

GRIMMIACEAE SUBFAM. RACOMITRIOIDEAE (BRYOPHYTA) IN HUNGARY

PETER ERZBERGER, HALINA BEDNAREK-OCHYRA & RYSZARD OCHYRA

Abstract. The subfamily Racomitrioideae of the Grimmiaceae is represented in Hungary by seven species belonging to four genera, including *Bucklandiella affinis* (F. Weber & D. Mohr) Bednarek-Ochyra & Ochyra, *B. heterosticha* (Hedw.) Bednarek-Ochyra & Ochyra, *B. microcarpa* (Hedw.) Bednarek-Ochyra & Ochyra, *Codriophorus aciculare* (Hedw.) P. Beauv., *C. aquaticus* (Brid.) Brid., *Racomitrium lanuginosum* (Hedw.) Brid. and *Niphotrichum canescens* (Hedw.) Bednarek-Ochyra & Ochyra. All species are briefly described and illustrated and their distribution in Hungary is mapped. A key for determination of genera and species is provided. Some ecological, bryogeographical and conservation questions related to particular species are discussed. The following new statuses and combinations are proposed: *Codriophorus* P. Beauv. sect. *Hydrophilus* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra, *stat. et comb. nov.*, *Codriophorus* sect. *Depressi* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra, *stat. et comb. nov.*, and *Codriophorus* sect. *Andicola* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra, *stat. et comb. nov.*

Key words. *Bucklandiella*, *Codriophorus*, distribution, *Niphotrichum*, nomenclature, *Racomitrium*, taxonomy

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INTRODUCTION

This is the third and last paper in a series of publications dealing with the moss family Grimmiaceae in Hungary (Erzberger & Schröder 2008; Erzberger 2009a). It aims to summarize the present state of knowledge of the taxa and their distribution in Hungary, with particular reference to modern taxonomic concepts. It deals with genera and species of the subfamily Racomitrioideae which traditionally have been classified in a single heterogeneous genus, *Racomitrium* Brid.

The Grimmiaceae are a very distinctive family of acrocarpous mosses. Most species are xerophytes which colonize bare, usually dry and exposed rocks and stones, forming usually dark green, brown to blackish cushions or tufts. A much smaller group of grimmialean mosses comprises species associated with wet or damp habitats, growing on rocks along watercourses, at the edges of lakes and in seepage sites. Only occasionally some species may grow epiphytically or inhabit soil (Hastings & Ochyra 2007; Ochyra *et al.* 2008).

Although the Grimmiaceae exhibit remarkable variation and diversity of gametophyte and sporophyte characters, the family as a whole is a distinct, clearly separated, monophyletic entity, and its monophyly is well supported by molecular data (Tsubota *et al.* 2003; Hedderson *et al.* 2004; Streiff 2006; Hernández-Maqueda *et al.* 2007, 2008). It was subsequently divided into two subfamilies, Grimmioidae Broth. and Racomitrioideae Ochyra & Bednarek-Ochyra (Ochyra *et al.* 2003); molecular investigations confirmed that these are monophyletic lineages (Hernández-Maqueda *et al.* 2007, 2008). The latter subfamily is clearly diagnosed by the combination of some character states, including the *Racomitrium* type of peristome, the sinuose-walled epidermal cells of the vaginula, the consistent absence of a central duct in the stem, and the presence of a preperistome.

The Grimmiaceae are a medium-sized family consisting of *ca* 280 species, but the real number of species may be higher when *Schistidium* Bruch & Schimp., the largest genus of the family, is

taxonomically revised on a global scale. The delimitation of genera in the Grimmiaceae is still controversial and not satisfactorily resolved. Traditionally, the vast majority of species of subfamily Grimmioidae have been placed in the large and all-encompassing genus *Grimmia* Hedw. There have been many attempts to divide this genus into smaller, homogeneous and better-circumscribed genera: for example, *Guembelia* Hampe, *Dryptodon*, Brid., *Schistidium* Bruch & Schimp., *Orthogrimmia* (Schimp.) Ochyra & Żarnowiec and *Streptocolea* (I.Hagen) Ochyra (Ochyra *et al.* 2003). Despite the general tendency in bryology to split large and heterogeneous genera into smaller and better-circumscribed ones, most segregates have not gained wide acceptance in the recent literature (e.g., Hill *et al.* 2006; Meinunger & Schröder 2007; Maier 2010), although molecular evidence clearly indicates that *Grimmia* is at least a paraphyletic taxon (Streiff 2006). The only exception is *Schistidium*, which for a long time was merged with *Grimmia* but in recent decades has gained universal acceptance.

The traditionally conceived genus *Racomitrium* exhibits a wide spectrum of distinct morphologies in the structure of both gametophytes and sporophytes. In view of this, it was split into four segregates, including *Racomitrium* s.str., *Bucklandiella* Roiv., *Niphotrichum* Bednarek-Ochyra & Ochyra and *Codriophorus* P. Beauv. (Ochyra *et al.* 2003). These segregates have not yet gained wide acceptance in moss checklists (e.g., Erzberger & Papp 2004; Hill *et al.* 2006; Sabovljević *et al.* 2008; Papp *et al.* 2010). However, they are well supported by molecular data based on mitochondrial phylogenomics (Sawicki *et al.* 2015). Moreover, these studies have revealed the polyphyly of *Codriophorus* and the need for recognition of additional segregates: *Frisvollia* Sawicki, Szczecińska, Bednarek-Ochyra & Ochyra and *Dilutineuron* Bednarek-Ochyra, Sawicki, Ochyra, Szczecińska & Plášek (Bednarek-Ochyra *et al.* 2015). Hence this concept is adopted in the present account.

In the latest checklist of Hungarian mosses (Papp *et al.* 2010), seven species of the broadly understood *Racomitrium* are recognized: *R. affine* (F. Weber & D. Mohr) Lindb., *R. heterostichum*

(Hedw.) Brid., *R. obtusum* (Brid.) Brid., *R. aciculare* (Hedw.) Brid., *R. aquaticum* (Brid.) Brid., *R. lanuginosum* (Hedw.) Brid., and *R. canescens* (Hedw.) Brid. Two of these, *R. aciculare* and *R. lanuginosum*, have only recently been shown to occur in Hungary as a result of a revisionary study of the herbarium specimens (Erzberger 2009b, 2010). The first three species in this listing are now transferred to the genus *Bucklandiella* and the next two to *Codriophorus*; the last two belong to the genera *Racomitrium* s.str. and *Niphotrichum*, respectively.

Subsequent revision of herbarium specimens has revealed one more racomitrialean species in the Gerecse Mts, *Bucklandiella microcarpa* (Hedw.) Bednarek-Ochyra & Ochyra (Bednarek-Ochyra *et al.* 2011). However, a revision of the voucher specimens of *B. obtusa* (Brid.) Bednarek-Ochyra & Ochyra from Hungary showed that they actually represent epilose ecads of *B. heterosticha* (Hedw.) Bednarek-Ochyra & Ochyra. Accordingly, the final number of species of the Racomitrioidae remains the same as recorded in the latest checklist of Hungarian mosses (Papp *et al.* 2010).

All aforementioned species are well circumscribed and illustrated in the global monographic treatments, including those belonging to the genera *Niphotrichum* (Frisvoll 1983), *Bucklandiella* (Frisvoll 1988) and *Codriophorus* (Bednarek-Ochyra 2006), as well as in a monograph of the broadly conceived *Racomitrium* in Poland (Bednarek-Ochyra 1995).

MATERIAL AND METHODS

All available specimens of *Racomitrium*-like mosses collected in Hungary have been examined. These are housed mainly in the bryophyte herbaria of the Hungarian Natural History Museum in Budapest (BP), the Eszterházy Károly University in Eger (EGR) and the personal collections of the first author which are deposited in the Botanical Garden and Botanical Museum Berlin-Dahlem (B-Erzberger). Altogether *ca* 300 specimens have been studied (excepting duplicates also seen in various European herbaria).

The results were evaluated with respect to floristic regions according to Boros (1968), and distribution maps were prepared on the basis of the Central European mapping scheme (Niklfeld 1971). Open circles represent

pre-1980 collections, and black dots refer to collections from 1980 onwards. Information on habitat, associated bryophytes and vertical distribution refers to Hungarian material and it is taken from the labels, and in part is based on field observations.

The nomenclature of bryophytes other than the Racomitrioideae follows Papp *et al.* (2010), and for mosses not listed in the last checklist it follows Hill *et al.* (2006). The descriptions of species are based on the Hungarian material. The illustrations are taken mostly from Bednarek-Ochyra (1995); some details are illustrated from the Hungarian specimens.

SELECTED TAXONOMIC CHARACTERS

For a long time the traditionally conceived genus *Racomitrium* was considered to be a good example of taxonomic chaos which could hardly be unravelled using traditional taxonomic methods. This was because of the considerable environmentally induced plasticity of some characteristics that were considered to be of high taxonomic importance: for example, the type of branching, the presence or absence of hyaline hair-points, the color of plants, leaf shape, and the length and stratosity of laminal cells. These characters are actually less valuable in the taxonomy of racomitrialean mosses or have only some importance for circumscription of individual species. The anatomical structure of the costa, the shape of the leaf hair-point, supra-alar cells, leaf margins, the papillosity of laminal cells, perichaetial leaves, and the morphology of the peristome teeth have proven to be of greater importance in the taxonomy of the Racomitrioideae. The following is a brief review of the taxonomically important characteristics of genera in this subfamily, with special reference to Central European taxa.

LEAF MARGINS

In the majority of species the margins are entire and only occasionally are irregularly dentate [in *Codriophorus acicularis* (Hedw.) P. Beauv.], erose-dentate towards the leaf apex in the decurrent part of the hyaline hair-point [in *Racomitrium lanuginosum* (Hedw.) Brid.], or lumpy (not in European species) at the apex. They usually are variously recurved to revolute on both sides but mostly plane

below the apex, and only occasionally the recurvature extends to the apex (in *Bucklandiella obtusa*). In transverse section the margins are either always unistratose [in *Racomitrium lanuginosum* and *Niphotrichum canescens* (Hedw.) Bednarek-Ochyra & Ochyra] or variously polystratose, and the multistratose cells may be arranged in one to several rows. In some species, including *Bucklandiella heterosticha* and *B. microcarpa*, the leaf margin is essentially unistratose with only occasional bistratose spots, whereas in *B. affinis* (F. Weber & D. Mohr) Bednarek-Ochyra & Ochyra and *Codriophorus aquaticus* (Brid.) Brid. the margins are unistratose with fairly frequent bistratose spots, especially near the leaf apex. Only in *Bucklandiella sudetica* (Funk) Bednarek-Ochyra & Ochyra are the leaf margins predominantly bistratose. Unistratose leaf margins mostly occur in Central European populations of *Codriophorus acicularis*, whereas in the Iberian Peninsula plants with bistratose leaf margins and laminal cells are quite frequent.

LEAF APEX

In most species the leaf apex is acute to subacute; only in the genus *Codriophorus* are the apices usually narrowly rounded-obtuse (in *C. aquaticus*) to broadly rounded-obtuse (in *C. acicularis*). The leaf apex generally is terminated by a hyaline hair-point, but this is absent from species of *Codriophorus* and some ecads of *Bucklandiella heterosticha*. The hyaline hair-points are very variable in length and are usually erect, straight or flexuose; in some species they are recurved. In general they differ markedly between genera. The most peculiar hair-points occur in the genus *Racomitrium*. They are long-decurrent down the leaf margins, erose-dentate and strongly papillose. In *Niphotrichum* the hair-points are terete and vary from stout to capillaceous and spinulose to denticulate. They are strongly papillose (in *N. canescens*) to nearly epapillose throughout or only in the central and distal parts. In contrast, the hair-points in *Bucklandiella* are usually thin and delicate, hyaline to brown, flattened and canaliculate (in *B. heterosticha*, *B. microcarpa*, *B. affinis*) but in some species they are stouter and less canaliculate to nearly terete (in *B. sudetica*).

COSTA

In all genera of the Racomitrioideae the leaves are unicostate. The costa is generally unbranched; it is forked or branched at the apex in *Niphotrichum canescens* and sometimes weakly laterally spurred in the upper part in *Codriophorus acicularis*. It reaches the leaf apex in most species of *Bucklandiella*, whereas in *Codriophorus* and *Niphotrichum* it vanishes clearly below the apex; in some species (e.g., *N. canescens*) it extends $\frac{1}{2}$ – $\frac{3}{4}$ the length of the leaf and gradually merges into the laminal cells. The costa is gradually narrowed towards the apex.

In species of *Codriophorus* and *Niphotrichum* the costa is situated at the bottom of a groove which is shallow and wide-angled, whereas in *Racomitrium* and *Bucklandiella* the costa is canaliculate to keeled. The profile of the costa in transverse section is very variable and hence of limited diagnostic importance. In some species it is distinctly flattened (in *Niphotrichum canescens*, *Bucklandiella heterosticha* and often in *Codriophorus acicularis* and *C. aquaticus*) to reniform, crescent-shaped (in *Bucklandiella microcarpa*) or, rarely, semi-terete (in *B. sudetica* and *B. affinis*) and distinctly exposed and convex on the abaxial side. On the adaxial surface the costa is mostly concave and keeled or widely channeled. In transverse section it is bistratose (in *Niphotrichum*) to polystratose, and the number of cell layers is an important taxonomic character. Most species show internal differentiation of the costa into an abaxial stereid group and an adaxial row of guide cells considerably larger than the stereid cells, and their number is of high taxonomic importance.

LAMINAL CELLS

The laminal cells are greatly variable both in size and form. The most peculiar feature is the strongly sinuose or nodulose longitudinal walls of the laminal cells, generally considered to be one of the basic diagnostic characters of *Racomitrium* broadly understood. The shape of the cells is variable and ranges from short and subquadrate or shortly rectangular to elongate or linear. Generally the laminal cells become elongate towards

the leaf base. In all Central European species the leaf lamina is always unistratose (except for the margins); only occasionally, bistratose streaks can be found in some populations.

One of the most important characters is the papillosity of the laminal cells. In all species of *Niphotrichum* the laminal cells are strongly papillose on both surfaces with tall conical papillae, and this is a unique character throughout the whole family Grimmiaceae. In *Bucklandiella* these are entirely smooth, or else pseudopapillose due to their longitudinal cuticular ridges, giving the leaf surface a papillose appearance in transverse section. Finally, in *Racomitrium* and *Codriophorus* the leaf cells are covered by large flat papillae situated over the longitudinal cell walls and usually covering a large part of the lamina, leaving only a narrow slit in their median part.

ALAR AND SUPRA-ALAR CELLS

The angular cells in the Racomitrioideae either are not differentiated from other basal cells or are larger and form distinct and often decurrent auricles. They are especially distinct in *Niphotrichum*, where they are composed of many hyaline to yellowish hyaline cells forming a pellucid, convex and decurrent alar group. In contrast, supra-alar cells are of high taxonomic value. They are either similar to laminal cells or are hyaline, esinuose, and form marginal borders of various length composed of 1–2(–5) rows of cells. In Central European species, prominent, distinct basal marginal borders are found in *Bucklandiella microcarpa* and in all species of *Niphotrichum*.

PERICHAETIA

The perichaetial leaves are very diverse in the Racomitrioideae. The outermost are mostly similar to vegetative leaves, whereas the innermost are of special taxonomic importance at generic and infrageneric levels. Three types can be recognized: (1) not or slightly differentiated, hyaline and sheathing at the base, piliferous, and with areolation in the upper part similar to that in the vegetative leaves (in *Bucklandiella sudetica* and *Racomitrium lanuginosum*); (2) strongly modified and sheathing, hyaline below but not above, mostly epilose (in *Bucklandiella microcarpa*); and (3) strongly

modified, epilose and hyaline throughout (in all species of *Niphotrichum* and *Codriophorus*, *Bucklandiella affinis* and *B. heterosticha*).

