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AFONINIA, A NEW MOSS GENUS OF FUNARIACEAE FROM TRANSBAIKALIA (EAST SIBERIA, RUSSIA)

AFONINIA – НОВЫЙ РОД ИЗ СЕМЕЙСТВА FUNARIACEAE ИЗ ЗАБАЙКАЛЬЯ (ВОСТОЧНАЯ СИБИРЬ, РОССИЯ)

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Abstract

Afoninia dahurica from the Transbaikal region of the East Siberia in Russia is described as a new species accommodated in a new genus of Funariaceae, based on molecular phylogenetic evidence from nrITS, *trn*L-F and *psb*A-*trn*H, that highlights the combination of strongly reduced double peristome with a well developed annulus of inflated revoluble cells. The exostome teeth are tapered to the base and attached to basal membrane with a plate that is less than one third of the cell of the endostome to which it adheres. The plant is known from few nearby localities in a xeric area of Dahuria, growing on soil near cliffs.

Резюме

Afoninia dahurica, новый род и вид из Funariaceae, описан из Забайкалья по результатам молекулярно-филогенетического анализа (nrITS, *trn*L-F and *psb*A-*trn*H) и на основании уникальной комбинации морфологических признаков (сильно редуцированного двойного перистома и отворачивающегося колечка, образованного вздутыми клетками). Для этого вида характерны суживающиеся книзу зубцы экзостома, которые в месте прикрепления к базальной мембране эндостома в три раза уже тех клеток, к которым они крепятся. Вид известен из немногочисленных местонахождений в засушливых районах Забайкалья; он растет на почве в основании скал.

KEYWORDS: *Afoninia,* Funariaceae, bryophytes, nrITS, *trn*L-F, *psb*A-*trn*H, taxonomy, phylogeny, Transbaikalia

Introduction

In the course of the bryofloristic exploration of the Zabaikalsky Territory, in southern Siberia, Russia, Olga M. Afonina collected a peculiar moss, which could not be attributed to any species known from Russia. The plants belong to the Funariaceae based on gametophytic and sporophytic characters: the spathulate leaves with obtusely serrulate leaf margins, large and thin-walled, elongate to rhombic laminal cells, incompletely divided stomatal guard cells, a double but strongly reduced peristome and long rostrate and cucullate calyptrae. The generic affinities of these plants seemed uncertain, as the specimen possessed combination of traits rather intermediate between typical *Funaria* and *Enhosthodon* species with a compound revoluble annulus, diagnostic of *Funaria* s. str. (Fife, 1985) and a smooth and symmetric rather cylindric urn and double peristome of short teeth and segments, hardly extending above the urn edge, known from *Entosthodon*.

The Funariaceae include 250-450 species accommodated in 13 to 16 genera (Fife, 1985; Crosby *et al.*, 1999). These genera were described mainly on the basis of sporophytic characters showing a great variation and representing morphological traits connected with an annual or ephemeral life strategies. The vast majority of species belong to *Funaria*, *Entosthodon* or *Physcomitrium*. The delimitation of the former two remained ambiguous for over a century as some authors broadly circumscribed *Funaria* by including *Entosthodon* (*e.g.*, Brotherus, 1924; Smith, 1978; Crum & Anderson, 1981; Savicz-Lyubi-

