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New record of bryophytes from Baltic and Bitterfeld amber

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ABSTRACT. Twenty one specimens from ten species of mosses are reported from Baltic and Bitterfeld amber, all of them already known from the Eocene. Four of them (*Campylopodiella himalayana*, *Ctenidium capillifolium*, *Haplocladium angustifolium*, *Hypnodontopsis mexicana*) are extant species which still exist, mainly in E- and SE-Asia. Two species (*Brotherella tortifolia* and *Hypnodontopsis casparyi*) are extinct species of extant genera. Four species (*Hypnites subflagellaris*, *Hypnites complanatus*, *Hypnites flagelliferus*, *Sematophyllites planus*) are pleurocarpous mosses described in form genera. *Sematophyllites planus* J.-P. Frahm is described here as new. The new combination *Hypnites subflagellaris* (Caspary & G.A.Klebs) J.-P. Frahm is made for *Dicranites subflagellaris* Caspary & G.A.Klebs to express that this is a pleurocarpous moss of the Hypnaceae and not an acrocarpous moss. A list of all moss species recorded from Baltic and Bitterfeld amber is given.

KEY WORDS: bryophytes, mosses, Baltic amber, Bitterfeld amber, Eocene

INTRODUCTION

Baltic and Bitterfeld (Saxonian) amber is the richest source of bryophyte fossils from the Palaeogene. The inclusions in amber allow a comparable very good identification of characters and species.

The knowledge of fossil bryophytes from amber has much increased over the past years. There were only five publications on this subject up to 1980 (Göppert & Berendt 1845, Göppert 1853, Caspary 1906, Dixon 1922, Mägdefrau 1957). Since that time, R. Grolle (Herbarium Haussknecht, Jena, Germany) has published 29 contributions on the liverworts known from Baltic and Bitterfeld amber, which were summarized shortly before his death in a book (Grolle & Meister 2004). This book describes 26 species of liverworts in 17 genera. The genera are all extant, six of them now extinct in Europe but present on the Azores or in Asia. Of the 26 species, only one is extant, all others are extinct, according to Grolle´s view. It can be assumed that a larger portion of species is in fact extant, as shown by the description of *Plagiochila groehnii*, which falls into the variability of *P. sciophila* Nees ex Lindenb., a species widespread Asia, from which it shall differ by "its coarser teeth and slightly smaller leaf cells".

RESULTS

The mosses from Baltic and Bitterfeld amber were published by Frahm (1994, 1996a, b, 1999a, b, 2000a, b, 2001a, b, 2004a, b, 2005a, b). They also belong to extant genera but also to extant species. In contrast to liverworts in which complanate habit of the plants predominate with distichous leaf arrangement, mosses have mostly non complanate habit with spiral leaf arrangement. Since characters important for the identification are often hidden (alar cells, paraphyllia) or hardly visible (for example papillae), a large deal of fossil specimens remains dubious. Nevertheless, 63 taxa of mosses have so far been reported from Baltic

and Bitterfeld amber and identified with more or less success:

extant species	10
not identified species of extant genera	18
species in form genera	6
extinct species of extant genera	9
unidentified species in extant families	4
dubious taxa (type specimens lost)	12
taxa incertis sedis	5

By the courtesy of Jürgen Velten (Idstein, Germany), I received in 2007 a large number of specimens with bryophyte inclusions from Baltic and Bitterfeld amber for study from the collection of Walter Ludwig (Berlin, Germany). Twenty three included mosses, which are illustrated and described here. Some of them were bought by Mr. Velten and are now kept in his collection. Another dozen specimens included liverworts, for which no specialist could be found. Included are some additional specimens from provided by Christel and Hans Werner Hoffeins (Hamburg, Germany), Even if few of them cannot be identified to the species, they are included here to show the broad variety of fossil mosses in amber. The specimens are kept in the private collections of Jürgen Velten, Walter Ludwig and Christel and Hans Werner Hoffeins as indicated in the text.

Ba = Baltic amber, Bi = Bitterfeld amber.

Brotherella tortifolia (Casp. & G.A.Klebs) J.-P. Frahm, (Ba 1033, coll. Velten, Fig. 1)

Muscites tortifolius Casp. & G.A. Klebs. ? *Muscites serratus* Göpp. & Berendt.

This species is a pleurocarpous moss with lanceolate, ecostate leaves and prosenchymatous laminal cells. As expressed by the species name of the putative synonym, the leaf margin is distinctly serrate.

