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Early lineages of Vespidae (Hymenoptera) in Cretaceous amber

(Preprint version of August 2016)

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Abstract. Three wasp (Hymenoptera: Vespidae) fossils in Cretaceous amber (Late Albian) of northern Myanmar are described. Two are new species of the Mesozoic genus *Curiosivespa* (Rasnitsyn): *C. zigrasi* **sp.n.** and *C. striata* **sp.n.**. The third species, *Protovespa haxairei* **gen.n. et sp.n.**, has a combination of features unique among Mesozoic Priorvespinae and the extant subfamilies. These well-preserved fossils provide new morphological data for a cladistic analysis of the basal lineages of Vespidae. Results suggest that Euparagiinae is the sister group of all other Vespidae. The new genus *Protovespa* appears more closely related to extant Masarinae, Eumeninae and social wasps than to Priorvespinae. We assign it to a new subfamily: Protovespinae. Finally, fossil information combined with a phylogenetic tree show that the main groups of Vespidae likely evolved during the Early Cretaceous.

Short title.

Vespidae in Cretaceous amber

Introduction

Social wasps are part of the family Vespidae (Hymenoptera) along with a huge diversity of solitary species. Their range of social behaviour, diversity of nest architecture and ecological importance make this group one of the best-studied families of wasps (e.g., Ross & Matthews, 1991, Turillazzi & West-Eberhard, 1996, Turillazzi, 2012, Archer, 2012). The fossil record indicates that the family evolved at least by the Early Cretaceous, with two genera (*Curiosivespa* Rasnitsyn and *Priorvespa* Carpenter & Rasnitsyn) preserved as lithified remains from the Early Cretaceous deposits of Russia and Mongolia (Carpenter & Rasnitsyn, 1990). However, the early history of this family is still poorly understood, since all of the Early Cretaceous fossils until now are known only as fragmentary compressions, mostly as wings. Of the several phylogenetic studies of Vespidae, only one considered the past diversity of deep relationships of the family (Carpenter & Rasnitsyn, 1990). Three well-preserved Vespidae fossils recently found in Burmese amber add significant new knowledge on the early lineages of the Vespidae and our view of the evolution of the group.

Vespidae is organized into six extant subfamilies. Three subfamilies are comprised of solitary wasps: Euparagiinae, once a widespread and diverse group of which only one genus remains today with 10 nearctic species (Carpenter & Kimsey, 2009); Masarinae, which feed on flower pollen (370 spp.) and the highly species-rich subfamily Eumeninae, or potter wasps (3746 spp.). The three other subfamilies are Stenogastrinae, primitively social wasps from South East Asia (63 spp.), Polistinae, or paper wasps, the most diverse group of social wasps (1003 spp.) and Vespinae, including yellow jackets and hornets (70 spp.). In addition to this extant diversity, 58 fossil species from four subfamilies have been described (Supplementary material, Table S.1). Six of these taxa belong to an extinct subfamily, Priorvespinae, previously known entirely as compression fossils (Carpenter & Rasnitsyn, 1990).

Several attempts at reconstructing the phylogenetic history of this group have resulted in disparate hypotheses, especially regarding the evolution of sociality (e.g., Carpenter, 1981; Hines *et al.*, 2007; Pickett & Carpenter, 2010; Piekarski *et al.*, 2014). The best-supported hypothesis placed Euparagiinae at the base of the family and Eumeninae as sister to a clade comprised of the three social subfamilies (Pickett & Carpenter, 2010; Piekarski *et al.*, 2014). The analysis including Priorvespinae presented similar relationships, with the Priorvespinae as sister group to the extant Vespidae (Carpenter & Rasnitsyn, 1990). These results raise the question as to whether Priorvespinae can be considered as a crown Vespidae or as a stem group taxon for the family. That previous study was based on a limited number of morphological characters, since fossil characters were drawn mostly from the wings. Here, we

test whether an analysis using new fossils, 3-dimensionally preserved with microscopic details and a significant number of characters, better resolves the position of the early lineages of Vespidae. In this study, we describe these new fossils from Burmese amber and we include them in a phylogenetic context based on samples from every tribe of the family.

Material and methods

The three fossils are from the Cretaceous amber deposit of the Hukawng Valley of Kachin State, northern Myanmar (26°15'N, 96°34'E). The formation is dated from between the Early Cenomanian (Shi *et al.*, 2012) to the Late Albian (99-105 Mya; Cruikshank & Ko, 2003; Grimaldi & Ross, 2016).

We follow here the wing venation nomenclature of Vespidae as described in Carpenter (1981), with abbreviations: *A* anal vein; *C* costal vein; *Cu* cubital vein; *M* median vein; *R* radial vein; *R₁* first radial; *R_S* radial sector; *Sc* subcostal vein; *Icu-a* crossvein between *M* and *Cu₁*; *2r-m* and *3r-m* crossveins between *R_S* and *M*; *1m-cu* and *2m-cu* crossveins between *M* and *Cu₁*; *r2* crossvein between *R_S* and *R₁*.

The relationship of these fossils to other Vespidae was explored through a cladistic analysis of 75 morphological and behavioural characters (Supplementary material, Table S.2). When possible, these characters were coded for the three vespid fossil genera from the Mesozoic. Two outgroups, Tiphidae and Rhopalosomatidae, were selected because of shared characteristics with the new fossils; namely a relatively complete venation and presence of emarginate eyes. The characters of the fossil genera *Curiosivespa* and *Priorvespa* were based on the descriptions of every species known for these groups. *Priorparagia* is known from a single fossil (*P. anancites* Brothers & Rasnitsyn, 2008). Several species and genera were observed per extant subfamily, but the morphological matrix was based on 14 species selected to represent the morphological diversity of every tribe of Vespidae. Similarly, the two outgroups were coded based on the species *Pseudotiphia beckeri* (Tournier) and *Rhopalosoma nearcticum* Brues. A phylogenetic analysis was performed under parsimony using TNT (Goloboff *et al.*, 2008), using 'implicit enumeration' and implied weighting (Goloboff, 1993). The concavity value *K* was set at 4.765625 using the script *setk.run* (J. S. Arias, pers. comm.). Node support was computed as GC-values from symmetric resampling of 10,000 replicates of traditional searches (group supported/contradicted values; Goloboff *et al.*, 2003: GC-values are the differences in group frequency between the group found in the most parsimonious tree

and the most frequent contradictory group). Only supported groups are shown (support value above zero, scaled 0-100).

Taxonomy

Family Vespidae Laicharting.

Subfamily *Protovespinae* Perrard & Carpenter, subfam. n.

Etymology. Named after *proto*, ‘first’, and genus *Vespa*. Gender feminine.

Type genus. *Protovespa* Perrard & Carpenter, **gen. n.**

Diagnosis: Forewing first discal cell shorter than subbasal, unlike other Vespidae except Priorvespinae and Gayellini. Hindwing *Cu* diverges basal to *cu-a*, unlike Gayellini. Forewing recurrent veins reaching M in the same cell, *3r-m* not sinuous, metasoma with first segment of similar width to second segment, unlike Priorvespinae.

Genus *Protovespa* Perrard & Carpenter, gen. n.

Type species. *Protovespa haxairei* Perrard & Carpenter, **sp. n.**

Description: Posterior part of head more produced dorsally than ventrally. Forewing venation reaching apex of wing, forewing subdiscal cell not produced, three submarginal cells present, third sub-marginal cell with anterior margin longer than posterior margin; apex of marginal cell pointed, touching margin of wing; vein *Icu-a* long, not curved.

Protovespa haxairei Perrard & Carpenter, sp. n.

