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Short communication

A new species of the iron maiden ant based on an alate female from mid-Cretaceous Burmese amber (Hymenoptera: Formicidae: †*Zigrasimecia*)

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ABSTRACT

The iron maiden ant, which was first described as †*Zigrasimecia* Barden & Grimaldi, 2013, received its nickname for bearing a unique mandible and ferocious mouthparts covered by spiky, columnar-shaped denticles. Here, we describe a new species based on an alate female preserved in 99-Ma Kachin amber – †*Zigrasimecia goldingot* sp. nov. – which displays several diagnostic features shared with the known species of this genus. Such features include the peg-like mandibular setae, setae of the labrum, clypeal denticles, and an omega-shaped head capsule. Our findings suggest a high diversity among †Zigrasimeciinae and support the grouping of this subfamily. Our work adds to the biodiversity of †*Zigrasimecia* and †Zigrasimeciinae, and explores the morphological and functional aspects, as well as the early appearance of the unique mouthparts in this ancient ant group.

1. Introduction

Ants are widely distributed eusocial insects in the terrestrial ecosystem, with a great quantity and morphological variety. It is estimated that the total number of ant individuals is greater than 10^{15}, accounting for 1% of the total biomass of the earth (Wheeler, 1965; Nowak et al., 1984; Wilson, 1990; Xu, 2002; Paukkunen et al., 2019). One of the scientific hotspots for myrmecologists is to trace back the evolutionary pathway of this successful group of insects over the last 120 million years (Brady et al., 2006; Perrichot et al., 2008a, b; Lucky et al., 2013; Qi et al., 2018; Robin et al., 2019).

In recent years, Kachin amber, the so-called burmite from the Hukawng Valley of Myanmar which contains various invertebrate inclusions, has received more and more attention from the academic community (Barden & Grimaldi, 2012; McKellar et al., 2013; Barden, 2015). The isotopic age of Kachin amber has been estimated at 98.79 ± 0.62 Ma (Shi et al., 2012; Zheng et al., 2018; Perrichot et al., 2020; Perkovsky et al., 2020; Wang et al., 2020), which has been further confirmed by a study that revealed that the Hukawng River Valley used to be a tropical saltwater lagoon from the Albian to the Cenomanian stages of the Lower Cretaceous (Yu et al., 2019). That environment facilitated high biodiversity and, in turn, ensured a great variety of inclusions in the amber, *ipso facto* (Yu et al., 2019; Wang et al., 2020). There are a large number of ant specimens found in the Kachin amber, which have been considered as the oldest inclusion of ants in amber (Lapolla, 2013). Those specimens have been shown to be an excellent source of material for understanding the evolution and ecology of this important group of insects. These include †Sphecomyrminae (Dlussky, 1996; Engel & Grimaldi, 2005; Perrichot, 2014; Barden & Grimaldi, 2016), †Haidomyrmecinae (Perrichot, 2016; Barden et al., 2016; Barden et al., 2017; Cao et al., 2019; Barden et al., 2020), and †Zigrasimeciinae (Barden & Grimaldi, 2013; Perrichot et al., 2014; Borysenko, 2017; Cao et al., 2020a, b; Boudinot et al., 2020). Another extinct group of early ants, †Brownimeciinae, is only known from the Raritan amber (Bolton, 2003).

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The subfamily †Zigrasimeciinae, or so-called iron maiden ants (Cao et al., 2020), was recently erected by Boudinot et al. (2020). Thus far, it comprises the genera †*Zigracimecia*, †*Protozigrasimecia*, and – doubtfully – †*Boltonimecia*. The latter two are monotypic while †*Zigrasimecia* contains three species. †*Zigrasimecia* is characterized by unique mouthparts and an omega-shaped head capsule with other genus in this subfamily and differ from other genus by its smaller body size and antenna segments number. The type species, †*Zigrasimecia tonsora*, was described from an amber piece with a single dealate gyne. The animal has its iconic needle-like setae densely distributed on the inner surface of the mandible, and the densely arranged clypeal base denticles and the labrum is covered by looming thick setae (Barden & Grimaldi, 2013). †*Z. tonsora* was named after its comb-like mandible, and therefore, received its nickname - the barber ant (Barden & Grimaldi, 2013). The second species of this genus is †*Zigrasimecia ferox* Perrichot, 2014, which was reported from two pieces of burmite with three complete workers and fragments of two other workers (Perrichot et al., 2014). Despite the different castes between the holotypes of †*Z. tonsora* and †*Z. ferox*, they share many morphological similarities, such as sting-like mandible and labral setae, clypeal denticles and an omega-shaped head (Perrichot et al., 2014). Recently, a third species, †*Zigrasimecia hoelldobleri*, was described based on the holotype and paratype of the worker caste (Cao et al., 2020b). The holotype of *Z. hoelldobleri*, with a pair of mandibles in open position, and a bristled labrum that appears almost parallel to the clypeal denticles, sheds new light on the functional morphology and possible predatory behaviour of these early ants (Cao et al., 2020b). Here, we report a fourth species, †*Zigrasimecia goldingot* sp. nov., which displays several diagnostic features shared with the described species of this genus. We also demonstrate a new female venational pattern within the genera †*Zigrasimecia*. Our findings suggest that †Zigrasimeciinae were relatively diverse, and support the grouping of this subfamily.

