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A PRELIMINARY STUDY OF *COSCINODON* (GRIMMIACEAE, MUSCI) IN EURASIA BASED ON MORPHOLOGY AND DNA SEQUENCE DATA

ПРЕДВАРИТЕЛЬНОЕ ИЗУЧЕНИЕ ЕВРАЗИАТСКИХ ТАКСОНОВ *COSCINODON* (GRIMMIACEAE, MUSCI) НА ОСНОВЕ АНАЛИЗА МОРФОЛОГИЧЕСКИХ ДАННЫХ И ПОСЛЕДОВАТЕЛЬНОСТЕЙ ДНК

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Abstract

The nuclear ITS1-5.8S-ITS2 DNA region is studied for 29 specimens of *Coscinodon* from Eurasia, mostly from Russia, and 4 specimens from North America. The sequences were found to be much less variable than in two other genera of the Grimmiaceae, *Grimmia* and *Schistidium*. *Coscinodon yukonensis* Hastings was found to be rather widespread in Asia, despite never having been reported before in this continent, being erroneously treated as *C. humilis* Milde. European *C. humilis* is quite distinct molecularly from Asian *C. yukonensis* and forms a sister clade to *C. cribrosus* (Hedw.) Spruce. Some Asian populations of *"C. cribrosus"* were unresolved, being found outside the main clade formed by *C. cribrosus* and *C. humilis*. *Coscinodon hartzii* C.E.O. Jensen forms a basal grade to the rest of the species in the genus. *Coscinodon pseudohartzii* is described as a species new to science from Siberia.

Резюме

Изучен участок ITS1-5.8S-ITS2 ядерной ДНК у 29 образцов рода *Coscinodon* из Евразии, б.ч. из России, и 4 образцов из Северной Америки. Последовательности оказались намного менее вариабельными по сравнению с таковыми у двух других родов Grimmiaceae, *Grimmia* и *Schistidium*. *Coscinodon yukonensis* Hastings ранее не был отмечен в Азии, ранее образцы этого вида с этого континента относили к *C. humilis* Milde. Типичный *C. humilis* из Европы, однако, молекулярно отличается от него очень сильно и в то же время более близок к *C. cribrosus* (Hedw.) Spruce. Европейские и часть азиатских популяций *C. cribrosus* образуют кладу, сестринскую *C. humilis,* но ряд азиатских популяций *"C. cribrosus"* оказывается в неразрешенном положении. *Coscinodon hartzii* C.E.O. Jensen образует граду в основании дерева рода. По результатам анализа в Сибири выявлен не описанный ранее вид, *C. pseudohartzii*.

KEYWORDS: mosses, *Coscinodon*, Grimmiaceae, taxonomy, ITS, molecular phylogenetics, Eurasia

Introduction

The genus *Coscinodon* Spreng. is closely related to the genus *Grimmia* Hedw., and has sometimes been treated as a subgenus of *Grimmia* (e. g. Crum & Anderson, 1981). However, it is currently separated by most authors at the generic

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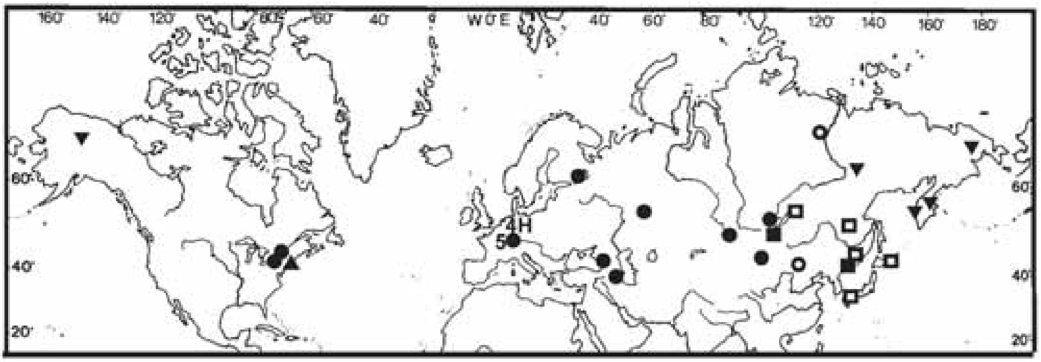


Fig. 1. Studied specimens of *Coscinodon cribrosus* (●), *C.* cf. *cribrosus* (○), *C. hartzii* (▼), *C. humilis* (**H**), *C. pseudohartzii* (■), *C.* cf. *pseudohartzii* (▲), and *C. yukonensis* (□). Dense sampling from Central Europe is indicated by 5 specimens of *C. cribrosus* and 4 of *C. humilis*.

level, mainly on the basis of a large, campanulate, plicate calyptra covering the capsule to the base of urn. Crosby & al. (1999) list nine species of *Coscinodon* in the world, one of them being insufficiently known, while Hastings (2007) lists 10 species. Six species are restricted to the Northern Hemisphere. Five species are known in North America with three of them considered to be endemic (*C. calyptratus* (Drumm.) C.E.O. Jensen, *C. hartzii* C.E.O. Jensen, and *C. yukonensis* Hastings); three species were reported from Eurasia, and one species is endemic (*C. humilis* Milde). *Coscinodon cribrosus* (Hedw.) Spruce occurs sporadically throughout the Holarctic and *C. arctolimnius* (Steere) Steere is represented in two continents by different subspecies, subsp. *arctolimnius* (North America) and subsp. *higuchii* Hastings & Deguchi (Asia, Mongolia). Records of *C. calyptratus* in Khazakhstan and Armenia (Muñoz, 1998) were confirmed by Hastings (1999), but later she referred them to an undescribed species (Hastings, 2007).

Only one species of the genus, *Coscinodon cribrosus,* was earlier reported from Russia (Ignatov, Afonina, Ignatova et al., 2006). It was considered to have a highly disjunctive distribution in mountainous areas throughout the country. However, a partial revision of herbarium collections of *Coscinodon* from Russia (MHA, MW, LE) by the first author revealed some specimens that are similar to the North American *C. hartzii*, and others similar to *C. humilis*, as it was circumscribed by Japanese authors (Deguchi, 1979; Noguchi, 1988). In addition to morphology we used nuclear ITS1-5.8S-ITS2 data to check species level identification. This method has been quite successful for elucidating taxonomy at the species level in the genus *Schistidium* (Goryunov & al., 2007) which is from the same family.

MATERIALS AND METHODS

Specimens used in this analysis were at first selected to check the identity of Far Eastern *'C. humilis'* with European *C. humilis*. However, the preliminary results revealed: (1) considerable differences between them; (2) high similarity of European *C. humilis* with *C. cribrosus* and (3) heterogenity of *'C. cribrosus'* in the eastern part of Asian Russia.

Further studies and especially morphological comparison with North American material, revealed the identity of 'Far Eastern *C. humilis*' with the recently described *C. yukonensis* (Hastings, 1999) previously known only from north-western North America. We tried to study as much comparative material as possible although collections from certain key areas were too old for sequencing.

Central European material was intensely sampled to determine the consistency of differentiation between *C. cribrosus* and *C. humilis.*

Some specimens from Asian Russia with exserted cylindric capsules on long setae were included in order to reveal their possible identity with *C. hartzii*; Alaskan specimens of this species were used for comparison.

As *Coscinodon cribrosus* was found to be the most variable species in DNA sequences, its sampling was expanded for better understanding this variation. One specimen of *C. cribrosus* from Maine was taken from GenBank, but found to be rather unrelated to most of other specimens of *C. cribrosus*, so additional material from North America was studied as well.

The tree was rooted on *Grimmia mollis* Bruch et al. and additionally *G. caespiticia* (Brid.) Jur. and *G. trinervis* R.S. Williams were included in analyzing the set. All three sequences were from GenBank. This choice was made after a number of attempts to align *Coscinodon* data with a number of *Grimmia* appeared to be exceedingly difficult. The above three species were found the most similar (= alignable) to *Coscinodon* by ITS. The close position of these species to *Coscinodon* was found also by Hernandez-Maqueda et al. (2008) using other gene regions.

Specimen distribution and data are given in Fig. 1 and Table 2.

The protocol of DNA extraction and amplification was the same as in Gardiner & al. (2005). Sequences were aligned manually, resulting in an alignment partially shown in Table 1. We performed parsimony ratchet analysis with NONA (Goloboff, 1994) within the Winclada (Nixon, 1999a) shell. A multi-ratchet option with five sequential parsimony ratchet runs was used (Nixon, 1999b). The jackknife support was calculated for 2000 replications.

RESULTS

The phylogenetic tree (Fig. 2) resolves *Coscinodon* (without *Grimmia trinervis* – sometimes placed in *Coscinodon*) to be monophyletic with high support. *Grimmia caespiticia* and *G. trinervis* form clade sister to *Coscinodon*.

Coscinodon hartzii forms a basal grade to the rest of the genus that was resolved as a clade but without support. Furthermore, the topology within this clade was found to be quite interesting and corresponded to morphology and geography of species/samples, although support of individual clades is low. Only the clade of *C. humilis* received a high support of 90. The *Coscinodon yukonensis*–clade received support of 68 (Fig. 2), although preliminary analyses (not shown) of a smaller set of specimens resulted in its support of 90. The final decrease can be explained by the inclusion of a specimen from southern Japan; its exclusion raises the support of the four specimen clade of *C. yukonensis* up to 84.

