061804); **Tatarstan Republic**, Volzhsko-Kamsky Nature reserve, Saraly, *Ignatov & Ignatova 05-2021* (MW9061773); **Republic of Mordovia**, Bolsheberezníkovsky Distr., Simkino Village, 26 Jul. 1994 *Filin s.n.* (MW9061765); **Uljanovsk Province**, Sakhchinskoe Forestry, 1973 *Kurnaev s.n.* (MW9061768); **Penza Province**, Penza Distr., Zasechnoe Settl., 2 Aug. 2008 *Kobozeva 21* (MW9061771); **Lipetzk Province**, Dankov Distr., Polibino Settl., *Seregin M-3033* (MW9061781); **Voronezh Province**, Khopersky State reserve, 25 Apr. 1982 *Popova s.n.* (MW9061777); **Tambov Province**, Gorelovskoe forestry, 11 Aug. 2926 *Samsel 472a* (MW9061779); **Karachaevo-Cherkessian Republic**, Teberda Nature Reserve, *Ignatov & Ignatova 05-3676* (MW9061797); **Republic of North Ossetia**, Ardon River valley, Nizhny Unal Settl., 1 Sept. 1997 *Petrunina s.n.* (MW9061801).

ASIAN RUSSIA: **Altai Republic**: Maima, flood valley of Katun River, 18 Jul. 1993 *Ignatov 35/23* (MHA9047324); Ongudai Distr., Malyj Yaloman, 30 Jul. 1991 *Ignatov & Ignatova 25/6* (9047329); Teletzkoe Lake, Bele, 3 Jul. 1989 *Ignatov 0/79* (MHA9047326); Kurkure Range, Kayakkatuyaryksky Creek basin, 6 Jul. 1991 *Ignatov 8/293* (MHA9047325). **Irkutsk Province**, Ust-Ilimsk Distr., Ust-Ilimsky reservoir, 8 Aug. 2007 *Seregin et al. M-2009* (MHA9047273). **Zabaikalsky Territory**, Kyra Distr., "Gornaya Step" Reserve, 31 Aug. 2005 *Afonina 7805* (MHA9130452). **Republic of Sakha/ Yakutia**: Momsky Distr., Ulakhan-Chistai Range, Tirekhtyakh River middle course, Mramornaya Mt., *Ignatov & Ignatova 18-1480* (MHA 9028262); Tomponsky Distr., a creek, right tributary of Sakkyryr River, *Ignatov & Ignatova 17-636* (MHA9025874; Tomponsky Distr., Suntar-Khayata Range, right bank of Kyurbelyakh Creek, *Ignatov & Ignatova 15-183* (MHA9047648); same place, Sukhaya Creek, *Ignatov & Ignatova 15-98* (MHA9047649); Tomponsky Distr., Sette Daban Range, Okraina Ridge between Ulakh and Nadezhda Creeks, *Ignatov & Ignatova 16-1083* (MHA9022767); Khangalassky Distr., Ulakhan Keteme Creek, *Ignatov & Ignatova 16-208* (MHA9021791). **Amurskaya Province**: Tukuringra Ridge, left bank of Gilyui Bay between Lugerkan and Tabuneika Rivers, *Dudov 2016_Br_0725* (MW9079158); same place, cape of Zeya reservoir between Razvedochny and Sukhoy Gulfs, *Dudov 2016_Br_0732* (MW9079153); same place, left side of Motovaya River vally, *Dudov 2016_Br_0721* (MW9079659). **Khabarovsk Territory**: Verkhnebureinsky Distr., Bureinsky State Reserve, Levaya Bureya River near Kolbond'o Creek mouth, *Iwatsuki 60553* (MHA9130436); Okhotsk Distr., Urak River, 15 Sep 1952 *Rozenberg s.n.* (MW9061906); Sovgavan Distr., Botchi Reserve, Kluych Dlinny, *Ignatov & Ignatova 13-452* (MHA9047650). **Primorsky Territory**: Partizansk Distr., Kamenisty Creek (south of Olkhovaya Peak), *Ignatov et al. 06-2448* (MW9061539); Vladivostok area, Bolshaya Sedanka Creek, *Ignatov et al. 06-3349* (MW9061905); Partizansk Distr., Lozovyj Range, Chandolaz Mt., *Ignatov 07-63* (MW9061902). **Sakhalinskaya Province**: Sakhalin, Tymovsk Distr., Chamginsky Pass, *Ignatov 06-493* (MW9061907);

2. **Pylaisia coreana** Nog., J. Hattori Bot. Lab. 12: 32, f. 12. 1954.

Figs. 10, 14A, 34F.

Note on taxonomy. *Pylaisia coreana* was described by Noguchi (1954) who compared it with *P. sublaevidens* Toyama, but later Noguchi (1984) synonymized *P. sublaevidens* with *P. polyantha*, without any discussion about *P. coreana*. Arikawa (2004) placed *P. coreana* to the synonymy of *P. polyantha*, but *P. sublaevidens* to the synonymy of *P. obtusa* (which well fits the illustrations of Toyama, 1938). *Pylaisia coreana* was described by Noguchi as having small plants, with leaves 1–1.2×0.3–0.35 mm, narrow laminal cells, 55–70×4–5.5 μm, and small spores, 10–13 μm; these characters exactly fit specimens from eastern part of Russia, which were found in a separate moderately supported clade. Therefore we apply the name *P. coreana* to the species of this clade.

The above mentioned quantitative characteristics of *Pylaisia coreana* are not totally exceptional in *P. polyantha*, but small spores are known in European populations of *P. polyantha,* while *P. polyantha* '*orientale*' has spores 12–18(–20) μm, i.e. is consistently different from *P. coreana*. The distinctions in peristome structure are discussed below.

Description. Plants small, light- to yellowish-green. Stem and branches straight, moderately densely foliate; leaves straight to indistinctly homomallous and turned outwards substrate. Stem leaves 0.6–1.1×0.2–0.4 mm, lanceolate, rarely ovate, gradually narrowed into a long or short acumen, slightly rounded to insertion; margins entire or serrulate above; median laminal cells 35–75×4–5 μm, alar cells subquadrate, few, forming small, slightly elongate triangular group to 10 cells long and 5 cells wide. Branch leaves somewhat smaller and narrower. Capsules cylindrical, 1.4–1.7 mm long (without operculum). Operculum conic to conic-rostrate. Peristome forming high conus when dry. Exostome teeth 250 μm long above the mouth, dorsal plates smooth below, and slightly papillose above; endostome to 300 μm above the mouth, not adherent to exostome, endostome segments narrow, not perforated along the keel, slightly papillose. Spores 9–12(–13) μm.

Differentiation and variation. In the whole range of *P. polyantha*–complex, *P. coreana* might be difficult to differentiate from some smaller morphs of the European group of haplotypes, especially from plants described as *P. suecica*, that was characterized by leaves up to 1.2 mm long and spores 8–10 μm (Limpricht, 1895). Currently, however, *P. suecica* is considered as a form of *P. polyantha* (and putatively of the European group of haplopytes). A sympatric plants of Asian *P. polyantha* however usually have larger plants with leaves 1.2–1.5 mm long and spores 12–14 μm, as probably most importantly, the exostome to 300 μm and endostome to 350 μm long, whereas in *P. coreana* exostome is to 250 μm and endostome to 300 μm long, and less papillose than in *P. polyantha* '*orientalis*'.

Among the samples referred here fo *P. coreana*, the most strongly dissimilar in morphology are Kamchatkan plants (Fig. 10: 37–40: **Cr9**). Its leaves are very short

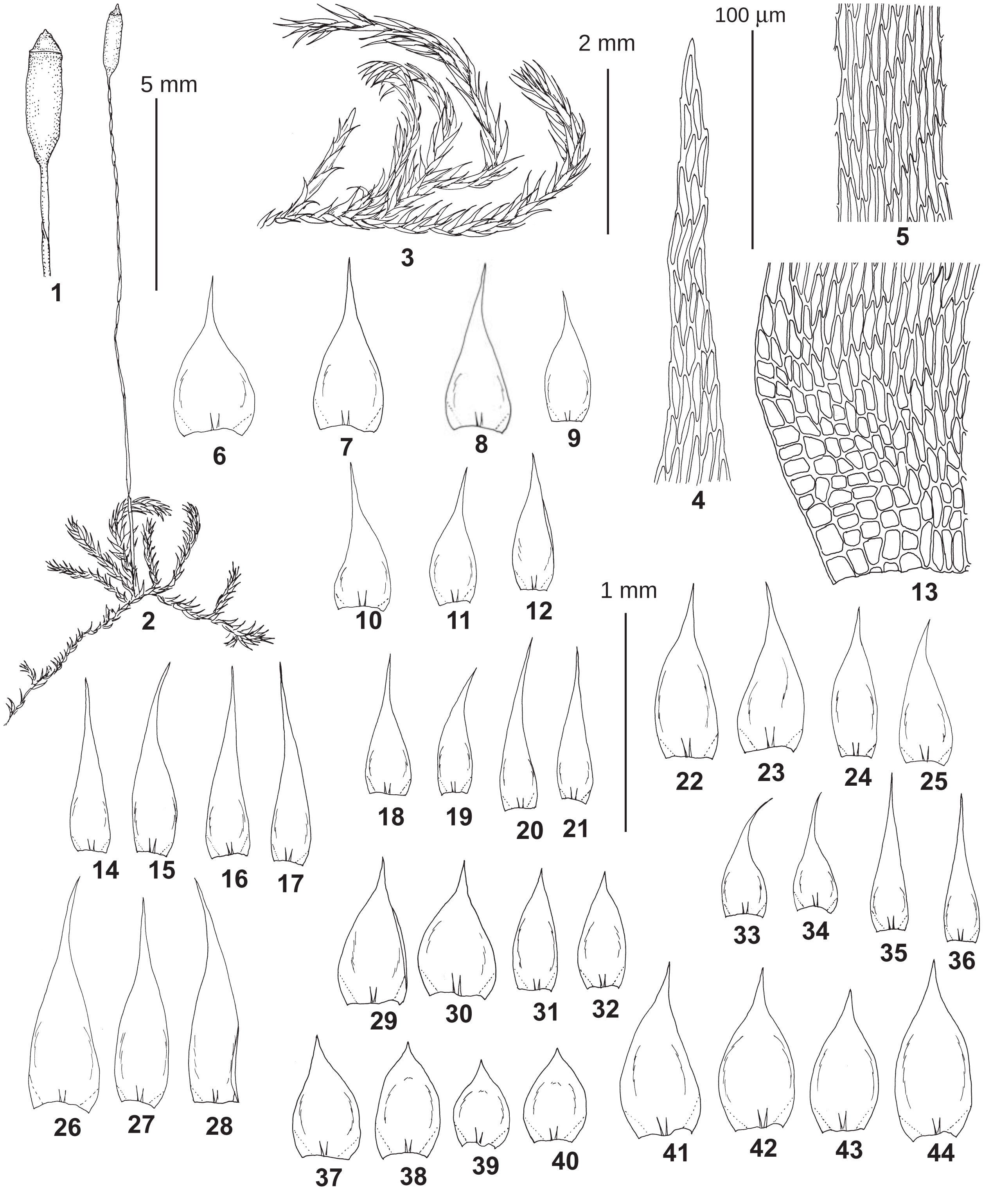

Fig. 10. *Pylaisia coreana* (all specimens from Russia): 1–13: **Cr4**, OK 2727, Khabarovsk Territory, Botchi Reserve; 14–17: **Cr6**, OK223, Primorsky Territory; 18–21: **Cr5**, OK2797, Primorsky Territory, Vladivostok; 22–25: **Cr2**, OK2726, Amurskaya Province, Zeya Reserve; 26–28: **Cr3**, OK2750, Yakutia, Sette Daban Mts.; 29–32: **Cr1**, OK2681, Yakutia, Sette Daban Mts.; 33–36: **Cr7**, OK2801, Amurskaya Province, Zeya Reserve; 37–40: **Cr9**, OK217, Kamchatka); 41–44: **Cr8**, OK224, Sakhalin. 1: capsule; 2–3: habit, dry; 4: upper laminal cells; 5: median laminal cells; 6–9, 14–15, 18–19, 22–23, 26–27, 29–30, 33–34, 37–38, 41–42: stem leaves; 10–12, 16–17, 20–21, 24–25, 28, 31–32, 35–36, 39–40, 43–44: branch leaves; 13: basal laminal cells. Scale bars: 5 mm for 2; 2 mm for 1, 3; 1 mm for 6–12, 14–44; 100 µm for 4–5, 13.

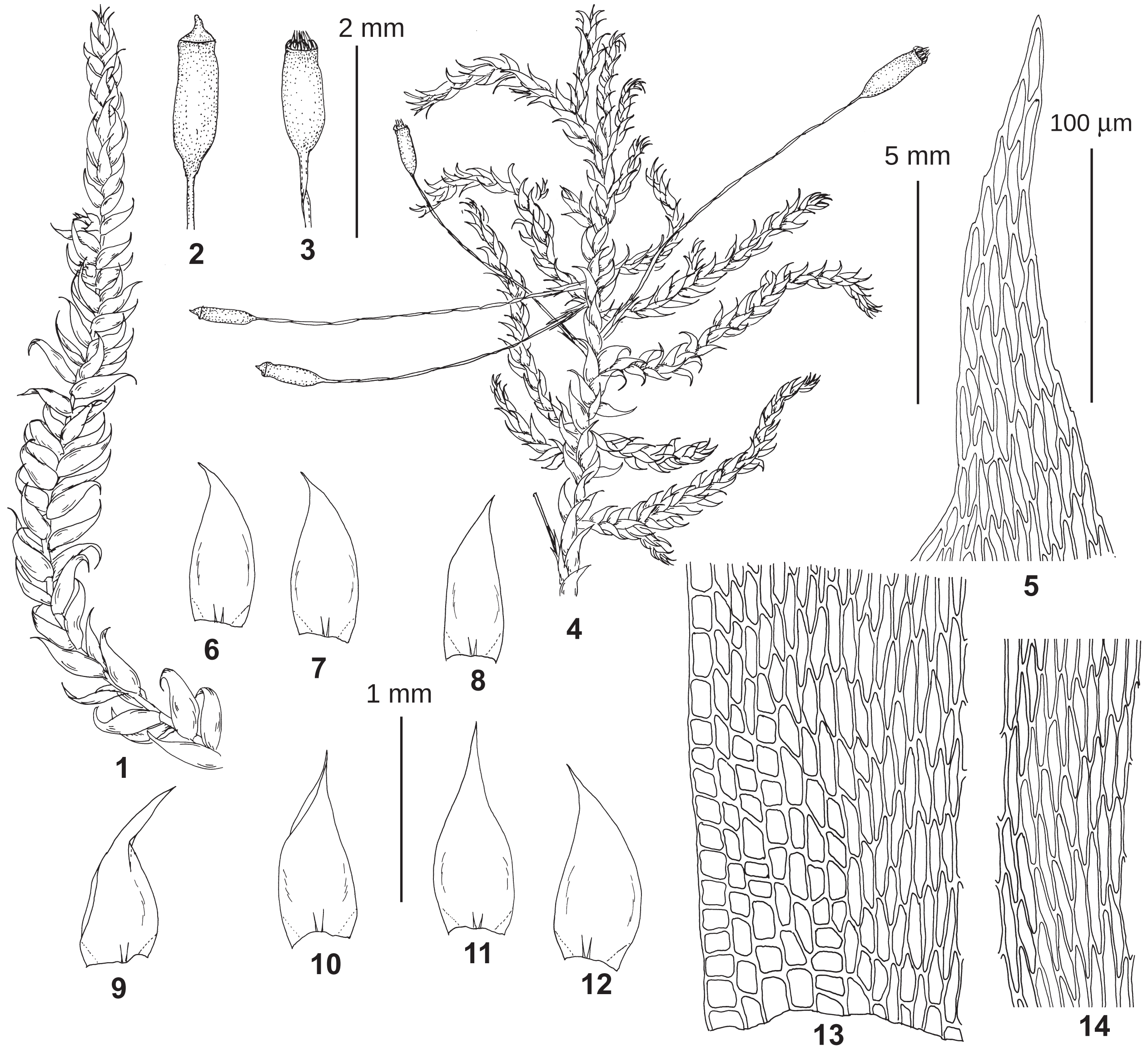

Fig. 11. *Pylaisia steerei* (**St4**, OK 2746, Russia, Yakutia, Ust–Maya Distr.). 1, 4: habit, dry; 2–3: capsules; 5: upper laminal cells; 6–8: branch leaves; 9–12: stem leaves; 13: basal laminal cells; 14: median laminal cells. Scale bars: 5 mm for 4; 2 mm for 1–3; 1 mm for 6–12; 100 µm for 5, 13–14.

and broad, resulting in julaceous habit similar to that of *P. curviramea*, but their narrow leaf cells and short peristome agree with its affinity to *P. coreana*, suggested from molecular phylogenetic analysis. We interpret such morphs as a result of an impact of severe environmental conditions, especially exposure to strong winds.

Distribution. Kamchatka, East Yakutia, Amurskaya Province, Khabarovsk and Primorsky Territories, Sakhalin.

Selected specimens examined: RUSSIA: East Siberia, **Republic Sakha (Yakutia)**, Ust-Maya Distr., left bank of Yudoma River, 2 km downstream Shchel Creek mouth, 8 Sep 2000 *Ivanova s.n.* (Bryophyta Sibiriae Exsiccata Fasc. I #48 (as *P. steerei*), MHA9130433); **Primorsky Territory**: Sudzhukhinsky Reserve, 27 Sept. 1944 *Zhudova 164* (MW9061904); Anuchino Distr., Anuchino, *Ignatov & Ignatova 13-1411* (MHA9130450).

3. **Pylaisia steerei** (Ando & Higuchi) Ignatov, Arctoa 10: 174. 2001. — *Pylaisiella steerei* Ando & Higuchi, Mem. New York Bot. Gard. 45: 211–215, f. 1–34. 1987.

Figs. 11–12, 14F, 15E-H, 34B.

