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Male dwarfism in the genus *Dicranum* (Dicranaceae) – a review

*Amélie PICHONET & S. Robbert GRADSTEIN**

Muséum National d'Histoire Naturelle, Dept. Systématique et Évolution, UMR 7205, C.P. 39, 57 rue Cuvier, 75231 Paris cedex 05, Paris, France

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Abstract – Understanding of male dwarfism in mosses is reviewed with special reference to the genus *Dicranum*. Dwarf males occur in about 20% of *Dicranum* species. Most species seem to be obligately nannadrous; in two species (*D. bonjeanii*, *D. scoparium*) male plant size may be normal or dwarfed. Variation in male plant size in *Dicranum* seems to be environmentally controlled. Male dwarfism in mosses is induced by genetic or environmental factors although the mechanisms leading to male dwarfism are poorly understood. Evidence suggests that male dwarfism increases reproductive success in dioicous species but many questions remain unanswered.

Bryophyta / dioicy / dwarf male / male dwarfism / nannandry / reproductive strategy / sexual dimorphism / *Dicranum*

INTRODUCTION

The occurrence of sexual reproduction in bryophytes was first suggested by Johann Jacob Dillenius (1684-1747) in his *Catalogus Plantarum circa Gissam sponte nascentium* (1719). His observations came only 25 years after the discovery of sexual reproduction in plants (Camerarius, 1694). Dillenius recognized two structures for sexual propagation in the moss now called *Aulacomnium androgynum* (Hedw.) Schwägr., the gemma stalk of this species being considered the female organ and the sporophyte the male organ. Ten years later, in his *Nova Plantarum Genera* (1729), Pier Antonio Micheli (1679-1737) published first observations on sex organs in liverworts and hornworts. In accordance with the opinion of Dillenius, Micheli interpreted the sporophyte as the male organ and various asexual reproductive structures, such as gemma cups in *Marchantia* and leaf-born gemmae in *Scapania*, *Radula* and *Calypogeia*, as female organs (Margadant, 1973). Micheli also illustrated archegonia, antheridia and paraphyses but did not name these structures nor describe their function. The function of the sporangium as the spore-producing organ of the bryophytes was first recognized in 1747 by Casimir Christoph Schmidel (1718-1792). Schmidel also correctly interpreted the antheridium as the male organ but did not observe the sperm cells (Schofield, 1985). Subsequently, Johann Hedwig (1730-1799) proposed the female function of the archegonia from his observations on growth and structure of the

* Correspondence and reprints: gradstein@mnhn.fr

sporophyte and the spores of mosses in his *Fundamentum Historiae Naturalis Muscorum Frondosorum* (1782). Hedwig also assumed that antheridia produce sperm (Margadant, 1973) although proof for this notion did not come until much later, in 1834, when Franz Joseph Andreas Nicolaus Unger (1800-1870) observed the release of antherozoids from antheridia in the genus *Sphagnum*. The sexuality and life cycle of the bryophytes was finally resolved by Wilhelm Hofmeister (1824-1877) in his epoch-making *Vergleichende Untersuchungen* (1851) in which he described the egg cell within the archegonium and the two distinct phases of the life cycle, comparing these with the life cycle of ferns and gymnosperms.

Although mosses, liverworts and hornworts share a similar life cycle and sexual reproduction by means of antheridia and archegonia, different reproductive strategies are observed among the three groups. An unusual reproductive feature distinguishing mosses from liverworts and hornworts is the occurrence in mosses of sexual dimorphism by male dwarfism or *nannandry* (derived from Greek *nann* = dwarf, *andro* = male), *i.e.* the growth of dwarfed male plants on the stems or leaves of normal-sized female plants. Size of the dwarf males varies from less than half to equal the length of the leaves of the female plant. Some dwarf males have very few leaves and contain a single antheridium while others have many of both (Ramsay, 1979).

Male dwarfism in mosses was first detected by Wilhelm Philipp Schimper (1808-1880), who in his *Bryologia Europeae* described the occurrence of annual male plants originating from the "adventive roots" of perennial female plants or from spores in the genus *Dicranum* (Schimper, 1837; see also Schimper, 1850). Schimper observed that the dwarf male plants occurred in the autumn and in the spring on fertile female plants but never on normal-sized male plants. He also noted that in some species of *Dicranum* normal-sized male plants are lacking and replaced by male "buds" originating from the the tomentum of the female plants. Forty-seven years later, Henri Philibert (1822-1901) described dwarf males in the mosses *Fissidens decipiens* De Not. (= *F. dubius* P. Beauv.) and *Camptothecium lutescens* (Gedw.) Schimp. (Philibert, 1883). Both Schimper and Philibert speculated that the dwarf male plants originated from female protonema, and Philibert (1883) in addition suggested that they might have originated from the female gametophore. Recent studies, however, have shown that dwarf males originate from spores (e.g., Ramsay, 1979; Une, 1985a,b).