Fourteen of 18 samples identified by morphology as *C. cribrosus* were found to form a sister clade to the *C. humilis*–clade. Certain groupings within this clade correspond to geography, e.g.: (1) five specimens from Central Europe and Karelia, NW European Russia; (2) three specimens from Caucasus and South Siberia. However, other samples show that specimens from such remote areas as North America, Siberia and Europe exhibit no grouping (Fig. 2). Four samples of '*C. cribrosus*' were found outside the main *C. cribrosus*–clade. Two of them represent the easternmost populations in Asia, in northern Yakutia and the Inner Mongolia Province of China. Two other samples are two DNA extractions from the same specimen from Maine in Eastern North America. The latter is grouped with two interesting specimens from Siberia and the Russian Far East that are here described as a new species, *Coscinodon pseudohartzii*.

Table 1. Molecular synapomorphies of 5 species of *Coscinodon*. Numbers above indicate position in alignment; numbers at abbreviated species names indicate number of samples. Shown are only those positions where all samples of species have consistent difference, except two cases (marked by *) where one sample is different from others. Two problematic samples of *C.* cf. *cribrosus* and two of *C.* cf. *pseudohartzii* (see discussion in text) were not considered for selection of positions to show; their nucleotides in the considered positions are shown in the bottom of table.

	56	97-99	127	156	277	302	396	592	602	760	819	889
hart 5	C	A--	T	A	G	-	-	C	T	C	C	C
yuko 5	C	CTT	T	A	A	-*	-	C	G	T	-	C*
pseu 2	C	A--	C	A	A	-	-	C	C	C	-	C
crib14	T	A--	T	G	A	A	T	C	T*	C	C	C*
humi 4	T	A--	T	A	C	-	-	-	T	C	C	T
cf-Yaku	C	A--	T	A	A	-	-	C	T	C	C	C
cf-Chin	C	A--	T	A	A	-	-	C	T	C	C	C
cf-Main	C	A--	C	A	A	-	-	C	C	C	-	C
cf-Mai2	C	A--	C	A	A	-	-	C	C	C	-	C

Molecular synapomorphies of studied species are summarized in Table 1.

DISCUSSION

Hernandez-Maqueda et al. (2008) demonstrated that the genus *Coscinodon* in its current circumscription is polyphyletic and nested within *Grimmia*. That study, however, used only two species in the genus, *C. cribrosus* and *C. calyptratus*. The latter species has a morphology deviating from all other *Coscinodon* species and does not occur in Russia, so it was not included in the present analysis.

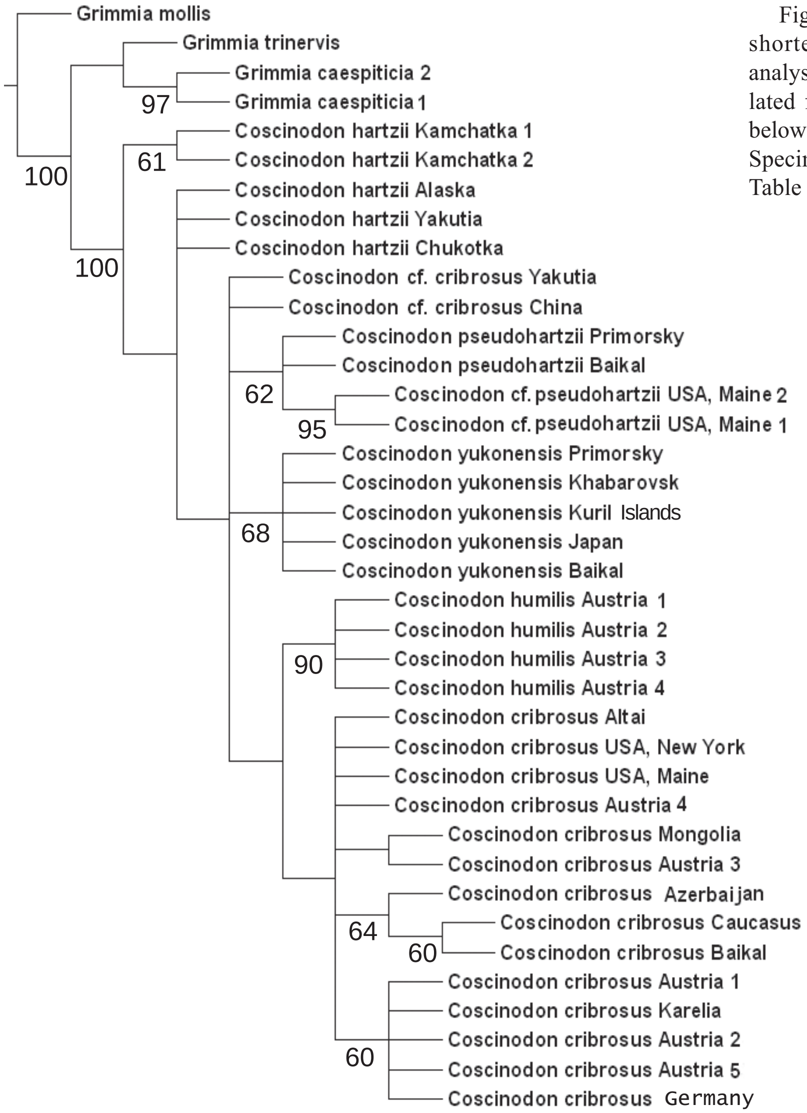


Fig. 2. Strict consensus of 75 shortest trees found in ratchet analysis. Jackknife values calculated for 2000 replicates (shown below branches if no less than 60). Specimen information is given in Table 1.

The other species of *Coscinodon,* however, were found to be monophyletic, as revealed in this analysis with rather poor outgroup taxa; however the broader outgroup sampling was almost impossible due to difficulties in ITS aligning. Other evidence of monophyly of the five studied *Coscinodon* species is the low variability between them in ITS, in comparison with species of both *Schistidium* (Goryunov & al., 2007) as well as of *Grimmia* (data of Hernandez-Maqueda & al. in GenBank, and our unpublished data).

Acceptance of *Coscinodon* makes the genus *Grimmia* paraphyletic and so Hernandez-Maqueda & al. (2008) merged the former genus into the latter one, following the cladistic approach. We, however, prefer to retain *Coscinodon* as a separate genus (not including *C. calyptratus* because it is outside of the present discussion and likely is not part of the genus) for three reasons: (1) this group has not been completely studied and the topology of phylogenetic tree may change after the inclusion of additional species; (2) the genus may become acceptable in the course of a division of *Grimmia* into a series of smaller genera (e. g. Ochyra & al., 2003); and (3) paraphyletic taxa (in contrast to polyphyletic), can be accepted for some specific reasons (cf. e. g. Zander, 2008; Huttunen et al., 2007).

Table 2. Specimens used in molecular analysis and GenBank data for nrITS1&2.

Coscinodon		
cribrosus Altai	Russia, Altai, *Ignatov #36/354* (MHA)	EU715359
cribrosus Baikal	Russia, Irkutsk Prov., Maloye Goloustnoe, 4.VIII.1993 *Bardunov s.n.* (MW)	FJ970945
cribrosus Caucasus	Russia, Kabardino-Balkaria, 2.VIII.2004 *Ignatov et al. s.n.* (MHA)	EU715364
cribrosus Karelia	Russia, Karelia, Hijtola, *Maksimov & Maksimova #23-67a* (PTZ)	FJ970944
cribrosus Austria 1	Austria, Mt. Hochwipfel, *Köckinger #14257* (Kl, MW)	EU715362
cribrosus Austria 2	Austria, Mörtschach, *Köckinger #14258* (KL, MW)	EU715363
cribrosus Austria 3	Austria, Mt. Hafner, *Köckinger #14259* (KL, MW)	EU715361
cribrosus Austria 4	Austria, Styria, Seetaler Alpen, *Köckinger #14594* (KL, MW)	FJ970943
cribrosus Austria 5	Austria, Tirol, Ötztaler Alpen, *Nebel et al. #323b* (KL, MW)	FJ970941
cribrosus Germany	Germany, Türingia, 16.IV.2008 *Meinunger & Schröder s.n.* (STU, MW)	FJ970942
cribrosus Azerbaijan	Azerbaijan, Zakatalsky Distr., Nurbazhi Mt., 7.VIII.2004 *Korotkov s.n.* (MW)	FJ970938
cribrosus Mongolia	Mongolia, Ikh-Bogd, *Ignatov #01-718* (MHA)	EU715360
cribrosus U.S.A., New York	U.S.A., State of New York, *Miller #15873* (MO)	FJ970939
cribrosus U.S.A., Maine	U.S.A., Maine, *Allen #20029* (MO)	FJ970940
cf. *cribrosus* Yakutia	Russia, Yakutia, Zhigansky Distr., 27.VIII.1991 *Nikolin s.n.* (MW)	FJ970930
cf. *cribrosus* China	China, Inner Mongolia, *Bai X.-l. #4345* (HIMC, MHA)	FJ970931
hartzii Chukotka	Russia, Chukotka, Baranie Lake, 6.VIII.1980 *Afonina s.n.* (MW)	FJ970933
hartzii Kamchatka 1	Russia, Kamchatka, 16.VII.2003 *Czernyadjeva #18* (LE)	EU715366
hartzii Kamchatka 2	Russia, Kamchatka, 15.VIII.2006 *Czernyadjeva #32* (LE)	EU715369
hartzii Yakutia	Russia, Yakutia, 22.VII.2003 *Zolotov & Ivanova s.n.* (MHA)	EU715367
hartzii Alaska	U.S.A., Alaska, *Perry & Murray #6330* (MHA, ex ALA)	EU715365
humilis Austria 1	Austria, Carinthia, Wangenitztal, *Köckinger #99-1337* (KL, MW)	EU715356
humilis Austria 2	Austria, Tirol, Platztal, *Köckinger #91-562* (KL, MW)	FJ970947
humilis Austria 3	Austria, Carinthia, Siflitzgraben, *Köckinger #14631* (KL, MW)	FJ970948
humilis Austria 4	Austria, Tirol, Obergurgl, *Nebel et al. #323a* (KL, MW)	FJ970946
pseudohartzii Baikal	Russia, Irkutsk Province, *Ignatov & Kazanovsky #05-6000* (MHA)	EU715368
pseudohartzii Primorsky	Russia, Primorsky Territory, Ryazanovka, 20.VI.2006 *Konovalova s.n.* (MHA)	FJ970937
cf. *pseudohartzii* Maine 1	U.S.A., Maine, *Allen #16698* (MO)	EU343763
cf. *pseudohartzii* Maine 2	U.S.A., Maine, *Allen #16698* (MO)	FJ970932
yukonensis Primorsky	Russia, Primorsky Territory, *Ignatov et al. #06-2231* (MHA)	EU715357
yukonensis Khabarovsk	Russia, Khabarovsk Territory, *Ignatov #97-1093* (MHA)	EU715358
yukonensis Kiril Islands	Russia, Kiril Islands, Shikotan, Notoro Mt., *Bakalin #K-43-8-07* (MHA)	FJ970934
yukonensis Baikal	Russia, Irkutsk Prov., Vitimsky Reserve, 14.VII.1991 *Bardunov s.n.* (MW)	FJ970936
yukonensis Japan	Japan, Kyushyu, Yakoshima Island, *Deguchi exs. #203* (MW)	FJ970935
Grimmia		
caespiticia 1		EU343760
caespiticia 2		EU343761
trinervis		EU343794
mollis		EU343779

