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Cretaceous braconid wasps from the Magadan Province of Russia

SERGEY A. BELOKOBYLSKIJ



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The Cretaceous genera of the hymenopteran family Braconidae are discussed. Overall, eight braconid subfamilies, including two only known from this period, and 17 genera together with two having unclear subfamily position, have been recorded in Cretaceous period. Two new genera, *Magadanobracon* gen. nov. (with two species, *Magadanobracon rasnitsyni* sp. nov. and *M. zherikhini* sp. nov.) and *Cretorhyssalus* gen. nov. (with type species *Cretorhyssalus brevis* sp. nov.) are described. The discussed position of the new genera in Protorhyssalinae remains putative owing to a lack of information about multiporous sensillae of the antenna and the poor preservation of the basal half of the hind wing. The earliest recorded thickened hind tibia in the female sex, as a probable apomorphic character of the subfamily Protorhyssalinae, and the evolutionary state of the antefurcal vs. postfurcal positions of the recurrent vein in the fore wing of Braconidae are discussed.

Key words: Insecta, Hymenoptera, Braconidae, Protorhyssalinae, parasitoids, ambers, prints, Cretaceous, Russia.

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Introduction

The study of the phylogenetic relations in different groups of Hymenoptera on the basis of morphological and/or molecular characters is often accompanied with the use of the palaeontological data (e.g., Quicke et al. 1999; Ronquist et al. 1999; Sharkey 2007). Unfortunately, the palaeontological information is not always strikingly helpful in understanding the group phylogeny, as it is hampered by scarcity of information on hymenopteran taxa, as well as with the often imperfection of the data on important morphological characters of these insects in fossils mostly due to limitation of the fossilization processes. Nevertheless, the data collected from fossils have been included in several studies on the phylogeny of Braconidae. They certainly have helped in the understanding of the natural history and origin time of particular taxa (Murphy et al. 2008; Zaldivar-Riveron et al. 2008a, b; Perrichot et al. 2009).

Cretaceous material (prints on mudstone) from Obeshchayushchiy Spring of the Magadan Province in Russia gives additional interesting information about the taxonomic composition of Cretaceous Braconidae and facilitates, at least partly, investigating possible relationships between extinct groups of these parasitoids.

Instititional abbreviation.—PIN, Laboratory of Palaeoentomology, Palaeontological Institute of the Russian Academy of Sciences, Moscow, Russia.

Other abbreviations.—1-M, second abscissa of basal vein of the fore wing, or second abscissa of mediocubital vein of the hind wing; 1-CU1, first abscissa of cubital vein of the for wing; 1-R1, metacarp of the fore wing; 2A, first transverse anal vein of the fore and hind wings; 2-SR, first radiomedial vein of the fore wing; 2-SR+M, second abscissa of medial vein of the fore wing; 3-SR, second abscissa of radial vein of the fore wing; a, second transverse anal vein of the fore wing; C, costal vein of the fore wing; C+SC+R, costal vein of the fore wing; CU1a, parallel vein of the fore wing; CU1b, brachial vein of the fore wing; cu-a, nervulus vein of the fore wing or nervellus vein of the hind wing; M+CU, first abscissa of mediocubital vein of the hind wing; M+CU1, first abscissa of mediocubital vein of the fore 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; SC, subcostal vein of the fore wing; SR1, third abscissa of radial vein of the fore wing.

Material and methods

The fossil material discussed in this paper was collected in tuffaceous mudstone of the lacustrine Ola Formation at Obeshchayushchiy Spring in the basin of the river Nil, a tributary of Arman' (Magadan Province, Russia). The stratigraphic horizon is Cenomanian, Upper Cretaceous 99.6±0.9–93.5±0.8 Myr (Rasnitsyn and Quicke 2002).

The wing venation terminology is given according to Belokobylskij and Tobias (1998) and (in parenthesis) to van Achterberg (1993).

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Systematic palaeontology

Class Insecta Linnaeus, 1758

Order Hymenoptera Linnaeus, 1758

Family Braconidae Nees, 1812

Subfamily Protorhyssalinae Basibuyuk, Quicke, and van Achterberg, 1999

Remarks.—The monotypic subfamily Protorhyssalinae was established from a single genus and species, *Protorhyssalus goldmani* Basibuyuk and Quicke, 1999, from the Late Cretaceous (Turonian) amber of New Jersey, USA (Basibuyuk et al. 1999). Recently Perrichot et al. (2009) described two new genera and species from French Cretaceous amber, *Protorhyssalodes arnaudi* Perrichot, Nel, and Quicke, 2009 (Protorhyssalinae) and *Aenigmabracon capdoliensis* Perrichot, Nel, and Quicke, 2009, which is similar to this subfamily but it was placed by the authors in Braconidae as "subfamily incertae sedis".

All these taxa were described from amber inclusions permitting thorough examination of the fossils. Rock fossils, like those described below, do not provide such detail and are much worse preserved. Some important details, including details of fore and hind wings, are missing. The multiporous plate sensillae of antennal segments which are the main synapomorphy of Protorhyssalinae (Perrichot et al. 2009) are also unclear in the studied fossils. The poor state of preservation of the basal half of the hind wings is particularly unfortunate because of the taxonomically important features concentrated there. As a result, the taxonomic position of the new taxa is somewhat uncertain, and assignment of both new genera to the subfamily Protorhyssalinae remains putative.

Genus *Magadanobracon* nov.

Etymology: From Magadan city, central to the area where the fossil material comes from, and the braconid genus *Bracon*.

Type species: *Magadanobracon rasnitsyni* sp. nov.; see below. By present designation.

Species included.—Two extinct species *M. rasnitsyni* and *M. zherikhini*.

Diagnosis.—This genus differs from *Protorhyssalus*, as well as *Protorhyssalodes* and *Aenigmabracon,* by the distinctly antefurcal position of the first recurrent vein (m-cu) in the fore wing, by the brachial (CU1b) vein closing the apicoposterior part of the brachial (subdiscal) cell of fore wing, and by the short flagellar segments.

The antefurcal position of the recurrent vein (m-cu) is common for many genera of the plesiomorphic non-cyclostome subfamily Helconinae. The new genus is similar to the helconine genus *Hellenius* Tobias, 1982, but distinctly differs by the presence of the second transverse anal vein (a), by the weakly antefurcal recurrent vein (m-cu), by the shortly postfurcal nervulus (cu-a), by the short first abscissa of the radial vein (r), by having the first tergite short and with complete and S-shaped dorsal keels, and by the wide hind femur.

