



Two new iron maiden ants from Burmese amber (Hymenoptera: Formicidae: †Zigrasimeciini)

Huijia CAO*, Brendon E. BOUDINOT*, Zhen WANG, Xiaofeng MIAO, Chungkun SHIH, Dong REN & Taiping GAO

Abstract

†*Zigrasimecia* BARDEN & GRIMALDI, 2013 is easily identified among the total diversity of the Formicidae by the unique form of the mandibles, presence of an antennal scrobe, and the massive, blocky cranium. Two species from mid-Cretaceous Burmese (Myanmar) amber are currently attributed to the genus, one is a dealate gyne and the other a worker. Herein, we describe two new species from Burmese amber based on workers: †*Zigrasimecia hoelldobleri* **sp.n.** and †*Protozigrasimecia chauli* **gen.n. sp.n.**, which display a suite of plesiomorphies which are retained relative to †*Zigrasimecia*. We also illustrate and provide a descriptive sketch of an unplaced alate. With the new morphological characters from the two new taxa, we provide a key to the genera of the †Zigrasimeciini. The remarkable preservation of †*Z. hoelldobleri* **sp.n.** sheds considerable light on the functional morphology of zigrasimeciine mouthparts. Due to the ferocious function of the mouthparts of †*Zigrasimecia* and †*Protozigrasimecia*, we colloquially dub these the iron maiden ants. Furthermore, we discuss wing venation of Mesozoic Formicidae and evolution of mesosomal form. Our work constitutes a contribution to a better understanding of the Mesozoic Formicidae and documents diversity for the phylogeny of the family.

Key words: Stem ants, alate gyne, mandibles, labrum, Cretaceous.

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Huijia Cao, Zhen Wang, Xiaofeng Miao, Chungkun Shih, Dong Ren (contact author) & Taiping Gao (contact author), College of Life Sciences and Academy for Multidisciplinary Studies, Capital Normal University, 105 Xisanhuanbeilu, Haidian District, Beijing 100048, China. E-mails: rendong@mail.cnu.edu.cn; tpgao@cnu.edu.cn

Brendon E. Boudinot, Department of Entomology & Nematology, University of California, Davis, CA 95616, USA.

Chungkun Shih, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013-7012, USA.

*These authors contributed equally to this work

Introduction

The earliest confirmed fossil ants are dated to the Albian-Cenomanian turnover of the Early Cretaceous (98.8 ± 0.6 million years ago, Mya) (PERRICHOT & al. 2008a, SHI & al. 2012, BARDEN 2017). Ants of this period, far more diverse than previously envisioned (e.g., HÖLLDOBLER & WILSON 1990), include an astonishing radiation of fierce and bizarre predators, for example, the †Haidomyrmecinae (PERRICHOT & al. 2020), and puzzling wasp-like species such as †*Camelomecia janovitzii* BARDEN & GRIMALDI, 2016. Of particular note is the variation in mouthpart structures, which occupy a considerable amount of morphospace (BARDEN & GRIMALDI 2016, PERRICHOT & al. 2016) and which indicate varying degrees of dietary spe-

cialization. These specialized mouthparts perhaps rendered the stem group ants more susceptible to extinction (BARDEN & GRIMALDI 2016), in analogy to macrofauna such as the saber-toothed cat, †*Smilodon*. Despite this diversity and increasing attention paid to Mesozoic Formicidae, the mouthpart structure and function of a particular genus, †*Zigrasimecia*, has yet to be clarified.

†*Zigrasimecia* was erected based on a single piece of Burmese (Myanmar) amber which contains a dealate gyne, designated as †*Zigrasimecia tonsora* BARDEN & GRIMALDI, 2013. The unique type specimen was only partially preserved, missing part of petiole and gaster, and details of the mouthparts were difficult to ascertain. The second

species of this genus, †*Zigrasimecia ferox* PERRICHOT, 2014, was described based on the worker caste. Numerous features are shared between †*Z. ferox* and †*Z. tonsora*, although PERRICHOT (2014: p. 168) adduced a list of specific features which distinguish the two species. The unique morphology of †*Zigrasimecia* is nowhere fully paralleled in the extant Formicidae, and is thought to represent habits that became extinct with the lineage (BARDEN & GRIMALDI 2013). †*Zigrasimecia* poses a further puzzle in its phylogenetic affinities; clearly the two described species are monophyletic due to an abundance of synapomorphies, but to which other Mesozoic ant taxa does the group relate?

To provide insight into the question of mouthpart anatomy and function, and to inform the phylogenetic position of †*Zigrasimecia*, we contribute two new taxa: †*Z. hoelldobleri* sp.n. and †*Protozigrasimecia chauli* gen.n. sp.n. The holotype of †*Z. hoelldobleri* has exceptionally well-preserved mouthparts, which allow for refined comparison between these stem ants and those of the crown. Moreover, we provide a descriptive sketch and figures of an alate gyne, which displays notable differences with †*Z. ferox*, thus expanding our knowledge of the morphological disparity of Mesozoic Formicidae. Finally, a discussion of mouthpart structure, wing venation, and mesosomal form is provided.

Material and methods

The studied material was collected from Noije Bum hill, some 18 km southwest of the Village of Tanai Village (26° 21' 33.41" N, 96° 43' 11.88" E) in the Hukawng Valley, of northern Myanmar (GRIMALDI & al. 2002, CHEN & al. 2019). The deposit is dated to 98.79 ± 0.62 Mya based on radiometric uranium-lead dating (SHI & al. 2012, LIN & al. 2019, YANG & al. 2019, GAO & al. 2019). Recently, an ammonite embedded in amber, supports the Albian-Early Cenomanian age of the amber (YU & al. 2019). The evidence of termite colonies reported from Myanmar amber recently indicate an early eusocial lifestyle, including large aggregation, cooperative brood care and overlapping generations (ZHAO & al. 2020). All the newly reported amber specimens are housed in the Key Lab of Insect Evolution and Environmental Changes, College of Life Sciences, Capital Normal University (CNU), Beijing, China. These specimens were examined under Nikon SMZ 25 microscope and imaged with a Nikon DS-Ri 2 digital camera system. Line drawings or reduction drawing were prepared using Adobe Illustrator CC and Adobe Photoshop CC graphics software.

Measurements of †*Protozigrasimecia* gen.n. were taken from photomicrographs using Adobe Illustrator CC. All measurements are provided in millimeters. The holotype of †*Zigrasimecia tonsora* was examined at the American Museum of Natural History (AMNH), New York, USA. Wing vein nomenclature follows BROWN & NUTTING (1949). Hairs which are short, stout, and in proximity of contact surfaces are termed traction setae because their location and microstructure physically increase friction, regardless of hypothetical ecological or behavioral function. The term traction seta has been used in prior works,

such as for the Ponerinae (e.g., BOLTON & FISHER 2008, SCHMIDT & SHATTUCK 2014).

Systematic palaeontology

Subfamily †Sphecomyrminae WILSON & BROWN, 1967

Tribe †Zigrasimeciini BORYSENKO, 2017

Constituent genera: †*Boltonimecia* BORYSENKO, 2017, †*Protozigrasimecia* gen.n., †*Zigrasimecia* BARDEN & GRIMALDI, 2013.

