



<http://dx.doi.org/10.11646/phytotaxa.170.3.4>

Towards a monophyletic classification of Lejeuneaceae III: the systematic position of *Leiolejeunea*

ALFONS SCHÄFER-VERWIMP¹, KATHRIN FELDBERG², SHANSHAN DONG³, HUUB VAN MELICK⁴, DENILSON F. PERALTA⁵, ALEXANDER R. SCHMIDT⁶, HARALD SCHNEIDER⁷, JOCHEN HEINRICH²

¹ Mittlere Letten 11, 88634 Herdwangen-Schönach, Germany. Email: moos.alfons@kabelbw.de

² Systematic Botany, Faculty of Biology, University of Munich (LMU), Menzinger Str. 67, 80638 Munich, Germany.

Email: jheinrichs@lmu.de, k.feldberg@biologie.uni-muenchen.de

³ Department of Systematic Botany, Albrecht von Haller Institute of Plant Sciences, Georg August University, Untere Karstraße 2, 37073 Göttingen, Germany. Email: shanshan.dong@stud.uni-goettingen.de

⁴ Merellaan 13, 5552 BZ Valkenswaard, The Netherlands. Email: hmhvanmelick@onsbrabantnet.nl

⁵ Instituto de Botânica, Caixa Postal 68041, 04045-972 São Paulo, SP, Brazil. Email: denilsonfp@yahoo.com.br

⁶ Courant Research Centre Geobiology, Georg August University, Goldschmidtstraße 3, 37077 Göttingen, Germany.

Email: alexander.schmidt@geo.uni-goettingen.de

⁷ Department of Life Science, Natural History Museum, London, SW7, 5BD, UK. Email: h.schneider@nhm.ac.uk

Abstract

The derived liverwort *Leiolejeunea grandiflora* was recollected at the type locality in Jamaica after more than 100 years. The characteristics of its oil bodies were described for the first time based on the new collections. Each leaf cell possesses 2-4(-6) rather small, subhomogeneous to very finely segmented, subglobose to ellipsoidal, colorless oil bodies. The plants were either dioicous or autoicous. DNA sequences of two chloroplast regions (*trnL-trnF*, *rbcL*) and the nuclear ribosomal ITS region were obtained for two accessions of *Leiolejeunea* to enable the inference of the phylogenetic relationships of these plants. Based on Bayesian inference of phylogeny as well as maximum parsimony and maximum likelihood analyses of a dataset including 87 representatives of Lejeuneaceae, *Leiolejeunea* was found as the putative sister to either Echinolejeuneinae or Cheilolejeuneinae. Thus, we propose the new monogeneric subtribe Leiolejeuneinae with relationships to Cheilolejeuneinae and Echinolejeuneinae. The analyses included also one accession of the generitype of *Cheilolejeunea*, *C. decidua* [= *Cheilolejeunea adnata*]. This species was found in a well supported sister relationship with *Cystolejeunea*. To avoid nomenclatural confusion, we propose a wide genus concept for *Cheilolejeunea* including *Aureolejeunea*, *Cyrtolejeunea*, *Cystolejeunea*, *Evansolejeunea*, *Leucolejeunea*, and *Omphalanthus*.

Key words: liverwort, Lejeuneae, molecular phylogeny, Porellales, taxonomy

Introduction

Evans (1908a) described a new genus of Lejeuneaceae based on three specimens from the Blue Mountain Peak of Jamaica including only a single species, *Leiolejeunea grandiflora* Evans (1908a: 378). The minute plants had conspicuous, terete perianths and a pair of very large, wide-spreading bracts that exceeded the size of the leaves more than twice. In habit, these liverworts resembled *Harpalejeunea* (Spruce 1884: 164) Schiffner (1893: 126), but differed by lobules with a hyaline papilla positioned distal to the apical lobule tooth, a lack of ocelli as well as perianth keels, and the absence of true subfloral innovations. Based on the distal position of the hyaline papilla of the leaf lobule Evans (1908a) assumed relationships of *Leiolejeuna* Evans (1908a: 377) with *Cheilolejeunea* (Spruce 1884: 251) Stephani (1890: 284) rather than with *Harpalejeunea*. Gradstein (2013) accepted Evans' interpretation (1908a) and placed *Leiolejeunea* in subtribe Cheilolejeuneinae of Lejeuneae.

