

New fossil bee flies (Diptera: Bombylioidea) in the Lowermost Eocene amber of the Paris Basin

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ABSTRACT

A new genus and two new species of bee flies are described from the Lowermost Eocene amber of the Paris basin: *Paradolichomyia eocenica* n. gen, n. sp. (Bombyliidae: Toxophorinae) and *Proplatypygus matilei* n. sp. (Mythicomyiidae). *Paradolichomyia eocenica* n. gen, n. sp. represents the oldest fossil record of Bombyliidae. It is closely related to the two modern genera *Dolichomyia* WIEDEMANN 1830 and *Zaclava* HULL 1973 (Toxophorinae: Systropodini). This discovery suggests that the present Gondwanan distribution of the Systropodini is an artefact related to the climatic changes in the Tertiary. *Proplatypygus matilei* n. sp. appears to be more closely related to the Baltic amber species *P. succineus* HENNIG 1969 than to the Upper Cretaceous amber *P. rohdendorfi* ZAITZEV 1986.

KEYWORDS | Insecta. Diptera. Bombyliidae. n. gen. n. sp. Eocene Amber. France.

INTRODUCTION

Bombyliid flies are not rare in the fossil record, with 33 described genera and 51 species (Evenhuis, 1991, 1994). We have recently discovered in the Eocene amber of the Paris basin an extraordinary fossil fly, with a rounded head and a very long 'neck', that we describe below.

The phylogenetic relationships, monophyly and composition of the Bombyliidae are still rather controversial. Among other authors, Yeates and Irwin (1992, fig. 55) excluded *Heterotropus* LOEW from the Bombyliidae and characterized the family on the sole basis of the potential autapomorphy 'larvae parasitic, with hypermetamorphosis', after Woodley (1989). Yeates (1992) excluded the *Pro-rates* group of genera and transferred it into the Scenopinidae. Wiegmann et al. (1993) indicated that the Bombyliidae *s.l.* is 'apparently paraphyletic'. Sinclair et al. (1994) supported the monophyly of the Bombyliidae, on the basis of the genital structures, but 'exclusive of

Mythicomyiinae and *Heterotropus* LOEW'. Yeates and Wiegmann (1999) added that 'morphologically, the monophyly of Bombyliidae is not well supported', even after the exclusion of several other lineages.

The subfamily classification of the Bombyliidae is also controversial. Important changes occurred between the works of Mülhenberg (1971), Hull (1973), Zaitzev (1992) and Yeates (1994). We follow the latter work because it is the only available cladistic analysis of the whole family.

We follow the body and wing venation terminology of McAlpine (1981a) and of Yeates (1994).

SYSTEMATIC PALAEONTOLOGY

Superfamily: Bombylioidea LATREILLE, 1802

Family: Bombyliidae LATREILLE, 1802

Subfamily: Toxophorinae SCHINER, 1868

GENUS *Paradolichomyia* n. gen.

Type species: Paradolichomyia eocenica, by monotypy.

Diagnosis: This new genus belongs to the Toxophorinae (*sensu* Yeates, 1994). It differs from all modern genera of this subfamily in the following characters: (1) antepnotum enlarged, saddle-like; (2) neck very elongate; (3) body nearly completely bare; (4) crossvein dm-cu straight, not sigmoidal; (5) occiput strongly tumid.

Etymology: After its close relationship with the genus *Dolichomyia*. Gender is feminine.

Paradolichomyia eocenica n. sp.
Figures 1 and 2

Material: Holotype specimen PA 8334, in collection De Ploëg deposited in Muséum National d'Histoire Naturelle, Paris.

Occurrence: Le Quesnoy, Chevrière, region of Creil, Oise department, France.

