

ON THE SYSTEMATIC POSITION OF DISCELIUM (BRYOPHYTA)
О СИСТЕМАТИЧЕСКОМ ПОЛОЖЕНИИ РОДА DISCELIUM (BRYOPHYTA)

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Abstract

Results of molecular phylogenetic analysis support the position of the genus *Discelium* in the group of diplolepidous opposite mosses, Funariidae; however, its affinity is stronger with Encalyptales than with Funariales, where it is currently placed. A number of neglected morphological characters also indicate that *Discelium* is related to Funariales no closer than to Encalyptales, and thus new order Disceliales is proposed. Within the Encalyptaceae a case of strong sporophyte reduction is revealed. *Bryobartramia* appeared to be nested in *Encalypta* sect. *Rhabdotheca*, thus this genus is synonymized with *Encalypta*.

Резюме

Молекулярно-филогенетический анализ подтвердил положение рода *Discelium* в группе диплолепидных мхов с перистомом с супротивным расположением его элементов, или подклассе Funariidae, однако указал на родство с порядком Encalyptales, а не с Funariales, в который его обычно относили. Ряд редко учитываемых морфологических признаков также свидетельствует в пользу лишь отдаленного родства с Funariaceae. Предложено выделение *Discelium* в отдельный порядок Disceliales. В Encalyptaceae выявлен случай сильной редукции спорофита. Выявлено положение *Bryobartramia* в пределах рода *Encalypta*, в котором он имеет близкое родство с терминальными группами видов с гетерополярными спорами. Таким образом, *Bryobartramia* отнесена в синонимы к роду *Encalypta*.

KEYWORDS: mosses, taxonomy, molecular phylogenetics, new order

INTRODUCTION

The genus *Discelium* Brid. represents a small moss with a strongly reduced gametophore. Photosynthetic function is delivered to protonema that densely covers expanded patches of bare wet soil. Stems are short in *Discelium*, bearing only few small leaves without or with quite indistinct costa. Absence of costa is a rare character in acrocarpous mosses; therefore the genus was segregated in a separate family by Schimper (1856) in “Corollarium Bryologiae Europaea...”, one of the first comprehensive accounts of mosses where all the genera were arranged in families.

Schimper (1856) placed Disceliaceae between Splachnaceae and Funariaceae, and since that time, Disceliaceae were almost invariably considered to be closely related to Funariaceae and placed in the order Funariales (Brotherus, 1924; Goffinet *et al.*, 2009; Frey & Stech, 2009).

Peristome development of *Discelium* was studied by Shaw & Allen (1985). Their anatomical study and SEM

observation revealed the peristomial formula of *Discelium* is 4:2(–4):4 with opposite position of exostome and endostome elements, which agrees with the Funariales and the Encalyptales, two diplolepidous opposite groups known that time (Edwards, 1984).

Already first molecular phylogenetic studies delimited diplolepidous opposite group (Goffinet & Cox, 2000). In addition to Funariaceae, Encalyptaceae and Disceliaceae, it was supplemented by Timmiaceae and Gigaspermaceae. These five families usually do not form a clade, but compose a paraphyletic grade or partly polytomy between *Diphyscium* and two major terminal moss clades, the Bryidae and Dicranidae (cf. Goffinet *et al.*, 2001; Hedderson *et al.*, 2004; Tsubota *et al.*, 2004; Cox *et al.*, 2010; Ignatov *et al.*, 2015; Fedosov *et al.*, 2016).

However, despite some incongruence in topologies obtained from different analyses that included representatives of these five families, three of them, Funariaceae, Encalyptaceae and Disceliaceae, are commonly resolved

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as a clade (Goffinet *et al.*, 2001; Larraín; Cox *et al.*, 2010). At the same time, Gigaspermales are always basal in the paraphyletic grade or in weakly supported clade, and the position of *Timmia* is variable, being however invariably between Gigaspermales and terminal clades of Dicranidae and Bryidae (cf. Goffinet *et al.*, 2001, Hedderson *et al.*, 2004, Fedosov *et al.*, 2016).