The systematic position of this species has controversely been discussed. Schimper (1896) referred the type specimen of *Muscites serratus* to the genus *Trichosteleum*. In contrast, Dixon (in Jongmans 1927) has attributed this fossil with some doubt as species of *Fabronia*, probably with regard to the serrate leaf margin. Frahm (2006) argued that this combination of characters is expressed in the genus *Brotherella* and therefore placed *Muscites tortifolius* in *Brotherella*. The illustration of the type of *Muscites serratus* Göpp. & Berendt looks much alike and could be conspecific. In this case, the epithet *serratus* would have the priority. The types of all these species are, however, no more available.

Campylopodiella himalayana (Broth.) J.-P. Frahm (Bi 2036, coll. Ludwig)

A common species, which has several times been reported from Baltic and Bitterfeld amber (Frahm 1996a, b, 2004b, 2005a, 2006). It occurs presently in the eastern Himalaya and Yunnan, where it grows on trunks and rotten wood.

Ctenidium capillifolium (Mitt.) Broth. (Ba 1034, coll. Velten, Ba 1035, 1037, 1040, coll. Ludwig; Figs 2–4).

So far only parts of branches have been reported. Ba 1034 shows an apical part of a plant with regularly pinnate branches, which are very typical for the genus. Ba 1040 consists of an almost complete regularly pinnate plant,

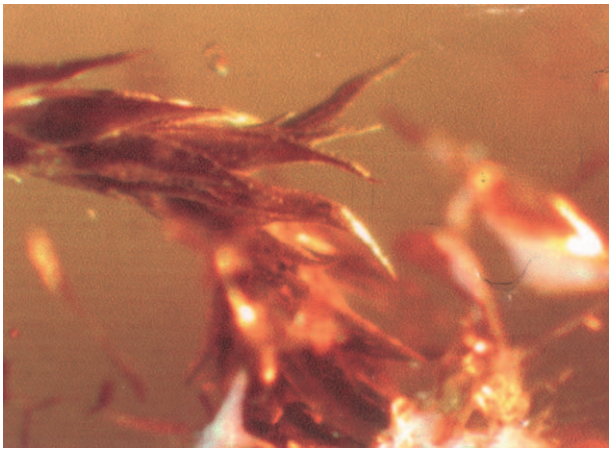


Fig. 1. *Brotherella tortifolia* (Casp. & G.A. Klebs) J.-P. Frahm (Ba 1033, coll. Velten)

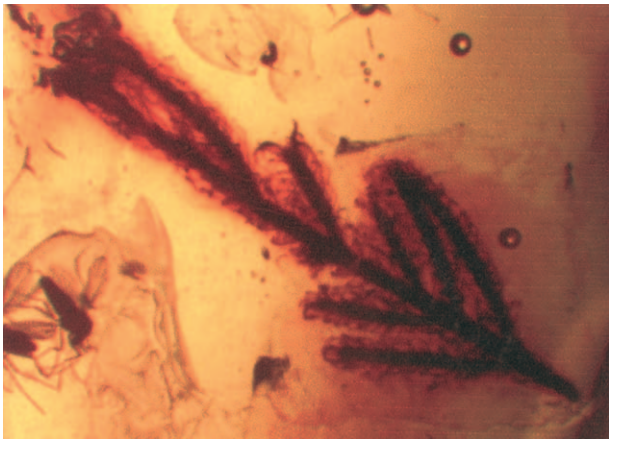


Fig. 2. *Ctenidium capillifolium* (Mitt.) Broth. (Ba 1034, coll. Velten)

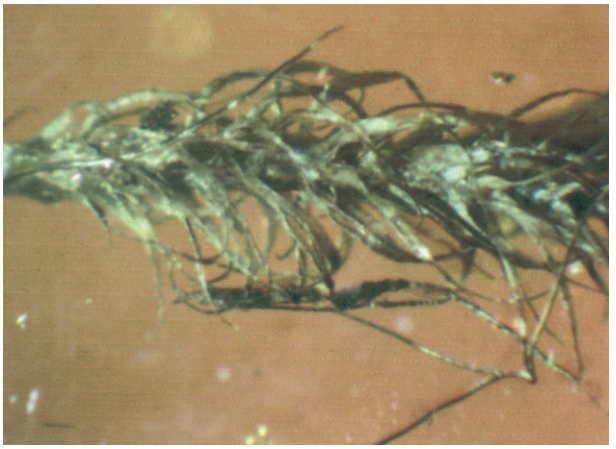


Fig. 3. *Ctenidium capillifolium* (Mitt.) Broth. (Ba 1035, coll. Ludwig

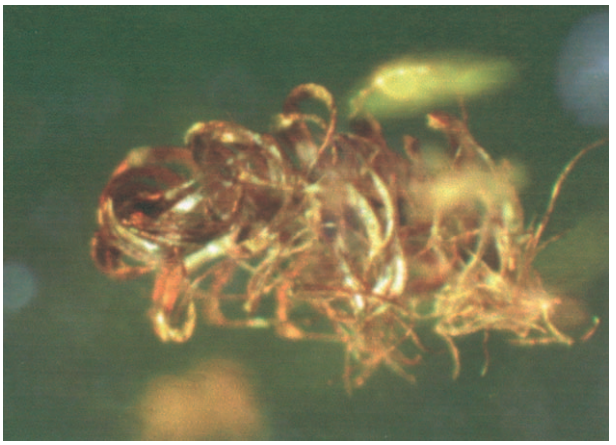


Fig. 4. *Ctenidium capillifolium* (Mitt.) Broth. (Ba 1037, coll. Ludwig)

together with several other remnants of pleurocarpous mosses. The species is native today in Japan, Korea, Taiwan and China.

