

ON THE PHYLOGENY AND TAXONOMY OF PALLAVICINIALES  
(MARCHANTIOPHYTA), WITH OVERVIEW OF RUSSIAN SPECIES

ФИЛОГЕНИЯ И ТАКСОНОМИЯ ПОРЯДКА PALLAVICINIALES  
(MARCHANTIOPHYTA) С ОБЗОРОМ РОССИЙСКИХ ВИДОВ

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Abstract

Integrative analysis of expanded sampling of Pallaviciniales revealed the heterogeneity of Moerckiaaceae. The new family Cordaeaceae Mamontov, Konstant., Vilnet & Bakalin is described based on morphology and molecular phylogenetic data. It includes one genus *Cordaea* Nees with two species, *C. flotoviana* (= *Moerckia flotoviana*), the type of the genus, and *C. erimona* (Steph.) Mamontov, Konstant., Vilnet & Bakalin *comb. nov.* Descriptions and illustrations of all species of the order known from Russia including newly reported *Pallavicinia subciliata* and provisional *P. levieri* are provided. Identification key for Pallaviciniales known from Russia and adjacent areas is given.

Резюме

В результате комплексного молекулярно-генетического и сравнительно-морфологического анализа расширенной выборки порядка Pallaviciniales выявлена гетерогенность сем. Моерckiaceae. Из него выделено новое семейство Cordaeaceae Mamontov, Konstant., Vilnet & Bakalin, включающее один род *Cordaea* Nees и два вида, *C. flotoviana* Nees (тип рода) и *C. erimona* (Steph.) Mamontov, Konstant., Vilnet & Bakalin *comb. nov.* Приведен ключ для определения видов порядка, встречающихся в России и на прилегающих территориях, даны описания и иллюстрации известных в России видов порядка, включая впервые выявленную для страны *Pallavicinia subciliata*, а также провизорно приводимую *P. levieri*, обнаруженную в республике Корея.

KEYWORDS: Pallaviciniales, molecular phylogeny, taxonomy, Moerckiaaceae, Cordaeaceae, Russia

INTRODUCTION

Pallaviciniales W. Frey & M. Stech (subclass Pellididae, class Jungermanniopsida) in recent treatments (Crandall-Stotler *et al.*, 2009) has been subdivided in two suborders: the Phyllohalliineae R.M. Schust. with the monotypic family Phyllohalliaceae E.A. Hodgs., and the Pallaviciniineae R.M. Schust., which includes the monotypic families Sandeothallaceae R.M. Schust. and Hymenophytaceae R.M. Schust., the oligotypic Moerckiaaceae Stotler et Crand.-Stotl. with two genera and Pallaviciniaceae Mig., with eight genera. The majority of the species of Pallaviciniales are restricted to the southern hemisphere. The latest and the most comprehensive molecular study on Pallaviciniaceae (Schaumann *et al.*, 2005: 39) shows “the clear molecular sep-

aration” of *Moerckia* that “supports Schuster’s (1992) view representing *Moerckia* as heterogeneous element in the family based on morphological characters”. It caused Crandall-Stotler & Stotler (2007) to describe a separate family for the latter genus. On the other hand the studies mentioned above pose several problems in the taxonomy of this group. Schaumann *et al.* (2005) studied 60 specimens of Pallaviciniaceae. The majority of them belong to species occurring in the southern hemisphere or in the tropics and subtropics whereas some Holarctic genera and species were not studied. Particularly *Moerckia blyttii* was not involved in the study. Some Holarctic species (*e.g.*, *Moerckia flotoviana*) were represented by single specimen. We expand this study of the holarctic species of the order.

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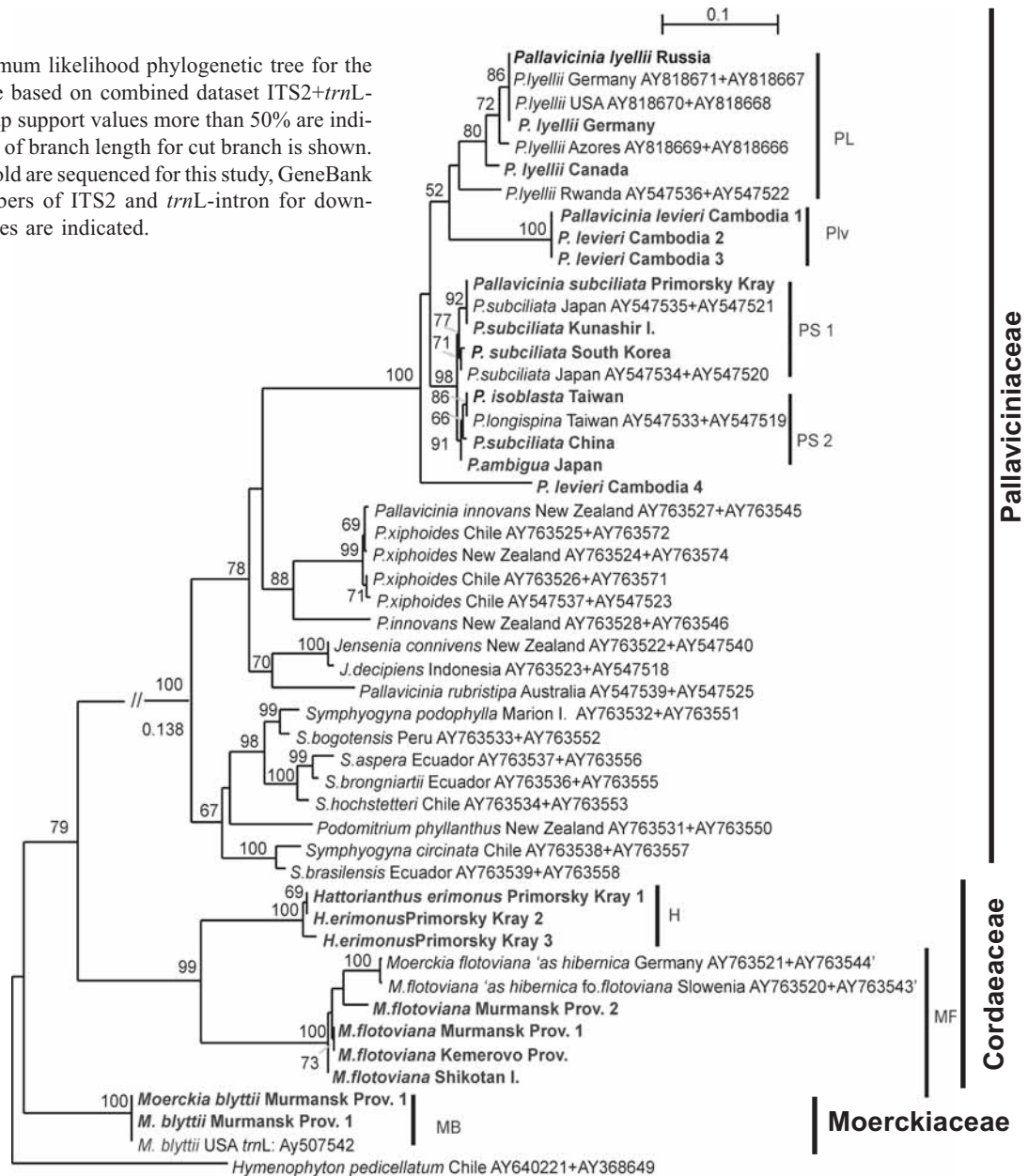
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Fig.1. Maximum likelihood phylogenetic tree for the Pallaviciniineae based on combined dataset ITS2+trnL-intron. Bootstrap support values more than 50% are indicated, the value of branch length for cut branch is shown. Specimens in bold are sequenced for this study, GeneBank accession numbers of ITS2 and trnL-intron for downloaded sequences are indicated.

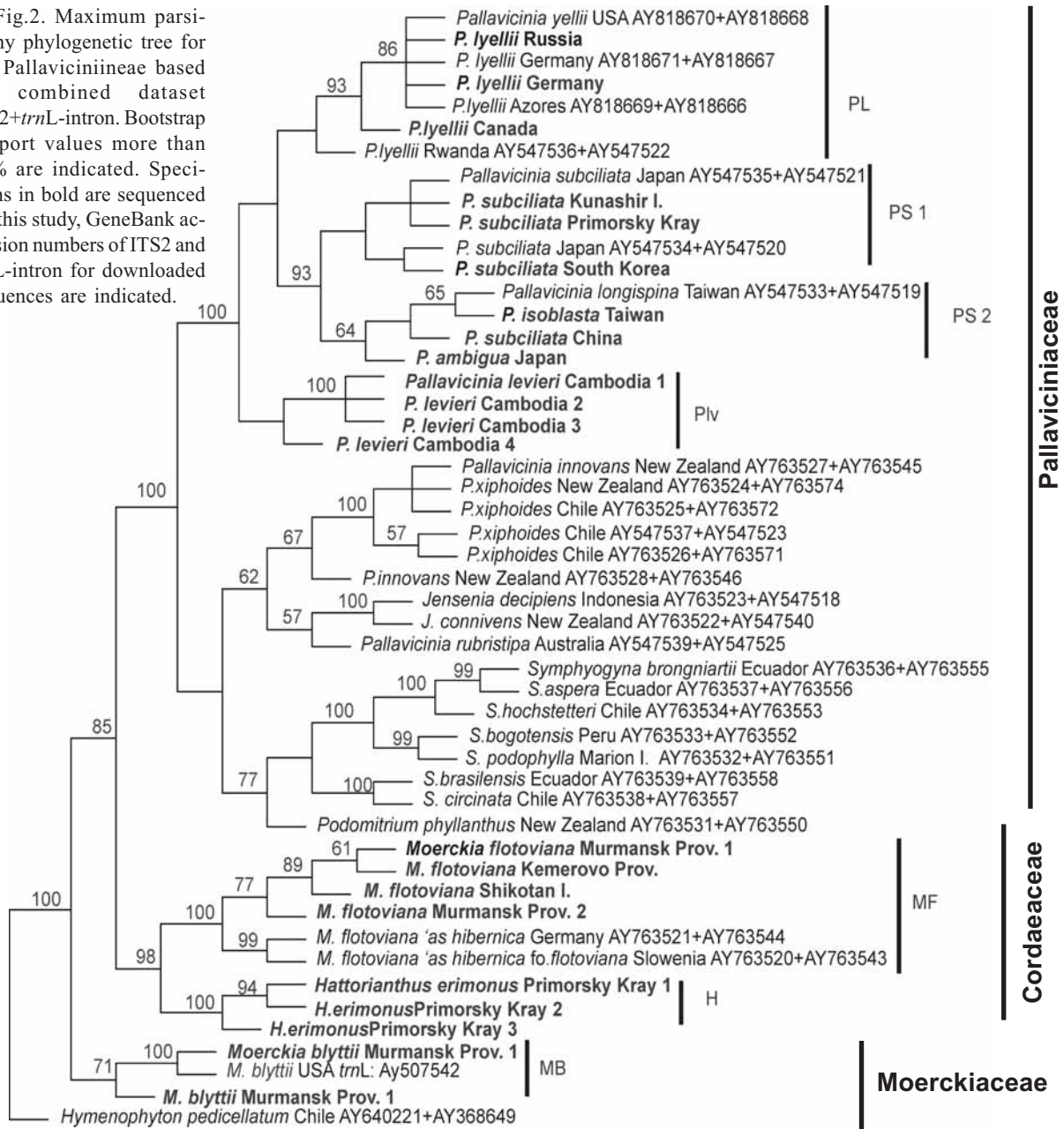


MATERIAL AND METHODS

According to the last checklist of Russian liverworts (Konstantinova, Bakalin *et al.*, 2009) the order Pallaviciniales is represented in Russia by five species from two families (Pallaviciniaceae and Moerckiaceae), and three genera (*Moerckia*, *Hattorianthus* and *Pallavicinia*). Species of *Moerckia* occur sporadically in Russia whereas *Hattorianthus* and *Pallavicinia* are extremely rare. All available specimens of Pallaviciniales from Russia were studied. The majority of them are preserved in KPABG (37). Apart from samples collected in Russia more than 50 specimens from the world were studied in KPABG, LE, VBGI, H, and E. The type specimens of *Pallavicinia levieri* (JE), *P. fistulosa* (LE), and *Sandeothallus japonicus* (NICH) were studied. In total ca. 100 specimens were revised.

Twenty-two specimens from the families Pallaviciniaceae and Moerckiaceae were selected for DNA analysis. The genus *Pallavicinia* was represented by three specimens of *P. lyellii* from Canada, Germany and Russia, four specimens from Cambodia that had preliminarily been identified as *P. lyellii*, four specimens of *P. subciliata* from the Russian Far East, South Korea and China and single specimens identified as *P. ambigua* from Japan and *P. isoblasta* from Taiwan. The family Moerckiaceae was represented by the genus *Moerckia* with four specimens of *M. flotoviana* and two of *M. blyttii* as well as three specimens from the monotypic genus *Hattorianthus*. All analyzed specimens are listed in Table 1, including GenBank accession numbers and voucher details. Additionally our analyses included earlier published data of ITS2 and trnL-intron for 28 specimens of Pallaviciniineae from Schau-

Fig.2. Maximum parsimony phylogenetic tree for the Pallaviciniaceae based on combined dataset ITS2+trnL-intron. Bootstrap support values more than 50% are indicated. Specimens in bold are sequenced for this study, GeneBank accession numbers of ITS2 and trnL-intron for downloaded sequences are indicated.



mann *et al.* (2005). *Hymenophyton pedicellatum* was chosen as an outgroup due to its earliest divergence within the suborder in this analysis. GenBank accession numbers for downloaded sequences are indicated in Figs.1-2.

**DNA isolation, PCR amplification and DNA sequencing** followed protocols described in Konstantinova & Vilnet (2011).

#### Phylogenetic analysis

The nucleotide sequences of ITS1-2, trnL-F and trnG-intron were obtained for 22 specimens studied here. To resolve phylogenetic affinities of the studied taxa we enlarged the data set by inclusion of earlier published sequences and produced alignments only for ITS2 and trnL-intron.

The two datasets, ITS2 and trnL-intron, were automatically aligned in BioEdit 7.0.1 (Hall, 1999) with Clust-

alW option and then manually corrected. The preliminary phylogenetic analysis revealed a lack of incongruence between ITS2 and trnL-intron and subsequently both datasets were combined. All positions of the final alignment were included in the phylogenetic analysis, lacking parts of sequences were coded as missing.

The combined dataset was analyzed by the maximum likelihood method (ML) with PhyML (Guindon *et al.*, 2010) and maximum parsimony method (MP) with TNT (Goloboff *et al.*, 2003). The program ModelGenerator (Keane *et al.*, 2004) determined that the K80+I+G model was the best-fit evolutionary model of nucleotide substitutions. That model was used in ML analysis and the rate of heterogeneity among sites was modelled using a gamma distribution with four rate categories. Bootstrap



Table 1. The list of taxa, specimens vouchers and GenBank accession numbers for studied samples.

Taxon	Specimen voucher	GeneBank accession number		
		ITS1-2	<i>trnL</i> -F	<i>trnG</i> -intron
<i>Hattorianthus erimonus</i>	Russia: Primorsky Kray 1, Bakalin, 105648 (KPABG)	KJ577207	KJ577220	—
	Russia: Primorsky Kray 2, Mamontov, 107/1-10 (KPABG)	KJ577205	KJ577218	KJ577228
	Russia: Primorsky Kray 3, Bakalin, 116-2-03 (KPABG)	KJ577206	KJ577219	KJ577229
<i>Moerckia blyttii</i>	Russia: Murmansk Prov. 1, Konstantinova, 9 (LE)	KJ577209	—	KJ577235
	Russia: Murmansk Prov. 2, Mamontov, 53/8 (KPABG)	KJ577208	KJ577221	KJ577234
<i>M. flotoviana</i>	Russia: Kemerovo Prov., Konstantinova, K202-1-04 (KPABG)	KJ577213	KJ577217	KJ577232
	Russia: Murmansk Prov. 1, Borovichev, BE-46-7-05 (KPABG)	KJ577211	KJ577215	KJ577231
	Russia: Murmansk Prov. 2, E. Borovichev, Yu-4-12 (KPABG)	KJ577210	KJ577214	KJ577230
	Russia: Sakhalin Prov. Shikotan I., Bakalin, K-54-1-07 (KPABG)	KJ577212	KJ577216	KJ577233
<i>Pallavicinia ambigua</i>	Japan, M. Higuchi, 1248 (KPABG, LE)	KJ577199	—	KJ577227
<i>P. isoblasta</i>	Taiwan, H. Inoue, 16822 (LE)	KJ577197	—	KJ577225
<i>P. levieri</i>	Cambodia, Bakalin, Cam-83-37-(KPABG, VGBI, VLA), 1	KP137574	—	KP137572
	Cambodia, Bakalin, Cam-83-42-11 (KPABG, VGBI, VLA), 2	KP137576	—	KP137571
	Cambodia, Bakalin, Cam-83-44-11 (KPABG, VGBI, VLA), 3	KP137575	—	KP137570
	Cambodia, Bakalin, Cam-89-5-11 (KPABG, VGBI, VLA), 4	KP137577	—	KP137573
<i>P. lyellii</i>	Canada, Brassard: Bryoph. Exs. Terr.-Nov. et Labrador # 176 (LE)	KJ577203	KJ577194	KJ577223
	Germany, M. Reimann, GLM-20968 (VGBI)	KJ577204	KJ577195	KJ577222
	Russia: Konstantinova, K523-2-07 (KPABG)	—	KJ577196	—
<i>P. subciliata</i>	China: Hunan Prov., T. Koponen, 51479 (LE)	KJ577198	—	KJ577226
	Russia: Primorsky Kray, Bardunov (KPABG)	KJ577202	—	—
	Russia: Sakhalin Prov.. Kunashir I., V. Bakalin, Hep. Ross. Ex. Fasc. VI, # 127 (KPABG)	KJ577200	—	—
	South Korea, S.-S. Choi, 96 (KPABG)	KJ577201	—	KJ577224

support (BS) for individual nodes was assessed using a resampling procedure with 1000 replicates. According to the stopping frequency criterion (FC) for the bootstrapping procedure (Pattengale *et al.*, 2010) for our dataset even 200 replicates were enough for reaching BS convergence with Pearson average  $\bar{n}100 = 0.994701$  realized in RAxML v7.2.6 (Stamatakis, 2006).

