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MICROAMBLYSTEGIUM – A NEW GENUS OF AMBLYSTEGIACEAE FROM SHIKOTAN ISLAND (SOUTH KURILS, RUSSIAN FAR EAST)

MICROAMBLYSTEGIUM – НОВЫЙ РОД МХОВ ИЗ СЕМЕЙСТВА AMBLYSTEGIACEAE С ОСТРОВА ШИКОТАН (ЮЖНЫЕ КУРИЛЫ, РОССИЙСКИЙ ДАЛЬНИЙ ВОСТОК)

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Abstract

A molecular phylogenetic study based on the plastid *trn*L-*trn*F, *atp*B-*rbc*L and nuclear ITS sequences resolved an unnamed tiny saxicolous moss recently collected in Shikotan Island in a clade with *Kandaea, Palustriella* and *Cratoneuron*. At the same time, it markedly differs from them morphologically in having homogeneous stem cross section, weak single costa reaching only 0.3 to 0.7 of leaf length, and very weakly differentiated alar cells. The moss is therefore described here as *Microamblystegium saxicola* gen. and sp. nov. We speculate that it represents another specialized evolutionary lineage with miniaturized and simplified morphology likely associated with adaptation to growth in shaded cliff niches, matching a similar pattern observed in the recently described amblystegiaceous genus *Arvernella*. Such specialized lineages of minute saxicolous mosses remain poorly known due to their outstanding rarity.

Резюме

Молекулярно-филогенетическое исследование, основанное на последовательностях пластидных маркеров *trn*L-*trn*F, *atp*B-*rbc*L и ядерного ITS доказало принадлежность миниатюрного эпилитного мха, собранного на острове Шикотан к кладе, также включающей роды *Kandaea, Palustriella* и *Cratoneuron*. В то же время он сильно отличается от них по морфологии, поскольку имеет стебель, гомогенный на поперечном срезе и сравнительно слабую простую жилку от 0.3 до 0.7 длины листа, а также слабо дифференцированные клетку в углях основания листа. Этот мох описан как *Microamblystegium saxicola* gen. and sp. nov. На основании молекулярно-филогенетических данных мы предполагаем, что он представляет еще одну специализированную филогенетическую линию, эволюция которой пошла по пути миниатюризации и упрощения морфологии, вероятно в связи с адаптацией к произрастанию в нишах скал, подобно недавно описанному в этом же семействе роду *Arvernella*. Такие специализированные группы мелких эпилитных мхов остаются слабо изученными ввиду их исключительной редкости.

KEYWORDS: Hypnales, molecular phylogeny, cryptic diversity, parallel evolution

INTRODUCTION

Among the collections from a recent expedition to Shikotan Island (South Kurils), we were puzzled by a specimen of a small saxicolous amblystegiaceous moss, which resembled species of the tiny amblystegiaceous genera *Serpoleskea* (Hampe ex Limpr.) Loeske, *Pseudoamblystegium* Vanderp. & Hedenäs or the recently described *Arvernella pisarenkoi* Ignatov & Ignatova (Ignatov *et al*., 2021). With respect to the little informative morphology of these mosses and having in mind the proved morphological parallelism among phylogenetically unrelated genera *Platydictya* Berk., *Heterocladium* Schimp., *Arvernella* Hugonnot & Hedenäs, *Serpoleskea* or *Pseudoamblystegium*, confident identification based solely on morphological ground is problematic. Therefore, we decided to explore the affinities of the newly found moss using molecular data. As we expected the unknown moss to be most likely member of Amblystegiaceae, our initial barcoding attempt included nrITS and chloroplast *atp*B–*rbc*L, two regions for which Amblystegiaceae have been rather well sampled in the course of earlier molecular phylogenetic studies (e.g., Vanderpoorten *et al*., 2001, 2002; Kučera & Hedenäs, 2020; Ignatov *et al*., 2021). These first obtained sequences, evaluated within an unpublished dataset by JK, showed an unexpected affinity with species from the clade containing members of *Cratoneuron* (Sull.) Spruce, *Palustriella* Ochyra, and the recently described *Kandaea* Jan

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Kučera & Hedenäs, rather than to *Arvernella*, *Amblystegium* Schimp., *Serpoleskea* or *Pseudoamblystegium* in which similar tiny morphotypes occur.

Therefore, we decided to compile a comprehensive dataset, aiming to obtain more solid evidence of molecular affinities of this unknown moss, which could either support the inclusion in one of existing genera in the Amblystegiaceae or prove the need for establishing a new genus for this moss.