(Figs. 1 & 2)

Material examined. Holotype, AMNH JZC-Bu1837 in the Division of Invertebrate Zoology, AMNH, New York.

Locality. MYANMAR, Kachin state, Cretaceous amber deposit of the Hukawng Valley. Early Cenomanian to Late Albian.

Etymology. Species named after Jean Haxaire, passionate entomologist and first mentor of AP.

Description. Female. Gena more produced in upper part than in lower part. Antenna with 12 articles. Scape longer than first flagellomere. Antennal flagellomeres short, approximately as wide as long. Eyes broadly emarginate. Ocelli closer to each other than to compound eyes. Clypeus wider than long, apex broken but without latero-apical teeth. Labrum protruding, pointed, with long setae. Mandible with small cutting edge. Occipital carina present,

potentially extending to mandible. Labial palp with 3 segments, without long setae on the terminal segment. Mesosoma relatively short, slightly longer than wide, dorsally rounded; pronotal carina absent; posterior pronotal lobe a distance of 1.5 times its length from posterior angle of pronotum; precoxal suture present; mesonotum with notauli and parapsidal furrows distinct; parategula absent; tegula rounded, longer than wide; transscutal furrow longitudinally ridged; scutellum laterally compressed; metanotum and propodeum almost vertical; lateral surfaces of propodeum produced posteriorly. Metasoma with six segments, last four segments partially retracted into second one; first tergum not fused to first sternum; second sternum with deep punctation; sixth sternum laterally compressed into a furrow around sting. Legs with trochanter longer than wide; tarsomeres symmetrical; claws large with small basal tooth and thinner, hooked apex; foreleg with one tibial spur; mid- and hind legs with two tibial spurs; hind leg spurs asymmetrical, larger spur with short comb. Forewing not plaited longitudinally, with three submarginal cells; *Icu-a* long and nearly straight, received at fork of *M* and *Cu*; subdiscal cell not produced apically; *Rs+M* longer than abscissa of *M* between *M+Cu* and *Rs*; recurrent veins both received in second submarginal cell; *M* segment between *Im-cu* and *2m-cu* longer than segment between *Rs* and *Im-cu*; pterostigma long, subtruncate apically; *Rs* angled far from pterostigma, then straight; *Rs* between *2r-m* and *3r-m* longer than *2r-rs* and apical segment of *Rs*; marginal cell elongate with apex pointed, no appendix; *2r-m* curved; basal angle of marginal cell acute; *A*, *M* and *Cu* veins almost reaching edge of membrane. *M+Cu*, *Cu*, *Im-cu* and *M* not aligned in straight line; first discal cell of similar size to subbasal cell, basal angle of first submarginal cell acute, angle between *Rs* and pterostigma obtuse, second submarginal cell narrowed above with basal angle acute, *2m-cu* close to *2r-m*, *3r-m* gently curved, apical part of *Im-cu* not angled, slightly curved, pterostigma shorter than pterostigma. Hind wing with three closed cells; jugal lobe present; axillary incision deep; subbasal cell broadest subapically, *cu-a* angled with *A*, *Cu* diverging basad of *cu-a*, *A* with free abscissa present; hamuli not present before divergence between *Rs* and *R1*. Measurements (mm): Forewing length: 8.6; Head width: 2.6; Head dorsal length: 1.25; Face height (top of the head to tip of the clypeus): 2.3; Mesosoma width: 2.4; Mesosoma length: 3.4.

Male and larvae: unknown for this species.

Subfamily Euparagiinae Ashmead

The two new species are classified as Euparagiinae based on their apically produced subdiscal cell, a distinctive apomorphy of the subfamily.

Genus *Curiosivespa* Rasnitsyn

The two new species are attributed to the genus *Curiosivespa* based on a combination of the reception of *Icu-a* at or after the divergence of *M* and *Cu*, the relatively straight *Icu-a* and the long first abscissa of *Rs*, excluding *Euparagia* and *Priorparagia*. In addition, *C. zigrasi* possesses elongated antennal flagellomeres, as does *Curiosivespa curiosa* Rasnitsyn. The second and third submarginal cells of *C. striata* are also of subequal size, excluding *Euparagia*, while the marginal cell is apically produced, excluding *Priorparagia*.

Curiosivespa zigrasi Perrard & Carpenter, sp. n.

(Figs. 3 & 4)

Material examined. Holotype, AMNH JZC-Bu245 (James Zigras leg.), in the Division of Invertebrate Zoology, AMNH, New York.

Locality. MYANMAR, Kachin state, Cretaceous amber deposit of the Hukawng Valley. Early Cenomanian to late Albian.

Etymology. Species named after James Zigras, collector of the specimen.

Diagnosis: Forewing recurrent veins received in separate cells, unlike *C. derivata* and *C. orapa*. Crossvein 1m-cu sharply angled into second submarginal cell, unlike *C. derivata* and *C. antiqua*. Reception of *Icu-a* at fork of *M* and *Cu*, unlike *C. curiosa*, *C. magna* and *C. striata*. In addition, pterostigma very short (absent on wing depicted in Fig. 4), unlike every other *Curiosivespa* species except *C. derivata*.

Description. Sex: possibly female based on number of antennal articles. Antenna with 12 articles, scape shorter than first flagellomere, flagellomeres longer than wide. Pronotum with dorsal part short; mesoscutum longer than wide, scutellum dorsally produced, compressed laterally and convex posteriorly, produced over metanotum; propodeum with posterolateral spine produced. Legs with basitarsomere very long (>2x length of tarsomere 2); claws broad with small basal tooth. Metasoma with short first segment. Forewing not plaited longitudinally; first abscissa of *M* longer than *Rs+M*; first subdiscal cell produced apically; abscissa of *Cu* beyond *1m-cu* almost aligned with *1m-cu*; first discal cell longer than subbasal cell; basal angle of first submarginal cell acute; recurrent veins received in separate cells; pterostigma very short, shorter than prestigma and truncate apically; angle between *Rs* and prestigma obtuse; apical part of *1m-cu* angled; *Rs* angled close to middle of marginal cell. Hind wing with three closed cells; *cu-a* vein received at fork of *M* and *Cu*; hamuli present

basal of divergence of R_1 and R_s . Measurements (in mm): Forewing (approximate) length: 16.5; Head width: 4.7; Mesosoma width: 4.4; Mesosoma length: 8.4.

Curiosivespa striata Perrard & Carpenter, sp. n.

(Figs. 5 & 6)

Material examined. Holotype, AMNH JZC-Bu1839 in the Division of Invertebrate Zoology, AMNH, New York.

Locality. MYANMAR, Kachin state, Cretaceous amber deposit of the Hukawng Valley. Early Cenomanian to Late Albian.

Etymology. Derived from the Latin 'striatus', based on the ridges observed on the sides of the specimen. This striation might be a taphonomic artefact, although it is difficult to assess based on a single fossil.

Diagnosis. Forewing recurrent veins received in separate cells, unlike *C. derivata* and *C. orapa*. Connection between Cu and $Icu-a$ after the divergence of M and Cu , unlike *C. antiqua*, *C. derivata* and *C. zigrasi*. Second submarginal cell slightly higher than long, with basal angle obtuse, unlike *C. curiosa* and *C. magna*.