In general, the phylogenetic tree (Fig. 2) provides a convincing model of the direction of evolution: from Orthogrimmealean ancestors with 1) small calyptrae, 2) long setae and 3) small and hardly perforated peristome teeth, to 1) large, campanulate calyptrae, 2) short setae and 3) large and strongly perforated teeth in *Coscinodon cribrosus*, which represents obviously the most advanced species in this genus. We can also observe an increasing loss of information in the sequences (large deletions) from *Orthogrimmia* to *Coscinodon*, which seems characteristic for modern groups in the Grimmiaceae (pronounced especially in *Schistidium*).

The taxonomy of *Coscinodon* at the species level is quite controversial. *Coscinodon humilis* and *C. cribrosus* were combined in Europe

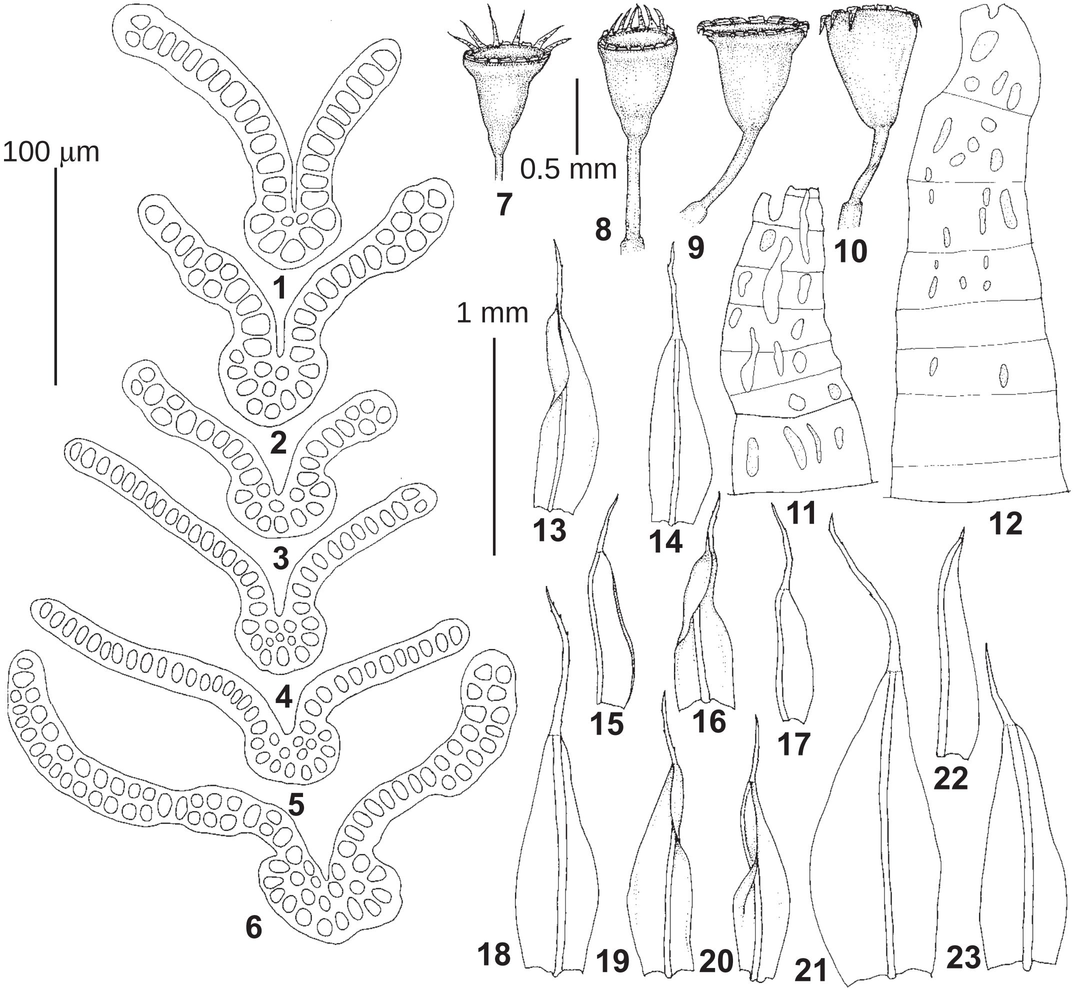


Fig. 3. *Coscinodon yukonensis* Hastings (1, 13-14 – from Primorsky Territory, *Ignatov & al. #06-2231,* MHA; 2-3, 15-17 – from Khabarovsk Territory, *Ignatov #97-1093*, MHA; 4-5, 7-8, 12, 18-20 – from Kamchatka, *Savicz #5790*, LE; 6, 9-10, 11, 21-23 – from Kuril Islands, Shikotan Island, *Bakalin #K-43-8-07*, MHA): 1-6 – leaf transverse sections; 7-10 – capsules (7, 9-10 – dry, 8 – wet); 11-12 – peristome teeth; 13-23 – stem leaves. Scale bars: 1 mm for 13-23; 0.5 mm for 7-10; 100 μm for 1-6, 11-12.

(Loeske, 1913; Podpera, 1954; Maier & Geissler, 1995) but later split again (Greven, 1995; Hill & al., 2006). In North America (again not counting *C. calyptratus*), Anderson & al. (1990) listed two species, whereas Hastings (2007) accepted four.

The present analysis demonstrates that marginal haplotypes and even undescribed species occur in Eurasia. In a parallel way, the molecular test of *Schistidium* between the 'lumper' approach of Bremer and 'splitter' one of Blom, revealed that the genus was not overly split by the second author, but rather a little undersplit (Goryunov et al., 2007). Individual species are discussed below.

COSCINODON YUKONENSIS HASTINGS

We did not sequence material of *C. yukonensis* from North America because no recent collections were found for molecular studies. At the same time, the study of morphological variation in the quite rich Asian material clearly indicates its identity with the relatively few specimens known up to now from northwestern North America.

Molecular definition of the species is very clear (Fig. 2, Table 1).

The important diagnostic characters of *C. yukonensis* include: ovate, non-plicate leaves with

