

ON THE SYSTEMATIC POSITION OF *LEPTODICTYUM MIZUSHIMAE* (BRYOPHYTA)
О СИСТЕМАТИЧЕСКОМ ПОЛОЖЕНИИ *LEPTODICTYUM MIZUSHIMAE* (BRYOPHYTA)

MICHAEL S. IGNATOV¹, OXANA I. KUZNETZOVA¹ & IRINA V. CZERNYADJEVA²

МИХАИЛ С. ИГНАТОВ¹, ОКСАНА И. КУЗНЕЦОВА¹, ИРИНА В. ЧЕРНЯДЬЕВА²

Abstract

Leptodictyum mizushimae (Sakurai) Kanda (= *Hygrohypnum mizushimae* Sakurai), a rare East Asiatic species, known from Japan, Kuril Islands and Kamchatka, is studied by three molecular markers, including nuclear ITS, chloroplastic *rps4* and mitochondrial *nad5*, and all of them indicate its affinity with Climaciaceae, despite lacking morphological similarity: plants are not dendroid and stem lacks any paraphyllia-like structures. A new genus, *Limnohypnum* is described to accomodate this species. Morphological description and illustrations are provided.

Резюме

Leptodictyum mizushimae (Sakurai) Kanda (= *Hygrohypnum mizushimae* Sakurai), редкий восточноазиатский вид, известный из Японии, с Курильских островов и Камчатки, изучен с помощью молекулярных маркеров, ядерного ITS, хлоропластного *rps4* и митохондриального *nad5*, причем все они выявили родство данного вида с Climaciaceae. При этом, однако, у данного вида отсутствуют морфологические признаки, которые обычно считаются диагностическими для Climaciaceae, а именно древовидные побеги и наличие парафиллий. Вид выделен в особый род *Limnohypnum*. Приводится его описание и иллюстрации.

KEYWORDS: mosses, taxonomy, molecular phylogenetics, *Limnohypnum* gen nov., Climaciaceae, East Asia, morphology

INTRODUCTION

Hygrohypnum mizushimae Sakurai has been described from Honsu in Japan (Sakurai, 1952), and later transferred to the genus *Leptodictyum* by Kanda (1975). This species is so rare, that it is absent in the “Illustrated moss flora of Japan” by Noguchi (1991), who included in the book only species checked by himself, and likely he failed to obtain any specimen for personal study.

Morphologically this species resembles neither *Hygrohypnum* nor *Leptodictyum*. It is a large and quite conspicuous plant looking like a big *Plagiothecium*, although with more extensive branching and a moderately long costa in the leaves. Unlike most *Leptodictyum* species, *L. mizushimae* (Sakurai) Kanda does not commonly occur with sporophytes, and its stem and branch leaves are much more shortly acute, in contrast to long acuminate leaves of *L. riparium* (Hedw.) Warnst. and other species of the genus described from East Asia (Kanda, 1975).

The genus *Hygrohypnum* appeared to be an unnatural assemblage in the recent molecular studies (Olivan et al. 2007; Ignatov et al., 2007), and it has been split into several genera. However, most species of all these genera have a double costa. Three species with the single costa provide exceptions: *Hygrohypnella polaris*, (Lindb.) Ignatov & Ignatova, which differs in well de-

fined hyalodermis, and *Hygrohypnum luridum* (Hedw.) Jenn. and *Platyhypnum smithii* (Sw.) Ochyra, which are relatively small plants, with rather rigid and concave leaves, quite unlike *Leptodictyum mizushimae*. The confusing habit forced us to check the systematic position of the latter species with molecular phylogenetic methods, which in many cases already solved long-standing problems of systematic placements of moss genera. The results of the molecular phylogenetic studies have rectified familial placements of *Anacamptodon* (Vanderpoorten et al., 2002), *Clasmatodon* (Buck et al., 2000), *Struckia* (Pedersen & Hedenäs, 2002), *Sasaokaea* (Ignatov & Milyutina, 2010), *Bissetia*, *Homaliadelphus* and *Miyabea* (Olsson et al., 2009), *Lecuraea* and *Pyralisia* (Gardiner et al., 2005), *Habrodon* (Budyakova et al., 2003), *Acrocladium* (Tangney et al., 2010) and at least a few tens of other moss genera.

MATERIAL AND METHODS

The species has been recently collected in Kuril Islands in Shikotan (Bakalin et al., 2008) and in Kamchatka (Chernyadjeva, 2012). These two specimens were compared with the set of pleurocarpous mosses used for previous molecular phylogenetic analyses. The ITS set included mostly samples used in analyses of Gardiner et al. (2005) and Ignatov

¹ – N.V. Tsitsin Main Botanical Garden, Russian Academy of Sciences, Botanicheskaya 4, Moscow 127276 Russia – Россия 127276 Москва, Ботаническая, 4, Главный ботанический сад РАН. e-mails: misha_ignatov@list.ru & oikuznets@gmail.com.

² – V.L. Komarov Botanical Institute Rus. Acad. Sci., Prof. Popov Str., 2, St. Petersburg, 197376 Russia – Россия 197376, г. Санкт-Петербург, ул. проф. Попова, д. 2, Ботанический институт им. В.Л. Комарова РАН; e-mail: irinamosses@gmail.com

GC values, 2000 replicates, cut=1 (tree 0) - Standard Bootstrap



Fig. 1. MP strict consensus tree based on ITS sequences. Bootstrap support >50 calculated for 2000 iterations in TNT is shown below branches. Clade with *Leptodictyum* (*Limnohypnum*) *mizushimae* and *Climaciaceae* is boxed.

