

A REVISION OF THE GENUS LINDBERGIA (LESKEACEAE, BRYOPHYTA)
IN RUSSIA

РЕВИЗИЯ РОДА LINDBERGIA (LESKEACEAE, BRYOPHYTA)
В РОССИИ

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Abstract

The genus *Lindbergia* is subdivided into 3 groups basing on morphological and molecular characters, and all these groups are represented in Russia. *Lindbergia brachyptera* is excluded from the Russian moss flora, it likely occurs only in North America; Russian plants referred to it belong to a closely related *L. grandiretis*. Specimens reported from the Russian Far East as *Lindbergia duthiei* and *L. japonica* are re-identified as *L. sinensis*. *Mamillariella*, a monospecific genus, is the closest relative to *L. sinensis* and is transferred to *Lindbergia*. *Lindbergia dagestanica* Ignatova & Ignatov sp. n. is described from the East Caucasus; this species is closely related to the American *L. mexicana* and African *L. patentifolia*. Plants of the latter group have never been reported from Eurasia before.

Резюме

По данным морфологического и молекулярно-филогенетического анализа род *Lindbergia* подразделен на 3 группы, причем все они представлены во флоре России. *Lindbergia brachyptera* исключена из флоры России, вероятно, она растет только в Северной Америке, а так определявшиеся растения с Кавказа и из Сибири относятся к близкому виду *L. grandiretis*. Образцы с Дальнего Востока, определявшиеся как *L. duthiei* и *L. japonica*, отнесены к *L. sinensis*. *Mamillariella*, монотипный род, очень близок к *L. sinensis* и переведен в род *Lindbergia*. Из Дагестана описан новый вид *Lindbergia dagestanica* Ignatova & Ignatov sp. n., близкородственный американской *L. mexicana* и африканской *L. patentifolia*. Представители последней группы ранее в Евразии известны не были.

KEYWORDS: *Lindbergia*, molecular phylogeny, mosses, peristome, Russia

INTRODUCTION

Lindbergia is a relatively small genus that has never been revised worldwide since Brotherus' treatment in "Die Naturlichen Pflanzenfamilien" (1925). At the same time, various regional treatments often described local species without sufficient comparison with other territories, so our study of the genus in Russia urged necessity of a revision in a broader scope.

The first finding of *Lindbergia* in Russia was made by V.F. Brotherus in the Caucasus. The specimen was described as *Leskea grandiretis* by S.O.Lindberg in Brotherus' "Musci Caucasicus" (1892). Later this species was synonymized with *Lindbergia austinii* (Sull.) Broth. (= *L. brachyptera*) by Holzinger (Bryologist 6: 75. 1903; cited by Wijk et al., 1964) and for a long time had not been accepted as a separate species until

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Ignatov, Afonina, Ignatova *et al.* (2006) resurrected it as an independent species, although without arguments, which we are going to present here.

Lazarenko (1941) reported *L. japonica* from Primorsky Territory of the Russian Far East, and this record was repeated without any revision in subsequent accounts of the Russian Far East bryoflora (Bardunov & Cherdantseva, 1982) and checklists (e.g. Ignatov, Afonina, Ignatova & al., 2006). Besides, Lazarenko (1934) described a monospecific genus *Mamillariella* from the same area, which was accepted by all subsequent authors in its original volume and status, including the revision of Buck (1980). The mamillate seta of this species is a unique character in the whole Leskeaceae, according to the traditional approach to the family. However, Gardiner *et al.* (2005) and Ignatov *et al.* (2007) have found in their molecular phylogenetic analyses that *Mamillariella* is closely related to *Lindbergia duthiei* (based on a specimen from the Russian Far East).

Bardunov (1969) reported from south Siberia, Transbaikalia *L. brachyptera*, the species described from eastern North America and then published for China by Levier (1906) and subsequent authors. Later on, Bardunov & Cherdantseva (1982) reported from Primorsky Territory one more species of *Lindbergia*, *L. duthiei*, a species originally described from the Western Himalayas (Brotherus, 1898).

Our interest to the genus was raised when attempting to identify one enigmatic specimen from Dagestan, eastern part of the Caucasus near the Caspian Sea. This area has a quite xeric climate and many interesting xerophytic mosses, including *Indusiella* and *Jaffueliobryum* (see also Ignatov *et al.*, 2010). After an expanded search, we found its surprising subidentity with *Lindbergia mexicana* (Besch.) Cardot from North and South America, and with *L. patentifolia* Dixon from the South and East Africa. Their morphological similarity with the Caucasian plant left no doubts on their relationship, but raised the question on their generic position, as this group of species has a number of differences from *Lindbergia brachyptera*, the type of the genus.

MATERIAL AND METHODS

Morphological studies include the material on *Lindbergia* from H, IRK, KW, LE, MW, MHA, S, SASY, VLA.

Peristomes were studied and photographed under Com Scan 2 SEM. Papillae were studied in both transmitted light and with fluorescence of the berberin stained specimens under Olympus SX41, $\lambda = 488$ nm.

Molecular studies include the sequencing of nr ITS and cp *trnL-F* of *Lindbergia*, which were analyzed with data from the previous analysis of pleurocarps (Ignatov *et al.*, 2007). This previous set was reduced, so mostly Leskeaceae species were retained. Specimen vouchers and GenBank accessions are in Appendix 1.

Laboratory protocol was essentially the same as in some of our previous analyses (e.g. Gardiner *et al.*, 2005). Maximum parsimony analysis was performed in Nona (Goloboff, 1994) under Winclada shell (Nixon, 1999).

One *trnL-F* short inversion region of 3 nucleotides exhibits strong variation (CCT – AGG), so it was omitted in the analysis according to the suggestion of Quandt & Stech (2005).

RESULTS

ITS analysis. The *Lindbergia* s. ampl. species were resolved into three clades, each having a high support (Fig. 1 A). These three clades form a bigger clade, which includes also a widespread Australian species, *Pseudoleskeopsis imbricata*. The support of this bigger clade was found to be low, 57.

The three well supported clades are as follows: (1) *L. brachyptera* + *L. grandiretis*; (2) *L. sinensis* + *Mamillariella geniculata*; (3) *L. mexicana* + *L. patentifolia*; their jackknife support is 99, 85 and 98 correspondingly.

Strict consensus tree based on *trnL-F* (Fig. 1 B) resolved *Lindbergia* species in one clade that includes also *Pseudoleskeopsis imbricata* (Fig. 1 B).

DISCUSSION

ITS tree provided topology that is in general congruent with those previously found in a number of analyses (Gardiner *et al.*, 2005; Ignatov *et al.*, 2007; Garcí'a-Avila *et al.*, 2009; Du *et al.*, 2005).

The obtained topology raises the question if the three clades are better to treat as separate genera or infrageneric units of *Lindbergia*. There are pros and cons in both ways, but we are now inclined to keep a conservative approach, minimizing nomenclatural changes by a two following reasons.

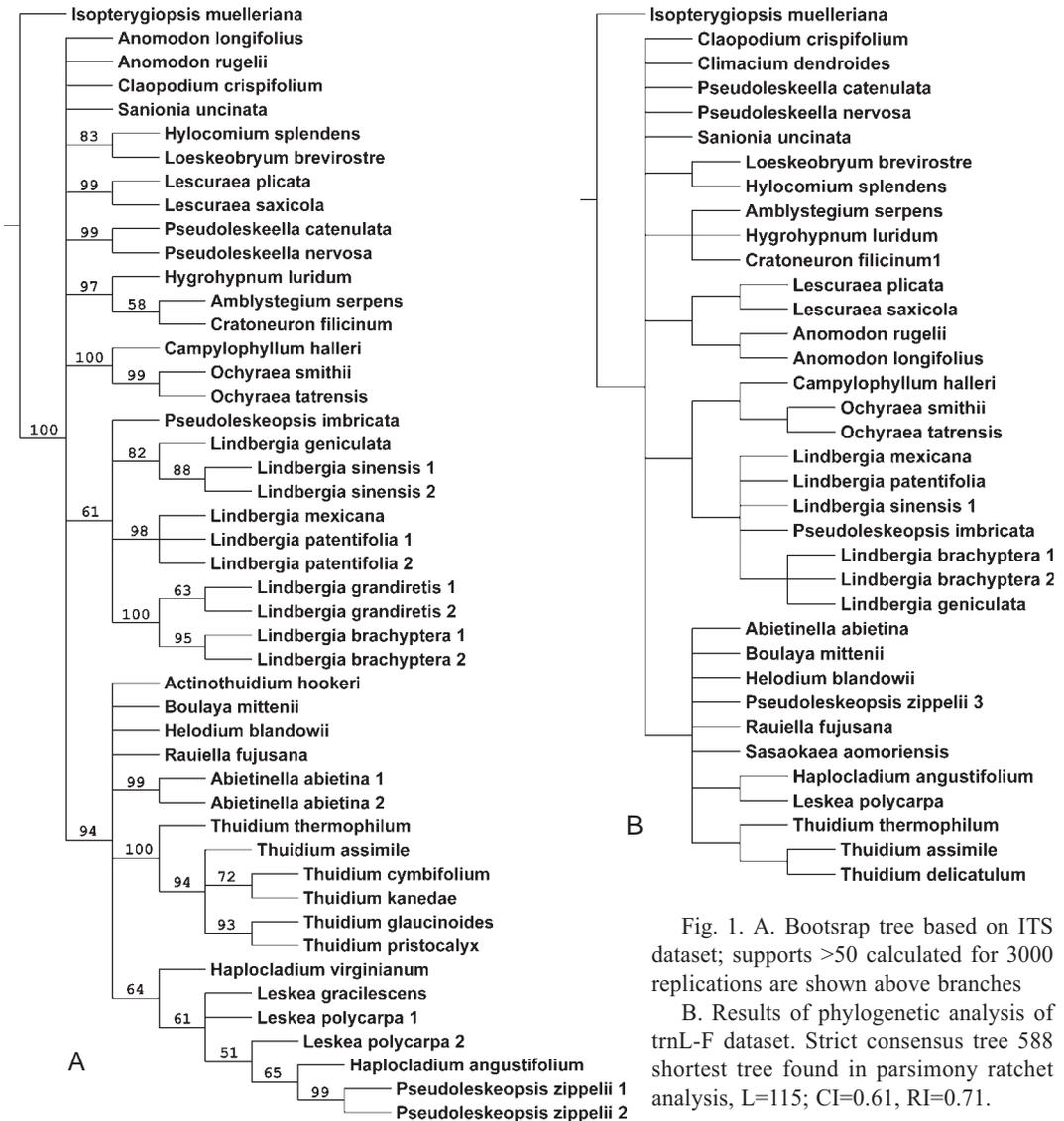


Fig. 1. A. Bootstrap tree based on ITS dataset; supports >50 calculated for 3000 replications are shown above branches

B. Results of phylogenetic analysis of trnL-F dataset. Strict consensus tree 588 shortest tree found in parsimony ratchet analysis, L=115; CI=0.61, RI=0.71.