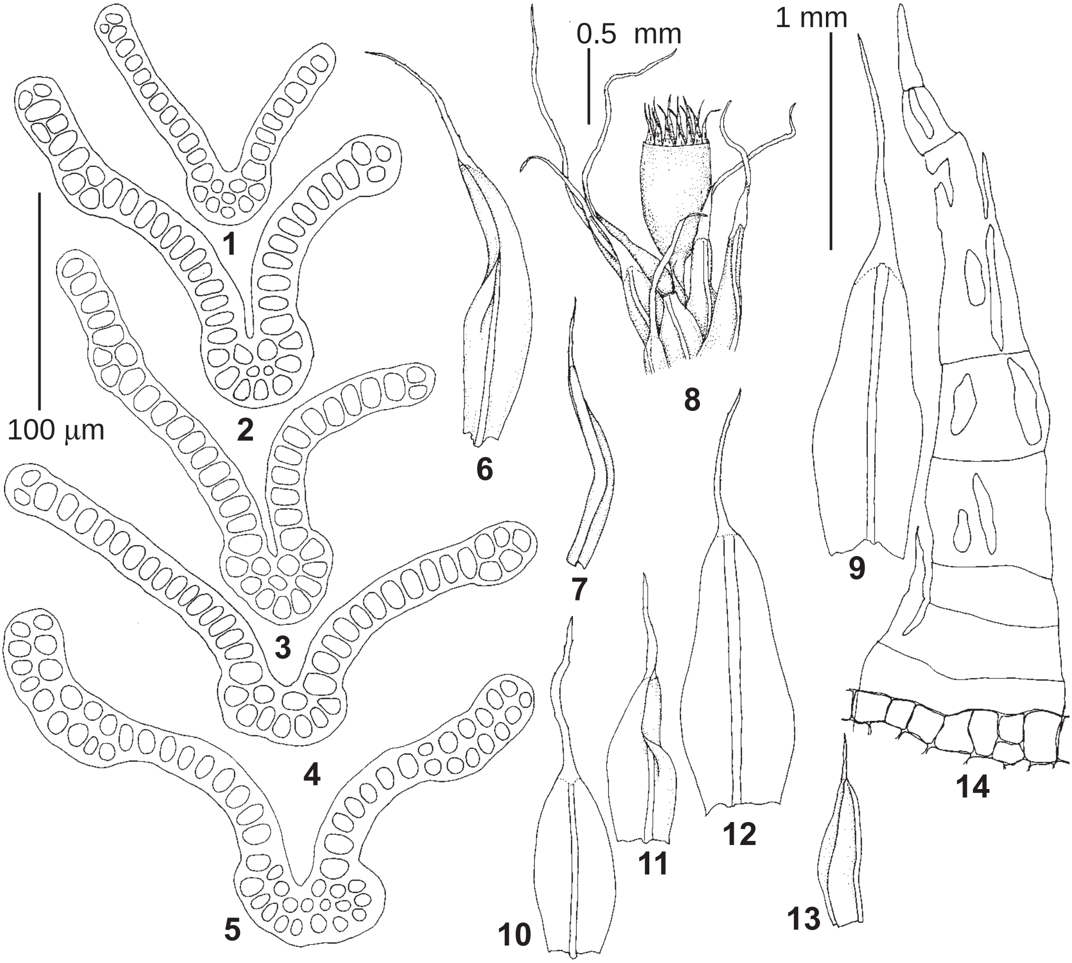


Fig. 4. *Coscinodon humilis* Milde (1,6-7 – from Meran, *Milde s.n.,* isotype, MO; 2, 8, 9, 14 – from Meran, *Milde s. n.,* isotype, LE; 3-4, 10-11 – from Austria, *Köckinger #99-1337*, KL; 5, 12-13 – from Austria, *Nebel et al. #323a*, KL): 1-5 – leaf transverse sections; 6-7, 9-13 – stem leaves; 8 – capsule, dry; 14 – peristome tooth. Scale bars: 1 mm for 6-7, 9-13; 0.5 mm for 8; 100 µm for 1-5, 14.

mostly unistratose leaf lamina; cupulate, deeply immersed capsules and xerocastique peristomes. Gametophytic characters are much like those of *C. humilis*, whereas these species differ in sporophytic ones: capsules are much smaller in *C. yukonensis*, about 0.5-0.6 mm long vs. 0.75-1.25 mm long in *C. humilis*, peristome teeth usually strongly reflexed after spore release (rarely spreading, cf. Fig. 3: 7) vs. erect in the latter species. Our observations reveal some differences in peristome teeth ornamentation. In a specimen of *C. yukonensis* from Kuril Islands, Bakalin #K-43-8-07, the outer surface of the peristome teeth has thickened trabeculae and vertical ridges and is very sparsely covered by low papillae (Fig. 9) but it is flat and densely papillose in *C. humilis* (Figs. 11-12). Papillae on their inner surface are also markedly different; in *C. yukonensis* they are more branched (cf. Figs. 10 & 14). However, Hastings (1999) describes the peristome of North American specimens of *C. yukonensis* as coarsely and densely papillose on both surfaces.

Unlike most other species of the genus, *C. yukonensis* often grows in considerable abundance, covering extensive faces of rock outcrops. However, tens to hundreds of square meters of pure populations are often totally sterile. It turns out that the species is not rare in the Russian Far East, both on the mainland and the islands, in zones of northern boreal coniferous forests and even in the alpine belt

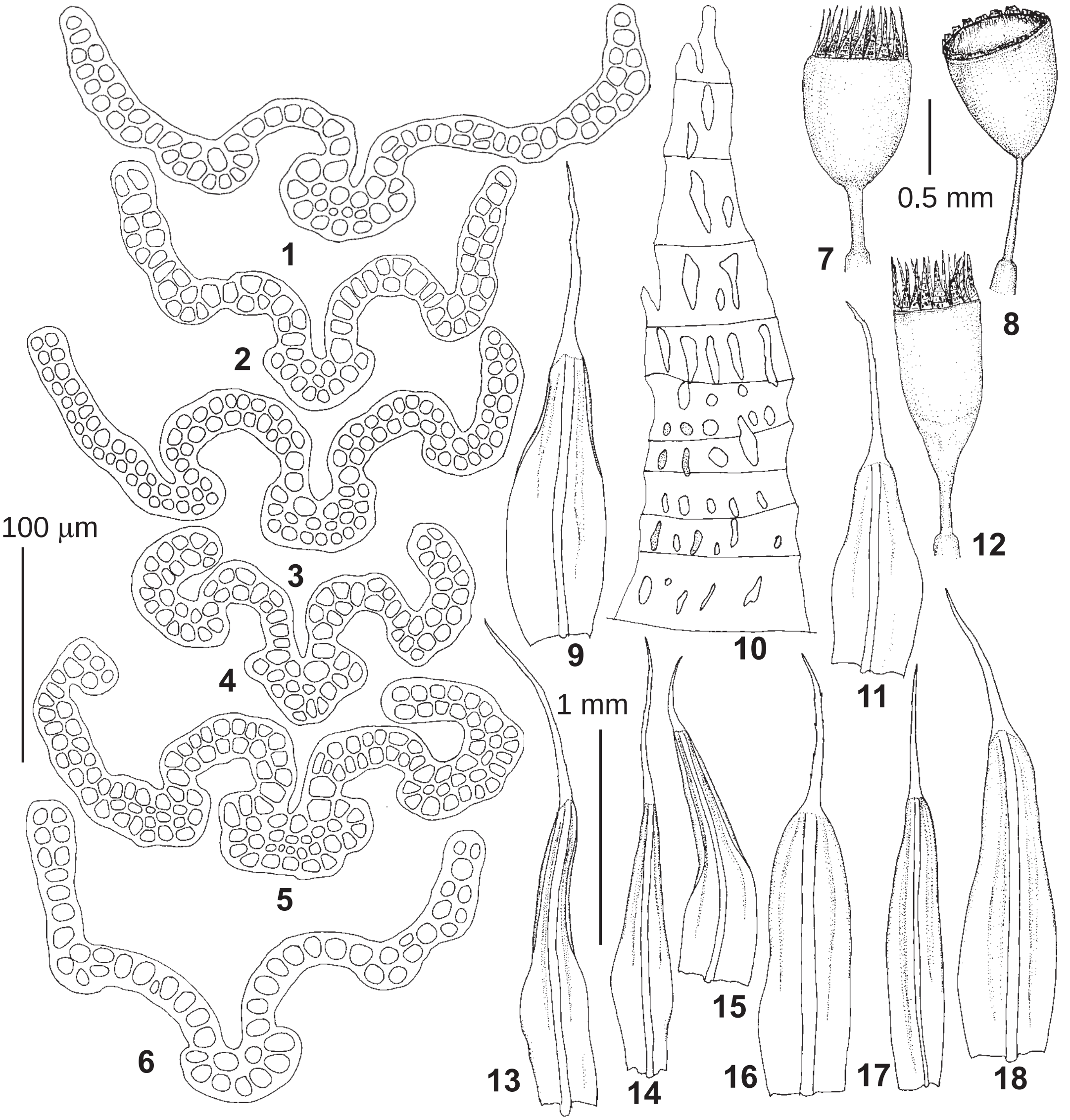


Fig. 5. *Coscinodon cribrosus* (Hedw.) Spruce (1, 7, 9-10 – from Austria, *Köckinger #14257*, KL; 2, 11 – from Austria, *Köckinger #14258*, KL; 3, 8, 17-18 – from Russia, Caucasus, Kabardino-Balkaria, 2.VIII.2004 *Ignatov & al. s.n.*, MHA; 4, 13-14 – from Russia, Altai Mts., *Ignatov #36/354*, MHA; 5, 15 – from Mongolia, *Ignatov #01-718*, MHA; 6, 12, 16 – from U.S.A., New York State, *Miller #15873*, MO): 1-6 – leaf transverse sections; 7-8, 12 – capsules, wet; 9, 11, 13-18 – stem leaves, 10 – peristome tooth. Scale bars: 1 mm for 9, 11, 13-18; 0.5 mm for 7-8, 12; 100 µm for 1-6, 10.

in mountains, as well as in deciduous north-temperate forests. The most western locality is in the Baikal Lake area, Vitim River. In Japan it occurs at least down to Kyushu, and undoubtedly will be found in northeastern China, although no material has yet been seen from that country. *Coscinodon yukonensis* obviously belongs to the distinct group of amphipacific bryophytes.

COSCINODON HUMILIS MILDE

According to various descriptions, e.g. that of Limpricht (1896) and Greven (1995), *C. humilis* differs from *C. cribrosus* by a combination of: (1) leaves non- or indistinctly plicate vs. strongly plicate, (2) leaf margins plane vs. incurved, (3) laminae mainly unistratose in its distal part vs. predominantly bistratose, and (4) peristome teeth with only few perforations vs. strongly cribrose. These characters were considered quite variable and exhibiting a continuous series of transitional forms by Maier & Geissler (1995), whereas Greven (1995) insisted that no transitions could be found, and thus *C. humilis* should be treated as a good species.