Description.—Ocelli medium-sized (Fig. $1C_2$, B_2). Antenna rather thick, setiform, 28-segmented (Fig. 2A). Scape rather short and thick; first flagellar segment longer than second; apical segment pointed apically. Mesosoma short and wide (Figs. 1A, B, 2B, 3A, B_1, 4A, B). Median lobe of mesoscutum distinctly protruding, weakly convex anteriorly. Notauli deep and complete. Prepectal carina developed. Sternaulus present but shallow and narrow. Propodeum with more or less distinctly delineated areas. Fore wing (Figs. 1C, 2C, $3B_2$, 4A). Pterostigma wide. Radial vein (r) arising shortly behind middle of pterostigma. Radial (marginal) cell not shortened. Both radiomedial veins (2-SR, r-m) present. Second radiomedial (submarginal) cell rather short and distinctly narrowed towards apex. Discoidal (discal) cell petiolate anteriorly, weakly narrowed anteriorly, with subparallel lateral margins. Recurrent vein (m-cu) antefurcal. Brachial (subdiscal) cell wide, distinctly closed posteroapically by brachial (CU1b) vein. Parallel vein (CU1a) arising almost from posterior 0.2 of distal margin of brachial (subdiscal) cell. Both transverse anal veins (a, 2A) present. In hind wing, submedial (subbasal) cell large; recurrent vein (m-cu) absent. Fore and hind femora distinctly widened, elongate-oval (Fig. 2E). Hind tibia of female distinctly thickened towards apex (Fig. 2E). Tarsal claws simple. Metasoma of female wide (Fig. 2D). First tergite short (Figs. 2D, $3A_2$, B_3, 4A, B), wide, with at least small dorsope, with distinct, more or less S-shaped and complete dorsal carinae; spiracular tubercles distinct. Second suture rather wide. Second tergite without delineated areas. Ovipositor long, about as long as costal vein (Fig. 1A, B).

Discussion.—*Magadanobracon* is putatively included in the subfamily Protorhyssalinae. The fossils available do not display all important diagnostic characters of this subfamily. Unknown character states include the presence vs. absence of the hypoclypeal depression in the mouth area, a crucial character state for assignment to the cyclostome group of subfamilies. Nevertheless the entire body of evidence looks suggestive of the cyclostome nature of the genus. Regrettably the basal posterior part of the hind wing is not preserved well enough to display the characters important for the definitive placing of the new genus to Protorhyssalinae.

Despite of limited information on the valuable diagnostic features, there is an important character of the new species, the distinctly thickened hind tibia, that represents a putative synapomorphy of the subfamily. A thick hind tibia is a characteristic of males of extant species of the cyclostome genus *Rhyssalus* (Rhyssalinae), and occurs only in some males of previously discussed Cretaceous braconids (Protorhyssalinae and related genera). The type species of *Magadanobracon* represents the first female of all known Protorhyssalinae along with genera of debatable subfamily position (*Protorhyssalodes* and *Aenigmabracon*) (Basibuyuk et al. 1999; Perrichot et al. 2009). It is noteworthy that this female shows thick hind tibia like supposedly related males and unlike any known females of fossil Braconidae.

The postfurcal position of the recurrent vein (meeting the second radiomedial cell distal of the first radiomedial vein) is

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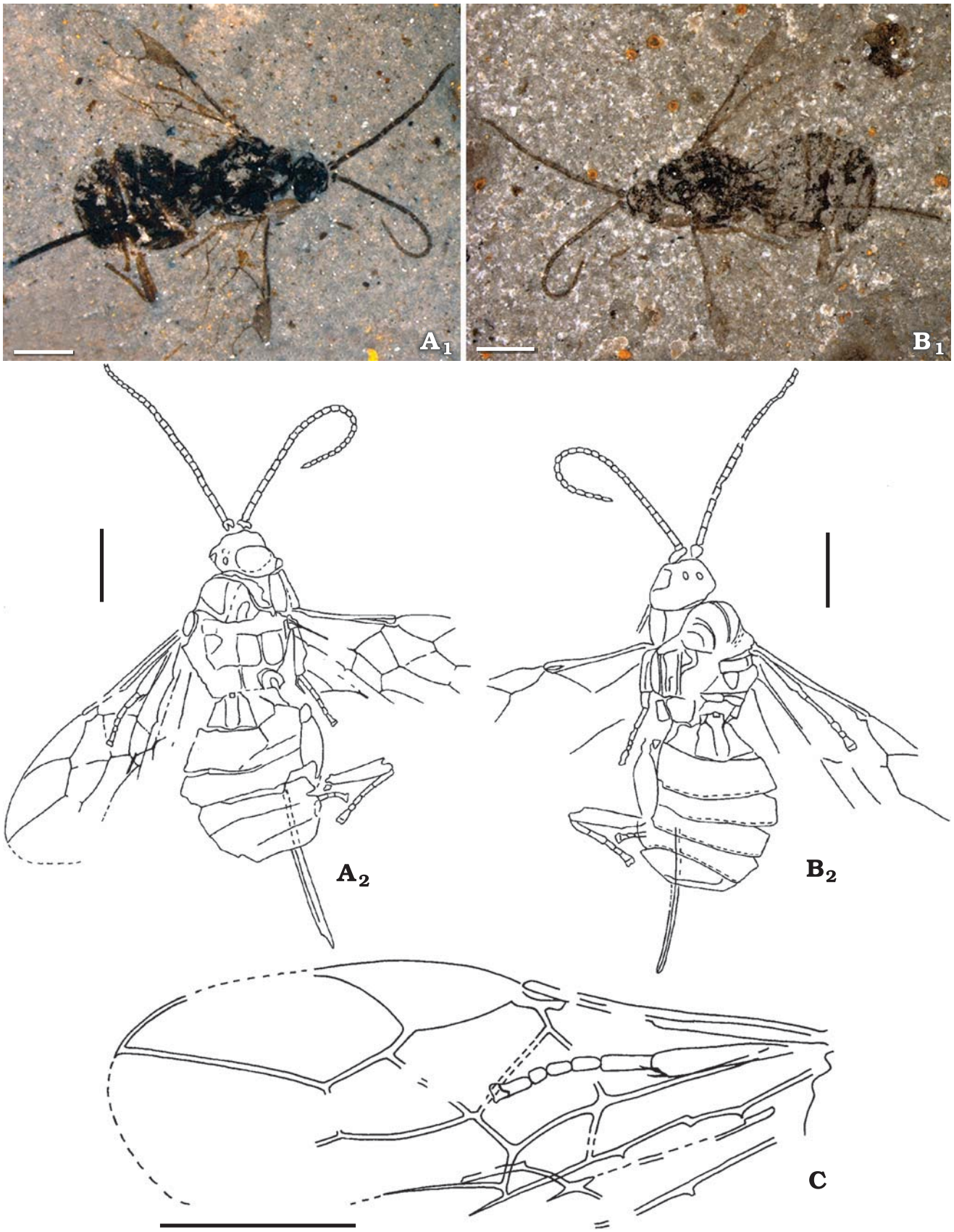


Fig. 1. Braconid wasp *Magadanobracon rasnitsyni* gen. et sp. nov., holotype of female, PIN, 3901/77 (part and counterpart), Obeshchayushchiy fossil site (Magadan Province, Russia), Earliest Upper Cretaceous. **A**. Habitus (part). **B**. Habitus (counterpart). **C**. Wings. Photographs (A_1, B_1) and drawings (A_2, B_2, C). Scale bars 1 mm.