Hedenäs & Bisang (2011) in a study on male dwarfism in pleurocarpous mosses found that nannandry was much more common than hitherto reported. It has been recorded from twenty-two moss families and may be a useful taxonomic feature at the family level. Male dwarfism occurs in all species of the genus *Garovaglia* (During, 1977) but in the majority of genera (and families) with male dwarfs the phenomenon is expressed in only part of the species. Hedenäs & Bisang (2011) also found that the majority of pleurocarpous species with dwarf males were facultatively nannandrous and produced normal-sized male plants as well. Species with obligate dwarf males appeared to be rare.

In the acrocarpous mosses male dwarfism has been reported in Dicranaceae, Fissidentaceae, Leucobryaceae and Orthotrichaceae. Much work has been done on male dwarfism in the orthotrichaceous genus *Macromitrium* where male dwarfism is associated with anisospory (e.g., Ernst-Schwarzenbach, 1939; Ramsay, 1979; Une, 1985a,b,c). In this paper we explore the occurrence of male dwarfism in the genus *Dicranum* (Dicranaceae). In addition, the biology of male dwarfism is briefly discussed.

MALE DWARFISM IN *DICRANUM*

Male dwarfism in *Dicranum* was first reported by Schimper (1837) who described the occurrence of dwarf males in five species (Table 1): *D. majus, D. robustum, D. schraderi* (now = *D. undulatum* Turn.), *D. spurium* and *D. undulatum*. He observed that normal-sized male plants occur as well in *D. majus D. robustum* and *D. undulatum*, but never in *D. schraderi* and *D. spurium* where they were always replaced by the small, bud-like male plants growing on the tomentous stems of the female plants ("*gemmulae masculae in tomento nascentes plus minus copiosae*").

Within 131 currently accepted species in *Dicranum* (van der Wijk *et al.,* 1962, 1969; Tropicos, 2010), 25 species are known to produce dwarf males, 21 lack male dwarfism and in more than 55 species male plants are unknown (Table 1). The occurrence of dwarf males in one species of *Dicranum*, *D. fragilifolium*, remains controversial. Bellolio-Trucco & Ireland (1990) reported the occurrence of normal-sized male plants in this species while Gao *et al.* (1999) recorded dwarf males. Only two species of *Dicranum* (*D. scoparium*, *D. bonjeanii*) are known to produce both normal-sized and dwarf male plants (Loveland, 1956; Briggs, 1965; Table 1). The apparent rarity of facultative nannandry in *Dicranum* is in contrast with pleurocarpous mosses where it is common (Hedenäs & Bisang, 2011).

Dwarf males have been recorded in ten genera of the Dicranaceae (Ramsay, 1979; Gao *et al.*, 1999), including four that are closely allied to *Dicranum*: *Dicranoloma, Eucamptodontopsis, Holomitrium* and *Pseudochorisodontium* (LaFarge *et al.*, 2002). Male dwarfism is apparently lacking in the dicranaceous genera *Chorisodontium*, *Orthodicranum* and *Paraleucobryum*.

The expression of male dwarfism in *Dicranum* was first studied by Loveland (1956). He found that in the facultatively nannandrous *D. scoparium* male plant size varies according to the proximity of the female shoot. Loveland concluded that at least two different mechanisms may lead to male dwarfism in this genus: 1) genetic or chromosomal determinism, and 2) chemical influences. Briggs (1964) confirmed that development of dwarf males in *D. scoparium* is environmentally controlled and also observed this phenomenon in *D. bonjeanii*. The influence of the environmental factors on the expression of male dwarfism has also been shown in *Macromitrium* (see below).

Since the pioneering work of Loveland and Briggs, no further experiments have been conducted on the mechanism of male dwarfism in *Dicranum*. However, several studies were carried out on the reproductive biology and phenology of nannandrous *Dicranum* species (Briggs, 1965; Hughes, 1980; Sagmo Solli *et al.*, 1998, 2000; Ehrlen *et al.,* 2000; Bisang & Ehrlen, 2002). Hughes (1980) showed that in the polysetous *D. majus* and *D. scoparium* dwarf males never occurred in association with female plants without sporophytes. In a study on the reproductive phenology of *D. majus*, Sagmo Solli *et al.* (1998, 2000) confirmed that dwarf males are annuals. Moreover, these authors demonstrated that the occurrence of dwarf males increases the number of plants with sporophytes and that the proportion of fertilized archegonia increases with the number of dwarf males on female shoots.

