

A new lovebug fly (Insecta, Diptera) from the lowermost Eocene amber of the Paris Basin

Julien GEE

André NEL

Jean-Jacques MENIER

Gaël DE PLOËG

Laboratoire d'Entomologie, Muséum national d'Histoire naturelle,
45 rue Buffon, F-75005 Paris (France)

anel@mnhn.fr

menier@mnhn.fr

Gee J., Nel A., Menier J.-J. & De Ploëg G. 2001. — A new lovebug fly (Insecta, Diptera) from the lowermost Eocene amber of the Paris Basin. *Geodiversitas* 23 (3): 341-348.

ABSTRACT

KEY WORDS

Insecta,
Diptera,
Bibionidae,
Plecia,
lower Eocene,
France,
amber,
new species.

A new species of *Plecia*, *P. parisiensis* n. sp., is described from the lower Eocene amber of the Paris Basin. It is compared to other Cretaceous, Paleocene and Eocene *Plecia*. Reexamination of the status of some bibionid species led to the following changes: *Plecia edwardsii* (Oustalet, 1870) n. comb. for *Bibio edwardsii* Oustalet, 1870; *Plecia chapuisii* (Oustalet, 1872) n. comb. for *Bibio chapuisii* Oustalet, 1872, and *Plecia oustaleti* (Brongniart, 1876) stat. rest.

RÉSUMÉ

Une nouvelle espèce de Bibionidae (Insecta, Diptera) de l'ambre éocène inférieur du Bassin parisien.

MOTS CLÉS

Insecta,
Diptera,
Bibionidae,
Plecia,
Éocène inférieur,
France,
ambre,
nouvelle espèce.

Une nouvelle espèce de *Plecia*, *P. parisiensis* n. sp., est décrite de l'ambre éocène inférieur du Bassin parisien. Elle est comparée aux autres espèces crétaçées, paléocène et éocène de *Plecia*. Le réexamen du statut de certaines espèces de Bibionidae entraînent les changements nomenclaturaux suivants : *Plecia edwardsii* (Oustalet, 1870) n. comb. pour *Bibio edwardsii* Oustalet, 1870 ; *Plecia chapuisii* (Oustalet, 1872) n. comb. pour *Bibio chapuisii* Oustalet, 1872, et *Plecia oustaleti* (Brongniart, 1876) stat. rest.

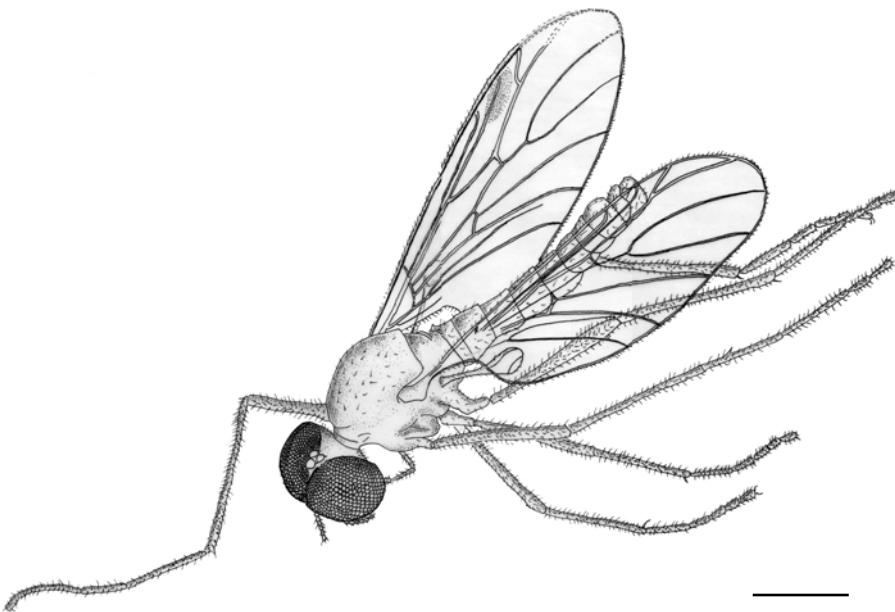


FIG. 1. — *Plecia parisiensis* n. sp.; reconstruction of the habitus, holotype (PA 74) (2/5). Scale bar: 1 mm.

