The leafy liverwort genus *Lejeunea* (Porellales, Jungermanniopsida) in Miocene Dominican amber

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Abstract

Lejeunea is a morphologically diverse subcosmopolitan genus of predominantly epiphytic leafy liverworts. We describe three *Lejeunea* fossils preserved in Miocene Dominican amber, *Lejeunea hamatiloba* sp. nov., *L. resinata* sp. nov. and *L. urbanoides* sp. nov., thereby increasing the *Lejeunea* fossil record to four species. The overall similarity of the fossils and extant species suggests the conservation of the generic composition of Caribbean epiphyte communities since the early Miocene, a pattern that was also confirmed for mosses and ferns.

Keywords: Caribbean; Cenozoic; fossil; Lejeuneaceae; Lejeuneae; Neogene

1. Introduction

With some 1,500 extant species (He & Zhu, 2011; Söderström et al., 2016), Lejeuneaceae represent the largest family of the Porellales, a predominantly epiphytic lineage of leafy liverworts with center of diversity in the humid tropics (Wilson et al., 2007; Feldberg et al., 2014). Lejeuneaceae are characterized by exclusively lateral branching, incubously inserted, complicate-bi(or tri-)lobed leaves, a lobule connected to the lobe with a long keel, a usually reduced stylus, bundled rhizoids, gynoecia with a single archegonium, usually beaked perianths, elaters attached to the capsule wall, 2-layered capsule valves, and spores with rosettes on the exine (Crandall-Stotler et al., 2009). Lejeuneaceae is currently subdivided in two subfamilies and three tribes of which Lejeuneae is by far the most speciose (Gradstein, 2013). Lejeuneaceae have a comprehensive Cenozoic fossil record (Heinrichs et al., 2015a), with the oldest Cenozoic fossil originating from early Eocene (Ypresian) Indian amber (Heinrichs et al., 2016a). Other Eocene fossils of Lejeuneaceae have been reported from Baltic (Grolle & Meister, 2004) and Rovno amber (Mamontov et al., 2013), from Oligocene Bitterfeld amber and from Miocene Mexican amber (Heinrichs et al., 2015a). However, the most important deposit for Lejeuneaceae fossils is the 15-20 million years old Miocene amber from the Dominican Republic (Itturalde-Vinent & McPhee, 1996). Representatives of the Fabaceae genus *Hymenaea* L. are considered to be the resiniferous trees of the Dominican amber forests (Poinar, 1991; Langenheim, 1995). To date, twenty one mostly extinct species of Lejeuneaceae have been described from this amber and assigned to sixteen extant genera (e.g., Grolle, 1984a, 1984b, 1993; Gradstein, 1993; Lee et al., 2015a, 2015b), thereunder two fossils of the speciose genus *Lejeunea* Libert, *Lejeunea* sp. (Reiner-Drehwald et al., 2012) and *Lejeunea miocenica* Heinrichs, Schäfer-Verwimp, M.A.M. Renner & G.E. Lee (Kasaaleinen et al., 2016). Here we describe two further species of *Lejeunea* based on inclusions from the Museum für Naturkunde at Berlin. These inclusions were found in the estate of the late hepaticologist Riclef Grolle (1934-2004) who annotated the material in 1988 but never

published a description of the fossils. We also propose a species name for a third *Lejeunea* fossil, earlier presented by Reiner-Drehwald et al. (2012).

2. Materials and methods

The ashlar-shaped, polished, and epoxy resin-embedded amber pieces MB.Pb.2016/1865 and 1866 were rediscovered in the legacy of Riclef Grolle in 2015. The inclusions were studied under a Carl Zeiss AxioScope A1 compound microscope equipped with a Canon 60D digital camera. Incident and transmitted light were used simultaneously. The images printed in Plates I and II are digitally stacked photomicrographic composites of up to 43 individual focal planes obtained using the software package HeliconFocus 6.7.1 for a better illustration of three-dimensional inclusions.