Note on taxonomy. This species was described from Alaska (Ando & Higuchi, 1987) by only one specimen, which was found very distinct from widespread *P. polyantha* in clearly falcate leaves. Later, plants with falcate leaves were found in Yakutia (Ignatov *et al.*, 2001), where they occur sporadically at places. Such plants grow at trunk bases in floodplains of creeks. Notably, the trees with such plants usually have an average-looking *P. polyantha* at 1.5 m above ground and higher. Preliminary tests confirmed the consistent ITS differences between such epiphytic and tree-base plants, e.g. confirming a

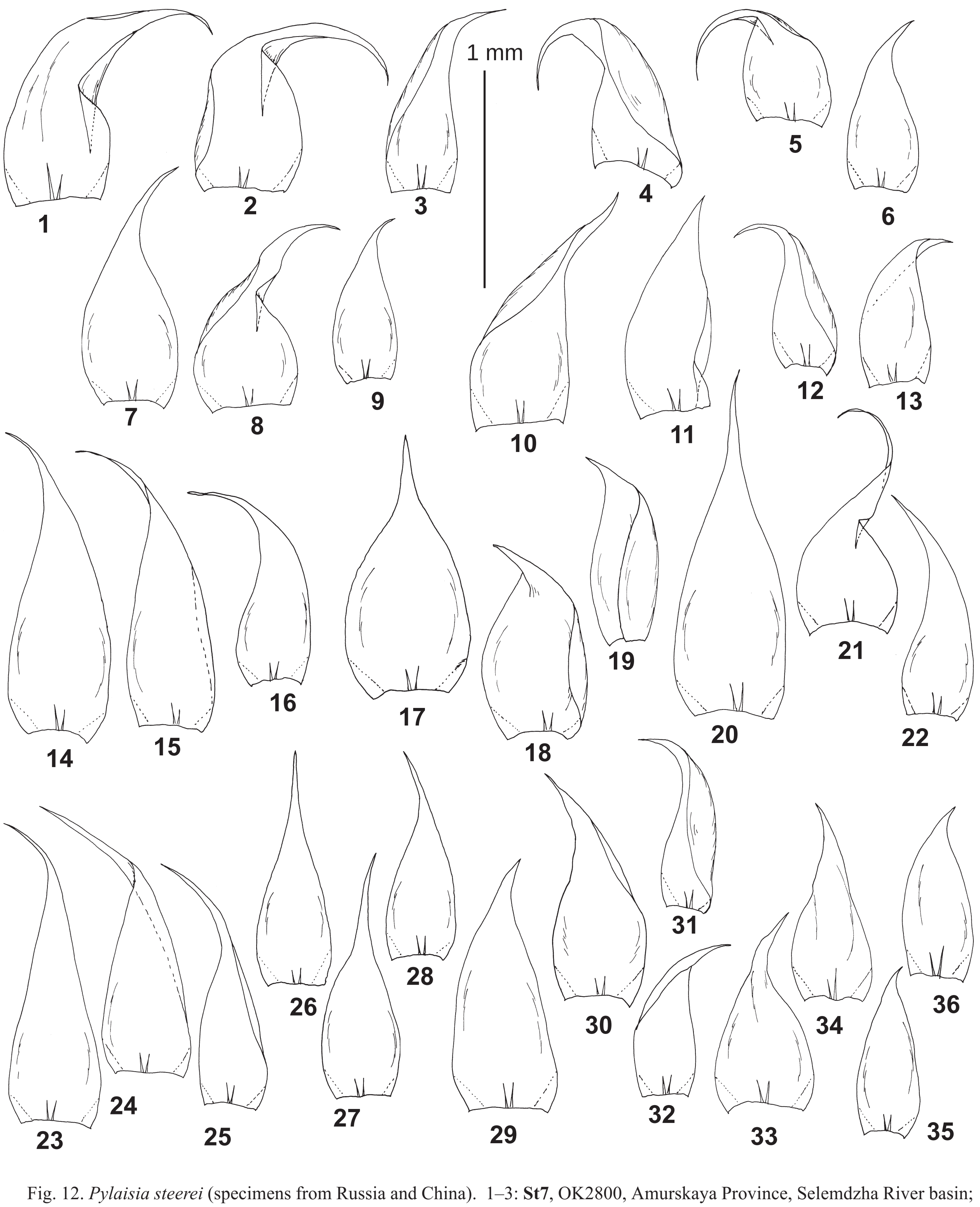

Fig. 12. *Pylaisia steerei* (specimens from Russia and China). 1–3: **St7**, OK2800, Amurskaya Province, Selemdzha River basin; 4–6: **St3**, OK2745, Amurskaya Province, Norsky Reserve; 7–9: **St5**, OK2749, Amurskaya Province, Norsky Reserve; 10–13: **St2**, OK2731, Amurskaya Province, Norsky Reserve; 14–16: OK2806, Amurskaya Province, Norsky Reserve; 17–19: admixture to **Cu1**, OK219, Khabarovsk Territory, Chegdomyn; 20–22: **St12**, OK2794(437), Russia, Altai Mts., Ust-Sema; 23–25: **St8**, OK2804, China, Xinjiang; 26–28: **St13**, OK220, Russia, Khabarovsk Territory, Bureinsky Reserve; 29–32: **St1**, OK2684, Yakutia, Khandyga settl.; 33–36: **St6**, OK215, Yakutia, Ust-Maya Distr.; 1–2, 4–5, 7–8, 10–11, 14–15, 17–18, 20–21, 23–24, 26–27; 29–30, 33–34: stem leaves; 3, 5–6, 9, 12–13, 16, 19, 22, 25, 28, 31–32, 35–36: branch leaves. Scale bar: 1 mm for all.

specific status of *P. steerei*. Arikawa (2004) also accepted *P. steerei,* although discussing our Yakutian plants he commented that only some their traits agree with *P. steerei*. Also Arikawa referred to *P. steerei* a specemen collected in NW China, Xinjiang.

Present molecular phylogenetic analysis revealed two facts that make circumscription of *P. steerei* more complicated. First, most specimens of *P. steerei* by ITS and also IGS appeared to be indistinguishable from *P. curviramea*, a species distinct in its morphology. Second, *Pylaisia* species with falcate leaves appeared in at least three groups of haplotypes. One of them, strongly gifferentiated genetically, is described below as a separate species, *P. bezgodovii*.

A rather substantial differentiation between two groups of haplotypes: (1) *P. polyantha* '*orientalis*' and (2) group of haplotypes of *P. steerei* + *P. curviramea* poses a question on the delimitation of *P. steerei* and even its acceptance as a species. The strong reticulation in this group and variation in most characters mentioned as diagnostic for *P. steerei* force us to accept simply a pragmatic decision and refer to this species all specimens with strongly falcate leaves, excepting *P. bezgodovii* that possesses differential characters discussed below.

Description. Plants moderately small to medium sized, yellowish- or brownish-green. Stem and branches straight, moderately densely complanately foliate; leaves falcate secund, turned towards substrate. Stem leaves 1.1–1.6×0.4–0.6 mm, ovate-lanceolate, gradually narrowed to apex, usually boradly acuminate, slightly rounded to insertion; margins entire or serrulate above; median laminal cells 30–55×5–6 µm, alar cells subquadrate, rather few, forming slightly elongate triangular group 10–15 cells long and 5–10 cells wide. Branch leaves somewhat smaller. Capsules cylindrical, 1.5–2.0 mm long without operculum. Operculum conic to conic-rostrate. Peristome forming high conus when dry. Exostome teeth 300 µm long above the mouth, dorsal plates smooth below, and slightly papillose above; endostome to 350–380 µm above the mouth, not adherent to exostome, endostome segments narrow, not perforated along keel, strongly papillose. Spores 12–18 µm.

Distribution: *Pylaisia steerei*, as it is circumscribed here, occurs in Eurasia in Chukotka, Yakutia, Amurskaya Province, Khabarovsk Territory, Transbaikalia, Buryatia, Altai Republic and Xinjiang Province of China.

Specimens examined: RUSSIA: **Chukotksky Autonomous District**, Anadyr river, 20 Aug.1981 *Afonina s.n.* (LE); **Republic of Buryatia**: Kabansky Distr., vicinity of settlement Rechka Vydrinaya, *Fedosov et al. 18-2-117* (MW9112045); **Amurskaya Province**: Norsky Reserve, valley of Nora River 1 km downstream cordon "Meunsky", 9 Jul. 2010 *Bezgodov 357* (MHA 9047656); Zeysky Reserve, Tukuringra Range, Garmakan River valley, *Duduv & Kotelnikova 2013_Br_0027* (MW9061982); **Altai Republic**: Altaisky State Reserve, Chulyshman River valley, Berekhtuyaryk Creek, 26 Jun. 1989 *Ignatov 0/1695* (MHA9130409); **Republic of Sakha (Yakutia)**: Lensky Distr., mouth of Pilka River, 2 Aug. 1999 *Ivanova s.n.* (MW9061980); Tomponsky Distr., right bank of Kuraanakh River (ca. 30 km from Yakutsk-Magadan Hwy), *Ignatov & Ignatova 17-186* (MHA9025955); Neryungri Distr., Chulma settl., 25 Jul. 1993 *Ivanova s.n.* (MHA9047655).

4. **Pylaisia curviramea** Dixon, Rev. Bryol., n.s. 1: 186. 1928.

Figs. 13, 16, 34C.

Note on taxonomy. Arikawa (2004) found that *P. polyantha* from Asian Russia and, specifically, collections from Bureya River Basin differ from European *P. polyantha* by *rbc*L sequences, and also found that these plants are identical by morphology with *Pylaisia curviramea* described from Central China.

The present analysis found specimens of this species homogeneous by applied DNA markers, posing only a question on its differentiation from *P. steerei.* However, these species are distinct morphologically when plants are well developed: *P. steerei* looks as *Hypnum cupressifirme* or miniature *Calliergonella lindbergii*, whereas optimally developed *P. curviramea* has short and broad leaves, dense foliage and curved branches, which make these plants more similar to *Entodon challengeri* (Paris) Cardot than to any *Pylaisia* species (Fig. 13). Less developed plants are still conspicuous due to imbricate, strongly concave leaves.

Description. Plants looks medium sized due to tumid foliage, despite its leaves are shorter than in many other species of *Pylaisia*, yellowish- or brownish-intense green. Stems and branches usually curved, occasionally straight, densely terete foliate; leaves straight or with slightly curved subapical part, in the latter case forming a homomallous apsect. Stem leaves 0.7–1.0×0.3–0.5 mm, ovate to broadly ovate, shortly narrowed to apex, slightly rounded to insertion; margin entire or serrulate above, median laminal cells rhomboidal, 20–45×5–6 µm, alar cells subquadrate in a rather expanded elongate group to 15 cells long and 7 cells wide. Branch leaves somewhat smaller. Capsules cylindrical, 1.5–2.0 mm long (without operculum). Operculum conic. Peristome forming high conus when dry. Exostome teeth 300 µm long above the urn mouth, dorsal plates smooth below, papillose above; endostome to 350 µm above the mouth, not adherent to exostome, endostome segments narrow, more or less perforated along keel, moderately papillose. Spores 12–15(–16) µm.

Differentiation and variation. A considerable variation in leaf size and shape between sequenced specimens of *P. curviramea* from Asian Russia is shown in Fig.13. The record of *Pylaisia curviramea* from Kamchatka is based on plants with a julaceous habit, but with slightly concave leaves and short, not curved branches. DNA sequence data place this specimen within *P. coreana* (specimen **Cr9**, OK217, Fig. 10: 37–40).

Distribution. *Pylaisia curviramea* is known from several areas in Russia; it usually grows in abundance. There are numerous collections (and observations in the

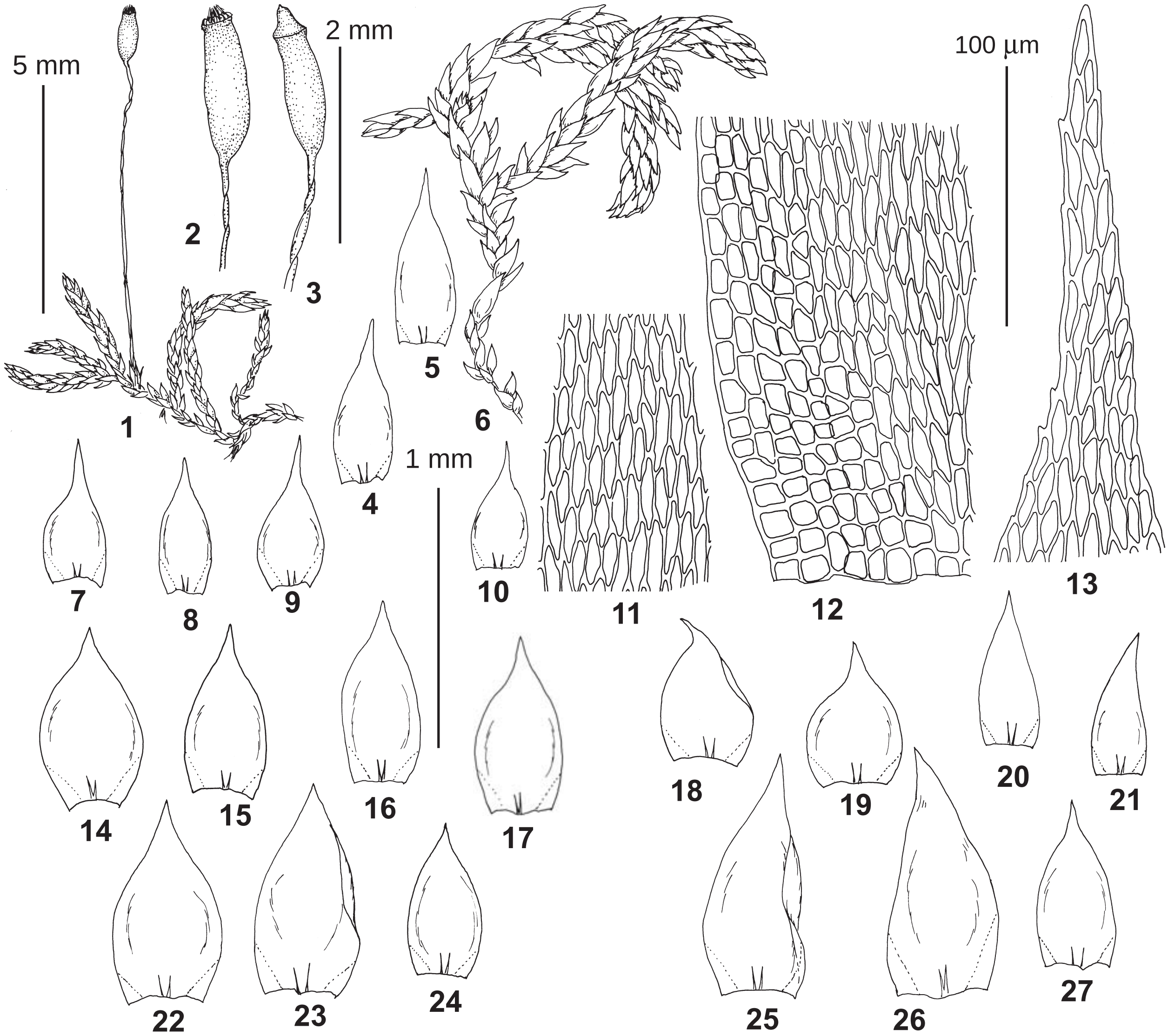

Fig. 13. *Pylaisia curviramea* (all specimens from Russia). 1–13: **Cu2**, OK 2682, Irkutsk Province, Listvyanka settl.; 14–17: **Cu3**, OK214, Yakutia, Ust–Maya Distr.; 18–21: **Cu4**, OK432, Amurskaya Province, Norsky Reserve; 22–24: **Cu1**, Khabarovsk Territory, Chegdomyn; 25–27: **Cu5**, OK1475, Yakutia, Khangalassky Distr. 1, 6: habit, dry; 2–3: capsules; 4–5, 16–17, 20–21, 24, 27: branch leaves; 7–10, 14–15, 18–19, 22–23, 25–26: stem leaves; 11: median laminal cells; 12: basal laminal cells; 13: upper laminal cells. Scale bars: 5 mm for 1; 2 mm for 2–3, 6; 1 mm for 4–5, 7–10, 14–27; 100 µm for 11–13.

field) in valleys of the left side tributaries of Amur River – Zeya and Bureya Rivers, in their middle courses which experience regular great floodings. An extensive population of *P. curviramea* was also found in Baikal Lake surroundings. *Pylaisia curviramea*, as it is circumscribed here, occurs in Yakutia, Irkutsk Province, Amurskaya Province, and Khabarovsk Territory.

Specimens examined: **Khabarovsk Territory**: Chegdomyn Settl., on street of the settlement, *Ignatov 97-1284* (MHA9130435); **Amurskaya Province**: Norsky Nature Reserve, valley of Nora River near cordon “Sorokaverstny”, 30 Jun. 2010 *Bezgodov 17* (MHA9130451); same place, island at the mouth of Meun River, 11 Jul 2010 *Bezgodov 397* (MHA9047653).

Peristome and spore size variations in *Pylaisia* species with free endostomes (Figs. 14–16).

Variation in peristome length and spore size was considered by Arikawa (2004) to be diagnostic for differentiation *P. steerei* from *P. polyantha*: endostome 380–500 µm mentioned in *P. steerei* vs. 300–380 µm in *P. polyantha,* and spores 15–18 µm vs. 11–14 µm corrrespondingly. Still somewhat indefinite understanding of these species forced us to discuss these quantative charactersists of *Pylaisia* with free endostomes in more details.

In most examined collections of *P. polyantha* from Russia spores were mainly 14–15 µm, occasionally 12 µm and 16 µm, and very rarely 10 and 17 µm, within the single capsules, mature but still operculate. In open capsules some spores were up to 20 µm, but as at the same

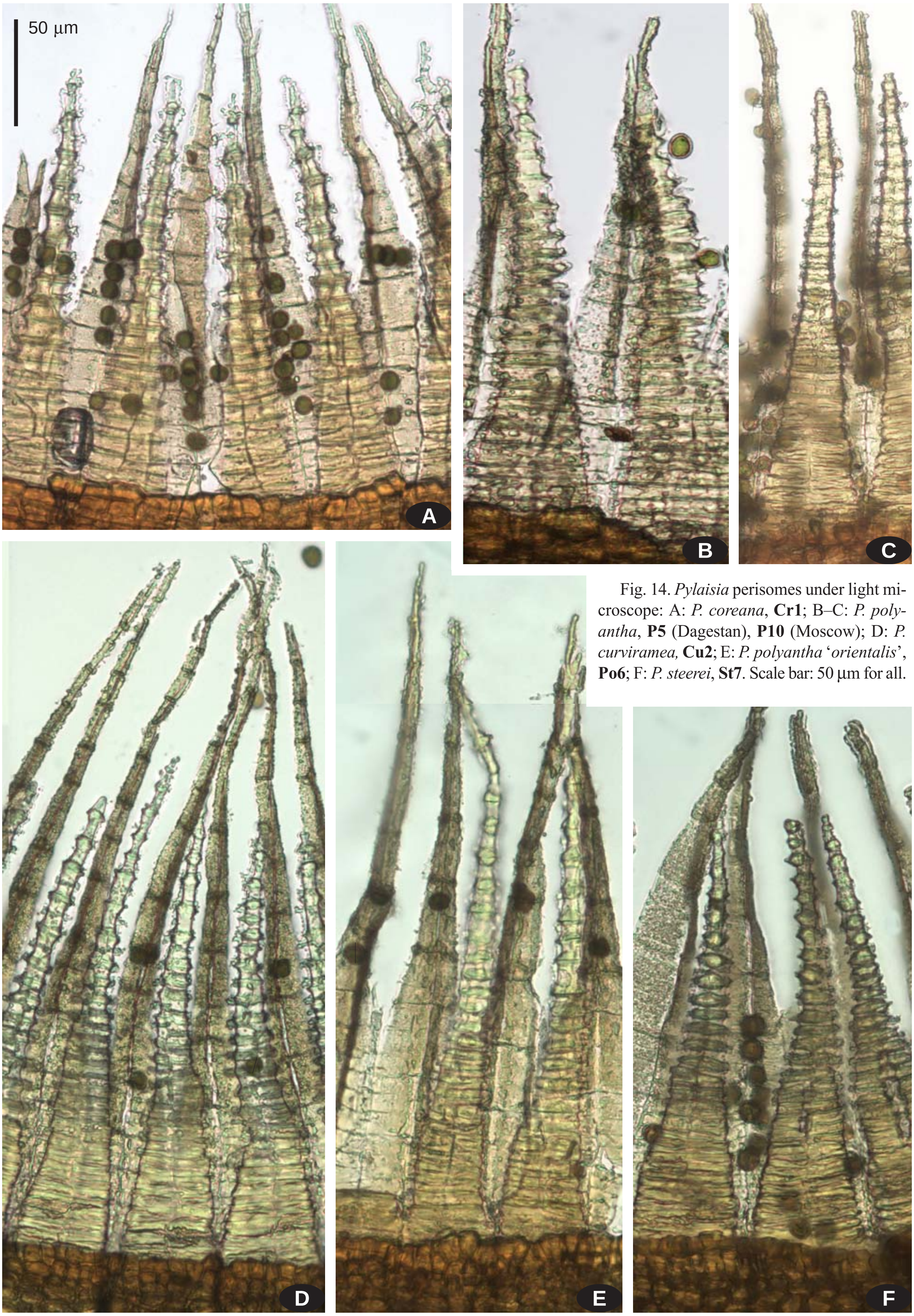

Fig. 14. *Pylaisia* perisomes under light microscope: A: *P. coreana*, **Cr1**; B–C: *P. polyantha*, **P5** (Dagestan), **P10** (Moscow); D: *P. curviramea,* **Cu2**; E: *P. polyantha* '*orientalis*', **Po6**; F: *P. steerei*, **St7**. Scale bar: 50 µm for all.

