A large hornet from the Upper Miocene of Saint-Bauzile, southeastern France (Hymenoptera, Vespidae)

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Abstract. – A new species of large hornet is described and figured from the Upper Miocene (end Tortonian) lacustrine diatomite of the paleolake la Montagne d'Andance of the Saint-Bauzile Konservat-Lagerstätte (Privas, Ardèche). *Vespa* (*Intervespa*) *tortonica* n. subgen., n. sp., is distinguished from extant and extinct species of *Vespa* Linnaeus on the basis of wing venation, which intermingles symplesiomorphic features of the Palaeocene-Eocene *Palaeovespa* Cockerell and other extant genera of Vespinae with the apomorphic elongation of the vertex present in *Vespa*. The historical diagnosis for *Palaeovespa* is clarified. Since *V. tortonica* bridges the character divide between *Vespa* and other vespines, the former is placed in its own subgenus, putatively sister to all other *Vespa*.

Résumé. – **Un gros frelon du Miocène supérieur de Saint-Bauzile, dans le sud-est de la France (Hymenoptera, Vespidae)**. Une nouvelle espèce de grand frelon est décrite et figurée à partir d'un fossile de la diatomite lacustre du Miocène supérieur (fin Tortonien) du paléolac de la Montagne d'Andance du Konservat-Lagerstätte de Saint-Bauzile (Privas, Ardèche). *Vespa* (*Intervespa*) *tortonica* n. subgen., n. sp., se distingue des espèces existantes et éteintes de *Vespa* Linnaeus sur la base de la nervation alaire, mêlant des caractères symplésiomorphes du genre *Palaeovespa* Cockerell (Paléocène-Éocène) et d'autres genres actuels de Vespinae, avec l'allongement apomorphe du vertex propre à *Vespa*. Le diagnostic historique pour *Palaeovespa* est clarifié. Puisque *V. tortonica* comble le fossé entre *Vespa* et les autres Vespinae, nous la plaçons dans son propre sous-genre, possiblement sœur de toutes les autres *Vespa*.

Keywords. – Aculeata, Montagne d'Andance, Tortonian, *Vespa*, Vespinae.

While southern France today enjoys a largely Mediterranean climate, with hot summers and mild winters, during the Miocene this same region was warm and humid. Indeed, during the Middle Miocene Climatic Optimum (16–11.6 Ma) the climate was such that the Arctic was still covered by permafrost forests, with humid subtropical

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climates extending as far north as Iceland (STEINTHORSDOTTIR *et al.*, 2020). Southern France was covered by dense humid tropical to subtropical forests. During the Late Miocene, the once consistently warm and humid forests experienced pronounced seasonality and significant temperature and precipitation differences throughout the year. Toward the end of the Miocene repeated desiccations (Messinian salinity crisis, 5.9–5.3 Ma) of the Mediterranean Sea led to considerable drying and seasonal aridity (KRIJGSMAN *et al.*, 1999; ROVERI *et al.*, 2014; HERBERT *et al.*, 2016), with extensive land connection across the Iberian Peninsula and southern France with northwestern Africa (KRIJGSMAN *et al.*, 1996; GARGANI & RIGOLETTE, 2007). Sclerophyllous woodlands replaced the humid temperate forests, which themselves had replaced earlier humid tropical forests (IKSANDER, 1990; KOVAR-EDER *et al.*, 2006). The Late Miocene is therefore an episode of considerable climatic and biotic changes during which the initial stages unfolded of the shift across Europe from a warm humid climate to a temperate seasonal environment (HERBERT *et al.*, 2016).

The lacustrine diatomite of the volcano-sedimentary paleolake of la Montagne d'Andance, Saint-Bauzile, near Privas, Ardèche is a rich Konservat-Lagerstätte from the Upper Miocene, and which preserves an exceptional and diverse assemblage of plants and animals (MÉTAIS & SEN, 2018). This site provides a rich record of life at the beginning of this period of critical climatic changes, with age estimates of 7.6–7.2 Ma and spanning the end of the Tortonian (11.61–7.25 Ma) and the earliest Messinian (7.25–5.33 Ma) stages. Most current age estimates favor an end-Tortonian age of 7.3 Ma for the fossils recovered from the quarry of la Montagne d'Andance (PASTRE *et al.*, 2004) and this is consistent with the palaeoflora from the locality representing a warm humid climate (BRICE, 1965; ISKANDER, 1990) preceding the drying that would shortly follow.

