

Lumping or splitting? The case of *Racomitrium* (Bryophytina: Grimmiaceae)

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Abstract The genus *Racomitrium* (Grimmiaceae: Racomitrioideae) was recently segregated into four genera—*Racomitrium*, *Niphotrichum*, *Codriophorus*, and *Bucklandiella*—following an infrageneric division originally proposed more than 100 years ago based on morphological traits such as the presence and shape of laminal cell papillae and hyaline leaf hairpoints, and differences in peristome teeth morphology and costa structure. Here we present a molecular phylogeny of *Racomitrium* s.l. based on nuclear ITS and plastid *rps4-trnL* and *trnK/matK-psbA* sequences, to test the monophyly of these four morphological entities. Our results solely support the monophyly of *Racomitrium* s.str., which includes only *R. geronticum*, *R. lanuginosum*, and *R. pruinosum*, while the members of the other segregate genera are distributed in different clades, rendering them polyphyletic (*Bucklandiella*, *Codriophorus*) or paraphyletic (*Niphotrichum*). Ancestral state reconstruction shows high levels of homoplasy in the characters usually used for the infrageneric division of *Racomitrium* s.l. (i.e., leaf papillae shape, perichaetial leaves morphology). Based on this evidence, we propose a return to a broader concept of *Racomitrium*, and adopt a revised sectional classification. Therefore, we propose new combinations for some recently described species of *Bucklandiella* and *Codriophorus*.

Keywords *Bucklandiella*; *Codriophorus*; Grimmiaceae; *Niphotrichum*; *Racomitrium*

Supplementary Material The Electronic Supplement (Tables S1–S2; Figs. S1–S30; Appendices S1–S2) is available in the Supplementary Data section of the online version of this article (<http://www.ingentaconnect.com/content/iapt/tax>).

Received: 23 Mar. 2013; revision received: 12 Nov. 2013; accepted: 12 Nov. 2013. DOI: <http://dx.doi.org/10.12705/626.45>

■ INTRODUCTION

Racomitrium Brid. s.l. (Grimmiaceae) comprises approximately 80 species distributed throughout the temperate and cold regions of the world (Ochyra & al., 2003). *Racomitrium* is one of the most distinctive genera of mosses, immediately identifiable under the light microscope by the rectangular basal and median laminal cells, which have strongly sinuose or nodulose walls. Outside *Racomitrium*, this trait is only present in some species of *Dryptodon* Brid., which is considered to be its sister group (Hedderson & al., 2004; Hernández-Maqueda & al., 2008a, b), and more obscurely in some species of the also closely related *Schistidium* Brid. (Ochyra & Afonina, 1986). *Racomitrium* is furthermore characterized by a cladocarpous habit, absence of a central strand in the stem, haplolepidous arthrodontous peristome of seligerioid type (16 teeth divided into two or three prongs or rarely entire, basal membrane and preperistome present), mitrate and basally lobed calyptra, and sinuose walls of the epidermal cells of the vaginula.

Despite the seemingly clear circumscription of *Racomitrium*, its taxonomic history is complex, especially with regard to the separation of *Racomitrium* and *Dryptodon*. Furthermore, the large number of species and high morphological diversity have encouraged taxonomists to define smaller taxonomic entities that would be easier to work with. These attempts have ranged from distinction of sections within *Racomitrium* to splitting the genus into separate genera, leading to renaming of long-recognized species.

Racomitrium was described by Bridel (1818) to accommodate some of the *Trichostomum* species of Hedwig (1801) characterized by deeply divided peristome teeth, shortly mitrate, basally lobed calyptrae, and annulate capsules. Later, the genus concept was refined by various authors, some of them proposing novel subgeneric classifications (Bridel, 1826; Huebener, 1833; Bruch & Schimper, 1845; Müller, 1849; Schimper, 1860).

The work of Kindberg (1898) represented a marked break in *Racomitrium* taxonomy and formed the basis for a still ongoing discussion. Kindberg ignored all previous divisions of the

genus *Racomitrium* and created four unranked species groups (*Lanuginosa*, *Canescentia*, *Papillosa*, *Laevifolia*), which were formalized as sections by Noguchi (1974). This concept was subsequently followed by Frisvoll (1983, 1988) and Bednarek-Ochyra (1995). The latter author, however, elevated the four taxa to subgeneric rank, as subg. *Racomitrium* (= *Lanuginosa*), subg. *Niphotrichum* Bednarek-Ochyra, nom. illeg. (= *Canescentia*), subg. *Cataracta* Vilh. (= *Papillosa*), and subg. *Ellipticodryptodon* (Vilh.) Bednarek-Ochyra & Ochyra (= *Laevifolia*). Finally, Ochyra & al. (2003) treated the four subgenera as separate genera within a newly erected subfamily Racomitrioideae of the Grimmiaceae. The generic names *Racomitrium* and *Niphotrichum* Bednarek-Ochyra & Ochyra were maintained, and for the other two taxa the already available generic names *Codriophorus* P. Beauv. (= *Cataracta*, *Papillosa*) and *Bucklandiella* Roiv. (= *Ellipticodryptodon*, *Laevifolia*) were used. A considerable number of sections and subsections were erected within the four (sub-)genera of *Racomitrium* s.l. by Bednarek-Ochyra (1995), Bednarek-Ochyra & Ochyra (1994, 1996), Frisvoll (1983), and Ochyra & al. (1988, 2003), and numerous new combinations of species names were made.

The four segregate taxa of *Racomitrium* s.l. are separated by morphological traits of papillae on the laminal cells, hyaline leaf hairpoints, alar cells, costa structure, and peristome teeth morphology. According to Ochyra & al. (2003), *Racomitrium* s.str. is characterized by a papillose seta and the presence of a long-decurrent hyaline hairpoint, which is eroded to sharply dentate and papillose, contrasting with the rest of the lamina cells which are bulging due to the presence of large, flat papillae. *Niphotrichum* stands out by the presence of high, conical papillae throughout the leaf surface, the inflated, yellowish-hyaline and thin-walled alar cells, as well as peristome teeth as long as the urn, usually more than 1 mm long. *Codriophorus* is characterized by the presence of flat papillae on the leaf surface, a distally verrucose to papillose calyptra, and a costa that generally ends well before the leaf apex. Finally, *Bucklandiella* has a smooth laminal surface (although sometimes with longitudinal cuticular thickenings or pseudopapillae) and generally short peristome teeth (<500 µm) that are divided to the middle (rarely deeper), or sometimes are entire. Although these characters seem to be useful for delimiting the four taxa at the generic level, circumscriptions are obscured because not all species show the traits considered diagnostic for the genera in which they are placed.

Due to these problems the generic division of *Racomitrium* s.l. has generally not been accepted by authors dealing with the Grimmiaceae, or at least has been questioned (e.g., Allen, 2005; Wagner, 2008). However, the publication of a monograph of *Codriophorus* (Bednarek-Ochyra, 2006) and the adoption of the new generic classification in the Bryophyte Flora of North America (Ochyra & Bednarek-Ochyra, 2007) has helped to increase its acceptance among bryologists. One of the most recent classifications of bryophytes has (provisionally) also accepted the division of *Racomitrium* at the generic level (Frey & Stech, 2009, but see Stech & al., 2013).

Phylogenetic inferences based on molecular data in *Racomitrium* s.l. are virtually absent. Few *Racomitrium* species have

been included in a study addressing overall phylogenetic relationships among the genera of the Grimmiaceae (Hernández-Maqueda & al., 2008b), which indicated that the genus *Racomitrium* is monophyletic in its traditional broad circumscription. Similarly, only a limited number of *Racomitrium* species were included in a study by Liu & al. (2011) testing the suitability of DNA barcoding markers in the Grimmiaceae. Only the *Racomitrium* (*Niphotrichum*) *canescens* complex has been subjected to more detailed analyses (Stech & al., 2013). Additionally, a subset of the data presented in this paper was used to support the description of the new species *Bucklandiella araucana* (Larraín & al., 2011). The evolutionary significance of morphological characters across *Racomitrium* s.l. has not yet been assessed, neither for those characters used for classification, nor for further potentially significant characters such as seta torsion.

Thus, the main objectives of this study are: (1) to reconstruct the phylogeny of *Racomitrium* s.l. using nuclear and plastid markers, (2) to test the monophyly of the four taxonomic entities recognized for more than 100 years, but rarely accepted at the generic level by most modern bryologists, and (3) to test the taxonomic relevance of the morphological characters defining the taxa of *Racomitrium* s.l. using ancestral state reconstruction.

■ MATERIALS AND METHODS

Taxon sampling and scoring of morphological characters. — A morphological data matrix was compiled based on all herbarium collections included in the molecular analyses (Electr. Suppl.: Appendix S1), plus some additional vouchers and literature information (Electr. Suppl.: Appendix S2). In total, 41 species out of approximately 80 species currently accepted in the group (Bednarek-Ochyra, 1995; Ochyra & al., 2003) were included in the analyses, representing all major currently accepted infrageneric taxa within *Racomitrium* s.l. (fide Frisvoll, 1983, 1988; Bednarek-Ochyra, 1995, 2006; Ochyra & al., 2003) spanning a representative sampling of the full range of morphological variation of the group. Outgroup taxa were chosen based on the traditional systematic knowledge of the family and recent molecular studies (Tsubota & al., 2003; Hedderson & al., 2004; Hernández-Maqueda & al., 2008a, b). For measurements of sporophytic continuous characters (seta length, peristome teeth length, spore diameter), 1–5 collections were examined, from each of which 3–10 sporophytes were dissected. For measurements of the single gametophytic continuous character (leaf size), 5–10 shoots were dissected from each examined collection, and for each shoot, 10–20 leaves were measured. For the species where few specimens were available, measurements were compared with available descriptions, and lacking data was taken from the literature (Electr. Suppl.: Appendix S2). The resulting morphological matrix comprised a total of 30 characters (22 gametophytic and 8 sporophytic; Appendix 1; Electr. Suppl.: Table S1). All characters traditionally considered systematically important for *Racomitrium* s.l., as well as other characters (e.g., leaf size, cross section shape, seta twist direction, peristome teeth morphology, spore size,

etc.) that could potentially be useful for interpreting patterns in the molecular phylogenetic reconstructions, were included.

