



Mitochondrial phylogenomics supports splitting the traditionally conceived genus *Racomitrium* (Bryophyta: Grimmiaceae)

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With 9 figures and 1 table

Abstract: The polyphyletic nature of the traditionally interpreted genus *Racomitrium* Brid. and the necessity of its division into some segregates is confirmed by mitochondrial phylogenomics. Phylogenetic analysis based on the complete mitochondrial genomes revealed some incongruence with plastid/nuclear data in the topology of the main clades and provided strong support for recognition of *Niphotrichum* Bednarek-Ochyra & Ochyra, *Codriophorus* P.Beauv. and *Bucklandiella* Roiv. as separate monophyletic genera. In addition, the new genus *Frisvollia* Sawicki, Szczecińska, Bednarek-Ochyra & Ochyra is recognised to accommodate *F. varia* (Mitt.) Sawicki, Szczecińska, Bednarek-Ochyra & Ochyra, a species which has so far been placed in *Codriophorus* as *C. varius* (Mitt.) Bednarek-Ochyra & Ochyra. In the phylogenetic analysis *Bucklandiella* is revealed to be the ancestral genus characterised by some primitive characters including smooth laminal cells and short peristome teeth which are variously divided into two broad segments, undivided or merely perforated. All segregates of the genus *Racomitrium* are characterised morphologically and a key to their determination is presented.

Key words: *Bucklandiella*, *Codriophorus*, *Frisvollia*, mitochondrial genome, *Niphotrichum*, phylogeny, taxonomy.

Introduction

A characteristic feature of early classifications of mosses has been the recognition of large and all-encompassing genera, comprising wide arrays of species which are currently considered to be only remotely related, for example *Bryum* Hedw., *Hypnum*

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Hedw., *Mnium* Hedw. and *Leskea* Hedw. With progress in taxonomic studies many of these catch-all genera were divided on morphological and anatomical grounds into smaller, more homogeneous and natural entities. In this way, a number of segregates have been recognised within such genera as *Mnium* (Koponen 1968), *Polytrichum* Hedw. (Smith 1972), *Sciaromium* (Mitt.) Mitt. (Ochyra 1985, 1986, 1987a, b), *Tortula* Hedw. (Zander 1989) and recently in *Grimmia* Hedw. and *Racomitrium* Brid. (Ochyra et al. 2003).

With the rapid development of phylogenetic studies on mosses which is associated with the wide application of molecular techniques, the number of newly recognised genera has increased markedly. Some large genera have still proven to be heterogeneous and polyphyletic taxa which needed to be split into smaller, monophyletic genera, for instance *Brachythecium* Schimp. and *Eurhynchium* Schimp. (Ignatov & Huttunen 2002), *Neckera* Hedw. and *Thamnobryum* Nieuwl. (Olsson et al. 2011), *Hygrohypnum* Lindb. (Oliván et al. 2007) and *Rhynchostegium* Schimp. (Huttunen & Ignatov 2010). These results have often been congruent with the results of studies based on morphology and the new genera have usually been earlier recognised as infrageneric taxa within the genera concerned.

In the case of the broadly understood genus *Racomitrium* the molecular phylogeny based on nuclear ITS and plastid *rps4-trnL* and *trnK/matK-psbA* sequences carried out by Larraín et al. (2013) revealed that two segregates, *Bucklandiella* Roiv. and *Codriophorus* P.Beauv. remained polyphyletic, whilst one segregate, *Niphotrichum* Bednarek-Ochyra & Ochyra, remained paraphyletic. Only the narrowly interpreted genus *Racomitrium* may be considered monophyletic.

A major problem which often markedly impedes the proper interpretation of molecular phylogeny is imperfect knowledge of the genera concerned at the basic level of alpha-taxonomy founded on morphological and anatomical traits. In the case of the segregates of *Racomitrium* only two of them are perfectly known taxonomically because they have been monographed worldwide, namely *Niphotrichum* (Frisvoll 1983) and *Codriophorus* (Bednarek-Ochyra 2006). The narrowly conceived genus *Racomitrium* is also quite accurately circumscribed on a worldwide scale (Vitt & Marsh 1988; Bednarek-Ochyra & Ochyra 2003; Ireland et al. 2005).

In contrast, the largest and most morphologically diverse segregate *Bucklandiella* is only partially revised taxonomically in the Northern Hemisphere (Frisvoll 1988), whilst exotic taxa from the Southern Hemisphere have not received modern taxonomic treatments. With ongoing monographic studies, a number of new species of this genus have been discovered in various parts of the world, including Europe (Köckinger et al. 2007), Asia (Bednarek-Ochyra & Ochyra 2010a), New Zealand and Australia (Bednarek-Ochyra & Ochyra 2010b, 2011; Bednarek-Ochyra et al. 2014), South America (Larraín et al. 2011) and Subantarctica (Bednarek-Ochyra & Ochyra 2012a) or resurrected from obsolence (Bednarek-Ochyra 2014). Moreover, exploration of some areas, especially the subantarctic islands where some species have their main centre of occurrence, has yielded rich material of some species and permitted a proper evaluation of their variability and their redescription, for example *B. orthotrichacea* (Müll.Hal.) Bednarek-Ochyra & Ochyra (Bednarek-Ochyra & Ochyra 2012b). These

discoveries have also enabled a revision of the internal classification of the genus and more precise circumscription of the sections and subsections. Unfortunately, some key species of *Bucklandiella* were not included in molecular studies by Larrain et al. (2013) and this seriously affected the nomenclature of infrageneric taxa adopted from an earlier preliminary treatment (Bednarek-Ochyra 1995) without consideration of any subsequent developments.

The phylogenetic relationships and taxonomic status of the segregates of *Racomitrium* were studied on the basis of two plastid and one nuclear intragenic spacers (Larrain et al. 2013, Bednarek-Ochyra et al. 2014), which have often demonstrated incongruent results. In the present study the phylogenetic status of the segregates of *Racomitrium* is tested using complete mitochondrial genomes, resulting in over 17 times larger dataset than in previous studies. This is also the first bryological study where complete genomes have been used to resolve the taxonomic status of the genera.

Material and methods

MATERIAL: In total, ten specimens representing the following nine species have been analysed: *Bucklandiella emersa* (Müll.Hal.) Bednarek-Ochyra & Ochyra, *B. orthotrichacea*, *Codriophorus acicularis* (Hedw.) P.Beauv., *C. laevigatus* (Mitt.) Bednarek-Ochyra & Ochyra, *Frisvolla varia* (Mitt.) Sawicki, Szczecińska, Bednarek-Ochyra & Ochyra, *Niphotrichum elongatum* (Frisvoll) Bednarek-Ochyra & Ochyra, *N. ericoides* (Brid.) Bednarek-Ochyra & Ochyra, *Racomitrium lanuginosum* (Hedw.) Brid. and *R. patagonicum* Bednarek-Ochyra & Ochyra. Specimen details are given in the Table 1. DNA quantity was estimated with the use of the Qubit fluorometer system (Invitrogen, Carlsbad, NM, USA) and the Quant-IT ds-DNA BR Assay kit (Invitrogen). The previously published mitogenome of *Orthotrichum speciosum* Nees (Sawicki et al. 2014) was used as an outgroup.

A genomic library for MiSeq sequencing was developed with the use of the Nextera XT Kit. 1 ng DNA was used in the procedure described in the Nextera XT protocol (Illumina, San Diego, CA).

The number and correctness of libraries was verified with the use of primers whose sequences are given in the Sequencing Library qPCR Quantification Guide (Illumina). PCR reactions were performed in 20 µl of reaction mixture containing 3 µl of genomic library, 1.0 µM of each primer, 1.5 mM MgCl₂, 200µl M dNTP (dATP, dGTP, dCTP, dTTP), 1× PCR buffer and 1 U OpenEx Taq polymerase (OpenExome, Warsaw, Poland). PCR reactions were performed under the following thermal conditions: (1) initial denaturation – 5 min at temperature of 94°C, (2) denaturation – 30 s at 94°C, (3) annealing – 30 s at 52°C, (4) elongation – 1 min at 72°C, final elongation – 7 min at 72°C. Stages 2–4 were repeated 34 times. The products of the PCR reaction were separated in the QIAxcel capillary electrophoresis system (Qiagen, Carlsbad, Germany). Electrophoresis was performed using the QIAxcel High Resolution Kit with the 15–1000 bp alignment marker (Qiagen) and the 25–1000 bp DNA size marker (Qiagen). Standard OL500 settings were used as the electrophoresis programme. Validated libraries were pooled according to the Nextera XT protocol. Genomic libraries were sequenced using the Miseq 500v2 and 600v3 cartridge that supported the acquisition of 2×250 and 3×300 bp pair-end reads respectively. The numbers of obtained reads for each of the sequenced specimens are given in Table 1.

DATA ANALYSIS: Obtained sequences were mapped on the previously published mitogenome of *Codriophorus laevigatus* (Szczecińska et al. 2014) using Geneious R6 software (Biomatters, Auckland, New Zealand) with default medium-low sensitivity settings. The contigs between gaps and overlapping but incongruent sequences were extracted to separate files. On the extracted sequences raw pair-ends reads were mapped with 100 iterations using customised settings (minimum sequence overlap set to 150 and overlap identity 99%). Obtained contigs were used for de novo assembly with default settings of the Geneious assembler. On the drafts of the mitogenomes all available reads were mapped to determine coverage and to check any incongruences between mapped raw reads.

Table 1. Specimen details and sequencing results.