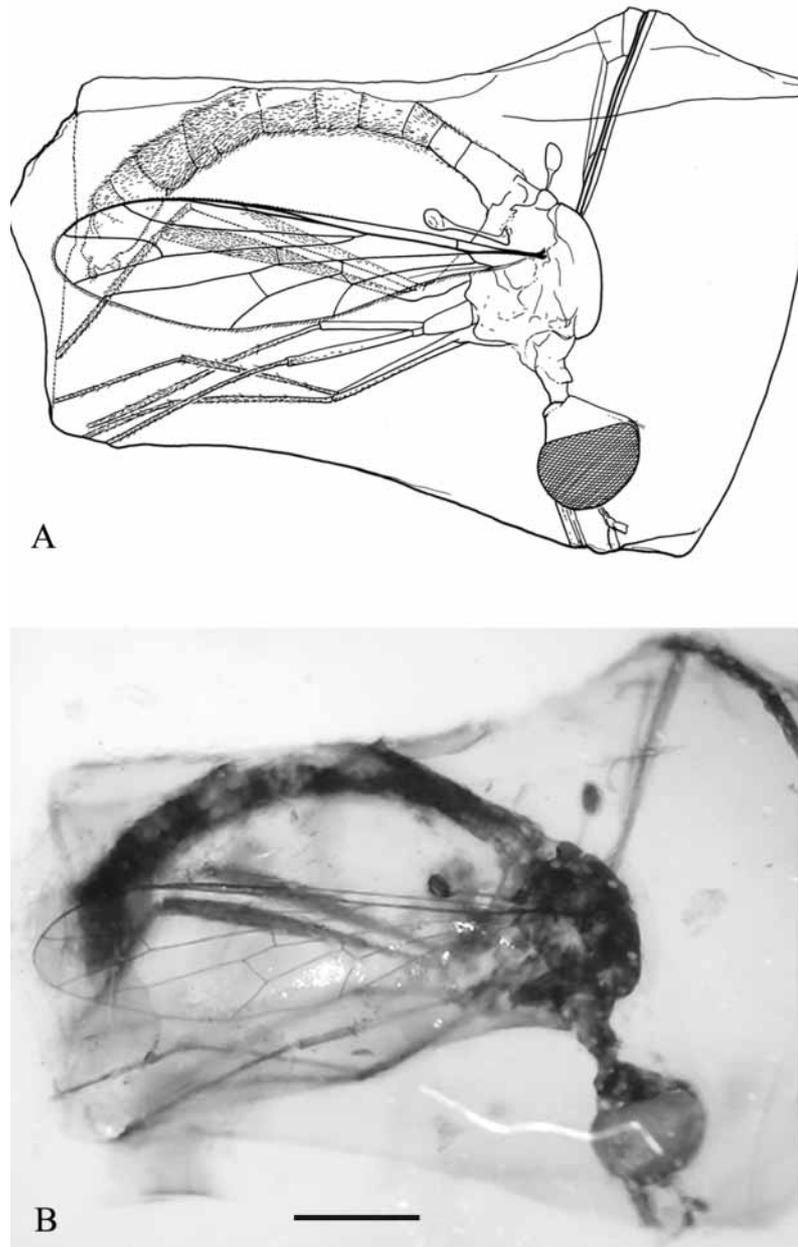


FIGURE 1 | *Paradolichomyia eocenica* n. gen., n. sp., holotype specimen PA 8334. A) Habitus reconstruction. B) Photograph of general habitus (scale bar: 1 mm).

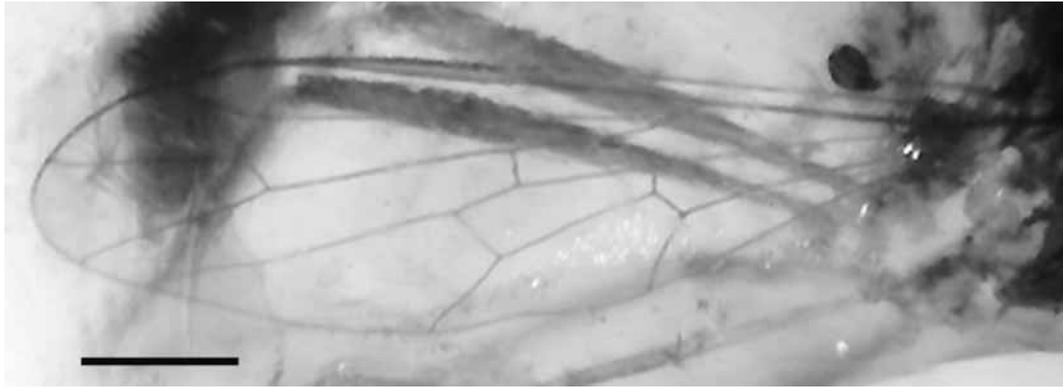


FIGURE 2 | *Paradolichomyia eocenica* n. gen., n. sp., holotype specimen PA 8334, photograph of wing (scale bar: 0,5 mm).

Geological age: Lowermost Eocene, Sparnacian, level MP7 of the mammal fauna of Dormaal. It was demonstrated that the amber is autochthonous and very different from Baltic amber in age, chemical composition, and origin (Nel et al., 1999).

Etymology: After the Eocene period.

Diagnosis: That of the genus.

Description: Head nearly bare, rounded, 0.88 mm long; face not tumid (Fig. 1A); vertex not concave; postcranium (occiput) strongly tumid, without concavity surrounding occipital foramen; only few short setae along occipital margin, occiput bare; maxillary palpus present, rather large, 0.1 mm long and 1-segmented; palpal pit absent; maxilla rather long, 2-3 times longer than palpus; apical end of antennae missing; eyes dorsally holoptic, meeting for long distance along midline, covering nearly all anterior part of head; facets subequal, not smaller ventrally than dorsally; posterior eye margin simple; ocellar tubercle posteriorly projected, with 2 large, anteriorly directed setae, 40 μ m long; 'labrum + mandibles + labrum-epipharynx' (proboscis) very long and slender (preserved part nearly as long as eye), but its distal part is missing; first antennal segment cylindrical long and slender, 0.1 mm long, with few short setae; second short, 0.04 mm long, widest apically and as long as its apical width, with crown of short setae; third segment long, laterally compressed, with numerous very short setae, but distal part missing.

Thorax bare (Fig. 1B); antepronotum enlarged, saddle-like with very long anterior part, 0.3 mm long, and two anterior humps; second laterocervical sclerite with large anterior part; first laterocervical sclerite triangular; neck very elongate; flange above wing base; prealar bristles present but small; anepimeron, laterotergite and mediotergite bare; laterotergite and mediotergite with small ridge; metepisternum and metepimeron enlarged.

