

# New fossil ants in French Cretaceous amber (Hymenoptera: Formicidae)

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**Abstract** Recent studies on the ant phylogeny are mainly based on the molecular analyses of extant subfamilies and do not include the extinct, only Cretaceous subfamily Sphecomyrminae. However, the latter is of major importance for ant relationships, as it is considered the most basal subfamily. Therefore, each new discovery of a Mesozoic ant is of high interest for improving our understanding of their early history and basal relationships. In this paper, a new sphecomyrmine ant, allied to the Burmese amber genus *Haidomyrmex*, is described from mid-Cretaceous amber of France as *Haidomyrmodes mammuthus* gen. and sp. n. The diagnosis of the tribe Haidomyrmecini is

emended based on the new type material, which includes a gyne (alate female) and two incomplete workers. The genus *Sphecomyrmodes*, hitherto known by a single species from Burmese amber, is also reported and a new species described as *S. occidentalis* sp. n. after two workers remarkably preserved in a single piece of Early Cenomanian French amber. The new fossils provide additional information on early ant diversity and relationships and demonstrate that the monophyly of the Sphecomyrminae, as currently defined, is still weakly supported.

**Keywords** Insecta · Formicidae · Sphecomyrminae · Haidomyrmecini · Cretaceous · France

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## Introduction

Ants are one of the most successful and widespread organisms on Earth. They have a crucial role in many ecosystems through their interactions with other arthropods, plants, or fungi (Hölldobler and Wilson 1990; Jolivet 1996). Despite the very extensive studies carried out on them, our understanding of their early history and evolution since they appeared in the Early Cretaceous is far from complete, owing to the relative scarcity of primitive fossils. The phylogeny of ants has recently gained clarity with the molecular studies of extant subfamilies (Brady et al. 2006; Moreau et al. 2006; Ouellette et al. 2006). However, these studies include fossils only for calibrating the divergent time estimates for major ant lineages and do not include the extinct Sphecomyrminae, which is considered the most basal subfamily and is therefore of major importance for the relationships of early ants.

Among these primitive sphecomyrmine ants, the very peculiar *Haidomyrmex cerberus* was described some years

ago from the Late Albian (Cretaceous) Burmese amber, after a partial worker characterized by highly specialized mandibles (Dlussky 1996). A photograph of the head was later provided by Ross and York (2000: Fig. 21), and Bolton (2003) erected the tribe Haidomyrmecini within the Sphecomyrminae for this unique genus. The ant was then refigured and discussed by Engel and Grimaldi (2005) who tentatively followed the past authors in placing *Haidomyrmex* within the Sphecomyrminae. In this paper, we describe (1) a new genus closely related to *Haidomyrmex*, after a gyne (alate female) and two workers fossilized in the Late Albian and Early Cenomanian amber of Charente-Maritime, SW France; (2) a new species of the genus *Sphecomyrmodes*, which was recently discovered in Burmese amber (Engel and Grimaldi 2005), and here represented by two worker specimens preserved in a distinct French amber deposit of Early Cenomanian age.

### Systematic palaeontology

Family Formicidae Latreille, 1809  
Subfamily Sphecomyrminae Wilson & Brown, 1967  
Tribe Haidomyrmecini Bolton, 2003

*Type genus Haidomyrmex* Dlussky 1996. Other genus: *Haidomyrmodes* gen. n.

*Emended diagnosis* Characters as defined by Bolton (2003: 74) but with the following modifications: females with slight but distinct constriction between third and fourth abdominal segments; gyne with ocelli; workers with or without ocelli; third funicular segment elongate or equal in length to other funicular segments.

Genus *Haidomyrmodes* gen. n.

*Type species Haidomyrmodes mammothus* sp. n.

*Diagnosis (gyne and worker)* This genus possesses all diagnostic characters of the tribe Haidomyrmecini but differs from *Haidomyrmex* as follows: part of mandible basal of elbow very short, so that distal part, which is strongly up-curved, is very close to head; mandibles smooth; eyes large (ratio eye length/head length about 0.4 vs 0.2 in *Haidomyrmex*); ocelli well developed; no brush of stiff setae on clypeus; antennal scape with distinct inner apical lobe; all funicular segments of same length and all less than two times as long as broad.