Description. Female. Head more developed in upper part; eyes emarginate; ocelli not visible; antenna with scape longer than first flagellomere. Pronotum without pronotal carina, lateral part vertical; pretegular carina with perpendicular marking; mesoscutum longer than wide; parategula absent; transscutal furrow smooth; scutellum compressed laterally and expanded posteriad over metanotum; metanotum vertical; mesepisternum striate; propodeum with lateral expansions wide and rounded; no valvula. Strong bristles present on legs, especially on tarsomeres; basitarsomere very long ($>2x$ length of tarsomere 2); each claw with a very elongate and straight basal tooth or a strong bristle, issuing from base of claw. Metasoma with six segments; first segment short; lateral parts of terga longitudinally striate. Forewing not longitudinally plaited; first discal cell longer than subbasal cell; basal angle of first submarginal cell acute; vein $Icu-a$ distal to fork of M and Cu ; R_s+M longer than abscissa of M between $M+Cu$ and R_s ; $Icu-a$ long but not markedly curved; abscissa of Cu beyond $Im-cu$ strongly recurrent, almost aligned with $Im-cu$; pterostigma short, approximately same length as prestigma; pterostigma truncate apically; angle between R_s and prestigma obtuse; apical part of $Im-cu$ angled; recurrent veins received in separate cells; R_s between $1r-m$ and $2r-m$ approximately of same length as $2r-rs$ and as the apex of R_s ; $1r-m$ straight; marginal cell with apex rounded, with appendix present; R_s angled close to middle of marginal cell; M and Cu veins almost reaching edge of membrane. Hind wing with three closed cells; $cu-a$ vein

received at fork of *M* and *Cu*; hamuli present basal to divergence between *R₁* and *R_s*. Measurements (in mm): Forewing length: 8.4; Head width: 2.6; Mesosoma width: 1.9; Mesosoma length: 3.2.

Phylogenetic analysis

A phylogenetic analysis of the 75 characters (Supplementary material, Table S.2) resulted in two trees (score of weighted characters: 16.812; consistency index (unweighted characters): 0.427; retention index (unweighted characters): 0.669). The two trees differed in how *Curiosivespa* was resolved within Euparagiinae, the genus being unresolved in the consensus (Fig. 7). Euparagiinae was recovered as the sister clade to the rest of Vespidae, instead of Priorvespinae. This novel arrangement was mostly supported by synapomorphies shared with *Protovespa* and most of the other non-Euparagiinae Vespidae (hindwing subbasal cell broadest subapically, *Cu1* diverging basad of *cu-a*, *cu-a* aligned with A).

This analysis also recovered the monophyly of established tribes and subfamilies. The relationships among extant subfamilies were congruent with previous analyses including mitochondrial and nuclear genes (Pickett & Carpenter, 2010; Piekarski *et al.*, 2014). Depending on the tree, *C. striata* either clusters with the other *Curiosivespa* or closer to *Priorparagia* and *Euparagia*. The fossil *P. anancites* is more related to extant Euparagiinae than to the other fossils. *Protovespa haxairei* is more related to extant non-Euparagiinae Vespidae than to Priorvespinae. In addition to the unresolved *Curiosivespa* in the consensus, symmetric resampling revealed one unsupported node within the subfamily Polistinae. Support values of the deep nodes were mostly relatively low.

Discussion

The two *Curiosivespa* fossils are readily attributed to the Euparagiinae by their specific venation pattern, with the subdiscal cell anteriorly produced. The position of *Protovespa haxairei* is more problematic. The combination of emarginate eyes, a reduced medio-dorsal part of the pronotum, the pronotum exceeding the tegula dorsally and the first tarsomere of foreleg elongate confirm that this fossil belongs to Vespidae. However, it could not be attributed to Euparagiinae (forewing subdiscal cell not produced), nor Masarini (three submarginal cells) or Gayellini (divergence of hindwing *Cu* basal to *cu-a*). It is not a eumenine (claws not bifid, no parategula) and not a social wasp (posterior part of the head more produced dorsally, forewing *1cu-a* long, *Rs+M* long relative to *M* between *M+Cu* and *Rs*). *Protovespa* has affinities with the Mesozoic subfamily Priorvespinae but with several

differences concerning the venation (e.g., recurrent veins received in the same cell, *2r-m* sinuous, *3r-m* not sinuous). This taxon was found to be more related to extant subfamilies (minus Euparagiinae) than Priorvespinae. In order to avoid a paraphyletic definition of Priorvespinae (Fig. 7), *Protovespa* is attributed to its own subfamily.

Addition of new taxa and characters to the analysis of Carpenter & Rasnitsyn (1990) modified the position of Priorvespinae within Vespidae. Despite its peculiar combination of plesiomorphic characters (short first discal cell, first abscissa of *Rs+M* longer than *M* between *Rs* and *M+Cu*, *3r-m* sinuous, first subdiscal cell not elongated dorso-apically and *Icu-a* long and curved), *Priorvespa* is more closely related to the five derived subfamilies of Vespidae than the genus is to Euparagiinae. The affinities between *Priorvespa* and *Protovespa haxairei*, combined with the new morphological characters that could relate *P. haxairei* to the Masarinae, Eumeninae and social wasps (retracted metasoma, forewing marginal cell shape and appendix, *1r-m* sinuous, hindwing *Cu1* diverging basad of *cu-a* and *cu-a* aligned with *A*), confirm *Priorvespa* as a member of Vespidae.

Considering that the oldest *Curiosivespa*, *C. antiqua* Carpenter & Rasnitsyn, had the subdiscal cell distinctly produced apically (Carpenter & Rasnitsyn, 1990), a clear synapomorphy of Euparagiinae, these wasps already diverged from the other Vespidae by the Hauterivian (129.4-132.9 Myo; Rasnitsyn & Zherikhin, 2002). The oldest priorvespines date back to the same time, with *P. bullata* Carpenter & Rasnitsyn, also from Baissa and *P. longiceps* Carpenter & Rasnitsyn, of a similar age from Turga in Russia (Rasnitsyn & Zherikhin, 2002). Thus, the origin of Vespidae occurred prior to these fossils and dates at least from the Hauterivian, but more likely before, in the very early Cretaceous.

The new fossil data suggest that, at the beginning of the Late Cretaceous, the ancestor of social wasps may already have had a metasoma that could be retracted within its second segment. This feature, apparently lost secondarily in Masarini, enables wider telescopic movements important in active breathing, especially at high temperatures (Papachristoforou *et al.*, 2007; Käfer *et al.*, 2013). It may have provided this lineage with an evolutionary advantage in the hot climate of the Cretaceous. Based on the known fossils, Cretaceous wasps also had non-plaited wings at rest, a protuberant scutellum and lateral propodeal extensions. The length of the first discal cell seems to have varied in the early stage of vespid evolution, the cell being somewhat short in Priorvespinae and Protovespinae, but also in some Stenogastrinae (e.g., *Liostenogaster topographica* Turilazzi,) and Gayellini. Similarly, the connection of the vein *Icu-a* at the fork of *M* and *Cu*, an apparent plesiomorphy, is present in these groups and varies within *Curiosivespa*.

The existence of a eumenine in the Turonian amber of New Jersey indicates that the divergence between the lineages of Masarinae, Eumeninae and social wasps occurred in the Cretaceous (Carpenter, 2000). Unfortunately, no fossil Masarinae has been found to confirm the timing of these events. The lack of a stenogastrine fossil is also an impediment to the dating of social evolution in the group. The fossil nest *Brownichnus* Genise was confirmed as belonging to social wasps (Wenzel, 1990; Genise, 2000) and is the only indication that sociality evolved as early as the Late Cretaceous in wasps. Unfortunately, the exact age is ambiguous for this fossil. Most Vespidae fossils were described from the Paleogene, hence offering little resolution of deep relationships within Vespidae. Furthermore, many of these fossils were attributed to extant genera and require taxonomic revisions (see Antropov *et al.*, 2014).

Finally, the low support values for the basal lineages of our analysis suggest that the deep relationships among vespid subfamilies may still be unstable and need further analysis. This result confirms the findings of a previous study, in which relationships among Vespidae subfamilies were found to be highly sensitive to data type and methods (Piekarski *et al.*, 2014). We hope that the new insights provided by the fossils described in this study will lead to inclusion of fossil data in future analyses of the Vespidae, to best infer the evolutionary history of the family.

