

## Short communication

A new species and one new wing type of the iron maiden ants from Kachin amber (Hymenoptera: Formicidae: *Zigrasimecia*)Yuhui Zhuang<sup>a, b, c</sup>, Yu Liu<sup>a, b</sup>, Hao Ran<sup>d</sup>, Edmund A. Jarzembowski<sup>c</sup>, Qingqing Zhang<sup>a, b, \*</sup><sup>a</sup> Yunnan Key Laboratory for Palaeobiology, Institute of Palaeontology, Yunnan University, South Waihuan Road, Chenggong District, Kunming 650500, China<sup>b</sup> MEC International Joint Laboratory for Palaeobiology and Palaeoenvironment, Yunnan University, Kunming 650500, China<sup>c</sup> State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, Jiangsu, China<sup>d</sup> State Key Laboratory of Genetic Resources and Evolution, Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming, 650223, China

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## ABSTRACT

The Cretaceous is a key period for the evolution of ants. *Zigrasimecia* is a genus endemic to mid-Cretaceous Kachin amber. In previous studies, four species of the genus based on worker and/or queen castes have been reported and three wing types of gyne within the genus have been described. We report here a new species, *Zigrasimecia zui* sp. nov., based on a worker specimen, the morphological details of which are investigated and reconstructed by using Micro-CT and other techniques. Moreover, a new wing type is reported based on a gyne specimen. By comparison with the compound eyes and other structures of extant ants, we propose that species of *Zigrasimecia* had the capability for surface-dwelling or burrowing. This work augments the species diversity of *Zigrasimecia*, and provides direct evidence for the variety of ecological niches that may have been occupied by members of this genus.

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## 1. Introduction

Ants are currently the dominant social insects in all terrestrial ecosystems world-wide except Antarctica (Hölldobler and Wilson, 1990). The variety of environments inhabited contributes to the diversity of ants, and the different morphologies of the ants also indicate that they are adapted to various niches. Thus, arboreal species usually have elongated appendages and their compound eyes may be more developed (Johnson and Rutowski, 2022); burrowing species may have highly reduced compound eyes, but their metapleural glands, which are used to inhibit bacterial growth, may be more advanced (Yek and Mueller, 2011); and nocturnal species with large compound eyes may have less melanin deposition resulting in a whitish body colour (Johnson and Rutowski, 2022). Moreover, compared to workers, the reproductive ants may have

better eyesight for mating (Gronenberg and Hölldobler, 1999; Ramirez-Esquivel et al., 2017). In the eusocial life of ants, however, the male is almost an outsider (Hölldobler and Wilson, 1990). In extant species, variations in body size, or the size of the compound eyes among workers, of the same species may also be determined during their larval period (influenced by environmental factors, such as the PH value and temperature) (Pontieri et al., 2020; Arganda et al., 2020; Casadei-Ferreira et al., 2022) and this morphological differentiation further affects the activities of worker ants.

One of the earliest known records of fossil ants is from Kachin amber, northern Myanmar (LaPolla et al., 2013) and the subfamily Sphecomyrminae was established by Dlussky in 1996 (Dlussky, 1996). The superbly preserved fossil ant specimens in Kachin amber have provided an unparalleled window into the morphological diversity of ants in the mid-Cretaceous. This former mining area has produced mainly Haidomyrmecinae, Sphecomyrminae (especially *Gerontofomica* Nel & Perrault, 2004) and *Zigrasimeciinae*. Haidomyrmecinae, with their uniquely shaped mandibles were possibly solitary predators (Cao et al., 2019; Barden et al., 2020; Guo et al., 2021); *Gerontofomica* may have transported