*Etymology* The name is a combination of *Haidomyrmex*, type genus of the tribe, and the suffix *-odes*, meaning “with the form of” (Figs. 1 and 2).

*Haidomyrmex* sp. Perrichot & Nel, In Perrichot 2005: 78, Fig. 26.

*Material* Holotype: MNHN ARC 50.2 (nearly complete alate gyne). Paratypes: MNHN ARC 242, MNHN AIX 1.2 (partial workers). Deposited in the department of Earth History, National Museum of Natural History, Paris, France.

*Localities* Archingeay/Les-Nouillers and Aix Island, Charente-Maritime, France.

*Stratigraphic horizon* Mid Cretaceous, Uppermost Albian to Lower Cenomanian (ca. 100 Ma old after Néraudeau et al. 2002; Perrichot 2005).

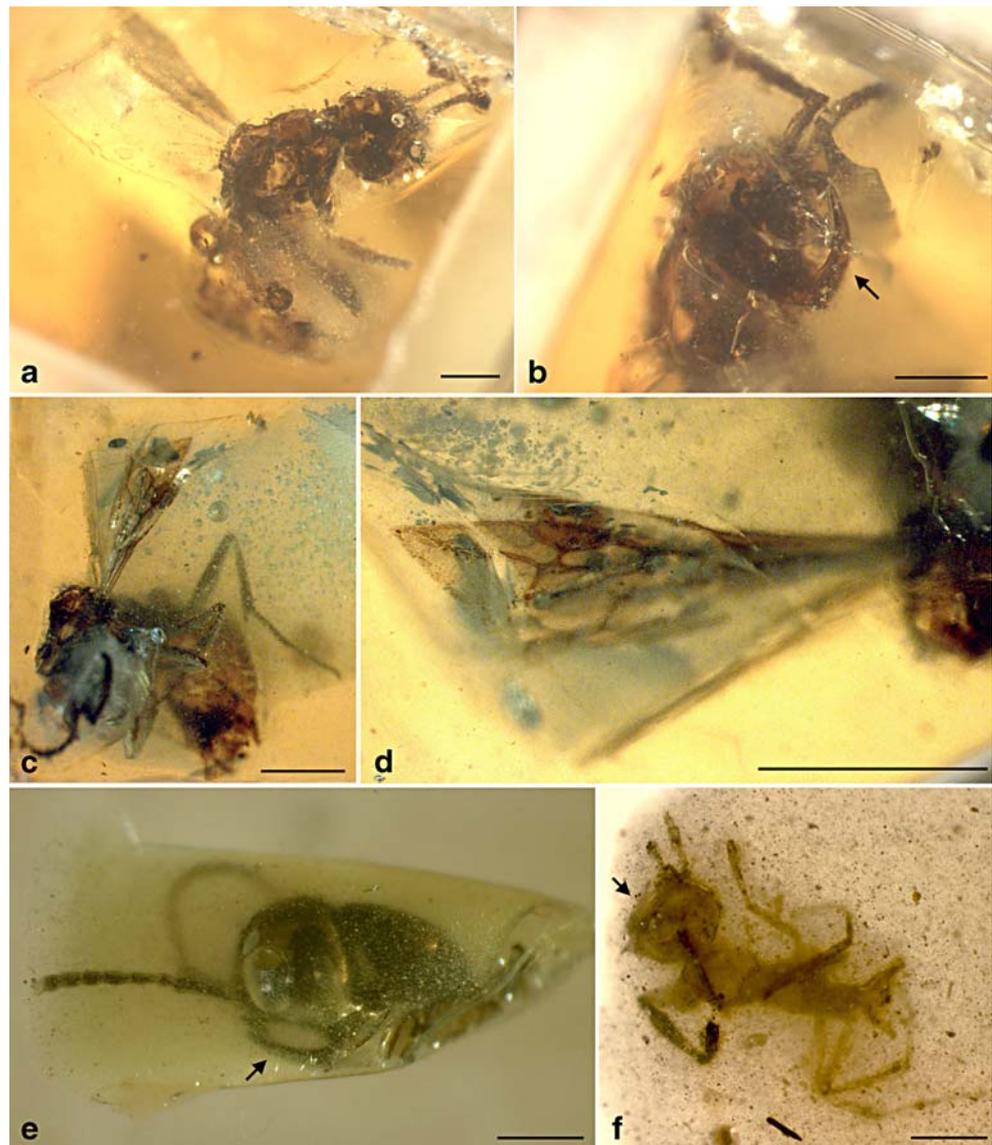
*Etymology* After the resemblance of the mandibles to the tusks of a mammoth.

