

## ***Dilutineuron*, a new moss genus of the subfamily Racomitrioideae (Grimmiaceae, Bryophyta)**

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**Abstract:** Based on available molecular and morphological evidence, the genus *Codriophorus* P.Beauv. (Grimmiaceae subfam. Racomitrioideae) proved to be a polyphyletic taxon. It consists of two distinct genera which correspond to two sections of *Codriophorus*, namely sect. *Codriophorus* and sect. *Fascicularia* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra. The latter section is raised to generic rank as *Dilutineuron* Bednarek-Ochyra, Sawicki, Ochyra, Szczecińska & Plášek. The new genus consists of the following five species: *D. fasciculare* (Hedw.) Bednarek-Ochyra, Sawicki, Ochyra, Szczecińska & Plášek, *comb. nov.*, *D. brevisetum* (Lindb.) Bednarek-Ochyra, Sawicki, Ochyra, Szczecińska & Plášek, *comb. nov.*, *D. anomodontoides* (Cardot) Bednarek-Ochyra, Sawicki, Ochyra, Szczecińska & Plášek, *comb. nov.*, *D. corrugatum* (Bednarek-Ochyra) Bednarek-Ochyra, Sawicki, Ochyra, Szczecińska & Plášek, *comb. nov.* and *D. laevigatum* (Mitt.) Bednarek-Ochyra, Sawicki, Ochyra, Szczecińska & Plášek, *comb. nov.*

**Keywords:** Bryophyta, *Bucklandiella*, *Codriophorus*, *Frisvollia*, *Niphotrichum*, nomenclature, *Racomitrium*, taxonomy

### **Introduction**

In the traditional circumscription (e.g. Bruch, Schimper & Gümbel 1845; Schimper 1860; Brotherus 1924; Loeske 1913, 1930), *Racomitrium* Brid. was a typical polythetic taxon that could not be defined on the basis of any single character, but it was given cohesion by a specific combination of characters. The most important of these were the leaf areolation of the thick and strongly sinuose to nodulose longitudinal cell walls, the consistent lack of the stem central strand, the usual presence of the prostome, the sinuose-walled epidermal cells of the vaginula, the cladocarpous position of sexual organs, and the special peristome type which, in its typical form, has linear teeth arising from a low or high basal membrane and is divided nearly to the base into two filiform, somewhat paired segments that are equally thickened and less prominently trabeculate on both dorsal and ventral sides. Therefore, some bryologists (Loeske 1930; Frisvoll 1983) argued that *Racomitrium* was a heterogeneous and unnatural genus which should be split into several distinct genera, well-defined by sets of sporophyte and gametophyte characters.

The infrageneric classification of *Racomitrium* was quite poorly developed. Kindberg (1898) divided the genus into four unranked groups, namely *Lanuginosa*, *Papillosa*, *Canescentia* and *Laevifolia*, which were subsequently validated as sections (Noguchi 1974). Bednarek-Ochyra (1995) presented a detailed infrageneric classification of *Racomitrium* which was largely based on the peristome structure, the shape of the perichaetial leaves and the ornamentation of the laminal cells. The genus was divided into four subgenera, namely subg. *Racomitrium*, subg. *Cataractarum* Vilh., subg. *Niphotrichum* Bednarek-Ochyra & Ochyra and subg. *Ellipticodryptodon* (Vilh.) Bednarek-Ochyra & Ochyra, which corresponded well to the four aforementioned groups recognised within this genus by Kindberg (1898).

A subsequent revisionary study of *Racomitrium* confirmed that the genus, in its traditional circumscription, was an artificial heterogeneous taxon and, as a result, it was split

into four genera, *Racomitrium* s. str., *Codriophorus* P.Beauv., *Niphotrichum* Bednarek-Ochyra & Ochyra and *Bucklandiella* Roiv. (Ochyra, Żarnowiec & Bednarek-Ochyra 2003). They are considered to be distinctive taxa through various combinations of unique or otherwise presumably advanced characteristics for the Grimmiaceae, such as the presence of pellucid alar cells, variously papillose laminal cells, papillosity of both seta and calyptra, torsion of the seta, shape of the peristome teeth, anatomy of the costa, and shape of the hair-point.

