New Fossil Non-Cyclostome Braconid Wasps from the Lowermost Eocene Amber of Paris Basin

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Source: Acta Palaeontologica Polonica, 55(3) : 519-527

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: https://doi.org/10.4202/app.2009.1114
New fossil non-cyclostome braconid wasps from the lowermost Eocene amber of Paris Basin

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Two braconid wasp taxa with enlarged eyes and ocelli indicative of probable nocturnal activity are discussed and described from the lowermost Eocene amber of the Paris Basin. The new tribe Palaeocharmontini nov., for new genus Palaeocharmon with type species Palaeocharmon basalis sp. nov. is described and illustrated in the subfamily Charmontinae. The similarity of this taxon with members of subfamilies Helconinae, Homolobinae, and Brachistinae is shown and the peculiar character [presence of hind wing recurrent vein (m-cu)] unknown previously in non-cyclostome braconids is discussed. A third fossil species of the genus Phanerotoma (Ph. menieri sp. nov.) is described and compared with known species from the Baltic amber.

Key words: Insecta, Hymenoptera, Braconidae, parasitoids, new taxa, fossil, amber, morphological peculiarities, Eocene, France.

Introduction

Fossil braconid wasps are not rare, especially from the Cenozoic, and many species of this period have been described from amber deposits (Brues 1923, 1933, 1939; Muesebeck 1960; Tobias 1987; Zuparko and Poinar 1997; Basiyuk et al. 1999; Martínez-Delclós et al. 1999; van Achterberg 2001; Hong 2001, 2002; Murphy et al. 2008; Perichot et al. 2009). Fossils representing twenty one subfamilies of braconids (including Aphidiinae, sometimes treated as a separate family) have been recorded from this period, with the subfamily Diopsilininae being endemic to the Baltic amber (Tobias 1987).

The first fossil representative of the subfamily Charmontinae is recorded in this paper from the lowermost Eocene amber of the Paris Basin. The peculiar combination of plesio- and apomorphic characters in this taxon allows us to propose it as a new monotypic tribe. Moreover, a new third species of the genus Phanerotoma is also described from the amber of Paris Basin in this paper. It is of particular interest that latter two taxa have considerably enlarged eyes and ocelli, a character indicating their probable nocturnal or crepuscular activity, as it has been observed on several extant ichneumonoids witness (Huddleston and Gauld 1988). This is apparently the earliest fossil record of nocturnal ichneumonoids wasp from the Upper Eocene Baltic amber which also possessed strongly enlarged eyes and ocelli (Kasparyan 1988). The material of this study supports the hypothesis of the existence of high braconid diversity during the Palaeogene.

A great number of amber inclusions has been obtained in the outcrop with the Lowermost Eocene sediments in the Oise Department (Nel et al. 2004). The crucial differences of this source from Baltic amber are connected to the age and taxonomic attribution of resin producing plant. The age depository of French amber in Oise falls on the end of the "thermoera”, while Baltic amber more or less coincides with the beginning “crioera”. The infrared spectrum of the French amber is rather similar to that of the Recent Hymenaea Linnaeus, 1753 (Caecalpiniaee) copal (Nel et al. 2004), while the resin for Baltic amber seemed to be produced by coniferous plants. These differences make possible to explain an essential distinction in composition of these amber entomofaunas.

Institutional abbreviation.—MNHN, Laboratoire de Paléontologie, Muséum National d’Histoire Naturelle, Paris, France.

Other abbreviations.—cu-a, nervulus vein of the fore wing, or nervellus vein of the hind wing; m-cu, recurrent vein of the fore and hind wings; r, first abscissa of radial vein of the fore wing; r-m, second radiomedial vein of the fore wing; 1r-m, basal vein of the hind wing; a, second transverse anal vein of the fore wing; 2A, first transverse anal vein of the fore and hind wings; C+SC+R, costal vein of the fore wing; CU1a, parallel vein of the fore wing; CU1b, brachial vein of the fore wing; SR, radial vein of the hind wing; SR1, third abscissa of radial vein of the fore wing; 1-SR, first abscissa of basal vein.
of the fore wing; 2-SR, first radiomedial vein of the fore wing; 3-SR, second abscissa of radial vein of the fore wing; 2-SR+M, second abscissa of medial vein of the fore wing; 1-M, second abscissa of basal vein of the fore wing, or second abscissa of mediocubital vein of the hind wing; 2-M, cubital vein of the hind wing; M+CU, first abscissa of mediocubital vein of the hind wing; 1-CU1, first abscissa of cubital vein of the fore wing.