3. Results and discussion

3.1 Systematic palaeontology

Phylum Marchantiophyta

Class Jungermanniopsida

Order Porellales

Family Lejeuneaceae

Tribe Lejeuneae

Subtribe Lejeuneinae

Genus *Lejeunea* Libert

3.1.1 Lejeunea hamatiloba Lee, Schäfer-Verwimp, M.A.M. Renner & Heinrichs, sp. nov.

Plate I, 1; Plate II, 1, 2; Fig. 1

80 *Holotype*: Liverwort amber inclusion MB.Pb.2016/1865, Museum für Naturkunde at Berlin.

81 According to an accompanying label the inclusion was classified as “*Lejeunea hamatiloba* n.
82 sp.” by R. Grolle in 1988. However, since Grolle did not approve publication we do not
83 attribute the name to him (Recommendation 23.A.3.i ICN)

84 *Syninclusions*: Detritus, poorly preserved Lejeuneaceae fragments, possibly also belonging to
85 *L. hamatiloba*.

86 *Etymology*: The epithet refers to the slightly falcate leaf lobes (“hamatus” = curved)

87 *Diagnosis*: Lejeuneoid liverwort with ventral merophyte two cells wide; underleaves small,
88 asymmetrically ovate to ovate triangular, bifid, lobes sometimes slightly falcate, margins
89 entire and cuticle smooth.

90 *Description*: Sterile gametophyte consisting of a shoot with ca. 10 pairs of leaves that
91 branches off from a poorly preserved, 0.7 mm long shoot fragment with ca. 3 leaf fragments,
92 thus possibly representing a lateral branch rather than a main shoot, ca. 1.85 mm long, 0.32-
93 0.41 mm wide, uppermost sector not preserved. Stem straight, uppermost 0.25 mm curved,
94 25-33 µm in diameter, with a two cells wide ventral merophyte, cells rectangular, ca. 8-12 x
95 18-25 µm, thin-walled to slightly thick walled. Leaves incubously inserted, remote to
96 contiguous, wide spreading, lobes asymmetrically ovate to ovate-triangular, sometimes
97 slightly falcate, apical lobe cells often shrunken, giving the lobe apex a more falcate shape
98 compared to fully turgescient lobes, 150-200 µm long and 150-160 µm wide, margin entire,
99 apex rounded to bluntly triangular, dorsal margin arched, ventral margin straight to concave.
100 Cells in midlobe isodiametric to slightly elongate, ca. 18-28 x 16-25 µm, towards base more
101 elongate, ca. 20-30 x 14-25 µm, marginal cells subquadrate to rectangular, ca. 10-15 x 12-20
102 µm; walls thin, without or with small, triangular trigones, intermediate thickenings absent,
103 cuticle smooth. Leaf lobules ovoid, 80-105 µm long and 60-75 µm wide, ca. ½ -1/3 the leaf
104 lobe length, free margin involute, apical tooth unicellular, rounded to elongate, keels with

ventral margin of lobe straight to slightly arched, apex truncate. Underleaves remote, small, distant, ca. 50 x 50 µm, ca. 1-1.5x stem width, ca. 50% bifid, sinus possibly U-shaped, lobes lanceolate to triangular, with a conspicuously thin-walled, blunt terminal cell, margin entire.

3.1.2 *Lejeunea resinata* Lee, Schäfer-Verwimp, M.A.M. Renner & Heinrichs, sp. nov.

Plate I, 2; Plate II, 3, 4; Fig. 2

Holotype: Liverwort amber inclusion MB.Pb.2016/1866, Museum für Naturkunde at Berlin.

Etymology: The epithet refers to the preservation of the holotype in amber, a fossil resin.

Diagnosis: Lejeuneoid liverwort with ventral merophyte two cells wide; leaf lobes asymmetrically ovate to ovate oblong with a smooth cuticle; and underleaves bifid and with a tooth on each outer margin.

