

New evidence on the taxonomic position of the Eocene *Jungermannites contortus* (Jungermanniales: Lejeuneaceae)

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Résumé – *Jungermannites contortus* Göpp. & Berendt, avec des gynoécies non fertilisées, des périanthes mûrs et un sporophyte portant une capsule ouverte, est décrit et illustré sur la base de nouvelles inclusions dans l'ambre de l'Eocène. Les auteurs concluent à son appartenance au genre *Mastigolejeunea* (Spruce) Schiffn., sous le nom *M. contorta* (Göpp. & Berendt) Gradst. & Grolle, comb. nov. (= *Lejeunea alifera* Casp., syn. nov.).

Eocène / *Jungermannites* / Lejeuneaceae / Ptychanthoideae / *Mastigolejeunea contorta* comb. nov. / ambre

Abstract – New amber inclusions of the Eocene *Jungermannites contortus* Göpp. & Berendt with unfertilized gynoecia, mature perianth and sporophyte bearing an opened capsule are described and figured. They require its attribution to *Mastigolejeunea* (Spruce) Schiffn. as *M. contorta* (Göpp. & Berendt) Gradst. & Grolle, comb. nov. (= *Lejeunea alifera* Casp., syn. nov.).

Eocene *Jungermannites* / Lejeuneaceae / Ptychanthoideae / *Mastigolejeunea contorta* comb. nov. / Baltic and Bitterfeld amber

The first record of liverworts in Baltic amber, and in amber at all, was published by Berendt (1845), who described three species under *Jungermannites* Göpp., among them *J. contortus* Göpp. & Berendt. Its holotype fortunately still exists in the amber collection of the 'Museum für Naturkunde' in Berlin (inv.-no. 1979/479) and has been studied by Grolle (1982).

Already Caspary (1887) recognized the relationship of *J. contortus* to the holostipous Lejeuneaceae and transferred it to *Phragmicoma* Dumort., a catchall of the majority of the holostipous Lejeuneaceae at that time.

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Since then, the knowledge on the holostipous Lejeuneaceae or Ptychanthoideae has grown considerably. Today within the Ptychanthoideae at least two dozen genera are distinguished, which comprise more than one hundred species, predominantly occurring in the tropics and subtropics. In Europe they are represented merely by the strictly Atlantic *Marchesinia mackaii* (Hook.) Gray and the African-Neotropical *Acanthocoleus aberrans* (Lindenb. & Gottsche) Kruijt (in Europe confined to the Azores).

It was challenging to find out whether the fossil *Jungermannites contortus* could be aligned with any of the extant genera of the Ptychanthoideae. Though the holotype of *J. contortus* proved to be well preserved and visible, it is sterile as are all available specimens in 1982. Its placement in *Trocholejeunea* Schiffn. by Grolle (1982) as *T. contorta* (Göpp. & Berendt) Gradst. & Grolle was merely based on the overall similarity of the sterile gametophyte to the extant *T. sandvicensis* (Gottsche) Mizut. Both have a lobule with (3)4 small, 1(2)-celled, often incurved teeth. A lobule with similar dentation, however, occurs also in other genera of the Ptychanthoideae, e.g.:

Acrolejeunea torulosa (Lehm. & Lindenb.) Schiffn. (see Gradstein, 1994: Fig. 33)

Brachiolejeunea laxifolia (Taylor) Schiffn. (see Gradstein, 1994: Fig. 45)

Frullanoides densifolia Raddi (see Gradstein, 1994: Fig. 35)

Marchesinia brachiata (Sw.) Schiffn. (see Gradstein, 1994: Fig. 29)

Mastigolejeunea indica Steph. (see Mizutani, 1987: Fig. 8; Thiers & Gradstein, 1989: Fig. 17)

Odontolejeunea lunulata (F.Web.) Schiffn. (see Gradstein, 1994: Fig. 54)

Recently, some inclusions of *J. contortus* in Baltic and Bitterfeld amber were discovered, which bear unfertilized gynoecia (private collection *Grabenhorst Le60*: Figs. 1e, 2c; private collection *Gröhn 2098*: Figs. 1c-d, 2a), perianth ('Museum für Naturkunde Berlin' inv.-no. 1997/15 (ser. 8/5a): Grolle (1989) Abb. 1c-d), and a perianth with exerted opened capsule (private collection *Kutscher Ku-98H02a*: Figs. 1a-b, 2b). These findings require a reconsideration of the taxonomic position of the species, for which we enjoyed a fruitful discussion with S. R. Gradstein.

