

Phylogenetic Relationships of Haploleptideous Mosses (Dicranidae) Inferred from *rps4* Gene Sequences

Terry A. Hedderson^{ad}, Donald J. Murray^b, Cymon J. Cox^c, and Tracey L. Nowell^a

^aBolus Herbarium, Department of Botany, University of Cape Town, Private Bag, Rondebosch 7701, Republic of South Africa

^bThe Birmingham Botanical Garden, Westbourne Road, Edgbaston, Birmingham, B15 3TR U. K.

^cDepartment of Biology, Duke University, Durham, North Carolina 27708

^dAuthor for Correspondence (thedders@egs.uct.ac.za)

Abstract

The haploleptideous mosses (Dicranidae) constitute a large group of ecologically and morphologically diverse species recognised primarily by having peristome teeth with a single row of cells on the dorsal surface. The reduction of sporophytes in numerous moss lineages renders circumscription of the Dicranidae problematic. Delimitation of genera and higher taxa within it has also been difficult. We analyse chloroplast-encoded *rps4* gene sequences for 129 mosses, including representatives of nearly all the haploleptideous families and subfamilies, using parsimony, likelihood and Bayesian criteria. The data set includes 59 new sequences generated for this study. With the exception of *Bryobartramia*, which falls within the Encalyptaceae, the Dicranidae are resolved in all analyses as a monophyletic group including the extremely reduced Archidiales and Ephemeraceae. The monotypic *Catoscopium*, usually assigned to the Bryidae is consistently resolved as sister to Dicranidae, and this lineage has a high posterior probability under the Bayesian criterion. Within the Dicranidae, a core clade is resolved that comprises most of the species sampled, and all analyses identify a proto-haploleptideous grade of taxa previously placed in various haploleptideous families. The data provide considerable resolution of relationships within the core Dicranidae, yielding a number of well-supported clades. These correspond only roughly to taxa that are currently recognised, and most families and orders of Dicranidae apparently are non-monophyletic under their current circumscriptions.

Literature Cited

Allen, B. 1987. On the costa of *Fontinalis* (Musci). *Lindbergia* 9:37–40.

