



Phylogenetic reconstructions of the Hedwigiaceae reveal cryptic speciation and hybridisation in *Hedwigia*

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Abstract

A molecular based study of relationships in the Hedwigiaceae, with a special focus on the genus *Hedwigia* in Europe was carried out. A combined approach using sequence data from all three genomes, information obtained from the secondary structures of the *nad5* group I intron, and morphological data was performed in order to clarify species concepts in the *Hedwigia ciliata*-complex. In agreement with earlier studies the separation of *Rhacocarpus* in its own family Rhacocarpaceae can be rejected. The genus is related to *Braunia* and therefore clearly belongs to the Hedwigiaceae. Based on molecular data *Pseudobraunia californica* is shown to be related to *Hedwigia*. Since several of the morphological characters are of questionable systematic value and the remaining characters are few, a separation in its own genus is inappropriate. We transfer *Pseudobraunia californica* back to *Hedwigia californica*. We show that the *Hedwigia ciliata*-complex in Europe consists of at least 4 species, *Hedwigia ciliata*, *Hedwigia stellata*, *Hedwigia striata* (which is here transferred back to species rank) and a cryptic species of which we do not have enough information yet to identify it as one of the existing taxa or as a new species. All Australian specimens included in our analyses, which were believed to be *Hedwigia ciliata* s. str., belong to this taxon rendering the occurrence of *Hedwigia ciliata* s. str. in Australia questionable. *Hedwigia ciliata* var. *leucophaea* cannot be maintained with its current morphological circumscription. The distinguishing characters can obviously be developed independently in some taxa of the *Hedwigia ciliata* complex. Furthermore we found evidence for potential hybridisation in some of the specimens determined as *Hedwigia ciliata* var. *leucophaea*, as nuclear and organellar DNA is originating from different taxa.

Based on the presented results, *Hedwigia striata* (Wilson) Bosw. is recognized as a distinct species with more or less distinctly plicate leaves and straight rather than flexuose perichaetial leaf cilia.

Keywords: *Hedwigia ciliata*-complex, *Hedwigia leucophaea*, *Hedwigia stellata*, *Hedwigia striata*, *nad5* intron secondary structure, molecular phylogenetics

Introduction

The family Hedwigiaceae was described in 1856, originally for the three genera *Hedwigia* Palisot de Beauvois (1804: 303), *Hedwigidium* Bruch & Schimper (1846: 155), and *Braunia* Bruch & Schimper (1846: 159). In the large overviews of the moss system from the early 20th Century, the Hedwigiaceae had grown to include also *Pseudobraunia* (Lesqeraux & James 1884: 153) Brotherus (1905: 715), *Bryowijkia* Noguchi (1973: 240), and *Rhacocarpus* Lindberg (1863: 607) (Fleischer 1906–1908, Brotherus 1909, 1925). This concept of the Hedwigiaceae was used by most authors until recently (e.g., Walther 1983). However, only the year after Walther's overview of the moss system Vitt & Buck (1984) transferred *Bryowijkia* to the Trachypodaceae based on features, such as the strong, single costa, seriate papillae on the leaf lamina cells, and the presence of a reduced diplolepideous-alternate peristome (absent in the Hedwigiaceae). Although some researchers did not follow this transfer (Vashistha 1998), the morphological evidence that places

England, Grasmere, August 1869, herb. Wilson (BM); England, Rydal, *Schimper* (S; B117464); Scotland, Dumyat, June 1869, herb. Wilson (BM); Scotland, Alva wood, 12 March 1850, herb. Wilson (BM); Scotland, summit of Alva, herb. Wilson (BM); Scotland, New Galloway, *J. Andrew* (S; B117463). **MOROCCO**. Larache mountains of Souk-el-Arba-des-Beni-Hassan, 30S2639, 630 m, 29 October 1994, *T.A.J. Hedderson* (MA; 15071).