The molecular phylogeny of the broadly understood genus *Racomitrium* based on nuclear ITS and plastid *rps4-trnL* and *trnK/matK-psbA* sequences, carried out by Larraín *et al.* (2013), revealed that *Bucklandiella* and *Codriophorus* remained polyphyletic, *Niphotrichum* was paraphyletic and only *Racomitrium* s. str. could be considered monophyletic. On the other hand, phylogenomic analysis based on complete mitochondrial genomes (Sawicki *et al.* 2015) fully supported splitting the traditionally conceived genus *Racomitrium* into four separate genera. In addition, the genus *Codriophorus* was resolved as paraphyletic mainly due to the phylogenetic position of one species, *C. varius* (Mitt.) Bednarek-Ochyra & Ochyra, which is sister to the genus *Niphotrichum* and forms a common clade with the representatives of this genus. A set of morphological characters, as well as large number of specific mutations in each of analysed genomes, justified the placement of this species in a separate monotypic genus *Frisvollia* Sawicki, Szczecińska, Bednarek-Ochyra & Ochyra, with *F. varia* (Mitt.) Sawicki, Szczecińska, Bednarek-Ochyra & Ochyra as a sole species.

Subsequent molecular studies on *Codriophorus* based on complete plastomes and mitogenomes as well as nuclear rRNA genes cluster revealed the polyphyletic nature of this genus and provided strong background for further splitting. The results of these studies will be presented in a separate account which is under preparation by the authors and in the present article taxonomic and nomenclatural conclusions are summarised. They confirm the results obtained by Larraín *et al.* (2013) based on analysis of nuclear ITS and plastid *rps4-trnL* and *trnK/matK-psbA* sequences.

### Morphological characterisation of the segregates of *Codriophorus*

*Codriophorus* is primarily diagnosed by a peculiar ornamentation of the laminal cells. They are distinctly papillose, with large flat papillae distributed on both abaxial and adaxial laminal surfaces, and over both the longitudinal walls and most of the lumina, leaving only a narrow slit in the centre. In this character *Codriophorus* is similar to *Racomitrium* s. str. but it differs in having the apical portion of the calyptra densely papillose, epilose innermost perichaetial leaves and an entirely smooth, dextrorse seta (exceptionally with one to several twists to the right immediately below the capsule and further down being twisted to the left).

In her monograph, Bednarek-Ochyra (2006) divided *Codriophorus* into two sections, namely the type section and sect. *Fascicularia* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra. The first of these was lectotypified by *C. acicularis* (Hedw.) P.Beauv (Bednarek-Ochyra, Lamy & Ochyra 2001) and it was characterised by several character states, although generally species of this section are markedly differentiated morphologically and this gave the basis to recognition of no fewer than four subsections within it. Species of sect. *Codriophorus* are generally characterised by simple to irregularly dichotomously branched stems, always without short lateral tuft-like branchlets. The leaves exhibit a broad range of variation, from lingulate to broadly ovate or ovate-lanceolate and they 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 section is further characterised by the multistratosity and strong dorsal convexity of the costa in the median and lower parts which, additionally, has a strongly developed stereid band on the dorsal side in the lower part and a single row of enlarged ventral guide cells. The costa is situated at the bottom of a shallow and wide-

angled groove and it is generally 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 states of stem branching, recurvature of leaf margins, leaf shape and seta torsion are more or less restricted to the type section, but are not shared by all species. For example, *Codriophorus dichelymoides* (Herzog) Bednarek-Ochyra & Ochyra, the only species of subsect. *Andicola* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra, has the seta twisted to the right but with only a single torsion to the left immediately below the capsule.

In contrast, *Codriophorus* sect. *Fascicularia* is primarily characterised by its peculiar costa. It is pale and concolorous with and usually not sharply set off from the laminal cells. It is situated at the bottom of a deep furrow that is mostly narrow-angled and partly enclosed by the plicate leaf base, less often wide-angled and open and it extends to mid-leaf or vanishes just below or in the leaf apex. In general, the costa is narrow, less than 80 µm wide at the base. In transverse section it is bistratose, except for the extreme base where it is in part tristratose or, rarely, it is entirely 3–4-layered. Both ventral and dorsal costal layers are composed of uniform cells and only in the proximal portion or only near the extreme base does the dorsal layer consist of small and thick-walled stereid cells. In addition, the costa varies from slightly prominent on the dorsal surface to nearly of the same thickness as the lamina. It is flat or convex on the ventral side and not prominently convex and crescent-shaped or flattened on the dorsal side.