(1) *Pseudoleskeopsis imbricata*. This species is really distinct gametophytically from the *P. zippellii*, the type of the genus *Pseudoleskeopsis*, and it obviously needs a more natural placement. However, the simple transfer to *Lindbergia* would be premature, as there are a number of other probably related genera in South Hemisphere, not included in the present analysis. Especially this concerns *Leskeadelphus*, which affinity with the *Pseudoleskeopsis* has recently been found by Cox et al. (2010). Both *Leskeadelphus* and *Pseudoleskeopsis imbricata* have more or less complete peristomes with cross striolate exostome teeth (Buck, 1980). On the other

hand, there is a number of pleurocarpous genera where species with perfect and reduced peristomes occur, e.g. *Homalothecium* (Huttunen et al., 2008), *Pylaisia* (Arikawa, 2004), and in acrocarpous families such examples are far more numerous.

(2) Excepting *Pseudoleskeopsis imbricata*, there are no other genera appearing in between the three groups of *Lindbergia*. Thus their acceptance both as genera or subgenera could be admitted, the latter being better, as no nomenclatural changes will be in need.

Morphological differences of representatives of these three clades are as shown in Table 1.

Table 1. A comparison of three groups of species in *Lindbergia*.

	<i>L. brachyptera</i> -group	<i>L. sinensis</i> -group	<i>L. mexicana</i> -group
Leaf shape	acuminate	acuminate	acute to acuminate
Acumen looks	±hyaline	green	green
Leaf margin	entire	entire	serrulate
Leaf papillae	large, simple to forked	small and indistinct to	absent
Seta	smooth	smooth or rough	smooth
Capsule shape	ovate	ovate	cylindrical
Segments	absent	absent	absent to present
Basal membrane	present	present or absent	present
Teeth outside	weakly to moderately papillose	strongly papillose	moderately papillose to smooth

TAXONOMY

Lindbergia Kindb., Gen. Eur. N. Amer. Bryin. 15. 1897.

Plants slender, dull, green, olivaceous or brownish, in thin mats. Stems creeping, irregularly or ± pinnately branching. Stem and branch leaves similar, crowded, appressed and imbricate when dry, widely spreading when moist, ovate or ovate-lanceolate, acute or acuminate, slightly concave, shortly decurrent; margins plane, entire or serrulate; costa single, stout, reaching 2/3–3/4 the leaf length or percurrent; lamina smooth or papillose on both sides, papilla single per cell on each side, simple or forked; upper and median laminal cells ± isodiametric, rounded, shortly ovate or rhombic and short rectangular, with thin or moderately thickened walls, with corner thickenings; basal juxtacostal cells not differentiated; basal marginal cells in 4–10 oblique rows transversely ovate, gradually transiting to isodiametric median cells. Autoicous. Perichaetial leaves pale, erect, long-acuminate from a sheathing base, not plicate, costa short, indistinctly delimited, cells rectangular, smooth. Setae erect, smooth or mamilllose. Capsules oblong-cylindrical, erect and symmetric or slightly asymmetric, narrowed to the mouth. Peristome double, inserted well below the mouth; exostome teeth lanceolate, smooth or papillose; endostome absent or present, consisting of low, smooth or papillose basal membrane, segments absent or present, narrow and fragile. Operculum low conic, with short, straight or curved obtuse beak. Calyptrae cucullate, naked.

Lindbergia grandiretis (Lindb. ex Broth.) Ignatov & Ignatova, Arctoa 15: 49. 2006. – *Leskea grandiretis* Lindb. ex Broth., Acta Soc. Sci. Fenn. 19(12): 97. 1892. Figs. 2-3; 4: 5-7; 8: 5-9

Lectotype (selected here): “*Leskea grandiretis* Lindb. n. sp., Caucasus: Balta ad fl. Terek, 19/5 1881, leg. V.F. Brotherus” (H-BR 2483003!); isotype in LE, small difference in date is: “V.1881”); Syntypes (same label as lectotype, H-BR 2483002! [scanty specimen]); Lars ad fl. Terek, 28/5 1881 leg. V.F. Brotherus” H-BR 2483004! [without sporophytes]). Lectotype is selected as the most representative collection.

Plants dull green, olivaceous or brownish green, in thin mats or growing as admixture to other bryophytes. Stems to 4 cm long, pinnately or irregularly pinnately branching, branches arcuate, 2–5 mm long. Stem and branch leaves 0.6–1.3×0.3–0.5 mm, weakly concave to almost plane, ovate-lanceolate, longly acuminate, with narrow, straight or recurved apices, looking hyaline when dry; margins entire, occasionally uneven; costa ending at 2/3–3/4 the leaf length; cells of leaf acumen elongate, smooth, uppermost 1–4 apical cells in one row; upper and median laminal cells rounded, 10–15 µm in diameter, with thin to moderately thickened walls, weakly collenchymatose, not or slightly bulging in transverse section, with one forked or occasionally simple papillae per cell on both surfaces. Seta smooth, 5–7 mm, reddish brown. Capsule ovate, ca. 1.0 mm long, symmetric, narrowed to the mouth, light reddish brown, red-brown at mouth, operculum conic, obtuse. Annulus of large cells, falling or persistent. Exostome ca. 200 µm long, teeth obtuse at apex, brown and smooth proximally, whitish and papillose distally on outer surface, dorsal trabeculae very low; endostome of basal membrane ca. 1/3 of exostome length, pale brownish, almost smooth, segments rudimentary. Spores 10–12 µm, finely papillose.

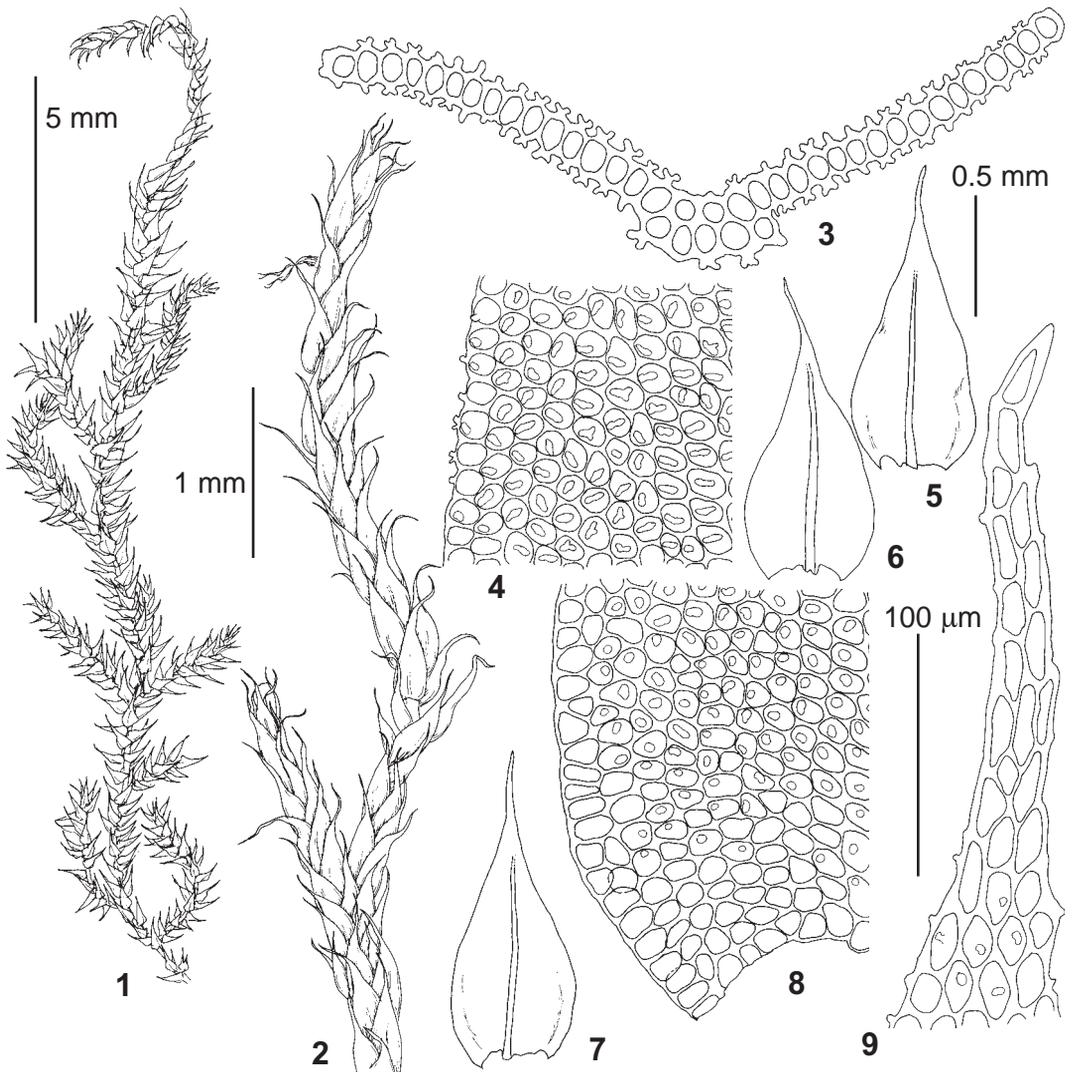
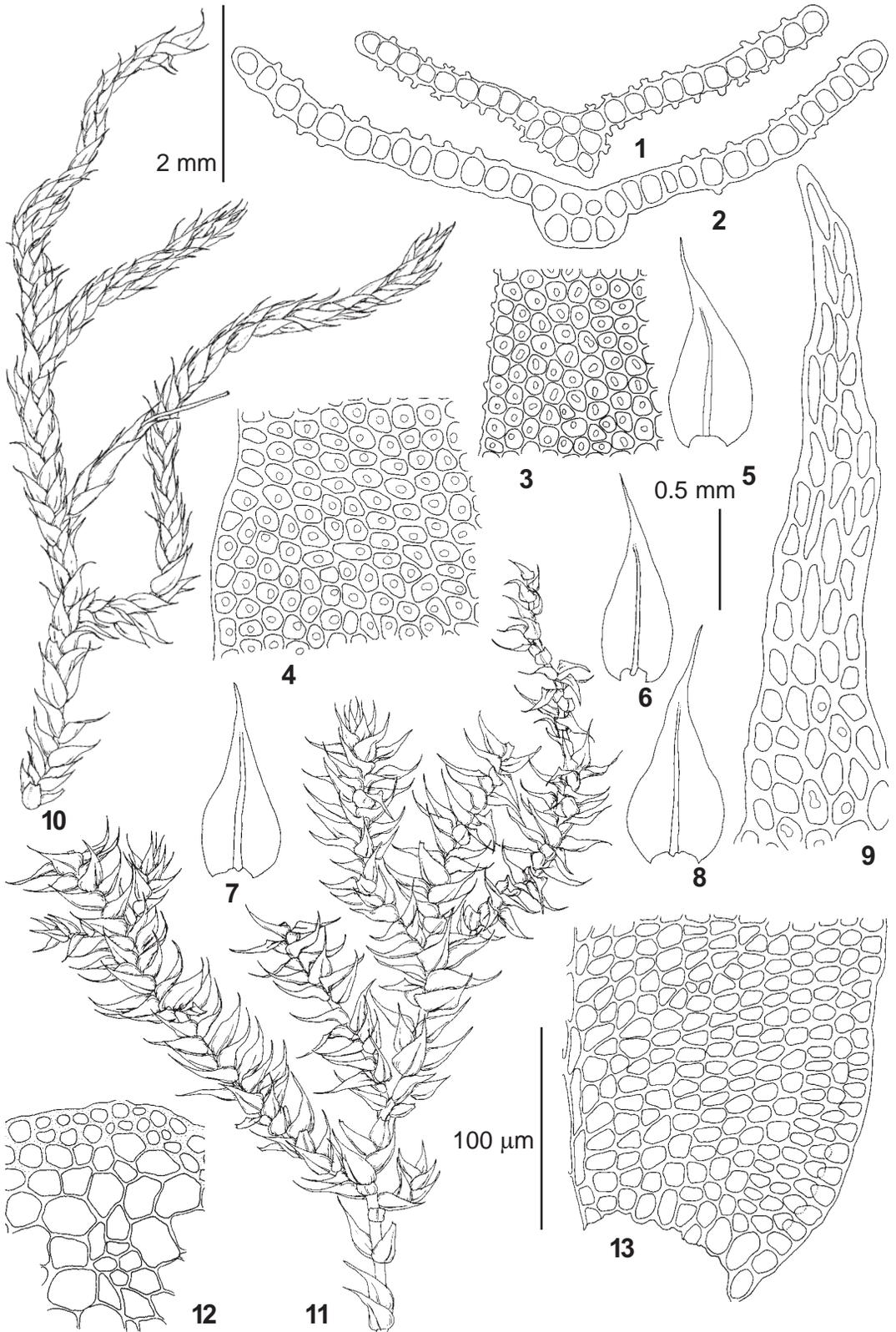