The position of *Discelium* within the clade of Funariaceae+Encalyptaceae+Disceliaceae varies in different analyses. It was found sister to Funariales+Encalyptales (Goffinet & Cox, 2000; Inoue & Tsubota, 2014), grouped either with Encalyptales or Funariales depending on the analysis parameter (Goffinet *et al.*, 2001), grouped with Funariales (Cox *et al.*, 2010), or formed a weakly supported clade with Encalyptales (Wahrmund *et al.*, 2009; Larraín *et al.*, 2009; Ignatov *et al.*, 2015). The aim of the present study was to check if the position of *Discelium* can be resolved more definitely after enriching the sampling by additional representatives of Encalyptales and Funariales. Morphological comparison of *Discelium* with Encalyptales and Funariales was also conducted.

MATERIALS AND METHODS

Molecular phylogenetic study

For molecular study we used three markers, the intronic region of the mitochondrial NADH dehydrogenase subunit 5 (*nad5*), chloroplast ribosomal small protein 4 (*rps4*) and chloroplast gene for ribulose biphosphate carboxylase large subunit (*rbcL*) gene, which are well represented in GenBank and quite useful for molecular-phylogenetic reconstructions at familial level (cf. Tsubota *et al.*, 2004; Cox *et al.*, 2010). The material used in the present study was sampled from MW and supplemented by sequences available in GenBank.

Dataset was compiled with special attention to the groups with diplolepidous-opposite peristome, *i.e.*, Disceliaceae itself, Gigaspermaceae, Funariaceae, and Encalyptaceae, while for Timmiaceae only one species was included, as it is known to form a clade apart from other diplolepidous opposite mosses. Bryobartramiaceae were included, as Goffinet *et al.* (2009) placed this family into Encalyptales. Several species of haplolepidous mosses and those with diplolepidous- alternate peristomes were involved to provide representation of major evolutionary lineages of mosses. *Takakia lepidozoioides*, *Polytrichum hyperboreum*, *Oedipodium griffithianum*, *Diphyscium foliosum* and *D. fulvifolium* were used as outgroups. Totally 142 sequences from 50 specimens, representing 49 species (sequences for *Discelium nudum*, downloaded from GenBank were supplied with originally studied specimen) were involved into the analysis, including 13 sequences of 5 species obtained de novo. Vouchers of newly sequenced specimens and GenBank accession numbers of all used sequences are compiled in Appendix 1. Laboratory protocol was essentially the same as in Fedosov *et al.*, (2016). Sequences

were aligned for each gene independently using BioEdit version 7.0.9.0 sequence alignment editor (Hall, 1999). Absent positions at the 3'- and 5'-ends were treated as missing data. All trees were rooted on *Takakia lepidozoioides*.

Four analyses were performed. The first three datasets corresponding to the individual gene alignments, *nad5* (1170 bp), *rps4* (571 bp) and *rbcL* (1376 bp), were analyzed separately to check their congruence. The fourth dataset represented concatenated *rps4* – *nad5* – *rbcL* sequences (3117 positions). Individual datasets were divided into unlinked partitions: three codon positions for coding portion of the *nad5* gene, the intron in the *nad5* gene; three codon positions of *rps4* gene; three codon positions of *rbcL* gene. Thus the combined dataset was separated into ten unlinked partitions. Best-fit substitution models were identified for each gene separately, and for combined dataset using ModelgeneratorV.8.5 (Keane *et al.*, 2006). Best-scoring Maximum Likelihood (ML) trees were estimated using RaxML (Stamatakis, 2006) from 1000 independent searches each starting from distinct random trees. Robustness of the nodes was assessed using the thorough bootstrapping algorithm (Felsenstein, 1985) with 1000 iterations. RaxML was performed on the Cipres Science Gateway (<http://www.phylo.org/portal2>), using RAXML-HPC2 on XSEDE.