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References

- Allen, B.H. (1987) A revision of the Dicnemonaceae (Musci). *Journal of the Hattori Botanical Laboratory* 62: 1–100.
- Axelrod, D.I. & Raven, P.H. (1978) Late Cretaceous and Tertiary vegetation history of Africa. In: Werger, M.J.A. (eds.) *Biogeography and ecology of southern Africa*. Dr. W. Junk b.v. Publishers, The Hague, pp. 79–130.
- Barthlott, W. & Schultze-Motel, W. (1981) Zur Feinstruktur der Blattoberflächen und systematischen Stellung der Laubmoosgattung *Rhacocarpus* und anderer Hedwigiaceae. *Willdenowia* 11: 3–11.
- Beckert, S., Steinhauser, S., Muhle, H. & Knoop, V. (1999) A molecular phylogeny of bryophytes based on nucleotide sequences of the mitochondrial *nad5* gene. *Plant Systematics and Evolution* 218: 179–192.
<http://dx.doi.org/10.1007/BF01089226>
- Biasuso, A.B. (2007) The genus *Hedwigia* (Hedwigiaceae, Bryophyta) in Argentina. *Lindbergia* 32: 5–17.
- Borsch, T., Hilu, K.W., Quandt, D., Wilde, V., Neinhuis, C. & Barthlott, W. (2003) Noncoding plastid *trnT-trnF* sequences reveal a well resolved phylogeny of basal angiosperms. *Journal of Evolutionary Biology* 16: 558–576.
<http://dx.doi.org/10.1046/j.1420-9101.2003.00577.x>
- Borsch, T. & Quandt, D. (2009) Mutational dynamics and phylogenetic utility of noncoding chloroplast DNA. *Plant Systematics and Evolution* 282: 169–199.
<http://dx.doi.org/10.1007/s00606-009-0210-8>
- Boswell, H. (1879) Reports of Societies: Manchester Cryptogamic Society. *The Naturalist* 5: 46.
- Brotherus, V.F. (1905) Musci (Laubmoose) III: Unterklasse Bryales. II. Gruppe: Pleurocarpi 222[I,3.] In: Engler, A. & Prantl, K. (Eds.) *Die Natürlichen Pflanzenfamilien*. W. Engelmann, Leipzig, pp. 673–698, [703]–715.
- Brotherus, V.F. (1909) Musci (Laubmoose) III: Unterklasse Bryales. Spezieller Teil. In: Engler, A. & Prantl, K. (Eds.) *Die Natürlichen Pflanzenfamilien*. W. Engelmann, Leipzig, pp. 701–1246.
- Brotherus, V.F. (1925) Musci (Laubmoose). 2. Hälfte. In: Engler, A. & Prantl, K. (Eds.) *Die natürlichen Pflanzenfamilien*. W. Engelmann, Leipzig, 542 pp.
- Bruch & Schimper (1846) *Bryologia Europaea* 3, fasc. 29–30. E. Schweizerbart, Stuttgart, pp. 146–202.
- Buck, W.R. (1995) The systematic position of the moss genus *Rhacocarpus*. *Fragmenta Floristica et Geobotanica* 40: 127–131.
- Buck, W.R., Cox, C.J., Shaw, A.J. & Goffinet, B. (2004) Ordinal relationships of pleurocarpous mosses, with special emphasis on the Hookeriales. *Systematics and Biodiversity* 2: 121–145.