Description: Sterile gametophyte consisting of the upper portion of a shoot, with 7 pairs of leaves, ca. 1.4 mm long, 0.40-0.57 mm wide. Stem straight, 45-50 µm in diameter, with a two cells wide ventral merophyte. Leaves incubously inserted, distant to subimbricate, wide spreading, decreasing towards shoot apex, lobes asymmetrically ovate to ovate-oblong, 0.17-0.30 mm long and 0.15–0.30 mm wide, margin entire, apex broadly rounded, dorsal margin arched, ventral margin ±straight. Lobe cell walls incompletely preserved, thin walled, trigones small, intermediate thickenings obviously absent, cuticle smooth. Cells in midlobe and towards base isodiametric to slightly elongate, 15-25 x 12-22 µm, marginal lobe cells subquadrate to rectangular, ca. 10-20 µm x 8-15 µm. Leaf lobules ovoid, reduced in upper leaves, 65-80 µm long and 60-75 µm wide when well-developed, ca. 0.27-0.35 the leaf lobe length, free margin involute, apical tooth unicellular, short, rounded, keels with ventral margin of lobe straight, apex truncate. Underleaves distant, 90-110 µm long and 70-90 µm wide, 1.5-2.0 x stem width, 50% bifid, sinus U-shaped, with rhizoid disc, lobes triangular, ending in a single cell, outer margins with a pronounced, 1-2 cells long tooth.

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132 **3.1.3 *Lejeunea urbanioides*** Lee, Schäfer-Verwimp, M.A.M. Renner & Heinrichs, sp. nov.

133 Plate I, 3; Plate II, 5, 6; Fig. 3; Reiner-Drehwald et al., 2012 (as *Lejeunea* sp.)

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135 *Holotype*: Liverwort amber inclusion NMNH 372452, National Museum of Natural History of
136 the Smithsonian Institution.

137 *Etymology*: The epithet refers to the morphological similarity with the extant *Lejeunea*
138 *urbanii* (Stephani) Stephani.

139 *Diagnosis*: Lejeuneoid liverwort with a ventral merophyte two cells wide, suborbicular to
140 ovate leaf lobes with an apparently smooth cuticle and entire-margined, $\pm$ oval, bifid
141 underleaves.

142 *Description* (modified from Reiner-Drehwald et al., 2012): Sterile gametophyte with eleven
143 pairs of leaves, ca. 2.5 mm long, 350-550 μ m wide; with two branches of the *Lejeunea*-type,
144 these smaller than the main shoot. Stem straight, $\pm$ 40 μ m wide, probably with a two cells
145 wide ventral merophyte. Leaves distant to contiguous, obliquely to widely spreading; leaf
146 lobes suborbicular to ovate, $\pm$ plane, 270-350 μ m long, 180-250 μ m wide, margin entire, apex
147 rounded, plane, dorsal margin arched, ventral margin slightly arched to straight. Leaf cells $\pm$
148 isodiametric in upper half of leaf, slightly elongated towards base, cell walls not clearly
149 visible, but walls probably thin and trigones lacking or minute; cuticle obviously smooth.
150 Lobule uniformly developed in the seven younger pairs of leaves, the four pairs of leaves at
151 the basal third of the stem with reduced lobule; when well developed, lobule rounded-
152 rectangular to ovate, strongly inflated, 110 μ m long, 70-90 μ m wide, ca 1/3 to 1/4 the lobe
153 length, lateral margin slightly incurved, tooth elongated, probably one cell large, apical
154 margin straight to lunulate, keel slightly to strongly arched, keel at the union with ventral
155 margin of lobe slightly angled. Underleaves distant, appressed to the stem, $\pm$ oval, 60-70 μ m

wide, 90 μm long, ca. 1.5-2 x the stem width, ca. 50 % bifid, sinus V-shaped, margins entire, rarely toothed due to an angular cell, rhizoids not seen.

3.2 Classification and implications on the Miocene epiphyte communities

Ricolf Grolle, authority on amber inclusions of liverworts, kept the specimens from the Museum für Naturkunde at Berlin for some 20 years but did not publish his taxonomic conclusions. It is possible that these fossils formed the basis for his listing of “*Lejeunea* sp.” in a note on amber fossils of liverworts (Grolle, 1988) yet this cannot be inferred with certainty.