Haplocladium angustifolium (Hampe & C. Müll.) Broth. (Bi 2034, coll. Ludwig, Ba 1039, coll. Velten, Fig. 5)

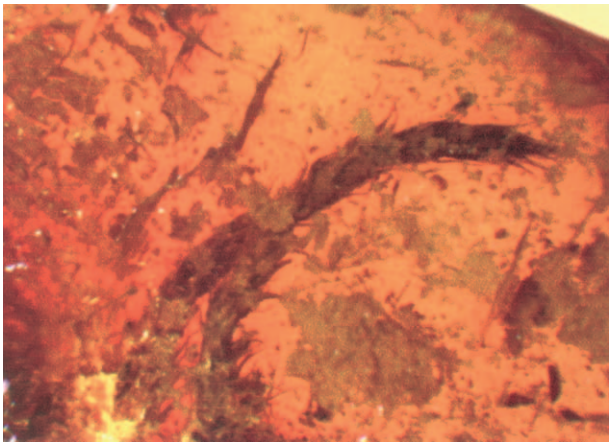


Fig. 5. *Haplocladium angustifolium* (Hampe & C. Müll.) Broth. (Bi 2034, coll.Ludwig)

This moss has been reported several times from Baltic and Bitterfeld amber (Frahm 1996a as isobryalean moss, Frahm 1999a, 2000, 2001). At present, it is widely distributed in Central America, southern Europe and SE-Asia, where it is still inhabiting oak pine forests, the dominant vegetation type of the amber forest.

Hypnites subflagellaris (Caspary & G.A. Klebs) J.-P. Frahm comb. nov. (Bi 2032, 2033, 2035, 2037, 2041, Ba 1033, coll. Ludwig, figs 6–7).

Dicranites subflagellaris Caspary & G.A. Klebs.

The name illustration of the type of *Dicranites subflagellaris* is apparently a flagellate branch of a pleurocarpous moss. Insofar the form genus *Dicranites* is misleading and therefore the new combination is proposed here. It cannot be excluded that the various specimens published under this name belong

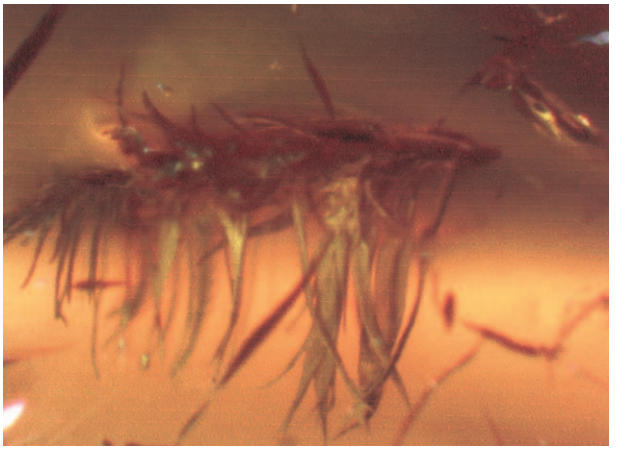


Fig. 6. *Hypnites subflagellaris* (Caspary & G.A. Klebs) J.-P. Frahm (Bi 2032, coll. Ludwig)

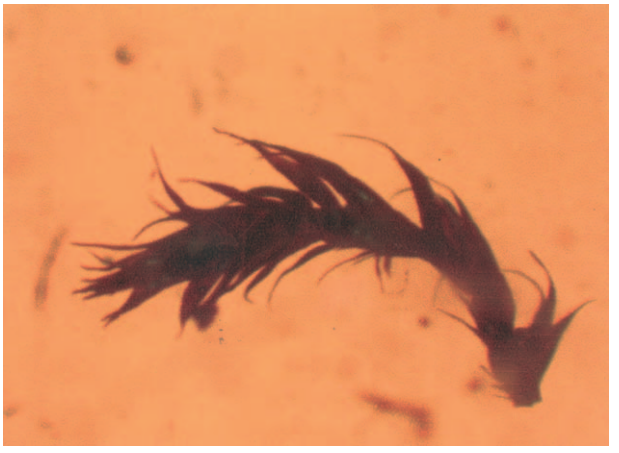


Fig. 7. *Hypnites subflagellaris* (Caspary & G.A. Klebs) J.-P. Frahm (Bi 2033, coll.Ludwig)

