

## Jochen Heinrichs March 14, 1969 – April 22, 2018

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Jochen Heinrichs in 2015 (with the permission of Springer Nature)

Dr. Jochen Heinrichs, professor for Molecular Systematics of Lower Plants at the Ludwig-Maximilians-University of Munich, Germany, passed away on April 22, 2018. A committed scientist and warm-hearted, selfless person, Jochen was an internationally renowned bryologist, paleobryologist, and plant evolutionary biologist, whose premature death has been devastating to his family, friends, colleagues, and students.

Jochen earned his master's degree in biology from the University of Düsseldorf (1989–1996) with a thesis on the moss genus *Syntrichia* (formerly *Tortula*) and his doctoral degree from the University of Göttingen in 2002 under the supervision of S. Robbert Gradstein, with a thesis on “A taxonomic revision of *Plagiochila* sect. *Hylacoetes*, sect. *Adiantoideae* and sect. *Fuscoluteae* in the Neotropics with a preliminary subdivision of Neotropical *Plagiochilaceae* into nine lineages.” In 2001, Jochen was appointed

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curator of the Göttingen University Herbarium (GOET), and in 2007 he completed his habilitation, also at the University of Göttingen. During his tenure as curator, Jochen reorganized the collection and initiated the establishment of a digital herbarium, which he supervised until he left Göttingen for Munich in 2013 to become a professor for Molecular Systematics of Lower Plants at the Ludwig-Maximilians-University.

Jochen devoted most of his time to collecting and studying liverworts. To gather his study objects, he undertook several expeditions to faraway countries, including Bolivia, Costa Rica, and Ecuador. The liverworts he collected during these trips are kept in the BRYOPHYTA EXSICCATA GENERIS PLAGIOCHILAE in 6 fascicles (300 numbers). Moreover, Jochen accumulated an impressive private collection of bryophytes, which is now part of the herbaria of the University of Munich, M and MSB.

Jochen published more than 200 research articles, which makes him one of the most prolific contemporary bryologists worldwide. A complete bibliography can be found in Krings *et al.* (2018). His most influential contributions focus on the systematics, taxonomy, and molecular phylogeny of leafy liverworts (e.g., Heinrichs *et al.*, 2012a; Feldberg *et al.*, 2010, 2016; Carter *et al.*, 2016), the taxonomy of genus *Plagiochila* (e.g., Heinrichs *et al.*, 1998a,b, 2000; Heinrichs 2002a,b), and the reclassification of Lejeuneaceae (e.g., Wilson *et al.*, 2004; Heinrichs *et al.*, 2014a,b,c,d, 2015a,b; Bechteler *et al.*, 2016a,b), as well as cryptic speciation and diversification patterns in various lineages of bryophytes (e.g., Kreier *et al.*, 2010; Heinrichs *et al.*, 2011; Heinrichs *et al.*, 2013; Bechteler *et al.*, 2016c). For the best paper published in *The Bryologist* in 2005, Jochen was awarded the Sullivant Award of the American Bryological and Lichenological Society.

Characterizing Jochen solely as a liverwort bryologist does not do him justice, because his research spanned a diverse spectrum of topics and organisms ranging from fungi to flowering plants. By about 2008, Jochen became increasingly interested in amber inclusions, and his dedicated research in this field resulted in more than 40 papers on fossils of leafy liverworts, mosses, ferns, lichens and fungi (e.g., Hartl *et al.*, 2015; Heinrichs *et al.*, 2012b, 2015b,c, 2016a,b, 2017a,b; Kaasalainen *et al.*, 2015; Schneider *et al.*, 2016; Regalado *et al.*, 2016, 2017, 2018). He also placed the results of his fossil studies into a broader evolutionary context by incorporating fossil evidence into molecular-clock analyses and biogeographic and trait change reconstructions. These papers have opened new avenues of research and have set standards in the investigation of amber fossils and their incorporation in phylogenetics. One of the last manuscripts Jochen was working on is “A comprehensive assessment of the fossil record of liverworts in amber,” an invited contribution to the commemorative volume for the late Thomas N. Taylor (1937–2016). Unfortunately, Jochen did not live to see the published version of his paper (Heinrichs *et al.*, 2018).

Jochen served the scientific community as an editorial board member of several scientific journals, including *Plant Systematics and Evolution* (since 2009), *Cryptogamie*, *Bryologie* (since 2002), *Journal of Bryology* (since 2013), and *Nature Scientific Reports* (since 2014), and as Editor-in-Chief of the publication series *Bryophytorum Bibliotheca* (since 2005). His contributions to *Cryptogamie*, *Bryologie*, as well as his high expectations with regard to the quality of manuscripts, have increased the impact factor of the journal and are greatly appreciated by the Editor-in-chief, Denis Lamy. Jochen was also a member of the Committee for Bryophytes of the International Association for Plant Taxonomy (1999–2005) and an executive board member of the GeoBio-Center<sup>LMU</sup> (since 2016). His commitment to the

society of German-speaking plant biologists is evident from his long-term service as vice-chairman of the Systematics sections of the German Botanical Society (since 2008). All these services to the community, Jochen conducted conscientiously, with enthusiasm, and with distinction.