Material and methods

The amber material described in this paper was collected in the Farm Le Quesnoy, Chevrière, region of Creil, Oise department of France. The stratigraphic horizon of this fossil is lowermost Eocene c. 53 Myr, Sparnacian, level MP7 of the mammal fauna of Dormaal (Nel et al. 1999).

We follow the wing venation terminology proposed by Belokobylskij and Tobias (1998) and (in parenthesis) van Achterberg (1979, 1993).

Systematic palaeontology

Class Insecta Linnaeus, 1758
Order Hymenoptera Linnaeus, 1758
Family Braconidae Nees, 1812
Subfamily Charmontinae van Achterberg, 1979

Remarks.—Charmontinae is a small subfamily of koinobiont parasitoids of Lepidoptera containing two extant genera: Charmon, with six species distributed in the Holarctic, Oriental and Australian regions, and the monotypic genus Charmontia, with type species Charmontia inopina van Achterberg, 1979 from Chile (van Achterberg 1979). This is the first fossil record of the subfamily Charmontinae.

Tribe Palaeocharmontini nov.

Type genus: Palaeocharmon gen. nov., see below.

Description.—Occipital carina possibly complete, but very fine medio-dorsally. Eyes very large; malar space very narrow, almost non-existent. Ocelli enlarged (Figs. 1A, B, 2A). Maxillary palpi 6-segmented; labial palpi 4-segmented, with third segment very small and suboval. Scape weakly thickened. First flagellar segment a little longer than second segment (Fig. 2B, E). Notauli complete, rather shallow, wide anteriorly and narrow posteriorly (Fig. 2B, C). Prescutellar depression shallow and wide, with shallow median carina. Scutellum posteriorly without furrow. Prepectal carina absent. Mesopleural pit transformed in shallow elongate furrow. Sternaulus rather wide, sigmoid (Fig. 2C). Metapleural flange distinct and long Propodeum without lateral tubercles and delineated areas. Legs rather long and more or less slender (Fig. 1B). Hind basitarsus 0.8 times as long as second to fifth segments combined (Fig. 1B). Telotarsus (fifth segment) of hind tarsus short and slender (Fig. 1B). Claws simple and weakly curved. Fore wing with radial (marginal) cell not shortened, recurrent vein (m-cu) strongly antefurcal, first radiomedial vein (2-SR) possibly present, second radiomedial vein (r-m) absent, brachial (sub-discal) cell large (Fig. 2G). Hind wing with 3 distal hamuli, submedial (subbasal) cell large, radial vein (SR) unsclerotised, almost parallel to anterior margin of wing, but very weakly divergent posteriorly; recurrent vein (m-cu) rather distinct, weakly sclerotised and almost straight (Fig. 2F). Metasoma distinctly elongate (Fig. 1A, B). First tergite short and wide (Fig. 1A, B), with narrow but distinct dorsosipe, with distinct, almost complete and convergent posteriorly dorsal carinae. Second suture indistinct. Spiracles of second tergite situated on the middle of its lateral sides. Tergites behind first one not modified. Ovipositor long (Fig. 1A, B).

Discussion.—The presence of the recurrent (m-cu) vein in the hind wing is very common in many groups of cyclostome braconids. This vein is developed in almost all taxa of Rhysalinae, Doryctinae, Exothecinae sensu lato, and Betylobraconinae (except for some specialised genera), in many taxa of Opiinae and Alysiinae, as well as in some taxa of Rogadinae and in several other small subfamilies. Otherwise, this vein is practically never recorded in the other non-cyclostomatous group of subfamilies (Tobias 1967; Quicke and van Achterberg 1990; van Achterberg 1993).
Fig. 1. Photographs of braconid wasp *Palaeocharmon basalis* gen. et sp. nov., holotype of female, MNHN A32944, from the French Amber (Farm Le Quesnoy, Oise, France), lowermost Eocene. **A.** Habitus in dorsal view. **B.** Habitus in lateral view. **C.** Part of the body and wing in dorsal view.
This new tribe represents the first member in the heliconine phylogenetic group, which either retained, or possibly re-stored, the recurrent vein (m-cu) in the hind wing. In addition to this characteristic feature, the new tribe also displays a set of plesiomorphic wing venation characters, such as a developed first transverse anal vein (2A) in the fore and hind wings and a distinctly petiolate anteriorly discoidal (discal) cell of fore wing. Unfortunately, the medio-anterior half of fore wing is not preserved in this fossil specimen and information about the second radiomedial vein (r-m) and therefore presence or absence of the second radiomedial (sub-marginal) cell cannot be recorded.

