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Systematic Palaeontology (Invertebrate Palaeontology)

The oldest bee fly in the French Paleocene (Diptera: Bombyliidae)

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Abstract

Paleolomatia menatensis gen. and sp. n., oldest Bombyliidae sensu stricto, is described from the Paleocene of Menat (France). The new genus, based on the wing venation, is attributed to the rather 'derived' subfamily Lomatiinae, strongly supporting a Late Cretaceous age for the diversification of the pollinator bee flies, in relation with the floristic changes and the angiosperm radiation that occurred at the same time. ***To cite this article: A. Nel, C. R. Palevol 7 (2008).***

Résumé

Le plus ancien bombyle dans le Paléocène français (Diptera : Bombyliidae). *Paleolomatia menatensis* gen. et sp. n., plus ancien Bombyliidae sensu stricto, est décrit du Paléocène de Menat (France). Ce nouveau genre, basé sur la nervation alaire, est attribué à la sous-famille relativement « dérivée » des Lomatiinae, ce qui étaye fortement l'hypothèse d'un âge Crétacé supérieur pour la diversification des insectes pollinisateurs que sont les bombyles, en relation avec les changements floristiques et la radiation des angiospermes concomitants. ***Pour citer cet article : A. Nel, C. R. Palevol 7 (2008).***

Keywords: Insecta; Diptera; Bombyliidae; Taxonomy; Paleocene; France; Radiation age

Mots clés : Insecta ; Diptera ; Bombyliidae ; Taxonomie ; Paléocène ; France ; Âge de radiation

1. Introduction

The Bombylioidea, or bee flies, are one of the largest groups of brachycerous flies with over 5500 species-group names [6]. They are pollen and nectar feeders. Thus, they are of great interest in the problems of the Cretaceous coevolution of plants and insects. If they can be dated as far back as the Middle Jurassic and the Early Cretaceous with representatives of the small family Mythicomyiidae Hennig, 1969 'microbombyliids' [11], the oldest known Bombyliidae sensu stricto are two species from the Lowermost Eocene amber of France (the toxophorine *Paradolichomyia eocenica* Nel and De Ploëg, 2004 and the phthiriine *Elektrophthiria magnifica* Nel, 2006) [17,18]. Previous oldest records were from the Eocene Baltic amber [7,9]. These bombyliids from the Earliest Eocene belong to recent subfamilies, suggesting that this family is much older. Grimaldi [10] hypothesized a Late Cretaceous age and Lamas and Nihei [13] an Early Cretaceous age for the radiation of the Bombyliidae sensu stricto, but these assumptions remain rather poorly supported because of the lack of fossil bombyliid before the Eocene. Thus,

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the present discovery of the oldest Bombyliidae sensu stricto in the Paleocene of France is of great interest for the correct estimation of the history of this family.

2. Geological setting and locality information

The Menat Pit fossil site is located within the department of Puy-de-Dôme, France, situated near the town of Gannat in the northwestern part of the Massif Central. The Menat Pit is an isolated former lake with sedimentary infill, interpreted as a maar lake, created by explosive volcanic activity [20]. The Menat Formation is biostratigraphically dated as Upper Paleocene, with a radiometric K/Ar analysis, which proposes a date in the neighbourhood of 56 My [19].

The Menat fossil site currently has yielded approximately 5000 fossil insects that are deposited mainly in the collections of the Muséum national d'Histoire naturelle, Paris and the Association Rhinopolis at Gannat. The insects from Menat comprise a diverse fauna, but flies are exceptionally rare among the Menat fossils (only 2% of the insect fauna) (personal observation). This rarity definitely is attributable to taphonomic reasons and not from a scarcity of Diptera in the surrounding habitats of former Lake Menat, similarly to what occurs for the Eocene Messel maar [21].

3. Systematic paleontology

The systematic classification of Bombyliidae follows Yeates [28], the nomenclature of the wing venation nomenclature follows Yeates [26].