Lejeunea has a complex taxonomic history because representatives of several dozen genera were originally placed in this genus (Reiner-Drehwald, 1999). However, molecular phylogenies have progressively refined and improved the classification of Lejeuneaceae, through the necessary recircumscription of numerous genera to achieve natural monophyletic taxa (e.g. Wilson et al., 2007; Dong et al., 2013; Ye et al., 2015; Bechteler et al., 2016). The taxonomically cleaned-up genus *Lejeunea* is currently circumscribed by long-inserted leaves, divided or more rarely undivided underleaves, leaf lobules with an unreduced first tooth and a marginal hyaline papilla, small, segmented or homogeneous oil bodies, lack of ocelli, lejeuneoid innovations, unwinged female bracts and inflated perianths with 0-5 smooth or toothed wings, and sporophytes with a 5+4 elater arrangement (Heinrichs et al., 2013). Although several taxonomically relevant structures are not preserved in the sterile fossils, the preserved plant fragments express sufficient characters to facilitate generic assignment to *Lejeunea* without much doubt. These characters are, the two-celled ventral merophyte, the bifid underleaves, the long-inserted leaf-lobes, the absence of differentiated ocelli, and the relatively small, quadrate lobules with the first tooth prominent. In 2012, only a single sterile *Lejeunea* fossil was available from Dominican amber. Reiner-Drehwald et al. (2012)

demonstrated morphological overlap of the preserved structures with an extant Neotropical species complex including the Caribbean *Lejeunea urbanii* but abstained from a species-level classification. Current divergence time estimates based on DNA sequence variation and information from the fossil record generally do not rule out Miocene origins for extant *Lejeunea* species (Heinrichs et al., 2016). However, *Lejeunea* taxonomy is considered notoriously difficult (Heinrichs et al., 2013) and representatives of different main lineages have been placed in a single species prior to molecular investigation and careful reconsideration of morphological evidence (Renner et al., 2010, 2011). Aligning incompletely preserved Miocene liverwort inclusions with extant species may thus be misleading and should only be considered if (a) divergence time estimates do not contradict such treatment (Heinrichs et al., 2015) and (b) vegetative and generative structures are preserved in ultrastructural fidelity allowing accurate comparison of extinct and extant material.

Understanding morphologically separable *Lejeunea* fossils is enhanced if they have names and therefore we classify them to species level. Up to now, the fossil record of *Lejeunea* comprises four species, all from Dominican amber, as the Mexican amber fossil *Lejeunea palaeomexicana* Grolle was recently transferred to *Ceratolejeunea* (Spruce) J.B. Jack & Stephani (Lee et al., 2015b). Although reproductive structures were not preserved, the four species can be separated by discrete character states. *Lejeunea resinata* is the only fossil *Lejeunea* species with lateral teeth on the underleaves (Plate II, 4; Fig. 2, A, D, E), a known but relatively uncommon feature among extant species (e.g., Reiner-Drehwald & Mustelier-Martínez, 2004). *Lejeunea hamatiloba* differs from the other fossil *Lejeunea* species by its small, deeply bifid underleaves (Plate II, 2; Fig. 1, C); its somewhat falcate leaf lobes (Plate I, 1) may to some extent result from the embedding process. *Lejeunea urbaniioides* has larger underleaves (Plate II, 6) and a more uniform leaf shape with rounded lobe apices (Plate I, 3). The recently described *Lejeunea miocenica* (Kaasalainen et al., 2017) has variably shaped leaf lobes with obtuse to acute apices, an asperulate cuticle and sometimes crenate lobe margins.

We do not provide a determination key since further *Lejeunea* species may turn up in Dominican amber.