Wing narrow (Fig. 2), subpetiolated, 3.46 mm long, 0.9 mm wide; C apparently continuing around wing, not ending at apex; basal section of Rs short, R_{2+3} branching obliquely from R_{4+5} , simple, slightly curved at its distal end; R_{4+5} branched; R_4 sigmoidal; R_5 nearly straight; spurious vein undeveloped; M_2 absent; discoidal cell dm 0.72 mm long and 0.24 mm wide; cell bm with 3 distal corners; CuA_2 reaching posterior wing margin; CuP reduced, not reaching CuA_2 and vanishing in narrow area between CuA_2 and posterior wing margin; A_1 and A_2 absent; alula very reduced; numerous scales present in posterior part of wing.

Legs very long and slender; prothoracic femur 0.9 mm long, tibia 1.14 mm long; mesothoracic femur 1.04 mm long, tibia about 1.44 mm long, metathoracic femur not strongly swollen, 1.9 mm long, 0.12 mm wide, tibia about 1.4 mm long; tarsi also very long but incomplete; mesothoracic and metathoracic coxae well separated.

Abdomen very elongated and narrow, about 4.1 mm long; spiracles not visible in tergites, probably located in pleural membrane; apical end of abdomen partly destroyed; epandrium with posterior margin concave.

Discussion: After the key to dipteran families proposed by McAlpine (1981b), this fossil taxon falls into the Bombyliidae, because of its large eyes meeting dorsally, wing venation, vertex not concave, ocellar tubercle in a posterior position, and one-segmented palpus.

If we follow the key to the Nearctic genera of Hall (1981), this fossil would fall into the Toxophorinae (*Lepidophora* WESTWOOD 1835 and *Toxophora* MEIGEN 1803). After the key of the Palearctic Bombyliidae of Greathead and Evenhuis (1997), it would fall in Toxophorinae close to *Systropus* WIEDEMANN 1820. After the key of Zaitzev (1992), it falls into the Systropodidae (= Sys-

tropodinae + Toxophorinae). After the key of Yeates (1994), it also falls into the Toxophorinae.

The significance of these groups has greatly varied in the literature. Rohdendorf (1960), followed by Krivosheina (1990, 1991), proposed to separate the Systropodidae from the Bombyliidae. Zaitzev (1992) followed her and proposed to divide Systropodidae into Systropodinae (*Systropus*, *Dolichomyia* WIEDEMANN 1830 and *Zaclava* HULL 1973) and Toxophorinae. He included in this last group the genera *Toxophora*, *Lepidophora* and *Palintonus* FRANÇOIS 1964. Yeates (1994) criticized Zaitzev's work and divided the Toxophorinae into Toxophorini (*Toxophora*), Gerontini (*Geron* MEIGEN 1820) and Systropodini (*Systropus*, *Dolichomyia* and *Zaclava*).

The antepnotum of *Paradolichomyia* n. gen. is as enlarged as that of *Toxophora* (main autapomorphy of Toxophorini), but it is bare, instead of having large setae and its shape is completely different, not rounded but saddle-like. Thus, it could correspond to a superficial convergency rather than to a synapomorphy. Nevertheless, *Paradolichomyia* n. gen. and *Toxophora* share the large anteriorly directed setae on ocellar tubercle and presence of scales on wings.

Paradolichomyia n. gen. has its metepisternum and metepimeron enlarged and its abdomen elongate and cylindrical as in Systropodini (main autapomorphies). Furthermore, the antennae of *Paradolichomyia* n. gen. are more similar to those of *Dolichomyia* than to any other Toxophorinae, with the second segment short and rounded (Hull, 1973). Also, its petiolated wing with anal vein very reduced is a potential synapomorphy with *Dolichomyia* and *Zaclava*. This vein is completely absent in *Zaclava*, also, its metathoracic femora are strongly swollen, unlike in *Paradolichomyia* n. gen. This would suggest a closer affinity between *Paradolichomyia* n. gen. and *Dolichomyia* but *Paradolichomyia* n. gen. shares with *Zaclava* the occiput well exposed and the presence of long anteriorly directed setae on the ocellar tubercle (Hull, 1973).

The exact affinities of *Paradolichomyia* n. gen. with Toxophorini and Systropodini remain difficult to establish, but it is probably more closely related to the two genera *Dolichomyia* and *Zaclava*.

Comparison with the fossil taxa attributed to the Toxophorinae sensu Yeates (1994)

Hull (1973) and Evenhuis (1994) listed 11 species attributed to the 'Toxophorinae' and 'Systropodinae'. All are fossil impressions on Oligocene lacustrine sediments from North America and Western Europe. All these species need redescription because they are rather incom-

pletely described and important characters of the head and thorax are not indicated. Only their wing venation is rather well known.

The fossil genus *Melanderella* COCKERELL 1909 (one species *M. glossalis* COCKERELL 1909, Oligocene, Florissant, Colorado, U.S.A.), attributed to the 'Systropinae' by Hull (1973), differs from *Paradolichomyia* n. gen. in its vein R_{2+3} separating from R_{4+5} at the very base of R_s and in its anal cell large and complete, closed on the posterior wing margin (which implies the presence of a complete anal vein) (Cockerell, 1909a). These fossils share a cross-vein dm-cu straight, not sigmoidal.

The fossil genus *Pachysystropus* COCKERELL 1909 (two species *P. rohweri* COCKERELL 1909 and *P. condemnatus* COCKERELL 1910, Oligocene, Florissant, Colorado, U.S.A.) has a closed anal cell (Cockerell, 1909b, 1910).

