A taxonomic contribution on the European cleistocarpous species of Pottiaceae (Musci)

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SUMMARY

The morphological characters of the sporophyte and gametophyte of the genera *Phascum* L. ex Hedw., *Microbryum* Schimp., *Acaulon* Müll. Hal. and *Aschisma* Lindb., are delimited. *Leptophascum* J. Guerra & M.J. Cano stat. nov. (type: *Leptophascum leptophyllum* (Müll. Hal.) J. Guerra & M.J. Cano comb. nov.), and *Protobryum* J. Guerra & M.J. Cano nom. nov. are proposed to replace *Mildeella* Limpr. hom. illeg., (as a genus with intermediate characteristics between *Phascum* and *Pottia* (Rchb.) Fürnr.). In addition, *Phascum cuynetii* Bizot & R.B. Pierrot ex J. Guerra et al. is transfered to the genus *Aschisma* Lindb. (*A. cuynetii* J. Guerra & M.J. Cano comb. nov.).

KEYWORDS: Pottiaceae, cleistocarpy, European taxa.

INTRODUCTION

During the last century, the taxonomy and systematics of mosses have been largely based on a balanced evaluation of both gametophytic and sporophytic characters. The structure of the sporophyte (stegocarpous or cleistocarpous) and the variation in the types of sporophytic opening have been considered essential in the definition of generic and suprageneric levels. In the current concept of the family Pottiaceae, the distinction between the stegocarpous and cleistocarpous sporophyte has been considered important in the separation of genera into different families (Phascaceae and Weissiaceae or Trichostomaceae) (cf. Bruch, Schimper & Gümbel, 1836-1855). The morphology of the peristome and its presence-absence can also be useful for the separation of closely related genera (e.g. Tortula Hedw. and Desmatodon Brid.), or between species from the same genus (e.g. Pottia lanceolata (Hedw.) Müll. Hal. and Pottia pallida Lindb.).

The Pottiaceae are one of the most extensive families in the mosses and there is still much work to be done in understanding them. It therefore seems logical that any serious taxonomic-systematic proposal should neither ignore nor undervalue the features of the sporophyte since, as a diploid structure, the features which develop during its evolution are more strongly fixed than most gametophytic structures.

In our opinion, the revolutionary and novel proposals of Zander (1993) do not follow a natural sequence in some cases, otherwise they would not include both cleistocarpous and stegocarpous species with complex peristomes in the same genus. These features are the expression of profound evolutionary processes about which not enough is known. However, they should not be underestimated in any serious taxonomic—systematic proposal.

In this paper, however, whilst taking into account the positive aspects of the proposals of Zander (1993) and others, regarding the taxonomy of the genera *Phascum*, *Pottia*, *Microbryum* and *Aschisma*, with the purpose of applying them to the European species of these genera, we intend to take a step towards a more natural classification of the family.

There is no doubt that some of the recent advances in molecular biological techniques could be used to shed much light on these problems. However, in the absence of such data, our aim is simply to put forward some taxonomic proposals which may, at the very least, serve as an alternative to the views of others.

Our taxonomic proposals, which we consider more natural, would create greater ease in the identification of taxa, using keys, and would also create a greater consonance between the evolutionary processes in mosses and their systematics. Allocating equal weight to gametophytic and sporophytic features is an important factor in our proposals. Not surprisingly this results in an increase in

the number of genera, especially among those which are very complex.

TAXONOMIC RESULTS AND DISCUSSION

Microbryum Schimp., Syn. 10. 1860.

Type: Microbryum floerkeanum (F. Weber & D. Mohr.) Schimp.

The proposal of Schimper (1860) for separating *Microbryum* and *Phascum* into different genera was not widely accepted, because the taxon was almost always considered as of infrageneric level (cf. Roth, 1904; Brotherus, 1924–25). However, we consider Zander's (1993) proposal, which considers this genus for inclusion within the Pottieae, as *pro parte* correct. Its characteristics are as follows:

Sporophytic characters: Capsule cleistocarpous, generally exerted, peristome absent (sometimes 1 or 2 rows of thickened cells forming a pseudo-operculum can be observed, particularly in *Microbryum rectum* (With.) R.H.Zander); spores mostly smooth or spinulose.