INTRODUCTION

Although the Bibionidae (“march flies”) are frequent in the Cenozoic lacustrine deposits, they are surprisingly very rare in ambers. Only 3.5% of the described fossil Bibionidae are from ambers (Evenhuis 1994). Weitschat & Wichard (1998) indicated that the Bibionidae represent between 0.03 and 0.2% of the Diptera, Nematocera in Baltic amber. This family has been recorded in Canadian amber (*Plecia myersi* Peterson, 1975; fragmentary material, Santonian, Upper Cretaceous, Cedar lake, Manitoba; Grimaldi & Cumming 1999), Baltic amber (*Plecia prisca* Meunier, 1899, *Plecia borussica* Meunier, 1907; upper Eocene) and Mexican amber (*Plecia pristina* Hardy, 1971; Oligocene, Chiapas).

Therefore, the present record of four adult specimens of *Plecia* in an amber outcrop from the lowermost Eocene of the Paris Basin (De Ploëg *et al.* 1998; Nel *et al.* 1999) is of great interest. These specimens belong to a new species hereunder described.

In the description we follow the wing venation nomenclature of McAlpine (1986), and the “generalized neurulation” of Melander (1949) for measures.

SYSTEMATICS

Order DIPTERA Linnaeus, 1758
Family BIBIONIDAE Macquart, 1838
Genus *Plecia* Wiedmann, 1828

Plecia parisiensis n. sp.
(Figs 1-4)

TYPE MATERIAL. — Holotype: male specimen (PA 74) (2/5). Paratypes: male specimen (PA 74) (3/5), female specimen (PA 74) (4/5) (these three specimens were fossilised in the same cylindrical piece of amber, which was 2 cm long and 0.5 cm in diameter, together with an Hymenoptera and a male Diptera, Psychodidae Bigot, 1854); male specimen (PA 2530) (1/2) (fossilised with an adult Ephemeroptera), collection Gaël De Ploëg and Indivision Langlois-Meurinne, deposited in the Muséum national d’Histoire naturelle, Paris. The amber pieces are mounted on microscope slides in glass cells, and embedded in Canada balsam.

TABLE 1. — Dimensions of the legs (in mm) of the holotype specimen of *Plecia parisiensis* n. sp. (PA 74).

	Fore	Median	Posterior
Femora	1.42	1.30	1.61
Tibia	1.56	1.01	1.68
Basitarsus	0.89	0.43	0.58
Tarsal segment 2	0.40	0.24	0.34
Tarsal segment 3	0.40	0.19	0.22
Tarsal segment 4	0.24	0.12	0.17
Tarsal segment 5	0.26	0.17	0.22

ETYMOLOGY. — *parisiensis* is made after Paris Basin.

TYPE LOCALITY. — Le Quesnoy, Chevrière, region of Creil, Oise department, Paris Basin, France.

TYPE HORIZON. — Lowermost Eocene, Ypresian (Sparnacian), level MP7 of the mammal fauna of Dormaal. It has been demonstrated before that this amber is native, and very different from the Baltic amber in age, chemical composition and origin (Feugueur 1963; De Ploëg *et al.* 1998; Nel *et al.* 1999).

