

## New taxonomical arrangement of the traditionally conceived genera *Orthotrichum* and *Ulota* (Orthotrichaceae, Bryophyta)

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**Abstract:** The traditionally conceived genera *Orthotrichum* Hedw. and *Ulota* F.Weber are here reclassified into six genera, *Orthotrichum*, *Dorcadion* Lindb., *Nyholmiella* Holmen & E.Warncke, *Pulviger* Plášek, Sawicki & Ochyra, *Plenogemma* Plášek, Sawicki & Ochyra, and *Ulota*, based on morphological differences and partially on molecular evidence. The genus *Pulviger* includes *P. lyellii* (Hook. & Taylor) Plášek, Sawicki & Ochyra (*Orthotrichum lyellii* Hook. & Taylor) which was selected as its generitype. The genus *Plenogemma* includes *P. phyllantha* (Brid.) Plášek, Sawicki & Ochyra (*Ulota phyllantha* Brid.) which was selected as its generitype.

**Key words:** *Orthotrichum*; *Dorcadion*; *Nyholmiella*; *Plenogemma* gen. nov.; *Pulviger* gen. nov.; *Ulota*; moss taxonomy

### Introduction

*Orthotrichum* Hedw. is a cosmopolitan moss genus consisting of 159 species (Sawicki, Plášek & Szczecińska 2012) and it is the second largest genus in the family Orthotrichaceae. Taxonomic subdivision within this genus has been the subject of continued debate since the late 19<sup>th</sup> century. Certain taxa were repeatedly included in or removed from the genus *Orthotrichum* in an attempt to better clarify infrageneric taxa, including subgenera and sections. The history of taxonomic classification of the genus *Orthotrichum* has been described in detail by Lewinsky (1993) and Lewinsky-Haapasaari and Hedenäs (1998). A phylogenetic analysis revealed the polyphyletic nature of the genus (Goffinet, Bayer & Vitt 1998; Goffinet *et al.* 2004; Sawicki, Plášek & Szczecińska 2009, 2010).

Previous research has demonstrated that the debate on the evolution and taxonomy of the genus *Orthotrichum* would not be complete without including those species of the genus *Ulota* whose close links to *Orthotrichum* subgenus *Gymnopus* (Braithw.) Limpr. have been proven by numerous studies (Goffinet, Bayer & Vitt 1998; Goffinet *et al.* 2004; Sawicki, Plášek & Szczecińska 2010).

The genus *Ulota* consists of around 60 species (Ramsay 2012), of which more than half are found only in the Southern Hemisphere.

Currently published phylogenetic studies (Goffinet *et al.* 2004; Sawicki, Plášek & Szczecińska 2009, 2010) as well as ongoing phylogenetic studies based on complete organellar genomes fully support the taxonomic concept presented in this work.

### A re-circumscription of the genera *Orthotrichum* and *Ulota*

The crucial feature for the reclassification of this group of taxa is the type and position of stomata. The only genus which has cryptoporous stomata is *Orthotrichum* s. str. Among the genera with phaneroporous stomata, an important character in the classification of taxa is the level of ploidy. Monoicous taxa include the genera *Ulota* and *Dorcadion*. Although they share superficial stomata and recurved leaf margins, species of *Ulota* can be easily distinguished from latter mainly by the presence of quadrate to rectangular hyaline cells forming a marginal border at leaf base. Moreover, in *Ulota* species brood bodies are never

produced and asexual reproduction by propagules within species of *Dorcadion* is extremely rare. The group of dioicous genera can be characterized mainly by production of gemmae in great profusion and this apparently compensates for the apparently very rare incidence of sexual reproduction. The group consists of *Nyholmiella*, *Pulvigera* and *Plenogemma*, the last two taxa being recognized here as new genera. *Nyholmiella* differs from *Pulvigera* and *Plenogemma* primarily by having an ovate leaf with an obtuse apex. The latter two genera have leaves that are linear-lanceolate or lanceolate with an acute to acuminate apex. While the gemmae in *Pulvigera* are scattered more or less equally on the adaxial leaf surface, in *Plenogemma* the conspicuous clusters of fusiform brownish gemmae are situated on the protruding costa of the upper leaves.