Family Bombyliidae Latreille, 1802.

Subfamily Lomatiinae Schiner, 1868.

Genus *Paleolomatia* gen. n.

3.1. Type species

Paleolomatia menatensis sp. n.

3.2. Etymology

Named after the Paleocene and the recent genus *Lomatia*.

3.3. Diagnosis

Wing venation characters only. R4 + 5 branched, M2 present, anal cell open, i-r cross-vein absent, vein m-cu long and sigmoidal, R2 + 3 arising very close to base of Rs but not at 90°, R2 + 3 very strongly sinuous at apex, with a distinctly pronounced loop, R4 strongly sinuous at apex with a basal appendix, r-m cross-vein entering discal cell very distally, in the outer 80%, cell r5 open, veins M2 and CuA1 well separated, not convergent, with cell m2 between them longer than broad, R5 and M1 apically separated.

Fig. 1. *Paleolomatia menatensis* gen. et sp. n., holotype R.63892, photograph of general habitus (scale bar represents 10 mm).
Paleolomatia menatensis gen. et sp. n., holotype R.63892, photographie de l'aspect général (la barre d'échelle représente 10 mm).

Paleolomatia menatensis sp. n (Figs. 1 and 2).

3.4. Description

Wing 8.8 mm long, 2.5 mm wide, hyaline; no visible elongate spine at basicosta; base of Rs 2.5 mm from wing base; R2 + 3 arising very close to base of Rs but not at 90°; R2 + 3 very strongly sinuous at apex, with a distinct loop, Radial Loop Index RLI = 2.2 (sensu Yeates [25]); 90° bend in apex of R2 + 3; R4 + 5 branched; R4 strongly sinuous at apex but with less pronounced apical curvature than R2 + 3; i-r cross-vein absent, but a basal appendix of R4 present; cells r5 open; r-m cross-vein entering discal cell very distally, in the outer 80%; vein M2 present; vein m-cu long and sigmoidal; cell m2 longer than broad, 1.0 mm long, 0.6 mm wide; M2 meeting wing margin closer CuA1 than M1; anal cell cup open; axillary cell narrow and parallel-sided; alula not preserved.

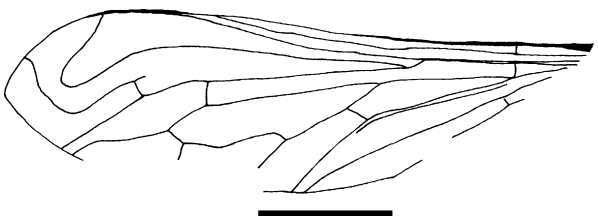

Fig. 2. *Paleolomatia menatensis* gen. et sp. n., holotype R.63892, drawing of wing venation (scale bar represents 2 mm).
Paleolomatia menatensis gen. et sp. n., holotype R.63892, dessin d'une aile veinée (la barre d'échelle représente 2 mm).

Head and abdomen missing; thorax 5.0 mm long, 3.0 mm wide; legs elongate but not very well preserved, apparent absence of midtibial spurs; tarsal setae elongate and lanceolate.

3.5. Material

Holotype MNHN-LP-R.63892, laboratoire de paléontologie, Muséum national d'Histoire naturelle, Paris.

3.6. Type locality

Menat, Puy-de-Dôme, France.

3.7. Type strata

Paleocene, –56 My, Spongo-diatom sediment of a volcano-sedimentary maar.

3.8. Etymology

Named after the small village Menat.

3.9. Discussion

The lack of information concerning the body structures of this fossil renders its attribution to a precise lineage very delicate. The present attribution is only tentative because we lack nearly all the body structures used by Yeates [28] in his phylogenetic analysis. Nevertheless, this fossil has its R2 + 3, very strongly sinuous at apex, R4 strongly sinuous at apex, which are rather infrequent characters, even among bombyliids.