SETA

The setae are mostly single per perichaetium, although in many species occasionally two or three sporophytes can be found in a single perichaetium (e.g., in *Racomitrium lanuginosum*). In all Racomitrioideae species the setae are entirely smooth, except in *Racomitrium lanuginosum* where they are strongly papillose. This character state is unique among the acrocarpous mosses. In *Bucklandiella* and *Codriophorus* the setae are dextrorse when dry (forming a right-handed helix, i.e. when moving upwards turning counter-clockwise as viewed from above), whereas in *Niphotrichum* and *Racomitrium* they are sinistrorse. The length of the setae is variable and has no special taxonomic value. They are usually more than 5 mm long, and consequently the capsules in all taxa of the Racomitrioideae are always exserted, never immersed.

PERISTOME

The peristome in the Racomitrioideae is haplolepidous, consisting of 16 teeth which are regularly or irregularly split into two or three branches. In *Niphotrichum* and *Racomitrium* the teeth are very long and regularly cleft to the base into two filiform prongs, whereas in *Bucklandiella* and *Codriophorus* the teeth are irregularly divided in the upper half only; less frequently the divisions are regular and extend below the middle. A basal membrane occurs in most species, usually 35–50 µm high. The length of the teeth varies considerably. The longest are found in *Niphotrichum* (to 2 mm) and *Racomitrium* (to 0.9 mm), and in other genera the length of the teeth varies from 200 to 800 µm. They are densely papillose on both surfaces but the basal membrane is less papillose and in some species nearly smooth.

HISTORICAL CONSIDERATIONS

The racomitrialean mosses are primarily associated with rocky habitats. In Central Europe they occur predominantly in the mountains. Because

Hungary is mainly lowland, suitable habitats are found mostly in the northern part of the country in some ranges of the Western Carpathians. The earliest documented collection is of *Niphotrichum canescens* from Vas County, collected on 24 September 1892 by J. Márton (BP 6475). This collector also contributed two additional collections which lack a collection date: *Racomitrium lanuginosum* (BP 6630, see below) and *Niphotrichum canescens* (BP 6626 as *R. lanuginosum*).

At the beginning of the twentieth century, collections of *Racomitrium*-like mosses were still scarce. They were made mainly by A. von Degen and J. Szurák (= J. Szepesfalvy), and some others. In subsequent decades there was an increase in the number of specimens collected, mainly by Á. Boros and L. Vajda; the most collections were made in the 1950s, coinciding with the exploration of the Börzsöny Mts (Vajda 1956, 1958, 1962, 1966), the number declining thereafter. Between 1980 and 1994 there is a conspicuous gap in collections of racomitrialean mosses in Hungary; only after 1995 the collecting activity of B. Papp and P. Erzberger contributed a number of new collections.

A SURVEY OF GENERA AND SPECIES

According to the present revision, the subfamily Racomitrioideae is represented in Hungary by seven species in four genera:

Bucklandiella Roiv.: *B. affinis* (F. Weber & D. Mohr) Bednarek-Ochyra & Ochyra, *B. heterosticha* (Hedw.) Bednarek-Ochyra & Ochyra and *B. microcarpa* (Hedw.) Bednarek-Ochyra & Ochyra;

Codriophorus P. Beauv.: *C. acicularis* (Hedw.) P. Beauv. and *C. aquaticus* (Brid.) Brid;

Racomitrium Brid.: *R. lanuginosum* (Hedw.) Brid.;

Niphotrichum Bednarek-Ochyra & Ochyra: *N. canescens* (Hedw.) Bednarek-Ochyra & Ochyra.

Bucklandiella Roiv.

Ann. Bot. Fenn. 9: 116. 1972.

This is the largest and taxonomically most difficult genus of the Racomitrioideae. It is also the most diverse morphologically; this gave rise

to its division into no fewer than nine sections (Bednarek-Ochyra 1995). However, it is a clearly defined and easily recognized genus, characterized by having smooth laminal cells which may eventually be pseudopapillose owing to numerous lengthwise cuticular ridges which make the leaf surface rugged and appearing papillose in transverse section. The smooth laminal cells are coupled with fairly short, lanceolate or triangular peristome teeth which are irregularly divided in the upper half into 2–3 or occasionally 4 branches, or sometimes undivided and solid to irregularly perforate along the median line. In addition, *Bucklandiella* is characterized by the following combination of traits: (1) ovate-triangular to narrowly lanceolate leaves; (2) always unbranched and percurrent costa; (3) if present, a hyaline hair-point that is smooth, denticulate to spinulose but never papillose; (4) 1- or 2(-4)-stratose leaf margins in one or several rows; (5) always smooth seta that is twisted to the right when dry; and (6) smooth calyptra.

The genus consists of ca 50 species distributed worldwide, nine of which occur in Europe. Three of these have been recorded in Hungary, including *Bucklandiella affinis* and *B. heterosticha* which belong to sect. *Laevifoliae* (Kindb.) Bednarek-Ochyra & Ochyra, and *B. microcarpa* in sect. *Marginatae* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra.

Bucklandiella affinis (F. Weber & D. Mohr) Bednarek-Ochyra & Ochyra Figs 1 & 2

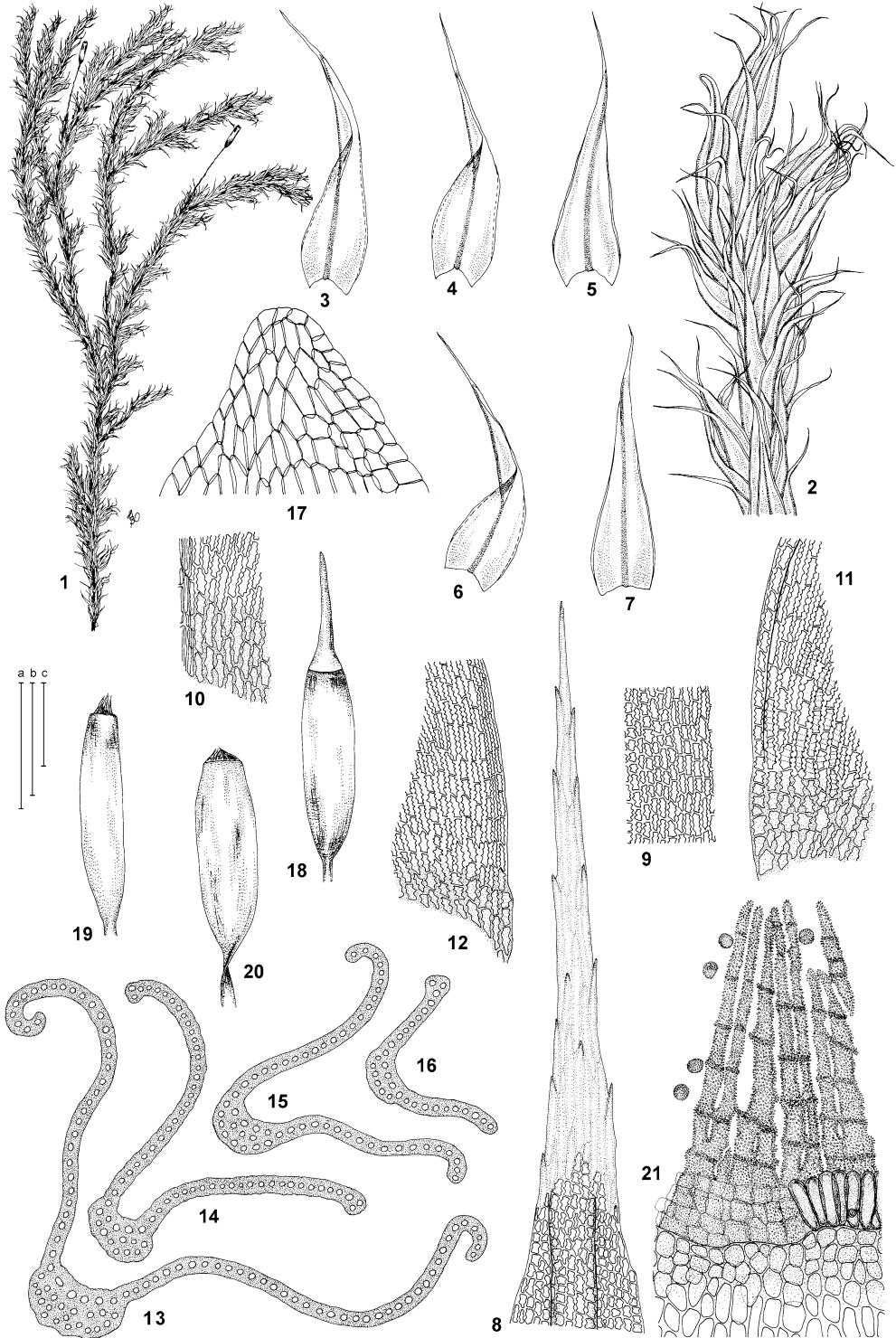
Racomitrium affine (F. Weber & D. Mohr) Lindb.; *R. heterostichum* (Hedw.) Brid. var. *alopecurum* Huebener; *R. heterostichum* var. *gracilescens* Bruch & Schimp.; *R. heterostichum* var. *limprichtii* Loeske

Plants medium-sized, rather slender, loosely caespitose, yellowish green to olivaceous or brownish above, brownish or blackish brown below. *Stems* 5–7 cm, erect to decumbent, subpin-

nately branched. *Leaves* loosely appressed, straight or secund when dry, erect-spreading to spreading when moist, lanceolate, channeled along costa, 2.3–3.2 mm (with hair-point) long, 0.5–0.8 mm wide; *margins* entire, smooth, recurved to revolute on both sides towards apex, unistratose distally or with bistratose patches, rarely predominantly bistratose near apex in 1 cell row; *hair-point* absent or present, erect-flexuose, more yellowish than whitish, flattened, (0.1–)0.5–1.1 mm, low-denticulate at margins and sometimes spinulose on dorsal side, usually not or slightly decurrent; *costa* percurrent or shortly excurrent into hair-point, prominently convex abaxially, 80–100(–110) µm wide at base, 60–70 µm wide distally, 3–4-stratose with 5–7 adaxial guide cells in proximal portion, 3-stratose in middle with 3–4 adaxial eurycysts and 2–3-stratose distally with 2–3 guide cells on adaxial side; *laminal cells* unistratose, not or slightly bulging on both adaxial and abaxial sides, rectangular to isodiametric in distal and middle parts, 10–25 µm long, 7–10 µm wide; *basal laminal cells* elongate, 15–35 µm long, 7–10 µm wide, with thick and sinuose-nodulose walls; *alar cells* usually slightly differentiated, yellowish, sometimes forming a small auriculate group of wider cells; *supra-alar cells* undifferentiated, not forming a marginal border. *Inner perichaetial leaves* ovate, hyaline, epilose. *Setae* brown, 4–10 mm. *Capsules* brown, somewhat lustrous, shortly cylindrical to obloid, 1.5–3.2 mm long, 0.6–0.8 mm wide; *operculum* long-rostrate, to 1.5 mm; *exothecial cells* irregularly rectangular; *peristome teeth* 16, lanceolate, 200–400 µm, reddish brown, papillose, mostly discontinuously divided into 2 prongs by median perforations, arising from a low basal membrane, to 30 µm high. *Spores* 12–20 µm, pale brown, finely papillose. *Calyptra* cucullate, smooth, 4–5-lobed at base.

NOTES. *Bucklandiella affinis* is closely related

Fig. 1. *Bucklandiella affinis* (F. Weber & D. Mohr) Bednarek-Ochyra & Ochyra. 1 – habit; 2 – portion of branch, dry; 3–7 – leaves; 8 – hyaline hair-point; 9 – mid-leaf cells; 10 – basal leaf cells; 11 & 12 – alar and supra-alar cells; 13–16 – leaf cross sections, sequentially from base to apex; 17 – uppermost cells of innermost perichaetial leaf; 18 – operculate capsule, wet; 19 – deoperculate capsule, wet; 20 – deoperculate capsule, dry; 21 – portion of peristome, spores and exothecial cells at orifice. [1 from *Klinggraeff s.n.*, 22 Jun 1884; 2–17, 21 from *Klinggraeff s.n.*, 19 Jun 1884; 18–20 from *Graw 4971*; all in KRAM]. Scale bars: a = 100 µm (8–17, 21); b = 1 cm (1) and 1 mm (3–7, 18–20); c = 1 mm (2).



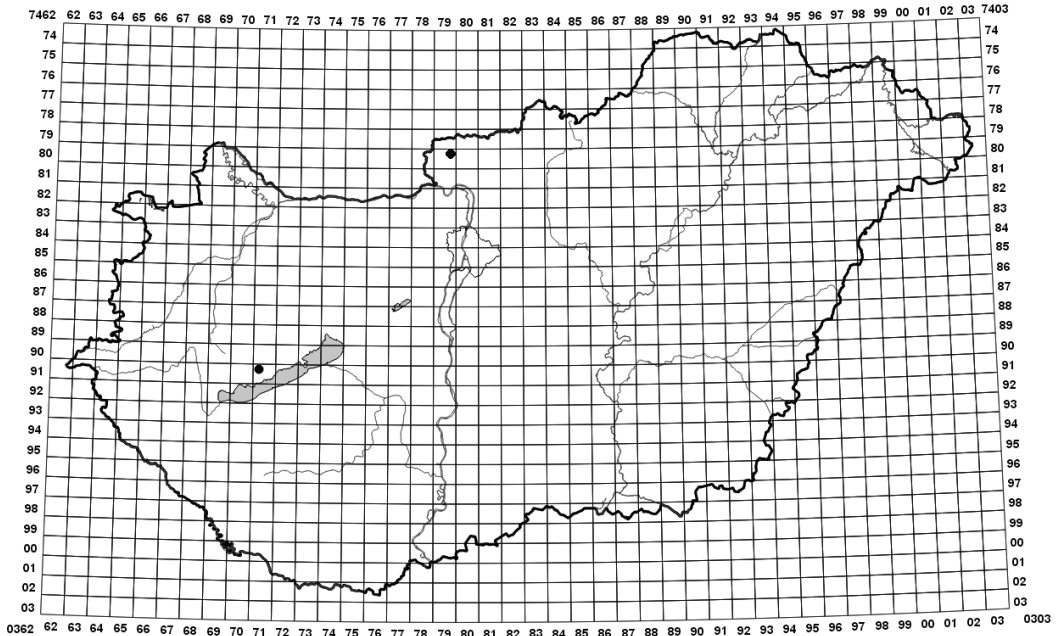


Fig. 2. Distribution of *Bucklandiella affinis* (F. Weber & D. Mohr) Bednarek-Ochyra & Ochyra in Hungary.

to and likely to be mistaken for *B. heterosticha* but they differ by their gross morphology, the former being a more yellowish green plant, the latter being a grayish green and often hoary plant. However, the safest character distinguishing the two species is the costal anatomy. In *B. affinis* the costa is tristratose in the middle and in the lower distal part of the leaf and distinctly convex on the abaxial side, whereas *B. heterosticha* has a canaliculate costa which is bistratose in the middle and in the lower distal part of the leaf and usually flattened on the abaxial side. All Hungarian specimens are in fine fruiting condition.

HABITAT: shaded andesite rock, northern aspect, in forest.

ASSOCIATED BRYOPHYTES: *Dicranum scoparium* Hedw., *Grimmia hartmanii* Schimp., *Hypnum cupressiforme* Hedw., *Polytrichum formosum* Hedw., *P. piliferum* Hedw., and *Codriophorus aquaticus*.

VERTICAL DISTRIBUTION: 650–700 m a.s.l.

SELECTED SPECIMENS EXAMINED: BÖRZSÖNY MTS: 8079.2 Comit. Hont. In rupibus andesit. sept. silvat.

supra vallem rivi Bacina = Bacsó-patak prope Királyháza, 700 m, 17.06.1958, leg. Á. Boros (BP 80545, 113723, 113724, 13725 & 113726 – all as *Racomitrium heterostichum* var. *limprichtii* Loeske). BALATON UPLANDS: 9171.1 Veszprém County, Mindszentkállya, Köves-hegy, basalt boulder scree, 340 m, N 46°52'34.2", E 017°31'33.4", 28.09.2014, leg. P. Erzberger & Cs. Németh (B-Erzberger 18909, KRAM, hb. Németh 6228).