Bayesian Analyses (BA) were performed running two parallel analyses. For single gene analyses each run consisted of six Markov chains and 10,000,000 generations with default number of swaps chains and a sampling frequency one tree each 5,000 generations. For concatenated dataset the analysis consisted of eight Markov chains and 50,000,000 generations with the number of swaps chains set to five and a sampling frequency one tree each 10,000 generations was performed. The chain temperature was set at 0.02 in all analyses. Convergence of each analysis was evaluated using Tracer1.4.1 (Rambaut & Drummond, 2007) to check that all ESS values exceeded 200. Consensus trees were calculated after omitting the first 25% trees as burn-in. Analyses were performed on the Cipres Science Gateway (<http://www.phylo.org/portal2>), using MrBayes 3.2.6 (Ronquist *et al.*, 2012) on XSEDE.

Morphology

Observations of perispome structure were done with the SEM Jeol 6380 for specimens coated by gold without additional preparation.

RESULTS

The trees from the analyses of the separate gene regions provided no supported conflicts, thus the concatenated dataset was used for the final analysis. The obtained tree (Fig. 1) is composed of paraphyletic grade formed by the putatively primarily eperistomate *Oedipodium*, then nematodontous *Polytrichum*, then the basal-most arthrodontous *Diphyscium*, then *Gigaspermales*, and then tritomy of (1) *Timmia*; (2) clade of Funariaceae+Encalyptaceae+Bryobartramiaceae+ Disceliaceae;

