

A new species of the Cretaceous ant *Zigrasimecia* based on the worker caste reveals placement of the genus in the Sphecomyrminae (Hymenoptera: Formicidae)

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Abstract

Zigrasimecia ferox sp.n. is described and illustrated based on workers fossilized in 99 million-year-old Burmese amber. The new specimens allow the confident assignment of *Zigrasimecia* BARDEN & GRIMALDI, 2013, a genus recently described based upon a gyne from the same amber deposit, to the extinct subfamily Sphecomyrminae, and more specifically to the tribe Sphecomyrmini.

Key words: Stem-group ants, Formicidae, Sphecomyrmini, amber, Myanmar, Cenomanian.

Myrmecol. News 19: 165-169

ISSN 1994-4136 (print), ISSN 1997-3500 (online)

Received 16 July 2013; revision received 10 October 2013; accepted 24 October 2013

Subject Editor: Herbert Zettel

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Introduction

Ants are a rare component of the Cretaceous paleoentomofauna. Since the first description of *Sphecomyrma*, from 92 million-year-old (Myo) New Jersey amber, 46 years ago by WILSON & al. (1967), only a few other Cretaceous ants have been discovered totalling no more than 28 species described in 22 genera (LAPOLLA & al. 2013: tab. 1; with addition of BARDEN & GRIMALDI 2013, MCKELLAR & al. 2013a, b). More than half of these species were described in the last decade (DLUSSKY & al. 2004, NEL & al. 2004, ENGEL & GRIMALDI 2005, PERRICHOT & al. 2008, BARDEN & GRIMALDI 2012, 2013, MCKELLAR & al. 2013a, b), reflecting the renewed interest in paleontological research on the origins of ants.

The greatest diversity of Cretaceous ants occurs in amber from Myanmar (ca. 99 Myo) and Canada (79 Myo). The latter is the only deposit revealing potential crown-group ants in the Aneuretinae, Dolichoderinae, and Ectatomminae, though the exact affinities of these fossils are still debated (DLUSSKY 1999, ENGEL & GRIMALDI 2005, MCKELLAR & al. 2013a). Most of the ants found in Burmese amber belong in the Sphecomyrminae, an exclusively Cretaceous and yet enigmatic subfamily, but a couple of fossils cannot be assigned to any extant or extinct subfamily. Among these, the latest contribution made recently by BARDEN & GRIMALDI (2013) depicted the gyne of *Zigrasimecia*, a new genus of highly specialized ants that they could not assign to any of the known subfamilies. Instead, they suggested possible affinities with the genera *Sphecomyrmodes* ENGEL & GRIMALDI, 2005 (Sphecomyrminae) and *Gerontiformica* NEL & PERRAULT, 2004 (subfamily incertae sedis). I was astonished when *Zigrasimecia* was published earlier this year, because at the same time I was completing a manuscript dealing with the description of a very similar morphotype, although from the worker

caste. Owing to the few occurrences of Cretaceous ants, this is a very rare case of concurrent and synchronous research work based on material from the same fossil deposit. I provide herein the supplemental description and illustration of the worker caste of *Zigrasimecia*, with the description of a new species, and a further discussion on its affinities within the Formicidae.

Material and methods

The present study comprises six new specimens originally preserved in two pieces of burmite, the Cretaceous amber from the State of Kachin in northern Myanmar. These were obtained at a mine near Tanai village, in the Hukawng Valley. A radiometric age of 98.79 ± 0.62 Ma (earliest Cenomanian) was recently established for burmite using U-Pb dating of zircons contained in volcanic rock clasts from the surrounding sediment (SHI & al. 2012).

Three complete worker specimens as well as fragments of two other workers (nine legs and two gastral apices preserved at surface of amber, revealing internal structures) were preserved within a piece of clear yellow amber along with four midges (Nematocera), one wasp (Platygastridae), two cockroaches (Blattaria), and eight mites (Acari). The presence of these syninclusions as well as organic debris made the detailed observation of each specimen difficult, so the piece has been cut into three parts then polished on all sides, with two complete and two fragmentary ants now in one small block and one complete ant in another block. A sixth, fragmentary (only the head and mesosoma preserved) specimen was found in another piece of clear yellow amber, with five workers of *Sphecomyrmodes orientalis* ENGEL & GRIMALDI, 2005 as syninclusions. All material is in the private collection of Jens-Wilhelm Janzen (Germany) but should be ultimately purchased by an academic institution.



Figs. 1 - 4: Photographs of worker specimens of *Zigrasimecia ferox* sp.n. (1) Paratype JWJ-Bu17, profile view. (2) Paratype JWJ-Bu17, dorsal view. (3) Holotype JWJ-Bu18a, profile view. (4) Paratype JWJ-Bu18b, profile view.