MATERIALS AND METHODS

Dataset

Since search for related taxa via blast and quick phylogenetic reconstructions based on ITS and the *atp*B–*rbc*L spacer revealed its affinity with morphologically rather dissimilar mosses, we performed a phylogenetic reconstruction of the Amblystegiaceae based on a dataset combining *atp*B-*rbc*L spacer and *trn*L-*trn*F region with nuclear ITS1-5.8S rRNA-ITS2. Sequences were obtained according to the protocols described by Gardiner *et al*. (2005), and Kučera *et al*. (2019). The core of the dataset originated from the recent study by Kučera & Hedenäs (2020). Our molecular dataset included 68 accessions including 57 representatives of the Amblystegiaceae. For GenBank accession numbers and voucher information of newly studied specimens see Fig. 1 and Appendix 1.

Three datasets used for phylogenetic inferences included 68 terminals and corresponded to the combined *trn*L-*trn*F & *atp*B-*rbc*L sequences (1228 aligned positions), nr ITS (924 positions) and their concatenation (2152 positions plus indels). Sequences were aligned using the E-INS-i strategy in MAFFT v. 7.487 (Katoh & Standley, 2013) and then edited manually in BioEdit (Hall, 1999). Indel data were scored using simple indel coding approach (Simmons and Ochoterena 2000) using SeqState 1.4.1. (Müller 2005). One of two alternative states of highly homoplasic inversion in the trnL-trnF spacer was coded as indel that allowed its inclusion in the analysis as a single mutation, not three substitutions. The combined dataset was divided into partitions using the algorithm described by Kučera & Hedenäs (2020) except for indels, which were divided into two partitions, corresponding to nuclear (151 indels) and plastid (66 indels) data.

Molecular phylogenetic analyses

Phylogenetic analysis was performed using Bayesian Inference by running two parallel analyses in MrBayes 3.2.7a (Ronquist *et al.*, 2012) with each run consisting of six Markov chains and 5,000,000 generations. The sampling frequency was one tree each 1 000 generations, and the chain temperature was set at 0.03 in all analyses and sampling across the GTR model space. Consensus trees were calculated after omitting the first 25% trees as burn-in. Convergence of analyses was assessed based on average PSRF values (1.000 in both analyses) and ESS values, checked using Tracer v.1.7.2. (Rambaut *et al.*, 2018) to be higher than 200. Analyses were performed on the Cipres Science Gateway (http://www.phylo.org/portal2) on XSEDE (Miller et al., 2010). Maximum Likelihood (ML) trees were estimated using RaxML 8.2.12 (Stamatakis, 2014). ML analyses were run at the cluster computer facilities of MetaCentrum VO (see acknowledgement) on identical matrices, the bootstrap analysis was stopped automatically using the autoMRE command. For ML analysis, the GTR model was used. Trees were rooted with the Scorpidiaceae clade in all analyses according to the topology of hypnalean mosses presented by Kučera *et al*. (2019).

RESULTS

The topologies of the ITS based trees are congruent with those based on the plastid dataset. Since the topology of the obtained single gene trees repeats already published ones with minor differences caused by different compositions of datasets, they are not considered here in details.

In the tree inferred from the combined dataset (Fig. 1) accessions of the Amblystegiaceae form a moderately supported clade sister to the Leskeaceae + Rhytidiaceae + Pseudoleskeellaceae clade. Within the Amblystegiaceae clade, a clade consisting of two accessions of *Myrinia pulvinata* (Wahlenb.) Schimp. split first, followed by the weakly supported *Drepanium* (Schimp.) Lange & C.E.O. Jensen, *Platyhypnum* Loeske, *Campylophyllum* (Schimp.) M. Fleisch. and *Arvernella* clade and the single accession of *Tomentypnum nitens* (Hedw.) Loeske, which forms a moderately supported sister group to the core Amblystegiaceae clade. The maximally supported core Amblystegiaceae clade includes four maximally supported major clades in a grade. These major clades include accessions of (1) *Leptodictyum* (Schimp.) Warnst. within which two remarkably distinct lineages appear; (2) *Kandaea, Cratoneuron*, *Palustriella* and the recently collected plant from Shikotan; (3) *Amblystegium, Hygroamblystegium* Loeske*, Drepanocladus* (Müll. Hal.) G. Roth, *Cratoneuropsis* (Broth.) M. Fleisch., *Hypnobartlettia* Ochyra*,* and *Vittia* Ochyra; (4) *Anacamptodon* Brid.*, Campylium* (Sull.) Mitt., *Campylophyllopsis* W.R. Buck*, Hygrohypnum* Lindb.*, Microhypnum* Jan Kučera & Ignatov*, Pseudoamblystegium, Pseudocampylium* Vanderp. & Hedenäs*,* and *Serpoleskea*.