Table 1. List of mosses recorded from Baltic and Bitterfeld amber in systematic arrangement. * = extinct species. ? = doubtful species (types lost or determination questionable)

Taxon	Baltic amber	Bitterfeld amber
Dicranaceae		
Camyplopodiella himalayana (Broth.) J.-P. Frahm	Frahm (2004b) as *C.* sp., Frahm (2005a, 2006)	Frahm (1996b, 1999a), Frahm (2004b) as *C.* sp.
Campylopus sp.		Frahm (2001a)
Campylopus sp., capsule	Frahm (1996a, 2004b)	
? Dicranum fuscescens Turn.	Göppert (1853)	
*? *Dicranum simplex* Göpp. & Menge nom. illeg..	Göppert (1853)	
**Dicranum subpellucidum* Göpp. & Menge [*Dichodontium subpellucidum*]	Göppert (1853)	
**Dicranum subscoparium* Göpp. & Menge	Göppert (1853)	
Pottiaceae		
**Barbula subcanescens* Göpp. & Berendt	Göppert & Berendt (1845) as *Muscites apiculatus*, Göppert & Berendt (1845)	
*? *Phascum cuspidatum* Hedw.	Göppert (1853)	
*? *Trichostomum substrictum* Göpp. & Menge	Göppert (1853)	
Grimmiaceae		
*? *Grimmia subelongata* Göpp. & Menge	Göppert (1853)	
Mniaceae		
Trachycystis flagellaris (Sull. & Lesq.) Lindb. (**Muscites hauchecornei* Caspary & G.A.Klebs, **Trachycystis szaferi* Szafran)	Caspary (1907), Frahm (1994, 2004b, 2005a)	Frahm (2004b)
Trachycystis microphylla (Dozy & Mplk.) Lindb.	Frahm (2000a, 2004b)	
**Trachycystis obtusus* J.-P. Frahm	Frahm (2001a, 2005a)	
Trachycystis sp.	Frahm (1999a)	
Rhizogoniaceae		
Calomnion sp.	Frahm (2000a, b)	
Rhizogonium sp.	Frahm (2004b)	Frahm (2001a, 2004b)
Bartramiaceae		
Bartramia sp.		Frahm (2001a)
Rhachitheciaceae		
**Hypnodontopsis fossilis* J.-P. Frahm	Frahm (2004b)	Frahm (2000a, 2004b)
Hypnodontopsis mexicana (Thér.) Robins. *(H. conferta* (Göpp. & Berendt) J.-P. Frahm*, Muscites confertus* Göpp. & Berendt*)*	Göppert & Berendt (1845) as *Muscites confertus*, Göppert (1853) and Caspari (1907) as *Hymenostomum microstomum (Weissia microstoma)*, Frahm (1999a) as akrokarpes Laubmoos, Frahm (2001b) as *Muscites confertus,* Frahm (2001a) as *Hypnodontopsis confertus,* Frahm (2004b) as *H. conferta,* Frahm (2006)	Frahm (1994), Frahm (1999a) as akrokarpes Laubmoos, Frahm (2000a) as *Dicranites casparyi,* Frahm (2004a) as *H. conferta*
**Hypnodontopsis casparyi* (G.A.Klebs) J.-P. Frahm **Dicranites casparyi*G.A. Klebs*, *Dicranites grollei* J.-P. Frahm, **Dicranites obtusifolius* Caspary & G.A.Klebs	Caspary (1907) as *Dicranites casparyi*, *D. obtusifolius*, Frahm (1999a) as *Dicranites c.,* Frahm (1999b) as *Dicranites grollei*, Frahm (2005a)	Frahm (1994, 2000a) als *Dicranites casparyi.*
**Hypnodontopsis lingulata* J.-P. Frahm	Frahm (2005a, 2005b)	
**Hypnodontopsis pilifer* J.-P. Frahm	Frahm (2004b)	
Echinodiaceae		
Echinodium sp.	Frahm (1999a) as *Haplocladium angustifolium*, Frahm (2004b)	
Fabroniaceae		
Fabronia ciliaris (Brid.) Brid.	Frahm (1999a)	Frahm (1994)
Fabronia sp. [*Muscites serratus* Göpp. & Berendt]	Göppert & Berendt (1845), Göppert (1853), Caspary (1907) als *Muscites serratus*	Frahm (1994) als *Muscites serratus*, Frahm (1999a)
Merilliobryum fabronioides Broth.		Frahm (1996b)
Helicodontium sp.	Frahm (2005a)	
Meteoriaceae		
Barbella sp.	Frahm (1996a), Frahm (1999a), Frahm (2004b)	
Symphyodontaceae		
Symphyodon sp.	Frahm (2004b, 2005a)	Frahm (1999a)

Table 1. Continued.

