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The oldest representative of the Trichomyiinae (Diptera: Psychodidae) from the Lower Cenomanian French amber studied with phase contrast synchrotron X-ray imaging

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Running title:

The oldest Trichomyiinae in Cretaceous French amber

Abstract. *Trichomyia lengleti* sp. nov., is described from the Lower Cenomanian amber of La Buzinie, Charente (SW France) from a piece of fully opaque amber. The Upper Albian *Trichomyia swinhoei* Cockerell, 1917 is transferred from the Trichomyiinae to the Sycoracinae incertae sedis stat. nov. *T. lengleti* is the oldest representative of the subfamily Trichomyiinae, supporting at least a Cretaceous diversification for the Psychodidae. The discovery of this fossil fly and its study thanks to propagation phase contrast synchrotron X-ray imaging improves our knowledge of the biodiversity and the historical evolution of psychodoid flies. A check list of fossil trichomyiine species is given.

Additional keywords: Diptera, Psychodidae, Trichomyiinae, Cretaceous amber, Charente, SW France, synchrotron, phase contrast.

Introduction

Psychodid flies are relatively well represented in the fossil record (Evenhuis 1994; Azar *et al.* 1999; 2003; 2007a; 2007b; Azar and Nel 2002; 2003; Azar and Ziadé 2005; Nel *et al.* 2002; Ansorge 1994; 1996; Wagner 2002; 2006). Their oldest definitive known fossil is from the Liassic (Ansorge 1994) but their occurrence could be as old as Triassic with *Triassopsychoda olseni* Blagoderov & Grimaldi, 2007 (tentatively included in ?Psychodidae), (Fraser *et al*. 1996; Blagoderov *et al.* 2007).

Trichomyiinae Tonnoir, 1922 is a subfamily of short-legged psychodid having the wing radial sector with only one vein between radial and medial forks. The monospecific Cenozoic genus *Eatonisca* Meunier, 1905 is characterized by a very particular wing venation. The other Cenozoic genus *Eotrichomyia* Nel *et al.*, 2002 has the same wing venation as *Trichomyia*, but is characterized by male genitalia with stylus bearing a sharp spine as in *Sycorax* (Sycoracinae). Recent representatives and remaining fossils are all included in *Trichomyia* Haliday, 1839. As a whole this genus embraces a wide range of structures that imposed the creation of different subgenera (Duckhouse 1965, 1978, 1980; Bravo 1999, 2001, etc.). Several other extant genera were created within Trichomyiinae like *Diplonema* Loew, 1845, *Lepria* Enderlein, 1936, and *Eubonetia* Vargas & Najera, 1953, but Satchell (1956) sank them in *Trichomyia*. The genus *Phalaenomyia* Loew, 1844 originally proposed without included species is considered by all the workers as a *nomen nudum*.

Duckhouse (1965) concluded that two or more groups are at present intermingled under *Trichomyia*, but he considered that it would be premature to form new genera. Nevertheless he subdivided the Trichomyiinae into two groups A and B based on antenna and palp structures.

Sycoracinae were first classified within the subfamily Trichomyiinae but Edwards (1929) recognized the difference between *Sycorax* and *Trichomyia* and suggested that *Sycorax* should be classified in a separate tribe of the Trichomyiinae or preferably as a separate subfamily. Jung (1954, 1956) recognized a separate subfamily for *Sycorax*, but thereafter Jung (1958) and Hennig (1972) reverted to the single subfamily Trichomyiinae. For Duckhouse (1972), Vaillant (1978) and Wagner (1997), Sycoracinae is considered as a separate subfamily.

The oldest fossil described in the subfamily Trichomyiinae is *Trichomyia swinhoei* Cockerell, 1917 from the Myanmar Lower Cretaceous (Upper Albian) amber, but this specimen was badly drawn and Cockrell's (1917) description was very succinct and insufficient for an accurate attribution of this fossil. We transfer below *Trichomyia swinhoei* Cockerell, 1917 from the Trichomyiinae to the Sycoracinae. Thus the current oldest published representative of the subfamily Trichomyiinae (*Eotrichomyia electronica* Nel *et al*., 2002) is from the Lower Eocene amber of the Paris Basin, Oise, France (Nel *et al*. 2002), but this subfamily occurs in the Turonian amber of New Jersey and the Upper Cretaceous amber of Myanmar (Azar *pers. obs*.). We describe herein a new *Trichomyia* species, from the Lower Cenomanian amber discovered at La Buzinie, in Charente, south-western France (Perrichot et al. 2007a, 2007b) and assess its age in relation to other Trichomyiinae. We used new Synchrotron X-ray imaging techniques (Tafforeau *et al*. 2006; Lak *et al*. 2008) that have enabled the discovery, imaging and 'virtual' extraction of the specimen from a totally opaque piece of amber