Fig. 2. *Lindbergia grandiretis* (from Russia, Caucasus, Ignatov & Ignatova 05-1874): 1 – habit, wet; 2 – habit, dry; 3 – leaf transverse section; 4 – median laminal cells; 5-7 – leaves; 8 – basal leaf cells; 9 – upper laminal cells. Scale bars: 5 mm for 1; 1 mm for 2; 0.5 mm for 5-7; 100 μ m for 3-4, 8-9.

Specimens examined: ARMENIA: Gorissky Distr., Vorotan River Canyon, between Galidzor and Khot, ca. 1000 m elev., on rotten trunk of *Juglans regia*, 25.V.1975, Manakyan (LE); RUSSIA: CAUCASUS: Stavropol Territory, Kislovodsk, on *Fraxinus*, 1915, leg. V.P. Savich, det L.I. Savich (LE); Kabardino-Balkaria, Verkhnyaya Balkaria, Ignatov et al. #05-1874, 1864 (MHA); Dagestan, Gunib, Ignatov & Ignatova #09-496; 674, 642, 645, 368, 371, 716a (MHA); SIBERIA: Buryatia, Bichura River near Bichura settlement 50°31'N, 107° 39'E, 753 m alt., on rocks 6.VII.2007 Afonina #01607 (LE); Zabaikalsky Territory: Nizhny Tsasuchey, in *Ulmis pumila* thicket, on *Ulmus*, 1-1,5 m above ground, common, 1.VII.1988,

Bardunov (LE); Buryat-Agin District, Alhanai Nat. Park 50°56'N, 113°13'E, on rocks, 9.VII.2006 Afonina #2206 (LE); Oka Distr., Tsagan-Oluy 12.X.1909, P. Mikhno (LE); Nercha River, Stary Olov, on rocks, 20.VI.1964, Bardunov (LE; KW#13138);

Both the type of *Leskea grandiretis* and numerous recent collections from Caucasus have distinct forked papillae (Fig. 2; 4; 5, 7). The latter differentiate it from the North American *L. brachyptera* where papillae are solid, quite massive, often with unclear outlines, as their 'foothills' are quite shallow (Figs. 4: 1-4). The forked papillae in *L. grandiretis* are best expressed at



the level of costa end, while below leaf middle they are also massive, sometimes two-topped or just round (Fig. 4: 6). Although in American plants the papillae are reported as ‘occasionally bluntly and minutely 2-3 forked’ (Crum & Anderson, 1981), we have seen such papillae very seldom among solid ones, and they always were only quite indistinctly forked.

Siberian plants have papillae somewhat less forked than in Caucasian plants, although in this character they are obviously closer to the latter than to American plants. ITS data fully support this conclusion: five substitutions and one indel differentiate both Caucasian and Transbaikalian specimens from two American ones. Search of *L. brachyptera* specimens from Japan and China have yielded no one which could be confirmed. Thus we suspect that *L. brachyptera* is a species confined to North America, while in East Asia there is only *L. grandiretis*. A recently described Chinese *L. brevifolia* C. Gao is likely the same, as the main its difference from *L. brachyptera* is described as forking vs. solid papillae (Cao Tong et al., 2002).

Lindbergia sinensis (Müll. Hal.) Broth., Nat. Pflanzenfam. 1(3): 993. 1907. – *Schwetschkea sinensis* Müll. Hal., Nuovo Giorn. Bot. Ital., n. ser. 3: 111. 1896. Figs. 5; 4: 8-9 & 13; 10

Type: Bryotheca E. Levier, *Schwetschkea sinensis* C. Müll., Nuovo Giornale botanico italiano 1985 p. 111 c.fr., China interior, provincia Schen-si sept., in medio monte Si-Ki-tzui-sau Jul 1984 legit Rev. Jos. Giralardi determ Prof. C. Müller sub n° 908” (isotype H-BR 2483031!, annotated by Cao Tong).

Lindbergia magniretis (Müll. Hal.) Broth., Nat. Pflanzenfam. 1(3): 993. 1907. – *Leskea magniretis* Müll. Hal., Nuovo Giorn. Bot. Ital., n. ser. 4: 274. 1897.

Type: Bryotheca E. Levier, *Leskea magniretis* C. Müll., Nuovo Giornale botanico italiano 1897 p. 274, 1898 p. 207 c.fr., China interior, provincia Schen-si sept., Zu-lu(caten. Lao-y-san) 22 Oct. 1896 legit Rev. Jos. Giralardi, determ Prof. C. Müller sub n° 2222” (H-BR 2483026!), annotated by Paulo Camara, 2004, Missouri Bot. Garden as isolectotype.

?*Lindbergia duthiei* (Broth.) Broth., Nat. Pflanzenfam. I(3): 993. 1907. – *Leskea duthiei* Broth., Acta Soc. Sci. Fenn. 24: 31. 1899.

Lectotype (*selected here*): “11459 Flora of Kashmir, *Leskea Duthie* Broth., Sind Valley 6-7000 ft. 24.6.92, Legit J.F.Duthie” (H-BR 2483024!). Protologue cited 2 places in Kashmir; both specimens are in H-BR and they are subidentical.

Plants dark green or brownish green, in thin mats. Stems 1-3 cm long, irregularly or almost pinnately branching, branches straight or arcuate, 2-5 mm long. Stem and branch leaves 0.9-1.3×0.4-0.7 mm, weakly concave to almost plane, ovate-lanceolate, shortly to longly acuminate, with straight or recurved apices when dry; margins entire, occasionally uneven; costa ending at 2/3-3/4 the leaf length; cells of leaf acumen elongate; upper and median laminal cells rounded, 10-12×10-14 µm, firm-walled, weakly collenchymatose, not bulging in transverse section, smooth or with one very small, hardly visible simple papilla per cell on dorsal or both surfaces. Seta smooth, 5-7 mm, reddish. Capsule ovate, 1.0-1.1 mm long, symmetric, narrowed to the mouth, reddish-brown, operculum conic, with short obtuse beak. Annulus absent. Exostome ca. 220 µm long, teeth obtuse at apex, whitish, finely papillose on outer surface, dorsal trabeculae moderately high; endostome of basal membrane ca. 1/4 of exostome length, white, finely papillose, segments absent. Spores 20-25 µm, reddish brown, finely papillose.

Specimens examined: RUSSIA: Primorsky Territory: Nakhodka, Sestra Mt., *Ignatov 08-257* (MHA); Khanka Distr., Melgunovka River, *Ignatov 08-370* (MHA); Vladivostok, Bolshaya Sedanka, *Ignatov et al., 06-2476* (MHA); Khabarovsk, *Ignatov 97-567* (MHA); Vladivostok, between Okeanskaya and Sanatoriumaya, *Gorobets #542* (MHA); Vladivostok, *Gorobets #60* (MHA); Lazo Distr., Kamenka 24.IX.1974 *Bardunov & Cherdantseva* (IRK, as *L. duthiei*); Lazo Distr., Kievka *Gorobets #84* (MHA); Lazovsky Distr., Kamenka 24.9.1974 *Bardunov & Cherdantseva* (MHA); Vladivostok, Okeanskaya, in forest above the line of frequent fog, on oak trunk, 30.IX.1933, *Lazarenko* (LE); Vladivostok surroundings, Bogataya Gri-

Fig. 3. *Lindbergia grandiretis* (from Russia, Zabaikalsky Territory, Nizhniy Tsasuchey, 1.VII.1988, *Bardunov*, LE): 1-2 – leaf transverse sections; 3-4 – median laminal cells; 5-8 – leaves; 9 – upper laminal cells; 10 – habit, dry; 11 – habit, wet; 12 – stem transverse section; 13 – basal leaf cells. Scale bars: 2 mm for 10-11; 0.5 mm for 5-8; 100 µm for 1-4, 9, 12-13.