Species	Specimen details	No. of reads	Mitogenome coverage	mitogenome length (bp)
<i>Bucklandiella emersa</i>	Tasmania: Bednarek-Ochyra & Ochyra 662/13, KRAM B-215912	3245322	78×	107299
<i>Bucklandiella orthotrichacea</i>	Chile: Ireland & Bellolio 35509, KRAM B-184501	2850244	68×	107329
<i>Codriophorus acicularis</i>	Poland: Fudali Ł147, KRAM B-187446	3646848	78×	106815
<i>Codriophorus laevigatus</i>	Chile: Garcia 4121, KRAM B-190278	3506616	79×	106809
<i>Frisvollia varia</i>	USA, Oregon: Shevock 26367, KRAM B-170926	2256810	49×	106410
<i>Frisvollia varia</i>	USA, California: Shevock 31759, KRAM B-186001	3685428	82×	106410
<i>Niphotrichum elongatum</i>	USA, Idaho: Gray 1811, KRAM-198065	5405600	107×	106745
<i>Niphotrichum ericoides</i>	Poland: Bednarek-Ochyra & Ochyra 197/90, KRAM-090360	2658220	59×	106727
<i>Racomitrium lanuginosum</i>	Poland: Cykowska 600, KRAM B-161321	1984408	45×	106795
<i>Racomitrium patagonicum</i>	Chile: Ireland & Bellolio 34898, KRAM B-163752	2450644	62×	106788

The annotated GenBank files of the mitochondrial genomes were used to draw gene maps using OrganellarGenome DRAW tool (Lohse et al. 2013). The maps were then examined for further comparison of gene order and content.

Obtained mitochondrial genomes were aligned using MAUFF genome aligner (Darling et al. 2004) and two regions containing tandem repeats were adjusted manually according to the criteria of reducing gaps. The unambiguously aligned DNA sequences were used for phylogenetic analyses.

Phylogeny reconstruction was carried out using two dataset: complete sequences of the mitogenomes and extracted coding regions.

For completed mitochondrial genomes the parameters of the likelihood model were those of the general time reversible model with gamma distributed rate variation among sites (GTR+G) in accordance with the best fitted nucleotide evolution model selected on the basis of Akaike Information Criterion scores in Modeltest 3.7 (Posada & Crandall 1998). In the case of coding regions the optimal model was GTR+I.

Bayesian analysis was carried out using MrBayes 3.2 (Huelsenbeck & Ronquist 2001). The MCM algorithm was run for 4 000 000 generations with four incrementally heated chains, starting from random trees and sampling one out every 1000 generations. Tracer 1.3 (Rambaut & Drummond 2003) was used to examine the parameters and determine the number of trees needed to reach stationarity (Burn-in), which happened at around 30 000 chains, and therefore the first 50 trees were discarded as burn-in. Remaining trees were used to construct the Bayesian consensus tree.

A brief historical account of *Racomitrium*

The history of the genus *Racomitrium* was presented in detail by Bednarek-Ochyra (1995, 2006), so herein only the most important details are presented. In the traditional circumscription it has been considered as a distinct and well defined genus practically since its inception (Bridel 1819). Although species placed in *Racomitrium* exhibited a remarkable morphological diversity, it was given cohesion by a specific combination of morphological and anatomical traits. These primarily include the strongly sinuose longitudinal walls of laminal cells; calyptrae frayed at the base into several lobes (from this feature the generic name was coined); peristome teeth split into two or more segments, having usually a distinct, low basal membrane and being equally and less prominently thickened on both dorsal and ventral sides; and epidermal cells of the vaginula with distinctly sinuose walls. Additionally, all species of *Racomitrium* are dioicous and lack a central strand in the stem. This combination of characters clearly separates this genus from all other genera of the large family Grimmiaceae in which the genus has been firmly rooted. On this basis *Racomitrium* was placed in a separate subfamily Racomitrioideae (Ochyra et al. 2003).

The traditionally understood *Racomitrium* was a large genus. Wijk et al. (1967, 1969) listed under this name over 200 species and nearly the same number of infraspecific taxa, but effectively they accepted only 81 species. Subsequent taxonomic studies of some complexes resulted in the reduction of many names to synonymy but at the same time a number of new species were described (Frisvoll 1983, 1988) or reinstated from oblivion. It was especially the case with many austral species which were lumped with *Racomitrium crispulum* (Hook.f. & Wilson) Wilson (Clifford 1955) but many of which proved to be distinct species (e.g. Roivainen 1955; Bell 1974; Deguchi 1984; Bednarek-Ochyra & Ochyra 1998, 2012c, 2013; Bednarek-Ochyra et al. 1999; Ochyra et al. 2008). In addition, a number of the aforementioned new species were discovered in various parts of the world. In her world synopsis of *Racomitrium*, Bednarek-Ochyra (1995) accepted 62 species in this genus but considering all subsequent additions and reductions one may assume that the subfamily Racomitrioideae may include in total nearly eighty species.

Considering the heterogeneous morphology of both gametophytes and sporophytes in *Racomitrium* species, Kindberg (1897) divided this genus into four groups which were not given formal taxonomic ranks, namely *Lanuginosa*, *Papillosa*, *Canescentia* and *Laevifolia*. The unranked group *Canescentia* was subsequently validated as a subgenus (Vilhelm 1926) and the remaining as sections of *Racomitrium* (Noguchi 1974). The first detailed infrageneric classification of *Racomitrium* including all the species then recognised in the genus was given by Bednarek-Ochyra (1995), with four subgenera, namely subg. *Racomitrium*, subg. *Cataractarum* Vilh., subg. *Niphotrichum* Bednarek-Ochyra and subg. *Ellipticodryptodon* (Vilh.) Bednarek-Ochyra & Ochyra, which corresponded well to the four unranked groups recognised within this genus by Kindberg (1897). Within each of these subgenera a number of sections and subsections were recognised.

The heterogeneity of *Racomitrium* was pointed out much earlier by some authors. For example, Loeske (1930, p. 18) stated that "Ich halte *Rh.[acomitrium] canescens* für die

abgeleitete und jüngste Art der Gattung, und ihre Beziehungen zu *Rh. lanuginosum* für sehr vage. Es ist allerdings auch keine andere Art ersichtlich, der sie näher stände, und in der Tat bildet *Rh. canescens* m. E. einen isolierten Typus". Also, Frisvoll (1983, p. 53) expressed the opinion that "The genus *Racomitrium* Brid. is heterogeneous", "*Racomitrium canescens* coll. is a well defined, monophyletic group, and there is a strong evidence that the group should be treated as a separate entity" and "Probably the large genus *Racomitrium* Brid. ought to be divided into monophyletic genera as suggested for the correspondingly large and heterogeneous genera *Grimmia* Hedw. and *Mnium* Hedw. by Bremer (1981) and Koponen (1968) respectively. The *Racomitrium canescens* group would constitute a natural genus with no intermediate taxa between it and the other groups of *Racomitrium* s. l.". These ideas regarding the heterogeneous nature of the traditionally understood *Racomitrium* were only effected by Bednarek-Ochyra & Ochyra (in Ochyra et al. 2003) who elevated four subgenera of *Racomitrium* to genera. They appeared to be natural, homogeneous and well defined taxa which sharply differed from each other in a set of gametophyte and sporophyte characters.

Results

The sequencing statistics and mitogenome length for each of sequenced specimens are given in Table 1. Content and order of mitogenomes of *Bucklandiella*, *Codriophorus*, *Niphotrichum* and *Racomitrium* were the same as previously published for the *Codriophorus laevigatus* genome (Szczecińska et al. 2014). The example view of the mitochondrial genome of *Bucklandiella emersa* is shown in Fig. 1. The aligned complete genome dataset comprised 107,423 positions.

Both phylogeny reconstruction methods and both datasets produced trees with identical topology, differing only with support values for each clade (Fig. 2). Each of the distinguished genera form monophyletic clades very well supported by bootstrap (BS) and Bayesian posterior probabilities (PP). Mitochondrial phylogenomic trees resolved evolutionary relationships among all analysed genera. The genus *Bucklandiella* resolved as sister to the remaining genera of *Racomitrium* s. lato which form a well supported clade (90% BS, 100% PP and 85% BB, 96% PP for complete and coding-only datasets respectively).

The genera *Codriophorus*, *Niphotrichum* and the newly established *Frisvollia* joined in a well supported clade (96% BS, 100% PP and 91% BB, 98% PP for complete and coding-only datasets respectively). Within this clade, representatives of the genera *Niphotrichum* and *Frisvollia* formed two separate, well supported monophyletic clades (100% BS and 100% PP for both datasets).

