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# New braconid wasps from French Cretaceous amber (Hymenoptera, Braconidae): synonymization with Eoichneumonidae and implications for the phylogeny of Ichneumonoidea

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Two new fossils of Braconidae are described from Albian-Cenomanian amber of south-western France, *Protorhyssalodes arnaudi* gen. n., sp. n., and *Aenigmabracon capdoliensis* gen. n., sp. n. The former appears superficially similar to the type genus and species of the extinct sub-family Protorhyssalinae, from Turonian New Jersey amber specimens, and the latter both to *Protorhyssalus* and to members of the extinct family Eoichneumonidae. However, both new taxa display unique combinations of wing venation characters making confident assignment to sub-family impossible. Indeed, they are the first braconids ever known to possess both vein 2-CU and a distinct trace of vein 2-1A on hindwing. The new fossil taxa are incorporated into a morphological analysis of extinct and extant ichneumonoids. As a result of the analyses we synonymize the Eoichneumonidae with the Braconidae.

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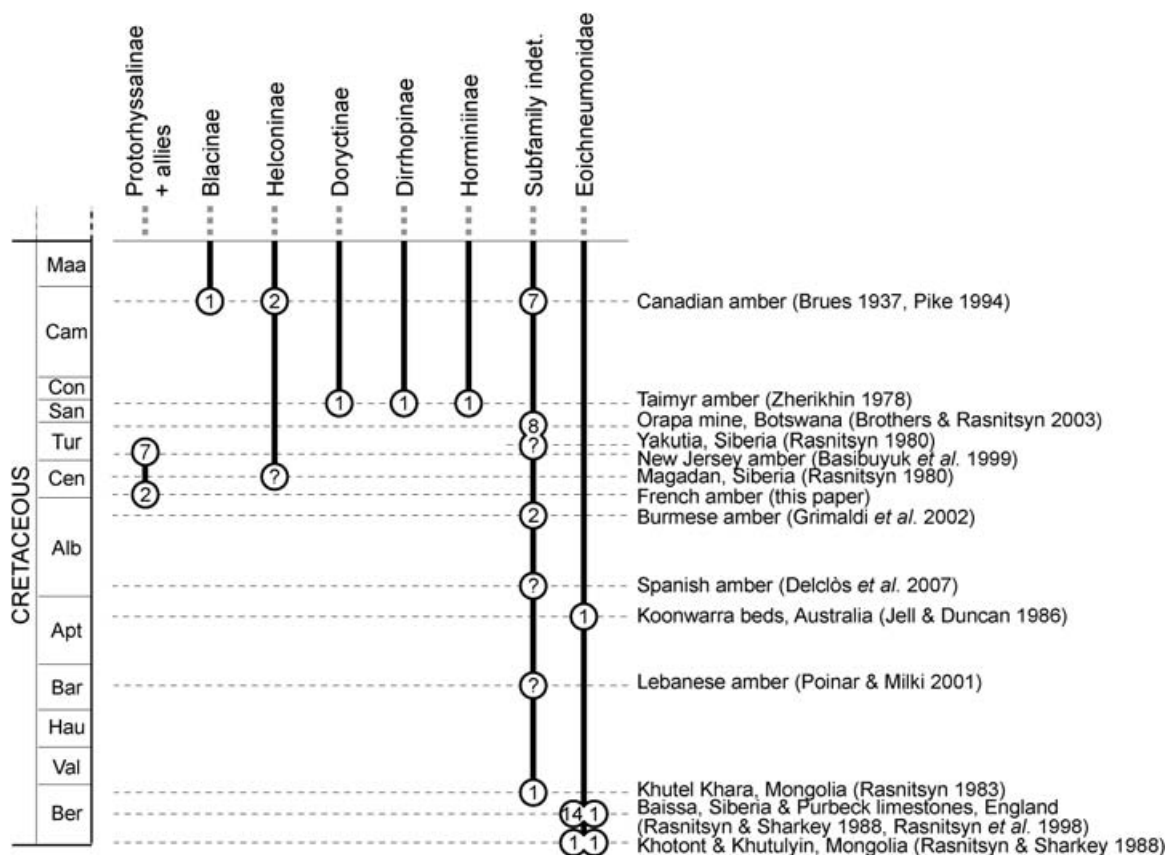
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## Introduction

The fossil record of the wasp family Braconidae is significant in the Cenozoic, whereas Mesozoic fossils are rather scarce with specimens being reported mainly from Cretaceous ambers (Fig. 1). Brues (1937) described three genera from the Campanian amber of Canada (estimated to be 76.5–79.5 myo), and Zherikhin (1978) reported representatives reputedly of the still extant genera *Heterospilus* Haliday, *Parahormius* Nixon, and *Dirrhope* Förster, from the Santonian amber of Yantardakh, Siberia (estimated to be 83.5–85.8 myo) though these should be treated with considerable caution as Zaldivar-Riverón *et al.* (2008) estimate the age of the Doryctinae to be between 44.45 and 59.89 myo (mean = 54.4; SD = 4.09). Basi-buyuk *et al.* (1999) described the Cretaceous sub-family Protorhyssalinae from the Turonian amber of New Jersey based on seven specimens, and suggested this could be basal in the braconid phylogeny. Some other mesozoic Braconidae have also been mentioned in the literature, though all are currently