2. Materials and methods

The material was originally collected from an amber mine located near Noije Bum Village (26° 21′ 33.41″ N, 96° 43′ 11.88″ E), Danai Town, northern Myanmar, and later purchased from a local dealer. The amber piece (YKLP-AMB-001) is housed at the Yunnan Key Laboratory for Palaeobiology, Institute of Palaeontology, Yunnan University, Kunming, China. The dimensions of the piece are 8.2 mm (length), 6.5 mm (width) and 5.5 mm (height). The weight of the piece is 0.137 g, including one alate gyne ant and one mite. The morphology of the ant has been well-preserved. A crack runs through the wings situated at the dorsal-lateral side. The mite (*circa* the size of the ant's head) was preserved near the ant's foreleg. Wing vein nomenclature follows Brown & Nutting (1949) and Cao et al. (2020).

The material was examined with a Keyence VHX-6000 3D microscope, allowing for measurement and high-resolution photography (nonreflective, 3D composition, and image stitching). Sketches and explanatory drawings were made in CorelDraw X8.

3. Systematic palaeontology

Subfamily †Zigrasimeciinae Boudinot et al., 2020

Genus †*Zigrasimecia* Barden et al., 2013

†***Zigrasimecia goldingot*** sp. nov. Zhuang, Ran, Li, Feng, Liu

Etymology. the species name is an allusion to shoe-shaped gold ingot (元宝), an ancient Chinese gold medium for exchanging expensive goods, in reference to the outline of the head, which clearly resembles the shape of gold ingot.

Material. holotype YKLP-AMB-001, alate female.

Type locality and horizon. Hukawng Valley, Kachin Province, northern Myanmar; upper Albian-lower Cenomanian (ca. 98.79 ± 0.62 Ma).

Diagnosis (female). Based on one complete alate gyne: ocelli small; compound eyes subcircular in shape; outline of clypeus nearly cylindrical; median portion of clypeus concave; anterior clypeal margin with 22 loosely arranged denticles; mandibles wedge-like from anterior perspective, with densely curved setae along outer edge; ring-like toruli; scape about 2.3 times the length of pedicel; flagellomeres (I-IX) sequentially and gradually shorter, terminal flagellomere (flagellomere X) longer than pedicel (ca. 1.85 = SL/FXL). Mesonotum with clusters of short comb-shaped setae near wing side. Petiolar node with dorsoventral axis vertical (not inclined anteriorly nor posteriorly), dorsum of node transversaly slightly concave medially; subpetiole wrinkled, half fan-shaped process extending ventrally; abdomen covered with minute, curvy setae; sting sheath surrounded by long, curvy setae (Table 1).

Description. Alate gyne. All sizes below in millimetres (mm) (Fig. 1). Head broad and flattened (oval-shape in lateral view). Frons convex and postero-dorsal vertexal strongly concave (omega-shape in dorsal view). Puffed small eyes subcircular. Ocelli small. Antennal fossa projecting outward from base of antenna to gena and lower eye sockets. Antenna with 12 flagellomeres; scape and flagellomeres VII-X covered with few curved setae, more densely distributed from flagellomeres VII to X. Frontal carinae between antennae, extending postero-laterally from posterior margin of clypeus to anterior margins of eyes. Clypeus broad and thick from front perspective, slightly bilobed from middle, extending to both sides with mildly downward curved, till wrapping base of mandibles; anterior clypeal margin has 22 clypeal denticles, which are slightly loosely arranged, and nearly cylindrical in shape, shortening from middle to sides. Labrum covered with dense, stout setae in three rows. Mandibles barely overlap each other, with only one large tooth on chewing side; outer edge with curved short setae; inner edge covered with two rows of hard and sharp needle-like setae, inner setae twice the length of outer setae. Palps obscured by bubbles and other mouthparts, only partly observable.