Discussion

The complete mitochondrial genome sequences presented in this study confirmed the hypothesis about stability of bryophyte mitogenomes (Liu et al. 2011, 2014). Phylogenomic analysis based on complete mitochondrial genomes fully support splitting the traditionally conceived genus *Racomitrium* into five genera. Monophyly

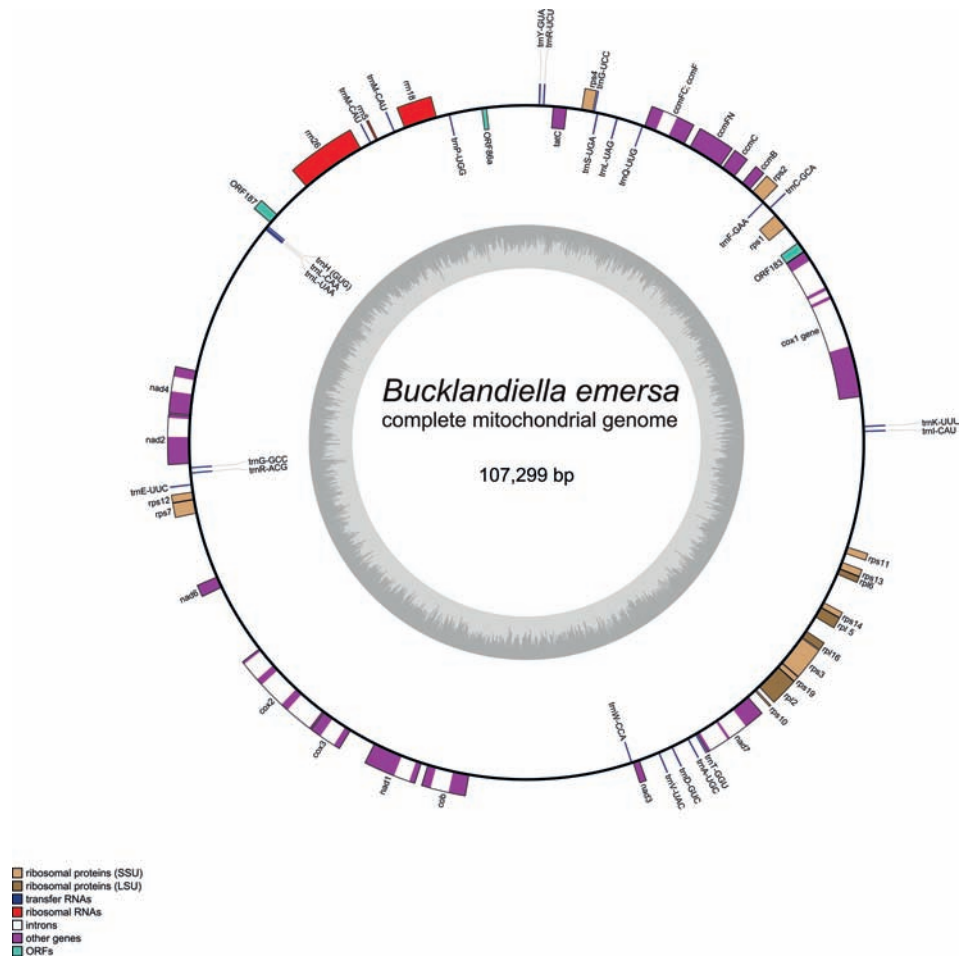


Fig. 1. Gene map of the mitochondrial genome of *Bucklandiella emersa*. Genes inside and outside the outer circle are transcribed in a counter-clockwise and clockwise direction, respectively. The genes are colour coded based on their function. The inner circle visualize G/C content.

of the studied genera was supported by both analysed datasets. Obtained results based on mitochondrial data are only partially congruent with earlier studies based on nuclear ITS and plastid sequences (Larraín et al. 2013; Bednarek-Ochyra et al. 2014). Combined plastid and ITS datasets confirmed monophyly of the genera *Racomitrium* and *Niphotrichum* (Larraín et al. 2013). Phylogenetic analysis of the complete mitochondrial genome confirmed also monophyly of the genus *Codriophorus* from which, however, is excluded *C. varius* which is positioned in the separate genus *Frisvollia*.

Earlier molecular analysis based on two plastid regions and the nuclear ITS region as well as morphological studies resolved *Frisvollia* as a sister to the genus *Niphotrichum*

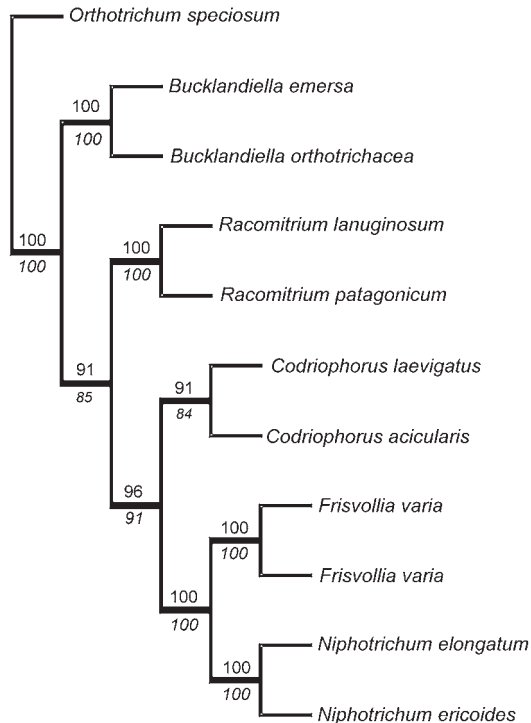


Fig. 2. The mitochondrial phylogenomic tree of the studied genera obtained with ML and BI methods. The bootstrap values are given above (whole dataset) and below (genes only) branches. The branches supported by BI analysis are thickened.

(Larraín et al. 2013). Based on plastid *rps4-trnL* and *trnK/matK-psbA* region analysis six studied species of *Codriophorus* formed two genetic groups, suggesting paraphyly of this genus. However paraphyly of *Codriophorus* (excluding *C. varius*) was not supported by the ITS dataset (Larraín et al. 2013; Bednarek-Ochyra et al. 2014).

To accept or reject the monophyly of the genus *Codriophorus* complete mitochondrial genomes of *Codriophorus laevigatus* and *C. acicularis* were sequenced and analysed. These two species are representatives of two separate sections: the type section *Codriophorus* and *C.* sect. *Fascicularia* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra represented by *C. acicularis* and *C. laevigatus*, respectively (Bednarek-Ochyra 2006). Splitting the genus *Codriophorus* into two sections, *Racomitrium* sect. *Stenotrichum* (Chevall.) Bednarek-Ochyra and *Fascicularia*, was also confirmed by molecular studies (Larraín et al. 2013). The phylogenetic trees obtained in the present study strongly support monophyly of the genus *Codriophorus*, despite the inclusion of two evolutionary distant species.

A monophyletic clade was also formed by two morphologically well-defined species from the genus *Bucklandiella*, *B. emersa* (Müll.Hal.) Bednarek-Ochyra & Ochyra and

B. orthotrichacea (Müll.Hal.) Bednarek-Ochyra & Ochyra. However, more morphological and molecular studies are needed to fully resolve the phylogeny and confirm the taxonomic status of this genus. Ongoing broad morphological and molecular studies on this genus should provide a better understanding of the taxonomy and evolution of *Bucklandiella* species.

Phylogenetic analysis based on the complete mitochondrial genomes also revealed some incongruence with plastid/nuclear data in the topology of the main clades. In previous studies based on plastid and nuclear genomic regions *Racomitrium* was resolved as the most ancestral to the remaining genera (Larraín et al. 2013; Bednarek-Ochyra et al. 2014), but mitochondrial phylogenetics reveal *Bucklandiella* as being closest to the ancestral state. The phylogenetic status of this genus is also implied by its gametophyte and sporophyte characters which form a clear link to the common ancestral grimmialean stock (Bednarek-Ochyra 1995). These features are primarily the entirely smooth laminal cells and relatively short peristome teeth which are variously divided into two broad segments or sometimes remain undivided or only perforated. This is in contrast to the variously papillose laminal cells and very long peristome teeth which are split nearly throughout into thread-like filiform prongs. These are evidently advanced character states and the genera *Racomitrium*, *Niphotrichum*, *Codriophorus* and *Frisvollia* are descendants which evolved from the ancestral state. The evolutionary relationships of the last four genera are congruent with previous studies based on plastid and nuclear genomic regions.

Observed incongruence between plastid and mitochondrial data could have several reasons, including size of the datasets (ca 3700 bp of plastid and 107000 bp of mitochondrial) and different rate of evolution of plastomes and mitogenomes (Drouin et al. 2008). The latter was observed in the genus *Pinus* L., where the substitution rate of the mitochondrial genome was four times slower than the plastid genome and eleven times slower than studied nuclear regions (Wang & Wang 2014). In the present and previous studies the genus *Codriophorus* is resolved as paraphyletic mainly due to the phylogenetic position of one species, *C. varius*, which is sister to the genus *Niphotrichum* and forms a common clade with the representatives of this genus. A set of morphological characters, as well as the large number of specific mutations in each of the analysed genomes justifies the placement of this species in the separate new genus *Frisvollia*.

A circumscription of the segregates of *Racomitrium*

Genera of the Grimmiaceae subf. Racomitrioideae which are all segregates of the broadly conceived genus *Racomitrium* are distinctive taxa through various combinations of unique or otherwise presumably advanced characteristics for the Grimmiaceae, including the presence of pellucid alar cells, variously papillose laminal cells, papillosity of the seta and calyptra, torsion of the seta, shape of the peristome teeth, anatomy of the costa, and shape and papillosity of the leaf hair-point. They are natural and well established taxa which are readily distinguished from one another on the basis of the following principal morphological traits.

***Bucklandiella* Roiv.**

Ann. Bot. Fenn. 9: 116. 1972 = *Bucklandia* Roiv., Arch. Soc. Zool. Bot. Fenn. "Vanamo" 9: 98. 1955, hom. illeg. [non *Bucklandia* Sternb. 1825; nec Brongn. 1828; nec R. Br. ex Griff. 1836]. TYPE: *Bucklandiella bartramii* (Roiv.) Roiv. (*Bucklandia bartramii* Roiv.).