Table 1. List of accepted species in *Dicranum* (van der Wijk *et al*. 1962, 1969; Tropicos, 2010) and male plant status. DWF = dwarf males; N = normal-sized males; U = male plant status unknown; * = species known only from the original diagnosis

	Species	*Male plant status*	*Reference*
1	*Dicranum acanthoneurum* Müll. Hal.	U	*Flora* 73: 474. 1890
2	*Dicranum acutifolium* (Lindb. *et* Arnell) C.E.O. Jensen	DWF	*Herzogia* 17: 179-197. 2004
3	**Dicranum alpinum* (P. Beauv.) Brid.	U	*Muscologia Recentiorum Supplementum* 1: 208. 1806
4	*Dicranum arcuatipes* Müll. Hal.	U	*Genera Muscorum Frondosorum* 299. 1900
5	*Dicranum assamicum* Dixon	N	*Moss Flora of China.* 1: 165. 1999
6	*Dicranum atratum* Geh.	U	*Flora* 62: 473. 1879
7	**Dicranum atro-viride* Cardot	U	*Annales botanici societatis zoologicae-botanicae Fennicae "Vanamo"* 9: 41. 1937
8	**Dicranum beyrichianum* (Duby) Hampe	U	*Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjøbenhavn* 9-10: 255. 1878
9	*Dicranum bonjeanii* De Not.	DWF, N	*Herzogia* 17: 179-197. 2004.
10	*Dicranum borbonicum* Renault *et* Cardot	U	*Prodrome de la Flore Bryologique de Madagascar des Mascareignes et des Comores* 160. 1898
11	*Dicranum braunsiae* Müll. Hal.	U	*Genera Muscorum Frondosorum* 290. 1900
12	*Dicranum brevifolium* (Lindb.) Lindb.	DWF	*Herzogia* 17: 179-197. 2004
13	*Dicranum caesium* Mitt.	U	*Transactions of the Linnean society of London, Botany* 3: 156. 1891
14	**Dicranum caldense* Müll. Hal.	U	*Hedwigia* 39: 250. 1900
15	**Dicranum capillatus* (Hook. *et* Wilson) L.C. Beck	U	*Transactions and proceedings of the New Zealand institute* 25: 301. 1893
16	**Dicranum carneum* Blandow	U	*Deutschlands Flora*, Abtheilung II, Cryptogamie 10: ic. 1809
17	*Dicranum cheoi* E.B. Bartram	DWF	*Moss Flora of China* 1: 167. 1999
18	**Dicranum clericii* Brizi	U	*Bollettino de società geologica Italiana* 9: 365. 1892
19	**Dicranum columbiae* (Kindb.) Renauld *et* Cardot	U	*Revue bryologique* 19: 77. 1892
20	*Dicranum condensatum* Hedw.	DWF	*Herzogia* 17: 179-197. 2004
21	**Dicranum conglomeratum* (Brid.) Wallr.	U	*Flora Cryptogamica Germaniae* 1: 169. 1831
22	**Dicranum craigieburnense* R. Br. bis	U	*Transactions and proceedings of the New Zealand institute* 29: 457. 1897
23	*Dicranum crassifolium* Sérgio, Ochyra *et* Seneca	DWF	*Herzogia* 17: 179-197. 2004
24	*Dicranum crispifolium* Müll. Hal.	N	*Botanische Zeitung (Berlin)* 22: 349. 1864
25	*Dicranum crispatulum* (Roll) Kindb.	U	*European and N. American Bryineae (Mosses*) 2: 189. 1897
26	*Dicranum decumbens* Thwaites *et* Mitt.	U	*Journal of the Linnean society, Botany* 13: 296. 1873

Table 1. List of accepted species in *Dicranum* (van der Wijk *et al*. 1962, 1969; Tropicos, 2010) and male plant status. DWF = dwarf males; N = normal-sized males; U = male plant status unknown; * = species known only from the original diagnosis *(continued)*