Emended diagnosis (female): Among Mesozoic Formicidae, uniquely defined by the presence of a facial scrobe for reception of scape which extends posterolaterally from antennal torulus to compound eye. †*Zigrasimecia* and †*Protozigrasimecia* gen.n. uniquely identified by the following: head massive, block-shaped, with broadly omega-shaped (Ω) occiput. These two genera additionally identified by rotation of the mandibles within their sockets (Note 1). Otherwise, the tribe shares the following states with †*Gerontoformica*: anterolateral clypeal margins lobate (albeit much expanded), covering mandibular bases; anterior clypeal margin lined by peg-like traction setae (Note 2); worker ocelli present or absent; propodeal spiracle slit-shaped (Note 3); tibial spur formula 2s,2(1p,1s) (Note 4); petiole anteriorly pedunculate and convex-nodiform or sessile / subsessile subsquamiform (latter not observed in †*Gerontoformica*); anteroventral process of petiolar sternum present (Note 5); and cinctus of abdominal segment IV, defining pre- and post-sclerites present or absent.

Note 1: The rotation of the mandibular base allows the mandibles to swing diagonally, which along the body axis is posterolateral during opening and anteromedial during closure, illustrated by Figures 1A, 1B, and 2D.

Note 2: Perioral traction setae of varying form also occur on the labrum of †*Zigrasimecia*, †*Protanilla*, †*Apo-myrrma*, †*Amblyopone*, among other taxa. Stout setae which may have a frictional function also occur on the ventral mandibular surfaces of various taxa, and are more difficult to delimit morphologically.

Note 3: All currently valid †*Gerontoformica* species were observed to have slit-shaped propodeal spiracles, except for †*G. cretacea* NEL & PERRAULT, 2004, †*G. occidentalis* PERRICHOT, NEL, NÉRAUDEAU, LACAU & GUYOT, 2008 (also see BARDEN & GRIMALDI 2016), and †*G. orientalis* (ENGEL & GRIMALDI, 2005), for which the spiracles are not visible or well-preserved enough for evaluation. Slit-shaped spiracles also occur in other stem ants, including †*Sphecomyrma freyi* WILSON & BROWN, 1967 and various †Haidomyrmecinae.

Note 4: The tibial spur formula follows BOLTON (2003). Specifically, s, simple; b, barbirulate; p, pectinate; when two spurs differ in formula, the conformation (s, b, or p) is indicated parenthetically. Despite description of Mesozoic Formicidae with two or more protibial spurs, this is a misnomer, as the calcar is the only true spur; it is attended posteriorly by one to two spur-like simple setae.

Note 5: The subpetiolar process is present in the majority of the Formicidae, and occurs in all valid, described stem ants to date.

Comments: BORYSENKO (2017) provided a list of nine characters to define the tribe †Zigrasimeciini, comprising at the time the poorly-preserved Canadian fossil taxon †*Boltonimecia* and two species of †*Zigrasimecia*. However, none of the nine characters uniquely define the tribe relative to other groups of Mesozoic Formicidae, and a number of revisions are necessitated by the discovery of †*Protozigrasimecia* **gen.n.** (genus defined below). The strongest character linking all three genera is the presence of the antennal scrobes, which is, surprisingly, unique among known stem ants, as far as their diversity is known to the present day (note that the antennal groove of †*Gerontoformica contega* (BARDEN & GRIMALDI, 2014) is not a scrobe as here used).

Borysenko's description of the cranium of †Zigrasimeciinae as "specialized, shield-like, with dorsal part thick and raised" is a mischaracterization of †*Zigrasimecia*, although it is apparently the case for †*Boltonimecia* – we do note that the preservation of the †*Boltonimecia canadensis* holotype is compromised at a gross scale due to desiccation and compression. Furthermore, Borysenko's definition of the group as having the "gastral constriction absent" is no longer valid, as †*Protozigrasimecia* has clearly defined pre- and postsclerites of abdominal segment IV. Critical reanalysis of the placement of †*Boltonimecia*, ideally with emphasis on the mandibular articulations, will be possible after the discovery and description of better-preserved material. In the meantime, we redefine the group as above, and provide a key to known generic taxa below.

Worker-based key to genera of †Zigrasimeciini

- 1 Head wedge-shaped, not omega-shaped (Ω), and not massive relative to mesosoma. Anterior clypeal margin evenly convex across its length between the anterolateral clypeal lobes. Face with shield-like dorsal thickening posterior to antennal scrobes. Face between antennae with several long, erect setae. Abdominal segment III (= metasomal II, gastral I) apparently without massive, longitudinal, keel-like prora. †***Boltonimecia***
 - Head omega-shaped (Ω), not wedge-shaped, and massive relative to mesosoma. Anterior clypeal margin evenly concave across its length between the anterolateral clypeal lobes. Face without shield-like dorsal thickening posterior to antennal scrobes. Face between antennae without several long, erect setae. Abdominal segment III with massive, longitudinal, keel-like prora. 2
- 2 Body small, total length < 5 mm. Mesosoma compact, with dorsal surface forming a single hump in profile view (a lumpy or even convexity). Promesonotal articulation completely fused. Flagellum relatively compact; fifth through terminal antennomeres with length < 3 × width. Masticatory margin of mandible with two very small denticles, or unidentate. Basal mandibular margin curving broadly to apical tooth, hence basal and masticatory margins indistinct. Median portion of cly-

peus, between lateral lobes, without traction setae except for even row along anterior clypeal margin. Labral traction setae aggressive and nail-shaped, longer than those of the anterior clypeal margin. Maxillary palps relatively short, palp length less than length of scape. Ocelli absent. Petiolar node high and squamiform, with short, poorly defined anterior peduncle. Abdominal segment IV without transverse sulcus defining pre- and postsclerites of tergum and sternum. †***Zigrasimecia***

- Body large, total length > 10 mm. Mesosoma comparatively elongate, with dorsal surface forming, approximately, a pair of humps in profile view (with convex mesonotum distinctly offset from propodeum). Promesonotal articulation well-developed, mobile. Flagellum relatively elongate; fifth through terminal antennomeres with length $\geq 4 \times$ width. Masticatory margin of mandible clearly bidentate, with two long, acute teeth. Basal mandibular margin obliquely meeting base of basal / subapical tooth, hence basal and masticatory margins clearly distinct. Median portion of clypeus, between lateral lobes, with traction setae in irregular rows in addition to even row along anterior margin. Labral traction setae relatively fine, approximately equal in size to those of the anterior clypeal margin. Maxillary palps relatively long, palp length greater than length of scape. Ocelli present. Petiolar node low and convex, with an apparently elongate anterior peduncle. Abdominal segment IV with transverse sulci (= cinctus) defining pre- and postsclerites of tergum and sternum. †***Protozigrasimecia* gen.n.**

Genus †*Zigrasimecia* BARDEN & GRIMALDI, 2013

Emended diagnosis (female): Distinguished from both †*Boltonimecia* and †*Protozigrasimecia* as outlined in the key above. Sharing uniquely with †*Protozigrasimecia* the large, dome-shaped head with deep and broadly concave occiput in posterior view, and evenly and broadly concave, arcuate clypeus. Additional definition provided by the following characters: antenna of worker and alate gyne 12-merous (see Note 5); worker body length 1.8 - 4.6 mm, gyne body length 2.7 - 4.0 mm; head massive, nearly as large as mesosoma; frontal carinae present; clypeus in form of an evenly arched transverse bar; anterior margin concave with dozens of denticulate traction setae; labrum with dense spiniform traction setae; inner surface of mandibles with traction setae distributed along their length; worker eyes small and rounded; scape at least twice length of pedicel; labrum covered with erect and strong spiniform traction setae; labrum apicomediaally bilobate; mesosoma strongly convex and anteroposteriorly compact, without external indication of segmental articulation; helcium (= articular sclerites of abdominal segment III) axial (situated at segment midheight). Gyne: most of characters similar with workers, except for the following: eyes reniform; mesoscutum and mesoscutellum demar-

cated by sulcus; mesosoma muscled for flight; forewing with seven closed cells: the costal, two submarginal, one marginal, the basal, subbasal, and first discal.

