

***Frullania cretacea* sp. nov.
(Porellales, Jungermanniopsida), a leafy liverwort
preserved in Cretaceous amber from Myanmar**

Jörn HENTSCHEL^{a, b}, Alexander R. SCHMIDT^c, Jochen HEINRICHS^{a*}

^aGeorg-August-Universität Göttingen, Abt. Systematische Botanik,
Albrecht-von-Haller-Institut für Pflanzenwissenschaften,
Untere Karspüle 2, 37073 Göttingen, Germany

^b« Friedrich Schiller Universität » Jena,
Institut für Spezielle Botanik mit Herbarium Haussknecht und Botanischem Garten,
Fürstengraben 1, 07737 Jena, Germany

^cGeorg-August-Universität Göttingen, Courant Research Centre Geobiology,
Goldschmidtstrasse 3, 37077 Göttingen, Germany

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Abstract – The extinct *Frullania cretacea* sp. nov. is described based on a gametophytic plant fragment preserved in Upper Albian amber from Myanmar (Burma). The fragment contains of a portion of a branched shoot with mamilllose leaf lobes and campanulate lobules forming watersacs. The Mesozoic species is assumed to be an early representative of the *Frullania* crown group and tentatively assigned to *F.* subg. *Frullania*.

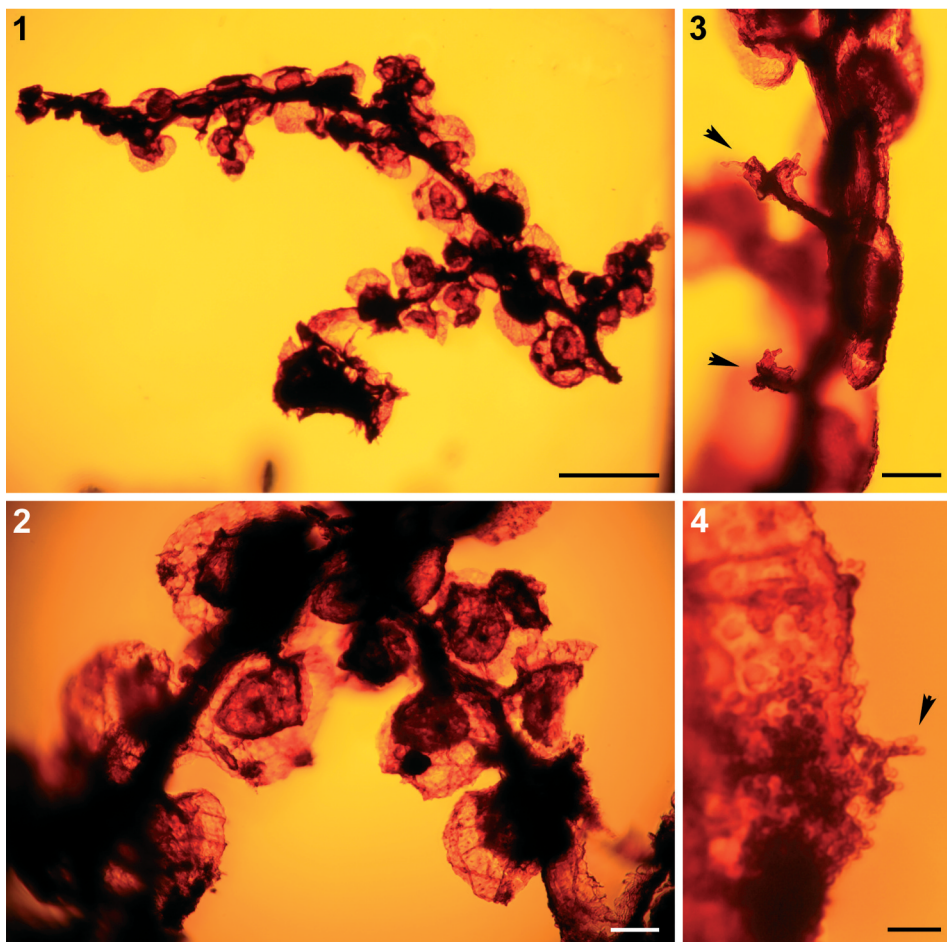
Porellales / *Frullania* / Cretaceous / amber / fossil / liverwort

INTRODUCTION

Cenozoic ambers such as that from the Baltic and Bitterfeld, Dominican Republic and Mexico are well known sources of excellently preserved liverwort inclusions (Grolle, 1984; Gradstein, 1993; Grolle & Meister, 2004). In contrast, Mesozoic amber deposits usually do not contain liverwort inclusions. Recently Grimaldi *et al.* (2002) reported the first liverwort fragments in Cretaceous amber from Myanmar (Burma), of which one was tentatively assigned to the extant genus *Frullania* Raddi. Both biostratigraphic data obtained from the amber-bearing sediment and the amber inclusions indicate a mid-Cretaceous age of the amber (Grimaldi *et al.*, 2002; Cognato & Grimaldi, 2009). Based on a recent re-investigation of the amber locality, Cruickshank & Ko (2003) suggest an Upper Albian age of the sediment. Thus, the recently found liverwort inclusions have an age of approximately 100 million years.