Among the many fossil insects recovered from Saint-Bauzile (RIOU, 1988), perhaps the largest and one of the most impressive is a large hornet preserved as a carbonaceous compression on a slab with a leaf impression of *Quercus* sp. (fig. 1-2). Hornets of the genus *Vespa* Linnaeus, 1758, are among the more substantial and recognizable of Vespidae, with a natural distribution in Asia (ARCHER, 2012; SMITH-PARDO *et al.*, 2020), and especially southern Asia and Malesia, one species in northern Africa and southern Europe, and the well-known *Vespa crabro* Linnaeus, 1758, common across Europe to the Caspian Sea. Several other species have been introduced and become established in North America and Western Europe (ARCHER, 2012). Species of *Vespa* are large, ranging from 1.5–4.5 cm in length, and are typically black to reddish or even yellowish brown and often with yellow or orange maculation. These are, of course, eusocial species living in large nests within enclosed spaces or may be in the open and suspended from the underside of branches or even on human constructions. Although some species obviously do well in temperate climates, hornets are largely tropical or subtropical, where colony sizes can reach an impressive 30,000 cells (ARCHER, 2012). The discovery of a large hornet in the Upper Miocene volcaniclastic diatomite of southern France is certainly consistent with the subtropical environment of the region at the time, as well as the modern-day habitats of many species of *Vespa* (ARCHER, 2012). The Miocene species is described and figured and then compared with *Palaeovespa* Cockerell, 1906, and *Vespa*.

Material and methods

The fossil reported here comprises the part and counterpart of a female (fig. 1–4), largely compressed laterally except the head is obliquely turned and slightly forward, thereby showing much of the face (fig. 2, 5, 9). The wings are folded, typical of most Vespidae, and extended straight back over the mesosoma and above the basal segments of the metasoma, which itself is turned downward (fig. 1-5). Overall, the wasp is in a hunched and folded position owing to the clustering of the legs beneath the mesosoma, the lowering of the head (and perhaps slightly detached from the mesosoma during deposition), and the ventrally bent metasoma. The part is represented by a carbonaceous material while the counterpart is merely an impression. At first glance, the fossil does not appear to preserve much detail but upon finer inspection a rather significant number of characters can be discerned, including additional traits when viewed using UV-A light, a method growing in application for paleoentomological studies (*e.g.*, Nel *et al.*, 2023; Boderau *et al.*, 2024a, b). With care the anterior wing veins can be followed, thus permitting identification of the fossil. However, given the nature of the preservation, the species description is kept rather limited so as to avoid any over-interpretation. Naturally, it is hoped that additional material will be discovered of this quite interesting species.

Fig. 1. – *Vespa* (*Intervespa*) *tortonica* n. subgen., n. sp., holotype (MNHN.F.A95075) female (part), entire stone. Scale bar = 1 cm.

Measurements of the specimen were taken with an ocular micrometer on an Olympus SZX9 stereomicroscope, while the morphological terminology follows that used elsewhere in the systematics of Vespinae (*e.g.*, ARCHER, 2012; PERRARD *et al.*, 2013, 2015; NGUYEN, 2020), except wing vein nomenclature is adopted from that of ENGEL *et al.* (2024).

SYSTEMATIC PALAEONTOLOGY

Family **Vespidae** Latreille, 1802

Subamily **Vespinae** Latreille, 1802

Genus ***Vespa*** Linnaeus, 1758

Intervespa n. subgen.

https://zoobank.org/NomenclaturalActs/88e09b28-5395-40e8-b486-3dc67bf996ad

Type species. – *Vespa* (*Intervespa*) *tortonica* n. sp.