Taxon	Baltic amber	Bitterfeld amber
Cyrtopodaceae		
Bescherellea sp.	Frahm (1999a)	
Thuidiaceae		
Boulaya mittenii (Broth.) Cardot	Frahm (2000a, b)	
Haplocladium angustifolium (Hampe & C. Müll.) Broth.	Frahm (1996a, 1999a, 2001a, 2004b, 2006)	Frahm (1999a)
Amblystegiaceae		
Campylium cf. *squarrosulum* (Besch.) Kanda	Frahm (2004b)	
Drepanocladus sp.	Frahm (2004b)	
Brachytheciaceae		
Brachythecium sp.	Frahm (2004b)	
Brachytheciites veltenii J.-P. Frahm	Frahm (2005a)	
Sematophyllaceae		
Brotherella tortifolia (Caspary & G.A. Klebs) J.-. Frahm, *Muscites tortifolius* Casp. & G.A. Klebs	Caspary (1907) als *Muscites tortifolius*, Frahm (1999a), Frahm (1996b, 2004b, 2006)	Frahm (2000a, 2001a)
Brotherella sp.	Frahm (1996a, 2000a, 2000b , 2004b)	Frahm (2001a) as *Muscites tortifolius*
Mastopoma sp.	Frahm (1999a)	
Aptychella sp.	Frahm (2004b, 2006)	
Sematophyllaceae		Frahm (2004b)
**Sematophyllites serratus* (Göpp. & Berendt) J.-P. Frahm, *Muscites serratus* Göpp. & Berendt	Frahm (1996a, 1999a) as *Hypnum* sp., Frahm (2004b), as *Muscites serratus*, Frahm (2006)	Frahm (2001a) as pleurocarpous moss, Frahm (2004b) as *Muscites serratus*
Hypnaceae *Hypnum* sp.	Frahm (1996a, 1999a), Frahm (2004b) as pleurokarpes Laubmoos, Frahm (2005a)	
Hypnum sp.	Frahm (2001a)	
Ctenidium capillifolium (Mitt.) Broth.	Frahm (2000a, b, 2004b, 2005a, 2006)	
?Hypnum squarrosum Hedw. [*Rhytidiadelphus squarrosus* (Hedw.) Warnst.]	Göppert (1853)	
**Eurohypnum revolutum* J.-P. Frahm		Frahm (2004b)
**Hypnites lanceolatus* J.-P. Frahm		Frahm (2004b)
**Hypnites complanatus* J.-P. Frahm	Frahm (2004b, 2005a)	
**Hypnites flagelliferus* J.-P. Frahm	Frahm (2006)	
**Hypnites subflagellaris* (Caspary & G.A. Klebs) J.-P. Frahm (*Dicranites subflagellare* Caspary & G.A. Klebs, *Dicranum subflagellare* Göppert & Menge nom. nud.)	Göppert (1853), Caspary (1907), Frahm (1999a, 2004b, 2005a)	Frahm (2004b)
Hypnaceous moss		Frahm (2004b)
Hypnaceae	Frahm (2000a, 2004b, 2005a)	
Plagiotheciaceae		
Plagiotheciaceae	Frahm (1999a, 2000a, b, 2004b)	
Polytrichaceae		
**Atrichum groehnii* J.-P. Frahm	Frahm (2000a, Frahm 2000b) as *Atrichum* sp., Frahm (2004a)	
**Atrichum mamillosum* J.-P. Frahm	Frahm 2004a	
**Atrichum subrhystophyllum* J.-P. Frahm	Frahm (2004a), Frahm (2004b) as *Atrichum* cf. *rhystophyllum*	
**Polytrichum subseptentrionale* Göpp. & Menge	Göppert (1853)	
**Polytrichum subundulatum* Göpp. & Menge	Göppert (1853)	
**Polytrichum suburnigerum* Göpp. & Menge	Göppert (1853)	
Musci incertis sedis		
Muscites convolutus Mägdefrau	Mägdefrau (1957)	
Muscites dubius Göpp. & Berendt	Göppert & Berendt (1845), Göppert (1853)	
Muscites elegans Göpp.	Göppert (1853)	
Muscites pilifer J.-P. Frahm	Frahm (1999b)	Frahm (2004b)

Excluded species from this list (obviously no bryophytes):

Muscites apiculatus Göpp. & Berendt, *Muscites hirsutissimus* Göpp. & Berendt, *Muscites dubius* Göpp. & Berendt

to several species producing convergent flagellae. The present fossil specimens revealed, however, for the first time more details of the plant. Bi 2041 shows a branch, Bi 2033 part of a stem with a flagellate branch. Ba 1033 shows a distinctly serrate leaf margin.