Although easy to recognize, *Leiolejeunea* has never been recollected at the type locality. Outside of Jamaica, it has been recorded only from Venezuela (Fulford 1972) but the identification requires confirmation (Dauphin *et al.* 2008). The lack of fresh collections prevented until now the study of oil bodies for these liverworts. This was required because Evans (1908a) did not describe the oil bodies of *Leiolejeunea*. However, these structures are recognized as valuable taxonomical characters in Cheilolejeuneinae (Heinrichs *et al.* 2014a). In December 2013, two of us (ASV, HvM) visited Jamaica and were able to locate three occurrences of *Leiolejeunea* in the upper regions of the Blue Mountain Peak. Based on this material, we describe the oil bodies of *Leiolejeunea*, and include the genus in molecular phylogenetic analyses of Lejeuneae. We also test genus concepts of Cheilolejeuneinae, and include a specimen of the *Cheilolejeunea* generitype in our analyses.

References

- Crandall-Stotler, B., Stotler, R.E. & Long, D.G. (2009) Phylogeny and classification of the Marchantiophyta. *Edinburgh Journal of Botany* 66: 155–198.
<http://dx.doi.org/10.1017/s0960428609005393>
- Darriba, D., Taboada, G.L., Doallo, R. & Posada, D. (2012) jModeltest 2: more models, new heuristics and parallel computing. *Nature Methods* 9: 772.
<http://dx.doi.org/10.1038/nmeth.2109>
- Dauphin, G., Morales, T. & Moreno, E.J. (2008) Catálogo preliminar de Lejeuneaceae (Hepaticae) de Venezuela. *Cryptogamie, Bryologie* 29: 215–265.
- Evans, A.W. (1903) Hepaticae of Puerto Rico III. *Harpalejeunea*, *Cyrtolejeunea*, *Euosmolejeunea* and *Trachylejeunea*. *Bulletin of the Torrey Botanical Club* 30: 544–563.
<http://dx.doi.org/10.2307/2478516>
- Evans, A.W. (1906) Hepaticae of Puerto Rico VI. *Cheilolejeunea*, *Rectolejeunea*, *Cystolejeunea*, and *Pycnolejeunea*. *Bulletin of the Torrey Botanical Club* 33: 1–25.
<http://dx.doi.org/10.2307/2478618>
- Evans, A.W. (1907) *Leucolejeunea*, a new genus of Hepaticae. *Torreya* 7: 225–229.
- Evans, A.W. (1908a) New West Indian Lejeuneae. *Bulletin of the Torrey Botanical Club* 35: 371–389.
<http://dx.doi.org/10.2307/2479284>
- Evans, A.W. (1908b) Hepaticae of Puerto Rico. IX. *Brachiolejeunea*, *Ptychocoleus*, *Archilejeunea*, *Leucolejeunea* and *Anoplolejeunea*. *Bulletin of the Torrey Botanical Club* 35: 155–179.
<http://dx.doi.org/10.2307/2478953>
- Felsenstein, J. (1985) Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39: 783–791.
<http://dx.doi.org/10.2307/2408678>