Diagnosis. – The new subgenus intermingles features of other vespine genera, including the extinct *Palaeovespa*, and *Vespa*. Like the former, the new subgenus has the prestigma short relative to *Vespa*, with 1Rs in a more apical position such that the prestigma is not pronouncedly more than 3× the pterostigmal length (closer to 2.7× pterostigmal length in *V. tortonica*). Unlike *Palaeovespa*, 2m-cu enters the second submarginal cell at the cell's midlength (*vs*. in the apical half of the cell's length, in *Vespa* 2m-cu usually enters within the proximal third of the cell). This new subgenus further differs from *Palaeovespa* in that 3Rs is scarcely angled and effectively continuous relative to 4Rs, such that the posterior margin of marginal cell is not pronouncedly angled at the juncture of 1rs-m and Rs (there is a pronounced angle in the posterior margin of the marginal cell at the 1rs-m/Rs juncture in *Palaeovespa*). The fossil shares with modern *Vespa* the apomorphy of a swollen vertex (*i.e.*, ocelloccipital area elongate), with the lateral ocelli separated from the posterior margin of the vertex by more than twice the interocellar distance (*Palaeovespa* and other vespine genera have the plesiomorphic condition of the ocelli separated from the posterior margin of the vertex by about the interocellar distance or less).

Etymology. – The new genus-group name is a combination of the Latin prefix *inter*– (from the preposition inter, meaning, "between") and the noun *vespa*, meaning, "wasp". The gender of the name is feminine.

Remarks. – Earlier authors recognized multiple subgenera for extant species of *Vespa* (*e.g.*, DALLA TORRE, 1904; VAN DER VECHT, 1959) but those were all synonymized by CARPENTER (1987). Phylogenetic estimates for *Vespa* support this decision (CARPENTER, 1987; ARCHER, 1993; PERRARD *et al.*, 2013, 2015). We do not advocate the resurrection of any further subgenera for extant species of *Vespa*. Accordingly, the system presented here is for two subgenera: *Intervespa* for *V. tortonica* and *Vespa s. str.* for all extant species of the genus (summarized by SMITH-PARDO *et al.*, 2020).

Vespa (Intervespa) tortonica n. sp. (fig. 1-9)

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Type material. – Holotype: ♀, MNHN.F.A95075, conserved in the Collections de Paléontologie, Muséum national d'Histoire naturelle, Paris, France..

Type locality and horizon. – La Montagne d'Andance [44.676451°N 4.670588°E], Saint-Bauzile, near Privas, Ardèche, France; volcaniclastic diatomite, Upper Miocene (Tortonian).

Diagnosis. – As for the genus (*vide supra*).

Description of female. – Total body length 41.18 mm (head length 5.89 mm, vertex to medial apex of clypeus; mesosoma length 10.62 mm; metasoma length 24.67 mm, not including sting); forewing length 21.3 mm. Integumental sculpturing and coloration not preserved (preserved as dark black carbonaceous compression). Head apparently slightly wider than long (oblique orientation prevents precise measurements so estimated by preserved contours); compound