The number of extant *Lejeunea* species is still unclear and should lie between “more than 100” (Gradstein & Costa, 2003) and 300 species (Lee, 2013) of which some 40 occur in the West Indies (e.g., Schäfer-Verwimp & Pócs, 2009; Schäfer-Verwimp, 2010; Lavocat Bernard & Schäfer-Verwimp, 2011; Söderström et al., 2011; Schäfer-Verwimp & van Melick, 2016). Our findings suggest high *Lejeunea* species diversity in the Miocene amber forests of the Caribbean. So far, Dominican amber fossils of liverworts were assigned to extant genera (Heinrichs et al., 2015a). The overall similarity of these fossils and extant species suggests the conservation of the generic composition of Caribbean epiphyte communities since the early Miocene, a pattern that was also confirmed for mosses (Frahm & Newton, 2005) and ferns (Lóriga et al., 2014; Schneider et al., 2015). Similar observations have been made for the Paleogene Baltic and Bitterfeld amber forests with a comparable diversity of liverworts (Grolle & Meister, 2004). The epiphytic liverwort diversity of these forests was dominated by *Frullania* Raddi rather than by Lejeuneaceae, possibly in consequence of the different phorophytes in the Dominican and European amber forests. The main resin producing trees of the Baltic and Bitterfeld amber forests were gymnosperms (Sadowski et al., 2016; Wolfe et al., 2016) which may have been disadvantageous for colonization by a diverse Lejeuneaceae flora, whereas the resin producing *Hymenaea* trees of the Dominican amber forests (Poinar, 1991) hosted more than 20 Lejeuneaceae species but only few *Frullania* species of the polyphyletic subg. *Diastaloba* Spruce (Heinrichs & Schmidt, 2010). It is possible that further Lejeuneaceae occurred on non-resiniferous angiosperm trees in the mixed forests of the Baltic region and Bitterfeld, however we are unable to present direct evidence. It is also possible that a different forest structure and climate influenced the composition of the local cryptogamic communities.

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References

- Bechteler, J., Lee, G.E., Schäfer-Verwimp, A., Pócs, T., Peralta, D.F., Renner, M.A.M., Schneider, H., Heinrichs J., 2016. 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.
- Crandall-Stotler, B., Stotler, R.E., Long, D.G., 2009. Phylogeny and classification of the Marchantiophyta. *Edinburgh Journal of Botany* 66, 155–198.
- Dong, S., Schäfer-Verwimp, A., Pócs, T., Feldberg, K., Czumaj, A., Schmidt, A.R., Schneider, H., Heinrichs, J., 2013. Size doesn't matter – recircumscription of *Microlejeunea* (Lejeuneaceae, Porellales) based on molecular and morphological evidence. *Phytotaxa* 85, 41–55.
- Feldberg, K., Schneider, H., Stadler, T., Schäfer-Verwimp, A., Schmidt, A.R., Heinrichs, J., 2014. Epiphytic leafy liverworts diversified in angiosperm-dominated forests. *Scientific Reports* 4, 5974.

260

261 Frahm, J.-P., Newton, A.E., 2005. A new contribution to the moss flora of Dominican amber.
262 The Bryologist 108, 526–536.

263

264 Gradstein, S.R., 1993. New fossil Hepaticae preserved in amber of the Dominican Republic.
265 Nova Hedwigia 57, 353–374.

266

267 Gradstein, S.R., 2013, A classification of Lejeuneaceae (Marchantiophyta) based on
268 molecular and morphological evidence. Phytotaxa 100, 6–20.

269

270 Gradstein, S.R., Costa, D.P., 2003. The Hepaticae and Anthocerotae of Brazil. Memoirs of the
271 New York Botanical Garden 87, 1–318.

272

273 Grolle, R., 1984a. *Bryopteris* und *Cyclolejeunea* fossil in dominikanischem Bernstein. Journal
274 of the Hattori Botanical Laboratory 56, 271–280.

275

276 Grolle, R., 1984b. *Cyrtolejeunea suzannensis* spec. nov. ein weiteres fossiles Lebermoos in
277 dominikanischem Bernstein. Cryptogamie Bryologie-Lichénologie 5, 27–32.