DNA extraction and sequencing. — DNA was extracted from recently collected herbarium specimens (Electr. Suppl.: Appendix S1). Selected shoots were cleaned manually by rinsing them several times with distilled water and by visual inspection under a compound microscope. Extraction followed the protocol described in Doyle & Doyle (1987) with some minor modifications. PCR reactions for the *rps4-trnL* region (including 125 bp of the *rps4* gene, the *rps4-trnT_{UGU}* intergenic spacer (IGS), *trnT_{UGU}*, *trnT_{UGU}-trnL_{UAA}* IGS, the *trnL_{UAA}* 5' exon, and the 5' part of the *trnL_{UAA}* intron until P6) were performed in a total volume of 50 μ l, including 0.2 μ l (5 U/ μ l) of polymerase (Ecogen, Madrid, Spain), 5 μ l of polymerase buffer [10 \times], 2.5 μ l MgCl₂ [50 mM], 5 μ l of dNTP mix [0.2 mM], 2 μ l of each primer [20 μ M], and 2 μ l of DNA template, completing the volume with 31.2 μ l of ultra-pure water. Primers used were *rps4-166F* (Hernández-Maqueda & al., 2008b), and *P6/7* (Quandt & al., 2004). Amplification cycles consisted of an initial period of 2 min at 94°C, followed by 29 cycles of 1 min at 94°C, 1 min at 55°C, and 1 min at 72°C, ending with a final extension period of 5 min at 72°C. Amplifications of *trnK/matK-psbA* were performed in a total volume of 25 μ l, adding 0.2 μ l (5 U/ μ l) of polymerase (Ecogen), 2.5 μ l of polymerase buffer [10 \times], 2.5 μ l MgCl₂ [50 mM], 2.5 μ l of dNTP mix [0.2 mM], 1 μ l of each primer [20 μ M], and 1 μ l of DNA template, completing the volume with 16.8 μ l of ultra-pure water. In a few cases where no PCR products could be obtained, 0.5 μ l of betaine and/or 1 μ l KCl were added, or the primer quantity was increased to 2 μ l each. Primers used were *trnK-F* (Wicke & Quandt, 2009), and *psbARbryo* (Hernández-Maqueda, 2007). In some cases, when this primer couplet did not produce amplification products, we used *trnK-F* together with the reverse primer *trnK-R4* (Wicke & Quandt, 2009). Amplification cycles consisted of an initial period of 3 min at 96°C, followed by 39 cycles of 30 s at 94°C, 90 s at 48°C, and 3 min at 72°C, ending with a final extension period of 20 min at 72°C. When this program did not produce products we modified it as follows: an initial cycle of 1 min at 96°C, 45 s at 50°C, 90 s at 68°C, followed by two cycles of 45 s at 95°C, 45 s at 48°C and 1 min at 68°C, and then 37 cycles of 30 s at 94°C, 30 s at 45°C and 1 min at 68°C, ending with a final extension period of 15 min at 68°C. Amplification reactions for ITS were performed in a total volume of 25 μ l, adding 12.5 μ l of FastStart polymerase mix (Roche, Basel, Switzerland), 5 μ l of each primer [10 μ M], and 1 μ l of DNA template, completing the volume with 6.5 μ l of ultra-pure water. Primers used were *ITS4* (White & al., 1990) and *18S* (Spagnuolo & al., 1999). Amplification cycles consisted of an initial period of 2 min at 94°C, followed by 40 cycles of 1 min at 94°C, 1 min at 48°C, and 1 min at 68°C (with a time increment of 4°C/cycle), ending with a final extension period of 4 min at 68°C. All reactions were performed in a Mastercycle Gradient thermocycler (Eppendorf, Hamburg, Germany) or a T3 Thermocycler (Biometra, Göttingen, Germany).

Sequencing reactions were performed by Macrogen Inc. (Seoul, South Korea), in a DNA Engine Tetrad 2 Peltier Thermal Cycler (BIO-RAD, Hercules, California, U.S.A.) using the

ABI BigDye Terminator v.3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, California, U.S.A.), following the protocols supplied by the manufacturer. Single-pass sequencing was performed on each template using the PCR primers indicated above, as well as the internal primers *trnKF426Grim* and *matK1024F* (Hernández-Maqueda, 2007) for the *trnK/matK-psbA* region, and primers *ITS2* and *ITS3* for the ITS region (White & al., 1990). Sequences were edited and manually aligned using *PhyDE v.0.995* (www.phyde.de) following the alignment rules and hotspot definitions presented in Kelchner (2000), Olsson & al. (2009), and Borsch & Quandt (2009).

Phylogenetic inferences. — Molecular phylogenetic reconstructions under maximum likelihood (ML) were performed with *RAxML v.7.2.8-alpha* (Stamatakis, 2006), specifying a random number seed for the parsimony inferences, including 10,000 bootstrap replicates, and applying the default settings in a rapid bootstrap (BS) search. Bayesian inference (BI) analyses were performed with *MrBayes v.3.1* (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003); all characters were given equal weight and gaps were treated as missing data. The default settings of the program for a priori probabilities were used. Four runs, each with four MCMC chains (5,000,000 generations each) were run simultaneously, with the temperature of the heated chain set to 0.2 (default setting). Chains were sampled every 1000 generations. Calculation of the consensus tree and posterior probabilities of clades was based on the set of trees sampled after the chains had converged, as observed graphically using *Tracer v.1.5* (Rambaut & Drummond, 2007). Maximum parsimony (MP) ratchet analyses were conducted with *PAUP* v.4.0b10* (Swofford, 2003) via the command files generated by *PRAP2* (Müller, 2004a), including bootstrap analyses with 10,000 replicates. Ratchet settings were as follows: 10 random addition cycles of 200 iterations each with a 25% upweighting of the characters in the iterations. For each of the tree construction methods, we analyzed the concatenated data matrix of the three sequenced regions, as well as each region individually in order to detect possible topological incongruences. Analyses were performed excluding hot spot regions (Electr. Suppl.: Table S2). Inversions were included as reverse complement for the analyses (cf. Quandt & al., 2003; Borsch & Quandt, 2009). In addition, the data matrix was analyzed using BI and MP searches with an indel matrix appended. Indels were coded using the simple indel coding (SIC) strategy (Simmons & Ochoterena, 2000) as implemented in *Seqstate v.1.4.1* (Müller, 2004b). Likelihood scores, as well as both the AIC and BIC criteria implemented in *jModelTest v.0.1* (Guindon & Gascuel, 2003; Posada, 2008), suggested the GTR+ Γ substitution model for the concatenated matrix. Although other substitution models were suggested by *jModelTest* for each partition separately, we used the GTR+ Γ model for the ML analyses as this had the best scores for our data among the available models in *RAxML*. For BI analyses we used the GTR+I+ Γ model by default, which should give best results under this method (see discussion in Huelsenbeck & Rannala, 2004). Indels were treated as restriction site data in BI analyses. Trees were edited and support values added using *TreeGraph v.2* (Stöver & Müller, 2010). For testing the relative

probabilities of the different topologies obtained by analyzing the different genetic regions selected, we performed an approximately unbiased (AU) test using CONSEL v.0.1k (Shimodaira & Hasegawa, 2001), by entering the site-log-likelihood values for each topology generated by Tree-Puzzle v.5.2 (Schmidt & al., 2002). For Tree-Puzzle we used the default settings, except for using neighbour-joining for parameter estimation, and the model was set to GTR with gamma distributed rates and eight gamma rate categories.

Ancestral character state reconstruction. — A total of 30 characters were scored for the ancestral state reconstructions (Table 1), including all characters that have been traditionally used for the classification of *Racomitrium*. Continuous characters (leaf size, seta length, peristome teeth length, spore size) were coded as discrete avoiding overlaps, and recording for

Table 1. Number of changes of all scored morphological characters along the molecular phylogeny of *Racomitrium* s.l., as inferred from ancestral state reconstruction.

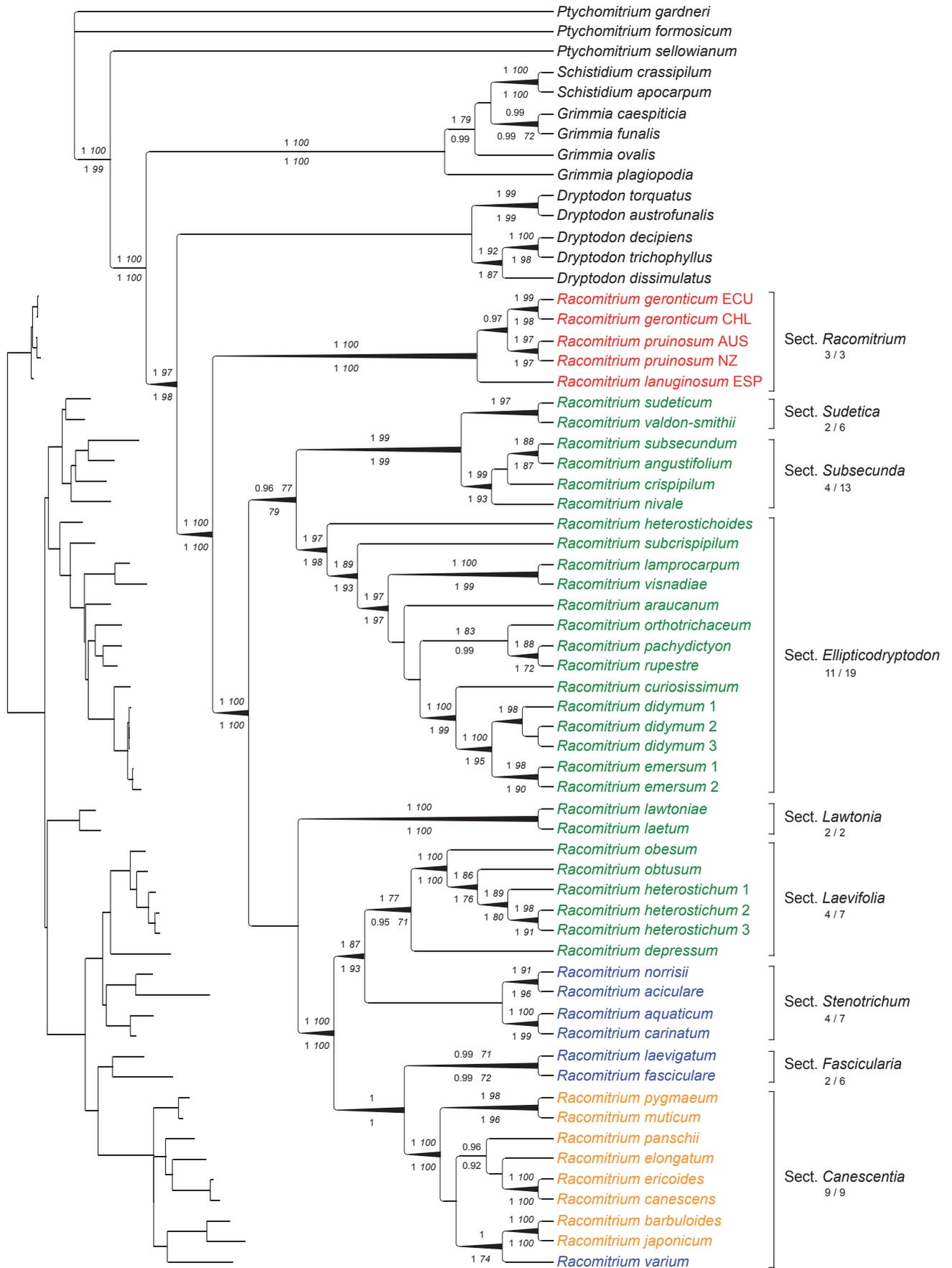
Character	Changes
Seta papillosity	1
Long decurrent hairpoint	1
Papillose hairpoint/low papillose lamina	1
Propagula	1
Leaves contorted when dry	1
Inner perichaetial leaves strongly modified	2
Leaf shape	2
Costa branched	2
Outer perichaetial leaves squarrose when wet	2
Peristome teeth divided	2
Spore size	2
Inner perichaetial leaves plicate	2
Calyptrae papillose	2
Costa length	3
Seta torsion	3
Leaves plicate	3
Leaf papillosity	4
Peristome teeth length	4
Inner perichaetial leaves hairpoint	4
Leaf cross section	5
Margin	9
Seta length	9
Inflated alar cells	9
Basal marginal band	9
Urn shape	9
Hyaline hairpoint	10
Margin stratosity	10
Inner perichaetial leaves hyaline	10
Costa thickness	13
Leaf size	14