Species of *Bucklandiella* are diagnosed by laminal cells which are either entirely smooth (Fig. 3C–D, 4D) or may eventually be pseudopapillose due to longitudinal cuticular ridges densely or thinly covering both dorsal and ventral surfaces of cells making the leaf surface rugged (Fig. 4A–B) and appearing papillose in leaf transverse section (Fig. 4C). The second diagnostic character of the genus is the relatively short, lanceolate or triangular peristome teeth which are irregularly divided in the upper half into 2–3 prongs (Fig. 3A) or occasionally they are only irregularly perforate along the median line or, in some cases, the teeth remain undivided (Fig. 3B). The leaves are lanceolate to ovate-triangular. The costa is unbranched and percurrent or very seldom excurrent, anatomically differentiated into a row of enlarged guide cells on the adaxial side and a 2–5-layered abaxial stereid or substereid band. The leaves usually terminate in a hyaline, smooth, denticulate or spinulose hair-point, or are epilose. The leaf margins are entire throughout or sometimes sinuate or lumpy near the apex, unistratose to variously polystratose and in the basal part they are often differentiated into a basal marginal border composed of various numbers of pellucid and straight-walled cells extending for a distance upwards along the margin. The laminal cells are uni- to 2–4-stratose in the upper half, very variable and range from short and nearly isodiametric in the distal part to rectangular or linear towards the base. The cells in the leaf basal angles are undifferentiated or enlarged, isodiametric to short-rectangular, often thick-walled and form distinct auricles. The seta is always smooth, twisted to the right when dry and the calyptra is always smooth.

Bucklandiella is the largest and taxonomically most diverse segregate of the broadly understood genus *Racomitrium*. It consists of about 50 species distributed worldwide, but only some of the Holarctic species have been revised taxonomically (Frisvoll 1988). Ongoing revisionary studies of the genus, especially in the Southern Hemisphere, constantly yield new species, so it is likely that the final number of the genus may approach 55 or so species.

***Racomitrium* Brid.**

Mant. Musc.: 78. 1818 = *Trichostomum* Bruch sect. *Racomitrium* (Brid.) Duby, Bot. Gall. Ed. 2, 2: 573. 1830 = *Grimmia* Hedw. sect. *Racomitrium* (Brid.) Müll.Hal., Syn. Musc. Frond. 1: 806. 1849 ['*Rhacomitrium*'] = *Racomitrium* Brid. 1. [unranked] *Lanuginosa* Kindb., Eur. N. Am. Bryin. 2: 235. 1898 = *Racomitrium* Brid. sect. *Lanuginosa* (Kindb.) Nog., J. Hattori Bot. Lab. 38: 346. 1974. ЛЕТОТІПЕ (vide Schimper 1860: cxxvi): *Racomitrium lanuginosum* (Hedw.) Brid. (*Trichostomum lanuginosum* Hedw.).

Racomitrium Brid. ex Lorentz, Bryol. Notizb.: 94. 1864, orthogr. pro *Racomitrium* Brid.

The narrowly defined *Racomitrium* is distinguished from all other congeners by a combination of several characteristics of which the sinistrorse and strongly papillose setae (Fig. 5C) do not occur in any other genus of the Grimmiaceae or in the acrocarpous mosses. Except for some depauperate plants, the leaves have always unusual hyaline hair-points that are papillose and distinctly eroso-dentate (Fig. 5D) and are longly

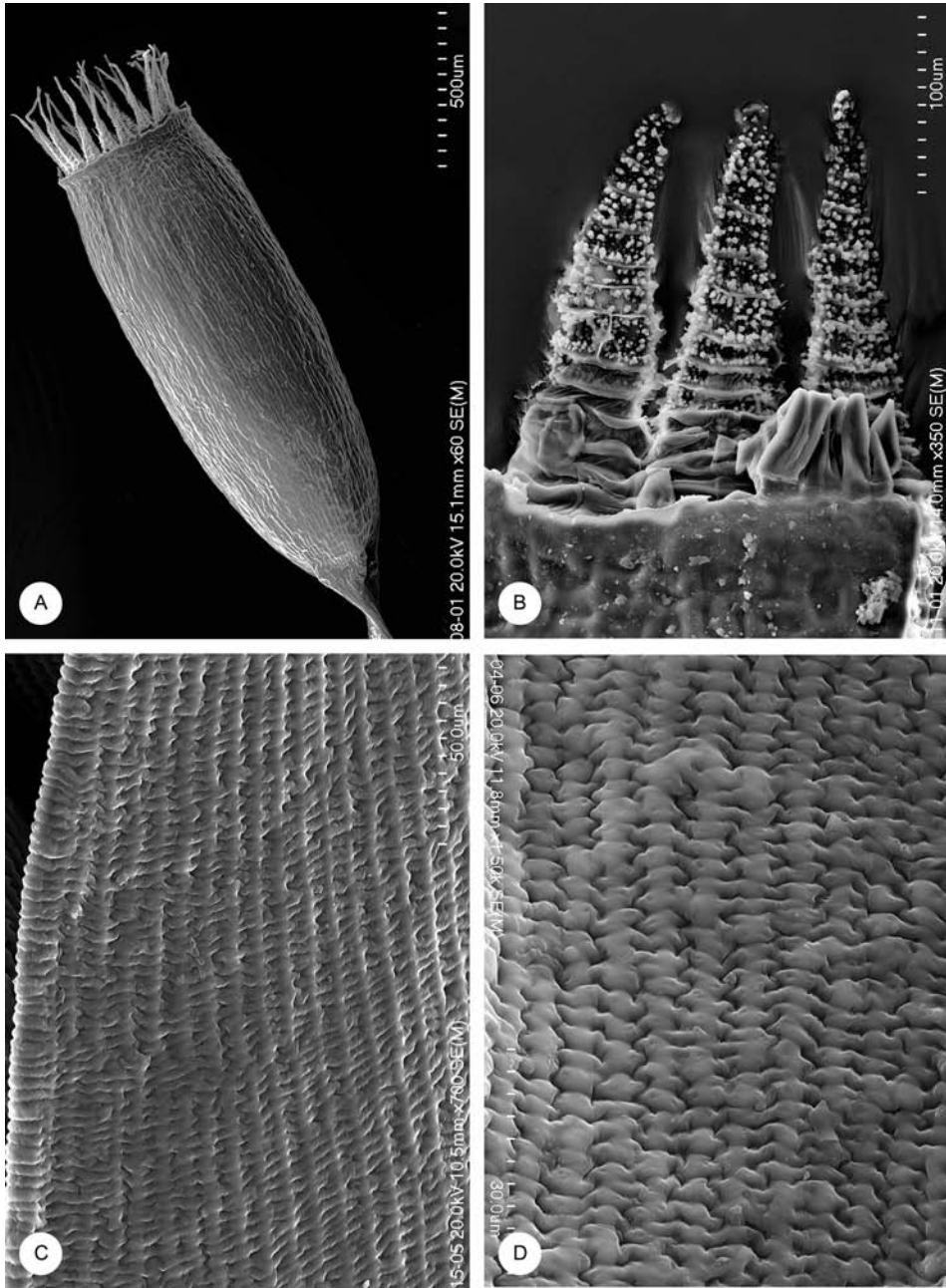


Fig. 3. *Bucklandiella didyma*: capsule (A); *B. orthotrichacea*: peristome teeth (B) and *B. pycnotricha*: upper laminal cells (C) and mid-leaf cells (D). (A from Matcham & Duckett s.n., 12 Sep 2006; B from Ochyra 825/06; C from Seppelt 19300; D from Shevock 31007, isotype; all in KRAM).