278

279 Grolle, R., 1988. Bryophyte fossils in amber. Bryological Times 47, 4–5.

280

281 Grolle, R., 1993. Ein autözisches Lebermoos mit Perianth in Dominikanischem Bernstein:
282 *Drepanolejeunea eogena* spec. nov. Nova Hedwigia 57, 375–380.

283

284 Grolle, R., Meister, K., 2004a. The liverworts in Baltic and Bitterfeld amber. Weissdorn, Jena.

285

286 He, Q., Zhu, R.-L., 2011. Spore output in selected species of Lejeuneaceae. *Cryptogamie,*
 287 *Bryologie* 32, 107–112.

288

289 Heinrichs, J., Schmidt, A.R., 2010. An inclusion of *Frullania* subgen. *Diastaloba* s. l.
 290 (Frullaniaceae, Porellales) in Dominican amber. *Tropical Bryology* 31, 91–94.

291

292 Heinrichs, J., Dong, S., Schäfer-Verwimp, A., Pócs T., Feldberg, K., Czumaj, A., Schmidt,
 293 A.R., Reitner, J., Renner, M.A.M., Hentschel, J., Stech, M., Schneider, H., 2013a. Molecular
 294 phylogeny of the leafy liverwort *Lejeunea* (Porellales): Evidence for a Neotropical origin,
 295 uneven distribution of sexual systems and insufficient taxonomy. *PloS ONE* 8, e82547.

296

297 Heinrichs, J., Kettunen, E., Lee, G.E., Marzaro, G., Pócs, T., Ragazzi, E., Renner, M.A.M.,
 298 Rikkinen, J., Sass-Gyarmati, A., Schäfer-Verwimp, A., Scheben, A., Solórzano Kraemer, M.,
 299 Svojtka, M., Schmidt, A.R., 2015a. Lejeuneaceae (Marchantiophyta) from a species-rich
 300 taphocoenosis in Miocene Mexican amber, with a short survey of liverworts fossilized in
 301 amber. *Review of Palaeobotany and Palynology* 221, 59–70.

302

303 Heinrichs, J., Scheben, A., Lee, G.E., Vána, J., Schäfer-Verwimp, A., Krings, M., Schmidt,
 304 A.R., 2015b. Molecular and morphological evidence challenges the records of the extant
 305 liverwort *Ptilidium pulcherrimum* in Eocene Baltic amber. *PLoS ONE* e0140977.

306

307 Heinrichs, J., Scheben, A., Bechteler, J., Lee, G.E., Schäfer-Verwimp, A., Hedenäs, L., Singh,
 308 H., Pócs, T., Nascimbene, P.C., Peralta, D.F., Renner, M.A.M., Schmidt, A.R., 2016. Crown
 309 group Lejeuneaceae and pleurocarpous mosses in early Eocene (Ypresian) Indian Amber.
 310 *PloS ONE* 11: e0156301.

311
312
313
314
315
316
317
318
319
320
321
322
323
324
325
326
327
328
329
330
331
332
333
334
335
336

Iturralde-Vinent, M.A., MacPhee R.D.E., 1996. Age and paleogeographical origin of Dominican amber. *Science* 273, 1850–1852.

Kaasalainen, U., Heinrichs, J., Renner, M.A.M., Hedenäs, L., Schäfer-Verwimp, A., Lee, G.E., Ignatov, M.S., Rikkinen, J., Schmidt, A.R., 2017. A Caribbean epiphyte community preserved in Miocene Dominican amber. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* (in press).

Langenheim, J.H., 1995. The biology of amber-producing trees: Focus on case studies of *Hymenaea* and *Agathis*. *ACS Symposium Series* 617, 1–31.

Lavocat-Bernard, E., Schäfer-Verwimp, A., 2011. Checklist of the bryophytes of the Guadeloupe archipelago and Martinique (French West Indies). *Cryptogamie, Bryologie* 32, 233–272.

Lee, G.E., 2013. A systematic revision of the genus *Lejeunea* Lib. (Marchantiophyta: Lejeuneaceae) in Malaysia. *Cryptogamie, Bryologie* 34, 381–484.

