

Bryophyte flora of the Huon Peninsula, Papua New Guinea. LXVII. *Amphidium* (Rhabdoweisiaceae, Musci)

Daniel H. Norris & Timo Koponen

Norris, D. H. & Koponen, T., Department of Ecology and Systematics, Division of Systematic Biology, P.O. Box 7, FIN-00014 University of Helsinki, Finland

Received 18 August 1999, accepted 1 November 1999

Norris, D. H. & Koponen, T. 1999: Bryophyte flora of the Huon Peninsula, Papua New Guinea. LXVII. *Amphidium* (Rhabdoweisiaceae, Musci). — *Ann. Bot. Fennici* 36: 265–269.

Amphidium tortuosum (Hornsch.) Cufod. is the only species of the family Rhabdoweisiaceae occurring in Western Melanesia and New Guinea. Both collections came from cliff walls, one of them was in an open grassland area and the other in closed montane rainforest. The placement of *Amphidium* Schimp. in the neighbourhood of Dicranaceae and in the family Rhabdoweisiaceae instead of Orthotrichaceae is based on the presence of epigametophytic plants in *Amphidium*, which are unknown in the Orthotrichaceae, on the rhizoid topography similar to Dicranaceae and different from that in Orthotrichaceae, the pattern of papillosity of leaf cells, and on recent evidence from nucleotide sequences.

Key words: *Amphidium*, Papua New Guinea, rhizoid topography, systematics, taxonomy, West Irian

INTRODUCTION

This paper belongs to a series dealing with the bryophyte flora of Western Melanesia, which includes West Irian, Papua New Guinea and the Solomon Islands. Essential background information of materials and methods, and abbreviations of collecting localities and geographical areas used in this study are given in part I (Koponen & Norris 1983) and VI (Norris & Koponen 1985). The previous parts of the Huon Peninsula series are listed in Koponen *et al.* (1991) and in Koponen (1993, 1995). The previous paper in the series is Norris

et al. (1999). Our studies are mainly based on the collections of Koponen and Norris from the Huon Peninsula, Papua New Guinea (H). *Amphidium tortuosum* was collected twice during Koponen-Norris mission and was previously reported therefrom in the literature.

FAMILY RHABDOWEISIACEAE Limpr. 1886

The systematic placement of the genus *Amphidium* Schimp. has been, and remains, a subject of controversy. Many workers have placed *Amphidium*

in the Orthotrichaceae because of the strongly sulcate capsule with the correlated character of longitudinally differentiated strips of exothecial cells, and they emphasized the resemblance to *Zygodon* Hook. & Tayl. in that family. However, *Amphidium* lacks a peristome, and cannot therefore be placed with certainty in the Haplolepidaceae or the Diplolepidaceae. Lewinsky (1976) attempted to deal with this gymnostomous condition by a comparison of cross-sections of capsules at spore sac level. She compared *Amphidium tortuosum* (Hornsch.) Cufod. (as *A. cyathicarpum* (Mont.) Broth.) and *Orthotrichum diaphanum* Brid., and found close parallels between the spore sacs of these two plants. Her observations of these spore sacs suggested to her that *Amphidium* is a doubly peristomate moss (see Kreulen 1972). She concluded that *Amphidium* is in the Orthotrichaceae near *Zygodon*.

More recently, however, Goffinet (1998) reported on studies of nucleotide sequences in bryophytes, and he finds *Amphidium* distant from the Orthotrichaceae. This suggests that an alternative placement of *Amphidium* may have to be weighed. Brotherus (1924) placed *Amphidium* in the Rhabdoweisioideae of the Dicranaceae. In that placement Brotherus partially followed Limpricht (1886), who erected a family Rhabdoweisiaceae to accommodate the two genera. Past systematic placements of *Amphidium* can partially be summarised on the basis of whether it is compared to *Rhabdoweisia* B.S. & G. or whether it is compared to *Zygodon*. The comparison with *Rhabdoweisia* takes two forms: placement in the Dicranaceae, or placement in a separate family, the Rhabdoweisiaceae.