each species the mean value taken from the measured specimens and literature information (Appendices 1, 2). Character reconstruction was done using maximum likelihood with Mesquite v.2.73 (Maddison & Maddison, 2010). The outgroup species were excluded from the analyses so as not to affect the probabilities of nodes for characters that could be variable among species of the outgroup genera, and branch lengths were included as a measure of the probability of change across time. For all characters a “Markov k-state 1 parameter” reconstruction model was used, which assumes that any particular change is equally probable (e.g., from state 0 to 1, or from 2 to 1).

RESULTS

The combined aligned dataset (alignment and tree from Fig. 1 were submitted to TreeBase [treebase.org], study number 14971) comprised 7210 positions, or 6633 positions excluding the hot spot regions listed in Table S2 (Electr. Suppl.) (1141 for *rps4-trnL*, 2652 for *trnK/matK-psbA*, 2840 for ITS 1 & 2), with 1298 variable sites. With simple indel coding (SIC), the number of variable sites increased to 2222. Regarding the MP analyses, 699 out of the 1298 variable sites were parsimony-informative. The use of SIC increased the number of parsimony-informative sites to 1114. From the MP ratchet analyses 86 trees were retained without SIC (lengths 2320, consistency index [CI] 0.674, retention index [RI] 0.791, rescaled consistency index [RC] 0.533) and 67 trees including SIC (lengths 3597, CI 0.691, RI 0.790, RC 0.546). We obtained the same tree topology when analyzing the concatenated dataset with ML, BI, and MP, with the only exception of the position of *Racomitrium laetum* and *R. lawtoniae* (sect. *Lawtonia*). These two species appear as sister to the *Laevifolia/Stenotrichum/Fascicularia/Canescentia* clade in the ML tree, sister to the “*Bucklandiella*” group in the MP strict consensus trees, and in an unresolved position together with the *Laevifolia/Stenotrichum/Fascicularia/Canescentia* and the “*Bucklandiella*” clades in the BI 50% majority-rule consensus tree, although none of these topologies received significant support. The strongly supported “*Bucklandiella*” clade includes *Racomitrium* sections *Sudetica*, *Subsecunda* and *Ellipticodryptodon*, which comprise the bulk of species of *Bucklandiella* fide Ochyra & al. (2003). Figure 1 shows the tree from the analysis of the concatenated dataset obtained

Fig. 1. Phylogenetic relations of the Racomitrioideae. ML tree of the concatenated dataset (ITS, *rps4-trnL*, *trnK/matK-psbA*) showing BI PP (normal font) and MP BS (italics) values, with SIC above branches, and without SIC below branches (SIC = Simple Indel Coding; Simmons & Ochoterena, 2000). MP BS values below 70, and BI PP below 0.95 are not shown. Wide lines indicate ML BS > 70. On the left a phylogram of the ingroup including branch lengths is shown. The current systematic placement of each taxon (fide Ochyra & al., 2003; Bednarek-Ochyra & Ochyra, 2011) is indicated by colors (*Racomitrium* in red, *Bucklandiella* in green, *Codriophorus* in blue, and *Niphotrichum* in orange). On the right the new sectional classification of *Racomitrium* s.l. proposed here is indicated, with the number of taxa used in this study of the total number of species on each section given below their names.



by the ML approach, including support values from the MP and BI analyses, and a phylogram for the ingroup showing branch lengths.

The individual analyses of the different datasets showed slightly different arrangements with regard to the backbone topology, but no conflict with significant support (BS > 70; PP > 0.95) could be identified (compare Fig. 2), except for the position of sect. *Canescentia*. This section is sister to sect. *Fascicularia* in all trees except in the ITS tree, where it appears as sister to the *Laevifolia/Stenotrichum/Fascicularia* clade (Fig. 2). Thus the topology from the concatenated matrix will be described and deviations from this mentioned where appropriate. Analysis of the concatenated matrix resulted in strong (i.e., BS > 70; PP > 95) to maximal support for nodes in the backbone topology, with one exception: the node grouping sect. *Lawtonia* with its sister clade in Fig. 1. In all analyses the first branching lineage is the monophyletic sect. *Racomitrium* (Figs. 1, 2), followed by “*Bucklandiella*”. The latter group, however, as circumscribed by Ochyra & al. (2003), is rendered polyphyletic in most analyses by the position of the monophyletic sect. *Lawtoniae* (*Racomitrium* sect. *Lawtonia*), the only

section of *Bucklandiella* sensu Ochyra & al. (2003) in which the seta is twisted to the right (Fig. 3C), and by sect. *Laevifoliae* (*Racomitrium* sect. *Laevifolia*). In the majority of analyses sect. *Lawtoniae* appears more closely related to *Codriophorus–Niphotrichum–Bucklandiella* sect. *Laevifoliae* (Figs. 1, 2A–C, E). Analysis of the *trnK/matK-psbA* dataset, however, resolved it as sister to the bulk of the *Bucklandiella* species (Fig. 2D). However, in all cases the relevant nodes are unsupported. The remaining *Bucklandiella* species (sensu Ochyra & al., 2003) included in the present study are resolved in two different clades, strongly to maximally supported in most analyses: (1) a clade (*Racomitrium* sect. *Ellipticodryptodon* in Fig. 1) comprising the austral species belonging to sections *Bucklandiella*, *Emersae*, *Marginatae*, and *Ptychophyllae* of Ochyra & al. (2003); and (2) a second clade (*Racomitrium* sect. *Sudetica* and sect. *Subsecunda* in Fig. 1) that includes the sampled species of sections *Sudeticae*, *Gemmiferae*, and *Subsecundae* of Ochyra & al. (2003). These two clades form a monophyletic group, albeit with only moderate support. As the position of sect. *Lawtonia* is weakly supported in all analyses (compare Figs. 1 and 2), the present data do not allow to unequivocally conclude that sections *Ellipticodryptodon*, *Lawtonia*, *Subsecunda*, and *Sudetica* form a monophyletic taxon.

In the clade sister to “*Bucklandiella*” (without considering the position of sect. *Lawtonia*) there is a dichotomy consisting of *Laevifolia/Stenotrichum* and *Fascicularia/Canescentia* (Figs. 1, 2A, 2B, 2D), other than in the ITS analyses, where *Fascicularia* appears as sister to the *Laevifolia/Stenotrichum* clade (Fig. 2E). Bootstrap support for both topologies ranges between 72 (ITS) and 73–100 (plastid), indicative of a conflict between plastid and nuclear data. The position of sect. *Laevifolia* as sister to sect. *Stenotrichum* is consistent in all analyses except for the *rps4-trnL* region analysis, which produced an unsupported topology that was also rejected by the AU test (Fig. 2C).

Ancestral state reconstruction analyses (Fig. 3A–D; Table 1; Electr. Suppl.: Figs. S1–S30) show that only three of the characters traditionally used to classify the different species groups within *Racomitrium* are free of homoplasy: the papillose seta, the long-decurrent hairpoints, and the combination of papillose hairpoints and smooth or low papillose laminal cells. This set of characters is diagnostic for *Racomitrium* s.str. Another two characters (leaves contorted when dry, and plants with propagules) would correspond to synapomorphies of *Racomitrium japonicum/R. barbulooides* and *R. nivale*, respectively, but both characters appear also in outgroup taxa, the former being common among *Ptychomitrium* species, and the latter present in most *Dryptodon* species. All other characters, including those most often used to define groups within *Racomitrium*, exhibit varying levels of homoplasy (Table 1).

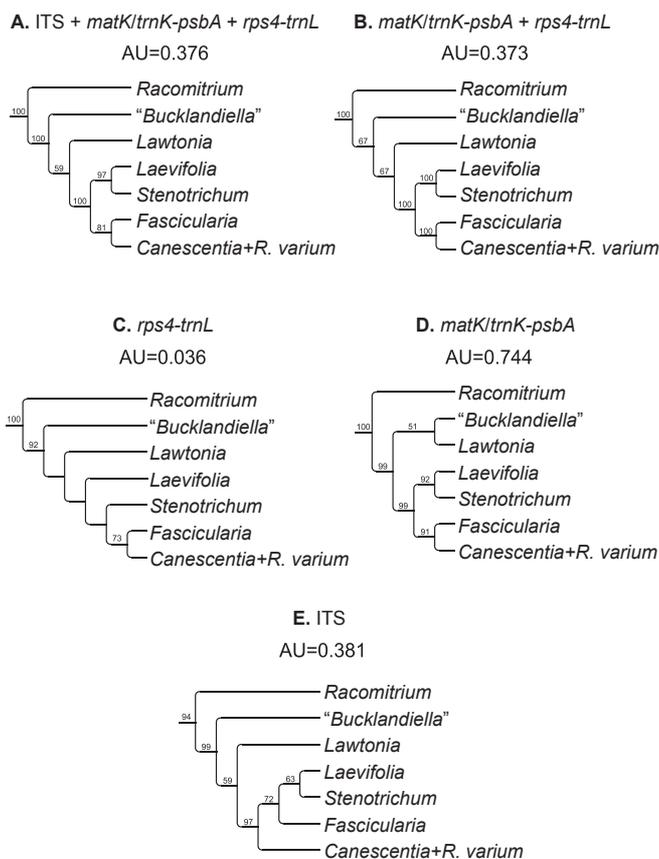


Fig. 2. Comparison of topologies obtained from the analyses of different datasets, indicating the results from the AU test for each. All trees correspond to ML analyses, indicating BS values only when greater than 50%. “*Bucklandiella*” refers to the clade including *Racomitrium* sections *Sudetica*, *Subsecunda* and *Ellipticodryptodon*; the position of *Racomitrium varium* is indicated for all analyses.

