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Fossil thrips of the family Uzelothripidae suggest 53 million years of morphological and ecological stability

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The new fossil thrips *Uzelothrips eocenicus* P. Nel and A. Nel sp. nov. (Thysanoptera: Uzelothripidae) is described from two lowermost Eocene amber-preserved specimens (one macropterous and one apterous). The family Uzelothripidae is only known so far from a single extant species, *Uzelothrips scabrosus*. The fossils differ from the extant species only by the antennal segments III and IV, which appear distinctly separated instead of being fused as in the extant *U. scabrosus*. Dark-coloured hyphae and conidia of the Dothideomycetes (Ascomycota) which are likely to belong to the sooty moulds (Capnodiales) are attached to the apterous fossil specimen. We consider this arthropod-fungus association not to be accidental since these fungi are also found in extant specimens of these uzelothripids, suggesting very specific long-term interactions and strong habitat specificity.

Key words: Arthropoda, Thysanoptera, Uzelothripidae, fossil fungi, Ascomycota, Capnodiales, sooty moulds, amber, Eocene, France.

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Introduction

The thysanopteran insect family Uzelothripidae Hood, 1952 is only known from a single extant species *Uzelothrips scabrosus* Hood, 1952. Specimens of this species are recorded from Belém in Brazil (Hood 1952), Singapore (Mound et al. 1980), and Brisbane in Australia (Tree 2009). We also found a specimen collected from Angola (Cambuacala River area, nearby Dundo) in the historic Alexandre Bournier collection at the MNHN. Specimens were recorded from dead branches of *Hevea* or *Bixa* from Brazil, dead twigs or litter from Singapore (Hood 1952; Mound et al. 1980), or soil litter from Angola; but specimens from Australia were collected after spraying *Eucalyptus major* trees with insecticide and collecting the fallen insects on a cloth sheet spread around the base of the trunk (Tree 2009).

Uzelothrips scabrosus presents an unusual combination of morphological features: (i) the wings are slender, rounded at the tip, and the unique vein present is the costal one; (ii) the antennae are whip-like, forming a flagellum beyond segment

III with one circular ventral plate-like sensillum on segment III; (iii) the sternum of the eighth abdominal segment and the whole surface of the ninth, except at its tip, are weakly sclerotized; and (iv) an external ovipositor is lacking. Consequently, the previously monospecific family Uzelothripidae was established (Bhatti 2006; Mound and Morris 2007). Within the Thysanoptera, the position of Uzelothripidae remains dubious because of the lack of evidence of shared characters with other families and because the phylogeny of the Thysanoptera remains unresolved. In particular most extant molecular analyses have failed to produce a resolved phylogeny (Mound and Morris 2007). The Thysanoptera are currently separated into two “sub-orders”, the Tubulifera and the Terebrantia, however, the latter is suspected to be paraphyletic (Mound and Morris 2007). A direct relationship of *Uzelothrips* to the Phlaeothripidae, the only family of the Tubulifera, could be supported by the potentially synapomorphic absence of radial, median, and cubital veins on wings, but Nel et al. (2010) described a Cretaceous Phlaeothripidae with these veins. Also *Uzelothrips* does not possess

