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 Pallavicinales revealed the heterogeneity of Moerckiaceae. 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 Pallavicinales known from Russia and adjacent areas is given.

В результате комплексного молекулярно-генетического и сравнительно-морфологического анализа расширенной выборки порядка Pallavicinales выявлена гетерогенность сем. Moerckiaceae. 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: Pallavicinales, molecular phylogeny, taxonomy, Moerckiaceae, Cordaeaceae, Russia

INTRODUCTION

Pallavicinales W. Frey & M. Stech (subclass Pellididae, class Jungermanniopsida) in recent treatments (Crandall-Stotler et al., 2009) has been subdivided in two suborders: the Phyllothalliineae R.M. Schust. with the monotypic family Phyllothalliaeae E.A. Hodgs., and the Pallaviciniineae R.M. Schust., which includes the monotypic families Sandothallaceae R.M. Schust. and Hymenophytaceae R.M. Schust., the oligotypic Moerckiaceae Stotler et Crand.-Stotl. with two genera and Pallaviciniaceae Mig., with eight genera. The majority of the species of Pallavicinales are restricted to the southern hemisphere. The latest and the most comprehensive molecular study on Pallavicinales (Schumann et al., 2005: 39) shows “the clear molecular separation” 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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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 Sandoeuthallus 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 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, *trn*L-F and *trn*G-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 *trn*L-intron.

The two datasets, ITS2 and *trn*L-intron, were automatically aligned in BioEdit 7.0.1 (Hall, 1999) with ClustalW option and then manually corrected. The preliminary phylogenetic analysis revealed a lack of incongruence between ITS2 and *trn*L-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.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Specimen voucher</th>
<th>GeneBank accession number</th>
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<tbody>
<tr>
<td></td>
<td></td>
<td>ITS2-2</td>
</tr>
<tr>
<td>Hattorianthus erinusus</td>
<td>Russia: Primorsky Kray 1, Bakalin, 105648 (KPABG)</td>
<td>KJ577207</td>
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<td></td>
<td>Russia: Primorsky Kray 2, Mamontov, 107/1-10 (KPABG)</td>
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<td>Russia: Primorsky Kray 3, Bakalin, 116-2-03 (KPABG)</td>
<td>KJ577206</td>
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<td>Moerckia blyttii</td>
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</tr>
<tr>
<td></td>
<td>Russia: Murmansk Prov. 2, Mamontov, 53/8 (KPABG)</td>
<td>KJ577208</td>
</tr>
<tr>
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<td></td>
<td>Russia: Sakhalin Prov. Shikotan I., Bakalin, K-54-1-07 (KPABG)</td>
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<td>Pallavicinia ambiguа</td>
<td>Japan, M. Higuchi, 1248 (KPABG, LE)</td>
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<td>Taiwan, H. Inoue, 16822 (LE)</td>
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<td>P. levieri</td>
<td>Cambodia, Bakalin, Cam-83-37-(KPABG, VGBI, VLA), 1</td>
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<td></td>
<td>Russia: Konstantinova, KGL-232-2-07 (KPABG)</td>
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<td>P. subciliata</td>
<td>China: Hunan Prov., T. Koponen, 51479 (LE)</td>
<td>KJ577198</td>
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<tr>
<td></td>
<td>Russia: Primorsky Kray, Bardunov (KPABG)</td>
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<td></td>
<td>South Korea, S.-S. Choi, 96 (KPABG)</td>
<td>KJ577201</td>
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The tree topologies obtained by the two methods are highly congruent and similar to those of Schumann et al. (2005), a number of internal nodes also have no support (Fig. 1, 2). Phylogenetic relation of Pallaviciniineae was discussed in details by Schumann et al. (2005). Here we focused on the relation of Holarctic species not or insufficiently studied previously to resolve some taxonomic 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. lyelli* from the Cambodia combined clade sister to *P. lyelli* 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. lyelli* (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. lyelli*. 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 Moerckiaeaceae 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 Slooover (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 molecular 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 Moerckiaeaceae 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 hepcities. 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.) Gottsch. 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 & Pippo, 1986). According to Grolle & Pippo (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 binominals 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 thallii 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 & Pippo (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” (I.e.), 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. ambiguia* by Grolle & Pippo (1986). Comparing all available literature data (Inoue, 1976; Koponen et al., 2000; Yamada & Iwatsuki, 2006) we found that *P. subciliata* and *P. ambiguia* differ neither ecologically, nor in their distribution, nor morphologically. Grolle & Pippo (1986) also noted that *P. fistulosa* is the synonym of *P. ambiguia*, and selected a specimen of *P. fistulosa* Elmer 9994, Island of Negros, Damaguete (G-22931) as a lectotype of *P. fistulosa*. Grolle & Pippo (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 (I.e.) as isolecotypes of *P. fistulosa*. They showed (I.e.) that the plants from these specimens agree with *P. ambiguia* 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 (isolecotype 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. ambiguia*.