■ DISCUSSION

Molecular data and ancestral state reconstruction of morphological characters do not support a division of *Racomitrium* into different genera. The four genera and many infrageneric taxa into which the classical *Racomitrium* has been divided

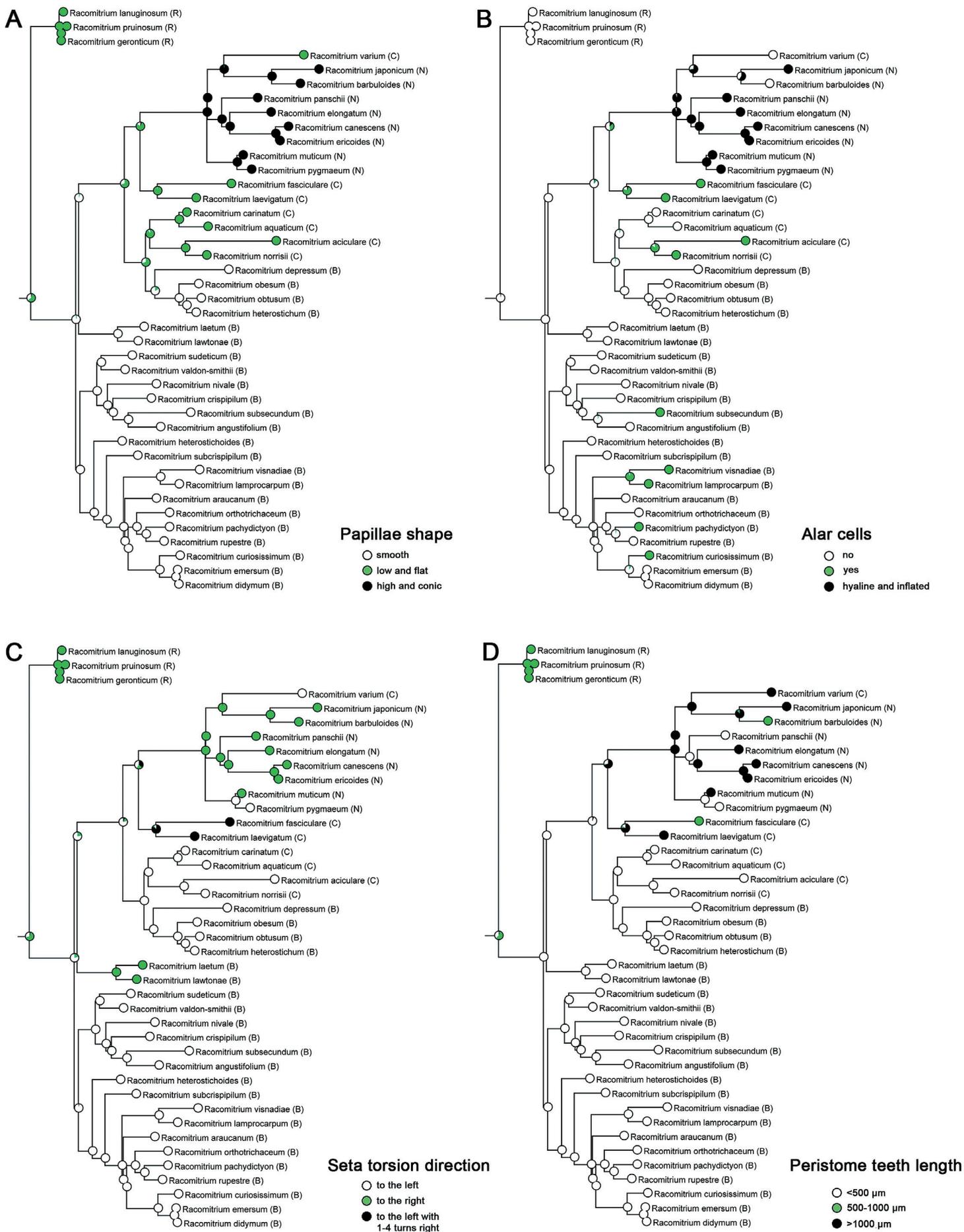


Fig. 3. Selected ancestral state reconstruction diagrams showing: **A**, leaf papillosity; **B**, alar cells; **C**, seta torsion; and **D**, peristome teeth length. In C and D, no data are available for *R. nivale*, *R. panschii* (only in D), *R. pygmaeum*, *R. valdon-smithii* and *R. visnadae* (sporophytes unknown). Placement of each species before this study is shown as a capital letter in parentheses next to each name (B = *Bucklandiella*; C = *Codiophorus*; N = *Niphotrichum*; R = *Racomitrium* s.str.).

(summarized in Ochyra & al., 2003) are mostly not monophyletic. However, the molecular groupings recovered in our analyses are supported by morphological characters; some of these characters are reinterpreted or newly proposed here. In the following discussion we use the nomenclature in Ochyra & al. (2003), and finish by presenting a revised infrageneric classification of an inclusive and monophyletic *Racomitrium*.

Circumscription of *Racomitrium* s.l. and the segregate genera distinguished by Ochyra & al. (2003). — *Racomitrium* s.l. is resolved as monophyletic with maximum support values in all analyses. Although some authors have included *Dryptodon* within *Racomitrium* (e.g., Huebener, 1833; Schimper, 1860; Husnot, 1884–1894), *Dryptodon* is clearly separated from *Racomitrium* s.l. based on molecular data (Hernández-Maqueda, 2007; Hernández-Maqueda & al., 2008a, b; this study) and also readily distinguished morphologically by its arcuate seta and ribbed capsules.

Within the *Racomitrium* s.l. clade two main groups are clearly separated, one comprising the *Racomitrium* s.str. species and a second comprising the *Niphotrichum*, *Codriophorus*, and *Bucklandiella* species of Ochyra & al. (2003). This result receives maximum support under all analytical approaches, no matter whether the regions were analysed separately or concatenated. Of the four segregate genera recognized by Ochyra & al. (2003), only *Racomitrium* s.str. is recognizable at the molecular level in its original circumscription, while *Niphotrichum* forms a monophyletic group together with a single species of *Codriophorus*. *Bucklandiella* and *Codriophorus* are resolved as polyphyletic (Fig. 1). At the sectional level in a broadly defined *Racomitrium* s.l., by contrast, well-supported clades corresponding to previously recognized or newly defined sections (see “Taxonomy” below), are resolved (Fig. 1).

The well-supported clade of *Racomitrium* s.str. (sect. *Racomitrium*) coincides with a set of morphological synapomorphies (papillose seta, long-decurrent hairpoints, and the combination of papillose hairpoint and smooth or slightly papillose laminal cells). Additionally, the seta is twisted to the right in all *Racomitrium* s.str. species, although this trait is shared with a number of other species in different sections (Fig. 3C).

A clade corresponding to *Niphotrichum* sensu Ochyra & al. (2003) but also including the western North American endemic *Racomitrium varium*, previously placed in *Codriophorus* subsect. *Pilifera* (Bednarek-Ochyra, 1995, 2006; Ochyra & al., 2003), is resolved with maximum support in all molecular analyses. The *Niphotrichum* clade (*Racomitrium* sect. *Canescentia*) is morphologically supported by synapomorphies such as the presence of high conical papillae over the cell lumina throughout the leaf (except *R. varium*, Fig. 3A) and the presence of inflated, hyaline to yellowish, thin-walled alar cells forming decurrent auricles (except *R. barbulooides* and *R. varium*, Fig. 3B). Other characters that were used to diagnose *Niphotrichum* are also present in other sections, such as the seta twisted to the right, which occurs in sections *Racomitrium* and *Lawtonia*, and long peristome teeth exceeding 1 mm, which are present in *R. laevigatum* of sect. *Fascicularia*. The shorter peristome teeth of *R. barbulooides* suggest that there have also been reversals in this character state in the sect. *Canescentia*

clade (Fig. 3D). The position of *R. varium* in this clade, however, seems to be only supported morphologically by the long peristome teeth. This challenging taxon has setae twisted to the left, leaf surfaces with weak papillae similar to the ones seen in sect. *Fascicularia*, and alar cells not as inflated and yellowish as in other members of sect. *Canescentia*, although the basal marginal border is clearly differentiated in a row of pellucid and straight-walled cells.

The morphological circumscription of *Codriophorus* was already obscured by the transfer of *R. dichelymoides* and *R. depressum*, two species having smooth leaves, to *Bucklandiella* (Bednarek-Ochyra & Ochyra, 2011). Unfortunately the authors neither explained the reasons for this transfer, nor discussed the implications of the papillose to verrucose calyptra observable in both species for the delimitation of *Codriophorus*, which also includes several species with smooth calyptrae (e.g., *R. fasciculare*, *R. laevigatum*). In contrast to the polyphyly of *Codriophorus* based on molecular data, two clades resolved in the present study correspond to the two sections already distinguished within the genus by Bednarek-Ochyra (2006). Her sect. *Codriophorus* (*Racomitrium* sect. *Stenotrichum* in this study) is characterized by simple to dichotomously branched stems, relatively short upper laminal cells (although there are exceptions), lingulate to oblong-lanceolate leaves, a generally obtuse leaf apex, and a broad and robust costa. It is resolved as sister to sect. *Laevifolia* with high support in all our molecular analyses. The two sections share a costa more than three layers thick in the proximal part, the lack of a differentiated basal marginal border of pellucid and straight-walled cells, a seta twisted to the left, innermost perichaetial leaves that are strongly modified, and generally the absence of a hyaline point (although this is conspicuous in *R. heterostichum* and *R. obesum*, and variably present in *R. obtusum*). Most of these morphological characters are, however, highly homoplastic according to the ancestral state reconstruction analyses (Table 1; Electr. Suppl: Figs. S1–S30). *Codriophorus* sect. *Fascicularia* sensu Bednarek-Ochyra (2006) (here *Racomitrium* sect. *Fascicularia*) differs by the presence of many short tuft-like branches on the main stems, a narrower costa, generally longer apical leaf cells, and (narrowly) lanceolate leaves. It is resolved (except for *R. varium*, see above) as sister to the sect. *Canescentia* clade in all analyses of the concatenated dataset and the cpDNA markers (Figs. 1, 2A–D), but as sister to the sect. *Stenotrichum*/sect. *Laevifolia* clade in the ITS tree (Fig. 2E). Both topologies are significantly supported, although only the cpDNA topology receives maximal support. Results from the AU topology test indicate that the topology obtained from the *rps4-trnL* analysis ($P = 0.036$) should be rejected, whereas the remaining topologies cannot be rejected (Fig. 2). Given these results, we cannot definitively conclude to which other section sect. *Fascicularia* is most closely related. The closer relationship based on molecular data between sect. *Fascicularia* and sect. *Canescentia* could be explained in terms of morphological, albeit homoplastic, traits such as a costa that vanishes at midleaf or is subpercurrent (seldom percurrent) and is both narrow and thin (except for *R. varium*), as well as the presence of a great number of short, tuft-like branches along the main stems. The recent

discovery of mature sporophytes of *R. laevigatum* (Larraín & al., unpub. data), which have very long peristome teeth (ca. 1.5 mm), further supports this relationship, as does the papillae shape, which is very variable, with typical “*Codriophorus*-like” (fide Bednarek-Ochyra, 2006) papillae in the proximal parts of leaves becoming almost conical at the leaf apex, as in the bulk of the species in *Niphotrichum*.