Widest part of mesosoma about 3/5 width of head in dorsal view. Neck short, from all angles, almost completely covered by pronutum, only one short part exposed in dorsal view. In lateral view, junctions well developed above each notum. Pronotum well developed and thick in lateral view. Mesonotum distinctly convex and fully developed, with short comb-shaped setae near wing margin. Mesopleuron well separated from rest of mesosoma by grooves, tilted through extension towards anterior. Propodeum thick in dorsal view. Propodeal spiracle slit-shaped and opening diagonally downward towards posterior. Metapleural gland opening large (facing posterior lateral, or bulla broken). Legs: Trochantellus present on all legs, well developed; foreleg and middle leg basis dorso-ventrally flattened; hind-leg basis, femora and developed tibia with heights and widths basically equal in length. All tibiae with several short setae facing tibial spur apically, one pair of long setae facing tibial spur on mid tibiae. Dense comb-shaped short setae (strigil-like) on ventral margin of protarsomere I; mid tarsomere I with minute sharp setae facing apex, needle-shaped; tarsomeres I-IV with two pairs of sharp setae apically on ventral side; every tarsomere V with one pair of claws. Petiole transversely slightly concave dorsally, its dorsoventral axis roughly perpendicular to body axis.

Gaster with five visible segments (retractable), with dense, minute downward curving setae laterally (segment I smoother than others), and distinctly broader than head and mesosoma. Sting

Table 1
Classified features among genus †*Zigrasimecia*.

Feature name \taxa name	*Z. tonsora*, Barden & Grimaldi, 2013	*Z. ferox*, Perrichot, 2014	*Z. hoelldobleri* Cao, Boudinot & Gao, 2020	*Z. goldingot* Zhuang, Ran, Li, Feng, Liu sp. n.
Holotype caste	dealate female	worker	worker	alate female
Head L/W	~ 0.87	~ 0.93	~ 0.89	~ 0.91
Head setae	short, erect	short, erect	long, erect	short, curved
Ocelli	present	absent	absent	present
Eye shape	drop-shaped	subcircular	round	round
Frontal carinae	absent	absent	present	present
Torulus shape	protruding	not significantly raised, ring-like	not significantly raised, ring-like	not significantly raised, ring-like
SL/PL	~ 1.69	~ 1.90	~ 2.67	~ 2.30
SL/FXL	~ 1.57	~ 1.58	~ 2.00	~ 1.85
Clypeus	shallow, broad, disc-shaped lobes absent	shallow, transverse, disc-shaped lobes present	disc-shaped lobes present	disc-shaped lobes present
Clypeal denticles number	30	48	>30 (holotype 48, paratype 34)	22
Mandible shape	slender, sickle-shaped	bottom half side is close to rectangle-shaped	long and thick, sickle-shaped	short, wedge-shaped
Mandible dorsal setae	single, straight, long	single, straight, long	single, straight, long	multiple, curved, short
Petiole shape	high, node inclined posteriorly	high, node inclined posteriorly	dorsum medially emarginate, node inclined posteriorly	dorsum medially emarginate, node vertical to body axis
Gaster setae	/	short, erect	short, curved, dense	long, erect

Abbreviations: L/W, length/width; SL, scape length; PL, pedicel length; FXL, flagellomere X length.

sheath conical-shaped, with slightly curved to dorsal side on the apex, surrounded by long curved setae (sting absent or retracted). Genital opening peach-like (upper margin convex and lower margin concave) when viewed from anterior, trapezoid-shaped protruding from ventral gastral surface when viewed laterally.