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considered to be the plesiomorphic condition for Braconidae (Tobias 1977), possibly except Doryctinae (Belokobylskij 1993). All other Protorhyssalinae and related genera (*Protorhyssalus*, *Protorhyssalodes*, and *Aenigmabracon*) have a postfurcal or sometimes (*Aenigmabracon*) subinterstitial position of this vein. *Magadanobracon* has the recurrent vein antefurcal, which is apparently an apomorphy of the described genus.

Stratigraphic and geographic range.—Type locality and horizon only.

Magadanobracon rasnitsyni sp. nov.

Figs. 1, 2.

Etymology: Dedicated to Alexandr Pavlovich Rasnitsyn, famous Russian palaeoentomologist and evolutionist, in honour of his 75-year jubilee.

Holotype: Female, PIN, 3901/77 (part and counterpart); wasp well preserved excepting posterior part of the hind wings.

Type locality: Obeshchayushchiy fossil site, Magadan Province, Russia.

Type horizon: Cenomanian, Late Cretaceous, 99.6±0.9–93.5 ±0.8 Myr, tuffaceous mudstone of the lacustrine Ola Formation.

Description.—Female. Body length 4.5 mm; metasoma 2.3 mm; fore wing 3.2 mm, ovipositor 1.4 mm.

Head: More or less transverse, about 1.5 times wider than its median length. Scape about 1.3 times longer than wide. First flagellar segment 2.4 times longer than maximum width, 1.2 times longer than second segment. Penultimate segment about twice longer than maximum width, 0.5 times as long as first segment, almost as long as apical segment.

Mesosoma: 1.3 times longer than its maximum width, 0.45 times as long as fore wing.

Fore wing: Length 2.7 times longer than maximum width. Costal vein (C+SC+R) thick, with rather distinct suture separated fused costal (C) and subcostal (SC) veins. Pterostigma subtriangular, 2.7 times longer than maximum width. Radial (marginal) cell wide, pointed apically, 2.7 times longer than maximum width. Metacarp (1-R1) 1.1 times longer than pterostigma. Radial vein (r) arising behind middle of pterostigma, distance from radial vein (r) to apex of pterostigma along its inner side about 0.8 times as long as distance from vein to base of pterostigma. First radial abscissa (r) 0.45 times as long as maximum width of pterostigma, forming almost straight line with second abscissa (3-SR). Second radial abscissa (3-SR) 2.4 times longer than first abscissa (r), 0.35 times as long as the straight third abscissa (SR1), 0.75 times as long as first radiomedial vein (2-SR), and 1.5 times longer than second radiomedial vein (r-m). Second radiomedial (submarginal) cell 1.7 times longer than maximum width, 1.2 times longer than brachial (subdiscal) cell. Recurrent vein (m-cu) 4.0 times longer than third medial abscissa (2-SR+M), 0.5 times as long as first radiomedial vein (2-SR), 0.55 times as long as second (posterior) abscissa of basal vein (1-M). Discoidal (discal) cell 1.4 times longer than width. Nervulus (cu-a) distinctly inclivous, distance from nervulus (cu-a) to basal vein (1-M) 0.3 times as long as nervulus length. Brachial (subdiscal) cell 2.5 times longer than its maximum width. Mediocubital vein (M+CU1) straight.

Legs: Fore femur about 3.0 times longer than wide. Median tibia weakly thickened. Hind femur 2.7 times longer than its maximum width. Hind tibia distinctly thickened, about 5.0 times longer than its maximum width, 1.4 times longer than hind femur, almost as long as hind tarsus.

Metasoma: First tergite wide, almost linearly widened towards apex, with rather distinct spiracular tubercles in basal 0.3. Apical width of tergite 1.3 times its width at level of tubercles, about 2.5 times its basal width; length of tergite about 0.7 times its apical width. Second tergite possibly smooth, rather short, 0.9 times as long as apical width of first tergite, 1.5 times longer than smooth third tergite. Ovipositor 0.65 times as long as metasoma, 0.85 times as long as mesosoma, 0.4 times as long as fore wing.

Colour: Body black. Fore and middle legs entirely, hind tibia in basal half and hind tarsus entirely yellowish brown. Fore wing hyaline. Pterostigma entirely and all veins brown.

Magadanobracon zherikhini sp. nov.

Figs. 3, 4.

Etymology: After Vladimir Vasilievich Zherikhin, well-known Russian palaeoentomologist and the collector of this specimen.

Holotype: male (?), PIN, 3901/80 (part), PIN, 3901/79 (counterpart); wasp in dorsoventral aspect lacking antenna excepting its bases, fore and middle legs, right fore wing, almost all hind wings, and metasomal apex.

Type locality: Obeshchayushchiy fossil site, Magadan Province, Russia.

Type horizon: Cenomanian, Late Cretaceous, 99.6±0.9–93.5 ±0.8 Myr, tuffaceous mudstone of the lacustrine Ola Formation.

Diagnosis.—This species is very similar to *M. rasnitsyni* sp. nov., but differs in having the hind tibia weakly widened, first metasomal segment with keels distinctly S-shaped, recurrent vein (m-cu) more strongly postfurcal, and fore wing metacarp (1-R1) longer.

Description.—Male. Body length 6.4 mm; mesosoma 2.2–2.3 mm, metasoma about 3.5 mm; first tergite 1.25 mm; fore wing 6.1–6.2 mm.

Head: More or less transverse, about 1.6 times as wide as long medially, roundly narrowed behind eyes. Head 1.35 times wider than its median length. Maximum diameter of ocellus equal to diameter of antennal socket. Scape rather wide, about 1.5 times longer than its width. Flagellar segments slender.