undescribed and their identities remain effectively unknown. These include specimens from the Barremian Lebanese amber (Poinar & Milki 2001), the Aptian/Albian Spanish amber of Álava (Delclòs *et al.* 2007), the Albian Burmese amber collection of the American Museum of Natural History (Grimaldi *et al.* 2002), and the Campanian amber of Grassy Lake, Canada (Pike 1994). A few impression fossils are also known from the Lower Cretaceous of Mongolia (Rasnitsyn 1983), the Cenomanian and Turonian of Siberia (Rasnitsyn 1980), and Brothers & Rasnitsyn (2003) cited eight specimens of putatively eight different species in the Turonian deposits of Orapa, Botswana. The Eoichneumonidae, here newly considered as Braconidae *incertae sedis* (see phylogenetic discussion below), consist of fewer than 20 fossil specimens found as impressions from the Berriasian of Mongolia, Siberia and England (Rasnitsyn & Sharkey 1988; Rasnitsyn *et al.* 1998), and the Aptian Koonwarra formation of Australia (Jell & Duncan 1986).



**Fig. 1** Mesozoic fossil record of the family Braconidae, including ‘Eoichneumonidae’. Labels in circles refer to the number of specimens identified.

Since braconids are specialized parasitoids typically with narrow relationships to their hosts, the mass extinctions (and especially that of the end-Cretaceous) would be expected to have had a greater impact on them than on similar but polyphagous insects. The present description of two new braconids from the middle part of the Cretaceous provides further insight for the Mesozoic diversity of this group and hopefully will improve our estimates of the impact of the K–T crisis on them.

Several phylogenies have been proposed for the Braconidae over the past two decades, based on morphological characters alone (Quicke & van Achterberg 1990; Sharkey & Wahl 1992; van Achterberg & Quicke 1992; Wharton *et al.* 1992; Quicke *et al.* 1999; Wharton 2000), or on combined molecular plus morphological characters (Shi *et al.* 2005; Zaldivar-Riverón *et al.* 2005; Pitz *et al.* 2007). These phylogenetic hypotheses are only partially congruent, indicating that much work remains to be done to obtain a robustly supported phylogeny for this highly diversified family. Here we modify the phylogenetic analysis of the Ichneumonoidea proposed by Quicke *et al.* (1999), in an effort to place the new fossils systematically.

### Materials and methods

The two wasps described below were found together with 44 other fossil arthropods, mainly dipterans and other hymenopterans, in a single piece of amber from the quarry of Cadeuil, Charente-Maritime, SW France. The amber-bearing stratum is Late Albian in age (Néraudeau *et al.* 2008).

Maximum parsimony phylogenetic analysis was carried out using PAUP\* (Swofford 1999). The data matrix is presented in Table 1 and is modified from that in table 1b of Quicke *et al.* (1999). The following changes to that matrix were made: (i) *Aenigmabracon* gen. n. and *Protorhyssalodes* gen. n. were added and scored separately; (ii) the taxon Agathidinae was removed and variation incorporated into the non-cyclostome braconid category; (iii) character 11 [i.e. hindwing vein r-m with (state 0) or without (state 1) a bulla] was correctly scored as in state 0 for *Tanychora*, instead of state 1 in Quicke *et al.* (1999: tables 1a and 1b, while a bulla is clearly visible in fig. 6B); (iv) character 13B was removed [i.e. just treating the presence (state 0) or absence (state 1) of hindwing vein 2-CU rather than interpreting distal occurrences as vein m-cu]; (v) an additional character, character 24 in Table 1, was added indicating the presence (state 0) or absence (state 1) of hindwing vein 2-1A.

**Table 1** Character states of taxa included in analysis of intraichneumonoid relationships, based on Quicke *et al.* (1999) but with additional taxa and character (see text for details).

Taxa	Characters																							
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
hypothetical_ancestor	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0
Praeichneumonidae	?	?	?	?	0	0	0	?	?	0	?	0	?	?	0	?	0	?	?	?	?	?	?	0
Eoichneumonidae	?	0	0	?	0	0	1	0	?	0	1	1	0	1	0	?	0	?	?	?	?	?	?	0
<i>Tanychora</i>	?	0	0	?	0	0	1	0	?	0	0	0	0	?	?	?	?	?	?	?	?	?	?	0
<i>Tanychorella</i>	?	0	0	?	1	0	1	1	1	0	0	0	0	?	0	?	0	?	?	?	?	?	?	0
Hybrizontinae*	0	0	2	1	1	0	2	1	1	0	0	1	0	1	1	1	0	0	?	1	1	1	0	0
Xoridinae	0	0	0	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0
Other_Ichneumonidae	0	0	0	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	P	1	0	0	0
<i>Aenigmabracon</i>	1	1	0	?	0	0	1	0	0	0	1	2	0	1	1	1	0	?	?	?	?	?	?	0
Apozyginae	1	0	0	0	0	1	2	1	1	0	1	2	0	1	1	1	1	0	?	?	0	?	?	1
<i>Protorhyssalus</i>	1	1	?	0	0	0	2	0	0	1	1	2	0	1	1	1	1	?	?	?	?	?	?	1
<i>Protorhyssalodes</i>	1	?	?	1	0	0	2	0	0	1	1	2	0	1	1	1	1	?	?	?	?	?	?	0
Rhyssalinae_group	1	1	1	0	0	1	2	1	1	1	1	2	1	1	1	1	1	0	0	2	0	1	1	0
Other_cyclostomes	1	1	1	0	0	1	2	1	1	1	1	2	1	1	1	1	1	0	0	1	0	1	1	0
Aphidiinae	P	1	2	1	P	1	2	1	1	1	1	2	1	1	1	1	1	1	2	1	P	1	0	0
Trachypetinae	0	0	0	0	P	0	1	1	0	1	1	1	0	1	0	1	1	1	?	1	1	0	0	1
Non-cyclostomes	0	0	0	0	P	P	Q	P	P	1	1	2	P	1	1	1	1	1	0	1	1	1	1	P

\*Hybrizontinae is currently recognized as having priority over Paxylommatinae.