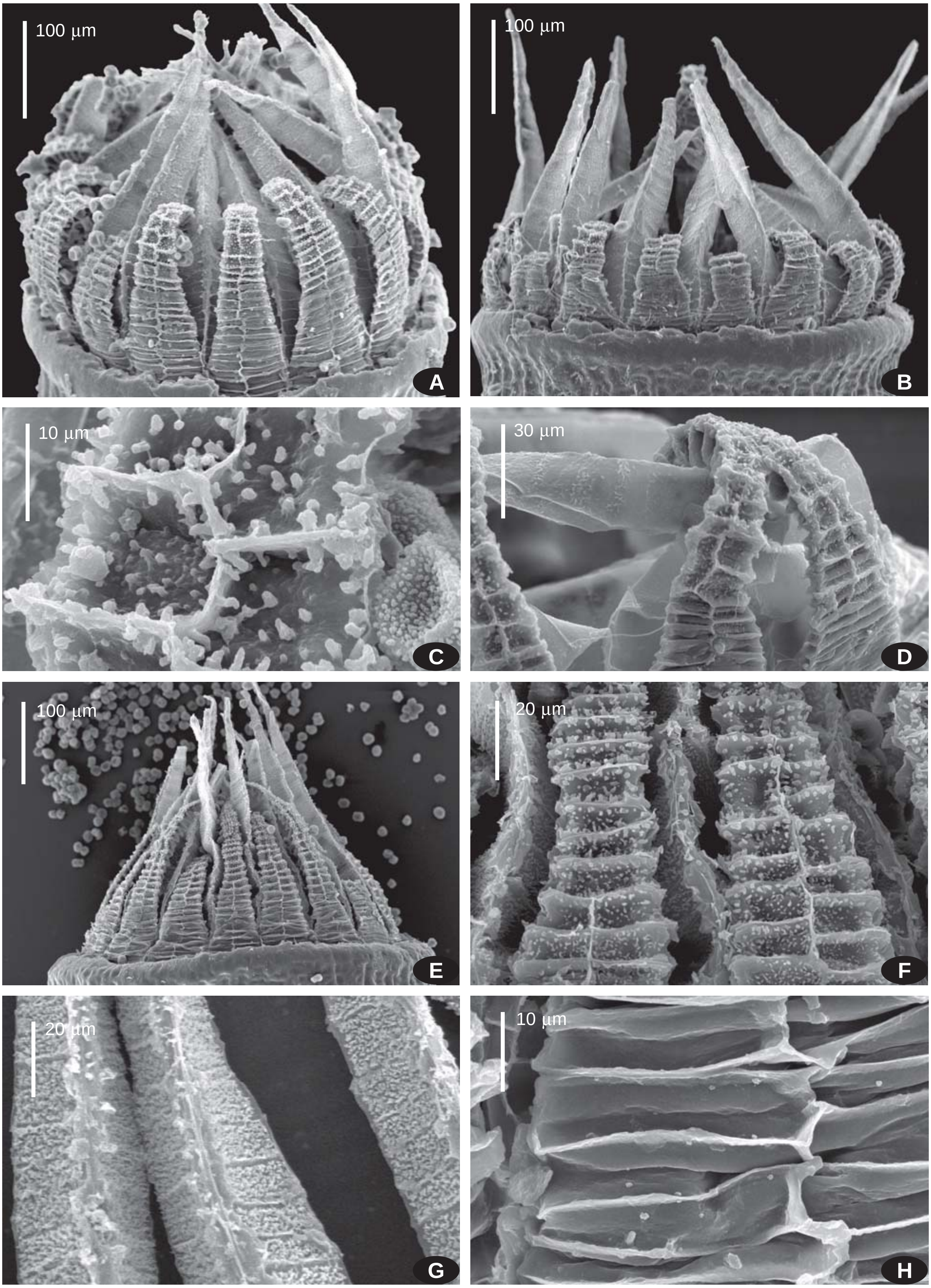

Fig. 15. *Pylaisia* perisomes under SEM: A–D: *P. polyantha*, **P10**; E–H: *P. steerei* (E–F: Yakutia, Ignatov 00-977, MHA; G–H: Yakutia, Ignatov 00-710, MHA). A, B, E: peristomes; C, F: exostome teeth distally, dorsal view; D, G: endostome segments in upper parts; H: exostome teeth proximally, dorsal view.

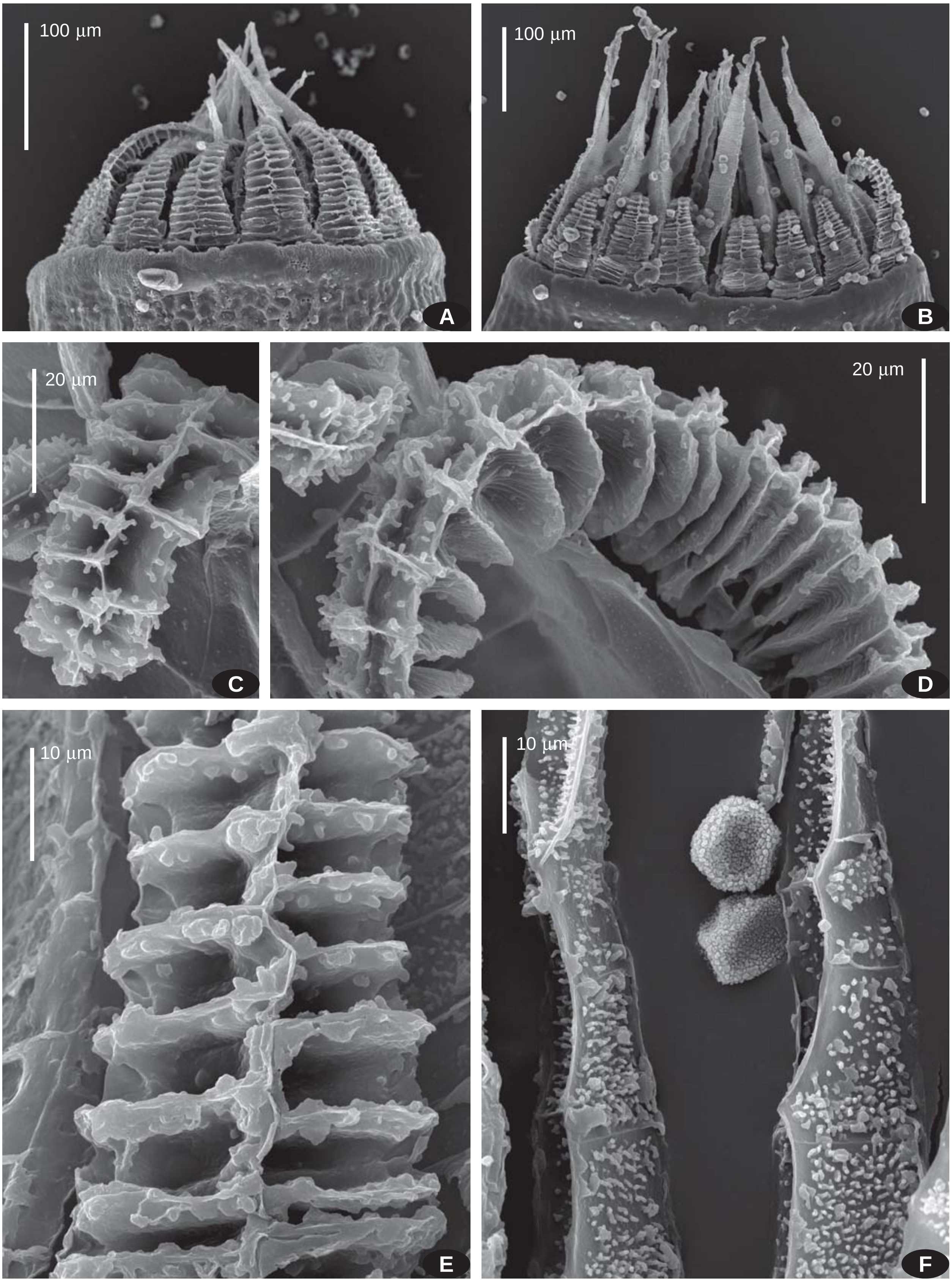

Fig. 16. *Pylaisia curviramea* perisomes under SEM: A, C–F from **Cu2** (Irkutsk); B from Yakutia, Ignatov 00-703 (MHA). A, B: peristomes; C, D, E: exostome teeth in upper part; F: endostome segments in upper parts.

time these capsules had at least few spores starting propagation (they also were enlarged to 20–22 µm in diameter); these measurements were ignored (such large spores usually slightly differ by more brownish color). However, in slightly immature capsules, although with separable operculum, spores about 8 µm only were sometimes observed. There are rather different data about the size of spores of *P. polyantha* in literature: 9.5–12.5 µm for Iberian Peninsula (Gallego, 2018), 11–14 µm for the whole world (Arikawa, 2004); 9–17 µm for eastern North America (Crum & Anderson, 1981), 9–17(–20) µm for Mexico (Sharp, 1994); 10–15 for Maine, USA (Allen, 2014), 12–16 µm for Europe (Limpricht, 1895), 11–17 for Netherlands (Touw & Rubers, 1989); 13–16 µm for Great Britain and Ireland (Smith, 2004), 13–18 µm for China (Zhang & He, 2005). Comparing *P. steerei* with *P. polyantha,* Ando & Higuchi provided for the latter species spore size 12–16, rarely 18 µm.

Considering the variation within one capsule and published data, it is difficult to prove any differentiation, except the general tendency for Asian plants of *P. polyantha* ‘*orientalis*’ to have a slightly larger spores (14–15 µm prevailing in most capsules), whereas in Europe many collections have only few spores over 14 µm (although in more northern part of Europe and in the Caucasus spore size is more similar to plants from Asian Russia). The sequenced collections of *P. steerei* have spores mostly 14–16 µm, also e.g. Xinjiang specimen has spores 12–14 µm, and several other falcate-leaved *Pylaisia* specimens from Russia have most spores less than 15 µm. Spore size variation in *P. curviramea* was identical to that in *P. polyantha* ‘*orientalis*’, and two genetically outlined entities, *P. coreana* and *P. bezgodovii* (described below), have spores smaller than 12 µm with solitary ones up to 13 µm in *P. coreana*.

Peristome length differentiation pattern in Russia is similar to that of spore size. Relatively short perisomes were observed in European *P. polyantha* and in *P. coreana*: exostome teeth to 200–250 µm long, and endostomes 250–300 µm long, while in *P. curviramea, P. polyantha* ‘*orientalis*’, and *P. steerei* exostome teeth were 250–300 µm long and endosotmes 300–380 (–400) µm long [e.g. in *P. steerei* from Xinjiang: 320–330 µm] (Fig. 14).

More densely papillose endostome segments are usually observed in *P. steerei*; it is better seen under SEM (Fig. 15 G), although light microscope is also sufficient for checking this character, cf. Fig. 14F, compare with Figs. 14D, E. The least papillose are endostomes in European and Caucasian *P. polyantha* (Fig. 15 B, D), and in *P. coreana* (Fig. 14A). In *P. curviramea* ornamentation of endostome is intermeriate between European *P. polyantha* and *P. steerei*: papillae are numerous but rather small and arranged at certain distance one from another (Fig. 16 F), not that densely as in *P. steerei* (Fig. 15 G). Endostome in *P. polyantha* ‘*orientalis*’ is similar to that in *P. curviramea* (Fig. 14E).

Exostome teeth on the dorsal surface are smooth below and papillose distally in all species with free endostome (Fig. 15A, H), and differences between species is not strong. Exostome teeth of *P. steerei* look more strongly papillose, which likely depends on more numerous dorsal trabeculae and larger size of papillae (cf. 15 C, F). In *P. curviramea* papillae in distal part of teeth on dorsal surface are not so numerous, but some of them are taller and under light microscope they form conspicuous projection from dorsal trabeculae (cf. Fig. 14D and 16 D).

5. Pylaisia bezgodovii Ignatov & Ignatova sp. nov.

Figs. 17, 18, 34A.

Type: “East Siberia, Republic Sakha/Yakutia, Ust-Maya District, Yugorenok, Khlebny Creek, 59°49’N – 137°59’E, 370 m alt., at base of *Salix* in regularly flooded part of the Yudoma River Valley, 7 Sept. 2000, Ignatov 00-711 (Holotype MHA9130416). Isolates: OK212 and OK2802.

Ethymology: the species name is given in honour of Andrej Gennadievich Bezgodov, an outstanding explorer of bryophyte flora of Urals and some areas in Sibera, who collected a specimen of the new species in Perm Province.

Diagnosis: Strongly falcate-secund leaves turned to the substrate make the species habit similar to that of *P. steerei*, although its leaves are smaller, 0.9–1.2×0.35–0.45 mm vs. 1.1–1.6×0.4–0.6 mm). Differences from *P. steerei* include also smaller spores (10–12 vs. 12–18 µm) and only slightly papillose endostome (vs. densely papillose in *P. steerei*). Alar cells are usually larger (to 12 µm wide) and more conspicuously differentiated than in *P. steerei*, forming larger alar group, 12–22 cells long and 5–6 cells wide vs. 10–15 cells long and 5–10 cells wide in the latter species. The strong unique substitutions in nuclear ITS and IGS sequences suggest a separate status of this species (Figs. 1–4).

Description. Plants small to medium-sized, light to whitish green, sometimes with glaucous tint. Stem and branches straight or only indistinctly curved, moderately densely foliate; leaves falcate-secund, turned towards substrate. Axillary hairs 4-celled, 70–90×9–11 µm. Proximal branch leaves triangular, irregualrly incised. Stem leaves 0.9–1.2×0.35–0.45 mm, ovate to ovate-lanceolate, gradually narrowed into a long acumen, slightly rounded to insertion; margin serrulate above, median laminal cells 35–70(–87)×5–6 µm, alar cells subquadrate, form elongate compact group 12–22 cells long and 5–6 cells wide; alar cells often to 12 µm wide. Branch leaves somewhat smaller. Inner perichaetial leaves erect, up 1.3×0.55 mm, not much elongated after fertilization. Capsules cylindrical, 1.5 mm long without operculum. Operculum high conic to conic-rostrate. Annulus deciduous. Peristome forming high conus when dry. Exostome teeth 250–300 µm long above the mouth, dorsal plates smooth below, papillose above; endostome up to 325 µm above the mouth, not adherent to exostome, endostome segments narrow, not perforated along keel, moderately papillose. Spores 9–12(–13) µm.

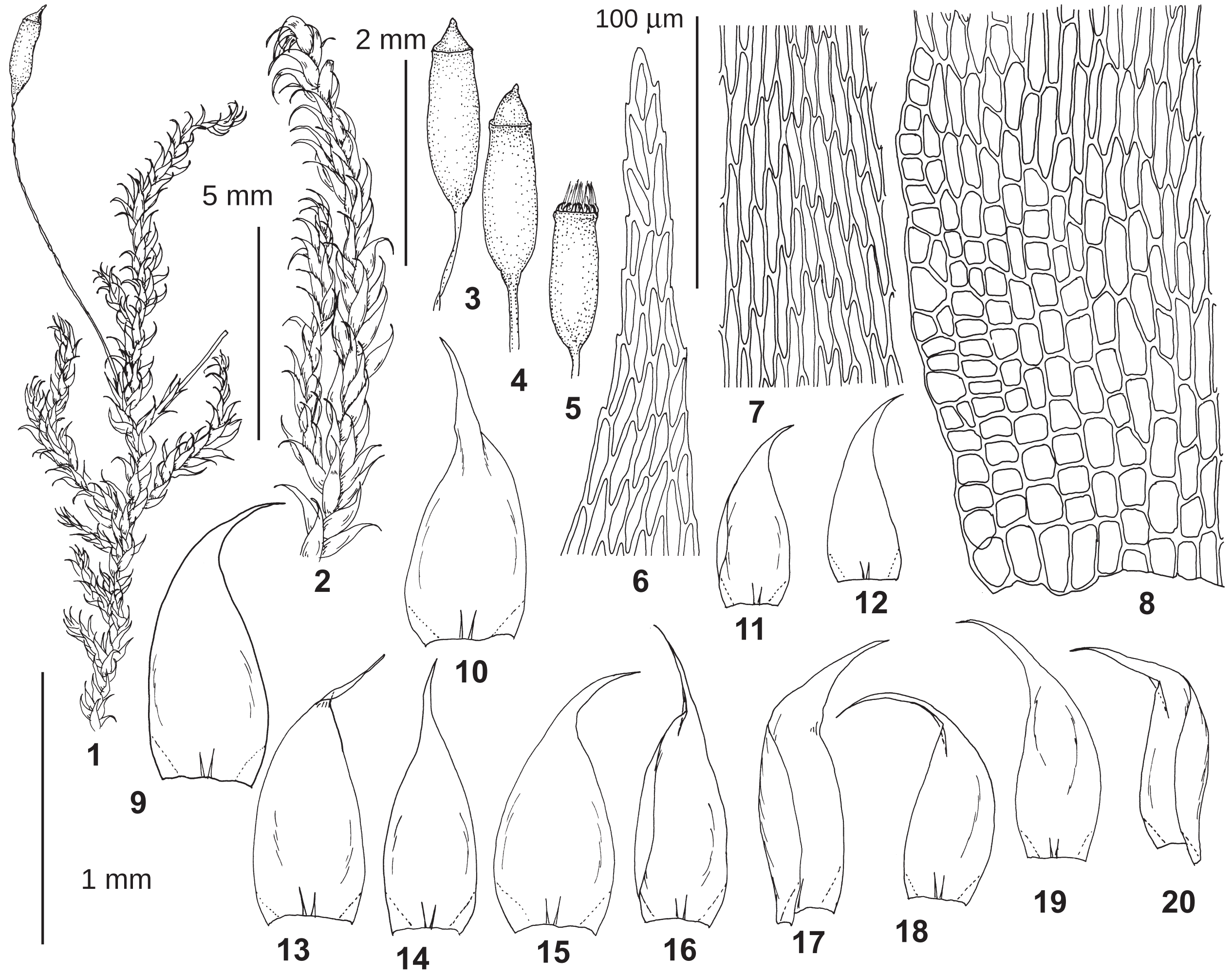

Fig. 17. *Pylaisia bezgodovii* (1–16: **Be1** & **Be3**, OK212, Yakutia, Ust–Maya Distr.; 17: **Be2**, OK835, Perm Province). 1–2: habit, dry; 3–5: capsules; 6: upper laminal cells; 7: median laminal cells; 8: basal laminal cells; 9–10, 18–19: stem leaves; 11–12, 20: branch leaves. Scale bars: 5 mm for 1; 2 mm for 2–5; 1 mm for 9–20; 100 µm for 6–8.