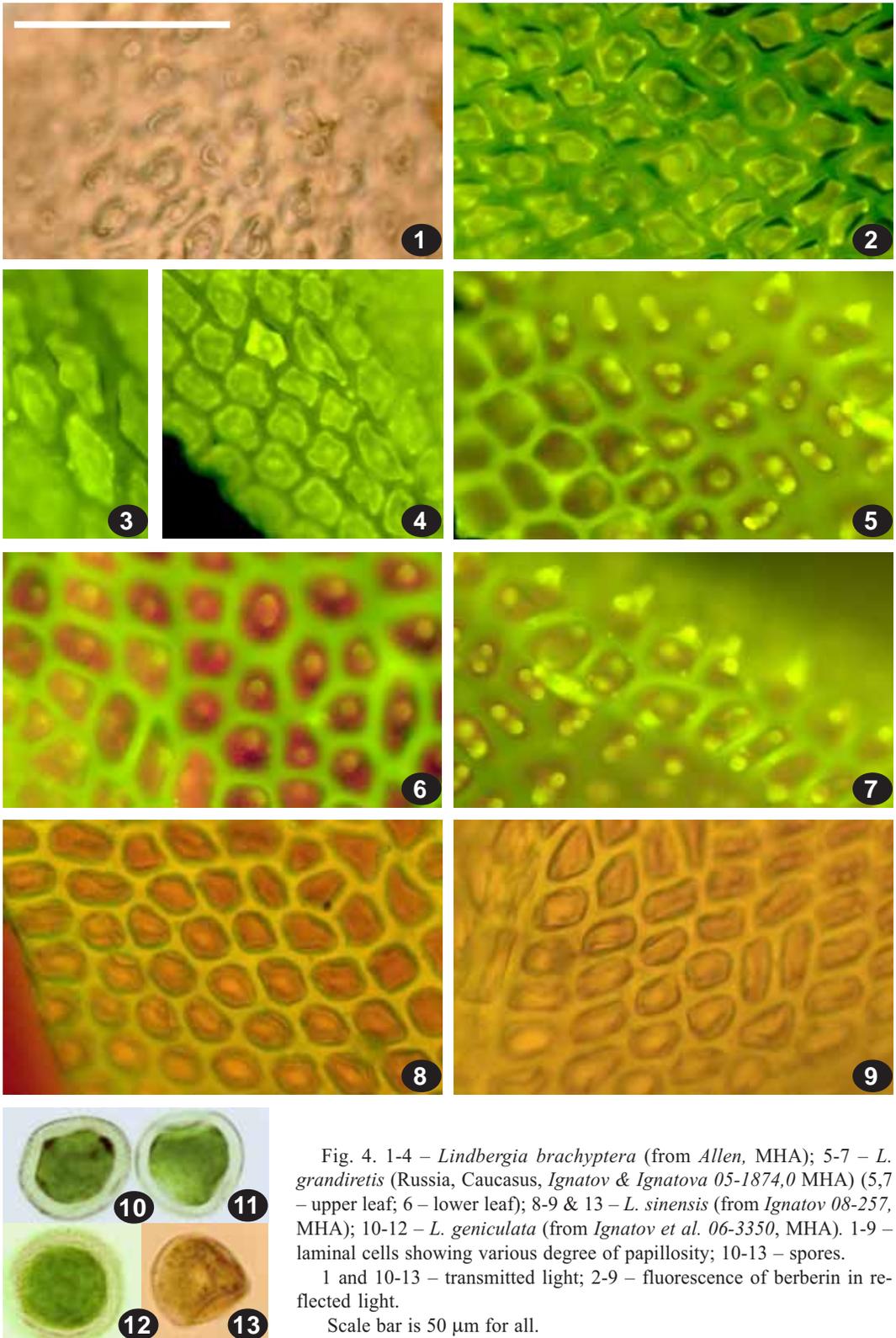


Fig. 4. 1-4 – *Lindbergia brachyptera* (from Allen, MHA); 5-7 – *L. grandiretis* (Russia, Caucasus, Ignatov & Ignatova 05-1874,0 MHA) (5,7 – upper leaf; 6 – lower leaf); 8-9 & 13 – *L. sinensis* (from Ignatov 08-257, MHA); 10-12 – *L. geniculata* (from Ignatov et al. 06-3350, MHA). 1-9 – laminal cells showing various degree of papillosity; 10-13 – spores.

1 and 10-13 – transmitted light; 2-9 – fluorescence of berberin in reflected light.

Scale bar is 50 μm for all.

va, on *Quercus mongolica* trunk, 30.IX.1933, Lazarenko (LE); Khabarovsk Territory (now Primorsky Territory), Bikin Distr., Krasnyj Pereval on Bikin River; on rocks. 2.X.1935, A.S. Lazarenko (KW13139, as *L. japonica*).

A revision of specimens from Primorsky and Khabarovsk Territories, including those reported as *Lindbergia japonica* by Lazarenko (1941) and as *L. duthiei* by Bardunov (1982), shows their identity with the widespread East Asiatic species *L. sinensis*.

Material of *L. duthiei* studied in H-BR does not show any substantial difference from *L. sinensis*, except for slightly larger plants. They quite likely belong to the same species, which is however better to prove genetically before their formal synonymization.

Note on *Lindbergia japonica*

Lindbergia sinensis differs from *L. japonica* (as described by Noguchi, 1972) mainly in rather uniform ovate to ovate-lanceolate, acuminate leaves (usually 1-1.3 mm long) and more or less frequent sporophyte production. Contrary to this, *Lindbergia japonica* has small leaves (0.5-0.9 mm long) and has never been reported with sporophytes. Leaf descriptions are strongly incongruent between authors: in the original description Cardot mentioned shortly acuminate leaves with costa less prominent comparatively with *L. magniretis* (synonymized with *L. sinensis*), whereas the illustration of Noguchi (l.c.) shows longly acuminate leaf with percurrent costa.

We studied putative isotypes of *Lindbergia japonica* in H and S, both being very scanty in material ["Herb. J. Cardot *Lindbergia japonica* Card. sp. nova, Japon: rocher de Zarnishi, Leg. Faurie, 1908, n. 3885" (H-BR 2483030!), same in S!]. Plants from these specimens are very variable, having stem leaves rather short acuminate, but branch leaves being lanceolate. The most important, however, is the fact that the leaf cells were not described by Cardot as papillose (implying that they are smooth?), but Noguchi described them as having one large papilla over the lumen. However, we found cells to be smooth in both isotypes we studied and have no explanation to this disagreement. Also, although plants of these isotypes have much in common with *Lindbergia sinensis* and *Mamillariella geniculata* in habit, their basal juxtacostal cells are

somewhat elongate, which disagrees with *Lindbergia*.

The further studies on identity of *L. japonica* should be done, but regardless to it, the specimens named as *L. japonica* and reported by Lazarenko from the Russian Far East in KW belongs to *L. sinensis*.

Notes on papillae in *Lindbergia sinensis*

Small papillae on laminal cells were not found in lectotype of *Lindbergia sinensis*, but they were observed in isolectotype in S. The presence and expression of papillae in this group need a comment.

The papillae in *L. sinensis* is not a very definite character: in some specimens low papillae occur in some leaves, while in others no traces of them can be discerned. In some collections we were able to find a leaf with papillae after checking many leaves, choosing the best developed ones. The expanded search, however, cannot be applied to scanty specimens of original collections. Likely because of this indefinite situation, papillae were almost never discussed in this group. Nothing is said about papillae in the original description of *Schwetschkea sinensis*, while Cao Tong et al. (2002) key out this species as smooth-celled.

This is true in general, but at places small papillae are observed in limited areas, being at best very low (Figs. 4: 8-9, 5: 4), like in a least expressed cases of *L. brachyptera* (Fig. 4: 1-4). In exceptional cases they are more apparent, and it is better to keep this in mind to avoid misinterpretation.

Lindbergia geniculata (Laz.) Ignatova & Ignatov comb. nov. – *Mamillariella geniculata* Laz., Izv. Kievsk. Bot. Sada 18: 104. 1-5. 1934.

Figs. 6; 4: 10-12; 9

Holotype: "ДСК, Приморська обл., Посьетський р-н, бухта Сідімі, парк, на деревах 28.X.1933 А.Лазаренко" [Far East Territory. Posiet Distr., Sidimi Bay, park, on trees, 28.X.1933 A.Lazarenko] (KW 13145).

Plants yellowish green or brownish green, in thin mats. Stems 1-2 cm long, irregularly or subpinnately branching, branches straight or arcuate, 2-4 mm long. Stem and branch leaves 0.6-0.9×0.3-0.4 mm, weakly concave to almost plane, ovate-lanceolate, acute or shortly to longly acumi-

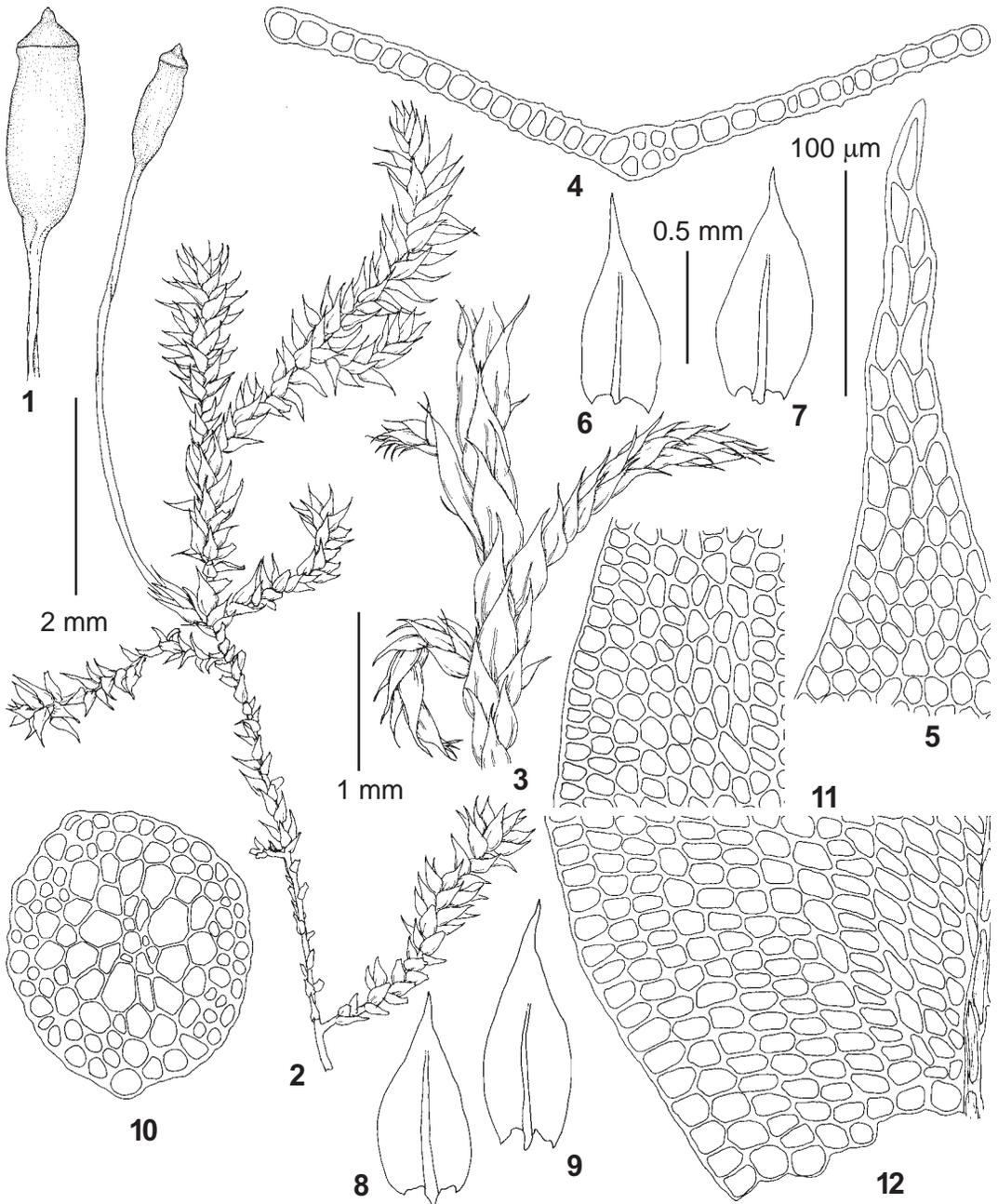


Fig. 5. *Lindbergia sinensis* (Müll. Hal.) Broth. (from Primorsky Territory, Lazo Distr., Kamenka 24.IX.1974 Bardunov & Cherdantseva (IRK, as *L. duthiei*): 1 – capsule; 2 – habit, wet; 3 – habit, dry; 4 – leaf transverse section; 5 – upper laminal cells; 6–9 – leaves; 10 – stem transverse section; 11 – median laminal cells; 12 – basal cells. Scale bars: 2 mm for 2; 1 mm for 1, 3; 0.5 mm for 6–9; 100 µm for 4–5, 10–12.