	Species	*Male plant status*	*Reference*
27	*Dicranum deflexicaulon* Müll. Hal.	U	*Linnaea* 38: 589. 1874
28	*Dicranum delavayi* Besch.	U	*Revue bryologique* 18: 88. 1891
29	*Dicranum dilatinerve* Cardot *et* P. de la Varde	U	*Revue bryologique* 49: 35. 1922
30	*Dicranum diplospiniferum* C. Gao *et* C. W. Aur	U	*Bulletin of botanical laboratory of North-Eastern forestry institute* 7: 99. 1980.
31	*Dicranum dispersum* Engelmark	DWF	*Herzogia* 17: 179-197. 2004
32	*Dicranum drummondii* Müll. Hal.	DWF	*Herzogia* 17: 179-197. 2004
33	*Dicranum dubium* Thér. *et* Dixon	U	*Revue bryologiqu*e 48: 12. 1921
34	*Dicranum eggersii* Müll. Hal.	U	*Genera Muscorum Frondosorum* 287. 1900
35	*Dicranum elongatum* Schleich. *ex* Schwägr.	N	*Herzogia* 17: 179-197. 2004
36	*Dicranum filum* Bory	U	*Voyage dans les quatre principales Îles des Mers d'Afrique* 3: 17. 1804
37	*Dicranum flagellare* Hedw.	N	*Herzogia* 17: 179-197. 2004
38	*Dicranum fragilifolium* Lindb.	DWF, N	*Herzogia* 17: 179-197. 2004
39	*Dicranum fragillimum* Warnst.	U	*Hedwigia* 57: 78. 14. 1915
40	*Dicranum frigidum* Müll. Hal.	DWF	*Moss Flora of Central America.* Tropicos®
41	*Dicranum fulvum* Hook.	N	*Herzogia* 17: 179-197. 2004
42	*Dicranum fuscescens* Turner	N	*Herzogia* 17: 179-197. 2004
43	*Dicranum gonoi* Cardot	U	*Bulletin de la Société Botanique de Genève*, Sér. 2 1: 121. 1909
44	*Dicranum gregoryi* B. H. Allen	U	*The bryologist* 91: 91. 1988
45	*Dicranum groenlandicum* Brid.	N	*Herzogia* 17: 179-197. 2004
46	*Dicranum hamulosum* Mitt.	N	*Moss Flora of China* 1: 173-174. 1999
47	*Dicranum himalayanum* Mitt.	N	*Moss Flora of China* 1: 175. 1999
48	**Dicranum homannii* Boeck	U	*Handbok i Skandinaviens Flora, Andra Upplagen* 314. 1832
49	*Dicranum howelli* Renauld *et* Cardot	DWF	*Revue bryologique* 15: 70. 1888
50	*Dicranum japonicum* Mitt.	DWF	*Moss Flora of China*. 1: 176. 1999
51	*Dicranum johnstonii* Mitt.	DWF	*Journal of the Linnean society, Botany* 22: 300. 1886
52	*Dicranum kashmirense* Broth.	N	*Moss Flora of China*. 1: 178. 1999
53	*Dicranum klauteri* Reimers	U	*Hedwigia* 70: 363. 1931
54	**Dicranum kwangtungense* (P.C. Chen) T. J. Kop.	U	*Bryobrothera* 1: 200. 1992
55	*Dicranum leiodontium* Cardot	N	*Moss Flora of China* 1: 178. 1999
56	*Dicranum leioneuron* Kindb.	DWF	*Herzogia* 17: 179-197. 2004
57	*Dicranum leucobryoides* Besch. *ex* Müll. Hal.	U	*Genera Muscorum Frondosorum* 285. 1900

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	Species	*Male plant status*	*Reference*
58	*Dicranum levieri* Müll. Hal.	U	*Genera Muscorum Frondosorum* 285. 1900
59	*Dicranum linzianum* C. Gao	N	*Acta phytotaxonomica Sinica* 17: 115. 1979
60	*Dicranum longicylindricum* C. Gao *et* T. Cao	U	*Bryobrothera* 1: 218. 1992
61	**Dicranum longipilum* Müll. Hal.	U	*Synopsis Muscorum Frondosorum omnium hucusque Cognitorum* 1: 411. 1848
62	**Dicranum longirostratum* (P. Beauv.) Brid.	U	*Muscologia Recentiorum Supplementum* 1: 228. 1806
63	*Dicranum lophoneuron* Müll. Hal.	U	*Synopsis Muscorum Frondosorum omnium hucusque Cognitorum* 2: 589. 1851
64	*Dicranum lorifolium* Mitt.	DWF	*Moss Flora of China* 1: 180. 1999
65	**Dicranum macrogaster* Müll. Hal.	U	*Hedwigia* 39: 252. 1900
66	*Dicranum majus* Turner	DWF	*Herzogia* 17: 179-197. 2004
67	*Dicranum mayrii* Broth.	DWF	*Moss Flora of China*. 1: 183. 1999
68	*Dicranum montanum* Hedw.	N	*Herzogia* 17: 179-197. 2004
69	**Dicranum morenoi* Müll.Hal.	U	*Hedwigia* 36: 97. 1897
70	*Dicranum muehlenbeckii* Bruch. *et* Schimp.	DWF	*Herzogia* 17: 179-197. 2004
71	**Dicranum myosuroides* DC.	U	*Flore Française. Troisième Édition* 6: 222. 1815
72	*Dicranum nipponense* Besch.	N	*Moss Flora of China* 1: 185. 1999
73	**Dicranum nitidum* (Dozy *et* Molk.) Dozy *et* Molk.	N	*Plantae Junghuhnianae* 3: 330. 1854
74	**Dicranum novae-hollandiae* Turton	U	*A General System of Nature* 2: 1717. 1806
75	*Dicranum novaustrinum* Margad.	U	*Lindbergia* 1: 127. 1972
76	*Dicranum obliquatum* Mitt.	U	*Journal of the proceedings of the Linnean society* 7: 148. 1863
77	*Dicranum ontariense* W.L. Peterson	DWF	*Canadian journal of botany* 68: 867-909. 1990
78	*Dicranum orthophylloides* Dixon	U	*Notes from the royal botanic garden Edinburgh* 19: 280. 1938
79	*Dicranum orthophyllum* Broth.	U	*Symbolae Sinicae* 4: 27. 1929
80	**Dicranum otii* (Sakurai) Sakurai	U	*Journal of Japanese botany* 27: 157. 1952
81	**Dicranum pachyneuron* (Molendo) Kindb.	U	*European and N. American Bryineae (Mosses)* 2: 190. 1897
82	**Dicranum pacificum* Ignatova *et* Fedosov	U	*Arctoa* 17: 76. 2008
83	**Dicranum pallescens* (Besch.) Müll. Hal.	U	*Genera Muscorum Frondosorum* 262. 1900
84	*Dicranum pallidisetum* (J.W. Bailey) Ireland	N	*The bryologist* 68: 447. 1965
85	*Dicranum papillidens* Broth.	N	*Akademie der Wissenschaften in Wien, Sitzungsberichte, Mathematisch-naturwissenschaftliche Klasse, Abteilung* 1, 133: 561. 1924