Gametophytic features: Stems extremely short 0.3–0.5 mm; leaves 0.6–1.6 mm in length, generally brown or reddish, with apiculate or mucronate apex; margins recurved from the mid-leaf to near apex; laminal cells papillose, with simple or branched papillae; costa in cross-section showing a well-developed ventral and dorsal epidermis and only 1-2(3) stereids in a dorsally-positioned group (Fig. 1a, b, c).

The European species which we include in this genus are as follows: *Microbryum floerkeanum* (F.Weber & D.Mohr) Schimp., *Microbryum longipes* (J.Guerra, J.J.Martínez & Ros) R.H.Zander, *Microbryum curvicolle* Ehrh. ex Hedw., *Microbryum rectum* (With.) R.H.Zander, *Microbryum piptocarpum* (Durieu & Mont.) J.Guerra & M.J.Cano comb. nov. (Basionym: *Phascum piptocarpum* Durieu & Mont., Syll. gen. sp. crypt: 51. 1856).

We do not consider that the stegocarpous species, such as *Pottia starckeana* (Hedw.) Müll. Hal. and *Pottia davalliana* (Sm.) C.E.O. Jensen should be included in this genus, in spite of their gametophytic resemblances to those of *Microbryum*. In our opinion, these species of *Pottia* (section *Muticae* Medelius in C.E.O. Jensen) are taxa phylogenetically closely related to *Mildeella* Limpr. and *Microbryum*. Some interspecific hybrids have been described (Ros, Guerra & Cano, 1994), but these need to be verified by investigations at genetic level.

Phascum L. ex Hedw., Spec. Musc. Frond.: 19. 1801.

Type: *Phascum acaulon* With., Syst. Arr. Brit. Pl. (ed. 4) 3: 768. 1801.

= Tortula acaulon (L. ex With.) R.H.Zander, Bull. Buffalo Soc. Nat. Sci. 32: 378. 1993; *Phascum cuspidatum* Schreb. ex Hedw., Spec. Musc. Frond.: 22, 1801.

Classically, cleistocarpous species with gametophytic characters very heterogeneous (or minimally homogenous) have been included in this genus (e.g. Guerra et al., 1991). Nevertheless, the discovery and greater knowledge of many species which were, at that time, poorly known has revealed that the genus *Phascum* (sensu Podpéra, 1954) can now be redefined, using the following combination of features:

Sporophytic characters: capsule subspherical, immersed; seta very short; peristome absent, sometimes with a line of dehiscence formed by one or two rows of differentiated cells; beak very short when mature; stomata phaneropore, at base of capsule.

Gametophytic characters: plants of middle size (or relatively big for this group of Pottiaceae); stems branched or not; leaves diversely papillose; costa well-developed in cross-section, at mid-leaf showing 3-4(5) dorsal stereid layers; in developed leaves some stereids or substereids are rarely included between the guide cells layer. (Fig. 1f, g)

The European species which can be included without any problem are: *Phascum cuspidatum* Schreb. ex Hedw. and *Phascum vlassovii* Laz.

Leptophascum stat. nov.

Basionym: *Phascum* sect. *Leptophascum* Müll. Hal., Flora 71: 7, 1888.

= Phascum subg. Leptophascum (Müll. Hal.) Roth, Aussereur. Laub. 2: 214, 1911.

Type: *Leptophascum leptophyllum* (Müll. Hal.) J.Guerra & M.J.Cano comb. nov.

Basionym: *Phascum leptophyllum* Müll. Hal., Flora 71: 6–7. 1888.

= Pottia splacnobryoides Müll. Hal., Nuov. Giornale Bot. Ital. N. Ser. 5: 174, 1998; Pottia denticulata Dixon & P. de la Varde., Arch. Bot. Bull. Mens. T.1 (8–9): 168 + pl. 4, 1927; Physcomitrium rhizophyllum Sakurai, Bot. Mag. Tokyo 52: 469, 1938; Funaria rhizophylla (Sakurai) Sakurai, Muscologia Japonica 68, 1954; Tortula vectensis E.F. Warb. & Crundw., Trans. Brit. Bryol. Soc. 4: 763, 1965; Tortula rhizophylla (Sakurai) Z.Iwats & K.Saito, Miscell. Bryol. et Lichénol. 6: 59, 1972; Chenia rhizophylla (Sakurai) R.H.Zander, Phytologia 65: 425, 1989; Chenia leptophylla (Müll. Hal.) R.H.Zander, Bull. Buffalo Soc. Nat. Sci. 32: 258. 1993.