nate, mostly with straight apices when dry; margins entire, occasionally uneven; costa ending at 2/3–3/4 the leaf length; cells of leaf apex isodiametric, occasionally several uppermost cells in one row; upper and median laminal cells rounded or

ovate, 8–10×10–15 µm, thick-walled, collenchymatose, not bulging in transverse section, smooth. Seta finely mamillate, 4–6 mm, yellow-green proximally, pale brownish distally. Capsule ovate, 1.0–1.3 mm long, symmetric, narrowed to the mouth,

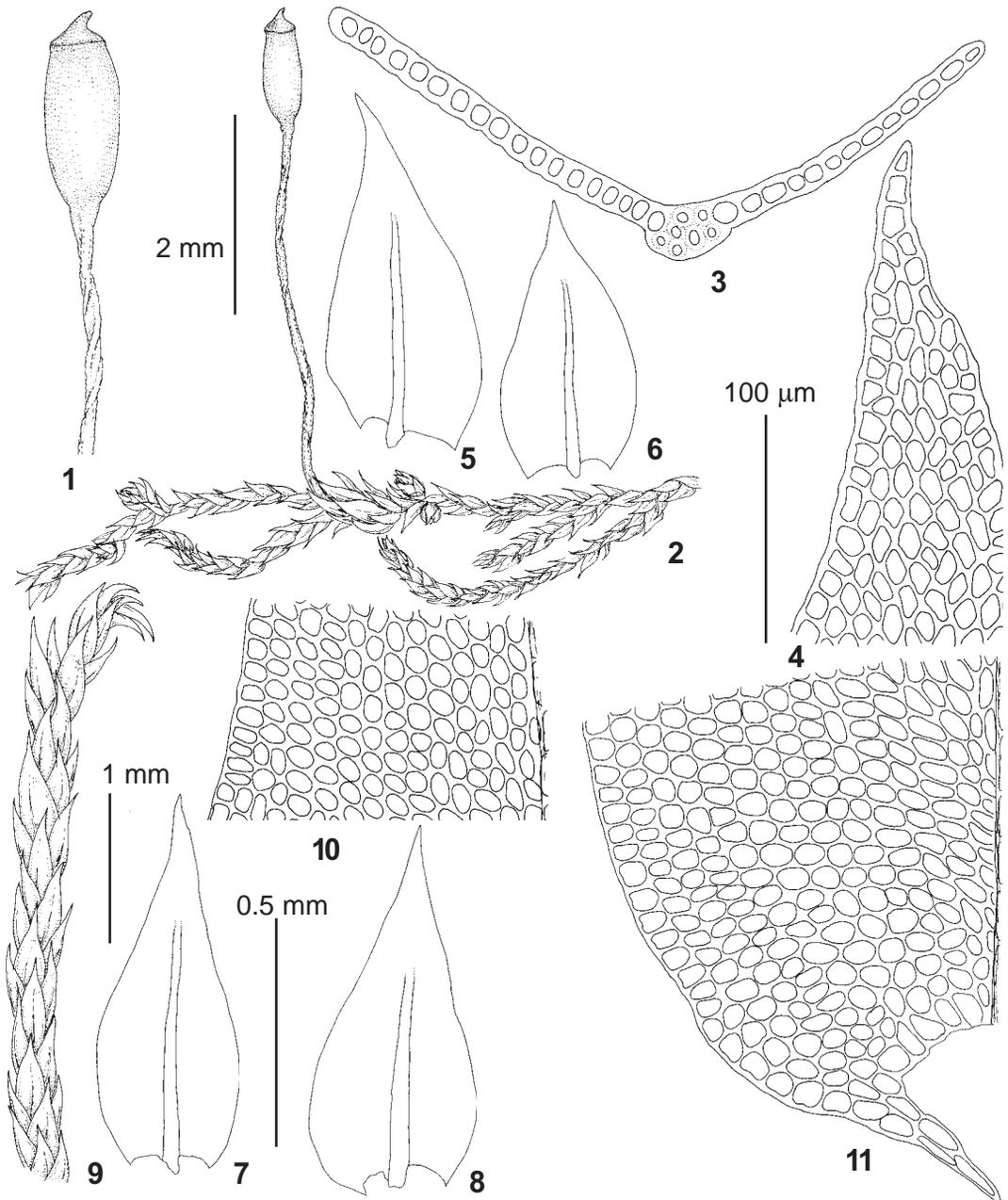


Fig. 6. *Lindbergia geniculata* (from Russia, Primorsky Territory, Ignatov 08-383, MHA): 1 – capsule; 2, 9 – habit, dry; 3 – leaf transverse section; 4 – upper laminal cells; 5-8 – leaves; 10 – median laminal cells; 11 – basal cells. Scale bars: 2 mm for 2; 1 mm for 1, 9; 0.5 mm for 5-8; 100 μm for 3-4, 10-11.

red-brown, operculum conic, with short straight or oblique beak. Annulus absent. Exostome ca. 200 μm long, teeth whitish, smooth distally, papillose proximally on outer surface, dorsal trabeculae moderately high, papillose; endostome absent. Spores 25-30 μm , finely papillose.

Specimens examined: RUSSIA: Primorsky Territory: same loc. as type (KW 13143); Okeanskaya, 30.IX. 1933, Lazarenko (KW 13142; 13146); Upper Suputinka, 11.IX.1934, Lazarenko (KW 13141); Tumannaya Peak, 2.IX.1936, Kolesnikov (KW 13140); Sichote-Alin, Fl. Volcha infer., 13.VII.1927, V.A.Petrov (KW 13144); Bolshaya Sedanka, Ignatov et al. 06-

3350 (MHA); Khasan Distr., Andreevka, 21.VII.1988, Mikulin (MHA ex VLA); Partizansky Distr., Lozovyy Range, 15.IX.1974, Bardunov & Cherdantseva (MHA ex VLA).

The broad generic concept urges to consider the genus *Mamillariella* within *Lindbergia*. By hametophytes *L. geniculata* is difficult to separate from *L. sinensis*, although their confusion is unlikely, since both commonly occur with sporophytes that have many differences. The most peculiar is the seta, which is mamillose, the mamillae varying from high and acute to rather moderate.

Two other important characters are almost complete reduction of endostome (*L. sinensis* has a rather high basal membrane), and very thick-walled spores (Fig. 4: 10-13).

Lindbergia dagestanica Ignatova & Ignatov sp. nov. Figs. 7; 11: 1-5

Species L. mexicana affinis sed dentes exostomii externi laevibus.

Holotypus: Dagestan, on bark of tree near waterfalls on summit of mountain opposite Gunib. 5.IX.1932. Samsel #119 (MW).

Plants yellowish-green, olivaceous or brownish, in thin mats. Stems to 1-3 cm long, irregularly branching, branches straight or arcuate, 3-6 mm long. Stem and branch leaves 0.7-0.9×0.5-0.6 mm, weakly concave to almost plane, broadly ovate, shortly acuminate, with straight apices when dry; margins entire or weakly serrulate, occasionally slightly wavy; costa ending few cells below the apex; upper and median laminal cells rhombic to short rectangular, 10-15×6-9 μm, with moderately thickened walls, weakly collenchymatose, not bulging in transverse section, smooth. Seta smooth, 7-8 mm, reddish brown. Capsule ovate, 1.8-2.1 mm long, symmetric or slightly asymmetric, erect, constricted below the mouth when dry, light reddish brown, red-brown at mouth; operculum and annulus not seen. Exostome ca. 230 μm long, teeth narrow, yellowish, smooth on outer surface, dorsal and ventral trabeculae very low; endostome pale yellowish, basal membrane ca. 1/4 of exostome length, finely and distantly papillose, segments narrow, not keeled, to 1/2 the exostome length. Spores 15-20 μm, finely papillose.

The species known only from the holotype.

An inegmatic plant from Dagestan that initi-

ated this study was first found to be very similar to *L. mexicana* (Besch.) Cardot. Overall habit, leaf shape, areolation and cylindric capsule strongly contracted below mouth clearly indicated their close affinity. As fresh collections of Dagestan plant were not available, sequences were studied only for Bolivian plant of *L. mexicana* and two specimens of *L. patentifolia* Dixon from South Africa. Surprisingly, ITS sequences of Bolivian and South African plants were found to be almost identical (mutations in ITS between Bolivian and South African specimens are at the same level as between two specimens from South Africa).

These two species have much in common, but leaves in *L. mexicana* are ovate, while in *L. patentifolia* ovate-lanceolate. More expanded analysis is needed to find out if this character is stable enough, but preliminary study indicates no reason to lump these species.

This group of the genus *Lindbergia* is represented by one species in America, from southern United States to Andes in South America, and in South Africa where it is far more diverse. *Lindbergia patentifolia* seems the most similar to *L. mexicana*; *L. haplocladioides* Dixon (isotype in H-BR 2482015!) has narrow leaves, often homomallous; *L. abbreviata* Broth. has recurved leaf tip and is habitually not similar; *L. pseudolekeelloides* Dixon has dull cells; while *L. viridis* Dixon differs from *L. mexicana* and other species of the group in somewhat narrower leaves and smaller plants.

Caucasian plants have almost no differences from *L. mexicana* in gametophyte, while the peristome characters are not identical. Plants from Bolivia (Fig. 12) have distinctly papillose outer exostome surface that has prominent joinings between plates, and endostome membrane is also slightly papillose. Contrary to this, *L. dagestanica* has smooth teeth and basal membrane, and in addition even in old capsule the segment fragments are retained (Fig. 11: 1, 5), while both our observations and literature data agree in absence of segments in *L. mexicana*.