The original description of *Dolichomyia tertiarica* COCKERELL 1917 (Oligocene, Florissant, Colorado, U.S.A.) is very poor and incomplete. The main information is that its 'venation is exactly like *Dolichomyia*' (Cockerell, 1917). A revision of this fossil is necessary.

Dolichomyia testea (MELANDER 1949) (Oligocene, Florissant, Colorado, U.S.A., named *Dolichomyia testacea* in Evenhuis, 1994). This species was originally placed in the genus *Melanderella*, maintained in this genus by Hull (1973), but transferred to *Dolichomyia* by Evenhuis (1994), without explanation and redescription. It differs from *Paradolichomyia* n. gen. (and *Dolichomyia*) in its metathoracic femora incrassate (Melander, 1949).

Only the wing venation of *Systropus acourti* COCKERELL 1921 (Upper Eocene, Gurnet Bay, Isle of Wight, U.K.) is described. It has a closed anal cell (Cockerell, 1921). *Systropus rottensis* MEUNIER 1917 (Oligocene, Rott-am-Siebengebirge, Germany) has also a closed anal cell, unlike *Paradolichomyia* n. gen.

The fossil genus *Alepidophora* COCKERELL 1909 (3 species from the Oligocene, Florissant, Colorado, U.S.A., *A. pealei* COCKERELL 1909, *A. cockerelli* MELANDER 1949, *A. minor* MELANDER 1949 and one species *A. maxima* LEWIS 1972 from the Oligocene of the Ruby River basin, Montana, U.S.A.) is considered as a Toxophorinae in Hull (1973). They have closed anal cells and rather broad abdomens (Cockerell, 1909b; Melander, 1949; Lewis, 1972).

Superfamily: Bombylioidea LATREILLE, 1802

Family: Mythicomyiidae MELANDER, 1902

GENUS *Proplatypygus* HENNIG 1969

Type species: Proplatypygus succineus HENNIG 1969.

Other species: Proplatypygus rohdendorfi ZAITZEV 1986, *Proplatypygus matilei* n. sp.

Remark: The mythicomyiid flies have been treated traditionally as a subfamily of the Bombyliidae. Zaitzev (1992) raised them to familial status and demonstrated they are probably monophyletic. Yeates (1994) corroborated this hypothesis but considered them as a subfamily of the Bombyliidae. Evenhuis (1994) considered them as a separate family.

***Proplatypygus matilei* n. sp.**

Figure 3

Material: Holotype specimen PA 2358 (sex unknown), in collection De Plöëg housed in Muséum National d'Histoire Naturelle, Paris.

Occurrence: Le Quesnoy, Chevrière, region of Creil, Oise department, France.

Geological age: Lowermost Eocene, Sparnacian, level MP7 of the mammal fauna of Dormaal.

Etymology: To the memory of Professor Loic Matile, Dipterologist at the Muséum National d'Histoire Naturelle, Paris.

Diagnosis: This species differs from *Proplatypygus succineus* and *Proplatypygus rohdendorfi* in its relatively narrow cell dm, more than twice longer than broad, veins CuA₂ and A₁ well separated, thorax excessively hump-backed and scutellum higher than long.

Description: Head nearly bare, rounded, 0.7 mm long; face not tumid (Fig. 3B); vertex not concave; postcranium (occiput) more or less flat, without concavity surrounding occipital foramen; no visible setae along occipital margin, occiput bare; maxillary palpus absent; maxillae not visible; labrum with short microtrichia at apex; 'labrum + mandibles + labrum-epipharynx' (proboscis) shorter than the head, 0.4 mm long; eyes strongly approximate with front very narrow; eyes not dorsally meeting, but broad and covering nearly all anterior part of head; facets not smaller ventrally than dorsally; posterior eye margin simple; ocellar tubercle posteriorly projected, but without any setae; first antennal segment cylindrical nearly as long as second; second short, broader than first; third segment pear-shaped, narrowed apically, longer than second, laterally compressed, with numerous very short setae; flagellum very slender, as long as third segment, with small apical flagellomere.

Thorax bare and high (Fig. 3A and 3C); anteprepronotum not enlarged, mesonotum strongly humped, rounded and

convex, 0.66 mm high, with several rows of minute setae; scutellum bare, flattened and narrow, higher than long.

Wing hyaline, not petiolated, 2.5 mm long, 0.72 mm wide; C ending at wing apex, midway between apices of R₄₊₅ and M₁; basal section of Rs 0.32 mm long, R₂₊₃ branching obliquely from R₄₊₅, simple, slightly curved at