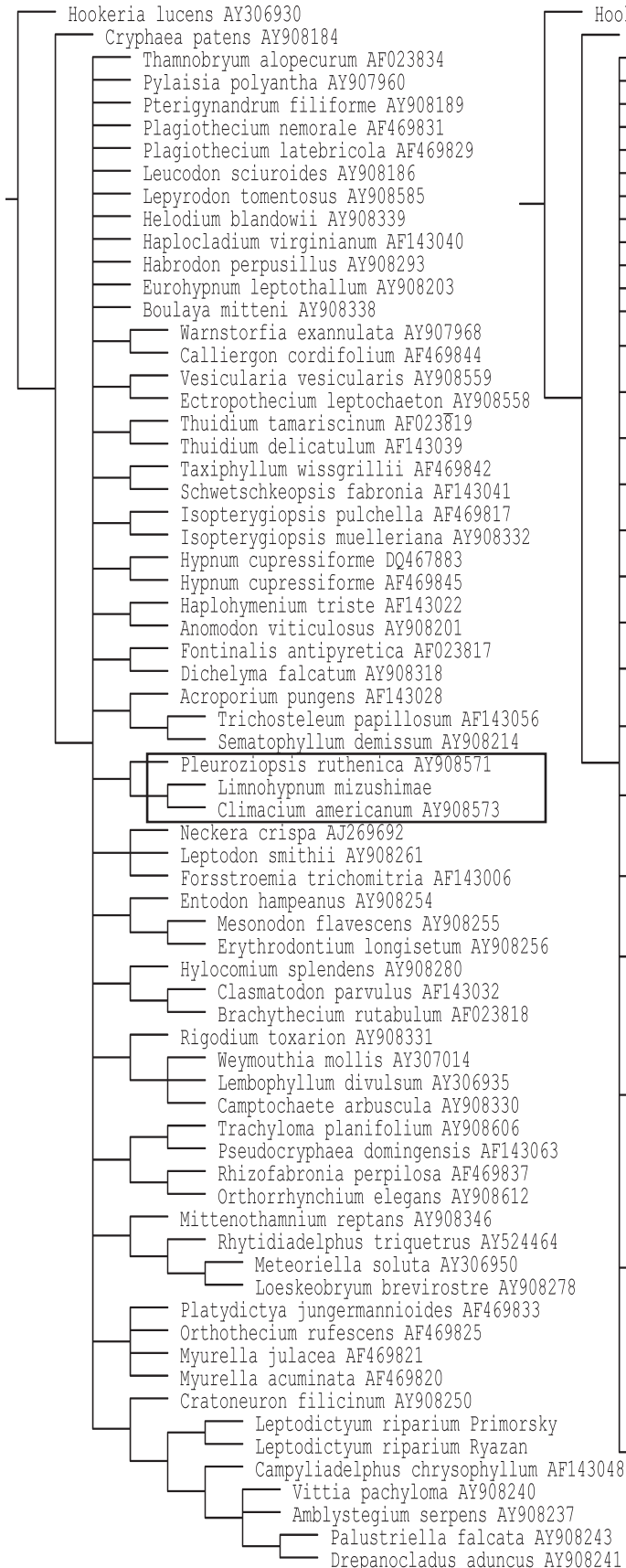


Fig. 3. MP strict consensus tree based on *rps4* chloroplastic sequences. Clade with *Leptodictyum* (*Limnophyllum*) *mizushimae* and Climaciaceae is boxed.

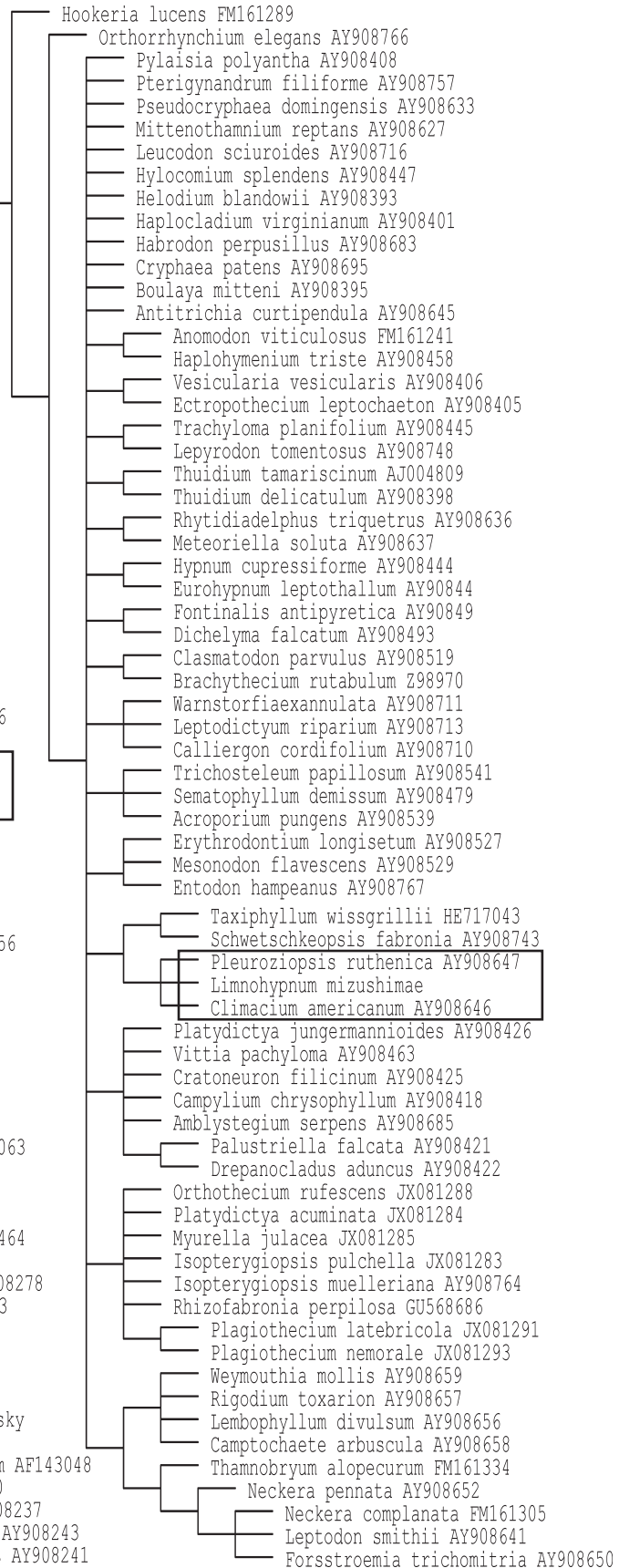


Fig. 2. MP strict consensus tree based on *nad5* mitochondrial sequences. Clade with *Leptodictyum* (*Limnophyllum*) *mizushimae* and Climaciaceae is boxed.

et al. (2007), with some subsequent addition from a limited analysis of *Sasaokaea* by Ignatov & Milyutina (2010).

A preliminary analysis of ITS placed the species in a strongly unexpected position, near *Climacium*, thus additional analyses using the chloroplast *rps4* and mitochondrial *nad5* were conducted, using GenBank data, mostly from the analysis of Huttunen et al. (2012), where a significant block of data was taken from Cox et al. (2010). This dataset made possible an analysis of a broader set of families, which was difficult with ITS as the alignment included too many gaps. New sequence data are given in Appendix 1.

We analysed the ITS, *rps4* and *nad5* datasets separately, as a putative hybrid origin and recombination were suspected because of known cases in pleurocarpous mosses (Ignatov & Milyutina, 2011).

The protocols of PCR and sequencing were standard (e.g., Gardiner et al., 2005), and the TNT program was used (Goloboff et al., 2003). Bootstrap support was calculated based on 2000 iterations.