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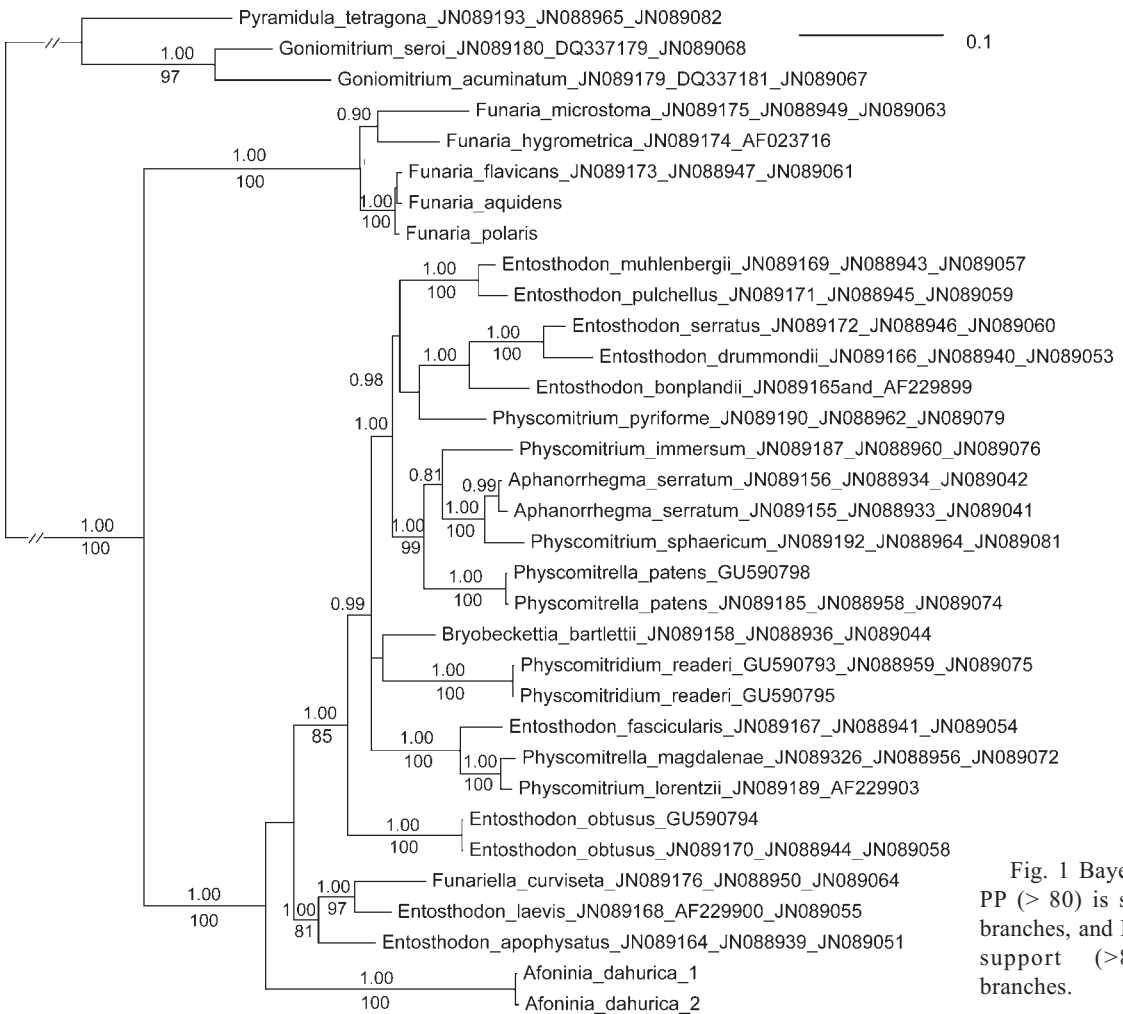


Fig. 1 Bayesian tree. BI PP (> 80) is shown above branches, and ML bootstrap support (>80) below branches.

tskaya & Smirnova, 1970; Noguchi & Iwatsuki, 1988), whereas others distinguished these genera (*e.g.*, Lawton, 1971; Li *et al.*, 2003; Smith, 2004) based on for example the inclined vs. straight capsule, or well developed vs. reduced peristome.

Fife (1985), as part of his worldwide generic revision of Funariaceae provided a numerical phenetic classification of the genera. He defined *Funaria* by the presence of a compound revoluble annulus, a structure that is always lacking in *Entosthodon*. This concept was, however, not universally adopted (*e.g.*, Noguchi & Iwatsuki, 1988) and in particular the group of intermediate species around *Funaria muhlenbergii* Turn. that has rather well developed peristome, but no revoluble annulus was placed by Miller & Miller (2007) in *Funaria* despite of the absence of a compound annulus, which points to an affinity with *Entosthodon* species as suggested by Fife (1985) and endorsed by Lönnel (2006) and Brugués & Ruiz (2010) among others.

A clear phylogenetic distinction of core *Funaria* and *Entosthodon* species was demonstrated by Liu *et al*. (2012) based on inferences from 10 loci sampled across all, albeit predominantly organellar, genomic compartments. The resolution of *Funaria* and *Entosthodon* in two distinct clades, with moreover a uniquely shared ancestry of *Entosthodon* with the remainder of the Funarioideae sensu Werner *et al.* (2007) highlighted the phylogenetic and hence systematic significance of the compound annulus as suggested by Fife (1985). Although a revoluble annulus occurs in one species outside of *Funaria*, namely the eperistomate *Physcomitrium hookeri* Hampe it has never been observed in any species of *Entosthodon*. Furthermore, the inferences by Liu *et al.* (2012) suggest that many sporophytic characters, traditionally used to define generic and subgeneric taxa in the Funariaceae were homoplasic and hence of limited systematic value, as none of the genera within the crown group of Funarioideae (*i.e.*, *Physcomitrella*, *Physcomitrium* and *Entosthodon*), with more than one species were resolved as monophyletic, a hypothesis further confirmed by Beike *et al*. (2014) for *Physcomitrella*.