Amber inclusions of liverworts are a valuable source of information on the morphological evolution of this early diverging land plant lineage (Qiu, 2008), and may be used to calibrate chronograms based on DNA sequences (Renner, 2005).

* Correspondence and reprints: jheinri@uni-goettingen.de

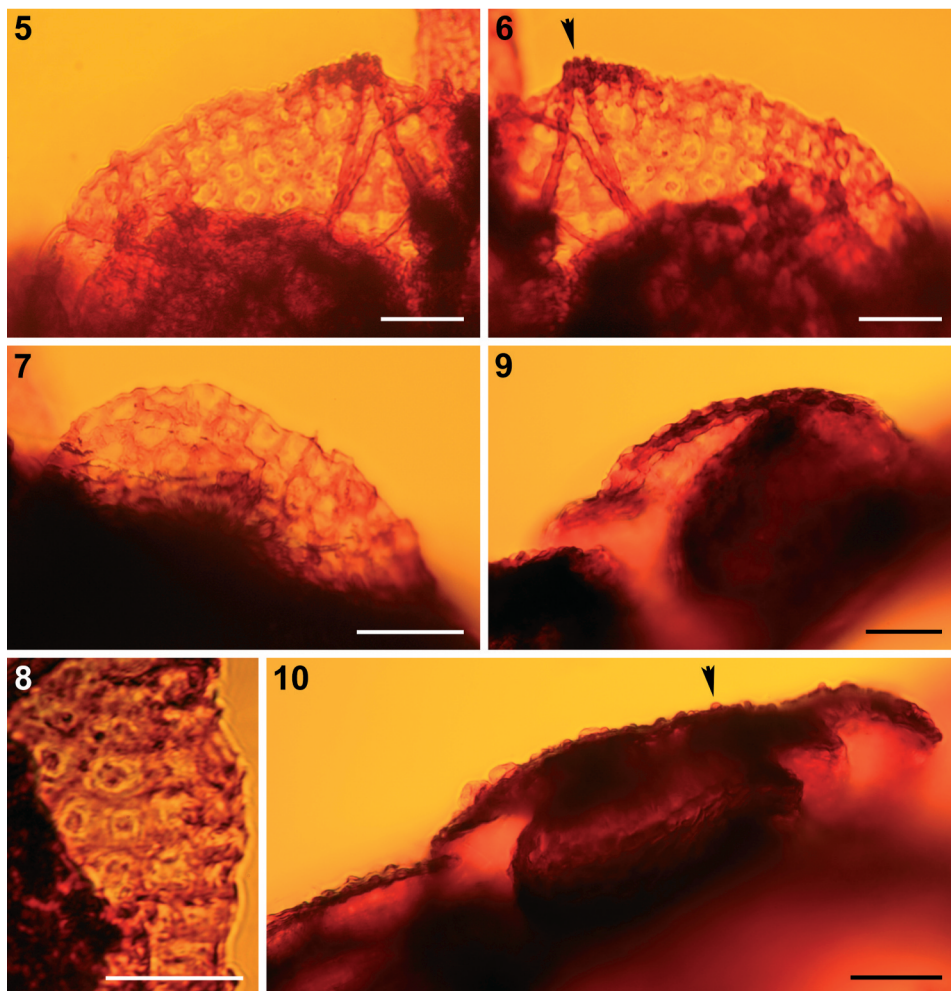


Figs 1-4. Habitus of *Frullania cretacea* sp. nov. **1.** Overview over the whole inclusion from the ventral side. **2.** Detail of the ventral side with highly visible watersacs. **3.** Rhizoids in bundles (arrows) at the apical part of the main branch. **4.** Detail of a leaf margin with a mycelium of epiphytic sooty moulds forming aerial hyphae protruding off the leaf (arrow). Scale bars represent 500 μm in 1, 100 μm in 2 and 3, and 20 μm in 4.

In the framework of ongoing studies on the phylogeny and historical biogeography of leafy liverworts (Hartmann *et al.*, 2006; Heinrichs *et al.*, 2007; Wilson *et al.*, 2007) we examined the amber inclusion assigned to *Frullania*. Here, we describe this fossil as a new species, *Frullania cretacea* J. Hentschel, A.R. Schmidt *et* J. Heinrichs.