After Zaitzev [29], *Paleolomatia* gen. nov. falls in the 'Bombyliidae' (sensu Zaitzev), to the exclusion of the Mythicomyiidae, Systropodidae, Phthriidae and Usiidae, because of the vein R4 + 5 branching apically, and anal cell closed. Following the phylogenetic analysis of Bombyliidae (sensu lato) of Yeates [28] and the catalogue of Bombyliidae of Evenhuis [6], only some Lomatiinae Schiner, 1868 have the following combination of characters also present in *Paleolomatia*: R4 + 5 branched, M2 present, anal cell open, i-r cross-vein absent, vein m-cu long and sigmoidal, R2 + 3 arising very close to base of Rs, R2 + 3 very strongly sinuous at apex, with a distinct loop, R4 strongly sinuous at apex, cell r5 open, R2 + 3 is not arising at 90° [12].

Among the lomatiine genera, *Paleolomatia* differs from *Docidomyia* White, 1916 and *Aleucosia* Edwards, 1934 in the lack of i-r cross-vein. It differs from *Comptosia* Macquart, 1840, *Ylasoia* Speiser, 1920, *Ulosometa* Hull, 1973, *Oncodosia* Edwards, 1934 and *Doddosia* Edwards, 1934 in its veins M2 and CuA1 well separated, not convergent, and with the cell between them longer than broad, although this character is rather variable in *Comptosia* [12,25–27]. *Paleolomatia* differs from *Macrocondyla* Rondani, 1863 in the r-m cross-vein entering the discal cell very distally, in the outer 80%, instead of the outer fourth to the outer sixth [12]. The genera *Brachydemia* Hull, 1973, *Bryodemina* Hull, 1973, *Canariellum* Strand, 1928, *Lomatia* Meigen, 1822, *Notolomatia* Greathead, 1998, *Edmundiella* Becker, 1915, *Ogcodocera* Macquart, 1840, and *Anisotamia* Macquart, 1840 have R2 + 3 and R4 distinctly less sigmoidal [8,12]. The fossil lomatiine genus *Alomatia* Cockerell, 1914 differs from *Paleolomatia* in the very basal position of the r-m cross-vein, and the veins R2 + 3 and R4 less sigmoidal [5]. Hull [12] considered the genus *Protolomatia* Cockerell, 1914 as a Lomatiinae, but Evenhuis [6,7] synonymized it with the recent tomomyzine genus *Paracosmus* Osten Sacken, 1877. *Paleolomatia* differs from it in the more proximal position of the base of R2 + 3 [4,12].

The wing venation of *Paleolomatia* looks similar to that of *Peringueyimyia* Bigot, 1886, except for the veins R5 and M1 apically separated, and a more pronounced radial loop in the former [12]. They share the presence of a basal appendix of R4 (but also present at least in *Anisotamia*, and some species of *Aleucosia* and *Canariellum*, etc.) [8,25].

Among the other fossil Bombyliidae with very sigmoidal veins R2 + 3 and R4, the lomatiine *Macrocondyla miranda* (Cockerell, 1909), originally described in the genus *Megacosmus* Cockerell, 1909 [6], has also very sigmoidal R2 + 3 and R4, similar to those of *Paleolomatia* [5], but it differs from the latter in the more basal position of r-m cross-vein (at the 73% of the discal cell) and the cell m2 between the veins M2 and CuA1, not really longer than broad (after Cockerell [1]). *Ylasoia secunda* (Cockerell, 1911), originally considered as a *Megacosmus* 1909 [6], differs from *Paleolomatia* in the cell m2, very narrow, as in the recent *Ylasoia* [3]. The genus *Alepidophora* Cockerell, 1909, currently considered as a Bombyliidae Eclimini [6], has also very sigmoidal R2 + 3 and R4 [5]. It differs from *Paleolomatia* in its veins, M2 and CuA1, strongly approximating near posterior wing margin [2,14,15].