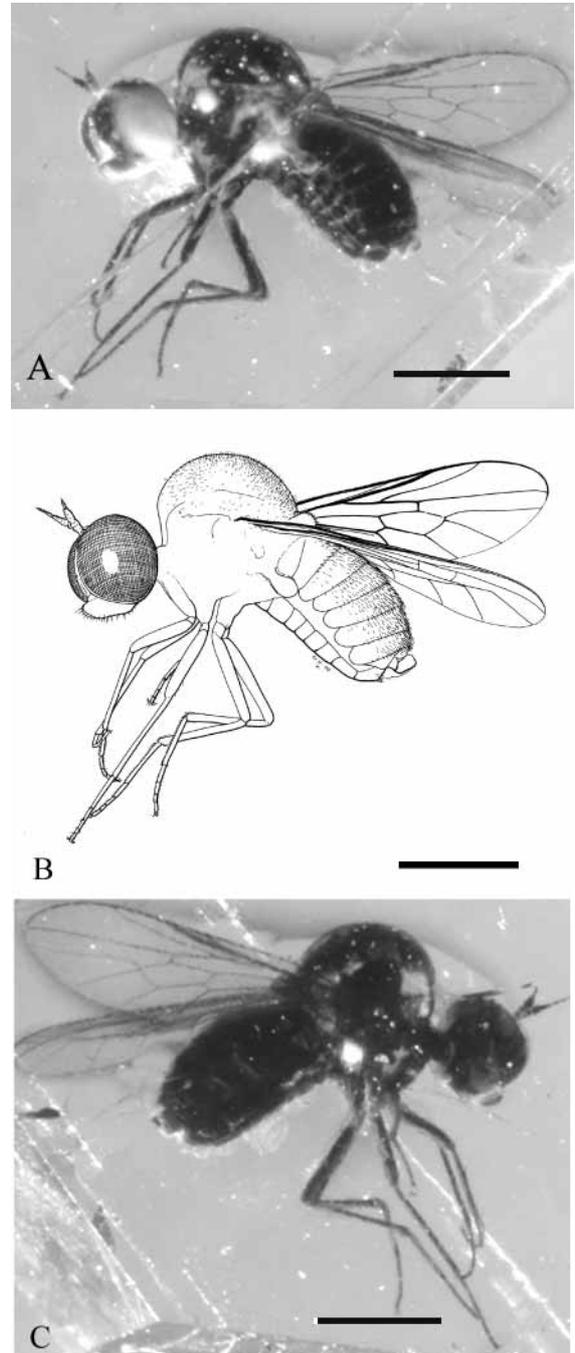


FIGURE 3 | *Proplatypygus matilei* n. sp., holotype specimen PA 2358. A) Photograph of general habitus, left. B) Habitus reconstruction. C) Photograph of general habitus, right. Scale bar: 1 mm.

distal end on anterior wing margin; R_{4+5} unbranched and straight; spurious vein undeveloped; M_1 sigmoidal; R_{4+5} and M_1 parallel at wing margin; M_2 present, straight; discoidal cell dm broad, 0.56 mm long and 0.20 mm wide; CuA_2 reaching A_1 very close to posterior wing margin; A_2 not visible; no scales on wing surface.

Legs long and slender; prothoracic femur 0.60 mm long, tibia 0.72 mm long; mesothoracic femur about 0.70 mm long, metathoracic femur, 0.80 mm long, 0.10 mm wide; tarsi five-segmented; pulvilli rounded; empodia absent; claws curved; both tibiae and femora with numerous setae but no spines.

Abdomen short and obtuse, about 1.40 mm long and 0.80 mm high; spiracles located on tergites; genital structures not visible.

Discussion: After the key of families proposed by McAlpine (1981b), this fossil falls into the 'Bombyliidae', because of its empodia absent, palpus absent, CuA_2 joining A_1 , spurious vein absent, structure of vein M, vertex not concave, ocellar tubercle rejected posteriorly, and cell dm present.

After the key of Zaitzev (1992), *Proplatypygus matilei* n. sp. falls into the 'Mythicomyiidae' because of the simple R_{4+5} , abdominal spiracles on tergites, head distinctly smaller than large mesothorax. *Proplatypygus matilei* n. sp. also falls into the 'Mythicomyiinae' sensu Yeates (1994) because of: (1) postcranium flat, without a concavity surrounding occipital foramen; (2) R_{4+5} simple (synapomorphy, after Yeates, 1994); (3) palpus absent (synapomorphy, after Yeates, 1994); (4) abdominal spiracles on tergites (synapomorphy, after Yeates, 1994); (5) labrum with small hair at apex; and (6) costal vein ending between apices of R_{4+5} and M_1 .

The division of the 'Mythicomyiinae' sensu Yeates (1994) into subgroups remains controversial. Yeates (1994) noted that 'the subfamily is urgently in need of revision using a larger spectrum of characters.' Nevertheless, this author recognized five tribes, i.e. the Psiloderini, Cyrtosiini, Platypygini, Mythicomyiini, and Empidideicini. Zaitzev (1992) divided his 'Mythicomyiidae' into Platypyginae, Cyrtosiinae and 'Mythicomyiinae'.

The [Platypyginae & Cyrtosiinae] sensu Zaitzev (1992) more or less corresponds the Platypyginae sensu Hull (1973) (= Psiloderini & Cyrtosiini & Platypygini sensu Yeates, 1994). The only difference is the genus *Cephalodromia* BECKER 1912, synonymized with *Cyrtosia* PERRIS 1839 by Hull (1973) but apparently restored by Zaitzev (1992). The Psiloderini contain the genus *Psiloderoides* HESSE 1967. The 'Mythicomyiinae' sensu Zaitzev (1992) comprise the same genera as in Hull

(1973), plus the genus *Mnemomyia* BOWDEN 1975. Zaitzev also considers *Acoecus* HULL 1973 and *Cyrtoides* ENGEL 1933 as genuine genera, unlike Hull (1973) who considered them as subgenera. Zaitzev (1992) and Yeates (1994) separated the 'Mythicomyiinae' into Empidideicini [= genera *Empidideicus* BECKER 1907, *Cyrtoides*, *Anomaloptilus* HESSE 1938, *Leylaiya* EFFLATTOUN 1945 and *Mnemomyia* (see Bowden, 1975)] and the Mythicomyiini. Lastly, Greathead and Evenhuis (2001) revised the African subfamilies and genera of Mythicomyiidae and proposed a new classification we follow herein.