In contrast to the results of the present study, Larraín & al. (2011) suggested that *Bucklandiella* is monophyletic. These results have already been used as evidence for supporting the validity of the segregated genera (Bednarek-Ochyra & Ochyra, 2012). However, species from *Bucklandiella* sect. *Laevifolia* (*Racomitrium* sect. *Laevifolia*: *R. heterostichum* and allied species) were not included in that study. This group now turns out to be a key taxon for assessing the circumscription of *Bucklandiella*, due to its close relationship to *Racomitrium* sect. *Stenotrichum*, as discussed above, and the fact that it includes *R. depressum*, which was considered to belong to either *Codriophorus* (Bednarek-Ochyra, 2006) or *Bucklandiella* (Bednarek-Ochyra & Ochyra, 2011).

The position of *Racomitrium dichelymoides* Herzog, a rheophyte endemic to Colombia, could not be assessed because PCR products could not be obtained from DNA extractions of available herbarium material. Bednarek-Ochyra (1995) placed this species in its own subsection *Andicola* within *Racomitrium*, but it has also been treated as a subsection of *Codriophorus* (Ochyra & al., 2003) and *Bucklandiella* (Bednarek-Ochyra & Ochyra, 2011). The species combines the seta twisting pattern observed in *Codriophorus* sect. *Fascicularia* (to the left with a few turns to the right just below the capsule, fide Bednarek-Ochyra 2006, fertile material not seen by us), a slightly verrucose calyptra (Bednarek-Ochyra, 2006), the costa shape of sect. *Stenotrichum*, and smooth laminal cells, together with short peristome teeth (350–400 µm) as in the bulk of the *Bucklandiella* species. The rheophytic habitat, falcate-secund leaves with obtuse and mucicous leaf apices, absence of a differentiated basal marginal border of pellucid cells, and presence of inflated leaf auricles, suggest that this taxon could either be related to species of sect. *Ellipticodryptodon* or sect. *Subsecunda*. However, possession of a costa which vanishes well below the leaf apex together with the seta twisting pattern make it difficult to place this taxon in any of the latter sections. Until more data is available, we prefer to keep it in its own section within *Racomitrium* (see Taxonomy).

Systematic significance of morphological characters. —

Concerning the traditional characters that have been used to define the different subdivisions of *Racomitrium* s.l., we find that some of them have been erroneously interpreted (e.g., leaf papilosity, squarrose outer perichaetial leaves) or are simply too variable and unstable to be used for classification (e.g., inner perichaetial leaf morphology, presence of hyaline hairpoint, presence of a differentiated marginal basal row of hyaline and straight walled cells, and branching pattern). Some of these characters are diagnostic for specific clades, but cannot be used for others. For example, the differentiated border of pellucid cells at the marginal bases of leaves is consistent with the close relationship between sections *Stenotrichum* and

Laevifolia based on molecular data, but cannot be used within sect. *Ellipticodryptodon* (e.g., for the strongly supported clade grouping *R. rupestre*, which lacks such a border, *R. pachydiction*, in which it is variably present, and *R. orthotrichaceum*, which has a well developed marginal border two cell rows wide). The same is true for leaf hair points: papillose, decurrent, and eroso-dentate to serrate hairpoints are diagnostic for sect. *Racomitrium*, but the character is quite variable, even within populations, in species such as *R. heterostichoides*, *R. obtusum*, *R. subsecundum*, and *R. sudeticum* (Bednarek-Ochyra & al., 1999; Frisvoll, 1986, 1988; Wagner, 2008).

The ancestral state reconstruction shows that even the characters regarded as most important for segregation of the classical *Racomitrium* by Ochyra & al. (2003), such as leaf cell papillae shape (Fig. 3A), are homoplastic. Although the strongly papillose hyaline hair point contrasting with flat papillae on the lamina exhibited by *Racomitrium* s.str., and the conical papillae located right over the cell lumen found in *Niphotrichum*, are characters that define these two taxa, variation in the leaf papillae shape between *Codriophorus* and *Bucklandiella* does not justify its use as diagnostic character, and this is corroborated by our molecular results. The pseudopapillae (cf. Frisvoll, 1988) of some taxa of *Bucklandiella* could be interpreted as an underdeveloped state of the massive flat papillae found in most *Codriophorus* species. Both types are situated over the longitudinal walls of the laminal cells. These structures are narrow, well-separated, and relatively tall in *Bucklandiella* and much wider in *Codriophorus*, where they cover the entire longitudinal cell wall, leaving a narrow groove just over the cell lumen. Additionally, *Racomitrium varium* has *Codriophorus*-type leaf papillae, although it always appears nested within the *Niphotrichum* clade in our results.

Another character that has been regarded as important for classification is the morphology of perichaetial leaves. Frisvoll (1988: 31) defined four main types of perichaetial leaves, i.e.: (1) innermost bracts slightly differentiated, thin-walled, hyaline and sheathing at the base but chlorophyllous and like vegetative leaves above, usually with hyaline point, and outer bracts not squarrose when wet; (2) innermost bracts strongly modified and sheathing, hyaline below but not above, epilose, and outer bracts not squarrose when wet; (3) innermost bracts strongly modified, strongly sheathing and pellucid below but not above, epilose, and outer bracts squarrose when wet; (4) innermost bracts strongly modified, hyaline and epilose, and outer bracts not squarrose when wet. We have observed that some of these characters have been erroneously interpreted for certain groups, e.g., sect. *Subsecunda* is supposed to have squarrose outer perichaetial leaves (Frisvoll, 1988), but in most of the Neotropical specimens of the type species of the section, *R. subsecundum*, this character is variable and the leaves are slightly erect to erect-spreading only when wet. Other characters are too variable even among closely related taxa, e.g., the extent to which the innermost perichaetial leaves are hyaline varies even within populations, and might be related to environmental conditions or to the state of development of the sporophytes.

The presence of inflated, hyaline alar cells forming a short-decurrent alar group can be considered a synapomorphy for

Niphotrichum, with the exceptions of *R. varium* and *R. barbulooides* that rarely have inflated alar cells. In addition to undifferentiated alar cells and the “*Niphotrichum*-type” hyaline alar cells, however, a third type (inflated alar cells in short decurrencies but often colored) occurs in various species in different sections, such as *R. fasciculare*, *R. laevigatum*, *R. norrisii*, *R. subsecundum*, *R. curiosissimum*, and *R. lamprocarpum* (Fig. 3B), which were placed in either *Bucklandiella* or *Codriophorus* by Ochyra & al. (2003).

Costa thickness seems to be a stable and useful character for some groups of species, although it is a highly homoplastic character within *Racomitrium* s.l. (Table 1). The thin (mostly two cell layers thick) and weakly differentiated costa is a shared character between sections *Canescentia* and *Fascicularia* (except for *R. varium* which has a costa that is three cell layers thick proximally). A thick and wide costa is shared by sections *Stenotrichum*, *Laevifolia*, most species of sect. *Ellipticodryptodon*, and *R. macounii* (sect. *Sudetica*).

Two sporophytic characters (seta torsion, peristome teeth length), although homoplastic, support some of the relationships found in our molecular analysis (Fig. 3C, D). Seta torsion has not previously been regarded as important taxonomically, perhaps due to a lack of consensus on a stable terminology for describing the direction in which the seta twists (Wagner, 2008). We have adopted here the terminology illustrated in Malcolm & Malcolm (2006), where “to the right” is synonymous with dextrorse, and “to the left” with sinistrorse. All species in sections *Racomitrium* and *Lawtonia*, and all in sect. *Canescentia* except *R. varium*, have setae twisted to the right (Fig. 3C). *Racomitrium varium* is again an exception because it has a seta that is twisted to the left. Members of sections *Ellipticodryptodon*, *Laevifolia*, *Subsecunda*, and *Sudetica* have setae twisted to the left, like those of sect. *Stenotrichum*. Finally, setae in sect. *Fascicularia* are slightly twisted to the left at the base, but just below the capsule they abruptly twist to the right. Peristome teeth length is also too variable to be used as a diagnostic character at the sectional level. They are generally longer than 1000 µm in all members of sect. *Canescentia* (including *R. varium*) as well as in *R. laevigatum*. Other members of sect. *Fascicularia* have shorter teeth (500–1000 µm). Further obscuring the distinction between *Codriophorus* and *Niphotrichum*, some members of sect. *Stenotrichum* (such as *R. rysardii*, not included in our molecular analyses) have peristome teeth generally longer than 500 µm, whereas in *R. barbulooides* they are shorter than 1000 µm (Fig. 3D). Finally, some species of the former *Bucklandiella* (*R. subsecundum*, *R. pacificum*) present extreme phenotypes with peristome teeth exceeding 500 µm, although generally these species have teeth shorter than 500 µm.

Final remarks. — The present molecular results do not support the current segregation of the traditional genus *Racomitrium* into four genera. In the light of the present data, three different approaches could be considered: (1) keeping the four genera proposed by Ochyra & al. (2003) and describing four new genera for *Codriophorus* sect. *Fascicularia*, *Bucklandiella* sect. *Laevifolia*, *Bucklandiella* sect. *Lawtonia*, and *Racomitrium varium*); (2) recognizing *Racomitrium* s.str. as

one genus and treating all other species in a second genus (i.e., *Codriophorus*, the oldest available name at the genus level); or (3) going back to the traditional use of *Racomitrium*, and proposing a novel infrageneric classification that corresponds to the molecular clades.

The first approach seems unjustified because there would be no morphological synapomorphies for the new genera. The second approach would reflect quite well our molecular results, but it would be necessary to recombine more than 60 names under *Codriophorus*, because *Racomitrium* was lectotypified by Schimper (1860) with *R. lanuginosum* (cf. Ochyra & al., 2003); we reject this solution because it would only increase the nomenclatural confusion surrounding the group. The third approach seems to be the most appropriate based on our molecular results. It involves returning to the traditional generic concept of the genus *Racomitrium*, which is diagnosed by a cladocarpous habit, lack of a stem central strand, conspicuously sinuose laminal cell walls, sinuose-walled epidermal cells in the vaginula, and the presence of a preperistome. A novel infrageneric classification of the genus *Racomitrium* is proposed below. For each recognised section we list the included species, indicating in bold letters all taxa assessed in the present molecular study.