DESCRIPTION

Holotype specimen PA 74 (2/5)

Body length 4.9 mm. Specimen complete (Fig. 2), except for the apex of the right forewing which is lacking. Eyes large and dorsally merging (male bibionid character). The three ocelli (diameter 0.1 mm each) are on a dorsal protuberance. Antennae with 10 antennomeres. Thorax gibbous, with sparse short dorsal setae, 1.4 mm long and 0.9 mm wide. Fore legs 4.7 mm long, median legs 3.85 mm long, and hind legs 4.8 mm long. Legs show no strong spine. For the detailed dimensions of the legs, see Table 1. Abdomen narrowly elongated, 2.65 mm long and 0.5 mm wide. Wings (Fig. 3): forewings rather narrow, 4.25 mm long and 1.45 mm wide (i.e. about 3.5 times longer than wide). Anal lobe well-developed. Vein R₂₊₃ short, strongly oblique, making an angle of 30° with R₄₊₅. R₂₊₃, 0.38 mm long. R₄₊₅, 0.96 mm long. Costal vein C ending at the apex of the wing, 0.3 mm distad of the apex of R₄₊₅. Vein R₁ reaching the wing margin halfway between Sc and R₂₊₃. Pterostigma elliptic, brown, 0.58 mm long and 0.19 mm wide. Crossvein r-m perpendicular to M and Rs. The distance between r-m and the fork of M is one fourth the length of M₁. M₁,

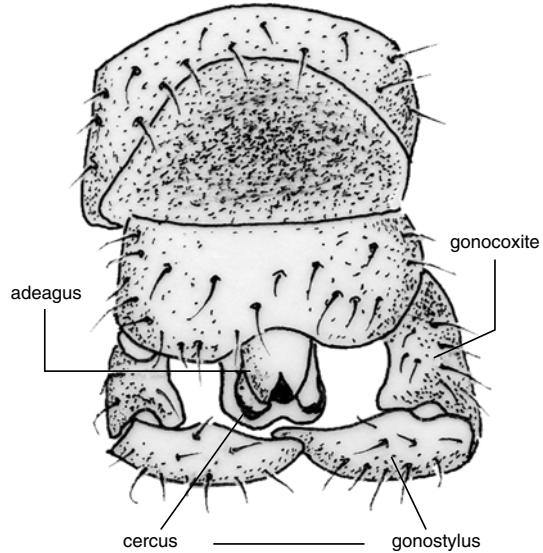


FIG. 2. — *Plecia parisiensis* n. sp.; male genital appendages, holotype (PA 74) (2/5). Scale bar: 2 mm.

1.56 mm long, M₂, 1.27 mm long. Wing hyaline. The notation of the points used here under to describe the wing venation are after Melander (1949: 18, fig. 1). Distances A-B 0.66 mm; A-C 1.46 mm; A-M 0.25 mm; B-G 0.22 mm; B-J 0.19 mm; C-D 0.10 mm; C-E 0.20 mm; D-H 0.19 mm; M-J 0.54 mm; M-K 0.88 mm; O-N 0.58 mm. Halters 0.85 mm long, ovoid with a blunt apex, brown in color (Figs 1; 2). Genital appendages (Fig. 4): gonostyli long (0.23 mm) and straight, with an obtuse apex. Cerci weakly developed. Ninth tergum 0.4 mm wide. It bears a strong median indentation.

Paratype specimen PA 74 (3/5)

Body length 3.9 mm. Specimen incomplete. The head and the wings are partly destroyed. This specimen is distinctly smaller than the holotype but it has the same general habitus. Fore legs 3.8 mm long, median legs about 3.4 mm long, and hind legs about 4.0 mm long. As in males, the legs show no strong spine. Abdomen narrowly elongated, 2.4 mm long and 0.4 mm wide. Wings (Fig. 3): forewings 3.8 mm long. Anal lobe well-developed. Vein R₂₊₃ short, strongly oblique, making an angle of 30° with R₄₊₅.