- Fulford, M.H. (1972) Hepaticae. In: Steyermark, J. & Maguire, B., The flora of the Meseta del Cerro Jaua. *Memoirs of the New York Botanical Garden* 23, pp. 838–845.
- Gola, G. (1907) Species novae in excelsis Ruwenzorensi in expeditione Ducis Aprutii lectae. III. Hepaticae. *Annali di Botanica* 6: 271–276.
- Gottschke, C.M., Lindenberg, J.B.W. & Nees von Esenbeck, C.G. (1845) *Synopsis Hepaticarum*, Part 2. Meissner, Hamburg, pp. 145–304.
<http://dx.doi.org/10.5962/bhl.title.15221>
- Gradstein, S.R. (2013) A classification of Lejeuneaceae based on molecular and morphological evidence. *Phytotaxa* 100: 6–20.
<http://dx.doi.org/10.11646/phytotaxa.100.1.2>
- Gradstein, S.R., Wilson, R., Ilkiu-Borges, A.L. & Heinrichs, J. (2006) Phylogenetic relationships and neotenic evolution of *Metzgeriopsis* (Lejeuneaceae) based on chloroplast DNA sequences and morphology. *Botanical Journal of the Linnean Society* 151: 293–308.
<http://dx.doi.org/10.1111/j.1095-8339.2006.00531.x>
- Grolle, R. (1977) Miscellanea hepaticologica 161–170. *Journal of Bryology* 9: 529–538.
<http://dx.doi.org/10.1179/jbr.1977.9.4.529>
- Grolle, R. (1983) Nomina generica Hepaticarum; references, types and synonymies. *Acta Botanica Fennica* 121: 1–62.
- Grolle, R. & Meister, K. (2004) *The liverworts in Baltic and Bitterfeld amber*. Weissdorn, Jena.
- Grolle, R., Zhu, R.L. & Gradstein, S.R. (2001) On *Cyrtolejeunea* A. Evans (Lejeuneaceae, Hepaticae). *Taxon* 50: 1067–1074.
<http://dx.doi.org/10.2307/1224721>
- Guindon, S. & Gascuel, O. (2003) A simple, fast and accurate method to estimate large phylogenies by maximum-likelihood. *Systematic Biology* 52: 696–704.
<http://dx.doi.org/10.1080/10635150390235520>
- Hall, T.A. (1999) BIOEDIT: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposia Series* 41: 95–98.
- Hamlin, B.G. (1972) Hepaticae of New Zealand, Parts I and II. Index of binomials and preliminary checklist. *Records of the Dominion Museum* 7: 243–266.
- Hartmann, F.A., Wilson, R., Gradstein, S.R., Schneider, H. & Heinrichs, J. (2006) Testing hypotheses on species delimitations and disjunctions in the liverwort *Bryopteris* (Jungermanniopsida: Lejeuneaceae). *International Journal of Plant Sciences* 167: 1205–1214.
<http://dx.doi.org/10.1086/508023>
- Heinrichs, J., Dong, S., Schäfer-Verwimp, A., Peralta, D.F., Feldberg, K., Schmidt, A.R. & Schneider, H. (2014a) Towards a monophyletic classification of Lejeuneaceae II: subtribes Pycnolejeuneinae and Xylojeuneinae subtr. nov., transfer of *Otolejeunea* to Lepidolejeuninae, and generic refinements. *Phytotaxa* 163: 61–76.