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FIGURES:

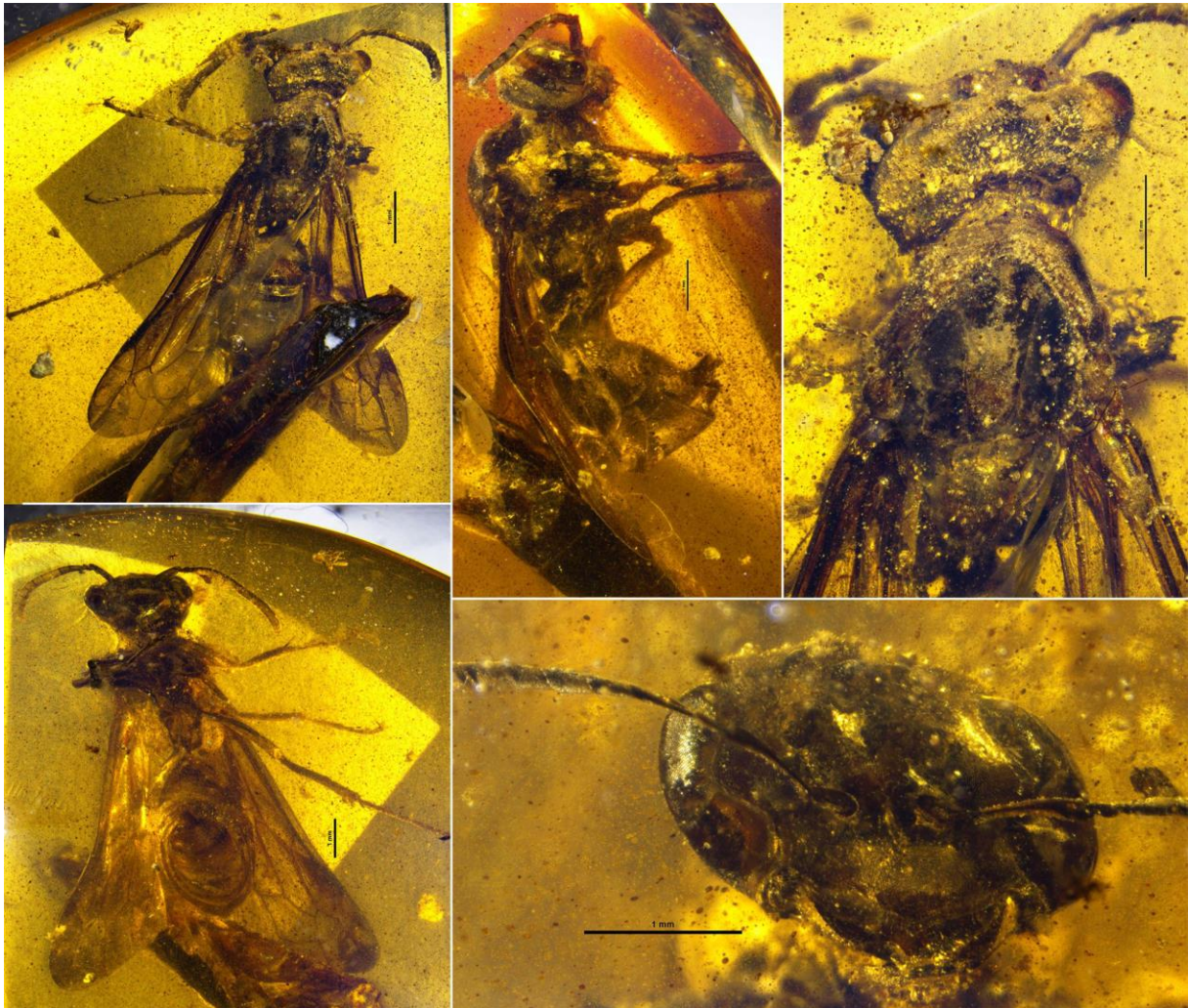


Figure 1. Holotype of *Protovespa haxairei*. Scale bars indicate 1 mm. From top right to bottom left: dorsal habitus; right lateral habitus; head and thorax, dorsal; habitus, ventral; head, frontal view

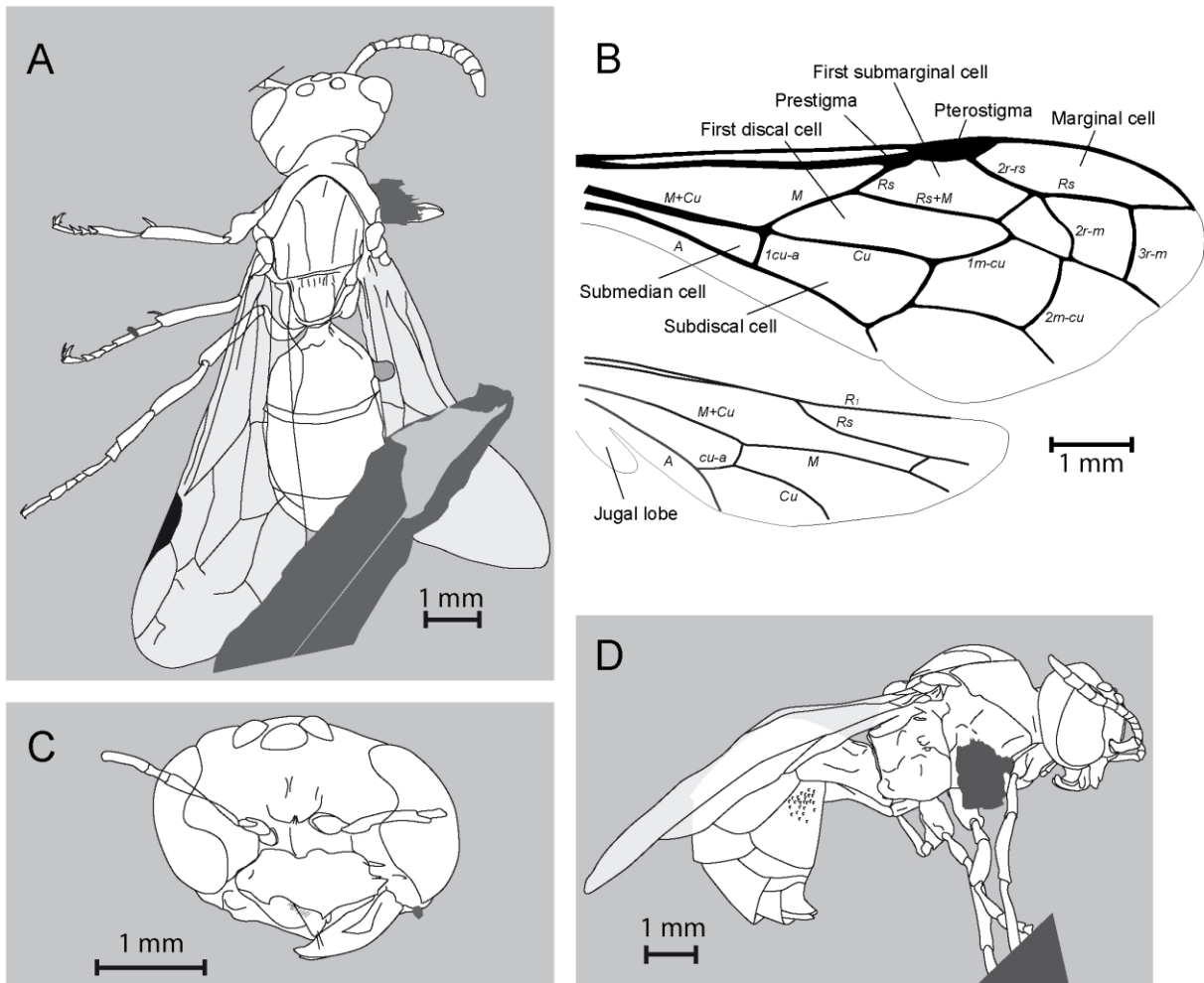


Figure 2. Details of the holotype of *Protovespa haxairei*. A: dorsal view. B: right wings, venation. C: frontal view of the head. D: lateral view. Parts obscured due to debris, bubbles, or surface of the amber are shaded in dark grey.