The MP analysis involved a New Technology Search with a search for the minimum-length tree by one reiteration and 1000 bootstrap resamplings; the default settings were used for other parameters, indels were taken into account by a modified complex coding algorithm in SeqState (Müller, 2005).

The infraspecific variability was evaluated as the *p*-distances for each DNA loci calculated in Mega 5.1 (Tamura *et al.*, 2011) using the pairwise deletion option for counting gaps. For specimens sequenced in this study *p*-distances were estimated for ITS1-2, *trnL*-F and *trnG*-intron, for both our and GenBank data *p*-distances were calculated for ITS2 and *trnL*-intron.

#### RESULTS

The nucleotide sequences of ITS1-2, *trnL*-F and *trnG*-intron were obtained for 21, 11 and 18 specimens respectively. Alignments for ITS2 includes 336 positions (182 variable, 153 parsimony informative) and *trnL*-intron has the 399/208/175 positions correspondingly. All alignments pose a high number of variable sites that correspond with data published by Schaumann *et al.* (2005) and suggest the deep divergence among the studied taxa.

The MP analysis of the combined ITS2+*trnL*-intron dataset yielded 15 most parsimonious trees with a length

of 1384 steps, with CI= 0.610010 and 0.875995 calculated in Mega 5.1. The arithmetic means of Log likelihood obtained in ML calculation for combined dataset was  $-5427.45796$ .

The tree topologies obtained by the two methods are highly congruent and similar to those of Schaumann *et al.* (2005), a number of internal nodes also have no support (Fig. 1, 2). Phylogenetic relation of Pallaviciniineae was discussed in details by Schaumann *et al.* (2005). Here we focused on the relation of Holarctic species not or insufficiently studied previously to resolve some taxonomical ambiguities. Three specimens of *Pallavicinia lyellii* sequenced in our study were located in the corresponding clade (PL) with specimens from Europe and USA (BS=80% in ML, BS=93% in MP). The specimens of *P. subciliata*, *P. isoblasta*, *P. ambigua*, and *P. longispina* composed an intermingled *Pallavicinia*-clade (BS=98% in ML, BS=93% in MP) with two subclades. One of these subclades (PS1) (BS=77% in ML, without support in MP) includes specimens of *P. subciliata* from the Russian Far East, Japan and South Korea. The other subclade (PS2) (BS=91% in ML, BS=64% in MP) includes specimens identified as *P. ambigua* (Japan), *P. isoblasta* (Taiwan), *P. longispina* (Taiwan) and *P. subciliata* (China). The means of *p*-distances (Table 2: see suppl. materials at <http://www.arctoa.ru/ru/Archive-ru/24/24.php>) suggest that the level of infraspecific variability in *Pallavicinia lyellii* by all studied DNA loci increased in 2-3 times the level of diversity between two subclades of intermingled *Pallavicinia*-clade. Thus the minute genetic divergence between specimens from subclades PS1

and PS 2 suggests that they belong to a single species. Four specimens provisionally identified as *P. lyellii* from the Cambodia combined clade sister to *P. lyellii* and *P. subciliata* clades on MP topology, or with separation of specimen Cam-89-5-11 as a clade in a poorly supported relation to *P. lyellii* (BS=52% in ML). The comparative molecular and morphological study refers these specimens to the Asian taxon *P. levieri*, which is quite similar to *P. lyellii*. The calculation of *p*-distances suggested both taxa as robustly diverged species (ITS1-2 – 12.2%, *trnG*-intron – 6.8%). The specimen Cam-89-5-11 differs from the three other Cambodian specimens both in ITS1-2 (13.1%) and *trnG*-intron (6%), but there are no significant morphological differences between the specimens.

Accordingly the tree topology the family Moerckiaceae appeared to be not monophyletic. The monotypic genus *Hattorianthus* (clade H) was found in relation with *Moerckia flotoviana*, including specimens identified as *M. hibernica*, but belonging to *M. flotoviana* (clades MF+MH; BS=100% in ML, BS=97% in MP), whereas *M. blyttii* (clade MB) was placed in a separate clade. The calculated values of *p*-distances for all studied *loci* also support greater divergence of *M. blyttii* from other *Moerckia* species and *Hattorianthus* than between the last two (on an average several percent, Table 3: see suppl. materials at <http://www.arctoa.ru/ru/Archive-ru/24/24.php>). The divergence of Central European specimens of *Moerckia* is well supported only in the MP tree (BS=100%). The value of *p*-distances between *Moerckia flotoviana* from the North of Europe, Siberia and Far East and Central European *Moerckia* is 6.1% by ITS2 and 2.3% by *trnL*-intron that greatly exceeds their infraspecific variability and could suggest these populations have recently diverged (Table 3).

#### DISCUSSION

In spite of many studies including molecular ones (Schaumann *et al.*, 2004; 2005) the taxonomy of the Pallaviciniales remains rather controversial.

**Moerckia.** De Sloover (1959) treated *M. flotoviana* as fo. *flotoviana* of *M. hibernica*, which was accepted by most bryologists (Schljakov, 1976; Schuster, 1992; Paton, 1999; Damsholt, 2002, *etc.*). Careful study by Crandall-Stotler & Stotler (2007) showed that *M. flotoviana* (= *Cordaea flotoviana* Nees) is very variable but distinct species and most descriptions and illustrations of *M. hibernica* s. lat. should be referred to *M. flotoviana*. According to Crandall-Stotler & Stotler (2007) *M. hibernica* (= *Jungermannia hibernica* Hooker) s. str. differs from *M. flotoviana* in 1) absence of conducting strands; 2) location of female scales (laterally behind gynoecia); 3) elongate-elliptical shape of capsule and 4) papillose surface of spores. *M. hibernica* s. str. is known from the type specimen from Ireland (Hooker, 1816, BM), as well as some specimens from Alaska, and Queen Charlotte and Vancouver Islands (Crandall-Stotler & Stotler, 2007). No specimens of this taxon have been included in mo-

lecular studies, but according available data on comparative morphology (lack of conducting strands, colored rhizoids, *etc.*, see Crandall-Stotler & Stotler, 2007 and see as well below) it is more closely related to *M. blyttii* than to *M. flotoviana*.

One of the results obtained by us is that Moerckiaceae as it is treated recently (Crandall-Stotler & Stotler, 2007; Crandall-Stotler *et al.*, 2009) is not monophyletic. In the molecular phylogenetic trees (Fig 1-2, see also results) *Hattorianthus* is closely related to *Moerckia flotoviana*, whereas *M. blyttii* is placed in a separate clade. This is supported by some morphological features, mainly by the presence of conducting strands in *Hattorianthus* and *M. flotoviana* whereas they never occur in *M. blyttii*. Conducting strands are usually treated as a quite ancient feature in hepatics. The lack of conducting strands in combination with the characteristic dense golden-yellow or brown rhizoids and DNA sequences clearly separate *M. blyttii* from *M. flotoviana* and *Hattorianthus*. Based on the obtained results we propose to keep *M. blyttii* and provisionally also *Moerckia hibernica* (Hook.) Gottsche in the genus *Moerckia*, while *M. flotoviana* and *Hattorianthus* should be combined in the separate genus *Cordaea* Nees (Nees, 1833). Both constructed trees and morphology support separation of *Cordaea flotoviana* Nees and *C. erimona* (Steph.) Mamontov, Konstant., Vilnet & Bakalin *comb. nov.* into a separate family Cordaeaceae Mamontov, Konstant., Vilnet & Bakalin *fam. nov.*

**Pallavicinia** is the largest genus of the order. Numerous species were described mostly from the south of East Asia and many of them were shown to be synonyms (Grolle & Piippo, 1986). According to Grolle & Piippo (1986) less than ten true species of *Pallavicinia* s. str. of ca. 60 described entities exist. The greatest diversity of the genus is represented in Eastern Asia, mostly in subtropics and tropics and only few species are found as far north as in Japan and the Russian Far East.

*P. ambigua* was described by Mitten (1861, as *Steetzia ambigua*) from India, but the original description is too short and formal. Several morphologically quite similar species were described later from different regions – *Steetzia subciliata* Austin (syn. *Pallavicinia subciliata*), *Pallavicinia longispina* Steph. from Japan and *Makednothallus isoblastus* Herzog (syn. *P. isoblasta*) from Taiwan. Some of these binomials have been synonymized with other species. Particularly *P. isoblasta* was shown to be a synonym of *P. ambigua*, and *P. longispina* to be synonym of *P. subciliata* (Inoue, 1981).

We studied several specimens identified as *P. ambigua*, *P. longispina*, *P. subciliata*, and *P. isoblasta* from Japan, Korea, China, and Taiwan including specimens from the Far East of Russia (Table 1) and did not find any essential differences in morphology or genetics (Figs. 1, 2). The thalli in all studied specimens are uniformly ciliate with marginal cilia of 3–6(–9) superimposed elongate cells. This agrees sufficiently with the description of *P. ambigua* given by Grolle & Piippo (1986: 63), where

they state "... margin shortly ciliate, without slime hairs" and "cilia ... uniseriate or rarely biseriate at base, formed of (2-)3-4(-5) strongly elongated persistent cells, often broken off their base in older frond sectors...". However this description contradicts illustrations presented in the paper mentioned above, particularly Fig. "1 b" (l.c.), where marginal bicellular slime hairs are clearly seen whereas cells of teeth are not elongated and only are 2-3 cells long. Thus, it is not clear what was treated as *P. ambigua* by Grolle & Piippo (1986). Comparing all available literature data (Inoue, 1976; Koponen *et al.*, 2000; Yamada & Iwatsuki, 2006) we found that *P. subciliata* and *P. ambigua* differ neither ecologically, nor in their distribution, nor morphologically. Grolle & Piippo (1986) also noted that *P. fistulosa* is the synonym of *P. ambigua*, and selected a specimen of *P. fistulosa* Elmer 9994, Island of Negros, Damaguete (G-22931) as a lectotype of *P. fistulosa*. Grolle & Piippo (1986) studied several duplicates of the latter specimens published as exsiccata (*Philippine Islands Plants, A.O.E. Elmer 9994, Island of Negros, Damaguete*) that are preserved in BM, G, JE, L, and W, and indicated them (l.c.) as isolectotypes of *P. fistulosa*. They showed (l.c.) that the plants from these specimens agree with *P. ambigua* in habit and the presence of short cilia at the thallus margins. We studied the specimen of *P. fistulosa* from the same series of exsiccata (*Elmer 9994, Island of Negros, Damaguete*) preserved in LE (isolectotype designated here). This specimen contains *Jensenia* sp. and some plants of *Pallavicinia* sp. The latter have remote slime hairs and few-celled teeth at the thallus margins (Fig. 7: 11-12, 15; Fig. 8: 4, 6, 8, 9, 11-13, 17) that agrees with *P. lyellii* and *P. levieri* rather than with *P. ambigua*.

Unfortunately, we could not study the type of *P. ambigua*, but all specimens of this complex studied by us match well the description of *Steetzia subciliata* (syn. *Pallavicinia subciliata*) provided by Austin (1879)<sup>1</sup> rather than *P. ambigua*. The latter taxon is probably conspecific with *Pallavicinia subciliata*, but study of the type material of *P. ambigua* is needed for resolving this problem.

We refer to *Pallavicinia levieri* the specimens of *Pallavicinia* collected by Bakalin in Cambodia (Tab. 1) and involved in this study. The most striking distinctions of Cambodian *Pallavicinia* are 3-4-stratose capsule walls, and the thalli mainly anisopleural, abruptly winged from a short stipe, without cylindrical rhizome. These features are also found in the studied specimen of *P. indica* (*Handel-Mazzetti, No. 3699, Crypt. exsic. Vind., LE*) that was treated as *P. levieri* by Grolle & Piippo (1986).

<sup>1</sup> "Dioica; Fronde stipitata erictiuscula bi-trifida, laciniis oblongo-linearibus (6-8 lineas longis, 1-2 lineas latis) subundulatis in medio fusco-vittatis margine remote ciliata, ciliis erectis, apice obtuso siccitate constricto, costa tereti tenui sub apice desinente, involucro subbasilari inciso-ciliato (immaturo)."

## TAXONOMIC TREATMENT

Key for the Holarctic species of the order Pallaviciniales

1. Thallus with a central conducting strand of sclerenchymatous cells; margins with remote slime hairs and small teeth, or shortly ciliate ..... 2
- Thallus with paired conducting strands of thin-walled sinuous (in cross section) cells, or conducting strands absent; margins entire ..... 4
2. Thallus margins always with remote slime papillae of 2-3 superimposed cells, sometimes with teeth of 1-4(-7) superimposed cells with multiple-row bases ..... 3
- Thallus margins without slime-hairs, but shortly ciliate. Cilia formed by 3-9 superimposed elongate cells ..... *Pallavicinia subciliata*
3. Female and sterile thalli mainly isopleural, more or less gradually winged from a long narrow stipe or narrow cylindrical rhizome. Antheridia arranged in two ranks on both sides of costa (or along costal area); tips of male bracts directed towards thallus margins and perpendicularly to stem axis .....  
..... *Pallavicinia lyellii*
- Female and sterile thalli mainly anisopleural, more or less abruptly winged from a short stipe, without cylindrical rhizome. Antheridia irregularly scattered along the midrib; tips of male bracts directed towards shoot apex ..... *Pallavicinia levieri*
4. Midrib with two distinct lateral conducting strands formed of thin walled elongate cells, which are sinuous in cross section (in plants from herbarium material) and sometimes brownish colored. Rhizoids colorless or pale yellowish ..... 5
- Midrib without any strands, but cells in cross section in lower half of costal region sometimes rather small and with purplish-red colored walls. Rhizoids pale to golden red or brown, seldom almost colorless ..... 6
5. Plants without subterete rhizome, from base become gradually wider, usually adhering to substrate throughout its length, but sometimes partly free; always procumbent. Multistratose part of thallus wings 3-44 cell rows wide. Female scales arranged in 1-4 rows circle around archegonia. Spores with irregular coarse ridges, or nearly reticulate. ....  
..... *Cordaea flotoviana*
- Plants usually with long subterete rhizome, become abruptly wider, adhering to a substrate mainly by stipe bases and almost free throughout its length; procumbent or ascendant. The costal region distinctly separated; multistratose part of thallus wings up to 5 cell rows wide, the wings almost entirely unistratose. Female scales mainly inserted laterally and posteriorly to archegonia, rarely surrounding archegonial cluster. Spores with small numerous low papillae. .... *Cordaea erimona*



6. Thallus / midrib width ratio 1.5-7:1. Rhizoids pale brownish to goldish or brown. Capsule wall without nodular thickenings ..... 7  
 — Thallus / midrib width ratio 7-34:1. Rhizoids dark red to purplish-violet. Capsule wall with nodular thickenings ..... 8
7. Midrib 16-30 cells high in cross section. Thallus wings almost entirely multistratose. Rhizoids goldish to brownish. Both male and female scales nearly square, rounded to truncate, or shallowly lobed, similar in size, erect to squarrose, arranged in several dense rows over the thallus and surrounding the gametangia. Spores with irregular and very short tuberculate ridges, 3-4  $\mu\text{m}$  high and 3-8  $\mu\text{m}$  long, at apex often truncate or distally divided .....  
 ..... *Moerckia blyttii*  
 — Midrib 12-18 cells high in cross section. Thallus wings almost entirely unistratose. Rhizoids pale-brownish or almost colorless. Male scales elongated-elliptical and shallowly toothed, single, remote, inserted in 1-2 rows along midrib, turned up inwards and formed oval chambers. Female scales lanceolate, incised to half of their length and lacinate-dentate, placed laterally and posteriorly to archegonia. Spores with numerous hemispherical papillae 3-8  $\mu\text{m}$  high and thick, at apex somewhat rounded .....  
 ..... [*Moerckia hibernica*]
8. Thallus / midrib width ratio 7-14:1. Midrib 16-20 cells high in cross section. Thallus wavy but not to extent of forming opposite lobe-like structures; wings multistratose to half (or more) of their width. Rhizoids reddish-brown. Spores with irregular coarse long sinuous ridges, 8-10  $\mu\text{m}$  high and thick, and 15-50  $\mu\text{m}$  long, at apex rounded ..... [*Sandeothallus japonicus*]  
 — Thallus / midrib width ratio 24-30:1. Midrib 9-12 cells high in cross section. Thallus wings entire or sometimes deeply divided towards midrib into opposite lobe-like structures; wings almost entirely unistratose. Rhizoids dark-red to purplish-violet. Spores with large cylindrical papillae, 6-8  $\mu\text{m}$  high and thick, at apex flat or rounded .....  
 ..... [*Sandeothallus radiculosus*]

**PALLAVICINIACEAE** Mig., Krypt.-Fl. Deutschl. 1: 423. 1904. — Subtribe Diplolaenineae Dumort., Syll. Jungerm. Europ.: 82. 1831. — Tribus Dilaeneae Dumort., Rec. d'Obs. Jungerm. [Tournay]: 25. 1835. — Diplomitriaceae Rabenh., Krypt.-Fl. Sachsen 1: 307 "Diplomitriaceae". 1863. — Diplolaenoideae T. Jensen, Bot. Tidsskr. 1: 78 "Diplolaeneae". 1866. — Leptothecaceae Spr., Trans. Proc. Bot. Soc. Edinburgh 15: 525. 1885. — Diplolaenaceae Breidl., Mitt. Naturwiss. Vereins. Steiermark 30: 278 "Diplolaeneae", non Diplolaenaceae J.G. Agardh (1858). 1894. — Blyttiaceae Debat, Fl. Musc.: 232. 1874. — Blyttiaceae Cavers, New Phytol. 9: 207. 1910. — Dilaenoideae Macvicar, Stud. Handb. Brit. Hepat.: 4. 1912.