In all four female specimens the gynoecia are innovated on both sides. This definitely excludes *Acrolejeunea* (Spruce) Schiffn., whose gynoecia lack innovation.

The recurved valves of the opened capsule (*Kutscher Ku-98H02a*) exclude *Brachiolejeunea* (Spruce) Schiffn. and *Odontolejeunea* (Spruce) Schiffn., whose valves of the opened capsule are incurved (Weis 2001).

In *Grabenhorst Le60* the upper portion of the subgynoecial underleaf is partly torn off "by preparation of the nature" (Fig. 2c). Thus, it becomes fortunately recognizable that the turn of segmentation and the sequence of underleaf/leaf of the left innovation branch is *not* pycnolejeuneoid. Therefore *Frullanoides* Raddi and *Marchesinia* Gray are excluded, whose gynoecial innovations are pycnolejeuneoid.

As candidates for the generic placement of *J. contortus* only remain *Mastigolejeunea* (Spruce) Schiffn. and *Trocholejeunea* Schiffn.

Knowledge about *Trocholejeunea* has been much improved by Mizutani (1989), who carefully described and illustrated its three extant species. Contrary to all other Lejeuneaceae their gynoecial innovation is frullanioid, i.e. the gynoecium is innovated by a branch of the *Frullania* type. The three species are palaeotropical in distribution and \pm widespread in tropical and subtropical Asia, Melanesia and Oceania. Indeed, Schuster (1992: 201) shifted three neotropical

species of *Frullanoides* Raddi to *Trocholejeunea*. But because of their pycnolejeuneoid gynoecial innovation, blackish pigmentation and different seta anatomy they should be excluded from *Trocholejeunea* (Gradstein & Costa, 2003).

Mastigolejeunea is a larger genus, whose species in Asia have been carefully studied by Mizutani (1987), those in Australasia by Thiers & Gradstein (1989), and those in the Neotropics by Gradstein (1994). The gynoecial innovation of *Mastigolejeunea* is lejeuneoid, contrary to the frullanioid one of *Trocholejeunea*.

In lejeuneoid gynoecial innovation the lobule of the innermost female bract is subtended by a branch of the *Radula* type, whereas in frullanioid gynoecial innovation the lobule of the innermost gynoecial bract is replaced by a branch of the *Frullania* type, i.e. lacking. Fortunately in *Grabenhorst Le60* the presence of the lobules of the innermost gynoecial bracts are recognizable (grey-marked in Fig. 2c). This demonstrates lejeuneoid gynoecial innovation. Therefore *J. contortus* has to be attributed to *Mastigolejeunea*, instead of *Trocholejeunea* where it has been placed hitherto.

The perianth of *J. contortus* is trigonous by three sharp straight far down reaching plicae, with two additional short very shallow straight plicae on ventral side, in accordance with most species of *Mastigolejeunea*. On the contrary, the perianth of the three extant *Trocholejeunea* species is pluriplicate by 6-10 equal, \pm inflated, undulate plicae. Thus the attribution of *J. contortus* to *Mastigolejeunea* is also supported by its perianth.

In the four specimens of *J. contortus* with gynoecia all are innovated on both sides and the innovating branches originate at the base of the innermost gynoecial bracts, in accordance with *Mastigolejeunea*. As shown by Mizutani (1989), in *T. sandvicensis* (Gottsche) Mizut. considerable variation in the origin of the innovating gynoecial branches and their number exists (six types were distinguished by him). A similar variation, though less so, is observed by him in the two other extant species of this genus. The constancy of gynoecial innovation on both sides at the base of the innermost gynoecial bracts favour the attribution of *J. contortus* to *Mastigolejeunea*, too.