Some species of *Codriophorus* sect. *Fascicularia*, especially *C. fasciculare* and *C. laevigatus*, often exhibit a characteristic bunched manner of branching owing to the presence of many short, tuft-like, horizontal, lateral branchlets giving the plants a nodose appearance. Branching of this type is unknown in sect. *Codriophorus*. Additionally, in all species of sect. *Fascicularia* (except for *C. brevisetum*) the leaf areolation is composed of elongate cells throughout the lamina, and the stem leaves are straight, lanceolate to ovate-lanceolate, gradually tapering to a short or long, canaliculate acumen. The seta is dextrorse but with a single torsion to the left immediately below the capsule, occasionally with six twists to the left in *C. laevigatus*.

The strict differences in morphological characters between sect. *Codriophorus* and sect. *Fascicularia* are well supported by molecular data. Accordingly, the genus *Codriophorus* is here split into two genera, *Codriophorus* s. str. and *Dilutineuron* warranted by gametophyte and sporophyte character states.

## Nomenclatural conclusions

The aforementioned discussion on morphological and molecular differences exhibited by species of the genus *Codriophorus* results in the following nomenclatural changes.

***Dilutineuron*** Bednarek-Ochyra, Sawicki, Ochyra, Szczecińska & Plášek, *gen. nov.*

*Racomitrium* sect. *Fascicularia* Bednarek-Ochyra, *Fragm. Florist. Geobot. Ser. Polon.* 2: 130. 1995 ≡ *Codriophorus* P.Beauv. sect. *Fascicularia* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra in Ochyra, Żarnowiec & Bednarek-Ochyra, *Cens. Cat. Polish Mosses*: 140. 2003. **Type:** *Dilutineuron fasciculare* (Hedw.) Bednarek-Ochyra, Sawicki, Ochyra, Szczecińska & Plášek (*Trichostomum fasciculare* Hedw., *Spec. Musc. Frond.*: 110. 1801).

**Plants** medium-sized to large and robust, mostly coarse and rigid, loosely caespitose, forming dull, yellow, green, yellowish- or brownish-green, olive-brown to brown tufts; sparsely or freely, irregularly, dichotomously to fasciculately branched, usually with many short, tuft-like, lateral, horizontal branchlets giving the plants a nodose appearance. **Leaves** straight to curved, sometimes falcate, erect and appressed to loosely erecto-patent when dry, erect-spreading or patent when wet, narrowly lanceolate to linear- or ovate-lanceolate, from an ovate, oblong- or ovate-lanceolate base

gradually tapering to a long, subulate or filiform, canaliculate-concave, straight, flexuous or sometimes wavy to serpentine acumen, smooth or with some longitudinal plicae, yellowish-brown at the insertion; **leaf apex** epilose, acute, subacute to narrowly rounded-obtuse, entire or dentate, denticulate-cristate to papillose-crenulate, occasionally terminated with a hyaline to yellowish-hyaline, denticulate to serrate hair-point; **margins** recurved to revolute on both sides from near the base to the apex, incurved and channelled in the upper part, entire throughout or nearly so, sometimes appearing somewhat crenulate due to large, low papillae in the upper part, unistratose throughout to variously bistratose in 1–2(–3) rows of cells distally; **costa** single, ending in mid-leaf to subpercurrent, situated at the bottom of a deep, narrow- or wide-angled groove below, in transverse section bistratose throughout, with occasional tristratose patches near the base, flattened or convex on the ventral side, weakly convex, lunate or flattened on the dorsal side, with costal cells of similar size and shape or with a dorsal row composed of stereid cells at the extreme base; **laminal cells** unistratose throughout, long-rectangular to linear or rarely variously bistratose, short-rectangular to isodiametric in the distal part; **basal cells** rectangular, with strongly incrassate, nodulose and porose walls, forming an intensely bright yellow or yellow-brown, 1–2(–3)-seriate strip along the leaf insertion; **basal marginal cells** differentiated into 1 (occasionally bi-seriate) row of hyaline, translucent cells with straight walls, forming a marginal border consisting of 5–25 cells; **alar cells** quadrate to short-rectangular, becoming much wider than the adjacent basal cells, with smooth to sinuose, incrassate walls, forming distinct, flat or often somewhat inflated and decurrent auricles. **Dioicous**. **Outer perichaetial leaves** oblong-lanceolate, rather abruptly narrowed to a long, filiform, mostly recurved acumen, hyaline at the extreme tip, with a weak costa extending to the acumen, concolorous with the laminal cells and areolation similar to that of the vegetative leaves; **innermost perichaetial leaves** oblong, oblong-lanceolate or oblong-ovate to elliptical, convolute, plicate, rounded-obtuse to shortly apiculate at the apex, with a faint subpercurrent costa, hyaline throughout, with entire or uneven margins. **Setae** 1–3 per perichaetium, erect, twisted to the left immediately below the urn, with 1–6 torsions, clockwise below, minutely grooved. **Capsules** exserted, erect, straight, ovoid, obloid to shortly cylindrical, smooth, lustrous, brown; **operculum** conical-rostrate, with a straight rostrum nearly as long as the urn; **peristome teeth** lanceolate, with a low basal membrane, brown to yellow- or reddish-brown, densely low or spiculate-papillose throughout, divided nearly to the base into 2(–3) filamentous branches. **Spores** spherical, brownish, minutely papillose. **Calyptra** conical-mitrate, 4–5-lobed at the base, scabrous at the apex.