Plants small to medium-sized, lanceolate to linear, or almost rosette-like; thalli prostrate or erect, with or without a stipe, sometimes dendroid. *Midrib* defined, dorsally convex or flat, ventrally convex, and thus in cross section elliptical or obtuse-trapezoidal, gradually to abruptly tapering into unistratose margins, with one or several vascular strands formed of sclerenchymatous cells. Cells of conducting strands throughout with pits produced by dissolution of secondary wall material and possess several perforations through the pit membrane. *Branching* both terminal (pseudodichotomous) and latero-ventral. Stalked filiform mucilage papillae present on both ventral and dorsal sides of midrib, especially towards apex. Thallus margins with remote slime hairs and few-celled marginal teeth, or shortly ciliate, or entire.

Dioicous. *Androecia* in discrete clusters or in elongate rows over the midrib of the main thallus (on abbreviated ventral branches in *Podomitrium*); associated with lamellate scales, or sunken in thallus depressions. *Gynoecia* anacrogynous on the dorsal surface of the thallus (acrogynous on ventral branches in *Podomitrium*); outer involucre represent by 1-several posterior lacinate-ciliate scale or forming a complete ring around archegonia; the scales free or connate into a cup-shaped structure. *Sporophytes* enclosed by a shoot calyptra and, if present, perichaetial tubular pseudoperianth, or by a coelocaul. *Seta* massive, usually 13-17 cells in diameter. *Capsule* long-elliptical, with the wall 2-4-stratose, with the radial walls of the epidermal cells evenly thickened and the inner wall cells without thickenings; dehiscing by 4 regular valves. *Elaterephore* absent. *Elateres* 2-4-spiral. *Spores* 17-40  $\mu\text{m}$  in diameter, surface delicately areolate or faintly granulate-punctate to ridged, or covered with short lamellae.

Type: *Jungermannia lyellii* Hook. = *Pallavicinia lyellii* (Hook.) Carruth.

Type genus: *Pallavicinia* Gray.

**Pallavicinia** Gray, Nat. Arr. Brit. Pl. 1: 775. 1821. "*Pallavicinius*" [corr. Trev., Rendiconti Reale Ist. Lomb. Sci. Lett. (Ser. 2) 7: 785. 1874. nom. & orth. cons.] — *Dilaena* Dumort., Comment. Bot.: 114. 1822. — *Diplomitrium* Corda, Naturalientausch 12: 653. 1829. — *Diplolaena* Dumort., Syll. Jungerm. Europ.: 82. 1831. — *Gymnomitrium* Huebener, Hepaticol. Germ.: 37. 1834. — *Blyttia* Endl., Gen. Pl.: 1339. 1840. — *Hollia* Endl., Gen. Pl. 2: 103. 1842. — *Thedenia* Fr., Bot. Not.: 178. 1842. — *Steetzia* Lehm., Pl. Preiss. 2: 129. 1846.

Plants dorsally flat or convex, ventrally convex, prostrate to nearly ascending, differentiated into a creeping subterete rhizomatous stipe, which becomes gradually or abruptly winged, ventrally branched or 1-3-pseudodichotomously furcate. *Midrib* sharply defined, obtuse-trapezoidal or elliptical in cross section, abruptly tapering into unistratose margin. Central water-conducting strand well developed, in situ visible from above. Thallus margin with remote slime-hairs or shortly ciliate. Asexual reproduction lacking.

*Androecia* in 2 ranks or arranged irregularly along the midrib associated with lamellate scales. *Archegonia* in well-defined clusters. Outer involucre forming a complete ring around archegonia, lacinate-ciliate; scales free or connate into a cup-shaped structure. Inner involucre forming a tubular pseudoperianth. *Seta* massive, 13–14 cells in diameter. *Capsule* long-elliptical, dehiscing by 4 regular valves. Capsule wall 2–4-layered. Cells of outer layer rather large, rectangular in transverse section and elongated in longitudinal section. Inner layer consists of flat elongated cells. *Spores* 17–24  $\mu\text{m}$  in diameter, surface delicately areolate or faintly granulate-punctate.

Type: *Jungermannia lyellii* Hook. = *Pallavicinia lyellii* (Hook.) Carruth.

***Pallavicinia lyellii*** (Hook.) Carruth., J. Bot. 3: 302. 1865. — *Jungermannia lyellii* Hook., Brit. Jungermann.: 77. 1816. — *Steetzia lyellii* Lehm., Pl. Preissi. 2(1): 129. 1846. — *Pallavicinia radiculosa* (Sande Lac.) Schiffn., Consp. Hep. Arch. Ind. 66. 1898.

The synonymy follows Grolle & Piippo (1986). For additional synonymy see Grolle & Piippo (1986) and Schuster (1992).

Illustrations: Figs. 3, 4.

Plants pale to yellow or dark green, locally brownish. Thalli 1–6 mm wide, 1–10 cm long, procumbent, flat to strongly undulate, mainly isopleural (equal-sided). Male and some sterile plants abruptly winged from a short thick stipe and subsequently narrowed to elongated apex, often with ventral-intercalary branches. Female plants usually with a long narrow creeping rhizomatous stipe or tuber-like “rhizome”, gradually or rarely more or less abruptly winged; simple or 1–2-pseudodichotomously furcate. *Rhizoids* pale brownish, developed on stipe bases and near thallus apex, or freely distributed throughout the midrib. *Midrib* sharply defined, dorsally concave to convex, ventrally convex, elliptical to obtapezoidal in cross section, abruptly tapering into unistratose margins. Stalked uniseriate mucilage papillae of 2(–4) cells long present on both ventral and dorsal sides of the midrib. Papillae 25–35  $\mu\text{m}$  wide, 100–160  $\mu\text{m}$  long (Fig. 3: 3–4; Fig. 4: 1). Midrib in cross section 10–14 cells high. Cells of both dorsal and ventral epidermis of the midrib weakly differentiated from medulla, 4–5-angled, 15–22  $\mu\text{m}$  high (in cross section), 25–35  $\mu\text{m}$  wide; the dorsal ones 65–135  $\mu\text{m}$  long. Inner cells of medulla 18–40  $\mu\text{m}$  high, 12–33  $\mu\text{m}$  wide (in cross section). Central strand formed of sclerenchymatous cells each with lumen of (2–)6–9  $\mu\text{m}$  (Fig. 3: 17). Thallus wings unistratose, margins locally bordered with elongated narrow cells in 1(–2) rows, usually with remote slime papillae 2(–3) cells long and with short rounded or long ciliate teeth. Teeth mostly with sharply defined base, where 2–3-seriate, then uniseriate and formed of 2–5(–7) superimposed cells (Fig. 3: 7–9), that are 15–35  $\mu\text{m}$  wide and 35–45  $\mu\text{m}$  long. Wing cells 5–6-angled, without trigones, obliquely oriented and elongated towards the margin, 22–65  $\mu\text{m}$  wide, 45–65

$\mu\text{m}$  long, in cross section 28–45  $\mu\text{m}$  high. Marginal cells 15–25  $\mu\text{m}$  wide, 45–70  $\mu\text{m}$  long, tending to be elongated parallel to margin.

*Androecia* arranged in two parallel ranks, hidden in bracts directed towards thallus margin and, thus, perpendicularly oriented to shoot axis (Fig. 3: 6, 13). *Archegonia* in well-defined clusters, 1–3 per frond. Outer involucre form a complete ring around archegonia and at base connate into a cup-shaped structure with lacinate-ciliate mouth; cilia 5–10 cells long (Fig. 4: 3–4). Cells of cilia 28–56  $\mu\text{m}$  wide, 40–115  $\mu\text{m}$  long. Posterior to the involucre often forming 1–2 supplementary dorsal lobes. Mouth of pseudoperianth ciliate. Spores finely reticulate.

**Ecology.** In Russia the species has been found in wetlands on the coast of the Baltic Sea (Dolnik & Napreenko, 2007) and on decaying wood in the valley of a tributary to the Khosta River (Western Caucasus, the Black Sea coast).

**Distribution.** Suboceanic, temperate-tropical. Russia: Kaliningrad Province (Dolnik & Napreenko, 2007) and Krasnodar Territory (Konstantinova & Savchenko, 2009). Europe: Ireland, Great Britain, Denmark, Spain, Portugal, France, Belgium, Netherlands, Austria, Italy, Germany, Czechoslovakia, Poland, Madeira, the Azores and the Balearic Islands (Damsholt, 2002), Georgia (Abramov *et al.*, 1966). North America: transcontinental in eastern North America, from Newfoundland to Florida, but not found in western North America (Schuster, 1992). Caribbean: Cuba, Dominica, and Puerto Rico (Schuster, 1992). South America: Colombia, Bolivia, Peru, Brazil, Uruguay, and Argentina (Hässel, 1961). Africa: Burundi, Malawi, Rwanda, South Africa, São Tome, Tanzania, Zaire, Zimbabwe (Wigginton & Grolle, 1996), Reunion Island (Grolle, 1995). Asia: Turkey (Keceli & Abay, 2007), Japan, China (Piippo, 1990), Indonesia (Grolle & Piippo, 1986). Oceania: Polynesia (Hawaii), Western Melanesia (Grolle & Piippo, 1984, 1986).

Reports of the species from the Russian Far East (Bakalin, 2007; Bakalin *et al.*, 2009) are erroneous and are referred by us to *P. subciliata* (see below).

Grolle & Piippo (1986) recorded the species from Western Melanesia (Grolle & Piippo, 1984 as *P. lyellii* and *P. radiculosa* (Sande Lac.) Schiffn.) and the Huon Peninsula, Papua New Guinea and stated that: “Types without androecia from the area, where *P. levieri* also occurs, have been tentatively attributed to *P. lyellii*, because the latter seems to be the more common species everywhere.” According to Schuster (1992) the reports of *P. lyellii* from Australasia “are based on total misunderstanding of *P. lyellii*” (l.c.). We studied the specimen identified as *P. radiculosa* from Java that is preserved in LE and found that it contains both male and female plants. Male plants have androecia arranged in two parallel ranks, with bracts directed towards the thallus margin which is characteristic for *P. lyellii*.

It is evident that all specimens from Asia referred to this group should be revised.



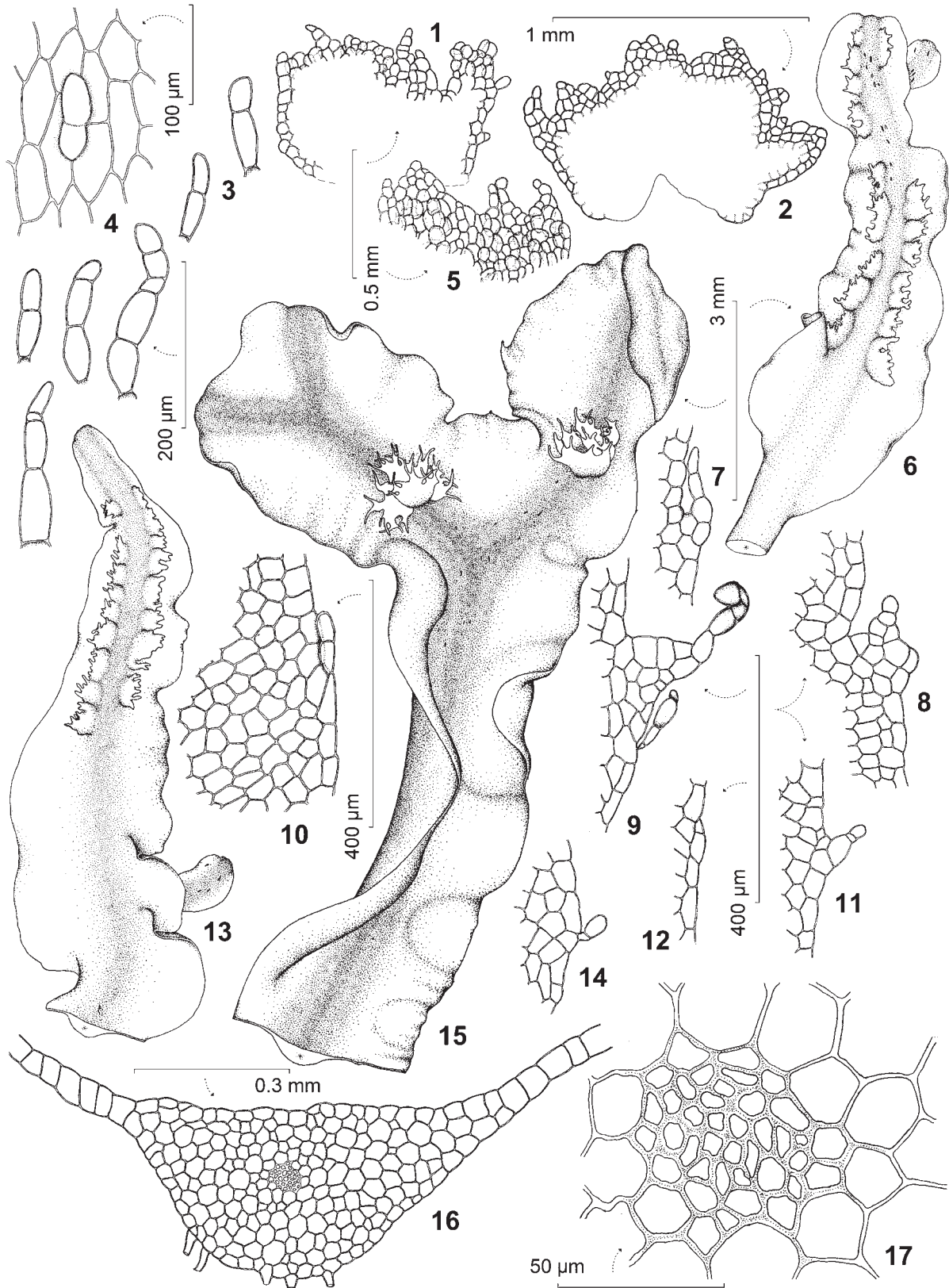


Fig. 3. *Pallavicinia lyellii*: 1, 2, 5 – male bracts with marginal cells indicated; 3, 4 – dorsal slime hairs; 6, 13 – male shoots, dorsal view; 7–12 – cells of thallus margin with marginal slime hairs or teeth indicated; 15 – female shoot; 16 – part of thallus cross section; 17 – inner cells of midrib in cross section, with central conducting strand indicated. 1, 2, 5, 6, 10, 13, 16, 17 from Russia, Krasnodar Territory, 29.X.2007, N.A. Konstantinova & A.N. Savchenko, # 523-2-07 (KPABG). 7-9, 11, 12, 14 from USA, North Carolina, 7.VI.1992, N.A. Konstantinova, ## 210, 242 (KPABG).