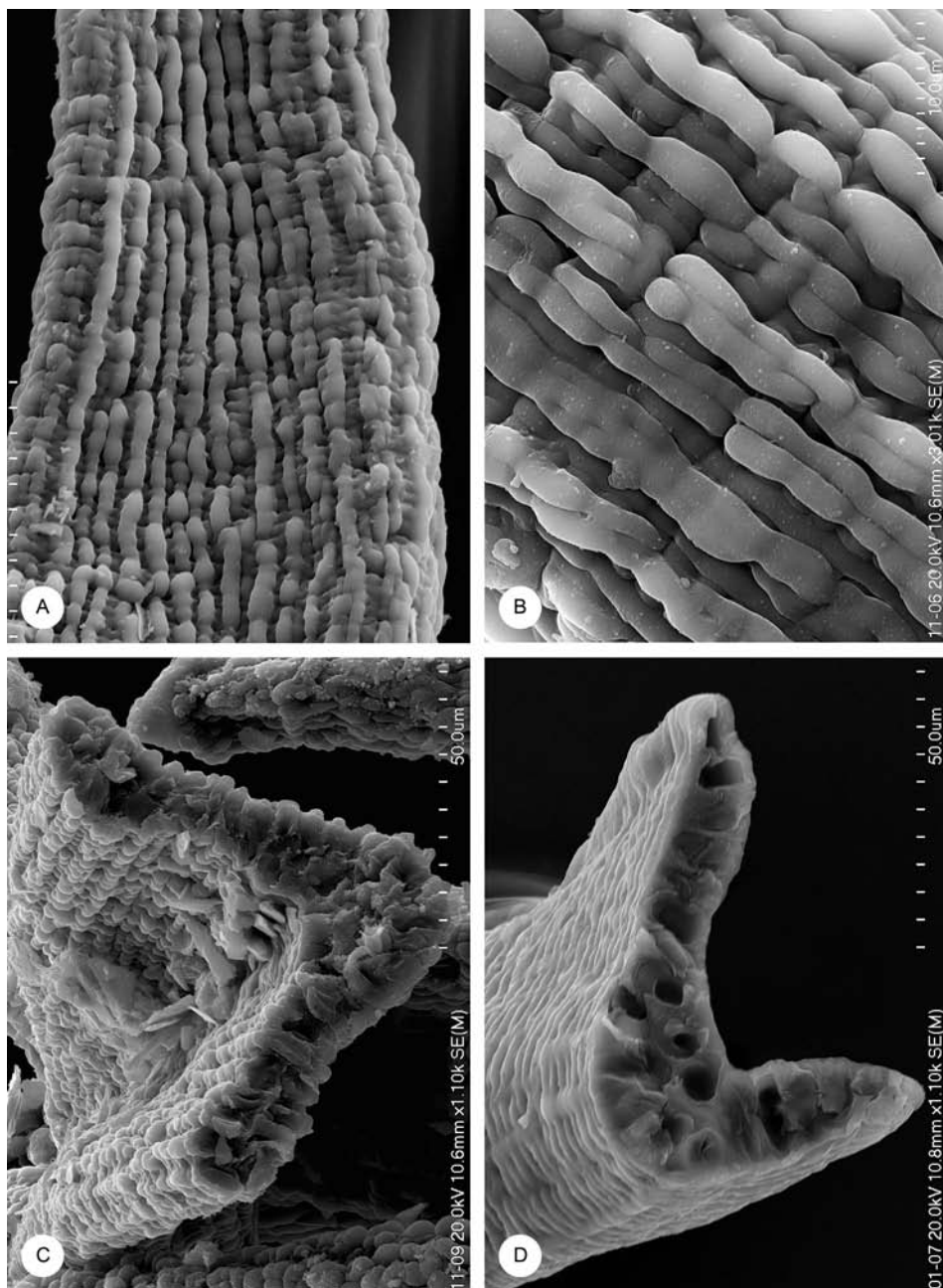


Fig. 4. *Bucklandiella orthotrichacea*: upper cells showing longitudinal cuticular ridges in (A–B) and leaf cross-section (C) and *B. crumiana*: leaf cross-section (D). (A–C from Ochyra 825/06; D from Bednarek-Ochyra & Ochyra 1333/13; all in KRAM).

decurrent down the leaf margins. The laminal cells are unistratose throughout and are regularly covered with large flat cuticular thickenings with small secondary papillulae situated over the longitudinal cell walls and almost the whole lumina, except for a narrow gap in the middle. This gives the leaf surfaces a regularly ridged appearance. The capsules are straight, ovoid to ovoid-cylindrical, somewhat ventricose in the base (Fig. 5A) and the peristome teeth are very long and divided to the base into 2(–3) filiform segments (Fig. 5B).

Racomitrium consists of only three species, namely *R. lanuginosum* with two subspecies, of which only the type subspecies has a wide bipolar distribution, with many intermediate stations in the tropical mountains, as well as *R. pruinosum* (Wilson) Müll.Hal. and *R. patagonicum* which are Southern Hemisphere species occurring in Australasia and southern South America (Vitt & Marsh 1988; Bednarek-Ochyra & Ochyra 2003).

***Codriophorus* P.Beauv.**

Mém. Soc. Linn. Paris 1: 445. 1822 = *Racomitrium* Brid. 3. [unranked] *Papillosa* Kindb., Eur. N. Am. Bryin. 2: 236. 1898 = *Racomitrium* sect. *Papillosa* (Kindb.) Nog., J. Hattori Bot. Lab. 38: 349. 1974 = *Racomitrium* subsect. *Papillosa* (Kindb.) Bednarek-Ochyra, Fragm. Florist. Geobot. Ser. Polon. 2: 144. 1995. LECTOTYPE (vide Bednarek-Ochyra et al. 2001: p. 109): *Codriophorus acicularis* (Hedw.) P.Beauv. (*Dicranum aciculare* Hedw.).

Codonophorus P.Beauv. ex Desv., Mém. Soc. Linn. Paris 3: 219. 1824, nom. illeg. incl. gen. prior. [*Codriophorus* P.Beauv., 1822].

Racomitrium Brid. subg. *Cataractarum* Vilh., Věstn. Král. České Společn. Nauk Tř. Mat.-Přir. 1925(5): 31. 1926 ['Cataractae']. LECTOTYPE (vide Bednarek-Ochyra 1995: p. 127): *Racomitrium protensum* (Duby) Bruch & Schimp. (*Trichostomum protensum* Duby) [= *Codriophorus aquaticum* (Schrad.) Bednarek-Ochyra & Ochyra (*Trichostomum aquaticum* Schrad.)].

Together with *Racomitrium* s. str. and the newly recognised genus *Frisvollia*, *Codriophorus* constitutes a distinct group of the genera characterised by a peculiar and unique ornamentation of the laminal cells. They are distinctly papillose, with large flat papillae distributed on both abaxial and adaxial laminal surfaces, both on the longitudinal walls and most of the lumina, leaving only a narrow gap in the middle (Fig. 6A–B). The main papillae are covered by secondary papillulae on their surface (Fig. 6C). This disposition of the papillae gives a peculiar appearance to the transverse leaf sections. It consists of a regular pattern of distinct hollows over lumen centres separated by the large, elevated and equally thickened flat cuticular elevations over the walls and sides of the lumina. Despite the great similarity of the papillosity pattern of the laminal cells, *Codriophorus* differs from *Racomitrium* s. str. in its densely papillose calyptra in the apical portion, epilose innermost perichaetial leaves and entirely smooth, dextrorse seta (with the exception of *C. fascicularis* in which the seta is only once twisted to the right immediately below the capsule and further down is twisted to the left). The peristome teeth are very variable in length, from 300 to 800 µm, and only exceptionally in *C. laevigatus* they are 1.0–1.6 mm long. They are deeply split nearly to the base into two segments and densely covered with spiculate or peg-like papillae (Fig. 6D).

Codriophorus exhibits a broad range of variation of leaf shape, from lanceolate or ovate-lanceolate to lingulate, elliptical, broadly ovate or broadly ovate-lanceolate.

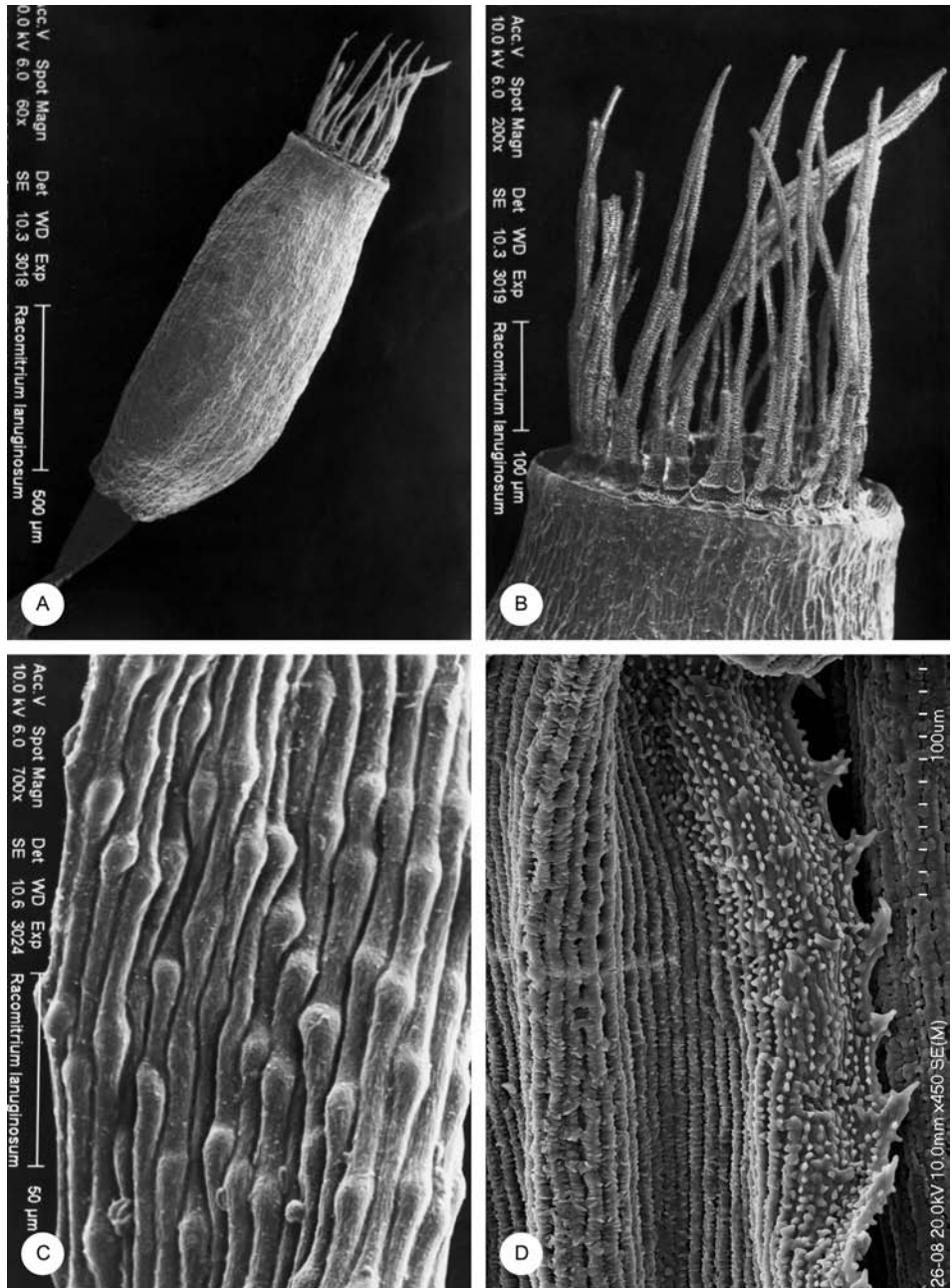


Fig. 5. *Racomitrium lanuginosum*: capsule (A), peristome teeth (B) and portion of seta (C) and *R. pruinosum*: portion of the decurrent part of the hair-point and adjacent laminal cells (D). (A–C from Hintze 1176; D from Streimann 51064; all in KRAM).