We have searched for new characters, which may help to resolve the affinities of *Amphidium*. One of the characters that may be useful is the frequent presence of small branchlets in upper leaf axils. These small branchlets do not seem to be gametangial but instead they may have some utility in vegetative expansion of the clone. They are very easily shed from the parent plant because of a strong constriction of that branch stem at its point of initiation. Such branches are not unique to *Amphidium*. Salazar-Allen (1985) describes "epigametophytic plants" in the haplolepidous genus *Leucophanes* Brid., and she notes that some of them are really short branching systems that early "lose their attachment from the parent plant". La

Farge-England (1996) further comments on such epigametophytic plants: "this type of fragile branching is common in *Leucoloma* Brid., and has been reported for other genera in the Dicranaceae". We have searched for similar basally constricted branchlets in *Rhabdoweisia crenulata* (Mitt.) Jameson, and we found them abundant in the first investigated specimen (Crum & Anderson, Mosses of North America 920: USA, North Carolina, Macon County, H!). We have been unsuccessful in our search for similar branches in numerous specimens of six genera of the Orthotrichales (*Erpodium* (Brid.) Brid., *Macromitrium* Brid., *Orthotrichum* Hedw., *Rhachithecium* Broth. ex Le Jol., *Schlotheimia* Brid. and *Ulota* Mohr). It is of some interest here that Hedenäs (1996) uses an observation of similar basally constricted branch stems in his cladistic analyses of the Hookeriales.

In continuing our investigation of the systematic placement of *Amphidium*, we directed our attention to the rhizoid insertion and morphology. Koponen (1968) and Tuomikoski and Koponen (1979) showed the importance of rhizoids and called attention to the "macronematal apparatus" in certain Eubryales. Crundwell (1979) distinguished rhizoids on the basis of their insertion on leaves or on various portions of stems. Hedenäs (1987) has given systematic importance to the position of rhizoid insertion on the stem relative to the leaves (adaxial versus abaxial), and we have found that even more precise description of position can be useful (Norris & Koponen 1996). In addition to adaxial and abaxial notations of position, one should note whether that insertion is all along the leaf base, or restricted to the area of costal insertion. Of very special importance in abaxial rhizoids is frequent pattern of insertion along a decurrent strip of cells below the alar region.

We have found that *Amphidium* has rhizoids inserted from the strip of cells decurrent from the alar region. This is a feature common among the Dicranaceae, including *Rhabdoweisia*. In the Orthotrichaceae, we find two basic patterns of rhizoid insertion: *Orthotrichum* and other sympodially branched plants (see Goffinet & Vitt 1998) have the rhizoids inserted on a patch of cells adaxial to the alar cells. In contrast, *Macromitrium* and other monopodially branched plants have the rhizoids inserted abaxially on the costa from its base even

to near its apex.

Furthermore, the pattern of papillosity shown by all species in the genus *Amphidium* is a feature essentially restricted to the Dicranaceae. The papillae of *Amphidium* are really streaks or bumps, which are in no way restricted to the confines of the lumen, but they instead are located over the lateral and transverse walls as well as over the lumens. A close examination will always show papillae, which seem to be partly located over the lumens, partly over the walls. Some species of Dicranoweisia show this same type of papillosity (cuticular papillosity).

After this quick morphological survey, we have decided to treat *Amphidium* as a genus close to *Rhabdoweisia*. The habitat ecology of these genera supports this placement; both are lithophytic, while the Orthotrichaceae and *Zygodon* have a wider selection of niches. Because of the somewhat ambiguous evidence for placement, we feel that burial within the large family Dicranaceae is unwise, and opt for its treatment in the Rhabdoweisiaeae in order to continue to point out the need for further research.

Genus *Amphidium* Schimp., *nom. cons.*

Amphidium is best recognised in the field by the extremely crispate leaves which are very narrow relative to width (mostly more than 10: 1). It is often with sporophytes, and the sulcate and stragulate, almost globular capsules are absolutely diagnostic on such a narrow-leaved plant. Without capsules, it may be confused with *Anoetangium aestivum* (Hedw.) Mitt., but this latter species has shorter leaves with broadly acute apices and not very keeled leaf bases.

Amphidium is most likely to be mistaken for some of the crispate genera of the Pottiaceae (example: *Anoetangium* Schwaegr.), or of the Dicranaceae (example: *Dicranoweisia* Lindb. ex Milde). The somewhat angular lumens of the laminal cells, and the pattern of papillosity shown by all species in the genus *Amphidium*, should tilt the decision toward the Dicranaceae, and the very ligulate leaves along with the lack of pitting of the juxtacostal basal cells will point toward *Amphidium*.