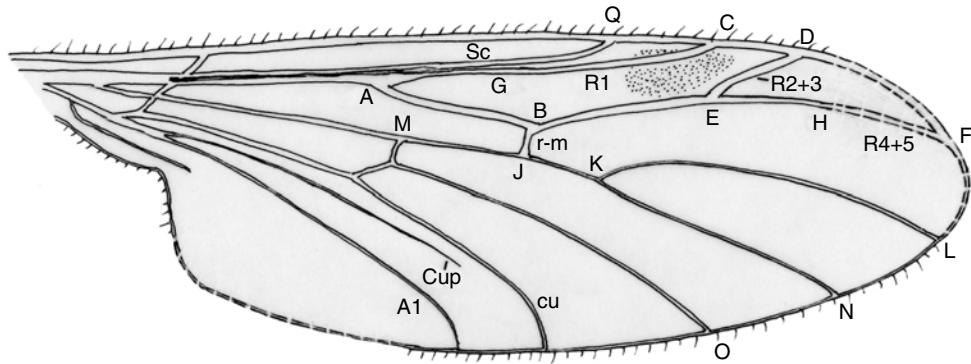


FIG. 3. — *Plecia parisiensis* n. sp.; wing, holotype (PA 74) (2/5). Abbreviations: **Sc**, subcostal vein; **R1**, **R2+3**, **R4+5**, branches of radial veins; **r-m**, crossvein between radial and median veins; **cu**, **Cup**, cubital veins; **A1**, anal vein; the points **A** to **Q** are after the nomenclature proposed by Melander (1949) for wing measures. Scale bar: 2 mm.

R2+3, 0.20 mm long. Costal vein C ending at the apex of the wing, 0.2 distal of the apex of R4+5. Vein R1 reaching the wing margin half-way between Sc and R2+3. Pterostigma elliptic, brown, 0.5 mm long and 0.1 mm wide. Wing hyaline. Halters identical to those of the holotype. Genital appendages poorly preserved.

Female paratype specimen PA 74 (4/5)

Body length about 4.5 mm. Specimen incomplete. The head and the wings are partly destroyed. This specimen is almost of the same size as the holotype and it has the same general habitus, except for the broader abdomen. Forewings hyaline, 4.2 mm long. The wing venation is identical to that of the male holotype. Abdomen broader than that of the male, 3.3 mm long and 1.1 mm wide. The genital appendages are retracted in the abdomen, then poorly visible.

Male paratype specimen PA 2530 (1/2)

Body length about 3.9 mm. Specimen complete, but its genital appendages are hidden by the wings. This specimen has almost the same size and habitus as the paratype PA 74 (3/5). Forewings hyaline, 3.7 mm long.

DISCUSSION

This species is attributed to the genus *Plecia* Wiedemann, 1828 because of the simple legs, i.e.

without large apical spur or spine, veins Rs furcated and R2+3 oblique and short.

About 150 species of fossil *Plecia* have been described from lacustrine Cenozoic sediments, but most of them are rather badly known because of poor descriptions and/or figures. A revision of these fossil species would be necessary. In most descriptions the genital appendages and body structures are not figured and not properly described by the authors (Oustalet 1870; Théobald 1937; Zhang et al. 1994 among others). The type specimens of some species were originally in a very poor state, especially the material described by Oustalet (1870), preserved in MNHN, Paris. Because of the lack of phylogenetic analysis of the Pleciinae that includes the fossil species, we cannot determine the exact affinities of *Plecia parisiensis* n. sp. We have compared *Plecia parisiensis* n. sp. to the *Plecia* species described from the Upper Cretaceous or Eocene lacustrine deposits. These later descriptions are mainly based on the wing venation. *Plecia parisiensis* n. sp. differs mainly from these taxa because of its smaller dimensions, all the Eocene *Plecia* being larger with longer and wider wings.

More precisely, *Plecia parisiensis* n. sp. differs from *Plecia undans* Zeuner, 1941 (upper Paleocene/Eocene, Ardtun Beds, Isle of Mull, Scotland, UK) in its distinctly smaller dimensions (wing lengths range 3.7–4.25 mm against more than 10.3 mm in