**Etymology:** The genus is named in reference to a costa which is usually of a pale tint and concolorous and imperceptibly merging with the laminal cells (*dilutus* means of pale tint, *neuron* means costa in Greek).

*Dilutineuron* includes the following five species which correspond to *Codriophorus* sect. *Fascicularia* sensu Bednarek-Ochyra (2006) from which *C. varius* (Mit.) Bednarek-Ochyra & Ochyra was excluded and placed in a separate monotypic genus, *Frisvollia* Sawicki, Szczecińska, Bednarek-Ochyra & Ochyra (Sawicki *et al.* 2015). It is divided into two sections, sect. *Dilutineuron* and sect. *Chrysea*. The former accommodates four species from the Northern Hemisphere centred around *D. fasciculare*, whereas the latter comprises only a single species, *D. laevigatum*, a south-temperate amphiatlantic species, which is the only species of the genus known exclusively from the Southern Hemisphere. It is worth noting that Larraín *et al.* (2013) placed *Bucklandiella shevockii* Bednarek-Ochyra & Ochyra (as *Racomitrium shevockii* (Bednarek-Ochyra & Ochyra) Larraín & J. Muñoz) in *Racomitrium* sect. *Fascicularia* Bednarek-Ochyra. Unfortunately, these authors neither explained the reasons for this placement, nor studied any material of the species concerned. They also failed to consider *Bucklandiella*

subsect. *Shevockia* Bednarek-Ochyra & Ochyra in which this otherwise distinct species from Yunnan Province in China was placed (Bednarek-Ochyra & Ochyra 2010). This species was merely mechanically transferred by these authors from *Bucklandiella* to *Racomitrium* sect. *Fascicularia*.

### ***Dilutineuron* sect. *Dilutineuron***

***Dilutineuron fasciculare*** (Hedw.) Bednarek-Ochyra, Sawicki, Ochyra, Szczecińska & Plášek, *comb. nov.*  
BASIONYM: *Trichostomum fasciculare* Hedw., Spec. Musc. Frond.: 110. 1801.

***Dilutineuron brevisetum*** (Lindb.) Bednarek-Ochyra, Sawicki, Ochyra, Szczecińska & Plášek, *comb. nov.*  
BASIONYM: *Racomitrium brevisetum* Lindb., Acta Soc. Sc. Fennica 10: 244: 1872.

***Dilutineuron anomodontoides*** (Cardot) Bednarek-Ochyra, Sawicki, Ochyra, Szczecińska & Plášek, *comb. nov.*  
BASIONYM: *Racomitrium anomodontoides* Cardot, Bull. Herb. Boissier Sér. 2, 8: 335. 1908.

***Dilutineuron corrugatum*** (Bednarek-Ochyra) Bednarek-Ochyra, Sawicki, Ochyra, Szczecińska & Plášek, *comb. nov.* BASIONYM: *Codriophorus corrugatus* Bednarek-Ochyra, Bryologist 107: 377, f. 1–77. 2004.

### ***Dilutineuron* sect. *Chrysea* (Bednarek-Ochyra) Bednarek-Ochyra, Sawicki, Ochyra, Szczecińska & Plášek, *comb. nov.***

BASIONYM: *Racomitrium* sect. *Chrysea* Bednarek-Ochyra, Fragm. Florist. Geobot. Ser. Polon. 2: 64. 1995.

***Dilutineuron laevigatum*** (A.Jaeger) Bednarek-Ochyra, Sawicki, Ochyra, Szczecińska & Plášek, *comb. nov.*  
BASIONYM: *Racomitrium laevigatum* A.Jaeger, Ber. Thät. S. Gall. Naturw. Ges. 1872–1873: 90. 1874.

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