Differentiation. Likewise *P. steerei, P. bezgodovii* differs from all other species of the genus in having complanate foliage and falcate leaves turned toward substrate. Differences from *P. steerei* are described in the diagnosis.

Variation. Contrary to *P. steerei*, specimens of *P. bezgodovii* from Yakutia and a specimen from Perm Territory show little variation in gametophyte and sporophyte characters, being easy to recognize.

Distribution. This species was revealed in the course of molecular phylogenetic studies, before is was kept just under *Pylasia steerei*. At the moment it is known by several specimens from eastern Yakutia and one specimen from Ural Mountains, Perm Territory. In the latter locality, *Pylaisa* with falcate leaves was noticed on the base of aspen tree, while average-looking *Pylaisia polyantha* grew on the trunk above the level of snow cover in winter, i.e. as it usually grows. We sequenced both plantsfrom that tree, confirming that the true epiphytic plants belong to the most common ITS-haplotype of European *P. polyantha*, while *P. steerei*-like plants from the trunk base were identical to Yakutian plants. Additional search of such plants in herbaria revealed several specimens of *P. bezgodovii* from few nearby localities in Ust-Maya District in Yakutia.

In the valley of Yudoma River where the holotype of *P. bezgodovii* was collected, *P. steerei* was also found in about the same habitats, but these two species provide no problem with identification by spore size and shape of the alar cell group, as given in the key.

Specimens examined: RUSSIA: East Siberia, **Republic Sakha/Yakutia**, Ust-Maya Distr., Yugorenok: Medvezhij Creek, *Ignatov 00-976* (MHA9130429); same place, Shchel Creek, *Ignatov 00-709* (MHA9130430).

6. Pylaisia camurifolia (Mitt.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges.: 307 (Gen. Sp. Musc. 2: 373). 1878. — *Stereodon camurifolius* Mitt., J. Proc. Linn. Soc., Bot., Suppl. 1: 96. 1859.

Figs. 19, 20, 34G.

Note on the taxonomy: *Pylaisia camurifolia* was placed in the synonymy of *P. falcata* by Arikawa (2004), and in our previous publications (Bakalin *et al.*, 2009;

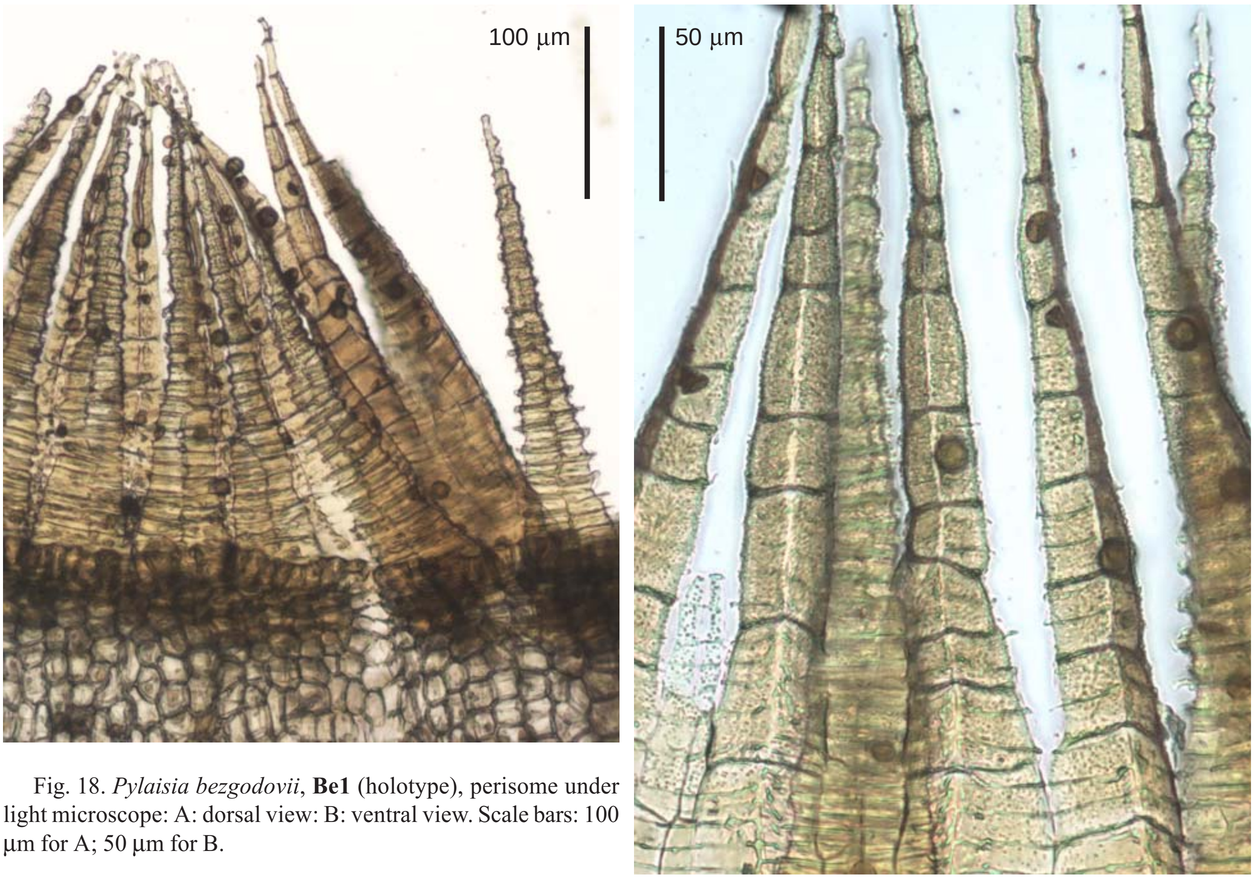

Fig. 18. *Pylaisia bezgodovii*, **Be1** (holotype), perisome under light microscope: A: dorsal view: B: ventral view. Scale bars: 100 µm for A; 50 µm for B.

Cherdantseva *et al.*, 2018) we reported it under that name. However, sequence data show a considerable genetic distance between *P. falcata* from Mexico (where from it has been originally described) and specimens from Asian Russia. In addition, plants referred to *P. falcata* from Asian Russia are somewhat smaller and also differ in smaller size of spores, ca. 20 µm only, while *P. falcata* is described as having spores 25–40 µm by Arikawa (2004), although Sharp *et al*. (1994) reported spores 20–40 µm, and Allen (2018) described them as16–30 µm. The protologue of *Pylaisia camurifolia*, which was described from Nepal, does not mention spore size; however, *Stereodon microsporus* Broth., described from China and subsequently synonymized with *Pylaisia falcata* (Ando, 1978), was described as having small spores, 20–25 µm, *i.e.*, quite similar to '*P. falcata*' from the Russian Far East.

Considering the fact that *Pylaisia camurifolia* is the eariest name of *Pylaisia falcata*-group described from Asia, and also that the type of *Stereodon microsporus* from Yunnan (BM001108723, with available high resolution scan) is habitually similar to plants from Russia, and also that according to Brotherus (1925) its spores are 20–25 µm, we use the name *Pylaisia camurifolia* for 'Asian *P. falcata*' instead of just retaining *P. falcata.* The further study with the additional sequencing of South-West Chinese and Himalayan specimens is obviously required for complete and correct naming of *P. falcata* s.l. plants in Asia.

Description. Plants medium-sized to moderately large. Stems and branches curved, loosely foliate; leaves homomallous to falcate-secund, turned outwards substrate. Stem leaves 1.2–1.7×0.5–0.6 mm, ovate to ovate-lanceolate, rather gradually narrowed into a long acumen, conspicuously and abruptly rounded to insertion; margins subentire; median laminal cells 30–55×5–6 µm, alar cells subquadrate, form a compact groups in basal leaf angles, alar groups quadrate or transverse rectangular, ca. 7 cells long and 7 cells wide. Branch leaves somewhat smaller. Inner perichaetial leaves erect to reflexed, not much elongated after fertilization. Capsules cylindrical. Peristome forming low conus when dry. Exostome teeth 230–260 µm long above the mouth, dorsal plates smooth below, papillose above; endostome up to 300 µm above the mouth, adherent to exostome only at base; segments rather broad, split only in lower 1/3 along the line that continues the segment keels; endostome moderately papillose. Spores 19–22 µm.

Differentiation. This species is unlikely to be mistaken with other species of *Pylaisia* known from Russia. It is a large plant, yellow-green with some reddish or orangish tint, with strongly falcate, rather loosely arranged leaves. Leaves have a triangular basal portion, are abruptly rounded to the insertion and have compact alar groups that are as broad as long. Peristomes are characterized by free upper parts of endostome segments which are broad and keeled. However, lower part of the

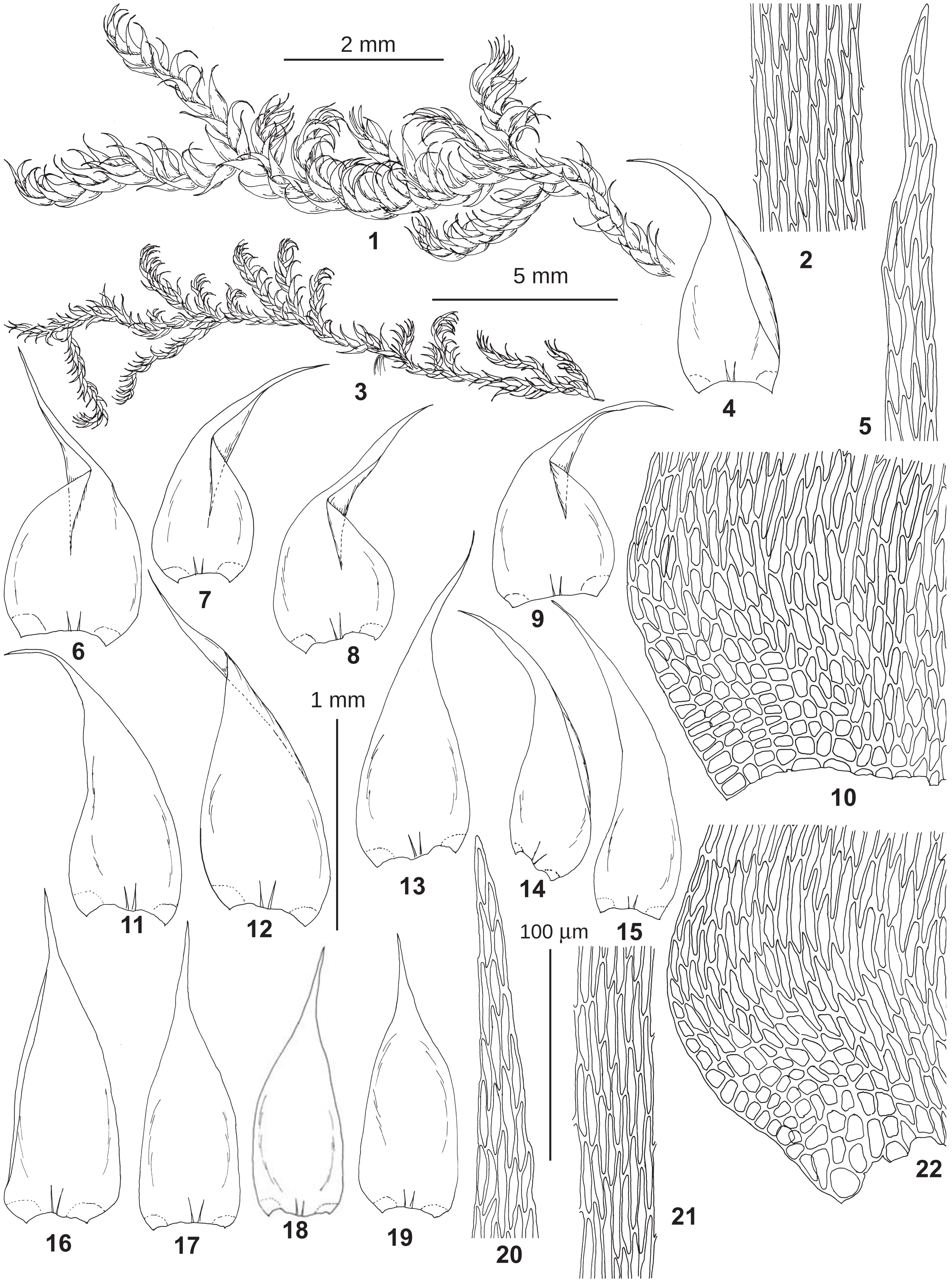

Fig. 19. *Pylaisia camurifolia* (1–10: **Ca1**, OK209, Russia, Kuril Islands; 11–15, **Ca2**, OK210, Sakhalin) and *P. falcata* (16–22: **F1**, OK546, Mexico). 1, 3: habit, dry; 2, 21: median laminal cells; 4, 6–7, 11–13, 16–17: stem leaves; 5, 20: upper laminal cells; 8–9, 14–15, 18–19: branch leaves; 10, 22: basal laminal cells. Scale bars: 5 mm for 3; 2 mm for 1; 1 mm for 4, 6–9, 11–19; 100 µm for 2, 5, 10, 20–22.

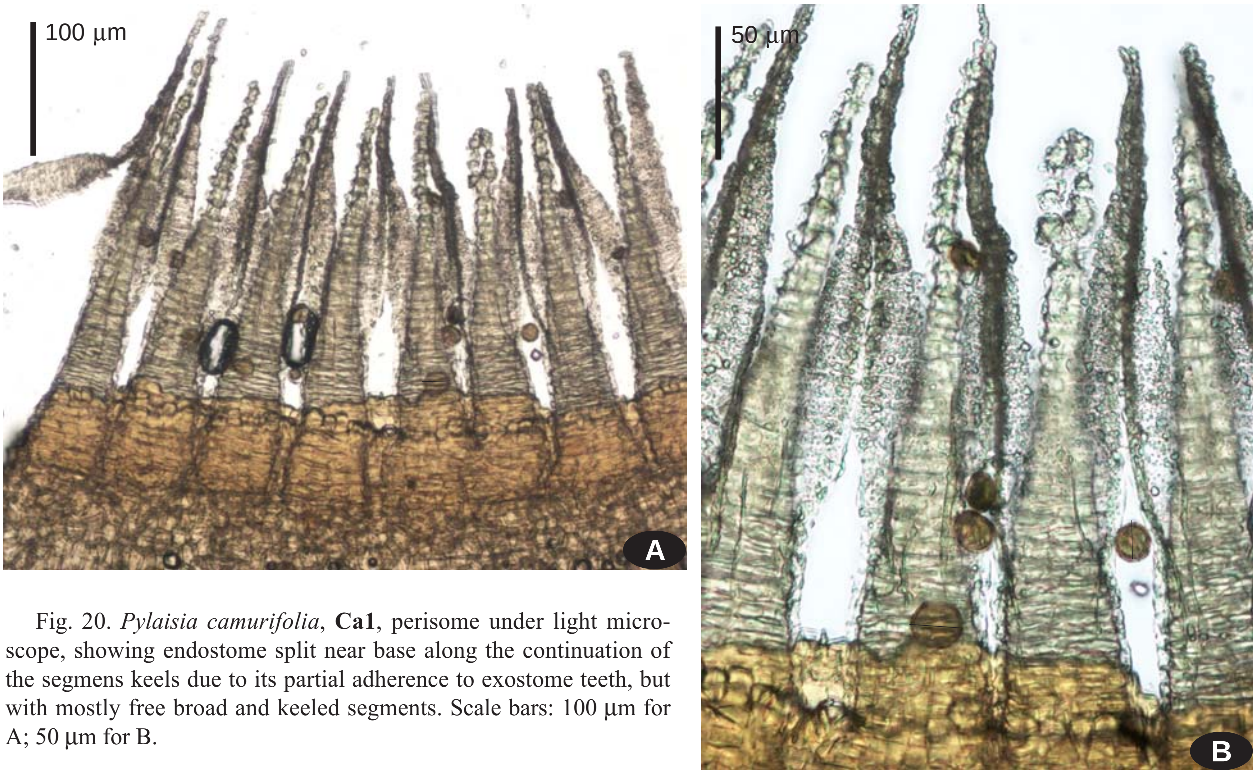

Fig. 20. *Pylaisia camurifolia*, **Ca1**, perisome under light microscope, showing endostome split near base along the continuation of the segmens keels due to its partial adherence to exostome teeth, but with mostly free broad and keeled segments. Scale bars: 100 µm for A; 50 µm for B.

endostome basal membrane is adherent to exostome teeth, resulting in splits of endostome in proximal part along the lines that are a continuations of the segment keels (Fig. 20).

Distribution. It seems that this species is rare in Asia. Only two collections, from Sakhalin and Kuril Islands, were found in Russia (see sequenced samples, Table 1).

7. Pylaisia condensata (Mitt.) A.Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1876–77: 306. 1878 (Gen. Sp. Musc. 2: 372). — *Stereodon condensatus* Mitt., J. Proc. Linn. Soc. Bot., Suppl. 1: 93. 1859.

Figs. 21–23; 24A,B; 25:1–16; 34I.

Notes on taxonomy: This species for a long time has been called *Pylaisia schimperi* Cardot (described from Canada), until Crum *et al.* (1964) found its name to be illegetimate and thus requiring substitution with *Pylaisia selwynii* Kindb. (described from Ottawa, Canada), which Crum *et al.* (1964) placed in the genus *Pylaisiella*. Recently Arikawa (2017) found that *Stereodon condensatus* Mitt. described from West Himalayas (Kumaon) belongs to the same species as *Pylaisia selwynii*, thus he suggested the substitution of the latter with *Pylaisia condensata*. The present study found a rather considerable difference between the western North American and Asian plants, thus we suggest to retain the name *Pylaisia selwynii* for the former. The distribution of *P. selwynii* in North America needs further studies: at least one specimen from Alaska called *P. selwynii* in Genbank seems to belong to *P. obtusa* (a species superficially rather similar to *P. selwynii).*

Morphological distinctions between the eastern North American plants referred here to 'true *P. selwynii*' and *P. condensata* (='Eurasian *P. selwynii*') includes a smaller spores of the former species, 16–24 µm vs. 18–30 µm, with at least some spores ca. 30 µm found in most collections. Also the number of dorsal trabeculae on the exostome teeth was found fewer in North American *P. selwynii* than in Eurasian plants (Fig. 24), although the latter character was studied by us on a limited material only.