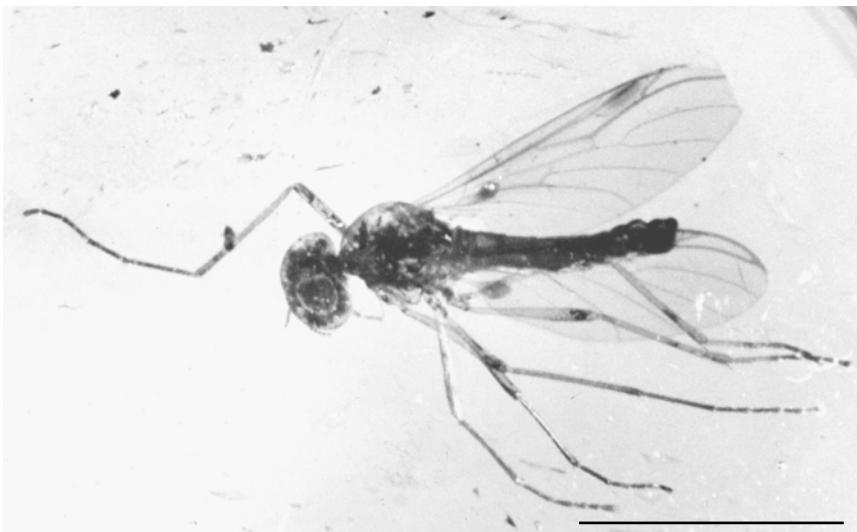


FIG. 4. — *Plecia parisiensis* n. sp.; photograph of the holotype (PA 74) (2/5), lower Eocene amber of Paris Basin. Scale bar: 2 mm.

P. undans). *Plecia akerionana* Fitzgerald, 1999 (Eocene, Green River Formation, Wyoming, USA) has smaller wings (3.47 mm long), light brown fumose. *Plecia rhodopterina* Cockerell, 1924 (Eocene, Green River Formation, Wyoming, USA) has wings of nearly the same length (5 mm) but they are dark ferruginous, R₂₊₃ is distinctly longer. *Plecia pealei* Scudder, 1890 and *Plecia dejecta* Scudder, 1890 (Eocene, Green River Formation, Wyoming, USA) have longer wings (respectively 10 mm and 7.5 mm long). *Plecia woodruffi* Cockerell, 1916 (Eocene, Green River Formation, Ute Station, Utah, USA) has longer wings (7 mm long) with the costal area suffusedly dusky. *Plecia winchesteri* Cockerell, 1917 (Eocene, Colorado, USA) also has longer wing (7.3 mm long) and “dilute fuliginous” (Scudder 1890; Cockerell 1916, 1917). *Plecia minutula* Rice, 1959 (Eocene, British Columbia, Canada) has wing slightly longer (5.5 mm long) with the apex distinctly more rounded than *P. parisiensis* n. sp. All the other species of *Plecia* described by Scudder (1890), Handlirsch (1910) and Rice (1959) from the Eocene of British Columbia have distinctly longer wings (more than 5.5 mm long). Schröder (1999) and Rust (1999) described and figured a *Plecia* sp. and a *Penthetria* sp. from the

Paleocene/Eocene of the Fur-Formation (Denmark). Both have a vein R₂₊₃ more or less straight, very different of that of *P. parisiensis* n. sp. *Plecia acourtii* Cockerell, 1921 (upper Eocene, Isle of Wight, UK) has longer wings (6.4 mm) entirely dark fuliginous (Cockerell 1921).

All the *Plecia* described by Théobald (1937) from the upper Eocene of the Gard department (France) have longer wings, ranging between 6.0 mm to 10 mm long.

Plecia fushunensis (Hong 1980: 47; 48, text-fig. 18, pl. 1; fig. 3) was described as *Lacibio fushunensis*, and renamed *Plecia* by Zhang (1989). Unfortunately, the successive drawings of the wings are unexploitable. After Evenhuis (1994), this fossil is supposed to originate from the Chinese Eocene amber of Fushun, but it appears to be clearly an impression of an isolated wing on a lacustrine rock, after the original photograph of Hong. This wing clearly differs from *Plecia parisiensis* n. sp. in its very long and oblique R₂₊₃, intermediate in shape between those of the modern species of *Plecia* and *Penthetria*. It is also about 9.5 mm long.

