A dendroid form of *Pogonatum cirratum* (Polytrichopsida, Bryophyta) from Mt. Kinabalu (Sabah, Malaysia)

Neil Bell¹ & Jaakko Hyvönen²

¹⁾ Botanical Garden and Museum (Bryology), P.O. Box 7 & Plant Biology, P.O. Box 65, FI-00014 University of Helsinki, Finland; e-mail: neil. bell@helsinki.fi

²⁾ Plant Biology, P.O. Box 65, FI-00014 University of Helsinki, Finland; e-mail: jaakko.hyvonen@helsinki.fi

Received Dec. 7, 2009, accepted Jan. 22, 2010

Bell, N. & Hyvönen, J. 2010: A dendroid form of *Pogonatum cirratum* (Polytrichopsida, Bryophyta) from Mt. Kinabalu (Sabah, Malaysia). — In: Koponen, T., Piippo, S. & Reinikka, E. (eds.), Dr. Ming-Jou Lai Memorial Volume. — *Acta Bryolichenologica Asiatica* 3: 39–45.

A dendroid form of *Pogonatum cirratum* (Sw.) Brid. *s.l.* is described and illustrated based on material collected in the unforested summit zone of Mt. Kinabalu in Sabah, Malaysia. In *Pogonatum* the dendroid habit is otherwise known only in *P. sinense* (Broth.) Hyvönen & Wu, a species sharing several other gametophytic features with *P. cirratum*. Phylogenetic and evolutionary implications are briefly discussed.

Key words: Bryophytes, Musci, Pogonatum, Polytrichopsida, taxonomy

Introduction

The genus Pogonatum, originally with 15 species, was separated from the complex genus Polytrichum by Palisot de Beauvois (1804). As currently delimited with over 50 species (Hyvönen 1989, Hyvönen & Wu 1993, Koskinen & Hyvönen 2004) it is the largest genus in the Polytrichopsida. All species are characterised by a set of sporophytic features that together are highly distinctive: lack of stomata, a deeply pigmented peristome with 32 broad compound teeth, and a mammillose exothecium. Gametophytically, however, the genus is very diverse, with much variation in size, habit and leaf morphology. Most species are confined to more or less disturbed and open habitats, although a few occur in dense tropical forests. The genus essentially has a world-wide distribution but is somewhat curiously absent from large parts of South America and westernmost Africa, while only two species, *P. dentatum* (Hedw.) P. Beauv. and *P. urnigerum* (Brid.) Brid., are widely distributed in the northern parts of the range. The largest number of species is found in South America and especially in SE Asia, ranging from extremely small species of the *Racelopus*-group (Touw 1986) to the largest plants of the genus such as *P. cirratum* subsp. *macrophyllum* (Dozy & Molk.) Hyvönen.

Based on morphology and manual Hennigian argumentation Hyvönen (1989) proposed a division of the genus into four subgenera: *Alienum* Hyvönen, *Dendroidea* (Schimp.) Hyvönen, *Catharinella* (Müll. Hal.) Hyvönen and *Pogonatum*. Later studies (Bell & Hyvönen 2009, Koskinen & Hyvönen 2004) did not support this division, although sampling, both in terms of terminals and characters, was limited. The most recent study (Bell & Hyvönen, 2010) suggests that members of subgenus *Dendroidea*

together with *P. japonicum* Sull. & Lesq. represent early diverging lineages while other species occur in a large, well supported apical clade within which subgenera *Pogonatum* and *Catharinella* are polyphyletic (the monospecific subgenus *Alienum* was not sampled).

In July and August 2007 the senior author had the opportunity to collect material during a short excursion to Mt. Kinabalu, Sabah, Malaysia as part of a post-conference field trip following the I.A.B. biennial meeting in Kuala Lumpur.