Amphidium is primarily a lithophytic plant of

the Northern Hemisphere. Scattered occurrences, primarily of *A. tortuosum*, are recorded for temperate parts of the Southern Hemisphere and for alpine areas of the tropics. There is no world-wide monograph of the genus, but such a monograph would probably yield little more than 5 species.

Amphidium tortuosum (Hornsch.) Cufod. (Fig. 1)

Österr. Bot. Zeitschr. 98: 221. 1951. — *Syrrhopodon tortuosus* Hornsch., Linnaea 15: 117. 1841.

Zygodon cyathicarpus Mont., Ann. Sci. Nat. Bot. III, 4: 106. 1845. — *Amphidium cyathicarpum* (Mont.) Broth. in Engler & Prantl, Nat. Pfl. 1(3): 460. 1902.

Plant tightly arranged in turfs or cushions, to 6 cm high, light-green to brownish-green. Stems brown to yellow brown, closely foliate, with leaves strongly keeled especially at base, erect-spreading when moist, not secund but strongly crispate. Leaves to 3 mm long, narrowly ligulate-lanceolate, mostly with parallel margins, somewhat broadened at extreme base, more than 12: 1 with the apex acute to acuminate. Margin recurved on at least one side toward the base, otherwise plane, not decurrent, entire or remotely and minutely serrulate. Cells throughout lamina in regular rows, mostly with 4 rows of cuticular papillae over each cell. Median cells of lamina moderately thick-walled with lumen: wall ratio 2–4: 1, with lumens angular, to 12 µm broad, rather variable in length with at least a few scattered cells wider than long, mostly isodiametric. Marginal cells of leaf of similar width to adjacent more interior cells but with transversely elongate cells frequent in that margin. Cells across the leaf base thin-walled and pellucid, lightly verruculose, to 12 µm broad, 3–6: 1. Cells of alar region not differentiated. Branching primarily by innovations below perichaetia but scattered additional erect branches present at leaf axils with the base of those branches strongly constricted to insertion and with those branches easily excised. Costa filling about 1/6 of the leaf base, gradually tapering to the subpercurrent to percurrent apex. Lamina unistratose throughout. Costa cross section with a strongly differentiated single layer of guide cells and with the dorsal stereid band prominent but with the ventral stereids few and inconspicuous, ventral epidermis obvious but dorsal epidermis absent or nearly so. Stem cross