Description. Plants small to medium-sized. Stems and branches curved, densely foliate; leaves homomallous, turned outwards substrate. Stem leaves broadly ovate to ovate-lanceolate, rather suddenly narrowed into a rather short acumen, 0.8–1.2(–1.4)×0.5–0.6 mm; margins subentire; median laminal cells 25–40(–50)×6–9 µm, alar cells subquadrate to rectangular, homogeneous, in a rather large group, 20–25 cells long and 6–7(–10) cells wide. Branch leaves somewhat smaller. Inner perichaetial leaves erect or somewhat reflexed, oblong-lanceolate, to 1.6 mm long. Capsules ovoid. Peristome in dry state forms a low conus due to adherence of its elements. Exostome teeth 150–200 µm long, dorsal plates smooth below, coarsely papillose above; endostome adherent to exostome teeth to about teeth halves; segments narrow, split except their uppermost part; endostome moderately papillose. Spores 16–30 µm.

Differentiation and variation. Despite *P. condensata* is a variable taxon, in most of its range, where it cooccurs with *P. polyantha,* this species is easy to recognize in the field by strongly homomallous to falcate leaves, curved branches and ovate capsules that are essentially cylindrical in *P. polyantha*. In southern Russian Far East, the region where other East Asian species of the genus

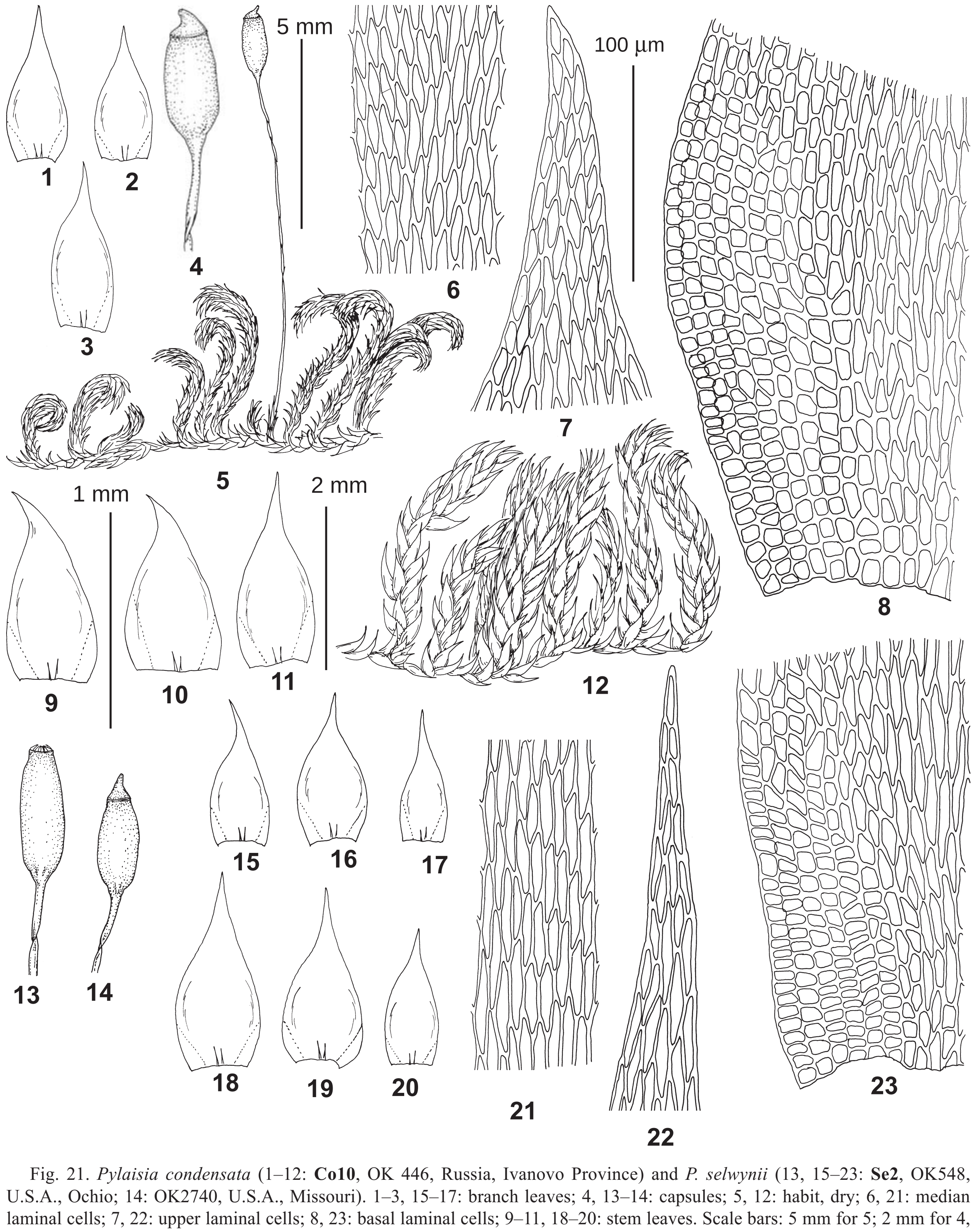

Fig. 21. *Pylaisia condensata* (1–12: **Co10**, OK 446, Russia, Ivanovo Province) and *P. selwynii* (13, 15–23: **Se2**, OK548, U.S.A., Ochio; 14: OK2740, U.S.A., Missouri). 1–3, 15–17: branch leaves; 4, 13–14: capsules; 5, 12: habit, dry; 6, 21: median laminal cells; 7, 22: upper laminal cells; 8, 23: basal laminal cells; 9–11, 18–20: stem leaves. Scale bars: 5 mm for 5; 2 mm for 4, 12–14; 1 mm for 1–3, 9–11, 15–20; 100 µm for 6–8, 21–23.

occur, variation of *P. condensata* is greater and its delimitation is problematic. Most difficult is its separation from *P. brotheri*. These difficulties were discussed by Noguchi (1994), who mentioned among the distinctive characters of *P. brotheri* broader leaves, rather triangular than elongate alar regions, and broader capsules. Some of these character states, however, were found in three specimens that belong to the same clade as *P. condensata*. These specimens are marked in the haplotype network as CoB1, 2, 3 (Fig. 4). They are not grouped to-

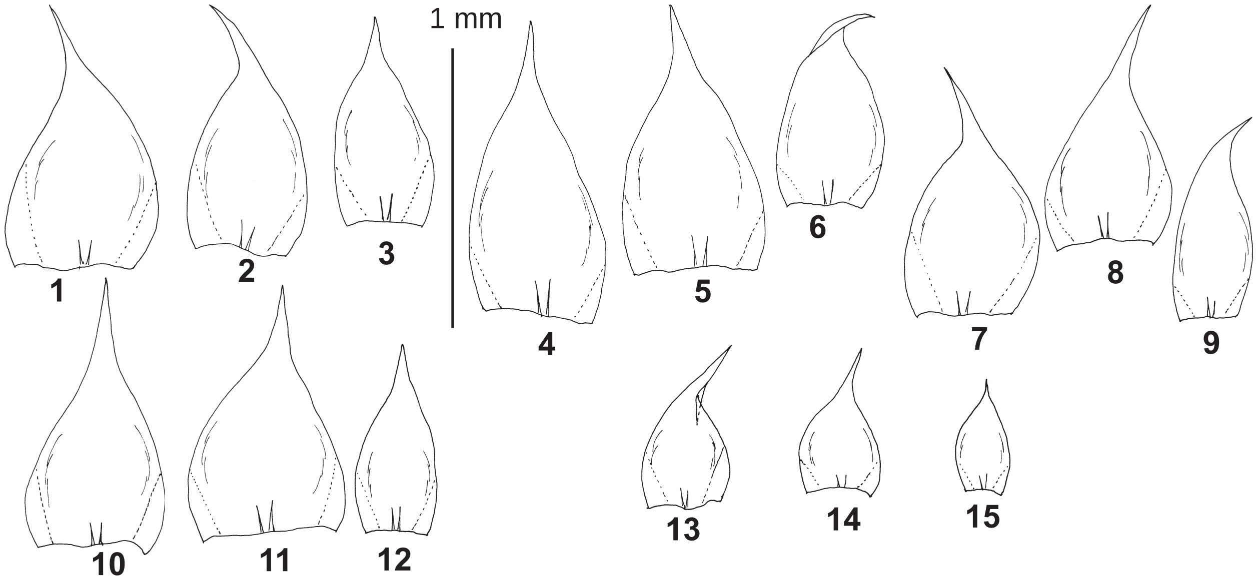

Fig. 22. *Pylaisia condensata* (all specimens from Russia); 1–3: **Co6**, OK2754, Amurskaya Province, Norsky Reserve; 4–6: **Co4**, OK221, Khabarovsk Territory, Bureinsky Reserve; 7–9: **Co1**, OK2744, Sakhalin; 10–12: **Co3**, OK448, Altai Mts; 13–15: **Co5**, OK2752, Primorsky Territory. 1–2, 4–5, 7–8, 10–11, 13–14: stem leaves; 3, 6, 9, 12, 15: branch leaves. Scale bar: 1 mm for all.

gether, thus we consider them as an infraspecific variation of *P. condensata*. Noteworthy, such morphotypes are especially similar in leaf shape to the type of *P. condensata* illustrated by Arikawa (2017).

Despite of certain doubts of Noguchi (1994) that *P. condensata* (referred that time to *P. selwynii)* and *P. brotheri* are good species, Arikawa & Higuchi (2003) found that *rbc*L sequences of these species are distinct enough to maintain their status of distinct species.

Distribution: *Pylaisia condensata* is a widespread Eurasian species known from Japan, China, and India; in Russia it is common in the Far East, northward to Kamchatka, and is sporadically distributed in southern Siberia, while in European Russia it is resticted to northern regions, westward to the border with Finland.

Selected specimens examined: EUROPEAN RUSSIA: **Republic of Karelia**: Kondopoga Distr., 8-10 km W of Kondopoga, 28 Aug.1990 *Smirnova s.n.* (MHA9047582). **Leningrad Province**: Podoporozhsk Distr., Terebsky Brook, 20 Aug. 2008 *Kushnevskaya s.n.* (MHA). **Vologda Province**: Gryazovetsky Distr., 19 Aug. 2001 *Ignatov & Ignatova 38* (MHA 9047555); Nikolsk Distr., Yug River ner Permas Village, 11 Aug. 2001 *Ignatov & Ignatova 28* (MHA9047558); Nyuksenitsy Dustr., Sukhona River opposite Nyuksenitsy Settl, 13 Aug. 2001 *Ignatov & Ignatova 31* (MHA9047559); Sokol Distr., Shorega Creek, 22 Sept. 1990 *Ignatov s.n.* (MHA9047568). **Kostroma Province**: Manturovo Distr., E of Unza River by the Hwy Kostroma-Verchnespasskoye, 18 Sept. 1990 *Ignatov s.n.* (MHA9047567); Sudislavl Distr., 30 km N of Sudislavl, 19 Sept. 1990 *Ignatov s.n.* (MHA9047570). **Komi Republic**: Syktyvkar, 1977 *Zheleznova s.n.* (MHA9047576). **Perm Territory**: Gornozavodsk Distr., Basegi Reserve, Vilva Rive near Koroostelevka Creek mouth, 08 Jun. 1994 *Ignatov & Bezgodov 215* (MHA9047577); Kosinsky Distr., Gorki Village, 04 Aug. 2012 *Bezgodov 252* (MHA9047580); Yurlinsky Distr., 30 km W of Yurla, 2 Aug. 2012 *Bezgodov 213* (MHA9047581). **Sverdlovsk Province**: Alapaevsk, 31 Aug. 1928 *Igoshina 38/2* (MHA9047634). **Bashkortostan Republic**: Beloretzk Distr., Maly Iremel Mt., 31 Aug. 1990 *Ignatova 2/1* (MHA9047579); Zilmerdak Range, Zuyakovo Settl., 1 May 1990 *Muldashev 64* (MHA9047578). **Ivanovo Province**: Provolzhsky Distr., Volga – Uvod' channel, 21 Apr. 2014 *Sorokin & Golubeva 1336* (MHA9047563). **Marij-El Republic**: Orshansk Distr., Hwy from Yoshkar-Ola to Yaransk, near the border of Kirovsk, 16 Sept. 1990 *Ignatov s.n.* (MHA9047566). **Nizhny Novgorod Province**: Bor Distr., Kerzhensky Reserve, 12 Sept. 1999 *Ignatov s.n.* (MHA9047554). **Tver Province**: Nelidovo Distr., Central Forest State Reserve, Stulovo, 5 Aug. 1994 *Ignatov s.n.* (MHA9047574). **Yaroslavl Provonce**: Danilov Distr., 2 km W of Danilov Town, 21 Sept. 1990 *Ignatov s.n.* (MHA9047565).

ASIAN RUSSIA: **Khanty-Mansi Autonomous District**: Surgut Distr., Yugansky State Reserve, 20 Jul. 1987 *Onipchenko s.n.* (MHA9047636). **Tyumen Province**: Uvatsky Distr., Moil River, 14 Sept. 2013 *Bezgodov 203* (MW). **Novosibirsk Province**: Salairsky Mts., Korotovo Settl., 26 Jun. 1993 *Pisarenko op00912* (MHA9047591). **Altai Republic**: Teletzkoe Lake, Yailyu, 06 Aug. 1988 *Zolotukhin s.n.* (MHA9047626); Ulagan Distr., 6 km upstream from Chulyshman River mouth, 17 Aug. 2012 *Ignatov & Ignatova 12-528* (MHA9047623); Chemal Distr., Chemal River, 12 Jul. 1993 *Ignatov 34/135* (MHA); **Amurskaya Province**: Zeysy Reserve, Teplyj Klyuch, 22 Sept. 1979 *Petelin 289* (MHA9047637). **Krasnoyarsk Territory**: Evenkia, Baikit Distr., Central-Siberian Reserve, 19 Jul. 1992 *Szerbina 141* (MW); Taimyr Distr., Khatanga settl. outskitrs, vicinity of Ko-

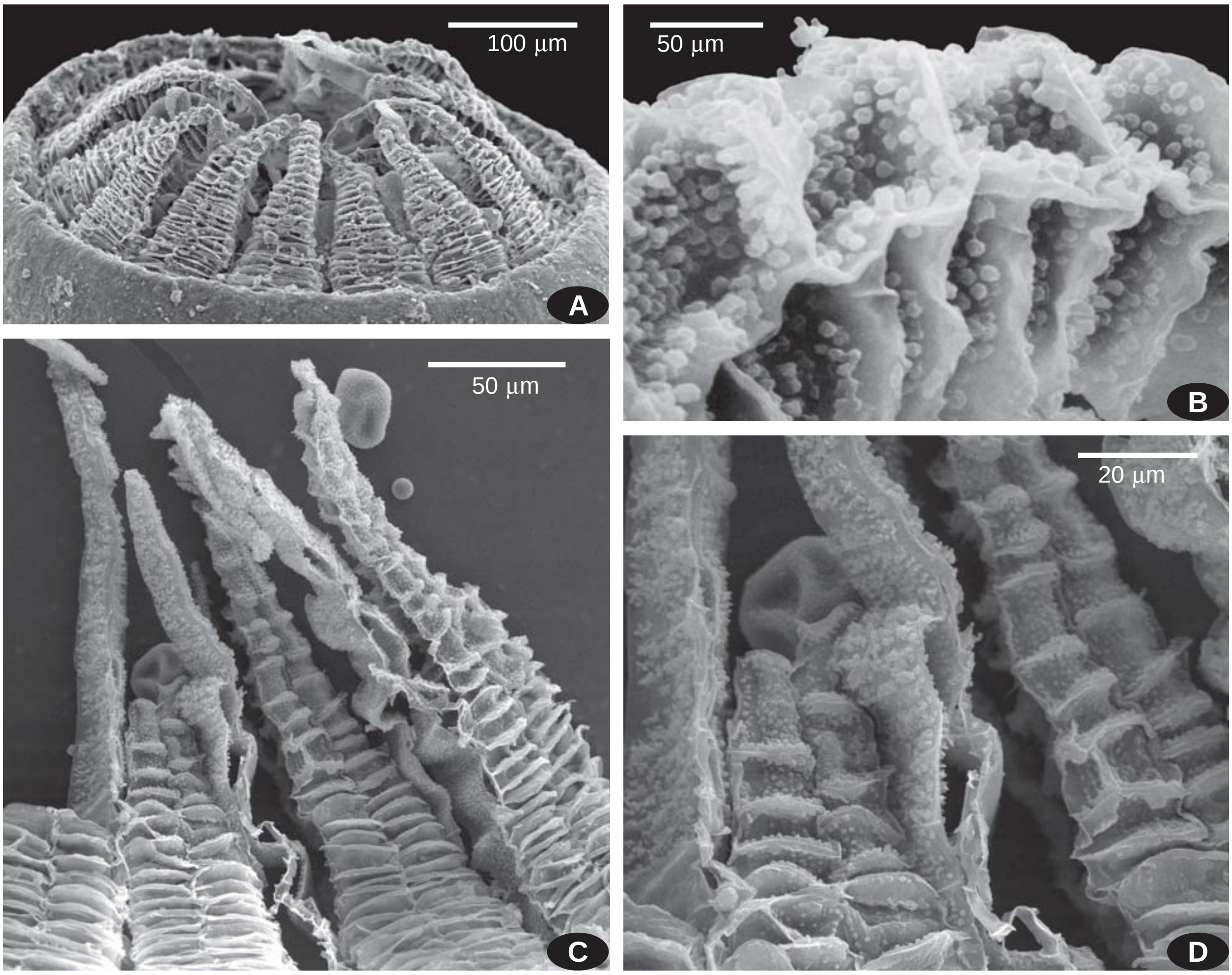

Fig. 23. *Pylaisia condensata,* SEM images of peristomes, from European Russia, A–B from Kostroma; C–D from **Co10**, OK 446, Russia, Ivanovo Province.