Bucklandiella heterosticha (Hedw.) Bednarek-Ochyra & Ochyra Figs 3 & 4

Racomitrium heterostichum (Hedw.) Brid.; *R. obtusum* auct. hung. non (Brid.) Brid.; *R. heterostichum* fo. *obtusum* auct. hung. non (Brid.) Boulay; *R. heterostichum* var. *obtusum* auct. hung. non (Brid.) Delogn.

Plants medium-sized, fairly slender but rigid, in loose or dense tufts or rather loose mats, often hoary and grayish (owing to the long hair-points) to olivaceous in the upper part, dark brown to blackish below. *Stems* 2–6 cm, prostrate to ascending, sparingly to copiously branched, often with many short lateral branchlets. *Leaves* loosely imbricate, twisted or secund when dry,

erect-spreading to patent when moist, lanceolate, channeled along costa, 2.3–3.5 mm long (with hair-points), 0.5–0.8 mm wide; *margins* unistratose throughout, with some bistratose patches distally, recurved on both sides towards apex, sometimes strongly so on one side and usually less recurved on the other side; *hair-point* absent to present, erect, hyaline, distinctly flattened, 0.5–1.5 mm, often decurrent down margins, distinctly denticulate at margins, often somewhat flexuose and wrinkled and spinulose on abaxial side; *costa* percurrent or subpercurrent, channeled on adaxial side throughout, weakly convex abaxially, 80–120 µm wide near base, 40–65 µm wide distally, 3–4-stratose with 4–9 enlarged adaxial guide cells at base, 2(–3)-stratose with 3–8 adaxial cells in mid-leaf and bistratose distally with 2–4 adaxial cells; *laminal cells* unistratose, smooth throughout; *basal cells* elongate, 15–35 µm long, 8–10 µm wide, with thick, sinuose-nodulose walls; *alar cells* not or weakly differentiated, yellowish; *supra-alar cells* not differentiated; *upper* and *mid-leaf cells* irregularly quadrate to rectangular, 10–25 µm long, 8–10 µm wide, usually becoming oblate at margins in upper part. *Sporophytes* not observed in Hungarian material. *Inner perichaetial leaves* (1–4) hyaline, obtuse, epilose. *Seta* brown, 4–9 mm. *Capsule* brown, shortly cylindrical, 1.5–3.0 mm long, 0.5–0.8 mm wide; *operculum* long-beaked, to 1 mm; *peristome teeth* 250–380 µm, yellowish brown, papillose, irregularly divided into 2 or rarely 3 branches in distal part, arising from a low, 35–45 µm high, basal membrane. *Spores* 14–18 µm. *Calyptra* cucullate, smooth, divided into 4–5 lobes at base.

NOTES. *Bucklandiella heterosticha* is closely related to *B. affinis*. The differences between them are discussed under that species. Some Hungarian specimens are distinctly epilose and are the only known specimens of this species lacking hair-points. They appear similar to *B. obtusa* but the leaf margins are weakly recurved and unistratose and the costa is predominantly bistratose, occasionally tristratose. These plants resemble also *Codriophorus aquaticus* and have often been misidentified as that species. How-

ever, the entirely smooth laminal cells immediately exclude any relationship of these specimens with *C. aquaticus*.

Bucklandiella heterosticha is characterized by a combination of several stable characters; a broad costa which is canaliculate throughout the adaxial side and moderately convex on the abaxial side, with as many as 5–9 enlarged guide cells on the adaxial side in the basal part; unistratose leaf margins with occasional bistratose patches above that are recurved to the apex, at least on one side; long, erect and weakly flexuose hyaline hair-points that are distinctly flattened and low-denticulate and spinulose; sinuose-nodulose, moderately thick-walled basal leaf cells; undifferentiated alar cells and basal marginal border; and strongly modified, entirely hyaline innermost perichaetial leaves.

HABITAT: siliceous, generally shaded andesite rock.

ASSOCIATED BRYOPHYTE: *Hypnum cupressiforme*.

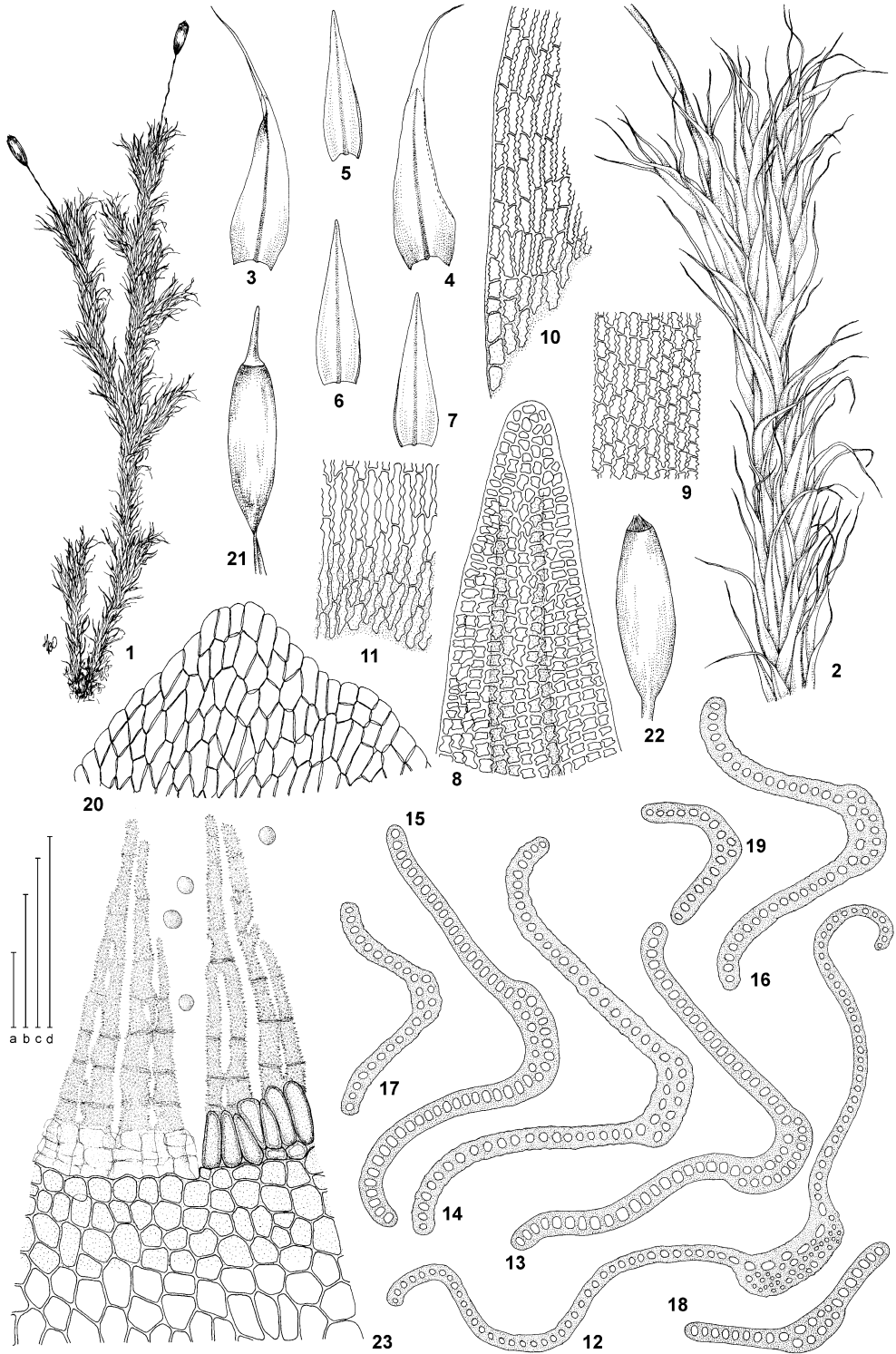
VERTICAL DISTRIBUTION: 600–800 m a.s.l.

SELECTED SPECIMENS EXAMINED: ZEMPLÉN MTS: 7594.3 Borsod-Abaúj-Zemplén County, Zemplén Mts, Kis-Péter-mennykő peak at Regéc, andesite rocks N48°25'00.2", E21°23'55.2", 632 m, 26.05.2007, *leg. B. Papp* (BP 174944); Comit. Abauj-Torna. In *Rupibus umbrosis cacuminis montis Kispétermenkő prope pag. Pálháza, montes Sátorhegység, 700 m, 14.07.1957, leg. L. Vajda* (BP 58022, 113732 & 113734). MÁTRA MTS: 8185.2 Heves County, Remete-bérc above Mátraháza, N of Széles parlag, andesite rockwalls, 780–800 m, 05.08.2000, *leg. B. Papp & P. Erzberger* (B-Erzberger 6316, BP 175286). Börzsöny Mts: 8079.2 Pest County, Kemence-Királyháza, Bacsina valley south of Királyháza, on rock outcrops (andesite), on the top of a cryoplanacious ridge, 04.04.1994, *leg. & det. P. Erzberger*, conf. S. Caspary & H. Bednarek-Ochyra (B-Erzberger 1089, KRAM).

Bucklandiella microcarpa (Hedw.) Bednarek-Ochyra & Ochyra Figs 5 & 6

Racomitrium microcarpon (Hedw.) Brid.; *R. ramulosum* Lindb.

Plants medium-sized, forming loose tufts, yellowish to olive green in the upper part, brown below. *Stems* erect-ascending, 2–5 cm, copiously



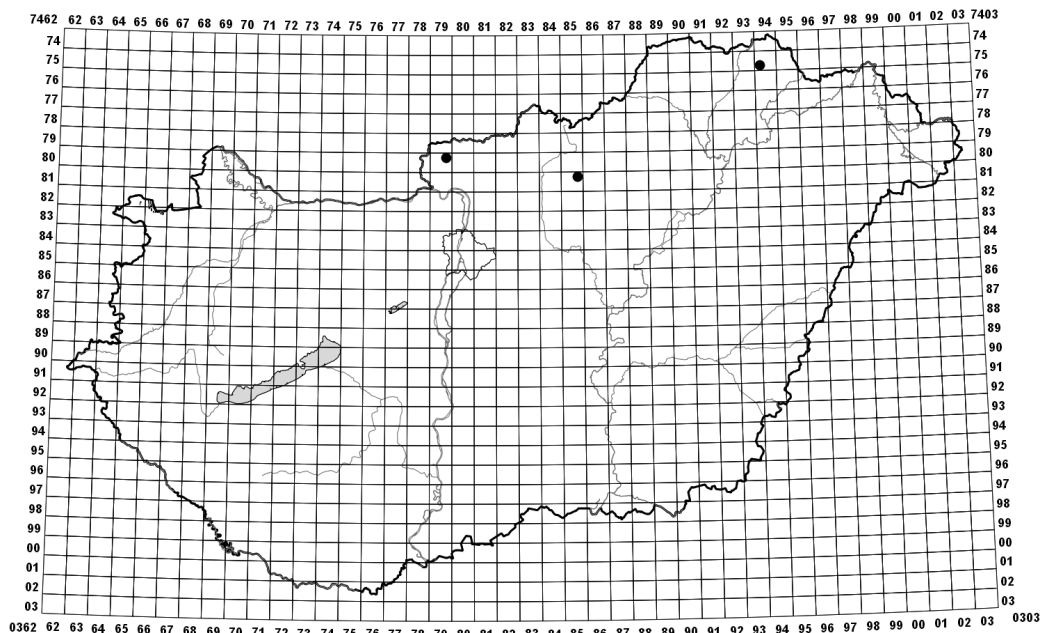
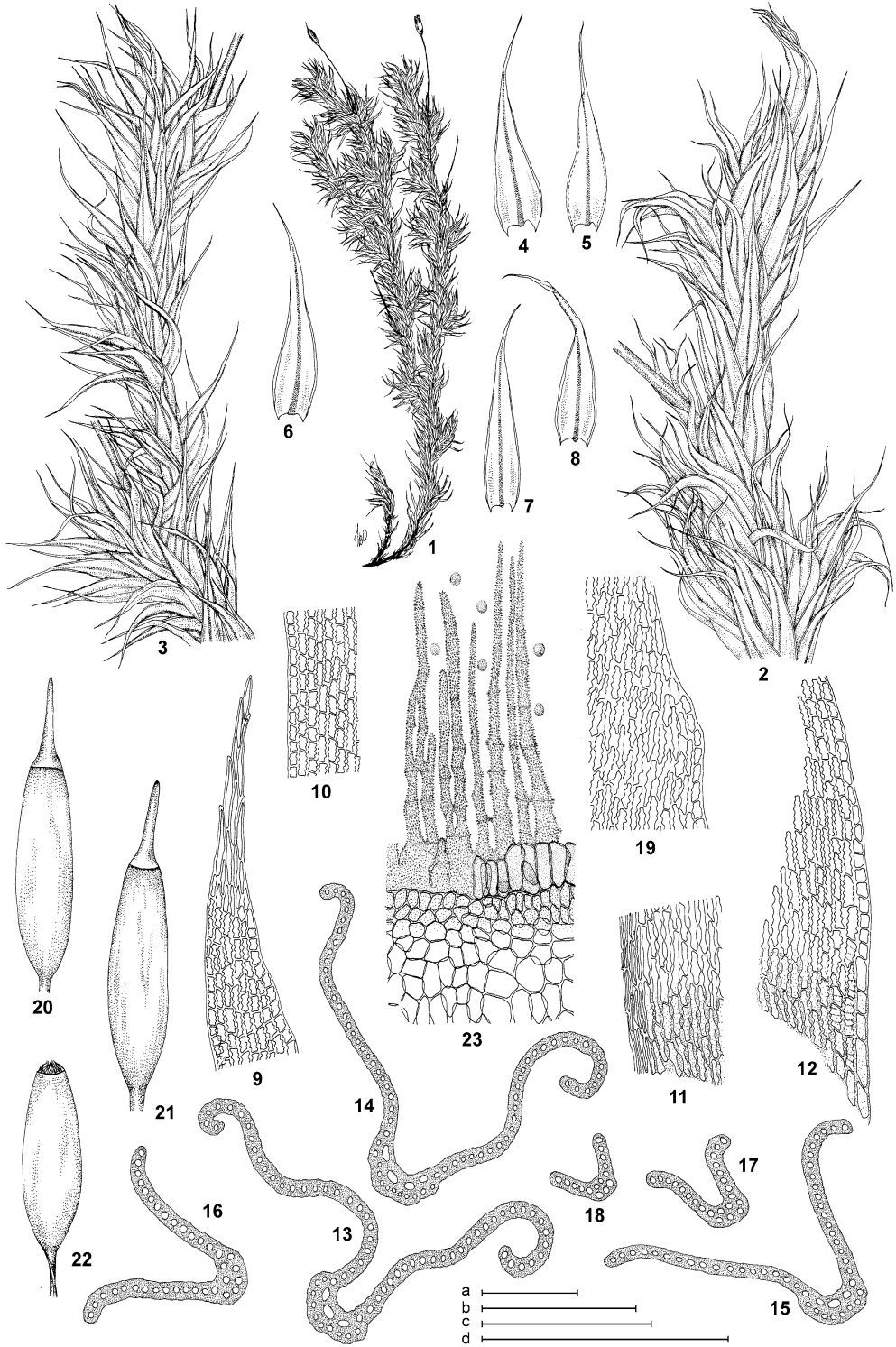


Fig. 4. Distribution of *Bucklandiella heterosticha* (Hedw.) Bednarek-Ochyra & Ochyra in Hungary.