Right fore wing unfolded, showing almost complete venation, left fore wing folded (Fig. 2D, E). Cell 1R1C/SMC1 irregular sector; cell 1 MC/DC1 with four sides, Cuf1a lost; Rs + M almost 1.5 times length of Mf1, slightly shorter than Cuf1; Rsf2-3 bent toward cell 1R1C/SMC1; Mf2 lost; Mf3 linear, almost twice as long as 2rs-m;

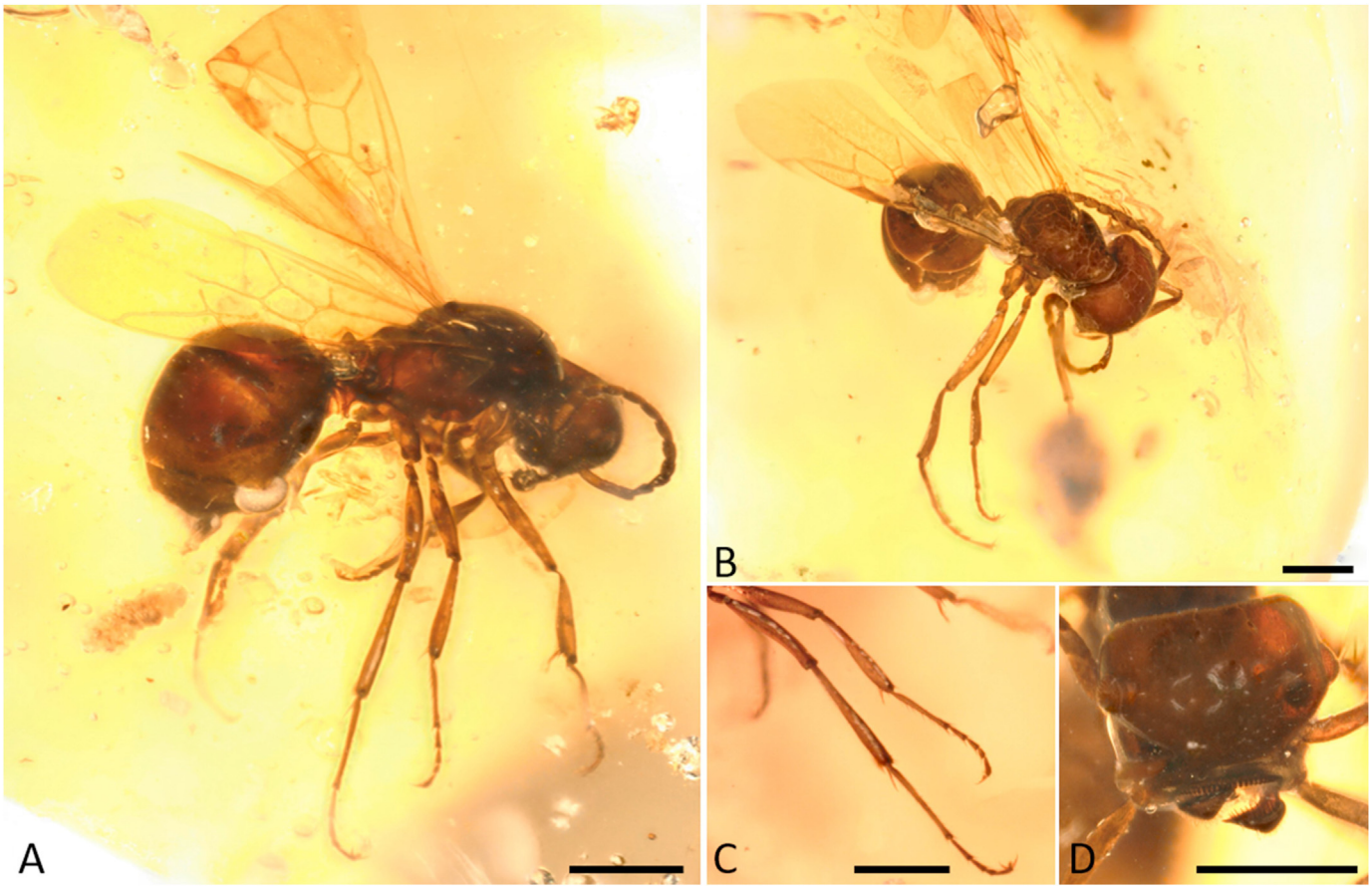

Fig. 1. Alate female of †*Zigrasimecia goldingot* sp. nov., holotype, YKLP-AMB-001; scale bars for all above = 0.5 mm. (A), photograph of body in lateral view. (B), photograph of body in dorsal view. (C), close-up hind-leg in lateral view. (D), head in full face view.

