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The genus *Lejeunea* in Miocene amber from the Dominican Republic

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Abstract – A sterile liverwort inclusion in a piece of Miocene amber from the Dominican Republic is described and assigned to the extant genus *Lejeunea*. The inclusion resembles a complex of extant American *Lejeunea* species (*L. angusta*, *L. aphanes*, *L. cladogyna*, *L. urbanii*) that share autoecy, a small size, and ovate to obovate leaf lobes with rounded apices. A definite assignment to one of these species is impossible due to inacessibility of several diagnostically relevant characters such as perianths and oil bodies. The inclusion is clearly different from the extinct *Lejeunea palaeomexicana*; hence at least two different *Lejeunea* species occured in the Miocene of Middle America.

Amber / Jungermanniopsida / Lejeuneaceae / Neogene / Porellales

INTRODUCTION

Cenozoic ambers are a valuable source of bryophyte inclusions and provide evidence for the presence of numerous extant genera of leafy liverworts in the Eocene and Oligocene (Grolle & Meister, 2004). Most Miocene amber inclusions of liverworts come from the Dominican Republic (Gradstein, 1993; Heinrichs & Schmidt, 2010). Some of these inclusions do not only match the morphology of extant genera but also of extant species, e.g., *Mastigolejeunea auriculata* (Wilson) Schiffn. and *Stictolejeunea squamata* (Willd. *ex* F.Weber) Schiffn., and demonstrate morphological stability of liverworts over a period of 15-20 million years (Gradstein, 1993).

Lejeuneaceae is the most species rich family of liverworts, and includes some 1000 extant species (Wilson *et al.*, 2007). Representatives of this family are also common in Dominican amber and the genera *Archilejeunea*, *Blepharolejeunea*, *Bryopteris*, *Ceratolejeunea*, *Cheilolejeunea*, *Cyclolejeunea*, *Cyrtolejeunea*, *Drepanolejeunea*, *Lopholejeunea*, *Marchesinia*, *Mastigolejeunea*, *Neurolejeunea*, *Prionolejeunea* and *Stictolejeunea* have been documented (Grolle,

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1984a, 1984b, 1990, 1993a, 1993b; Gradstein, 1993; Ye & Zhu, 2010). Grolle (1988) and Gradstein (1993) also list the genus *Lejeunea*, but related inclusions have not yet been described and illustrated.

In the course of a study of amber collections from the Dominican Republic housed at the National Museum of Natural History of the Smithsonian Institution, we recognized a liverwort inclusion that we assign to the genus *Lejeunea*. We illustrate and describe this inclusion, and discuss relationships to extinct and extant *Lejeunea* species.

MATERIALS AND METHODS

The amber piece is part of the Dominican amber collection of the National Museum of Natural History of the Smithsonian Institution (coll. no. NMNH 372452). Iturralde-Vinent and MacPhee (1996) demonstrated that Dominican amber is early to middle Miocene in age (15 to 20 million years old). Representatives of the Fabaceae genus *Hymenaea* are considered to be the resin-bearing trees (Poinar, 1991; Langenheim, 1995).