The fossils were examined under incident and transmitted light using a Leica MZ APO stereomicroscope, and imaged with the aid of an attached Canon 5D Mark II camera. Stacks of photographs taken at different depths of field were merged using HeliconFocus 5.2 software. Photographs and final repository data will be available on AntWeb (<http://www.antweb.org>). Measurements were taken at 63× and 80× magnification using a dual-axis micrometer.

Systematic paleontology

Sphecomyrminae WILSON & BROWN, 1967

Sphecomyrmini WILSON & BROWN, 1967

Zigrasimecia BARDEN & GRIMALDI, 2013

Supplemental diagnosis, worker: Small wingless females of varied body length (2.0 - 2.8 mm) without remarkable cuticular sculpturing. Head very similar to that of gyne (see BARDEN & GRIMALDI, 2013) but without ocelli and without rugose patches on vertex; with toruli ring-like, not raised; with a single row of clypeal denticles (i.e., no rows of subclypeal combs); with vertexal (posterodorsal) margin strongly concave. Mesosoma entirely smooth, without distinctive spine, foveae, or carinae; promesonotal suture indistinct, in profile view dorsal mesosomal surface a continuous curve; posterior (declivous) propodeal surface distinctly concave, high, strongly angled with dorsal pro-

pedeal surface; bulla hemispherical. All legs with femur and tibia dorso-ventrally flattened, tibiae carinate anteriorly and posteriorly; tibial spur formula 3 - 2 - 2. Petiole consists of high scale strongly inclined posteriorly, with anterior surface flat, posterior surface convex and nearly half as tall; subpetiolar process present, in profile view a moderately high, short longitudinal lamella pointing antero-ventrally. Gaster with five visible segments (abdominal segments AIII-AVII); tergite of AIII with anterior surface vertical, sternite of AIII anteriorly with large medial longitudinal flange protruding underneath helcium; tergite IV largest abdominal sclerite; sting large, retractable, external part basally enclosed by gonostyli.

Zigrasimecia ferox sp.n. (Figs. 1 - 10)

Type material: Holotype JWJ-Bu18a, paratypes JWJ-Bu17, JWJ-Bu18b, three complete workers; paratypes JWJ-Bu18c and JWJ-Bu18d, two partial workers preserved by legs and gastral apices; paratype JWJ-Bu23, a partial worker missing the metasoma. In amber from early Late Cretaceous (Earliest Cenomanian, 98.79 ± 0.62 Ma) of Hukawng Valley, Kachin State, northern Myanmar. Provisionally in J.-W. Janzen collection.

Diagnosis, worker: As for the genus.

Description: Head broad, crescent-shaped in dorsal view, with frons strongly convex and vertexal (posterodorsal) margin strongly and regularly concave. In full-face view the anterior clypeal margin broad, concave; sides con-

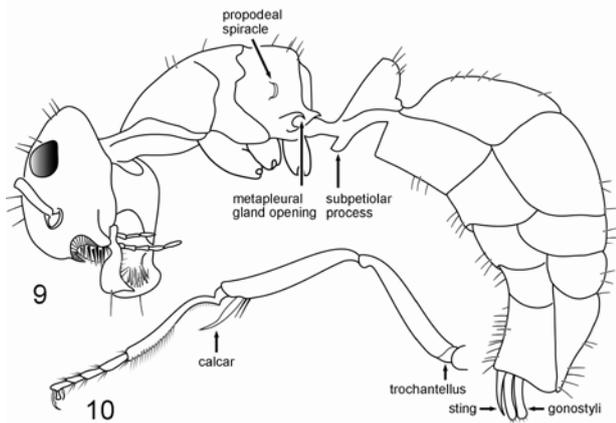


Figs. 5 - 8: Photographs of worker specimens of *Zigrasimecia ferox* sp.n. (5) Holotype JWW-Bu18a, full-face view. (6) Paratype JWW-Bu18b, full-face view. (7) Holotype JWW-Bu18a, close-up of the mouthparts. (8) paratype JWW-Bu18c, detail of gaster preserved at amber surface, showing the sting apparatus. Abbreviations: cd, clypeal denticles; go, gonostyli; fl, hypostomal flange; ls, labral spicules; ms, mandibular spicules; sb, sting bulb; st, sting shaft.

vex, with small protruding eyes located posteriorly to mid-length of head; posterior corners broadly rounded; base of mandibles concealed by large anterior genal expansion (hypostomal flange). Clypeus shallow, transverse, 8× wider than high; anterior clypeal margin entirely lined with 48 contiguous denticles decreasing in length laterally; denticles peg-shaped, with rounded apices. Labrum covered with dense brush of spine-like setae arranged in three transverse rows; each row with approximately 20 setae stouter (about twice as broad basally) and increasingly longer (2× longer in row immediately ventral to clypeus, 3× longer in third row) than clypeal denticles, tapered. Mandibles barely overlapping medially, with one large apical tooth and one smaller subapical tooth; outside surface with one long decumbent seta medially; oral surface covered with dense brush of stiff, sharp, spicule-like setae, inner setae 4× longer than outer setae. Palps very short, maxillary palps with five segments, labial palps apparently with three segments. Frontal carinae absent. Antennae well-separated; toruli not significantly raised, ring-like, directed laterad; antennal scrobes shallow, projecting outward laterally from bases of antennae to ventral margin of eyes; antenna with 12 antennomeres: scape short, barely twice as long as pedicel, third and last antennomeres longest flagellar articles.