The specimen *Ku-98H02a* has been handed to G. Weis for study of a fossil capsule of the Lejeuneaceae. She detected that the cells of the inner stratum of the capsule have plurifenestrate incrassations, an important character of extant Ptychanthoideae. For any reason, however, Weis (2001: 112-113) treated her findings under "fossile Kapsel von *T.[rocholejeunea] sandvicensis*". This identification is no doubt wrong. Even in sterile state the fossil *J. contortus* and the extant *T. sandvicensis* (Gottsche) Mizut. are clearly distinct by the lobule, as has already been pointed out by Grolle (1982) and could be confirmed by all specimens which have been studied so far. In addition the perianth of *J. contortus* proved to be sharply trigonous with straight narrow keels. By this the latter is drastically distinct from all three extant *Trocholejeunea* species including *T. sandvicensis*, which all have perianths with 6-10 \pm undulate, \pm inflated equal keels.

After study of several additional specimens since Grolle (1982, 1985) we are now convinced that *Lejeunea alifera* Casp. is merely a weak branch of *J. contortus*, whose underleaves are torn off, as already supposed by Grolle (1985).

The new findings require the following recomposing:

Mastigolejeunea contorta (Göpp. & Berendt) Gradst. & Grolle, *comb. nov.*
Figs 1-2

≡ *Jungermannites contortus* Göpp. & Berendt in G. C. Berendt (ed.), *Die im Bernstein befindlichen organischen Reste der Vorwelt* 1(1): 114. 1845. ≡ *Phragmicoma contortum* (Göpp. & Berendt) Casp., *Schriften Physik.-Ökon. Ges.*