Hypnites complanatus J.-P. Frahm (Ba 1010, coll. Velten, Ba 1038 with *Frullania* sp., coll. Ludwig, Fig. 8)

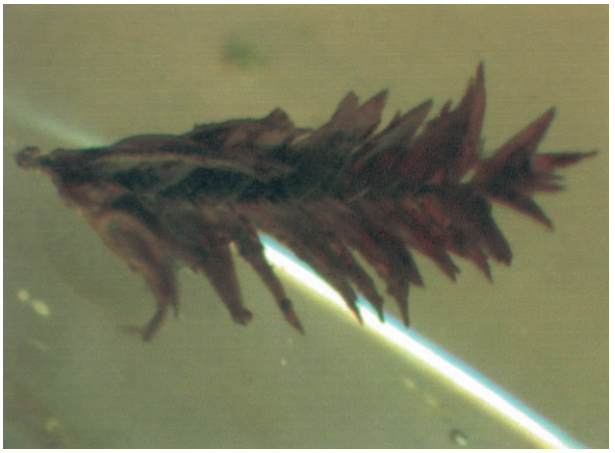


Fig. 8. *Hypnites complanatus* J.-P. Frahm (Ba 1010, coll. Velten)

As expressed by the epithet, the species has conspicuously complanate leaves. They are ecostate and have prosenchymatous laminal cells. In contrast to other similar fossils with the same combination of characters, it has entire and not serrate leaf margins. This species was named as Plagiotheciaceae (Frahm 1999a, 2000a, b) before it was described as new (Frahm 2004b).

Hypnites flagelliferus J.-P. Frahm (Ba 1569.1, coll. Hoffeins, Fig. 9)

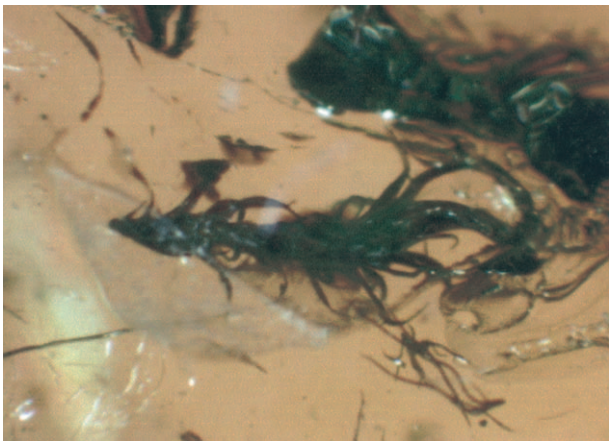
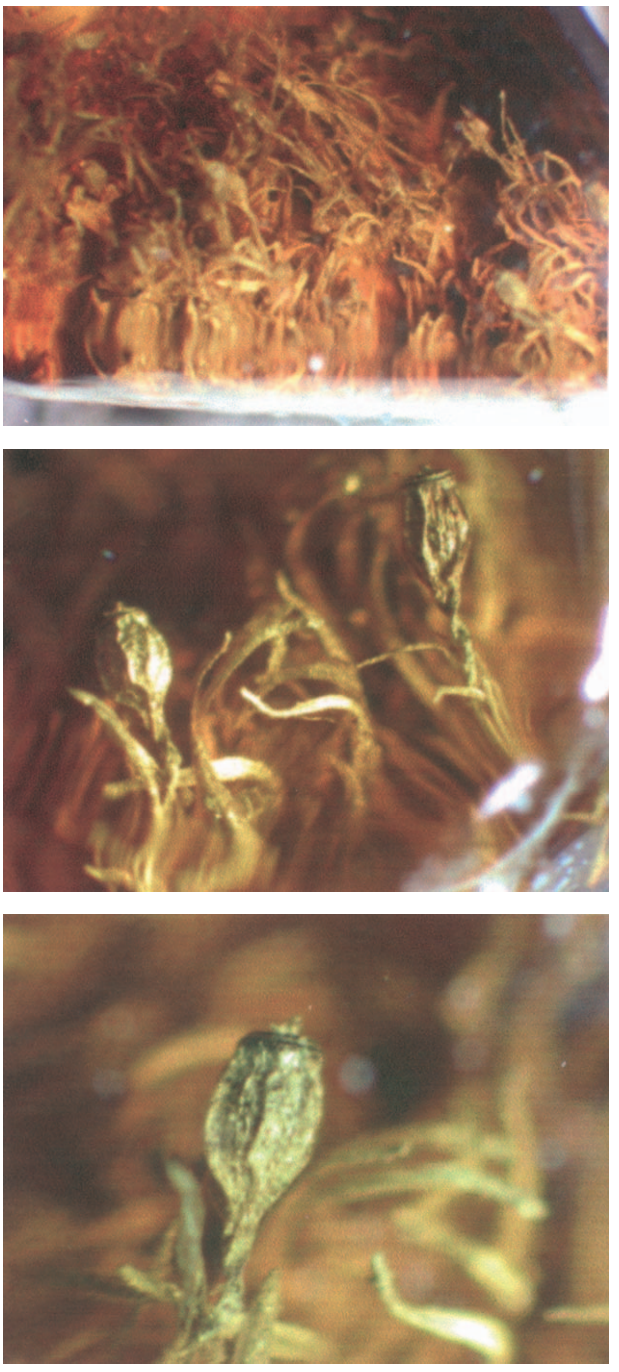