Table 2 compares the few species described from different ambers. It clearly shows that our new species cannot be one of these already described

TABLE 2. — Comparison of some characters of *Plecia* species from different ambers or fossil resins. Abbreviations: **CD/QD**, refer to Fig. 3 after Melander 1949; **CuP**, cubital veins.

	<i>P. pristina</i>	<i>P. prisca</i>	<i>P. borussica</i>	<i>P. myersi</i>	<i>P. parisiensis</i>	<i>n. sp.</i>
Length/width (wing)	2.5	3	unknown	2	3.5 (holotype)	
CD/QD	0.20	0.35	unknown	0.31	0.47	
Anal lobe	nearly absent	weakly developed	unknown	well-developed	well-developed	
Anal vein A	short	very short	unknown	long	long	
CuP	very short	absent	unknown	short	short	
Costa ends distal of	R2+3	unknown	unknown	R4+5	R4+5	
Nb. Antennomeres	8	unknown	10	unknown	10	
Gonostyli	short, curved	unknown	unknown	unknown	long, straight	

taxa. In particular, *Plecia parisiensis* n. sp. cannot be attributed to any of the species of *Plecia* described from Baltic amber. The original descriptions and figures of *Plecia prisca* Meunier, 1899 and *Plecia borussica* Meunier, 1907 are very unclear. Nevertheless, *Plecia borussica* differs from *P. parisiensis* in having 10 antennomeres and its third antennomere drop-shaped, this making it different from all others (Meunier 1899, 1907). This once again corroborates our previous observations that the entomofauna of Le Quesnoy shows great differences when compared to the Baltic amber.

MISCELLANEOUS REMARKS AND NEW SYNONYMIES
Oustalet (1870) described *Bibio edwardsii* from the Oligocene of Corent (Puy-de-Dôme, France). Evenhuis (1994) attributed it to the genus *Penthetria* Meigen, 1803. After a thorough re-examination of the type specimen preserved in the collection of the Laboratoire de Paléontologie, Muséum national d'Histoire naturelle, Paris (specimen MNHN-LP-R.06669), it is clearly visible that vein R2+3 is short and not parallel to R4+5. Thus, we reattribute this species to the genus *Plecia*, under the name *Plecia edwardsii* (Oustalet, 1870) n. comb.

Oustalet (1872) described an adult bibionid from the Eocene of the "Gypse de Paris" (Buttes-

Chaumont, Paris, France), under the name *Bibio chapuisii*. This species is not listed by Evenhuis (1994). We could not find the type specimen in the collections of the Paris Museum. Nevertheless, it is clear after the original description of Oustalet who indicated that this fossil is nearly identical to *Plecia edwardsii* (Oustalet, 1870), that *B. chapuisii* belongs to the genus *Plecia*. We propose to rename it *Plecia chapuisii* (Oustalet, 1872) n. comb. The wing of *P. chapuisii* is 6.25 mm long, distinctly longer than that of *P. parisiensis* n. sp.

Penthetria oustaleti (Brongniart, 1876), from the Oligocene of Chadrat (Puy-de-Dôme, France), described under the name *Protomyia oustaleti* by Brongniart (1876a, b), has been attributed to the genus *Penthetria* by Evenhuis (1994) who apparently ignored the revision of Brongniart (1878) who reattributed it to the genus *Plecia*. A thorough reexamination of the type specimen, preserved in the collections of the Laboratoire de Paléontologie, Muséum national d'Histoire naturelle, Paris (specimen MNHN-LP-R.06698), showed that it is a true *Plecia*. Thus, we restore it into this genus, under the name of *Plecia oustaleti* (Brongniart, 1876) stat. rest.