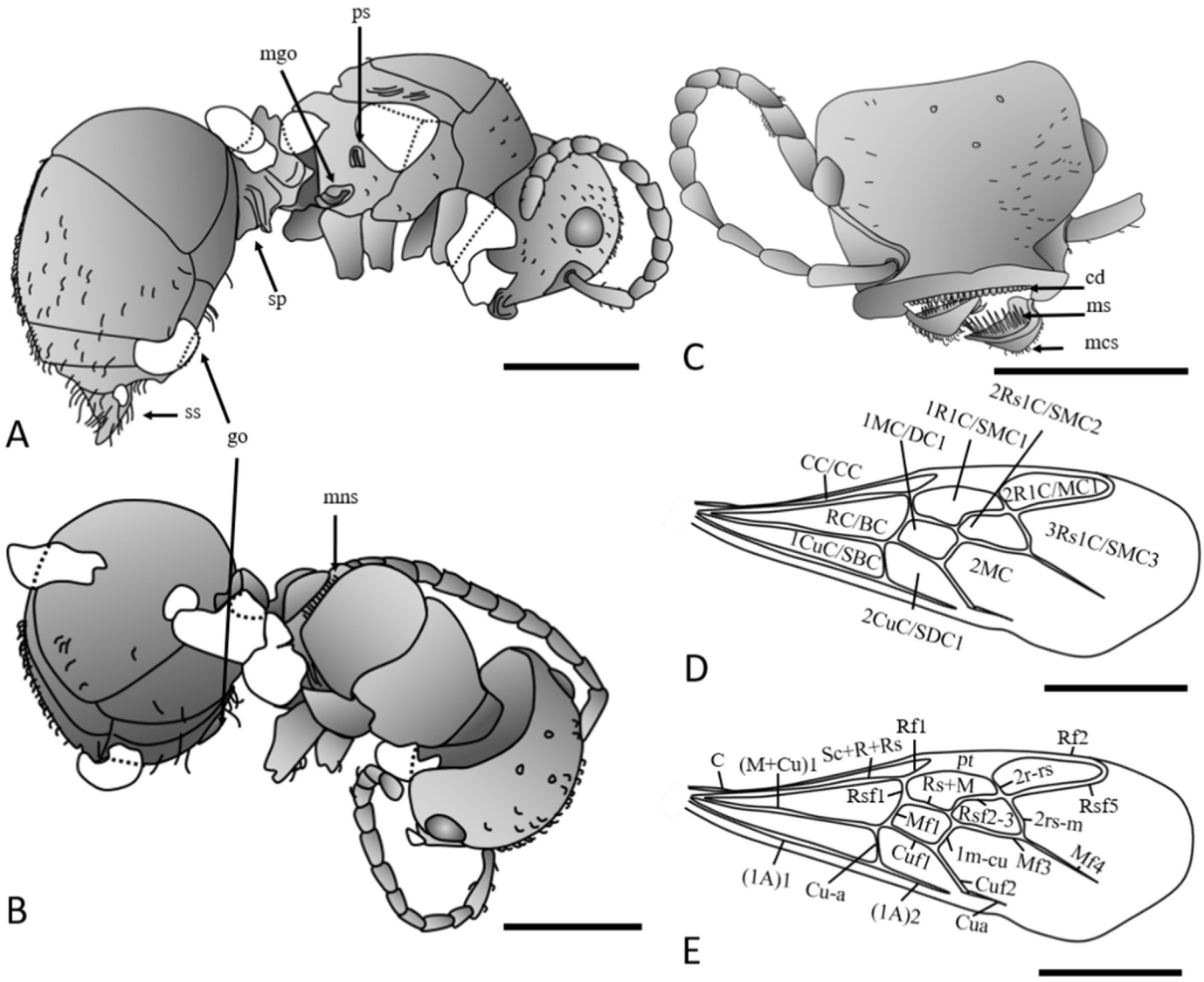

Fig. 2. Reconstructive drawings of †*Zigrasimecia goldingot* sp. nov., holotype, YKLP-AMB-001; scale bars for all above = 0.5 mm. (A), body in lateral view. (B), body in dorsal view. (C), head in full face view. (D) and (E), fore wing with terminology of cells (D) and veins (E). Abbreviation: cd = clypeal denticles; go = genital opening; mgo = metapleural gland opening; mcs = mandibular curved setae; mns = mesonotum setae; ms = mandibular spicules; ps = propodeal spiracle; sp = subpetiolar process; ss = sting sheath.

cell 2R1C/MC1 wedge-shaped. Right hind wing (Fig. 1A, B) folded (by bubble and crack), slightly damaged.