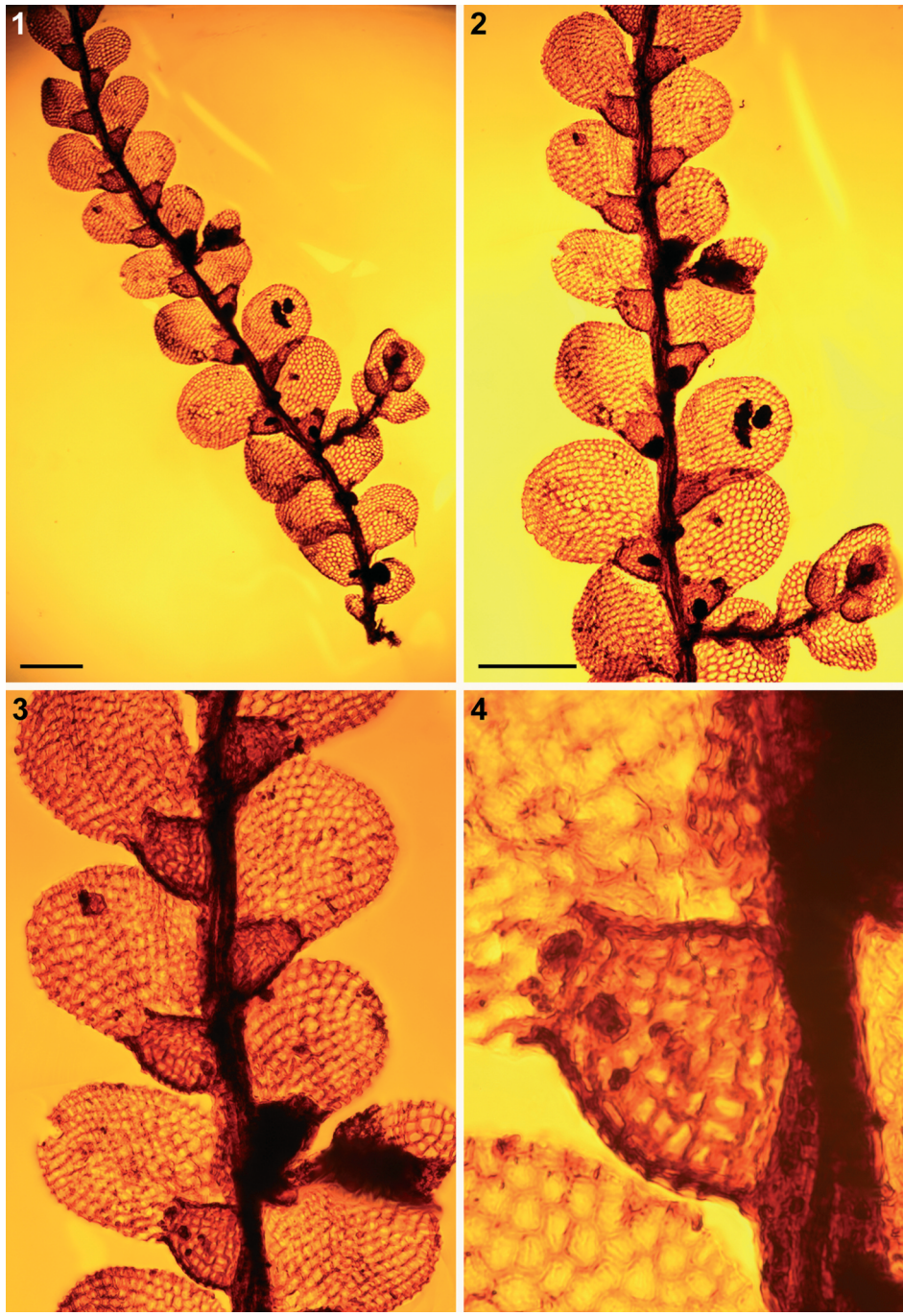
The putative fossil liverwort was investigated using a transmitted-light microscope (Carl Zeiss AxioScope A1) equipped with a Canon 450D digital camera. In some instances, incident and transmitted light were used simultaneously. In order to better illustrate the three-dimensional inclusion, the photomicrographs were combined from 20 to 40 optical sections using the software package HeliconFocus 4.45.

The amber inclusion was compared to herbarium specimens including types (BM, G, GOET, JE, MANCH, NY, S, US, W, YU), and to the fossil *Lejeunea palaeomexicana* Grolle from the Miocene of Mexico (Grolle, 1984c).

RESULTS AND DISCUSSION

Lejeunea sp. **Figs 1-5**

Description: Sterile shoot with eleven pairs of leaves, ca 2.5 mm long, 350-550 µm wide; with two branches of the *Lejeunea*-type, these smaller than the main shoot. Stem straight, ± 40 µm wide, probably with a two cells wide ventral merophyte. Leaves distant to contiguous, obliquely to widely spreading; leaf lobes suborbicular to ovate, ± plane, 270-350 µm long, 180-250 µm wide, margin entire, apex rounded, plane, dorsal margin arched, ventral margin slightly arched to straight. Leaf cells +/– isodiametric in upper half of leaf, slightly elongated towards base, cell walls not clearly visible, but walls probably thin and trigones lacking or minute. Lobules uniformly developed in the seven younger pairs of leaves, the four pairs of leaves at the basal third of the stem with reduced lobules; when well developed, lobules rounded-rectangular to ovate, strongly inflated, 110 µm long, 70-90 µm wide, *ca* 1/3 to 1/4 the lobe length, lateral margin slightly incurved, tooth elongated, probably one cell large, apical margin straight to lunulate, keel slightly to strongly arched, keel at the union with ventral margin of lobe slightly angled. Underleaves distant, appressed to the stem, ± oval, 60-70 µm wide, 90 µm long, ca 1.5-2 × the stem width, *ca* 50% bifid, sinus V-shaped, margins entire, rarely toothed due to an angular cell, rhizoids not seen. Androecia and gynoecia unknown.