*Description* Holotype gyne (Figs. 1a–d, 2a–d). Head with large eyes; two visible ocelli; frons hardly visible but frontal carina apparently absent; clypeus concave in lateral view, forming angle with frons, without visible setae; genae very large; mandibles strongly developed, L-shaped in lateral view, dorsally elbowed at right angle, with acute tip and small outer tooth at elbow; maxillary/labial palps only partly visible, with at least four/two segments respectively; antennae geniculate, with 12 segments; scape rather long and thick, not reaching occipital border when folded backward, with a distinct inner apical lobe; funicular segments of equal length.

Mesosoma narrow, elongated, bare; cuticle nearly smooth; anterior margin of pronotum forming elongate neck; suture between pronotum and mesoscutum distinct; propodeum in lateral view elongate, with rather high anterior edge; metathoracic/propodeal spiracles, propodeal lobes, metapleural gland orifices not detected by preservation. Legs: all long; tarsal claws with extra tooth; tibial spur formula 1/2/2; mid and hind legs with major tibial spur finely pectinate, that of foreleg corresponding to setose notch at base of tarsus. Fore wing hyaline; pterostigma broad; cells [1R1], [2R1], [1Rs], [1M] closed but cell [2Rs] distally open; vein 2r–m just distal of vein r–rs. Hind wing poorly preserved.

*Metasoma* Petiole with short anterior peduncle and strong node, well separated from gaster by a narrow articulation; presence/absence of tergo-sternal fusion not determinable by preservation. Gaster globose, with slight but distinct constriction between third and fourth abdominal segments; spiracles not detected by preservation; distal part of sting visible.

**Fig. 1** Photomicrographs of *Haidomyrmodes mammothus* gen. and sp. n. **a–d** Holotype specimen MNHN ARC 50.2; **b** head in ventral view; **d** forewing; **e** paratype specimen MNHN ARC 242, head and prothorax in left lateral view; **f** paratype specimen MNHN AIX 1.2, in dorsal view. *Arrows* indicate the mandibles. Scale bars represent 0.5 mm