Mesosoma: 1.8–1.9 times longer than maximum width at level of tegulae, 0.4 times as long as fore wing. Mesoscutum distinctly rounded apically, 1.2 times as wide as long medially; median lobe convex. Notauli deep and complete, joined before posterior margin of mesoscutum. Prescutellar depression deep, long, smooth, with median carina. Metanotum rather long. Propodeum with delineated areas, mostly sculptured. Sternaulus (or possibly at least distinct fold in lower part of metapleuron) rather deep, long, and smooth.

Fore wing: Length 2.8 times longer than maximum width. Costal vein (C+SC+R) thick, with rather distinct suture separated costa (C) and subcosta (SC). Pterostigma subtriangular, 2.6 times longer than maximum width. Radial (marginal) cell almost not shortened, wide, pointed apically, 2.3 times lon-

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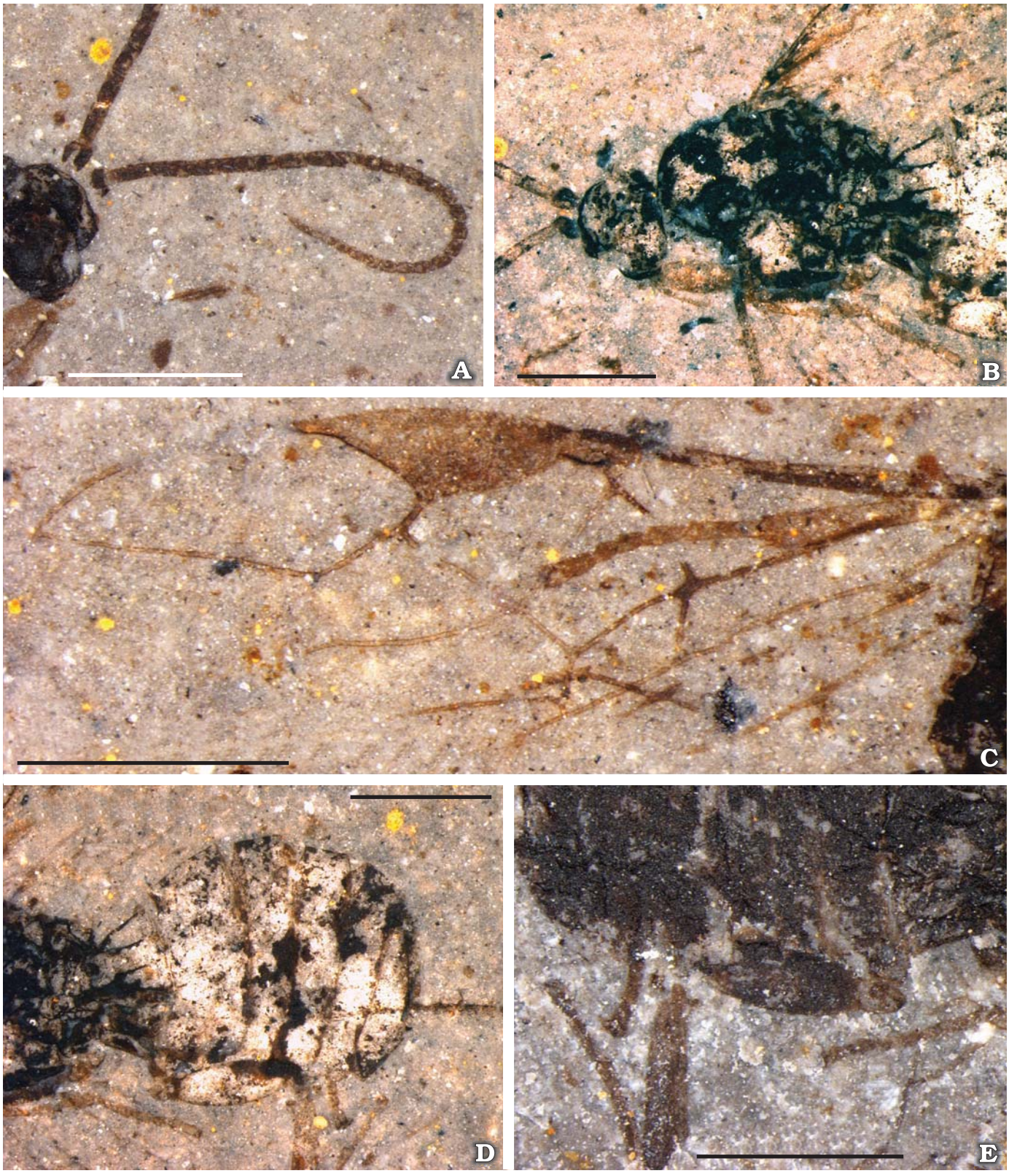


Fig. 2. Photographs of braconid wasp *Magadanobracon rasnitsyni* gen. et sp. nov., holotype of female, PIN, 3901/77 (part and counterpart), Obeshchayushchiy fossil site (Magadan Province, Russia), Earliest Upper Cretaceous. **A**. Antenna. **B**. Head and mesosoma. **C.** Fore and hind wings. **D**. Propodeum and metasoma. **E**. Hind leg. Scale bars 1 mm.

ger than its maximum width. Metacarp (1-R1) 1.25 times longer than pterostigma. Radial vein (r) arising almost from or weakly behind middle of pterostigma, distance from this vein to apex of pterostigma along its inner side 0.7 times as