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larvae or cocoons to avoid calamities or enemies, like living ants (Boudinot et al., 2022; Richter et al., 2022); Zigrasimeciinae, especially *Zigrasimecia* Barden & Grimaldi, 2013, with an armed labrum and mandibles suggests a special type of predation (Perrichot, 2014; Cao et al., 2020b; Zhuang et al., 2022a, 2022b; Chaul, 2023). In terms of morphology, both Haidomyrmecinae and Sphecomyrminae have elongated appendages, well-formed claw pads and well developed compound eyes, hence it is likely that they were arboreal or surface foraging ants (Perrichot et al., 2016; Boudinot et al., 2020, 2022). Normally, the gyne and male engage in more frequent activity on tree trunks and are therefore more likely to be captured by resin – a possible explanation why the gyne and the male are frequently found in amber (Guo et al., 2021; Zhuang et al., 2022a, 2022b). Due to different ecological niches inhabited, ant fossil preservation can vary. Burrowing insects, including several ant species, are more difficult to encapsulate in resin than arboreal taxa and more difficult for researchers to investigate. In contrast, reproductive-grade ants, which normally stay on tree branches or trunks due to their poor flight ability, irrespective of whether burrowing or arboreal, are more susceptible to resin capture than burrowing worker ants (Hölldobler and Wilson, 1990). The study of cavity-dwelling hidden worker ants though is essential to fully understand the ecological characteristics and niche partitioning of Cretaceous ants.

Here we report a new species, *Zigrasimecia zui* sp. nov., and a new female wing type in *Zigrasimecia*. The holotype of *Z. zui* sp. nov. is a worker caste specimen with relatively small compound eyes and only approximately 26 ommatidia on each compound eye; its appendages are stubby and short, probably indicative of the earliest fossil evidence of burrowing ants. The new wing type reported in this paper has a more complex wing-vein structure, augmenting our understandings of wingvein variation in this taxon. Iron-maiden *Zigrasimecia* ants are so-called as their mouthparts show a superficial resemblance to ancient iron-maiden torture machines.

## 2. Materials and methods

### 2.1. Materials

The fossils were originally collected from an amber mine located near Noije Bum Village (26° 21' 33.41" N, 96° 43' 11.88" E), Danai Town, northern Burma. The amber pieces (YKLP-AMB-005, YKLP-AMB-006) are housed in the Yunnan Key Laboratory for Palaeobiology, Institute of Palaeontology, Yunnan University, Kunming, China, and were legally sourced without any conflict of interest. These amber materials were obtained before June 2017 (See supplementary material 1, statement). The dimensions of YKLP-AMB-005, which include the *Z. zui* holotype are 5.1 mm (length) × 5.0 mm (width) × 1.2 mm (height). The weight of the piece is 1.1 g, including one ant, one millipede and one dipteran fly. The dimensions of YKLP-AMB-006 are 11.0 mm (length) × 7.2 mm (width) × 3.1 mm (height). The weight of the piece is 3.3 g. The morphology of the ant is wellpreserved. Wing-vein nomenclature follows Brown and Nutting (1949).

The material was examined under a Keyence VHX-6000 3D microscope enabling measurement and high-resolution photography (with non-reflective, 3D composition and image stitching). Sketches and explanatory drawings were made in Illustrator 2020 (Adobe Systems Incorporated, San José, USA).

### 2.2. Methods

#### 2.2.1. Micro-CT scanning and 3D rendering

The specimen was scanned at the micro-CT laboratory of YKLP with an X-ray microscope (3D-XRM), ZeissXradia 520 versa.

Scanning parameters are as follows: YKLP-AMB-005 (worker): Beam strength: 60 kV/5w, Filter: no, Resolution: 1.98  $\mu$ m, Exposure time: 5 s, Number of TIFF images: 990. The three-dimensional model enabled a more comprehensive view of the specimen, especially the morphology and number of ommatidia.

Volume rendering and 3D reconstruction were performed using the open-source software Drishti 2.4 (Limaye and Stock, 2012).

## 3. Systematic palaeontology

**Subfamily** *Zigrasimeciinae* Borysenko, 2017

**Genera** *Zigrasimecia* Barden & Grimaldi, 2013

***Zigrasimecia zui*** Zhuang et al. sp. nov.

**Etymology.** The name of the species is taken from the pseudonym “Zuni” (祖尼) of Mr Liu Hao, the donor of the specimen. The word “Zu” (祖) also means the ancestor in Chinese and represents the relationship between this group of ants and extant ants. Masculine. **Material.** Holotype YKLP-AMB-005, worker.