If we assume that the second radiomedial vein (r-m) and second radiomedial (submarginal) cell are present, then this genus can be included in subfamily Helconinae and would be similar to *Hellenius*, although on the basis of mainly plesiomorphic characters, i.e., discoidal (discal) cell is petiolate, the propodeal bridge being absent, the prescutellar depression long, and the second transverse anal vein (2A) in hind wing is present. The new genus differs distinctly from *Hellenius*, however, and besides the presence of the hind wing recurrent vein (m-cu), also in the following characters: the eyes and ocelli are strongly enlarged, the malar space is very short, the mandible is large, the palpi are long, the third segment of the labial palpus is very short, the prepectal carina is absent, the propodeum is without delineated areas, the nervulus in fore wing is antefurcal, and the eyes are distinctly emarginated opposite the antennal sockets.

On the other hand, the new genus is also similar to *Homolobus* (Homolobinae) in having enlarged eyes and ocelli, a reduced number of labial palpal segments, rather large hind coxae, a spine on the apical segment of antenna, and a well-developed laterope on the first metasomal tergite. Unfortunately, information about such important subfamily character as the antescutal depression is not available for study because of the preservation state of the unique specimen. At the same time, *Palaeocharmon* gen. nov. differs distinctly from *Homolobus* in the following features: the spurs of all legs are short, the discoidal (discal) cell is petiolate anteriorly on long distance, the second transverse anal (2A) and recurrent (m-cu) veins of hind wing are present, the radial (marginal) cell of hind wing is very weakly divergent apically, the first metasomal tergite has dorsal carinae and rather distinct laterope, and the ovipositor is very long.

In the case of absence of the second radiomedial vein (r-m) and second radiomedial (submarginal) cell, *Palaeocharmon* gen. nov. can be compared to the subfamilies Brachistinae and Charmontinae. Differences between this new genus and brachistine genera, especially from the most similar one, *Eubazus*, are distinct, i.e., the discoidal (discal) cell is distinctly petiolate, the second transverse anal (2A) and recurrent (m-cu) veins of hind wing are present, the radial (marginal) cell of hind wing is not narrowed apically, the eyes and ocelli are much enlarged, the malar space is very short, the eye has an emargination opposite the antennal socket, the nervulus (cu-a) is antefurcal, and the hind basitarsus is long.

Comparison of the new genus with all aforementioned taxa suggests the placement of the new genus in the subfamily Charmontinae as most reasonable because of the set of following apomorphic and peculiar plesiomorphic features: the eyes and ocelli are enlarged, the labial palpus has the third segment strongly reduced, the areola on propodeum is absent, and the occipital carina is possibly reduced mediodorsally. Moreover, the shape and proportions of the hind leg in *Palaeocharmon* are the same as in *Charmon*, as well as the laterope of the first tergite and the first transverse anal (2A) vein in both fore and hind wings are present. A number of apomorphic characters (the apical antennal segment with very long apical spine, the rather distinct dorsorse and the nervulus [cu-a] of fore wing antefurcal) and the principal plesiomorphic characters (not thickened scape, the narrow and petiolate discoidal [discal] cell, the weakly divergent apically radial [marginal] cell of hind wing, the distinct and long metapleural flange) as well as the presence of recurrent (m-cu) vein in hind wing show an isolated position of this new genus within the Charmontinae. For this reason we erect the new tribe *Palaeocharmontini* for this genus.

*Palaeocharmon basalis* sp. nov.
Figs. 1, 2.

*Etymology:* After the inferred morphologically basal position of this genus within the subfamily Charmontinae.

*Holotype:* Female, MNHN A32944.

*Type locality:* Farm Le Quesnoy, Chevrière, region of Creil, Oise department.

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

*Description.*—Body 6.1 mm long; fore wing about 4.0 mm.

Head transverse, 1.65 times as wide as maximum long (lateral view), 1.5 times as wide as maximum width of mesoscutum. Head behind eyes distinctly and roundly narrowed.