Lee, G.E., Bechteler, J., Schäfer-Verwimp, A., Heinrichs, J., 2015a. *Microlejeunea miocenica* sp. nov. (Porellales, Jungermanniopsida), the first fossil of a subcosmopolitan genus in Miocene Dominican amber. *Review of Palaeobotany and Palynology* 222, 16–21.

Lee, G.E., Schäfer-Verwimp, A., Schmidt, A.R., Heinrichs, J., 2015b. Transfer of the Miocene *Lejeunea palaeomexicana* to *Ceratolejeunea*. *Cryptogamie Bryologie* 36, 335–341.

337 Lóriga, J., Schmidt, A.R., Moran, R.C., Feldberg, K., Schneider, H., Heinrichs, J., 2014. The
338 first fossil of a bolbitidoid fern belongs to the early-divergent lineages of *Elaphoglossum*
339 (*Dryopteridaceae*). *American Journal of Botany* 101, 1466–1475.

340

341 Mamontov, Y., Heinrichs, J., Schäfer-Verwimp, A., Ignatov, M.S., Perkovski, E.E., 2013.
342 Hepatics from Rovno amber (Ukraine), 2. *Acrolejeunea ucrainica* sp. nov. *Arctoa* 22, 93–96.

343

344 Poinar, G.O. Jr., 1991. *Hymenaea protera* sp. n. (*Leguminosae*, *Caesalpinioideae*) from
345 Dominican amber has African affinities. *Experientia* 47, 1075–1082.

346

347 Reiner-Drehwald, M.E., 1999. Catalogue of the genus *Lejeunea* Lib. (*Hepaticae*) of Latin
348 America. *Bryophytorum Bibliotheca* 54, 1–101.

349

350 Reiner-Drehwald, M.E., Mustelier Martínez, K., 2004. On *Lejeunea multidentata*, a new
351 species from Cuba. *Journal of Bryology* 26, 103–106.

352

353 Reiner-Drehwald, M.E., Schmidt, A.R., Heinrichs, J., 2012. The genus *Lejeunea* in Miocene
354 amber from the Dominican Republic. *Cryptogamie, Bryologie* 33, 33–38.

355

356 Renner, M.A.M., Brown, E.A., Wardle, G.M., 2010. The *Lejeunea tumida* species group
357 (*Lejeuneaceae*, *Jungermannniopsida*) in New Zealand. *Australian Systematic Botany* 23, 443–
358 462.

359

360 Renner, M.A.M., Brown, E.A., Wardle, G.M., 2011. The *Lejeunea tumida* species group is
361 positively polyphyletic (*Lejeuneaceae*: *Jungermannniopsida*). *Australian Systematic Botany* 24,
362 10–18.

363

364 Sadowski, E.-M., Schmidt, A.R., Kunzmann, L., Gröhn, C. Seyfullah, L., 2016. *Sciadopitys*
365 cladodes from Eocene Baltic amber. Botanical Journal of the Linnean Society 180, 258–268.

366

367 Schäfer-Verwimp, A., 2010. A checklist of the liverworts and hornworts of Dominica, West
368 Indies. Cryptogamie, Bryologie 31, 313–415.

369

370 Schäfer-Verwimp, A., Pócs, T., 2009. Contributions to the hepatic flora of the Dominican
371 Republic, West Indies. Acta Botanica Hungarica 51, 367–425.

372

373 Schäfer-Verwimp, A., van Melick, H.M.H., 2016. A contribution to the bryophyte flora of
374 Jamaica. Cryptogamie Bryologie 37, 305–348.

375

376 Schneider, H., Schmidt, A.R., Nascimbene, P.C., Heinrichs, J., 2015. A new Dominican
377 amber fossil of the derived genus *Pleopeltis* confirms generic stasis in the epiphytic fern
378 diversity of the West Indies. Organisms, Diversity and Evolution 15, 277–283.

379

380 Söderström, L., Hagborg, A., Váňa, J., von Konrat, M., 2011. Land of wood and water. A
381 checklist of liverworts and hornworts of Jamaica. The Bryologist 114, 67–91.