Lindbergia patentifolia in respect to peristome papillosity is similar to *L. mexicana* (Fig. 11: 6-7), although a certain caution is needed, as the species was described from Uganda by sterile

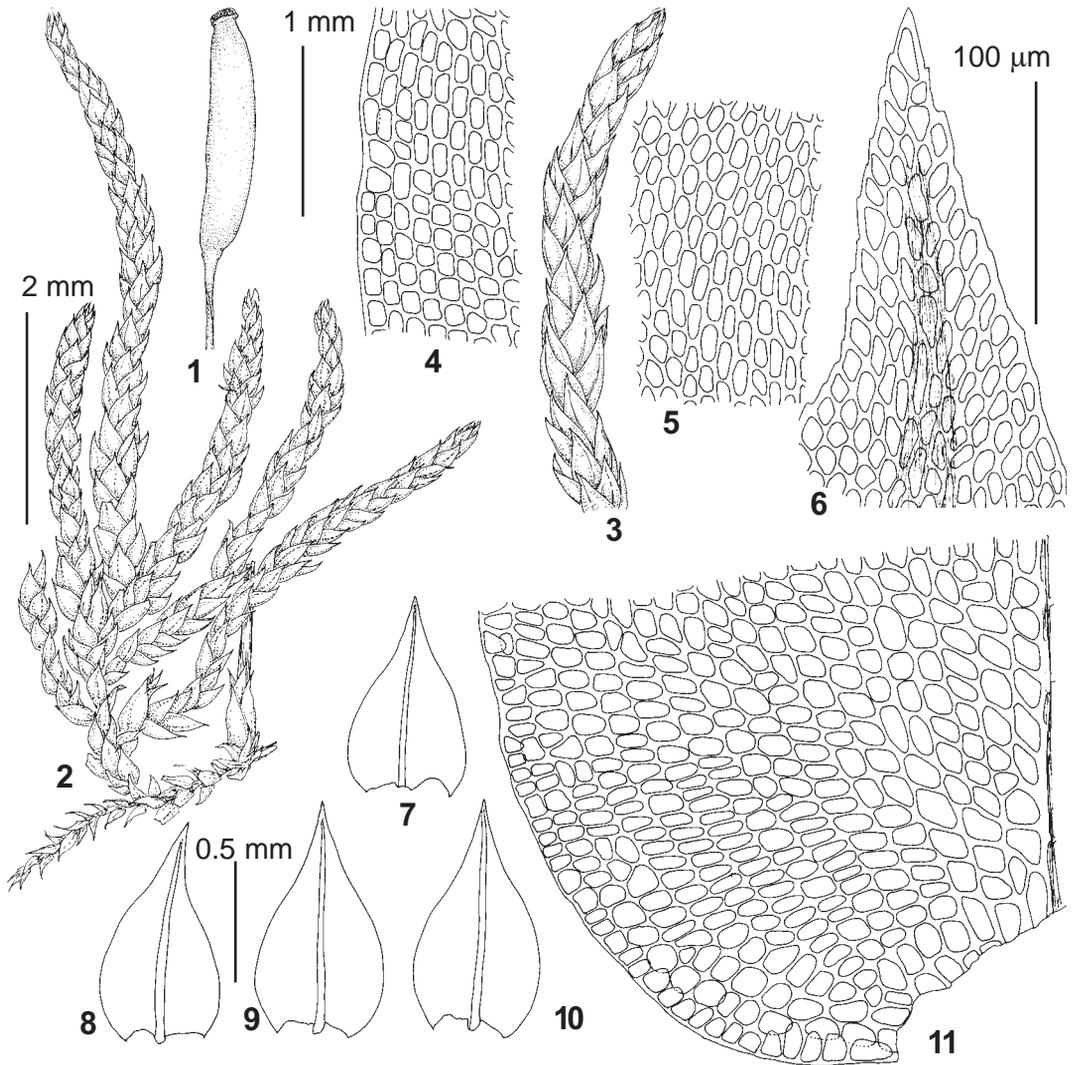


Fig. 7. *Lindbergia dagestanica* sp. nov. (from holotype: Russia, Dagestan, Gunib, 5.IX.1932. *Samsel* #119, MW): 1 – capsule; 2, 3 – habit, dry; 4–5 – median laminal cells; 6 – upper laminal cells; 7–10 – leaves; 11 – basal cells. Scale bars: 2 mm for 2; 1 mm for 1, 3; 0.5 mm for 6–9; 100 µm for 4–5, 10–11.

plants (Dixon, 1918). Subsequently Sims (1926) provided an expanded description of peristome, with teeth being finely striolate, terminal joints papillose; membrane nearly half as high as peristome [although in illustrations 1/3–1/4 high], firm, densely papillose, without processings and cilia. Seemingly, this observation had been done on South African material. Our SEM micrographs (done from one of specimens used for DNA study brought the same results. And in addition the studied plants from Ethiopia (ex Dixon Herb. 2100 m Piovano 13.X.1937, MHA) also have papillose exostome.

Thus the collection from Dagestan appears to be different in peristome structure, which is (1) completely smooth on abaxial surface and with only very slightly exerted dorsal trabeculae vs. papillose, especially along more or less exerted dorsal trabeculae; (2) has smooth basal membrane of endostome vs. papillose; (3) has segments, although narrow and fragile, but nevertheless clearly seen at least in several places even in old capsules. These differences forced us to describe Caucasian plants as a separate new species, *Lindbergia dagestanica*.

KEY TO IDENTIFICATION
OF *LINDBERGIA* SPECIES IN RUSSIA

1. Leaf lamina distinctly papillose; papillae mostly forked *L. grandirete*
— Leaf lamina smooth or with few very small, hardly visible papillae 2
2. Leaves broadly ovate, short acuminate; upper and median leaf cells rhombic to short rectangular; costa ending few cells below leaf apex; capsule ca. 2 mm long, cylindrical, constricted below the mouth; endostome with narrow segments; Caucasus, very rare
..... *L. dagestanica*
— Leaves broadly ovate-lanceolate, short to long acuminate; upper and median leaf cells rounded or ovate; costa reaching 2/3–3/4 the leaf length; capsule ca. 1 mm long, ellipsoidal, not constricted below the mouth; endostome consists of basal membrane only or absent; Russian Far East, sporadic 3
3. Setae smooth; endostome present; cells of attenuate leaf apices elongate; spores 20–25 μm *L. sinensis*
— Setae mamilliose; endostome absent; cells of attenuate leaf apices short; spores 25–30 μm *L. geniculata*

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Appendix 1. Taxon sampling and Genbank accession numbers.
Species

Species	GenBank		
	ITS1	ITS2	trnL-F
<i>Abietinella abietina</i> (Hedw.) M. Fleisch. 1	AY009802	AY009802	AY009850
<i>A. abietina</i> (Hedw.) M. Fleisch. 2	AJ417494	AJ417494	
<i>Actinothuidium hookeri</i> (Mitt.) Broth.	AY568547	AY568547	
<i>Amblystegium serpens</i> (Hedw.) Bruch & al.	AF168152	AF168152	AY009827
<i>Anomodon longifolius</i> (Brid.) Hartm.	AY695750	AY695766	AY683562
<i>A. rugelii</i> (Müll. Hal.) Keissl.1	AJ288420	AJ277232	
<i>Anomodon rugelii</i> (Müll. Hal.) Keissl.2			AF161116
<i>Boulaya mittenii</i> (Broth.) Cardot	FM161080	FM161080	AM990347
<i>Campylophyllum halleri</i> (Hedw.) M. Fleisch.	AY683610	AY693655	AY693655
<i>Claopodium crispifolium</i> (Hook.) Ren. & Cardot	AY695739	AY695778	AY683583
<i>Climacium americanum</i> Brid.			AF161158
<i>Cratoneuron filicinum</i> (Hedw.) Spruce	AY009812	AY009812	AY009817
<i>Haplocladium angustifolium</i> (Hampe & Müll. Hal.) Broth.	AY528884	AY528885	AY527129
<i>Helodium blandowii</i> (F. Weber & D. Mohr) Warnst.	AY009803	AY009803	AY009852
<i>Hygrohypnum luridum</i> (Hedw.) Jenn.	AF168137	AF168137	AY009862
<i>Hylacomium splendens</i> (Hedw.) Bruch et al.	AJ288336	AJ270021	AF152385
<i>Isopterygiopsis muelleriana</i> (Schimp.) Z. Iwats.	AY528882	AY528882	AY527138
<i>Lescuraea plicata</i> (Schleich. ex F. Weber & D. Mohr) Schimp.	AY695740	AY695765	AY683596
<i>L. saxicola</i> (Bruch & al.) Mol.	AF516165	AY695774	AY683569
<i>Leskea gracilescens</i> Hedw.	AF176277	AF176277	
<i>L. polycarpa</i> Hedw. 1	AY528889	AF516151	AY527134
<i>L. polycarpa</i> Hedw. 2	AY568554	AY568554	
<i>Lindbergia brachyptera</i> (Mitt.) Kindb.1 (USA, Churchill 1328, H)	AY695760	AY695763	AY683571
<i>L. brachyptera</i> (Mitt.) Kindb.2 (USA: H: H3194519)	FM161151	FM161151	AM990407
<i>L. geniculata</i> (Laz.) Ignatova & Ignatov (Primorsky Territory, 21.VII.1988 Cherdantseva s. n., MHA)	AY693652	AY693652	AY683597
<i>L. grandiretis</i> (Lindb. ex Broth.) Ignatov & Ignatova 1 (Dagestan, Ignatov & Ignatova 09-496, MHA)	JF280965	JF280965	
<i>L. grandiretis</i> (Lindb. ex Broth.) Ignatov & Ignatova 2 (Zabaikalsky Territory, 1.VII.1988 Bardunov, MHA)	JF280966	JF280966	
<i>L. mexicana</i> (Besch.) Cardot (Bolivia, Churchill 24643, MHA)	JF280967	JF280967	JF280979
<i>L. patentifolia</i> Dixon 1 (South Africa, Rooy 9771800, H)	JF280968	JF280968	
<i>L. patentifolia</i> Dixon 2 (South Africa, Phephu 28, H)	JF280969	JF280969	JF280980
<i>L. sinensis</i> (Müll. Hal.) Broth. 1 (Primorsky Territory, Ignatov 97-567, MHA)	AF516170	AF516153	AY683572
<i>L. sinensis</i> (Müll. Hal.) Broth. 2 (Primorsky Territory, Ignatov & al. 06-2476, MHA)	JF280970	JF280970	
<i>Loeskeobryum brevirostre</i> (Brid.) M. Fleisch.	JF280975	AJ270022	AF161172
<i>Ochryaea smithii</i> (Sw.) Ignatov & Ignatova	AF168139	AF168139	AY009856
<i>Ochryaea tatrensis</i> Váňa		AF260916	AF260915
<i>Pseudoleskeella catenulata</i> (Brid. ex Schrad.) Kindb.	AY695747	AF516154	AY683578