Mt. Kinabalu, hot spot of bryophytes in East Asia

The montane vegetation of Mt. Kinabalu can be

divided into zones determined by altitude and geology. Montane oak (Quercus subg. Cyclobalanopsis) forests with a wide range of taxa abruptly give way at about 2600 m to ultrabasic montane forest dominated by Leptospermum recurvum and Dacrydium gibbsiae, while above the treeline at approximately 3500 m there is only limited shrub and dwarf scrub vegetation (Leptospermum recurvum, Schima wallichii, Diplocosia kinabaluensis, several species of Ericaceae) amongst the predominating exposed granite rock (Menzel 1988). The summit zone itself has a very different bryophyte flora from the typically Malesian (although uniquely diverse) forested areas lower down and is well known to host species such as Racomitrium lanuginosum (Hedw.) Brid. and Grimmia ovalis (Hedw.)

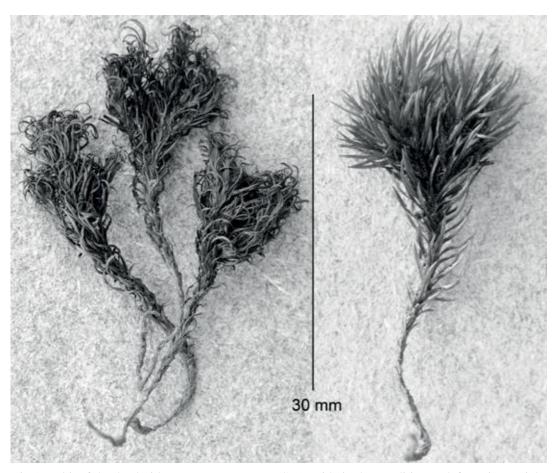


Fig.1. Habit of the dendroid *Pogonatum cirratum* (Sw.) Brid., in dry condition on left, moist on right (*Bell 01.08.07.001*, H).

Lindb. that are otherwise characteristic of temperate regions of the world (Menzel 1988).

Although Mt. Kinabalu (alt. 4095 m) is the most heavily bryologised locality in Borneo (Mohamed 1998), new records and occasionally taxa new to science continue to be found (Mohamed 1998, Akiyama *et al.* 2001, 2003). Tan and Iwatsuki (1996) marked Mt. Kinabalu as one of the hot spots of mosses in East Asia. Even during this short two day "tourist trip" with limited opportunities for collecting, the senior author found one other moss species new to Borneo (unpublished data) in addition to the plant described here. Thus even in a group such as mosses in which dispersal is accomplished relatively easily, the tremendous biological diversity of this unique site should not be underestimated.

In the upper part of the transition zone between the ultrabasic montane forest and the unforested summit area a prominent tufted patch of a dendroid polytrichaceous moss was seen growing in a moderately exposed, damp hollow near the base of a cliff (Fig. 1). The habitat was not dissimilar to that of the shorter montane variants of *Dendroligotrichum microdendron* (Müll. Hal.) G. L. Sm. in New Zealand or *D. squamosum* (Hook. f. & Wilson) Cardot in Tierra del Fuego, although the dendroid nature of the plant was not immediately obvious due to the closely packed, tufted growth form. Closer examination revealed the specimen to be a member of the *Pogonatum cirratum s.l.* complex.

A detailed description of the collected material (*Bell 01.08.07.001*, H!) is provided to enable comparison with descriptions of *P. cirratum* and *P. sinense* as presented for example by Hyvönen (1986) and Hyvönen & Wu (1993).

Pogonatum cirratum (Sw.) Brid. (Figs. 1–3)

Bryol. Univ. 2: 110. 1827. — *Polytrichum cir-ratum* Sw., J. f. Bot. 1800(2): 176. 1802.

Plants medium-sized, loosely caespitose, dark green. Stems tightly dendroid above, erect, up to 45 mm high. Leaves crowded, contorted when dry; erect-spreading when moist, narrowly line-

ar-lanceolate. Blade 5-6 mm long and 0.5-0.6 mm wide, very gradually narrowed to sharp serrate apex. Margins upcurved, uni- or bistratose, 2(-3) cell-rows wide, serrate with fairly large, multicellular teeth. Costa excurrent, light brown, with 160-190 µm wide dorsal stereid band, ventral stereid band 130-170 µm wide, cells of stereid bands with distinctly incrassate walls, costa apically sharply serrate with dorsal teeth. Dorsal cells of blade ovate to round with extremely incrassate walls, cell-lumen 7-10 µm. Ventral lamellae 28-32 per leaf, 1-2(-3) cells high, with essentially straight upper margin. Cells subquadrate to ovate with incrassate to firm walls, lumen 5-13 µm. Sheath ovate, gradually narrowed to blade, cells subquadrate to rectangular with firm walls, lumen 5–9 x 20–75 µm. Some perichaetia with few archegonia, 450-530 µm long, surrounded by long, uniformly uniseriate paraphyses. Perigonia and sporophytes unknown.