Note 6: The antennomere counts of alate †*Boltonimecia* and †*Protozigrasimecia* are unknown.

Note 7: The coronal rugosities described on the vertexal area of the holotype of †*Z. tonsora* are almost certainly artefacts derived from the taphonomic process (BEB, pers. obs., AMNH). The rugosities are asymmetrical, and similar apparent bubble streaks can be observed on other, distantly related taxa.

†*Zigrasimecia hoelldobleri* CAO, BOUDINOT & GAO sp.n.

(Fig. 1 to Fig. 3)

Etymology: The specific name is in honor of myrmecologist Dr. Bert Hölldobler, for his outstanding contributions on studying evolution and social organization in ants.

Material: Holotype: No. CNU-HYM-MA2019053, worker; Paratype: No. CNU-HYM-MA2019054, worker.

Locality and horizon: Kachin (Hukawng Valley) of northern Myanmar. The lowermost Cenomanian (near Albian boundary).

Diagnosis: Worker. **Differs from †*Zigrasimecia tonsora* as follows:** (1) apical concavity of mandible, subtending distal tooth on the external surface, less pronounced; (2) basal mandibular margin distinctly but shallowly convex along its length to the basal tooth, rather than being more-or-less linear to its apex; (3) one long seta situated on ventral mandibular margin, about 2/3 length of mandible (versus several; single seta state shared with †*Z. ferox*); (4) labral traction setae stouter; (5) clypeus with > 30 traction setae; (6) face just posterad posterior clypeal margin without paired transverse sulci; (7) body (head, mesosoma, metasoma) with more-or-less even layer of long erect setae (versus setae much shorter, stubblier); (8) propodeum without median longitudinal groove. **Differs from †*Z. ferox* as follows:** (1) numerous long erect setae present in malar space of head (versus absent); (2) scape relatively longer (SI [SL / HW] = 0.44 vs. ~ 0.29 - 0.39); (3) foretibia with single spur-like seta posterad calcar; (4) mesosoma evenly arched, propodeum without distinct dorsal and posterior faces (versus mesosoma with dorsal propodeal face angled relative to mesonotum and posterior propodeal face); and (5) body setation longer, denser. **Identification supported by the following conditions which are not necessarily unique among †*Zigrasimecia* species:** (1) entire body covered with long and erect setae; (2) body length ranging from 2.6 mm to 3.5 mm; (3) labrum bilobed, with a distinct median notch; (4) eyes small and elliptical to circular; (5) ocelli absent; (6) scape to flagellomeres I or III covered with long and erect setae; (7) antennomeres sequentially and gradually shorter toward antenna apex; (8) anterior labral margin with a row of cincinate (curved) setae; (9) mandible weakly bidentate, with two small denticles; (10) apex of subapical mandibular denticle aligning with apical

denticle; and (11) oral face of mandible with 3 rows of erect spiniform setae.

Description: Worker. Holotype No. CNU-HYM-MA2019053; Paratype, No. CNU-HYM-MA2019054, characters of paratype differing from holotype are described in brackets [].

Whole body (Fig. 1A, B) covered with long, erect setae; many of the setae clavate [pointed, setae sharp at apex (Fig. 2 A, B)]; setae denser on legs, shorter and fewer on antennal flagellum.

Head (Fig. 1C to E): broad [In lateral view, head (Fig. 2D) triangular; frons and lower face forming a plane (Fig. 2B)]. Eyes bulging. Ocelli absent. Antenna with 12 antennomeres (Fig. 2A). Scape, pedicel as well as flagellomeres I - III covered with a few erect setae on ventral surface, which is shortening in each antennomere. Frontal carinae present between antennae, extending posterolaterally from posterior clypeal margin to anteromedian eye margin, carinae forming posterior margin of short, shallow scrobe. Clypeus (Fig. 1C) curved across its length; lateralmost portions of clypeus, dorsal to mandibular insertion, expanded as disc-shaped lobes; anterior clypeal margin slightly emarginate medially; anterior clypeal margin with at least 48 [34] peg-shaped denticles arranged in a single row. Labrum (Fig. 1C) large, filling most of oral area; distalmost margin covered with a row of short, crooked setae; distal margin with median slit-like cleft; at least 30 [54] suberect spiniform setae present across labral disc; these setae somewhat cone-shaped, with the proximalmost row relatively shorter and thinner. Mandibles with three rows of stiff and spicule-like setae along basal margin; these setae of three different level lengths, the outermost row shortest and the innermost row longest (Fig. 2D); apex of subapical tooth aligning with apical tooth; both teeth of masticatory margin short, being subequal in length to clypeal traction; a single long seta present on outer mandibular surface. Maxillary palp 6-merous, with erect setae.

Mesosoma (Fig. 1A, B): very compact, with dorsal margin evenly convex in lateral view; dorsal lines between each sclerite completely effaced. Mesothorax narrow; metathorax and propodeum in profile with dorsum distinctly rounded [paratype: posterior flange of propodeum forms an angle that is slightly smaller than 90° (Fig. 2C)]; propodeal spiracle slit-shaped. Tibial spur formula 2s, 2(1s,1p); protibia with single spiniform seta posterior to calcar; pectinate metatibial spur large relative to simple spur, which is also subtended by a spiniform seta. Proboscis covered with patch of dense setae on ventral surface. Pretarsal claws dentate. Apicomedian lobate setae (plantar lobes) on ventral apex of tarsomeres I - IV absent.

Abdomen with seven exposed segments. Petiolar node squamiform (compressed anteroposteriorly); vertex of petiolar node medially emarginate [for paratype: ventral surface of petiole even, subpetiolar process presence uncertain]. Helcium short. Gaster five segments. Gastral tergum I evenly convex to posterior margin; posterior margins of tergum and sternum I not cinched, that is, not having posteriorly-directed surfaces. Gastral segment II without