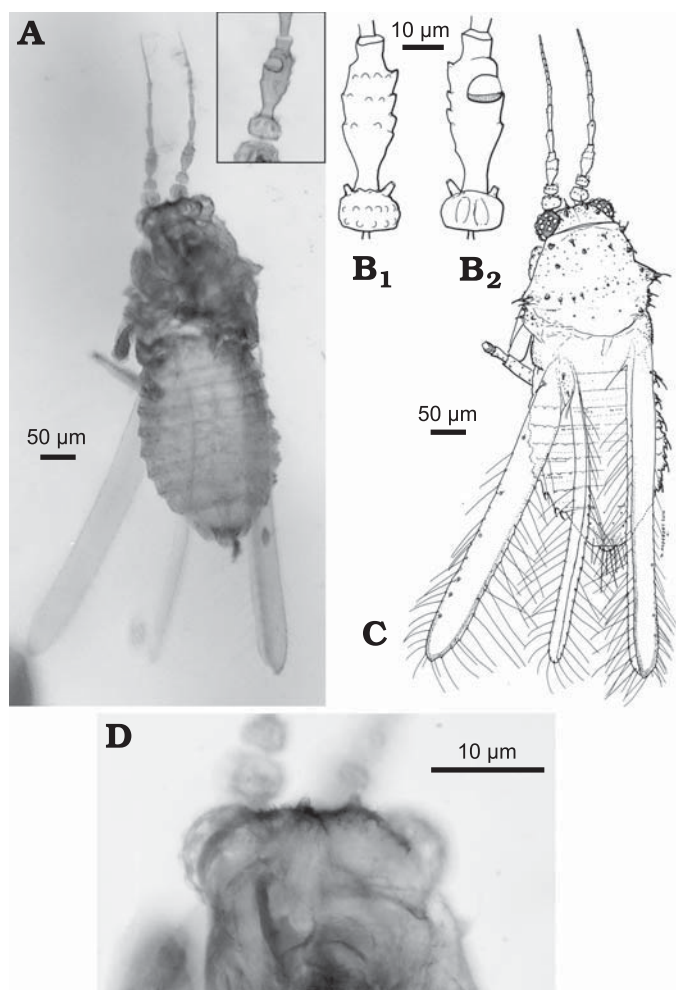


Fig. 1. Macropterous specimen of uzelothripid insect *Uzelothrips eocenica* P. Nel and A. Nel sp. nov., Lowermost Eocene, Le Quesnoy, Oise, France. **A.** Dorsal habitus; inset: detail of antennal segments III and IV. **B.** Drawings of right antennal segments III and IV in dorsal (B_1) and ventral (B_2) views. **C.** Camera lucida drawing of dorsal habitus. **D.** Detail of the head showing symmetrical pair of humps between eyes, each bearing three prominent tubercles from which arise setae.

an important apomorphy of this last family, i.e., the presence of a tube-like tenth abdominal segment. The Uzelothripidae are therefore currently placed provisionally inside the “Terebrantia” (Bhatti 2006; Mound and Morris 2007).

Here, we present two lowermost Eocene amber-preserved specimens of the Uzelothripidae which are distinguished from the extant *Uzelothrips scabrosus* by the antennal segments III and IV, which appear distinctly separated instead of being fused as in the extant *U. scabrosus*. This fossil feature allows us to confirm the original assumption by Hood (1952) interpreting the antennal segment III of the only extant species as being possibly III + IV. Dark-coloured hyphae and conidia of the Dothideomycetes (Ascomycota) which are likely to belong to the sooty moulds (Capnodiales) are found associated with a fossil and with extant *Uzelothrips* specimens, indicating long-term and very specific fungus-animal interactions and strong habitat specificity.

Institutional abbreviations.—MNHN, Muséum National d’Histoire Naturelle, Laboratory of Palaeontology, Paris, France.

Material and methods

The Oise amber deposit is located near Creil at the place known as “Le Quesnoy” (Oise, northern France). The lignite layers containing the amber belong to the Lower Eocene of the Paris basin (~53 Ma). This age corresponds to Paleocene–Eocene Thermal Maximum (PETM), one of the most important periods of global warming. Data from the evaluation of flora and fauna in Oise amber suggest a semideciduous forest under a hot climate with a wet and a dry season. Representatives of the Combretaceae or Caesalpinaceae are considered as amber producing trees in this region. Up to date, 20 000 amber inclusions have been collected from this site, including hexapods, mites, spiders, and two pseudoscorpions. Plant remains (leaves, seeds, flowers, pollen), fungi and microorganisms are also very abundant (see Brasero et al. 2009, for review).

The amber pieces were ground and polished and placed in Canada balsam between two cover slips as described by Azar et al. (2003). Fossils were examined and measured using an incident light (Olympus SZX9), and a Leitz Wetzlar binocular microscope.

Systematic paleontology

Kingdom Animalia Linnaeus, 1758

Phylum Arthropoda Latreille, 1829

Class Insecta Linnaeus, 1758

Order Thysanoptera Haliday, 1836

Family Uzelothripidae Hood, 1952

Genus *Uzelothrips* Hood, 1952

Type species: *Uzelothrips scabrosus* Hood, 1952, Recent species, Bélem, Brazil.

Uzelothrips eocenica P. Nel and A. Nel sp. nov.

Figs. 1, 2.

Etymology: In reference to the Eocene age.

Type material: Holotype MNHN-F.A38530, PA 6818, macropterous female (Fig. 1). Paratype MNHN-F.A38531, PA 1794, apterous of unknown sex (Fig. 2).

Type locality: Farm Le Quesnoy, Chevière, Region of Creil, Oise Department (northern France).