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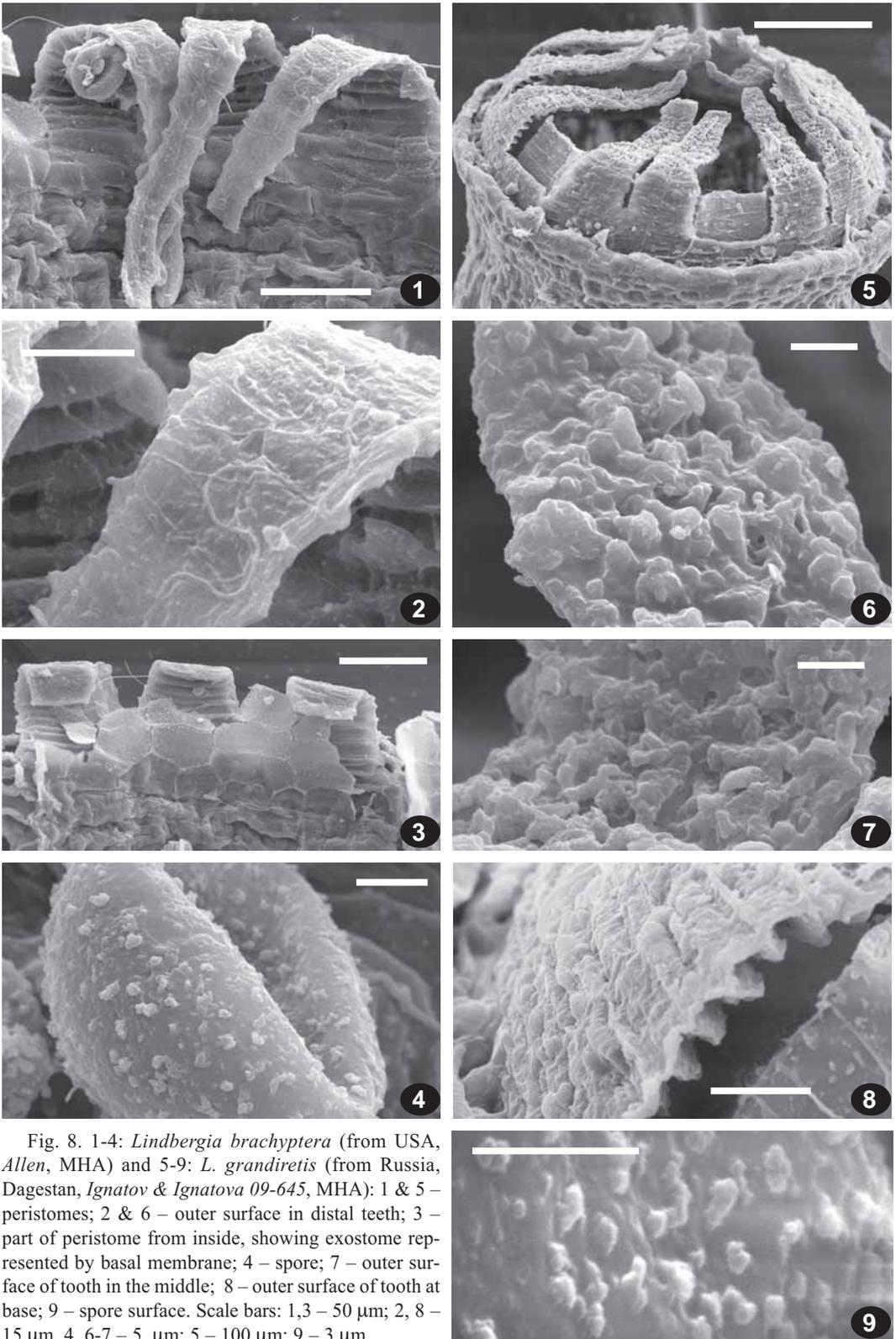


Fig. 8. 1-4: *Lindbergia brachyptera* (from USA, Allen, MHA) and 5-9: *L. grandiretis* (from Russia, Dagestan, Ignatov & Ignatova 09-645, MHA): 1 & 5 – peristomes; 2 & 6 – outer surface in distal teeth; 3 – part of peristome from inside, showing exostome represented by basal membrane; 4 – spore; 7 – outer surface of tooth in the middle; 8 – outer surface of tooth at base; 9 – spore surface. Scale bars: 1,3 – 50 μm ; 2, 8 – 15 μm . 4, 6-7 – 5 μm ; 5 – 100 μm ; 9 – 3 μm

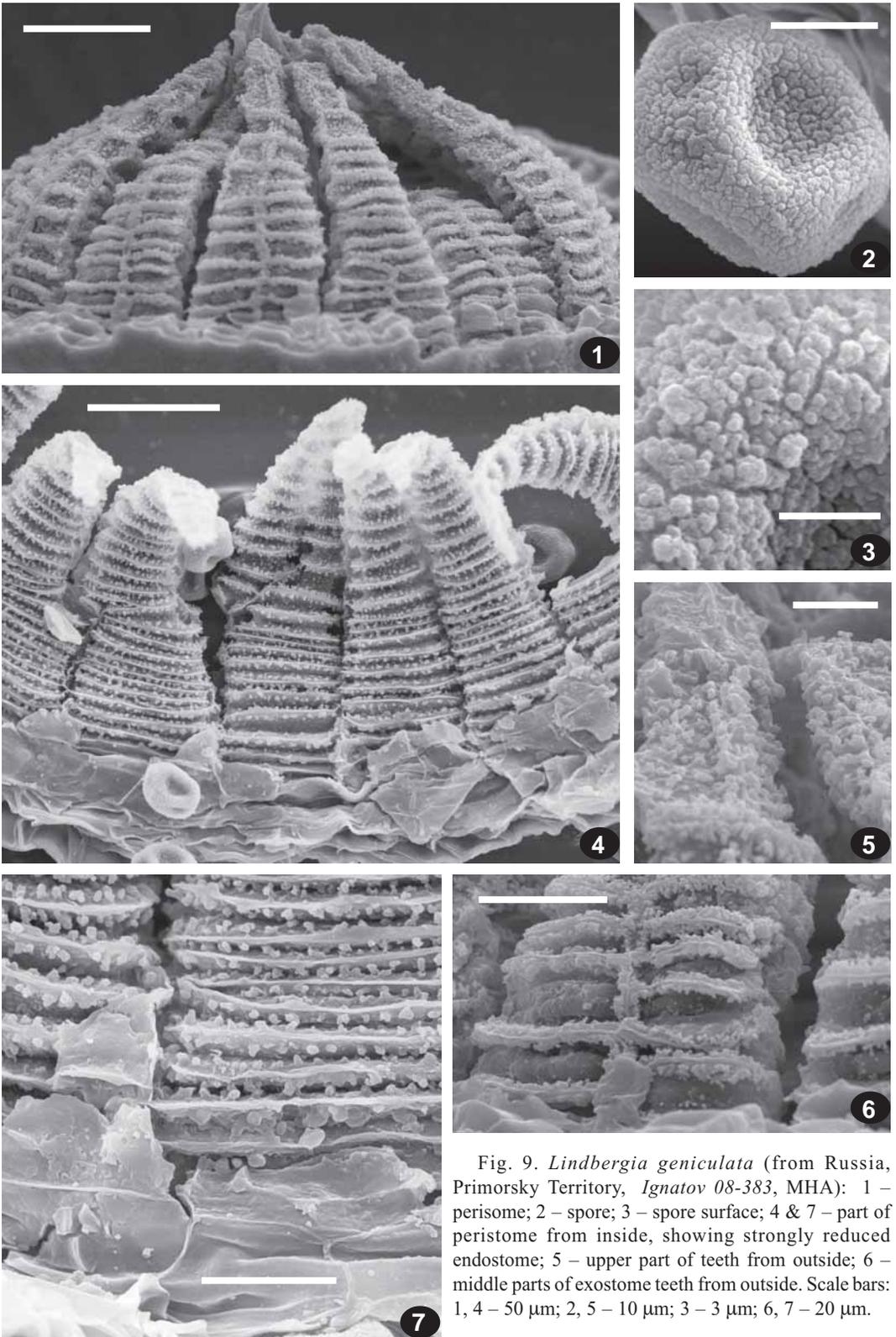


Fig. 9. *Lindbergia geniculata* (from Russia, Primorsky Territory, *Ignatov 08-383*, MHA): 1 – perisome; 2 – spore; 3 – spore surface; 4 & 7 – part of peristome from inside, showing strongly reduced endostome; 5 – upper part of teeth from outside; 6 – middle parts of exostome teeth from outside. Scale bars: 1, 4 – 50 µm; 2, 5 – 10 µm; 3 – 3 µm; 6, 7 – 20 µm.