The specimen from Shikotan was found in a well-supported C2 clade of core Amblystegiaceae as delimited by Kučera & Hedenäs (2020), where it forms a marginally supported clade with accessions of *Palustriella*.

DISCUSSION

The topologies of the obtained trees are congruent with those obtained in earlier studies focused on the Amblystegiaceae (Vanderpoorten *et al*. 2001, 2002; Kučera & Hedenäs, 2020; Ignatov *et al.*, 2021). The *Arvernella* clade was found deeply nested in the maximally supported C1 clade of the Amblystegiaceae, which also includes *Drepanium, Platyhypnum* and *Campylophyllum* (cf. Kučera & Hedenäs, 2020), and similar affinity was suggested by Hugonnot & Hedenäs (2015) and Ignatov

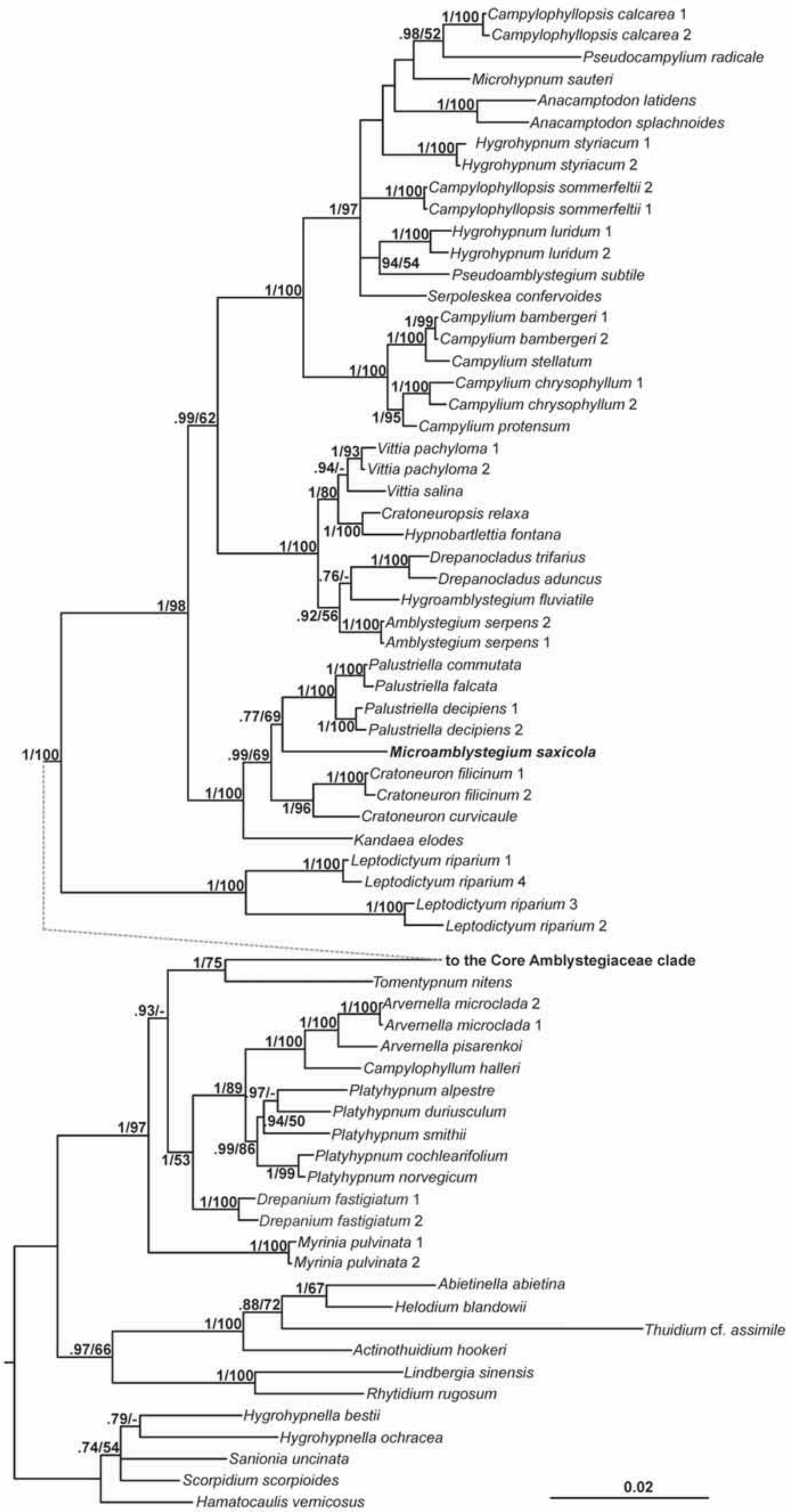

Fig. 1. Bayesian tree of Amblystegiaceae inferred from the combined nuclear and plastid data. Bayesian posterior probabilities higher than 0.7 and Bootstrap support values higher than 50 are shown at branches; «-» indicates low support in the ML tree.