RESULTS OF MOLECULAR PHYLOGENETIC ANALYSIS

The phylogenetic analysis of ITS sequences resulted in a moderately resolved tree, which is not discussed here in detail as its topology is almost identical to those that has been discussed already several times for analyses where ITS has been used (Gardiner et al., 2005; Ignatov et al., 2007; Huttunen et al., 2012). The bootstrap tree is composed of a basal grade formed by four small clades of the Plagiotheciaceae (*Herzogiella*, *Isopterygiopsis*, *Myurella*, *Orthothecium*, *Plagiothecium*, *Platydictya*), Habrodontaceae (*Habrodont*), Leucodontaceae (*Leucodon*), Pterigynandraceae plus Hypnaceae (*Pterigynandrum*, *Hypnum*, *Eurohypnum*) and then the terminal clade represents a polytomy, where most species are grouped in small clades, formed by species of one genus or one family. Bootstrap support was found for clades of Amblystegiaceae (98) and Calliergonaceae (100) with several genera. Many families represented by 2 genera were also supported, e.g., *Leskea*+*Haplodcladium* of Leskeaceae (73); *Taxiphyllum*+*Glossadelphus* of Taxiphyllaceae (98), *Leptodon*+*Neckera* of Neckeraceae (98). The clade formed by *Leptodictyum mizushimae* (shown in the tree as *Limnohypnum*), *Climacium americanum* and *Pleuroziopsis ruthenica* received bootstrap support 77, i.e., close to the value 83 obtained for the subclade *Pleuroziopsis*+*Climacium*, and 100 was found for two specimens of *Leptodictyum mizushimae* from Kamchatka and Shikotan Island (ca. 1000 km apart). This clade is nested in a bigger clade with the species of Hylocomiaceae (*Loeskeobryum*, *Rhytidiadelphus*, *Neodolichomitria*) and Antitrichiaceae (*Antitrichia*), i.e., having a topology similar to that in previous analyses, although without support.

Two trees built by ITS1 and ITS2 separately (not shown) have low support (calculated in TNT for 1000 iterations). However, in both of them the clade composed of *Pleuroziopsis*+*Climacium*+*Limnohypnum* was found.

The chloroplast *rps4* and mitochondrial *nad5* regions are less variable, and branches in their trees have only very low support (not shown). Figures 2 & 3 present strict consensus trees for them (both built in TNT, with maximal precision and accuracy).

The tree by *rps4* in Fig. 2 displayed a large polytomy, with a number of small clades combining species of the families Anomodontaceae (*Anomodon* and *Haplohy-menium*), Fontinalaceae (*Fontinalis* and *Dichelyma*), tropical Hypnaceae (*Ectropothecium* and *Vesicularia*), Calliergonaceae (*Calliergon* and *Warnstorfia*), Taxiphyllaceae (*Taxiphyllum* and *Schwetschkeopsis*), Sematophyllaceae (*Acroporium*, *Sematophyllum*, *Trichosteleum*), Neckeraceae (*Forsstroemia*, *Leptodon*, *Neckera/Exsertotheca*), Entodontaceae (*Entodon*, *Erythrodontium*, *Mesonodon*), Hylocomiaceae (*Rhytidiadelphus*, *Loeskeobryum*, *Meteoriella*, *Mittenothamnium*), but *Hylocomium splendens* grouped with the two Brachytheciaceae genera *Brachythecium* and *Clasmatodon*, Lembophyllaceae (*Camptochaete*, *Lembophyllum*, *Rigodium*, *Weymouthia*), Plagiotheciaceae (*Myurella*, *Orthothecium*, *Platydictya*), Amblystegiaceae (*Amblystegium*, *Campyliadelphus*, *Cratoneuron*, *Drepanocladus*, *Palustriella*, *Vittia*). One clade combined species that were found in the analysis by Huttunen et al. (2012) as members of basal Hypnaceae families (*Orthorrhynchium*, *Pseudocryphaea*, *Rhizofabronia*, *Trachyloma*). *Leptodictyum mizushimae* was found in the same clade as with ITS, with *Pleuroziopsis* and *Climacium*, but the clade was not grouped with Hylocomiaceae.

The *nad5* tree differs from the *rps4* one in a larger number of species/genera which do not group with any other one. However, species from individual families formed clades, e.g., Amblystegiaceae, Anomodontaceae, Brachytheciaceae, Calliergonaceae, Entodontaceae, Hypnaceae, Neckeraceae, Lembophyllaceae, Plagiotheciaceae + Rhizofabroniaceae, and Sematophyllaceae (Fig. 3). The clade joining *Pleuroziopsis*+*Climacium*+*Limnohypnum* appeared in this analysis as well.

Summing up, all three genome regions independently provide an evidence that *Leptodictyum mizushimae* is not a member of Amblystegiaceae, but closely related to *Climacium* and *Pleuroziopsis*. This 'impossible' placement will be discussed below, but in any case, it is clear that the moss has to be segregated in its own genus.

TAXONOMIC TREATMENT

***Limnohypnum* Ignatov & Czernyadjeva, gen.nov.**

Plants robust. Stem prostrate or floating, irregularly pinnately branched, subcomplanately foliate, with central strand, hyalodermis absent, sclerodermis 2-3-stratose, only slightly differentiated. Proximal branch leaves broadly triangular. Axillary hairs 5(-6)-celled, with 3(-4) elongate upper cells. Rhizoids below leaf insertion, reddish-brownish, smooth. Stem leaves erecto-patent, ovate-lanceolate, gradually tapered to apex or shortly and indistinctly acuminate, decurrent; margin plane, subentire; costa single or rarely with lateral spurs, reaching