4. Conclusion

The Toxophorinae and Usiinae: Phthiriini are relatively in inclusive positions in Yeates's [28] phylogeny of the Bombylioidea, which is rather coherent with their

presence in the Lowermost Eocene as oldest known bee flies. The Paleocene *Paleolomatia* has a wing venation with apomorphic structures such as a very pronounced radial loop and can be tentatively attributed to the more 'derived' subfamily Lomatiinae. The previously earliest records of Lomatiinae were from the Middle to Late Eocene (Messel pit and Baltic amber) [23]. The present discovery suggests that nearly all the bombyliid subfamilies, except maybe the Anthraciinae, Tomyzinae and Antoniinae, are clearly older than the Paleocene and can probably be dated from the Late Cretaceous, supporting the hypothesis of Grimaldi [10]. Of course, the clade of the nonmythicomyiid bee flies is probably a phantom group since the Upper Jurassic, as their sister group Mythicomyiidae, is recorded from this period (if the Mythicomyiidae are really monophyletic). This is congruent with the estimation of a Jurassic age for the Bombylioidea after a molecular divergence times proposed by Wiegmann et al. [24]. But this does not mean that the diversification of the true bee flies into modern subfamilies can be dated from this very remote period.

The lack of Cretaceous bombyliid fossils is surprising. It could be due either to a gap in the fossil record related to a hypothetical taphonomic bias or to a Late Cretaceous major radiation of the clade. The abundance of other brachyceran flies in the Cretaceous suggests that this lack of bombyliids rather reflects their rarity or absence during this period. Adult bombylioid flies are pollen and nectar feeders, even with specialized setae on the fore tarsi, present in nonmythicomyiid taxa, and visible in *Paleolomatia* [16]. Interestingly the Nemestrinidae or tangle-veined flies, oldest brachyceran group of pollen feeders and pollinators, are more frequent during the Mesozoic than the Cenozoic, while symmetrically the Bombyliidae were very rare in Mesozoic and relatively abundant in the Cenozoic. Bee flies could have replaced tangle-veined flies, in relation with the floristic changes and the angiosperm radiation that occurred during the Late Cretaceous [22].

References

[1] T.D.A. Cockerell, Fossil Diptera from Florissant, Colorado, Bull. Am. Museum Nat. Hist. 26 (1909) 9–12.

[2] T.D.A. Cockerell, Description of Tertiary insects. Part 5, Am. J. Sci. 27 (4) (1909) 53–58.

[3] T.D.A. Cockerell, Fossil insects from Florissant, Colorado, Bull. Am. Museum Nat. Hist. 30 (1911) 71–82.

[4] T.D.A. Cockerell, New and little-known insects from the Miocene of Florissant, Colorado J. Geol. 22 (1914) 714–724.

[5] T.D.A. Cockerell, The fossil and recent Bombyliidae compared, Bull. Am. Museum Nat. Hist. 33 (1914) 229–236.

[6] N.L. Evenhuis, World catalog of genus-group names of bee flies (Diptera: Bombyliidae), Bishop Museum Bull. Entomol. 5 (1991) 1–105.

[7] N.L. Evenhuis, Catalogue of the fossil flies of the World (Insecta: Diptera), Backhuys Publishers Leiden, The Netherlands, 1994, 600 pp.

[8] D.J. Greathead, A review of the Afrotropical and Palaearctic genera of Lomatiinae (Diptera: Bombyliidae), Entomol. Scand. 29 (1998) 211–222.

[9] D.J. Greathead, N.L. Evenhuis, Annotated keys to the genera of African Bombylioidea (Diptera: Bombyliidae; Mythicomyiidae), Afr. Invert. 42 (2001) 105–224.

[10] D.A. Grimaldi, The co-radiations of pollinating insects and angiosperms in the Cretaceous, Ann. Mo. Bot. Gard. 86 (1999) 373–406.