**Type locality and stratigraphy.** Hukawng Valley, Kachin Province, northern Myanmar. Upper Albian–lower Cenomanian (ca. 98.79  $\pm$  0.62 Ma).

**Diagnosis. Worker. Differs from *Z. ferox* as follows:** (1) scape relatively longer, flagellomere X relatively short (SL/PL = 2.70 vs 1.90; SL/FXL = 2.44 vs 1.58); (2) compound eye flat, not convex (3) less numerous ommatidia, ~30 vs >200; (4) frontal carinae present not absent; (5) ring-like toruli shallow, not convex; (6) mandible with smooth surface, without setae on dorsal side; (7) petiole more developed; (8) gastral setae curved and sparse, rather than straight and dense.

**Differs from *Z. hoelldobleri* as follows:** (1) scape relatively longer, flagellomere X relatively short (SL/FXL = 2.44 vs 2.00); (2) compound eye flat, not convex (3) less numerous ommatidia, ~30 vs >200; (4) head setae sparse and short, not long and straight; (5) ring-like toruli shallow not convex; (6) mandible with smooth surface, without setae on dorsal side; (7) propodeal posterodorsal margin concave; (8) petiole more developed; (9) gastral setae curved and short, rather than straight and long.

**Differs from *Z. boudinoti* as follows:** (1) small body size not large (2) body setae curved and short not erected and long (3) less numerous ommatidia, ~30 vs >150; (4) propodeal posterodorsal margin concave; (5) petiolar node apex smooth not sharp.

**Differs from *Z. caohuijiae* as follows:** (1) head frontal view with edges approximating obtuse rectangles; (2) less numerous ommatidia, ~30 vs ~50; (3) propodeal posterodorsal margin concave; (4) Petiolar node dorsal surface middle concave.

**Differs from *Z. chuyangsui* as follows:** (1) more smaller body size; (2) head flat; (3) Mesosoma more slender not compact; (4) short body setae sparsed and curved, not abundant and long (5) less numerous ommatidia, ~30 vs ~90; (6) propodeal posterodorsal margin concave; (7) petiole node more developed.

**Differs from *Z. perrichoti* as follows:** (1) more smaller body size; (2) head surface more smooth; (3) body setae more pronounced; (4) less numerous ommatidia, ~30 vs ~90; (5) propodeal posterodorsal margin concave; (6) petiole apex bilobed not transversally.

**Differs from *Z. thate* as follows:** (1) more smaller body size; (2) no subflagellate or hook-shaped setae on the frontovertexal region, rather curved and short; (3) head more flatter not convex; (4) clypeal lobes absent not developed; (5) petiolar node not particularly tilted in lateral view.