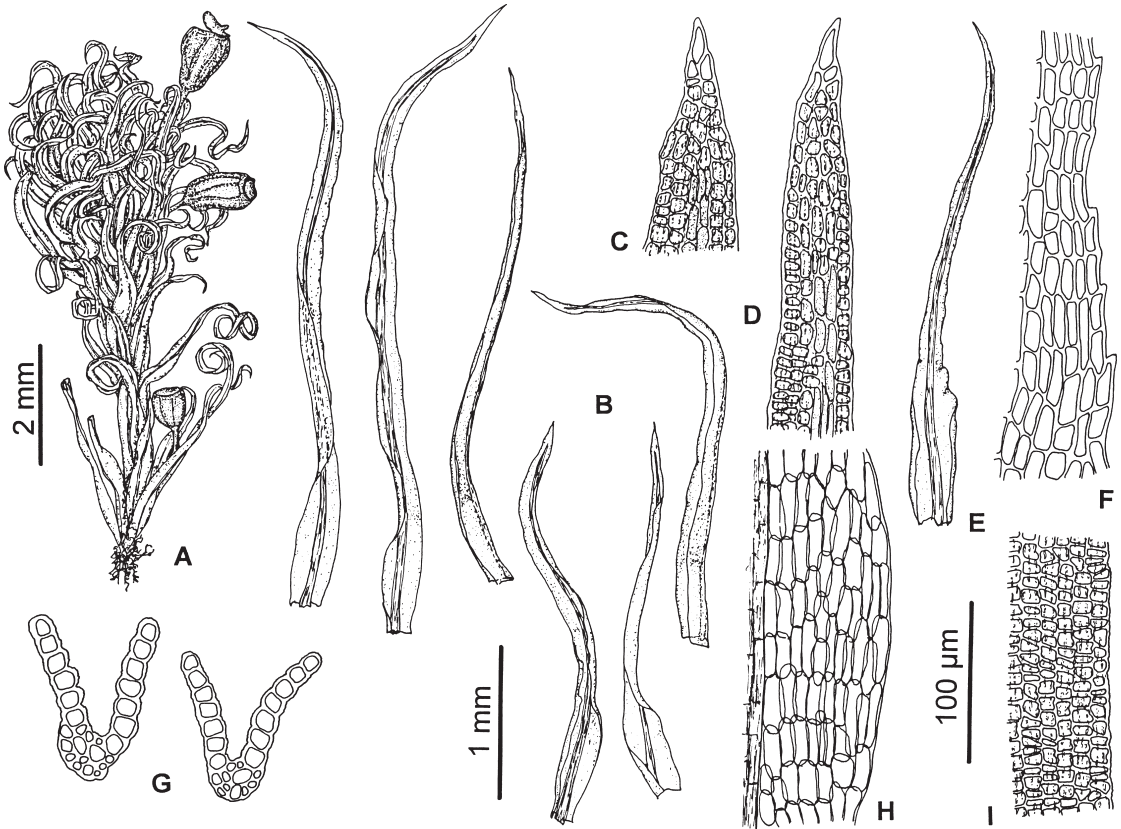


Fig. 1. *Amphidium tortuosum* (Hornsch.) Cufod. (from Koponen 32413, H). — A: Habit of plant. — B and E: Leaves. — C and D: Leaf apices. — F: Leaf margin at mid-leaf. — G: Cross-section of leaves. — H: Leaf base. — I: Leaf margin. Scale bars: 2 mm for A, 1 mm for B and E, 100 µm for C, D and F–I.

section rounded triangular, with a stereome of 1–2 very strongly differentiated, small, red-brown and pachydermous cells, and without a central strand. Rhizoids to 15 µm broad at insertion, arising from decurrent strips from below the lateral angles of leaf insertion, smooth to verruculose, monopodially branched with ultimate branchlets formed of very much curled cells. Axillary hairs to 200 µm long with about 8 rather elongate hyaline cells uniform in length and diameter.

Autoicous with perigonia placed in leaf axils near the perichetia or on separate short branchlets. Perichaetia terminal but with subsequent growth making them appear lateral. Perichaetial bracts similar or identical to vegetative leaves. Seta to 1 mm long, straight to slightly arcuate, very stout above the narrow vaginulum, brown to yellow brown. Urn symmetrical, to 1 mm long, nearly globose, brown to yellow brown, regularly and

strongly sulcate. Operculum short rostrate. Calyptra cucullate, without hairs or plications. Suboral exothelial cells rather thick-walled, transversely elongate in 3–5 rows, 0.5–0.8: 1, to 20 µm broad. Median exothelial cells in longitudinally differentiated rows with the cells of the ridges of the sulcate capsule to 15 µm broad, rectangular, about 3: 1, thick-walled and pitted with lumen: wall ratio 2–3: 1; and with the cells of the valleys similar to those of the ridges but thin-walled. Stomata phaneroporously, restricted to base of urn. Annulus poorly defined. Peristome absent. Spores spherical, nearly smooth, to 14 µm.

Illustrations: Sharp *et al.* 1994 (fig. 448).

Amphidium tortuosum was found at 1 850–3 600 m in an alpine grassland (1 collection) and in a moss forest (1 collection). Both our specimens grew on a cliff.

Range on the Huon Peninsula: 3a. 29377. 6g. 32413.

Range in Western Melanesia: Papua New Guinea. 11.

Present report. 15. (Bartram 1965, Wade & McVean 1969).

Total range: Am 2; Afr 1; Afr 2; As 4; PNG; Oc: Haw; Aust 1; Aust 2.