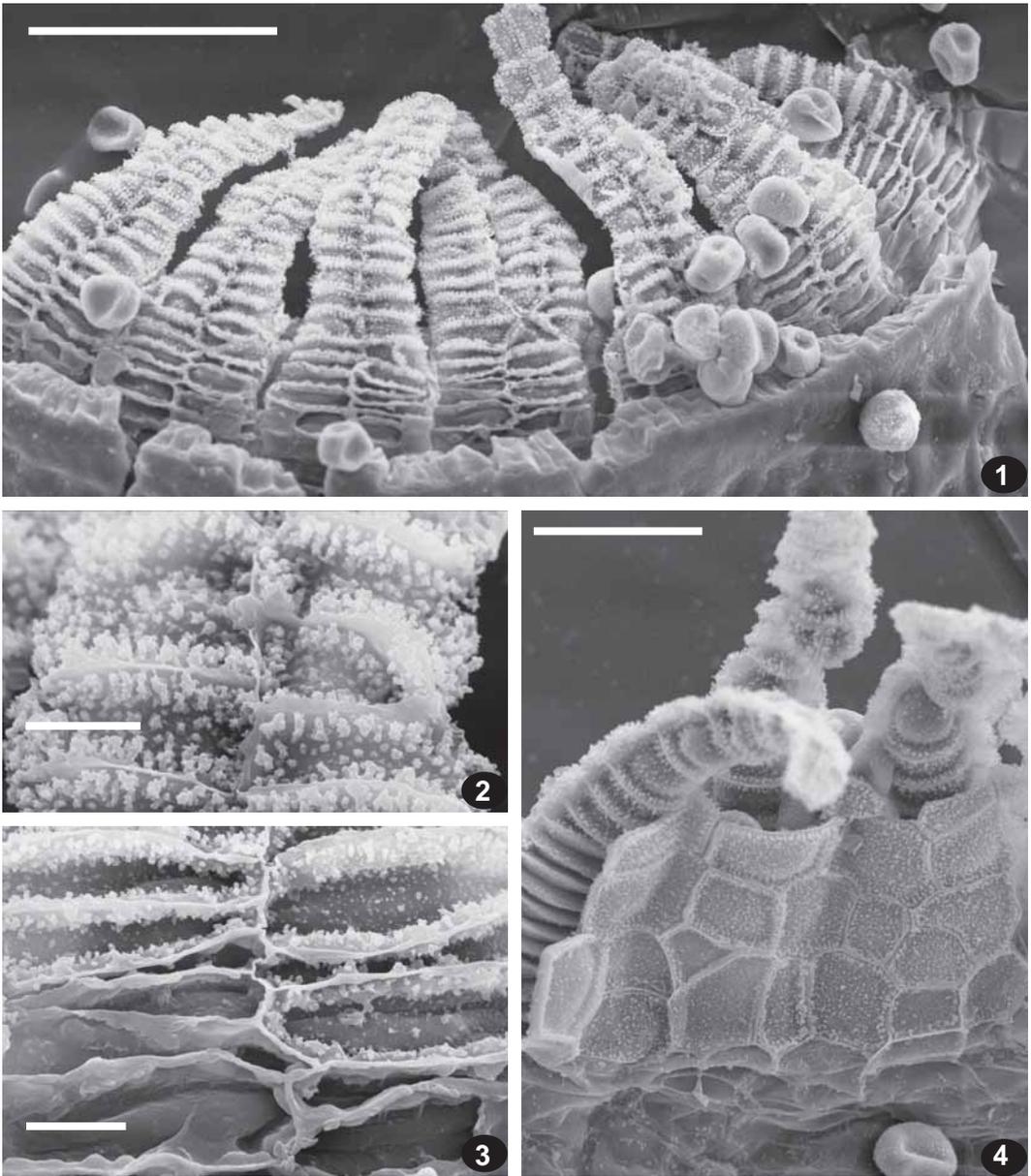
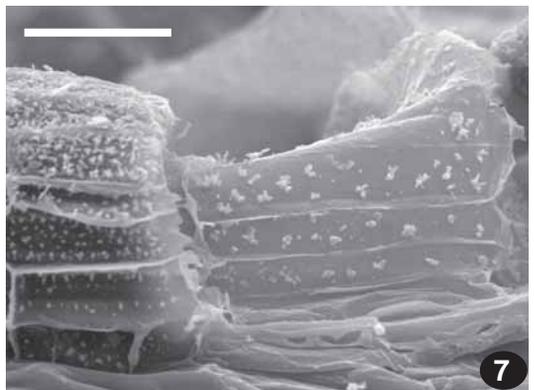
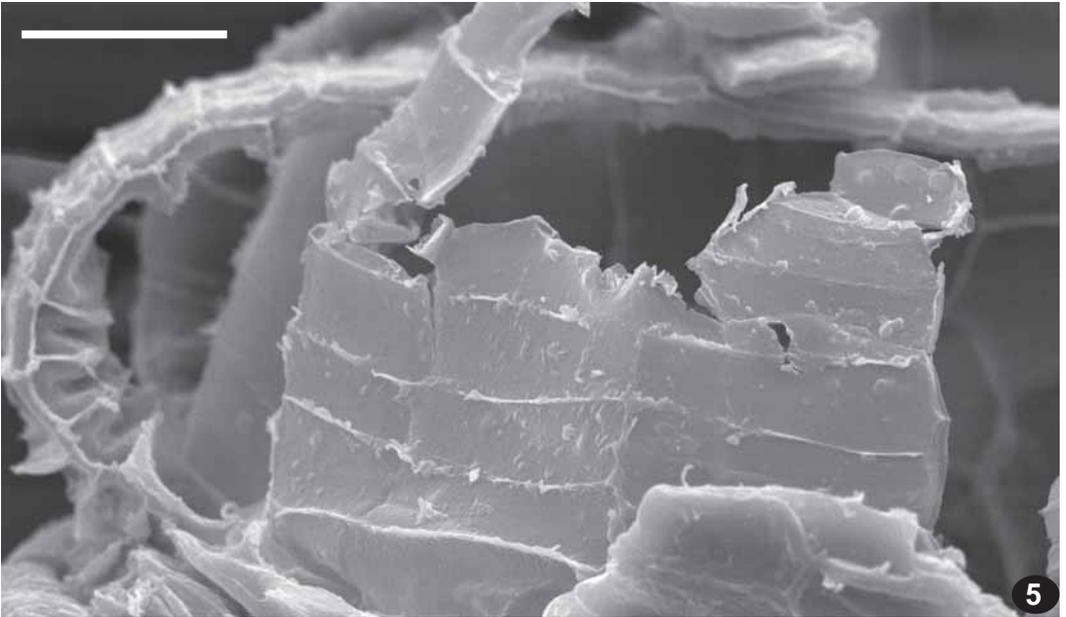
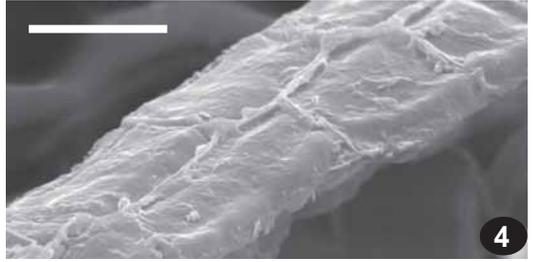
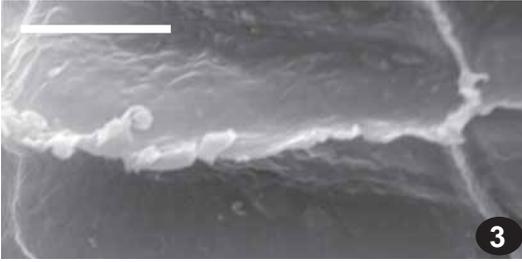
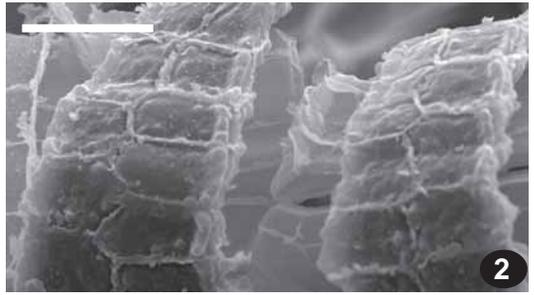
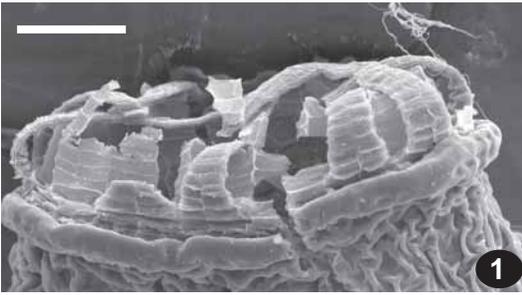


Fig. 10. *Lindbergia sinensis* (from Russia, Primorsky Territory, *Ignatov 08-257*, MHA): 1 – part of peristome from outside; 2 – outer surface of exostome tooth above the middle; 3 – outer surface of exostome tooth near base; 4 – peristome from inside, showing strongly papillose teeth and endostome reduced and represented by the basal membrane only, the latter being papillose and lacking segments. Scale bars: 1 – 100 μm ; 2-3 – 10 μm ; 4 – 50 μm .

Fig. 11 (opposite page). 1-5 – *Lindbergia dagestanica* (from type: Russia, Dagestan, *Samsel*, #119, MW); 6-7 – *L. patentifolia* (from South Africa, *Phephu* #28, H): 1 – peristome; 2 – outer surface of exostome teeth in the middle; 3,6, 7 – outer surface of exostome tooth at base (3 – high dorsal (sic!) trabeculae); 4 – outer surface of exostome tooth in distal part; 5 – part of peristome, showing lateral view of exostome tooth (note smooth and strongly incrassate ventral trabeculae), almost smooth basal membrane and moderately developed segment. Scale bars: 1 – 50 μm ; 2, 5-7 – 20 μm ; 4 – 10 μm ; 3 – 5 μm .



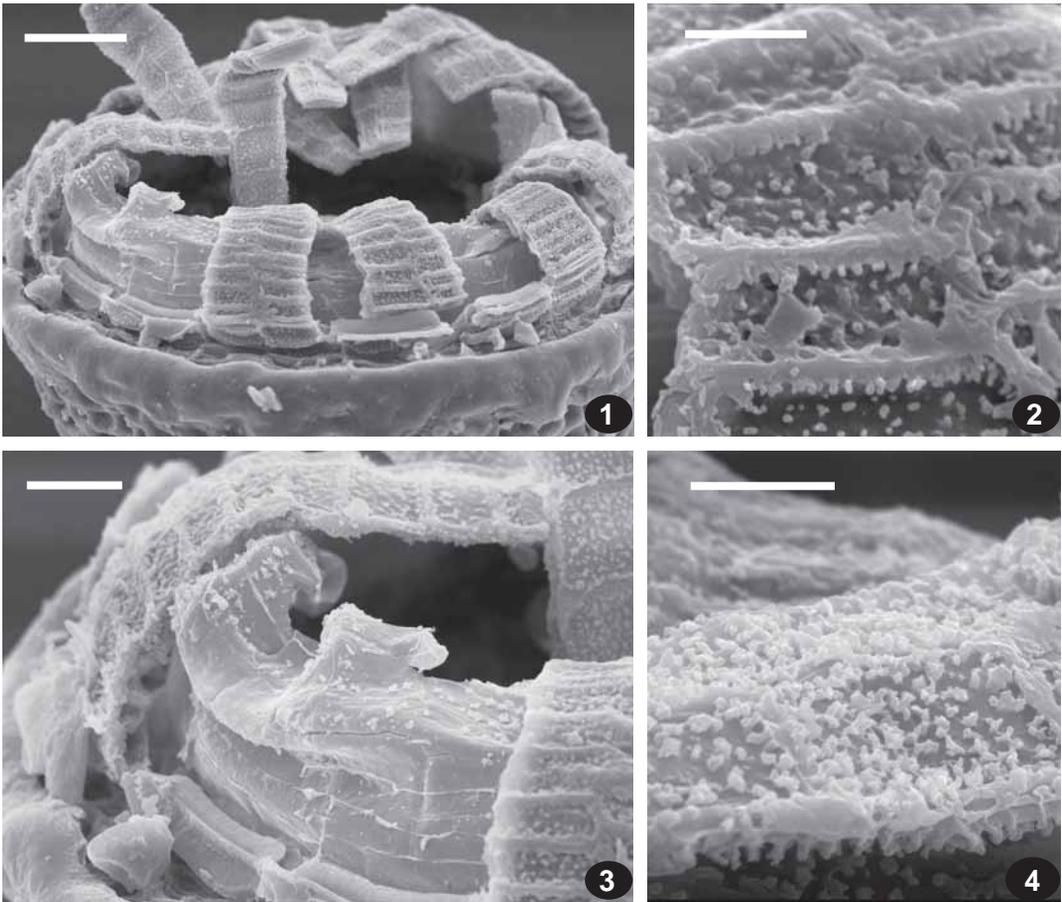


Fig. 12. *Lindbergia mexicana* (from Bolivia, Churchill #24643, MHA ex MO): 1 – peristome; 2 – outer surface of exostome tooth in the middle; 3 – part of peristome, showing lateral view of exostome tooth; note papillose and only moderately incrassate ventral trabeculae, slightly papillose basal membrane and strongly reduced segments; 4 – outer surface of exostome tooth distally. Scale bars: 1 – 50 µm; 3 – 20 µm; 2, 4 – 10 µm.

Appendix 1. Taxon sampling and Genbank accession numbers (continued from p. 111).

<i>P. nervosa</i> (Brid.) Loeske	AF516167	AF516152	AY527135
<i>Pseudoleskeopsis imbricata</i> (Hook. & Wilson) Thér.	AY693653	AY693653	AY683581
<i>P. zippelii</i> (Dozy & Molk.) Broth. 1	AY568548	AY568548	
<i>P. zippelii</i> (Dozy & Molk.) Broth. 2	FM161206	FM161206	
<i>P. zippelii</i> (Dozy & Molk.) Broth. 3			AY683603
<i>Rauiella fujisana</i> (Paris) Reimers 2			AY683600
<i>Rauiella fujisana</i> (Paris) Reimers 1	AY568546	AY568546	
<i>Sanionia uncinata</i> (Hedw.) Loeske	AF168148	AF168148	AY009860
<i>Sasaokea aomoriensis</i> (Paris) Kanda			JF280981
<i>Thuidium assimile</i> (Mitt.) A. Jaeger	AJ416442	AJ416442	
<i>T. cymbifolium</i> (Dozy & Molk.) Dozy & Molk.	AY568542	AY568542	
<i>T. delicatulum</i> (Hedw.) Bruch & al.			AF161132
<i>T. glaucinoides</i> Broth.	AY568544	AY568544	
<i>T. kanedae</i> Sakurai	AY568541	AY568541	
<i>T. pristocalyx</i> (Müll. Hal.) A. Jaeger	AY568540	AY568540	
<i>T. tamariscinum</i> (Hedw.) Bruch et al.			AF023770
<i>T. thermophilum</i> Czernyadjeva	EF368013	EF368013	EF368012