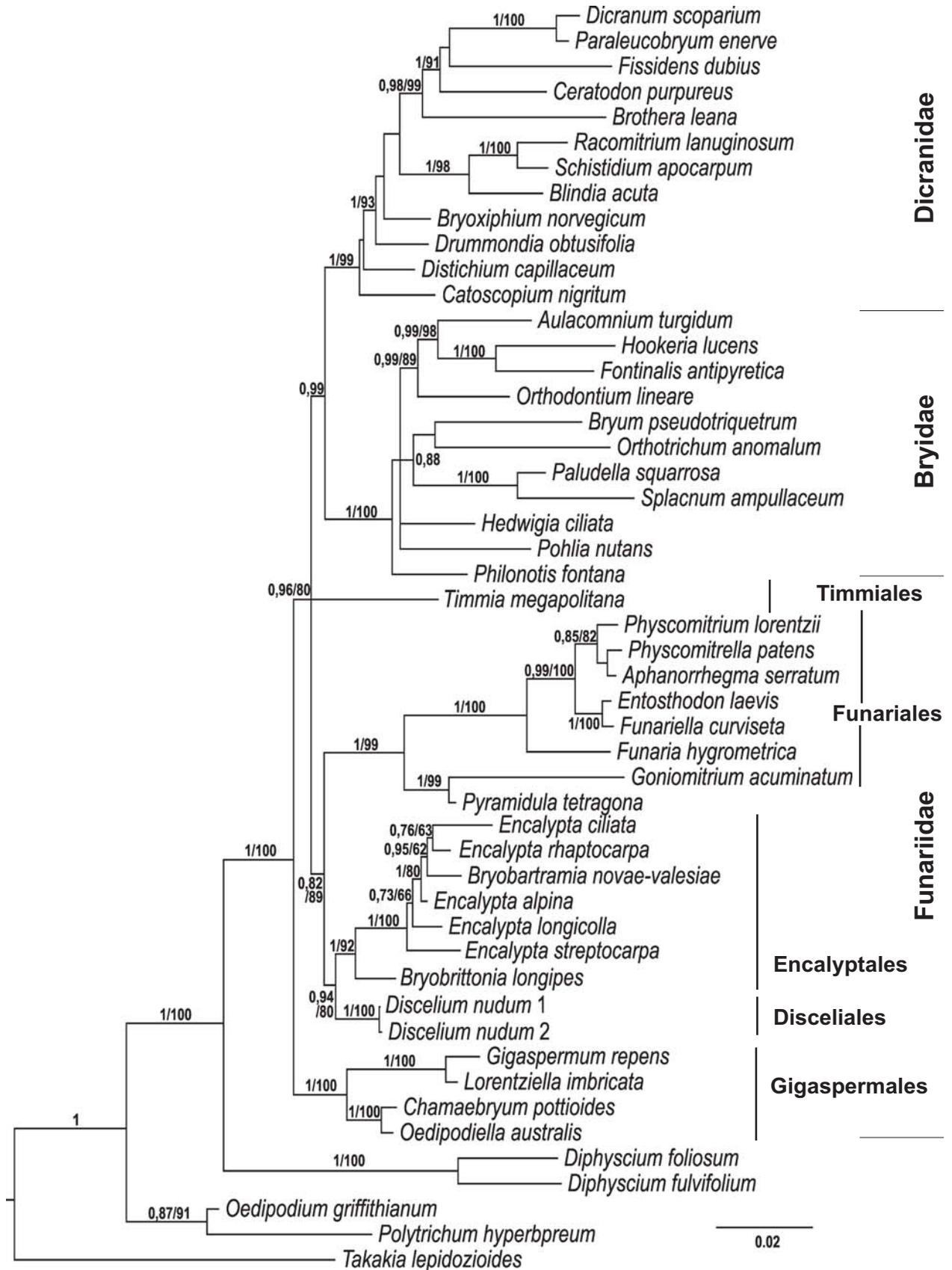


Fig. 1. Bayesian tree obtained from a concatenated data set of mitochondrial *nad5* and chloroplastic *rps4* and *rbcL*. Posterior probabilities (>0.7) are Bootstrap supports (>50) is indicated above branches.