According to Arts & Sollman (1991), the taxonomic status of *Phascum leptophyllum*, as Müller (1888) defined it, creating the monotypic subgenus *Leptophascum* (later adopted by Roth, 1911) is more suitable than its inclusion in *Tortula* (Iwatsuki & Saito, 1972) or *Chenia* (Zander, 1989). In our opinion, its relationship with *Tortula* is practically non-existent, at both sporophytic and gametophytic level. The same could be applied to its placement in *Chenia* where stegocarpous (*Chenia subobliqua* (Wilson) R.S.Williams) and cleistocarpous species (*Chenia leptophylla*) coexist.

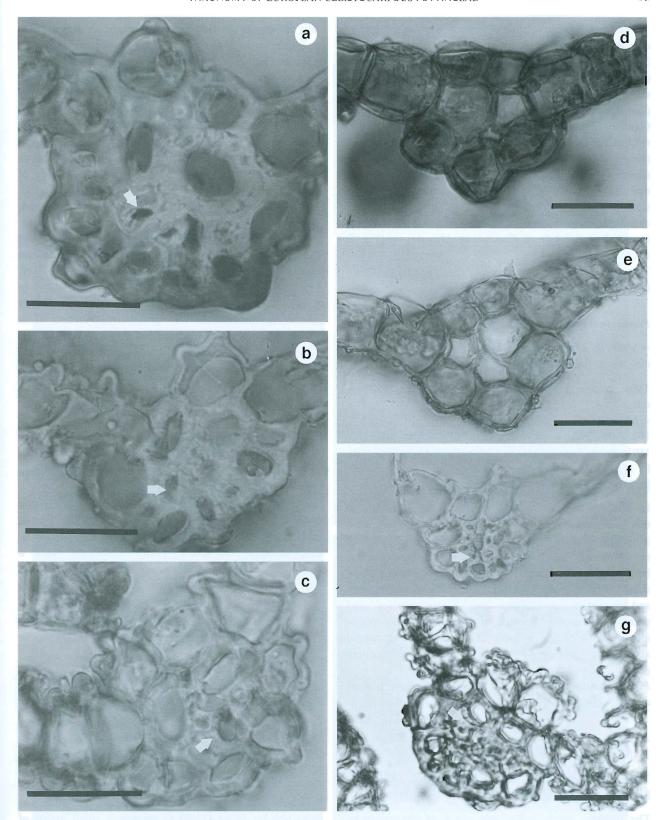


Figure 1. Leaf cross-sections, showing variation in the costa. a: Microbryum floerkeanum. b: M. piptocarpum. c: M. curvicolle. d, e: Leptophascum leptophyllum. f: Phascum vlassovii. g: P. cuspidatum. Scale bars: a, b, c, f, $g = 20 \mu m$; d, $e = 30 \mu m$. Arrows mark areas with stereids.

The features which define the new genus *Leptophascum*, extending those proposed by Müller (1888), are as follows: Sporophytic characters: capsule ovoid or subspherical, immersed cleistocarpous, without any trace of operculum; seta very short; beak *ca* 0.25 mm in length, rostrate; phaneropore stomata at base of capsule.

Gametophytic characters: plants of middle size with rhizoidal tubers, reported by Warburg & Crundwell (1965); costa in cross-section at middle part of the leaf showing a very well-developed dorsal and ventral epidermis and 2–3 guide cells in 1 layer and no stereids. (Occasionally there is 1 substereid in a central position). These characters represent a considerable difference with respect to costal anatomy from *Phascum* or *Microbryum* (Fig. 1: d, e).

There is only one known species *Leptophascum leptophyllum*. It is probably a monospecific genus.

Protobryum nom. nov.

= *Mildeella* Limpr., Laubm. Deutschl. 1: 191, 1985, hom. illeg. (later homonym)

Type: Protobryum bryoides J. Guerra & M.J. Cano nom. nov.