The data set was analysed using the branch and bound search option that is guaranteed to recover trees of the shortest length, followed by heuristic search using 10 000 random additions. The five distinct most parsimonious trees obtained were each used as starting trees for further heuristic searches to determine whether more than one distinct island of trees had been discovered. Successive approximations character weighting was carried out using both the maximum and the minimum values of the retention index as the reweighing function (see Quicke *et al.* 1999). The raw data were bootstrapped using 100 bootstrap replicates each with 100 random addition heuristic searches and unlimited maxtrees.

The terminology of van Achterberg (1993) is employed throughout for morphological features.

### Systematic palaeontology

Superfamily Ichneumonoidea *sensu* Rasnitsyn, 2002

Family BRACONIDAE Stephens, 1829

Subfamily INCERTAE SEDIS

### Genus *Protorhyssalodes*, Perrichot, Nel & Quicke, gen. n.

*Type species.* *Protorhyssalodes arnaudi* sp. n., by present designation and monotypy.

*Etymology.* The name is a combination of *Protorhyssalus*, its most similar genus, and the Greek suffix *-odes* meaning 'with the form of'.

*Diagnosis.* Antennae with 19 segments; forewing vein R and parastigma contiguous; veins C+SC and R merged but with a

distinct groove between them in dorsal profile, no costal cell present apically; vein 1-SR oblique; veins CU1b and 2m-cu absent; vein m-cu entering second sub-marginal cell; vein cu-a strongly post-furcal; vein 'a' present; hindwing veins 2-CU and 2-1A present; veins SC+R and C completely fused for a considerable distance from hindwing base; vein 1r-m without a bulla, approximately half length of 1-M; a bulla present between 2-CU and 2-1A; dorsal carinae on metasomal tergite 1; probably cyclostome. Hind basitarsus shorter than combined length of following segments.

### *Protorhyssalodes arnaudi* Perrichot, Nel & Quicke, sp. n. (Figs 2–3)

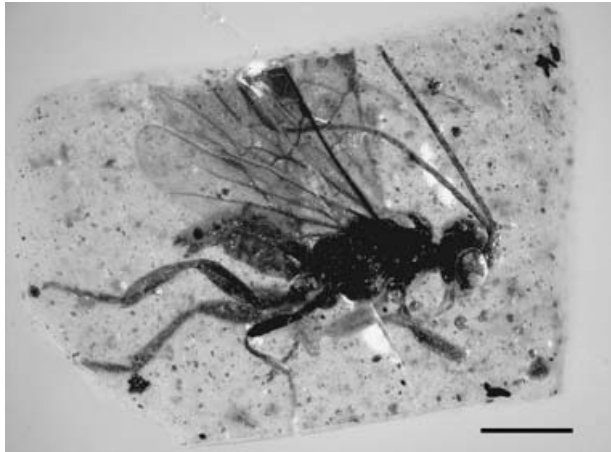
*Holotype.* Specimen MNHN CDL 2.4, deposited in the amber collection of the Earth History Department, Muséum National d'Histoire Naturelle, Paris, France.

*Type locality.* Cadeuil, Charente-Maritime, SW France. Mid-Cretaceous (Uppermost Albian-Lower Cenomanian) amber.

*Etymology.* The name is dedicated to Eugène Arnaud, collector of the type specimen.

*Diagnosis.* As for the genus.

*Description.* Head orthognathous, probably cyclostome (a distinct depression visible above mandibles in lateral aspect); mandibles poorly visible; maxillary palps five-segmented unless there is a small basal 6th one, fourth segment the longest;



**Fig. 2** *Protorbysalodes arnaudi* gen. n., sp. n., holotype specimen MNHN CDL 2.4. General habitus in right lateral view. Scale bar is 0.50 mm.