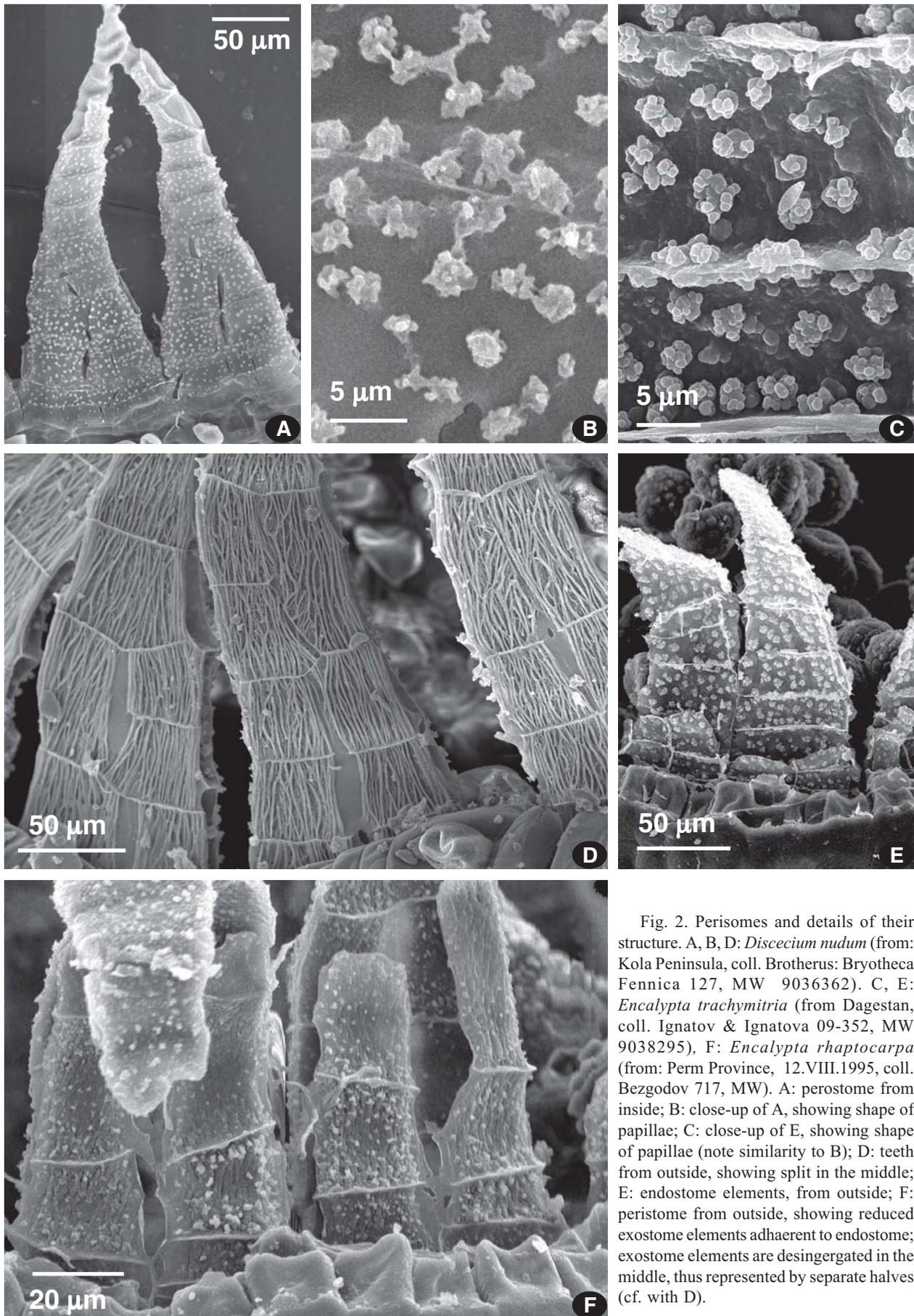


Fig. 2. Peristomes and details of their structure. A, B, D: *Disceium nudum* (from: Kola Peninsula, coll. Brotherus: Bryotheca Fennica 127, MW 9036362). C, E: *Encalypta trachymitria* (from Dagestan, coll. Ignatov & Ignatova 09-352, MW 9038295), F: *Encalypta rhaptocarpa* (from: Perm Province, 12.VIII.1995, coll. Bezgodov 717, MW). A: peristome from inside; B: close-up of A, showing shape of papillae; C: close-up of E, showing shape of papillae (note similarity to B); D: teeth from outside, showing split in the middle; E: endostome elements, from outside; F: peristome from outside, showing reduced exostome elements adhaerent to endostome; exostome elements are desingergated in the middle, thus represented by separate halves (cf. with D).

and (3) clade with two subclades of Bryidae and Dicranidae.

Only the clade of Funariaceae+Encalyptaceae+Bryobartramiaceae+Disceliaceae is described here in details. It obtained a rather moderate support ($P=0.82$; $BS=89$), while three lineages within it, namely Funariaceae, Encalyptaceae+Bryobartramiaceae and Disceliaceae received the maximal support. *Discelium* has a sister position to the Encalyptaceae+Bryobartramiaceae, and their common clade has a rather high support ($P=0.94$; $BS=80$).

Within the Encalyptaceae+Bryobartramiaceae, the topology is as follow. *Bryobrittonia* is sister to the rest of species, the latter having maximal support. Then, the grade in composed of the species with isopolar spores: *Encalypta streptocarpa*, then *E. longicollis*, then *E. alpina*. The inner clade of *E. alpina*, *E. ciliata*, *E. rhaptocarpa* and *Bryobardtramia novae-valesiae* obtained a high support ($P=1$; $BS=80$). *Bryobardtramia novae-valesiae* is found in sister position to *E. ciliata* and *E. rhaptocarpa*, with $P=0.95$ (Bayesian analysis) or sister to *E. ciliata*, though with weak support (ML).

DISCUSSION

Discelium

The position of *Discelium* within Funariidae raised no doubts in recent literature, especially after the excellent study of peristome morphology of *Discelium nudum* by Shaw & Allen (1985). All molecular phylogenetic studies, since Goffinet & Cox (2000), invariably found *Discelium* in the group of species with diplolepidous opposite peristome.