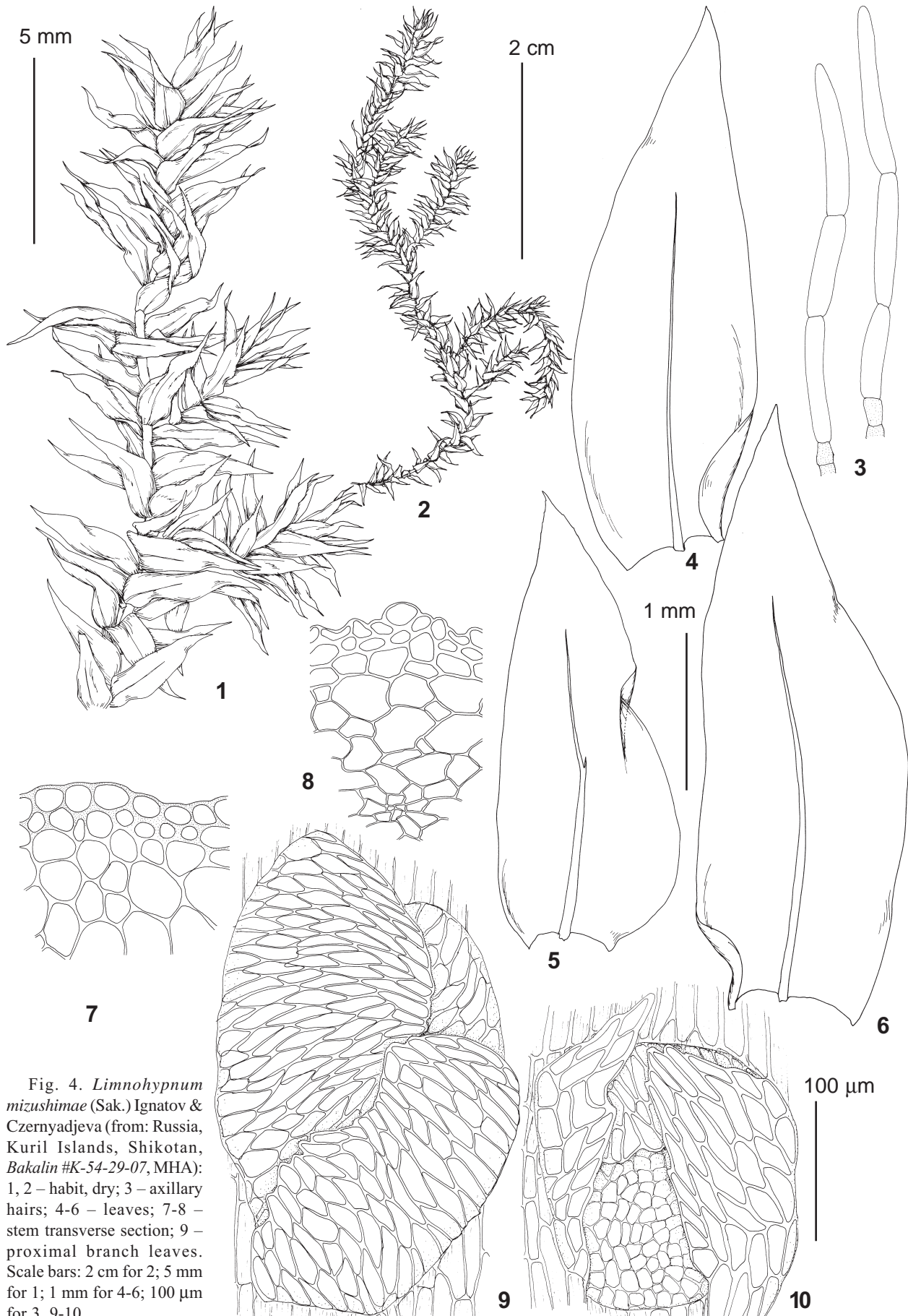


Fig. 4. *Limnohypnum mizushimae* (Sak.) Ignatov & Czernyadjeva (from: Russia, Kuril Islands, Shikotan, Bakalin #K-54-29-07, MHA): 1, 2 – habit, dry; 3 – axillary hairs; 4-6 – leaves; 7-8 – stem transverse section; 9 – proximal branch leaves. Scale bars: 2 cm for 2; 5 mm for 1; 1 mm for 4-6; 100 µm for 3, 9-10.

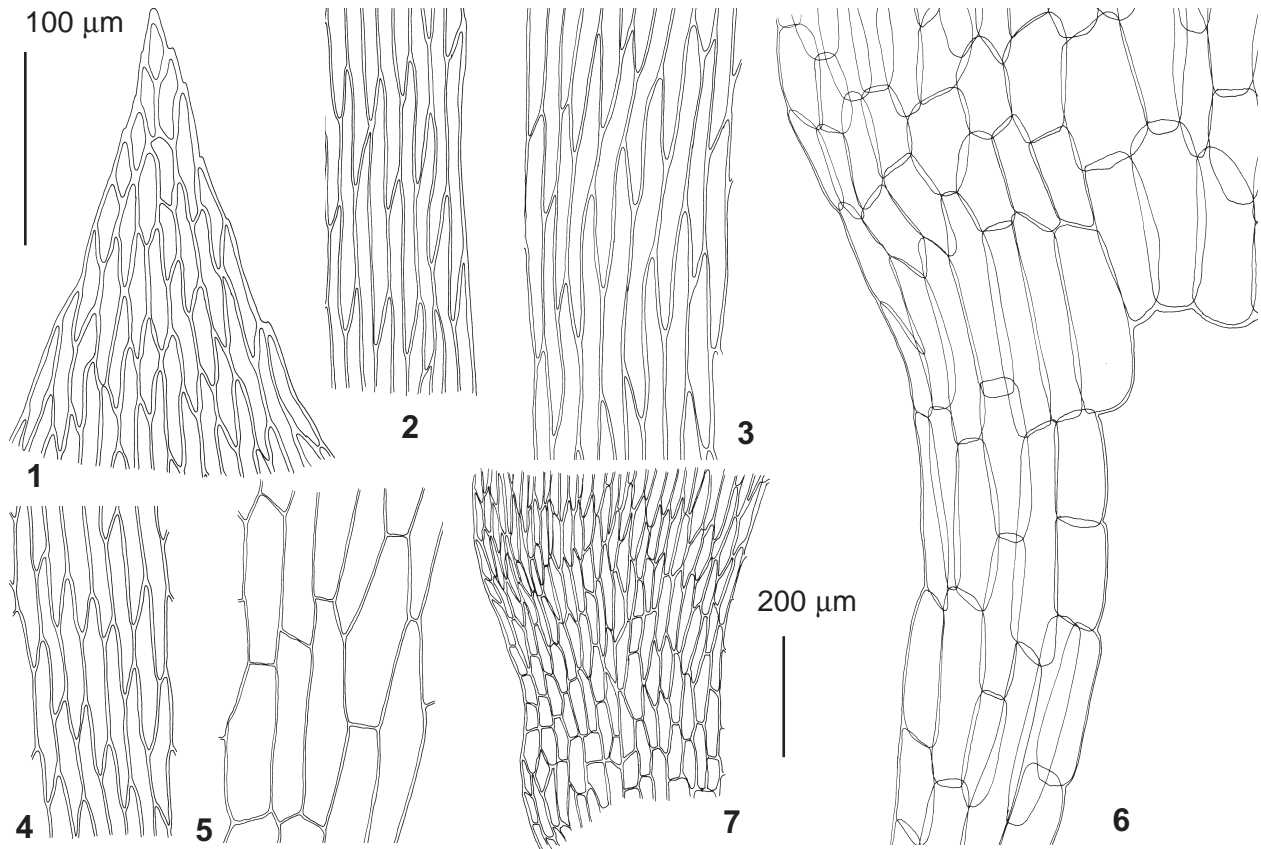


Fig. 5. *Limnophyllum mizushimae* (Sak.) Ignatov & Czernyadjeva (from: Russia, Kuril Islands, Shikotan, *Bakalin* #K-54-29-07, MHA): 1 – upper laminal cells; 2 – marginal cells at mid-leaf; 3-4 – median laminal cells; 5-7 – basal laminal cells. Scale bars: 200 µm for 7; 100 µm for 1-6.