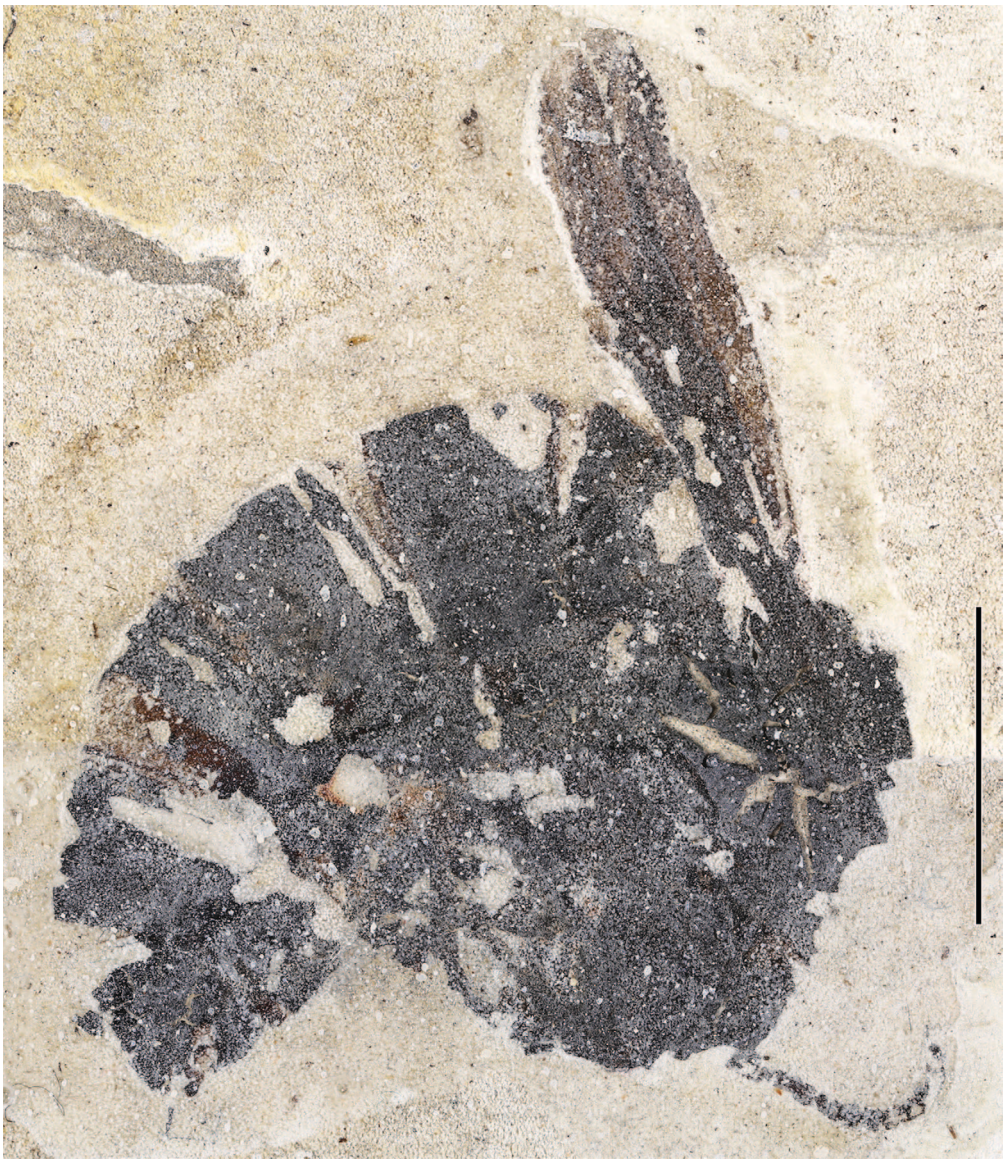

Fig. 2. – *Vespa* (*Intervespa*) *tortonica* n. subgen., n. sp., holotype (MNHN.F.A95075) female (part), detail of wasp only. Scale bar = 1 cm.

eye seemingly slightly narrower than gena; gena of apparent equal width above as below; ocelli at upper tangent of compound eyes, not enlarged, lateral ocelli closer to each other than to inner orbit of compound eye; vertex swollen, lateral ocelli separated from posterior margin of vertex by twice interocellar distance; apical margin of clypeus without median tooth or tubercle, apicolateral angles relatively small, bluntly but narrowly rounded, concavity of medioapical margin weak.

Forewing prestigma comparatively short, approximately 2.7× pterostigmal length; pterostigma short, approximately squarish, r-rs originated at is apicoposterior angle; 1M proximad 1cu-a, shorter than 1m-cu; Rs+M weakly curved; 2Rs straight; 2M strongly angled posteriorly from Rs+M; 1m-cu meeting 2M and continuing straight into 3M; 2m-cu meeting second submarginal cell at cell midlength; 1rs-m and 2rs-m straight; 3Rs scarcely angled at origin of 4Rs, effective continuous with adjoining abscissa, thus posterior margin of marginal cell a continuous curve, not angled; r-rs longer than 3Rs; 3rs slightly longer than 4Rs.