Type horizon: Lowermost Eocene amber, Sparnacian (53 Myr), level MP7 of the mammal fauna of Dormaal (Nel et al. 1999).

Material.—Type material only.

Diagnosis.—Antennal segments III and IV clearly separated, while they are fused in the Recent species.

Description.—Body stout, 488 µm long (Figs. 1A, C). Head

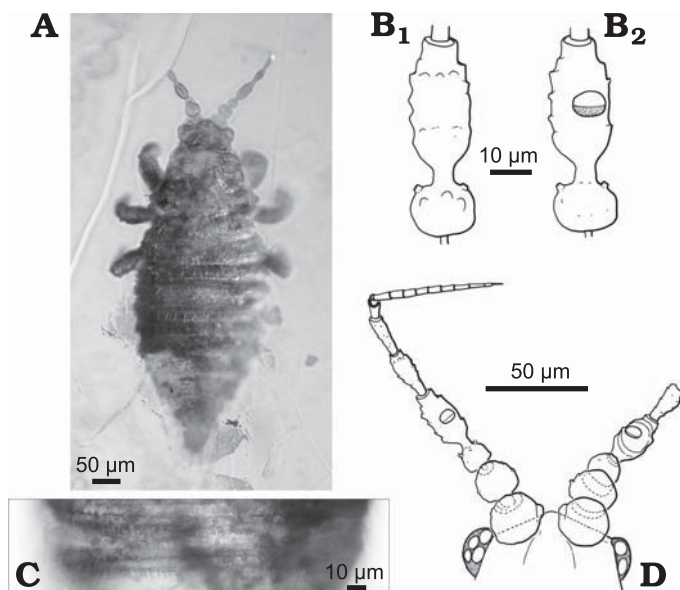


Fig. 2. Apterous specimen of uzelothropid insect *Uzelothrips eocenicus* P. Nel and A. Nel sp. nov., Lowermost Eocene, Le Quesnoy, Oise, France. A. Dorsal habitus. B. Drawings of right antennal segments III and IV in dorsal (B₁) and ventral (B₂) views. C. Detail of tergites IV and V showing comb of short teeth on posterior margins. D. Camera lucida drawing in ventral view of head and antenna.

36 µm median dorsal long; 112 µm wide; eyes large, 40 µm long, 32 µm wide; presence of a symmetrical pair of humps between eyes, each bearing three infundibuliform setae arising from prominent tubercles (especially well seen on macropterous specimen) (Fig. 1D); mouth cone longer than head; antennae eight-segmented, antennal segment I 20 µm long, segment II 24 µm long, segment III 14 µm long with one truncated cone on each lateral side (whether tubercle or sensilla is unknown; more pronounced in macropterous than in apterous specimen) (Figs. 1A, B, 2B, D); segment IV 44 µm long, narrower than III, with one large and broad rounded tympanum-like sensory area in its upper middle part (Figs. 1A, B, 2B, D); segment V 32 µm long with a thumb-like sensorium on outer lateral margin; segment VI 36 µm long, VII 32 µm long; segment VIII slender with seven long and narrow divisions, 66 µm long. Transverse median dorsal sclerite attached to anterior margin of pronotum. Pronotum trapezoidal 100 µm long, 190 µm wide at posterior margin (inclusive of lateral tubercles); posterior angles conically projecting bearing each two infundibuliform setae arising from prominent tubercles; heavily tuberculate, posterior margin with projecting teeth only distinctly visible on apterous specimen; mesonotum and metanotum posteriorly margined with projecting teeth well seen on apterous specimen, unknown for macropterous specimen. Legs with numerous tubercles; tarsi one-segmented. Fore wing 480 µm long, 40 µm wide; rounded at apex; margins running parallel; indiscernible venation, one clear seta at base, a second one seems highly probable because on the left wing base, a structure resembling an insertion of seta (but no seta) is discernible; two discal setae on clavus; fringe straight. Hind wing 440 µm long, 12 µm wide, one vestigial vein visi-

ble. Abdomen 260 µm long, 188 µm wide; tergites with mostly twelve setae arising from tubercles (particularly well seen on apterous specimen); a comb of short teeth on posterior margin of tergites I–VII clearly visible on apterous specimen (Fig. 2C); combs of short teeth are discernible at some places on abdominal segments of macropterous specimen (Fig. 1C); sternite I as wide as other sternites on apterous specimen; ovipositor only weakly sclerotized.