0.6-0.75(-0.9) leaf length, rather thin, 3-4-stratose, ending without tooth; lamina cells elongate, at and below mid-leaf 3-7:1, at 3/4 leaf length narrower, thin-walled; basal cells broader, forming lax areolation across the base, indistinctly enlarged in alars. Gametangia and sporophytes unknown.

Type species of the genus: *Limnophyllum mizushimae* (Sak.) Ignatov & Czernyadjeva.

Ethymology: Limne – lake, often applies for various inland water-bodies; *Hypnum* – genus of pleurocarps, commonly used in sense of an indefinite ‘hypnalean’ moss.

Limnophyllum mizushimae (Sak.) Ignatov & Czernyadjeva, comb. nov.

Basionym: *Hygrohypnum mizushimae* Sak., J. Jap. Bot. 27: 281. f. 6. 1952. Type: Japan, Honshu, Ozegahara, Sakurai 20370 (holotype MAK, isotype in Herb. U. Mizushima, according to Kanda, 1975). Figs. 4-5

Plants in very loose tufts, pale-green, yellowish-green to goldien, slightly glossy. Stem 5-8 cm, remotely irregularly pinnately branched, subcomplanately to complanately foliate, with weak central strand 5-7 cells across, sclerodermis 2-3-stratose, its cells moderately thick-walled; branches 3-10(-40) mm; proximal branch leaves broadly triangular, the first having 4 o'clock position; axillary hairs 5(-6)-celled, to 300 µm long, with two brownish proximal cells and 3 upper cells to 18 µm wide. Stem leaves 2.5-4.0×0.9-1.9 µm, broadest at 1/3–1/4 leaf

length, gradually tapered to apex or shortly and indistinctly acuminate, ovate-lanceolate, slightly to conspicuously asymmetric, decurrent; margin plane, subintire; costa single or, rarely, with lateral spurs, reaching 0.6-0.75(-0.9) leaf length, rather slender, 40-80(-100) µm wide at base, 3-4-stratose, without tooth at its end; laminal cells thin-walled, in distal part linear, 90-130×8-12 µm (8-12:1), in median part elongate, 65-100×8-14 µm (5-9:1), towards margins longer, to 120-180 µm long, in many leaves along the margin in 1-2 rows very long and narrow, 160-240×5-7 µm; cells just below apex shorter, 3-7:1, basal cells broader, rectangular, forming lax areolation across base, indistinctly to distinctly enlarged in alars, cells in decurrencies rectangular to round, inflated. Branch leaves usually smaller than stem leaves. Gametangia and sporophytes unknown.

Variation. Japanese specimens are larger than Russian ones, to 15 cm long, leaves 5-5.5×2-2.5 mm and lamina cells 100-125×15-18 µm. Such a difference is rather common for moss sizes between the northern limit and more southern areas, in this case likely accentuated because the only two Russian collections do not represent optimally developed plants (cf. Kanda, 1975).

Ecology. In Kamchatka, the species has been found in as individual shoots among *Calliergon richardsonii* and *Warnstorfia exannulata*, in a flooded hollow of a sedge mire with thermal springs in Paratun'ka River Valley.

The species composition in this place include: *Carex cryptocarpa* C.A. Mey (projective cover 60%), *Carex vesicata* Meinsh. (10%), *Calamagrostis purpurea* (Trin.) Trin. (10%), *Equisetum fluviatile* L. (5%), *Comarum palustre* L. (1%), *Warnstorfia exannulata* (Bruch et al.) Loeske (3%), *Calliergon richardsonii* (Mitt.) Kindb. (1%), *Sphagnum riparium* Ångstr. (1%), *Sphagnum subsecundum* Nees (1%).

According to Bakalin et al. (2009), in Shikotan the species grew on very wet soil among *Phragmites australis* on low lake bank.

Distribution. The species occurs in Hokkaido and Honshu, and until recently it had been considered as an endemic of Japan (Kanda, 1975). Despite a considerable distance of more than 2000 km between the localities in Kamchatka (52°N) and Honshu (36°N), such a distribution pattern is not unique, and can likely be explained by dispersal with the migratory birds. *Campylopus umbellatus* and *Entodon flavescens* provide additional examples of southern species found in Kamchatka, disjunct from localities in Japan (Ignatov & Samkova, 2006; Czernyadjeva, 2012). Noticeably, both of them occur in Kamchatka near thermal springs, like *Limnophyllum mizushimae*.

Specimens examined: Kuril Islands, Shikotan, Bakalin K-54-29-07 (VLA, MHA); Kamchatka, Termalny, 7.VIII.2001, Czernyadjeva (LE, MHA).

DISCUSSION

All previous authors kept *Limnophyllum mizushimae*, either in *Leptodictyum* or *Hygrohypnum*, in the family Amblystegiaceae (Sakurai, 1934; Kanda, 1975; Iwatsuki, 2004). The gametophyte morphology of *Limnophyllum* does not contradict Amblystegiaceae in its current circumscription, but this family is peculiar mostly in perichaetial and sporophytic characters (plicate perichaetial leaves, long arcuate capsules, long-pored stomata), which are not useful for the present discussion, as sporophytes are unknown in this genus. A certain difference in proximal branch leaves is briefly discussed below. Traditionally, the family Amblystegiaceae has been a “waste-basket” for various hygrophilous groups, thus the species ecology has often been crucial for this familial placement. Mostly or solely for ecological reasons, the Amblystegiaceae included the genera *Platyhypnidium* (now included in *Rhynchostegium*, Brachytheciaceae, cf. Huttunen & Ignatov, 2010), *Donrichardsia* (now in Brachytheciaceae, cf. Huttunen & Ignatov, 2004), *Sasaokaia* (now in Leskeaceae, Ignatov & Milyutina, 2010), genera of the Calliergonaceae, i.e., *Calliergon*, *Loeskypnum*, *Straminergon*, *Warnstorfia* (Vanderpoorten et al., 2002).