Within this systematic context the specimens from the Zabaikalsky Territory should be accommodated within *Funaria* on the basis of their compound annulus. The peristome of *Funaria* species is, however, typically well developed with exostome teeth fused at their tips, and reduced peristomes are rare, and then never reduced to tiny teeth or segments. Furthermore, the capsule of *Funar-*

ia is always asymmetric, typically furrowed and most often on a curved seta. The specimens at hand, however, have straight urns, a condition reminiscent of *Entosthodon*. The morphological traits of the material from the Zabaikalsky Territory thus overlap with the diagnostic traits of *Funaria* and *Entosthodon*. To determine if the combination marks the evolutionary transition between *Funaria* and its sister-group, which comprises *Entosthodon* or represents a case of reversal or reduction within either one lineage, we inferred the relationships of these specimens based on phylogenetic analyses of DNA sequences of some loci sampled by Liu *et al*. (2012) complemented by data available on GenBank.

MATERIAL AND METHODS

We sampled the nuclear ITS and two spacers of the chloroplast loci *trn*L-F and *psb*A-*trn*H from two of five known collections of an enigmatic species. These sequences were inserted in a matrix drawn from Funariaceae sequenced by Liu *et al.* (2012) to which we added also two species of *Funaria* with ± symmetric capsules and more or less reduced peristomes, *F. polaris* Bryhn and *F. aequidens* Lindb. ex Broth. Specimen vaucher data and accession numbers are in Appendix 1.

Sequences were aligned manually in Bioedit following preliminary Clustal aligning (ITS: 1297 bp, *trn*L-F: 575 bp, *psb*A-*trn*H: 530 bp). Phylogenetic inferences were based on maximum parsimony using TNT (Golobov, 2003) and maximum likeklihood (Stamatakis, 2006) complemented by Bayesian analysis (Huelsenbeck & Ronquist 2001).

Bayesian analyses were performed using MrBayes 3.2.0, running in two parallel analyses, consisting each of six Markov chains of 10 000 000 generations with a sampling frequency of one tree each ten thousand generations and the chain temperature at 0.05. Parameters of the substitution model were estimated during the analysis (six substitution categories, a gamma-distributed rate variation across sites approximated in four discrete categories and a proportion of invariable sites). The consensus tree was then combined after the first 25% of trees were discarded as a burn-in. All analyses were performed on the Cipress Science Gateway (http://www. phylo.org/portal2). Maximum likelyhood analysis (RAxML, Stamatakis, 2006) was performed to estimate support of nodes in resulting tree.

The tree is rooted with the *Pyramidula* and *Goniomitrium*, the two genera of the Pyramiduloideae.

RESULTS

The topology of the strict consensus tree obtained from the ratchet MP analysis (not shown) are congruent with those proposed by Liu *et al.* (2012) based on 10 loci. Within the Funarioideae, species of *Funaria*, including *F. polaris* and *F. aequidens* compose a well defined and supported clade. The specimens from Zabaikalsky Territory compose the sister-group to the crown group comprising *Entosthodon* and the remaining Funariaceae. Within this heterogeneous lineage, the relationships are not well supported but overall similar to those reported by Liu *et al.* (2012) with *Funariella curviseta* (Schwägr.) Sérgio, *Entosthodon laevis* (Mitt.) Fife and *E. apophysatus* (Taylor) Mitt. composing a lineage sister to the remaining crown group species, and thus with *Entosthodon* resolved as a polyphyletic genus.

The Bayesian analysis (Fig.1) yields a similar topology: within the Funarioideae *Funaria* is sister to the remaining taxa, followed by *Afoninia*, and then the *Entosthodon-Physcomitrium-Physcomitrella* complex. The monophyly of this complex is not supported, but that of the two main clades corresponding to those recovered by Liu *et al.* (2012), *i.e*., with *Funariella* and the main crown group, is robust (PP=1.00).