However, alternative placement of *Discelium* either in Funariales or in Encalyptales was briefly discussed only once by Shaw & Allen (1985). Funariales were suggested to accommodate Disceliaceae, because *Discelium* was thought to be very different both gametophytically and sporophytically from *Encalypta* and *Bryobrittonia*, two genera in the Encalyptales known that time. Among the evidences for the placement of *Discelium* in Funariaceae the authors mentioned its ephemeral life cycle and the leaf areolation typical for the Funariales. Actually, its great difference from the Encalyptaceae that have densely papillose leaves and straight urn covered by peculiar campanulate calyptrae is really conspicuous. However, it is easy to note that its similarity with Funariaceae in gametophytic characters relates mostly to those that are associated with reduction.

During the last thirty years the traditional approach in the systematics was challenged, and the cases interpreted as reduction were especially strongly reconsidered. The re-evaluation of reductional changes was accelerated with the application of cladistic approach, already in the pre-molecular era. Thus, Zander (1993) brought a new look of a number of lineages of Pottiaceae. The genus *Phascum* was found to be the ultimate stage of reduction of *Tortula* through transitional stages represented by *Desmatodon* and *Pottia*. Similarly, *Astomom*, which

was accepted as a separate genus in check-lists of 1980s and early 1990s (Corley *et al.*, 1981; Anderson *et al.*, 1990) appeared to be just a reduced *Wessia*, and so on.

One of the best known examples of reduction concerns epiphytic pleurocarpous mosses. Traditional subdivision of pleurocarps into Isobryales (Leucodontales) and Hypnobryales (Hypnales) universally accepted during almost throughout 20th century was crushed by the molecular phylogenetic tests (Tsubota *et al.*, 2004; Huttunen *et al.*, 2004, 2012a,b). It became clear, that the circumscriptions of these orders were based on over-evaluation of peristomial reduction, which was one of the main characters for their separation.

Considering these cases, it is unlikely that the lack of costa and small size of leaves with thin-walled cells in *Discelium* may necessarily serve as an evidence for its affinity with the Funariaceae. The nested position of the *Ephemerum* in Pottiaceae (Werner *et al.*, 2004; Goffinet *et al.*, 2009) may serve as a useful parallel case. In the most well-known species of *Ephemerum*, *E. serratum*, costa is reduced and cells are smooth.

The number of characters, which indicate more similarity of *Discelium* with Encalyptaceae than with Funariaceae are not many.

(1) The most obvious is dioicous sexual conditions in *Discelium*. All Funariales are autoicous. Most Encalyptaceae, and especially those forming terminal part of their phylogenetic lineage, also are autoicous. However, two basalmost species, *Bryobrittonia longipes* and *Encalypta streptocarpa*, are dioicous, being similar in this respect to *Discelium* (cf. Fig. 1).

(2) Endostome is ornamented with papillae of a quite similar shape (Fig. 2A–C, E).

(3) Endostome in *Discelium* is adherent to exostome along all its length and is even hardly observed, and exostome is commonly split along the median line, which is reflected in the name of the genus.

In Funariaceae, a well developed peristomes occur only in *Funaria* and few *Entosthodon* species (*E. muhlenbergii*-group). In these genera exostome is better developed than the endostome. The latter is either free or somewhat adherent to exostome, occasionally along its whole length (e.g., in *Funaria aequidens*), however even in this case, ventral trabeculae are developed, making endostome and exostome more or less separated. In *Encalypta*, in contrary, exostome and endostome are often fused throughout. In basal species, like *E. procera*, they are fused to the middle; in *E. longicollis* 3–5 cell layers form peristome teeth of a 'secondary nematodontous' type (Edwards, 1984); in advanced species of *Encalypta*, e.g. in *E. rhaptocarpa*, exostome is represented by short remnants fully adherent to stout endostome. Exostome material in this case is not united, like in basal part of *Discelium* teeth (Fig. 2D, F).

By the strong fusion between exostome and endostome, as well as by teeth split *Discelium* is rather similar to Encalyptaceae. At the same time, delicate tex-

ture of its endostome is more similar to *Funaria*, as in Encalyptaceae, especially in their terminal groups, endostome evolves towards being more robust than exostome.

