

**Phylogeny, Character Evolution, and Biogeography of the Gondwanic Moss Family
Hypopterygiaceae (Bryophyta)**

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Abstract

Phylogenetic relationships among the seven genera of the Hypopterygiaceae, represented by 14 of the 21 species recognized in the family, were reconstructed based on variation in nucleotide sequences of six nuclear, mitochondrial, and plastid loci. Monophyly of the Hypopterygiaceae is strongly supported, whereas the genera *Cyathophorum* and *Dendrohypopterygium* are unambiguously polyphyletic. *Cyathophorum bulbosum* and *C. adiantum* make up a lineage sister to the remainder of the family. A lineage comprising four monotypic genera (*Arbusculohypopterygium*, *Canalohypopterygium*, *Catharomnion*, and *Dendrocyathophorum*) is sister to *Lopidium* plus a heterogenous clade that includes *Dendrohypopterygium*, *Hypopterygium*, *Cyathophorum hookerianum*, and *C. parvifolium*. The later two species are transferred to *Hypopterygium* as *H. hookerianum* and *H. parvifolium*. The Hypopterygiaceae are distinguished from their sister family, the Hookeriaceae, by their anisophylly, and by a border of two or more differentiated cells on lateral leaves, although this character also occurs in some Hookeriaceae and has been lost at least twice in the Hypopterygiaceae. Intermediate cells in the axillary hairs arose early in the evolution of the family but are lacking in the two species of *Cyathophorum* that form a sister group to the remainder of the Hypopterygiaceae.

Keywords: [Bryophyta phylogenetics](#), [Gondwana biogeography](#), [Hookeriales](#), [Hypopterygiaceae](#), [Hypopterygium](#)

Literature Cited

- Blöcher, R. and I. Capesius. 2002. The systematic position of the Hypopterygiaceae (Bryopsida) inferred from *rps4* gene sequences. *Cryptogamie, Bryologie* 23:191–207.
- Brotherus, V. F. 1925. Hypopterygiaceae. 270–278. in Die natürlichen Pflanzenfamilien. vol. 11. Engler, A. and K. Prantl, editors. Leipzig W. Engelmann.
- Buck, W. R. 1987. Taxonomic and nomenclatural rearrangement in the Hookeriales with notes on West Indian taxa. *Brittonia* 39:210–224.
- Buck, W. R. and B. Goffinet. 2000. Morphology and classification of mosses. 71–123. in *Bryophyte biology*. Shaw, A. J. and B. Goffinet, editors. Cambridge Cambridge University Press.
- Buck, W. R. and D. H. Vitt. 1986. Suggestions for a new familial classification of pleurocarpous mosses. *Taxon* 35:21–60. [CrossRef](#)
- Buck, W. R., C. J. Cox, A. J. Shaw, and B. Goffinet. 2005. Ordinal relationships of pleurocarpous mosses, with special emphasis on the Hookeriales. *Systematics and Biodiversity* 2:121–145. [CrossRef](#)
- Cox, C. J., B. Goffinet, A. J. Shaw, and S. B. Boles. 2004. Phylogenetic relationships among the mosses based on heterogeneous Bayesian analysis of multiple genomic compartments. *Systematic Botany* 29:234–250. [BioOne](#)
- Crosby, M. R. 1974. Toward a revised classification of the Hookeriales (Musci). *The Journal of the Hattori Botanical Laboratory* 38:129–141.
- Davis, E. C. 2004. A molecular phylogeny of leafy liverworts (Jungermanniidae, Marchantiophyta). 61–86. in *Molecular systematics of bryophytes: progress, problems and perspectives*. Goffinet, B., V. Hollowell, and R. Magill, editors. Monographs in systematic botany from the Missouri Botanical Garden. vol. 48. St. Louis Missouri Botanical Garden.
- Farris, J. S. 1989. The retention index and the rescaled consistency index. *Cladistics* 5:417–419. [CrossRef](#)
- Felsenstein, J. S. 1981. Evolutionary trees from DNA sequences: a maximum likelihood approach. *Journal of Molecular Evolution* 17:368–376. [CrossRef](#), [PubMed](#)
- Felsenstein, J. S. 1985. Confidence-limits on phylogenies: an approach using the bootstrap. *Evolution* 39:783–791. [CrossRef](#)
- Frey, W., M. Stech, and K. Meissner. 1999. Chloroplast DNA-relationships in palaeoaustral *Lopidium concinnum* (Hypopterygiaceae, Musci). An example of stenoevolution in mosses. *Studies in austral temperate rain forest bryophytes 2. Plant Systematics and Evolution* 218:67–75. [CrossRef](#)
- Goffinet, B. and W. R. Buck. 2004. Systematics of the Bryophyta (mosses); from molecules to a revised classification. 205–209. in *Molecular systematics of bryophytes: progress, problems and perspectives*. Goffinet, B., V. Hollowell, and R. Magill, editors. Monographs in systematic botany from the Missouri Botanical Garden. vol. 48. St. Louis Missouri Botanical Garden.
- Huelsenbeck, J. P. and F. Ronquist. 2002. MrBayes version 3.0B. Available from the authors. <http://morphbank.ebc.uu.se/mrbayes3/info.php>
- Kluge, A. G. and J. S. Farris. 1969. Quantitative phyletics and the evolution of Anurans. *Systematic Zoology* 18:1–32. [CrossRef](#)
- Kruijer, H. 2002. Hypopterygiaceae of the world. *Blumea supplement*. 13:1–388.
- Kruijer, H. and R. Blöcher. 2007. Reevaluation of the phylogeny of the Hypopterygiaceae (Bryophyta) based on morphological and molecular data. 61–103. in *Pleurocarpous mosses. Systematics and Evolution*. Newton, A. E. and R. S. Tangney, editors. Boca Raton CRC Press.
- Maddison, W. P. and D. R. Maddison. 2004. Mesquite: a modular system for evolutionary analysis. Version 1.05. <http://mesquiteproject.org>