Friends, colleagues, and students will keep Jochen in grateful remembrance. We will miss Jochen as a mentor, colleague, and friend, and honor his legacy through the continuation of the work that he so loved.

## REFERENCES

- BECHTELER J., LEE G.E., SCHÄFER-VERWIMP A., PÓCS T., PERALTA D.F., RENNER M.A.M., SCHNEIDER H., HEINRICHS J., 2016a - Towards a monophyletic classification of Lejeuneaceae IV: reinstatement of *Allorgella*, transfer of *Microlejeunea aphanella* to *Vitalianthus* and refinements of the subtribal classification. *Plant systematics and evolution* 302: 187–201.
- BECHTELER J., LEE G.E., SCHÄFER-VERWIMP A., RENNER M.A.M., PERALTA D.F., HEINRICHS J., 2016b - Towards a monophyletic classification of Lejeuneaceae V: the systematic position of *Pictolejeunea*. *Phytotaxa* 280: 259–270.
- BECHTELER J., SCHÄFER-VERWIMP A., LEE G.E., FELDBERG K., PÓCS T., PERALTA D.F., RENNER M.A.M., HEINRICHS J., 2016c - Geographical structure and narrow species ranges in a pantropical clade of epiphyllous leafy liverworts. *Ecology and evolution* 7: 638–653.
- CARTER B.E., LARRAÍN J., MANUKJANOVÁ A., SHAW B., SHAW A.J., HEINRICHS J., de LANGE P., SULEIMAN M., THOUVENOT L., von KONRAT M., 2017 - Species delimitation and biogeography of a southern hemisphere liverwort clade, *Frullania* subgenus *Microfrullania* (Frullaniaceae, Marchantiophyta). *Molecular phylogenetics and evolution* 107: 16–26.
- FELDBERG K., VÁŇA J., LONG D.G., SHAW A.J., HENTSCHEL J., HEINRICHS J., 2010 - A phylogeny of Adelanthaceae (Jungermanniales, Marchantiophyta) based on nuclear and chloroplast DNA markers, with comments on classification, cryptic speciation and biogeography. *Molecular phylogenetics and evolution* 55: 293–304.
- FELDBERG K., VÁŇA J., KRUSCHE J., KRETSCHMANN J., PATZAK S.D.F., PÉREZ-ESCOBAR O.A., RUDOLF N.R., SEEFELDER N., SCHÄFER-VERWIMP A., LONG D.G., SCHNEIDER H., HEINRICHS J., 2016 - A phylogeny of Cephaloziaceae (Jungermanniopsida) based on nuclear and chloroplast DNA markers. *Organisms diversity and evolution* 16: 727–742.
- HARTL C., SCHMIDT A.R., HEINRICHS J., SEYFULLAH L.J., SCHÄFER N., GRÖHN C., RIKKINEN J., KAASALAINEN U., 2015 - Lichen preservation in amber: morphology, ultrastructure, chemofossils and taphonomic alteration. *Fossil records* 18: 127–135.
- HEINRICHS J., GRADSTEIN S.R., GROLLE R., 1998a - A revision of the neotropical species of *Plagiochila* (Dumort.) Dumort. (Hepaticae) described by Olof Swartz. *Journal of the Hattori botanical laboratory* 85: 1–32.
- HEINRICHS J., GROLLE R., DREHWALD U., 1998b - The conspecificity of *Plagiochila killarniensis* Pearson and *P. bifaria* (Sw.) Lindemb. (Hepaticae). *Journal of bryology* 20: 495–497.
- HEINRICHS J., ANTON H., GRADSTEIN S.R., MUES R., 2000 - Systematics of *Plagiochila* sect. *Glaucescentes* Carl (Hepaticae) from tropical America: a morphological and chemotaxonomical approach. *Plant systematics and evolution* 220: 115–138.
- HEINRICHS J., 2002a - A taxonomic revision of *Plagiochila* sect. *Hylacoetes*, sect. *Adiantoidae* and sect. *Fuscoluteae* in the Neotropics with a preliminary subdivision of Neotropical *Plagiochilaceae* into nine lineages. *Bryophytorum bibliotheca* 58 (Append. 1–5): 1–184.
- HEINRICHS J., 2002b - New synonyms in *Plagiochila* II. *Cryptogamie, Bryologie* 23: 351–353.
- 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.