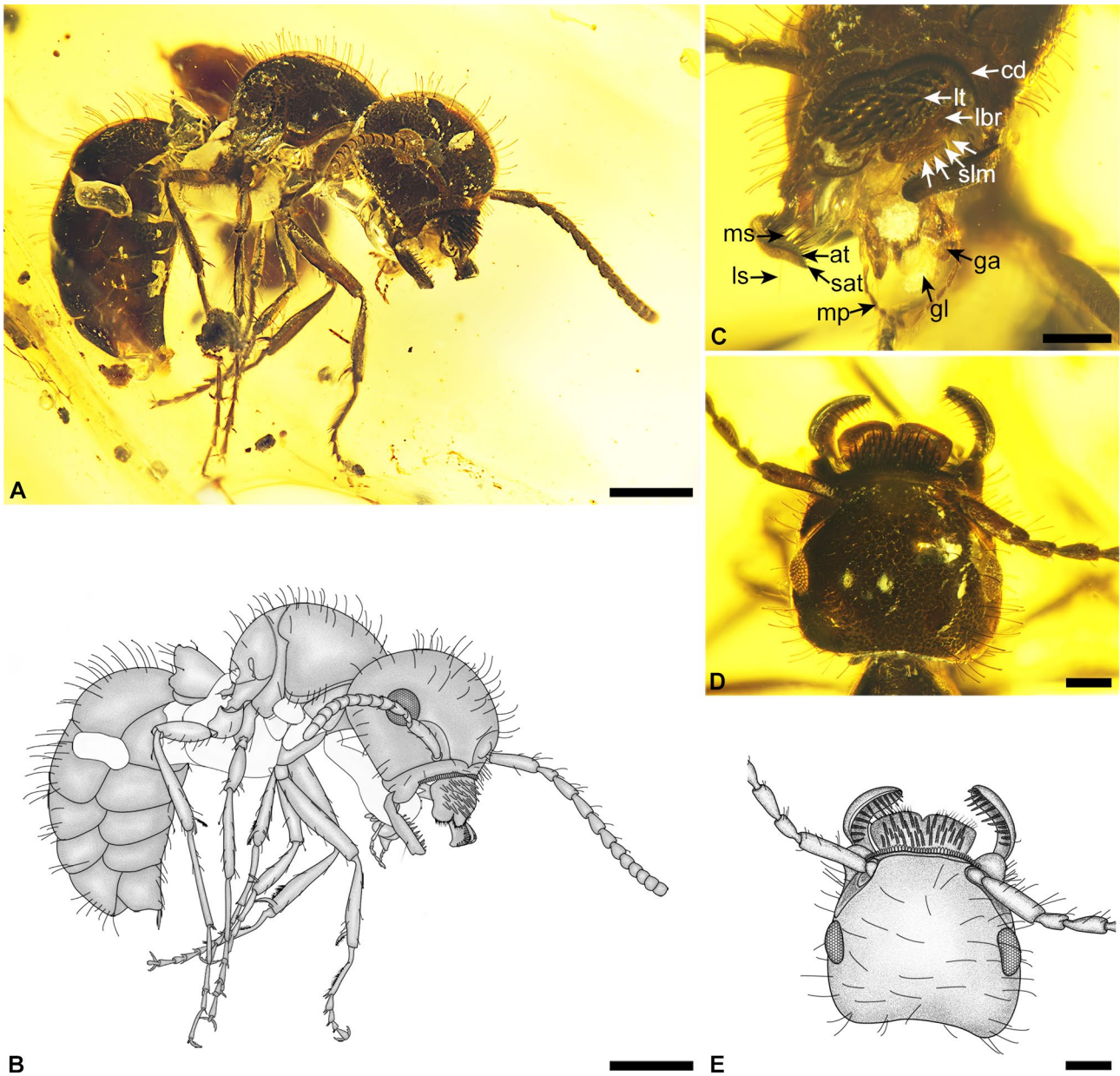


Fig. 1: Worker of *Zigrasimecia hoelldobleri* sp.n., holotype, No. CNU-HYM-MA2019053; scale bars for (A), (B) = 0.5 mm, for (C) - (E) = 0.2 mm. (A) photograph of worker in lateral view; (B) line drawing; (C) detail of the mouthparts; (D) photograph of head in dorsal view; (E) line drawing of head. Abbreviations: at, apical tooth; cd, clypeal denticles; ga, galea; gl, glossa; lt, labral tubercle; mp, maxillary palpus; ms, mandibular spicules; ls, long seta on outer surface of mandibles; sat, subapical tooth. Traction setae = cd, lt, ms.

defined cinctus [for paratype, the second gastral segment distinctly larger; sternite of gastral segment V larger than tergite, connected with tergite closely, gradually narrowing to apex, slightly upcurved apically]. Sting short but stout, largely internalized and only an element of sting exposed.

Measurements (in millimeters) for holotype (No. CNU-HYM-MA2019053) and paratype (No. CNU-HYM-MA2019054, in brackets []) specimens: Body length 3.53 [2.6]; head length (from vertex to clypeal margin) 0.8 [0.55], width (excluding eyes) 0.9 [0.5]; eyes diameter 0.2 [0.14]; total length of antenna 1.87 [1.11], scape 0.40 [0.12], pedicel 0.15 [0.07], flagellomeres I - X 0.17, 0.15, 0.12, 0.12, 0.12, 0.10, 0.10, 0.10, 0.10, 0.20 [0.12, 0.09, 0.09, 0.09,

0.08, 0.08, 0.07, 0.08, 0.08, 0.15], respectively; maxillary palp: 0.16, 0.12, 0.07, 0.04, 0.03, 0.05, respectively; labral palpomeres I - V: 0.04, 0.04, 0.04, 0.05, 0.07, respectively; mesosomal length 1.25 [0.57], maximum height [0.35]. Legs: forefemur 0.64, mesofemur 0.61, metafemur 0.73; protibia 0.52 in length; mid tibia 0.51 in length; hind tibia 0.62 in length. Petiole length [0.3], height (including subpetiolar process) ~ 0.4; [0.34]. Gastral length (excluding sting): gaster comprising segments III - VII of seven segments exposed of holotype: 0.6, 0.34, 0.18, 0.18, 0.16; total length [1.2] of paratype, sting [0.04].

Undetermined alate gyne:

No. CNU-HYM-MA2019055, (Fig. 3).



Fig. 2: Photograph of worker of *Zigrasimecia hoelldobleri* sp.n., paratype, No. CNU-HYM-MA2019054; scale bar for (A) = 0.5 mm, for (B) = 0.2 mm, for (C) = 0.25 mm, and for (D) = 0.1 mm. (A) photograph of profile in dorsal view; (B) profile in lateral view; (C), petiole of paratype; (D) head in full face view.

Whole body covered with clavate setae (Fig. 3A, B). In dorsal view, head (Fig. 3C) flattened, ocelli absent. Antenna 12-merous, right antenna lost except scape, clavate setae gradually shorter on left antenna. Frontal carinae present. At least 44 clypeal denticles visible, mandibles slightly overlapping at closure (Fig. 3C). Posterior margin of propodeum weakly sloping and relative rounded. Petiole with anteroventral process (subpetiolar process present), in small bulge shape, not very conspicuous. Most of gaster shielded by a bubble, anterior of gaster poorly preserved, but well-developed sting clearly present.

Right forewing (Fig. 3D, E) venation almost complete, distal part of posterior margin not preserved. Cell 1R1C / SMC1 pentagonal; cell 1MC / DC1 with five sides, Cuf1a very short, nearly half of Rsf1; Rs + M almost twice as long as Mf1, and almost parallel to Cuf1; Rsf2 - 3 linear, length about equal to Rs + M; Mf2 lost to juncture of Rs + M and 1 m-cu; cross-vein 2rs-m slightly bent. Nearly whole right hind wing (Fig. 3A) folded together with forewing, but six distal hamuli distinctly visible. (M + Cu)2 nearly twice as long as cross-vein cu-a; Mf1 aligned with Mf2 (Fig. 3E).

Other characters are similar to those of †*Z. hoelldobleri*.

Measurements (in millimeters).

Alate gyne. Body length 4.0; head length (from vertex to clypeal margin) 0.74, width (excluding eyes) 0.8; eyes length 0.3; scape 0.41, pedicel 0.13, flagellomeres I - X 0.21, 0.14, 0.15, 0.1, 0.13, 0.09, 0.07, 0.06, 0.07, 0.17, respectively; mesosomal length 1.43, maximum height 0.76; petiole length 0.3, height (including subpetiolar process) 0.58; gastral length (excluding sting) 1.5; forewing length 3.21, width 0.68 at the widest point.