Mesosoma at most half as broad as head in dorsal view. Neck long. Junction of mesoscutellum and dorsal surface

of propodeum mostly indistinct, only slightly angled on specimens JWW-Bu18a and JWW-Bu23 (where dorsal propodeal surface is short, about 0.25× length of mesosoma excluding neck); posterior margin of propodeal dorsum distinctly concave. In profile view, propleuron well developed; mesopleuron fully separated from the rest of the mesosoma by distinct sulci, distinctly higher than long. Propodeum high, declivity steep; propodeal spiracle slit-like, facing posteriad, located around midpoint of propodeal sides; metapleural gland opening semicircular, facing posteroventrad; metapleural bulla developed, roughly hemispherical. Legs: all femora and tibiae dorso-ventrally flattened, tibiae with anterior and posterior margins bordered by a carina; small trochantellus present on all legs; foreleg with patch of dense, elongate setae on ventral surface of tibia (apically) and basitarsomere (entire length following strigil); protibia with three spurs apically on ventral margin, large one ("calcar") gently curved, with minute setae apically, two other ones about half as long as calcar, straight and simple; protarsomere I with "antennal cleaner" (strigil) a velvety notch proximally on ventral margin; tarsomeres I - IV of all legs with two pairs of stiff setae apically on ventral surface; mesotibial apex with two simple spurs straight and subequal in length; metatibial apex with one large pectinate spur gently curved apically and one small, straight and simple spur; pretarsal claws with minute subapical tooth.



Figs. 9 - 10: Drawings of holotype of *Zigrasimecia ferox* sp.n. (9) Habitus without legs in profile view. (10) Left foreleg in dorsal view.

Gastral segments sometimes telescoped, with apparent small constriction between segments I and II (AIII - AIV) likely an artefact of preservation; anterior flange of sternite of AIII lamellar, with anterior and ventral margins straight and right angled. Sting long but largely internalized, stout, slightly upcurved apically, externalized part basally enclosed by sting sheaths (gonostyli); sting bulb (visible on two fragmentary specimens with mesosoma "opened" by the polishing of the amber surface) large.

Integument minutely rugose throughout except legs and gaster smooth; dorsofrontal portion of head and dorsal surfaces of mesosoma, petiole, and gaster sparsely covered by fine erect hairs; slightly longer and decumbent hairs present ventrally on mesosoma and gaster; apical segment of gaster more densely setose, with longer decumbent hairs.

Measurements (in millimetres) for smallest (paratype JWJ-Bu17) and largest (holotype JWJ-Bu18a, in brackets, {}) specimens: body length 2.00 {2.80}; head length (from vertex to clypeal margin) 0.52 {0.66}, width (excluding eyes) 0.56 {0.70}; maximum diameter of eye 0.15; length of antennomeres: scape 0.19 {0.27}, pedicel 0.10 {0.12}, flagellomeres I - X 0.12, 0.10, 0.09, 0.09, 0.08, 0.06, 0.06, 0.06, 0.05, 0.12 {0.19, 0.14, 0.12, 0.12, 0.12, 0.12, 0.11, 0.11, 0.11, 0.19}, respectively; mesosomal length 0.66 {0.87}, maximum width 0.30; petiole length 0.21 {0.36}, height (including subpetiolar process) 0.33 {0.41}; gastral length (excluding sting) 0.82 {1.36}.

Etymology: The specific epithet is taken from the Latin word *ferox*, meaning "fierce", and refers to the head appearance of this ant.

Discussion

The new worker specimens are attributed to *Zigrasimecia* based on the similar, very peculiar head, particularly the unique structures of the mouthparts with clypeal denticles, labral and mandibular spine-like setae, and large hypostomal flange (the latter is absent in figure 2c of BARDEN & GRIMALDI (2013), but is visible in figure 1c). Both morphotypes also have the mandibles, antennae, pronotal neck, propodeal spiracle, propodeum, and petiole of similar shape (though the subpetiolar process was not seen in the gyne of *Z. tonsora*, but this may be a matter of observation – see BARDEN & GRIMALDI 2013: fig. 2a, the anteroventral