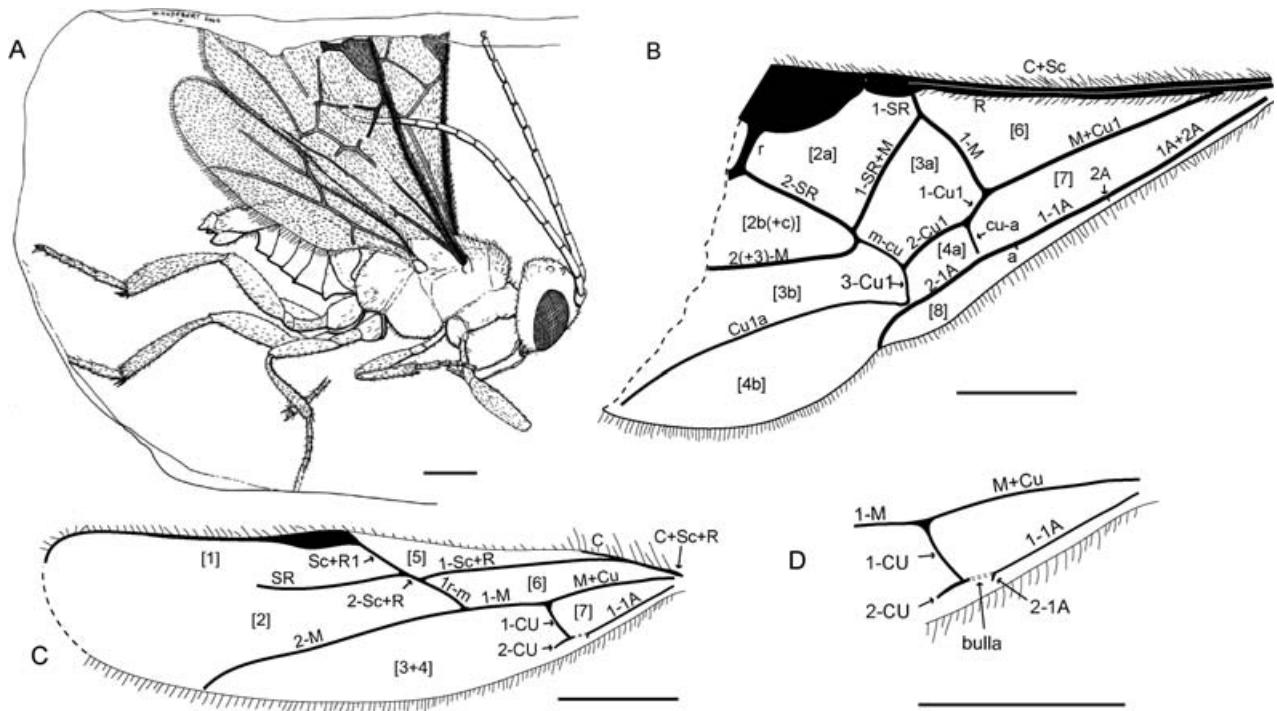
labial palps four-segmented; eyes glabrous, not emarginate; antenna with 19 segments; multiporous plate sensilla not visible by preservation; scape sub-cylindrical, about as long as wide, distinctly wider than pedicel; combined length of scape and pedicel about same length as first flagellomere; flagellomeres cylindrical, becoming gradually shorter from basal to apical one; terminal flagellomere strongly acuminate.

*Mesosoma.* 1.6 times longer than high; mesoscutum and scutellum finely setose; pronotal collar long; notauli partly visible; metacoxa narrower at base, mesoscutum without sulcus; scutellum without tooth.

*Forewing.* Apex destroyed; veins C+SC and R merged, with a distinct groove between them, without narrow costal cell apically; R and parastigma contiguous; first sub-marginal cell longer than first discal cell; vein CU1b absent; vein 2m-cu apparently absent; vein 1-SR distinct, oblique; vein r probably originating beyond middle of pterostigma; vein m-cu entering second sub-marginal cell; vein cu-a strongly post-furcal; traces of veins 2A and a present.

*Hindwing.* SC+R and C completely fused for a considerable distance from base; secondary hamuli present beyond apex of C+SC+R and C, setiform; vein 1r-m without a bulla, 0.5 × length of 1-m; vein 2-CU present, short; vein 2-1A present, very short and rudimentary; a bulla between 2-CU and 2-1A, slightly angled compared with 1-1A.

*Legs.* Tibiae and tarsi more densely setose than coxae and femora; hind tibia moderately robust; tibial spur formula ?-2-2; hind tibial spurs short, about 0.2 × length of basitarsus; hind basitarsus rather long but shorter than combined length of following segments; tarsal claws simple.



**Fig. 3.** A–D. Line drawings of *Protorbysalodes arnaudi* gen. n., sp. n., holotype specimen MNHN CDL 2.4. —A. General habitus. —B. Forewing. —C. Hindwing. —D. Detail of the posterior margin of hindwing showing veins 2-1A and 2-CU. The terminology of wing venation and cells is according to van Achterberg (1993: figs H–K). Scale bars are 0.25 mm.

*Metasoma*. Inserted above hind coxae; seven visible tergites, first one with a well-pronounced dorsal carina but organization poorly visible; ornamentation and spiracles of other tergites not visible by preservation; parameres broad, apically oblique in lateral aspect and with apical 1/4 densely setose.

*Measurements (in mm)*. Total length of head and body 1.75 mm; length of head 0.35, of antenna 1.90, of mesosoma 0.65, of metasoma 0.75. Forewing distance from base to vein r 1.10; ratio of veins 3-CU1:m-cu = 1.00 : 1.70; vein 1-SR 0.06 long. Hindwing 1.30 long, 0.40 wide. Ratios of length of fore femur : tibia : tarsus = 1.00 : 1.00 : 1.23; ratios of length of middle femur : tibia : tarsus = 1.00 : 1.20 : 1.30; ratios of length of hind femur : tibia : tarsus = 1.00 : 1.25 : 1.25.

## Discussion

According to Quicke *et al.* (1999), the new fossil shows characteristic features of the Braconidae in its forewing vein 2A present, the hindwing vein 1r-m without a bulla (apomorphy), the secondary hamuli setiform (apomorphy), and the forewing vein 2m-cu absent (apomorphy).