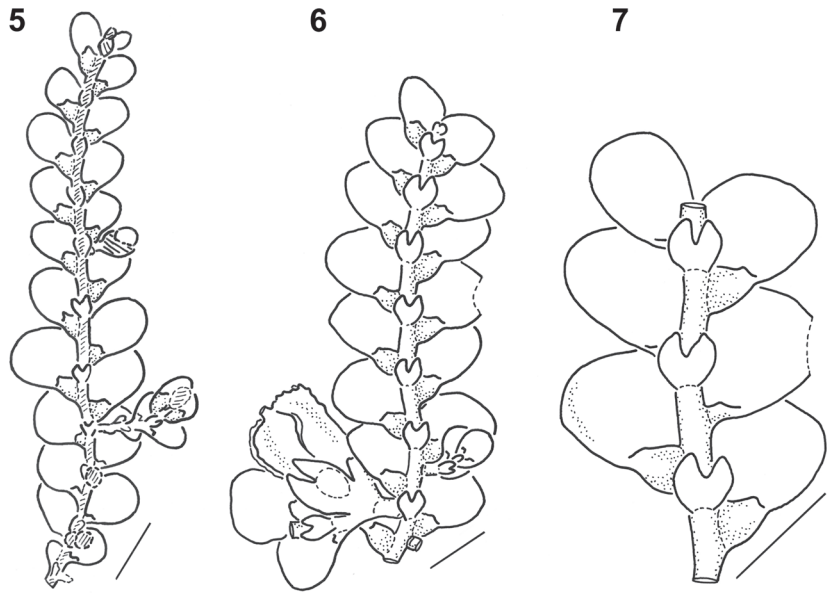


Figs 1-4. Photomicrographs of the ventral side of *Lejeunea* sp. from Miocene Dominican amber (coll. no. NMNH 372452). **1.** Shoot with two branches. **2-3.** Higher magnification images of shoot sectors. **4.** Detail of leaf lobule and margin of adjacent underleaf. Scale bars represent 200 µm in 1 and 2, and 50 µm in 3 and 4.

Lejeunea is one of the largest genera of Lejeuneaceae (Reiner-Drehwald, 1999). A worldwide monograph is still lacking, however, numerous recent revisions allow for a better understanding of the geographical distribution and morphological variation of *Lejeunea* species (e.g., Zhu & Cheng, 2008; Ilkiu-Borges, 2005; Reiner-Drehwald & Schäfer-Verwimp, 2008). The genus is widespread throughout the tropics and in warm-temperate regions, and includes numerous epiphytes, especially in the lowlands and lower montane areas. To date, only two fossil species of *Lejeunea* have been published, *Lejeunea* sp. in a list of liverwort inclusions in amber from the Dominican Republic (Grolle, 1988, without description or specimen citation) and *Lejeunea palaeomexicana* from Mexican amber (Grolle, 1984c).

Lejeunea species are usually characterized by thin stems with a two cells wide ventral merophyte, bifid underleaves, cell walls without brownish pigmentation, leaf lobules with a proximal hyaline papilla, and gynoecia with lejeuneoid innovations.

The morphological features observed in the Miocene amber inclusion (Figs 1-5) match perfectly those of a group of extant neotropical species of *Lejeunea*, namely *L. angusta* (Lehm. & Lindenb.) Mont., *L. aphanes* Spruce, *L. cladogyna* A.Evans and *L. urbanii* (Steph.) Spruce. These species share a small size (0.4-1.0 mm wide shoots), autoecy and leaves with ± ovate to obovate lobes and ± rounded apices. *Lejeunea angusta* and *L. aphanes* are both widely distributed in the Neotropics. The rather poorly known *Lejeunea urbanii* (Figs 6-7) is until now only known from the Dominican Republic and from Dominica;



Figs 5-7. Comparison of the Dominican amber fossil with *Lejeunea urbanii* (Steph.) Spruce. **5.** Reconstruction of the Miocene *Lejeunea* sp. in ventral view (hatched areas represent dark sectors in the amber inclusion). **6-7.** Extant *Lejeunea urbanii* (holotype specimen, G 026041) in ventral view with perianth (6) and portion of a sterile shoot sector (7). Scale bars represent 250 µm.

Lejeunea cladogyna occurs in the Southern U.S.A. and in the West Indies (Evans, 1918; Schuster, 1980 [*Lejeunea aphanes* as *L. autoica*]; Stephani 1985 [icon no. 2666]; Reiner-Drehwald 2000 [*L. aphanes* as *L. filipes*]).

The diagnostic characters of these *Lejeunea* species are found in the lobule apex, leaf surface (smooth to papillose), underleaf cells, oil bodies and perianths. These features can not be determined in the small and sterile shoot of the amber inclusion here described. Therefore, it is not possible to decide if the inclusion belongs to one of these extant *Lejeunea* species or if it represents another taxon. The extinct *Lejeunea palaeomexicana* differs from the new inclusion by the peculiar leaf lobe with a notch at the junction of the ventral leaf lobe margin with the lobule keel (Grolle, 1984c, fig. 1). It is clearly different at the species level, and morphologically not closely related to the newly described inclusion.

Accordingly, our study provides evidence for a second Miocene species of *Lejeunea*. However, a species assignment of this *Lejeunea* morphotype should await the detection of generative structures.

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