To resolve this puzzle we sequenced a number of 'typical' and 'intermediate' specimens from Central Europe (where *C. humilis* had been described), including a mixed collection (Nebel et al. specimens 323a and 323b). The quite sharp molecular differentiation (Fig. 2, Table 1) confirms the species status of *C. humilis*. Some specimens preliminarily identified as intermediates or 'not very good' *C. humilis* were found among *C. cribrosus*. It looks that underdeveloped, sterile plants of the latter species are very difficult if not impossible to differentiate from *C. humilis* based on gametophyte morphology alone.

In well-developed plants, however, the differences in leaf structure are usually enough for species discrimination. *Coscinodon humilis* normally does not have true leaf plications although bistratose strips may look like plicae in that species; the lamina is distally mostly unistratose (except the bistratose margin and occasional longitudinal strips) and the peristome is not cribrose. *Coscinodon cribrosus* by contrast has well-developed leaf plications, the lamina is mostly bistratose distally, and the peristome is cribrose (cf. Figs. 4 and 5).

Our study of the peristome teeth provides some additional characters, although since the number of studied specimens is limited, the stability of these characters should not be taken as a proven fact. First, in *C. cribrosus* the outer surface has numerous 'bald' areas (Fig. 15) surrounded by large round papillae, whereas the outer surface of the teeth in *C. humilis* is evenly papillose (Fig. 11), and papillae are smaller and fused at the base (Fig. 12). The inner tooth surface in *C. cribrosus* has similar 'bald' areas (Fig. 16), whereas nothing similar is seen in *C. humilis* (Fig. 13). Also papillae on the inner surface are narrower and more branched in *C. humilis* than in *C. cribrosus* (Figs. 14 & 17). These differences obviously affect peristome movements. Most specimens of *C. cribrosus* have dome-like incurved peristome teeth in dry condition, at least in recently deoperculate capsules. When moistened the teeth move outwards and become more or less erect but only rarely distinctly spreading. In *C. humilis* mature sporophytes were not found in recent collections, but they occur in Milde's specimens in different herbaria (KL, LE, MO). Even in these old plants peristome teeth show a xerocastique type of hygroscopic movement: being erect when dry, they start to move inwards when moistened.

The lectotypification of *C. humilis* was made by Maier & Geissler (1995), who came to the conclusion that the two species were identical. The illustrated leaf transverse sections in their paper indeed resemble those of *C. cribrosus*, forcing us to re-examine the lectotype from G which was done by HK. The lectotypification proved to be correct. The specimen contains a mixture of disintegrated *Coscinodon* cushions and *Andreaea rupestris*, similarly present also in the majority of isotype-specimens; in addition, a revision label by RH from 1990 confirms the belonging to *C. humilis*. Most of the leaves show flat and unistratose upper laminae, only a minor part is weakly plicate and irrigularly bistratose. The drawings in Maier & Geissler (1995) certainly represent an extreme case. We can exclude the possibility of an admixture of *C. cribrosus*, as one shoot with partly weakly plicate leaves bears an old capsule with few remaining peristome teeth which fit the protologue in being only sparsely and irregularly perforated.

Sporophytes are obviously extremely rare in *C. humilis* and also missing in the four molecularly tested collections. How can we be sure that they represent true *C. humilis*? In their leaf characters they all fit the protologue and isotypes very well. Characteristic for *C. humilis* seem to be the longer hair-points in comparison to *C. cribrosus*. This is especially obvious in alpine environments, where *C. cribrosus* tends to reduce hair-length. The two of the tested specmens from the highest altitudes appear even whitish due to extreme hair-development. Such a form is also mentioned in Limpricht (1895) (sub fo. *subsulcata*) which was collected only 15 km SW of "Austria 2" and at about the same altitude. Remarkably, this plant is given as having capsules and its teeth as "wenig durchbrochen" which means "with few perfora-

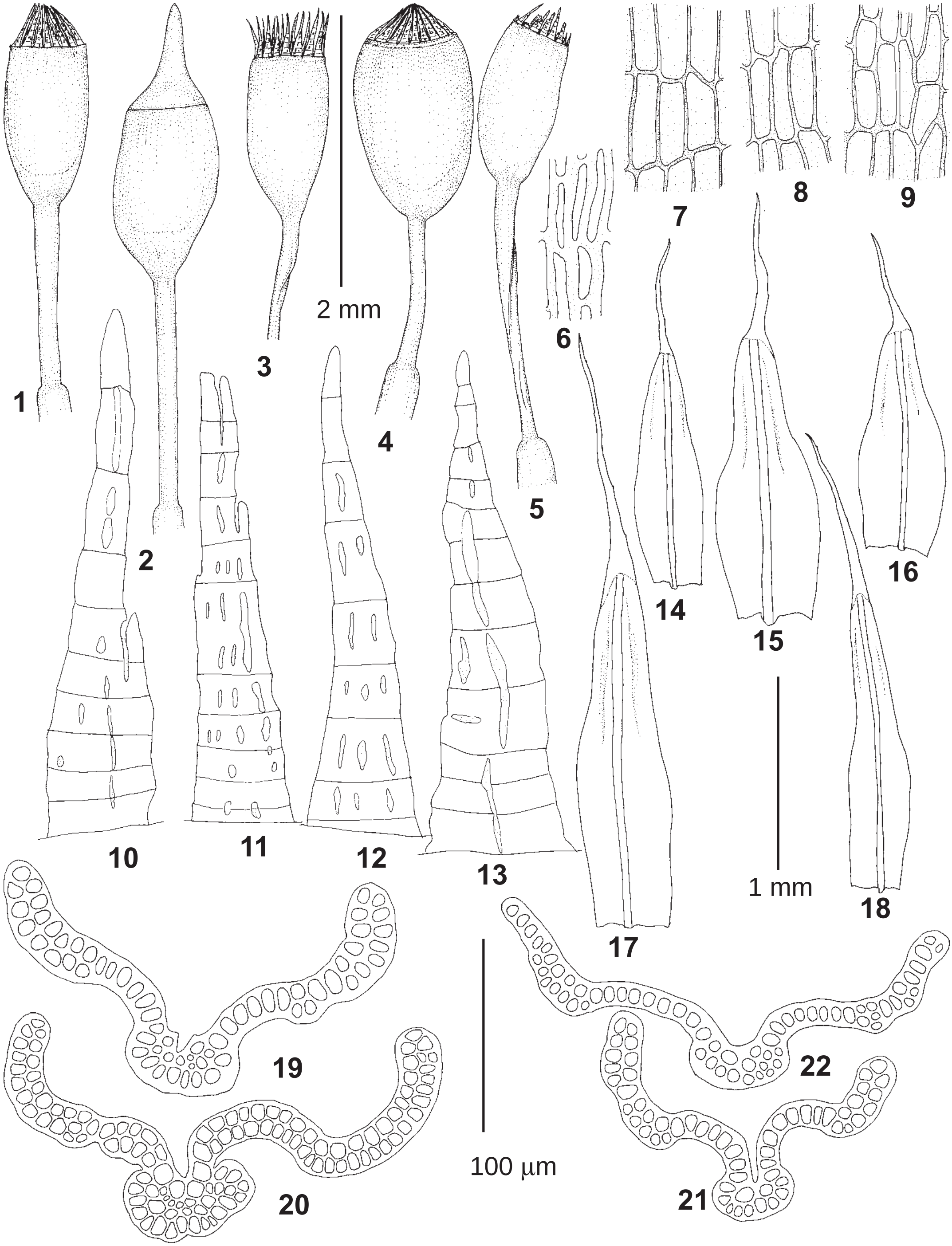


Fig. 6. *Coscinodon hartzii* C.E.O. Jensen (1, 6, 11, 14, 21 – from U.S.A., Alaska, *Perry & Murray #6330*, MO; 2-3, 7, 10, 16, 19 – from Kamchatka, *Chernyadjeva #18*, LE; 4, 8, 13,15, 20 – from Kamchatka, *Chernyadjeva #32*, LE; 5, 9, 12, 17, 18, 22 – from Yakutia, 22.VII.2003 *Zolotov & Ivanova s.n.*, MHA): 1-5 – capsules (1-2, 4-5 – wet, 3 – dry); 6-9 – exothecial cells; 10-13 – peristome teeth; 14-18 – stem leaves; 19-21 – leaf transverse sections. Scale bars: 2 mm for 1-5; 1 mm for 14-18; 100 µm for 6-13, 19-21.