Unfortunately, we could not study the type of *P. ambiguia*, but all specimens of this complex studied by us match well the description of *Stezzia subciliata* (syn. *Pallavicinia subciliata*) provided by Austin (1879) rather than *P. ambiguia*. The latter taxon is probably conspecific with *Pallavicinia subciliata*, but study of the type material of *P. ambiguia* 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. excis. Vind., LE*) that was treated as *P. levieri* by Grolle & Pippo (1986).

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**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..........................
   — 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. .........................
   — 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 square, arranged in several dense rows over the thallus and surrounding the gametangia. Spores with irregular and very short tuberculate ridges, 3-4 μm high and 3-8 μm long, at apex often truncate or distally divided ......................
   — 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 laciniate-dentate, placed laterally and posteriorly to archegonia. Spores with numerous hemispherical papillae 3-8 μm high and thick, at apex somewhat rounded ...........................................
   — Thallus / midrib width ratio 7-14:1. Rhizoids dark red to purplish-violet. Capsule wall without nodular thickenings ..............................................  8

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 μm high and thick, and 15-50 μm long, at apex rounded .... [Sandothallus 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 μm high and thick, at apex flat or rounded .............................. [Sandothallus radiculosus]


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 obtapezoidal, 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 possesses 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.

Dioicus. *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. *Gynoecea* anacrogynous on the dorsal surface of the thallus (acrogynous on ventral branches in *Podomitrium*); outer involucres represent by 1-several posterior laciniate-ciliate scale or forming a complete ring around archegonia; the scales free or connate into a cup-shaped structure. *Sporo-phylies* enclosed by a shoot calyptra and, if present, perichaetial tubular pseudoperianth, or by a coelocaula. *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. *Elaterophore* absent. *Elateres* 2-4-spiral. *Spores* 17-40 μm in diameter, surface delicately areolate or faintly granulate-punctate to ridged, or covered with short lamellae.


Type genus: *Pallavicinia* Gray.


Plants dorsally flat or convex, ventrally convex, prostrate to nearly ascending, differentiated into a creeping subteterate rhizomatous stipe, which becomes gradually or abruptly winged, ventrally branched or 1-3-pseudodichotomously furcate. *Midrib* sharply defined, obtapezoidal 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 involucres forming a complete ring around archegonia, laciniate-ciliate; scales free or connate into a cup-shaped structure. Inner involucres 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 μm in diameter, surface delicately areolate or faintly granulate-punctate.

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


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 obtrapezoidal in cross section, abruptly tapering into unistratose margins. Stalked uniseriate mucillage papillae of 2(–4) cells long present on both ventral and dorsal sides of the midrib. Papillae 25–35 μm wide, 100–160 μm 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 μm high (in cross section), 25–35 μm wide; the dorsal ones 65–135 μm long. Inner cells of medulla 18–40 μm high, 12–33 μm wide (in cross section). Central strand formed of sclerenchymatous cells each with lumen of (2–)6–9 μm (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 μm wide and 35–45 μm long. Wing cells 5–6-angled, without trigones, obliquely oriented and elongated towards the margin, 22–65 μm wide, 45–65 μm long, in cross section 28–45 μm high. Marginal cells 15–25 μm wide, 45–70 μm 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 involucres form a complete ring around archegonia and at base connate into a cup-shaped structure with laciniate-ciliate mouth; cilia 5–10 cells long (Fig. 4: 3-4). Cells of cilia 28–36 μm wide, 40–115 μm 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).


Reports of the species from the Russian Far East (Bakalin, 2007; Bakalin et al., 2009) are erroneous and are referred to us by 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” (i.e.). 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).
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.


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 μm
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.


Ecology. *P. subciliata* has been found in Russia on humus, probably in shaded places in coniferous-broadleaved forest, where it occurs with *Plagiothecium* sp. (Bar- dunov, *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. lon- gispina* (IRK, KPABG).
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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).


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-intercalar branching. *Rhizoids* pale brownish, developed on stipe bases or freely throughout. *Midrib* sharply defined, dorsally concave to convex, ventrally convex, elliptical to obtrapezoidal 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...
wards thallus middle; bracts multistratose at base, becoming unistratose at margins, irregularly incised and laciniate-ciliate, usually with additional wings on outer surface; antheridia spherical, almost subsessile.