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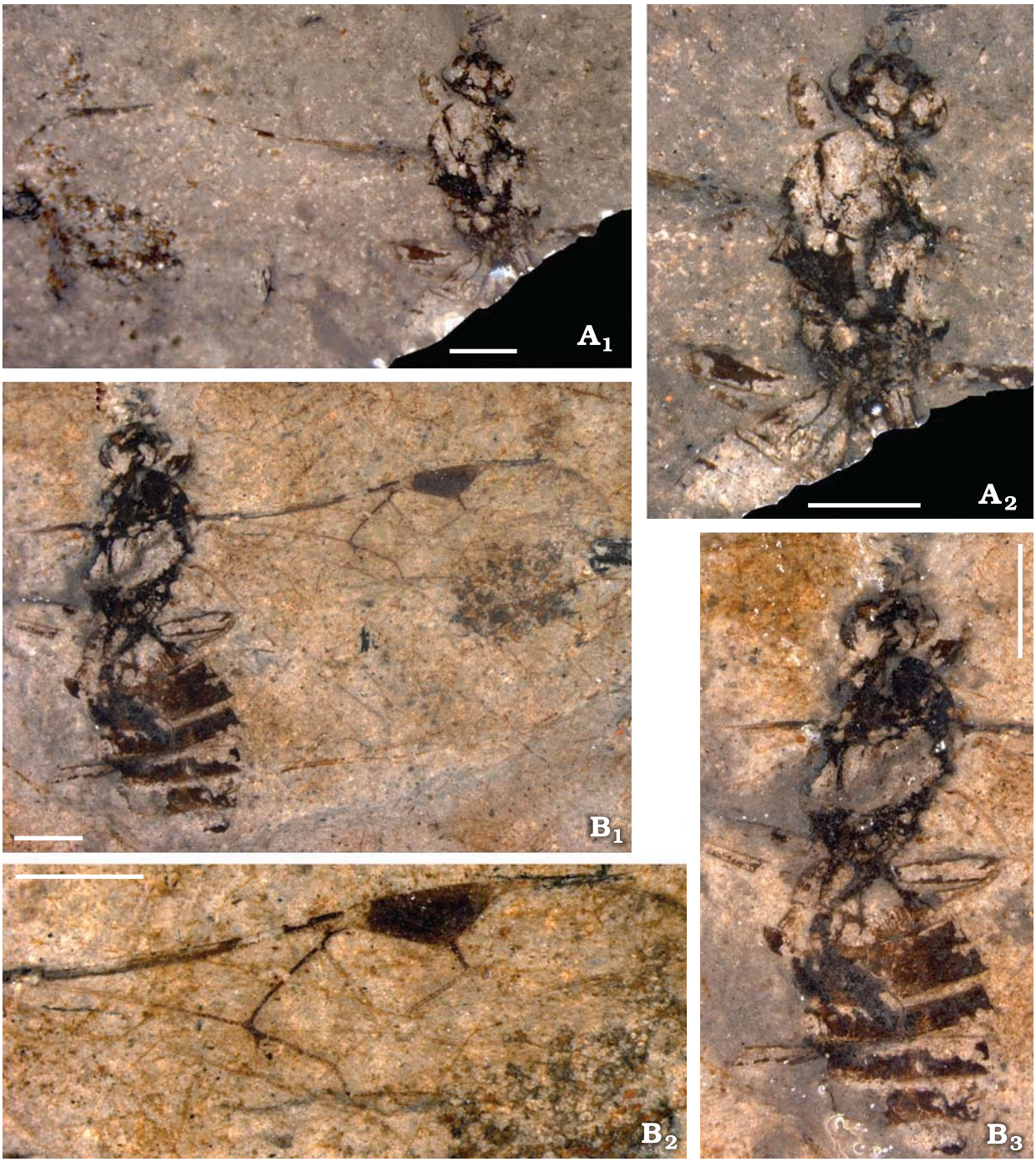


Fig. 3. Photographs of braconid wasp *Magadanobracon zherikhini* gen. et sp. nov., holotype of male (?), Obeshchayushchiy fossil site (Magadan Province, Russia), Earliest Upper Cretaceous. **A**. PIN, 3901/79, counterpart; A_1, habitus; A_2, head, mesosoma, and basal part of metasoma. **B**. PIN, 3901/80, part; B_1, habitus (part); B_2, fore wing (part); B_3, body (part). Scale bars 1 mm.

long as distance from vein to base of pterostigma. First radial abscissa (r) about 0.6 times as long as maximum width of pterostigma, forming very obtuse angle with second abscissa (3-SR). Second radial abscissa (3-SR) 2.2 times longer than first abscissa (r), 0.4 times as long as the straight third abscissa (SR1), 0.8 times as long as first radiomedial vein (2-SR), 1.5 times longer than second radiomedial vein (r-m). Second radiomedial (submarginal) cell not narrowed distally, about twice as long as maximum width, 1.3 times longer than brachial (subdiscal) cell. Recurrent vein (m-cu) 3.5 times longer than third medial abscissa (2-SR+M), 0.6 times as long as first radiomedial vein (2-SR), 0.55 times as long as second (posterior) abscissa of basal vein (1-M). Discoidal (discal) cell 1.2 times longer than wide. Nervulus (cu-a) inclivous, distance from nervulus (cu-a) to basal vein (1-M) 0.4 times as long as nervulus (cu-a) length. Brachial (subdiscal) cell about 3.0 times longer than its maximum width. Mediocubital vein (M+CU1) straight.

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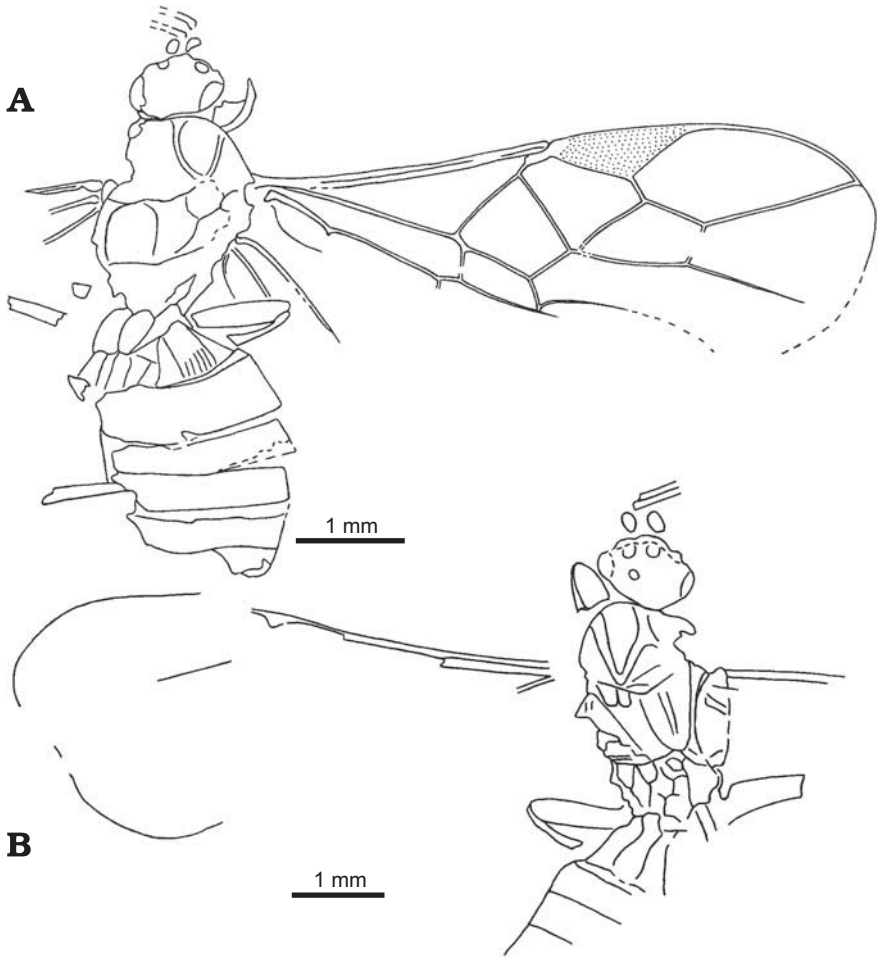


Fig. 4. Drawings of braconid wasp *Magadanobracon zherikhini* gen. et sp. nov., holotype of male (?), Obeshchayushchiy fossil site (Magadan Province, Russia), Earliest Upper Cretaceous. **A**. PIN, 3901/80 (part), habitus. **B**. PIN, 3901/79 (counterpart), habitus.