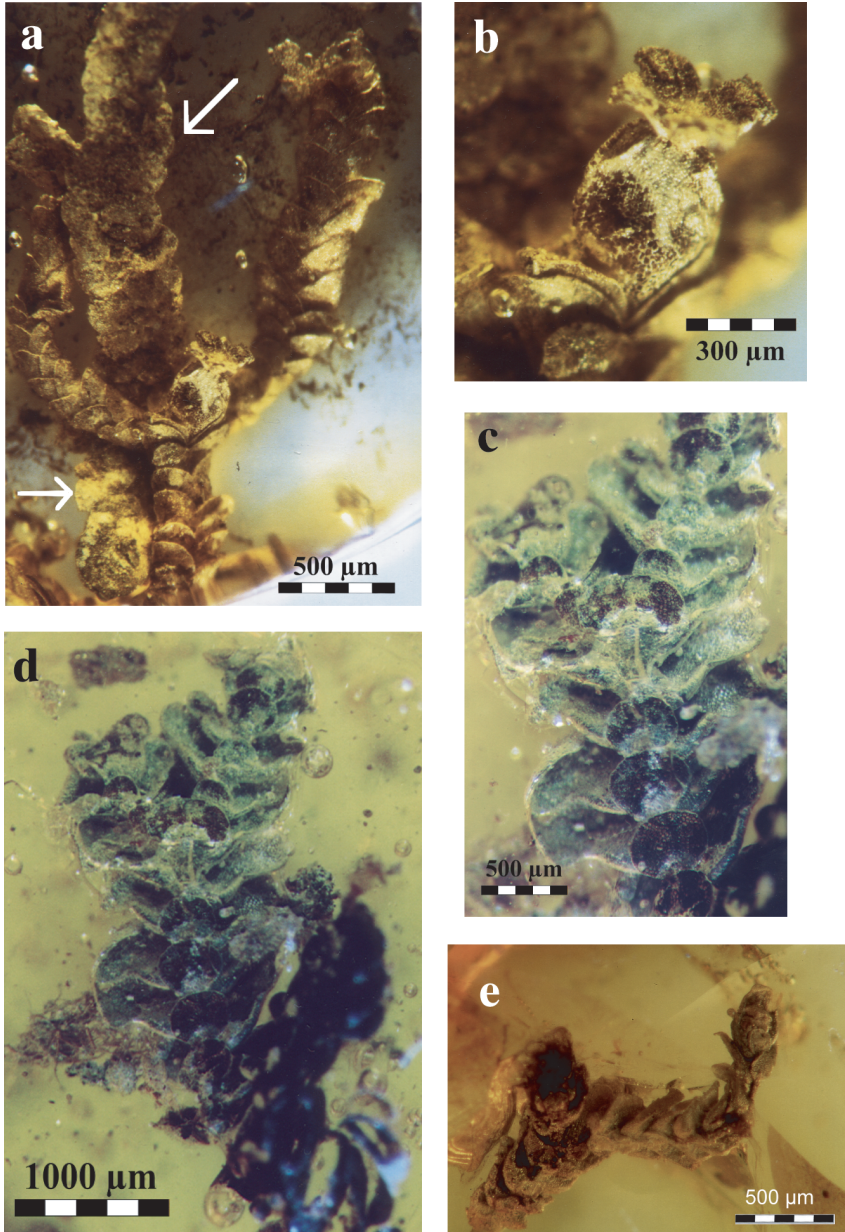


Fig. 1. *Mastigolejeunea contorta* (Göpp. & Berendt) Gradst. & Grolle: **a** : plant with perianth, exserted opened capsule and gynoecial innovations on both sides, dorsal view (accompanied by *Frullania schumannii* (Casp.) Grolle, see arrows). **b** : sector of the former showing perianth and exserted opened capsule enlarged. **c** : plant with undamaged unfertilized gynoecium and gynoecial innovations on both sides, ventral view. **d** : sector of the former showing gynoecium and innovations, enlarged. **e** : plant with partly damaged unfertilized gynoecium and innovations on both sides, ventral view. (a-b micrographs from *Kutscher Ku-98H02a*, c-d from *Gröhn 2098*, e from *Grabenhorst Le60*).