**All six genera can be distinguished in the following key.**

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|--|---------------------|
| 1a. Stomata cryptoporous   | <i>Orthotrichum</i> |
| 1b. Stomata phaneroporous  | 2                   |
| 2a. Monoicous; gemmae mostly absent  | 3                   |
| 2b. Dioicous; gemmae always present  | 4                   |
| 3a. Basal marginal cells of leaves shorter and pale with thickened cross-walls, forming a border sharply differentiated from inner cells | <i>Ulota</i>        |
| 3b. Basal marginal cells of leaves not particularly differentiated   | <i>Dorcadion</i>    |
| 4a. Leaf margins erect, incurved or involute throughout; leaves ovate, concave, broadly obtuse or rounded at the apex                    | <i>Nyholmiella</i>  |
| 4b. Leaf margins plane above, partly recurved below; leaves lanceolate, narrower at the apex, acute or acuminate                         | 5                   |
| 5a. Gemmae forming conspicuous clusters on excurrent part of costa of uppermost leaves   | <i>Plenogemma</i>   |
| 5b. Gemmae scattered more or less equally on adaxial leaf surface  | <i>Pulvigera</i>    |

**Principal morphologic features of the genera**

The following characters are not an exhaustive list of the distinguishing features, but represent a selection of those that are of fundamental importance for taxonomic delimitation of individual genera.

***Orthotrichum* Hedw.**

Spec. Musc.: 162. 1801. **Lectotype:** *Orthotrichum anomalum* Hedw. (*vide* Grout 1935: 106).

Species of *Orthotrichum* s. str. are characterized by having appressed to erect leaves, which are only occasionally flexuose when dry (e.g. *O. pulchellum*). They are narrowly lanceolate to oblong- or ovate-lanceolate, keeled, acuminate to acute or rounded with the margins mostly recurved. The costa is single, usually vanishing below the apex, rarely excurrent. Short cylindrical, unbranched gemmae are occasionally present on the leaves. Species of the genus are monoicous. The capsules are immersed to somewhat long exserted and mostly ribbed. The stomata are immersed. The vaginula is naked or hairy. The peristome is double or, rarely, reduced and single, with the teeth erect or reflexed on drying. The exostome consists of 16 teeth which are typically arranged in 8 pairs. The endostome contains 8 or 16 segments. The calyptra is naked or sparsely to densely hairy.

### ***Dorcadion*** Lindb.

Utkast Eur. Bladmoss.: 7. 1878. **Lectotype** (*selected here*): *Dorcadion affine* (Brid.) Lindb. (*Orthotrichum affine* Brid.)

Species of *Dorcadion* are characterized by having appressed to erect leaves that are narrowly lanceolate to oblong- or ovate-lanceolate, keeled, acuminate to acute or rounded with the margins mostly recurved. The costa is single, usually subpercurrent. Short cylindrical und unbranched gemmae are occasionally present on the leaves. Sexual condition is always monoicous. The capsules are immersed to somewhat long exserted, smooth or less often furrowed when dry. The stomata are superficial. The vaginula is naked or hairy. The peristome is double (rarely reduced or single), erect or reflexed when dry. It consists of 16 exostome teeth that are usually arranged in 8 pairs and an endostome of 8 or 16 segments. The calyptra is naked or sparsely to densely hairy.

The name *Dorcadion* was introduced by Adanson (1763) and as a pre-Hedwigian name it was subsequently validated by Lindberg (1878). These two authors placed in this genus three species which Dillenius (1741) placed in his genus *Polytrichon* for which he had used phrase names and presented on plate 55 in figures 8–10. In current taxonomic usage these are *Dorcadion affine*, *D. stramineum* (Hornsch.) Lindb. and *D. rupestre* (Schwägr.) Lindb. The first of these is here selected as a lectotype of this generic name.