ramified, mostly with short lateral, tuft-like sub-pinnate branchlets giving the plants a nodose appearance. *Leaves* loosely imbricate and secund when dry, erect-spreading to recurved when moist, 2.0–3.2 mm long, 0.5–0.7 mm wide, keeled in distal part, narrowly canaliculate in proximal part, piliferous; *hair-point* erect, hyaline, capillaceous, flexuose, 0.4–0.8 mm, not or slightly decurrent down leaf margins; *margins* broadly recurved to revolute on one or both sides for $\frac{1}{2}$ – $\frac{3}{4}$ the leaf length, unistratose throughout; *costa* percurrent, convex abaxially, 60–80 μ m wide near base, 40–55 μ m wide distally, 2–3-stratose near base with 3–4 markedly enlarged guide cells, 2–3-stratose in middle with 2–3 large guide cells and bis-tratose distally with 2 adaxial cells; *laminal cells* unistratose, smooth to distinctly pseudopapillose;

upper and *median* cells strongly sinuose, rectangular, 20–30 μ m long, 9–10 μ m wide, becoming shorter or oblate towards margins; *basal cells* elongate to linear, 25–95 μ m long, 8–12 μ m wide, with strongly incrassate and porose walls; *alar cells* not differentiated; *basal marginal cells* quadrate to short-rectangular, esinuose, hyaline, pellucid, forming uniseriate border of 10–20 cells. *Sporophytes* not observed in Hungarian material. *Innermost perichaetial leaves* (4–6) markedly modified, ovate, acuminate, epilose, hyaline to yellowish hyaline in proximal half, chlorophyllose in distal half with strongly incrassate cell walls. *Setae* dark red to reddish brown, 4–8 mm. *Capsules* obloid-cylindrical to elongate-ovoid, 1.5–2.0 mm long, 0.3–0.6 mm wide, brown, dull; *peristome teeth* yellow-reddish, 310–350 μ m, papillose, irregularly

Fig. 3. *Bucklandiella heterosticha*. 1 – habit; 2 – portion of branch, dry; 3–7 – leaves; 8 – leaf apex of epilose plant; 9 – mid-leaf cells; 10 – alar and supra-alar cells; 11 – basal juxtacostal cells; 12–19 – leaf cross sections, sequentially from base to apex; 20 – apical cells of innermost perichaetial leaf; 21 – operculate capsule, dry; 22 – deoperculate capsule, wet; 23 – portion of peristome, spores and exothecial cells at orifice. [1–4, 14, 16, 17, 19, 20, 22, 23 from *Golenz s.n.*, 9 Apr 1864; 5–8, 13, 15, 18 from *Vajda s.n.*, 17 Jul 1957; 9–12 from *Ochyra s.n.*, 23 Jun 1974; 21 from *Žmuda s.n.*, Jul 1910; all in KRAM]. Scale bars: a = 1 mm (2–7, 21, 22); b = 100 μ m (8–19); c = 1 cm (1); d = 100 μ m (20, 23).



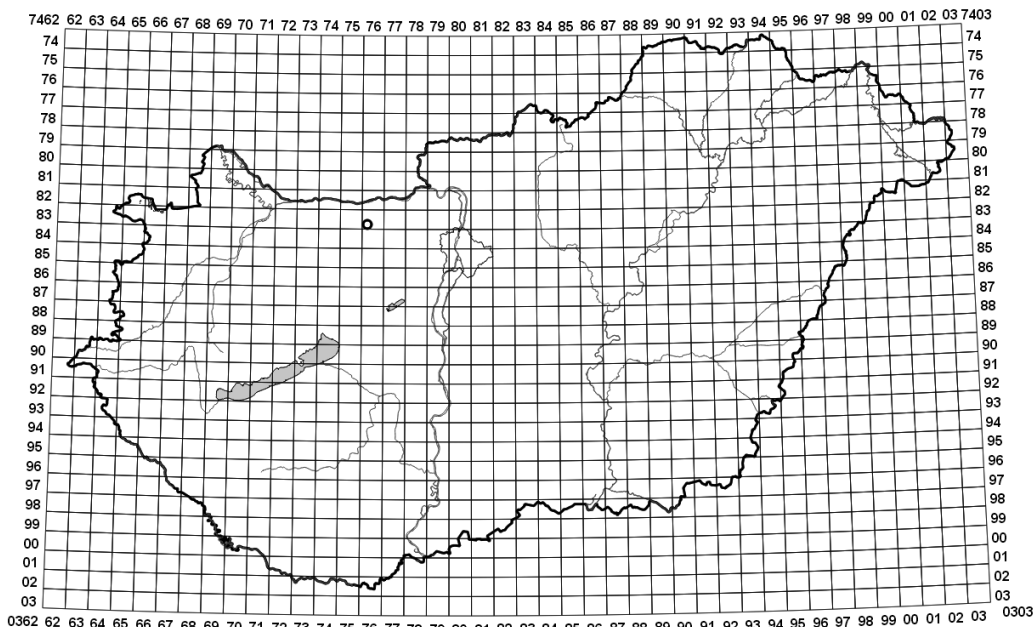


Fig. 6. Distribution of *Bucklandiella microcarpa* (Hedw.) Bednarek-Ochyra & Ochyra in Hungary.

split nearly to base into 2 branches, without or with low basal membrane, 10–15 µm high. *Operculum* conic-rostrate, to 1 mm, with straight or slanted beak. *Spores* 12–14 µm in diameter.

NOTES: *Bucklandiella microcarpa* is a very distinct and unmistakable species which is immediately recognized by its long, pellucid basal marginal border of straight-walled cells, basal laminal cells which are esinuose and have porose and prominently thickened lateral walls, and markedly modified innermost perichaetial leaves, with chlorophyllose distal cells having strongly incrassate walls and basal laminal cells that are esinuose and have porose and prominently thickened lateral walls.

HABITAT: not available.

ASSOCIATED BRYOPHYTE: *Polytrichum formosum*.

VERTICAL DISTRIBUTION: 270–300 m a.s.l.

SPECIMEN EXAMINED: GERECE Mts: 8376.3 [Komárom-Esztergom County, Tatabánya], Kiszgalla, Tarjáni mélyút, 07.05.1938, leg. L. Vajda (BP 160790 as *R. heterostichum*) (see also Bednarek-Ochyra et al. 2011).

Codriophorus P. Beauv.

Mém Soc. Linn. Paris 1: 445. 1822.

This genus is characterized by having large, flat papillae distributed over the longitudinal cell walls and covering a major part of the lumina, leaving only a narrow central slit. Additionally, the leaves lack a hyaline hair-point or occasionally are minutely hyaline tipped, the calyptra is densely



Fig. 5. *Bucklandiella microcarpa*. 1 – habit; 2 – portion of branch, wet; 3 – portion of branch, dry; 4–8 – leaves; 9 – hyaline hair-point; 10 – mid-leaf cells at margin; 11 – basal leaf cells; 12 – alar and supra-alar cells; 13–18 – leaf cross sections, sequentially from base to apex; 19 – upper cells of innermost perichaetial leaf; 20 & 21 – operculate capsules, wet; 22 – deoperculate capsule, dry; 23 – portion of peristome, spores and exothecial cells at orifice. [1–3 from *Žmuda* 116; 4–18, 22, 23 from *Bornmüller s.n.*, 16 May 1932; 19 from *Ochyra* 957; 20, 21 from *Limpricht* 63; all in KRAM.] Scale bars: a = 1 cm (1); b = 1 mm (20–22) and 100 µm (9–18); c = 1 mm (2) and 100 µm (19, 23); d = 1 mm (3–8).

papillose above, the costa vanishes well below the leaf apex, the innermost perichaetial leaves are epilose and the seta is dextrorse. *Codriophorus* was monographed by Bednarek-Ochyra (2006), who included 15 species in the genus. However, subsequent molecular studies on this genus based on complete plastomes and mitogenomes as well as nuclear rRNA gene clusters (Sawicki *et al.* 2015), and on analysis of nuclear ITS and plastid *rps4-trnL* and *trnK/matK-psbA* sequences (Larrain *et al.* 2013), revealed its polyphyletic nature. Accordingly, two segregates have been split from the broadly understood *Codriophorus*: the monotypic *Frisvollia* Sawicki, Szczecińska, Bednarek-Ochyra & Ochyra (Sawicki *et al.* 2015) and *Dilutineuron* Bednarek-Ochyra, Sawicki, Ochyra, Szczecińska & Plášek which consists of five species (Bednarek-Ochyra *et al.* 2015).

Codriophorus s.str. is diagnosed by the simple to irregularly dichotomously branched stems, always lacking short lateral tuft-like branchlets. The leaves vary from lingulate to broadly ovate or ovate-lanceolate and are concave to broadly canaliculate-concave. The leaf margins are variously recurved on one or both sides in the lower half (rarely to three quarters). The costa is multistratose and distinctly convex abaxially in the median and lower parts, with a strongly developed stereid band on the abaxial side in the lower part and a single layer of enlarged adaxial guide cells appearing as a row in cross section. It is situated at the bottom of a shallow and wide-angled groove and generally is very broad, 85–200 µm wide at the base. The laminal cells are mostly isodiametric in the distal portion and the setae are dextrorse.

The narrowly conceived *Codriophorus* consists of nine species distributed mainly in the Northern Hemisphere, with one species restricted in its range to the northern Andes in South America. It

is divided into four sections: *Codriophorus* sect. *Codriophorus*, *C.* sect. *Hydrophilus* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra, *stat. et comb. nov.* (BASIONYM: *Racomitrium* Brid. subsect. *Hydrophilus* Bednarek-Ochyra, *Fragm. Florist. Geobot. Ser. Polon.* 2: 157. 1995 [‘-um’]), *C.* sect. *Depressi* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra, *stat. et comb. nov.* (BASIONYM: *Codriophorus* P. Beauv. subsect. *Depressi* Bednarek-Ochyra, *Taxon. Monogr. Codriophorus*: 151. 2006) and *C.* sect. *Andicola* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra, *stat. et comb. nov.* (BASIONYM: *Racomitrium* Brid. subsect. *Andicola* Bednarek-Ochyra, *Fragm. Florist. Geobot. Ser. Polon.* 2: 64. 1995).

Two species of *Codriophorus* are known to occur in Hungary: *C. acicularis* which represents the type section of the genus, and *C. aquaticus* belonging within sect. *Hydrophilus*.

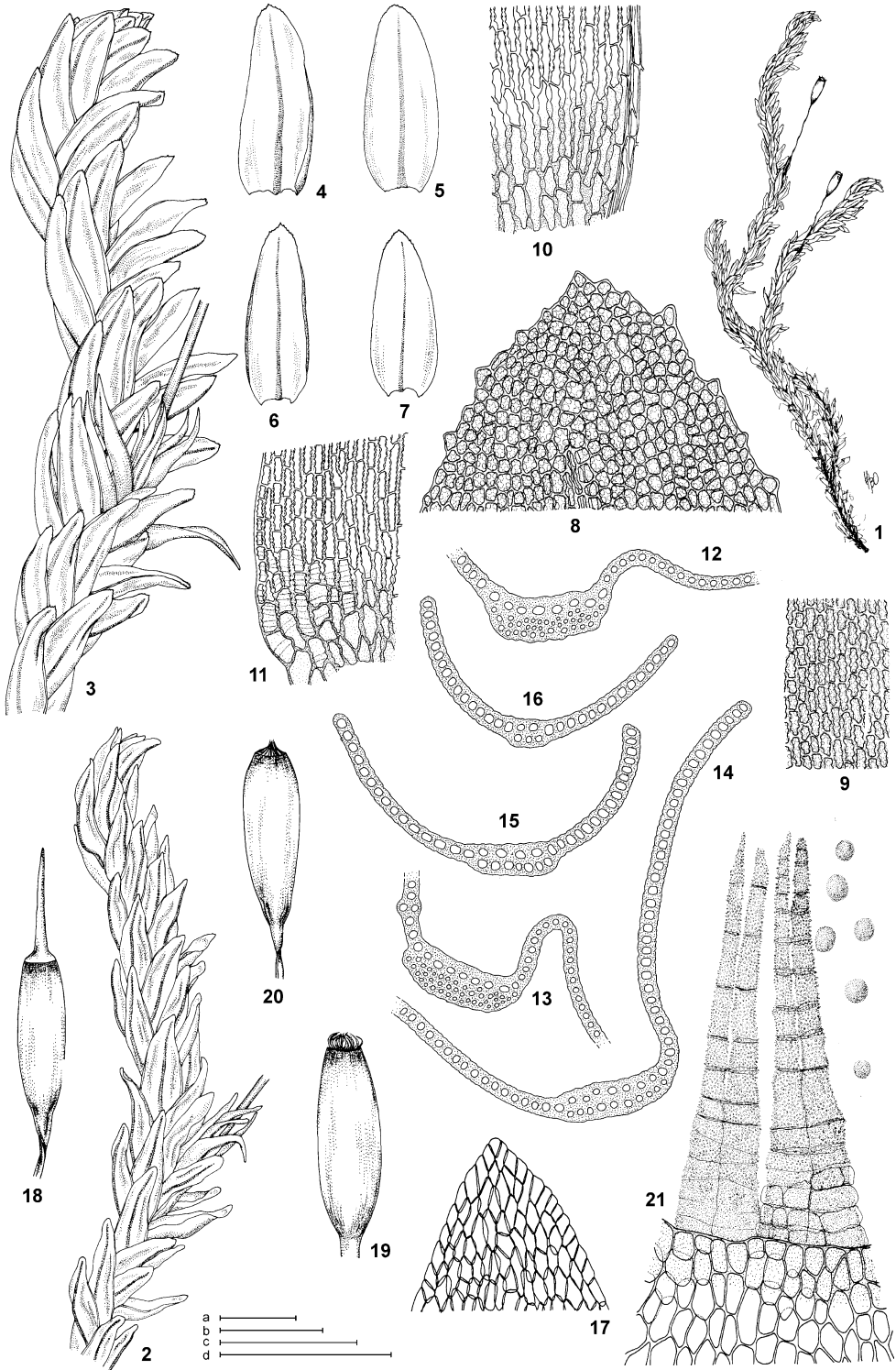
Codriophorus acicularis (Hedw.) P. Beauv.

Figs 7 & 8

Racomitrium aciculare (Hedw.) Brid.

Plants mostly coarse, forming loose tufts or mats, olivaceous above, brown to blackish brown below. *Stem* ascending, 2–5 cm, repeatedly forked or dichotomously branched, rigid. *Leaves* erect-appressed, secund when dry, erect-spreading when wet, lingulate or elliptical to oblong-ovate, 2.1–2.8 mm long, 1.0–1.2 mm wide, subacute, rounded to broadly rounded-obtuse at apex, mucous; *margins* recurved on both sides in proximal half, plane, erect or somewhat inflexed in distal part, unistratose, entire for ca $\frac{3}{4}$ – $\frac{7}{8}$ of distance to apex, bluntly or sharply toothed or erose-dentate to sinuate at apex; *costa* subpercurrent, entire, 70–110 µm wide near base, in cross section 2–3-stratose, flat adaxially and reniform or lunate, weakly to distinctly convex on abaxial

Fig. 7. *Codriophorus acicularis* (Hedw.) Bednarek-Ochyra & Ochyra. 1 – habit; 2 – portion of branch, dry; 3 – portion of branch, wet; 4–7 – leaves; 8 – leaf apex; 9 – mid-leaf cells; 10 – basal leaf cells; 11 – alar and supra-alar cells; 12–16 – costa and leaf cross sections, sequentially from base to apex; 17 – uppermost cells of innermost perichaetial leaf; 18 – operculate capsule, dry; 19 – deoperculate capsule, wet; 20 – deoperculate capsule, dry; 21 – portion of peristome, spores and exothecial cells at orifice. [1, 17, 19 from *Ochyra s.n.*, 23 Jun 1973; 2, 3, 8 from *Ochyra 629*; 4–7, 9–11, 18, 20, 21 from *Lisowski 93776*; 12–16 from *Shlyakov s.n.*, 27 Jul 1957; all in KRAM.] Scale bars: a = 1 mm (2–7, 18–20); b = 100 µm (12–16); c = 100 µm (8–11, 17, 21); d = 1 cm (1).