<http://dx.doi.org/10.1017/S147200004001410>

- Buck, W.R. & Norris, D.H. (1996) *Hedwigia stellata* and *H. detonsa* (Hedwigiaceae) in North America. *Nova Hedwigia* 62: 361–370.
- Buck, W.R. & Vitt, D.H. (1986) Suggestions for a new familial classification of pleurocarpous mosses. *Taxon* 35: 21–60.
<http://dx.doi.org/10.2307/1221034>
- Cox, C.J., Goffinet, B., Wickett, N.J., Boles, S.B. & Shaw, A.J. (2010) Moss diversity: A molecular phylogenetic analysis of genera. *Phytotaxa* 9: 175–195.
<http://dx.doi.org/10.11646/phytotaxa.9.1.10>
- Dalton, N.J., Kungu, E.M. & Long, D.G. (2012) The misapplication of *Hedwigia integrifolia* P.Beauv. and identity of *Gymnostomum imberbe* Sm. (Hedwigiaceae, Bryophyta). *Journal of Bryology* 34: 59–61.
<http://dx.doi.org/10.1179/1743282011Y.0000000041>
- Dalton, N.J., Kungu, E.M. & Long, D.G. (2013) A taxonomic revision of Hedwigiaceae Schimp. from the Sino-Himalaya. *Journal of Bryology* 35: 96–111.
<http://dx.doi.org/10.1179/1743282012Y.0000000043>
- De Luna, E. (1990) Protonemal development in the Hedwigiaceae (Musci) and its systematic significance. *Systematic Botany* 15: 192–204.
<http://dx.doi.org/10.2307/2419173>
- De Luna, E. (1995) The circumscription and phylogenetic relationships of the Hedwigiaceae (Musci). *Systematic Botany* 20: 347–373.
<http://dx.doi.org/10.2307/2419500>
- Doyle, J.J. & Doyle, J.L. (1990) Isolation of plant DNA from fresh tissue. *Focus* 12: 13–15.
- Draper, I., Hedenäs, L. & Grimm, G.W. (2007) Molecular and morphological incongruence in European species of *Isoetecium* (Bryophyta). *Molecular Phylogenetics and Evolution* 42: 700–716.
<http://dx.doi.org/10.1016/j.ympev.2006.09.021>
- Dusén, P. (1905). Musci nonnulli novi e Fuegia et Patagonia reportati. *Botaniska Notiser* 1905: 299–310.
- Edelmann, H.G., Neinhuis, C., Jarvis, M., Evans, B., Fischer, E. & Barthlott, W. (1998) Ultrastructure and chemistry of the cell wall of the moss *Rhacocarpus purpurascens* (Rhacocarpaceae): a puzzling architecture among plants. *Planta* 206: 315–321.
<http://dx.doi.org/10.1007/s004250050406>
- Erzberger, P. (1996) Zur Verbreitung von *Hedwigia stellata* in Europa. *Herzogia* 12: 221–238.
- Fleischer, M. (1906–1908) *Die Musci der Flora von Buitenzorg. Band 3*. E.J. Brill, Leiden, pp. 645–1103.
- Frahm, J.-P. (1996) Revision der Gattung *Rhacocarpus* Lindb. (Musci). *Cryptogamie, Bryologie Lichenologie* 17: 39–65.
- Frahm, J.-P., Capesius, I. & Geiger, H. (1997) Zur systematischen Position von *Rhacocarpus* Lindb. (Musci. Rhacocarpaceae). *Nova Hedwigia* 64: 231–241.
- Frahm, J.-P. & Frey, W. (2004) *Moosflora, 4. Neubearbeitete und erweiterte Auflage*, 4 edn. Eugen Ulmer GmbH & Co., Stuttgart, 538 pp.
- Goffinet, B., Buck, W.R. & Shaw, A.J. (2008) Morphology, anatomy, and classification of the Bryophyta. In: Goffinet, B. & Shaw, A.J. (Eds.) *Bryophyte biology*. Cambridge University Press, Cambridge, pp. 55–138.
- Guerra, J., Cano, M.J. & Brugués, M. (Eds.) (2013) *Flora Briofítica Ibérica, vol. 5. Orthotrichales: Orthotrichaceae; Leucodontales: Fontinalaceae, Climaciaceae, Anomodontaceae, Cryphaeaceae, Leptodontaceae, Leucodontaceae, Neckeraceae; Hedwigiales: Hedwigiaceae; Hookeriales: Hypopterigiaceae, Hookeriaceae, Leucomiaceae, Pilotrichaceae*. Universidad de Murcia/Sociedad Española de Briología, Murcia, 261 pp.
- Hampe, G.E.L. (1865) Prodrómus florae novo-gratens [sic]. [sér. 5] *Annales des Sciences Naturelles; Botanique* 4: 337–376.
- Hedenäs, L. (1994) The *Hedwigia ciliata* complex in Sweden, with notes on the occurrence of the taxa in Fennoscandia. *Journal of Bryology* 18: 139–157.
<http://dx.doi.org/10.1179/jbr.1994.18.1.139>
- Hedenäs, L. (2008) Molecular variation and speciation in *Antitrichia curtispindula* s. l. (Leucodontaceae, Bryophyta). *Botanical Journal of the Linnean Society* 156: 341–354.
<http://dx.doi.org/10.1111/j.1095-8339.2007.00775.x>
- Hedenäs, L. (2011) Incongruence among morphological species circumscriptions and two molecular data sets in *Sarmentypnum* (Bryophyta: Calliergonaceae). *Taxon* 60: 1596–1606.
- Hedwig, J. (1801) *Species Muscorum Frondosorum*. J.A. Barth, Leipzig, 353 pp.
- Hernández-Maqueda, R., Quandt, D. & Muñoz, J. (2008) Testing reticulation and adaptive convergence in the Grimmiaceae (Bryophyta). *Taxon* 57: 500–510.
- Hespanhol, H., Vieira, C., Garcia, C. & Sérgio, C. (2013) New distribution data on *Hedwigia striata* (Wilson) Bosw., a forgotten and misplaced taxon, in Portugal. *Boletín de la Sociedad Española Briología* 40(4): 49–53.
- Hooker, W.J. (1833) *The English flora*. Vol. 2. Cryptogamia. Longman, Rees, Orme, Brown, Green, & Longman, London, 432 pp.