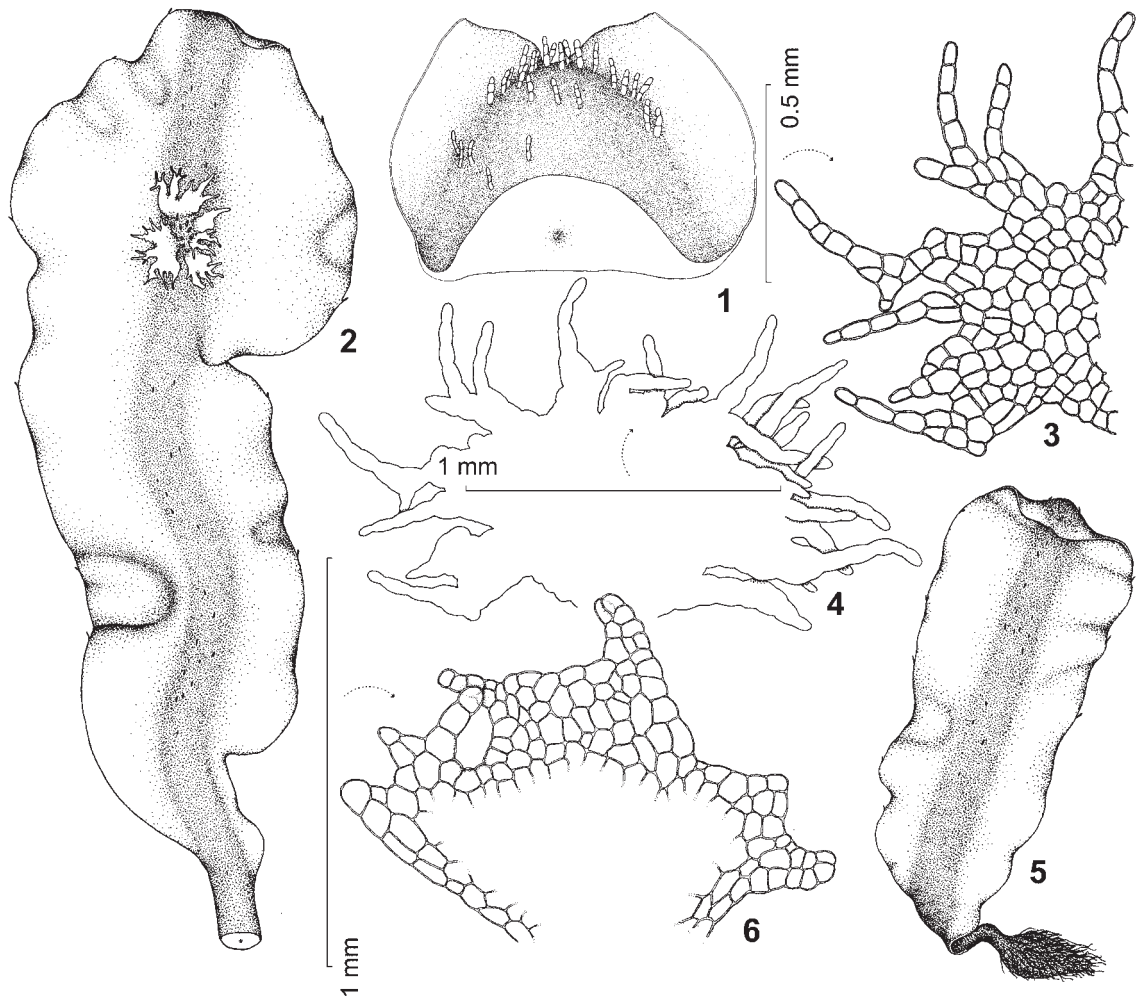


Fig. 4. *Pallavicinia lyellii*: 1 – part of thallus apex with ventral slime hairs indicated; 2 – female shoot, dorsal view; 3 – part of outer female involucre (4), with cells indicated; 4, 6 – outer female involucre; 5 – sterile shoot, dorsal view. All from USA, North Carolina, 7.VI.1992, N.A. Konstantinova, ## 210, 242 (KPABG).

**Differentiation.** In Europe and North America *P. lyellii* is the only species of the genus. It can be mistaken for *Cordaea flotoviana* and *Moerckia hibernica*. It differs from these species by remote slime-hairs and small inconspicuous teeth on the thallus margins as well as by one central conducting strand of sclerenchymatous cells vs. absent in *Moerckia* or two conducting strands in *Cordaea*. *Cordaea* occur mostly in cool regions whereas *Pallavicinia* is restricted mostly to temperate and tropical regions.

**Specimens examined.** **EUROPE:** RUSSIA: Krasnodar Territory, 29.X.2007, N.A. Konstantinova & A.N. Savchenko #523-2-07 (KPABG). GERMANY: Sachsen, 15.VII.2000, M. Reimann #B-20968 (VLA). UKRAINE: Kiev Province, Teteriv Station, 12.IX.1968, Zerov s.n. (KPABG); same, 6.V.1969, Zerov s.n. (KPABG). REPUBLIC OF ABKHAZIA: Pitsunda, 16.VI.1953, Z. Lavitsky s.n. (KPABG). **NORTH AMERICA:** U.S.A.: New York, Erie County, 11.IX.1963, N.G. Miller 1712 (KPABG); Maine, Kennebunkport [York County], 26.IV.1945, A.M. Pier & A.B. Seymour s.n. (KPABG); North Carolina, Bladen County, 7.VI.1992, N.A. Konstantinova 210, 242 (KPABG). **CARIBBEAN:** TRINIDAD and TOBAGO: Island of Trinidad, 1878-1880, A. Fendler s.n. (LE); Saint-Martin Island, Vallée St-Louis, 1868, Husnot s.n. (LE). **OCEANIA:** POLYNESIA:

Hawaii, Kalua, VI.1909, M. Faurie #343, as *Pallavicinia cylindrica* (LE). **ASIA:** INDONESIA: Java, VI. Lipsky s.a.n., as *Pallavicinia radiculosa* (LE). All studied specimens from Asia (excl. Java) are sterile and need to be verified.

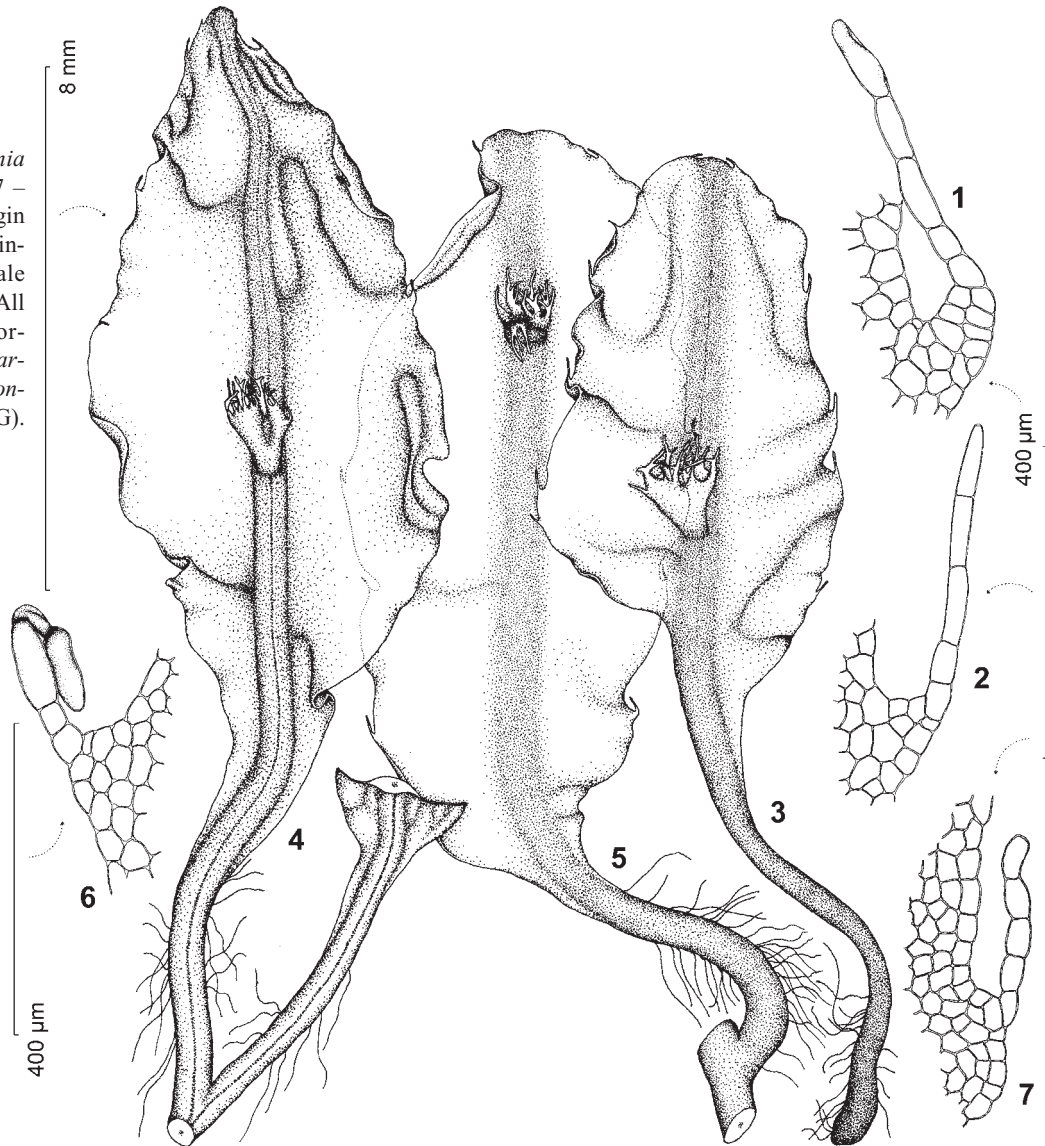
***Pallavicinia subciliata*** (Austin) Steph., Mém. Herb. Boissier 11: 9. 1900 — *Steetzia subciliata* Austin, Bull. Torrey Bot. Club 6: 303. 1879. — *Pallavicinia longispina* Steph., Bull. Herb. Boissier 5: 102 1897.

The synonymy follows Inoue (1981).

Illustrations: Figs. 5, 6.

*Plants* pale to yellow-green, brownish locally, 3.0–3.5 mm wide (1.5–2.5 mm according to Grolle & Piippo, 1986), procumbent to slightly ascendant from a long creeping stipe that is often with numerous ventral intercalary branches, gradually to (rarely) abruptly winged, mainly isopleural (equal-sided), wings unbranched or pseudodichotomously furcate. *Rhizoids* pale brownish, developed on stipe bases, rarely on sides and thallus apex. *Midrib* sharply defined, dorsally and ventrally convex, elliptical in cross section, abruptly tapering into unistratose margin, 9–12 cells high, with inner cells 18–45  $\mu\text{m}$

Fig. 5. *Pallavicinia subciliata*: 1, 2, 6, 7 – cells of thallus margin with marginal cilia indicated; 3-5 – female plants, dorsal view. All from Russia, Primorskiy Territory, L.V. Bardunov, s. a. n., as *P. longispina* (IRK, KPABG).



high and 15–45 µm wide. Stalked uniseriate mucilage papillae 2 cells long present on both ventral and dorsal sides of the midrib and on ventral side near apex. The papillae 15–30 µm wide, 70–100 µm long. Cells of both dorsal and ventral epidermis of the midrib 4–5-angled, 20–40 µm wide, 40–100 µm long, in cross section 15–30 µm, medulla weakly differentiated. Central strand formed by sclerenchymatous cells each with lumen of (2–)4–9 µm (Fig. 6: 1). Thallus margin slightly undulate to plane, shortly ciliate with (3–)5–9 (or even more) opposite pairs of cilia; the cilia are formed of 3–6(–9) superimposed elongate cells 30–45 µm wide and 70–100 µm long (Fig. 5: 1-2, 6-7). Cells of unistratose part of thallus 25–60 µm wide, 40–100 µm long, and 35–45 µm high (in cross section), 4–6-angled, with small concave trigones, obliquely oriented and elongated towards the margin. Marginal cells 25–40 µm wide, 40–100 µm long, somewhat elongated along thallus margin.

*Androecia* arranged in two parallel ranks and subtended with bracts directed towards thallus margin and, thus, ori-

ented perpendicularly to shoot axis (Inoue, 1976). *Archeogonia* in well-defined clusters, usually one per frond. Outer involucres forming a complete ring around archegonia, highly connate into a cup-shaped structure with laciniate-ciliate mouth with cilia 5–10 cells long. Cells of cilia 30–55 µm wide, 50–150 µm long. Spores finely reticulate (Inoue & Hibino, 1984). Otherwise unknown.

**Ecology.** *P. subciliata* has been found in Russia on humus, probably in shaded places in coniferous-broadleaved forest, where it occurs with *Plagiothecium* sp. (Bardunov, *sine anno et numero*) and in *Picea glehnii* boggy mossy forest with admixture of *Sorbus*, *Betula*, *Taxus cuspidata*, and *Abies sachalinensis* (Bakalin, No. 127 (Fasc. VI) *Hep. Ross. Exs.*, as *P. lyellii*). There it occurs in dense patches with admixture of *Calypogeia muelleriana*, *Plagiothecium* sp. and *Sanionia uncinata*. According to Koponen *et al.* (2000) in China *P. subciliata* is restricted to rather low altitudes, from 315 m to 1385 m a.s.l., where it grows on sand, soil, humus, gravel and twigs in different mountain habitats: cliffs, outcrops, boul-



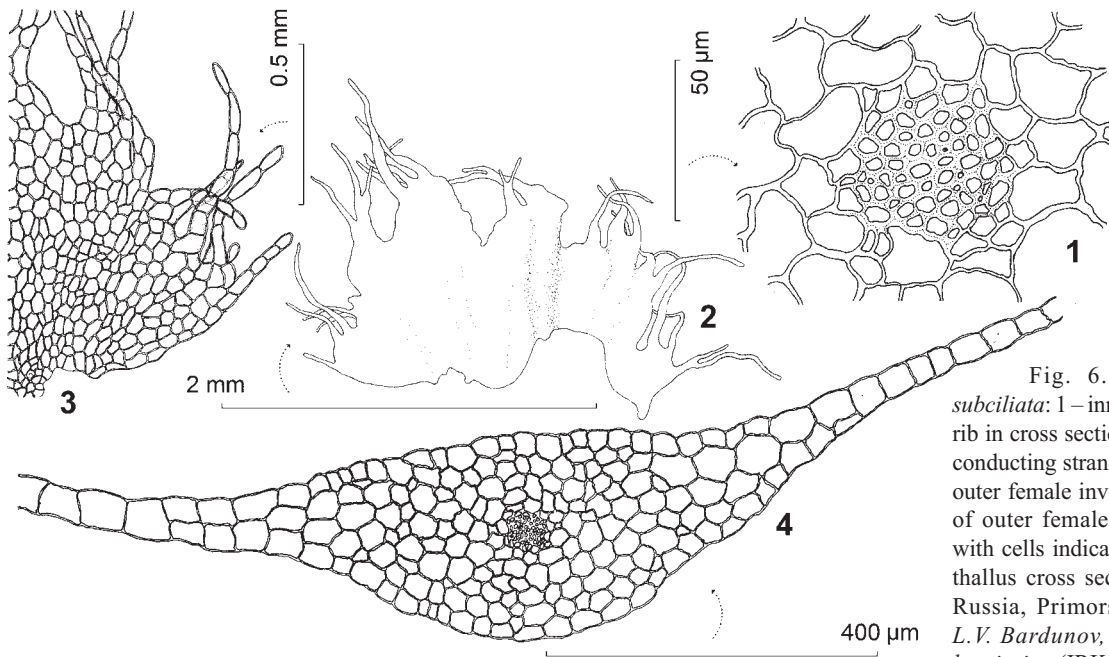


Fig. 6. *Pallavicinia subciliata*: 1 – inner cells of midrib in cross section, with central conducting strand indicated; 2 – outer female involucre; 3 – part of outer female involucre (2), with cells indicated; 4 – part of thallus cross section. All from Russia, Primorskiy Territory, L.V. Bardunov, s. a. n., as *P. longispina* (IRK, KPABG).

ders, along streams in second growth and primeval evergreen mixed forests, on road sides.

**Distribution.** *Pallavicinia subciliata* is an oceanic temperate-tropical mountain Asian species. It is known from Russia: Primorskiy Territory and Sakhalinskaya Province; Japan: Honshu, Shikoku, Kyushu, Ryukyu (Inoue, 1976; Yamada & Iwatsuki, 2006); China: Zhejiang, Guangdong (Piippo, 1990; Zhu *et al.*, 1998), Hong Kong (So & Zhu, 1996), Hunan Province (Koponen *et al.*, 2000); Republic of Korea (Park, 2007); Taiwan (Piippo, 1990).

**Specimens examined:** RUSSIA: Primorskiy Territory, Ussuriyskiy State Reserve, L.V. Bardunov s.a.n., as *P. longispina* (IRK, KPABG). Sakhalinskaya Province, Kuril Island Chain, Kunashir Island, 17.IX.2006, V.A. Bakalin, No. 127 (*Fasc. VI Hepaticae Rossicae Exsiccatae*, as *P. lyellii* (KPABG)). JAPAN: Kyushu, Miyazaki, V.1946, S. Hattori, No. 33, *Hepaticae Japonicae, Ser. I.* (1946), as *P. longispina* (LE). Kyushu, Kagoshima Prefecture, 19.III.2002, M. Noguchi, No. 1248, *Bryophytes Selecta Exsiccatae*, as *P. ambigua* (LE). Prope Saijo, Ehime Prefecture, 6.II.1947, K. Oti, No. 378, *Hepaticae Japonicae, Ser. 8.* (1956), as *P. longispina* (LE). Kuki, Owase City, Mie Prefecture, 17.VI.1984, H. Inoue, No. 763, *Bryophyta selecta exsiccata*, as *P. subciliata* (KPABG). CHINA: Hunan Province, Yizhang Co., Mt. Mangshan, Yiashui, 4.X.1997, T. Koponen, S. Huttunen & P.-C. Rao #51479, as *P. subciliata* (LE). Hunan Province, Walinguan Global Cultural Heritage Area, Zhangjiajie, 10.X.1997, T. Koponen, S. Huttunen & P.-C. Rao # 53021, as *P. subciliata* (LE). SOUTH KOREA: Jeju-do, 28.X.2010, S.-S. Choi, No. 96 (*Fasc. II Hepaticae Korea Exsiccatae*, as *P. subciliata* (KPABG)). TAIWAN: Chia-yi Co.: Mt. A-li., 13.X.1970, T. Koponen #16822, as *P. isoblata* (LE).