Discussion

Pogonatum cirratum, as broadly circumscribed by Hyvönen (1989), has a wide distribution ranging from eastern and southern parts of the Indian subcontinent and Japan south to New Guinea and the Solomon Islands (Fig. 3). Hyvönen (1989) distinguished three subspecies; P. cirratum subsp. fuscatum (Mitt.) Hyvönen, P. cirratum subsp. macrophyllum (Dozy & Molk.) Hyvönen and P. cirratum subsp. cirratum. While the status of these is controversial, it is fairly clear, based on our preliminary unpublished molecular data, that P. cirratum in this inclusive sense (henceforth referred to as *P. cirratum s.l.*) is a monophyletic, natural entity. Furthermore, Hyvönen & Wu (1993) noted obvious similarities in leaf morphology between P. cirratum s.l. and the dendroid P. sinense (Broth.) Hyvönen & Wu, while an affinity between these species was suggested by Koskinen & Hyvönen (2004) and Liu et al. (2005) based on morphology and sequence level data. While our as yet incomplete molecular data do not suggest that these taxa are sister species, they may nonetheless be relatively

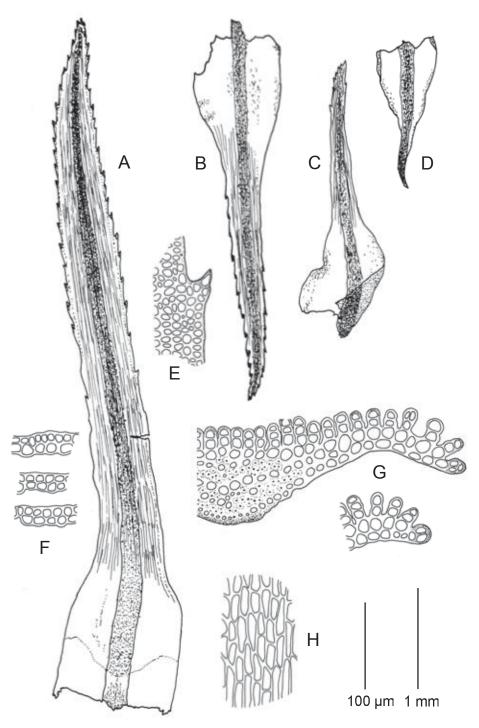


Fig. 2. Dendroid form of *Pogonatum cirratum* (Sw.) Brid. (from *Bell 01.08.07.001*, H). — **A–D.** Leaf sequence from apex towards basal part of branch. – **E.** Marginal teeth. – **F.** Lamellae in side view. – **G.** Leaf cross-section. – **H.** Sheath cells. – Use the 1 mm scale for A–D and 100 μm scale for E–H.

closely related.

Pogonatum sinense was described by Brotherus (1929) as Microdendron sinense based on specimen collected in the eastern part of the Himalayas (Handel-Mazzetti 8098, holotype H-BR!). The obvious reason for the initial recognition of this plant as a new genus was its dendroid habit that closely resembles the wellknown Dendroligotrichum (Müll. Hal.) Broth., found in South America and New Zealand. However, Brotherus was only able to study a specimen that lacked sporophytes, and so was not able to note the close resemblance between the capsules of Microdendron and Pogonatum. While the dendroid habit of P. sinense is strikingly different from that of other species of the genus, it is worth noting that besides sporophyte morphology, gametophytic characters (excepting the dendroid habit) very closely resemble those of many species of *Pogonatum*, especially P. cirratum and allied species.