Measurements (in millimeters) for holotype (YKLP-AMB-001): body length 2.416; head length 0.405, height (basic of mandible to vertex) 0.447, width (excluding eyes) 0.498; eyes diameter 0.105; length of antennomeres: total 1.116, scape 0.252, pedicel 0.111, flagellomeres I-X 0.108 0.088 0.086 0.074 0.073 0.071 0.075 0.067 0.071 0.136; mandible (basic to apex) 0.156; clypeus 0.485.

4. Discussion

The new specimen displays a set of diagnostic characters with the known species of the genus †*Zigrasimecia* (Table 1). These include 12-segmented antennae, peg-like labial and mandibular setae (similar to the extant group Leptanillinae, e.g., *Protanilla beijingensis* (Man et al., 2017)), an omega-shaped head capsule, and three ocelli in the head of gyne caste (worker caste does not possess ocelli). On the other hand, the new specimen also bears unique features that are not known in the known species of the genus †*Zigrasimecia*.

Take the characters comparison with *Z. tonsora*. These are (1) Different shapes of clypeus: although the clypeal thickness (up and down height) of *Z. tonsora* objectively more thicker, and the upper edge of the clypeus is obviously thickened in the upper middle part, the clypeus upper edge of this specimen relatively flat and more uniform in its width; (2) Different clypeal denticles' number: 30 of *Z. tonsora*, whereas 22 of this specimen, the difference ratio is close to 1/3 (Since the clypei of the two specimens are relatively well preserved, the difference in preservation states cannot explain the obvious difference between the samples.); (3) Both of the compound eyes are preserved intact, but they are not the same: the one of *Z. tonsora* slightly long and drop-shaped, and similar compound eye forms also exist in modern ants such as *Tetramorium polymorphum* and *Tetramorium kraepelini* (Forel, 1905; Liu et al., 2015), and the compound eyes among these ants are stable in shape and can be used as a diagnostic feature. While the compound eyes of this specimen are large, full, and nearly round; (4) The ratios of SL/

PL are definitely different, with nearly 30% difference; (5) This specimen have the head and mesosoma significantly less setae than *Z. tonsora*, considering that this specimen is better preserved; for example, the outer setae of mandible are preserved intact, it cannot be considered that the loss of setae of this specimen is more serious than that of *Z. tonsora*, which is in a worse state. The number of setae is one of the characteristics of morphological identification and should be regarded as the morphological difference between the two specimens; (6) Different petioles' shapes (Figs. 1A and 2A) (The differences between this sample and other known species can be found in Table 1). We, therefore, consider the new specimen representing a new species within †*Zigrasimecia*. This study increases the biodiversity of †Zigrasimeciinae – a subfamily recently proposed by Boudinot et al. (2020).

The peg-like setae of the labrum and mandibles suggest that they can grasp the bodies of small invertebrates, securely, prey on small animals like ticks, mites and springtails, regardless of athletic ability, and make escape difficult. The prominent compound eyes on both sides of the head are indicative of good vision in †*Zigrasimecia*. The hook-like structures of long and flexible legs suggest a scansorial to arboreal habits, rather than fossorial, such as *Oecophylla smaragdina* (Wheeler, 1930). Before the present study, Cao et al. (2020b) found that the shape of eyes in workers was more spherical than in female caste specimens (more drop-shaped compound eyes in females), so that the round-like eyes of this female reveal the unique habitat of the specimen differ from other queens, although further research is required. YKLP-AMB-001 possesses loosely arranged clypeal denticles with columnar-shaped apexes which differs from other species of †*Zigrasimecia*, providing evidence that the clypeal denticle is probably adapted to fixing or defence, rather than trapping prey.

5. Conclusion

The study of †*Zigrasimecia goldingot* sp. nov. enriches the detailed descriptions and characterization of species within the genus, and reveals the possibility of discussing more functions of this ant's highly specialised mouthpart.

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