DISCUSSION

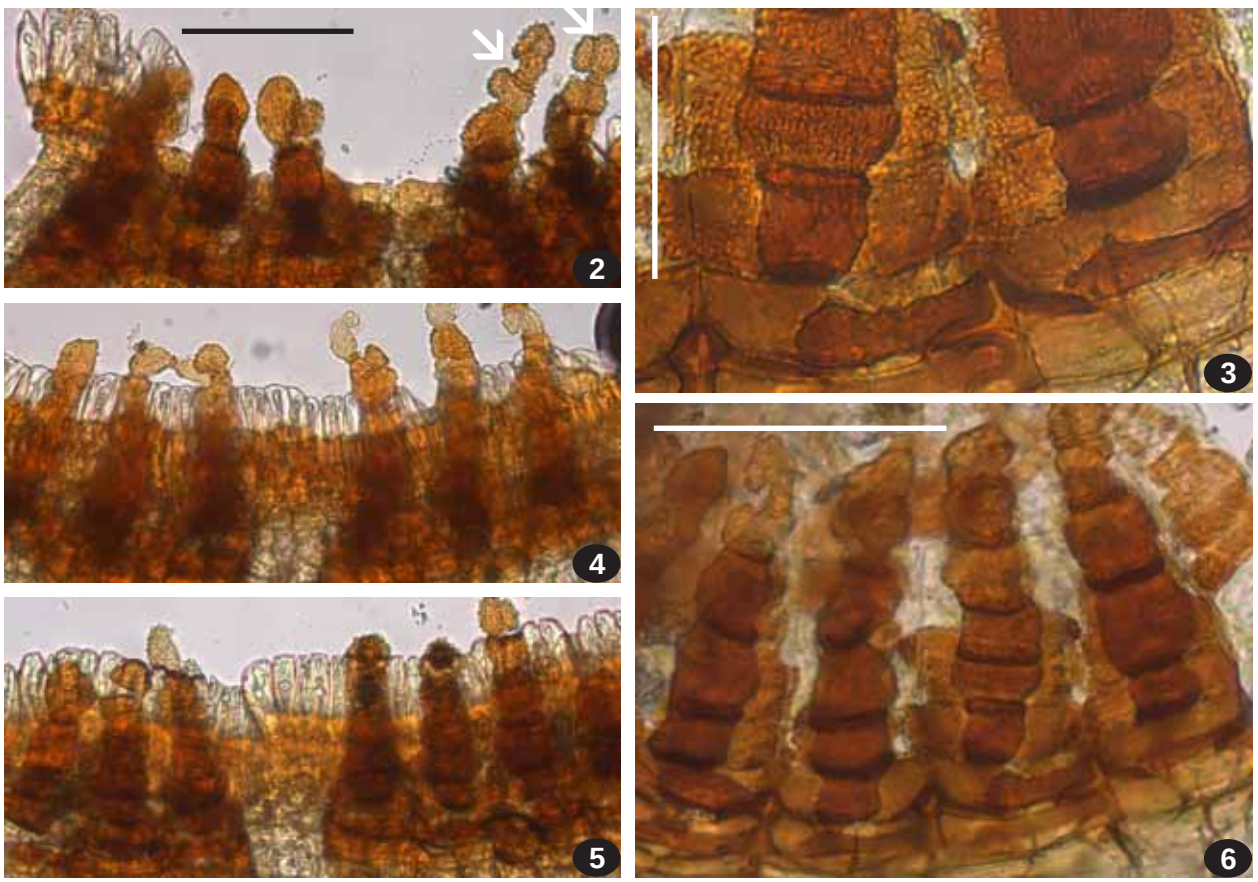
The Funariaceae display a broad variation in morphological traits and in particular of their sporophyte due in part of reductionary trends (Fife, 1985). Phylogenetic inferences by Liu *et al.* (2012) strongly suggest that homoplasy of traits used to diagnose supraspecific taxa is rampant except for the compound annulus, a character already considered by Fife (1985) to diagnose *Funaria.* Species of *Entosthodon*, which may exhibit asymmetric peristomate capsules but always lack such annulus evolved from an ancestor that also gave rise to *Physcomitrium* and all other taxa within the Funarioideae. Thus *Funaria* and *Entosthodon* are segregated in two distinct lineages. The specimens of the Zabaikalsky Territory with their intermediate morphology (*i.e.*, erect capsules dehiscing via a compound annulus) are resolved as a sister lineage to the crown group composed of the *Entosthodon-Physcomitrium* complex. They evolved from an ancestor shared with this group but distinct from the unique ancestor to extant *Funaria* species. In this position the specimens from Transbaikalia seem to mark a transition in the evolution of the Funarioideae, from a *Funaria* type to an *Entosthodon* type sporophyte.