Remarks: We provide this morphological sketch of the gyne (Fig. 3) as it is clearly a member of †*Zigrasimecia* due to the typical mandibular spines, clypeal denticles and trapezoidal shape of head in dorsal view. Although there is evidence that this gyne probably represents a distinct species, we do not provide it with its own specific epithet. The most salient differences include: dense setae, a small subapical mandibular tooth, three rows mandibular spines in different lengths, and a more rounded propodeum. We expect that additional alate material of †*Zigrasimecia* will help refine species boundaries.

Genus †*Protozigrasimecia* CAO, BOUDINOT & GAO gen.n.

Type species: †*Protozigrasimecia chauli* by monotypy.

Diagnosis: Uniquely identified among all Formicidae by the diagnostic features listed for †*Zigrasimeciini* and in the Key to the genera of †*Zigrasimeciini* (both above). The new genus is defined by the following combination of character states (see Note 8): **(1)** head massive, omega-shaped (Ω); **(2)** anterior clypeal margin broadly concave and arcuate; **(3)** traction setae present on the anterior clypeal margin and labrum; **(4)** clypeal traction setae not restricted to single row on anterior margin, but doubling and tripling on clypeus toward cranial midlength; **(5)** basal mandibular margin evenly convex, ending apically at base of basal tooth; **(6)** masticatory margin bidentate, comprising well-developed, acute basal and apical teeth (Fig. 4D); **(7)** flagellomeres elongate, length $> 2 \times$ width; **(8)** diagonal antennal scrobes present (extending from toruli to anteromedian eye margins); **(9)** ocelli present; **(10)** mesosoma diagonal, with domed promesonotum; **(11)** promesonotal articulation clearly defined and probably mobile;

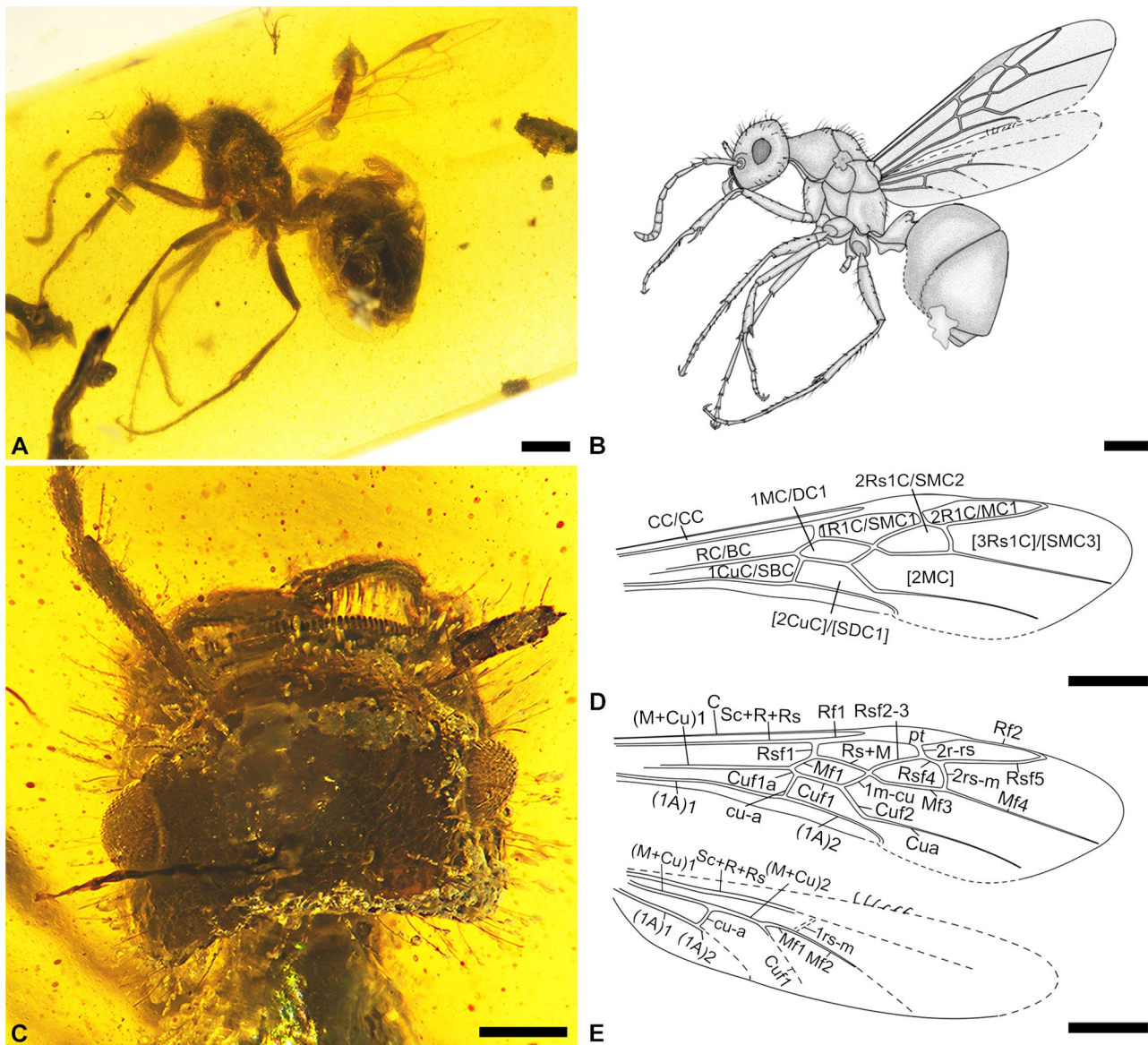


Fig. 3: Alate gyne of the unplaced *Zigrasimecia*, No. CNU-HYM-MA2019055; scale bars for (A), (B) = 0.5 mm, for (C) = 0.2 mm, and for (D) - (E) = 0.5 mm. (A), Photograph of alate gyne in lateral view, (B), reconstructive drawing of alate gyne, (C), head of alate gyne in dorsal view, (D) and (E), venation reconstructions, where (D), indicates cells and (E), indicates veins.

(12) mesonotum well-developed, comprising only mesoscutum; (13) mesoscutellum and metanotum not expressed; (14) propodeum rectangular and box-shaped; (15) propodeal spiracle situated low and laterally on segment; (16) propodeal spiracle slit-shaped; (17) tibial spur formula 2b, 2(1b, 1s) (b = barbirulate, i.e., with fringed margin, but spur not pectinate); (18) pretarsal claws with denticle situated in basal half; (19) helcium apparently infraaxial (anterior articular sclerites of abdominal segment III situated below segment midheight); (20) prora of abdominal sternum III in form of longitudinal keel; (21) abdominal tergum III constricted posteriorly, almost nodiform, albeit segment large; (22) abdominal segment IV with cinctus (tergum and sternum IV divided into pre- and postsclerites by transverse sulcus); and (23) sting robust (Fig. 5D).

Note 8: Because the uniqueness of these characters in comparison to other \dagger Zigrasimeciini has already been addressed in the \dagger Zigrasimeciini definition, the \dagger *Zigrasimecia* diagnosis, and the key, we simply provide these characters in sequence from anterior to posterior along the body axis. The taxon definition provided here includes characters which encompass meaningful variation among all described and many undescribed stem Formicidae, as well as with relevant comparisons with crown groups. See, for example, FISHER & BOLTON (2016) for a comparable approach.

Etymology: The generic name refers to the set of retained plesiomorphic features which distinguish the new taxon from \dagger *Zigrasimecia* (namely, the mandibular dentition and mesosomal form).