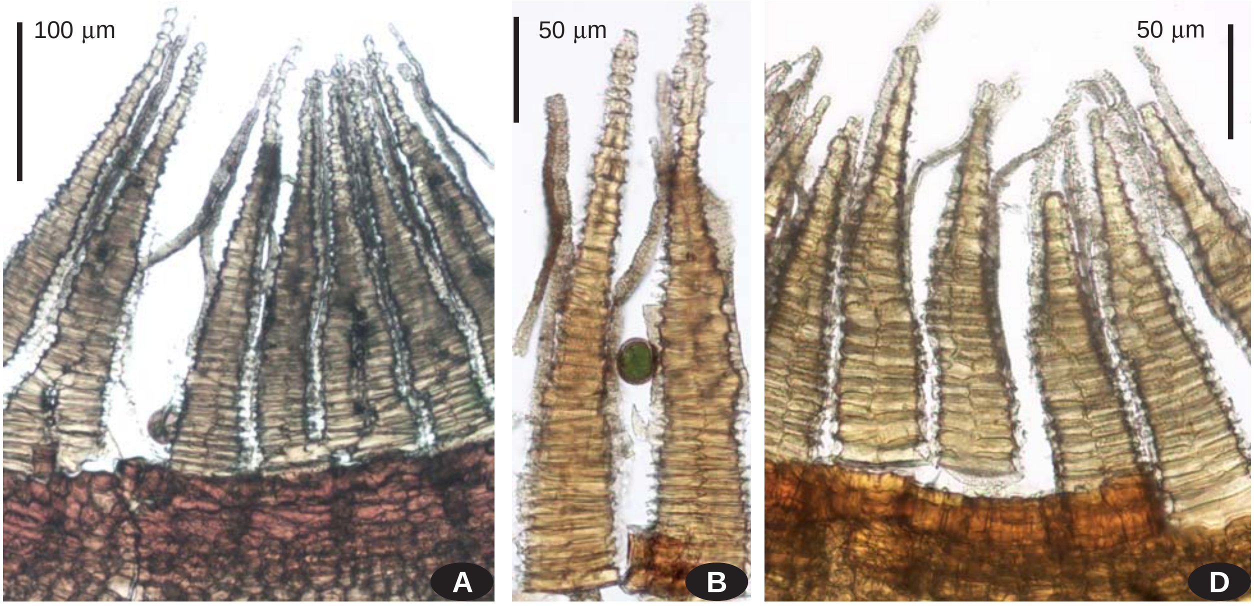

Fig. 24. Peristomes of *Pylaisia* under light microscope, showing endostome split along the keel nearly to the top of segments and its extensive adherence to exostome teeth. A–B: *Pylaisia condensata*, **Co10**, European Russia, Ivanovo; and C: *P. selwynii* (USA, Missouri, Allen 13400, Mosses of the Interior Highlands Exsiccatae #325; LE).

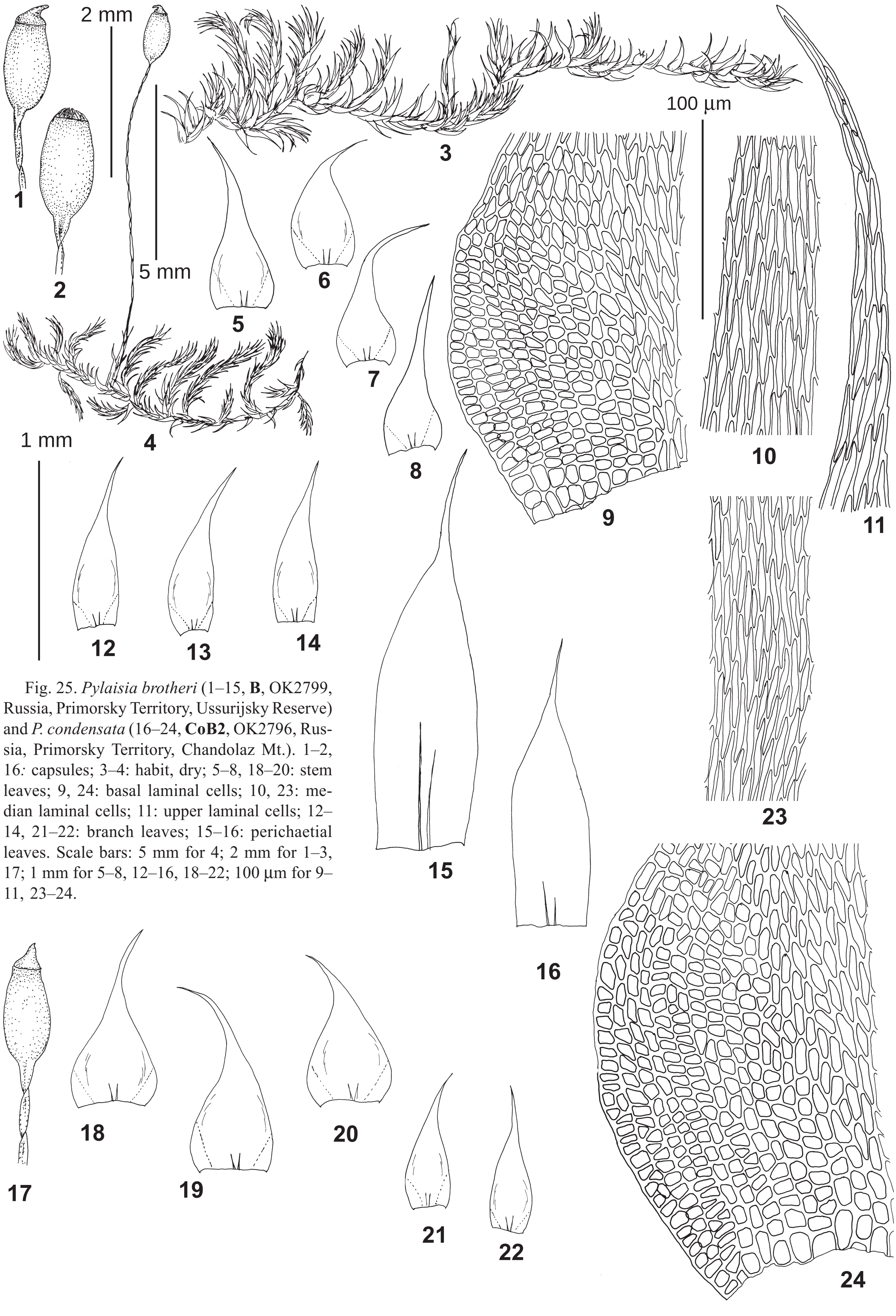

Fig. 25. *Pylaisia brotheri* (1–15, **B**, OK2799, Russia, Primorsky Territory, Ussurijsky Reserve) and *P. condensata* (16–24, **CoB2**, OK2796, Russia, Primorsky Territory, Chandolaz Mt.). 1–2, 16*:* capsules; 3–4: habit, dry; 5–8, 18–20: stem leaves; 9, 24: basal laminal cells; 10, 23: median laminal cells; 11: upper laminal cells; 12–14, 21–22: branch leaves; 15–16: perichaetial leaves. Scale bars: 5 mm for 4; 2 mm for 1–3, 17; 1 mm for 5–8, 12–16, 18–22; 100 µm for 9–11, 23–24.

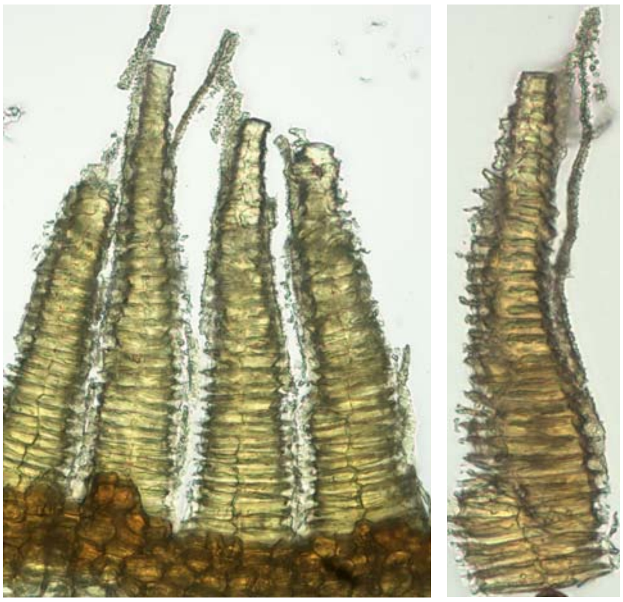

Fig. 26. *Pylaisia brotheri* (**B**, OK2799, Russia, Primorsky Territory, Ussurijsky Reserve), perisome under light microscope, showing endostome split along the keel nearly to the top of segments and its extensive adherence to exostome teeth. Scale bars: 100 µm for A; 50 µm for B–C.

tuykan River mouth, 9 Aug. 2011 *Fedosov 11-390* (MW). **Republic of Sakha/Yakutia**: Khangalassky Distr., National Park "Lena Pillars", 05 Aug. 2016 *Ignatov & Ignatova 16-434* (MHA9021361); Tomponsky Distr., Sette-Daban, Okraina Ridge, between Ulakh and Nadezhda Creeks, 17 Jul. 2016 *Ignatov & Ignatova 16-957* (MHA9022653). **Irkutsk Province**: East Sayan Mts, Udinsky Range, Kara-Buren' River, 13.VIII.1961 *Bardunov s.n.* (MHA9047632); Slyudyanka Distr., Slyudyanka Creek, 08 Jun. 2005 *Ignatov & Kazanovskii s.n.* (MHA 9047604). **Zabaikalsky Territory**: ca. 40 km W of Chita Town, 4 Aug. 1988 *Bochkin et al. s.n.* (MHA9047633). **Amurskaya Province**: Zeisky Reserve, Tukuringra Range, 21 Sept. 2012 *Dudov Br_12_059* (MW9061951). **Khabarovsk Territory**: Sarapulskoe Settl., 22 Aug.1988 *Bochkin et al. s.n.* (MHA 9047644); Verkhnebureinsky Distr., upper course of Bureya River, 04 Aug. 1997 *Ignatov 97-195* (MHA9047607); Bureinsky Reserve, Levaya Bureya River 2 rm upstream Chapkhoz Creek mouth, 16 Aug. 1989 Grigor'eva 89-M-90 (MHA9047642); Sovgavan Distr., Botchi Reserve, Mulpa River, *Ignatov & Ignatova 13-239* (MHA9047583); Badzhal Mts., Yarap River valley, 14 Aug. 2016 *Fedosov 16-48* (MW9130180). **Primorsky Territory**: Lazovsky Reserve, Perekatnaya River, 21 Sept. 1977 *Bardunov s.n.* (ex IRK, MHA); Vladivostok Area, Okeanskaya Station, 20 Aug. 1952 *Voroshilov 6748* (MHA9047638); Dalnegorsk Distr., 5 km N of Sedaya Mt., *Ignatov & Ignatova 13-1496* (MHA9047617); Lazo Distr., Elomovsky Klyuch Creek, *Ignatov et al. Pr-5-13-13* (MHA9047594); Vadivostok, Bolshaya Sefdanka Creek, *Ignatov et al. 06-2453* (MHA); Olga Distr., waterfall on Milogradovka Creek, 21 Aug. 2007 *Ignatov 07-434* (MHA9047600); Partizansk Distr., Olkhovaya Mt., 4 Oct. 2006 *Ignatov et al.* 06-2551 (MHA); Partizansk Distr., Chandolaz Mt., *Ignatov et al. 06-2718* (MHA9047596); Ussurijsky Reserve, Komarovka Creek, *Ignatov & Ignatova 06-3426* (MHA). Chuguevka Distr., Izvilinka Creek ca. 5 km downstream Bereznyaki village, 15 Aug. 2007 *Ignatov 07-502* (MHA9047602). **Sakhalinskaya Province**: Kuril Islands, Shikotan Island, *Nyushko N-1-06a* (MHA9047590); Sakhalin, Tymovsky Distr., Tym' River, *Ignatov & Teleganova 06-424* (MHA9047589). **Kamchatsky Territory**: Kamchatka, Pravy Kikhchik River basin, 22 Jul. 2004 *Czernyadjeva 12* (MHA9047603).

8. **Pylaisia brotheri** Besch., Ann. Sci. Nat. Bot. ser. 7, 17: 369. 1893.

Figs. 25: 1–15; 26.

Note on taxonomy. Previous authors considered this species only moderately rare in the southern part of the Russian Far East (Bardunov & Cherdantseva, 1982), relying probably on the leaf shape and broader group of alar cells. As already discussed above, molecular phylogenetic analysis does not support a separate status of such morphotypes. Instead, a separate position was found for only one sample, which in addition to the mentioned leaf characters has also long perichaetial leaves clasping the seta base, a character used as one of diagnostic by Arikawa (2004). Therefore our circumscription of this species is based on this morphotype, which seems to be very rare among available collections (some collections previously referred to *P. brotheri* are transferred to *P. condensata*). The opinion of Bardunov & Cherdantseva (1982) is likely biased by their extensive field observations in the southernmost part of the Russian Far East, Khasan District, near the border with North Korea, there *P. brotheri* seems to be more common in rather open and more dry forest dominated by *Quercus dentata*.

Arikawa mentioned the spore size of *P. brotheri* being 20–30 µm as a distinctive character from *P. condensata* (as *P. selwynii*) where they are 16–25 µm. However, Noguchi (1994) reported for *P. condensata* (as *P. selwynii*) also rather large spores, 20–30 µm, which agree with Russian specimens of *P. condensata.*

The type material of *P. brotheri* in BM has in general more broad, subglobose capsules, although in the sequenced collection of *P. brotheri* from Russia capsules are not so broad (Fig. 25). Some capsules in the type are also similar in shape to those from Russian collection.

Description. Plants small to medium-sized. Stems and branches straight to curved, loosely to densely foliate; leaves homomallous, turned outwards substrate. Stem leaves from ovate-triangular base gradually tapered to narrowly lanceolate acumina, 0.8–1.2×0.3–0.5 mm; margins subentire; median laminal cells 40–55×4–5 µm, alar cells subquadrate and transversely rectangular, in a rather large, more or less triangular group, 20–25 cells long and ca. 10 cells wide. Branch leaves markedly smaller, lanceolate. Inner perichaetial leaves erect, to 2.1 mm long. Capsules ovoid or broadly so. Peristome in dry state forms a low conus due to adherence of its elements. Exostome teeth to 200 µm long, dorsal plates smooth below, papillose above; endostome adherent to exostome teeth to about teeth halves; segments narrow, split except their uppermost part; endostome moderately papillose. Spores 20–30 µm.

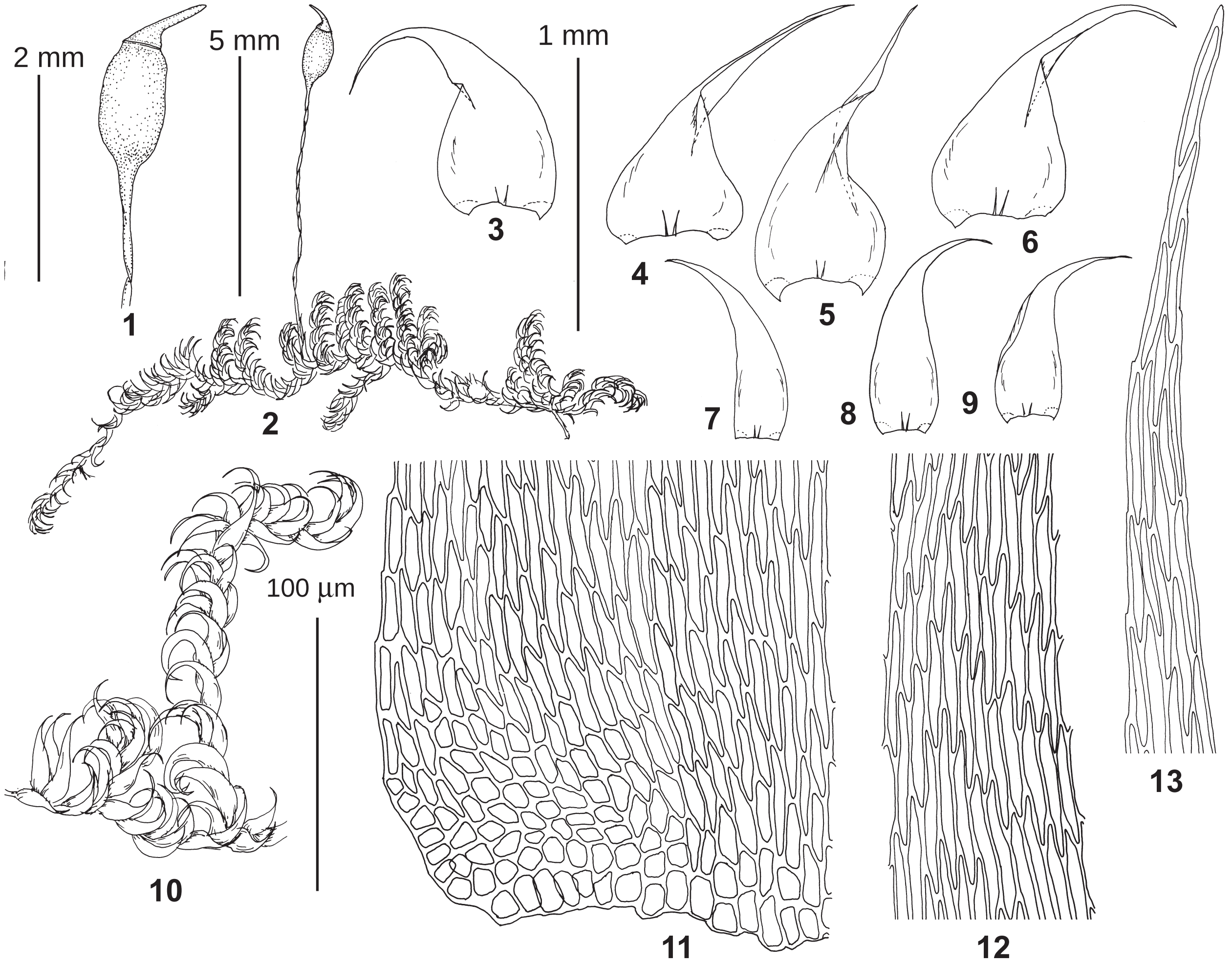

Fig. 27. *Pylaisia subcircinata* (**Sc**, OK 830, Russia, Sakhalin). 1: capsule; 2, 10: habit, dry; 3–6: stem leaves; 7–9: branch leaves; 11: basal laminal cells; 12: median laminal cells; 13: upper laminal cells. Scale bars: 5 mm for 2; 2 mm for 1, 10; 1 mm for 3–9; 100 µm for 11–13.

Distribution. *Pylaisia brotheri* occurs in Japan and SE China (Arikawa, 2004); in the Russian Far East it is apparently a rare species in Primorsky Territory.

Specimens examined: RUSSIA: **Primorsky Territory**, Vityaz Bay, 13 Oct 1978, L.V. Bardunov (ex IRK, MHA9047211).

9. **Pylaisia subcircinata** Cardot, Bull. Soc. Bot. Genève 3: 287. 1911.

Figs. 27, 28, 34J.

Description. Plants small to medium-sized. Stems and branches straight to curved, loosely to densely foliate; leaves homomallous, turned outwards substrate. Stem leaves falcate, 0.8–1.2×0.3–0.5 mm, from ovate-triangular base gradually tapered to narrowly lanceolate acumina; margins subentire; median laminal cells 45–80×4–6 µm, alar cells subquadrate and transversaly rectangular, in a small group, 7–10 cells long and ca. 10 cells wide. Branch leaves smaller, lanceolate. Capsules ovoid-cylindrical. Operculum long-rostrate. Peristome in dry state forms low conus due to adherence of its elements. Exostome teeth to 200 µm long, dorsal plates smooth below, slighlty papillose above; endostome adherent to exostome teeth almost thoughout its length, except the upper part; segments rather broad, shortly exserted above teeth ends; endostome slightly papillose. Spores 25–32 µm.