Legs: Fore femur rather thick. Middle (?) femur 4.2 times longer than its maximum width. Hind tibia basally slender, weakly widened distally.

Metasoma: First tergite wide, distinctly and curvedly widened towards apex, with rather distinct and wide subbasal tubercles, with more or less distinct dorsope; dorsal carinae distinct, complete, subparallel in basal half and weakly roundly widened in apical half; more or less sculptured at least in apical half. Apical width of first tergite about 2.0 times its basal width; length of first tergite 0.7–0.8 times its apical width. Second tergite with narrow basal area, or possibly it is wide gape between first and second tergites; tergite smooth, rather short, 0.35 times as long as basal width, about as long as smooth third tergite.

Colour: Head and mesosoma black, metasoma brown or black. Middle femur dark brown, hind tibia pale. Fore wing possibly faintly or very faintly infuscate, especially along veins. Pterostigma dark brown, pale in basal 0.2 and apically; veins brown.

Genus *Cretorhyssalus* nov.

Etymology: After combination of Cretaceous, the geological period from which the genus was discovered, and the braconid genus *Rhyssalus*.

Type species: *Cretorhyssalus brevis* sp. nov.; see below. By monotypy.

Diagnosis.—*Cretorhyssalus* differs from *Magadanobracon* gen. nov. in having the hind femur slender and long, fore wing with brachial (subdiscal) cell is open in postero-apical corner, recurrent vein (m-cu) almost interstitial, first radial abscissa (r) short and arising before middle of pterostigma, and body size small.

Description.—Mesosoma short and high (Fig. 5A, B), about 1.3 times longer than maximum height. Prepectal carina present and distinct. Sternaulus indistinct. Fore wing (Fig. 5A, B). Fused costal (C) and subcostal (SC) veins thick. Pterostigma wide. Radial vein (r) arising distinctly before middle of pterostigma. First abscissa of radial vein (r) short. Both radiomedial veins (2-SR, r-m) possibly present. First radiomedial vein (2-SR) long. Discoidal (discal) cell petiolate anteriorly, weakly narrowed anteriorly, with subparallel lateral margins (recurrent (m-cu) and basal (1-M) veins). Recurrent vein (m-cu) almost interstitial. Brachial (subdiscal) cell wide, open postero-apically, brachial vein (CU1b) absent. At least first transverse anal vein (2A) present. Hind femur narrow and long, elongate-oval (Fig. 5B). Metasoma rather long (Fig. 5A, B).

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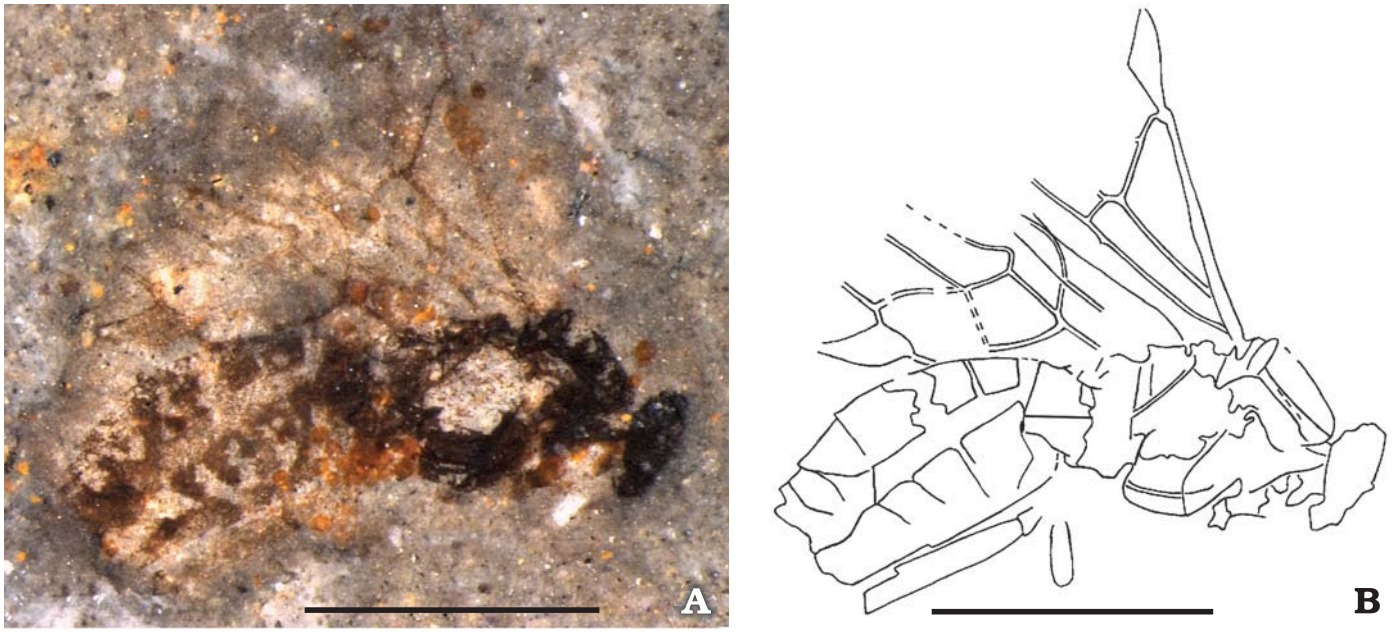


Fig. 5. Braconid wasp *Cretorhyssalus brevis* gen. et sp. nov., holotype of male (?), PIN, 3901/81, Habitus in lateral view, Obeshchayushchiy fossil site (Magadan Province, Russia), Earliest Upper Cretaceous. Photograph (**A**) and drawing (**B**). Scale bars 1 mm.

Cretorhyssalus brevis sp. nov.

Fig. 5.

Etymology: From the Latin *brevis,* short; to emphasize the short body.