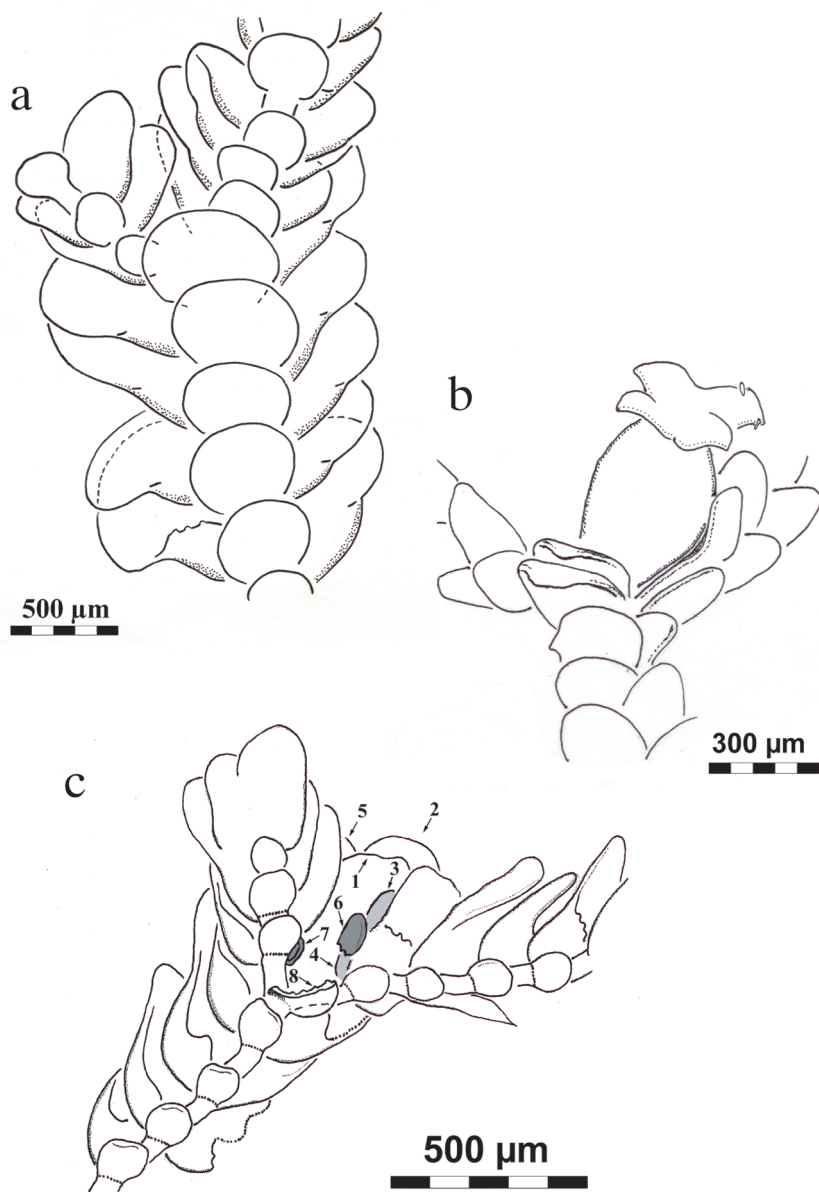


Fig. 2. *Mastigolejeunea contorta* (Göpp. & Berendt) Gradst. & Grolle: **a** : same plant sector as Fig. 1d with undamaged unfertilized gynoecium and gynoecial innovations on both sides, ventral view. **b** : same plant sector as Fig. 1b with perianth and exserted opened capsule perianth, dorsal view. **c** : enlarged plant sector of Fig. 1e with partly damaged unfertilized gynoecium and innovations on both sides, ventral view. (a drawn from Gröhn 2098, b from Kutscher Ku-98H02a, c from Grabenhorst Le60). [1 = innermost female bracteole, 2 = lobe of the innermost female bract, 3-4 = lobule parts (grey-marked) of the former, 5 = lobe of the second innermost bract, 6 = ruptured displaced part of lobule (grey-marked) of the former, 7 = small basal part of the same lobule (grey-marked) in its natural place, 8 = subgynoecial underleaf, whose upper part is partly torn off].

Königsberg 27: 2. 1887. ≡ *Trocholejeunea contorta* (Göpp. & Berendt) Gradst. & Grolle, *J. Hattori Bot. Lab.* 51: 178. 1982. – **Holotype**: Amber collection of the Museum für Naturkunde Berlin inv.-no. 1979/479 (Coll. Berendt) !

= *Lejeunea alifera* Casp., *Abhandl. Königl. Preuss. Landesanst.* N. F. 4: 29, 1907; *syn. nov.* – **Holotype**: Amber collection of the Physikalisch-Ökonomische Gesellschaft at the former Königsberg no. 134 (destroyed).

= *Trocholejeunea sandvicensis* sensu G. Weis, *Bryophytorum Bibliotheca* 57: 112-113. 2001; *syn. nov.* [*non* (Gottsche) Mizut.].

For further synonyms see Grolle (1982).

Illustrations

Berendt (1845): Tafel 6, figs 40-41 as *Jungermannites contortus*.

Caspary (1887): Tafel 1, Bild 6 as *Phragmicoma contortum*; Tafel 1, Bild 5 as *Phragmicoma magnistipulatum*; Tafel 1, Bild 7 as *Phragmicoma suborbiculatum*; Tafel 1, Bild 8 as *Phragmicoma suborbiculatum* var. *sinuatum*.

Caspary & Klebs (1907): Tafel 2, Bild 16, 16a-c as *Phragmicoma contortum*; Tafel 2, Bild 15, 15a-c as *Phragmicoma magnistipulatum*; Tafel 2, Bild 17, 17a-c as *Phragmicoma suborbiculatum*; Tafel 2, Bild 18, 18a-c as *Phragmicoma suborbiculatum* var. *sinuatum*; Tafel 3, Bild 24a-c as *Lejeunea alifera*.

Grolle (1982) : Figs 1a-b, Tables 1-7 as *Trocholejeunea contorta*.

Grolle (1985): Fig. 2a as *Lejeunea alifera*.

Grolle (1989): Abb. 1c-d as *Trocholejeunea contorta*.

Most of the extant *Mastigolejeunea* species have a lobule with a single, angular, usually straight tooth, which is 1-6 cells long and 1-2 cells wide at base. Exceptions are the neotropical *M. innovans* (Spruce) Steph. (Gradstein 1994) and the Asian-Australian *M. indica* Steph. (Mizutani, 1987; Thiers & Gradstein, 1989). The lobules of the former have on main axis 2-3 blunt, triangular teeth and those of the latter 3-4 straight triangular teeth, which are (4)6 cells long and (4)6 cells wide at base. Thus the fossil *M. contorta* clearly differs from all extant species of the genus by lobules with (3)4 small, 1(2)-celled, often incurved teeth.

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