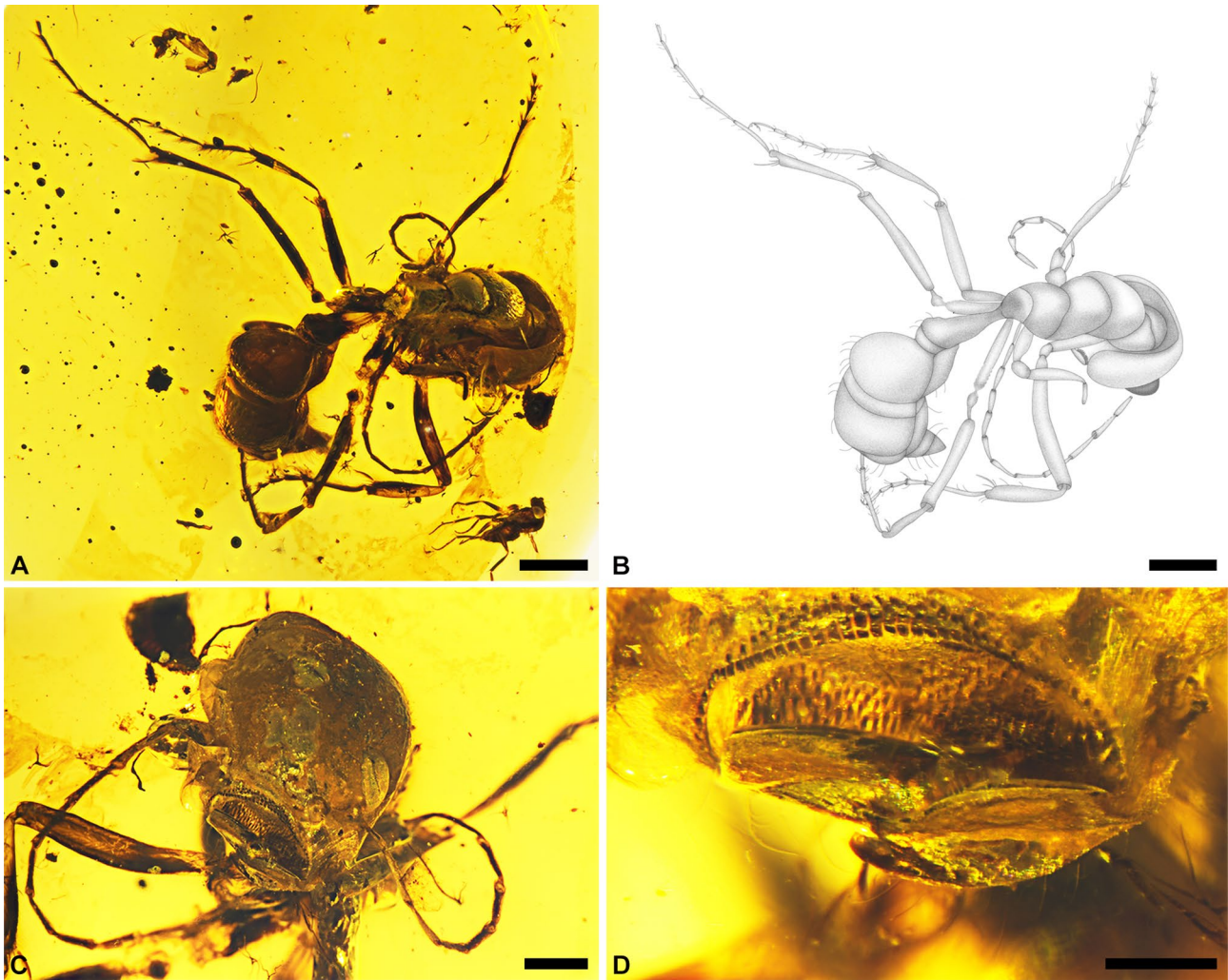


Fig. 4: †*Protozigrasimecia chauli* gen.n. sp.n. worker holotype, No. CNU-HYM-MA2020001; scale bars for (A), (B) = 1.0 mm, for (C), (D) = 0.25 mm, (A) Habitus, posterodorsal lateral oblique view; (B) line drawing of habitus, body in approximate lateral view; (C) head in anterolateral oblique view, (D), clypeus, labrum, and mandibles in approximate full-face view.

†*Protozigrasimecia chauli* CAO, BOUDINOT & GAO sp.n.

(Figs. 4 and 5)

Etymology: The specific name is in recognition and appreciation of Júlio C. M. Chaul, a Brazilian myrmecologist who has undertaken a taxonomic review of †*Zigrasimecia*; his insights have definitively shaped our understanding of the group, and particularly for the new genus.

Material: Holotype: No. CNU-HYM-MA2020001, worker.

Locality and horizon: Kachin (Hukawng Valley) of northern Myanmar. The lowermost Cenomanian (near Albian boundary).

Diagnosis: As for genus (above).

Description: Worker. All measurements in millimeters.

Total body length as defined by the addition of head and mesosomal lengths, plus the lengths of abdominal segments III - V and VII: 11.75. Mesosoma and meta-

soma covered by variably-dense layers of erect, curved pubescence; longer erect setae present on metasoma and legs; long setae especially dense on sixth (= terminal) abdominal segment; dense setal brushes present apically on fore- and hind-tibiae, plus the tarsomeres of each leg; stout, long setae present on ventral surfaces of tarsomeres, and ring the tarsomere apices; a pair of long stout setae accompany protibial calcar, situated posterad; outer / ventral mandibular margin with six widely-spaced and evenly distributed long setae; malar space apparently without long standing setae.

Head (Fig. 4A - D): broad, blocky; head width 1.60; head length to anterior margin of clypeal lobes 1.77, head length to anteromedian clypeal margin 1.42. Eyes bulging, maximum diameter 0.55. Ocelli present. Antenna 12-merous; total length uncertain due to poor preservation of apical antennomeres. Scape with short, curled pubescence; pedicel and flagellum apparently without standing setation or pubescence. Scape length 0.45; pedicel length