REFERENCES

- Bartram, E. B. 1965: Mosses of the Eastern Highlands, New Guinea, from the 6th Archbold Expedition, 1959. — *Contrib. U.S. Natl. Herb.* 37: 43–67.
- Brotherus, V. F. 1924: Musci (Laubmoose) Gruppe: Acrocarpi. — In: Engler, A. & Prantl, K. (eds.), *Die Natürlichen Pflanzenfamilien*. Ed. 2, 10: 192–194. W. Engelmann, Leipzig.
- Crundwell, A. C. 1979: Rhizoids and moss taxonomy. — In: Clarke, G. C. S. & Duckett, J. (eds.), *Bryophyte systematics*: 347–363. Acad. Press, London.
- Goffinet, B. 1998: A reconsideration of the affinities of *Kleioweisiopsis*, *Pleurozygodontopsis*, *Trigonodictyon*, and the Microtheciellaceae (Bryopsida, Orthotrichales). — *J. Bryol.* 20: 69–82.
- Goffinet, B. & Vitt, D. H. 1998: Revised generic classification of the Orthotrichaceae based on a molecular phylogeny and comparative morphology. — In: Bates, J. W., Ashton, N. W. & Duckett, J. G. (eds.), *Bryology for the twenty-first century*: 143–159. Maney Publ. & British Bryol. Soc., Leeds.
- Hedenäs, L. 1987: North European mosses with axillary rhizoids. — *J. Bryol.* 14: 429–439.
- Hedenäs, L. 1996: A cladistic overview of the “Hookeriales”. — *Lindbergia* 21: 107–143.
- Koponen, T. 1968: Generic revision of Mniaceae Mitt. (Bryophyta). — *Ann. Bot. Fennici* 5: 117–151.
- Koponen, T. 1993: The project “Bryophyte flora of the Huon Peninsula, Papua New Guinea”. — *Bryol. Times* 76: 6–8.
- Koponen, T. 1995: News from Helsinki. — *Bryol. Times* 86: 5.
- Koponen, T. & Norris, D. H. 1983: Bryophyte flora of the Huon Peninsula, Papua New Guinea. I. Study area and its bryological exploration. — *Ann. Bot. Fennici* 20: 15–29.
- Koponen, T., Piippo, S. & Norris, D. H. 1991: Bryophyte flora of the Huon Peninsula, Papua New Guinea. XLVII. Generic and family indexes to parts I–XLVI. — *Acta Bot. Fennica* 143: 107–111.
- Kreulen, D. J. W. 1972: Features of single- and double-peristomate capsules. Homology of layers and ontogeny of outer spore sac. — *Lindbergia* 1: 153–160.
- La Farge-England, C. 1996: Growth form, branching pattern and perichaetial position in mosses: cladocarp and pleurocarpy redefined. — *Bryologist* 99: 170–186.
- Lewinsky, J. 1976: On the systematic position of *Amphidium* Schimp. — *Lindbergia* 3: 227–231.
- Limpricht, K. G. 1885–1889: *Die Laubmoose Deutschlands, Oesterreichs und der Schweiz*. Ed. 2. I. *Sphagnaceae, Andreaeaceae, Archidiaceae, Bryineae (Cleistocarpae, Stegocarpae)* [Acrocarpae]. — E. Kummer, Leipzig. 836 pp.
- Norris, D. H. & Koponen, T. 1985: Bryophyte flora of the Huon Peninsula, Papua New Guinea. VII. Trachypodaceae, Thuidiaceae and Meteoriaceae (Musci). — *Acta Bot. Fennica* 131: 1–51.
- Norris, D. H. & Koponen, T. 1996: Bryophyte flora of the Huon Peninsula, Papua New Guinea. LVII. *Hypnodendron* (Hypnodendraceae, Musci). — *Acta Bot. Fennica* 156: 23–48.
- Norris, D. H., Koponen, T. & Piippo, S. 1999: Bryophyte flora of the Huon Peninsula, Papua New Guinea. LXVI. Meesiaceae (Musci), with lists of boreal to temperate disjunct, bipolar, and widely spread species in New Guinea. — *Ann. Bot. Fennici* 36: 257–263.
- Salazar-Allen, N. 1985: The life-form and presence of epigametophytic plants in the genus *Leucophanes*. — *Bryologist* 88: 94–97.
- Sharp, A. J., Crum, H. A. & Eckel, P. M. 1994: The moss flora of Mexico. Vol. II. — *Mem. New York Bot. Garden* 69: 591–1113 + XVII.
- Tuomikoski, R. & Koponen, T. 1979: On the generic taxonomy of *Calliargon* and *Drepanocladus* (Musci, Amblystegiaceae). — *Ann. Bot. Fennici* 16: 213–227.
- Wade, L. K. & McVean, D. N. 1969: Mt. Wilhelm Studies I. The alpine and subalpine vegetation. — *Res. School Pacific Stud., Dept. Biogeogr. Geomorph. Publ.* BG/1: 1–225. Australian Nat. Univ., Canberra.