Metasoma swollen as preserved (likely bloated from partial decay at the time of deposition); six segments, with short sting partially exserted.

Male. – *Latet*.

Etymology. – The specific epithet is taken from the Tortonian stage with the Latin suffix –*icus*, meaning, "belonging to".

DISCUSSION

The current fossil, despite its rather challenging preservation, can be attributed to the subfamily Vespinae based on several characters. Based on apomorphies established by CARPENTER (1982), the fossil can be assigned to various clades within the family. Like Eumeninae + Zethinae + Stenogastrinae + Polistinae + Vespinae, the forewing first medial cell (= discal cell) is greatly elongate (fig. 7). Euparagiinae and Masarinae may be further excluded by the marginal cell apex on the costa rather

Fig. 3. – *Vespa* (*Intervespa*) *tortonica* n. subgen., n. sp., holotype (MNHN.F.A95075) female (counterpart), entire stone. Scale bar = 1 cm.

than truncate and appendiculate, and variably separated from the costa, and 1cu-a prefurcal or confluent with 1M. As in Stenogastrinae + Polistinae + Vespinae, the marginal cell is pointed apically on the costa and is not appendiculate (fig. 7), and it shares with Vespinae + Polistinae the pretarsal claws secondarily simple (fig. 8). The fossil can be excluded from Polistinae as the apical margin of the clypeus is broadly straight between short, rounded, apicolateral angles (fig. 9) (in polistines the clypeus is pointed medioapically, sometimes appearing trilobate when apicolateral angles are produced). Furthermore, the metasoma is sessile with tergum I abruptly declivitous anteriorly (fig. 2, 8), while it is petiolate to subsessile in Polistinae. In addition, the fossil can be excluded from Stenogastrinae owing to the plaited forewings (fig. 1-5, 7)