Holotype: male (?), PIN, 3901/81; wasp in lateral aspect lacking antenna, fore and middle legs entirely and apical half of hind leg, distal halves of fore wings, distal and posterior parts of hind wing and metasomal apex.

Type locality: Obeshchayushchiy fossil site, Magadan Province, Russia.

Type horizon: Cenomanian, Late Cretaceous, 99.6±0.9–93.5± 0.8 Myr, tuffaceous mudstone of the lacustrine Ola Formation.

Description.—Male (?). Body length 2.2 mm; metasoma 1.1 mm.

Head. Without characters for description. Antenna not preserved.

Mesosoma. Short and height, 1.3 times longer than maximum height, 0.75 times as long as metasoma. Mesoscutum not highly, but distinctly and roundly elevated above pronotum. Prepectal carina distinct. Propodeum quite possibly with areas delineated by carinae, or at least sculptured.

Fore wing. Apical half of fore wing absent. Costal vein (C+SC+R) thick. Pterostigma triangular, not wide, 2.5 times longer than maximum width. Radial vein (r) arising distinctly before middle of pterostigma, distance from this vein to apex of pterostigma along inner side 1.5 times longer than distance from vein to base of pterostigma. First radial abscissa (r) short, 0.4 times as long as maximum width of pterostigma, forming very obtuse angle with second radial abscissa (3-SR). First radiomedial vein (2-SR) 1.7 times longer than recurrent vein (m-cu), about 4.5 times longer than first radial abscissa (r). Second radiomedial (submarginal) cell possibly not narrowed distally. Recurrent vein (m-cu) almost interstitial, subparallel to basal vein (1-M), 0.7 times as long as second (posterior) abscissa of basal vein (1-M). Discoidal (discal) cell 1.3 times longer than wide. Nervulus (cu-a) postfurcal, distance from nervulus (cu-a) to basal vein (1-M) 0.3 times as long as nervulus (cu-a). Brachial (subdiscal) cell 2.5 times longer than its maximum width. Mediocubital vein (M+CU1) straight. First transverse anal vein (2A) fine and short.

Metasoma: First tergite wide, without clear spiracular tubercles, its length about 0.9 times apical width. Second tergite smooth, 0.8 times as long as first tergite, about as long as smooth third tergite. Laterotergites of second and third tergites possibly not separated.

Colour: Head and mesosoma black, metasoma brown. Fore wing almost hyaline. Pterostigma entirely and veins more or less brown.

Concluding remarks

The oldest recorded fossils of Braconidae are known from the Cretaceous (Carpenter et al. 1937; Zherikhin 1978; Rasnitsyn 1983; Basibuyuk et al. 1999; Perichot et al. 2007, 2009), and have been recorded almost exclusively from amber. Only a single Cretaceous braconid wasp, *Eobraconus inopinatus*, is known from the rocks of Mongolia (Rasnitsyn 1983). Although Cretaceous braconids are represented mainly by non-specialised taxa, nonetheless several genera recorded from this geological period (*Heterospilus* Haliday, 1836; *Paraharmius* Nixon, 1940; *Dirrhope* Foerster, 1851; *Eobraconus* Rasnitsyn, 1985) are morphologically advanced and display many apomorphic features. In total, eight subfamilies of Braconidae have been recorded from the Cretaceous period so far

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Table 1. Mesozoic and Cenozoic fossil records of the family Braconidae.

Subfamilies of Braconidae and number of genera (in parenthesis)	Geological period, age and collecting sites
Acampsohelconinae (1)	Late Eocene, 34–37 Myr (Baltic amber)
Agathidinae (4)	Late Eocene, 34–37 Myr (Florissant, USA; Bembridge Marls, Isle of Wight, England; Baltic amber).
Alysiinae (4)	Earliest Miocene, 20–23 Myr (Rott am Siebengebirge, Germany); Late Oligocene, c. 28 Myr (Aix-en-Province, France); Late Eocene, 34–37 Myr (Florissant, USA)
Brachistinae (3)	Late Eocene, 34–37 Myr (Florissant, USA; Bembridge Marls, Isle of Wight, England; Baltic amber).
Braconinae (2)	Middle Miocene, 11–16 Myr (Shanwang, China); Early Miocene, 16–23 Myr (Radoboj, Croatia); Earliest Miocene, 20–23 Myr (Rott am Siebengebirge, Germany); Oligocene, 23–34 Myr (Sieblos, Bayern, Germany; Brunstatt, Altsatia, Germany; Similkameen River, British Columbia, Canada); Late Oligocene, c. 28 Myr (Aix-en-Province, France); Late Eocene, 34–37 Myr (Baltic amber; Bembridge Marls, Isle of Wight, England; Florissant, USA)
Charmontinae (1)	Earliest Eocene, c. 53 Myr (French amber, Oise, France)
Cheloninae (5)	Late Eocene, 34–37 Myr (Baltic amber; Bembridge Marls, Isle of Wight, England; Florissant, USA); Middle Eocene; 40–48 Myr (Green River, Colorado, USA); Earliest Eocene, c. 53 Myr (French amber, Oise, France).
Diospilitinae (1)	Late Eocene, 34–37 Myr (Baltic amber)
Dirrhopinae (1)	Late Cretaceous (Santonian), 83.5–85.8 Myr (Yantardakh, Taimyr, Russia)
Doryctinae (13)	Middle Miocene, 11–16 Myr (Shanwang, China); Early–Middle Miocene, 16–20 Myr (Dominican amber, Dominican Republic; Chiapas, Mexico); Earliest Miocene, 20–23 Myr (Rott am Siebengebirge, Germany); Late Eocene, 34–37 Myr (Baltic amber; Bembridge Marls, Isle of Wight, England; Florissant, USA); Middle Eocene; 40–48 Myr (Green River, Colorado, USA); Late Cretaceous (Santonian), 83.5–85.8 Myr (Yantardakh, Taimyr, Russia)
Eoichneumoninae (5) (insectae sedis)	Earliest Cretaceous (Berriasian–Aptian), 112–145 Myr (Koonwarra, Australia; Khotont, Khutuliin-Khira, Mongolia; Baissa, Siberia; Purbeck, England)
Euphorinae (13)	Earliest Miocene, 20–23 Myr (Rott am Siebengebirge, Germany); Late Eocene, 34–37 Myr (Baltic amber; Bembridge Marls, Isle of Wight, England; Florissant, USA); Late Cretaceous (Campanian), 76.5–79.5 Myr (Canadian Amber, Cedar Lake, Canada)
Exothecinae (7)	Middle Miocene, 11–16 Myr (Shanwang, China); Earliest Miocene, 20–23 Myr (Rott am Siebengebirge, Germany); Late Oligocene, c. 28 Myr (Aix-en-Province, France; Late Eocene, 34–37 Myr (Baltic amber; Bembridge Marls, Isle of Wight, England; Florissant, USA); Late Cretaceous (Santonian), 83.5–85.8 Myr (Yantardakh, Taimyr, Russia)
Helconinae (12)	Earliest Miocene, 20–23 Myr (Rott am Siebengebirge, Germany); Late Oligocene, c. 28 Myr (Aix-en-Province, France); Late Eocene, 34–37 Myr (Baltic amber; Bembridge Marls, Isle of Wight, England; Florissant, USA); Late Cretaceous (Campanian), 76.5–79.5 Myr (Canadian Amber, Cedar Lake, Canada)
Ichneutinae (1)	Late Eocene, 34–37 Myr (Baltic amber)
Macrocentrinae (1)	Late Eocene, 34–37 Myr (Baltic amber)
Masoninae (1)	Early–Middle Miocene, 16–20 Myr (Dominican amber; Dominican Republic)
Microgastrinae (7)	Earliest Miocene, 20–23 Myr (Rott am Siebengebirge, Germany); Oligocene, 23–34 Myr (Camoins, Bassin de Marseille, France); Late Eocene, 34–37 Myr (Baltic amber; Bembridge Marls, Isle of Wight, England; Florissant, USA)
Miracinae (1)	Late Eocene, 34–37 Myr (Baltic amber)
Opiinae (1)	Late Eocene, 34–37 Myr (Bembridge Marls, Isle of Wight, England)
Orgilinae (2)	Late Eocene, 34–37 Myr (Baltic amber; Bembridge Marls, Isle of Wight, England)
Protorhyssalinae (4)	Late Cretaceous (Turonian), 89–92 Myr (New Jersey, USA); Late Cretaceous (Cenomanian), 93.5–99.6 Myr (Obeshchayushchiy Spring, Magadan Province, Russia)
Rhyssalinae (2)	Late Eocene, 34–37 Myr (Baltic amber)
Rogadinae (4)	Earliest Miocene, 20–23 Myr (Rott am Siebengebirge, Germany); Late Eocene, 34–37 Myr (Baltic amber; Florissant, USA)
Unknown subfamily (insertae sedis) (2)	Late Cretaceous (Albian–Cenomanian); 93–99 Myr (French amber); Earliest Cretaceous (Berriasian), 140–145 Myr (Khutel-Khara-Ula, Mongolia)