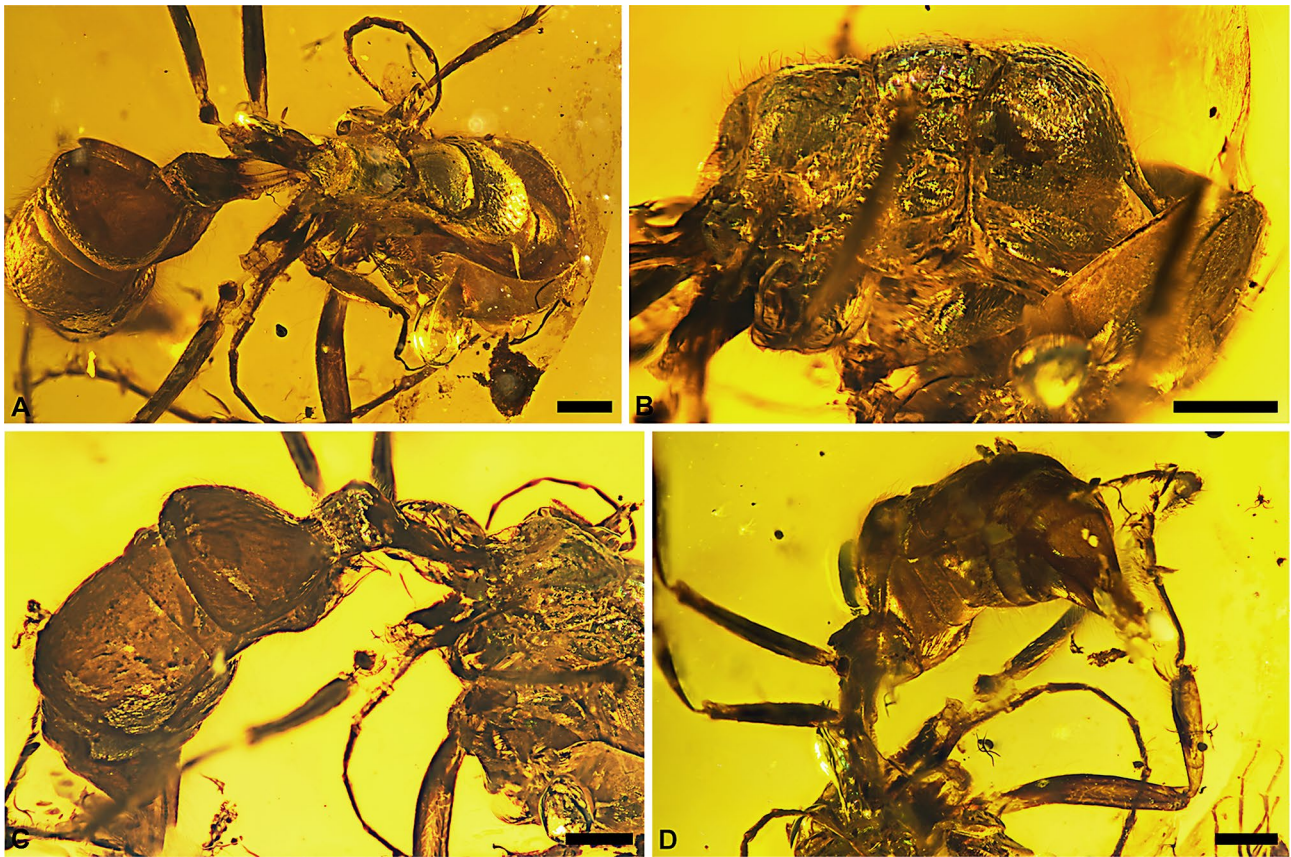


Fig. 5: *Protozigrasimecia chauli* **gen.n. sp.n.** worker holotype, No. CNU-HYM-MA2020001; scale bars for (A) - (D) = 0.5 mm. (A) Body in posterodorsal lateral oblique view; (B) mesosoma in approximate lateral view; (C) propodeum and metasoma in dorsolateral oblique view; (D) metasoma in ventrolateral oblique view.

0.11; length of flagellomeres I - VII (VIII - X too poorly preserved to measure): 0.43, 0.47, 0.40, 0.40, 0.29, 0.28, 0.32, respectively. Frontal carinae poorly developed, margining antennal scrobe posteriorly / dorsally. Clypeus (Fig. 4C, D) curved for its entire length; lateralmost portions of clypeus, dorsal to mandibular insertion, expanded as disc-shaped lobes; malar space, continuous with lateral clypeal lobes, apparently explanate laterally; anterior clypeal margin apparently not emarginate medially; anterior clypeal margin margined with an even row of about 44 peg-shaped traction setae; a second, messier row of traction setae begins at about the 8th traction seta from the lateral margin; second row including about 36 traction setae. Labrum (Fig. 4D) of holotype partially concealed by mandibles, which overlap in closure; disc of labrum covered in > 50 traction setae which are similar in size to those of the clypeus, but are acutely pointed apically; labral traction setae absent from a lentil- or lens-shaped area located proximomedially on labral disc; labral traction setae approaching the glabrous lentil-shaped area decreasing in size. Mandibles (Fig. 4D) with comparatively thin and short traction setae on their oral surfaces, these setae apparently too fine for impalement; basal mandibular margin forming even, shallow convexity, ending distally at base of basal / subapical tooth; masticatory mandibular margin short, comprising just the two large, acute teeth; apical

tooth larger than subapical / basal tooth; aboral surface of mandible with carina extending from mandibular base onto base of subapical / basal tooth. Maxillary palps long, length of visible palp (obscured at base) 0.95; labial palp and maxillary palp base obscured as preserved.

Mesosoma (Fig. 5A, B): relatively compact, mesosoma length (= Weber's length, from inflection between anterior pronotal face and pronotal neck in profile view to posteriormost point of metapleuron) 4.28; dorsal mesosomal margin interrupted by promesonotal articulation and transversely-impressed mesonotal-metathoracopropodeal suture; promesonotal articulation apparently unfused and mobile. Pronotal length including neck 1.94; mesothorax anteroposteriorly narrower than pronotum and propodeum, minimum length 0.91, height 2.30; metathoracopropodeal complex box-shaped, taller dorsoventrally (1.57) than long anteroposteriorly (0.91); dorsal and posterior faces of propodeum rounding into one another along a relatively narrow curve. Legs (Fig. 4A, B): mesofemur length 1.49. Pretarsal claws dentate, with tooth occurring in basal half of claw. Apicomedian lobate setae (plantar lobes) of tarsomeres I - IV absent, apparently replaced functionally by apical crown of spur-like setae.

Metasoma (Fig. 5A, C, D): Abdomen with seven exposed segments, of these gaster comprising segments III - VII: segment III length 2.24, postsclerite IV length 2.10,

length of remaining abdominal segments as preserved 1.37. Petiole apparently long-pedunculate; petiolar node low and convex, not squamiform; vertex of petiolar node apparently without median emargination; posterior petiolar and helcium long. Helcium apparently infraaxial. Prora massive, longitudinal, keel-like. Abdominal tergum III with anterior face steeply angled; posterior margin constricted, giving tergum nodiform-appearance. Abdominal segment IV with cinctus dividing tergum and sternum into pre- and postsclerites; poststernite distinctly shorter than posttergite; abdominal segment V and VI telescoped within segment IV; tergum and sternum VII long, conical. Sting robust.

Discussion

Mouthpart structure and function: The mandibles of ants are characteristically modified relative to other Hymenoptera. Among these modifications are enlargement of the cranial condyle (= dorsal or anterior mandibular condyle) and swelling of the mandibular abductor swelling (= atala of R. Keller; RICHTER & al. 2019, RICHTER & al. 2020). The posterolateral view of the †*Zigrasimecia hoelldobleri* holotype (Fig. 6) shows that the mandibular abductor swelling and mandibular condyle (= ventral or posterior mandibular condyle) are rotated in the mandibular sockets, such that they are aligned in the transverse plane of the head, rather than the sagittal. This conformation is also observed in the micro-CT scan of the haidomyrmecine †*Linguamyrmex* BARDEN & GRIMALDI, 2017: fig. 7. Because condyles and acetabula are functional elements of any pair of articulating parts, the rotation of the abductor swelling and mandibular condyle indicate distinct function relative to crown ants and less specialized stem ants, such as †*Gerontoformica*. Indeed, the mandibles of †*Z. hoelldobleri* in death can be seen to have swung open posterolaterally from the closed condition (Figs. 1, 6), relative to the lateral motion of other stem and crown Formicidae.