- HEINRICH S J., BOMBOSCH A., FELDBERG K., KREIER H.P., HENTSCHEL J., ECKSTEIN J., LONG D., ZHU R.L., SCHÄFER-VERWIMP A., SCHMIDT A.R., SHAW B., SHAW A.J., VÁŇA J., 2012a - A phylogeny of the northern temperate leafy liverwort genus *Scapania* (Scapaniaceae, Jungermanniales). *Molecular phylogenetics and evolution* 62: 973–985.
- HEINRICH S J., REINER-DREHWALD M.E., FELDBERG K., von KONRAT M., HENTSCHEL J., VÁŇA J., NASCIMBENE P.C., GRIMALDI D.A., SCHMIDT A.R., 2012b - The leafy liverwort *Frullania* in the Cretaceous amber forest of Myanmar. *Review of palaeobotany and palynology* 169: 21–28.
- HEINRICH S J., DONG S., SCHÄFER-VERWIMP A., PÓCS T., FELDBERG K., CZUMAJ A., SCHMIDT A.R., REITNER J., RENNER M.A.M., HENTSCHEL J., STECH M., SCHNEIDER H., 2013 - Molecular phylogeny of the leafy liverwort *Lejeunea* (Porellales): Evidence for a Neotropical origin, uneven distribution of sexual systems and insufficient taxonomy. *PLoS ONE* 8: e82547.
- HEINRICH S J., CZUMAJ A., DONG S., SCHEBEN A., SCHÄFER-VERWIMP A., PERALTA D.F., FELDBERG K., SCHMIDT A.R., SCHNEIDER H., 2014a - The Bromeliaceae tank dweller *Bromeliophila* (Lejeuneaceae, Porellales) is a member of the *Cyclolejeunea-Prionolejeunea* clade. *Plant systematics and evolution* 300: 63–73.
- HEINRICH S J., DONG S., SCHÄFER-VERWIMP A., PERALTA D.F., FELDBERG K., SCHMIDT A.R., SCHNEIDER H., 2014b - Towards a monophyletic classification of Lejeuneaceae II: subtribes Pycnolejeuneinae and Xylolejeuneinae subtribe nov., transfer of *Otolejeunea* to Lepidolejeuneinae, and generic refinements. *Phytotaxa* 163: 61–76.
- HEINRICH S J., SCHÄFER-VERWIMP A., BOXBERGER J., FELDBERG K., SOLÓRZANO KRAEMER M.M., SCHMIDT A.R., 2014c - A fossil species of *Ceratolejeunea* preserved in Miocene Mexican amber. *The bryologist* 117: 10–14.
- HEINRICH S J., SCHÄFER-VERWIMP A., CZUMAJ A., DONG S., SCHEBEN A., FELDBERG K., SCHNEIDER H., 2014d - Towards a monophyletic classification of Lejeuneaceae I: subtribe Leptolejeuneinae subtribe nov. *Phytotaxa* 156: 165–174.
- HEINRICH S J., FELDBERG K., BECHTELER J., SCHEBEN A., CZUMAJ A., PÓCS T., SCHNEIDER H., SCHÄFER-VERWIMP A., 2015a - Integrative taxonomy of *Lepidolejeunea* (Porellales, Jungermanniopsida): ocelli allow the recognition of two neglected species. *Taxon* 64: 216–228.
- HEINRICH S J., KETTUNEN E., LEE G.E., MARZARO G., PÓCS T., RAGAZZI E., RENNER M.A.M., RIKKINEN J., SASS-GYARMATI A., SCHÄFER-VERWIMP A., SCHEBEN A., SOLÓRZANO KRAEMER M., SVOJTKA M., SCHMIDT A.R., 2015b - Lejeuneaceae (Marchantiophyta) from a species-rich taphocoenosis in Miocene Mexican amber, with a short survey of liverworts in amber. *Review of palaeobotany and palynology* 221: 59–70.
- HEINRICH S J., SCHEBEN A., LEE G.E., VÁŇA J., SCHÄFER-VERWIMP A., KRINGS M., SCHMIDT A.R., 2015c - Molecular and morphological evidence challenges the records of the extant liverwort *Ptilidium pulcherrimum* in Eocene Baltic amber. *PLoS ONE* 10: e0140977.
- HEINRICH S J., SCHEBEN A., BECHTELER J., LEE G.E., SCHÄFER-VERWIMP A., HEDENÄS L., SINGH H., PÓCS T., NASCIMBENE P.C., PERALTA D.F., RENNER M.A.M., SCHMIDT A.R., 2016a - Crown group Lejeuneaceae and pleurocarpus mosses in early Eocene (Ypresian) Indian Amber. *PLoS ONE* 11: e0156301.
- HEINRICH S J., SCHMIDT A.R., SCHÄFER-VERWIMP A., BAUERSCHMIDT L., NEUMANN C., GRÖHN C., KRINGS M., RENNER M.A.M., 2016b - Revision of the leafy liverwort genus *Radula* (Porellales, Jungermanniopsida) in Baltic and Bitterfeld amber. *Review of palaeobotany and palynology* 235: 157–164.
- HEINRICH S J., FELDBERG K., BECHTELER J., MÜLLER P., RENNER M.A.M., VÁŇA J., SCHÄFER-VERWIMP A., SCHMIDT A.R., 2017a - A fossil genus of the Frullaniaceae (Porellales, Jungermanniopsida) from the mid-Cretaceous of Myanmar. *Cretaceous research* 74: 223–226.
- HEINRICH S J., FELDBERG K., MÜLLER P., SCHÄFER-VERWIMP A., von KONRAT M., ILSEMANN B., KRINGS M., 2017b - *Frullania pinnata* spec. nov. (Frullaniaceae, Porellales), a new leafy liverwort in mid-Cretaceous Burmese amber from Myanmar. *Cretaceous research* 78: 56–60.
- HEINRICH S J., FELDBERG K., BECHTELER J., REGALADO L., RENNER M.A.M., SCHÄFER-VERWIMP A., GRÖHN C., MÜLLER P., SCHNEIDER H., KRINGS M., 2018 - A comprehensive assessment of the fossil record of liverworts in amber. In: Krings M., Harper C.J., Cuneo N.R., Rothwell G.W. (eds), *Transformative Paleobotany, papers to commemorate*