Figure 3. Holotype of *Curiosivespa zigrasi*. Scale bar indicates 1 mm.

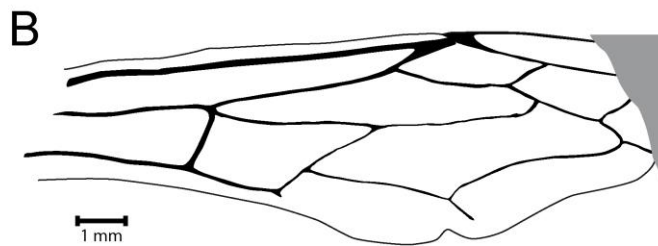
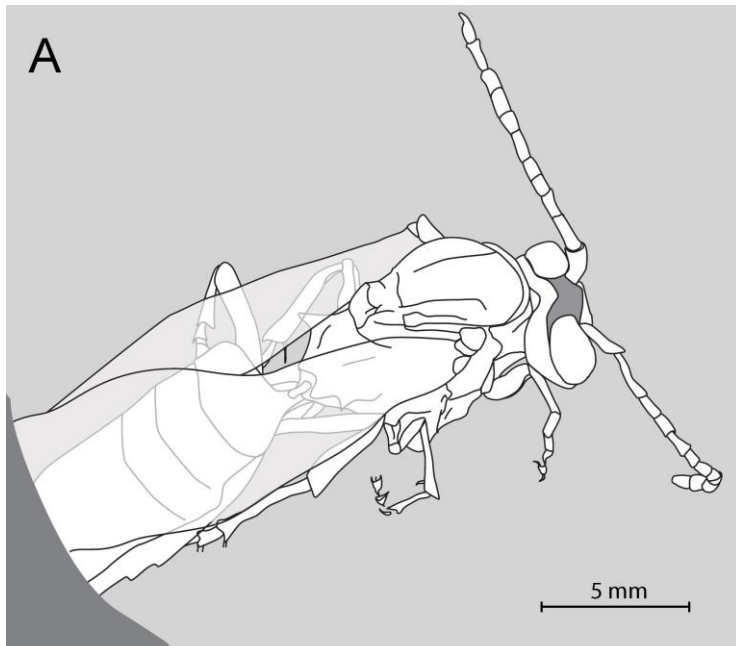


Figure 4. Details of *Curiosivespa zigrasi*. A: dorsal view. B: right forewing venation. Obscured parts are shaded in dark grey.

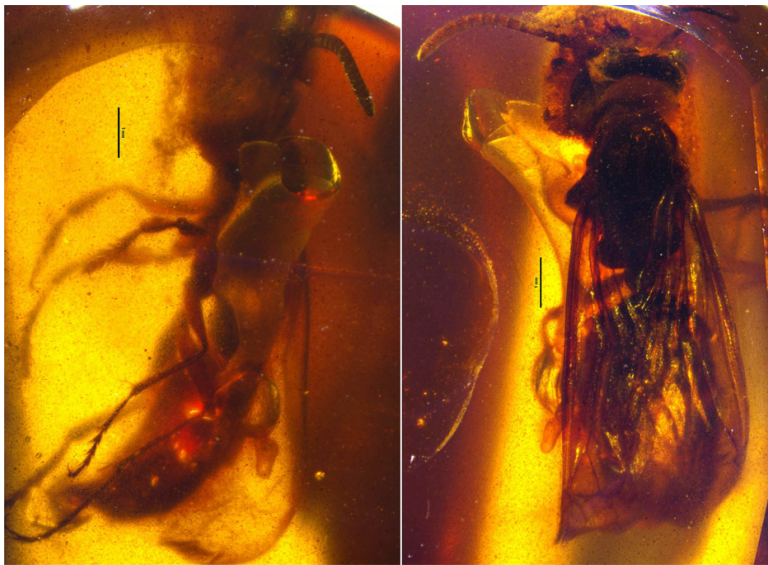


Figure 5. Holotype of *Curiosivespa striata*. Scale bars indicate 1 mm.

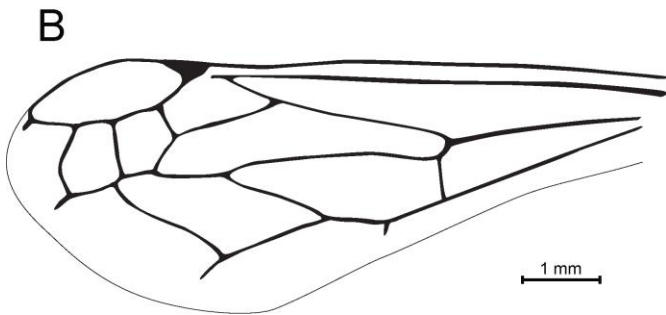
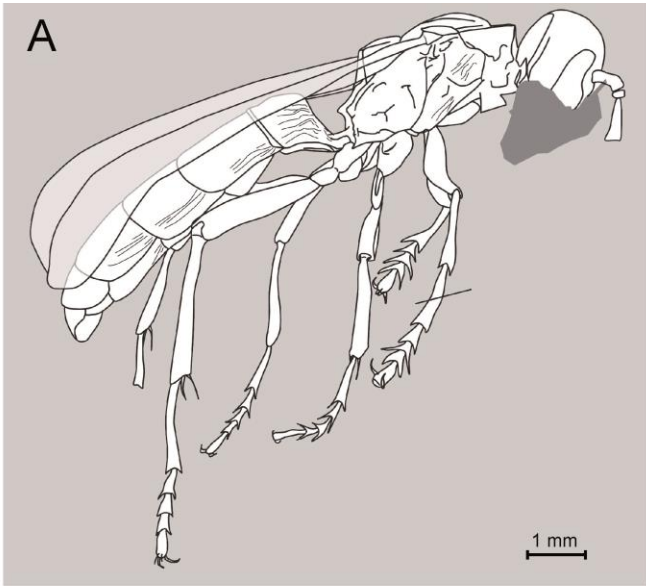


Figure 6. Details of *Curiosivespa striata*. A: Lateral view. B: left forewing. Obscured parts are shaded in dark grey.