- Howe, M. (1897) Notes on California Bryophytes. *Erythea* 5(8): 87–94.
- Huttunen, S., Olsson, S., Buchbender, V., Enroth, J., Hedenäs, L. & Quandt, D. (2012) Phylogeny-based comparative methods question the adaptive nature of sporophytic specializations in mosses. *PLoS ONE* 7(10), e48268, 48261–48210.
<http://dx.doi.org/10.1371/journal.pone.0048268>
- Jones, G.N. (1933) Grimmiaceae. In: A.J. Grout (Ed.) *Moss Flora of North America. Volume 2, Part 1*. A. J. Grout, Newfane, Vermont, pp. 1–66.
- Kelchner, S.A. (2000) The evolution of non-coding chloroplast DNA and its application in plant systematics. *Annals of the Missouri Botanical Garden* 87: 482–498.
<http://dx.doi.org/10.2307/2666142>
- Kelchner, S.A. (2002) Group II introns as phylogenetic tools: structure, function, and evolutionary constraints. *American Journal of Botany* 89: 1651–1669.
<http://dx.doi.org/10.3732/ajb.89.10.1651>
- Kindberg, N.C. (1894) Check-list of European and North American mosses (Bryinae). *Canadian Record of Science* 6: 17–28, 72–76.
- Kindberg, N.C. (1899) Studien über die Systematik der pleurokarpischen Laubmoose. *Botanisches Centralblatt* 77: 49–55.
- Koponen, T. & Norris, D.H. (1986) Bryophyte flora of the Huon Peninsula, Papua New Guinea. XVII. Grimmiaceae, Racopilaceae and Hedwigiaceae (Musci). *Acta Botanica Fennica* 133: 81–106.
- LaFarge-England, C. (1996) Growth form, branching pattern, and perichaetial position in mosses: cladocarp and pleurocarpy redefined. *Bryologist* 99, 170–186.
<http://dx.doi.org/10.2307/3244546>
- Lesquereux, C.L. (1865) On Californian mosses. *Transactions of the American Philosophical Society, new series* 13: 1–24.
<http://dx.doi.org/10.2307/1005344>
- Lesquereux, C.L. & James, T.P. (1884) *Manual of the Mosses of North America*. Boston, 447 pp.
- Limpricht, K.G. (1885–1890) *Die Laubmoose Deutschlands, Oesterreichs und der Schweiz. I. Abtheilung*. Verlag von Eduard Kummer, Leipzig, 836 pp.
- Lindberg, S.O. (1863) Om ett nytt slägte, Epipterygium. *Öfversigt af Förhandlingar: Kongl. Svenska Vetenskaps-Akademiens* 19: 599–609.
- Mathews, D.H., Disney, M.D., Childs, J.L., Schroeder, S.J., Zuker, M. & Turner, D.H. (2004) Incorporating chemical modification constraints into a dynamic programming algorithm for prediction of RNA secondary structure. *Proceedings of the National Academy of Sciences of the United States of America* 101: 7287–7292.
<http://dx.doi.org/10.1073/pnas.0401799101>
- Mathews, D.H., Sabina, J., Zuker, M. & Turner, D.H. (1999) Expanded sequence dependence of thermodynamic parameters improves prediction of RNA secondary structure. *Journal of Molecular Biology* 288: 911–940.
<http://dx.doi.org/10.1006/jmbi.1999.2700>
- Mitten, W. (1869) Musci austro-americi. *Journal of the Linnean Society, Botany* 12: 1–659.
<http://dx.doi.org/10.1111/j.1095-8339.1871.tb00633.x>
- Müller, C. (1851) *Synopsis muscorum frondosorum omnium hucusque cognitorum* 2. A. Foerstner, Berlin, 772 pp.
- Müller, J. & Müller, K. (2004) TREEGRAPH: automated drawing of complex tree figures using an extensible tree description format. *Molecular Ecology Resources* 4: 786–788.
<http://dx.doi.org/10.1111/j.1471-8286.2004.00813.x>
- Müller, K. (2005) SeqState. *Applied Bioinformatics* 4: 65–69.
<http://dx.doi.org/10.2165/00822942-200504010-00008>
- Mönkemeyer, W. (1927) *Die Laubmoose Europas. IV. Band, Ergänzungsband. Andreaeales-Bryales*, Leipzig, 960 pp.
- Natcheva, R. & Cronberg, N. (2004) What do we know about hybridization among bryophytes in nature? *Canadian Journal of Botany* 82: 1687–1704.
<http://dx.doi.org/10.1139/b04-139>
- Noguchi, A. (1973) Contributions to the bryology of Thailand. *Journal of the Hattori Botanical Laboratory* 37: 235–250.
- Noguchi, A. (1985) The isobryalean mosses collected by Dr. Z. Iwatsuki in New Caledonia. *Journal of the Hattori Botanical Laboratory* 58: 87–109.
- Nyholm, E. (1998) *Illustrated flora of Nordic mosses. Fasc. 4*. Nordic Bryological Society, Copenhagen and Lund, pp. 249–405.
- Olsson, S., Buchbender, V., Enroth, J., Hedenäs, L., Huttunen, S. & Quandt, D. (2009a) Phylogenetic analyses reveal high levels of polyphyly among pleurocarpous lineages as well as novel clades. *Bryologist* 112, 447–466.
<http://dx.doi.org/10.1639/0007-2745-112.3.447>
- Olsson, S., Buchbender, V., Enroth, J., Huttunen, S., Hedenäs, L. & Quandt, D. (2009b) Evolution of the Neckeraceae (Bryophyta): resolving the backbone phylogeny. *Systematics and Biodiversity* 7: 419–432.