Fig. 9. *Hypnites flagelliferus* J.-P. Frahm (Ba 1569.1, coll. Hoffeins)

Two framents of a pleurocarpous moss, 2 and 3 mm long, with homomallous leaves, especially at the leaf apices. Such fragments were detected several times before but could not be identified and were described in a form genus instead (Frahm 2006). The fragments resemble much *Hypnites subflagelliferus* (see above), but have entire leaf margins.

Hypnodontopsis casparyi (Klebs) J.-P. Frahm (Bi 2040, coll. Ludwig, figs. 10–12)

This extraordinary specimen includes



Figs 10–12. *Hypnodontopsis casparyi* (Klebs) J.-P. Frahm (Bi 2040, coll. Ludwig)

a part of a tuft of this species with several sporophytes. The capsules with eight striae and the twisted setae are significant for the genus *Hypnodontopsis* in the Rhachitheciaceae. The long, narrow leaves separate the species from all other species of the genus. *Hypnodontopsis casparyii* is an extinct species, which is frequently recorded from Baltic and Bitterfeld amber. Fossil specimens known before 2005 were all sterile. Therefore the generic affiliation was not clear and accordingly the species was described under different names such as *Dicranites grollei* J.-P. Frahm and before as *Dicranites casparyi* Klebs or *Dicranites obtusifolius* Caspary & G.A.Klebs.

Hypnodontopsis mexicana (Thér.) Robins.(Ba 1585.1, coll. Hoffeins, fig. 13)

Preserved is a complete plant of 3 mm width with a sporophyte. The capsule is shortly ovoid, with 8 striae, 0,5 mm wide, contracted at the mouth and with slightly differentiated neck. The seta is curved, curved about 1 mm long, else perhaps 1.5 mm.

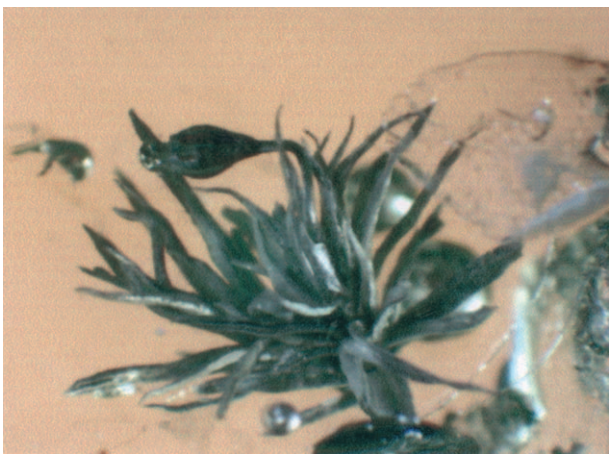


Fig. 13. *Hypnodontopsis mexicana* (Thér.) Robins. (Ba 1585.1, coll. Hoffeins)

This is the only extant species of *Hypnodontopsis* amongst the five species known from Baltic and Bitterfeld amber, which has been found only twice in Mexico and Uganda (Frahm 2005b). It is (together with *Hypnodontopsis casparyi* and unidentified specimens of the genus) the most common acrocarpous moss in Baltic and Bitterfeld amber.

Hypnodontopsis sp. (Ba 1036, coll. Velten, Fig. 14; Bi 1585.3, coll. Hoffeins, Fig. 15; Bi 2038, coll. Ludwig)

Preserved are single complete plants consisting of a rosette of leaves which are about ten

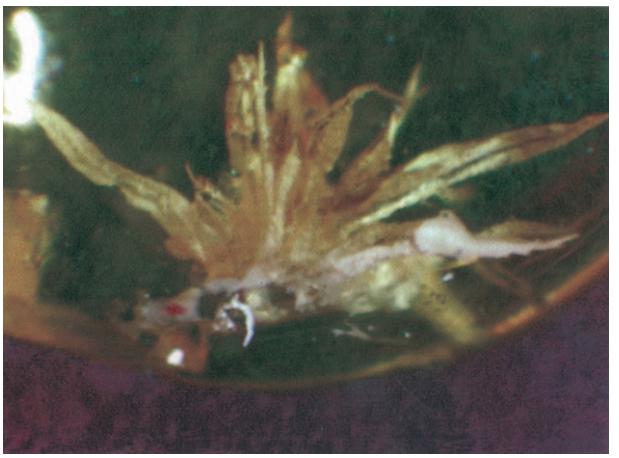


Fig. 14. *Hypnodontopsis* sp. (Ba 1036, coll. Velten).