(Carpenter 1992; Perichot et al. 2009), though the taxonomic status of some of some these taxa needs clarification.

Brues (in Carpenter et al. 1937) studied the Campanian amber of Canada (Cedar Lake, Manitoba) and described three taxa from the subfamilies Helconinae and Euphorinae. Of these, *Neoblacus* (= *Blacus*) *facialis* Brues, 1937 quite possibly has a correct generic position in Blacinae. On the other hand, the placement of *Pygostolus patriarchicus* Brues, 1937 in this genus is undoubtedly erroneous since its fore wing has a second radiomedial vein (r-m), a feature that is unknown in the extant species of the euphorine genus *Pygostolus*. *Diospilus allani* Brues, 1937 was originally placed in the subfamily

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Helconinae. However, its wing venation is very similar to the extant cyclostome rhyssaline genus *Pseudobathystomus*, as well as to the Cretaceous *Protorhyssalus*, *Protorhyssalodes*, and *Aenigmabracon* and it possibly belongs with the group of genera mentioned above.

Members of the specialised extant genera *Heterospilus* (Doryctinae), *Parahormius* (Exothecinae, Hormiini), and *Dirrhope* (Dirrhopinae) have been recorded from Santonian (Late Cretaceous) Taimyr amber (Zherikhin 1978), but this needs reconsideration (unfortunately, respective amber material is badly damaged and hardly permits verification).

Rasnitsyn (1983) described the new genus and species *Eobraconus inopinatus* based on a print on rock from Khutel-Khara-Ula (Mongolia) that has quite specialised wing venation, but its subfamily position is unresolved. The Cretaceous subfamily Protorhyssalinae (Basibuyuk et al. 1999) was described for *Protorhyssalus goldmani* Basibuyuk and Quicke, 1999 from Turonian amber of New Jersey (USA). Some other undescribed Cretaceous Braconidae have been mentioned from Lebanon, Spanish, Burmese, Canadian and South African ambers (for a short review of this see: Perrichot et al. 2009).

Two new Cretaceous taxa, *Protorhyssalodes arnaudi* Perrihot, Nel, and Quicke, 2009 (Protorhyssalinae) and *Aenigmabracon capdoliensis* Perrihot, Nel, and Quicke, 2009 (with an ambiguous subfamily position) have been described recently from French Albian–Cenomanian ambers (Perrichot et al. 2009). The latter genus provides the first record in the fossil Braconidae having the second recurrent vein (2-m-cu) in the fore wing (known also in extant Apozyginae [Mason 1978, 1987; Quicke and Achterberg 1990] and as aberrant venation in some non-advanced braconid taxa [Tobias and Belokobylskij 1983]). Study of the wing venation and phylogenetic analysis of the fossil braconid taxa, as well as of the extinct and extant ichneumonoids as a whole, led to synonymization of the extinct family Eoichneumonidae with Braconidae, although as an *insertae sedis* group in the latter family (Perrichot et al. 2009). New and more comprehensive information on the morphological structures of the members of these fossil taxa (especially of Eoichneumonidae) are required to support or refute this judgment.

The three new taxa of Cretaceous Braconidae described in this paper, *Magadanobracon rasnitsyni* sp. nov., *M. zherikhini* sp. nov., and *Cretorhyssalus brevis* sp. nov., yield additional information about the diversity of the fossil braconid fauna in this palaeontological period. The female of *Magadanobracon rasnitsyni* exhibits for the first time in this sex of braconids, the unique feature of a distinctly thickened hind tibia which, together with the same hind tibial condition in males, may be an apomorphic character of the whole subfamily Protorhyssalinae. The members of the genus *Magadanobracon* have an antefurcal position of the recurrent vein in the fore wing. This putatively apomorphic character is also recorded for the first time in the subfamily Protorhyssalinae and related genera. However, such alternative representation of both antefurcal and postfurcal positions of the recurrent vein in the oldest braconid fossils leaves the plesiomorphic state in the evolution of Braconidae uncertain.

A comprehensive overview of the diversity of the fossil Braconidae subfamilies and genera recorded in the Mesozoic and Cenozoic eras is shown in the Table 1.

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