<http://dx.doi.org/10.1017/S1477200009990132>

- Ochyra, R., Lewis Smith, R.I. & Bednarek-Ochyra, H. (2008) *The illustrated moss flora of Antarctica*. Cambridge University Press, Cambridge, 685 pp.
- Palisot de Beauvois, A.M.F.J. (1804) Prodrôme de l'Aethéogamie ou d'un Traité sur les familles de plantes dont la fructification est extraordinaire; famille des mousses. *Magasin Encyclopédique* 5(19): 289–330.
- Palisot de Beauvois, A.M.F.J. (1805) *Prodrome des Cinquième et Sixième Familles de l'Aethéogamie*. Fournier f., Paris, 114 pp.
- Podpěra, J. (1954) *Conspectus muscorum Europaeorum*. Československé Akademie Věd, Praha, 697 pp.
- Quandt, D., Bell, N. & Stech, M. (2007) Unravelling the knot: the Pulchrinodaceae fam. nov. (Bryales). *Beihefte zur Nova Hedwigia* 131: 21–39.
- Quandt, D., Müller, K. & Huttunen, S. (2003) Characterisation of the chloroplast DNA *psbT*-H region and the influence of dyad symmetrical elements on phylogenetic reconstructions. *Plant Biology* 5: 400–410.
<http://dx.doi.org/10.1055/s-2003-42715>
- Quandt, D., Müller, K., Stech, M., Hilu, K.W., Frey, W., Frahm, J.P. & Borsch, T. (2004) Molecular evolution of the chloroplast *trnL*-F region in land plants. *Monographs in Systematic Botany from the Missouri Botanical Garden* 98: 13–37.
- Quandt, D. & Stech, M. (2004) Molecular evolution of the *trnT_{UGU}*-*trnF_{GAA}* region in bryophytes. *Plant Biology* 6: 545–554.
<http://dx.doi.org/10.1055/s-2004-821144>
- Quandt, D. & Stech, M. (2005) Molecular evolution and secondary structure of the chloroplast *trnL* intron in bryophytes. *Molecular Phylogenetics and Evolution* 36: 429–443.
<http://dx.doi.org/10.1016/j.ympev.2005.03.014>
- Reichardt, H.W. (1870) *Reise der österreichischen Fregatte Novara um die Erde: Botanischer Theil*. Pilze, Leber- und Laubmoose. K.K. Hof- u. Staatsdruckerei, in Commission bei Gerold, 64 pp., 17 pl.
- Robinson, H. (1971) Scanning electron microscope studies on moss leaves and peristomes. *Bryologist* 74: 473–483.
<http://dx.doi.org/10.2307/3241307>
- Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic biology* 61: 539–42.
<http://dx.doi.org/10.1093/sysbio/sys029>
- Roth, G. (1904) *Die europäischen Laubmoose. Erster Band*. Verlag von Wilhelm Engelmann, Leipzig, 598 pp.
- Sainsbury, G.O.K. (1945) New and Critical Species of New Zealand Mosses. *Transactions and Proceedings of the Royal Society of New Zealand* 75: 169–186.
- Schimper, W.P. (1856) *Corollarium bryologiae Europaeae*. E. Schweizerbart, Stuttgartiae, 140 pp.