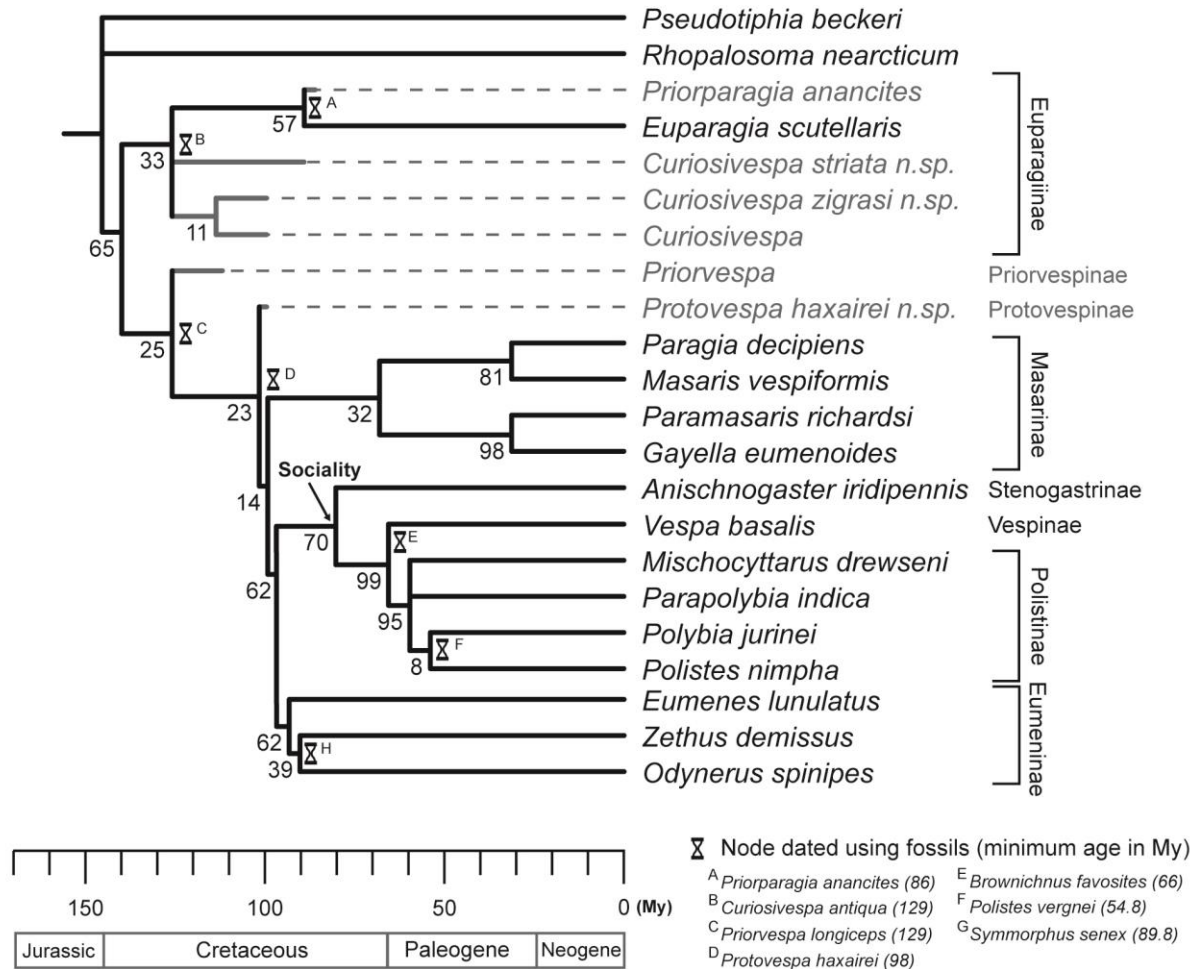


Figure 7. Chronogram of the evolution of the Vespidae. Relationships among taxa are based on the consensus of the two most parsimonious trees resulting from the analysis of 75 characters with implied weighting. Only supported nodes (GC-value > 0) are shown. Time scale is in millions of years. Fossil taxa and extinct lineages are depicted in grey. Fossil branches end at the youngest possible age of the most recent fossil known for the corresponding taxon. Only nodes marked by an hourglass are dated and to be compared to the timeline. The age of these nodes is based on the youngest possible age of the earliest fossil of the clade.

Supplementary material

Table S.1. Table of the Vespidae found in the fossil record. The list is in chronological order, from the most recent to the most ancient species. ‘N’ indicates species described based on fossil nests.

Genus	Species	Author, date	Deposit	Geological period	Country
<i>Polistes</i>	<i>kirbyanus</i>	Cockerell, 1914	Oeningen	Sarmatian	Germany
<i>Polistes</i>	<i>primitiva</i>	Heer, 1865	Oeningen	Sarmatian	Germany
<i>Polistes</i>	<i>attavinus</i>	(Heer, 1849)	Parschlug	Miocene	Austria
<i>Agelaia</i>	<i>electra</i>	Carpenter & Grimaldi, 1997	Dominican amber	Miocene	Dominican Rep.
<i>Eumenes</i>	<i>shanwangensis</i>	(Hong, 1983)	Shanwang	Middle Miocene	China
<i>Rotundipetiolus</i>	<i>longiantennus</i>	Zhang, 1989	Shanwang	Middle Miocene	China
<i>Harmorhynchium</i>	<i>reflexum</i>	Zhang et al., 1994	Shanwang	Middle Miocene	China
<i>Provespa</i>	<i>nobilis</i>	Zhang et al., 1994	Shanwang	Middle Miocene	China
<i>Vespa</i>	<i>ciliate</i>	Zhang et al., 1994	Shanwang	Middle Miocene	China
<i>Vespa</i>	<i>picea</i>	Zhang et al., 1994	Shanwang	Middle Miocene	China
<i>Vespa</i>	<i>crabroniformis</i>	Heer, 1867	Radoboj	Lower Miocene	Croatia
<i>Alastor</i>	<i>rottensis</i>	(Meunier, 1915)	Rott	Rupelian	Germany
<i>Eunortonia</i>	<i>sepulta</i>	(Timon-David, 1944)	Camoins-les-Bains	Rupelian	France
<i>Polistes</i>	<i>signata</i>	Statz, 1936	Rott-am	Rupelian	Germany
<i>Vespa</i>	<i>bilineata</i>	Statz, 1936	Rott-am	Rupelian	Germany
<i>Vespa</i>	<i>cordifera</i>	Statz, 1936	Rott-am	Rupelian	Germany
<i>Vespa</i>	<i>nigra</i>	Statz, 1936	Rott-am	Rupelian	Germany
<i>Odynerus</i>	<i>oligopunctatus</i>	Theobald, 1937	Cereste	Rupelian	France
<i>Polistes</i>	<i>industrius</i>	Theobald, 1937	Cereste	Rupelian	France
<i>Odynerus</i>	<i>palaeophilus</i>	Cockerell, 1906	Florissant	Rupelian	U.S.A.
<i>Odynerus</i>	<i>praesepultus</i>	Cockerell, 1906	Florissant	Rupelian	U.S.A.
<i>Odynerus</i>	<i>terryi</i>	Cockerell, 1909	Florissant	Rupelian	U.S.A.
<i>Odynerus</i>	<i>percontusius</i>	Cockerell, 1914	Florissant	Rupelian	U.S.A.
<i>Odynerus</i>	<i>wilmattae</i>	Cockerell, 1914	Florissant	Rupelian	U.S.A.
<i>Palaeovespa</i>	<i>florissantia</i>	Cockerell, 1906	Florissant	Rupelian	U.S.A.
<i>Palaeovespa</i>	<i>gillettei</i>	Cockerell, 1906	Florissant	Rupelian	U.S.A.
<i>Palaeovespa</i>	<i>relecta</i>	Cockerell, 1923	Florissant	Rupelian	U.S.A.
<i>Palaeovespa</i>	<i>scudderi</i>	Cockerell, 1906	Florissant	Rupelian	U.S.A.
<i>Palaeovespa</i>	<i>wilsoni</i>	Cockerell, 1914	Florissant	Rupelian	U.S.A.
<i>N – Eumenes</i>	<i>roemeri</i>	Handlirsch, 1910	Flörsheim	Rupelian	Germany
<i>Palaeopolybia</i>	<i>anglica</i>	(Cockerell, 1921)	Gurnard Bay	Oligoc. – Eocene	U.K.
<i>Protopolistes</i>	<i>oblita</i>	(Cockerell, 1921)	Gurnard Bay	Oligoc. – Eocene	U.K.
<i>Sphaerancistrocerus</i>	<i>petiolatus</i>	Antropov, 2014	Gurnard Bay	Oligoc. – Eocene	U.K.
<i>Palaeopolistes</i>	<i>jattioti</i>	Perrard, 2014	Monteils	Upper Eocene	France
<i>Alastor</i>	<i>solidescens</i>	(Scudder, 1890)	Green River Beds	Eocene	U.S.A.
<i>Palaeovespa</i>	<i>baltica</i>	Cockerell, 1909	Baltic	Eocene	Baltic
<i>Palaeovespa</i>	<i>socialis</i>	Poinar Jnr, 2005	Baltic	Eocene	Baltic
<i>Vespa</i>	<i>dasypodia</i>	Menge, 1856	Baltic	Eocene	Baltic
<i>Paleovespa</i>	<i>menatensis</i>	Nel & Auvray, 2006	Menat	Paleocene	France
<i>Ancistrocerus</i>	<i>berlandi</i>	Piton, 1940	Menat	Paleocene	France
<i>Ancistrocerus</i>	<i>eocenicus</i>	Piton, 1940	Menat	Paleocene	France
<i>Eumenes</i>	<i>projaponica</i>	Piton, 1940	Menat	Paleocene	France
<i>Odynerus</i>	<i>manevali</i>	Piton, 1940	Menat	Paleocene	France
<i>Polistes</i>	<i>vergnei</i>	Piton, 1940	Menat	Paleocene	France
<i>Rhynchium</i>	<i>andrei</i>	Piton, 1940	Menat	Paleocene	France
<i>N – Brownichnus</i>	<i>favosites</i>	(Brown, 1941)	Utah	Upper Cretaceous	U.S.A.
<i>Curiosivespa</i>	<i>orapa</i>	Brothers, 1992	Orapa	Coniacian-Cenomanian	Botswana
<i>Priorparagia</i>	<i>anancites</i>	Brothers & Rasnitsyn, 2008	Orapa	Coniacian-Cenomanian	Botswana
<i>Curiosivespa</i>	<i>curiosa</i>	Rasnitsyn, 1975	Kzyl-Zhar	Turonian	Kazakhstan
<i>Symmorphus</i>	<i>senex</i>	Carpenter, 2000	New Jersey	Turonian	U.S.A.
<i>Curiosivespa</i>	<i>zigrasi</i>	Perrard & Carpenter, 2016	Burmese amber	late Albian	Myanmar
<i>Curiosivespa</i>	<i>striata</i>	Perrard & Carpenter, 2016	Burmese amber	late Albian	Myanmar
<i>Proovespa</i>	<i>haxairei</i>	Perrard & Carpenter, 2016	Burmese amber	late Albian	Myanmar
<i>Curiosivespa</i>	<i>derivata</i>	Carpenter & Rasnitsyn, 1990	Bon-Tsagan	Aptian	Mongolia
<i>Priorvespa</i>	<i>directa</i>	Carpenter & Rasnitsyn, 1990	Bon-Tsagan	Aptian	Mongolia
<i>Priorvespa</i>	<i>minuta</i>	Carpenter & Rasnitsyn, 1990	Bon-Tsagan	Aptian	Mongolia
<i>Priorvespa</i>	<i>quadrata</i>	Carpenter & Rasnitsyn, 1990	Bon-Tsagan	Aptian	Mongolia
<i>Priorvespa</i>	<i>recidiva</i>	Carpenter & Rasnitsyn, 1990	Bon-Tsagan	Aptian	Mongolia
<i>Priorvespa</i>	<i>longiceps</i>	Carpenter & Rasnitsyn, 1990	Turga	Hauterivian	Russia
<i>Curiosivespa</i>	<i>antiqua</i>	Carpenter & Rasnitsyn, 1990	Baissa	Hauterivian	Transbaikalia
<i>Priorvespa</i>	<i>bullata</i>	Carpenter & Rasnitsyn, 1990	Baissa	Hauterivian	Transbaikalia