Female plants (the description of female involucres 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 – elater; 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).
branching. Archegonia in well-defined clusters, 1 per frond. Outer involucres forming a complete ring around archegonia, at base conate into a cup-shaped structure, multistratose, becoming unistratose at margins, variously incised, with laciniate-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 broad-leaved 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 (isolectotyputs, JE). CAMBODIA: Mongul-Kiri Province, 19.XII.2011, V.A. Bakalin #Cam-79-13-11 (VGBI,
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 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.

 Dioious. 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. Archeogonia 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. Elaterophore 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 Pallavicinaceae it differs in the type of vascularisation, particularly in two lateral conducting strands vs. one (or several in Symphyogyna) in Pallavicinaceae. 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 Pallavicinaceae 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 Pallavicinaceae stalked filiform mucilage papillae are present on both ventral and dorsal sides of midrib, especially towards the apex.

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

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


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 ascendent 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 ascendent, 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 obturpezoideal 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 gynoeicum, 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 gynoeicum 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
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).

Cordaea erimona is a sub-oceanic East-Asian montane 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., Campylium sp., Serpolekea 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 et al., Prim-4-4 (KPABG); Prim-4-3, Prim-4-1 (KPABG); Prim-107-1 (KPABG); Vladivostok, V.A. Bakalin #116-2-03 (KPABG).


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 unistratose 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, 30–40×45–65(–73) μm, thin-walled; outer cells of the wings more elongated, 27–40(–50)×60–90(–116) μm. Cells of unistratose part of wings rounded-hexagonal to quadrate, (27–)30–40(–50)×(35–)40–50(–70) μm; marginal cells somewhat elongated, 27–32×40–46 μm. Cells of ventral epidermis of midrib with brown pigmentation, mostly elongated-hexagonal, or rounded to elongated-rectangular, (20–)24–32(–40)×(20–)45–60(–80) μm. Ventral slime hairs uniseriate, up to 12 cells long, with cells 19–23×31–44 μm. Inner cells of midrib rounded-polygonal in cross section, (19–)24–46(–54) μm in diameter.
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Male scales in clusters or covering surface of midrib, erect to squarrose, broad, foliaceous, subquadrate or rectangular, with laciniate-dentate margins, sometimes on posterior face with low vertical dentate lamellae. Cells of scales elongated and 5–6-angled to rounded, 35–50×50–60 μm. 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, 20–40(–50)×(35–)65–95(–110) μm. Pseudoperianth ovoid or cylindrical, 3–5 times as long as wide, plicate distally; the mouth contracted, mostly 3-lobed and then laciniate, 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, 35–40 μm high in cross section, cells of inner layers colorless, thin-walled, 9–13 μm high. Spores brownish, 35–50 μm in diameter, with reticulate to ridged surface. The outgrowths on spore surface rounded, 2–3 μm 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 rhizoids; 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, Scorphidium, Fissidens adiantoides, F. osmundoides, Calliergonella lindbergii, Cinclidium stigium, 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 Russia, Primorsky Territory, Yu.S. Mamontov, # Prim-4-4 (KPABG).
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, 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).
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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).
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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 f.o. 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).


Type genus: **Moerckia** Gottsche.

**Plants** short or elongated, moderately to very wide, dorsally flat or concave, ventrally convex. **Midrib** sharply defined, triangular to obtrapezoidal 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.

**Dioious.** **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 subsessile globose antheridia; antheridal stalk multicellular. Archegonia in well-defined clusters surrounded by broad laminar involucres 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-transparent, 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 sectional view and elongated in longitudinal section. Inner layers consist 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).


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

In Russia the genus is represented by one species.


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 stipule 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 obtrepezooidal, 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 emarginate, 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 gynoecium per thallus, rarely, if divided, then forming up to three gynoeccia 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 induplicate 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 incinate-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 Sandeothallus 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 incinate-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 – Moerkia 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 acidophilous or neutrophilous cryophytic 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, *e.g.*, *Anthelia juratzkana*, *Cephalozia ambiguca*, *C. leucantha*, *Diplphyllum taxifolium*, *Gymnocolea inflata*, *Marsupella boeckii*, *M. emarginata*, *Pleurocladula albsencs*, *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, 1996), Solar Uras (Zinovjeva, 1973), Yamal Peninsula (Potemkin, 1993), Taimyr Peninsula (Zhukova & Matveeva, 2000), Kurils (Zinovjeva, 1973), Yamal Peninsula (Potemkin, 1993), Taimyr Peninsula (Zhukova & Matveeva, 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, 1992), Newfoundland, Alberta, British Columbia, and Washington (Schuster, 1992). In East Asia it was recorded from Japan (Inoue, 1985).


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