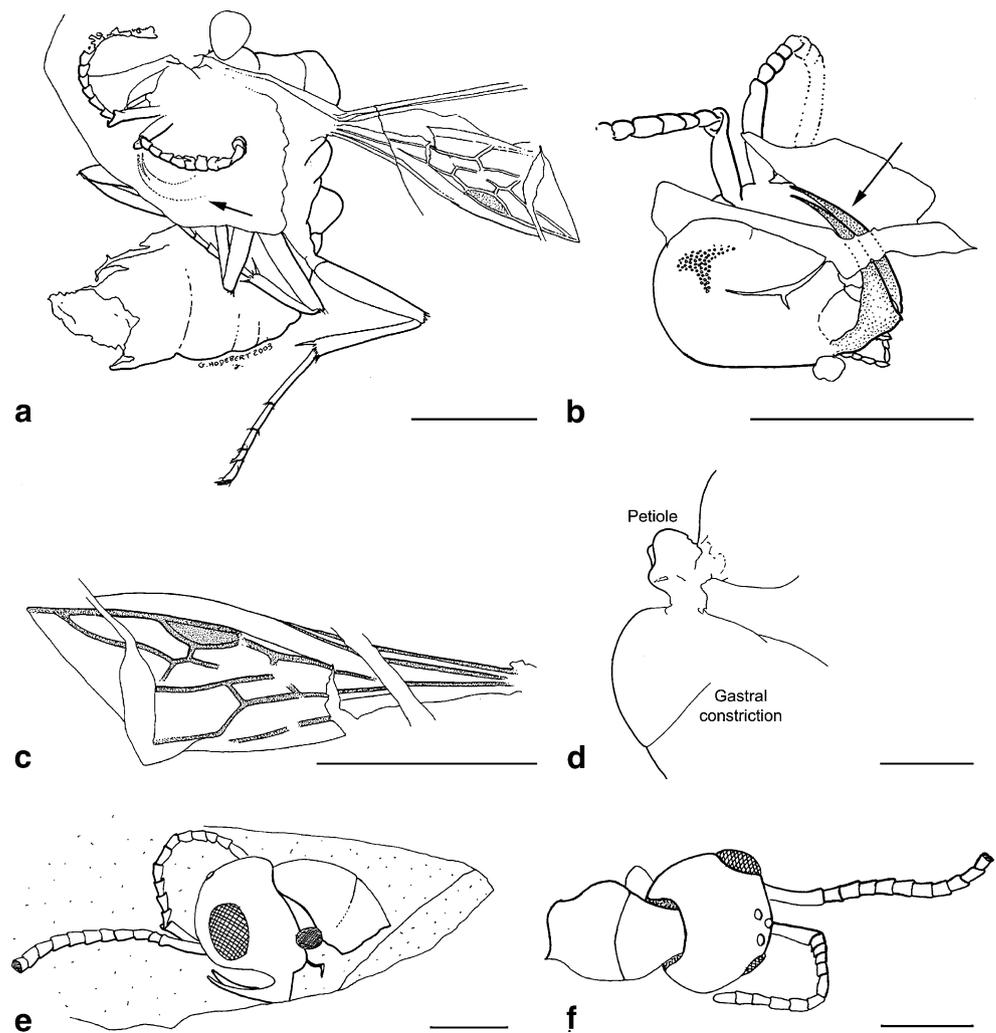


Paratype specimens (workers, see “Discussion” Figs. 1e–f and 2e–f). They differ from the holotype specimen by their smaller size and the following characters: clypeus with two rather long setae (ARC 242); part of mandible basal of elbow shorter; basal part of masticatory margin of mandibles with distinct carina, basal of elbow; antennae shorter.

*Measurements (in mm)* For [holotype], paratypes {ARC 242} and [AIX 1.2], respectively: total length of body [about 3.7]; head length (excluding mandibles) [0.85] {0.75} |0.70|, width [0.90] {0.80}, height [0.65] {0.58}; eyes length {0.34} |0.32|, width {0.20}, ratio eye length/head length {0.45} |about 0.4|; length of parts of mandible basal/distal of elbow [0.30/0.75] {0.18/0.50} |about 0.1/0.40|; antenna length [2.37] {1.40}; scape length [0.50] {0.37} |0.37|, width [0.10] {0.08} |0.09|, scape length/scape

width [5] {4.62} |4.11|; scape index (scape length/head width) [0.55] {0.46}; funiculus length [1.87] {1.10} (all segments [0.17] {0.10}, preserved segment [0.09]); ratio (scape length/funiculus length)=[0.27] {0.33}; indice (scape length/antenna length)=[0.21] {0.26}; mesosoma length [about 1.5] |1.35|; pronotum length [0.30] {about 0.3} |0.40|. Legs: fore femur [0.80], tibia [0.70], tarsi [0.60]; mid femur [0.95], tibia [0.55], basitarsomere [0.40], tarsi 2–5 [0.50]; hind femur [1.0], tibia [0.85], basitarsomere [0.60], tarsi 2–5 [0.65]; length of fore wing [2.35], width [0.75]; pterostigma length [0.35], width [0.01]; cell [1M] [0.25] long, [0.10] wide; cell [1R1] [0.50] long, [0.12] wide; cell [2R1] [0.60] long, [0.25] wide; length of hind wing [about 1.4], width [0.60]; length of petiolar segment [0.40] |0.30|, petiolar node [0.25] high, [0.30] |0.25| wide; length of gaster [about 1.85] |0.25 visible|, maximum width [1.0]; length of visible part of sting [0.25].