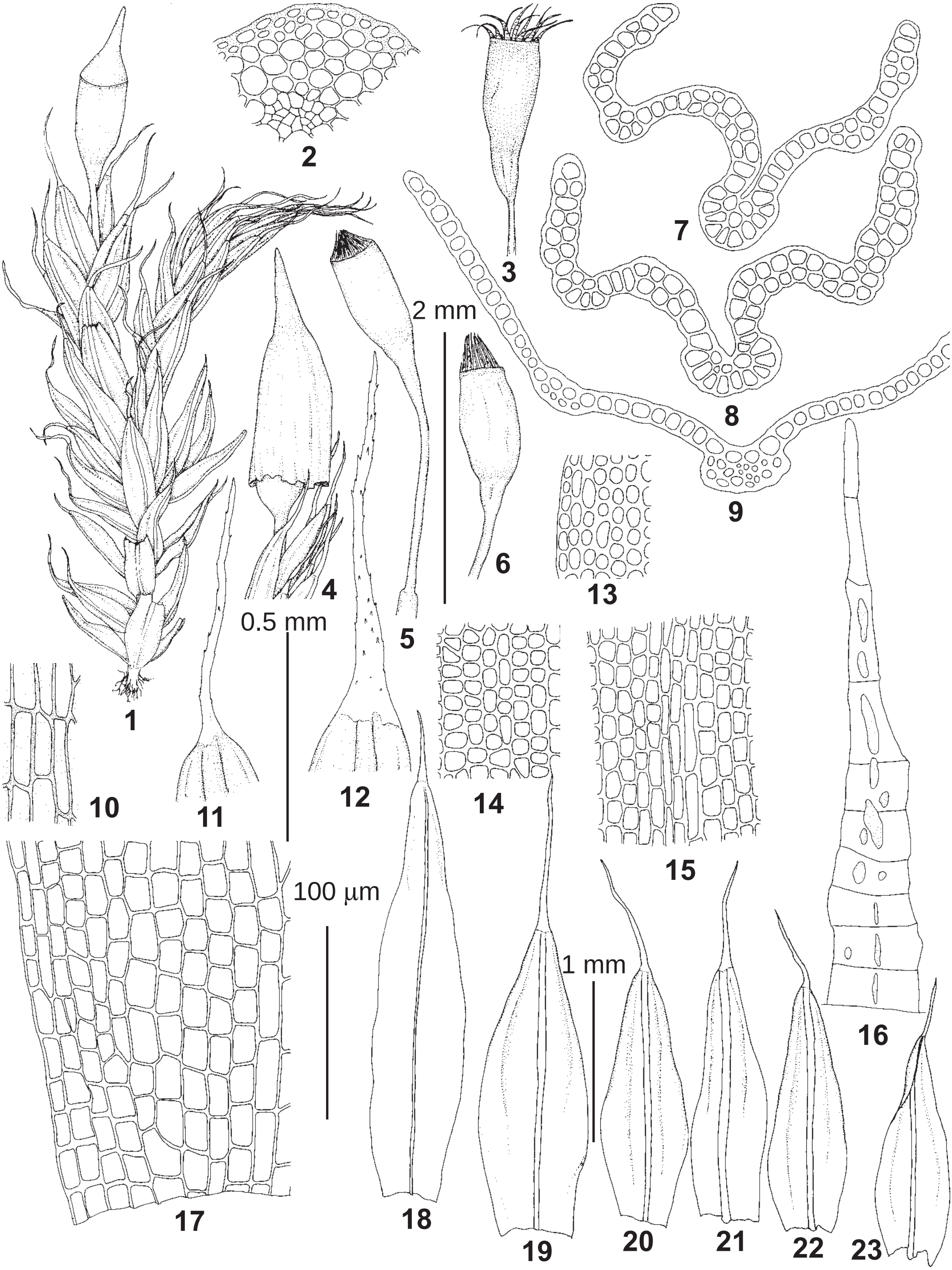
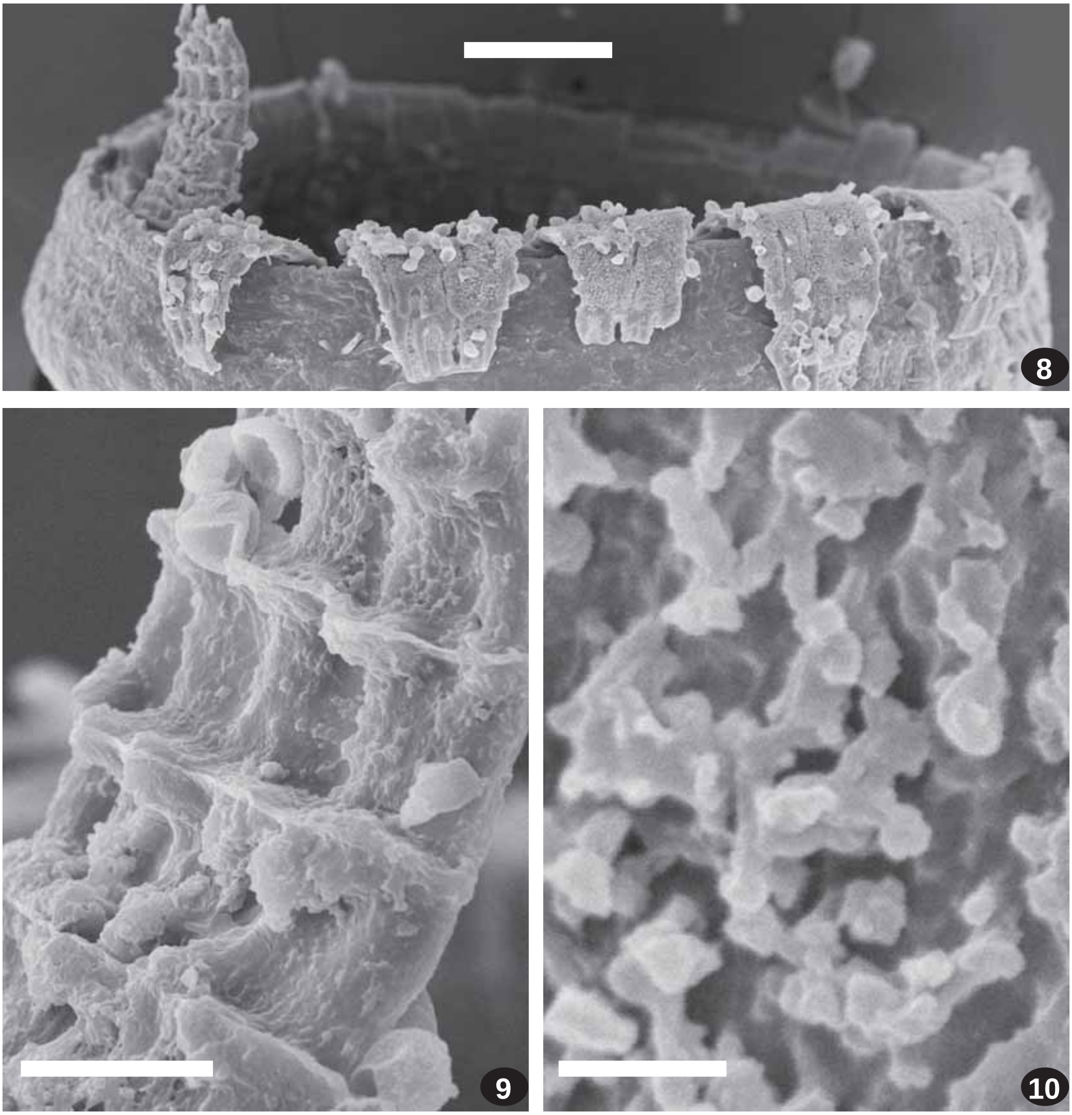


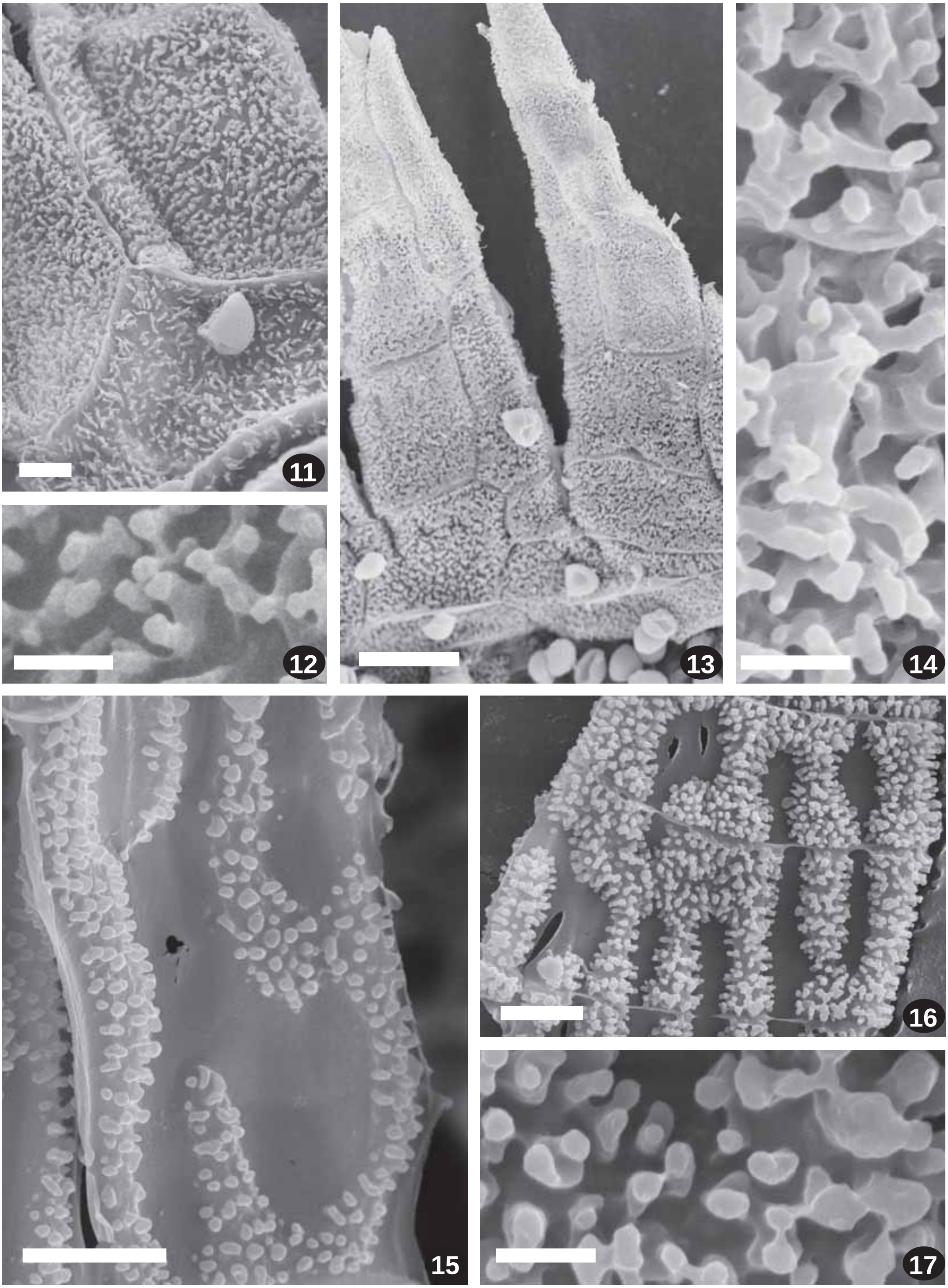
Fig. 7. *Coscinodon pseudohartzii* sp. nov. (from Irkutsk Prov., *Ignatov & Kazanovsky #05-6000*, MHA): 1 – habit, dry; 2 – stem transverse section; 3, 5-6 – capsules (3 – dry, 5-6 – wet); 4 – capsule & calyptra; 7-9 – leaf transverse sections; 10 – exothecial cells; 11-12 – leaf hair-points; 13 – upper laminal cells; 14-15 – median laminal cells; 16 – peristome tooth; 17 – basal laminal cells; 18-19 – perichaetial leaves; 20-23 – stem leaves. Scale bars: 2 mm for 1, 3-6; 1 mm for 18-23; 0.5 mm – for 11-12; 100 µm for 2, 7-10, 13-17.