= Mildeella bryoides (Dicks.) Limpr., Laubm. Deutschl. 1: 192, 1886; *Phascum bryoides* Dicks., Pl. Crypt. Brit. 4: 3, 1801; *Pottia bryoides* (Dicks.) Mitt. Ann. Mag. Nat. Hist. 8: 311, 1851; *Tortula protobryoides* R. H. Zander, Bull. Buffalo Soc. Nat. Sci. 32: 226, 1993.

In our opinion, there is a need for the retention of this monospecific genus. Only one species (*P. bryoides*) is included, which shows gametophytic features similar to *Phascum*, but sporophytic features intermediate between *Phascum* and *Pottia*: i.e. capsule emergent or shortly exerted, cleistocarpous but with a rudimentary and persistent operculum, and a rudimentary and papillose peristome. Because of its imprecise taxonomic identity, and taking account of the evidence presented above, we propose *Protobryum* as an independent genus.

Protobryum replaces Mildeella according to the article 53 of ICBN (Greuter et al., 1994).

Aschisma Lindb., Utkas Nat. Grupp. Eur. Bladm. 28, 1878.

Type: Aschisma carniolicum (F.Weber & D.Mohr.) Lindb.

The features which define this genus of cleistocarpous mosses are numerous and very clear. Basically, they are as follows:

Sporophytic characters: plants very small; leaves with margins plane to occasionally weakly incurved, bordered by 1–3 rows of weakly or epapillose cells, and the leaf base not very differentiated in shape; costa with two bands of stereid or substereid cells separated by a band of guide

cells; epidermis not very differentiated; upper laminal cells quadrate with 3-4 stout papillae per lumen, densely disposed (Fig. 2: a, d, e).

Gametophytic characters: Capsule cleistocarpous; exothecial cells rectangular 4–5:1, circling capsule longitudinally in several even bands with the appearance of a pallisade (Fig. 2: c, f); stomata cryptopore (Fig. 2: b).

In Europe, only one species (A. carniolicum) had previously been known. After new localities and better material were found, a detailed morphological study of Phascum cuynetii was carried out. We conclude that P. cuynetii should be transferred to the genus Aschisma. Therefore we propose the following combination: Aschisma cuynetii (Bizot & R.B.Pierrot ex J.Guerra et al.) J.Guerra & M.J.Cano comb. nov. (Basionym: Phascum cuynetti Bizot & R.B.Pierrot ex J.Guerra et al., Rev. Bryol. Lichénol. 36 (3–4): 505, "1969" 1970).

It is a species with very clear features indicating it should be included in this genus; it is distinct from *Aschisma kansanum* A.L.Andrews (cf. Guerra *et al.*, 1991: Figs 130–146). The main differences between *A. cuynetti* and another European species, *A. carniolicum*, are shown in Table 1.

Acaulon Müll. Hal, Bot. Zeit. 5: 99. 1847.

Type: Acaulon muticum (Hedw.) Müll. Hal.

This genus is highly diversified in the Mediterranean region and is fairly easily delimited.

Sporophytic characters: capsule globose immersed, with a minute or absent apiculus, calyptra extremely tiny, flimsy, mitriform, often persistent.

Gametophytic characters: plants bulbiform with a basal tuft of fine pale rhizoids; tiny, up to ca 2–2.5 mm high; leaves few, concave, rounded on the back, sometimes keeled; costa in cross section at middle part of the leaf consists of 2(3) stereid bands and lacks guide cells; lamina cells thick on abaxial surface (Fig. 3a–f).

At present the genus comprises seven species in Europe: Acaulon casasianum Brugués & H.A.Crum, A. dertosense Casas, Sérgio, Cros & Brugués, A. piligerum (De Not.) Limpr. (subgenus Alaticosta I.G.Stone), A. triquetrum (Spruce) Müll. Hal., A. muticum (Hedw.) Müll. Hal., A. mediterraneum Limpr. and A. fontiquerianum Casas & Sérgio. The latter species, due to the anatomical features of the costa, could be included in Phascum subgenus Acaulonopsis I.G.Stone. This subgenus was described by Stone (1989) to include a small group of species from Australia and Africa which do not fit satisfactorily into either Phascum or Acaulon as they possess some features of each. Nevertheless, the anatomy of the costa described in this subgenus is closer to Acaulon than Phascum (except for the large adaxial cells, also present in A. fontiquerianum) (cf. Casas & Sérgio, 1990).