*Protorhyssalodes* gen. n. shares with the clade Braconidae excluding the Trachypetinae hindwing veins SC+R and C fused completely for a considerable distance from base (apomorphy). Also, forewing vein 'a' is present and rather long, as in the Protorhyssalinae and the group 'other non-cyclostomes' *sensu* Quicke *et al.* (1999) (reverse specialization), but not in the clade A = ('Agathidinae group' + (Apozyginae + ('other cyclostomes' + (Aphidiinae + 'Rhyssaline group')))). One of the main synapomorphies of the Protorhyssalinae is unknown in *Protorhyssalodes*, that is, the distribution of the multiporous plate sensilla of antennal segments. However, the vein 2-CU is present on the hindwing, as in the Protorhyssalinae and unlike in its sister group 'other non-cyclostomes'. *Protorhyssalodes* does not have the synapomorphy of the clade A, namely forewing vein R and parastigma separated. Nevertheless, its forewing veins C+SC and R are merged, with a distinct groove between them in dorsal profile, but without costal cell apically, which is a plesiomorphic state of character present in the Trachypetinae.

The body and wings dimensions of *Protorhyssalodes* agree closely with those of *Protorhyssalus*. However, the two taxa were never recovered as forming a monophyletic group in any of the analyses conducted, instead forming a grade leading to the extant Braconidae. They differ in the following characters: the mesosoma of *Protorhyssalodes* is 1.6 longer than high, instead of 1.45 in *Protorhyssalus*; the ratio forewing veins 3-CU1 : m-cu is 1 : 1.7 in *Protorhyssalodes*, instead of 1 : 1.5 in *Protorhyssalus*; forewing vein cu-a is distinctly more post-furcal in *Protorhyssalodes* and it has a trace of hindwing vein 2-1 A. Because of these differences and the apparent absence of synapomorphies, we therefore provisionally consider it as a closely related but separate genus.

## Genus *Aenigmabracon* Perrichot, Nel & Quicke, gen. n.

*Type species*. *Aenigmabracon capdoliensis* sp. n., by present designation and monotypy.

*Etymology*. Combination of the Latin aenigma, for the enigmatic puzzle of characters displayed by this specimen, and the genus *Bracon*.

*Diagnosis*. Cyclostome; antennae with 23 segments; multiporous plate sensilla shorter than length of flagellomeres; mesosomal prepectal carina complete, postpectal carina absent; forewing vein R and parastigma well-separated; veins C+SC and R merged, with a distinct groove between them basally, and a narrow costal cell present apically; vein cu-a strongly post-furcal and straight; veins 2m-cu and a present; hindwing veins 2-CU and 2-1A present; fore tibia with five apical pegs; 1st metasomal tergite with a well-pronounced dorsal carina.

## *Aenigmabracon capdoliensis* Perrichot, Nel & Quicke, sp. n. (Figs 4 and 5)

*Holotype*. Specimen MNHN CDL 2.30, deposited in the amber collection of the Earth History Department, Muséum National d'Histoire Naturelle, Paris, France.

*Type locality*. Cadeuil, Charente-Maritime, SW France. Mid-Cretaceous (Uppermost Albian to Lower Cenomanian) amber.

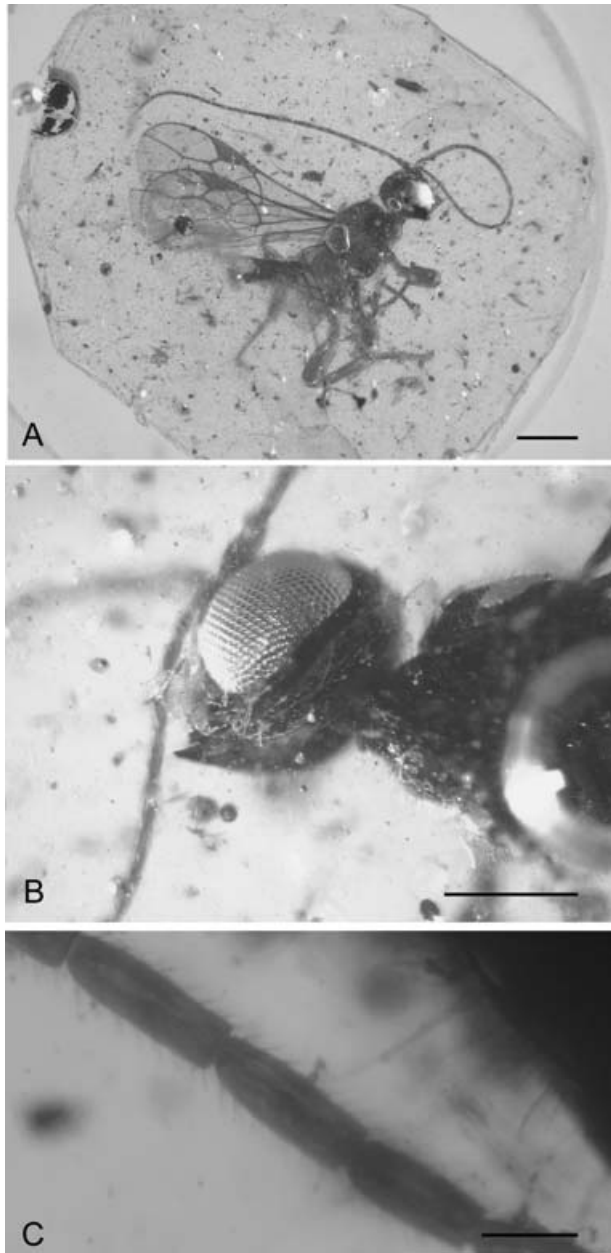
*Etymology*. After Capdoliium, the Latin name for Cadeuil where was found the amber piece containing the type specimen.