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	Species	*Male plant status*	*Reference*
86	**Dicranum perichaetiale* (P. Beauv.) Brid.	U	*Muscologia Recentiorum Supplementum* 1: 204. 1806
87	*Dicranum peruvianum* H. Rob.	DWF	*The bryologist* 70: 317. 1967
88	*Dicranum petrophylum* G. Negri	U	*Annali di botanica* 7: 162. 1908
89	**Dicranum pinetorum* Griff.	U	*Calcutta journal of natural History and miscellany of the arts and sciences in India* 2: 497. 1842
90	*Dicranum polysetum* Sw.	DWF	*Herzogia* 17: 179-197. 2004
91	*Dicranum psathyrum* Klazenga	DWF	*Journal of the Hattori botanical laboratory* 87: 118. 1999
92	**Dicranum pseudacutifolium* OtnyUova	U	*Arctoa, a journal of bryology* 16: 163. 2007
93	*Dicranum pseudofalcatum* Seppelt	U	*The bryologist* 83: 591. 1980
94	**Dicranum pseudojulaceum* (Müll. Hal.) Müll. Hal.	U	*Hedwigia* 39: 259. 1900
95	*Dicranum pseudoleucoloma* Müll. Hal.	U	*Linnaea* 43: 397. 1882
96	*Dicranum pseudorobustum* Müll. Hal. *ex* Geh.	U	*Revue bryologique* 4: 53. 1877
97	*Dicranum rectifolium* Müll. Hal.	U	*Nuovo giornale botanico Italiano*, new series 3: 98. 1896
98	*Dicranum rhabdocarpum* Sull.	N	*Moss Flora of Central America. Part 1. Sphagnaceae-Calymperaceae. Monogr. Syst. Bot. Missouri Bot. Gard.* 49. 242 pp.
99	**Dicranum richardsoni* Drumm.	U	*Musci Americani;* or, Specimens of the Mosses Collected in British North America 104. 1828
100	*Dicranum rodriguezii* Müll. Hal.	U	*Genera Muscorum Frondosorum* 285. 1900
101	*Dicranum savatieri* (Besch.) Schimp. *ex* Paris	U	*Index Bryologicus, editio secunda* 2: 57. 1904
102	**Dicranum saxatile* Lag., D. Garcia *et* Clemente	U	*Anales de ciencias naturales* 5: 178. 1802
103	*Dicranum schensianum* Müll. Hal.	U	*Nuovo giornale botanico Italiano*, new series 4: 249. 1897
104	*Dicranum scoparium* Hedw.	DWF, N	*Herzogia* 17: 179-197. 2004.
105	**Dicranum scopellifolium* Müll. Hal.	U	*Nuovo giornale botanico Italiano*, new series 5: 169. 1898
106	*Dicranum scottianum* Turner *ex* Scott, Robert	N	*The Moss Flora of Britain & Ireland* 210. 1978
107	**Dicranum scrabrophyllus* Müll.Hal.	U	*Hedwigia* 36 : 84-144. 1897
108	**Dicranum seligeri* Brid.	U	*Muscologia Recentiorum Supplementum* 4: 59. 1819
109	*Dicranum semperi* Hampe	U	*Genera Muscorum Frondosorum* 297. 1900
110	*Dicranum setifolium* Cardot	N	*Moss Flora of China* 1: 189. 1999