382

383 Söderström, L., Hagborg, A., von Konrat, M., Bartholomew-Began, S., Bell, D., Briscoe, L.,
384 Brown, E., Cargill, D.C., Cooper, E.D., Costa, D.P., Crandall-Stotler, B.J., Dauphin, G.,
385 Engel, J.J., Feldberg, K., Glenney, D., Gradstein, S.R., He, X., Heinrichs, J., Hentschel, J.,
386 Ilkiu-Borges, A.L., Katagiri, T., Konstantinova, N.A., Larraín, J., Long, D.G., Nebel, M.,
387 Pócs, T., Puche, F., Reiner-Drehwald, M.E., Renner, M.A.M., Sass-Gyarmati, A., Schäfer-
388 Verwimp, A., Segarra-Moragues, J.G., Stotler, R.E., Sukkharak, P., Thiers, B.M., Uribe, J.,

Váňa, J., Villarreal, J.C., Wigginton, M., Zhang, L., Zhu, R.L., 2016. World checklist of
hornworts and liverworts. *PhytoKeys* 59, 1–828.

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.

Wolfe, A., McKellar, R.C., Tappert, R., Sodhi, R.N.S., Muehlenbachs, K., 2016. Bitterfeld
amber is not Baltic amber: Three geochemical tests and further constraints on the botanical
affinities of succinite. *Review of Palaeobotany and Palynology* 225, 21–32.

Ye, W., Gradstein, S.R., Shaw, A.J., Shaw, B., Ho, B.C., Schäfer-Verwimp, A., Pócs, T.,
Heinrichs, J., Zhu, R.L., 2016. Phylogeny and classification of Lejeuneaceae subtribe
Cheilolejeuneinae (Marchantiophyta) based on nuclear and plastid molecular markers.
Cryptogamie Bryologie 36, 313–333.

Captions

Plate I: Habit of the three new *Lejeunea* species in ventral view [scale bars = 150 µm]

1 Holotype of *Lejeunea hamatiloba* sp. nov. (MB.Pb.2016/1865)

2 Holotype of *Lejeunea resinata* sp. nov. (MB.Pb.2016/1866)

3 Holotype of *Lejeunea urbanioides* sp. nov. (NMNH 372452)

413 Plate II: Leaves (1, 3, 5) and underleaves (2, 4, 6) of the three new *Lejeunea* species in ventral
414 view [scale bars 1, 3, 4, 5, 6 = 50 μm ; 2 = 20 μm]

415 1, 2 Holotype of *Lejeunea hamatiloba* sp. nov. Arrowhead in 2 points to underleaf lobe.

416 Note the thin-walled terminal cell (MB.Pb.2016/1865).

417 3, 4 Holotype of *Lejeunea resinata* sp. nov. Arrowhead in 4 points to underleaf lobe. Note
418 that some marginal cells are collapsed (MB.Pb.2016/1866).

419 5, 6 Holotype of *Lejeunea urbanioides* sp. nov. Arrowhead in 2 points to underleaf lobe.
420 (NMNH 372452)

421

422 Figure 1: Reconstruction of the gametophyte of *Lejeunea hamatiloba* based on the holotype.

423 (A) Gametophyte in ventral view, (B) Portion of shoot with two leaves in ventral view, (C)

424 Portion of shoot showing one leaf and a deeply bifid underleaf in ventral view, (D) Median

425 leaf lobe cells.

426

427 Figure 2: Reconstruction of the gametophyte of *Lejeunea resinata* based on the holotype. (A)

428 Gametophyte in ventral view, (B) Median leaf lobe cells, (C) Portion of stem with leaf lobule,

429 (D, E) Underleaves.

430

431 Figure 3: Reconstruction of the gametophyte of *Lejeunea urbanioides* based on the holotype.

432 (A) Gametophyte in ventral view, (B) Portion of stem with two pairs of leaves and two

433 underleaves, (C) Portion of stem with leaf lobule.