et al. (2021). Our plant from Shikotan appeared in the well-supported C2 clade (referred to as the clade 2 of the core Amblystegiaceae clade in the Results section), where no such minute mosses have previously been known. Our morphological observations provided insufficient information regarding the affinity of the studied plant. With the combination of small size of plants, not differentiated cells in the stem cross section, ovate-lanceolate, acute to acuminate leaves, weak to moderately developed single costa, short, smooth leaf cells and not or weakly differentiated alar regions, this plant does not exactly match the circumscription of any amblystegiaceous genus. In particular, it differs rather significantly from other species of the C2 clade except for sharing short leaf cells with species of the genus *Cratoneuron*, where both *C. filicinum* (Hedw.) Spruce and *C. curvicaule* (Jur.) G. Roth can also form relatively small plants. Other species of the C2 clade are medium-sized to large plants with a well-differentiated stem central strand and sclerodermis, strong costae usually reaching leaf tips, and typically markedly differentiated alar cells in large groups (except for *Kandaea*). Most species also possess paraphyllia, except *Cratoneuron curvicaule* and *Kandaea* (Ignatov & Ignatova, 2004; Lüth, 2019). Although our plant lacks sporophytes, they usually are not very informative in terms of phylogenetically important traits within the Amblystegiaceae except for several specialized epiphytic lineages.

In its lack of central strand, the plant from Shikotan fits the circumscription of *Platydictya* sensu Kanda (1976), who considered this genus within the Amblystegiaceae. While it is obvious from recent phylogenies that the type of *Platydictya*, *P. jungermannioides* (Brid.) H.A. Crum, together with *P. acuminata* (Lindb. & Arnell) Ignatov, is a member of the Plagiotheciaceae (Hedenäs & Pedersen, 2002; Ignatov & Kuznetsova 2011; Huttunen *et al*., 2013), the affinities of several insufficiently known Japanese species referred to this genus are unknown. However, none of the species presented by Kanda (1976) and Noguchi (1991) matches satisfactorily our plants (see the Taxonomy section).

Several morphological trends, such as reduction of stem layers, costa and alar cells seem result from parallel evolution associated with miniaturization. Miniaturization is a common adaptive trend in many groups of organisms, which enables them to occupy previously inaccessible niches. In bryophytes, it most prominently occurs in epiphyllous liverworts but there are examples of saxicolous lineages with reduced morphology, particularly among sciotolerant mosses occupying sheltered niches beneath rock overhangs. Examples of such specialized groups include the genera *Tetrodontium* Schwägr. (reduced central strand and costa), *Seligeria* Bruch & Schimp. (reduced central strand), *Platydictya* (reduced central strand and costa), *Heterocladium* (in case of *H. flaccidum* (Schimp.) A.J.E. Sm. also with undifferentiated stem cells and costa, in others at least reduced costa), *Ignatovia* U.B. Deshmukh (reduced central strand), *Serpoleskea* (reduced central strand, reduced costa), and *Arvernella* (reduced central strand and costa). No representative of these reduced saxicolous lineages has well-developed and differentiated alar cells, and this appears particularly prominent among other taxa of the C2 clade of the Amblystegiaceae, which otherwise have the alar cells well-differentiated, together with the strong costa. As a result of such parallelisms extremely similar morphotypes originated in unrelated lineages of mosses, representing unusual instances of cryptic diversity when molecular data reveal new genera or possibly even higher level taxa instead of cryptic species.