*Diagnosis*. As for the genus.

*Description*. Head orthognathous and cyclostome (Figs 4B, 5A: a distinct depression strongly developed above mouthparts); mandibles poorly visible; no visible palp; eyes glabrous, not emarginate; antenna with 23 sub-cylindrical segments; pedicel large, 0.65 × length of scape; flagellomeres with internal aperture of placoid sensilla (clearly visible in transmitted light) occupying approximately 0.4 × length of external sensilla; basal six flagellomeres of nearly same length, following ones becoming gradually shorter; back of head with distinct medial groove behind stemmaticum; occipital carina complete, joining hypostomal carina before base of mandible.

*Mesosoma*. Pronotal collar long, transverse groove situated far from posterior margin; notauli partly visible; prepectal carina complete; postpectal carina absent; mesoscutum without sulcus; scutellum without tooth; mid longitudinal mesosomal groove deep but not crenulate.

*Forewing*. Veins C+SC and R merged, with a distinct groove between them basally and a short and narrow costal cell



**Fig. 4** A–C. *Aenigmabracon capdoliensis* gen. n., sp. n., holotype specimen MNHN CDL 2.30. —A. General habitus in right lateral view. —B. Head in left lateral view, showing the deep depression above mouthparts. —C. Ichneumonid-type placoid sensilla on antennal segments. — Scale bars: A–B, 0.50 mm; C, 0.10 mm.

present apically; R and parastigma well separated; first sub-marginal cell [2a] longer than first discal cell [3a]; second sub-marginal cell [2b] longer than first; vein CU1b absent, CU1a and 3-CU1 forming a smooth curve; vein 2m-cu present; vein 1-SR distinct, oblique; vein r originating beyond middle of pterostigma; vein m-cu aligned with 2-SR, entering second

sub-marginal cell; vein cu-a strongly post-furcal and straight; traces of veins 2A and a present.

*Hindwing.* Deformed; SC+R and C completely fused for a considerable distance from base; single strongly differentiated setiform secondary (basal) hamulus present beyond apex of C+SC+R and C; three well-developed slightly sinuous distal hamuli; vein 1r-m longitudinal, without a bulla; vein 1-M present; vein 2-CU short; vein 2-1A very short and rudimentary; a bulla between 2-CU and 2-1A, slightly angled compared with 1-1A.

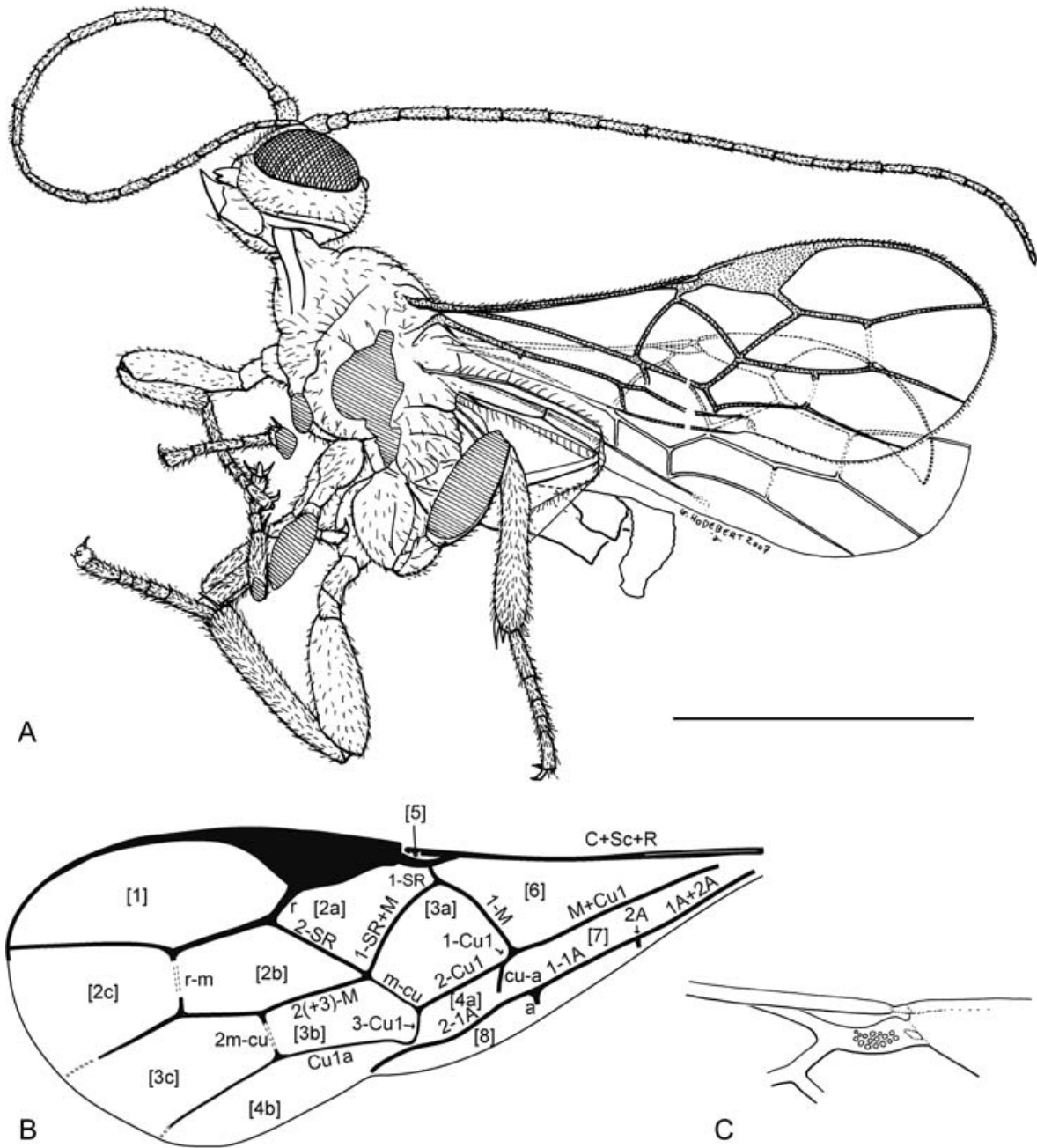
*Legs.* Moderately setose; apex of fore tibia with transverse group of five pegs (chaetobothria); metacoxa narrower at base; tibial spur formula 1-2-2; hind tibial spurs short, about  $0.2 \times$  length of basitarsus; hind basitarsus rather long but shorter than combined length of following segments; tarsal claws simple.