This plant has a combination of morphological characters unknown in any other genus of Funariaceae. Therefore we propose a new genus, with the name honouring Olga M. Afonina, the bryologist from Komarov' Botanical Institute, St. Petersburg, Russia, a well-known researcher of the moss flora of Russia as a whole, and Transbaikalia in particular, a collector of this species.

Afoninia dahurica Ignatova, Goffinet & Fedosov, gen. et sp. nov. Figs. 2-12.

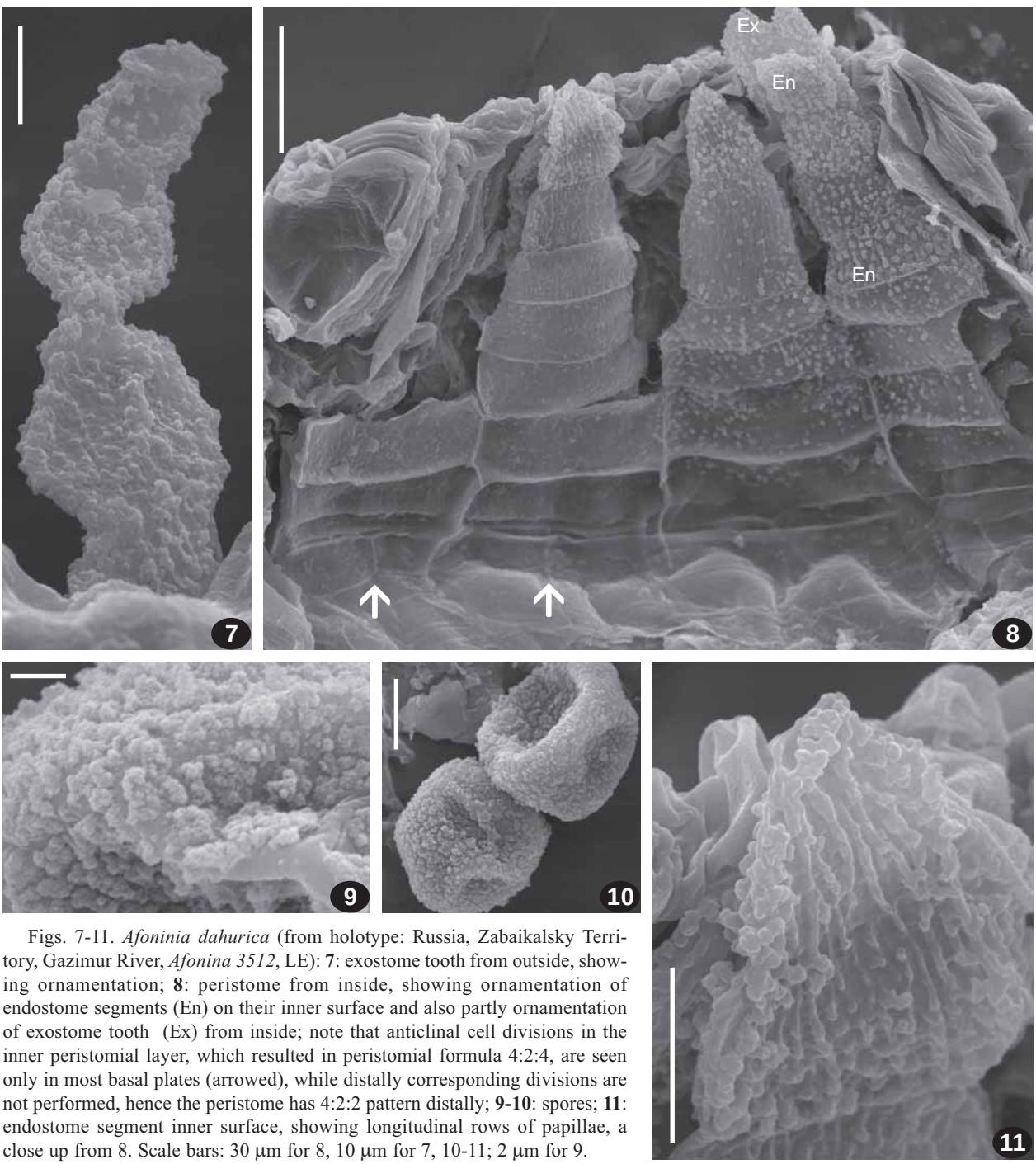
Type: Russia, Southern Siberia, Zabaikalsky Territory, Gazimuro-Zavodskoy District, midstream of Gazimur River, circa 12 km SW of Batakan Settlement, 51°50'46"N, 118°43'48"E, alt. 635 m. Rock outcrops. 23.VII.2012. Coll. O.M. Afonina #3512 (Holotype LE, isotypes MHA, MW).