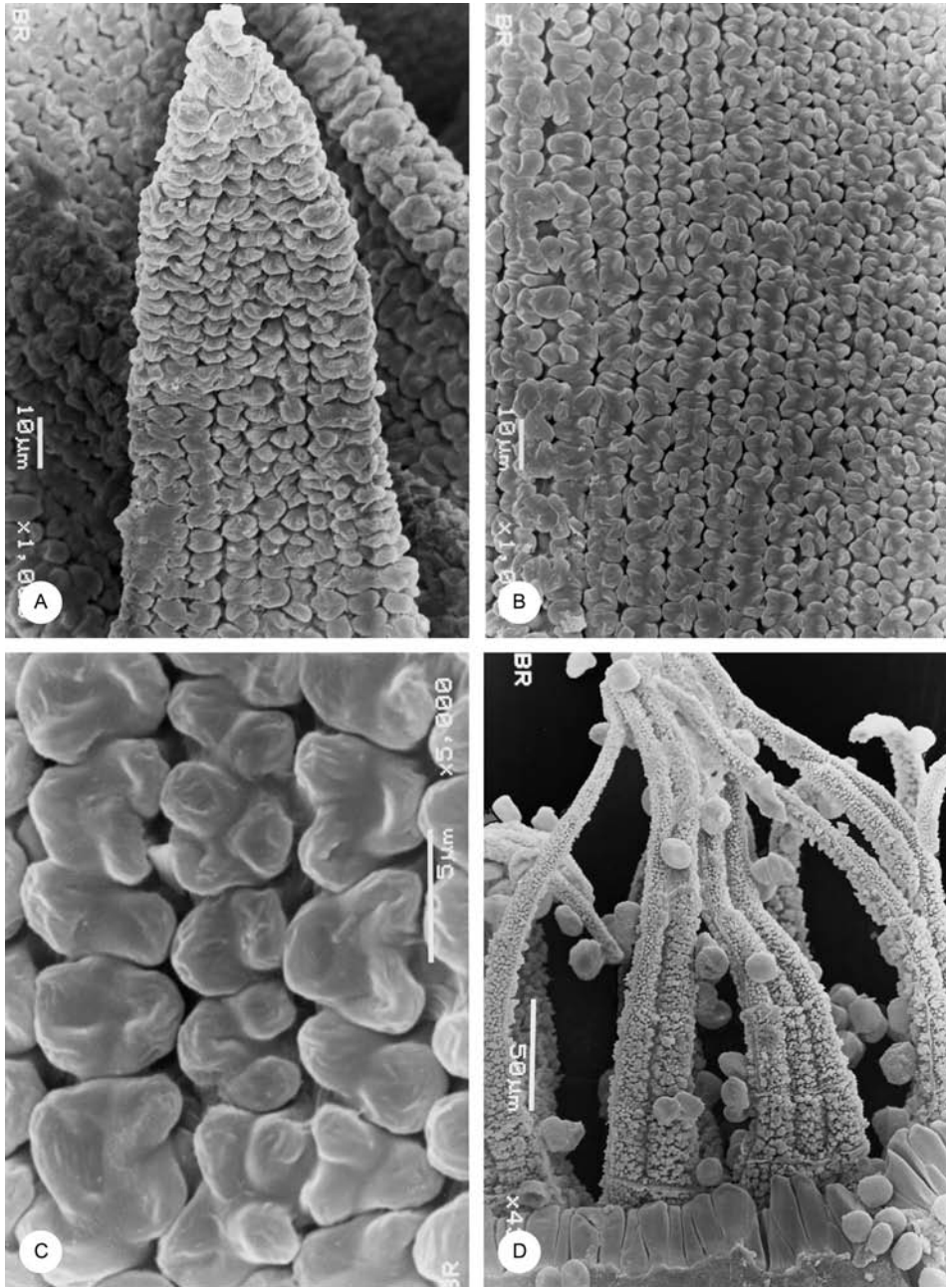


Fig. 6. *Codriophorus fascicularis*: leaf apex (A) and *C. acicularis*: mid-leaf cells (B), upper cells (C) and peristome (D). (A from Lisowski 59922; B–C from Sergio et al. 8296, paratype of *Racomitrium hespericum*; D from Allen 27; all in KRAM).

Leaves are generally acute or rounded-obtuse to broadly rounded at the apex, entire throughout or variously toothed at the apex. With two exceptions, the leaves are always epilose. Only in *C. carinatus* (Cardot) Bednarek-Ochyra & Ochyra they are minutely hyaline tipped, to 0.1 mm, and in *C. laevigatus* the leaves are terminated with a short, 0.1–0.3 mm, non-decurrent, hyaline or yellowish-hyaline, subentire to weakly denticulate awn. The costa is single and variable in its length and anatomy. It vanishes in mid-leaf or is subpercurrent and ceases a few cells below the apex and often it is forked or spurred in the distal portion. It is either bistratose throughout, not or weakly convex on the abaxial side and not or slightly differentiated into guide and stereid cells or 3–4-layered and distinctly convex abaxially, with a prominent abaxial stereid band and an adaxial row of enlarged guide cells.

Codriophorus is the earliest recognised (Bednarek-Ochyra et al. 2001) and, besides *Niphotrichum*, the best known taxonomically segregate of *Racomitrium*. The genus has been monographed by Bednarek-Ochyra (2006), who included 15 species in it. They are primarily distributed in the Holarctic, except for *C. laevigatus* from southern South America, Tristan da Cunha and Gough Island, and *C. dichelymoides* (Herzog) Bednarek-Ochyra & Ochyra of the northern Andes of Colombia.

***Frisvollia* Sawicki, Szczecińska, Bednarek-Ochyra & Ochyra, gen. nov.** Figs 7–8

Racomitrium Brid. sect. *Pilifera* Bednarek-Ochyra, *Fragm. Flor. Geobot. Ser. Polon.* 2: 64. 1995 = *Codriophorus* P.Beauv. subsect. *Piliferi* (Bednarek-Ochyra) Bednarek-Ochyra. TYPE: *Frisvollia varia* (Mitt.) Sawicki, Szczecińska, Bednarek-Ochyra & Ochyra, comb. nov. (Basionym: *Grimmia varia* Mitt., *J. Linn. Soc. Bot.* 8: 21. 1864).

Plants large and robust, coarse, stiff and rigid, caespitose, yellow, yellow-green or dirty green. Stems erect, ascending or procumbent, sparingly dichotomously or fasciculately branched, sometimes pinnate-branched because of numerous short, lateral, horizontal branches, or nodose owing to lateral tuft-like branchlets. Leaves crowded, closely imbricate to loosely appressed, often falcato-secund, broadly keeled to narrowly canaliculate-concave distally, ovate-lanceolate to lanceolate, from an ovate, plicate base slenderly or broadly acuminate, terminated by a hyaline, straight or flexuose, finely and irregularly spinulose-denticulate hair-point, or occasionally muticous; margins entire and unistratose throughout, recurved to revolute from the base almost to the apex; costa single, unbranched, percurrent or subpercurrent, lying at the bottom of a deep, fairly narrow-angled and partly enclosed furrow, in cross-section distinctly convex on the abaxial side, flat adaxially, bistratose, reniform to elliptical, with 3(–4) adaxial cells not differentiated from the abaxial ones in the distal portion, 3–4-stratose, rectangular to lunate and strongly flattened in the proximal part, with 4–7 adaxial cells approximately of the same size and shape as those in the central row and small stereid cells in 1 or sometimes 2 dorsal rows; laminal cells unistratose throughout, pellucid, with thickened and strongly sinuose longitudinal walls, short-rectangular to quadrate at the extreme tip, becoming elongate in mid-leaf and long rectangular towards the base; basal cells rectangular, with strongly incrassate, nodulose and porose walls; alar cells short-rectangular, broader, forming a yellow-brown or yellow, pellucid, flat, somewhat decurrent group; supra-alar cells rectangular, with moderately thickened and straight or somewhat sinuose walls, forming a pellucid hyaline marginal border

of 15–19 cells, often with the second, shorter row consisting of up to 9 similar cells. Dioicous. Inner perichaetial leaves convolute, longitudinally plicate, oblong-lanceolate, broadly acute to rounded-obtuse and apiculate, bluntly serrate due to projecting cell ends at the apex, hyaline throughout, with a thin-walled areolation and a faint costa ending far below the apex. Setae single in the perichaetium, rarely geminate, straight, erect, smooth, glossy, twisted clockwise. Capsules exserted, erect, straight, cylindrical, (2.5–)3.0–4.2 mm long, 0.8–1.0 mm wide, smooth or somewhat sulcate when old and empty, lustrous, pachydermous; operculum subulate, with a straight rostrum; annulus deciduous, consisting of 2–3 rows of large, vesiculose cells; exothecial cells mostly elongate, oblong to longly rectangular, arranged in regular longitudinal rows, becoming rounded, quadrate to shortly rectangular, intensely dark or orange-brown in 4–7 tiers at the orifice, and short-rectangular to rounded with strongly incrassate walls at the base of the urn; stomata many at the urn base, 18–20 per capsule, arranged in 2–3 rows, bicellular, superficial, with rounded pori; peristome teeth 16, dark reddish-brown, 1.0–1.8 mm long, fragile and often broken, faintly papillose to nearly smooth, regularly split nearly to the base into 2, thread-like, terete, equal or unequal branches, nodose on account of distinct articulations, with a short basal membrane, and a low, hyaline preperistome. Spores spherical, pale brown, 12–15 µm in diameter, faintly papillose. Calyptra long, conic-mitrate, brown, darker and verrucose at the apex, naked, 4–5-lobed at the base.