**Fig. 2** Line drawings of *Haidomyrmodes mammuthus* gen. and sp. n. **a–d** Holotype specimen MNHN ARC 50.2. **a** General habitus; **b** head in right lateral view, showing the antennal scapes and mandibles; **c** forewing; **d** petiole in right dorso-lateral view; **e–f** paratype specimen MNHN ARC 242 in left lateral and dorsal views. *Arrows* indicate the mandibles. *Scale bars* represent 0.5 mm



**Comments** The attribution of the three type specimens to the same species is based on their very particular mandibles and head shape, the presence of ocelli, and the eye size. Engel and Grimaldi (2005) suggested that the position of mandibles as preserved in *Haidomyrmex* results from post-mortem damage. If such was the case for this genus and the new specimens described in this paper, it is logical that some cracks or folds would therefore be visible at the level of distortion (i.e., at elbow). However, there is no trace of such distortion in the mandibles of the three new specimens, and their position as preserved in three distinct amber pieces is identical. Thus, the observed position is very unlikely to have resulted from post-mortem damage but merely corresponds to their original position. The only differences between the holotype and paratypes of *Haidomyrmodes* are observed in the length of their antennae and the basal parts of their mandibles. Although partially preserved, the paratypes are very unlikely to be males because they possess specialized mandibles identical to those of the gyne, although slightly smaller. In modern ants having females with highly modified mandibles (e.g.,

Dacetini, *Polyergus*, *Odontomachus*, *Harpegnathos*), it is observed that male mandibles are always more acutely reduced and their shape simpler (Hölldobler and Wilson 1990). Moreover, the paratypes are wingless and have 12-segmented antennae, whereas nearly all males of modern and fossil ants are winged and have 13-segmented antennae. Given that *Haidomyrmex* and *Haidomyrmodes* are primitive ants, some doubts could remain about the value of this actualistic biological inference (Nel 1997). Nevertheless, in our purposes in this study and in the related paper (Perrichot et al. 2007), the paratype specimens are considered as workers.

*Haidomyrmodes* is closely related to *Haidomyrmex* by the following characters: mandibles with highly specialized shape (unique synapomorphy); genae long; clypeus with two rather long setae; tarsal claws with basal tooth; petiolar segment with short peduncle and strong node dorsally convex (Dlussky 1996). Nevertheless, we consider that they correspond to two distinct genera based on the characters given in the generic diagnosis.

Dlussky (1996) tentatively placed the genus *Haidomyrmex* within the Sphecomyrminae based on the following plesiomorphies: scape and pedicel short (see Wilson et al. 1967: Fig. 2). Grimaldi et al. (1997) discussed the attribution to this subfamily because of the absence of ocelli, the head shape and the scape, which is distinctly shorter than that of other Cretaceous sphecomyrmines. As seen above, at least two castes of *Haidomyrmodes* have ocelli and a rather long scape. Dlussky's (1996) placement of *Haidomyrmex* was followed by Bolton (2003: 74, 261) and Engel and Grimaldi (2005), although the latter note similarities of *Haidomyrmex* with the Cretaceous genus *Brownimecia*. *Haidomyrmodes* differs from this genus in having ocelli and distinctly larger eyes. In addition, *Haidomyrmodes* has a high petiolar node, a long scape and a long pedicel. This could argue against its placement and consequently that of *Haidomyrmex* and the tribe Haidomyrmecini, within the Sphecomyrminae (see the diagnosis of the subfamily by Grimaldi et al. 1997: 7–8; Bolton 2003: 74). As the tribe shares only plesiomorphies and no known synapomorphy with the Sphecomyrminae, its attribution to this subfamily is therefore not very well supported. Representatives of the modern dorylomorph and poneromorph subfamilies have a more or less pronounced constriction between the second and third abdominal segments, in some cases similar to that of *Haidomyrmodes*, viz. the doryline *Dorylus* sp. (Bolton 1995: Fig. 60). Such a girdling constriction corresponds to the differentiation of a presclerite on the fourth abdominal segment and it is sometimes variously reduced, as in *Odontomachus* and *Thaumatomyrmex* (Bolton 2003). They also have an apparent, well-developed sting. *Haidomyrmodes* shares a pectinate tibial spur on hind legs with Formicinae, Dolichoderinae, and some Ponerinae (Brothers 1975; Hölldobler and Wilson 1990). However, without further evidence for assignment to any of these subfamilies, we prefer to maintain the current position of the Haidomyrmecini within the Sphecomyrminae.