Etymology: The species name indicates the collecting locality, Dahuria, a part of Trans-Baikal area, called by Russian colonists after a local population name.



Figs. 2-6. *Afoninia dahurica* (from holotype: Russia, Zabaikalsky Territory, Gazimur River, *Afonina 3512*, LE): 2, 4, 5 – capsule mouth from outside, showing annulus and peristome variation; 3, 6 – peristome attached to spore sac wall from outside: note the teeth tapering towards the bases, so their lower parts are narrower than endostome segments, while distally the teeth and segments have about the same width. Median line is seen on few teeth (arrowed in 2). Scale bars: 100 μm for 2, 4-5; 50 μm for 3, 6.

Plants pale green, dull green or yellowish, growing on soil as individual shoots or forming loose tufts. Stems 2.5–4.0 mm, green or brownish at base, with well-differentiated hyalodermis, abruptly delimited sclerodermis consisting of 1–2 rows of thick-walled red-brown cells, very thin-walled medullar cells and narrow central strand. Lower leaves small and distant, upper leaves enlargered and crowded in distal part of stem, contorted when dry, erect-spreading when moist, (1.8–)2.5–3.5×(0.8–)1.2–1.6 mm, spatulate, slightly concave, widely acute or obtuse at apex; margins obtusely serrulate in distal 1/2, entire in proximal part, plane; costa moderately strong, slightly narrowing upwards, ending 4–6 cells below leaf apex; distal and median laminal cells 40–60×(18–)22–28(–40) μm, 4-6-angled, thin-walled, not differentiated or colored at margins, basal laminal cells elongate rectangular, 90–120×30–40 μm, basal marginal cells slightly shorter. Apparently autoicous (smaller male shoot mixed among plants with sporophytes, but seems so easily broken off that no one obvious junction was seen in a limited material available for study). Male shoots slightly smaller than female ones. Androecia terminal, perigonial leaves similar to stem leaves, obtusely serrulate throughout. Paraphyses mostly 5-celled, 3 basal cells narrow rectangular, two upper cells inflated, more than twice wider, both spheric, or terminal cell pyriform, all cells not colored. Seta 1.0–1.6 mm, light reddish brown. Capsules 2.0–2.6 mm long, ca. 0.8 mm wide, symmetric, cylindric, erect or slightly inclined, yellowish to light brownish when mature, urn smooth, neck ca. 1/4–1/3 the capsule length, weakly delimited; exothecial cells oblong, ± irregular, rhombic and hexagonal, slightly bulging, with moderately thickened outer walls, with cuneate thickenings of radial walls, at urn mouth in 3 rows transversely rectangular to quadrate, with numerous one-celled stomata at the neck and urn base. Annulus compound, revoluble, consisting of 2 rows of large inflated cells. Peristome double, hardly extending above urn mouth; exostome teeth 16, attached to endostome, 120–140 μm long, slightly narrowing distally, obtuse, occasionally irregularly notched in upper part, finely papillose throughout on outer surface, with low ventral trabeculae; endostome segments 16, opposite to teeth, ca. 150 μm long, fused at base and forming low basal membrane, segments irregular in shape, slightly wider than exostome teeth, vertically papillose-striolate on outer surface. Operculum flat or weakly convex, indistinctly mamillate, with red rim. Spores 18–21 μm, brownish, finely verrucose. Calyptra cucullate, inflated below, with rostrum ca. 0.9 mm long.



Figs. 7-11. *Afoninia dahurica* (from holotype: Russia, Zabaikalsky Territory, Gazimur River, *Afonina 3512*, LE): **7**: exostome tooth from outside, showing ornamentation; **8**: peristome from inside, showing ornamentation of endostome segments (En) on their inner surface and also partly ornamentation of exostome tooth (Ex) from inside; note that anticlinal cell divisions in the inner peristomial layer, which resulted in peristomial formula 4:2:4, are seen only in most basal plates (arrowed), while distally corresponding divisions are not performed, hence the peristome has 4:2:2 pattern distally; **9-10**: spores; **11**: endostome segment inner surface, showing longitudinal rows of papillae, a close up from 8. Scale bars: 30 μm for 8, 10 μm for 7, 10-11; 2 μm for 9.

