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.

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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; Basibuyuk 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 Diospilitinae 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, the next oldest being probably the Pherombinae ichneumonid wasps 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 (Caecalpiniaeae) 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, nervellus 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, Chevrerie, 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 Charmonia, with type species Charmonia inopina van Achterberg, 1979 from Chile (van Achterberg 1979). This is the first fossil record of the subfamily Charmontinae.

Tribe Palaeocharmontini nov.

Type species: Palaeocharmon basalis sp. nov., by monotypy.

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 palp 6-segmented; labial palp 4-segmented, with third segment very small and suboval. Scape weakly thickened (Fig. 2B). Apical segment of antenna with long and slender apical spine (Fig. 2D). Scuto-scutellar suture indistinct. Scutellum posteriorly without furrow (Fig. 1C). Sternalus very shallow (Figs. 1B, 2B, C). Prepectal and postpectal carinae absent (Figs. 1B, 2B, C, E). Propodeum possibly without propodeal bridge between metasomal and coxal cavities. Tibial spurs and claws short and simple (Fig. 2D). Discoidal (discal) cell of fore wing anteriorly distinctly petiolate (Fig. 2G). Nervulus (cu-a) weakly antefurcal (Fig. 2G). First transverse anal vein (2A) present but fine and spectral; second transverse anal vein (a) absent. Brachial (subdiscal) cell closed apico-posteriorly by brachial (CU1b) vein (Fig. 2G). In hind wing, first transverse anal (2A) and recurrent (m-cu) veins present (Fig. 2F); anal (plical) lobe not separated and rather narrow. Metasoma without carapace (Fig. 1B, C). First tergite with distinct lateroioe and distinct dorsal carinae (Fig. 2B, C).

Genera included.—One type genus is known.

Genus Palaeocharmon nov.

Etymology: After palaios, the Greek for ancient, and the Recent genus Charmon. Gender masculine.

Type species: Palaeocharmon basalis sp. nov., by monotypy.

Description.—Occipital carina fused ventrally with hypostomal carina not far from the base of mandible. Eyes possibly glabrous, distinctly emarginated opposite of antennal sockets. Ocelli almost forming equilateral triangle. Frons and face weakly convex. Clypeus weakly convex ventrally. Mandible large. Palpi long. Scape weakly thickened. First flagellar segment a little longer than second segment (Fig. 2B, E). Mesosoma rather short and high (Figs. 1B, 2B, C). 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 (subdiscal) 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 dorsore, 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 Opiniinae 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 (Farml 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 helconine 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 thus presence or absence of the second radiomedial (submarginal) 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 Heliocominae 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 prepectoral 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, *Eubrachus*, are distinct, i.e., the discoidal (discal) cell is distinctly petiolate, the second transverse anal (2A) and recurrent (m-cu) veins of the 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 antennal scape is very long apical spine, the rather distinct dorcus 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, Sparnian, 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 roundingly narrowed. Eye 2.8 times longer than temple (lateral view, on median line). Eye oval, 1.25 times as high as maximum long. Clypeal 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 antennaal socket. Diameter of ocellus 2.3 times interocular 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-
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. Mesoscutum smooth. Subalar depression 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. Metapleural furrow along mesopleural suture distinctly and densely crenulate. Metapleural part of ovipositor sheath about 1.3 times longer than apex of wing.

Dial (SR) and cubital (2-M) veins weakly divergent towards apex. 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 3.0 times longer than wide. Secundal vein (1-M) 0.4 times 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. Radical (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 Palaearctic 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 Diadontogaster are also recorded in amber and rocks. The fossil genus Chelonohelcon has been transferred to Cheloniinae within the monogeneric tribe Chelonoconini (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 zoographic 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 petiolute 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.

Eymology: After our colleague Professor Jean-Jacques Menier.

Holotype: Female, MNHN A32945, mounted in Canada balsam.

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

Type horizon: Lowermost Eocene, 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-
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

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Fig. 3. Photographs of braconid wasp *Phanerotoma menieri* sp. nov., holotype of female, A32945, from the French Amber (Farm Le Quesnoy, Oise, France), lowermost Eocene. A. Habitus in lateral view. B. Metasoma in lateral view. C. Head and mesosoma in lateral view. D. Head in front view. E. Habitus in dorsal view. F. Metasoma in dorsal view.
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 medially, 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 vertex smooth, face sparsely and rather finely punctate.

Antennae thickened, setiform, 27-segmented, about 0.8 times as long as body. Scapes 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.


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.

Colour: Metasoma pale reddish brown, head and mesosoma darker. Antenna yellow, basally and apically infuscated. Wings hyaline; pterostigma dark brown.

A key to fossil species of the genus Phanerotoma

1. Antenna 31-segmented. Upper angles of propodeum strongly produced to conical tooth.—Verte transversely striate. Mesopleuron with smooth area posteriorly Ph. extensa
– Metasoma pale reddish brown, head and mesosoma darker. Face

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