PALAEOCOLOGICAL CONSIDERATIONS

The insect fauna of Le Quesnoy shows a great number of Diptera, mainly Nematocera. On a total of 10 000 fossil insects identified today from this location, four Bibionidae specimens have been found, making this family relatively more frequent in this amber than in any other amber (only two specimens described from the very rich fauna of the Baltic amber). The genus *Plecia* is very frequent in the upper Eocene, Oligocene and Miocene lacustrine sediments of western Europe, but it seems somewhat less frequent in the Paleocene and lower Eocene lacustrine sediments of the same areas (Menat, Messel) where, nevertheless, they still remain more frequent than in ambers. The origin of this difference between ambers and lacustrine outcrops is still questioned. One hypothesis could be that the Bibionidae are usually larger than other flies and thus more difficult to preserved in

resins. Tipulids are distinctly larger than bibionids but also more frequent in Baltic and Oise ambers. Thus, this hypothesis is clearly not sufficient. Another one could be that the Bibionidae are not attracted by resins, similarly to what Skalski (1976) demonstrated for the some Lepidoptera, but this would need confirmation after experimentation on living taxa. A last hypothesis is that "march flies" appear quite early in the season, perhaps when resin production is at a low level. This shift in periods of appearance could be a reason why bibionids are so rare in ambers.

Bibionidae larvae feed on "decaying organic material" and "root of grasses and other plants" (Hardy 1986), in wet environments, which fits with the reconstruction of the palaeoenvironment proposed by Nel *et al.* (1999).

Acknowledgements

We thank the company Lafarge-Granulat for the help with the sampling of the fossil and the family Langlois-Meurinne for the authorization of working in their property. We thank G. Hodebert (MNHN) for the realization of the habitus drawings and mounting of the figures. We also thank Dr E. A. Jarzemowski (Maidstone Museum, UK) and an anonymous referee for their useful remarks and corrections. This is a contribution No. 04 to the knowledge of the fauna of the lowermost Eocene of the Paris Basin.