- Buck, W. R. and B. Goffinet. 2000. Morphology and classification of mosses. Pp. 71–123 in *Bryophyte Biology*, eds. A. J. Shaw and B. Goffinet. Cambridge: Cambridge University Press.
- Capesius, I. and M. Stech. 1997. Molecular relationships within mosses based on 18S rRNA sequences. *Nova Hedwigia* 64:525–533.
- Churchill, S. 1981. A phylogenetic analysis, classification and synopsis of the genera of the Grimmiaceae (Musci). Pp. 127–144 in *Advances in Cladistics: Proceedings of the first meeting of the Willi Hennig Society*, eds. V. A. Funk and D. R. Brooks. New York: The New York Botanical Garden.
- Cox, C. J. and T. A. J. Hedderson. 1999. Phylogenetic relationships among the ciliate arthrodontous mosses: evidence from chloroplast and nuclear DNA sequences. *Plant Systematics and Evolution* 215:119–139. [CrossRef](#)
- Cox, C. J., B. Goffinet, A. E. Newton, A. J. Shaw, and T. A. J. Hedderson. 2000. Phylogenetic relationships among the diplolepidous-alternate mosses inferred from nuclear and chloroplast DNA sequences. *The Bryologist* 103:224–241. [BioOne](#)
- Crum, H. A. 1994. Grimmiaceae. Pp. 386–415 in *The moss flora of Mexico*, eds. A. J. Sharp, H. A. Crum and P. M. Eckel. Memoirs of the New York Botanic Garden 69.
- Crosby, M. R. 1980. The diversity and relationships of mosses. Pp. 127–144 in *The mosses of North America*, eds. R. J. Taylor and A. E. Leviton. San Francisco: California Academy of Science.
- Edwards, S. R. 1979. Taxonomic implications of cell patterns in haplolepidous moss peristomes. Pp. 317–346 in *Bryophyte systematics*, eds. G. C. S. Clarke and J. G. Duckett. London: Academic Press.
- Edwards, S. R. 1984. Homologies and inter-relationships of moss peristomes. Pp. 658–695 in *New Manual of Bryology*, ed. R. M. Schuster. Nichinan: The Hattori Botanical Laboratory.
- Edwards, S. R., K. C. Johnstone, and C. Thompson. 1991. A simple and rapid method for the preparation of plant genomic DNA for PCR analysis. *Nucleic Acids Research* 19:1349. [CrossRef](#), [PubMed](#)
- Farris, J. S. 1969. A successive approximations approach to character weighting. *Systematic Zoology* 18:374–385. [CrossRef](#)
- Farris, J. S. 1989. The retention index and the rescaled consistency index. *Cladistics* 5:417–419. [CrossRef](#)
- Fleischer, M. 1902–23. *Die Musci der Flora von Buitenzorg (Zugleich Laubmoosflora von Java)*. Vols. 1–4. Brill.
- Frahm, J. P. 1991. A phenetic and cladistic study of the Campylopodioideae. *Journal of the Hattori Botanical Laboratory* 69:65–78.
- Goffinet, B. 1998. The Rhachitheciaceae: revised generic circumscription and ordinal affinities. *The Bryologist* 100:425–439.
- Goffinet, B. and C. J. Cox. 2000. Phylogenetic relationships among basal-most arthrodontous mosses with special emphasis on the evolutionary significance of the Funariineae. *The Bryologist* 103:212–223. [BioOne](#)
- Goffinet, B., C. J. Cox, A. J. Shaw, and T. A. Hedderson. 2001. The Bryophyta (mosses): systematic and evolutionary inferences from a *rps4* gene (cpDNA) phylogeny. *Annals of Botany* 87:191–208. [CrossRef](#)
- Goloboff, P. A. 1993. Estimating character weights during tree search. *Cladistics* 9:83–91. [CrossRef](#)
- Greven, H. C. 1995. *Grimmia Hedw. (Grimmiaceae, Musci) in Europe*. Leiden: Backhuys Publishers.