Material and methods

The amber containing the Trichomyiinae has been collected in the mid part of the Lower Cenomanian series of La Buzinie road works (Angoulême area, Charente, SW France) (Perrichot *et al*. 2007b), in the B2 lithological subunit sensu Néraudeau *et al*. (1997). The amber pieces collected in this subunit are more or less opaque, so the specimen has been detected and 3D-reconstructed using phase contrast X-ray synchrotron imaging according to the protocol published in Lak *et al*. (2008). All the experiments were performed at the ESRF – Grenoble (France) on the Beamline ID19. The microradiograph of the fossil fly

being not sufficiently accurate to describe the specimen precisely; therefore the following description is based on a 3D-reconstruction, obtained by local propagation phase contrast microtomography (Tafforeau *et al*. 2006, Lak *et al.* 2008). The parameters of the scan were the following: monochromatic beam set at an energy of 20.5 keV using a multilayer monochromator, 100 mm of propagation distance between the sample and the detector, 25 µm thick YAG scintillator screen, isotropic voxel size of 1.4 µm, 1500 projections of 0.2 s each taken over 180 degrees. After tomographic reconstruction and 8 bits conversion, the volume was segmented in 3D using the software VGStudioMax 1.2.1 (Volume Graphics, Heidelberg, Germany), in order to virtually extract the specimen from the opaque amber. We could have a vision of the rotating fossil in order to examine very minute structures, such as the apical flagellomeres, the pattern of the dorsal setae, and the genitalia.

We follow the wing venational nomenclature of McAlpine (1981), with the following abbreviations: h, humeral vein; Sc, subcosta; R1, R2, R3, R4+5, radial veins; M1, M2, M3, median veins; CuA1, CuA2, cubital veins; A1, anal vein; r-m, radial-median cross-vein.

Systematic palaeontology

Family PSYCHODIDAE Newman, 1834

Subfamily TRICHOMYIINAE Tonnoir, 1922

Genus ***Trichomyia*** Haliday (*in* Curtis 1839)

Type species. *Trichomyia urbica* Haliday, 1939 by monotypy.

Trichomyia swinhoei Cockerell, 1917

Material. Holotype In.19101, Natural History Museum, London, UK.

Type locality and horizon. Late Albian, Burmese amber, Myanmar.

Discussion

The reexamination of this fossil material in the Natural History Museum (London) by one of us (DA) and by Derek A. Duckhouse, indicates that this specimen is definitely not a Trichomyiinae but a Sycoracinae as its CuA2 is rather short as in all known sycoracine flies (*pers. obs.*; and Duckhouse *pers. comm. to DA*). We transfer *Trichomyia swinhoei* Cockerell, 1917 from the Trichomyiinae to the Sycoracinae incertae sedis stat. nov. Its detailed redescription will be done in another paper.

?*Trichomyia lengleti*, sp. nov.

(Plate 1, Figs 1-3)

Material. Holotype BUZ 2.7 (female), from the collection of T. Lenglet, deposited in the Muséum National d'Histoire Naturelle, Département Histoire de la Terre, Paris, France. All the tomographic data as well as a surface model of the specimen are available upon request to the first author, and will be deposited in the public palaeontological database project of the ESRF when available. Reference 3D prints of the extracted specimens are deposited in the Muséum National d'Histoire Naturelle (Paris, France), in the Géosciences laboratory (Rennes, France), and at the ESRF (Grenoble, France).

Etymology. The species name is dedicated to Mr. Thierry Lenglet, who discovered the type specimen and donated it to the MNHN.

Type locality and horizon. Lower Cenomanian (subunit B2 *sensu* Néraudeau *et al*. 1997) of La Buzinie, Charente, SW France (Perrichot *et al*. 2007b).

Diagnosis

Head with well-developed vertex puffed out behind antenna; antenna with 15 flagellomeres bearing well-developed digitiform and sigmoid ascoids, flagellomeres 12 to 15 gradually reduced with the last one extremely reduced and drop-like; wing venation of

Trichomyia-type with CuA2 elongated and Rs separated from R1 at the same level where Sc meets with R1, and beyond fork of M into M1+2 and M3.