Recently, phylogenetic studies have shown that lineages of specialized tiny saxicolous mosses are remarkably phylogenetically isolated, necessitating the erection of new genera based mostly on molecular arguments (Vanderpoorten & Hedenäs 2009, Ignatov *et al.*, 2019, Ignatov *et al*., 2021). At the same time, the diversity within such groups of miniaturized saxicolous mosses can be overlooked, as shown in the example of the saxicolous moss genus *Heterocladium* where most of the described taxa were synonymized with the type species, *H. heteropterum*, in the past, but the molecular diversification accompanied by slight morphological differences could be demonstrated in a recent morpho-molecular study by Hugonnot *et al.* (2020). It is thus arguable whether the miniaturization in saxicolous bryophytes can be considered as a kind of a dead end of evolution, since all revealed lineages remain monotypic and often thought to be rare or extremely rare, or rather is just the consequence of inadequate exploration of some regions and habitats in combination with the insufficient molecular sampling of seemingly morphologically little variable tiny saxicolous plants. The latter might be more probable, as the relatively recently discovered *Arvernella microclada* Hugonnot & Hedenäs (Hugonnot & Hedenäs, 2015) was described from a bryologically relatively well-known and often visited region and subsequent discovery of this species in likewise well-explored Vosges mountains (Tinguy *et al.*, 2019) seems to confirm this view. Russian Far East and Japan is the area where the diversity of such minute mosses seems to be underexplored, as witnessed by the recent discoveries of *Ignatovia microphylla* (Ignatov & Ignatova) U.B. Deshmukh (Ignatov *et al.*, 2019), *Arvernella pisarenkoi* (Ignatov *et al.*, 2021), and the present find. The status of the earlier described stenotopic temperate East Asian taxa *Amblystegium fauriei* Broth. & Paris, *Platydictya hattorii* Kanda, *P. shiroumensis* Kanda (cf. Kanda, 1976) and other ones should be revisited in this context and bryologists should be aware of the importance of such unapparent plants which might be genetically isolated and possibly relict, as are the remarkable mosses *Takakia* S. Hatt. & Inoue and *Oedipodium* Schwägr., which also share the habitat of sheltered rock niches with stable humidity and low competition.

Among the advantages of molecular phylogenetic approaches is that they allow an estimation of the phylo-