### ***Nyholmiella*** Holmen & E. Warncke

Bot. Tidsskr. 65: 179. 1969. **Lectotype**: *Nyholmiella obtusifolia* (Brid.) Holmen & E. Warncke (*Orthotrichum obtusifolium* Brid.) (*vide* Vitt 1971: 704).

Species of *Nyholmiella* have leaves erect-spreading when moist but loosely appressed when dry. They are ovate with bluntly rounded apices, erect, incurved or involute margins and a single costa that is obscure distally and ceases far below the apex. The gemmae are usually abundantly produced, primarily on the adaxial surface of the leaf lamina. They are uniseriate or with a few biseriate areas, branched (in *N. gymnostoma* (Brid.) Holmen & Warncke) or unbranched (in *N. obtusifolia*). The plants are always dioicous. The capsules are immersed to somewhat emergent. The stomata are superficial and the vaginula is naked. The peristome is present only in *N. obtusifolia* and consists of 8 exostome teeth, which are reflexed on drying, and 8 endostome segments, whereas *N. gymnostoma* has gymnostomous capsules. The calyptra is essentially glabrous.

The distinctness from other taxa of the genus *Orthotrichum* of the species now placed in the genus *Nyholmiella* has been already noted by Delogne (1885) and these differences were effected by Hagen (1908) who established the separate genus *Stroemia* I. Hagen to accommodate *Orthotrichum gymnostomum* and *O. obtusifolium*. Since *Stroemia* was an illegitimate name, it was replaced by *Nyholmiella* by Damsholt, Holmen & Warncke (1969). This genus has not been universally accepted by bryologists (Vitt 1973; Goffinet *et al.* 2004; Sawicki, Plášek & Szczecińska 2010) provided convincing molecular evidence to support of the generic distinctness of *Nyholmiella*.

### ***Pulviger*** Plášek, Sawicki & Ochyra, *gen. nov.*

*Orthotrichum* Hedw. sect. *Lyelliana* Schimp., Syn. Musc. Eur. (ed. 2) 2: 336. 1876 [‘*Orthotricha Lyelliana*’]. **Type**: *Orthotrichum lyellii* Hook. & Taylor, *Musc. Brit.*: 76, pl. 22. 1818 ≡ *Pulviger* *lyellii* (Hook. & Taylor) Plášek, Sawicki & Ochyra, *comb. nov.*

**Etymology**: The generic name refers to the leaves that are covered with numerous brown gemmae giving them a dusty appearance.

*Pulviger* is a monotypic genus comprising only *P. lyellii* which is its generitype. Although formerly placed in genus *Orthotrichum*, its position there is no longer sustainable

with respect to its dioicous sexuality and the production of gemmae in great profusion. Moreover, the species has plane leaf margins.

The leaves are erect-spreading to loosely-erect when moist, but slightly contorted when dry, lanceolate to linear-lanceolate, narrowly acute to acuminate. The leaf margin is plane above but sometimes lightly recurved near the base. The costa is strong, ending near the apex.

Fertile plants with mature capsules have been recorded several times for *Pulviger a lyellii* but they are always considered to be very rare (Smith 2004). The stomata are superficial. Detailed description of the double peristome (16 exostome teeth + 16 endostome segments) in this species was published by Lewinsky (1989) and Lewinsky-Haapasaari (1994).

*Pulviger a lyellii* are easily recognized mainly by the gemmae and sharply tipped leaves. Quantity of brownish gemmae situated over the leaf surfaces gives the impression that the leaves are dusty by them. *Plenogemma phyllantha* also has gemmae, but its leaves are strongly crisped when dry, and the gemmae cluster are situated rather on the leaf apices.