Description

Head with well-developed vertex puffed out behind antenna; eyes elliptical, 148 µm of large diameter and 107.5µm of small diameter; antenna 617 µm long, with 15 flagellomeres, viz. 13 of normal size, the 14th reduced and the 15th (apiculus) very reduced and drop-like (Pl. 1, Fig. 1A); first flagellomere the longest, 42.5 µm, nearly 1.5 times as long as each of following ten flagellomeres; flagellomeres 2 to 11 pyriform and of nearly same length 38 µm long; flagellomeres 12 and 13 of equal length and slightly shorter than the preceding, 30 µm long each; flagellomere 14 well reduced and shorter than half of flagellomere 12 or 13, 17 µm long, bearing the terminal flagellomere apiculus which is much reduced and drop-like; scape subspherical, nearly 34 µm long and 34 µm wide; pedicel subspherical, about 46.8 µm long and 38.3 µm wide; flagellomeres 1-6 with well-developed, digitate, and sigmoid ascoids in their ventral sides (Fig. 1B, 1C); maxillary and labial palps not visible.

Wing 1011 µm long, 393 µm wide (Pl. 1, Fig. 2); humeral vein (h) reaching costal margin at 129 µm from wing base; subcostal vein Sc distally fused with R1 in a strong angle, 337 µm from wing base, and a possible cross-vein reaching costal margin, but rather unclear character; R1 reaching costal margin 747 µm from wing base; Rs separated from R1 337 µm from wing base, at same level where Sc meets with R1, and beyond fork of M into M1+2 and M3; Rs three-branched; R2 and R3 separated 708 µm distally, slightly before level where R1 meets with costal margin; R2 sigmoid-shaped reaching costal margin at 921 µm from wing base; R3 slightly curved at base and reaching costal margin at 989 µm from wing base; R4 and R5 fused forming R4+5, 612 µm long, slightly curved at its middle toward posterior side; cross-vein r-m 421 µm distal of wing base; fork of M into M1+2 and M3 112 µm distal of arculus; fork of M1+2 into M1 and M2 269 µm distal of base of M1+2; M1 slightly curved; M2 slightly shorter than M1; M3 reaching wing margin at 803 µm from wing base; CuA1 separating from CuA 309 µm distal of wing base; CuA2 rather long, 444 µm long; A1 hardly visible on right wing but reaching posterior wing margin.

Halteres 191 µm long; knob 101 µm long; stem 90 µm long.

Thorax nearly 358 µm long, 260 µm wide and 377 µm high; vestiture indicated by the insertion holes of setae, grouped into three anterior longitudinal zones and two posterior zones on scutum, and two zones on scutellum (Pl. 1, Fig. 3A).

Legs short, shorter than whole body.

Abdomen 828 µm long excluding genital appendages, 379 µm wide; dorsal surfaces of all abdominal segments bearing few setae, indicated by insertion holes; female genital appendages: two elongated subgenital plates (Sub), 95 µm long and 77 µm wide; cerci (Cer) 132 µm long and 77 µm wide (Fig. 3B, 3C).

Discussion

As *Trichomyia lengleti* sp. nov. is a psychodid that has a typical trichomyiine-wing structure characterized by the radial sector with only one vein between radial and medial forks, and CuA2 vein well-developed, we assign it to the Trichomyiinae.

Trichomyia lengleti differs from all the recent and fossil species belonging to Trichomyiinae in its antenna with 15 flagellomeres, while Trichomyiinae have usually antenna with 16 antennomeres, the sixteenth being very diminutive or occasionally fused to fifteenth (Duckhouse 1965). *T. lengleti* has flagellomeres 12 to 15 gradually reduced comparing to the more basal ones, a character inexistent in all known Trichomyiinae. Such a reduction in the terminal three or more flagellomeres is known in some Psychodinae.

Even if the antennal structures of *T. lengleti* are unique within the Trichomyiinae, we prefer to assign it to *Trichomyia sensu lato*, as the male genital appendages are not available (*Eotrichomyia* differs from *Trichomyia* in the male genital appendages), and the palps are not visible. There are not enough arguments to create a new genus. *T. lengleti* would fall in the group A of Duckhouse (1965) after its head with well-developed vertex, first flagellomere almost 1.5 times as long as other flagellomeres, elongate-pyriform flagellomeres, and in addition to very reduced and drop-like last flagellomere. Nevertheless *T. lengleti* shares with the group B of Duckhouse (1965) the well-developed digitate ascoids.