Differentiation. This species has leaves that are similar to *P. brotheri* in ovate-triangular basal part shape and gradual tapering to acumen. However, leaves of *P. brotheri* are only slightly curved, whereas in *P. subcircinata* they are falcate to almost circinate. The most distinctive feature of *P. subcircinata* is a small alar group, often broader than long that differentiate this species from *P. brotheri* and *P. condensata*, but makes it more similar to *P. obtusa*, a species that appeared most closely related to *P. subcircinata* basing on our molecular phylogenetic reconstruction. This similarity led to a number of misidentifications in herbaria, as *P. obtusa* is often superficially rather similar and has homomallous to falcate leaves when they are attached to stem. However, in microscope slides leaves of *P. obtusa* are straight, with ovate basal part, while leaves of *P. circinata* are strongly curved and have triangular basal part. The easiest way to distinguish *P. circinata* from *P. obtusa* is checking the opecu-

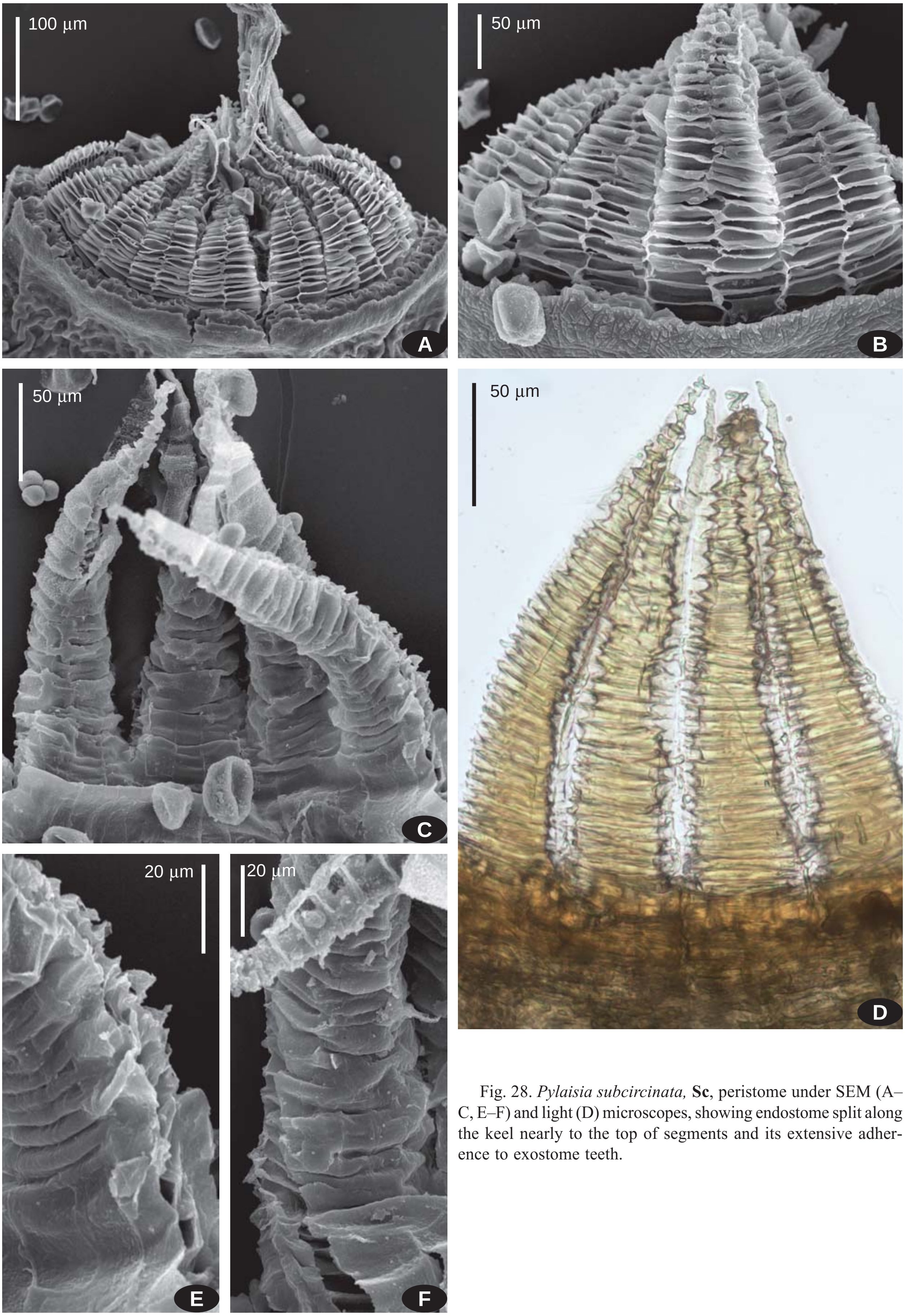

Fig. 28. *Pylaisia subcircinata,* **Sc**, peristome under SEM (A–C, E–F) and light (D) microscopes, showing endostome split along the keel nearly to the top of segments and its extensive adherence to exostome teeth.

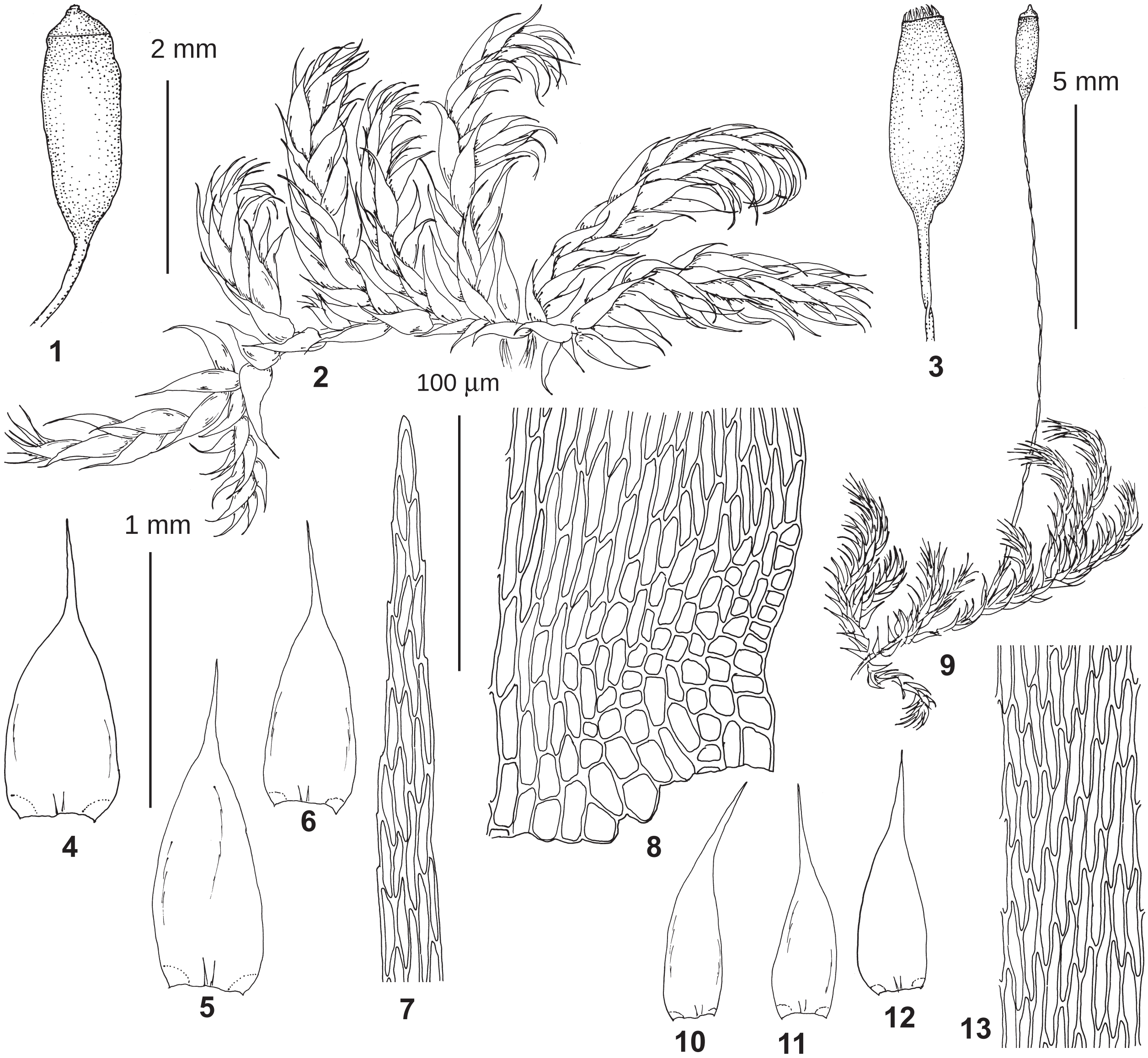

Fig. 29. *Pylaisia obtusa* (**O1**, OK211, Russia, Sakhalin). 1, 3: capsules; 2, 9: habit, dry; 4–6: stem leaves; 7: upper laminal cells; 8: basal laminal cells; 10–12: branch leaves; 13: median laminal cells. Scale bars: 5 mm for 9; 2 mm for 1–3; 1 mm for 4–6, 10–12; 100 µm for 7–8, 13.

lum shape: long rostate vs. short and blunt, but as the capsules appear in late autumn, this character cannot be observed in some specimens.

Distribution. *Pylaisia subcircinata* is common in Japan and know from Korea (Arikawa, 2004). It is apparently a rare species in Russia: Bardunov & Cherdantseva (1982) cited it only from one locality in Primorsky Territory; Cherdantseva (1976) listed it for Sakhalin based only on the record of Sakurai (1935), and Bardunov & Cherdantseva (1984) reported it from few localities in Kuril Islands (Kunashir and Shikotan). Chernyadjeva (2012) reported this species as sporadic in Kamchatka; however, it was likely based on misidentification of *P. obtusa*.

Specimens examined: RUSSIA: **Primorsky Territory**, Lazovsky Reserve, Perekatnaya Creek, 21 Sept. 1974, *Bardunov s.n.* (ex IRK, MHA9130434); **Sakhalinskaya Province**: Kuril Islands, Shikotan Island, area of Malokurilsk Village, *Bakalin K-37-48-07* (ex VLA, MW9061987); Sakhalin, Dolinsky Distr., mouth of Bakhura River, 19 Jul. 2001, *Cherdantseva s.n.* (ex VLA, MHA).

10. **Pylaisia obtusa** Lindb., Contr. Fl. Cryptog. Asiae 257. 1872.

Figs. 29–31, 34L.

Description. Plants small to medium-sized. Stem and branches curved, rather densely foliate; leaves homomallous, turned outwards substrate. Stem leaves 1.1–1.5 ×0.4–0.5 mm, ovate to ovate-lanceolate, gradually or moderately abruptly narrowed into narrow acumen, gradually and slightly rounded to insertion; margins subentire; median laminal cells 40–60×4–6 µm, alar cells subquadrate, form compact subquadrate to triangular or oc-

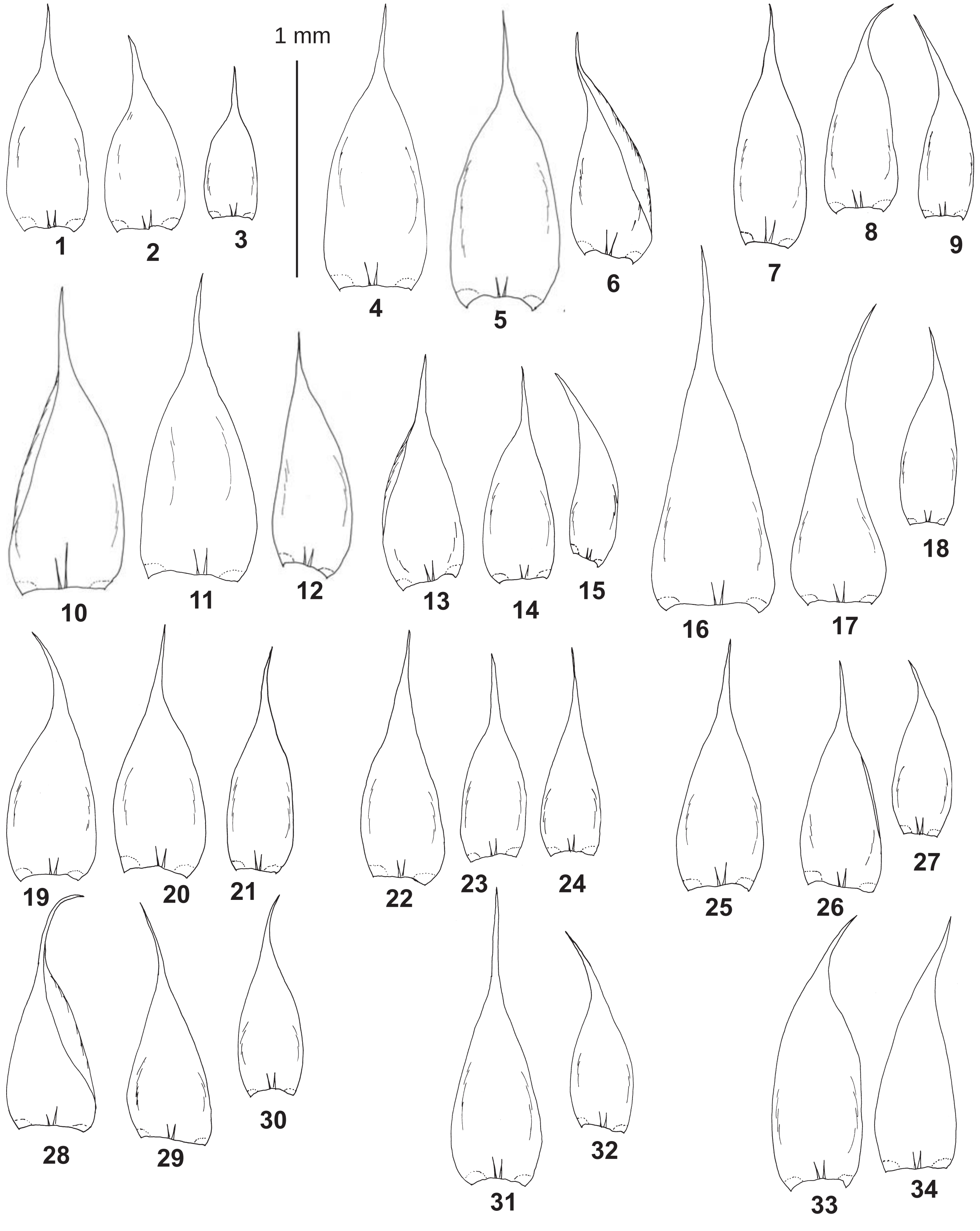

Fig. 30. *Pylaisia obtusa* (all specimens from Russia). 1–3: **O12**, OK813, Sakhalin; 4–6: **O2**, OK225, Sakhalin; 7–9: **O8**, OK441, Sakhalin; 10–12: **O6**, OK433, Sakhalin; 13–15: **O10**, OK810, Sakhalin; 16–18: **013**, OK811, Sakhalin; 19–21: **O7**, OK434, Sakhalin; 22–24: **O4**, OK226, Dakhalin; 25–27, **O11**, OK812, Sakhalin; 28–29: **O9**, OK443, Kuril Islands, Shikotan; 31–32: **O5**, OK2795, Kuril Islands, Kunashir; 33–34: **O3**, OK2748, Sakhalin. 1–2, 4–5, 7–8, 10–11, 13–14, 16–17,19–20, 22–23, 25, 26, 28–29, 31, 33: stem leaves; 3, 6, 9, 12, 15, 18, 21, 24, 27, 30, 32, 34: branch leaves. Scale bar: 1 mm for all.

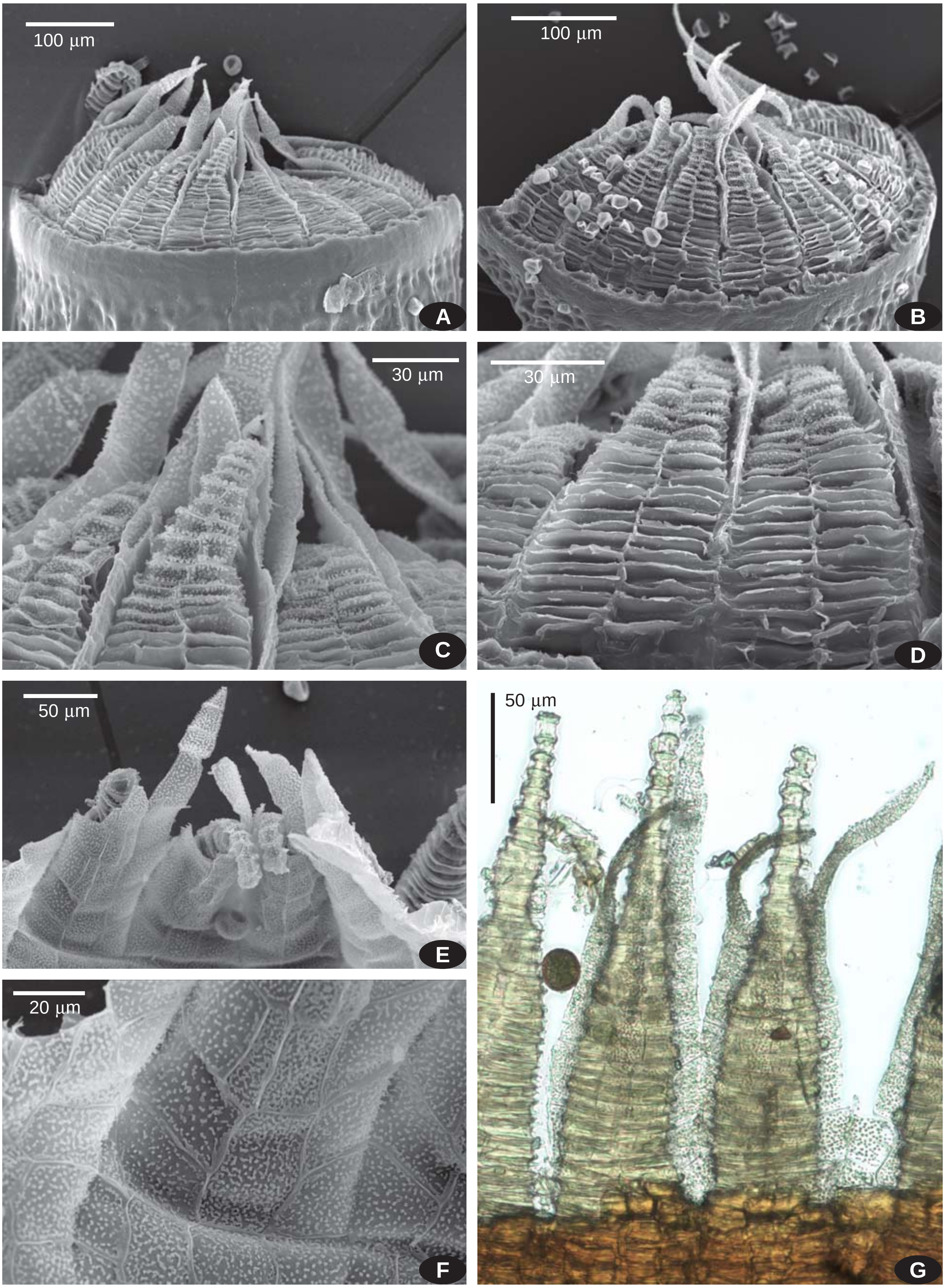

Fig. 31. Peristome of *Pylaisia obtusa* under SEM (A–F) and light (G) microscopes, showing endostome segments split into two branches distally and rather moderate adherence to exostome teeth. A–F: from Sakhalin, Pisarenko, 20.VIII.2012, op I448 (MHA), G from **O4,** Sakhalin, Ignatov & Teleganova 06-268 (MHA).