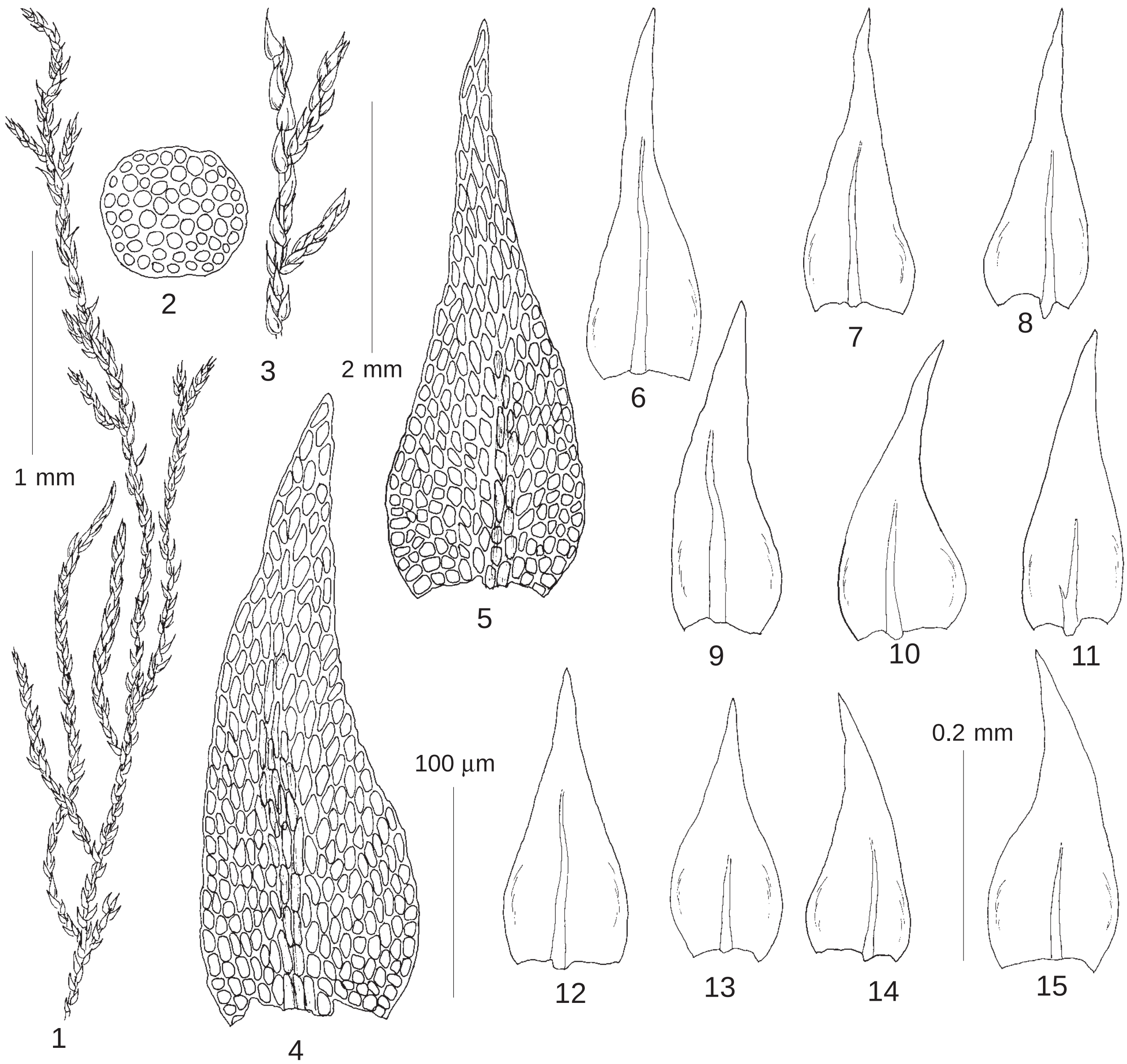

Fig. 2. *Microamblystegium saxicola* (from holotype). 1, 3: habit, dry; 2: stem transverse section; 4–5: leaf cells; 6–15: stem leaves. Scale bars: 2 mm for 3; 1 mm for 1; 0.2 mm for 6–15; 100 µm for 3–5.

genetic position of a single specimen and therefore, in well sampled groups, enable the description of new taxa based on a single specimen. Earlier this was considered as a rather inappropriate practice since aberrant morphotypes of already known species might be erroneously described as something new, but after the wide introduction of molecular phylogenetic methods several groups were described in such a way (Ignatov *et al*., 2019; 2021; Bakalin *et al.*, 2021a,b, etc.). Moreover, molecular data provide an essential view of a specimen's affinity in case morphology is incompletely known or uninformative and the identification and description based on traditionally used morphology is thus unreliable. In such a case, sequences obtained from the type specimens become an essential reference, reflecting the identity of the newly described taxa, and should thus be included in the protologue.

Taxonomy

Microamblystegium saxicola Fedosov, Ignatova & Jan Kučera gen. et spec. nov.

Type: Russia, Shikotan Island, Tymovo Distr., vicinity of Malokurilskoe Village, 43.88292°N, 146.83257°E, 230 m alt. In shaded niche of rock outcrops. 7 August 2021, coll. Fedosov V.E. & Shkurko A.V. (holotype MW).

Etymology: The generic name originates from *Amblystegium* (a genus of mosses) and refers to its small size. The specific epithet refers to the habitat where it was discovered.

Diagnosis: *Microamblystegium* differs from most other genera of pleurocarpous mosses in combination of minute size of plants; stem not differentiated internally, composed of thin-walled cells; a weak single costa reaching above mid-leaf at least in several leaves; short and wide rhomboidal, smooth laminal cells and scarcely differentiated alar cells. It differs from the similar *Arvernella pisarenkoi*, *Amblystegium fauriei* and *Platydictya hattorii* in a longer single vs. forked costa, somewhat shorter leaf cells and scarcely developed groups of quadrate cells in leaf angles.

Sequences: Plastid, *trn*S-*trn*F OL689422 ; *atp*B-*rbc*L OL689420; nr ITS OL689127.

Description. Plants small, in moderately dense, delicate mats, green, yellowish or olivaceous green. Shoots creeping, to 10 mm long, with terete foliation, loosely irregularly branched, stem in transverse section composed of homogeneous thin-walled cells, without central strand and sclerodermis, outermost cells somewhat smaller, with slightly thicker outer walls than cells inwards; paraphyllia absent. Axillary hairs few, pellucid, 3–4-celled, 30×6 μm, apical cell 10 μm long; proximal branch leaves of branch primordia variable in size, lanceolate or triangular. Leaves appressed when dry, spreading when moist, (0.22–)0.27–0.35(–0.40)×0.10–0.13(–0.16) mm, from ovate base gradually narrowed into lanceolate or narrowly triangular acumen, apex acute to subobtuse , some leaves with weak shoulders, slightly narrowed to base, not or shortly decurrent, concave; costa single, to 0.3–0.7 of leaf length, occasionally geniculate, gradually disappearing distally; margins plane, uneven to obtusely serrulate at shoulders; laminal cells rhomboidal or elongate-rhomboidal, (9–)15–17(–25)×5–6(–7) μm, with length to width ratio 1.5–2.5(–3):1, moderately thick-walled, smooth; cells along margin in 1–2 rows subquadrate to short-rectangular, 9–18×4–6 μm, alar cells not or weakly differentiated, subquadrate, transition to adjacent laminal cells gradual. Branch leaves somewhat smaller and narrower than stem leaves. Sexual condition, reproductive structures, and sporophytes unknown.