Thus, *Discelium* has similar features with both Funariaceae and Encalyptaceae, and the obvious conclusion will be the segregation of Disceliaceae into their own order. This suggestion has been proposed by Ignatov & Ignatova (2003), but these authors failed to validate this name properly, thus here we recover this error:

DISCELIALES Ignatov, Ignatova & Fedosov, ordo nov.

Type: Disceliaceae Schimp., Corollarium Bryologiae Europaeae 59. 1856.

Included families: Disceliaceae Schimp.

Diagnosis: Protonema persistent. Dioicous. Stem short. Leaves in female plants few, small, ecostate. Seta long. Capsule inclined. Peristome double opposite, exostome teeth 16, prominent, erect, endostome thin.

A note on *Bryobartramia*

In the course of this study another case of reduction was observed. It concerns mostly sporophytic structures, but it is worthy comment it in order to compare, how much faster reductional changes in sporophyte are possible.

The genus *Bryobartramia* and the monogeneric family Bryobartramiaceae were described by Sainsbury (1948) for peculiar Australian endemic species, characterized by capsule retaining in epigonium. Later, Stone (1977) exhaustively described the type species of the genus. In the discussion of leaf cell structure and papillosity, differentiation of costa, spores and other structures, she repeatedly addressed *Encalypta* for comparison. Despite the final decision to retain the genus and the family as their own, her publication indicate so much similarity with *Encalypta*, that it looks that just a last drop is lacking to merge the *Bryobartramia* to *Encalypta*.

The present analysis places the type species of *Bryobartramia* not only within the genus *Encalypta*, but in the group of species with heteropolar spores, sect. *Encalypta* Hedw. (or *E. ciliata*-group) and sect. *Rhabdotheca* Müll. Hal. (or *E. rhaptocarpa*-group), being considered as the most advanced part of the genus (Horton, 1983). Indeed, the species of *Bryobartramia* demonstrate the same trend of sporophyte reduction that is well known in the genera *Tortula* and *Weissia* (see discussion above), some lineages of Ditrichaceae (Fedosov *et al.*, 2015, 2016) and some other lineages of acrocarpous mosses (Vitt, 1981). Epigonium of *Bryobartramia* are just calyptrae of *Encalypta* with exerted capsules. Both *E. ciliata*-group and *E. rhaptocarpa*-group comprise species with papillose calyptrae, *i.e.*, *E. sibirica* (Weinm.) Warnst. and *E. sinica* J.-C. Zhao & M. Li, correspondingly; it is also characteristic for *Bryobartramia*. Spores of *B. novae-valesiae* (Stone, 1977, Fig. 5) are very similar to *E. rhaptocarpa* at the view from the distal pole. Thus, we consider *Bryobartramia* as a synonym of *Encalypta*.

Taxonomic implications

Encalypta novae-valesiae (Broth. ex G. Roth) Ignatov & Fedosov, comb. nov. – *Trachycarpidium novae-valesiae* Broth. ex G. Roth, Hedwigia 53: 94. pl. 2: f. 8. 1913. – *Bryobartramia novae-valesiae* (Broth. ex G. Roth) I.G. Stone & G.A.M. Scott, J. Bryol. 7: 604. 1973 [1974].

Encalypta schelpei (Hedd.) Ignatov & Fedosov, comb. nov. – *Bryobartramia schelpei* Hedd., J. Bryol. 34(4): 258. 2012.

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Appendix 1. List of taxa used in molecular phylogenetic analysis with GenBank accession numbers for *nad5/rps4/rbcL*. Newly obtained sequences (in bold) are shown with the voucher specimen data.