Following their key, this fossil would fall in the subfamily Platypyginae because the following characters: vein R_{4+5} ending in C at a level clearly well beyond end of vein M_2 ; R_{2+3} present, well separated from R_1 and long, similar to R_{4+5} . Nevertheless, it shares with the subfamily Leylaiyinae Greathead and Evenhuis 2001 the veins R_{4+5} and M_1 parallel at wing margin. Thus, its subfamily position remains uncertain.

We exclude our fossil taxon from the Empidideicinae because they have no free vein R_{2+3} , the Mythicomyiinae because their R_{2+3} ends in R_1 , and the Glabellulinae because their R_{4+5} and M_1 are diverging. The Psiloderoidinae have their vein R_{2+3} distinctly shorter than that of *P. matilei* n. sp. and very divergent from R_{4+5} . Evenhuis (2001, p. 137) described the African genus *Hesychastes* that 'does not fit in any of the existing subfamilies'. It differs from *P. matilei* in its R_{2+3} ending in the C just beyond the junction of R_1 with the C.

Within the Platypyginae, this fossil does not fall in *Cephalodromia* and *Cyrtosia* because of its closed cell dm. *Cyrtosia* SÉGUY 1930 has a very long proboscis, its vein Sc is incomplete and its thorax is not excessively humpbacked, unlike *P. matilei* n. sp. The species of *Platypygus* LOEW 1844 have a long proboscis, 'a little longer than the length of the head' (Hull, 1973). *Ahessa* GREATHEAD and EVENHUIS 2001 has its R_1 short, ending in C before level of r-m cross-vein, unlike *P. matilei* n. sp.

Among the fossil taxa attributed to the Mythicomyiidae sensu Evenhuis (1994), *Glabellula electrica* (HENNIG 1966) [Upper Eocene Baltic amber, originally described under the fossil genus *Proglabellula* HENNIG 1966 and synonymized with the Recent taxon *Glabellula arctica* ZETTERSTEDT 1838 by Schumann (1991), followed by Evenhuis (1994)], *Glabellula hannemanni* SCHUMANN 1991 (Miocene Saxonian amber, Germany) and *Glabellula kuehnei* SCHLÜTER 1976 (Oligo-Miocene amber of Dominican Republic) have the typical wing venation of the Mythicomyiini (Hennig, 1966; Schlüter, 1976; Schumann, 1991).

Palaeoplatypygus zaitzevi KOVALEV 1985 (in Kalugina and Kovalev, 1985) [Middle Jurassic of Siberia] has a very broad cell dm, only slightly longer than broad, unlike *P. matilei* n. sp. *Protocyrtosia sukatshevae* ZAITZEV 1986 (Upper Cretaceous, Taymyr, Siberian amber) has its veins M_1 and M_2 arising from a common base, unlike *P. matilei* n. sp.

The fossil genus *Proplatypygus* comprises two species, *P. succineus* from the Baltic amber and *P. rohdendorfi* from the Taymyr amber (Upper Cretaceous, Siberia). *Proplatypygus matilei* n. sp. shares with this genus a very similar wing venation, shape of the thorax, abdomen, head, antenna, and short probosci. *P. rohdendorfi* differs from *P. matilei* n. sp. in its broader cell dm and veins CuA_2 and A_1 well separated. *P. succineus* and *P. matilei* n. sp. have nearly the same wing venation, the main difference being the distal fusion of CuA_2 with A_1 in *P. matilei* n. sp. This last species also differs from *P. succineus* in its excessively humpbacked thorax and its higher than long scutellum.

Zaitzev (1986) considered that *Proplatypygus* is 'closest to the modern *Platypygus*'. Greathead and Evenhuis (2001, p. 129) included it in the Psiloderoidinae, but the vein R_{2+3} is not much shorter than R_{4+5} in this genus. Because of the lack of phylogenetic analysis of the Mythicomyiinae *sensu* Yeates (1994), it is impossible to precisely determine its exact affinities within this group.

Biogeographic and palaeoclimatic implications

The genus *Systropus* is Nearctic, Neotropical, Afrotropical, Indo-Malaysian, Australian and Eastern Palaearctic (South China) (Evenhuis and Greathead, 1999). *Zaclava* is known from the Australian and Pacific region. *Dolichomyia* is Nearctic and Neotropical (Hull, 1973; Zaitzev, 1986; Evenhuis, 1979). The presence of a fossil species closely related to the Systrophorini in the Lowermost Eocene (and probably also Oligocene, if the previously described species are correctly attributed) of Europe suggests that the primarily Gondwanan pattern of distribution of this group is not relictual but just an artefact of extinction due to climatic changes in the Tertiary. The previous oldest fossil records of the Bombyliidae *sensu stricto* were from the Upper Eocene Baltic amber (Evenhuis, 1994; Greathead and Evenhuis, 2001). The present new genus and species together with the very recent discoveries (June 2002) in the same French amber and in the Paleocene paleolake of Menat (Puy-de-Dôme, France) of other Bombyliidae belonging to very different subfamilies suggest that this family is older than previously supposed and probably appeared during the Upper Cretaceous (Nel, under study).