***Pallavicinia levieri*** Schiffn., Denkschr. Math.-Nat. Cl. Kais. Akad. Wiss., Wien 67: 184 [31 in reprint]. 1898.

The description below is based mainly on the type specimen Schiffner 379 (JE).

Illustrations: Figs. 7-9.

**Male plants** pale to yellow, brownish locally. **Thalli** 2–5 mm wide, 1.5–4 cm long, procumbent, flat to somewhat undulate at margins, abruptly winged from a short thick stipe and subsequently narrowed to elongated apex, anisopleural (unequal-sided), with both terminal and ventral-intercalary branching. **Rhizoids** pale brownish, developed on stipe bases or freely throughout. **Midrib** sharply defined, dorsally concave to convex, ventrally convex, elliptical to obtuse-trapezoidal in cross section, abruptly tapering into unistratose margins. Stalked uniseriate mucilage papillae of 2–3 cells long present on both ventral and dorsal sides of the midrib. Papillae 25–35 µm wide, 70–120 µm long. Cells of dorsal epidermis of the midrib 4–5-angled, 25–40 µm wide, 65–130 µm long; cells of the ventral epidermis strongly collapsed, then unavailable to study. **Central strand** formed of 4–6-angled (in cross section), sclerenchymatous cells each with lumen of 5–10(–16) µm (Fig. 7: 1). **Thallus wings** unistratose, margins locally bordered with elongated narrow cells in 1(–2) rows, usually with remote slime papillae 2(–3) cells long, sometimes with short rounded teeth. Teeth at the base 1–2 celled wide, 1–2-seriate, formed of 1–2 superimposed cells (Fig. 7), ending sometimes with slime papillae. Wing cells polygonal, without trigones, obliquely oriented and elongated towards the margin, 30–60 µm wide, 60–110 µm long, in cross section 30–40 µm high. Marginal cells 25–40 µm wide, 45–75 µm long, tending to be elongated parallel to margin.

**Androecia** irregularly scattered along the midrib subtended with bracts directed mostly towards shoot apex, or obliquely oriented towards thallus margins. Bracts located at thallus apex, then remote, or densely cover almost all the midrib surface from the thallus base to-

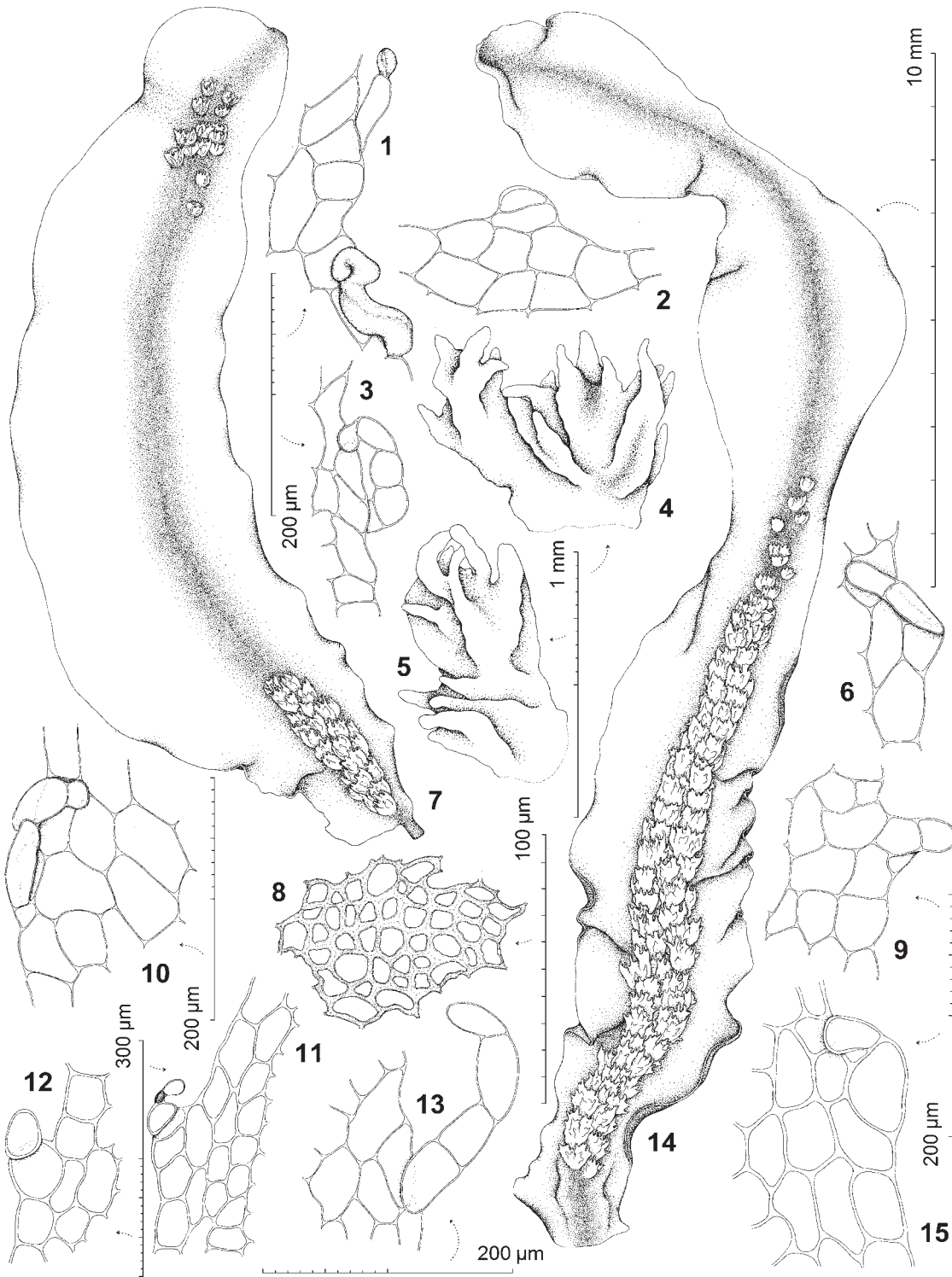


Fig. 7. *Pallavicinia levieri* (1-10, 13, 14) and *P. fistulosa* (11, 12, 15): 1-3, 6, 9-13, 15 – cells of thallus margin with marginal slime hairs or teeth indicated; 4, 5 – male bracts; 7, 14 – habit, dorsal view; 8 – cells of central conducting strand in cross section. 1-10, 13, 14 from Java, *V. Schiffner* 379 (JE). 11, 12, 15 from Philippine, Island of Negros, *A.O.E. Elmer* 9994 (LE).

wards thallus middle; bracts multistratose at base, becoming unistratose at margins, irregularly incised and lacinate-ciliate, usually with additional wings on outer surface; antheridia spherical, almost sessile.

*Female plants* (the description of female involucre of *P. levieri* is based on specimens from Cambodia and

Hunan Province, China) 3–5 mm wide, 1–3 cm long, procumbent, flat to somewhat undulate at margins, more or less abruptly winged from a short stipe, sometimes narrowed to elongated apex, almost all anisopleural (unequal-sided); with both terminal (*Cam-83-44-11*, *Cam-79-13-11*) and ventral-intercalary (*Handel-Mazzetti* No.

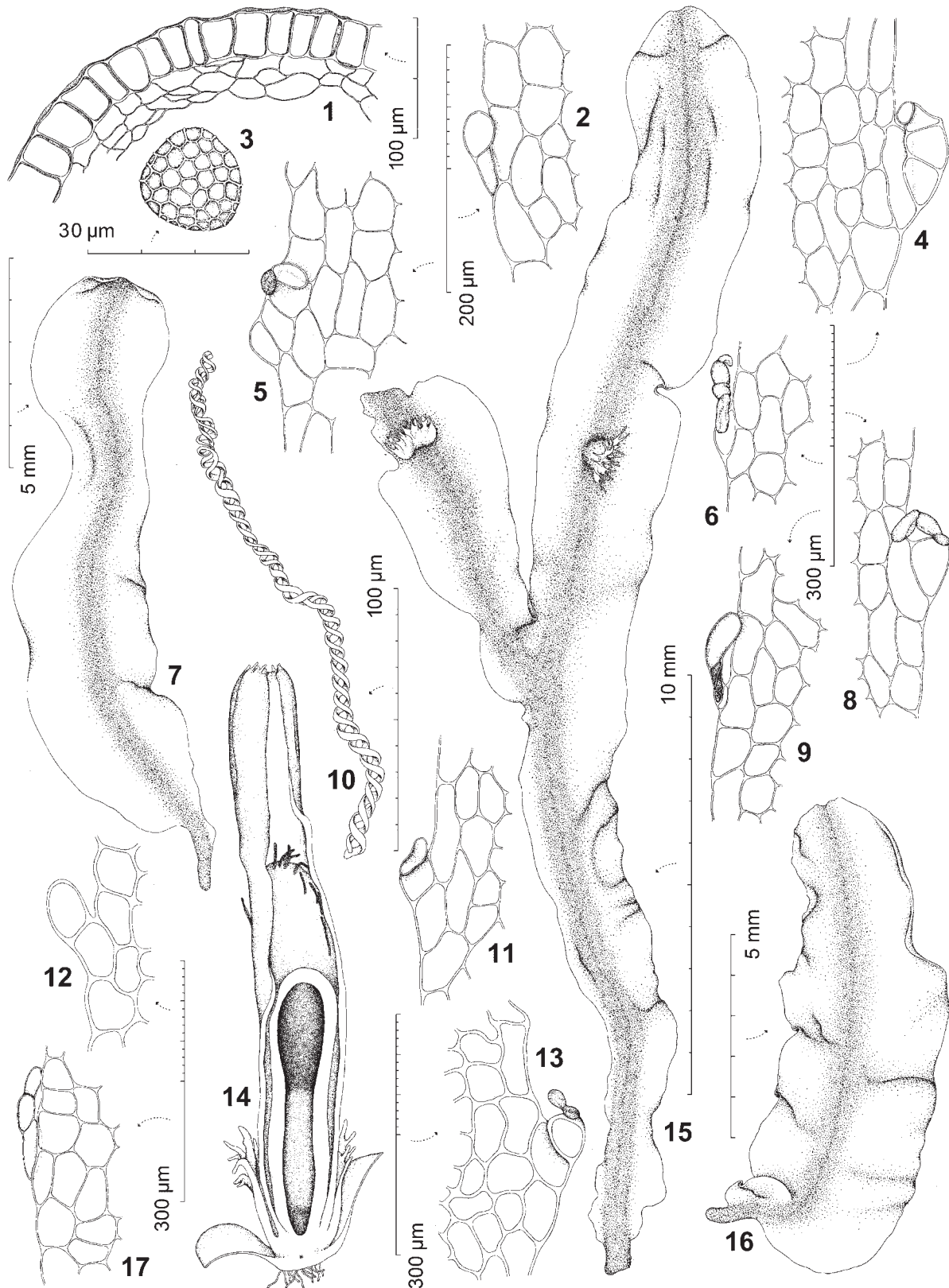


Fig. 8. *Pallavicinia levieri* (1-3, 5, 7, 10, 14, 15, 16) and *P. fistulosa* (4, 6, 8, 9, 11-13, 17): 1 – capsule wall in cross section; 2, 4, 5, 6, 8, 9, 11-13, 17 – cells of thallus margin with marginal slime hairs or teeth indicated; 3 – spore; 7, 16 – sterile shoots, dorsal view; 15 – female shoot, dorsal view; 10 – elatere; 14 – pseudoperianth in cross section with shoot calyptra and juvenile sporophyte indicated. 1, 4 from Cambodia, 19.XII.2011, V.A. Bakalin # Cam-79-13-11 (VGBI, KPABG). 2, 5, 7, 15 from Cambodia, 23.XII.2011, V.A. Bakalin # Cam-83-44-11 (VGBI, KPABG). 4, 6, 8, 9, 11-13, 17 from Philippine, Island of Negros, A.O.E. Elmer 9994 (LE, KPABG). 16 from China, Hunan Province, II.1918, H. Handel-Mazzetti, No. 3699, as *Pallavicinia indica* (LE, KPABG).



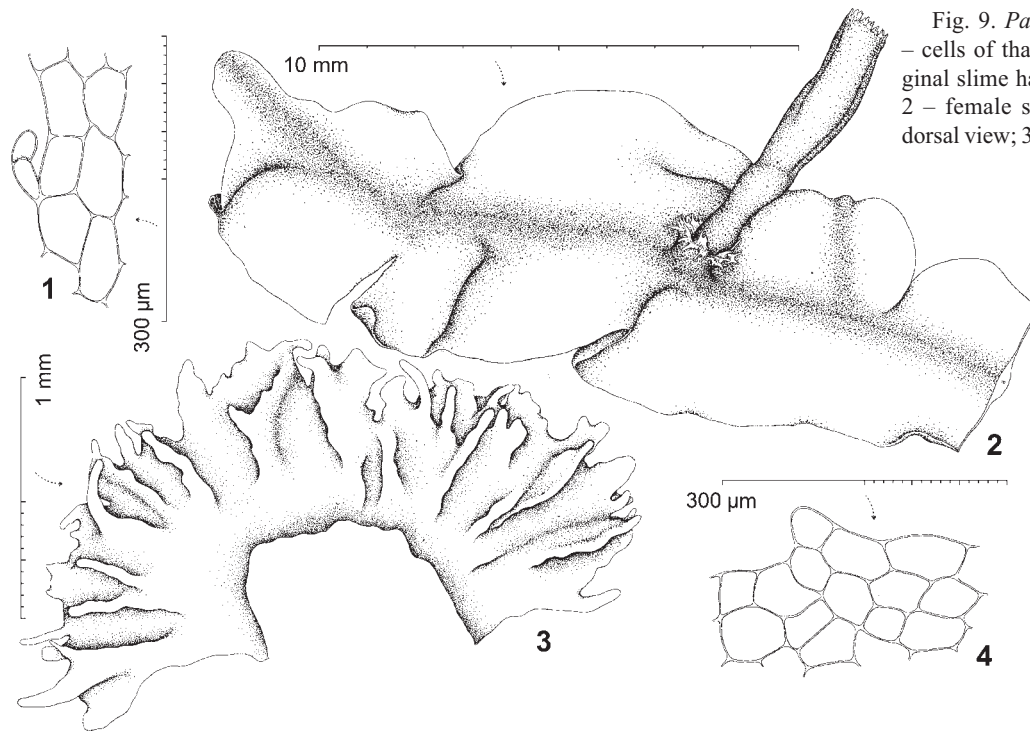


Fig. 9. *Pallavicinia levieri*: 1, 4 – cells of thallus margin with marginal slime hairs or teeth indicated; 2 – female shoot with a perianth, dorsal view; 3 – outer female involucre, external surface. All from China, Hunan Province, II.1918, H. Handel-Mazzetti, No. 3699, as *Pallavicinia indica* (LE, KPABG).

3699) branching. *Archegonia* in well-defined clusters, 1 per frond. Outer involucre forming a complete ring around archegonia, at base connate into a cup-shaped structure, multistratose, becoming unistratose at margins, variously incised, with lacinate-ciliate mouth, usually with additional wings on outer surface; cilia 3–5 cells long. Cells of cilia 25–55 µm wide, 75–110 µm long. Mouth of pseudoperianth dentate-ciliate. Capsule fusiform, with 3–4-layered wall. Pseudoperianth long, cylindrical, with dentate-ciliate mouth. *A single sterile archegonium on external surface of the pseudoperianth* found in *Cam-79-13-11* (Fig. 8: 14). Fleshy shoot calyptra hidden inside the pseudoperianth, in distal 1/4 with scattered sterile archegonia. Capsule fusiform, with somewhat acute tip. Capsule wall 3–4-layered. Cells of outer layer hard, with somewhat incrassate walls, yellow-brownish colored, 40–48 µm high and 20–30 µm wide in cross section, without thickenings; cells of inner strata soft, 10–25 µm high and 20–50 µm wide in cross section. Elaters 2(–3)-spiral, 6.5–7.6 µm wide, up to 200 µm long. Spores finely reticulate, 17–22 µm in diameter.

**Variation and differentiation.** Sterile and female plants of *P. levieri* are hardly different from *P. lyellii*. All studied specimens of *P. lyellii* from Europe, America, and Java have almost isopleural thalli, winged more or less gradually from a long stipe whereas most thalli of *P. levieri* are more or less anisopleural and winged abruptly from a short stipe. Only few specimens of *P. lyellii* from Europe and North America have long uniseriate slime hairs and multiseriate-based teeth up to 5–7 cells long on the thallus margins, that never is seen in the specimens of *P. levieri*. The majority of the studied plants of *P. lyellii* from Central and North America, especially

submerged ones, have almost entire thallus margins with few remote slime hairs of 2–3 cells long.

According to Grolle & Piippo (1986) the specimen of *P. indica* in *Handel-Mazzetti No. 3699* (LE, KPABG) belongs to *P. levieri*. This specimen is morphologically quite similar to specimens collected by Bakalin in Cambodia (*Cam-79-13-11*, *Cam-83-37-11*, *Cam-83-42-11*, *Cam-83-44-11*, *Cam-89-5-11*, VBGI, KPABG) in having reticulate spore surface (Fig. 9), 3–4-layered capsule wall, as well as more or less anisopleural and abruptly winged from the short stipe thallus, just as in the type of *P. levieri*. We found (see above) that Cambodian plants clearly differ genetically from *P. lyellii*, which is the single morphologically similar species also occurring in South-East Asia. Thus we treat Cambodian plants as *P. levieri*.