ETYMOLOGY: The new genus honours Dr Arne A. Frisvoll, Trondheim, Norway, in recognition of his great contribution to the taxonomy of *Racomitrium* s. lato. In his studies he paid special attention to some characters which proved to be of the paramount importance in taxonomy of this genus and which were generally neglected or ignored by former students and thus directed the taxonomy of this genus into new pathways. He also accepted the polyphyletic nature of *Racomitrium* and suggested the necessity of its division into some smaller, natural genera.

Frisvollia is a monotypic genus that consists of only *F. varia*, a western North American endemic. It is characterised by the following set of characters: (1) hyaline, flat, denticulate leaf hair-point; (2) plicate leaf base; (3) rectangular to lunate and strongly flattened costa on the adaxial side, bistratose in the upper half, 3–4-layered in the lower half with 1–2 layers of abaxial stereids; (4) shortly to long rectangular laminal cells; (5) convolute, plicate and entirely hyaline innermost perichaetial bracts, subacute to rounded-obtuse and bluntly serrate at the apex; (6) long cylindrical capsule with a long rostrate operculum; (7) peristome teeth very long, 1.0–1.8 mm, deeply split nearly to the base into two thread-like branches. The single species of this genus is thoroughly described and illustrated in the monograph of *Codriophorus* (Bednarek-Ochyra 2006).

Frisvollia varia shares some characters with *Codriophorus laevigatus* including the presence of a leaf hair-point, plicate leaf bases, leaf areolation, convolute and plicate innermost perichaetial leaves and very long peristome teeth. However, they differ in the shape of the hair-point, anatomy of the costa, areolation of the innermost perichaetial leaves and shape of the capsules. The distinctness of *Frisvollia* is strongly supported by the complete mitochondrial genome as well as phylogeny based on nuclear ITS and plastid *rps4-trnL* and *trnK/matK-psbA* sequences (Larraín et al. 2013).

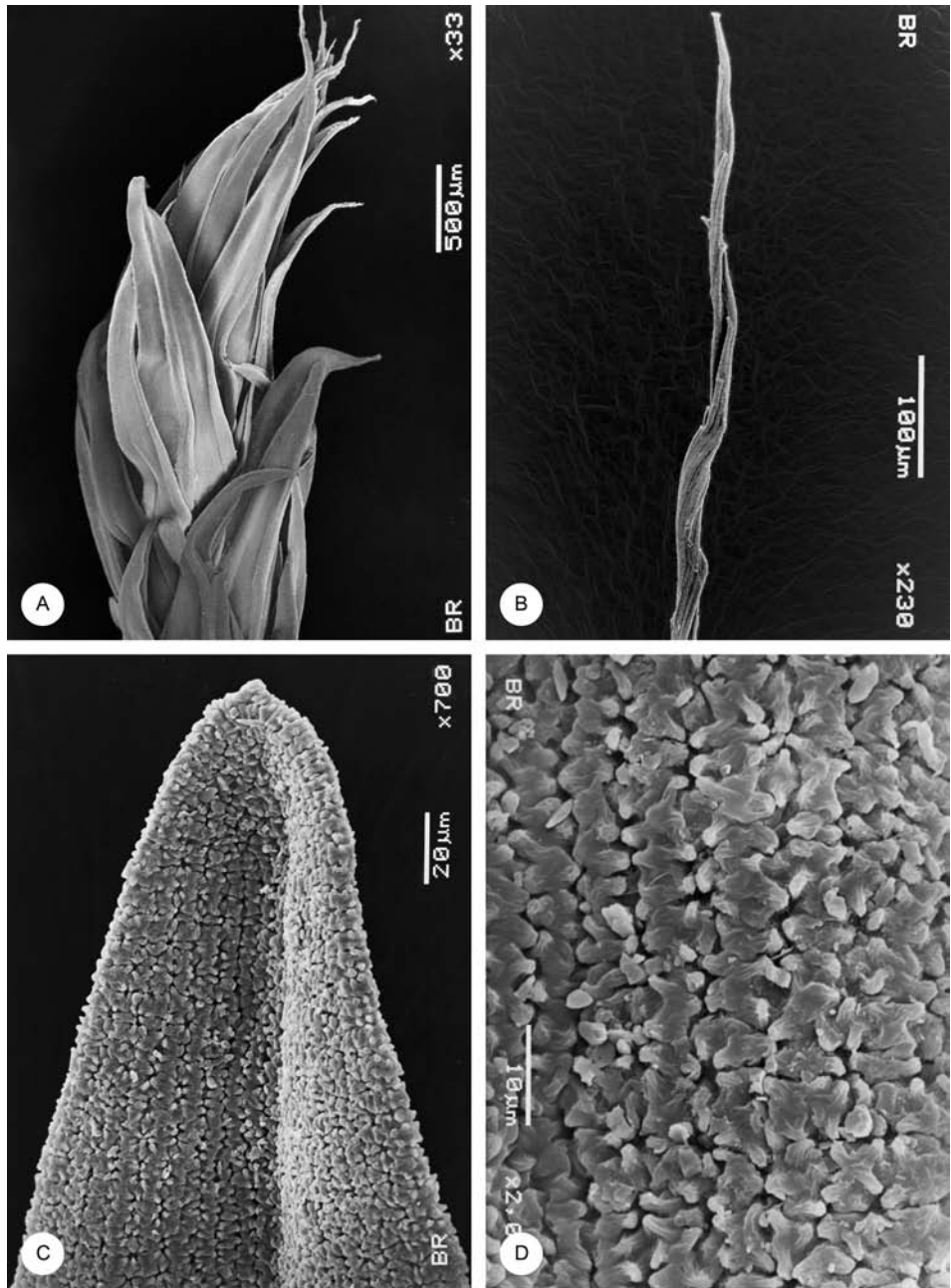


Fig. 7. *Frisvollia varia*: tip of the shoot showing piliferous leaves (A), hair-point (B), mucous leaf apex (C) and upper laminal cells (D). (A from Schofield 22633; B from Henderson 17040; C–D from Lyford 200; all in KRAM).

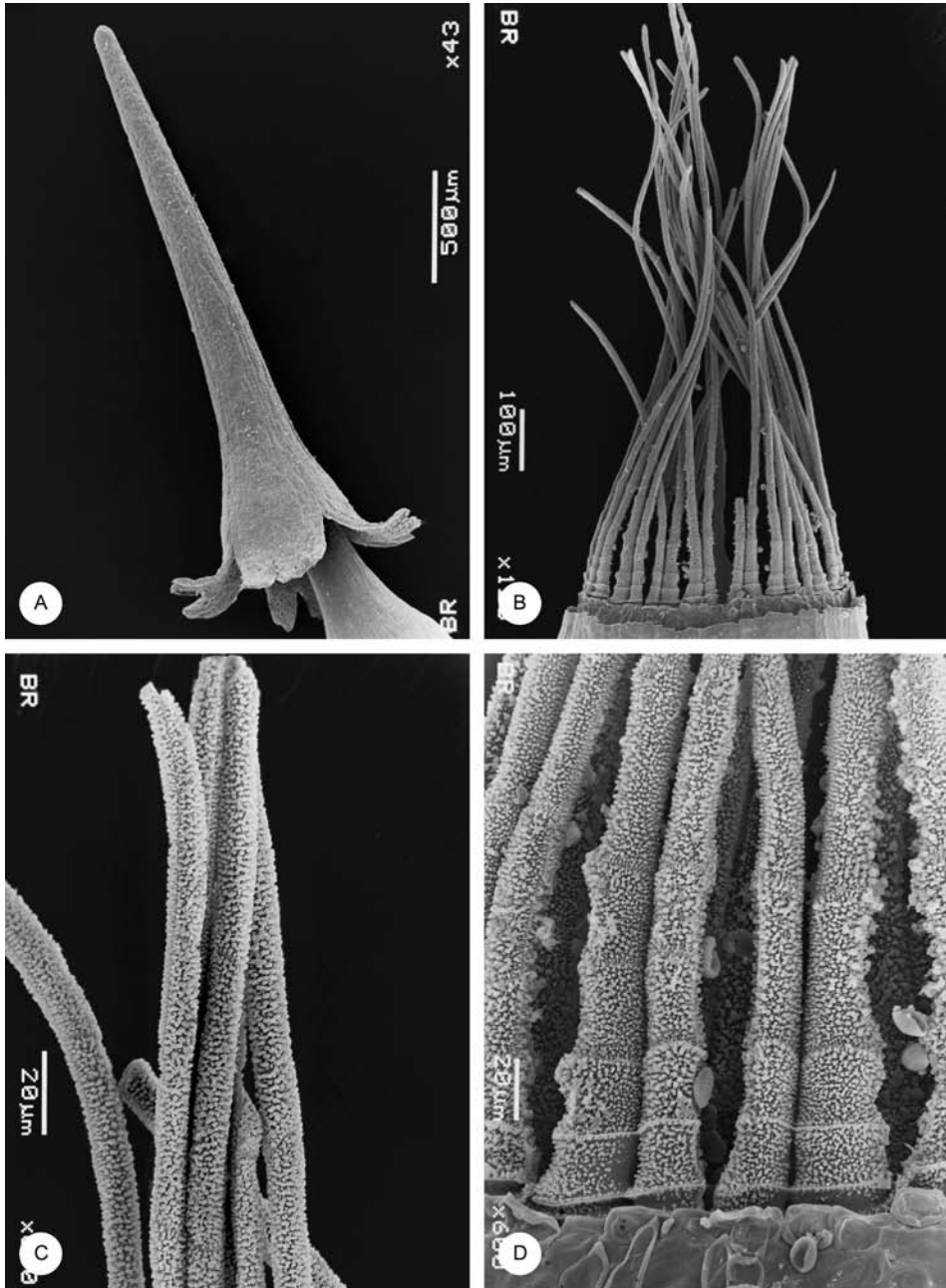


Fig. 8. *Frisvollia varia*: calyptra (A), peristome teeth (B), upper part of the peristome teeth (C) and basal part of the peristome teeth (D). (A from Lyford 200; B-D from Schofield 22633; all in KRAM).