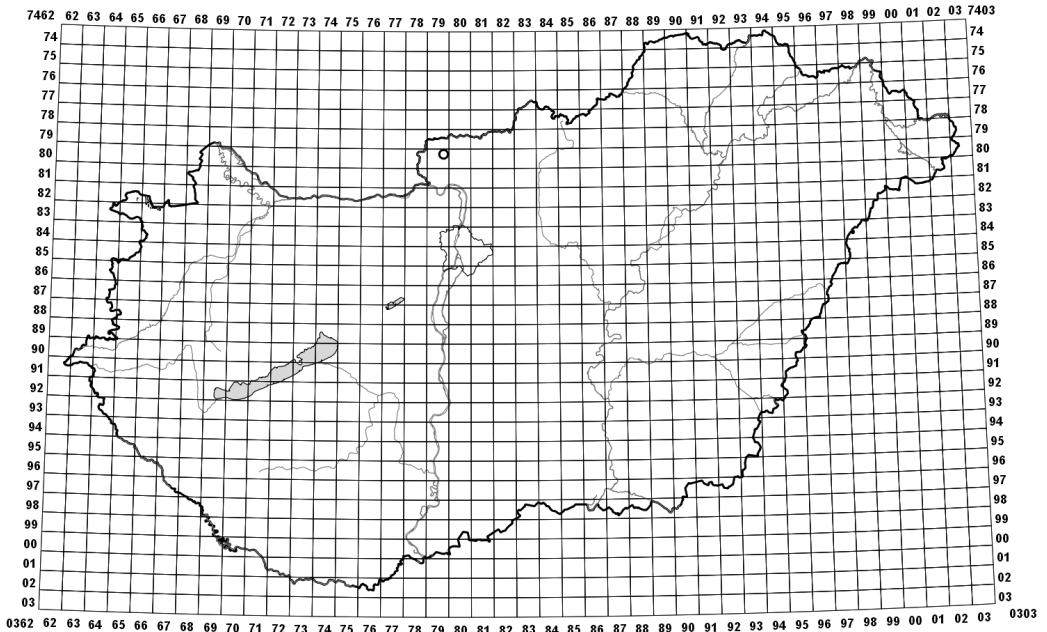


Fig. 8. Distribution of *Codriophorus acicularis* (Hedw.) Bednarek-Ochyra & Ochyra in Hungary.

side, with 3–7 ventral epidermal cells in distal and median parts, plano-convex and strongly flattened or crescent-shaped abaxially, 3–6-layered in basal part, situated in a shallow and wide-angled furrow, with 5–10 enlarged adaxial guide cells in a single layer and 2–5 layers of small, thick-walled sclerenchymatous cells forming a distinctly convex stereid band on abaxial side; *laminal cells* unistratose and papillose throughout, isodiametric, from irregularly rounded or rounded hexagonal to shortly rectangular, 5–15 μm long, 6–10 μm wide in upper and median parts, becoming long rectangular to linear, with strongly incrassate, nodulose and porose longitudinal walls, 25–55 μm long, 8–10 μm wide in basal part; *alar cells* subquadrate to short-rectangular, with rather thin to strongly incrassate, straight or sinuose walls, forming distinct, inflated or flat, brownish yellow or brown, somewhat decurrent auricles; *supra-alar cells* shortly rectangular, chlorophyllous, thick- and sinuose-walled, not differentiated from adjacent laminal cells. *Sporophytes* not found in Hungarian material. *Inner perichaetial leaves* hyaline to yellowish hyaline throughout. *Seta* blackish or reddish

brown, 4–15 mm, twisted to the right on drying. *Capsule* brown, obloid to shortly cylindrical, 1.5–2.5 mm, smooth; *peristome teeth* lanceolate, 350–450 μm , yellowish brown to dark reddish brown, densely low- or spiculate-papillose, bifid down to the middle or two thirds of their length. *Spores* 15–20 μm in diameter, globose to ellipsoid, finely papillose. *Calyptra* conic-mitrate, dark brown, verrucose at apex, naked, 4–5-lobed at base.

NOTES. *Codriophorus acicularis* is central to a group of four species constituting the type section of the genus. It is one of the most distinctive and easily recognisable species of racomitrialean mosses on account of its lingulate or elliptical to broadly ovate leaves with subacute to broadly rounded apices which are irregularly bluntly or sharply and coarsely dentate or eroso-dentate. Additionally, the costa ceases below the apex and is situated at the bottom of a shallow, wide-angled and open groove. It is a hydrophilous moss, usually growing on blocks in stream beds that are submerged or periodically washed by wave action.

HABITAT: shaded andesite rock.

ASSOCIATED BRYOPHYTE: *Grimmia hartmanii*.

VERTICAL DISTRIBUTION: 700 m a.s.l.

SPECIMEN EXAMINED: BÖRSZÖNY MTS: 8079.2 Nógrád. In rupibus umbrosis montis Rakottyásbérc supra vallem rivi Bacsinapatak prope Királyháza, montes Börzsöny, 23.05.1958, leg. L. Vajda [originally as admixture to *Grimmia hartmanii*, BP 59411, see Erzberger 2009b] (BP 175909).

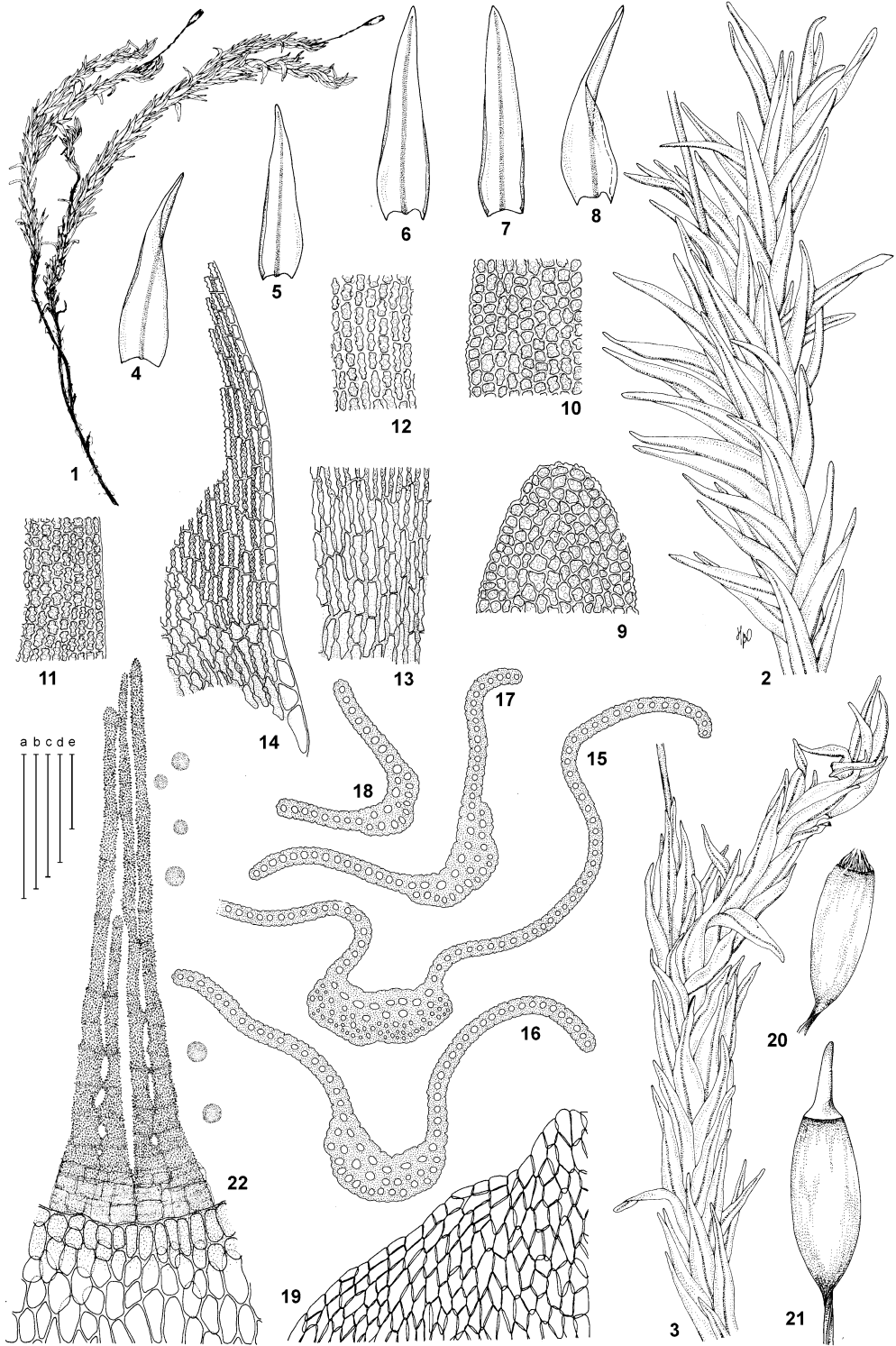
Codriophorus aquaticus (Brid.) Bednarek-Ochyra & Ochyra Figs 9 & 10

Racomitrium aquaticum (Hedw.) Brid.; *R. protensum* (Duby) Bruch & Schimp.

Plants medium-sized, coarse, in dense or loose tufts, stiff and rigid, dull, olivaceous to olive-green above, blackish brown. *Stems* decumbent or erect, 2.5–7.5 cm long, tough, irregularly, sparingly dichotomously or fastigiately branched, rarely almost unbranched, sparsely radiculose at base with dark brown, smooth rhizoids. *Leaves* crowded, rigid and stiff, imbricate to loosely appressed, erect when dry, erecto-patent to patent and often subsecund when wet, straight to somewhat curved, 2.1–2.7 mm long, 0.7–1.0 mm wide, not or slightly decurrent, lanceolate to oblong-lanceolate, gradually tapering to a narrowly rounded-obtuse or subacute, muticous apex, narrowly to broadly canaliculate to obtusely carinate above, broadly canaliculate-concave; *margin* broadly recurved to $\frac{1}{2}$ – $\frac{2}{3}$ of leaf length on one side and more narrowly recurved to about the same length on the other side, nearly plane above, entire and unistratose throughout; *costa* single, robust 90–160 μm wide at base, vanishing a few cells below leaf apex, shallowly or deeply grooved in a wide- or narrow-angled furrow in proximal part, strongly convex abaxially over its whole length, in transverse section often somewhat asymmetric, lunate to reniform or rectangular above, often distinctly flattened below, in distal part 2–3-stratose, with 4–7 adaxial epidermal cells, usually equal in size to median and abaxial cells, 3(–4)-stratose in middle, with (3–)5–8 adaxial cells, 3–5-stratose below, consisting of a row of 7–14 large, circular or elliptical adaxial guide cells and small, substeroid or steroid central and abaxial cells; *laminal*

cells densely covered on both surfaces with large, flat papillae covering the longitudinal walls and most of the lumina, leaving only a narrow slit in the middle, isodiametric to shortly elongate, irregularly rounded-quadrate to short-rectangular in distal part, thick- and weakly sinuose-walled, 10–15 μm long, 8–10 μm wide, becoming elongate towards mid-leaf, 15–25 μm long, 5–8 μm wide, and somewhat longer above base, 25–45 μm , with incrassate, porose and nodulose longitudinal walls; *alar cells* not differentiated from adjacent basal cells; *supra-alar cells* not differentiated or quadrate to short-rectangular, with moderately thickened, straight walls, pellucid, hyaline to yellowish hyaline, forming a distinct, uniseriate marginal border consisting of 7–15 cells. *Sporophytes* very rare in Hungarian material, found only in a single gathering. *Inner perichaetial leaves* (2–3) ovate-lanceolate to lingulate, obtuse or subacute to broadly rounded at the apex, yellowish hyaline throughout, with lax areolation of thin-walled cells. *Setae* reddish brown to blackish brown, erect, straight, 5–10 mm long, smooth, dextrorse. *Capsules* exserted, erect, straight, obloid to cylindrical, 2.1–3.1 mm long, 0.8–1.0 mm wide, smooth, pale brown or olive-brown, becoming dark brown with age, pachydermous; *operculum* conic-rostrate, 1.1–1.5 mm long, long-beaked, with straight rostrum up to $\frac{2}{3}$ of urn length; *peristome* single, consisting of 16, brown- or orange-reddish, densely and finely papillose teeth, 400–480 μm long, split to near the middle into 2 terete prongs, with short basal membrane, 15–30 μm tall. *Spores* globose, 13–17 μm in diameter, pale brownish, nearly smooth to finely papillose. *Calyptra* conic-mitrate, 4–5-lobate at base, verrucose at apex.

NOTES. *Codriophorus aquaticus* differs from the closely related *C. aciculare* in having lanceolate to narrowly lanceolate leaves which are narrowly rounded and entire at the leaf apex, narrowly canaliculate costa in the distal portion, esinuose supra-alar cells forming a pellucid marginal border and non-differentiated alar cells. The species can be confused in the field with the epilose plants of *Bucklandiella heterosticha* (for difference see under that species) and *Dryptodon patens* (Hedw.) Brid.,



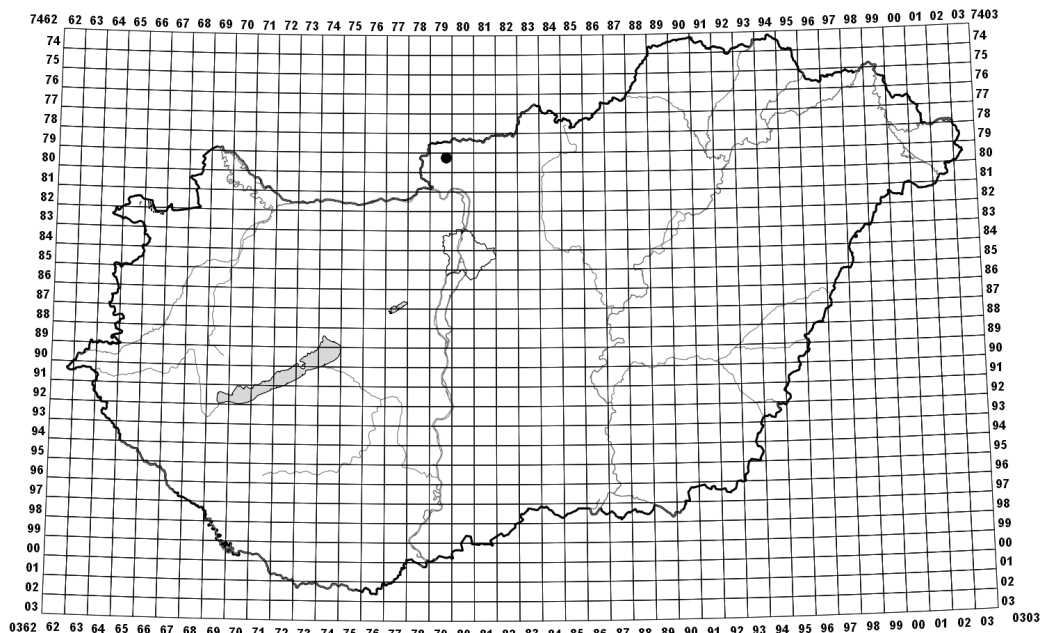


Fig. 10. Distribution of *Codriophorus aquaticus* (Brid.) Bednarek-Ochyra & Ochyra in Hungary.

especially when sterile. However, the latter can easily be distinguished microscopically because the presence of longitudinal abaxial lamellae on the costa precludes any possibility of misdetermination.

HABITAT: shaded and/or humid fissures or horizontal faces of andesite rock, often on northern or northeastern aspects, in forest, sometimes near a stream.