- the life and legacy of Thomas N. Taylor*. Burlington MA, London, San Diego CA, New York NY, Academic Press, Elsevier Inc., 213-252.
- KAASALAINEN U., HEINRICHS J., KRINGS M., MYLLIS L., GRABENHORST H., RIKKINEN J., SCHMIDT A.R., 2015 - Alectorioid morphologies in Paleogene lichens: new evidence and re-evaluation of the fossil *Alectoria succini* Mägdefrau. *PLoS ONE* 10: e0129526.
- KREIER H.P., FELDBERG K., MAHR F., BOMBOSCH A., SCHMIDT A.R., ZHU R.L., von KONRAT M., SHAW B., SHAW A.J., HEINRICHS J., 2010 - Phylogeny of the leafy liverwort *Ptilidium*: cryptic speciation and shared haplotypes between the Northern and Southern Hemispheres. *Molecular phylogenetics and evolution* 57: 1260–1267.
- KRINGS M., SCHNEIDER H., BECHTELER J., FELDBERG K., RENNER S.S., SCHÄFER-VERWIMP A., SCHMIDT A.R., 2018 - Jochen Heinrichs: March 14, 1969–April 22, 2018. *Plant systematics and evolution* (<https://doi.org/10.1007/s00606-018-1521-4>).
- SCHNEIDER H., SCHMIDT A.R., HEINRICHS J., 2016 - Burmese amber fossils bridge the gap in the Cretaceous record of polypod ferns. *Perspectives in plant ecology, evolution and systematics* 18: 70–78.
- REGALADO L., SCHMIDT A.R., MÜLLER P., KOBBERT M.J., SCHNEIDER H., HEINRICHS J., 2016 - The first fossil of Lindsaeaceae (Polypodiales) from the Cretaceous amber forest of Myanmar. *Cretaceous research* 72: 8–12.
- REGALADO L., SCHMIDT A.R., APPELHANS M.S., ILSEMANN B., SCHNEIDER H., KRINGS M., HEINRICHS J., 2017 - A fossil species of the enigmatic early polypod fern genus *Cystodium* (Cystodiaceae) in Cretaceous amber from Myanmar. *Scientific reports* 7: 14615.
- REGALADO L., SCHMIDT A.R., KRINGS M., BECHTELER J., SCHNEIDER H., HEINRICHS J., 2018 - Fossil evidence of eupolypod ferns in the mid-Cretaceous of Myanmar. *Plant systematics and evolution* 304: 1–13.
- WILSON R., GRADSTEIN S.R., HEINRICHS J., GROTH H., ILKIU-BORGES A.L., HARTMANN F.A., 2004 - Phylogeny of Lejeuneaceae: a cladistic analysis of chloroplast gene *rbcl* sequences and morphology with preliminary comments on the mitochondrial *nad4-2* spacer region. In: *Molecular Systematics of Bryophytes. Monographs in systematic botany from the Missouri botanical garden* 98: 189–202.