Eye 2.8 times longer than temple (lateral view, on median line). Eye oval, 1.25 times as high as maximum long. Clypeus suture distinct. Clypeus weakly convex, 0.5 times as high as face. Mandibles enlarged, distinctly curved, weakly twisted in apical half, with long and pointed anterior tooth. Face rather narrow, its width 1.2 times median height. Eye with distinct emargination opposite antennal socket. Diameter of ocellus 2.3 times interocellular distance, almost twice longer than distance between ocellus and eye. Vertex smooth.

Antenna setiform, 31-segmented, longer then body.

Scape 1.7 times longer than its maximum width, 2.3 times longer than pedicel. First flagellar segment 1.2 times longer than scape, 3.5 times longer than apical width, 1.1 times lon-

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Fig. 2. Braconid wasp *Palaeocharmon basalis* gen. et sp. nov., holotype of female, A32944, from the French Amber (Farm Le Quesnoy, Oise, France), lowermost Eocene. A. Head and anterior part of mesosoma in dorsal view. B. Head, mesosoma and anterior part of metasoma in lateral view. C. Mesosoma and anterior part of metasoma in lateral view. D. Legs and basal part of ovipositor in lateral view. E. Habitus in lateral view. F. Hind wing. G. Fore wing. Photographs (A–D) and drawings (E–G).
ger than second segment. Penultimate segment 1.8 times longer than width, 0.6 times as long as apical segment (spine included).

Mesosoma 1.7 times maximum high. Sides of pronotum with rather deep and oblique furrow, almost entirely smooth. Mesoscutum smooth, rounded anteriorly, 1.3 times wider than its median length. Notauli distinctly crenulate. Prescutellar depression medially 0.45 times as long as scutellum. Mesopleuron smooth. Subalar depression deep above and shallow below, mostly smooth. Sternalus finely and quite sparsely punctate-areolate. Mesopleural pit very shallow. Furrow along mesopleural suture distinctly and densely crenulate. Metanotal tooth absent. Suture between metapleuron and propodeum deep, wide, crenulate. Ventral metapleural flange wide, rather long and rounded apically. Propodeum distinctly and irregularly reticulate-areolate for most part, almost smooth basally.

Legs: Fore and middle femora slender, 4.8–5.0 times longer than maximum wide. Hind coxa without basiventral corner, 1.5 times longer than maximum wide. Trochantellus without subapical comb of pegs. Hind femur 4.5 times longer than wide. Hind tibia more or less thickened towards apex. Outer and inner tibial spurs of equal length, 0.3 times as long as hind basitarsus. Second tarsal segment 0.4 times as long as basitarsus, 1.4 times longer than third segment, 2.6 times longer than fourth segment, twice longer than telotarsus; fourth segment almost half as long as third segment and 0.75 times as long as telotarsus.

Wings: Fore wing about 3.0 times longer than wide. Second abscissa of basal vein (1-M) 6.0 times longer than its first abscissa (1-SR), 2.2 times longer than recurrent vein (m-cu); Second abscissa of basal (1-M) and recurrent (m-cu) veins more or less convergent posteriorly. Recurrent vein (m-cu) 1.5 times longer than second abscissa of medial vein (2-SR+M). Discoidal (discal) cell 1.15 times longer than its maximum width. Brachial (subdiscal) cell wide, 1.8 times longer than width. Parallel vein (CU1a) arising from posterior 0.2 of distal side of brachial (subdiscal) cell. Hind wing about 4.0 times longer than its width. Second abscissa of mediocubital vein (1-M) 0.4 times as long as its first abscissa (M+CU), almost as long as nervellus (cu-a), 1.6 times longer than basal vein (1r-m). Medial (basal) cell 6.5 times longer than its width. Radial (SR) and cubital (2-M) veins weakly divergent towards apex of wing.

Metasoma: First tergite short, distinctly convex, more or less distinctly and sparsely striate, 1.3 times longer than apical width, 1.6 times longer than propodeum. Tergites behind first one smooth. Ovipositor sheaths densely and short setose, preserved part of ovipositor sheath about 1.3 times longer than metasoma, 1.5 times longer than head and mesosoma combined.

Colour: Body probably entirely black. Wings hyaline.