**Ecology.** The species grows preferably on decaying wood, and only occasionally on soil and rocks (Grolle & Piippo, 1986). According to Koponen *et al.* (2000), it occurs along river beds in primeval forests, along stream beds and slopes in second growth mixed evergreen forests, in second growth broad-leaved forests, at brook sides in deep gorges, at trails, in bamboo and *Cunninghamia* cultivations. In Cambodia, it was collected in broadleaved evergreen forests, on decaying wood (with *Heteroscyphus* sp.), on soil-covered stones, and on wet cliffs near waterfalls, with *Riccardia* sp. and *Plectocolea* sp.

**Distribution.** *Pallavicinia levieri* is an oceanic temperate-tropical mountain Asian species. It is known from Japan, China, Vietnam, Indonesia, Philippines, Papua New Guinea (Grolle & Piippo, 1984, 1986), and Cambodia.

**Specimens examined.** ASIA: INDONESIA: Java, *V. Schiffner* #379 (isolectotypus, JE). CAMBODIA: Mongul-Kiri Province, 19.XII.2011, *V.A. Bakalin* #*Cam-79-13-11* (VBGI,

KPABG); Koh-Kong Province, 23.XII.2011, *V.A. Bakalin* ##Cam-83-37-11, Cam-83-42-11, Cam-83-44-11 (VGBI, KPABG); Koh-Kong Province, 24.XII.2011, *V.A. Bakalin* #Cam-86-9-11 (VGBI, KPABG). CHINA: Hunan Province, II.1918, *H. Handel-Mazzetti*, No. 3699, *Cryptogamae exsiccatae editae a Museo Hist. Natur. Vindobonensi*, as *Pallavicinia indica* (LE, KPABG).

**CORDAEACEAE** Mamontov, Konstant., Vilnet & Bakalin *fam. nov.*

*Plants* medium sized, 0.7 to 7 cm long, up to 7 mm wide. *Midrib* with two lateral conducting strands formed of thin-walled cells, which are smaller than cells of the medulla. *Branching* both terminal and ventral-intercalary. *Rhizoids* from colorless to slightly yellowish. *Thallus wings* wavy, crispate or undulate, or almost flat, unistratose for 1/3–2/3 of their width, margins edentate but on ventral side uniseriate hairs up to 2–12 cells long ending with slime papillae are present.

Dioicous. *Androecia* restricted to the midline of the thallus, mostly in basal or apical part of the frond, or cover almost all surface of midrib, antheridia subtended with bracts. *Archegonia* in well-defined clusters encircled with or protected posteriorly by broad laciniate-dentate scales. *Pseudoperianth* short or elongated, cylindrical or elliptical. *Calyptra* 1–6-layered, hidden inside the pseudoperianth. *Seta* long, massive, 14–18 cells in diameter. *Capsule* short- or long-elliptical, dehiscing by 2–4 regular valves. Capsule wall 4–5-stratose. Cells of outer layer rather large, rectangular in transverse section and elongated in longitudinal section. Inner layers of capsule wall consist of flat elongated cells. *Elatrophore* absent or vestigial. *Spores* 38–50 µm in diameter. Spores surface papillose or ridged, seldom nearly reticulate.

Type genus: *Cordaea* Nees.

Cordaeaceae differ from Moerckiaceae in presence of vascular system in the thallus midrib, and from Pallaviciniaceae it differs in the type of vascularisation, particularly in two lateral conducting strands vs. one (or several in *Symphyogyna*) in Pallaviciniaceae. Moreover, conducting cells in Cordaeaceae are thin-walled and only slightly smaller than adjacent cells, but often hydrolyzed and collapsed and then have stellate or sinuous lumen, whereas in Pallaviciniaceae conducting cells are thick-walled, sclerenchymatous, with lumens much smaller than lumens of adjacent cells, and with numerous pits where several perforations through the pit membrane are produced by dissolution of secondary wall material. The Cordaeaceae also differ in distribution of slime hairs that occur on the ventral side only, whereas in Pallaviciniaceae stalked filiform mucilage papillae are present on both ventral and dorsal sides of midrib, especially towards the apex.

**Cordaea** Nees, *Flora* 16: 401. 1833.

*Cordaea* is the only genus of the family. It includes 2 species. Type species: *Cordaea flotoviana* Nees, *Flora* 16: 405. 1833.

**Cordaea erimona** (Steph.) Mamontov, Konstant., Vilnet & Bakalin *comb. nov.* Basionym: *Pallavicinia erimona* Steph., *Bull. Herb. Boissier* 5: 102. 1897. – *Hattorianthus erimonus* (Steph.) R.M.Schust. et Inoue, *Bull. Nat. Sci. Mus., Ser. B, Bot.* 1(3): 103. 1975. – *Moerckia erimona* (Steph.) S.Hatt., *J. Jap. Bot.* 18: 472. 1942.

Illustrations: Figs. 10, 11, 25–30.

*Plants* greyish to yellowish, or dark green to black, 5–6 mm wide, up to 7 cm long. *Thallus* with elongated, almost cylindrical, rhizomatous stipe, with abruptly winged to long-lingulate, procumbent or ascendant frond. Wings of the frond wide, almost from the base unistratose and thus translucent. Fronds not strongly adhering to the substrate, thus procumbent or somewhat ascendant, mostly growing as isolated thalli among mosses and hepatics. *Branching* 1–2 times ventral-intercalary, rarely terminal. *Rhizoids* pale to yellowish, occurring mainly on the ventral surface of the stipe, rarely developed throughout the ventral surface of the thallus midrib; on ventral branches rhizoids sometimes occur near the thallus apex. *Midrib* obtapezoidal in cross section, 10–15(–17) cells high, dorsally concave, ventrally convex. Cells of the midrib rounded-hexagonal, (10–)15–30(–40) µm high in cross section. Multistratose part at the base of the thallus wings 3–5 cells wide. Paired conducting strands are developed in the thallus midrib (Fig. 11: 3, 7; Fig. 25–30) and are visible from dorsal surface *in situ*. The strands are formed of outer brownish thin-walled cells, which are smaller, but more elongated than colorless cells of the medulla. Both ventral and dorsal epidermis weakly differentiated from medulla; the epidermal cells colorless, rectangular to 5–6-angled, 27–40 µm wide and 108–150 µm long. Cells of the thallus wings rectangular or elongated 5–6-angled, (20–)30–40(–45) µm wide and (55–)60–70(–95) µm long. On the ventral side of the midrib, numerous uniseriate slime hairs of 4–6 superimposed cells are present; cells 28–40 µm wide and 70–125 µm long.

Female scales usually 1–3 per gynoeceium, entire or deeply lobed (Fig. 11: 1, 4–6), placed laterally and posterior to archegonia. Cells of scales thin-walled, large, elongate, 30–40(–67) µm wide and (30–)65–100(–150) µm long. In specimens from Japan, eight to thirteen linear-lanceolate, dentate, partially connate scales surrounding each archegonial cluster and obvious dorsal lamella frequently encountered on the gynoeceial plants were described by Renzaglia (1982). *Androecia* restricted to the midline of the thallus, mostly in basal half of the main thallus or apically on ventral branches, antheridia hidden in laciniate-dentate scales. [Pseudoperianth elliptical, cylindrical or clavate. *Seta* massive, 14–17 cells in diameter. *Capsule* long-elliptical, 2.5–3 times as long as wide, dehiscing by 2 valves; wall 4–5-layered in cross section. Cells of the external layer brownish, large, 41–63 µm high; cells of the internal layers colorless or yellowish, 6–9 µm high, relatively thick-walled. Spores

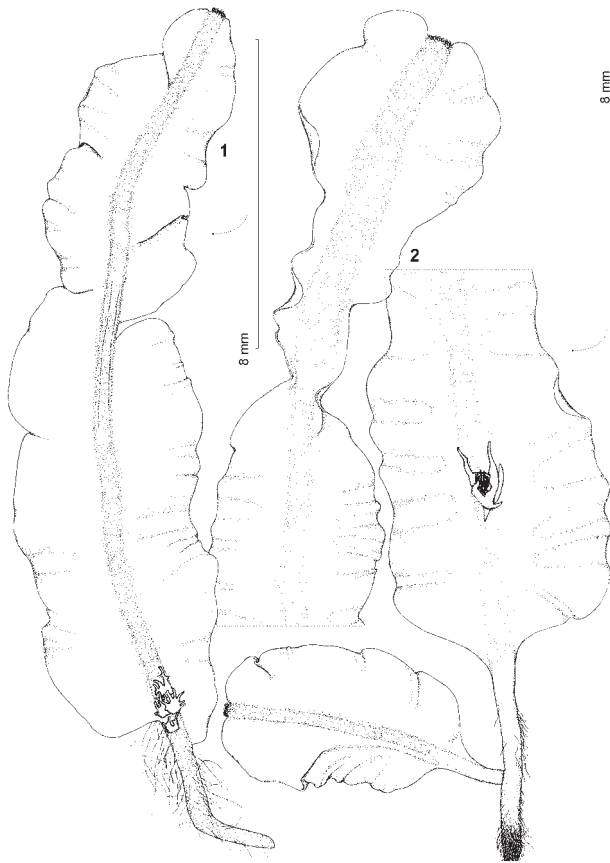


Fig. 10. *Cordaea erimona*: 1 – male shoot, dorsal view; 2 – female shoot with the ventral branching indicated, dorsal view. All from Russia, Primorsky Territory, Yu.S. Mamontov, # Prim-4-4 (KPABG).

38–43  $\mu\text{m}$  in diameter; the surface covered by very numerous, dense, small semispherical outgrowths, thus finely papillose.]<sup>2</sup>

**Differentiation.** *Cordaea erimona* can be confused mainly with *C. flotoviana* but differs from it in habit. Particularly thalli of *C. erimona* usually have an elongate, almost cylindrical, rhizomatous stipe abruptly tapered in the long-lingulate procumbent or ascendant winged frond, whereas thalli of *C. flotoviana* gradually transform from narrow stipe to the winged fronds, that are lanceolate or almost rosette-like, and procumbent to strongly adhering to the substrate. The thallus wings of *C. erimona* are almost entirely unistratose, whereas they are multistratose to a great extent in *C. flotoviana*. According to Schuster & Inoue (1975) and Crandall-Stotler & Stotler (2007), *C. erimona* has finely papillose spores, while *C. flotoviana* has reticulate to ridged spores.

**Distribution.** *Cordaea erimona* is a sub-oceanic East-Asian mountane species. It is known from the Russian Far East (Konstantinova, Bakalin *et al.*, 2009), Japan

(Yamada & Iwatsuki, 2006), China (Zhongling, 1988) and Republic of Korea (Park, 2007).

**Ecology.** The species occurs on humus soil in deciduous and coniferous forests, on slopes to the streams and rivulets in shade of ferns, horsetails, or under the overhanging roots of trees usually in mats with dominance of *Brachythecium rivulare*, *Eurhynchiastrum pulchellum*, *Plagiomnium ellipticum*, *Trachycystis flagellaris*, and admixture of *Plagiothecium* sp., *Campylidium* sp., *Serpoleskea* sp., *Conocephalum salebrosum*, *Lejeunea japonica* and *Porella oblongifolia*.

**Specimens examined:** RUSSIA: Primorsky Territory: Verkhne-Ussuriyskiy Station, 21.IX.1976, L.V. Bardunov s.n. (KPABG); Ussuriyskiy State Nature Reserve, Yu.S. Mamontov ##Prim-4-4, Prim-4-3, Prim-4-1 (KPABG); Elomovskije Waterfalls, Yu.S. Mamontov #Prim-107-1 (KPABG); Vladivostok, V.A. Bakalin #116-2-03 (KPABG).

***Cordaea flotoviana*** Nees, Flora 16: 405. 1833. — *Moerckia flotoviana* (Nees) Schiffn., Oesterr. Bot. Zeitschr. 51: 41, 43. 1901. — *Moerckia hibernica* fo. *flotoviana* (Nees) De Sloover, Bull. Jard. Bot. Etat. 29: 180. 1959. — *Calycularia flotoviana* (Nees) Steph. ex Bonner, Index Hepat. 3: 477. 1962.

For additional synonymy see Crandall-Stotler & Stotler (2007).

Illustrations: Figs. 12, 13, 19–24, 31–32.

**Plants** 2–6 [7] mm wide, 0.5–4 [7] cm long, from almost flat to strongly undulate margins, pale to dark green, often with brown secondary pigmentation. **Branching** usually terminal, less often (in male plants) ventral. Thalli simple or pseudodichotomously 1–3 times furcate, gradually winged from base to the fronds adhered to substrate. Thallus wings wavy, crispate or undulate, or almost flat, unistratose for 1/3–2/3 of their width; width of multistratose part of the thallus wings 3–44 rows of epidermal cells in cross section. **Rhizoids** colorless, origin throughout the ventral surface of thallus. Midrib 11–26 cells high in cross section, triangular or obtrapezoidal, gradually thinning out into unistratose margins, with two lateral conducting strands (Fig. 13: 10–11, 13–14) formed of brownish or colorless thin-walled cells, which have stellate or narrow sinuous lumen; the strands are sometimes weakly developed, and then visible only in the median part of the frond. Cells of dorsal epidermis of midrib elongated hexagonal or rectangular to quadrate, 30–40 $\times$ 45–65(–73)  $\mu\text{m}$ , thin-walled; outer cells of the wings more elongated, 27–40(–50) $\times$ 60–90(–116)  $\mu\text{m}$ . Cells of unistratose part of wings rounded-hexagonal to quadrate, (27–)30–40(–50) $\times$ (35–)40–50(–70)  $\mu\text{m}$ ; marginal cells somewhat elongated, 27–32 $\times$ 40–46  $\mu\text{m}$ . Cells of ventral epidermis of midrib with brown pigmentation, mostly elongated-hexagonal, or rounded to elongated-rectangular, (20–)24–32(–40) $\times$ (20–)45–60(–80)  $\mu\text{m}$ . Ventral slime hairs uniseriate, up to 12 cells long, with cells 19–23 $\times$ 31–44  $\mu\text{m}$ . Inner cells of midrib rounded-polygonal in cross section, (19–)24–46(–54)  $\mu\text{m}$  in diameter.

<sup>2</sup> The description of the pseudoperianths, the capsule anatomy and the spore size are given according to Schuster *et al.* (1975), the spores surface is described according to Crandall-Stotler & Stotler (2007).



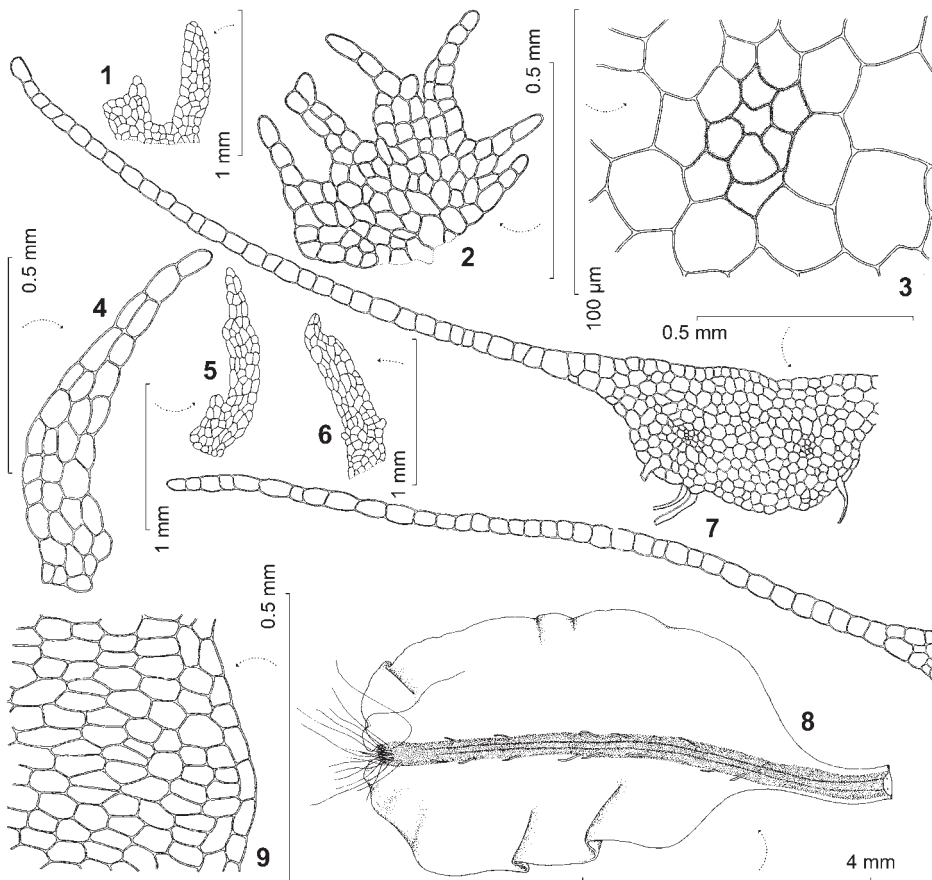


Fig. 11. *Cordaea erimona*: 1, 4-6 – female scales; 2 – male scale; 3 – inner cells of midrib in cross section, with a lateral conducting strand indicated; 7 – two part of thallus cross section; 8 – an isolated ventral shoot with slime hairs and apical cluster of rhizoids indicated, ventral view; 9 – cells of thallus margin. All from Russia, Primorsky Territory, Yu.S. Mamontov, # Prim-4-4 (KPABG).