MATERIAL AND METHODS

The ground and polished amber piece of ca $10 \times 9 \times 5$ mm size is housed in the American Museum of Natural History in New York (collection number AMNH B-011). The original amber piece was prepared by embedding in epoxy



Figs 5-10. Cellular details of *Frullania cretacea* sp. nov. **5-6.** Mature leaf in dorsal (5) and ventral (6) view with covering hyphae of sooty moulds (arrow). **7.** Small apical leaf from the ventral side. **8.** Detail of figure 6. Note the visible border of the cell walls and the mamillae. **9.** Lateral view of leaf, the dark area in the fore ground is a watersac. **10.** Leaf and watersac in lateral view, the dorsal leaf surface with mamillae. A well-exposed mamilla is indicated by the arrow. Scale bars represent 50 µm.

resin under vacuum using the method described by Nascimbene & Silverstein (2000). The inclusion of the liverwort was investigated using a transmitted-light microscope (AxioScope A1 with long-distance objectives, Carl Zeiss, Germany) equipped with a Canon 450D digital camera (Canon Inc., Tokyo, Japan). In order to better illustrate the three-dimensional oriented inclusion, some photomicrographs were combined using the software package HeliconFocus 4.45. Figure 7 was obtained from three, Figure 9 from four, Figures 1 and 10 from six, and Figures 2 and 3 from nine optical sections.

The morphological characters of the AMNH B-011 were compared to extant *Frullania* species, as well as to species described from Paleogene amber inclusions (Grolle, 1985). The supraspecific classification of AMNH B-011 was based on the results of Hentschel et al. (2009).

RESULTS

Frullania cretacea J. Hentschel, A.R. Schmidt et J. Heinrichs, spec. nov.

Holotype: amber inclusion in sample AMNH B-011 from Myanmar [Figs 1-10].

Diagnosis: Sterile, 3.12 mm long, irregularly branched gametophyte fragment, stem diameter *ca* (40-)50-(60) μm , rhizoids in bundles, up to *ca* 200 μm long, leaf lobes imbricate to remote, dorsally extending *ca.* 1/2-1 the stem width beyond the farther edge of stem, slightly concave to nearly flat, entire, *ca* 300-350 μm long and 230-300 μm wide, broadly rounded, cells in upper half of lobe subisodiametric, *ca* 15-27 \times 15-20 μm in diameter, each dorsally with a distinctly protruding, central mamilla, mamillae up to 5 μm high, with a diameter of 6.5-8.0 μm ; cells walls possibly with subnodulose trigones; mature leaf lobules campanulate, forming *ca* 140-220 μm long and 110-160 μm broad watersacs. Underleaves not observed, possibly aborted.

Syninclusions of the liverwort are *ca* 20 tricolpate pollen grains, two branched plant hairs resembling those of the extant fern genus *Dicranopteris* Bernh., indeterminable remnants of insects and several insect faecal pellets. Furthermore, the surface of the liverwort is sometimes densely covered by sooty moulds, an epiphytic group of saprotrophic fungi, mostly belonging to the Capnodiales (Ascomycota). A tiny remnant of the substrate (probably tree bark) is also attached to one branch of the liverwort.

DISCUSSION

Frullania with an estimated number of 300 to 375 morphologically-circumscribed extant species (Schuster, 1992; Gradstein et al., 2001) is the largest genus of Porellales, a mainly epiphytic lineage of leafy liverworts (Heinrichs et al., 2005). For a long time *Frullania* taxonomy has been based nearly exclusively on morphological evidence. Recently, Hentschel et al. (2009) presented a phylogeny of *Frullania* that was based on four molecular markers and about 170 specimens. They proposed a well supported, subcosmopolitan clade that corresponds to *Frullania* subgen. *Frullania*. Schuster (1992) defined members of *F.* subgen. *Frullania* [as *F.* subgen. *Trachycolea* Spruce] by their galeate to rounded-quadrate lobules. This type of lobule precisely characterises the Mesozoic *F. cretacea*. The majority of extant *Frullania* species has smooth leaf surfaces, however, several species are provided with dorsally mamilliose leaves similar to those of *F. cretacea*. Examples from *F.* subgen. *Frullania* include *F. hamaticoma* Steph. (Hattori, 1979) and forms of *F. ericoides* (Nees) Mont. (Kamimura, 1961, as *F. squarrosa* var. *verrucosa* Kamim.). Several species of *F.* subgen. *Microfrullania* (R.M. Schust.) R.M. Schust.

[*F. parhamii* R.M. Schust., *F. caledonica* (R.M. Schust.) R.M. Schust. (Schuster, 1970, 1992)] have mamilllose dorsal leaf surfaces, as has *F. hattorii* von Konrat & Braggins (von Konrat & Braggins, 2003) of *F.* subgen. *Diastaloba* Spruce “I” (Hentschel *et al.*, 2009). The diffuse distribution of *Frullania* species with mamilllose dorsal leaf surfaces indicates that this character state is homoplastic and not applicable to place a species in one of the main clades of *Frullania*.

The gametophyte morphology of *F. cretacea* fully matches the range of morphological variation of extant *Frullania*. Thus, we assume the Mesozoic species to be an early representative of the *Frullania* crown group. The lack of perianths or androecia prevents us from a more extensive comparison of *F. cretacea* to extant species. However, based on the the campanulate watersacs observed in *F. cretacea* we tentatively assign this species to *F.* subgen. *Frullania*.

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