[11] D.A. Grimaldi, M.S. Engel, Evolution of the insects, xv, Cambridge University Press, Cambridge, 2005, 755 pp.

[12] F.M. Hull, Bee flies of the World. The genera of the family Bombyliidae, Bull. U. S. Natl. Museum 286 (1973) 1–687.

[13] C.J.E. Lamas, S.S. Nihei, Biogeographic analysis of Crocidiinae (Diptera, Bombyliidae): finding congruence among morphological, molecular, fossil and paleogeographical data, Rev. Bras. Entomologia 51 (2007) 267–274.

[14] S.E. Lewis, A new species of fossil bee fly (Diptera: Bombyliidae) from the Ruby River basin (Oligocene) of southwestern Montana, Ann. Entomol. Soc. Am. 65 (1972) 1421.

[15] A.L. Melander, A report on some Miocene Diptera from Florissant, Colorado, Am. Museum Novitates 1407 (1949) 1–63.

[16] J.L. Neff, B.B. Simpson, N.L. Evenhuis, G. Dieringer, Character analysis of adaptations for tarsal pollen collection in the Bombyliidae (Insecta: Diptera): the benefits of putting your foot in your mouth, Zootaxa 157 (2003) 1–14.

[17] A. Nel, Oldest records of Bombyliidae: Phthiriinae and Mythicomyiidae: Glabellulinae from the Lowermost Eocene amber of France (Diptera: Bombylioidea), Eur. J. Entomol. 103 (2006) 109–114.

[18] A. Nel, G. De Ploëg, New fossil bee flies in the Lowermost Eocene amber of the Paris basin (Diptera: Bombylioidea), Geologica Acta 2 (2004) 57–65.

[19] D.E. Russel, The geology of the Menat basin, France, Palaeontographica (B) 182 (1982) 87–150.

[20] P. Vincent, M. Aubert, P. Boivin, J.M. Cantagrel, J.F. Lenat, Découverte d'un volcanisme paléocène en Auvergne : les maars de Menat et leurs annexes : étude géologique et géophysique, Bull. Soc. geol. France 19 (7) (1977) 1057–1070.

[21] S. Wedmann, Annotated taxon-list of the invertebrate animals from the Eocene fossil site Grube Messel near Darmstadt, Germany, Courier Forschungsinstitut Senckenberg 255 (2005) 103–110.

[22] S. Wedmann, A nemestrinid fly (Insecta: Diptera: Nemestrinidae: cf.Hirmoneura) from the Eocene Messel pit (Germany), J. Paleontol. 81 (2007) 1114–1117.

[23] S. Wedmann, D.K. Yeates, Eocene records of bee flies (Insecta, Diptera, Bombyliidae, Comptosia): their paleobiogeographic implications and remarks on the evolutionary history of bombyliids, Palaeontology 51 (2008) 231–240.

[24] B.M. Wiegmann, D.K. Yeates, J.L. Thorne, H. Kishino, Time flies, a new molecular time-scale for brachyceran fly evolution without a clock, Syst. Biol. 52 (2003) 745–756.

[25] D.K. Yeates, Phylogenetic relationships of the Australian lomatines (Diptera: Bombyliidae), Syst. Entomol. 15 (1990) 491–509.

[26] D.K. Yeates, Revision of the Australian bee fly genus *Aleucosia* Edwards (Diptera: Bombyliidae), Invert. Taxonomy 5 (1991) 133–209.
[27] D.K. Yeates, Revision of the Australian bee fly genus *Comptosia* Edwards (Diptera: Bombyliidae), Invert. Taxonomy 5 (1991) 1023–1178.
[28] D.K. Yeates, The cladistics and classification of the Bombyliidae (Diptera: Asiloidea), Bull. Am. Museum Nat. Hist. 219 (1994) 1–191.
[29] V.F. Zaitzev, Contribution to the phylogeny and systematics of the superfamily Bombylioidea (Diptera), Entomol. Rev. 71 (1992) 94–114.