■ TAXONOMY

Taxonomic changes

Racomitrium allanfifei (Bednarek-Ochyra & Ochyra) Larraín & J. Muñoz, **comb. nov.** ≡ *Bucklandiella allanfifei* Bednarek-Ochyra & Ochyra in J. Bryol. 32(4): 247. 2010 – Holotype: NEW ZEALAND. South Island. Canterbury Region, Arthur Pass National Park, east face of Mount Bealey, basin on upper slope, lat. 42°58.1'S, long. 171°33.7'E, alt. 1550 m, near a small stream and late snow bed; hab. keys: greywacke, alpine, slope, rock, wet, open, sunny, 16 Nov. 1988, *Huang Guangbin 13* (with A.J. Fife) (CHR n.v.).

Racomitrium angustissimum (Bednarek-Ochyra & Ochyra) Larraín & J. Muñoz, **comb. nov.** ≡ *Bucklandiella angustissima* Bednarek-Ochyra & Ochyra in Cryptog. Bryol. 32: 14. 2011 – Holotype: NEW ZEALAND. Auckland Islands. Adams Island, on summit of S.W. Adams Trig, lat. 50°52' S, long. 165°56' E; elev. 520 m; on rock cliffs and open stones in alpine moor with abundant cushion plants and mosses; 30 Dec. 1972, *Vitt 9668* (ALTA n.v.).

Racomitrium araucanum (Larraín) Larraín & J. Muñoz, **comb. nov.** ≡ *Bucklandiella araucana* Larraín in Bryologist 114: 737. 2011 – Holotype: CHILE. Provincia de Cautín, Parque Nacional Villarrica, poco más arriba de la entrada a las cuevas volcánicas, 39°22'38" S, 71°56'31" W, 1150 m, en afloramientos rocosos sobre el límite de la vegetación arbórea, sobre rocas; 18 Sep. 2009, *Larraín 31884* (CONC!; isotypes: KRAM!, MA!, NY!).

Racomitrium corrugatum (Bednarek-Ochyra) Larraín & J. Muñoz, **comb. nov.** ≡ *Codriophorus corrugatus* Bednarek-Ochyra in Bryologist 107: 377. 2004 – Holotype: CHINA. Prov. Sichuan, Song Fan County, near Huang Long Temple, lat. 32°20' N, long. 103°30' E; on soil in primeval *Abies-Picea* forest, alt. 3040–3460 m; 8 Jun. 1983, *Si He 30455* (MO n.v.; isotype: KRAM!).

Racomitrium shevockii (Bednarek-Ochyra & Ochyra) Larraín & J. Muñoz, **comb. nov.** ≡ *Bucklandiella shevockii* Bednarek-Ochyra & Ochyra in Polish Bot. J. 55: 500. 2010 – Holotype: CHINA. Yunnan Province, Gongshan county, Gaoligong Shan mountains, Cikai Xiang, along the Qi Qi Trail, about 2.5 km below the Qi Qi Forestry Field Station and 0.5 km above the Qi Qi He Bridge; on slopes on north side of the Qi Qi He, lat. 27°41'21.5" N, long. 98°34'59.4" E; elev. 1945 m; mixed hardwood forest along cascading stream, on top of granitic boulder in filtered light, rheophyte, 1 Oct. 2007, *Shevock 31007* (with David G. Long and Xuezhong Fan) (CAS n.v.; isotypes: E n.v., KRAM n.v., KUN n.v.).

Sectional classification of *Racomitrium*

Racomitrium Brid., Muscol. Recent. 4: 78. 1818 (“1819”) – Type (designated by Schimper, 1860, cf. Bednarek-Ochyra, 1995: 281): *R. lanuginosum* (Hedw.) Brid. (≡ *Trichostomum lanuginosum* Hedw.).

= *Codriophorus* P. Beauv. in Mém. Soc. Linn. Paris 1: 445. 1822 (synonymized by Allen, 2005) – Type (designated by Bednarek-Ochyra & al., 2001): *C. aciculare* (Hedw.) P. Beauv. (≡ *Dicranum aciculare* Hedw.).

= *Niphotrichum* Bednarek-Ochyra & Ochyra 2003 (see under *Racomitrium* sect. *Canescentia* (Kindb.) Bednarek-Ochyra).

= *Bucklandiella* Roiv. in Ann. Bot. Fenn. 9: 116. 1972 (synonymized by Allen, 2005) ≡ *Bucklandia* Roiv. in Arch. Soc. Zool. Bot. Fenn. “Vanamo” 9: 98. 1955., non Sternb. 1825 nec Brongn. 1828, R. Br. ex Griff. 1836 – Type: *B. bartramii* (Roiv.) Roiv. (≡ *Bucklandia bartramii* Roiv.).

Plants cladocarpous, saxicolous or terricolous. Stems dichotomously to pinnately branched, without central strand. Leaves lanceolate to ligulate; costa excurrent to just vanishing at apex; laminal cell walls thick, conspicuously sinuose throughout; margins often recurved. Dioicous. Vaginula with sinuose-walled epidermal cells; peristome arthrodontous, haplolepidous, of seligerioid type (16 teeth divided into two or three prongs or rarely entire); basal membrane and preperistome present; spores smooth to slightly verrucose, 10–28 μm in diameter; calyptra mitrate and basally lobed.

Racomitrium Brid. sect. *Racomitrium*

– “*Racomitrium* [unranked] *Lanuginosa*” Kindb., Eur. N. Amer. Bryin. 2: 235. 1898, invalidly published (Art. 22.2).

– “*Racomitrium* sect. *Lanuginosa*” Noguchi in J. Hattori Bot. Lab. 38: 346. 1974, invalidly published (Art. 22.2). incl. type genus.

Included species: *R. geronticum*, *R. lanuginosum*, *R. pruinosum*.

Stems dichotomously or pinnately branched; leaf surface with low, blunt papillae contrasting with conical, tall papillae on the hyaline points; hyaline hairpoints long-decurrent; cells towards leaf apex rectangular to linear, rarely isodiametric; differentiated basal marginal border of pellucid and straight-walled cells present; costa weak, bistratose in proximal portion; leaf margins unistratose, serrate to dentate (sometimes only eroded) in distal half. Innermost perichaetial leaf differentiated, hyaline to yellowish, convolute, fragile. Seta papillose, twisted to the right; peristome teeth long (>500 μm) deeply divided in 2–3 prongs; calyptra smooth.

Racomitrium sect. *Sudetica* Bednarek-Ochyra in Fragm. Florist. Geobot., Ser. Polon. 2: 221. 1995 ≡ *Bucklandiella* sect. *Sudeticae* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra in Ochyra & al., Cens. Cat. Polish Mosses (Biodivers. Poland 3): 143. 2003 – Type: *R. sudeticum* (Funck) Bruch & Schimp. (≡ *Trichostomum sudeticum* Funck).

Included species: *R. afoninae*, *R. brevipes*, *R. macounii*, *R. occidentale*, *R. sudeticum*, *R. valdon-smithii*.

Stems dichotomously branched; leaf surface smooth or with longitudinal cuticular ridges (appearing papillose in cross section); hyaline hairpoint of vegetative leaves terete and straight, robust, often denticulate; cells towards leaf apex usually isodiametric or oblate; differentiated basal marginal border of pellucid and straight-walled cells variable, either absent or conspicuous; costa strong, often of 3 or 4 cell layers in proximal portion; leaf margins often bistratose, entire; innermost perichaetial leaf slightly differentiated from vegetative leaves, chlorophyllose in distal half or more and piliferous, sheathing at the base but not above. Seta smooth, twisted to the left; peristome teeth generally short (<500 μm), divided to the middle (rarely deeper); calyptra smooth.

Racomitrium sect. *Subsecunda* Bednarek-Ochyra in Fragm. Florist. Geobot., Ser. Polon. 2: 65. 1995 ≡ *Bucklandiella* sect. *Subsecundae* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra in Ochyra & al., Cens. Cat. Polish Mosses (Biodivers. Poland 3): 143. 2003 – Type: *R. subsecundum* (Hook. & Grev. ex Harv.) Mitt. (≡ *Trichostomum subsecundum* Hook. & Grev. ex Harv.).

= *Racomitrium* subg. *Microcarpa* Vilh. in Věstn. Král. České Společn. Nauk, Tř. Mat.-Přír. 1925(5): 22. 1926 (“*Microcarpa*”), **syn. nov.** ≡ *R.* sect. *Marginata* Bednarek-Ochyra in Fragm. Florist. Geobot., Ser. Polon. 2: 175. 1995, **syn. nov.** ≡ *Bucklandiella* sect. *Marginatae* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra in Ochyra & al., Cens. Cat. Polish Mosses (Biodivers. Poland 3): 143. 2003 – Type: *R. microcarpum* (Hedw.) Brid. (≡ *Trichostomum microcarpum* Hedw.).

= *Racomitrium* subsect. *Cucullaria* Bednarek-Ochyra in Fragm. Florist. Geobot., Ser. Polon. 2: 64. 1995, **syn. nov.** ≡ *Bucklandiella* subsect. *Cucullaria* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra in Ochyra & al., Cens. Cat. Polish Mosses (Biodivers. Poland 3): 143. 2003 – Type: *R. cucullatifolium* Hampe.

= *Bucklandiella* sect. *Gemmiferae* Köckinger, Bednarek-Ochyra & Ochyra in Bryologist 110: 97. 2007, **syn. nov.**

– Type: *B. nivalis* Köckinger, Bednarek-Ochyra & Ochyra.

Included species: *R. albipiliferum*, ***R. angustifolium***, ***R. crispipilum***, *R. cucullatum*, *R. fuscescens*, *R. himalayana*, *R. joseph-hookeri*, *R. microcarpum*, *R. nitidulum*, ***R. nivale***, ***R. subsecundum*** (= *R. cucullatifolium*), *R. verrucosum*, *R. vulcanicola*.

Stems dichotomously branched; leaf surface smooth or with longitudinal cuticular ridges (appearing papillose in cross section); hyaline hairpoint often long and flexuose; cells towards leaf apex generally much longer than wide; differentiated basal marginal border of pellucid and straight-walled cells variable, lacking to well developed; costa bi- to tri-stratose in proximal portion; leaf margins often unistratose; innermost perichaetial leaf strongly modified, and generally lacking a hyaline point (except in some populations of *R. microcarpum*). Seta smooth, twisted to the left; peristome teeth generally short (<500 µm), divided to the middle (rarely deeper); calyptra smooth.