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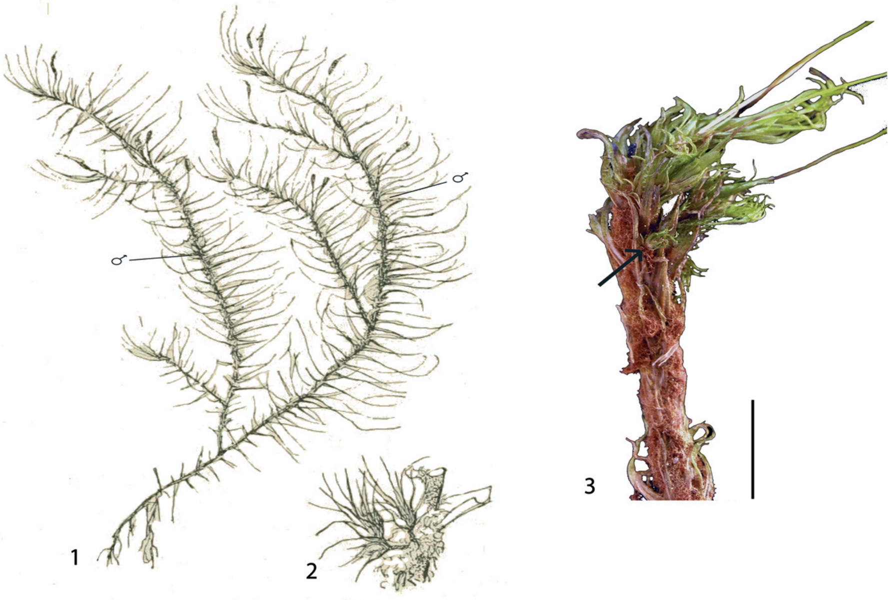
	Species	*Male plant status*	*Reference*
111	*Dicranum spadiceum* J.E. Zetterst	DWF	*Herzogia* 17: 179-197. 2004
112	*Dicranum speirophyllum* Mont.	U	*Annales des sciences naturelles ; Botanique*, sér. 2, 20: 295. 1843
113	**Dicranum splachnoides* Brid.	U	*Journal für die Botanik* 1800: 295. 1801
114	*Dicranum spurium* Hedw.	DWF	*Herzogia* 17: 179-197. 2004
115	**Dicranum strictum* (Dicks.) Sm.	U	*Flora Britannica* 3: 1218. 1804
116	**Dicranum stygium* Brid.	U	*Muscologia Recentiorum Supplementum* 4: 64. 1819
117	**Dicranum sulphureo-flavus* Müll. Hal.	U	*Index Bryologicus Supplementum Primum* 98. 1900
118	*Dicranum sumichrastii* Duby	U	*Mémoires de la société de physique et d'histoire naturelle de Genève* 20: 353. 1870
119	*Dicranum symblepharoides* Cardot	U	*Bulletin de la société botanique de Genève,* Sér. 2 1: 121. 1909
120	*Dicranum syrrhopodontoides* Müll. Hal.	U	*Hedwigia* 36: 96. 1897
121	*Dicranum tauricum* Sapjegin	N	*Herzogia* 17: 179-197. 2004
122	*Dicranum thelinotum* Müll. Hal.	U	*Nuovo giornale botanico Italiano*, new series 3: 98. 1896
123	*Dicranum thraustophyllum* Müll. Hal.	U	*Genera Muscorum Frondosorum* 297. 1900
124	*Dicranum toninii* Müll. Hal.	U	*Hedwigia* 36: 97. 1897
125	**Dicranum torquatum* Mitt.	U	*Journal of the proceedings of the Linnean society* 4: 69. 1859
126	*Dicranum transsylvanicum* Luth	DWF	*Herzogia* 17: 179-197. 2004
127	**Dicranum truncatum* (Müll. Hal.) Müll. Hal.	U	*Synopsis Muscorum Frondosorum omnium hucusque Cognitorum* 1: 410. 1848
128	*Dicranum truncicola* Broth.	U	*Akademie der Wissenschaften in Wien, Sitzungsberichte, Mathematisch-naturwissenschaftliche Klasse, Abteilung* 1, 133: 561. 1924
129	*Dicranum tubulifolium* Ireland	DWF	*The bryologist* 87: 355. 1984
130	*Dicranum undulatum* Schrad. *ex* Brid.	DWF	*Herzogia* 17: 179-197. 2004
131	*Dicranum viride* (Sull. *et* Lesq.) Lindb.	N	*Herzogia* 17: 179-197. 2004