ITS sequence data (Fig. 1) placed *Limnophyllum* in a clade with the Climaciaceae, which is nested in a larger clade with the Antitrichiaceae and Hylocomiaceae, families unrelated to the Amblystegiaceae according to previous analyses (Tsubota et al. 2004; Cox et al., 2010; Huttunen et al., 2012). Ignatov et al. (2007) showed that the Amblystegiaceae, on the one hand, and the Climaciaceae,

Antitrichiaceae and Hylocomiaceae, on the other, belong to two major different lineages, found earlier in the cladistic analysis of morphological characters by Hedenäs (1989, 1995, 1997). Contrary to the Amblystegiaceae, the three latter families belong to a group called by Hedenäs ‘taxa with Brachythecium-like capsules’. They are characterized, among other things, by eplicate perichaetial leaves, relatively short capsules and round-pored stomata. Although sporophytes of *Limnophyllum* are unknown, we may predict that it has the latter character states.

The new familial position requires a discussion, as the Climaciaceae is one of the best delimited families of pleurocarps, immediately recognized by habit, representing the only clearly dendroid plants in the boreal zone of the Northern Hemisphere, while almost none of their character states occur in *Limnophyllum*.

According to most classifications, the family Climaciaceae includes two genera, *Climacium* and *Pleuroziopsis* (Brotherus, 1925; Frey & Stech, 2009; Goffinet, 2009; Iwatsuki, 2004; Ignatov et al. 2006). Ireland (1968) suggested to separate *Pleuroziopsis* in its own family, but Norris & Ignatov (2000) disagreed, finding a specific stem structure in these genera as likely homologous. A doubt regarding the position of Pleuroziopsidaceae close to *Climacium* was expressed by Hedenäs (1995), who included it in the Hylocomiaceae. The recent molecular phylogenetic analyses based on different gene regions, e.g., nuclear ITS and chloroplast *trnL-F* (Ignatov et al., 2007) or chloroplast *rps4*, mitochondrial *nad5* and part of nuclear 26S rRNA (Cox, 2010) found them closely related, although some analyses did not join them, as in the *rbcL*-based analysis of Tsubota et al. (2004). All the analyses with nuclear ITS showed Climaciaceae related to the Hylocomiaceae and *Antitrichia* (e.g., Gardiner et al., 2005; Huttunen et al., 2012). The latter genus was thus segregated in its own family (Ignatov & Ignatov, 2004), removed from the Leucodontaceae, which was also supported by the arrangement of the proximal branch leaves (Spirina & Ignatov, 2010; Ignatov & Spirina, 2013).

The tree topologies obtained here indicate that *Limnophyllum* is related to *Climacium* and *Pleuroziopsis*, and *rps4* even indicates that it is more closely related to *Climacium*, than to *Pleuroziopsis*. There are likely five possible solutions for how to reflect the current tree topologies in the classification: 1) separate *Limnophyllum* in its own family, distinct from the Climaciaceae (with *Climacium* and *Pleuroziopsis*); 2) accept three genera, *Limnophyllum*, *Climacium* and *Pleuroziopsis* in three families of their own; 3) expand the circumscription of the Climaciaceae, to include the third genus *Limnophyllum*; 4) include *Limnophyllum*, *Climacium* and *Pleuroziopsis* (and then also *Antitrichia*) in Hylocomiaceae, reducing Climaciaceae (and then likely also Antitrichiaceae) into synonymy of Hylocomiaceae; 5) leave Hylocomiaceae paraphyletic, accepting Climaciaceae as a separate family, but place *Limnophyllum* in the Hylocomiaceae, considering it as a transitional step from Hylocomiaceae to Climaciaceae.

Advantages and disadvantages of each solution can be evaluated from different point of views, such as practical classification and ease of building keys, strictly following cladistic rules, or a balance between molecular and morphological approaches, with variable weighting of different data sets.

The idea of a separate family will allow avoiding a very indefinite circumscription of Climaciaceae, but it will indicate nothing about their relationship.

Expansion of Hylocomiaceae may have a certain basis, as this family includes both plants with paraphyllia, e.g., *Hylocomium*, *Hylocomiastrum*, *Loeskeobryum*, and some without them, e.g., *Rhytidiadelphus* and *Neodolichomitra*. However, inclusion of additional genera will make the circumscription of the family even more vague, and the interesting fact of the close relationship between *Limnophyllum*, *Climacium* and *Pleuroziopsis* will be neglected.

Thus we suggest acceptance of these tree genera in one family, the Climaciaceae, despite that the key characters of the family will almost disappear. Thus the rule that aquatic habitat strongly modifies moss morphology, making them superficially very different from the most closely related terrestrial ancestors will obtain additional support.

Similarly, the transition from terrestrial to epiphytic growth of pleurocarps often results in strong changes (cf. Hedenäs, 2012; Huttunen et al., 2004, 2008, 2013; Ignatov et al., 2012; Vanderpoorten et al., 2002). Naturally, a numerous striking familial displacement happened due to investigations of these facts: *Anacamptodon* (was Fabroniaceae, now Amblystegiaceae), *Clasmatodon* (was Fabroniaceae, now Brachytheciaceae), *Struckia* (was Fabroniaceae, now Plagiotheciaceae), and many other ones.

The transition from terrestrial to epiphytic growth affects mostly sporophytic characters (Hedenäs, 2012; Huttunen et al., 2004), although common trends to relatively smaller plants, with shorter and more thick-walled cells occur in many groups like Leskeaceae, Taxiphyllaceae, Brachytheciaceae, and Amblystegiaceae. Hedenäs (2012) found that the short double costa significantly correlates with the epiphytism in pleurocarpous mosses.

Morphological traits associated with the change of environmental preference from terrestrial to aquatic include larger plant size, a tendency to hyalodermis development, enlarged alar cells, longer leaf decurrencies and longer axillary hairs. These traits are not as many and also not so specific to aquatic plants, being present in some terrestrial lineages as well, as, for example, in *Plagiothecium*.

The sharp differentiation between clearly dendroid *Climacium* and *Pleuroziopsis* and not dendroid at all in *Limnophyllum* may appear less impossible considering one recently studied case in the genus *Kindbergia* (Brachytheciaceae). This genus includes 4–8 species, and one of them, the Japanese endemic *K. arbuscula*, is very distinct in its dendroid plant architecture. At the same

time, molecularly it has been found not to differ from the widespread *K. praelonga* by Hedenäs (2010), who suggested to consider such abrupt change as a result of mutation in development regulation, where shoot differentiation was redirected along another path. A similar, but much older case may be present in the evolution of Climaciaceae. Concerning paraphyllia, abundantly present in both *Climacium* and *Pleuroziopsis*, in the related family of Hylocomiaceae, the stronger the sympodial branches with a 'stipe' zone at base of the sympodial innovations, the better developed are the paraphyllia: cf. *Hylocomium*, *Hylocomiastrum* and *Loeskeobryum* versus *Rhytidiadelphus*, *Pleurozium* and *Neodolichomitra*.