Differentiation. *Microamblystegium saxicola* resembles *Arvernella pisarenkoi* in its combination of small size, sparse branching, not differentiated stem cells in transverse section, rather weak costae, short leaf cells, and saxicolous habitat. It differs from it in single, somewhat longer costae, which typically reach mid-leaf or higher vs. usually forked costae extending to 0.2–0.4 the leaf length; leaves often with shoulders and narrower acumina vs. gradually tapered into wider acumina, and shorter cells with length/width ratio up to 2.5(–3):1 vs. usually 3–4:1 in *A. pisarenkoi*. *Microamblystegium saxicola* also resembles the insufficiently known Japanese species *Amblystegium fauriei*, as illustrated by Kanda (1976) from type material, in its stem not differentiated in transverse section, but that species differs in having elongate, thick-walled, prorate laminal cells and subquadrate cells along basal leaf margin in 2–3 rows (in 1 row in *Microamblystegium saxicola*). The likewise saxicolous *Serpoleskea confervoides* also lacks a central strand, but has a well-developed sclerodermis. Another minute saxicolous Far Eastern pleurocarpous species, *Ignatovia microphylla*, differs from *Microamblystegium saxicola* in having a strong costa nearly reaching the leaf apex, and smaller, rounded, thick-walled laminal cells. The insufficiently known Japanese species *Hygroamblystegium calcareum* Kanda resembles *Microamblystegium saxicola* in having a small size, a rather long single costa and weakly differentiated alar cells. However, *H. calcareum* has a stem with a differentiated sclerodermis and a central strand that differentiate it from *M. saxicola*. Another small and poorly known amblystegiaceous moss, which likely represents the C2 Amblystegiaceae clade (cf. Kučera & Hedenäs, 2020), *Cratoneuron tenerrimum* Kanda, according to illustration in Kanda (1976), also has a well differentiated sclerodermis and central strand in the stem, and its alar group is remarkably differentiated, composed of strongly inflated cells.

Ecology and distribution. The new species is at the moment known from a single locality in the northern part of Shikotan Island. Shikotan differs from all other areas of Russia in a very mild and humid climate. The specimen was collected from shaded humid niche of an acidic rock, where it formed a pure mat. Among other epilithic species growing there, *Bryoxiphium japonicum* (Berggr.) E. Britton, *Calohypnum plumiforme* (Wilson) Jan Kučera & Ignatov, *Dozya japonica* Sande Lac., and *Forsstroemia yezoana* (Besch.) S. Olsson, Enroth & D. Quandt are the most common ones.

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Appendix 1. Sequences used for molecular phylogenetic study. Specimens originally studied in course of the present study in newly obtained sequences are shown in bold.

species	voucher/isolate	ITS	trnL-trnF	AtpB-rbcL
Abietinella abietina	Allen 19816	AY009802	AY009850	AF322308
Actinothuidium hookeri	Yunan	KF770664	KF770502	KF770610
Amblystegium serpens 1	Czechia, Osule, Kučera 20081CBFS	MK327283	MK313964	MK313876
Amblystegium serpens 2	S B55399 Vanderpoorten 4158	FJ535778	FJ535739	FJ535758
Anacamptodon latidens	Kučera 18134	MK327284	MK313965	MK313877
Anacamptodon splachnoides	Schofield et al. 96529	AY009810	AY009816	AF322336
Arvernella microclada 1	Hugonnot CBNMC 5186	KC914873	KC914874	KC914875
Arvernella microclada 2	Kučera 18824 CBFS	MH613350	MH613576	MH613491
Arvernella pisarenkoi	OK106, Sakhalin Province, Sakhalin Island, Pisarenko op03738 MHA	MZ417374	**OL689423**	MZ447838
Microamblystegium saxicola	BF44, Russia, Sakhalin Province, Shikotan Island, 7.VIII.2021 Fedosov s.n., MW	**OL689127**	**OL689422**	**OL689420**
Campylium bambergeri 1	Kučera 15845 CBFS	MK327315	MK313997	MK313909
Campylium bambergeri 2	Scharnock 9204	MH613390	MH613616	MH613516
Campylium chrysophyllum 1	Anderson 26799	AF168150	AF161141	AF322355
Campylium chrysophyllum 2	Kučera 15609	MH613361	MH613587	MH613496
Campylium protensum	Kučera 13219 CBFS	MH613364	MH613590	MH613499
Campylium stellatum	Kučera 15972 CBFS	MK327292	MK313974	MK313886