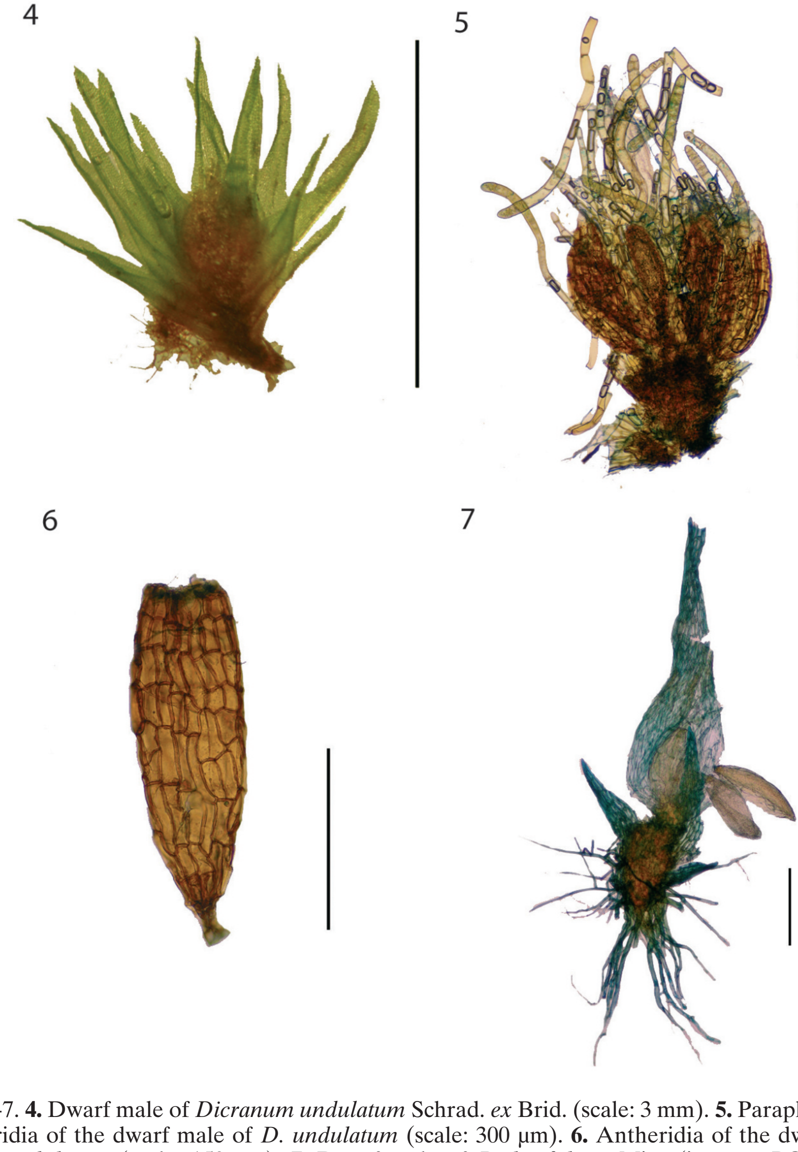


Figs 1-3. **1.** Female plant of *Dicranum undulatum* Schrad. *ex* Brid. **2.** Dwarf males of *Dicranoloma brevisetum* (Dozy *et* Molk.) Paris (after Fleischer, 1900-1922). **3.** Dwarf males on a female stem in *Dicranum undulatum* Schrad. *ex* Brid. (scale: 0.5 cm).

GENERAL DISCUSSION

Male dwarfism may be induced by genetic factors (Ernst-Schwarzenbach, 1939; Une, 1985a) environmental factors (Une, 1985a), and unfavourable nutrient conditions (Woesler, 1935). It is considered a strategy to enhance reproduction in dioicous species, which include about 40% of all moss species (Wyatt, 1994). Suppression of sexuality is often observed in these dioicous taxa due to the spatial separation of male and female plants and their limited fertilization range (Longton & Schuster, 1983; Bisang *et al.,* 2004). Male dwarfism may counterbalance the reproductive constraints in these taxa, however may also lead to an increase in the rate of inbreeding. Following fertilization of the haploid parental plants by offspring of the F_1-generation, recessive alleles may become expressed in the offspring of the F_2-generation, resulting in large phenotypic variability (Mogensen, 1981; Hedenäs & Bisang, 2011). The latter authors suggested that the taxonomic difficulties encountered in genera with male dwarfism (e.g. *Dicranum, Macromitrium*) may be due to the commonness of back-crossing in these groups and the resulting phenotypic complexity.

Evidence for increase in fertilization and outbreeding when males are closer to the female plants has been demonstrated in *Macromitrium* (Une, 1985b). The latter author also found a correlation between temperature and male plant size in Japanese *M. gymnostomum* Sull. *et* Lesq. and *M. japonicum* Dozy *et* Molk. In



Figs 4-7. **4.** Dwarf male of *Dicranum undulatum* Schrad. *ex* Brid. (scale: 3 mm). **5.** Paraphyses and antheridia of the dwarf male of *D. undulatum* (scale: 300 µm). **6.** Antheridia of the dwarf male of *D. undulatum* (scale: 150 µm). **7.** Dwarf male of *D. lorifolium* Mitt. (isotype: PC0128679) (scale: 250 µm).

these two species, normal-sized male plants are only found in regions where mean January temperature is higher than 6°C. This suggests that male dwarfism in these species is an adaptation to low temperatures. Une (1985c) also found that germination of male spores at low temperatures is slower than that of female spores.