Niphotrichum Bednarek-Ochyra & Ochyra

Cens. Cat. Polish Mosses: 137. 2003 = *Racomitrium* Brid. 2 [unranked] *Canescentia* Kindb., Eur. N. Am. Bryin. 2: 235. 1898 = *Racomitrium* subg. *Canescentia* (Kindb.) Vilh., Věstn. Král. České Společn. Nauk Tř. Mat.-Přír. 1925(5): 15. 1926 ['Canescentes'] = *Racomitrium* subsect. *Canescentia* (Kindb.) Frisvoll, Gunneria 41: 106. 1983 ['Canescens'] = *Racomitrium* sect. *Canescentia* (Kindb.) Bednarek-Ochyra, Fragm. Flor. Geobot. Ser. Polon. 2: 71. 1995 = *Racomitrium* subg. *Niphotrichum* Bednarek-Ochyra, Fragm. Florist. Geobot. Ser. Polon. 2: 70. 1995, nom. illeg. incl. subg. prior. TYPE: *Racomitrium canescens* (Hedw.) Brid. (*Trichostomum canescens* Hedw.).

Niphotrichum is the most distinctive and sharply delimited segregate of *Racomitrium*. It is well characterised by the following combination of morphological traits. The laminal cells are strongly papillose with tall conical papillae situated over the lumina (Fig. 9D), the peristome teeth are very long, regularly divided to the base into 2–3 thread-like branches (Fig. 9B) and the angular cells are hyaline or yellowish-hyaline, thin-walled and form prominent, convex and often decurrent auricles. Additionally, the leaves are triangular, elliptic or broadly ovate-lanceolate and they are terminated with massive, hyaline, papillose and denticulate hair-points (Fig. 9C). The costae are spurred or branched at the tip, ceasing at mid-leaf or well below the leaf apex, bi- or imperfectly tristratose and consist of an adaxial row of enlarged guide cells and an abaxial layer of smaller substereid cells. The innermost perichaetial leaves are hyaline, sheathing and pilose. The setae are smooth and sinistrorse on drying (Fig. 9A). The operculum is longly beaked, with a rostrum as long as the urn or longer and the capsules are plicate when dry (Fig. 9A). *Niphotrichum* is a small genus of eight species which belong within two sections and three subsections.

In the traditionally understood *Racomitrium* species of *Niphotrichum* constituted a distinct group centred around *R. canescens* (Hedw.) Brid. It was taxonomically revised by Frisvoll (1983) who recognised eight species, having mainly Holarctic distribution. In the Southern Hemisphere only *N. japonicum* (Dozy & Molke.) Bednarek-Ochyra & Ochyra reaches to Lord Howe Island (Vitt et al. 1993) and *N. elongatum* to New Zealand, where it is apparently introduced in the South Island (Malcolm & Shevock 2012). The record of *N. canescens* from Chile in South America (He 1998, as *Racomitrium canescens*) is dubious and the voucher specimen, which correctly represents *N. elongatum*, was apparently mislabelled (Bednarek-Ochyra et al. 2011).

All the genera of the Racomitrioideae can be distinguished in the following key:

- 1 Laminal cells smooth or pseudopapillose due to longitudinal cuticular ridges; peristome teeth short, irregularly divided to the middle, rarely lower, into 2–3 prongs*Bucklandiella*
- 1' Laminal cells papillose; papillae tall and conical, situated over the lumina or large and flat, placed over the longitudinal walls and covering a major part of the lumina except for a narrow central slit; peristome teeth long, split at least to the middle into 2(–3) filiform, somewhat paired, regular segments 2
- 2 Laminal cells with tall, conical papillae placed over the lumina; alar cells hyaline or yellowish-hyaline, thin-walled forming prominent, decurrent auricles*Niphotrichum*
- 2' Laminal cells with large, flat papillae placed over the longitudinal walls; alar cells absent, indistinct or prominent, brown to yellowish-orange, never hyaline, thick-walled, forming auricles ...3

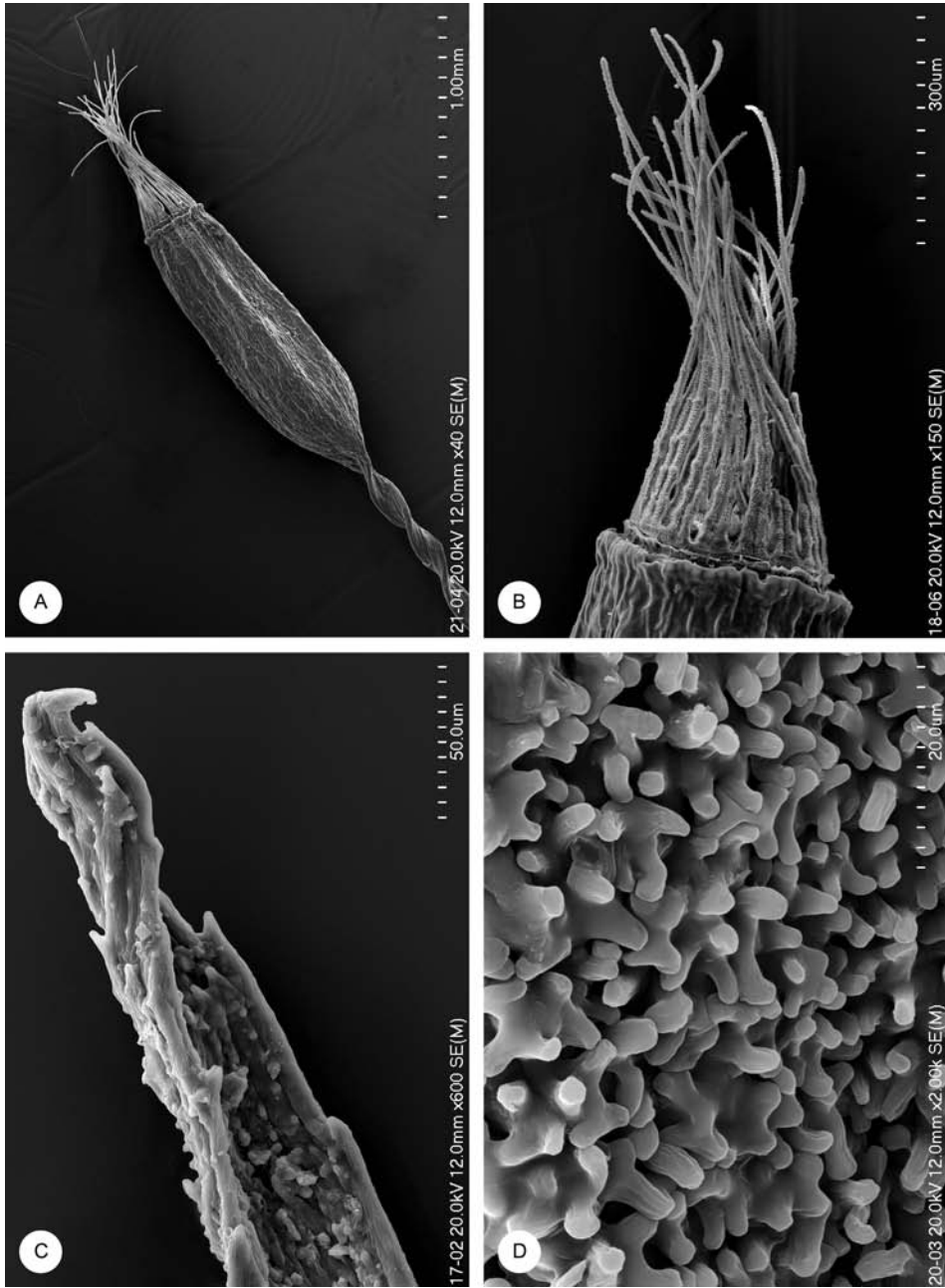


Fig. 9. *Niphotrichum barbuloides*: capsule with the peristome (A); *N. muticum*: peristome teeth (B); *N. japonicum*: tip of the hair-point (C); and *N. elongatum*: mid-leaf cells (D). (A from Smith J-277; B from Ireland 6097; C from Koponen 11604; D from Gos s.n., Jun 1990; all in KRAM).

- 3 Leaf hair-point eroso-dentate, mostly strongly papillose, long decurrent down the leaf margins; seta strongly papillose, sinistrorse when dry; capsule slightly ventricose at base; calyptra smooth or minutely roughened..... *Racomitrium*
- 3' Leaf hair-point absent or, if present, smooth to denticulate, never papillose and decurrent down the leaf margins; seta smooth, dextrorse when dry (in *C. fascicularis* only once twisted to the right immediately below the capsule and below twisted to the left); calyptra distinctly verrucose to papillose..... 4
- 4 Capsules ovoid to obloid-cylindrical, 1.2–3.0 mm; peristome teeth to 900 µm, if 1000–1600 µm then costa bistratose throughout, ceasing in three fourth the leaf length and the innermost perichaetial leaves thick-walled at the apex; leaves epilose or very seldom with a short, 0.1–0.3 mm, weakly denticulate, hyaline or yellowish-hyaline hair-point..... *Codriophorus*
- 4' Capsules long cylindrical, (2.5–)3.0–4.2 mm; peristome teeth 1000–1800 µm; leaf hair-point almost always present, at least on the upper leaves, (0.1–)0.4–0.7(–1.2) mm, very seldom absent, hyaline, sharply denticulate to spiculose-dentate..... *Frisvollia*

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