Subfamily Cheloninae Nees, 1816

Remarks.—The subfamily Cheloninae is one of the most specialised groups within the braconid wasps of the non-cyclostome phylogenetic branches. Members of this subfamily are koinobiont egg-larval parasitoids of Lepidoptera and are easily recognised by the coarsely sclerotised and immovably fused three anterior metasomal tergites, the presence of the postpectal carina and by some features of the fore wing venation. More than 15 genera from five tribes of this subfamily are known in the world fauna and only five of which are distributed in the Palearctic region (Zettel 1990).

The fossil chelonine parasitoids are particularly common as inclusions in the Eocene Baltic amber (Brues 1933; Tobias 1987), and nearly all of these are members of the genus Ascogaster. A few members of the genera Chelonus, Phanerotoma, and endemic Diosdonthagaster are also recorded in amber and rocks. The fossil genus Chelonohecon has been transferred to Cheloninae within the monogenic tribe Chelonoheconini (Tobias 1987). Probably Anacanthobracon, described originally in the subfamily Doryctinae, is an additional genus of this tribe (Belokobylskij in press).

Genus Phanerotoma Wesmael, 1838

_Type species:_ Chelonus dentatus Panzer, 1805 (Germany; extant species).

Remarks.—The genus Phanerotoma is one of the less derived, but peculiar and polymorphic chelonine genera, embracing more than 100 species from the almost all zoogeographic regions (Zettel 1990; van Achterberg 1990; Tobias 2000). The members of this genus have two anterior metasomal sutures complete and deep and a fore wing venation complete. Otherwise, both very fine metasomal sutures are retained only in the fossil species of Ascogaster separated as the subgenus _Syntaphus_ (Belokobylskij in press). Discovery of a similar character in _Ascogaster_ reduces the gap between that genus and _Phanerotoma_. Species of _Ascogaster_ have discoidal (discal) cell petiolate and body usually dark coloured, in contrast to _Phanerotoma_ that has discoidal (discal) cell distinctly and more or less widely sessile anteriorly and body colour of many taxa pale.

Only two species of _Phanerotoma_ have been described previously from the Eocene Baltic amber, _Phanerotoma baltica_ Brues, 1933 and _Phanerotoma extensa_ Brues, 1933 (Brues 1933). A third species of this genus from the French amber is described below.

*Phanerotoma menieri* sp. nov.

Figs. 3, 4.

_Etymology:_ After our colleague Professor Jean-Jacques Menier.

_Holotype:_ Female, MNHN A32945, mounted in Canada balsam.

_Type locality:_ Farm Le Quesnoy, Chevrière, region of Creil, Oise department.

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

_Diagnosis:_ This new species is very similar to _Phanerotoma baltica_ Brues, 1933 in the strongly enlarged eyes, the same number of antennal segments and the less strongly produced angles on the propodeum. _Phanerotoma menieri_ sp. nov. dif-

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fers from the latter in having the pale colour of the body, the finely punctate face, the not deeply excavate occiput, the very short temple, the weakly and not completely sculptured propodeum, the not flattened metasoma, the short second metasomal tergite, and the short ovipositor.

**Description.**—Body length 3.2 mm; fore wing length 2.6 mm.

Head distinctly transverse, possibly not deeply excavate posteriorly, about twice as wide as maximum length, 1.4 times as wide as mesoscutum, strongly and roundly narrowed behind eyes. Ocelli enlarged. Eye very large, without...
emargination opposite antennal socket, medially about 3.5 times longer than temple (in lateral view of head), 1.2 times as high as median width. Malar space very short, almost indistinct. Face quite narrow, 1.2 times as wide as high medi ally, 0.7 times as wide as eye high. Clypeus subround, weakly convex (lateral view), distinctly and roundly convex on the ventral margin and with two distinct, small and obtuse medioventral teeth, 1.4 times as wide as high medially, 0.85 times as wide as face, 0.8 times as high as face medially. Mandible long, not twisted apically, subparallel-sided in apical 0.7, with long, wide and pointed teeth. Temple and possibly vertext smooth, face sparsely and rather finely punctate.

Antennae thickened, setiform, 27-segmented, about 0.8 times as long as body. Scapate distinctly thickened, about twice longer than its maximum width, 4.5 times longer than pedicel. First flagellar segment almost 3.0 times longer than its apical width, 1.2 times longer than second segment. Segments much shortened in apical third of antenna, 16th and 17th ones almost square. Four apical segments narrow; penultimate one 1.4 times longer than width, 0.8 times as long as apical segment; the latter obtuse apically.