Tribe Sphecomyrmini sensu Bolton, 2003

Genus *Sphecomyrmodes* Engel and Grimaldi 2005

*Sphecomyrmodes* Engel and Grimaldi 2005: 5. Type species: *S. orientalis* Engel and Grimaldi 2005, by monotypic and original designation. Other species: *S. occidentalis* sp. n. (Figs. 3 and 4).

**Material** Two nearly complete worker specimens, references MNHN FRS 4.4 (holotype) and MNHN FRS 4.3 (paratype), initially preserved in a same piece of amber, now separated into two pieces each embedded in Canada balsam for study. Deposited in the department of Earth History, National Museum of Natural History, Paris, France.



**Fig. 3** *Sphecomyrmodes occidentalis* sp. n., photomicrographs of specimens preserved in Early Cenomanian amber from Fouras, SW France. Scale bars represent 0.5 mm. **a** Holotype specimen MNHN FRS 4.4; **b** paratype specimen MNHN FRS 4.3

**Locality deposit** Fouras, Charente-Maritime, France.

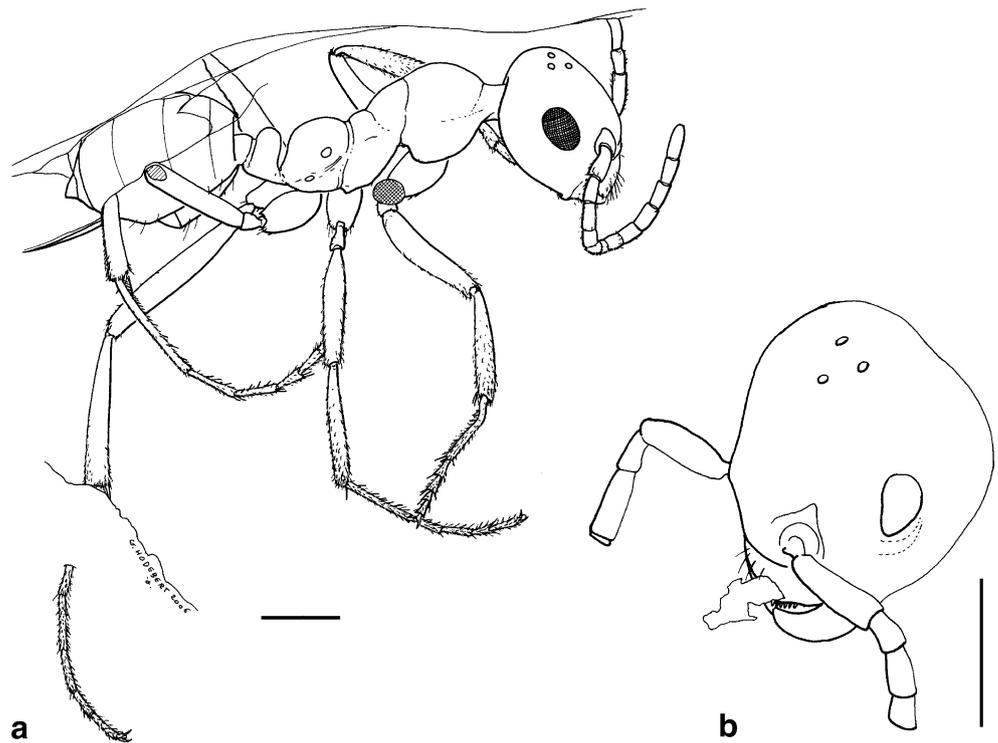
**Stratigraphic horizon** Upper Cretaceous, Lower Cenomanian (Néraudeau et al. 2003).