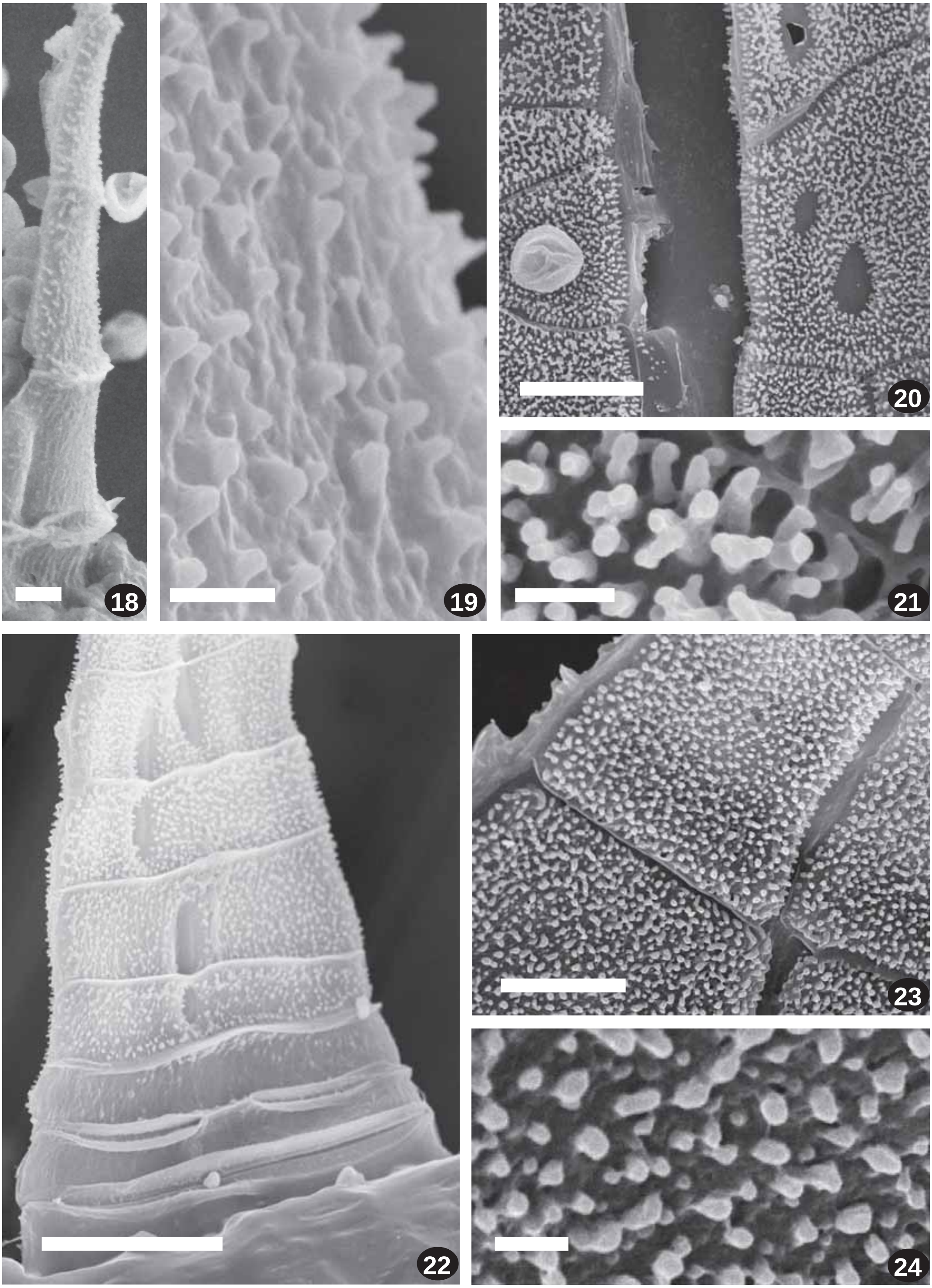
Figs. 8-10. *Coscinodon yukonensis* Hastings (from Kuril Islands, *Bakalin K-43-8-07*, MHA): 8 – peristome, showing mostly reflexed teeth; 9 – outer surface of peristome tooth; 10 – inner surface of peristome tooth. Scale bars: 100 µm for 8, 30 µm for 9; 3 µm for 10.

tions”. Hence, it is very likely that both represent *C. humilis*. Alpine plants are very dense but easily disintegrating, whereas another tested plant (Austria 3) from a much lower, montane locality exhibits extraordinarily loose, tuft-like plants, totally uncommon for a “normal” *Coscinodon.* Additionally, it is worth noting that despite of its latin epithet *C. humilis* tends to be a coarser plant than *C. cribrosus*. This is obvious in the mixed collection (Nebel & al. 323a, b) which was collected only about 20 km north of the type-locality. The minor element which molecularly proved to belong to *C. humilis* is a distinctly larger-leaved, easily disintegrating plant whereas the major element of *C. cribrosus* consists of small-leaved, dense cushions.

Until now *C. humilis* seems to be confined to the Alps, where it obviously prefers the inner ranges with a more continental climate. There it occurs rarely from the lower mountain valleys up to the upper alpine belt, growing at the same poor rock habitats as *C. cribrosus*.



Figs. 11-14: *Coscinodon humilis* Milde (from Meran, *Milde s.n.,* isotype, LE) and 15-17: *Coscinodon cribrosus* (Hedw.) Spruce (from Thuringia, 16.IV.2008, *Meinunger & Schröder s.n.,* STU): 11-12 & 15 – outer surface of peristome teeth; 13-14 & 16-17 – inner surface of peristome teeth. Scale bars: 30 µm for 13; 10 µm for 11, 15-16; 3 µm for 12, 14, 17.



Figs. 18-21: *Coscinodon hartzii* C.E.O. Jensen (from Kamchatka, 16.VII.2003, *Czernyadjeva #18*, LE) and 22-24: *C. pseudohartzii* Hastings, Ignatova & Köckinger (from holotype: Irkutsk Province, *Ignatov & Kazanovsky #05-6000*, MHA): 18-19 & 22 – outer surface of peristome teeth; 20-21 & 23-24 – inner surface of peristome teeth. Scale bars: 30 µm for 20, 22; 10 µm for 18, 23; 3 µm for 19, 21, 24.

COSCINODON CRIBROSUS (HEDW.) SPRUCE

This species is the most widespread in the genus and also the most polymorphous in its ITS sequences. It is also the most well-known and many taxonomic treatments and floras provide its description and illustrations. The cribrose peristome, immersed capsules and strongly plicate leaves are important species' diagnostics.

Easternmost Asian populations were not resolved within the main group of samples of this species. Among them, the Inner Mongolian plants deviate from 'typical' *C. cribrosus* in some morphological characters, e. g. reduced peristome teeth with irregular outline and few perforations (Bai & Tan, 2004). The North Yakutian plants are similar to *C. cribrosus* in most morphological characters, except their peristome is xerocastique. Their placement in *C. cribrosus* is problematic.

Weakly developed plants, as was discussed above, can be confused with *C. humilis*. Another problem is the separation of *C. cribrosus* and *C. hartzii*, as is discussed below.