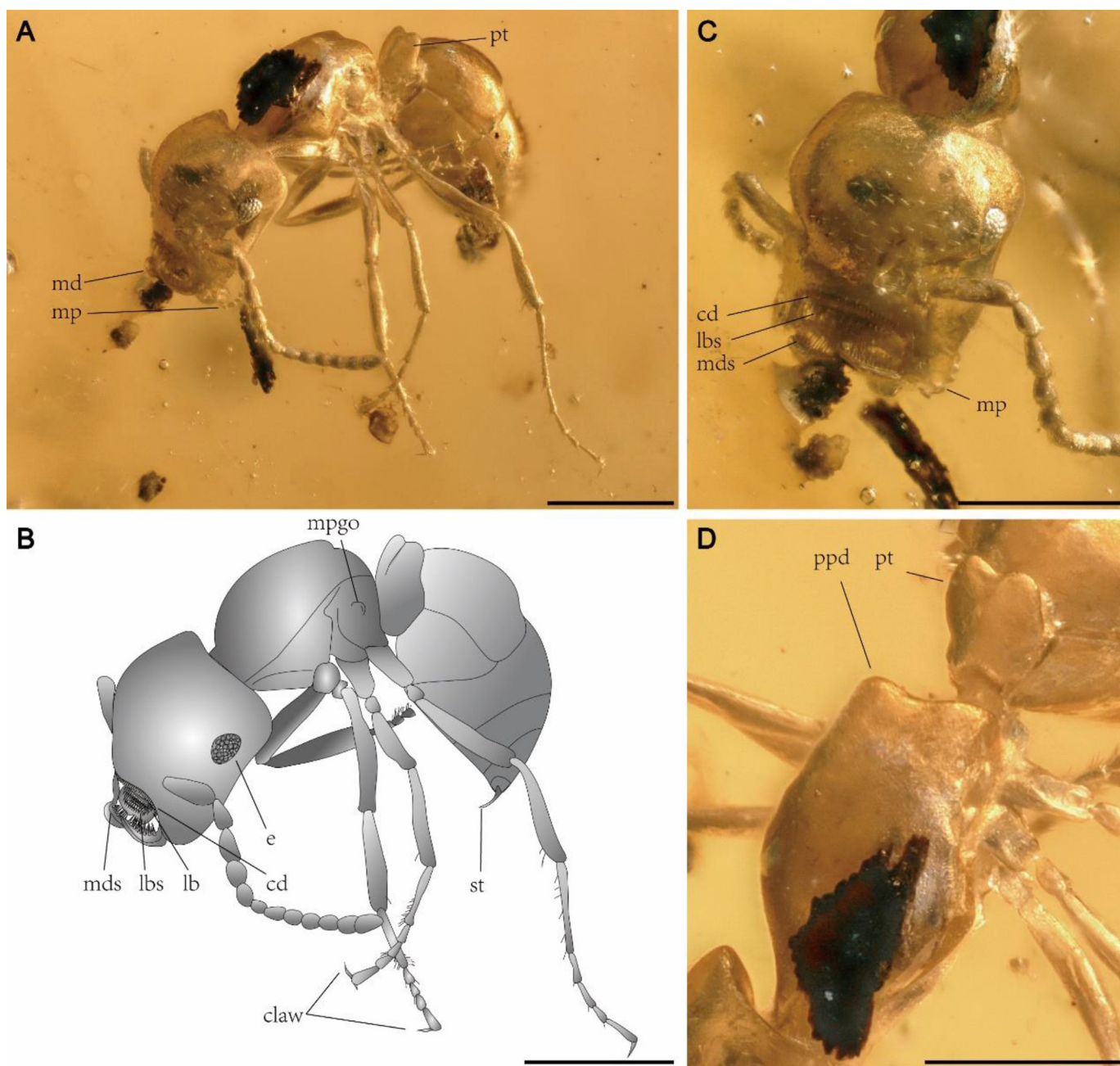
**Identification is supported by the following features which are, however, not necessarily unique among *Zigrasimecia* species.** frontal aspect of head nearly square (aspect ratio approx. 1). Compound eyes small, hemispherical. Clypeus sub-rectangular. Posterior clypeal margin not distinct. Mandible flattened and

sickle-shaped with smooth surface in frontal view. Notum in mesosoma not evident. Propodeum concave in middle. Petiolar node broad, apically slightly concave. Abdominal segment III large. *Description* (Fig. 1).

**Head:** broad and forehead flat. Posterior edge of head strongly concave (omega-shaped in dorsal view). Head setae sparse and curved. Ocelli absent. Frontal carinae developed. Antennal fossa flattened, projecting outwards from base of antenna to lower compound eyes margin. Antenna with 12 flagellomeres; scape about 2.75 times length of pedicel; scape and flagellomeres III-X covered with few short setae. Frontal carinae between antennal fossa. In frontal view, rectangular clypeus developed on both sides and with shallow superior margin; clypeus developed with disc-shaped lobes wrapped