Mesosoma 1.5 times longer than maximum high. Posterior flange of propodeum present, long and narrow. Mesoscutum wide, 1.4 times as wide as long medially, possibly densely punctate. Notauli distinct, rather deep anterior and shallow posterior, distinctly crenulate. Prescutellar depression narrow. Mesopleuron distinctly convex, clearly punctate posteriorly and finely punctate anteriorly. Subalar depression narrow, short and distinctly crenulate. Prepectal carina complete but not strong. Postpectal carina possibly present. Sternauli distinct, shallow, oblique. Propodeum weakly rugose, almost smooth basally, in lateral view almost horizontal in basal 0.3, strongly abrupt in apical 0.7, with very low and wide lateral tubercles, with transverse submedian carina not strong.

Wings: Fore wing about 2.5 times longer than maximum width. Costal vein (C+SC+R) wide. Pterostigma wide, first abscissa of radial vein (r) arising almost from apical 0.3 of pterostigma. Radial ( marginal) cell weakly shortened, 2.5 times longer than maximum width, its anterior margin 1.6 times longer than pterostigma. First abscissa of radial vein (r) long, 0.8 times as long as pterostigma wide, 1.3 times longer than second abscissa of radial vein (3-SR). Second abscissa of radial vein (3-SR) 0.2 times as long as distinctly curved third abscissa (SR1), about 0.4 times as long as weakly S-shaped first radiomedial vein (2-SR), 0.8 times as long as second radiomedial vein (r-m). Parastigma large, subround. Discoidal (discal) cell rather narrow sessile anteriorly, almost twice longer then its width. Recurrent vein (m-cu) far postfurcal, 1.5 times longer than second abscissa of median vein (2-SR+M). Second radiomedial (submarginal) cell large, about 1.8 times longer than maximum wide. Nervulus (cu-a) far postfurcal, first abscissa of cubital vein (1-CU1) almost as long as nervulus (cu-a). Brachial (subdiscal) cell closed apico-posteriorly by brachial vein (CU1b). Hind wing incompletely known due to vein discoulouration.

Legs: Fore and middle femora and tibiae rather slender; fore femur 4.5 times, middle one about 5.5 times longer than their width; both tibiae weakly widened apically. Hind femur about 3.5 times longer than wide. Hind tibia distinct ly widened towards apex, 4.8 times longer than maximum width, 1.1 times longer than hind femur, almost as wide as hind f emur. Inner tibial spur about 0.8 times as long as maximum width of tibia, 1.7 times longer than outer spur.

Metasoma not strongly convex (lateral view), not flattened, with two rather deep and crenulate sutures, a little longer than mesosoma, 1.7 times longer than its maximum width. In lateral view, first tergite 1.4 times longer than second one and almost as long as third tergite. First tergite in basal 0.7 with distinct and convergent dorsal carinae. Second tergite 0.5 times as long as maximum width, 0.8 times as long as first and third tergites. Third tergite distinctly, regularly and roundly narrowed posteriorly, without postero-ventral processes. Metasomal carapace entirely covered by dense rugose-areolate sculpture. Ovipositor sheath 0.7 times as long as third metasomal tergite.


A key to fossil species of the genus Phanerotoma

1. Antenna 31-segmented. Upper angles of propodeum strongly produced to conical tooth.—Vertex transversely striate. Mesopleuron with smooth area posteriorly .......................... Ph. extensa
Acknowledgements

We thank the company Lafarge-Granulat for the help with the sampling of the fossils and the family Langlois-Meurin for the authorisation of working on their property. We also thank Gilbert Hodebert (MNHN) for the execution of the habitus drawing. We are very thankful to Alexandr P. Rasnitsyn (Palaeontological Institute RAS, Moscow, Russia) and Don- ald L.J. Quicke (Imperial College, London, UK) for valuable comments of the first draft of this paper, James B. Whitfield (University of Illinois, Urbana, USA), Alejandro Zaldívar-Riverón (University of Mexico, Mexico City, Mexico), and anonymous referee for the critical review of our manuscript. The present work is supported for the senior author in part by the grants of the Russian Foundation for Basic Research (Nos. 07-04-00454 and 10-04-00265) and by the Presidium RAS Program “Origin and evolution of Biosphere, Subprogram II”.

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