*Male scales* in clusters or covering surface of midrib, erect to squarrose, broad, foliaceous, subquadrate or rectangular, with lacinate-dentate margins, sometimes on posterior face with low vertical dentate lamellae. Cells of scales elongated and 5–6-angled to rounded,  $35\text{--}50 \times 50\text{--}60\ \mu\text{m}$ . Male scales partly connate basally to form chambers, each usually 1–3-androus. *Female plants* usually bears 1–2 or more archegonial clusters each surrounded by an imperfect ring of 1–4 rows of scales. The scales deeply incised into elongated ciliate-dentate segments (Fig. 12: 3-5, 9-10; Fig. 13: 4, 9, 12). Cells of scales elongated to isodiametric,  $20\text{--}40\text{--}(50) \times (35\text{--})65\text{--}95\text{--}(110)\ \mu\text{m}$ . Pseudoperianth ovoid or cylindrical, 3–5 times as long as wide, plicate distally; the mouth contracted, mostly 3-lobed and then lacinate, usually with brownish coloration. Seta massive, 16–17 cells in diameter. Capsule ovoid-cylindrical, 3–5 times as long as wide, dehiscing by 2–3 valves. Capsule wall 3–5-layered (Fig. 13: 1). Cells of outer layer brownish,  $35\text{--}40\ \mu\text{m}$  high in cross section, cells of inner layers colorless, thin-walled,  $9\text{--}13\ \mu\text{m}$  high. Spores brownish,  $35\text{--}50\ \mu\text{m}$  in diameter, with reticulate to ridged surface. The outgrowths on spore surface rounded,  $2\text{--}3\ \mu\text{m}$  high and broad (Fig. 13: 6).

**Differentiation.** The species can mostly be confused with *Cordaea erimona* and *Moerckia hibernica*. Distinctions from *C. erimona* are given under the latter species. *Cordaea flotoviana* differs from *Moerckia hibernica* in having 1) paired conducting strands; 2) colorless rhiz-

oids; 3) wider multistratose part of the thallus wings; 4) position of archegonial scales that are arranged in 1–4 rows circle around archegonia vs. laterally and posteriorly inserted in *M. hibernica*; 5) form and position of male scales; 6) 3–5-layered capsule wall vs. 2–3-layered in *M. hibernica*; 7) reticulate or with irregular ridges spores vs. papillose spores in *M. hibernica*.

Since mature sporophytes and spores are very rare in *C. flotoviana*, the most important distinction of this species is the presence of lateral conducting strands that can be better visible in polarized light (Figs. 21-24, 31).

**Ecology.** *Cordaea flotoviana* is an eutrophic hygrophyte often restricted to Ca-rich habitats. It occurs in coastal areas on moist meadows and along streams, in mesic or eutrophic wetlands, rarely in mountains in crevices of cliffs, often mixed with eutrophic hygrophytes such as *Philonotis* spp., *Hamatocaulis*, *Scorpidium*, *Fissidens adianthoides*, *F. osmundoides*, *Calliergonella lindbergii*, *Cinclidium stigmatum*, *Harpanthus flotovianus*, etc.

**Distribution.** *Cordaea flotoviana* can be characterized as an arcto-boreo-montane species restricted mainly to Europe and North America, with single localities in Asia (Shikotan Island).

As it was shown previously, all literature records of *M. hibernica* from Russia should be referred to *C. flotoviana* (Mamontov & Konstantinova, 2012). The species is not rare in the north of European part of Russia (Murmansk Province, Republics of Karelia, Republic of

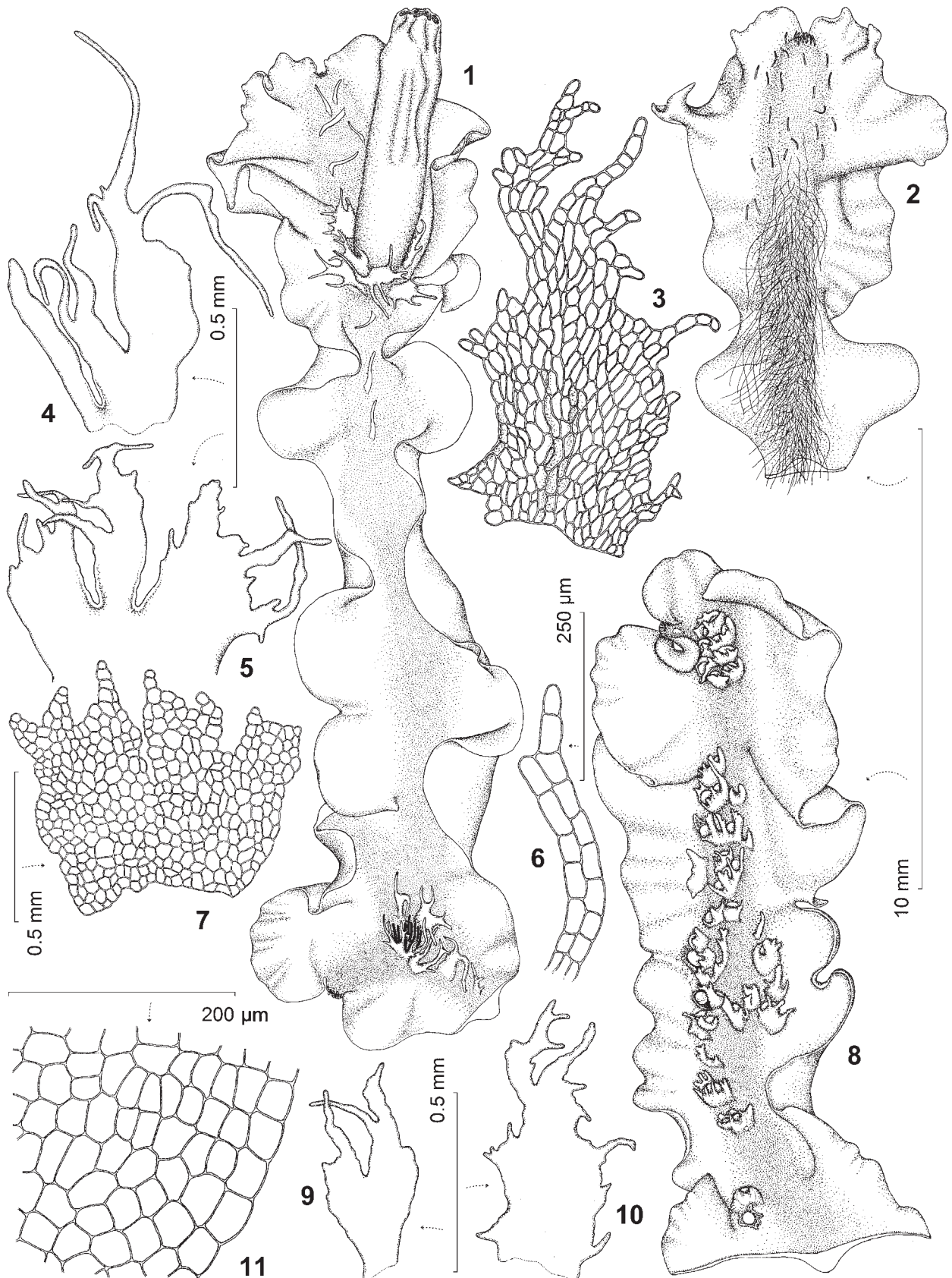


Fig. 12. *Cordaea flotoviana*: 1 – female shoot with a perianth, dorsal view; 2 – ventral surface of the female shoot, with slime hairs indicated; 3 – enlarged female scale; 4, 5, 9, 10 – female scales; 6 – dorsal scale from the female shoot; 7 – male scale; 8 – female shoot, dorsal view; 11 – cells of thallus margin. 1, 2, 6, 11 from Russia, Murmansk Province, *E.A. Borovichev* # 24-22/1-06 (KPABG). 3-5, 7-10 from Russia, Murmansk Province, *N.A. Konstantinova*, # 66-2-86 (KPABG).

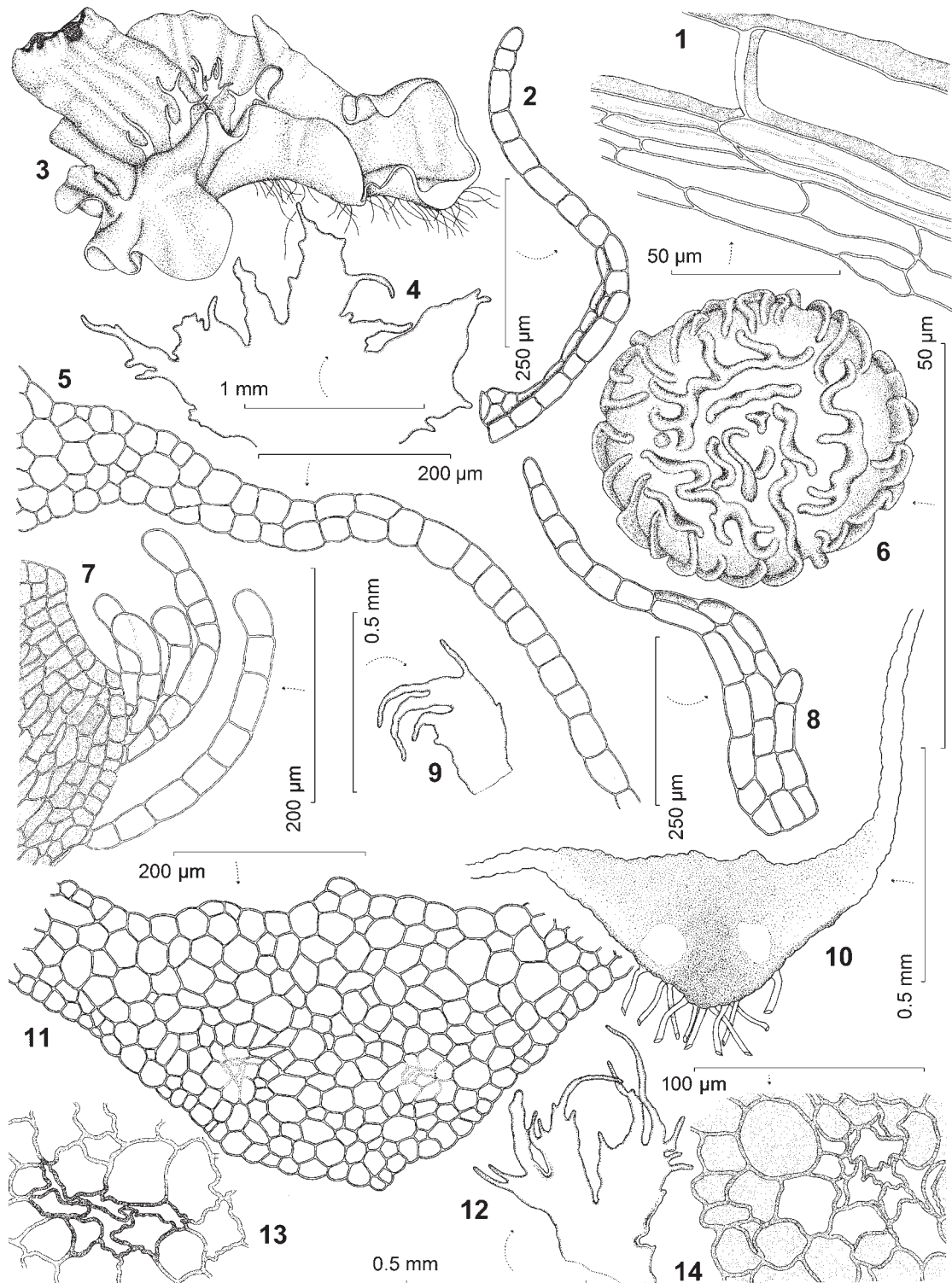


Fig. 13. *Cordaea flotoviana*: 1 – part of capsule wall in longitudinal section; 2, 8 – dorsal scales from the female shoot; 3 – female shoot with a perianth, dorsal view; 4, 9, 12 – female scales; 5 – lateral part of thallus cross section; 6 – spore; 7 – thallus apex in longitudinal section, with ventral slime hairs protected the grow point indicated; 10 – thallus cross section with places of two lateral conducting strands (clear areas) indicated; 11 – midrib cross section with two lateral conducting strands (cells pictured with dotted lines) indicated. 13 – inner cells of midrib in cross section, with tinted cells of lateral conducting strand indicated; 14 – hyphae-filled inner cells of midrib in cross section, with a lateral conducting strand indicated. 1 from Germany, Brandenburg, V. Schiffner, No. 1302 Exs. Eur. Hep. (LE). 2, 3, 8 from Russia, Murmansk Province, E.A. Borovichev # 24-22/1-06 (KPABG). 4, 5, 7, 9-14 from Russia, Murmansk Province, N.A. Konstantinova, # 66-2-86 (KPABG). 6 from Germany, Rügen Insel, V. Schiffner, No. 1303 Exs. Eur. Hep. (LE). 2, 6, 11 from Russia, Murmansk Province, E.A. Borovichev # 24-22/1-06 (KPABG). 3-5, 7-10 from Russia, Murmansk Province, N.A. Konstantinova, # 66-2-86 (KPABG).





Fig. 14. *Moerckia blyttii*: 1 – female shoot with a perianth, dorsal view; 2 – male shoot, dorsal view; 3 – epidermal cell of thallus with oil-bodies and chloroplasts indicated; 4 – sterile shoot, lateral aspect; 5, 7 – male scales; 6 – midrib cross section with the area of tinted cells indicated. 1, 3, 4 from Russia, Murmansk Province, 24.VI.2011, Yu.S. Mamontov, # YuSM-51 (KPABG). 2, 5, 7 from Russia, Bering Island, V.A. Bakalin # K-22-16-02-VB (KPABG).

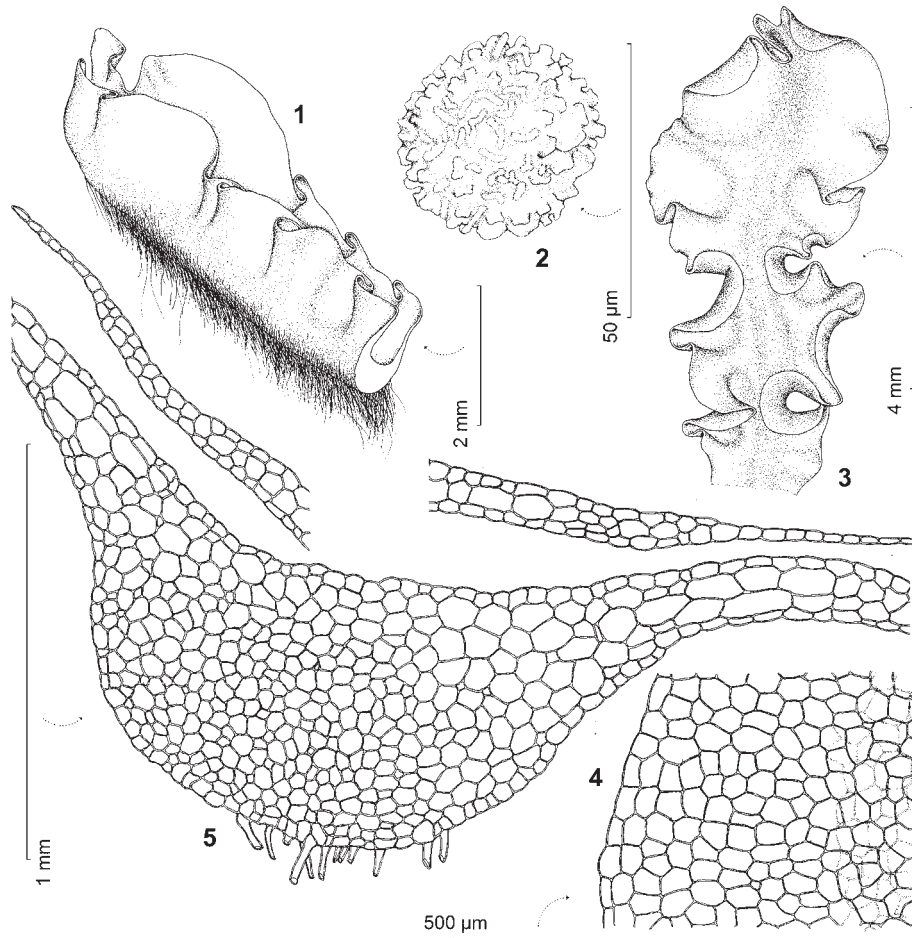


Fig. 15. *Moerckia blyttii*: 1, 3 – sterile shoots, dorsal view; 2 – spore; 4 – cells of thallus margin; 5 – tree parts of thallus cross section. All from Russia, Paramushir Island, V.A. Bakalin # K-102-03-04 (KPABG).

Komi), in Asia it has been reported from Kuznetskiy Alatau (Konstantinova *et al.*, 2003) and Shikotan Island (Bakalin, 2012). We refer all studied samples of *M. hibernica* from Sweden, Denmark, Finland, Germany and Romania (Mamontov & Konstantinova, 2012) to *C. flotoviana*. *C. flotoviana* [as *Moerckia flotoviana* (Nees) Schiffn.] has also been recorded from Great Britain (Crandall-Stotler, Stotler, 2007). In eastern North America, the species has been recorded (as *Moerckia hibernica* fo. *flotoviana*) by R.M. Schuster (1992) from many localities in U.S.A. and Canada. In western North America, *C. flotoviana* has been recorded from the arctic Alaska (Steere & Inoue, 1978), it has also been found in collections of N.A. Konstantinova and A.D. Potemkin from the state of Washington and South Alaska (KPABG, LE).