Male dwarfism occurs in both isosporous and anisosporous mosses. Anisospory is always linked with sexual dimorphism but the opposite is not true (Ramsay, 1979; Mogensen, 1981). In anisosporous *Macromitrium* species

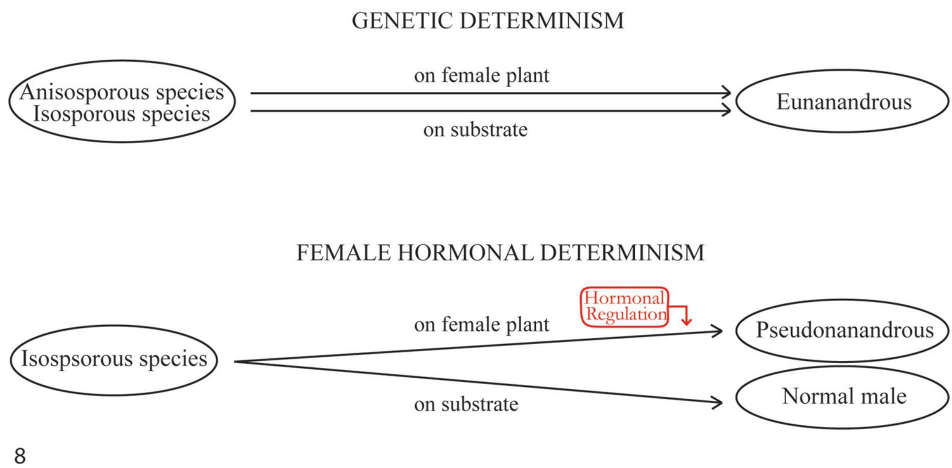


Fig. 8. Determinisms driving male dwarfism, modified from Une (1985a).

cultivated in vitro, dwarf males were always obtained from microspores, whether grown isolated or together with female plants (Une, 1985a). In isosporous *Macromitrium*, Une (1985a) showed that the initiation of male dwarfism was induced by a phytohormone from auxin family (2, 4-dichlorophenoxyacetique acid: 2, 4D) known to increase the rate of DNA, RNA and protein synthesis. He concluded that the development of dwarf males in the isosporous species was hormonally regulated. He also found that small spores of isosporous *Macromitrium* give rise to dwarf males much more often that randomly sampled spores under phytohormone regulation (75% of small spores *vs* 25% of randomly sampled spores). Une (1985a) concluded that small spores of isosporous *Macromitrium* are male. Based on his results, Une (1985a) proposed a new terminology for male dwarfism, taking into account underlying developmental mechanisms. Since Schimper (1837), various terms have been employed to characterize species with dwarf males (e.g. "pseudo-monoicous", "pseudo-autoicous", "phyllodioïcous"). Following Une, genetically determined dwarf males are called "eunanandrous" and those influenced by female phytohormones "pseudonanandrous".

Dwarf males seem to generally establish on female plants of the same species, and a single female plant may host a variety of dwarf males, including siblings or conspecific populations. Pedersen *et al.* (2006) in a molecular study using ITS markers found that the dwarf males of *Garovaglia elegans* (Dozy *et* Molk.) Bosch *et* Sande Lac. and *G. powellii* Mitt. were conspecific with their respective female hosts. The results needed confirmation by further sampling, however, as phylogenetic relationships within the clade containing the two species were poorly resolved. Growth of dwarf males on either the stem or the leaves of the female plant seems to depend on the suitability of leaves and stems for the establishment and germination of the spores (Ernst-Schwarzenbach, 1939). In a study on the occurrence of male dwarfism in the Ptychomniales, Pedersen & Newton (2007) found that male dwarfism was more common in plants with rugose or toothed dorsal leaf surfaces than in plants with smooth leaves. They proposed that the roughened leaf surfaces promoted the establishment of spores, and thus male dwarfism. The mechanisms inhibiting the germination of "foreign" spores and/or stimulating the germination of those of the same species remain unknown, however.

CONCLUDING REMARKS

Male dwarfism is known in about 20% of *Dicranum* species but in almost half of the species of the genus male plants remain unknown. Phenotypic plasticity of male plant size has been observed in two species of *Dicranum* (*D. bonjeanii*, *D. scoparium*), all other species of the genus with dwarf males seem to be obligately nannandrous. The percentage of obligately nannandrous species in *Dicranum* is higher than in pleurocarpous mosses where it is rare (Hedenäs & Bisang, 2011). The mechanisms leading to male dwarfism are still poorly understood and may include genetic, environmental and physiological factors. In their recent overview of nannandry in pleurocarpous mosses, Hedenäs & Bisang (2011) emphasized that male dwarfism in bryophytes is an overlooked phenomenon. In the acrocarpous mosses, where male dwarfism occurs in four different families, nannandry has been little studied with exception of the genus *Macromitrium*. A comprehensive study on male dwarfism in acrocarpous mosses would be desirable and might contribute to a better understanding of the origin, evolution and biological relevance of this neglected phenomenon in mosses.

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