ASSOCIATED BRYOPHYTES: *Barbilophozia barbata* (Schreb.) Loeske, *Bryum moravicum* Podp., *Dicranum scoparium*, *Grimmia hartmanii*, *Hypnum cupressiforme*, *Marsupella* sp., *Polytrichum formosum*, *Rhizomnium punctatum* (Hedw.) T. J. Kop., *Schistidium* cf. *apocarpum* (Hedw.) Bruch & Schimp. and *Tritomaria exsecta* (Schmidel) Loeske.

VERTICAL DISTRIBUTION: 650–850 m a.s.l.

SELECTED SPECIMENS EXAMINED: BÖRZSÖNY MTS: 8079.2 Nógrád County, Királyháza (Diósjenő), Kopolya kövek rocks, shaded andesite rock, with *Cephalozia bicuspidata* (L.) Dumort., *Tritomaria exsecta*, 650–700 m, 04.08.1999, leg. P. Erzberger & B. Papp (B-Erzberger 5575, BP 170513 [many collections from 1957–1959 by Boros and Vajda in BP and EGR]. Mont Magosfa prope Kemence, 850 m, 30 Jun 1957, Boros (c. spor.) (BP 113348).

Racomitrium Brid.

Muscol. Recent. Suppl. 4: 78. 1818

Narrowly understood *Racomitrium* is distinguished from all other congeners of the Racomitrioideae by a combination of several traits, of which

←
Fig. 9. *Codriophorus aquaticus* (Brid.) Bednarek-Ochyra & Ochyra. 1 – habit; 2 – portion of branch, wet; 3 – portion of branch, dry; 4–8 – leaves; 9 – leaf apex; 10 – upper laminal cells; 11 – mid-leaf cells at margin; 12 – mid-leaf cells; 13 – basal leaf cells; 14 – alar and supra-alar cells; 15–18 – leaf cross sections, sequentially from base to apex; 19 – uppermost cells of innermost perichaetial leaf; 20 – deoperculate capsule, dry; 21 – operculate capsule, dry; 22 – portion of peristome, spores and exothecial cells at orifice. [1–3, 19, 20 from Lisowski 58991; 4–14 from Kola s.n., 22 Sep 1968; 15–18 from Kaalaas s.n., 27 Jul 1896; 21 from Schoepke s.n., KRAM B-79999; 22 from Limpricht 314; all in KRAM.] Scale bars: a = 1 cm (1); b = 100 µm (19, 22); c = 100 µm (9–14); d = 100 µm (15–18); e = 1 mm (2–8, 20, 21).

the sinistrorse and strongly papillose setae do not occur in any other genus of the Grimmiaceae or in the acrocarpous mosses. Moreover, the leaves always have unusual hyaline hair-points which are papillose and distinctly eroso-dentate and are longly 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 slit in the middle. This gives the leaf surfaces a regularly ridged appearance. The capsules are straight, ovoid to ovoid-cylindrical and somewhat ventricose in the base, and the peristome teeth are very long and divided to the base into 2(–3) filiform segments. Additional features helpful in characterizing this genus are (1) the absence of alar cells; (2) a very long 1–2-seriate marginal border composed of 25–30 yellowish hyaline transparent cells; (3) a single undivided costa, 3(–4)-stratose below and bistratose above. This genus contains only three species: the cosmopolitan *Racomitrium lanuginosum*, and *R. pruinosum* (Wilson) Müll. Hal. and *R. patagonicum* Bednarek-Ochyra & Ochyra which occur in Australasia and southern South America (Vitt & Marsh 1988; Bednarek-Ochyra & Ochyra 2003).

***Racomitrium lanuginosum* (Hedw.) Brid.**

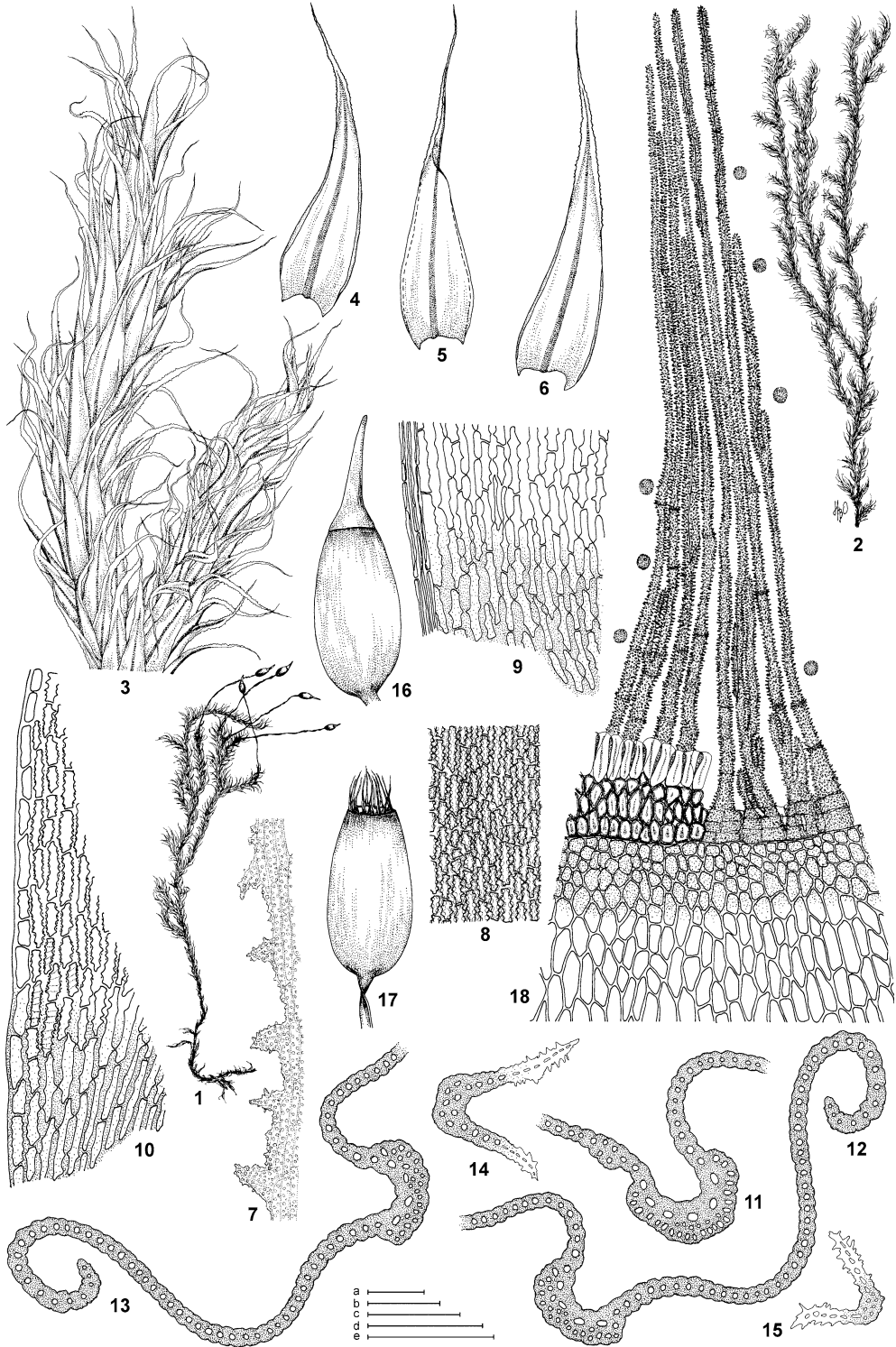
Figs 11 & 12

Plants medium-sized, coarse and rigid, forming grayish to yellowish green tufts or patches, hoary when dry. *Stems* erect, 5–6 cm long, stiff, variously branched, usually with elongate lateral branches or with short tuft-like horizontal branchlets. *Leaves* erect to slightly falcato-secund and appressed when dry, erecto-patent when moist, 2.5–3.5 mm long, 0.6–0.9 mm wide, narrowly lanceolate to oblong-lanceolate, gradually narrowed to long slender hair-point, non-decurrent, canaliculate distally, concave

to broadly carinate in proximal part; *hair-point* hyaline, flat to canaliculate, densely papillose, broadly evenly decurrent to $\frac{1}{4}$ – $\frac{1}{3}$ along margins, eroso-dentate, with teeth short, to 30 μm long, sharp or blunt, spreading at 30°–90° angle, moderately papillose throughout; *margins* unistratose all around, recurved on one side to middle, plane to erect elsewhere, entire below, toothed to sinuate in echlorophyllose part formed by decurrencies from the hyaline hair-point; *costa* percurrent, 60–80 μm wide at base, in transverse section rectangular to reniform, strongly convex on abaxial surface, bistratose with two large adaxial guide cells in distal half, becoming partially tristratose, with 2–3 enlarged adaxial guide cells towards base; *laminal cells* unistratose throughout, short-rectangular, 15–40 μm long, 7–8 μm wide in distal part, becoming long-rectangular, 50–60 μm long, 6–8 μm wide in median and lower parts, with thickened, sinuose longitudinal walls, distinctly papillose with large flat papillae over these walls, covering almost the whole lumina except for a narrow central slit, with rounded secondary papillae over both ventral and dorsal surfaces; *basal cells* long-rectangular, to 80 μm long, 7–8 μm wide, strongly nodulose, forming broad orange strip along insertion; *alar cells* not differentiated; *supra-alar cells* rectangular, pellucid, with straight or weakly nodulose walls, forming a uniseriate translucent border consisting of up to 20 cells. *Sporophytes* unknown in Hungarian material. *Inner perichaetial leaves* oblong-lanceolate to elliptical, concave and sheathing at base, abruptly contracted into short, hyaline-tipped, smooth or nearly so acumen. *Seta* papillose, brown to reddish brown, 3–7 mm, erect, flexuose, sinistrorse when dry. *Capsule* brown, ovoid to obloid, 1.2–1.5 mm long, 0.6–0.7 mm wide, smooth, lustrous, somewhat ventricose at base; *operculum* straight, erect, conic-rostrate; *peristome teeth* 16, 500–700 μm long, arising from



Fig. 11: *Racomitrium lanuginosum* (Hedw.) Brid. 1 – fertile plant, dry; 2 – sterile plant, dry; 3 – portion of branch, dry; 4–6 – leaves; 7 – marginal teeth of hyaline hair-point in middle; 8 – mid-leaf cells. 9 – basal leaf cells; 10 – alar and supra-alar cells; 11–15 – leaf cross sections, sequentially from base to apex; 16 – operculate capsule, wet; 17 – deoperculate capsule, dry; 18 – portion of peristome, spores and exothecial cells at orifice. [1, 4–15 from *Lützw s.n.*, 2 Oct 1885; 2 from *Kuc s.n.*, KRAM B-10457; 3 from *Woloszczak s.n.*, 8 Aug 1886; 16, 17 from *Rieher & Hintze s.n.*, 2 Aug 1915; 18 from *Vrang 673b*; all in KRAM.] Scale bars: a = 1 cm (2); b = 1 mm (4–6); c = 1 cm (1); d = 1 cm (3) and 1 mm (16 & 17); e = 100 μm (7–15, 18).



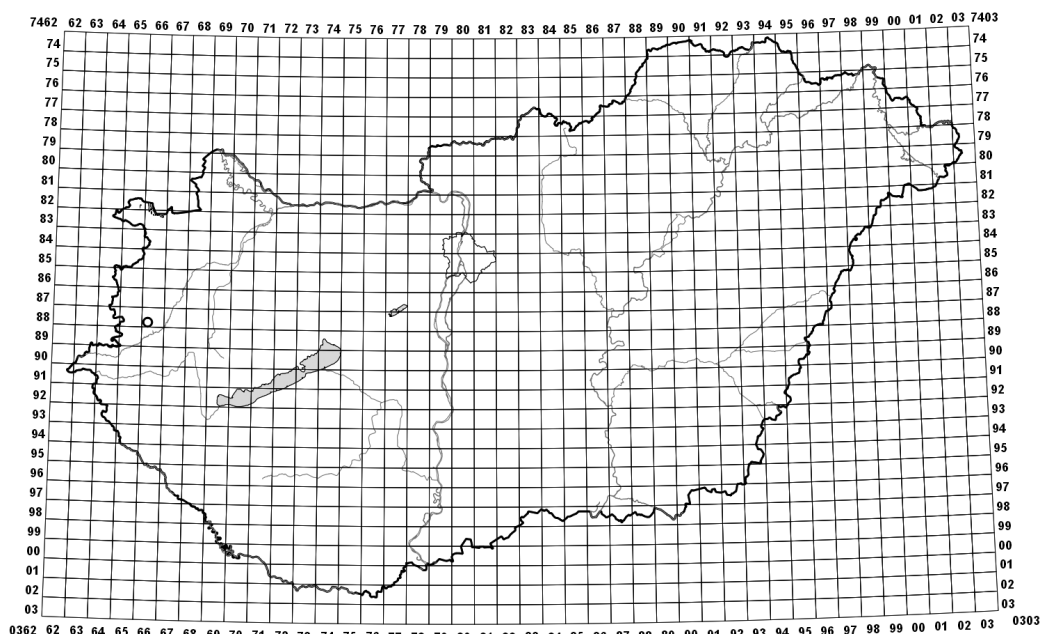


Fig. 12. Distribution of *Racomitrium lanuginosum* (Hedw.) Brid. in Hungary.

low basal membrane, divided almost to base into 2 thread-like, terete, strongly papillose branches. Spores spherical, 9–12 µm in diameter, pale yellowish, finely roughened to nearly smooth. Calyptra cucullate, smooth to slightly scabrous above.

NOTES. *Racomitrium lanuginosum* is one of the most distinctive and easily distinguished of all mosses. Its most characteristic feature is the hyaline, eroso-dentate and strongly papillose leaf hair-point which is long-decurrent as a white border along the upper portion of the leaf. Other characteristic traits of this species are (1) large, flat papillae densely covering the longitudinal walls of the leaf cells with additional secondary small papillulae over both the abaxial and adaxial surfaces; (2) the lack of alar cells; (3) the long basal marginal border of yellowish hyaline, translucent, straight-walled cells; (4) papillose setae; (5) barrel-shaped capsules distinctly ventricose at the base; and (6) long peristome teeth divided to the base into two filiform segments.

Recently doubts have arisen concerning the trustworthiness of the collector of this specimen

and, additionally, the region seems unsuitable to support *Racomitrium lanuginosum*. This species must therefore be considered doubtfully recorded from Hungary.

HABITAT: 'in silvi'.

ASSOCIATED BRYOPHYTES: none.

VERTICAL DISTRIBUTION: 185–210 m a.s.l.

SPECIMEN EXAMINED: VAS REGION (CASTRIFERREICUM): 8866.3 Cottus Castriferrei (Vas Megye) S-Kápolna (Sorkikápolna) in silvis (without date) (BP 6630) (see Erzberger 2010).

Niphotrichum Bednarek-Ochyra & Ochyra

Cens. Cat. Polish Mosses: 137. 2003.

Niphotrichum is a very distinctive genus which is well characterized by the following set of morphological features: the laminal cells are strongly papillose with tall conical papillae situated over the lumina, the peristome teeth are very long, regularly divided to the base into 2–3 filiform branches, and the angular cells are hyaline or yellowish hyaline, thin-walled, and form prominent, convex and often

decurent auricles. Moreover, the leaves are elliptic or broadly ovate-lanceolate to triangular and are terminated with massive, hyaline, papillose and denticulate hair-points. The costae are spurred or branched at the tip and vanish at mid-leaf or well below the leaf apex. They are bi- or imperfectly tristratose and consist of an adaxial layer 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 twisted to the left when dry. The operculum is longly beaked, with a rostrum as long as the urn or longer, and the capsules are plicate when dry. *Niphotrichum* is a small genus consisting of eight species which are predominantly distributed in the Northern Hemisphere. One species is known to occur in Hungary.

Niphotrichum canescens (Hedw.) Bednarek-Ochyra & Ochyra Figs 13 & 14
Racomitrium canescens (Hedw.) Brid.