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1 **Table S2. Matrix and list of the morphological and behavioural characters.**

2 ‘?’ refers to missing data; ‘-’ refers to non-applicable character; ‘#’ refers to multistate characters ‘0 and 1’; ‘*’ refers to multistate characters ‘1
 3 and 2’. *Curiosivespa* and *Priorvespa* were scored on the basis of every known fossil for these taxa. Fossil taxa are in grey. Characters 06, 24, 38,
 4 39, 48, 56, 60 and 74 were treated as additive.

5
6
7

8 TAXA	CHARACTERS	0000000000	1111111111	2222222222	3333333333	4444444444	5555555555	6666666666	77777
		0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	01234
9 <i>Pseudotiphia beckeri</i>		0000020000	1000000000	0001201100	0200000001	000-0#0111	0--0--1-0	--11110000	00000
10 <i>Rhopalosoma nearcticum</i>		11100-0001	0000001000	0000000001	0100100000	0000010020	0-1-1--1-0	2000011010	00000
11 <i>Priorvespa</i>		?01???00??	?0???01???	?01????1??	1??????21	0000000110	0100100010	20?#0?2101	?????
12 <i>Protovespa haxairei</i>		00100?0*01	10???11011	0011201111	11011???21	0010010110	0011110101	2100012101	?0???
13 <i>Euparagia scutellaris</i>		001101*20#	1000011011	0011201111	1000001021	0001101101	0010000010	0011001000	00000
14 <i>Curiosivespa</i>		0110??#0?1	00???11???	001?2?1???	1??????2*	0001110##1	0000###10	#0#0??100?	?????
15 <i>Curiosivespa striata</i>		00100?????	???0?11011	00?02001?1	10??????20	0011110111	0100001110	000?0010?0	?0???
16 <i>Curiosivespa zigrasi</i>		11????????	???0?11?11	?0102001??	11????????1	0001110001	0110000??0	???001000	?????
17 <i>Priorparagia anancites</i>		???????????	?????0???	??1?2?????	?????????20	0001?01011	0110000010	0?110?????	?????
18 <i>Gayella eumenoides</i>		0011002100	1010111111	1011011110	1101100021	001101011#	0010100101	1000010001	11010
19 <i>Masaris vespiformis</i>		00110-1301	1010111111	1001211110	110000101#	0110110110	0-1-1-00-1	1010002211	11010
20 <i>Paramasaris richardsi</i>		0011002200	1010111111	1001211110	1101100021	0011010010	0010100101	1000010001	11010
21 <i>Paragia decipiens</i>		0000101001	0010111111	0011211110	1100101010	0110110120	0-1-1-0010	0010002211	11010
22 <i>Zethus demissus</i>		0010010300	1010011111	0111110111	1211100020	1111110100	1001110110	0010002101	11000
23 <i>Eumenes lunulatus</i>		0011012301	0010011111	0101011111	1211100020	1111110110	1011110100	1010002101	11000
24 <i>Odynerus spinipes</i>		001#011301	1010011111	0101111111	1211000020	1111110110	1011110110	0010002101	11000
25 <i>Anischnogaster iridipennis</i>		1010122100	1000011011	0010001011	1111100021	0111110110	1111110101	2110102101	11101
26 <i>Polistes nimpha</i>		1010111110	1011011111	1000000111	1011111120	1111110020	1021111110	2110002101	11102
27 <i>Mischocyttarus drewsenii</i>		00101-1110	1011011111	0000000011	1011111120	1111110120	1021111110	2110002101	11102
28 <i>Parapolybia indica</i>		0010111110	1011011111	0000000011	1011111120	1111110120	1021112110	2110002101	11102
29 <i>Polybia jurinei</i>		0010111110	1011011111	1000000111	1011111120	1111110120	1020112110	2110002101	11102
30 <i>Vespa basalis</i>		0010111300	1111011101	0000101011	1011111120	1111110020	1021110100	2111002101	21102