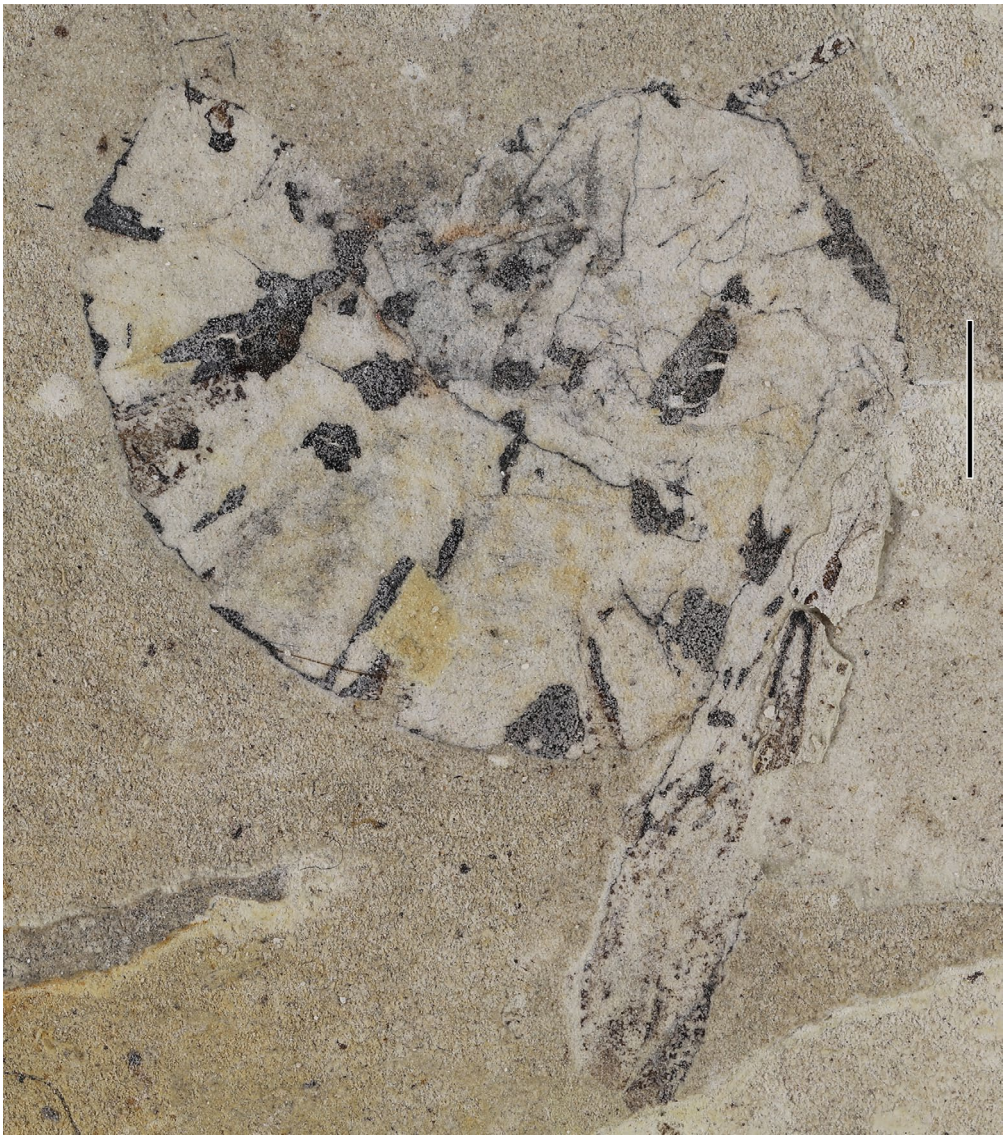

Fig. 4. – *Vespa* (*Intervespa*) *tortonica* n. subgen., n. sp., holotype (MNHN.F.A95075) female (counterpart), detail of wasp only. Scale bar = 1 cm.

(secondarily absent in stenogastrines), the clypeus is not produced into a point (fig. 9), the tegula is separated from the pronotum laterally by about its length (fig. 2) (separated by 2× its length in stenogastrines), the simple pretarsal claws (fig. 8) (toothed in stenogastrines), metasoma sessile (fig. 2, 8) (elongate petiolate in stenogastrines), and metasomal tergum I and sternum I not fused (fig. 2, 5, 8) (fused in stenogastrines).

Although COCKERELL (1906) cited several venational differences between *Palaeovespa*, which was widespread through North America and Europe during the Palaeocene and Eocene (COCKERELL, 1906, 1909, 1914, 1923; POINAR, 2005; NEL & AUVRAY, 2006), nearly all of these occur across species of *Vespa* and so are of little value to consider *Palaeovespa* distinct. For example, COCKERELL (1906) placed emphasis on the fact that 2M was oblique relative to the apex of 1m-cu, and yet this is also a feature of *Vespa* and therefore identical to that of the extant species (ARCHER, 2012; PERRARD *et al.*, 2013). There are seemingly only three traits that distinguish the Palaeocene-Eocene group, although even these have some intermediates. First, in *Palaeovespa* 1Rs originates in a more apical position relative to modern species, such that the anterior side of the first submarginal cell is about as long as 1Rs, rather than many times the length of 1Rs in modern species. Second, in *Vespa*, the junctures of 1m-cu and 2m-cu on M are