***Campylophyllopsis calcarea* 1**	Ca2022, Czechia, Horni Alberice, Kučera 22342 CBFS	**OL740037**	**OL792053**	**OL792051**
Campylophyllopsis calcarea 2	Navarov 14800	MH613366	MH613592	MH613501
Campylophyllopsis sommerfeltii 1	Hedenäs, S B175748	MH613368	MH613594	MH613502
***Campylophyllopsis sommerfeltii* 2**	Ca2020, Czechia, Salajka, 25.IX.2019 Mikulaskova, CBFS22454	**OL740036**	**OL792052**	**OL792050**
Campylophyllum halleri	Kučera 18388	MK327293	MK313975	MK313887
Cratoneuron curvicaule	Kučera 15725, CBFS	MN646798	MN635410	MN635403
Cratoneuron filicinum 1	Kučera 18759, CBFS	MN646797	MN635411	MN635404
Cratoneuron filicinum 2	Lewis 87262	AF168155	AY009817	AF322332
Cratoneuropsis relaxa	Streimann 49394	FJ535787	FJ535748	FJ535768
Drepanium fastigiatum 1	Kučera 12468	MH613449	MH613674	MH613552
Drepanium fastigiatum 2	Kučera 18282	MK327338	MK314022	MK313936
Drepanocladus aduncus	S B1047	EU216317	EU216109	FJ535761
Drepanocladus trifarius	S B73402	KC601928	FJ535737	FJ535756
Hamatocaulis vernicosus	S B1068	AY625994	AY626012	AY625976
Helodium blandowii	Schofield 108637	AY009803	AY009852	AF322313
Hygroamblystegium fluviatile	Vanderpoorten 3739	AF464979	AF465000	AF464956
Hygrohypnella bestii	Schofield S B81888	AY857598	AY857555	AY857576
species	voucher/isolate	ITS	trnL-trnF	AtpB-rbcL
Hygrohypnella ochracea	S B818976	AY857605	AY857563	AY857584
Hygrohypnum luridum 1	Kučera 18482 CBFS	MH613385	MH613611	MH613512
Hygrohypnum luridum 2	S B81975	AY857601	AY857559	AY857580
Hygrohypnum styriacum 1	CBFS18850	MH613386	MH613612	MH613513
Hygrohypnum styriacum 2	S B81902	AY857608	AY857566	AY857587
Hypnobartlettia fontana	isolate Hypno.1477	AY242368	AY242376	HQ268437
Kandaea elodes	Kučera 20960 CBFS	MN646796	MN635412	MN635405
Leptodictyum riparium 1	Kučera 17055	MH613473	MH613698	MH613564
***Leptodictyum riparium* 2**	LF1, Russia, Vladimir Province, MW6046724	**OL6891231**	**OL689427**	–
***Leptodictyum riparium* 3**	LF5, Russia, Tatarstan Republic, MW9046928	**OL6891230**	**OL689426**	–
***Leptodictyum riparium* 4**	LF8, Russia, Volgograd Province, MW9046941	**OL689129**	**OL689425**	–
Lindbergia sinensis	Jiangsu	KF770668	KF770506	KF770614
Microhypnum sauteri	Kučera 16814	MH613460	MH613684	MH613558
Myrinia pulvinata 1	Chernyadyeva 3.VII.2015	MK327351	MK314034	MK313949
***Myrinia pulvinata* 2**	ThF11, Russia, Nenets autonomous Distr., MHA9024223	**OL689128**	**OL689424**	**OL689421**
Palustriella commutata	Kučera 20946 CBFS	MN646799	MN635409	MN635402
Palustriella decipiens 1	Kučera 20956 CBFS	MN646800	MN635408	MN635401
Palustriella decipiens 2	MACB 90037	AY857615	AY857572	AY857594
Palustriella falcata	S B61810	GU237137	AY626006	AY625966
Platyhypnum alpestre	S B81980	AY857596	AY857553	AY857574
Platyhypnum cochlearifolium	S B81890	AY857599	AY857556	AY857577
Platyhypnum duriusculum	Kučera 10940	MH613476	MH613701	–
Platyhypnum norvegicum	S B81898	AY857604	AY857562	AY857583
Platyhypnum smithii	Schofield 104556	AY857607	AY857565	AY857586
Pseudoamblystegium subtile	Kučera 16368	MH613478	MH613703	MH613566
Pseudocampylium radicale	Kučera 18708	MH613480	MH613705	MH613568
Rhytidium rugosum	Kučera 12871	MK327361	MK314044	MK313960
Sanionia uncinata	S B96458	GQ849964	GQ849841	AF322321
Scorpidium scorpioides	S B61836	AY625995	AY626014	AY625977
Serpoleskea confervoides	Kučera 14744	MH613488	MH613713	MH613573
Thuidium cf. *assimile*	Yunnan	KF770638	KF770476	KF770584
Tomentypnum nitens	Schofield 103470	AF168161	AY009854	AF322352
Vittia pachyloma 1	Goffinet 5605	AY062886	AY062889	AY062883
Vittia pachyloma 2	isolate Vittia1303	AY242367	AY242375	AY242358
Vittia salina	isolate Vittia1466	AY242370	AY242378	AY24236