Stratigraphic and geographic range.—Type locality and horizon only.

Kingdom Fungi R.T. Moore, 1980

Phylum Ascomycota Cavalier-Smith, 1998

Class Dothideomycetes O.E. Eriksson and Winka, 1997

Order ?Capnodiales Woronichin, 1925

?Capnodiales gen. et sp. indet.

Fig. 3.

Description.—Melanized fungal remains are found attached to the cuticle of the fossil apterous specimens (Fig. 3A). Most of these structures are obviously fragments of a pigmented mycelium and consist of few mostly globose to subglobose cells of 3 to 6 µm diameter. A few elongate cells of 8 to 10 µm length and 4 µm diameter are also preserved. Other structures represent four-celled *Capnosporium*-like conidia (see arrowhead in the uppermost left panel of Fig. 3A). The occurrence of hyphae with tapering tips with dividing stages (indicated by the arrowhead in the middle right panel of Fig. 3A) suggests that these fossil fungi may belong to the sooty moulds (Capnodiales). However, based on the few visible features an assignment to this order is tentative.

Discussion

The differences between both fossil thrips (one macropterous and one apterous) range within the intraspecific variability of the only modern relative; this being the reason why we consider both fossils to be representatives of the same species. Both fossils show a particular combination of the antennal segments III and IV that is unknown in any other extant or fossil Thysanoptera (Figs. 1B, 2B). Apart from the specific antennal segments III and IV, all other characters of these two specimens are consistent with the original description of the genus *Uzelothrips* by Hood (1952). These are (i) the whip-like antennae (Fig. 2D), (ii) large tuberculate humps between eyes (Fig. 1D), (iii) a dorsal sclerite ahead the pronotum, (iv) a heavily tuberculate trapezoidal pronotum with conically projecting posterior angles bearing each two infundibuliform setae, (v) slender wings that are rounded at tip and without discernible venation (at least in forewing, very weak in hind wing) (Fig. 1A), (vi) tergites that are posteriorly emarginated with projecting teeth (Fig. 2C), (vii) an external ovipositor lacking, and (viii) numerous dorsal tubercles and setae arising