31
32

00 Scape: 0 = longer than 1st flagellum;
1 = shorter than 1st flagellum.

01 Flagellum articles: 0 = short (length~width); 1 = long (length>>width).

02 Eyes: 0 = with interior margin straight or slightly curved; 1 = emarginate.

03 Posterior ocelli: 0 = closer to each other than to the eyes; 1 = closer to the eyes than to each other.

04 Gena width: 0 = upper part > lower part;
1 = lower part > or = upper part.

05 Preoccipital and postocular carinae:
0 = present and separated; 1 = fused;
2 = evanescent.

06 Clypeus shape: 0 = wider than long;
1 = square; 2 = longer than wide.

07 Clypeus apex: 0 = continuous; median tooth; 1 = two central teeth; 2 = two lateral teeth.

08 Lateral lobes of clypeus: 0 = absent or reduced; 1 = pronounced.

09 Labrum: 0 = hidden; 1 = protruding.

10 Labrum apex: 0 = wide (similar width to clypeus apical area); 1 = narrow (<1/2 width than clypeus apical area).

11 Mandible: 0 = with small cutting edge;
1 = with long cutting edge.

12 Acroglossal buttons: 0 = absent;
1 = present.

13 Posterior lingual plate: 0 = narrow;
1 = broad.

14 Hypostomal apodemes: 0 = absent;
1 = present.

15 Mesosoma shape: 0 = short or as long as wide; 1 = longer than wide.

16 Pronotum dorsum: 0 = long (horizontal part >1/4 of length mesonotum); 1 = short (horizontal part absent or <1/4 of mesonotum).

17 Pronotal carina: 0 = absent; 1 = present.

18 Posterior pronotal lobe: 0 = next to the tegula; 1 = distinctly distant from the tegula (from ~1/2x length of the lobe to 3x length of the lobe).

19 Prescutal sculpture: 0 = absent;

1 = present.

20 Tegula shape: 0 = about as long as wide;
1 = distinctly elongated.

21 Parategula: 0 = absent; 1 = present.

22 Pronotum posterior angle: 0 = stopping at the tegula; 1 = produced above the tegula.

23 Transscutal furrow: 0 = smooth;
1 = ridged.

24 Metanotum: 0 = roughly aligned with scutellum; mostly vertical but no overlap with scutellum; 1 = mostly vertical and partially under scutellum, scutellum produced.

25 Scutal lamella: 0 = present; 1 = absent.

26 Propodeum posterior part: 0 = not vertical (angle with mesonotum dorsum > 110°);
1 = vertical (angle with mesonotum dorsum < or = 110°).

27 Propodeum posterolateral angles:
0 = blunt, without clear delimitation of lateral and posterior parts; 1 = sharp (sometime produced), clearly delimited.

28 Mesosternal sclerite before mid-legs:
0 = large and produced; 1 = short and rounded.

29 Trochantellus: 0 = absent; 1 = present.

30 First tarsomere: 0 = length < or = 2x 2nd tarsomere; 1 = length > 2x 2nd tarsomere.

31 Claws: 0 = simple; 1 = with a basal small tooth; 2 = bifid.

32 First metasomal segment: 0 = tergum and sternum distinct; 1 = tergum and sternum fused.

33 Metasomal retraction: 0 = absent;
1 = present.

34 Sixth metasomal sternum: 0 = apical part straight or slightly curved; 1 = apical part laterally compressed in a furrow.

35 Van der Vecht's gland: 0 = absent;
1 = present.

36 Parameral spines: 0 = elongated; 1 = short.

37 Volsella: 0 = no apodeme; 1 = apodeme present.

38 Forewing, number of closed cells: 0 = 7 cells; 1 = 8 cells; 2 = 9 cells.

39 Forewing, M connection with Cu: 0 = before Cu and 1cu-a; 1 = at the same point; after.

40 Forewing, longitudinal plaiting: 0 = absent; 1 = present.

41 Forewing, 1cu-a length: 0 = long, more than 3x its width; 1 = short.

42 Forewing, 1cu-a shape: 0 = curved; 1 = straight.

43 Forewing, RsM: 0 = longer than M between MCu and Rs; 1 = same length or shorter.

44 Forewing, first discal cell: 0 = shorter than submedian cell; 1 = at least the equal of submedian cell.

45 Forewing, basal angle of first submarginal cell: 0 = obtuse; 1 = acute.

46 Forewing, first Rs abscissa: 0 = long; 1 = short.

47 Forewing, pterostigma size: 0 = short (< or = 1/4th of marginal cell length); 1 = long (> 1/4th of marginal cell length).

48 Forewing, pterostigma shape: 0 = truncate apically; 1 = subtruncate, basal angle of marginal cell acute; pointed apically.

49 Forewing, 2nd segment of Cu: 0 = distinctly angled with 1m-cu; 1 = in the prolongation of 1m-cu.

50 Forewing, vein alignment: 0 = absent; 1 = MCuA, CuA, m-cu1 and M aligned in almost straight line.

51 Forewing, second submarginal cell shape: 0 = narrowed above; 1 = quadrate.

52 Forewing, second submarginal cell: 0 = basal angle obtuse, M and Rs angled; 1 = basal angle acute, M and Rs angled; 2 = basal angle obtuse, M and Rs aligned.

53 Forewing, 1r-m: 0 = straight or curved; 1 = sinuous.

54 Forewing, first recurrent vein: 0 = distal part angled sharply into second

submarginal cell; 1 = distal part running straight into second submarginal cell.

55 Forewing, 1r-m connection to M: 0 = before 2m-cu; 1 = after 2m-cu.

56 Forewing, M segment between 1m-cu and 2m-cu: 0 = longer than between Rs and 1m-cu; 1 = same length; 2 = shorter.

57 Forewing, third submarginal cell: 0 = apically rounded; 1 = apically subtruncate.

58 Forewing, Rs between 1r-m and 2r-m: 0 = longer than 2r-rs; 1 = same size or shorter.

59 Forewing, marginal cell shape: 0 = Rs angled near middle of cell; 1 = Rs angled close to pterostigma, then straight.

60 Forewing, marginal cell apex: 0 = short and rounded; 1 = elongated and rounded;

2 = elongated with apex pointed.

61 Forewing, marginal cell appendix: 0 = present; 1 = absent.

62 Forewing, M vein: 0 = almost reaches the margin; 1 = stops shortly after the 3rd submarginal cell.

63 Forewing, Cu vein: 0 = almost reaches the margin; 1 = stops shortly after the cell.

64 Hindwing, cell number: 0 = three; 1 = two.

65 Hindwing, hamuli placement: 0 = beginning basad of fork of R1 and Rs; 1 = beginning at fork.

66 Hindwing, Cu1: 0 = diverging apicad of cu-a; 1 = diverging at cu-a; 2 = diverging basad of cu-a.

67 Hindwing, cu-a: 0 = transverse; 1 = aligned with A; 2 = angled with apex of A.

68 Hindwing, apical part of hindwing anal vein: 0 = free; 1 = fused with cu-a.

69 Hindwing, subbasal cell: 0 = broadest apically; 1 = broadest subapically.

70 Hindwing, preaxillary excision: 0 = shallow; 1 = deep; 2 = absent.

71 Hindwing, anal lobe: 0 = long; 1 = short or absent.

72 Larva, clypeus: 0 = broad; 1 = narrow.

73 Provisions: 0 = insects; 1 = pollen.

74 Sociality: 0 = solitary; 1 = temporary eusociality; 2 = permanent eusociality.