**Etymology** The specific name is the Latin word *occidentalis*, meaning “of the west” and is given in opposition to the Burmese type species *S. orientalis*.

**Description** Head smooth; eyes well developed; ocelli small, disposed back to posterior margin of eyes; clypeus without medial extension but with minute, peglike denticles running along entirety of anterior margin, with surface slightly setose; mandible with two teeth, without setae on outer surface. Antenna with small scape; pedicel shortest antennal segment, second funicular segment (fall) longest of funiculus.

Mesosoma entirely smooth and glabrous; metapleural gland orifice present; coxae large, ventrally setose; meta-

**Fig. 4** *Sphecomyrmodes occidentalis* sp. n., preserved in Early Cenomanian amber from Fouras, SW France. Scale bars represent 0.5 mm. **a** Holotype specimen MNHN FRS 4.4, line drawing of the general habitus; **b** paratype specimen MNHN FRS 4.3, details of clypeal margin and mandibles



notal constriction well impressed; foreleg with basitarsomere basally curved, longer than combined lengths of more distal tarsomeres, with three pairs of apical strong setae; strigil (antennal cleaner) well developed; protarsomeres II–IV each with two pairs of apical strong setae; protibial apex with two short and one long spinelike setae; tarsal claws with minute subapical tooth.

*Metasoma* Attachment of petiole to propodeum narrow, with thickness (measured in lateral view) of anterior end of petiolar peduncle  $0.3\times$  greatest depth of propodeum; petiole slightly higher than long; gaster smooth; long, curved sting.

*Measurements (in mm)* Body length 3.84; head length (with mandibles closed) 0.99; eyes length/width 0.30/0.22; length of antennal segments: scape 0.25, pedicel 0.14, faII 0.22, faIII 0.12, faIV 0.12, faV 0.12, faVI 0.12, faVII 0.14, faVIII 0.16, faIX 0.16, faX 0.16, faXI 0.20. Mesosoma length 1.42; petiole length 0.31; petiole height 0.38; gaster length 1.18; length of visible part of sting 0.62.

*Comments* These two worker ants are nearly identical to the Burmese type specimen of *Sphecomyrmodes orientalis*, but the metasoma of the latter is too damaged for accurate morphometric comparisons of the petiole and gaster. Indeed, antennae and legs are the only structures that are well preserved enough. The French specimens are assigned to a distinct species based on the following species-level

differences: faII shorter; mandibles bare on outer surface; protarsomeres II–III with two pairs of apical stiff setae on ventral surface instead of three; hind legs with combined lengths of tarsomeres II–IV longer than length of tarsomere I; petiole slightly higher than long.

## Conclusion

The ant systematics has remained in a state of flux until recently (Brothers 1975, 1999; Taylor 1978; Bolton 1990a, b, 2003; Ward 1990; Baroni Urbani et al. 1992; Shattuck 1992; Brothers and Carpenter 1993; Grimaldi et al. 1997; Ohnishi et al. 2003; Ward and Brady 2003; Astruc et al. 2004; Saux et al. 2004; Ouellette et al. 2006). However, new results recently reported by Brady et al. (2006) and Moreau et al. (2006) now support the monophyly of most of the subfamilies and clarify their relationships, although they still disagree in some important aspects (see Crozier 2006). However, as an extinct subfamily of still conflicting systematic assignment, the Sphecomyrminae is not considered in these molecular phylogenies. Further sphecomyrmines displaying a larger set of characters have yet to be discovered, as such a phylogenetic work would require the combined analyses of both molecular and morphological characters, including the earliest known fossils.

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