Aphanorrhagma serratum AY908931/ AF223048/ –;
Aulacomnium turgidum AY312869/ AF023809/ AJ275180;
Brothera leana AY908911/ AY908129/ AF226830;
Bryobartramia novae-valesiae AY908967/ AY908160/ –;
Bryobrittonia longipes AY908790/ JN088970/ AJ275168;
Bryoxiphium norvegicum AY908957/ AF231267/ JN162305;
Bryum pseudotriquetrum DQ640127/ JF277327/ AY163040;
Catoscopium nigrum AY908927/ AF307001/ AB914712;
Ceratodon purpureus AY908862/ AB848717/ DQ463103;
Chamaebryum pottioides AY908983/ AF223051/ FJ870761;
Dicranum scoparium AY908884/ AF234158/ AF231067;
Diphyscium foliosum AY312874/ AF223034/ AF231063;
Diphyscium fulvifolium JX241614/ AF478266/ AF478222;
Discelium nudum AY908956/ EU095320/ EU095320;
***Discelium nudum* Russia, Khabarovsk Territory, Botchinsky Nature Reserve, coll. Ignatov & Ignatova 10.VIII.2013 #13-61 (MHA, MW) KY358071/ KY358066/ KY358062;**
Distichium capillaceum AY908786/ AB853082/ AB853072;
Drummondia obtusifolia AY908926/ AF223038/ AF232697;
Encalypta streptocarpa AJ622818/ AF478282/ AF478239; ***E. alpina* Russia, Krasnoyarsk Territory, Taimyr Municipal Distr., vicinity of Khatanga settl. near Nyamakit-Daldyn Creek mouth, coll. Fedosov 30.VII.2013 #13-3-0662 (MW) KY358074/ KY358068/ KY358063;** *E. ciliata* AY312875/ AF223040/ AY312929; ***E. longicolla* Russia, Krasnoyarsk Territory, Taimyr Municipal Distr., vicinity of Khatanga settl. near Afanas'evskie Lakes, coll. Fedosov 9.VIII.2006 #06-635 (MW) KY358073/ KY358069/ KY358064;** ***E. rhaptocarpa* Russia, Krasnoyarsk Territory, Taimyr Municipal Distr., vicinity of Khatanga settl. near Fomich River mouth, coll. Fedosov 10.VII.2008 #08-754 (MW) KY358075/ KY358070/ KY358065;** *Entosthodon laevis* AY312876/ AF223043/ –; *Fissidens dubius* JX241619/ AF231281/ AF231303; *Fontinalis antipyretica* AY908494/ AF023817/ AJ275183; *Funaria hygrometrica* Z98959/ JN088980/ AF005513; *Funariella curviseta* AY908791/ AY908157/ –; *Gigaspermum repens* AY908974/ JN088984/ AF231064; *Goniomitrium acuminatum* AY908820/ DQ337185/ –; *Hedwigia ciliata* AY908380/ AF478289/ AF231073; *Hookeria lucens* AY908489/ AY306930/ AY631185; *Lorentziella imbricata* AY908973/ AF223053/ –; *Oedipodium griffithianum* AY312880/ AF306968/ AF478202; *Oedipodiella australis* FJ870754/ JN088987/ FJ870763; *Orthodontium lineare* AY312881/ AF023800/ AJ275174; *Orthotrichum anomalum* AY908979/ JQ836889/ AF005538; *Paludella squarrosa* AY908375/ AF306996/ KC250533; *Paraleucobryum nerve* AY908883/ AY908106/ AF226827; *Philonotis fontana* AY908384/ AF023801/ AY631192; *Physcomitrella patens* Z98960/ AF223044/ X74156; *Physcomitrium lorentzii* AY908933/ AF223046/ –; *Pohlia nutans* AY908369/ AY631156/ AY631193; *Polytrichum hyperboreum* GU569580/ GU569840/ GU569487; ***Pyramidula tetragona* Ukraine, Vinnitsakaja Province, coll. March 1938 KY358072/ DQ337184/ –;** *Racomitrium lanuginosum* AJ291561/ AJ553982/ GU809015; *Schistidium apocarpum* AY908920/ JQ40708/ AF231065; *Scouleria aquatica* AY312887/ AF023780/ AF226822; *Splachnum ampullaceum* EU095308/ AY039044/ AF231071; *Takakia lepidosoides* AJ291553/ AB299143 / AY312936; *Timmia megapolitana* AY312890/ AF222902/ AF478242.