The Mythicomyiidae are more or less distributed over all continents and are present under a wide range of climates, although they seem to be less frequent in the intertropical regions (Hull, 1973, text-figs. 36 and 39). Because of the lack of phylogenetic analysis, the fossil species of *Proplatypygus* cannot be used to infer any palaeoclimatic information (Nel, 1997).

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REFERENCES

- Bowden, J., 1975. Studies in African Bombyliidae. 10. Taxonomic problems relevant to a catalog of Ethiopian Bombyliidae, with description of new genera and species. *Journal of the Entomological Society of Southern Africa*, 38(2), 305-320.
- Cockerell, T.D.A., 1909a. Fossil insects from Florissant, Colorado. *Bulletin of the American Museum of Natural History*, 26, 67-76.
- Cockerell, T.D.A., 1909b. Description of Tertiary insects. Part 5. *American Journal of Science*, 4(27), 53-58.
- Cockerell, T.D.A., 1910. Fossil insects and a crustacean from Florissant, Colorado. *Bulletin of the American Museum of Natural History*, 28, 275-288.
- Cockerell, T.D.A., 1917. A fossil tse-tse fly and other Diptera from Florissant, Colorado. *Proceedings of the Biological Society of Washington*, 30, 19-22.
- Cockerell, T.D.A., 1921. Fossil arthropods in the British Museum. 6. Oligocene insects from Gurnet Bay, Isle of Wight. *Annals and Magazine of Natural History*, 9(7), 453-480.
- Evenhuis, N.L., 1979. Studies in Pacific Bombyliidae (Diptera). 1. A new species of *Zaclava* from the Loyalty Islands and New Caledonia, with a key to species in the genus. *Pacific Insects*, 20(1), 87-89.
- Evenhuis, N.L., 1991. World catalog of genus-group names of bee flies (Diptera: Bombyliidae). Honolulu, Bishop Museum Bulletin in Entomology, 5, 1-105.
- Evenhuis, N.L., 1994. Catalog of the fossil flies of the World (Insecta: Diptera). Leiden, ed. Backhuys Publishers, 570 pp.
- Evenhuis, N.L., 2001. A new 'microbombyliid' genus from the Brandberg Massif, Namibia (Diptera: Mythicomyiidae). *Cimbebasia*, 17, 137-141.
- Evenhuis, N.L., Greathead, D.J., 1999. World catalogue of bee flies (Insecta: Diptera). Leiden, ed. Backhuys Publishers, xviii + 756 pp.
- Greathead, D.J., Evenhuis, N.L., 1997. Family Bombyliidae. In: Papp, L., Darvas, B. (eds.). *Contributions to a manual of Palaearctic Diptera* (with special reference to flies of eco-