*Metasoma.* Incomplete, with distal segments missing, inserted above hind coxa, with three visible tergites, without visible ornamentation; a well-pronounced dorsal carina on first metasomal tergite but its organization is poorly visible by preservation; laterotergite of first segment pendulous; first sternite separated from tergite and reaching approximately  $0.3 \times$  along length of tergite; second and third tergites separated; second spiracle visible on lateral part separated from dorsal part by a longitudinal fracture, but it is not clear whether this is the laterotergite.

*Measurements (in mm).* Length of head 0.56, of antennae 2.60; mesosomal length 0.90, height 0.50. Forewing 1.80 long; distance from base to vein r 1.10; length of vein 1-SR 0.04, of veins 2A 0.01, of vein a 0.02; ratios of lengths r : 3-SR : SR1 = 1.00 : 2.75 : 4.75; ratios of lengths of vein r-m : 3-SR : 2-SR = 1.00 : 1.80 : 1.80; ratio of veins 3-CU1 : m-cu = 1.00 : 2.33; Hindwing 1.40 long; length of vein 1r-m 0.08, of vein 1-m 0.12, of vein 2-CU 0.04. Ratios of length of fore femur : tibia : tarsus = 1.0 : 0.52 : 1.0; of middle femur : tibia : tarsus = 1.0 : 1.4 : 1.6; of hind femur : tibia : tarsus = 1.0 : 1.47 : 1.0.

## Discussion

*Aenigmabracon* differs from *Protorhyssalus* and *Protorhyssalodes* in its number of antennal segments and its forewing venation with vein R and parastigma separated (synapomorphy of the clade A as defined above), presence of a distinct costal cell, and presence of vein 2m-cu. The latter character is present in the modern Apozyginae and the Ichneumonoidea excluding the Braconidae. Quicke *et al.* (1999) considered it as a reversal of the Apozyginae. The metasoma of *Aenigmabracon* is too poorly preserved to determine if it has a very long and broad



**Fig. 5** A–C. Line drawings of *Aenigmabracon capdoliensis* gen. n., sp. n., holotype specimen MNHN CDL 2.30. —A. General habitus. Scale bar is 1.00 mm. —B. Forewing. —C. Detail of the posterior margin of forewing showing parastigma.

second tergite and the second and third sternites united (van Achterberg 1993). The distribution of the multiporous plate sensilla of antennal segments is of ichneumonoid type, that is, not occupying the entire length of the flagellomeres. Therefore *Aenigmabracon* has a unique combination of characters and does not fit in any of the known braconid sub-families. Nevertheless, we prefer not to create a new sub-family for

this fossil because numerous characters remain unknown, especially those of the metasoma. *Aenigmabracon* is most easily confused with the genera previously included in the Eoichneumonidae but it can be distinguished from the five described genera as follows: from *Eoichneumon* Jell and Duncan it differs in having m-cu interstitial with 2-SR, vein 2m-cu largely unpigmented and rather spectral, and vein r less than 0.5 ×

2-SR; from *Baissobracon* Rasnitsyn and Sharkey it differs in having forewing vein cu-a strongly post-furcal, and in having metasomal tergites 1 and 2 smooth rather than strongly striate; from *Cretobraconus* Rasnitsyn and Sharkey it differs in having forewing vein r short (it is about as long as 1-SR in *Cretobraconus* except for *C. mongolensis* Rasnitsyn and Sharkey) and in having 2m-cu arising approximately half-way along the second sub-marginal cell whereas it is very distal in *Cretobraconus*; and from *Archobraconus* Rasnitsyn and Sharkey and *Cretobraconus* in that both these genera have forewing vein r approximately as long as veins 2-SR and 3-SR; from *Purichneumon* Rasnitsyn and Jarzembowski (preserved from an isolated forewing only) it differs in the presence of a parastigma, veins 1-SR+M, 2A, and a.