- http://dx.doi.org/10.11646/phytotaxa.163.2.1
- Heinrichs, J., Kreier, H.-P., Feldberg, K., Schmidt, A.R., Zhu, R.L., Shaw, B., Shaw, A.J. & Wissemann, V. (2011) Formalizing morphologically cryptic biological entities: New insights from DNA taxonomy, hybridization, and biogeography in the leafy liverwort *Porella platyphylla* (Jungermanniopsida, Porellales). *American Journal of Botany* 98: 1252–1262.
<http://dx.doi.org/10.3732/ajb.1100115>
- Heinrichs, J., Schäfer-Verwimp, A., Boxberger, J., Feldberg, K., Solórzano Kraemer, M. & Schmidt, A.R. (2014b) A fossil species of *Ceratolejeunea* (Lejeuneaceae, Porellales) preserved in Miocene Mexican amber. *The Bryologist* 117: 10–14.
<http://dx.doi.org/10.1639/0007-2745-117.1.010>
- Hillis, D.M. & Bull, J.J. (1993) An empirical test of bootstrapping as a method for assessing the confidence in phylogenetic analysis. *Systematic Biology* 42: 182–192.
<http://dx.doi.org/10.2307/2992540>
- Hooker, J.D. (1855) The botany of the Antarctic voyage of H.M. discovery ships Erebus and Terror in the Years 1839–1843 under the command of Captain Sir James Clark Ross. II. Flora Novae Zelandiae. Part 2: Flowerless Plants. Lovell Reeve, London.
<http://dx.doi.org/10.5962/bhl.title.16029>
- Larget, B. & Simon, D.L. (1999) Markov chain Monte Carlo algorithms for the Bayesian analysis of phylogenetic trees. *Molecular Biology and Evolution* 16: 750–759.
<http://dx.doi.org/10.1093/oxfordjournals.molbev.a026160>
- Lehmann, J.G.C. (1832) *Novarum et Minus Cognitarum Stirpium Pugillus IV addita enumeratione plantarum omnium in his pugillis descriptarum*. Meissner, Hamburg, 64 pp.
<http://dx.doi.org/10.5962/bhl.title.45011>
- Lehmann, J.G.C. (1834) *Novarum et Minus Cognitarum Stirpium Pugillus VI addita enumeratione plantarum omnium in his pugillis descriptarum*. Meissner, Hamburg, 66 pp.
<http://dx.doi.org/10.5962/bhl.title.45011>
- Mason-Gamer, R.J. & Kellogg, E.A. (1996) Testing for phylogenetic conflict among molecular data sets in the tribe Triticeae (Gramineae). *Systematic Biology* 45: 524–545.
<http://dx.doi.org/10.2307/2413529>
- Miller, M.A., Pfeiffer, W. & Schwartz, T. (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *Proceedings of the Gateway Computing Environments Workshop (GCE), 14 Nov. 2010, New Orleans, LA*: 1–8.
<http://dx.doi.org/10.1109/gce.2010.5676129>
- Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Hoehna, 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: 539–542.
<http://dx.doi.org/10.1093/sysbio/sys029>
- Schiffner, V. (1893) Hepaticae. In: Engler, A. & Prantl, K., *Die natürlichen Pflanzenfamilien* 1. Engelmann, Leipzig, pp. 97–141.
- Schuster, R.M. (1978) Studies on Venezuelan Hepaticae, II. *Phytologia* 39: 425–432.
- Schuster, R.M. (1992) The oil-bodies of the Hepaticae. II. Lejeuneaceae (Part 2). *Journal of the Hattori Botanical Laboratory* 72: 163–359.
- Sprengel, C.P.J. (1827) *Systema Vegetabilium, editio decima sexta* 4(2). Dieterich, Göttingen, pp. 1–410.
- Spruce, R.M. (1884) Hepaticae Amazonicae et Andinae. Tribus I: Jubuleae. *Transactions and Proceedings of the Botanical Society of Edinburgh* 15: 1–308.
- Stephani, F. (1890) Hepaticae africanae novae in insulis Bourbon, Maurice et Madagascar lectae. *Botanical Gazette* 15: 281–292.
<http://dx.doi.org/10.1086/326585>
- Swofford, D.L. (2000) PAUP*, phylogenetic analyses using parsimony (* and other methods), version 4.01b10. Sinauer Associates, Sunderland, Massachusetts.
- Vanden Berghe, C. (1948) Un nouveau genre d'Hépatiques *Evansiolejeunea* nov. gen. *Revue Bryologique et Lichenologique* 17: 86–90.
- Vanden Berghe, C. (1960) Hépatiques récoltées par le Dr. J.J. Symoens dans la région péri Tanganyikaise. *Bulletin de la Société Botanique de Belgique* 92: 111–138.
- Wilson, R., Gradstein, S.R., Schneider, H. & Heinrichs, J. (2007) Unravelling the phylogeny of Lejeuneaceae (Jungermanniopsida): evidence for four main lineages. *Molecular Phylogenetics and Evolution* 43: 270–282.
<http://dx.doi.org/10.1016/j.ympev.2006.10.017>
- Ye, W., Zhu, R.L., Shaw, J. & Gradstein, S.R. (2011) Proposal to conserve the name *Cheilolejeunea* against *Omphalanthus* (Lejeuneaceae). *Taxon* 60: 588–589.
- Zwickl, D.J. (2006) Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion. GARLI version 2.0 available online at <https://code.google.com/p/garli/>.