Summing up, *Limnophyllum* is yet another case where molecular phylogenetic inference indicates an 'unbelievably' different position, akin to what was found in the genera *Leptodon* (Sotiaux et al., 2009) and *Pinnatella* (Enroth et al., 2010). However, it also points at the ability of pleurocarps for a relatively fast morphological evolution, especially in connection with change of environment.

ACKNOWLEDGEMENTS

We are grateful to V.A. Bakalin for making to our disposal his specimen, to L. Hedenäs for critical comments and corrections of the manuscript, E. Ignatova for making drawing. The work was partially supported by RFBR № 13-04-01592 and RAS program "World Life, Current State and Development: Biodiversity".

LITERATURE CITED

- BAKALIN, V.A., V.YA. CHERDANTSEVA, M.S. IGNATOV, E.A. IGNATOVA & T.I. NYUSHKO 2009. Bryophyte flora of the South Kuril Islands (East Asia). – *Arctoa* **18**: 69–114.
- BROTHERUS, V. F. 1925. Musci (Laubmoose). 2. – In: A. Engler & K. Prantl Nat. Pflanzenfam. (ed. 2). Duncker & Humblot, Berlin: 1–542.
- BUCK, W. R., B. GOFFINET & A. J. SHAW. 2000. Testing morphological concepts of orders of pleurocarpous mosses (Bryophyta) using phylogenetic reconstructions based on trnL-trnF and rps4 sequences. – *Molec. Phylogen. Evol.* **16**: 180–198.
- BUDYAKOVA, A.A., M.S. IGNATOV, S.P. YATSENTYUK & A.V. TROITSKY 2003 [2004] Systematic position of *Habrodon* (Habrodonaceae, Musci) as inferred from nuclear ITS1 and ITS2 and chloroplast trnL intron and trnL-trnF spacer sequence data. – *Arctoa* **12**: 137–150.
- [CZERNYADJEVA, I.V.] ЧЕРНЯДЬЕВА И.В. 2012. Мхи полуострова Камчатка. – [Mosses of Kamchatka Peninsula] *СПб. [Sankt-Petersburg]*: 459 pp.
- COX, C.J., B. GOFFINET, N.J. WICKETT, S.B. BOLES & A.J. SHAW 2010. Moss diversity: a molecular phylogenetic analysis of genera. – *Phytotaxa* **9**: 175–195.
- ENROTH, J., S. OLSSON, S. HE, J. R. SHEVOCK & D. QUANDT 2010. When morphology and molecules tell us different stories, part 2: *Pinnatella homaliadelphoides* (Neckeraceae), a new moss species from China and India. – *Trop. Bryol.* **31**: 67–75.
- FREY, W. & M. STECH 2009. Bryophyta (Musci, mosses). – In: Frey, W. [ed.], *Syllabus of plant families A. Engler's Syllabus der Pflanzenfamilien. Part 3. Bryophytes and seedless vascular plants. 13th ed.. Gebr. Borntraeger Verlagsbuchhandlung, Stuttgart, Germany*: 116–257.
- GARDINER, A., M. IGNATOV, S. HUTTUNEN & A. TROITSKY 2005. On resurrection of the families Pseudoleskeaceae Schimp. and Pylaisiaceae Schimp. (Musci, Hypnales). – *Taxon* **54**: 651–663.
- GOFFINET, B., W.R. BUCK & A.J. SHAW 2009. Morphology, anatomy, and classification of the Bryophyta. – In: B. Goffinet & A.J. Shaw,

eds. *Bryophyte biology*, 2nd edn. Cambridge: Cambridge University Press: 55-138.