REFERENCES

- BRONGNIART C. 1876a. — Observations sur un insecte fossile de la famille des diptères trouvé à Chadrat (Auvergne) (*Protomyia oustaleti*). *Annales de la Société géologique de France* 7, 2 p.
- BRONGNIART C. 1876b. — Note sur une nouvelle espèce de diptère fossile du genre *Protomyia* (*P. oustaleti*), trouvé à Chadrat (Auvergne). *Bulletin de la Société géologique de France* (3) 4: 459-460.
- BRONGNIART C. 1878. — Note rectificative sur quelques diptères tertiaires et en particulier sur un diptère des marnes tertiaires (Miocène inférieur) de Chadrat (Auvergne), la *Protomyia oustaleti* qui devra s'appeler *Plecia oustaleti*. *Bulletin de la Société scientifique du Département du Nord* 1: 74-81.
- COCKERELL T. D. A. 1916. — Some american fossil insects. *Proceedings of the United States National Museum* 51: 89-106.
- COCKERELL T. D. A. 1917. — New Tertiary insects. *Proceedings of the United States National Museum* 52: 373-384.
- COCKERELL T. D. A. 1921. — Fossil Arthropods in the British Museum. VI: Oligocene insects from Gurnet Bay, Isle of Wight. *Annals and Magazine of Natural History* (9) 7: 453-480.
- DE PLOËG G., DUTHEIL D., GHEERBRANT E., GODINOT M., JOSSANG A., NEL A., PAICHELER J.-C., PONS D. & RAGE J.-C. 1998. — Un nouveau gisement paléontologique "Konservat-Lagerstätte" à la base de l'Éocène dans la région de Creil (Oise), in *The Paleocene/Eocene Boundary in Europe: Events and Correlations. Symposium de la Société géologique de France, Paris, 19-20 janvier 1998*. Société géologique de France, Paris, 5 p.
- EVENHUIS N. L. 1994. — *Catalogue of the Fossil Flies of the World (Insecta: Diptera)*. Backhuys Publishers, Leiden, 570 p.
- FEUGUEUR L. 1963. — L'Yprésien du Bassin de Paris. Essai de Monographie stratigraphique, in *Mémoires pour servir à l'Explication de la Carte géologique détaillée de la France*. Publication du Ministère de l'Industrie, Paris: 1-568.
- GRIMALDI D. & CUMMING J. 1999. — Brachyceran Diptera in Cretaceous ambers and Mesozoic diversification of the Eremoneura. *Bulletin of the American Museum of Natural History* 239, 124 p.
- HANDLIRSCH A. 1910. — Canadian Fossil Insects. *Contributions to Canadian Palaeontology* 2: 93-129.
- HARDY D. E. 1986. — Family Bibionidae, in ALEXANDER C. P. (ed.), *Manual of Nearctic Diptera*, 1. Research branch, Agricultural Canada Monograph, Ottawa 27: 209-222.
- HONG Y. C. 1980. — Insecta, in HONG Y. C., YANG T. C., WANG S. T., SUN X. J., DU N. Q. & SUN M. R. (eds), *Study of Stratigraphy and Palaeontologic Biota from Fushun Coal Field, Liaoning Province*. Beijing, Science Press, 98 p. (in Chinese).
- MCALPINE J. F. 1986. — Morphology and terminology – adult, in ALEXANDER C. P. (ed.), *Manual of Nearctic Diptera*, 1 Research branch, Agricultural Canada Monograph, Ottawa 27: 9-63.
- MELANDER A. L. 1949. — A report on some Miocene Diptera from Florissant, Colorado. *American Museum Novitates* 1407: 1-63.
- MEUNIER F. 1899. — Révision des Diptères fossiles types de Loew. *Miscellanea Entomologica* 7: 1-17.
- MEUNIER F. 1907. — Beitrag zur Fauna der Bibioniden, Simuliden, und Rhyphiden des Bernsteins. *Jahrbuch der Königlich Preussischen Geologischen Landesanstalt und Bergakademie zu Berlin* 24: 391-404.
- NEL A., DE PLOËG 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., LAPPARENT DE BROIN F. DE, 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, Sciences de la terre et des planètes*, Paris 329: 65-72.
- OUSTALET J. F. E. 1870. — Recherche sur les insectes fossiles des terrains tertiaires de la France. *Annales des Sciences géologiques de Paris* 2: 1-178.
- OUSTALET J. F. E. 1872. — Sur l'empreinte d'une aile de Diptère. *Bulletin de la Société philomathique de Paris* séance du 27 juillet 1872: 161-163.
- RICE H. M. A. 1959. — Fossil Bibionidae (Diptera) from British Columbia. *Bulletin of the Geological Survey of Canada* 55: 1-37.
- RUST J. 1999. — *Biologie der Insekten aus dem ältesten Tertiär Nordeuropas*. Habilitationsschrift, Georg-August-Universität Göttingen, Göttingen, Germany, 482 p.
- SCHRÖDER F. 1999. — *Ursprüngliche Dipteren aus dem Alttertiär der Fur- und Ølst-Formationen von Dänemark (Moler, oberes Paleozän/unteres Eozän)*. Unveröff. Dipl.-Arb., Georg-August-Universität Göttingen, Göttingen, Germany, 169 p.
- SCUDDER S. H. 1890. — The Tertiary insects of North America. *United States Geological Survey of the Territories* 13: 1-734.
- SKALSKI A. W. 1976. — Les Lépidoptères fossiles de l'ambre, état actuel de nos connaissances. *Linneana Belgica* 6: 154-169; 195-208; 221.
- THÉOBALD N. 1937. — *Les Insectes Fossiles des Terrains oligocènes de France*. Thomas G., Nancy, 473 p.
- WEITSCHAT W. & WICHARD W. 1998. — *Atlas der Pflanzen und Tiere im Baltischen Bernstein*. Pfeil, München: 1-256.
- ZHANG J. F. 1989. — *Fossil Insects from Shanwang, Shandong, China*. Shandong Science and Technology, Beijing, 455 p. (in Chinese).
- ZHANG J. F., SUN B. & ZHANG X. 1994. — *Miocene Insects and Spiders from Shanwang, Shandong*. Science Press, Beijing, i-iv + 298 p. (in Chinese with English summary).

*Submitted on 11 July 2000;
accepted on 23 January 2001.*