- onomic importance), volume 2, Nematocera and lower Brachycera. Budapest, Science Herald, 487-512.
- Greathead, D.J., Evenhuis, N.L., 2001. Annotated keys to the genera of African Bombylioidea (Diptera: Bombyliidae; Mythicomyiidae). *African Invertebrates*, 42, 105-224.
- Hall, J.C. 1981. Bombyliidae. In: McAlpine, J.F., Peterson, B.V., Shewell, G.E., Teskey, H.J., Vockeroth, J.R., Wood, D.M. (coord.). *Manual of Nearctic Diptera*, 1, Research Branch, Ottawa, Ontario, Agricultural Canada Monograph, 27, 589-602.
- Hennig, W., 1966. Bombyliidae im Kopal und im Baltischen Bernstein. *Stuttgarter Beiträge zur Naturkunde*, 166, 1-21.
- Hennig, W., 1969. Kritische Betrachtungen über der phylogenetischen Bedeutung von Bernsteinfossilien: die Gattungen *Proplatypygus* (Diptera, Bombyliidae) und *Palaeopsylla* (Siphonaptera). *Memorie della Societa Entomologica Italiana*, 48, 57-67.
- Hull, F.M., 1973. Bee flies of the World. The genera of the family Bombyliidae. *Bulletin of the United States National Museum*, 286, 1-687.
- Kalugina, N.S., Kovalev, V.G., 1985. Insecta Diptera of the Jurassic in Siberia. *Akademiya nauk SSSR, Paleontologicheskij Institut, Moskovskogo Obshchestva Ispytatelej Prirody*, 198 pp. [in Russian.]
- Krivosheina, N.P., 1990. Phyletic relationships and evolution of the lower Diptera Brachycera. *Entomological Review*, 69(3), 138-150.
- Krivosheina, N.P., 1991. Phylogeny of lower Brachycera (Diptera), a new view. *Acta Entomologica Bohemoslovaca*, 88, 81-93.
- Latreille, P.A., 1802. *Histoire naturelle, générale et particulière des Crustacés et des Insectes. Partie 3. Familles naturelles et genres*, Paris, ed. Dufart, 479 pp.
- Lewis, S.E., 1972. A new species of fossil bee fly (Diptera: Bombyliidae) from the Ruby River basin (Oligocene) of Southwestern Montana. *Annals of the Entomological Society of America*, 65(6), 1421.
- McAlpine, J.F., 1981a. Morphology and terminology - adult. In: McAlpine, J.F., Peterson, B.V., Shewell, G.E., Teskey, H.J., Vockeroth, J.R., Wood, D.M. (coord.). *Manual of Nearctic Diptera*, 1, Research Branch, Ottawa, Ontario, Agricultural Canada Monograph, 27, 9-63.
- McAlpine, J.F., 1981b. Key to families - adult. In: McAlpine, J.F., Peterson, B.V., Shewell, G.E., Teskey, H.J., Vockeroth, J.R., Wood, D.M. (coord.). *Manual of Nearctic Diptera*, 1, Research Branch, Ottawa, Ontario, Agricultural Canada Monograph, 27, 89-124.
- Melander, A.L., 1902. A monograph of the North American Empididae. Part 1. *Transactions of the American Entomological Society*, 28, 195-367.
- Melander, A.L., 1949. A report on some Miocene Diptera from Florissant, Colorado. *American Museum Novitates*, 1407, 1-63.
- Meunier, F., 1917. *Sur quelques insectes de l'Aquitainien de Rott (Sept-Montagne, Prusse rhénane)*. Amsterdam, Verhandelingen der Koninklijke Academie van Wetenschappen, 2^o série, 20(1), 3-17.
- Mühlenberg, M., 1971. Phylogenetisch-systematische Studien an Bombyliiden (Diptera). *Zeitschrift für Morphologie der Tiere*, 70(1), 73-102.
- Nel, A., 1997. The probabilistic inference of unknown data in phylogenetic analysis. In: Grancolas, P. (ed.). *The origin of Biodiversity in Insects: phylogenetic tests of evolutionary scenarios*. Paris, Mémoires du Muséum National d'Histoire Naturelle, 173, 305-327.
- Nel, A., de Plöeg, G., Dejax, J., Dutheil, D., de Franceschi, D., Gheerbrant, E., Godinot, M., Hervet, S., Menier, J.-J., Augé, M., Bignot, G., Cavagnetto, C., Duffaud, S., Gaudant, J., Hua, S., Jossang, A., de Lapparent de Broin, F., Pozzi, J.-P., Paicheler, J.-C., Bouchet, F., Rage, J.-C., 1999. Un gisement sparnacien exceptionnel à plantes, arthropodes et vertébrés (Éocène basal, MP7): Le Quesnoy (Oise, France). *Comptes-Rendus de l'Académie des Sciences, Paris, Sciences de la Terre et des Planètes*, 329, 65-72.
- Rohdendorf, B.B., 1960. Neue Angaben über das System der Dipteren. 11 Internationaler Kongreß für Entomologie, Verhandlungen, Wien, 17-25 August 1960, 1, 123-158.
- Schiner, J.R., 1868. Diptera. In: Wüllerstorff, U. (ed.). *Reise der österreichischen Fregatte Novara 1857-1859. Zoologische Theil*, 2(1), i-vi + 388 pp.
- Schlüter, T., 1976. Die Wollschweber-Gattung *Glabellula* (Diptera: Bombyliidae) aus dem oligozänen Harz der Dominikanischen Republik. *Stuttgart, Entomologica Germanica*, 2(4), 355-363.
- Schumann, H., 1991. Eine neue *Glabellula*-Art aus dem sächsischen Bernstein. *Deutsche Entomologische Zeitschrift*, (N.F.), 38(1-3), 79-84.
- Sinclair, B.J., Cumming, J.M., Wood, D.M., 1994. Homology and phylogenetic implications of male genitalia in Diptera - Lower Brachycera. *Entomologica Scandinavica*, 24(4), 407-432.
- Wiegmann, B.M., Mitter, C., Thompson, F.C., 1993. Evolutionary origin of the Cyclorrhapha (Diptera): tests of alternative morphological hypotheses. *Cladistics*, 9(1), 41-81.
- Woodley, N.E., 1989. Phylogeny and classification of the "Orthorrhaphous" Brachycera. In: McAlpine, J.F., Wood, D.M. (eds.). *Manual of Nearctic Diptera*, 3, Research Branch, Ottawa, Agricultural Canada Monograph, 32, 1371-1395.
- Yeates, D.K., 1992. Towards a monophyletic Bombyliidae (Diptera): the removal of the Proratinae (Diptera: Scenopinidae). *American Museum Novitates*, 3051, 1-30.
- Yeates, D.K. 1994. The cladistics and classification of the Bombyliidae (Diptera: Asiloidea). *Bulletin of the American Museum of Natural History*, 219, 1-191.
- Yeates, D.K., Irwin, M.E., 1992. Three new species of *Heterotrophus* Loew (Diptera: Bombyliidae) from South Africa with descriptions of the immature stages and a discussion of the phylogenetic placement of the genus. *American Museum Novitates*, 3036, 1-25.
- Yeates, D.K., Wiegmann, B.M., 1999. Congruence and contro-

versy: toward a higher-level phylogeny of the Diptera. Annual Review of Entomology, 44, 397-428.

Zaitzev, V.F., 1986. New species of Cretaceous fossil bee flies and a review of paleontological data on Bombyliidae (Diptera). Entomologicheskoe Obozrenie, 65, 815-824. [In Russian] [English translation in 1987, Entomological

Review, 66(3), 150-160.]

Zaitzev, V.F., 1992. Contribution to the phylogeny and systematic of the superfamily Bombylioidea (Diptera). Entomologicheskoe Obozrenie, 70, 716-736. [In Russian] [English translation in 1992, Entomological Review, 71(4), 94-114.]

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