- Miller, H. A. 1971. An overview of the Hookeriales. *Phytologia* 21:243–252.
- Milne, R. I. 2006. Northern hemisphere plant disjunctions: a window on Tertiary land bridges and climate change. *Annals of Botany* 98:465–472. [CrossRef](#), [PubMed](#)
- Newton, A. E., N. Wikström, N. Beil, L. L. Forrest, and M. S. Ignatov. 2007. Dating the diversification of the pleurocarpous mosses. 337–366. in *Pleurocarpous mosses. Systematics and Evolution*. Newton, A. E. and R. S. Tangney, editors. Boca Raton CRC Press.
- Nylander, J. A A. 2002. MrModeltest, version 1.1b. Available from the author.
<http://www.ebc.uu.se/systzoo/staff/nylander.html>
- Pacak, A. and Z. Szweykowska. 2003. Organellar inheritance in liver-worts: an example of *Pellia borealis*. *Journal of Molecular Evolution* 56:11–17.
- Pelser, P. B., H. Kruijer, and R. Verpoorte. 2002. What is the function of oil-containing rudimentary branches in the moss *Canalohypopterygium tamariscinum*. *New Zealand Journal of Botany* 40:149–153.
- Pfeiffer, T., H. Kruijer, W. Frey, and M. Stech. 2000. Systematics of the *Hypopterygium tamarisci* complex (Hypopterygiaceae, Bryopsida): implications from morphological and molecular study. *Studies in austral temperate rain forest bryophytes. The Journal of the Hattori Botanical Laboratory* 89:55–70.
- Shaw, A. J., C. J. Cox, and B. Goffinet. 2005. Global patterns of moss biodiversity: taxonomic and molecular inferences. *Taxon* 54:337–352. [CrossRef](#)
- Stech, M., T. Pfeiffer, and W. Frey. 1999. Molecular systematic relationships of temperate austral Hypopterygiaceae (Bryopsida): Implications for taxonomy and biogeography. *Studies in austral temperate rain forest bryophytes 3. Hausknechtia Beiheft* 9:359–367.
- Stech, M., T. Pfeiffer, and W. Frey. 2002. Molecular generic classification of the Hypopterygiaceae (Bryopsida), with the description of a new genus, *Arbusculohypopterygium* gen. nov. *Studies in austral temperate rain forest bryophytes 10. New Zealand Journal of Botany* 40:207–221.
- Swofford, D. L. 2002. PAUP*. Phylogenetic analysis using parsimony (*and other methods), version 4.0. Sunderland Sinauer Associates.
- Williams, T. and C. Kelley. 1999. Gnuplot, version 3.7.1. Software and documentation.
<http://sourceforge.net/projects/gnuplot>
- Yang, Z. and B. Rannala. 1997. Bayesian phylogenetic inference using DNA sequences: A markov chain Monte Carlo method. *Molecular Biology and Evolution* 14:717–724. [CrossRef](#), [PubMed](#)