Our ongoing research on the molecular sys-

tematics of *P. cirratum s.l.* (manuscript in prep.) suggests that there are several highly distinct groups in the complex that may or may not correspond precisely to previously recognized species, and that sequences from the dendroid specimen are distinct from those of *P. cirratum* collected in the lower forested zones of Mt. Kinabalu. Thus while it is possible that the plant represents a new species, further sampling from other parts of the geographical range of *P. cirratum s.l.* is required before taxa are delimited in order to avoid the risk of creating paraphyletic species unnecessarily.

It is intriguing that the dendroid growth form, otherwise not known in *Pogonatum*, occurs in this plant as well as in *P. sinense*, and that *P. cirratum s.l.* and *P. sinense* share multiple other characters. Nonetheless they have distinct differences and most likely occur in different clades of as yet uncertain affinity. Based on our current evidence it seems probable that they have acquired the dendroid habit independently, although a

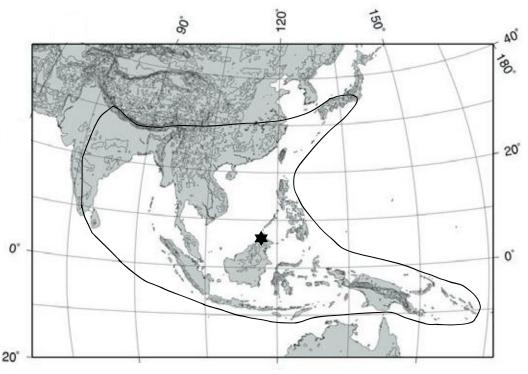


Fig. 3. Total range of *P. cirratum* (Sw.) Brid. *s.l.* — The collecting locality of the dendroid specimen is marked with an asterisk *. Map created using the on-line service @ www.aquarius.geomar.de.

related possibility is that a facilitated potential to evolve a dendroid growth form under appropriate environmental pressures can be regarded as a plesiomorphy that both have exploited. Such a potential could result from epigenetic factors, phenotypic accommodation (Badyaev 2009), or simply a shared exaptation such as a robust stem. This would be consistent with the phylogenetic distribution of the dendroid form in other groups of mosses. In pleurocarpous mosses for example, the dendroid habit tends to be restricted to particular families or higher level groupings, although recent evidence indicates that it has been gained and lost on several occasions within many of these groups (Bell & Newton 2005, Bell et al. 2007, Shaw et al. 2008). As has been argued previously (Bell & Newton 2005), the dendroid morphology may be an example of a phenotypic trait that has been overemphasised in traditional classifications because it has an impact on human visual perception that is out of proportion to its genuine complexity or significance as a conserved evolutionary feature; such questions provide fascinating topics for future study.

Acknowledgements. We thank two anonymous reviewers for their constructive comments. Financial support to the senior author from a Marie Curie Intra-European Fellowship (FP6-2004-Mobility-5, proposal No. 024896 - POLYPHY-MON) and the Academy of Finland projects (nos. 108629 and 128112) are cordially acknowledged. The senior author also thanks the organizers of the I.A.B. post-conference field trip in 2007, during which the material was collected. The junior author wishes to express his gratitude to Prof. Ming-Jou Lai for hosting the visit to Taiwan in late 1987. This provided a unique chance to collect and observe in natural habitats numerous species of Pogonatum. Specimens collected proved to be very important for timely completion of his Ph.D. thesis in 1989.