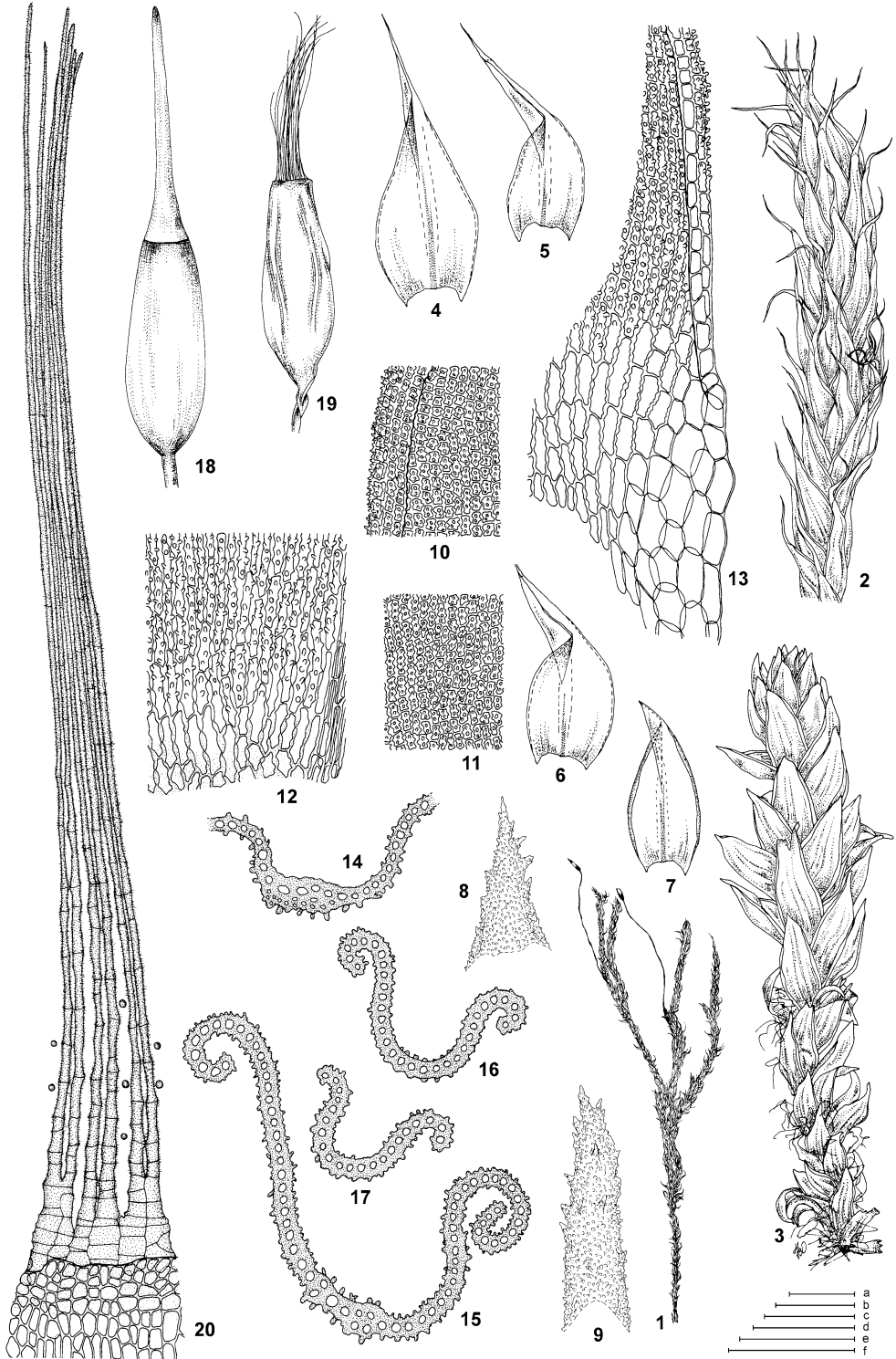
Plants medium-sized and fairly slender to large, forming loose or dense patches or tufts, dull green, grayish, yellow-green or yellow-brown, often hoary when dry. *Stems* prostrate to ascending, 3–10 cm long, sparingly or profusely irregularly branched or often regularly pinnately branched with short tuft-like branchlets. *Leaves* straight to distinctly falcate, imbricate when dry, patent to recurved when moist, ovate to broadly ovate-lanceolate, 1.9–2.8 mm long, 0.8–1.3 mm wide, rather abruptly narrowed to hyaline or yellowish hyaline hair-point or sometimes muticous; *hair-points* broad and stout to subulate, not reflexed, not or distinctly decurrent, mostly serrulate and spinulose, papillose distally and strongly so basally; *margins* broadly recurved to revolute throughout; *costa* weak, extending $\frac{1}{2}$ – $\frac{3}{4}$ up the leaf, strongly flattened and weakly convex on abaxial side, 90–120 μm wide near base; *laminal cells* with moderately thickened, sinuouse walls, quadrate to short-rectangular in upper part, 10–25 μm long, 5–10 μm wide, densely covered with tall conical papillae, becoming elongate-rectangular in base, 30–50 μm long, 4–7 μm wide, strongly porose and often epapillose in 1–3 rows at insertion; *alar*

cells usually rounded and inflated in 3–5 rows, thin-walled, hyaline to yellowish hyaline, forming prominent, decurrent, somewhat inflated auricles; *supra-alar cells* elongate, thin- and straight-walled, producing a pellucid marginal border of 20–30 cells. *Sporophytes* occasional in Hungarian material. *Inner perichaetial leaves* membranous, hyaline, acute, usually with hyaline awns. *Seta* dark red to reddish brown, 5–25 mm long, twisted to left on drying. *Capsules* brown, narrowly ellipsoid to cylindrical, 1.5–2.5 mm long, smooth to somewhat furrowed when dry; *operculum* longly beaked, with straight rostrum as long as urn; *peristome teeth* 16, reddish brown, 600–800 μm long, regularly divided to base into 2–3 thread-like branches, densely papillose. *Spores* spherical, 8–11 μm in diameter, yellowish brown, minutely roughened. *Calyptra* cucullate, scabrous, 4–5-lobed at base.

NOTES. *Niphotrichum canescens* is a distinct species which is readily separated from all other congeners by its broadly canaliculate to obtusely keeled leaves in the distal portion, massive hair-points that are strongly papillose throughout and weakly serrulate, and short, forked costae ceasing well before the apex, usually in mid-leaf or at three quarters of leaf length, and very large papillae throughout the leaf lamina. It is a xerothermic moss growing in dry and open sites, and is only occasionally found in shaded and moist habitats. It is indifferent to the reaction of the substrate and grows on both acidic and basic ground. Phytosociologists generally consider it to be a characteristic species of the class *Sedo-Scleranthetea*.

HABITAT: Andesite tufa, andesite grassland, sand, on soil over and among andesite rocks, on soil over and among sandstone rocks, on soil among dolomite rocks, on the wall of a railway bridge, on andesite stones on a bridge, in rocky grassland, on glauconite sandstone, sandstone rocks, on andesite rocks, on rhyolite, on sandstone rocks, in fissures of andesite and dolomite rock, in fissures and on soil among granite and quartzite rocks, on soil among conglomerate rocks, in open situations, often dry, such as forest margins or forest clearings.

ASSOCIATED BRYOPHYTES: *Bryum alpinum*



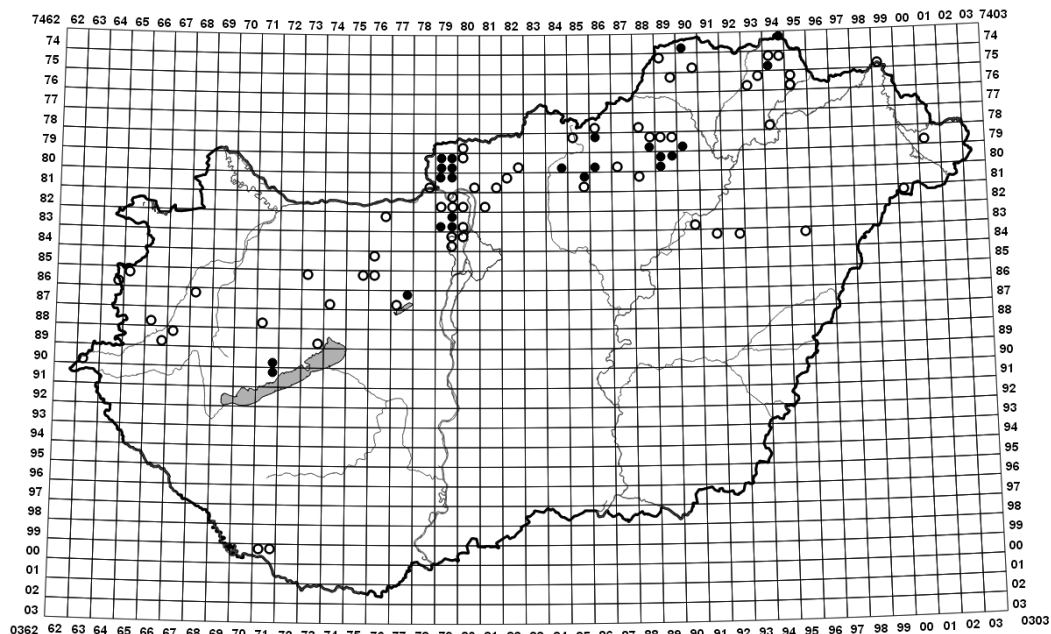


Fig. 14. Distribution of *Niphotrichum canescens* (Hedw.) Bednarek-Ochyra & Ochyra in Hungary.

With., *Bryum* sp., *Ceratodon purpureus* (Hedw.) Brid., *Dicranum scoparium*, *Ditrichum flexicaule* (Schwägr.) Hampe, *Entosthodon fascicularis* (Hedw.) Müll. Hal., *Grimmia laevigata* (Brid.) Brid., *G. pulvinata* (Hedw.) Sm., *Homalothecium sericeum* (Hedw.) Schimp., *Hypnum cupressiforme*, *H. lacunosum* Brid., *Pleurochaete squarrosa* (Brid.) Lindb., *Pogonatum aloides* (Hedw.) P. Beauv., *Polytrichum juniperinum*, *P. piliferum*, *Rhytidium rugosum* (Hedw.) Kindb., *Schistidium* sp., *Thuidium abietinum* (Hedw.) Schimp., *Tortula ruralis* (Hedw.) P. Gaertn., B. Mey. & Scherb.

VERTICAL DISTRIBUTION: 92–800 m a.s.l.

SELECTED SPECIMENS EXAMINED: ZEMPLÉN MTS: 7494.2 Borsod-Abaúj-Zemplén County, around hunting house (Vadászház) at Füzér, andesite grassland. N 48°33', 147', E 21°27', 217', 460 m, 08.04.2004, leg.

B. Papp (BP 171517). CSEREHÁT HILLS: 7590.4 Comit. Borsod. In petrosis arenac. ad Ördögrét prope Meszes, 160 m, 27.10.1957, leg. Á. Boros (BP 122080 as *Hedwigia albicans*, rev. P. Erzberger Feb 1996). Aggtelek Karst: 7589.1 Comit. Gömör. In collibus glareosis Nagy-völgy prope Aggtelek, 350 m, 11.10.1952, leg. Á. Boros (BP 113608). RUDABÁNYA HILLS: 7689.2 Rudabánya. In rupibus siccis in fruticetis, 26.05.1979, leg. L. Vajda (BP 159735 as *Hedwigia albicans*, rev. P. Erzberger, Feb 1996). BÜKK Mts: 7989.1 Comit. Borsod. Ad marg. silvarum sub monte Nagykörös prope Jávorkút (Bükkfenntárség), 750 m, 29.06.1948, leg. Á. Boros (BP 6496 & 113594). 8089.2 Borsod-Abaúj-Zemplén County, Bükk Mts; Latorút-Latorvár, N47°58'41.9", E20°38'29.4" on soil, 240 m, 27.03.2008, leg. P. Erzberger & T. Pócs (B-Erzberger 12863). TARNA REGION: 7986.1 Heves County, Istenmezeje, Noé szőlője, on glauconite sandstone rocks in village, 200–230 m, 26.03.2008, leg. P. Erzberger & T. Pócs (B-Erzberger



Fig. 13. *Niphotrichum canescens* (Hedw.) Bednarek-Ochyra & Ochyra. 1 – habit; 2 – portion of branch, dry; 3 – portion of branch, wet; 4–7 – leaves; 8 & 9 – hyaline hair-points; 10 – upper leaf cells at margin; 11 – mid-leaf cells; 12 – basal leaf cells; 13 – alar and supra-alar cells; 14–17 – leaf cross sections, sequentially from base to apex; 18 – operculate capsule, wet; 19 – deoperculate capsule, dry; 20 – portion of peristome, spores and exothecial cells at orifice. [1, 3–6, 9–17, 20 from *Bednarek-Ochyra & Ochyra* 36/88; 2, 7, 8 from *Torka* 29; 18 from *Krupa s.n.*, Nov 1877; 19 from *Woloszczak s.n.*, Apr 1888; all in KRAM.] Scale bars: a = 100 µm (8 & 9); b = 1 cm (2 & 3) and 100 µm (20); c = 1 mm (4–7); d = 1 cm (1); e = 1 mm (18 & 19); f = 100 µm (10–17).

12858). MÁTRA Mts: 8084.4 Heves County, Bárány-kő rocks in valley of Csörgő stream at Mátraszentimre, andesite rocks N47°54'35.2", E19°49'05.8", 490 m, 01.07.2007, leg. B. Papp (BP 175100). KARANCS-MEDVES Mts: 7985.2 Comit. Nógrád. Ad margines silvarum montis Háromhatár prope Bárna, solo arenac., 400 m, 17.06.1936, leg. Á. Boros (BP 113589); CSERHÁT HILLS: 8182.1 Comit. Nógrád. In petrosis andesiticis montis Berceli-hegy prope Bercei, 450 m, 27.05.1956, leg. Á. Boros (BP 113586). GÖDÖLLŐ HILLS: 8281.3 Comit. Pest. In rupestribus collium Kigyós prope pag. Vácrotót, 21.05.1952, leg. L. Vajda (BP 646, EGR). BÖRZSÖNY Mts: 8079.1 Comit. Nógrád. In rupibus in sylvestribus supra pag. Perőcsény, montes Börzsöny, 20.05.1962, leg. L. Vajda (BP 67996). VISEGRÁD Mts: 8279.4 [Pest County] Bucšina patak, Izbék felett, Pest m., 17.08.1911, leg. J. Szurák [= Szepesfalvi; collector not noted, identified by handwriting] (BP 6450). NASZÁLY: 8180.4 Comit. Nógrád. In silvis meridionalis-orientalis montis Nagyszál prope pag. Kosd, 300 m, 19.04.1919, leg. Á. Boros (BP 6521 & 113609). PILIS Mts: 8379.4 Comit. Pest. In monte Fehérhegy prope Boros-Jenő, 05.07.1901, leg. Á. Degen (BP 37059 & 37060). BUDA Mts: 8479.2 Comit. Pest. In locis arenaceis montis Tök-hegy inter mont. Csúcs-hegy et Szarvas-hegy prope pag. Pesthidegkút, 350 m, 15.03.1941, leg. Á. Boros (BP 6442 & 113615). GERECE Mts: 8376.2 Comit. Komárom. Ad margines silvarum vallis Tüzköves-völgy prope Tardos, 300 m, 25.03.1941, leg. Á. Boros (BP 6459 & 113564). VÉRTES Mts: 8675.2 Comit. Fejér. Inter saxa dolomit. (!) Pap-irtás prope Csákerény, 400 m, 18.04.1949, leg. Á. Boros (BP 6454 & 113551, EGR). VELENCE Mts: 8777.2 Comit. Fejér. In declivibus graniticis siccis montis Meleghegy prope pagum Nadap, 300 m, 04.04.1921, leg. Á. Boros (BP 113554). BAKONY Mts: 8871.3 Comit. Veszprém. In petrosis conglom. calcar. ad Bakonygyepes, 220 m, 23.10.1950, leg. Á. Boros (BP 80490 & 116540, EGR). BALATON UPLANDS: 9171.2 Veszprém County, Kötenger at Kővágóörs, andesit rocky grassland N46°51'15.4", E17°36'34.9", 160 m, 19.06.2007, leg. B. Papp (BP 175042). KŐSZEG Mts: 8665.1 Kőszeg, prope lacune in colle Gubahegy dicto, solo glareoso arido, 350 m, 28.03.1931, leg. A. Visnya (BP 6465). VEND REGION: 9163.1 Comit. Vas. In apertis silvarum montis Dugosz-erdő prope Felsőszőlők, 350 m, 09.10.1949, leg. Á. Boros (BP 6477 & 116580). ŐRSÉG REGION: 9165.1 Comit. Vas. Ad margines silvarum pr. pag. Szőce Solo glareoso, 250 m, 08.07.1954, leg. Á. Károlyi (BP 113579) and leg. Á. Boros (EGR). VAS REGION: 9065.4 Praenoricum: Vasi Hegyhát, pr. pag. Nádasd. Betuleto-Callunetum in silv. Nádasd-erdő, 240 m, 24.04.1954, leg. T. Pócs & I. Gelencsér

(BP 58477). ZALA: 9465.3 Comit. Zala. In arenosis ad ripas fluvii Kerka pr. pag. Lovászi, 01.05.1948, leg. Á. Károlyi (BP 6463, EGR). BELSŐ SOMOGY: 0071.2 Comit. Somogy. In collibus arenosis Pupos erdő prope Darány, 120 m, 14.04.1923, leg. Á. Boros (BP 6466, 6469 & 113568). MECSEK Mts: 9974.2 Comit. Baranya. In petrosis glareosis versus Cserkut prope Pécs, 300 m, 30.04.1962, leg. Á. Boros (BP 113558, EGR). TISZÁNTÚL: 8495.2 Comit. Hajdu. In graminosis arenosis ad Régi Lötér prope oppid. Debrecen. Festucetum pseudovinae, 14.04.1940, leg. R. Soó, Szűcs & L. Felföldy (BP 113501). NORTHERN PLAIN: 7599.3 Comit. Ung. In muris pontis viae ferreae ad Záhony, 100 m, 07.09.1925, leg. Á. Boros (BP 113500).