Racomitrium* sect. *Ellipticodryptodon (Vilh.) Ochyra, Sérgio & Schumacker in Bull. Jard. Bot. Natl. Belg. 58: 246. 1988 ≡ *Dryptodon* subg. *Ellipticodryptodon* Vilh. in Acta Bot. Bohem. 2: 53. 1923 ≡ *Racomitrium* subg. *Ellipticodryptodon* (Vilh.) Bednarek-Ochyra & Ochyra in Fragm. Florist. Geobot. 39: 362. 1994 – Type: *R. ellipticum* (Turner) Bruch & Schimp. (≡ *Dicranum ellipticum* Turner).

= *Bucklandiella* Roiv. 1972 (see entry under *Racomitrium*).

= *Racomitrium* sect. *Emersa* Bednarek-Ochyra in Fragm. Florist. Geobot., Ser. Polon. 2: 65. 1995, **syn. nov.** ≡ *Bucklandiella* sect. *Emersae* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra in Ochyra & al., Cens. Cat. Polish Mosses (Biodivers. Poland 3): 142. 2003 – Type: *R. emersum* (Müll. Hal.) A. Jaeger (≡ *Grimmia emersa* Müll. Hal.).

= *Racomitrium* sect. *Ptychophylla* Bednarek-Ochyra in Fragm. Florist. Geobot., Ser. Polon. 2: 65. 1995, **syn. nov.** ≡ *Racomitrium* subsect. *Diaphana* Bednarek-Ochyra & Ochyra in Fragm. Florist. Geobot. 41: 982. 1996, **syn. nov.** ≡ *Bucklandiella* sect. *Ptychophyllae* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra in Ochyra & al., Cens. Cat. Polish Mosses (Biodivers. Poland 3): 143. 2003 ≡ *Bucklandiella* subsect. *Diaphanae* (Bednarek-Ochyra & Ochyra) Bednarek-Ochyra & Ochyra in Ochyra & al., Cens. Cat. Polish Mosses (Biodivers. Poland 3): 143. 2003 – Type: *R. ptychophyllum* (Mitt.) Mitt. (≡ *Grimmia ptychophylla* Mitt.).

= *Racomitrium* subsect. *Grimmiiformia* Bednarek-Ochyra in Fragm. Florist. Geobot., Ser. Polon. 2: 64. 1995, **syn. nov.** ≡ *Bucklandiella* subsect. *Grimmiiformes* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra in Ochyra & al., Cens. Cat. Polish Mosses (Biodivers. Poland 3): 143. 2003 (“*Grimmiaeformes*”) – Type: *R. grimmioides* Herzog.

= *Racomitrium* subsect. *Horrida* Bednarek-Ochyra & Ochyra in Fragm. Florist. Geobot. 41: 982. 1996, **syn. nov.** ≡ *Bucklandiella* subsect. *Horridae* (Bednarek-Ochyra & Ochyra) Bednarek-Ochyra & Ochyra in Ochyra & al., Cens. Cat.

Polish Mosses (Biodivers. Poland 3): 143. 2003 – Type: *R. curiosissimum* Bednarek-Ochyra & Ochyra.

Included species: *R. allanfifei*, *R. angustissimum*, ***R. araucanum***, *R. bartramii*, *R. crispulum*, *R. crumianum*, ***R. curiosissimum***, ***R. didymum***, *R. ellipticum*, ***R. emersum***, ***R. heterostichoides***, ***R. lamprocarpum***, ***R. orthotrichaceum*** (= *R. grimmioides*), ***R. pachydictyon***, *R. ptychophyllum*, ***R. ruprestre***, *R. stenocladum*, ***R. subcrispipilum***, ***R. visnadiae***.

Stems dichotomously branched; leaf surface smooth or with longitudinal cuticular ridges (appearing papillose in cross section); hyaline hairpoint flat, variable in length, lacking to very long and flexuose; cells towards leaf apex variable, generally longer than wide; differentiated basal marginal border of pellucid and straight-walled cells variable, lacking to well developed; costa 2- to 5-stratose in proximal portion; leaf margins variable, unistratose to bistratose in several rows; innermost perichaetial leaf strongly differentiated from vegetative leaves, hyaline or with a smaller chlorophyllose area distally, without or with a very short hyaline hairpoint, sheathing (sometimes for all its length). Seta smooth, twisted to the left; peristome teeth generally short (<500 µm), divided to the middle (rarely deeper), or sometimes even entire; calyptra smooth.

Racomitrium* sect. *Lawtonia Bednarek-Ochyra in Fragm.

Florist. Geobot., Ser. Polon. 2: 65. 1995 ≡ *Bucklandiella* sect. *Lawtoniae* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra in Ochyra & al., Cens. Cat. Polish Mosses (Biodivers. Poland 3): 142. 2003 – Type: *R. lawtoniae* Ireland.

Included species: ***R. laetum***, ***R. lawtoniae***.

Stems scarcely branched, dichotomous; leaf surface smooth. Hyaline hairpoint flat; cells towards leaf apex generally longer than wide; differentiated basal marginal border of pellucid and straight-walled cells absent or very weak; costa weak, 2–3 cell layers in proximal portion; leaf margins unistratose, entire; innermost perichaetial leaf strongly differentiated from vegetative leaves, hyaline or with a smaller chlorophyllose area distally, without or with a very short hyaline hairpoint, sheathing (sometimes for all its length). Seta smooth, twisted to the right; peristome teeth generally short (<500 µm), divided to the middle (rarely deeper); calyptra smooth.

Racomitrium* sect. *Andicola (Bednarek-Ochyra) Larraín

& J. Muñoz, **stat. nov.** ≡ *Racomitrium* subsect. *Andicola* Bednarek-Ochyra in Fragm. Florist. Geobot., Ser. Polon. 2: 64. 1995 ≡ *Codriophorus* subsect. *Andicola* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra in Ochyra & al., Cens. Cat. Polish Mosses (Biodivers. Poland 3): 140. 2003 ≡ *Bucklandiella* subsect. *Andicola* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra in Cryptog. Bryol. 32: 23. 2011 – Type: *R. dichelymoides* Herzog.

Included species: *R. dichelymoides*.

Stems dichotomously branched; leaf surface smooth; hyaline hairpoint lacking; cells towards leaf apex usually isodiametric or oblate; differentiated basal marginal border of pellucid and straight-walled cells lacking; costa weak, often of 3 or more cell layers in proximal portion, abruptly failing at leaf apex; leaf margins unistratose; innermost perichaetial

leaf slightly differentiated from vegetative leaves, chlorophyllose throughout, sheathing (sometimes for all its length). Seta smooth, twisted to the left with a few turns to the right just below the capsule; peristome teeth short (<500 µm), irregularly divided; calyptra smooth.

Racomitrium* sect. *Laevifolia (Kindb.) Noguchi in J. Hattori Bot. Lab. 38: 361. 1974 ≡ *Racomitrium* [unranked] *Laevifolia* Kindb., Eur. N. Amer. Bryin. 2: 235. 1898 ≡ *Bucklandiella* sect. *Laevifoliae* (Kindb.) Bednarek-Ochyra & Ochyra in Ochyra & al., Cens. Cat. Polish Mosses (Biodivers. Poland 3): 142. 2003 – Type: *R. heterostichum* (Hedw.) Brid. (≡ *Trichostomum heterostichum* Hedw.)

= *Codriophorus* subsect. *Depressi* Bednarek-Ochyra in Ochyra, Taxon. Monogr. Codriophorus: 151. 2006, **syn. nov.** ≡ *Bucklandiella* subsect. *Depressae* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra in Cryptog. Bryol. 32: 23. 2011 – Type: *C. depressus* (Lesq.) Bednarek-Ochyra & Ochyra (≡ *Racomitrium depressum* Lesq.)

Included species: *R. affine*, ***R. depressum***, ***R. heterostichum***, ***R. obesum***, ***R. obtusum***, *R. pacificum*, *R. venustum*.

Stems scarcely dichotomously branched; leaf surface smooth; hyaline hairpoint flat, often long, flexuose and denticulate; cells towards leaf apex usually isodiametric or oblate; differentiated basal marginal border of pellucid and straight-walled cells lacking; costa strong, often of 3 or more cell layers in proximal portion; leaf margins often unistratose (except in *R. obesum*); innermost perichaetial leaf strongly modified, generally lacking a hyaline point (conspicuous in *R. heterostichum* and *R. obesum*, and variably present in *R. obtusum*). Seta smooth, twisted to the left; peristome teeth generally short (<500 µm), divided to the middle (rarely deeper); calyptra smooth.

Racomitrium* sect. *Stenotrichum (Chevall.) Bednarek-Ochyra in Fragm. Florist. Geobot., Ser. Polon. 2: 143. 1995 ≡ *Trichostomum* sect. *Stenotrichum* Chevall., Fl. Gén. Env. Paris 2: 44. 1827 ≡ *Codriophorus* P. Beauv. 1822 (see entry under *Racomitrium*) ≡ *Racomitrium* [unranked] *Papillosa* Kindb., Eur. N. Amer. Bryin. 2: 235. 1898 ≡ *Racomitrium* sect. *Papillosa* (Kindb.) Noguchi in J. Hattori Bot. Lab. 38: 349. 1974, nom. superfl. (Art. 52.1, 52.3) ≡ *Racomitrium* subsect. *Papillosa* (Kindb.) Bednarek-Ochyra in Fragm. Florist. Geobot., Ser. Polon. 2: 144. 1995 – Type: *R. aciculare* (Hedw.) Brid. (≡ *Dicranum aciculare* Hedw.)

= *Racomitrium* subg. *Cataracta* Vilh. in Věstn. Král. České Společn. Nauk, Tř. Mat.-Přír. 1925(5): 31. 1926 (“*Cataractae*”) – Type: *R. protensum* (A. Braun ex Duby) Huebener (≡ *Trichostomum protensum* A. Braun ex Duby).

= *Racomitrium* subsect. *Hydrophilus* Bednarek-Ochyra in Fragm. Florist. Geobot., Ser. Polon. 2: 157. 1995, **syn. nov.** ≡ *Codriophorus* subsect. *Hydrophilus* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra in Ochyra & al., Cens. Cat. Polish Mosses (Biodivers. Poland 3): 140. 2003 – Type: *R. aquaticum* (Schrad.) Brid. (≡ *Trichostomum aquaticum* Schrad.)

Included species: ***R. aciculare***, *R. aduncoides*, ***R. aquaticum*** (= *R. protensum*), ***R. carinatum***, *R. molle*, ***R. norrisii***, *R. ryszardii*.

Stems dichotomously branched; leaf surface with low, blunt papillae over longitudinal cell walls and lumen, leaving only a narrow groove between consecutive thickenings; hyaline hairpoint absent, apices often obtuse or wide-acute; cells towards leaf apex usually isodiametric or oblate; differentiated basal marginal border of pellucid and straight-walled cells weak or lacking; costa weak, spurred, often of 3 or more cell layers in proximal portion but abruptly fading towards leaf apex; leaf margins often unistratose; innermost perichaetial leaf strongly differentiated from vegetative leaves, hyaline, lacking a hyaline point. Seta smooth, twisted to the left; peristome teeth generally short (<500 µm), divided to the middle (rarely deeper); calyptra verrucose.