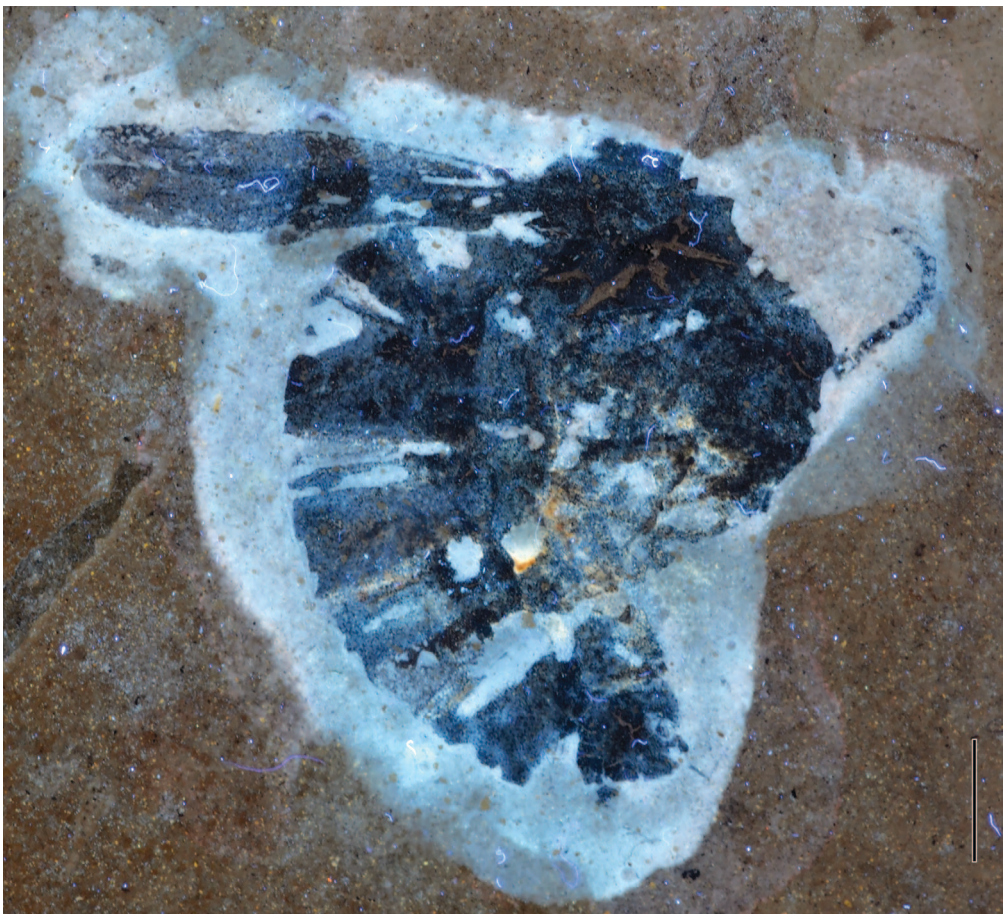

Fig. 5. – *Vespa* (*Intervespa*) *tortonica*, n. subgen., n. sp., holotype (MNHN.F.A95075) female (part), viewed under UV-A light. Scale bar = 1 cm.

comparatively close together, with 2m-cu at about midlength or less of the second submarginal cell, while in *Palaeovespa* 2m-cu is slightly to greatly beyond the cell's midlength. The position of 2m-cu is quite variable and there is a gradation across extant species and those of *Palaeovespa*, with 2m-cu in the most proximal position near midlength. However, despite the fact these are individually quantitative traits, their combination seems to group the Palaeocene-Eocene species relative to other *Vespa*, and even other Vespinae. An overlooked difference is also the short vertex of *Palaeovespa*, which is similar to *Provespa* Ashmead, *Dolichovespula* Rohwer, and *Vespula* Thomson. As noted by the morphometric analysis of Perrard *et al*. (2015), *Palaeovespa* may belong to the stem group of Vespinae.

The current Miocene fossil is interesting in that one might immediately conclude based on the comparatively shorter prestigma that it should be classified in *Palaeovespa* or perhaps in one of the other extant genera of Vespinae. However, on closer inspection it is evident that the short prestigma is merely a retained plesiomorphy as