Differentiation. There is no species in the Zabaikalsky Territory that can be confused with *Afoninia*. The Funariaceae are represented in the area by *Funaria hygrometrica* and *Entosthodon pulchellus*, both having asymmetric and inclined capsules and well-developed peristome, while species of *Physcomitrum* and *Entosthodon hungarius*, reported from there, are eperisomate.

The species of the clade most closely related to *Afoninia*, *i.e.*, Mediterranean *Funariella curviseta*, South American *Entosthodon laevis*, and Australian *E. apophysatus*, all have inclined and more or less asymmetric capsules, non-revoluble annulus, and different peristomes: *Funariella* is eperistomate, *Entosthodon laevis* has well developed double peristome, *E. apophysatus*,in contrast, develops only a rudimentary endostome, whereas *Afoninia* has a strongly reduced double peristome. Other differences include mitrate calyptrae in both these *Entosthodon species* versus *Afoninia* and *Funariella*, both sharing cucullate calyptra. However, the latter genus is characterized by a short rostrum of the calyptra, whereas in *Afoninia* the rostrum is long, resembling that of *Funaria hygrometrica*.

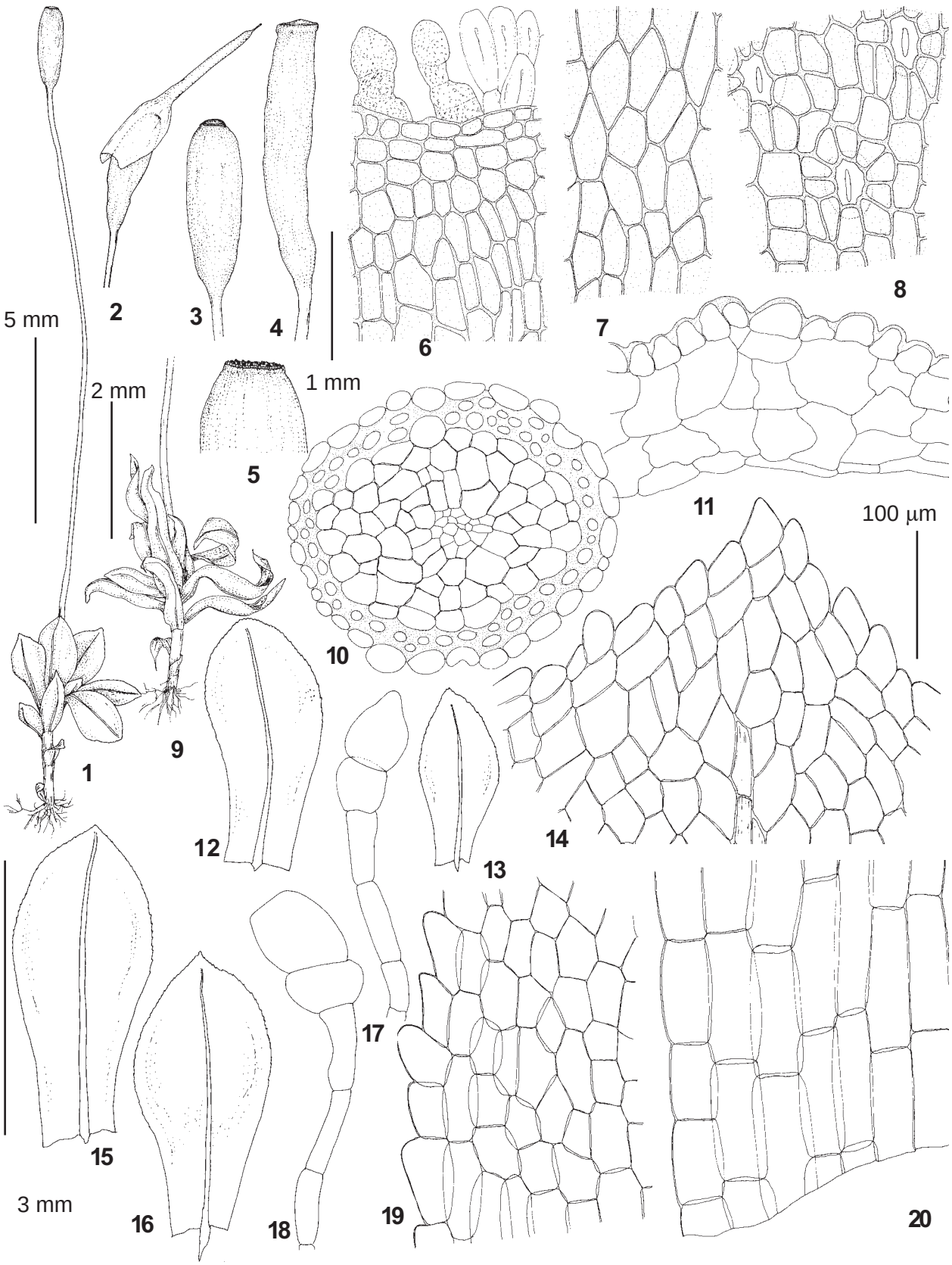


Fig. 12. *Afoninia dahurica* (from holotype: Russia, Zabaikalsky Territory, Gazimur River, *Afonina 3512*, LE): 1 – habit, wet; 2, 4 – capsules; dry; 3,5 – capsules, wet; 6 – peristome & exothecium at urn edge; 7 – exothecium in the middle part of urn; 8 – exothecium & stomata at urn base; 9 – habit, dry; 10 – stem transverse section; 11 – transverse section of urn wall in the middle part of urn; 12-13, 15-16 – leaves; 14 – upper laminal cells; 17-18 – paraphyses from perigonium; 19 – median laminal cells; 20 – basal laminal cells. Scale bars: 5 mm for 1; 3 mm for 12-13, 15-16; 2 mm for 2-3, 9; 1 mm for 4-5; 100 μm for 6-8, 10-11, 14, 17-20.

Although the *Funaria*-like annulus and the long rostrate calyptra may point to affinities of *Afoninia* to species of *Funaria*, inferences from DNA data do not support this hypothesis, and similarities with *F. aequidens*, *F. flavicans* and *F. polaris*, must hence reflect homoplasy. Resolving *Afoninia* outside of *Funaria* s. str. is consistent with it developing a smooth and symmetric urn, an erect capsule and a peristome only slightly exceeding the level of annulus, all features not known from *Funaria*.