BRYOGEOGRAPHICAL CONSIDERATIONS

The species of the subfamily Racomitrioideae show a very interesting distribution pattern in Hungary. *Racomitrium lanuginosum* was found only once in the nineteenth century and no later records are known from the country. This species probably does not grow any longer in Hungary.

On the other hand, *Niphotrichum canescens* is the most widespread member of the genus, occurring in 25 of 43 floristic regions, which is nearly 60% of those units. In fact this number seems still too small, since the regions where no data for *R. canescens* are available are less attractive bryologically and may be underexplored. It is interesting that no specimen of *N. elongatum* (Frisvoll) Bednarek-Ochyra & Ochyra has been found in Hungary. It is a distinct species, only recently described in the *N. canescens* group (Frisvoll 1983) which occurs in some adjacent countries including Austria (Grims 1999), Slovenia (Martinčič 2003), Romania and Serbia (Sabovljević *et al.* 2008) and the Czech Republic (Kučera & Váňa 2003). The species has only recently been reported from Slovakia (Hodgetts 2015). According to Meinunger and Schröder (2007), *N. canescens* and *N. elongatum* show a tendency to occupy different areas, the latter preferring more acidic substrates and avoiding warm lowland areas, although there is an overlap in their ecological requirements, as documented by findings of mixed stands. The same tendency is observed in Poland, where *N. elongatum* is bicentric in distribution and exhibits some oceanic

tendency, occurring in Western Pomerania and in the mountains and their foreland in the south of the country, where humidity generally is higher than in the central Polish lowlands (Bednarek-Ochyra 1995). It would appear that Hungary, with its dominance of calcareous or at least base-rich substrates and warm and rather dry climate, is not suited for *N. elongatum*.

Codriophorus acicularis and *C. aquaticus*, as well as *Bucklandiella affinis*, are restricted in their occurrence in Hungary to the Börzsöny Mts, a region with andesite as bedrock, formed by volcanic activity in the Miocene, and with nearly continuous cover of mainly beech forest. This is the floristic region of Hungary with the highest number of species of racomitrialean mosses. *Bucklandiella heterosticha* occurs in the Börzsöny Mts but has a wider distribution, being also found in the Mátra Mts and Zemplén Mts, two areas of similar geology and bedrock, which together with the Börzsöny Mts form part of the northeastern range of the Hungarian highlands.

More enigmatic is that *Bucklandiella affinis*, *Codriophorus acicularis* and *C. aquaticus* appear to be absent in the Mátra Mts and Zemplén Mts. Possibly these species have been overlooked in particular areas, but in view of the number of specimens examined and the length of the collection periods this seems not very likely.

KEY TO DETERMINATION OF TAXA OF SUBFAM.
RACOMITRIOIDEAE IN HUNGARY

1. Laminal cells smooth or pseudopapillose, with longitudinal cuticular ridges; peristome teeth short, irregularly divided to the middle, rarely lower, into 2–3 broad branches (*Bucklandiella*) 2
- 1* Laminal cells papillose; papillae tall and conical, situated over the lumina, or else 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 4
2. Basal leaf cells not sinuose, with strongly incrassate and porose, not nodulose walls; basal marginal border present, uniseriate, consisting of 10–20 hyaline to yellowish hyaline, pellucid, esinuose cells; costa narrow, 60–80 µm wide, with 3–4 adaxial guide cells in the proximal part; innermost perichaetial leaves hyaline below, chlorophyllose above, with an areolation of cells with strongly incrassate walls ***Bucklandiella microcarpa***
- 2* Basal leaf cells sinuose; basal marginal border absent; costa broad, 80–120 µm wide, with 4–9 adaxial guide cells in the proximal part; innermost perichaetial leaves hyaline or yellowish hyaline throughout 3
3. Costa broadly canaliculate throughout on the adaxial side, bistratose in the distal and median parts, weakly convex abaxially, with 4–9 enlarged adaxial guide cells in the lower part ***Bucklandiella heterosticha***
- 3* Costa keeled, at least distally, on the adaxial side, 3–4-stratose in the median and lower parts and prominently convex on the abaxial side, 5–7 enlarged adaxial guide cells in the lower part ***Bucklandiella affinis***
4. Laminal cells with tall, conical papillae; alar cells hyaline or yellowish hyaline, thin-walled, forming distinct, decurrent auricles ***Niphotrichum canescens***
- 4* Laminal cells with large, flat papillae over longitudinal walls; alar cells indistinct or distinct but never hyaline 5
5. Hyaline hairpoint present, often long and strongly papillose, eroso-dentate; costa percurrent ***Racomitrium lanuginosum***
- 5* Hyaline hairpoint absent; costa vanishes well below the leaf apex (*Codriophorus*) 6
6. Leaves lingulate, elliptic to oblong-ovate, broadly channelled in the upper part, broadly rounded and bluntly or sharply denticulate to sinuate at the apex ***Codriophorus acicularis***
- 6* Leaves lanceolate to oblong-lanceolate, canaliculate in the upper part, rounded-obtuse or subacute and entire at the apex ***Codriophorus aquaticus***

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REFERENCES

- BEDNAREK-OCHYRA H. 1995. The genus *Racomitrium* (Musci, Grimmiaceae) in Poland: taxonomy, ecology and phytogeography. *Fragm. Florist. Geobot. Ser. Polon.* **2**: 3–307 (in Polish with English summary).
- BEDNAREK-OCHYRA H. 2006. *A taxonomic monograph of the moss genus Codriophorus P. Beauv. (Grimmiaceae)*. Polish Academy of Sciences, Institute of Botany, Kraków.
- BEDNAREK-OCHYRA H. & OCHYRA R. 2003. *Racomitrium patagonicum*, a new species from southern South America. *J. Bryol.* **25**: 181–187.
- BEDNAREK-OCHYRA H., ERZBERGER P. & OCHYRA R. 2011. New national and regional bryophyte records, 29. 5. *Bucklandiella microcarpa* (Hedw.) Bednarek-Ochyra & Ochyra (Hungary). *J. Bryol.* **33**: 317–318.
- BEDNAREK-OCHYRA H., SAWICKI J., OCHYRA R., SZCZECIŃSKA M. & PLÁŠEK V. 2015. *Dilutineuron*, a new moss genus of the subfamily Racomitrioideae (Grimmiaceae, Bryophyta). *Acta Musei Silesiae, Scientiae Naturales* **64**: 163–168.
- BOROS Á. 1968. *Bryogeographie und Bryoflora Ungarns*. Akadémiai Kiadó, Budapest.
- ERZBERGER P. 2009a. The genera *Grimmia* and *Coscinodon* (Grimmiaceae, Musci) in Hungary. *Stud. Bot. Hung.* **40**: 37–124.
- ERZBERGER P. 2009b. New national and regional bryophyte records, 20. 17. *Racomitrium aciculare* (Hedw.) Brid. (Hungary). *J. Bryol.* **31**: 57.
- ERZBERGER P. 2010. New national and regional bryophyte records, 25. 32. *Racomitrium lanuginosum* (Hedw.) Brid. (Hungary). *J. Bryol.* **32**: 317.
- ERZBERGER P. & PAPP B. 2004. Annotated checklist of Hungarian bryophytes. *Studia Bot. Hung.* **35**: 91–149.
- ERZBERGER P. & SCHRÖDER W. 2008. The genus *Schistidium* (Grimmiaceae, Musci) in Hungary. *Stud. Bot. Hung.* **39**: 27–88.
- FRISVOLL A. A. 1983. A taxonomic revision of the *Racomitrium canescens* group (Bryophyta, Grimmiales). *Gunneria* **41**: 1–181.
- FRISVOLL A. A. 1988. A taxonomic revision of the *Racomitrium heterostichum* group (Bryophyta, Grimmiales) in N. and C. America, N. Africa, Europe and Asia. *Gunneria* **59**: 1–289.
- GRIMS F. 1999. Die Laubmoose Österreichs. *Catalogus Florae Austriae*, Teil 2, Bryophyten (Moose). Heft 1, Musci (Laubmoose). *Biosystematics and Ecology Series* **15**: 1–418.
- HASTINGS R. I. & OCHYRA R. 2007. Grimmiaceae Arnott. In: *FLORA OF NORTH AMERICA EDITORIAL COMMITTEE* (ed.), *Flora of North America north of Mexico*. 27 *Bryophyta*, part 1, pp. 204–205. Oxford University Press, New York – Oxford.
- HEDDERSON T. A., MURRAY D. J., COX C. J. & NOWELL T. L. 2004. Phylogenetic relationships of haplolepidous mosses (Dicranidae) inferred from *rps4* gene sequences. *Syst. Bot.* **29**: 29–41.
- HERNÁNDEZ-MAQUEDA R., QUANDT D. & MUÑOZ J. 2007. Testing reticulation and adaptative convergence in the Grimmiaceae (Bryophyta). *Taxon* **57**: 500–510.
- HERNÁNDEZ-MAQUEDA R., QUANDT D., WERNER O. & MUÑOZ J. 2008. Phylogeny and classification of the Grimmiaceae/Ptychomitriaceae complex (Bryophyta) inferred from cpDNA. *Molec. Phylog. Evol.* **46**: 863–877.
- HILL M. O., BELL N., BRUGGEMAN-NANNENGA M. A., BRUGUÉS M., CANO M. J., ENROTH J., FLATBERG K. I., FRAHM J.-P., GALLEGO M. T., GARILLETI R., GUERRA J., HEDENÄS L., HOLYOAK D. T., HYVÖNEN J., IGNATOV M. S., LARA F., MAZIMPAKA V., MUÑOZ J. & SÖDERSTRÖM L. 2006. An annotated checklist of the mosses of Europe and Macaronesia. *J. Bryol.* **28**: 198–267.
- HODGETTS N. B. 2015. Checklist and country status of European bryophytes – towards a new Red List for Europe. *Irish Wildlife Manual* **84**: 1–124.
- KUČERA J. & VÁŇA J. 2003. Check- and Red list of bryophytes of the Czech Republic. *Preslia* **75**: 193–222.
- LARRAÍN J., QUANDT D., STECH M. & MUÑOZ J. 2013. Lumping or splitting? The case of *Racomitrium* (Bryophytina: Grimmiaceae). *Taxon* **62**: 1117–1132.
- MAIER E. 2010. The genus *Grimmia* Hedw. (Grimmiaceae, Bryophyta). A morphological-anatomical study. *Boissiera* **63**: 1–377.
- MARTINČIČ A. 2003. Seznam listnatih mahov (Bryopsida) Slovenije. *Hacquetia* **2**(1): 91–166.
- MEINUNGER L. & SCHRÖDER W. 2007. *Verbreitungsatlas der Moose Deutschlands*. Band 2. Regensburgische Botanische Gesellschaft, Regensburg.
- NIKL FELD H. 1971. Bericht über die Kartierung der Flora Mitteleuropas. *Taxon* **20**: 545–571.
- OCHYRA R., ŻARNOWIEC J. & BEDNAREK-OCHYRA H. 2003. *Census catalogue of Polish mosses*. Polish Academy of Sciences, Institute of Botany, Kraków.
- OCHYRA R., LEWIS SMITH R. I. & BEDNAREK-OCHYRA H. 2008. *The illustrated moss flora of Antarctica*. Cambridge University Press, Cambridge.
- PAPP B., ERZBERGER P., ÓDOR P., HOCK ZS., SZÖVÉNYI P., SZURDOKI E. & TÓTH Z. 2010. Updated Checklist and Red List of Hungarian Bryophytes. *Stud. Bot. Hung.* **41**: 31–59.
- SABOVLEVIĆ M., NATCHEVA R., DIHORU G., TSAKIRI E., DRAGIČEVIĆ S., ERDAĞ A. & PAPP B. 2008. Check-list of the mosses of SE-Europe. *Phytol. Balcan.* **14**: 207–244.
- SAWICKI J., SZCZECIŃSKA M., BEDNAREK-OCHYRA R. & OCHYRA R. 2015. Mitochondrial phylogenomics supports splitting the traditionally conceived genus *Racomitrium* (Bryophyta: Grimmiaceae). *Nova Hedwigia* **100**: 293–317.

- STREIFF A. 2006. Phylogenetic study of *Grimmia* (Grimmiaceae) based on plastid DNA sequences (*trnL-trnF* and *rps4*) and on morphological characters. *Bryologist* **109**: 224–235.
- TSUBOTA H., AGENO Y., ESTÉBANEZ B., YAMAGUCHI T. & DEGUCHI H. 2003. Molecular phylogeny of the Grimmiiales (Musci) based on chloroplast *rbcL* sequences. *Hikobia* **14**: 55–70.
- VAJDA L. 1956. *Fissidens algarvicus* Solms-Laubach aus dem Börzsönygebirge (Mittelungarn). *Ann. Hist.-Nat. Mus. Natl. Hung.* **48** (ser. nov. 7): 299–301.
- VAJDA L. 1958. *Fissidens košaninii* Latzel dans la Montagne Börzsöny en Hongrie. *Rev. Bryol. Lichénol.* **27**: 49–51.
- VAJDA L. 1962. Die Verbreitung einiger seltener Leber- und Laubmoose in Ungarn. *Fragm. Bot. Mus. Hist.-Nat. Hung.* **2**: 23–31.
- VAJDA L. 1966. Die Moosflora des Börzsöny-Gebirges. *Fragm. Bot. Mus. Hist.-Nat. Hung.* **4**: 79–100 (in Hungarian with German summary).
- VITT D. H. & MARSH C. 1988. Population variation and phyto-geography of *Racomitrium lanuginosum* and *R. pruinosum*. *Nova Hedwigia Beih.* **90**: 235–260.

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