part of petiole is hidden by right metacoxa). However, the workers differ from the gyne of *Z. tonsora* by the following features, regarded here as species-specific: clypeal margin with more peg-like denticles (48 as opposed to 30 in *Z. tonsora*), denticles decreasing in size laterally (as opposed to subequal in length); labral spicules apparently stouter; mandibular spicules apparently longer; absence of V-shaped groove above clypeus; toruli not raised; antenna with scape and apical flagellomere relatively longer (scape index SI = scape length / head width: 34 - 38 as opposed to 29 in *Z. tonsora*; flagellomere X as long as flagellomere I in *Z. ferox* sp.n., as long as flagellomere II in *Z. tonsora*); legs with femora and tibiae flattened, tibiae carinate; propodeal dorsum without median concavity. The absence of ocelli and head rugosities, and the simplified mesosoma without suture or foveae may be regarded as differences of conspecific castes, with alate specimens having larger mesosomal segments due to flight muscles. But what we know of Cretaceous ant castes so far and basal ant lineages today (e.g., Leptanillinae and poneromorph subfamilies), merely suggests the new specimens represent workers of a distinct species. For example, in *Haidomyrmodes* PERRICHOT & al., 2008, workers and gyne identified as conspecific vary mostly in size but are otherwise remarkably similar in their components, with ocelli and same mesosomal sutures or foveae present in both castes. In the present case, the worker specimens vary quite significantly from the described gyne of *Z. tonsora*, and are thus considered a closely related but distinct species.

BARDEN & GRIMALDI (2013) were equivocal on the exact placement of *Zigrasimecia*, as they suggested affinities with the Sphecomyrminae but without formally assigning it to this subfamily. Instead, they emphasized a close relationship with the sphecomyrmine genus *Sphecomyrmodes* and the enigmatic genus *Gerontoformica*, which both possess a similar row of stout, peg-like setae along the anterior clypeal margin. Another similarity with *Gerontoformica* pointed out by these authors would include the presence of peg-like setae on the labrum. But I have re-examined the type of *Gerontoformica cretacica* and there are no such labral setae: apparently these features were erroneously reported in the original account by NEL & al. (2004). Recently, I also discovered an additional, partial specimen of *Gerontoformica* which provides strong support for the placement of this genus within the Sphecomyrminae (Vincent Perrichot, unpubl.). Therefore, there is little doubt that *Zigrasimecia* also belongs in the Sphecomyrminae, and more specifically, the tribe Sphecomyrmini. With respect to the Sphecomyrminae, it possesses most of the worker characteristics given by BOLTON (2003), viz. the antennae are geniculate and with relatively short antennal scapes, the funiculus is filiform, the propodeal lobes are absent, the mesotibia and metatibia each bear two spurs, the pretarsal claws have a preapical tooth, the petiole is nodiform with a short anterior peduncle, and a distinct sting is present. Assignment of *Zigrasimecia* to the tribe Sphecomyrmini is also supported by the female mandible with only two teeth, the antennal segment III elongate, and the anterior surface of AIII vertical. Another diagnostic feature of the tribe as proposed by BOLTON (2003) was the presence of ocelli, a character missing in workers of *Zigrasimecia*, but this is also variable among genera of the other tribe Haidomyrmecini (e.g., ocelli present in workers of

Haidomyrmodes, but absent in workers of *Haidoterminus* MCKELLAR, GLASIER & ENGEL, 2013, and *Haidomyrmex* DLUSSKY, 1996). The dorsal surface of the mesosoma being continuously curved is a unique feature among Sphecomyrminae and even among Cretaceous ants, strikingly similar to what is seen in the Formicinae with the genus *Camponotus* MAYR, 1861. But contrary to *Camponotus*, the promesonotal suture is indistinct in *Zigrasimecia*. Finally, the protibiae with three spurs and gonostyli apically externalized are unique characters not seen in any extinct or modern ant so far, thus with potential phylogenetic value.

The simultaneous presence of a partial specimen of *Zigrasimecia* and several workers of *Sphecomyrmodes* in a same piece of amber demonstrates that these two genera were present at exactly the same time, ruling out the diachronism that is always a minor concern with amber deposits. It also suggests that both taxa shared at least a part of their ecological niche, and even possibly fought against each other. Burmese amber provides some of the earliest known ants, yet with a surprising diversity for the time. Sphecomyrmines remain the most enigmatic of these early ants, as they display a wide array of specialized morphologies, and any new discovery challenges the definition and monophyly of this subfamily.

Acknowledgements

I am grateful to Jens-Wilhelm Janzen (Seevetal, Germany) who made possible the study of these ant specimens from his collection. Comments by Ryan McKellar and two other anonymous reviewers significantly improved this manuscript. This work was partly supported by the program Interrvie (research project NOVAMBRE 2 to D. Néraudeau, Univ. Rennes 1) from the French National Institute for Universe Sciences (CNRS-INSU).

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