***Plenogemma* Plášek, Sawicki & Ochyra, gen. nov.**

*Dense pulvinata, foliis longis, valde tortilis, lanceolatis longe acuminatisque, marginibus integris, planis in parte superiori, inferne recurvis, costis fuscis, longe styloso-excurrentibus, in parte stylosa foliorum supremorum densissime propagulis cylindraceis articulatis fuscis obtectis, cellulis superioribus ellipticis vel rotundatis cum (1–)2 papillis humilibus praeditis. Dioica. Capsulae perrarae, stomata phaneropora, peristomium duplex. Gemmae semper effecta. Type: *Plenogemma phyllantha* (Brid.) Sawicki, Plášek & Ochyra, comb. nov. BASIONYM: *Ulota phyllantha* Brid., Mant. Musc.: 113. 1819.*

**Etymology:** The generic name alludes to gemmae that are produced in great profusion on the excurrent part of the costa at the leaf apex.

*Plenogemma* is a monotypic genus comprising a single species, *P. phyllantha*, which serves as its generitype. Although formerly placed in *Ulota*, there are at least two undisputed features for its exclusion, namely the dioicous sexuality (and accordingly extremely rare production of sporophytes), and production of gemmae in great profusion on the excurrent costa. Moreover, the species has narrowly elongate basal laminal cells with nodose and incrassate lateral walls, not quadrate to rectangular hyaline cells as in *Ulota* s. str. species.

The leaves, on drying, are contorted to strongly crisped and erect-spreading when moist. They are ovate to narrowly lanceolate with acute apices. The leaf margin is plane or recurved below. The costa is brownish and protrudes from the tip, where a conspicuous cluster of brown gemmae is formed.

The sexual condition is dioicous and sporophytes are produced exceedingly rarely. The stomata are superficial but detail description of the sporophyte characters of *P. phyllantha* is usually absent in the literature.

*Plenogemma phyllantha* is easily recognized due to the mass-production of brownish to dark brown cylindrical and multi-septate gemmae forming clusters on the excurrent part of the costa of the uppermost leaves. Some species of *Orthotrichum* and the two known species of *Nyholmiella* also produce gemmae on the leaves, but they are pale green, not brown. In *Pulviger a lyellii* gemmae are brown colored but they are scattered more or less equally on the leaf surface or very occasionally arise from the ends of rhizoids and protonema (Correns 1899; Piccioli 1932; Duckett & Ligrone 1992; Lewinsky 1993).

SEM micrographs of the peristome in this species were published by Shaw (1986) who suggested that its peristome structure agrees well with that observed in species of the broadly conceived genus *Orthotrichum*. This argument may also support the transfer of the species from the genus *Ulota* to *Plenogemma*.

## *Ulot* D.Mohr

Ann. Bot. (König & Sims) 2(3): 540. 1806. **Type:** *Ulota crispa* (Hedw.) Brid. (*Orthotrichum crispum* Hedw.).

Species of *Ulot* are characterized by having contorted-cripsed to slightly twisted leaves that are erect-curved when dry. They are oblong- to linear-lanceolate, usually from an ovate base, acuminate, acute with the margins mostly recurved. The costa is percurrent. The inner basal laminar cells radiate from the insertion and are elongate-rectangular to elliptic, often with nodose and very incrassate walls. The leaf base also has a well differentiated border of one or few rows of quadrate to rectangular hyaline cells. Brood bodies are always absent. The plants are monoicous. The capsules are fully exerted and the stomata are superficial. The vaginula is naked or hairy. The peristome is double or single (if the endostome is lacking). The exostome consists of 8 or sometimes 16 reflexed or erect teeth. The endostome comprises 8 segments which may be lacking. The calyptra is conic, hairy and usually deeply split for several lobes at base.

All species of *Ulot* are monoicous and often produce sporophytes but never propagate vegetatively by gemmae. *Ulot phyllantha* has had always been a discordant element within the genus. It was the only dioicous species which produced sporophytes exceedingly rarely, but it reproduced very successfully by gemmae. The shape of the leaves in *U. phyllantha* differs from that of other congeners in the lack of an ovate base and by having an excurrent costa. These morphological differences are strongly supported by molecular data and accordingly *U. phyllantha* is transferred to the separate genus *Plenogemma*.

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