Racomitrium* sect. *Fascicularia Bednarek-Ochyra in Fragm. Florist. Geobot., Ser. Polon. 2: 130. 1995 ≡ *Codriophorus* sect. *Fasciculares* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra in Ochyra & al., Cens. Cat. Polish Mosses (Biodivers. Poland 3): 140. 2003 (“*Fascicularia*”) ≡ *Codriophorus* subsect. *Fasciformes* Bednarek-Ochyra in Ochyra, Taxon. Monogr. Codriophorus: 168. 2006 – Type: *R. fasciculare* (Hedw.) Brid. (≡ *Trichostomum fasciculare* Hedw.)

= *Racomitrium* sect. *Chrysea* Bednarek-Ochyra in Fragm. Florist. Geobot., Ser. Polon. 2: 64. 1995, **syn. nov.** ≡ *Codriophorus* sect. *Chrysei* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra in Ochyra & al., Cens. Cat. Polish Mosses (Biodivers. Poland 3): 140. 2003 ≡ *Codriophorus* subsect. *Chrysei* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra in Ochyra, Taxon. Monogr. Codriophorus: 225. 2006 – Type: *R. laevigatum* (Mitt.) A. Jaeger (≡ *Grimmia laevigata* Mitt.)

Included species: *R. anomodontoides*, *R. brevisetum*, *R. corrugatum*, ***R. fasciculare***, ***R. laevigatum***, *R. shevockii*.

Stems pinnately branched; leaf surface with low, blunt papillae over longitudinal cell walls and lumen, leaving only a narrow groove between consecutive thickenings, papillae occasionally turning conical towards leaf apex; hyaline hairpoint short or absent, flat; cells towards leaf apex generally longer than wide; differentiated basal marginal border of pellucid and straight-walled cells present, sometimes weak; costa weak, 2–3 cell layers in the proximal portion, failing at leaf apex; leaf margins unistratose; innermost perichaetial leaf modified, oblong, chlorophyllose, apex longly acuminate. Seta smooth, twisted to the left with a few turns to the right just below the capsule; peristome teeth very long (often >1000 µm), deeply divided; calyptra smooth or slightly verrucose.

Racomitrium* sect. *Canescentia (Kindb.) Bednarek-Ochyra in Fragm. Florist. Geobot., Ser. Polon. 2: 71. 1995 ≡ *Racomitrium* [unranked] *Canescentia* Kindb., Eur. N. Amer. Bryin. 2: 235. 1898 ≡ *Racomitrium* subg. *Canescentia* (Kindb.) Vilh. in Věstn. Král. České Společn. Nauk, Tř. Mat.-Přír. 1925(5): 15. 1926 (“*Canescentes*”) ≡ *Racomitrium* subsect.

- Canescentia* Frisvoll in *Gunneria* 41: 106. 1983 (“*Cane-scens*”), nom. illeg. (Art. 41.5) ≡ *Racomitrium* subg. *Niphotrichum* Bednarek-Ochyra in *Fragm. Florist. Geobot.*, Ser. Polonica 2: 70. 1995, nom. superfl. et illeg. (Art. 52.1) ≡ *Niphotrichum* Bednarek-Ochyra & Ochyra in *Ochyra & al.*, *Cens. Cat. Polish Mosses (Biodivers. Poland 3)*: 137. 2003 – Type: *R. canescens* (Hedw.) Brid. (≡ *Trichostomum canescens* Hedw.).
- = *Racomitrium* sect. *Elongata* Bednarek-Ochyra in *Fragm. Florist. Geobot.*, Ser. Polon. 2: 94. 1995 ≡ *Niphotrichum* sect. *Elongata* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra in *Ochyra & al.*, *Cens. Cat. Polish Mosses (Biodivers. Poland 3)*: 138. 2003, **syn. nov.** – Type: *R. elongatum* Ehrh. ex Frisvoll.
- = *Racomitrium* sect. *Pilifera* Bednarek-Ochyra in *Fragm. Florist. Geobot.*, Ser. Polon. 2: 64. 1995 ≡ *Codriophorus* sect. *Piliferi* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra in *Ochyra & al.*, *Cens. Cat. Polish Mosses (Biodivers. Poland 3)*: 140. 2003 ≡ *Codriophorus* subsect. *Piliferi* (Bednarek-Ochyra) Bednarek-Ochyra in *Ochyra*, *Taxon. Monogr. Codriophorus*: 236. 2006, **syn. nov.** – Type: *R. varium* (Mitt.) A. Jaeger (≡ *Grimmia varia* Mitt.).
- = *Racomitrium* subsect. *Ericoides* Frisvoll in *Gunneria* 41: 58. 1983 ≡ *Niphotrichum* subsect. *Ericoides* (Frisvoll) Bednarek-Ochyra & Ochyra in *Ochyra & al.*, *Cens. Cat. Polish Mosses (Biodivers. Poland 3)*: 138. 2003, **syn. nov.** – Type: *R. ericoides* (Brid.) Brid. (≡ *Trichostomum ericoides* Brid.).
- = *Racomitrium* subsect. *Japonica* Bednarek-Ochyra in *Fragm. Florist. Geobot.*, Ser. Polon. 2: 63. 1995 ≡ *Niphotrichum* subsect. *Japonica* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra in *Ochyra & al.*, *Cens. Cat. Polish Mosses (Biodivers. Poland 3)*: 138. 2003, **syn. nov.** – Type: *R. japonicum* Dozy & Molk.
- = *Racomitrium* subsect. *Minima* Bednarek-Ochyra in *Fragm. Florist. Geobot.*, Ser. Polon. 2: 63. 1995 ≡ *Niphotrichum* subsect. *Minima* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra in *Ochyra & al.*, *Cens. Cat. Polish Mosses (Biodivers. Poland 3)*: 138. 2003, **syn. nov.** – Type: *R. barbuloide*s Card.
- “*Racomitrium* sect. *Racomitrium*” Noguchi in *J. Hattori Bot. Lab.* 38: 343. 1974, invalidly published (Art. 22.4).
Included species: *R. barbuloide*s, *R. canescens*, *R. elongatum*, *R. ericoides*, *R. japonicum*, *R. muticum*, *R. panschii*, *R. pygmaeum*, *R. varium*.
- Stems pinnately branched (except in *R. varium*); leaf surface with high, conical papillae throughout (except in *R. varium*); hyaline hairpoint often present, robust and papillose (except in *R. varium*); cells towards leaf apex generally longer than wide; differentiated basal marginal border of pellucid and straight-walled cells present, strong; costa weak and narrow, 2 cell layers in proximal portion and vanishing at leaf apex (except in *R. varium*); leaf margins unistratose; innermost perichaetial leaf modified, hyaline to yellowish. Seta smooth, twisted to the right (except *R. varium*, where it is twisted to the left); peristome teeth very long (often > 1000 μm), except in *R. barbuloide*s, deeply divided; calyptra smooth.

■ ACKNOWLEDGEMENTS

We acknowledge Ryszard Ochyra, Halina Bednarek-Ochyra, Jim Shevock, Blanka Shaw, Bill Buck, Ben van Zanten and Dale Kruse for providing valuable herbarium specimens for our morphological and molecular studies, as well as the curators of the herbaria mentioned in Appendices 1 and 2. Rafael Hernández, Fátima Durán and Emilio Cano (Real Jardín Botánico, CSIC, Madrid), as well as Susan Wicke and Monika Ballmann (Bonn) are greatly acknowledged for technical help and kindness, and A. Herrero (Real Jardín Botánico, CSIC, Madrid) for advice on nomenclatural issues. Boon-Chuan Ho, Reinaldo Vargas and Jorge Avaria provided valuable help with the use of phylogenetic software. JL & DQ are grateful for the hospitality of the Real Jardín Botánico (CSIC, Madrid). This contribution was funded by CONICYT (no. 21061080) and MECESUP scholarships given to JL, and the grants CGL2009-09530-BOS of the Ministry of Science and Technology of Spain and “DNA-barcoding de musgos de páramo y bosques altoandinos; herramienta de identificación ante el cambio global” of the Universidad Tecnológica Indoamérica to JM. We also thank the DAAD (Deutscher Akademischer Austauschdienst) for financing a two months internship in Bonn/Germany for JL.

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Appendix 1. List of morphological characters included and their codification (gametophytic: 1–23; sporophytic: 23–31).

1. Leaf shape: lanceolate (0), ovate-lanceolate to elliptical (1). 2. Leaf size: mostly less than 2.5 mm (0), ca. 2.5 mm (1), mostly more than 2.5 mm (2). 3. Leaf cross section: keeled (0), concave to U-shaped (1). 4. Leaves plicate: no (0), yes (1). 5. Leaves contorted when dry: no (0), yes (1). 6. Papilosity: no or pseudo-papillose (0), low and flat (1), high and conic (2). 7. Papillose hairpoint/smooth lamina: no (0), yes (1). 8. Hyaline hairpoint: generally long (0), short or absent (1). 9. Decurrent hairpoint: no (0), yes (1). 10. Margin: entire (0), crenulate to dentate (1), serrate (2). 11. Margin stratosity: unistratose (0), bi- to multistratose (1). 12. Costa: simple (0), branched (1). 13. Costa thickness at base: two layers (0), 2–3 layers (1), more than three layers (2). 14. Costa extension: percurrent to excurrent (0), subpercurrent or less (1). 15. Presence of alar cells: no (0), yes (1), hyaline and inflated (2). 16. Basal marginal band: >10 cells (0), <10 cells or absent (1). 17. Propagules: no (0), yes (1). 18. Outer perichaetial leaves squarrose when wet: no (0), yes (1). 19. Inner perichaetial leaves strongly modified: no, normal above (0), yes (1). 20. Inner perichaetial leaves hyaline: only at base (0), almost throughout (1). 21. Hyaline point of inner perichaetial leaves: absent (0), present (1). 22. Innermost perichaetial leaves plicate: no (0), yes (1). 23. Seta length: generally less than 5 mm (0), generally more than 5 mm (1). 24. Seta papilosity: no (0), yes (1). 25. Seta torsion: to the left (0), to the right (1), to the left with 1–4 turns to the right below the capsule (2). 26. Urn shape: nearly spheric (0), elliptic (1), cylindrical (2). 27. Peristome teeth length: <500 µm (0), 500–1000 µm (1), >1000 µm (2). 28. Peristome teeth divided: yes (0), no (1). 29. Spore size: <20 µm (0), >20 µm (1). 30. Calyptra papillose: no (0), yes (1).