- Harvey, P. H. and M. D. Pagel. 1991. *The comparative method in evolutionary biology*. Oxford: Oxford University Press.
- Hedderson, T. A. and R. E. Longton. 1995. Patterns of life history variation in the Funariales, Polytrichales and Pottiales. *Journal of Bryology* 18:639–676.
- Hedderson, T. A., R. L. Chapman, and C. J. Cox. 1998. Bryophytes and the origins and diversification of land plants: new evidence from molecules. Pp. 65–77 in *Bryology for the twenty-first century*, eds. J. W. Bates, N. W. Ashton and J. G. Duckett. Leeds: Maney.
- Hedderson, T. A., C. J. Cox, and J. G. Gibbings. 1999. Phylogenetic relationships of the Wardiaceae (Musci): evidence from 18S rRNA and *rps4* gene sequences. *The Bryologist* 102:26–31.
- Hillis, D. M. and J. J. Bull. 1993. An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analyses. *Systematic Biology* 42:182–192. [CrossRef](#)
- Huelsenbeck, J. P. and F. Ronquist. 2001. MrBayes 2.0: Bayesian Analysis of Phylogeny. Distributed by the author.
- La Farge, C., A. J. Shaw, and D. H. Vitt. 2002. The circumscription of the Dicranaceae (Bryopsida) based on the chloroplast regions *trnL-trnF* and *rps4*. *Systematic Botany* 27:435–452.
- La Farge, C., B. D. Mishler, J. A. Wheeler, D. P. Wall, K. Johannes, S. Schaffer, and A. J. Shaw. 2000. Phylogenetic relationships within the haplolepideous mosses. *The Bryologist* 103:257–276. [BioOne](#)
- Munoz, J. and F. Pando. 2000. *A world synopsis of the genus Grimmia*. Monographs in Systematic Botany from the Missouri Botanical Gardens. 83.
- Newton, A. E., C. J. Cox, J. G. Duckett, J. Wheeler, B. Goffinet, T. A. J. Hedderson, and B. D. Mishler. 2000. Evolution of the major moss lineages: phylogenetic analyses based on multiple gene sequences and morphology. *The Bryologist* 103:187–211. [BioOne](#)
- Nadot, S., G. Bittar, L. Carter, R. Lacroix, and B. Lejeune. 1995. A phylogenetic analysis of monocotyledons based on the chloroplast gene *rps4*, using parsimony and a new numerical phenetics method. *Molecular Phylogenetics and Evolution* 4:257–282. [CrossRef](#), [PubMed](#)
- Philibert, H. 1984a. De l'importance du péristome pour les affinités naturelles des mousses. *Revue Bryologique* 11:49–52.65–72.
- Philibert, H. 1984b. Études sur le péristome,. *Revue Bryologique* 11:80–87.
- Pursell, R. A. and W. D. Reese. 1980. The taxonomic status of the Nanobryaceae (Bryopsida). *The Bryologist* 83:559–562.
- Schofield, W. B. 1985. *Introduction to Bryology*. New York: Macmillan.
- Shaw, A. J., B. D. Mishler, and L. E. Anderson. 1989. Peristome development in mosses in relation to systematics and evolution. IV. Haplolepideae: Ditrichaceae and Dicranaceae. *The Bryologist* 92:314–325.
- Shoemaker, J. S., I. S. Painter, and B. S. Weir. 1999. Bayesian statistics in genetics—a guide for the uninitiated. *Trends in Genetics* 15:9354–358.
- Snider, J. A. 1975a. A revision of the genus *Archidium* (Musci). *Journal of the Hattori Botanical Laboratory* 39:105–201.
- Snider, J. A. 1975b. Sporophyte development in the genus *Archidium* (Musci). *Journal of the Hattori Botanical Laboratory* 39:85–104.
- Stech, M. 1999. A reclassification of the Dicranaceae (Bryopsida) based on non-coding cpDNA sequence data. *Journal of the Hattori Botanical Laboratory* 86:137–159.
- Stone, I. G. 1977. Some morphological and anatomical features of the monotypic genus *Bryobartramia* Sainsbury (Musci). *Australian Journal of Botany* 25:141–157.

- Swofford, D. L. 1998. PAUP*. Phylogenetic analysis using parsimony (and other methods). Version 4. Sunderland: Sinauer.
- Vitt, D. H. 1984. Classification of the Bryopsida. Pp. 696–759 in *New Manual of Bryology*, ed. R. M. Schuster. Nichinan: The Hattori Botanical Laboratory.
- Vitt, D. H., B. Goffinet, and T. A. Hedderson. 1998. The Ordinal classification of the Mosses: Questions and Answers for the 1990's. Pp. 113–123 in *Bryology for the twenty-first century*, eds. J. W. Bates, N. W. Ashton and J. G. Duckett. Maney.
- Williams, P. 'and others'. 1999. Gnuplot 3.71. Distributed by the authors: <http://www.gnuplot.vt.edu/>.
- Yang, Z. 1993. Maximum likelihood estimation of phylogeny from DNA sequences when substitution rates vary over sites. *Molecular Biology and Evolution* 10:1396–1304. [PubMed](#)
- Yang, Z. 1994. Maximum likelihood estimation of phylogeny from DNA sequences when substitution rates vary over sites: approximate methods. *Journal of Molecular Evolution* 39:306–314. [CrossRef](#), [PubMed](#)
- Zander, R. H. 1993. Genera of the Pottiaceae: mosses of harsh environments. *Bulletin of the Buffalo Society of Natural Sciences* 32:1–378.
- Zander, R. H. 1998. A phylogrammatic evolutionary analysis of the moss genus *Didymodon* in North America north of Mexico. *Bulletin of the Buffalo Society for Natural Science* 36:81–115.