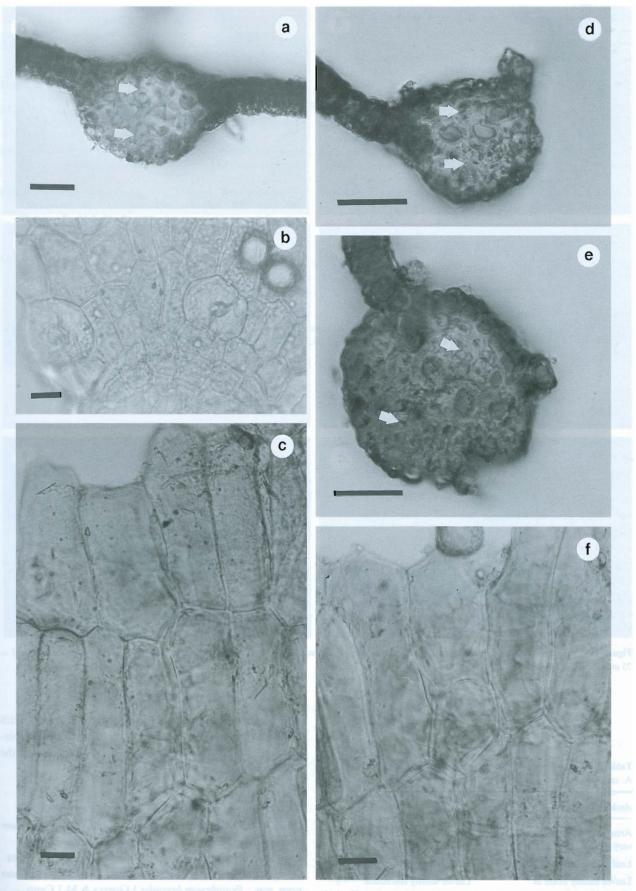


Figure 2. Leaf cross-sections (a, d, e), stomata (b) and exothecial cells (c, f). a, b: Aschisma carniolicum. c, d, e, f: Aschisma cuynetii. Scale bars: a, d, $e = 15 \mu m$; $b = 40 \mu m$; c, $f = 25 \mu m$. Arrows mark areas with stereids.

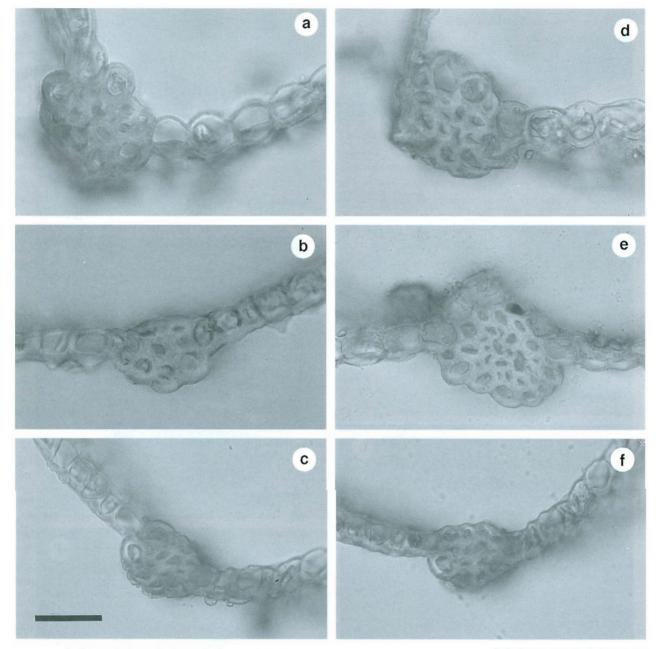


Figure 3. Leaf cross-sections of Academ (a-f). a: A. dertosense. b: A. casasiamom. c, f: A. triquetrum. d, e: A. fontiquerianum. Seale bars: $a-f=35 \mu m$.

Table 1. The differences between Aschisma cuyuctii and A. carniolicum.

Aschisma cușnetii	Aschisma earniolicum
Areolation obscure, papillae very dense	Arcolation pellucid, papillae not very dense
Leaf apex cucudlate	Leaf apex plane
Leaves mostly ovate or obovate-lanceolate	Leaves mostly lanceolate
Capsule yellowish when mature	Capsule reddish when mature

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