Taken altogether, the mandibles of †*Zigrasimecia* may be conceived to have the following function. To open, the mandibles swing posterolaterally, with closure affected via the opposite, anteromedial motion. Shutting the mandibles traps prey between the spiniform traction setae of the oral mandibular face and the aboral (dorsal / outer) labral face. Prey, as if situated in a myrmecological iron maiden, are further immobilized by pressure from mandibular closure, forcing the victim against the numerous peg-like traction setae of the anterior clypeal margin. Stings, death, and sacrifice to larvae might have ensued. With this scenario in mind, we hypothesize that †*Zigrasimecia* was a predator of small, soft-bodied prey such as various arthropods, including Collembola or other Pterygota (see also BARDEN & GRIMALDI 2013). Mandibular channels, speculated to funnel liquids such as hemolymph (BARDEN & al. 2017), are absent (Fig. 1C). An explicit survey of small soft-bodied arthropods of Burmese amber may shed further light on the paleoecology of these unique and probably predatory stem Formicidae.



Fig. 6: †*Zigrasimecia hoelldobleri* sp.n., holotype, No. CNU-HYM-MA2019053; scale bar = 0.5 mm. Posterolateral view of head, showing lateral and ventral craniomandibular articulations.

We present this interpretation in the context of prior descriptions of mandibular morphology, which did not account for function. Although †*Zigrasimecia tonsora* and †*Z. ferox* are known to bear ferocious mandibular and labral spiniform setae (labral spicules, BARDEN & GRIMALDI 2013, PERRICHOT 2014), anatomical details of the mandibular articulations and their function remained unclear. Based on †*Z. hoelldobleri* and additional specimens with opened mandibles in the CNU collection, we observed that the entire labrum is covered with stiff traction (or impaling) setae. The proximal row of labral traction setae is probably the structure marked as sub-clypeal comb in the original description of †*Z. tonsora* BARDEN & GRIMALDI, 2013. Further, we suspect that the three transverse rows of spines of †*Z. ferox* (PERRICHOT 2014) represent just the proximal portion of the labral disc, given the preservation of the mandibles at near closure.

Although the labrum is generally appreciated as a device for protecting the buccal cavity at closure (e.g., GOTWALD 1969), †*Zigrasimecia* and †*Protozigrasimecia* provide a unique and, sadly, extinct example of labral weaponization. Extant examples include predatory Attini SMITH, 1858 (Myrmicinae LEPELETIER DE SAINT-FARGEAU, 1835), such as the *Rhopalothrix* genus group sensu WARD & al. 2015 (e.g., *Rhopalothrix* MAYR, 1870: LONGINO & BOUDINOT 2013; *Eurhopalothrix* BROWN & KEMPF, 1961: LONGINO 2013; *Protalaridris* BROWN, 1980: LATKE & al. 2018; and *Basiceros* SCHULTZ, 1906: PROBST & al. 2019; among others). Of course, the labral traction setae are a homology conundrum, as they are observed in various stem Formicidae, and a few extant taxa (some Leptanillinae, some Amblyoponinae) (BOUDINOT 2015). It is possible that presence of these setae in the extant taxa are exceptional plesiomorphic retentions, or simply secondary gains. That various species of *Leptogenys* (Ponerinae) have stout traction setae on the clypeus (e.g., LATKE 2011) circumstantially supports functional convergence

of modified mouthpart setae (BARDEN & GRIMALDI 2013). Regardless, it is clear that mouthpart traction setae were used in a variety of predatory functions, as evinced by †Haidomyrmecinae (BARDEN & GRIMALDI 2012, 2013, PERRICHOT & al. 2016, CAO & al. 2020b, PERRICHOT & al. 2020).

The diversity of the Cretaceous ant venation:

Alate gynes are rare in the Mesozoic fossil record relative to workers. Remarkably, however, alates have been recorded for eight genera, most of which are †Haidomyrmecinae (BARDEN & GRIMALDI 2016, CAO & al. 2020a, PERRICHOT & al. 2020). Notably, alate gynes of †*Zigrasimecia ferox* and that of the unplaced alate above show variation in the positioning of the anterior juncture of 1 m-cu and cu-a (CAO & al. 2020a); in comparison to †*Z. ferox*, abscissae Rsf2 and Rsf3 of †*Z. hoelldobleri* are merged, the basal 1 / 4 part of Mf3 is bent and Mf2 is decreased to a junction (Fig. 3E). While not mirroring the total diversity of crown ants (e.g., OGATA 1991, PERFILIEVA 2008, 2011, 2015), this documented variation within †*Zigrasimecia* confirms parallel evolution of venational patterns among the Cretaceous ant fauna. The venation of three Cretaceous genera (†*Haidomyrmodes* PERRICHOT, NEL, NÉRAUDEAU, LACAU & GUYOT, 2008, †*Gerontoformica* NEL & PERRAULT, 2004, †*Camelomecia* BARDEN & GRIMALDI, 2016) as well as that of †*Zigrasimecia* is uniform but complete: †*Z. hoelldobleri* and †*Camelomecia* are nearly same Ogata type (OGATA 1991), †*Gerontoformica* and †*Z. ferox* are same Ogata type, demonstrating a multiplicity of venational forms in stem ants.

Mesosomal evolution: Mesosomal form has been used for well over a century in the classification of the Formicidae (e.g., MAYR 1861, BOLTON 2003). Recent molecular phylogenies (e.g., WARD & al. 2015) have shown that the mesosoma, as characterized for classification, is more prone to homoplasy than previously suspected. Specifically, it is now clear that compact mesosomata have arisen multiple times in the crown ants from a groundplan morphology similar to the form observed in †*Gerontoformica*, namely having a bihumped mesosoma, with a high promesonotum and low metathoracic-propodeal complex. With the discovery of †*Protozigrasimecia*, this pattern is now clearly documented in the Mesozoic fossil record as a definitively independent origin of the compact mesosoma, a state unique to †*Zigrasimecia* among stem Formicidae. This leads us to suspect that the anatomical study of compact mesosomata in a comparative, phylogenetic context will reveal multiple, distinct patterns of mesosomal integration. Moreover, if compact mesosomata have indeed arisen numerous times, this strongly implies functional advantage of this form, which must be evaluated in future studies, ideally employing micro-CT, as in KHALIFE & al. (2018), RICHTER & al. (2019), and LIU & al. (2019), for example. Given that it is possible to segment out (render in 3D from micro-CT scan data) internal structures in well-preserved fossils, such as the tentorium (A. Richter & R.G. Beutel, pers. comm.) or genital skeletal musculature (POHL & al. 2010), generating 3D data for the

†*Zigrasimeciini* should be seen as a priority for myrmecological systematics and evolutionary biology. Moreover, should specimens be found with sufficient preservation of internal anatomy, comparison of †*Zigrasimecia* and †*Protozigrasimecia* could be used to evaluate the effects of miniaturization, given the disparity in size between the two taxa.

Conclusion: Our study of †*Zigrasimecia hoelldobleri* sp.n. and †*Protozigrasimecia chauli* gen.n. sp.n. reveals both morphological and functional diversity in stem Formicidae. The holotype of †*Z. hoelldobleri* is shockingly well-preserved for light microscopy, and has yielded insights into mandibular, labral, and clypeal function of the Burmese †*Zigrasimeciini*. Based on the interpreted mouthpart function, we colloquially recognize †*Zigrasimecia* and †*Protozigrasimecia* as the iron maiden ants. Among the †*Zigrasimeciini*, we severely doubt that the monotypic genus †*Boltonimecia* from Canadian amber is correct to include, and recommend revised study. In summary, there are ample opportunities for discovery, characterization, and evolutionary analyses of the †*Zigrasimeciini*, which we have attempted to facilitate through the present work.

Compliance and ethics

The authors declare that they have no conflict of interest.

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