- GOLOBOFF, P., S. FARRIS & K. NIXON 2003. TNT (Tree analysis using New Technology) (BETA) ver. 1.0. – *Program and documentation*, available from the authors, and at www.cladistics.com/aboutTNT.html.
- HEDENÄS, L. 1989. Some neglected character distribution patterns among the pleurocarpous mosses. – *Bryologist* **92**: 157-163.
- HEDENÄS, L. 1995. Higher taxonomic level relationships among diplolepidous pleurocarpous mosses – a cladistic overview. – *J. Bryol.* **18**: 723-781.
- HEDENÄS, L. 1997. An evaluation of phylogenetic relationships among the Thuidiaceae, the Amblystegiaceae, and the temperate members of the Hypnaceae. – *Lindbergia* **22**: 101-133.
- HEDENÄS, L. 2010. Global relationships and European phylogeography in the *Kindbergia praelonga* complex (Brachytheciaceae, Bryophyta). – *Trop. Bryol.* **31**: 81-90.
- HEDENÄS, L. 2012. Morphological and anatomical features associated with epiphytism among the pleurocarpous mosses – one basis for further research on adaptations and their evolution. – *J. Bryol.* **34**(2): 79-100.
- HUTTUNEN, S., N. BELL, V.K. BOBROVA, V. BUCHBENDER, W.R. BUCK, C.J. COX, B. GOFFINET, L. HEDENÄS, B.-C. HO, M.S. IGNATOV, M. KRUG, O. KUZNETSOVA, I.A. MILYUTINA, A. NEWTON, S. OLSSON, L. POKORNY, J.A. SHAW, M. STECH, A. TROITSKY, A. VANDERPOORTEN & D. QUANDT 2012. Disentangling knots of rapid evolution: origin and diversification of the moss order Hypnales. – *J. Bryol.* **34**: 187-211.
- HUTTUNEN, S. & M.S. IGNATOV 2004. Phylogeny of the Brachytheciaceae (Bryophyta) based on morphology and sequence level data. – *Cladistics* **20**: 151-183.
- HUTTUNEN, S. & M.S. IGNATOV 2010. Evolution and taxonomy of aquatic species in the genus *Rhynchostegium* (Brachytheciaceae, Bryophyta). – *Taxon* **59**(3): 791-808.
- HUTTUNEN, S., L. HEDENÄS, M.S. IGNATOV, N. DEVOS & A. VANDERPOORTEN 2008. Origin and evolution of the Northern Hemisphere disjunction in the moss genus *Homalothecium* (Brachytheciaceae). – *Am. J. Bot.* **95**(6): 720-730.
- HUTTUNEN, S., M. S. IGNATOV, K. MÜLLER & D. QUANDT 2004. Phylogeny and evolution of epiphytism in the three moss families Meteoriaceae, Brachytheciaceae and Lembophyllaceae. – *Monographs in Systematic Botany Missouri Bot. Garden* **98**: 328-361.
- IGNATOV, M.S., O.M. AFONINA, E.A. IGNATOVA et al. 2006. Checklist of mosses of East Europe and North Asia. – *Arctoa* **15**: 1-130.
- IGNATOV, M.S., O.M. AFONINA, O.I. KUZNETSOVA & E.A. IGNATOVA 2012. The genus *Leptopterigynandrum* (Taxiphyllaceae, Bryophyta) in Russia. – *Arctoa* **21**: 207-220.
- IGNATOV, M.S., A.A. GARDINER, V.K. BOBROVA, I.A. MILYUTINA, S. HUTTUNEN & A.V. TROITSKY 2007. On the relationships of mosses of the order Hypnales, with special reference to taxa traditionally classified in the Leskeaceae. – In: Newton, A. E. & R. S. Tangney (eds.), *Pleurocarpous mosses: systematics and evolution*. Syst. Assoc. Special Vol. **71**: 177-213.
- IGNATOV, M. S. & L. HEDENÄS 2007. Homologies of stem structures in pleurocarpous mosses, especially of pseudoparaphyllia and similar structures. – In: Newton, A. E. & R. S. Tangney (eds.), *Pleurocarpous mosses: systematics and evolution*. Syst. Assoc. Special Vol.: **71**: 269-286.
- [IGNATOV, M.S. & E.A. IGNATOVA] ИГНАТОВ М.С., Е.А. ИГНАТОВА 2003-2004. Флора мхов средней части европейской России. Т. 1-2. – [Moss flora of the Middle European Russia. Vols. 1-2] М., КМК [Moscow, KMK]: 960 pp.
- IGNATOV, M.S. & I.A. MILYUTINA 2010. On the familial position of the genus *Sasaokea* (Bryophyta). – *Arctoa* **19**: 63-68.
- IGNATOV, M.S. & I.A. MILYUTINA 2011. Intrafamilial hybridization in mosses? An enigmatic case in the genus *Podperaea* (Hypnales, Bryophyta). – *Arctoa* **20**: 107-118.
- IGNATOV, M.S. & U.N. SPIRINA 2012. Morphogenesis of proximal brach leaves in Mosses. – *Russian J. Develop. Biol.* **43**(3): 148-156.
- IGNATOVA, E. A. & T. YU. SAMKOVA 2006. *Campylopus umbellatus* (Arn.) Paris (Leucobryaceae, Musci) – a new species for Russia. – *Arctoa* **15**: 215-218.
- IRELAND, R.R. 1968. Pleuroziopsidaceae, a new family of mosses. – *J. Hattori Bot. Lab.* **31**: 59-64.
- IWATSUKI, Z. 2004. New catalog of the mosses of Japan. – *J. Hattori Bot. Lab.* **96**: 1-182.
- KANDA, H. 1975. A revision of the family Amblystegiaceae of Japan I. – *J. Sci. Hiroshima Univ., Ser. B, Div. 2, Bot.* **15**: 201-276.
- NOGUCHI, A. 1991. Illustrated moss flora of Japan. Pt. 4. – *Hattori Bot. Lab., Nichinan*: 743-1012.
- NORRIS, D.H. & M.S. IGNATOV 2000. Observations on stem surface anatomy in *Climacium* and *Pleuroziopsis* (Climaciaceae, Musci). – *Arctoa* **9**: 151-154.
- OLSSON, S., V. BUCHBENDER, J. ENROTH, L. HEDENÄS, S. HUTTUNEN & D. QUANDT 2009. Phylogenetic analyses reveal high levels of polyphyly among pleurocarpous lineages as well as novel clades. – *Bryologist* **112**(3): 447-466.
- OLIVÁN, G., L. HEDENÄS & A.E. NEWTON 2007. Phylogeny of *Hypogryhnum* Lindb. based on molecular data. – In: A. E. Newton & R. S. Tangney (eds.), *Pleurocarpous mosses: systematics and evolution*. Syst. Assoc. Special Vol. **71**: 215-226.
- PEDERSEN, N. & L. HEDENÄS 2002. Phylogeny of the Plagiotheciaceae based on molecular and morphological evidence. – *Bryologist* **105**: 310-324.
- SAKURAI, K. 1952. Reports of some interesting mosses in Japan (3). – *J. Jap. Bot.* **27**: 279-284.
- SOTIAUX, A., J. ENROTH, S. OLSSON, D. QUANDT & A. VANDERPOORTEN 2009. When morphology and molecules tell us different stories: a case-in-point with *Leptodon corsicus*, a new and unique endemic moss species from Corsica. – *J. Bryol.* **31**: 186-196.
- SPIRINA, U.N. & M.S. IGNATOV 2010. On the branch development in *Leucodon* (Leucodontaceae, Bryophyta). – *Arctoa* **19**: 139-152.
- TANGNEY, R., S. HUTTUNEN, M. STECH & D. QUANDT 2010. A review of the systematic position of the pleurocarpous moss genus *Acrocladium* Mitten. – *Tropical Bryology* **31**: 164-170.
- TROITSKY, A.V., M.S. IGNATOV, V.K. BOBROVA & I.A. MILYUTINA 2008. Contribution of genosystematics to current concepts of phylogeny and classification of Bryophytes. – *Biochemistry (Moscow)* **72**(12): 1368-1376.
- TSUBOTA, H., E. DE LUNA, D. GONZÁLEZ, M.S. IGNATOV & H. DEGUCHI 2004. Molecular phylogenetics and ordinal relationships based on analyses of a large-scale data set of 600 rbcL sequences of mosses. – *Hikobia* **14**: 149-170.
- VANDERPOORTEN, A., L. HEDENÄS, C.J. COX & A.J. SHAW 2002. Circumscription, classification, and taxonomy of the Amblystegiaceae (Bryopsida) inferred from nuclear and chloroplast DNA sequence data and morphology. – *Taxon* **51**: 115-122.

Appendix 1. Genbank accession numbers and voucher specimen data for of specimens other than taken from Genbank. *Limnophyllum mizushimae* Kuril Islands, Shikotan, *Bakalin K-54-29-07* (MHA ex VLA): ITS KM392103, *nad5* KM392096, *rps4* KM392099; *Limnophyllum mizushimae* Kamchatka, Termalnyi, 7.VIII.2001, *Czernyadjeva* (MHA ex LE): ITS KM392102. *Leptodictyum riparium* Russia, Ryazan Province, Pryamoglyadovo, 5 May 2010 Volosnova (MHA): ITS KM392101, *rps4* KM392098; *Leptodictyum riparium* Russia, Primorsky Territory, Steklyanukha, Ignatov 07-241b (MHA): ITS KM392100, *rps4* KM392097.