T. lengleti is in a piece of amber which contains at least 15 well-preserved arthropods (among which Diptera notably represented by Dolichopodidae [*Microphorites* Hennig, 1971] and Psychodidae, Hymenoptera: Diapriidae [*Lengletia chanieraudi* Lak & Nel, 2008], Blattodea, and decapod Tanaidacea), and five plant remains and micro-inclusions (mainly freshwater testate amoebae) (Girard *pers. com.*). The sedimentological characteristics of the amber deposit and the arthropod species found in other amber pieces allow interpreting the palaeoenvironement of *T. lengleti* as an estuarine forest, located at the boundary between marine and freshwater influences (Perrichot *et al*. 2007a, 2007b). Although the piece of amber is translucent enough to see some of the macro-inclusions, phase contrast X-ray imaging is necessary for most of them and remains preferable as a non-destructive technique.

Two other psychodoid flies, *Eophlebotomus carentonensis* Azar *et al.*, 2003, and *Sycorax neli* Azar *et al*., 2007, were hitherto described from the Albian amber of Charentes, SW France (Perrichot *et al*. 2007a) and Lebanon respectively (Azar *et al.* 2003, 2007b). These discoveries confirm those from the study of the Lower Cretaceous Lebanese psychodoids about the very high diversity of this group in the Mesozoic.

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Appendix: List of fossil Trichomyiinae:

Fossil taxa	**Age**	**Deposit**
Trichomyia buceras Loew, 1845	Holocene	Copal of "Ostindische"= eastern India or the Indonesian Archipelago
Trichomyia antiquaria Quate, 1961 *Trichomyia declivivena* Quate, 1963 *Trichomyia discalis* Quate, 1963 *Trichomyia glomerosa* Quate, 1963 *Trichomyia mecocerca* Quate, 1963 *Trichomyia smithi* Quate, 1963	Oligocene/Miocene	Mexican Amber
Eatonisca tertiaria Meunier, 1905 *Trichomyia brevicornis* Loew, 1850 *Trichomyia concinna* Meunier, 1905 *Trichomyia crassicornis* Meunier, 1905 *Trichomyia decora* Meunier, 1905 *Trichomyia distincta* Meunier, 1905 *Trichomyia formosula* Meunier, 1905 *Trichomyia longicornis* Loew, 1850 *Trichomyia nova* Meunier, 1905 *Trichomyia procera* Meunier, 1905 *Trichomyia pulchra* Meunier, 1905 *Trichomyia tenera* Meunier, 1905	Eocene	Baltic and Saxonian ambers Baltic amber
Eotrichomyia electronica Nel et al., 2002	Lower Eocene	Oise French Amber
Trichomyia lengleti sp. nov.	Lower Cenomanian	Charente French amber

N.B. *Trichomyia swinhoei* Cockerell, 1917 has been omitted from the list as this species undoubtedly belongs to the subfamily Sycoracinae.

Figure captions

Pl. 1: *Trichomyia lengleti* sp. nov., General habitus, 3D-reconstruction using local phase contrast microtomography. *A*, dorsal view; *B*, left-side view; *C*, dorsal view. Scale bar = 500 µm, pixel size = 1.4 µm.

Fig. 1: *Trichomyia lengleti* sp. nov. *A*, detail of head, 15 flagellomeres visible on left antenna. Pixel size = 1.4 µm, scale bar = 200 µm; *B*, detail of antennae, white arrows: sigmoidal ascoids. Pixel size = 1.4 µm, scale bar = 200 µm; *C*, drawing of sigmoid ascoids on a: inner view; b: outer view; c: ventro-lateral view. Scale bar = 50 µm.

Fig. 2: *Trichomyia lengleti* sp. nov. *A*, left wing, missing parts of veins appear in grey dotted lines. Pixel size = 1.4 µm; *B*, drawing of wing. Scale bar = 500 µm.

Fig. 3: *Trichomyia lengleti* sp. nov. *A*, thorax in latero-dorsal view. Scale bar = 500 µm, pixel size = 1.4 µm; *B*-*C*, details of female genitalia, respectively 3D-reconstruction and drawing, subgenital plates Sub, cerci Cer. Pixel size = 1.4 µm, scale bars = 200 µm.