- Shaw, A.J., Cox, C.J. & Boles, S.B. (2003) Polarity of peatmoss (*Sphagnum*) evolution: who says bryophytes have no roots? *American Journal of Botany* 90: 1777–1787.
<http://dx.doi.org/10.3732/ajb.90.12.1777>
- Simmons, M.P. & Ochoterena, H. (2000) Gaps as characters in sequence-based phylogenetic analyses. *Systematic Biology* 49: 349–381.
<http://dx.doi.org/10.1093/sysbio/49.2.369>
- Smith, A.J.E. (2004) *The moss flora of Britain and Ireland. Second edition*. Cambridge University Press, Cambridge, 1026 pp.
<http://dx.doi.org/10.1017/CBO9780511541858>
- Spagnuolo, V., Caputo, P., Cozzolino, S., Castaldo, R. & De Luca, P. (1999) Patterns of relationships in *Trichostomoideae* (Pottiaceae, Musci). *Plant Systematics and Evolution* 216: 69–79.
<http://dx.doi.org/10.1007/BF00985101>
- Stamatakis, A. (2006) RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22: 2688–2690.
<http://dx.doi.org/10.1093/bioinformatics/btl446>
- Stech, M. (1999) *Molekulare Systematik haplolepider Laubmoose (Dicranaceae, Bryopsida)*. PhD thesis. Freie Universität Berlin, Berlin, 114 pp.
- Taberlet, P., Gielly, L., Pautou, G. & Bouvet, J. (1991) Universal primers for the amplification of three non-coding regions of chloroplast DNA. *Plant Molecular Biology* 17: 1105–1109.
<http://dx.doi.org/10.1007/BF00037152>
- Tsubota, H., Arikawa, T., Akiyama, H., De Luna, E., González, D., Higuchi, M. & Deguchi, H. (2002) Molecular phylogeny of hypnobryalean mosses as inferred from a large-scale dataset of chloroplast *rbcl*, with special reference to the Hypnaceae and possibly related families. *Hikobia* 13: 645–665.
- Vanderpoorten, A., Rumsey, F.J. & Carine, M.A. (2007) Does Macaronesia exist? Conflicting signal in the bryophyte and pteridophyte floras. *American Journal of Botany* 94: 625–639.

<http://dx.doi.org/10.3732/ajb.94.4.625>

Vashistha, B.D. (1998) Distribution of mosses in India. *In*: Chopra, R.N. (Eds.) *Topics in Bryology*. Allied Publishers Limited, New Delhi, pp. 86–111.

Vitt, D.H. & Buck, W.R. (1984) The familial placement of *Bryowijkia* (Musci: Trachypodaceae). *Brittonia* 36: 300–306.

<http://dx.doi.org/10.2307/2806531>

Walther, K. (1983) Bryophytina, Laubmoose. *In*: Gerloff, J. & Poelt, J. (Eds.) *A. Englers Syllabus der Pflanzenfamilien*. Gebrüder Borntraeger, Berlin & Stuttgart, pp. I–X, 1–108.

Zuker, M. (2003) Mfold web server for nucleic acid folding and hybridization prediction. *Nucleic Acids Research* 31: 3406–3415.

<http://dx.doi.org/10.1093/nar/gkg595>