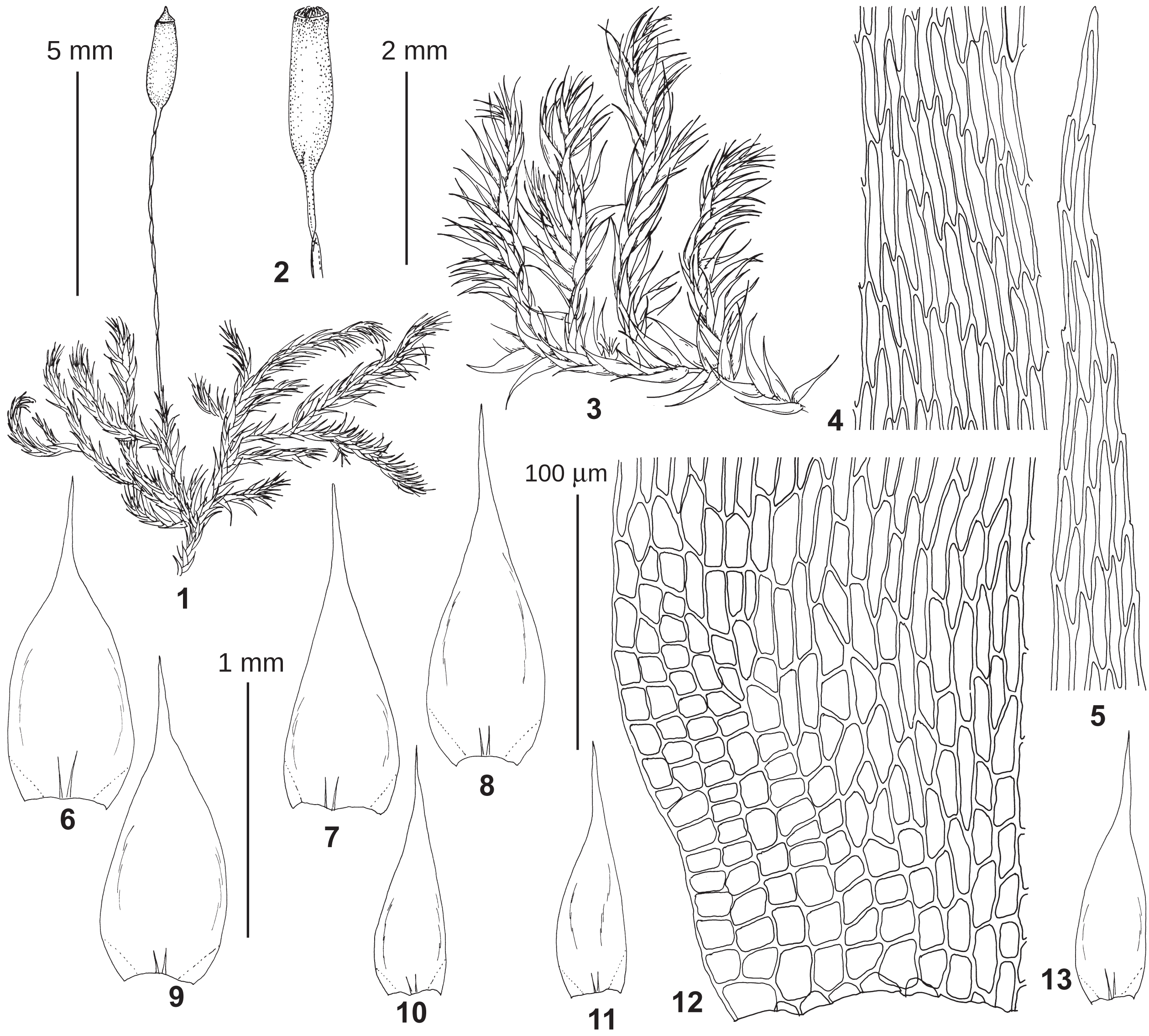

Fig. 32. *Pylaisia stereodontoides* (**Str3**, OK 2747, Russia, Primorsky Territory). 1, 3: habit, dry; 2: capsule; 4: median laminal cells; 5: upper laminal cells; 6–8: stem leaves; 10–11, 13: branch leaves; 12: basal laminal cells. Scale bars: 5 mm for 1; 2 mm for 2–3; 1 mm for 6–11, 13; 100 µm for 4–5, 12.

casionally transversely elongate alar group, 7–10 cells long and 12 cell wide. Branch leaves smaller, narrowly ovate-lanceolate. Inner perichaetial leaves erect to reflexed, long. Capsules oblong-cylindrical. Operculum conic, with short, obtuse beak. Peristome forming high conus when dry. Exostome teeth 230–260 µm long above the mouth, dorsal plates smooth below, papillose above; endostome up to 300 µm above the mouth, adherent to exostome only at base; segments bifid; endostome moderately papillose. Spores 15–22 µm.

Differentiation: *Pylaisia obtusa* is habitually similar to *P. subcircinata*, and these species were often confused in herbarium collections. Their distinctions are described in comments to the latter species. Combination of markedly differentiated stem and branch leaves, stem leaves with ovate base and narrow acumen, small, subquadrate alar group, obtuse opercula and bifid endostome segments is unique for this species.

Distribution. *Pylaisia obtusa* is the commonest species of the genus in Sakhalin; it is also known from Kuril Islands and Kamchatka. In Japan it occurs only on Hokkaido (Arikawa, 2004). Our molecular data also suggest the presence of this species in Alaska.

Specimens examined: RUSSIA: **Sakhalinskaya Province**: Kuril Islands: Kunashir, Mysovoy Cape, *Ignatov 06-1822* (MHA9029876); Iturup Island, Bogatyr Range, Stokap Volcano, *Bakalin K-23-19-07a* (ex VLA, MW9061988); Sakhalin: near Yuzhno-Sakhalinsk Town, Bolshevik Mt., 18 Aug 2009 *Pisarenko op03713* (MHA9130437); Tymosvky Distr., Kamyshovy Range, Kamyshovy pass, 5 Sept. 2009 *Pisarenko op03716* (MHA9130438); Dolinsky Distr., Sokol, *Ignatov & Teleganova 06-598* (MHA9130439); Anivsky Distr., Bystraya River, 7 Sep 1966 *Ardeeva (Cherdantseva) s.n.* (MHA9130440).

11. **Pylaisia stereodontoides** Broth. & Yasuda ex Ihsiba, Classif. Mosses Japan 92. 1932.

Figs. 32, 33, 34K.

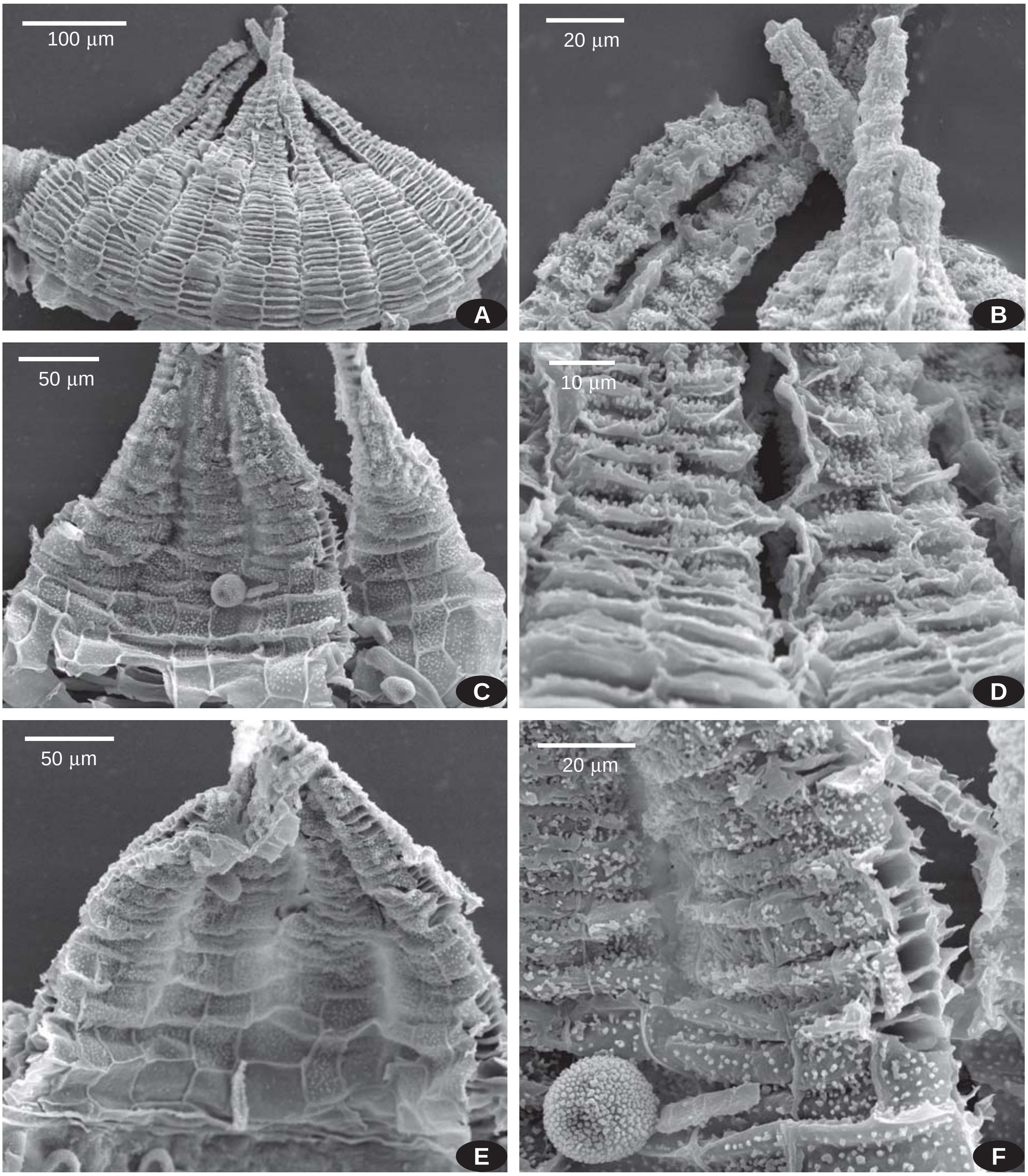

Fig. 33. Perisome of *Pylaisia stereodontoides,* from specimen **Sd4**. A: part of peristome, dorsal view; B, D, F: dorsal surface of exostome teeth in distal (B), middle (D) and proximal (F) parts; C, E: ventral surface of peristome, showing adherent parts of endostome.

Description. Plants small to medium-sized. Stems creeping, branches straight or slightly curved, rather densely foliate; leaves erect-spreading when dry, slightly homomallous. Stem leaves 1.3–1.7×0.4–0.45 mm, ovate-lanceolate, gradually or moderately abruptly narrowed into narrow acumen, gradually rounded to insertion; margins subentire; median laminal cells 30–65×5–6 µm, alar cells subquadrate, form triangular alar group 10–14 cell long and 6–8 cells wide. Branch leaves markedly differentiated, smaller, narrowly ovate-lanceolate. Inner perichaetial leaves erect to reflexed, long. Capsules oblong-cylindrical. Operculum conic, with short, obtuse beak. Capsules ovoid-cylindrical. Operculum long-rostrate. Peristome in dry state forms low conus due to adherence of its elements. Exostome teeth ca. 230 µm long above the mouth, long acuminate, dorsal plates smooth below, slightly papillose above; endostome totally adherent to exostome theeth, fragmentary. Spores 14–25 µm.

Differentiation: *Pylaisia stereodontoides* can be recognized from other species occuring in the Russian Far East by combination of only slightly homomallous leaves with narrow acumina, triangular alar group formed of rather large cells, long cylindrical capsules and low conic peristome due to fragmentary endostome totally adherent to exostome teeth. *Pylaisia subcircinata* and *P. obtusa* have smaller, subquadrate alar group consisting of smaller, often dark-colored cells, and less strongly modified endostomes. Shape of alar group in leaves of *P. stereodontoides* is more similar to *P. polyantha*, but this species is readily recognized from it due to high-conic, free endostome with wide, keeled segments and exostome teeth usually incurved into the urn mouth between endostome segments.

Distribution: Arikawa (2004) reported *P. stereodontoides* only from Japan (Hokkaido and eastern Honshu) and Korea. In Russia it is known from several localities in Primorsky Territory. It was also reported (as *P. intricata*) from Judish Autonomous District (Cherdantseva, 2007) and south of Khabarovsk Territory (Lazarenko, 1941), but we haven't seen specimens.

Specimens examined: RUSSIA: **Primorsky Territory**: Khasansky Distr., Kedrovaya Pad' Reserve, 16 Sept. 1958 *Cherdantseva s.n.* (ex VLA, MHA); Lazovsky Reserve, Petrov Island, 25 Aug. 1986 *Cherdantseva* (s.n. ex VLA, MHA); Ussurijsky Nature reserve, upper course of Artyomovka River, *Ignatov 08-217* (MW9061983); Ussurijsky Nature Reserve, Komarovka Creek, *Ignatov & Ignatova 06-3522* (MW9061984); Lazovsky Distr., Lazovsky Reserve, 1 Jul. 2008 *Dudov s.n.* (MW9061986); Partizansk Distr., Lozovy Range, Chandolaz Mt., *Ignatov et al. 13-1887* (MHA9047654); Chuguevka Distr., ridge S of Pravaya Sokolovka Creek, *Ignatov 07-603* (MHA9130443); Vladivostok area, Bolshaya Sedanka Creek, *Ignatov et al. 06-3361* (MHA9130448); Terney Distr., surroundings of Taiga village, *Galanina & Yakovchenko Pr-430-1-11* (MHA9130449); Okeanskaya Station, Markovsky Peninsula, 6 Sept. 1931 *Popov s.n.* (MHA9047212).

* * *

Despite *Pylaisia* is a not very large genus, a number of misinterpretations of species was rather great, which at least partly may be explained by a difficulty in presenting species characters. Habitually many species are recognizable at once. Thus we provide the species habit comparison in Fig. 34, where all Russain species are shown at the same magnification.

ACKNOWLEDGMENTS

The work on SEM was performed at User Facilities Center of M.V. Lomonosov Moscow State University under financial support of Ministry of Education and Science of Russian Federation. The study of M.S. Ignatov and E.A. Ignatova was conducted in the framework of the MSU research project № AAAA-A16-116021660039-1.

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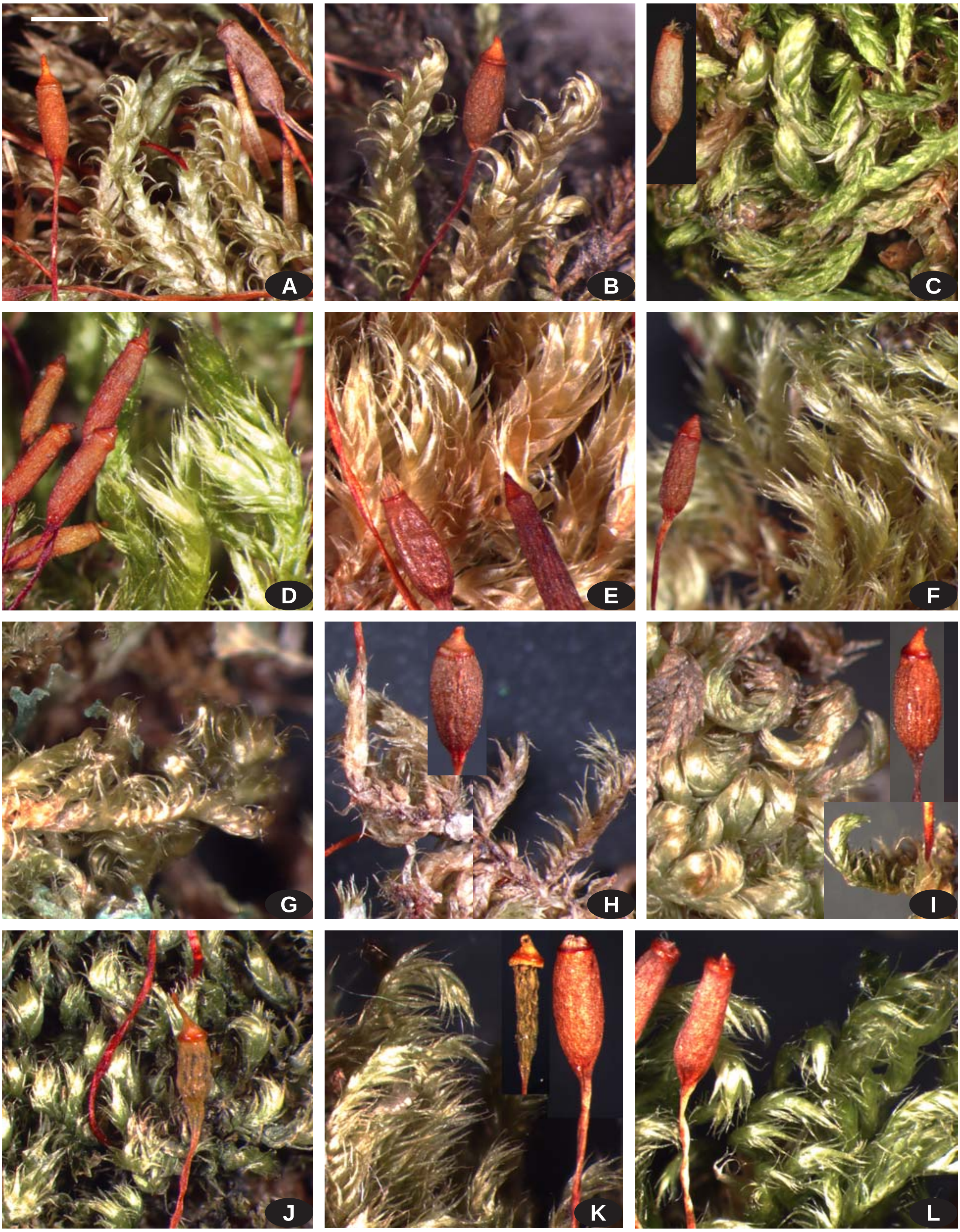

Fig. 34. Habit of the Russian species of the genus *Pylaisia.* A: *P. bezgodovii*, OK212; B: *P. steerei*, OK212; C: *P. curviramea*, Irkutsk, OK2682; D: *P. polyantha*, Moscow, **P10**; E: *P. polyantha,* haplotype'orientalis', Altai, OK2729; F: *P. coreana,* Yakutia, OK2722; G: *P. camurifolia*, Kurils, OK209; H: *P. condensata*, OK446; I: *P. brotheri*, OK2799; J: *P. subcircinata*, OK830; K: *P. stereodontoides*, OK2811; L: *P. obtusa*, OK226. Scale bar: 1 mm for all.

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