The sequence from the Germany can be seen as a standard sequence for what we have to understand as *C. cribrosus* s.str., as it was collected ca. 100 km S of the type-locality in Goslar, Germany, in an environments quite similar to that in the latter. Four further specimens belong to the same, genetically invariably group, originating from Karelia (NW Russia) and Austria. This is certainly the common European morph of lowland areas and low mountain ranges; in the Alps it ascends to the tree-line. From the alpine to the nival belt of the Alps, however, additional genotypes of *C. cribrosus* s. lato occur. There is, for example, a subnival plant with short hair-points and reduced peristome teeth which is molecularly hardly different from a sterile Mongolian plant which points to a Pleistocene immigration of this plant from the East. Possibly, this plant has something to do with the non-peristomate *C. arctolimnius* ssp. *higuchii*, recently described from Central Asia (Hastings & Deguchi 1997). An additional group within *C. cribrosus* s.lato is formed by collections from the Baikal area, the Caucasus and Azerbaijan, which have two molecular synapomorphies in common. However, the few specimens tested, partly even sterile, do not allow a taxonomic segregation of infraspecific taxa.

COSCINODON HARTZII C.E.O. JENSEN

This species was considered to be endemic to North America by Hastings (1999 and 2007). However, a number of specimens from the eastern part of Russia fit the concept of *C. hartzii* better than *C. cribrosus*. They have: (1) seta longer than 1.5 mm; (2) capsules cylindric, exserted; (3) peristome xerocastique and (4) leaves with plicae only in distal part. Some characters show considerable variability in the studied specimens, i. e. the seta length typically varies from 1.6 to 2 mm, but one specimen from Kamchatka has the seta only ca. 1 mm long. This specimen, however, is referred to *C. hartzii* because of its xerocastique peristome, and its ITS sequence is virtually identical with the second specimen from Kamchatka, which is 'typical' *C. hartzii* with a longer seta.

Hastings (1999) describes the peristome teeth of *C. hartzii* as cribrose and similar to that of *C. cribrosus*, albeit exhibiting xerocastique movements. In specimens from Asian Russia, however, peristome teeth are longer and narrower than in *C. cribrosus* and only slightly perforated. The hygroscopic movements in Asian *C. hartzii* are rather xerocastique, the teeth being erect to spreading when dry and dome-shaped when wet (Fig. 6), although not always totally covering the urn mouth.

Furthermore, all studied Asian specimens of *C. hartzii* have thin-walled elongate exothecial cells (Fig. 6: 9-12), which is unusual for the genus. In all studied capsules of different *Coscinodon* species, as well as in *C. hartzii* from Alaska, the exothecial cells have strongly thickened cell walls. By the position in the phylogenetic tree (Fig. 2) and by the presence of the single molecular synapomorphism (Table 1), the Alaskan specimen does not differ from Russian specimens with a thin-walled exothecium.

Thus, we refer all five studied specimens to *C. hartzii*, despite the differences in exothecium and peristome structure. This decision seems to be the only one possible for so few specimens studied.

COSCINODON PSEUDOHARTZII SP. NOV.

Among the specimens preliminarily sorted out as *C. hartzii*, primarily based on long setae, one specimen from the Baikal Lake area looked anomalous. It had unusually narrow capsules on long setae, ca. 2 mm, with a long and indistinctly delimited neck gradually tapered to seta; stomata were few and small in contrast to those seen in *C. hartzii*; peristome teeth long attenuate at tips and semiperforate; leaves with inrolled leaf margins and deep plicae extending far below mid-leaf in many leaves. Such character combinations are out of the range of variation of *C. hartzii*, thus a new species, *C. pseudohartzii* is described below.

ITS data showed considerable similarity with a sterile specimen preliminarily called '*C. cribrosus*' from the southern Primorsky Territory. Also, one specimen of '*C. cribrosus*' from Maine was found in a clade with *C. pseudohartzii*. Unfortunately, it too is sterile, so we are not able to discuss it in much detail. Morphologically it perfectly fits the concept of *C. cribrosus* in gametophyte characters. To ensure that its ITS sequence was correct we re-sequenced the specimen. The newly obtained sequence, however, was identical to that previously found by Hernandez-Maqueda (EU343763). Two other samples from Maine and New York State were found to be quite different, virtually identical to European *C. cribrosus*. Further discussion must be left until the sporophytes of this enigmatic plant from Maine are discovered. However, if we trust the molecular results, then the Baikal, the Primorsky and the Maine plant belong to the same species (the three have also two molecular synapomorphies in common), despite the obvious impossibility to distinguish sterile collections (which is a general problem in *Coscinodon*).

* * *

Coscinodon pseudohartzii Hastings, Ignatova & Köckinger sp. nov.

Coscinodon hartzii similis, sed hypophysibus elongatis, dentibus peristomii attenuatis, foliis margine involutis et usque ad basin plicatis differt.

Holotypus: Russia, Provincia Irkutsk, Slyudyanka, saxicola. M.S. Ignatov & S.G. Kazanovsky, #05-6000 (MHA). Isotypi MW, LE, PMAE.

Plants small, in dense hoary cushions, dark greyish-green or olivaceous-green. Stems 2-4 mm long, branching from the base, with distinct central strand. Stem leaves erect-appressed when dry, erect-patent when moist, 1.0-1.5 mm long, 0.3-0.4 mm wide at shoulder, from ovate base gradually to rather abruptly tapered into lanceolate acumen, keeled above, concave below, lower leaves muticous, median and upper leaves with hyaline hair-points to 0.5(-0.6 mm) long, hair-points distantly denticulate, mostly narrowly attached, more widely attached in uppermost leaves, not decurrent, flexuose when dry; leaf lamina smooth, partially or completely bistratose distally, unistratose proximally with bistratose strips, with deep plicae extending well below mid-leaf in many leaves, cells of plicae differentiated at places, elongate to linear (Fig. 7:15), leaf margins incurved distally, plane proximally; laminal cells with moderately thickened, not sinuose walls, rounded to shortly rectangular or elliptical, upper laminal cells 10-15×8-10 μm, median laminal cells 10-20×10-12 μm, basal juxtacostal cells 15-35×10-15 μm, with uniformly thickened walls, basal marginal cells shorter, with more strongly thickened transverse walls and thin longitudinal walls, in uppermost stem leaves becoming hyaline and thin-walled; costa strongly prominent abaxially, narrowly grooved adaxially, 2-3(-4)-layered, cells of costa mostly not differentiated in transverse section. Sexual condition dioicous. Perichaetial leaves enlargered, 1.8-2.5 mm long, to 0.7 mm wide, with thin-walled and hyaline cells across the base or at margins in proximal 1/2 of leaf, hyaline hair-points to 1.0 mm long, widely attached, not to shortly decurrent. Capsules exserted, setae ca. 2 mm long, straight to slightly arcuate. Urn cylindric, ca. 1 mm long, 0.5-0.6 mm wide, light orange-brownish or yellow-brownish, slightly striolate when dry, with long indistinctly differentiated neck gradually narrowing into seta. Peristome xerocastique, teeth light yellowish-brown or orange, 350-400 μm long, 40-60 μm wide at base, narrowly attenuate distally, semiperforate, finely and densely papillose throughout on both surfaces. Exothecial cells thin-walled, rectangular, stomata few and tiny, 1-2 at urn base. Annulus absent. Operculum conic, with a straight narrow beak, ca. 0.6 mm long. Spores 8-13 μm, smooth. Calyptra campanulate, plicate, golden-brown, almost covering mature capsules.

Specimens examined*:* Russia, *Irkutsk Province*, Slyudyanka River valley, *Ignatov & Kazanovsky #05-6000* (MHA). One more sterile specimen agrees with the type specimen in all details of gametophyte structure, as well as in sequence: Primorsky Territory, Khasansky Distr., Ryazanovka, 20.VI.2006, *Konovalova s.n.* (MHA).

Ecology. The fertile specimen from the Irkutsk Province was collected on a cliff at slope base in an open *Larix* & *Betula* forest. Its association with *Mielichhoferia mielichhoferiana* (Funck) Loeske indicates a high concentration of heavy metal and in general the valley is known to be rich in copper. In the Primorsky Territory the specimen was found growing on a cliff along the sea shore.

Differentiation. Gametophytically *C. pseudohartzii* is practically indistinguishable from *C. cribrosus* due to deep and long leaf plicae extending below mid-leaf and sometimes almost reaching the leaf base, bistratose lamina and incurved margins in distal part of leaf. However, sporophytically *C. pseudohartzii* is closer to *C. hartzii*: its capsules are well-exserted and the peristome is xerocastique. It differs from the latter species in: (1) the absense of annulus vs. usually present, (2) semiperforated but not cribrose peristome teeth vs. usually cribrose teeth, (3) neck of urn longer and indistinctly delimited, gradually narrowing into seta vs. neck shorter, distinctly delimited, and (4) stomata tiny and very few (1-2) vs. stomata prominent and common (6-8). In addition, exothecial cells are thin-walled in *C. pseudohartzii*, while they are thick-walled in North American specimens of *C. hartzii*, but all Russian collections of *C. hartzii* also have thin-walled exothecia. In gametophyte characters *C. pseudohartzii* is readily separated from *C. hartzii* in longer leaf plicae, incurved leaf margins in distal part of leaf, absence of 3-stratose patches in distal leaf lamina and narrowly attached hyaline hair-points, whereas in *C. hartzii* leaf plicae never extend below midleaf, leaf margins are plane, distal lamina is often 3-stratose at places and hyaline hair-points are widened at the base.

* * *

Summing up, the present analysis demonstrated that the diversity of the genus *Coscinodon* in Russia and adjacent regions was greater than previously thought. It also pointed out difficulties, especially in North-East Asia, where taxa delimitation and possible introgression have to be especially addressed. More collections from this poorly studied area have to be made. Extensive molecular comparison with Western North America is also needed with more variable markers than the ITS region.

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