The hindwing vein 2-1A is present in *Protorhyssalodes* and *Aenigmabracon*, although very short. Indeed, the new fossils are the first braconids ever known to possess both vein 2-CU and a distinct trace of vein 2-1A on hindwing. This supports the hypothesis that the vein with a posterior bulla in other braconids such as Agathidinae, Sigalphinae (including Pselaphaninae), Acampsohelconinae (see van Achterberg 2002) and Meteorideinae is 2-CU. Possession of vein 2-CU is probably plesiomorphic for Braconidae as it is also the state shown by the Trachypetinae, the genus *Apozyx* of the Apozyginae, the Acampsohelconinae, and *Protorhyssalus* (van Achterberg 2002).

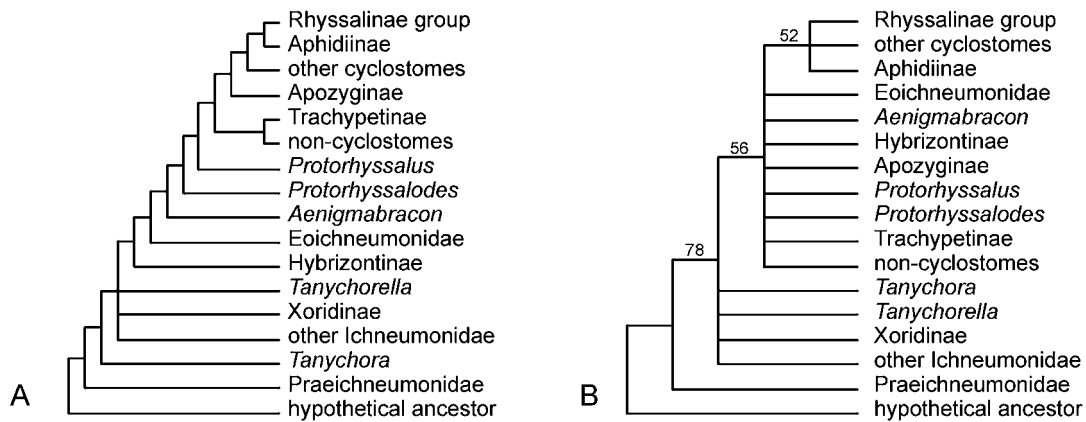
**Results of phylogenetic analysis**

Parsimony analysis of the morphological data set presented in Table 1 yielded five equally most parsimonious trees (MPTs) of length 62 steps (same minimum length was found both from branch and bound search and heuristic searches). Searching on all individual trees as starting trees revealed only one island of trees (see Maddison 1991). The strict

consensus of these (Fig. 6A) was rather well resolved, with (i) Ichneumonidae forming a sister group to the monophyletic (Eoichneumonidae + Braconidae); (ii) Eoichneumonidae and all exclusively Cretaceous Braconidae (i.e. *Aenigmabracon*, *Protorhyssalodes* and *Protorhyssalus*) forming a group basal to all extant Braconidae (iii) Apozyginae forming a sister group to the ((Rhyssalinae + Aphidiinae) + other cyclostome braconids). This tree has *Tanychorella* forming part of a polytomy with Xoridinae and other Ichneumonidae, this clade being sister to Hybrizontinae and all Braconidae. Bootstrap analysis showed only one node to be supported, that being the separation of Praeichneumonidae from the other included ichneumonoids which had 78% support (Fig. 6B).

Successive approximation weighting was then carried out to try to reduce the number of trees and obtain a better-resolved consensus. As per Quicke et al. (1999) we used the maximum value of the retention index as the primary reweighing function. Use of the minimum instead of the maximum value of the retention index had no effect.

Of the results, two appear likely to be disproved when more data become available. The inclusion of the Trachypetinae with the non-cyclostome braconids rather than basal to all extant braconids (except perhaps *Apozyx*) is at odds with its distinctly open costal cell and, probably more importantly, with its high 28S rDNA G+C content and numerous base agreements with the Ichneumonidae, both of which are likely to be plesiomorphies not shared by other braconids. The inclusion of *Apozyx* in the cyclostome clade of braconids (with the Aphidiinae) seems unlikely because (i) as shown here, the stem lineage leading to the braconids was apparently cyclostome, (ii) the males of *Apozyx* possess a well-developed, toothed and articulated distal cuspidal process (as in the non-cyclostome braconids) whereas it is at most poorly developed in the Rhyssalinae group of cyclostomes, and (iii) it possesses forewing



**Fig. 6** A, B. Strict consensus of five trees obtained from maximum parsimony analysis (and successive approximations parsimony analysis) of data set in Table 1. —A. Strict consensus of all 5 MPTs. —B. Bootstrap majority rule consensus tree showing bootstrap values for nodes with greater than 50% support.

vein m-cu and hindwing vein 2-CU which seem most likely to be plesiomorphies rather than secondarily acquired. It is hoped that the discovery of more well-preserved fossils along, eventually with molecular data from *Apozyx*, will help resolve these matters.

As the new genus *Aenigmabracon* shares no synapomorphy with either the Braconidae nor with the Eoichneumonidae, and because the latter is defined only on the basis of symplesiomorphies with respect to the Braconidae (Rasnitsyn & Sharkey 1988), we hereby synonymize Eoichneumonidae with Braconidae and leave its rank undefined (*incertae sedis*). The possibility exists to treat it as a sub-family and to include *Aenigmabracon* within it, but such a taxon would not be supported by any synapomorphy.

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