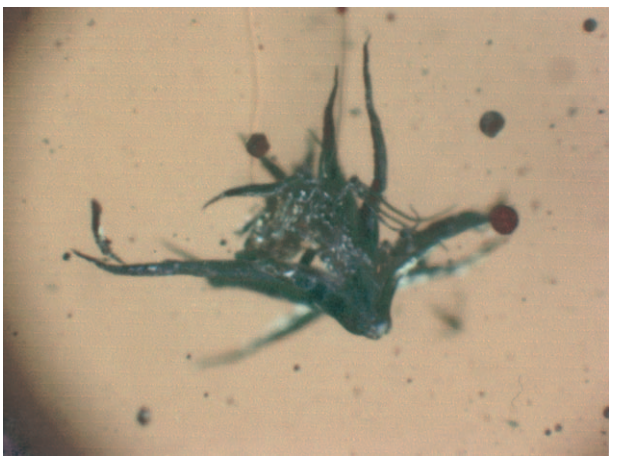


Fig. 15. *Hypnodontopsis* sp. (Bi 1585.3, coll. Hoffeins)

times as long as wide. This character refers to two species, the extinct *H. fossilis* J.-P. Frahm and the extant *H. mexicana* Thér., which can only be distinguished by the shape of the capsule (Frahm 2005b).

Sematophyllites planus J.-P. Frahm sp. nov. (Fig. 16)

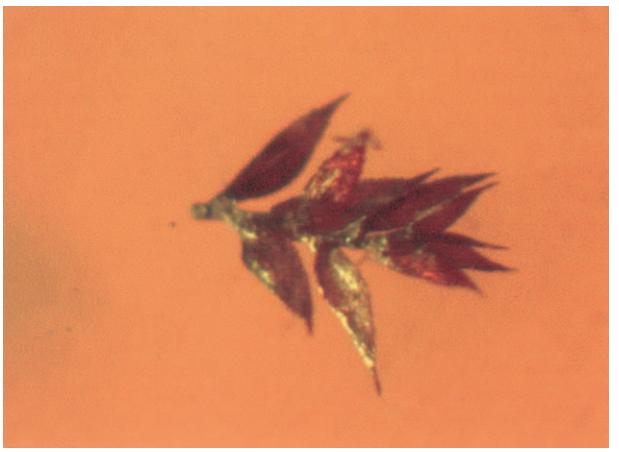


Fig. 16. *Sematophyllites planus* J.-P. Frahm sp. nov. (Ba 1041, coll. Velten, type)

Species muscorum pleurocarporum foliis complanatis, lancecolatis, apice valde acutis, cellulis laminae anguste linearibus, ecostatis, marginibus distincte serratis.

Holotype: Ba 1041, coll. Velten.

Type locality: Baltic coast, exact locality unknown.

Stratigraphy: Eocene

Preserved is an apical part of a stem. The leaves are ovate – lanceolate, have no costa, and are distinctly serrate. The leaves are complanate. The specimen resembles what was named a Sematophyllaceae (Frahm 2004b). Although the identity is not clear, the fossil shall be described here as new that it can be cited.

CONCLUSION

All taxa reported here have been published before, which means that the moss flora of the Eocene amber forest is relatively well known. Naturally most of the species preserved in amber are epiphytic species. They are, however, also species growing on rotten wood (*Rhizogonium* spp.) or even soil (*Campylopus* sp.). Usually only small fragments are preserved, which were most likely blown into the resin. In a few cases, pieces of bark are preserved showing fossil compositions of plants. The latter leads to the conclusion that the trees producing the resin was covered with epiphytes. This aspect, epiphyte covered conifers, is rarely met nowadays but still in subtropical forests. Conspicuously, most of the species are pleurocarpous mosses. This is insofar of interest as this group is interpreted as the youngest branch in evolution, which has radiated in the Tertiary when habitats became available on the forest floor. This lead to a reduction of structures such as hydroids or costae. Insofar it is interesting that pleurocarpous mosses were already so numerous as epiphytes in the Palaeogene. It has to be kept in mind that the bryophyte fossils from amber are the first fossils of epiphytic bryophytes. We have no evidence of epiphytic bryophytes from earlier geological periods, for example the carboniferous forest.

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