References

- Akiyama, H., Yamaguchi, T. & Suleiman, M. 2001: The bryophyte flora of Kinabalu National Park (Sabah, Malaysia), based on the collections by Japan-Malaysia collaborative expeditions in 1997. *Nature Human Activities* 6: 83–99.
- Akiyama, H., Tsubota, H., Yamaguchi, I. & Suleiman, M. 2003: The new genus *Benitotania* (Daltoniaceae, Bryopsida) from Mt. Kinabalu. *Bryologist* 106: 454–459.
- Badyaev, A. V. 2009: Evolutionary significance of phenotypic accommodation in novel environments: an empirical test of the Baldwin effect. *Philosophical Transact. Royal Soc.* B 364: 1125–1141.
- Bell, N. & Hyvönen, J. 2009: Rooting the Polytrichopsida: the phylogenetic position of *Atrichosis* and the independent origin of the polytrichopsid peristome. In: Mohamed, H., Baki, B. B., Nasrulhaq-Boyce A., & Lee, P. K. Y. (eds), *Bryology in the New Millennium*: 227–239. University of Malaya, Kuala Lumpur.
- Bell, N. E. & Hyvönen, J. 2010: Phylogeny of the moss class Polytrichoipsida (Bryophyta): generic-level structure and an anomalous 18S gene tree. *Molecular Phylogenetics and Evolution* 55: 381–398.
- Bell, N. E. & Newton, A. E. 2005: The paraphyly of *Hypnodendron* and the phylogeny of related non-hypnanaean pleurocarpous mosses inferred from chloroplast and mitochondrial sequence data. *Syst. Bot.* 30: 34–51.
- Bell, N. E., Quandt, D., O'Brien, T. J. & Newton, A. E. 2007: Taxonomy and phylogeny in the earliest diverging pleurocarps: square holes and bifurcating pegs. *Bryologist* 110: 533–560.
- Brotherus, V. F. 1929: Musci. In: Handel-Mazzetti, H. (ed.), Symbolae Sinicae. Botanische Ergenisse der Expedition der Akademie der Wissenschaften in Wien nach Südwest-China 1914/1918, IV: i–v, 1–147, Tafel i–v. Julius Springer, Wien.

- Hyvönen, J. 1986: Bryophyte flora of the Huon Peninsula, Papua New Guinea. XVIII. Polytrichaceae and Buxbaumiaceae (Musci). *Acta Bot. Fennica* 133: 107–149.
- Hyvönen, J. 1989: A synopsis of genus *Pogonatum* (Polytrichaceae, Musci). *Acta Bot. Fennica* 138: 1–87.
- Hyvönen, J. & Wu, P.-C. 1993: The identity of *Microdendron sinense* (Polytrichaceae). *Bryologist* 96: 631–634.
- Koskinen, S. & Hyvönen, J. 2004: *Pogonatum* (Polytrichales, Bryophyta) revisited. In: Goffinet, B. *et al.* (eds.), Molecular systematics of bryophytes. *Monographs in Systematic Botany* 98: 255–269.
- Liu, Y., Jia, Y., Wang, W. & Chen, Z.-D. 2005: A taxonomic reassessment of *Microdendron* inferred from molecular and morphological evidence. *Bryologist* 108: 591–599.
- Menzel, M. 1988: The bryophytes of Sabah (North Borneo) with special reference to the BRYO-TROP transect of Mount Kinabalu. I. The study area and its bryological exploration. *Will-denowia* 18: 281–300.
- Mohamed, H. 1998: Mosses of Sayap-Kinabalu Park, Sabah. *ASEAN review of biodiversity and environmental conservation. Article V*, 1998: 1–16.
- Palisot de Beauvois, A. M. F. J. 1804: Prodrome des cinquième et sixième familles de l'Aetheogamie. Les Mousses. Les Lycopodes. *Mag. Encycl.* 9. *Ann.* 5: 289–330.
- Smith, G. L. 1971: A conspectus of the genera of Polytrichaceae. *Mem. New York Bot. Gard.* 21: 1–83.
- Smith Merrill, G. L. 1994: Subclass Polytrichidae. In: Sharp, A. J., Crum, H. & Eckel, P. M., The moss flora of Mexico. *Mem. New York Bot. Gard.* 69: 1068–1092.
- Shaw, A. J., Holz, I., Cox, C. J. & Goffinet, B. 2008: Phylogeny, character evolution, and biogeography of the Gondwanic moss family Hypopterygiaceae (Bryophyta). *Syst. Bot.* 33: 21–30.
- Tan, B. C. & Iwatsuki, Z. 1996: Hot spots of mosses in East Asia. *Anales Inst. Biol. Univ. Nac. Autón. México, Ser. Bot.* 67(1): 159–167. 1996.
- Touw, A. 1986: A revision of *Pogonatum* sect. *Racelopus*, sect. nov., including *Racelopus* Dozy & Molk., *Pseudoracelopus* Broth. and *Racelopodopsis* Thér. *J. Hattori. Bot. Lab.* 60: 1–33.