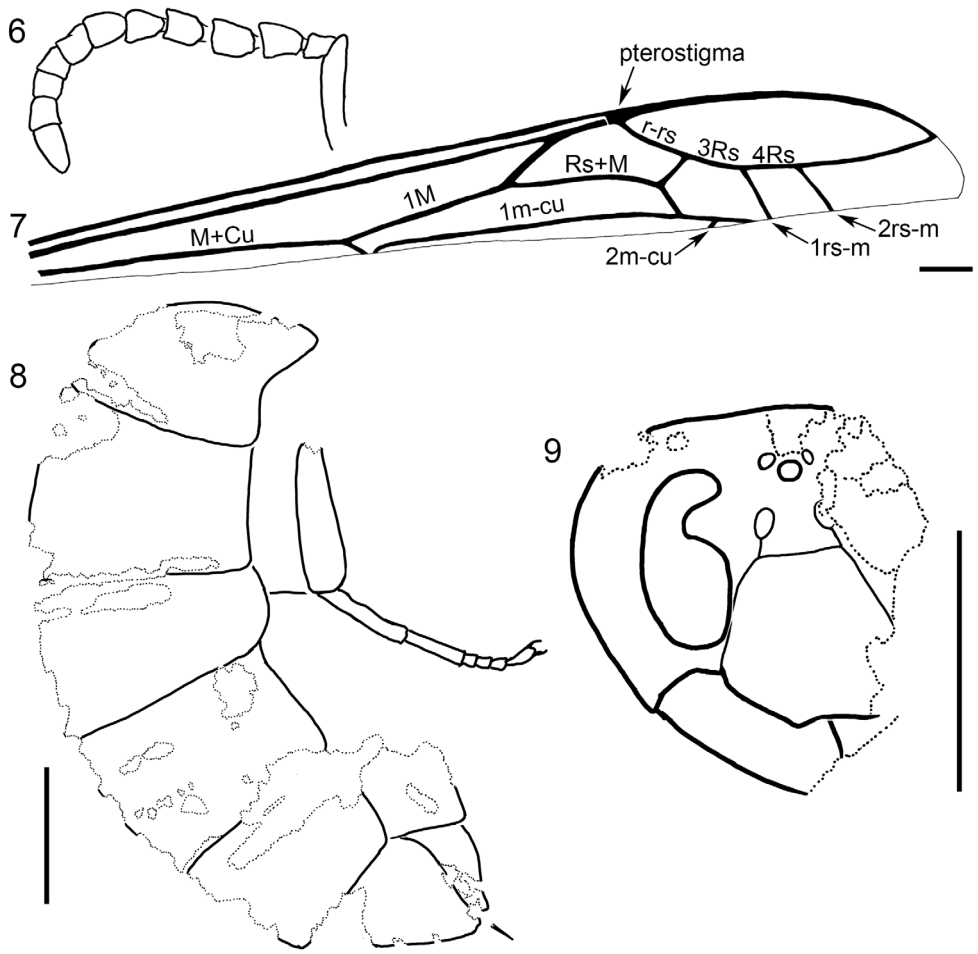

Fig. 6–9. – *Vespa* (*Intervespa*) *tortonica*, n. subgen., n. sp., holotype (MNHN.F.A95075) female, line drawings. – 6, Antenna, as preserved. – 7, Anterior portion of folded forewing. – 8, Visible details of metasoma and mesofemur through mesopretarsus. – 9, Head. Scale bars: 6, 7 = 1 mm (same scale); 8, 9 = 5 mm.

the position of 2m-cu is at the midlength of the second marginal cell, and therefore the distance between 1m-cu and 2m-cu is shorter than that of species of *Palaeovespa*. More importantly, however, the new fossil shares the apomorphy of an elongate ocelloccipital distance, indicative of the genus *Vespa*. However, including the current fossil within *Vespa* proper would vitiate one of the key apomorphies for the genus —the elongate prestigma (ARCHER, 2012; PERRARD *et al.*, 2013, 2015). In this respect, the combination of traits in the Miocene species is seemingly osculant between extant *Vespa* and the other vespine genera. Rather than establish a monotypic genus for the new species we have adopted the conservative position of considering the elongate ocelloccipital area as key to the distinction of *Vespa* relative to other vespines and classify the new fossil in an early-diverging subgenus, putatively sister to all other *Vespa*.

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