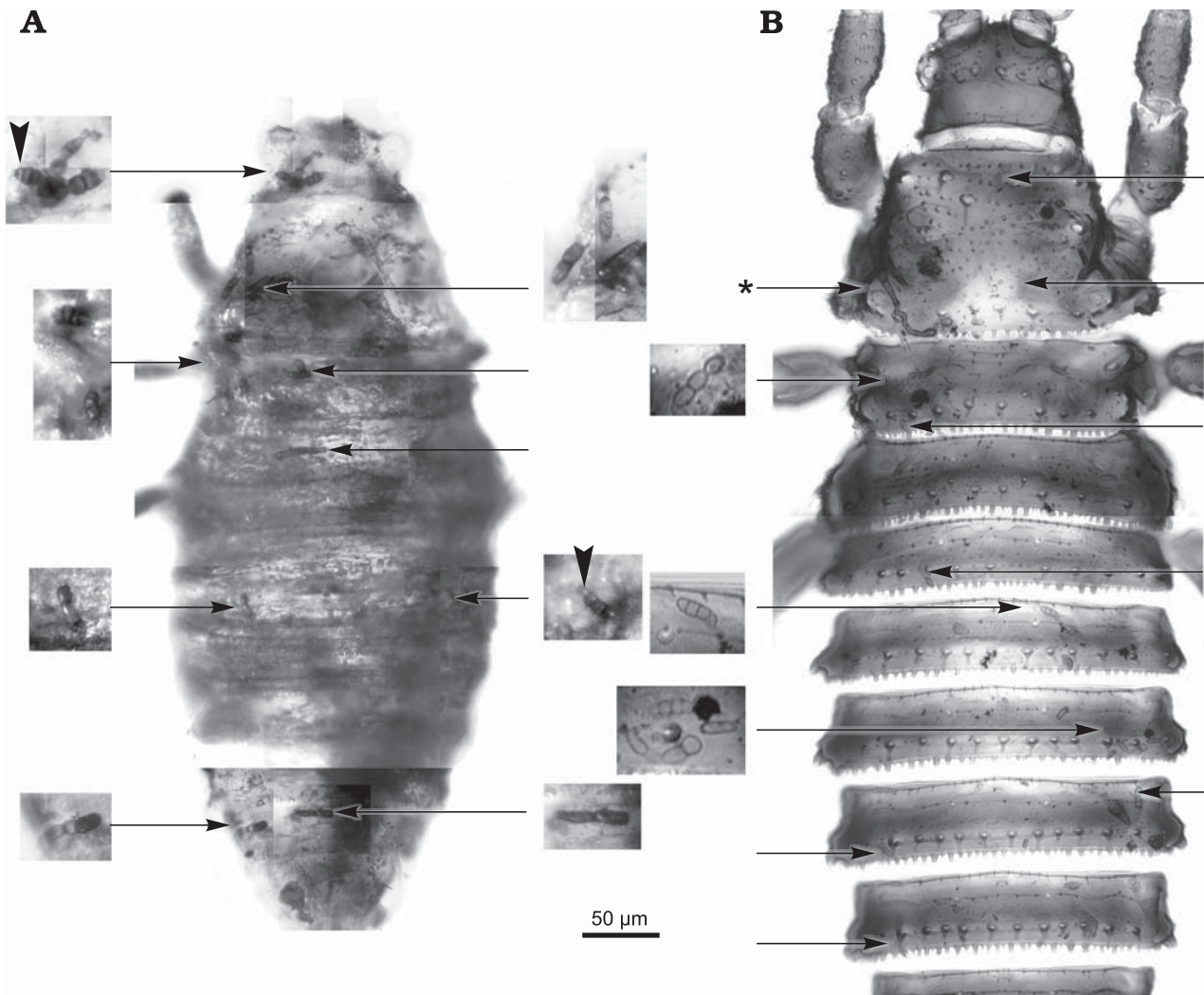


Fig. 3. Ascomycetes found attached to the cuticle of the fossil and extant uzelothripid insects. The small panels show higher magnification images of some fossil and extant fungi found at the locations indicated by the arrows. **A.** Fossil apterous specimen of *Uzelothrips eocenicus* P. Nel and A. Nel sp. nov. The image is composed of photographs obtained from those optical sections which show the attached fungi most clearly. The arrowhead in the uppermost left panel indicates a *Capnosporium*-like conidium; the arrowhead in the middle right panel indicates a tapering hypha tip with dividing stage. **B.** Recent specimen of *Uzelothrips scabrosus* Hood, 1952 (reconstitution of two photographs by Laurence A. Mound, see also Mound 2011). The asterisk refers to the elongated hypha that has possibly grown on the surface of the thrips after attachment.

from tubercles on whole body. The antennae of the fossils do not fit exactly to the original description of *Uzelothrips* by Hood (1952). This does not concern the whip-like shape which is present in fossils in the same way as in extant species, but it concerns the number of antennal segments (eight in fossils instead of seven in extant species) as well as the shape and supposed sensilla on the antennal segments III (short segment with truncated cones in fossils instead of long segment with ventral circular sensorium in extant species) and the antennal segment IV (long segment with ventral circular sensorium in fossils instead of long segment with thumb-like sensorium in extant species). However, Hood (1952) also stated in his original description that the antennal segment III of Recent *Uzelothrips scabrosus* has a pronounced constriction between its distal part and the proximal part of the segment and suggested it was the result of a fusion when writing: “segment III (possi-

bly III + IV, morphologically)”. The fossil uzelothripids have the antennal segments IV and V resembling very much the distal part of antennal segment III and the antennal segment IV, respectively, in extant species. Therefore it is highly probable that the antennal segment III of extant species *U. scabrosus* is in fact the result of a fusion of the antennal segments III and IV that are still well distinguished in our fossils. During fusion antennal segment III became condensed and the truncated cones get reduced. We noticed that one truncated cone is figured by Wilson (1975: fig. 190, collection from Beltsville) on extant specimen from Belém. Apart from the shape of the antennal segments III and IV and from the truncated cones on antennal segment III, all other parts of the body of *Uzelothrips eocenicus* P. Nel and A. Nel sp. nov. strikingly resemble the extant *U. scabrosus*. It is particularly well-visible in the fossil apterous specimen, that the setae of meso- or metanotum, and

those of the abdominal tergites, have the same pattern of distribution in both the fossil and some representatives of the extant species (Fig. 3A, B). However, we noticed that apparently, two different patterns exist regarding the number of setae on abdominal tergites: (i) *U. eocenicus* bears mostly 12 setae on each abdominal tergite, which is consistent with some specimens of *U. scabrosus* (Fig. 3B); (ii) in contrast, the specimen of *U. scabrosus* from Angola which we found in Alexandre Bournier's collection at the MNHN Paris bears only six setae on each abdominal tergite. This character state was also illustrated by Moritz (2006: fig. 68c), as well as by Wilson (1975: fig. 320, from specimens from Belém in Brazil, collection from Beltsville). This may indicate polymorphism in *U. scabrosus* and it should be checked whether these two morphs could represent two different species instead of one; genetic analyses may contribute to resolve this question.