*Selected specimens examined*: RUSSIA: Murmansk Province: Kola Peninsula: Lapland Reserve, E.A. Borovichev ##18-42-05, 42-1-07, 24-22/1-06, 24-22/2-06, 26-23-09, 36-24-09 (KPABG). Republic of Karelia: Konchozero, M.L. Ramenskaya #108541 K (KPABG). Karelia ladogensis, Exs. Lindb. No. 219 (H). Leningrad Province: Belyi Kamen' Sanctuary, 18.VII.1984, E.O. Kuz'mina #49A (LE). Republic of Komi: Elva Mezenskaya River, I.D. Kildjuschevsky #10 (SYKO); Upper of Bolshaya Kedwa River, G.V. Zheleznova #652 (SYKO); Nizhnyayja Omra River valley, M.V. Dulin #262MBI (SYKO). Kemerovo Province: Kuznetskiy Alatau Mts., N.A. Konstantinova #100-2-00 (KPABG). Sakhalinskaya Province: Shikotan Island, Ostrovnoy

Cape Area, 31.VIII.2007, V.A. Bakalin #K-51-1-07 (KPABG). GERMANY: Rügen Island: Heringsdorf, V. Schiffner, No. 1303 Exs. Eur. Hep. (LE); Brandenburg: Berlin, V. Schiffner, No. 1302 Exs. Eur. Hep. (LE). GREAT BRITAIN: Scotland, Pert, Ben Oss, 4.VIII.1981, J.A. Paton #6386 (E); Shetland Islands, Yell, 14.VIII.1974, J.A. Paton #3504 (E). U.S.A.: Michigan: Presque Isle Co., 22.VII.1987, *Si He s. n.* (LE).

**MOERCKIACEAE** Stotler et Crand.-Stotl., Nova Hedwigia, 131: 54. 2007. — Moerckiaceae K.I. Goebel, Organogr. Pflanz. (ed. 3): 911. 1930 [nom. inval.: “Moerckiaceen”].

Type genus: *Moerckia* Gottsche.

*Plants* short or elongated, moderately to very wide, dorsally flat or concave, ventrally convex. *Midrib* sharply defined, triangular to obtuse-trapezoidal in cross section, gradually or rather abruptly tapering into unistratose margin. Inner cells of midrib mainly thin-walled, isodiametric and homogenous, lacking any strands. Stalked filiform slime-hairs present on ventral side along midrib (Fig. 14: 1, 4). The slime-hairs uniseriate, up to 12 cells long, with apical slime papillae. Thallus margin without any slime hairs, teeth, or cilia.

*Dioicous*. *Sexual* organs on dorsal surface of the midrib. *Androecia* more or less clustered, mostly in several rows along midrib, subtended by lamellate and lacini-



ate-dentate bracts; each bract with 1–4 sessile globose antheridia; antheridial stalk multicellular. *Archeogonia* in well-defined clusters surrounded by broad lacinate involucre for more than 6 cells broad (Fig. 14: 6–7). *Pseudoperianth* short or elongated, cylindrical or elliptical (Fig. 14: 1). *Calyptra* in large part unistratose and semi-translucent, hidden inside the pseudoperianth. *Seta* massive, 2–3 cm long and 14–18 cells in diameter. [*Capsule* short- or long-elliptical, dehiscing by 2–4 regular valves. Capsule wall composed of an outer layer and 2–4 inner layers. Cells of outer layer dark brown, rather large, rectangular in transverse section and elongated in longitudinal section. Inner layers consists of flat elongated cells with thin walls.] *Spores* 30–60 µm in diameter. Spore surface with coarse, short hemispherical (papilliform) outgrowths, or with short trabeculate ridges (Fig. 15: 2).

**Moerckia** Gottsche, in Rabenh., Hep. Eur. Exsicc. no. 121. 1860. — *Pallavicinius* Gray, Nat. Arr. Brit. Pl. 1: 755. 1821. — *Dilaena* Dumort., Comm. Bot. Tournay: 114. 1822. — *Diplomitron* Corda in Opiz, Beitr. 1: 653. 1828. — *Diplolaena* Dumort., Syll. Jungerm. Europae: 82. 1831. — *Gymnomitron* Huebener, Hepat. Germ.: 37, 44. 1834. — *Moerckia* Jørg., Bergens Mus. Skrifter 16: 49. 1934. — *Moerchia* S.W. Arnell, Illus. Moss. Fl. Fennosc. 1: 23. 1956.

Type: *Jungermannia hibernica* Hook. = *Moerckia hibernica* (Hook.) Gottsche (l.c.).

In Russia the genus is represented by one species.

**Moerckia blyttii** (Mørch ex Hornem.) Brockm., Arch. Vereins Freunde Naturgesch. Mecklenburg 17: 190, 191. 1863. — *Jungermannia blyttii* Mørch ex Hornem., Fl. Danicae 12(34):6, pl. 2004, 1830. — *Cordaea blyttii* (Mørch ex Hornem.) Corda, ibid., 2: 126. 1835. — *Cordaea contorta* Nees, Diar. Bot. Ratisb. 1 (Suppl.): 59. 1836. — *Calycularia blyttii* (Mørch ex Hornem.) Steph., Sp. Hepat. 1: 360. 1900.

The synonymy follows Crandall-Stotler & Stotler (2007). For additional synonymy see Schuster (1992) and Crandall-Stotler & Stotler (2007).

Illustrations: Figs. 14–15, 16–18.

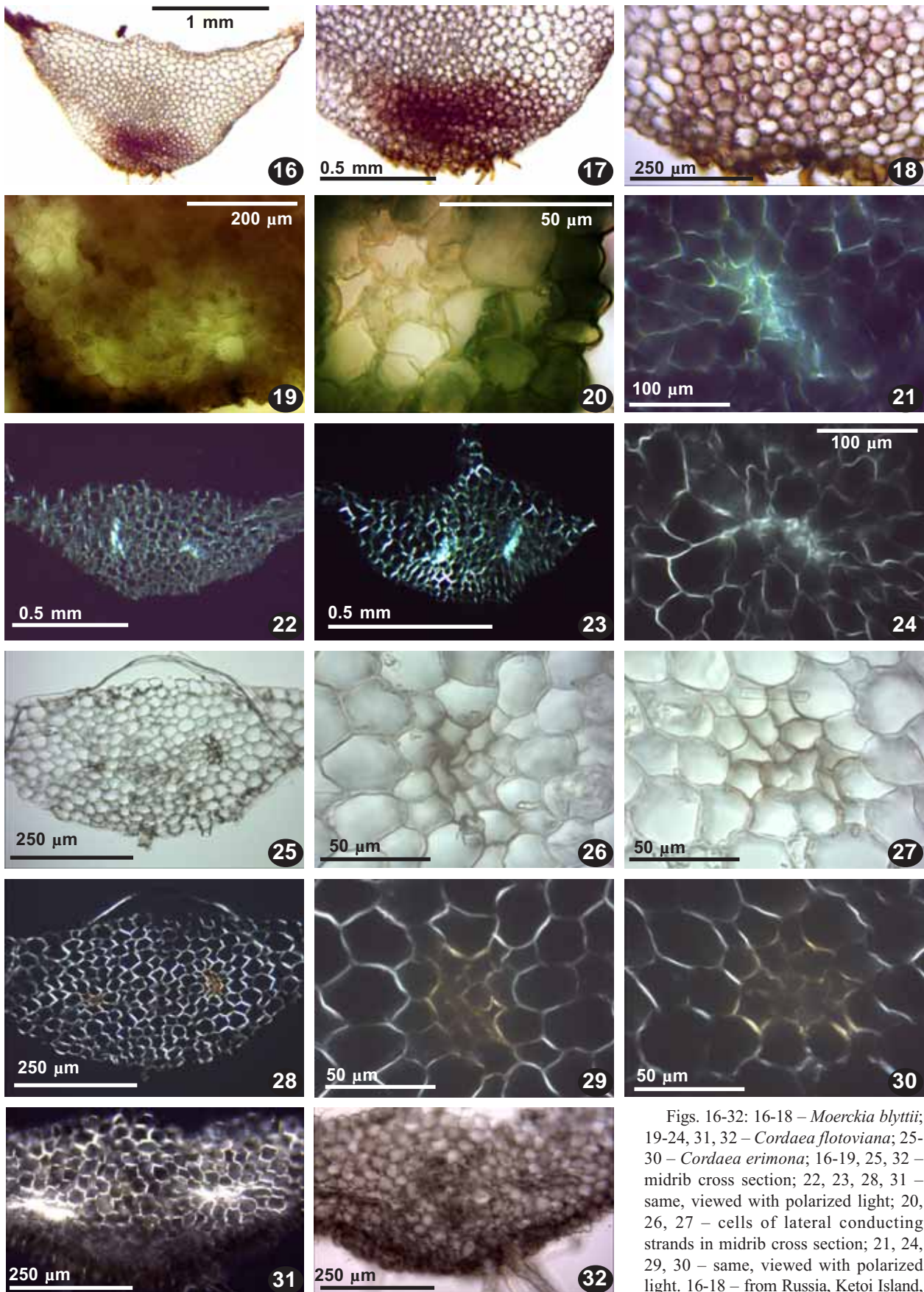
*Plants* 4–10×12–20 mm, pale or yellowish-green to dark-green, usually with brownish marginal pigmentation, rarely plants dark brown; simple or pseudodichotomously furcate, ventral branching unknown. *Thalli* gradually winged from narrow cylindrical stipe base to the fronds strongly adhering to the substrate. *Thallus* wings wavy, usually ascending and strongly crispate or undulate, unistratose for 3–11(–16) rows. *Rhizoids* goldish to brownish. *Midrib* obtapezoidal, 20–30 cells high in cross section, gradually thinning out into unistratose margins; an elliptical area of reddish tinted smaller cells is in the lower part of the midrib (Fig. 14: 6; Fig. 16–18). *Cells* of dorsal epidermis of midrib elongated hexagonal or rectangular to quadrate, 29–46(–54)×(40–)54–65(–90) µm,

thin-walled; outer cells of the wings more elongated, 27–40(–52)×81–97(–154) µm. *Cells* of unistratose part of wings rounded-hexagonal to quadrate, 22–54 µm in diameter; marginal cells somewhat elongated along the margin, 27–32×40–46 µm. *Cells* of ventral epidermis of midrib mostly elongated-hexagonal, or rounded to elongated-rectangular, 25–50×45–60 µm. *Inner cells* of midrib rounded-polygonal in cross section, (35–)45–55(–70) µm in diameter; in the lower part of midrib cells smaller, (30–)35–40(–50) µm. *Inner cells* of the thallus wings larger, up to 90–105 µm high and 180 µm long.

*Male* and *female scales* cover the entire surface of midrib, erect to squarrose, broad, foliaceous, entire-margined or emarginated, to somewhat incised, at base multistratose (2–3-layered) to 1/3 of high, then unistratose, sometimes provided on posterior face with low vertical lamellae. *Cells* of scales elongated to rounded, 19–40×32–62 µm. *Male scales* partly connate basally to form chambers, each usually enclosing a single antheridia. *Female plants* usually undivided, rarely divided; with one gynoeceum per thallus, rarely, if divided, then forming up to three gynoecea on the single thallus. A ring of female scales, free from each other, surround the archegonia; other scales more or less connate with each other, often forming a partial, incised, low sheath, divided into lingulate to oblong segments. *Pseudoperianth* ovoid (up to twice as long as wide) or short cylindrical, plicate distally; the mouth contracted, mostly 3-lobed and then lacinate-dentate, usually with brownish coloration. *Seta* massive, (13–)17–18 cells in diameter. *Capsule* ovoid-cylindrical, 1.5–2 times as long as wide, dehiscing by 2–4 valves. *Capsule wall* 4–5-layered. *Spores* brownish, (25–)35–46 µm in diameter, with truncate to emarginated ridges, 3–4 µm high and broad.

**Differentiation.** Japanese *Sandethallus japonicus* morphologically is closely related (probably congeneric) to *Moerckia blyttii* and may be found in the Russian Far East. It differs from *Moerckia blyttii* as follows: 1) the ratio of width of thallus to that of costa is about 1.5–7:1 in *M. blyttii* vs. 7–14:1 in *S. japonicus*; 2) the rhizoids goldish-brown in *M. blyttii* vs. reddish-brown in *S. japonicus*; 3) thallus wings almost entirely multistratose in *M. blyttii* vs. the wings multistratose to half (or more) of their width in *S. japonicus*; 4) female scales numerous, cover the entire surface of midrib, broad, foliaceous, entire-margined to somewhat incised in *M. blyttii* vs. the female scales 2–4 in count, elongate-lanceolate, incised to half of their length and lacinate-dentate, placed laterally and posteriorly to archegonia in *S. japonicus*; 5) cells of outer layer of capsule wall with equally thickened walls in *M. blyttii* vs. cells of outer layer of capsule wall with nodular thickenings on longitudinal walls in *S. japonicus*; 6) spore surface with very short tuberculate ridges, 3–4 µm high and 3–8 µm long, at apex often truncate in *M. blyttii* vs. spore surface with sinuous ridges, 8–10 µm high and thick, and 15–50 µm long, at apex rounded in *S. japonicus*. The phylogenetic relationships of the both taxa need in further investigation.





Figs. 16-32: 16-18 – *Moerckia blyttii*; 19-24, 31, 32 – *Cordaea flotoviana*; 25-30 – *Cordaea erimona*; 16-19, 25, 32 – midrib cross section; 22, 23, 28, 31 – same, viewed with polarized light; 20, 26, 27 – cells of lateral conducting strands in midrib cross section; 21, 24, 29, 30 – same, viewed with polarized light. 16-18 – from Russia, Ketoi Island,

*T.I. Hyushko* # *K-42-06* (LE); 19-24 – from Russia, Murmansk Province, *N.A. Konstantinova*, # 66-2-86 (KPABG); 25-30 – from Russia, Primorsky Territory, *Yu.S. Mamontov*, # *Prim-4-4* (KPABG); 31, 32 – from USA, Michigan, 22.VII.1987, *Si He s.n.* (LE).

**Ecology.** *Moerckia blyttii* is slightly acidophyllous or neutrophyllous cryophilic hygrophyte mostly restricted to late snow sites. It occurs mostly on sandy and peat soil, on fine earth along streams and lakes, in depressions with temporary streams, on rocky slopes, associated with other arcto-montane and arcto-boreomontane species, *i.e.*, *Anthelia juratzkana*, *Cephalozia ambigua*, *C. leucantha*, *Diplophyllum taxifolium*, *Gymnocolea inflata*, *Marsupella boeckii*, *M. emarginata*, *Pleurocladula albescens*, *Orthocaulis floerkei*, *Pseudolophozia sudetica*, *etc.*

**Distribution.** *Moerckia blyttii* is mostly a suboceanic arcto-montane species. In Russia it is known from Murmansk Province (Schljakov & Konstantinova, 1982; Konstantinova, 2004), Republic of Karelia (Bakalin, 1999), Archangelsk Province (Konstantinova & Potemkin, 1996), Novaya Zemlya (Schljakov, 1976), Polar Urals (Zinovjeva, 1973), Yamal Peninsula (Potemkin, 1993), Taimyr Peninsula (Zhukova & Matweeva, 2000), Kurils and Commander Islands (Bakalin, 2009; Bakalin *et al.*, 2009). In Europe it is more or less widespread from the Scandinavian countries in the north to Italia in the south, from Iceland and Great Britain in the west to Ukraine and Caucasus in the east (Damsholt, 2002). In North America the species was recorded from South Greenland (Schuster, 1988), Newfoundland, Alberta, British Columbia, and Washington (Schuster, 1992). In East Asia it was recorded from Japan (Inoue, 1985).

**Specimens examined:** RUSSIA: Murmansk Province: Keivy Mts., 23.VII.1965, *R.N. Schljakov s.n.* (KPABG); Semuzhye Lake, *N.A. Konstantinova #59-1-97* (KPABG); Lavna-Tundra Mts., *N.A. Konstantinova #114-6-87* (KPABG); Chiltald Mts., 28.VI.1988 *N.A. Konstantinova s.n.* (KPABG); Laplandskiy State Nature Reserve, *N.A. Konstantinova #8-1-93* (KPABG); Valley of Teriberka River, 24.VI.2011, *Yu.S. Mamontov, # YuSM-51* (KPABG). Yamalo-Nenetsky Autonomous District: Yamal Peninsula, 18.VII.1977 *E.N. Andrejeva s.n.* (LE). Kamchatskiy Territory: Bering Island, *V.A. Bakalin #E-22-16-02-VB, K-22-19-02-VB* (KPABG). Sakhalinskaya Province: Paramushir Island, *V.A. Bakalin #K-96-10-04, K-102-03-04* (KPABG); Ketoi Island, *T.I. Hyushko #K-42-06* (LE). UKRAINE: Ivano-Frankovsk Province, Vorokhta Town, Chornogora Range, 29.VIII.1953, *L. Komandor s.n.* (KPABG). CANADA: Newfoundland, West coast, Portland Creek, 12-13.VIII.1982, *R.J. Belland #5641* (No. 173 *Bryophyta exsiccata Terrae-Novae et Labradoricae*, LE).

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