Entosthodon is very variable and likely will be split in the future into monophyletic entities; however, in any case all its species in modern definition lack a revoluble annulus, and *E. attenuatus*, the type of the genus has long peristome teeth.

Ecology: *Afoninia dahurica* was collected in five localities in the eastern part of Zabaikalsky Territory, at altitudes ranging from 635 m to 1170 m a.s.l., on soil-covered rock outcrops, on fine soil in crevice and in niches between rocks, and on bare soil on rocky slope with steppe-like vegetation. In the type locality, in the end of July the plants had both immature and almost ripe capsules and well-preserved male and female inflorescences, while in other places, plants had mostly mature and deoperculate sporophytes despite of approximately the same time of collecting.

Additional specimens examined: ASIATIC RUSSIA: **Zabaikalsky Territory**: ***Kalgansky District,*** Nerchinsky Mt. Range, 10 km from Kalga Settlement to Aleksandrovsky Zavod Settlement, 50°56’37”N, 118°41’23”E, 754 m alt., 26.VII.2012, *Czernyadjeva 31-12* (LE, MHA); ***Kyra District***, Sokhondinsky Nature Reserve: Enda River, ca. 49°27’N, 110°51’E, 1070 m alt., 14.VII.2010, *Czernyadjeva 19-10* (LE, MHA); Agutsa River, ca. 49°38’N, 111°27’E, 1170 m alt., 18.VII.2010, *Czernyadjeva 28-10* (LE, MHA); Gazimuro-Zavodsky District, Pryamoy Mulday River, 52°14’48”N, 119°23’22”E, 664 m alt., 22.VII.2012, *Afonina* #2812 (LE, MHA).

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APPENDIX 1.

GenBank accession number are given in the following order: ITS, *trn*L-F, *psb*A-*trn*H.

Afoninia dahurica 1 (holotype: Russia, Zabaikalsky Territory, *Afonina #3512*, LE): KP342459, KP342465, KP342461; *Afoninia dahurica* 2 (Russia, Zabaikalsky Territory, *Afonina #2812*, LE): KP342458, KP342464, KP342460; *Funaria polaris* (Russia, Krasnoyarsk Territory, Taimyrsky Autonomous District, *Fedosov #13-3-0670*, MW): KP342456, KP342463, –; *Funaria aequidens* (Russia, Caucasus, Kabardino-Balkaria, *Ignatov & Ignatova #05-1766*, MW): KP342457, KP342462, –.