The presence of numerous fungal remains attached to the surface of the apterous specimen of *Uzelothrips eocenicus* P. Nel and A. Nel sp. nov. (Fig. 3A) motivated us to check their possible occurrence on specimens of the Recent species *U. scabrosus*. Similar fungi are actually visible on some published photographs of specimens of *U. scabrosus* (see, e.g., Fig. 3B; Moritz 2006); however, they are absent in the Angolan specimen from Alexandre Bournier's collection. It is conspicuous that fossil and extant fungal remains at the surfaces of the thrips look very alike. Based on the sometimes visible tapering hyphae tips and the *Capnosporium*-like conidia we assume that these fungi belong to the sooty moulds (Capnodiales, Ascomycota). Sooty moulds are epiphytic saprophytic fungi that often possess globular dark-coloured cells. Hyphae easily detach from the loose mycelium and, as they are sometimes a bit sticky, they attach to plant surfaces. Hence it may be assumed they could also easily attach to some insects. The long hypha visible on the Recent thrips specimens (indicated by an asterisk in Fig. 3B) may even have grown on the surface after initial attachment. Sooty moulds produce mycelia forming extensive patches on the surface of living plants. Many sooty moulds obtain their nutrients mainly from insect excretions of aphids, scale insects and other producers of honey-dew, or from plant exudates (Hughes 1976). Aphids, scale insects, as well as other producers of honeydew are rather frequent in Oise amber (AN personal observation; see also Brasero et al. 2009). Some representatives of the sooty mould families Antennulariellaceae and Metacapnodiaceae of the Capnodiales possess hyphae that resemble the hyphae on the thrips. Fossils of the Metacapnodiaceae are recorded from several pieces of Eocene Baltic amber and Oligocene Bitterfeld amber (Rikinen et al. 2003) as well as from Albian amber of France (Girard et al. 2009). Schmidt et al. (2010) recently reported fragments of a mycelium of the Antennulariellaceae from Cenomanian amber from Ethiopia. These amber fossils suggest that at least some representatives of the Capnodiales did not change their morphology since the Early Cretaceous.

We consider the association of these fungi and *Uzelothrips eocenicus* P. Nel and A. Nel sp. nov. not to be acciden-

tal because these fungi are also found in extant specimens of *U. scabrosus*, and because dark-coloured hyphae of the Dothideomycetes have never been reported from the cuticle of other fossil and modern insects. This suggests a long-term interaction such as fungivory along with accidental attachment of loose mycelia fragments.

We assume that the uzelothripids live near or inside clusters of epiphytic fungi such as sooty moulds, their assumed food source, at least since 53 million years. It would be worth clarifying the ecology of *U. scabrosus* in order to verify its presumed fungivorous mode of life (Mound et al. 1980; Tree 2009) and to further discover their preferred microhabitats such as litter, tree trunks and twigs. The extant *Uzelothrips* specimens are found in warm environments with at least one wet period, in analogy to the Eocene climate of central and Western Europe. Thus the climatic constraints may be similar for the two species.

Anyway, the new fossil uzelothripids provide evidence of long term ecological stability in their association with dark-coloured fungi of the Dothideomycetes. We hypothesize that the morphological stability of uzelothripids over geologic periods is correlated with a long-term stability of its microhabitats and food sources, resulting in less selection pressure.

Because of their excellent mode of preservation, insect fossils from ambers are excellent models for studying this phenomenon. Preliminary studies on the insect fauna from the lowermost Eocene Oise amber suggest that the taxa belonging to the soil, litter or bark fauna (e.g., the fossil Psocoptera from this amber are nearly identical to their Recent relatives, Nel et al. 2005) show a higher morphological stability than those living in forest habitats above the soil surface such as Diptera: Chironomidae, Odonata; Hymenoptera: Apoidea, etc., which were more influenced by environmental changes (Fleck et al. 2000; Michez et al. 2007; Doitteau and Nel 2007).

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