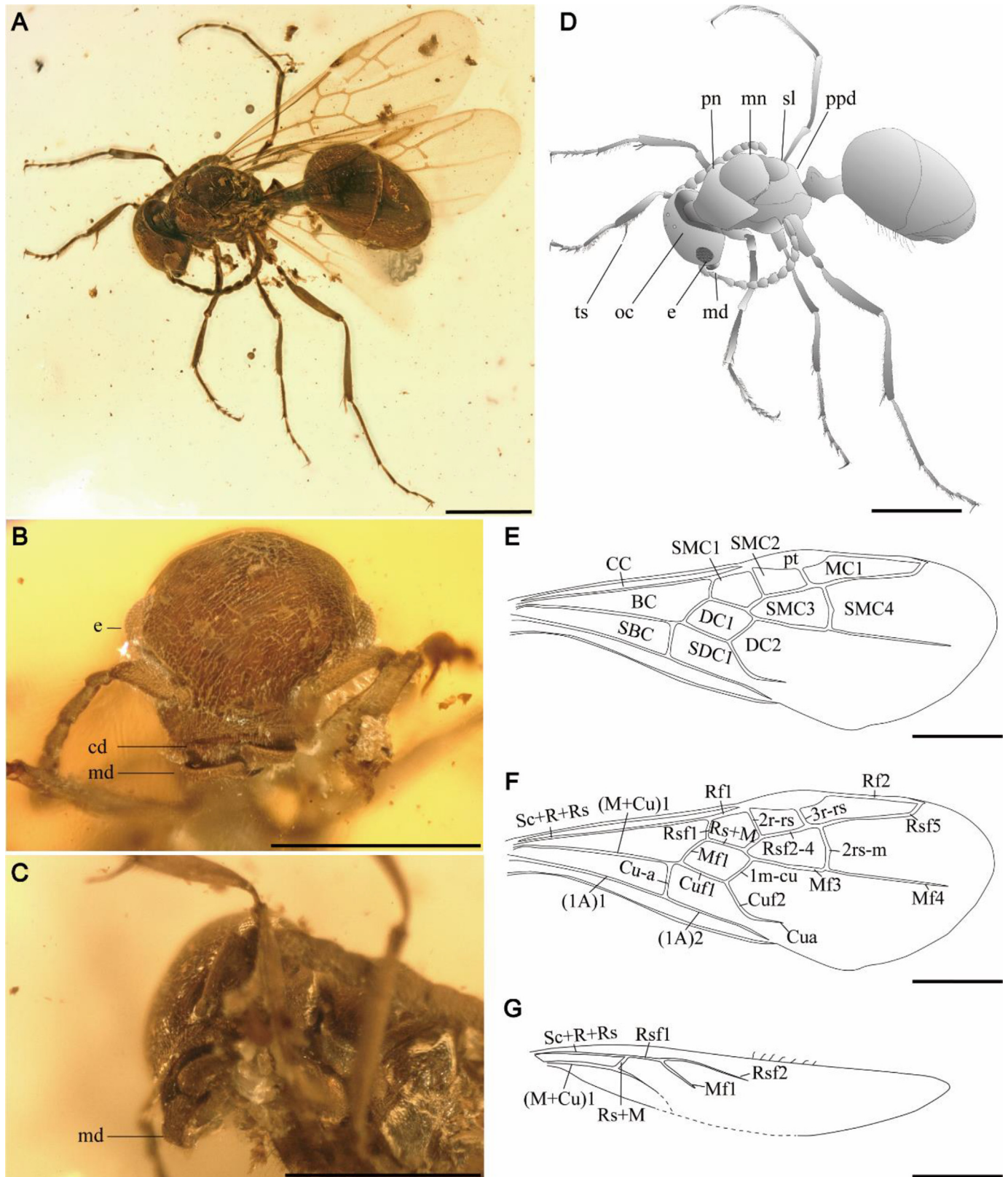
around base of mandibles. Anterior clypeal margin with 36 cylindrical clypeal denticles, closely aligned; clypeal denticles gradually shortening from middle to both sides. Outer surface of labrum covered with dense and robust spine-like setae in 3–5 lines arranged in rows. Less overlapped area between mandibles; chewing side of mandible with two teeth; outer side of mandible smoother; inner side of mandible covered with two rows of hard needle-like setae (length of inner needle-like setae about twice as long as outer ones). Labial palp 3-segmented. Maxillary palp 5-segmented.

**Mesosoma:** smooth. Narrow in dorsal view, about one-half width of head. Neck short and slender, almost completely covered by pronotum from all sides. In both dorsal and lateral views, junctions and grooves almost absent on thoracic nota. Propodeum narrower in

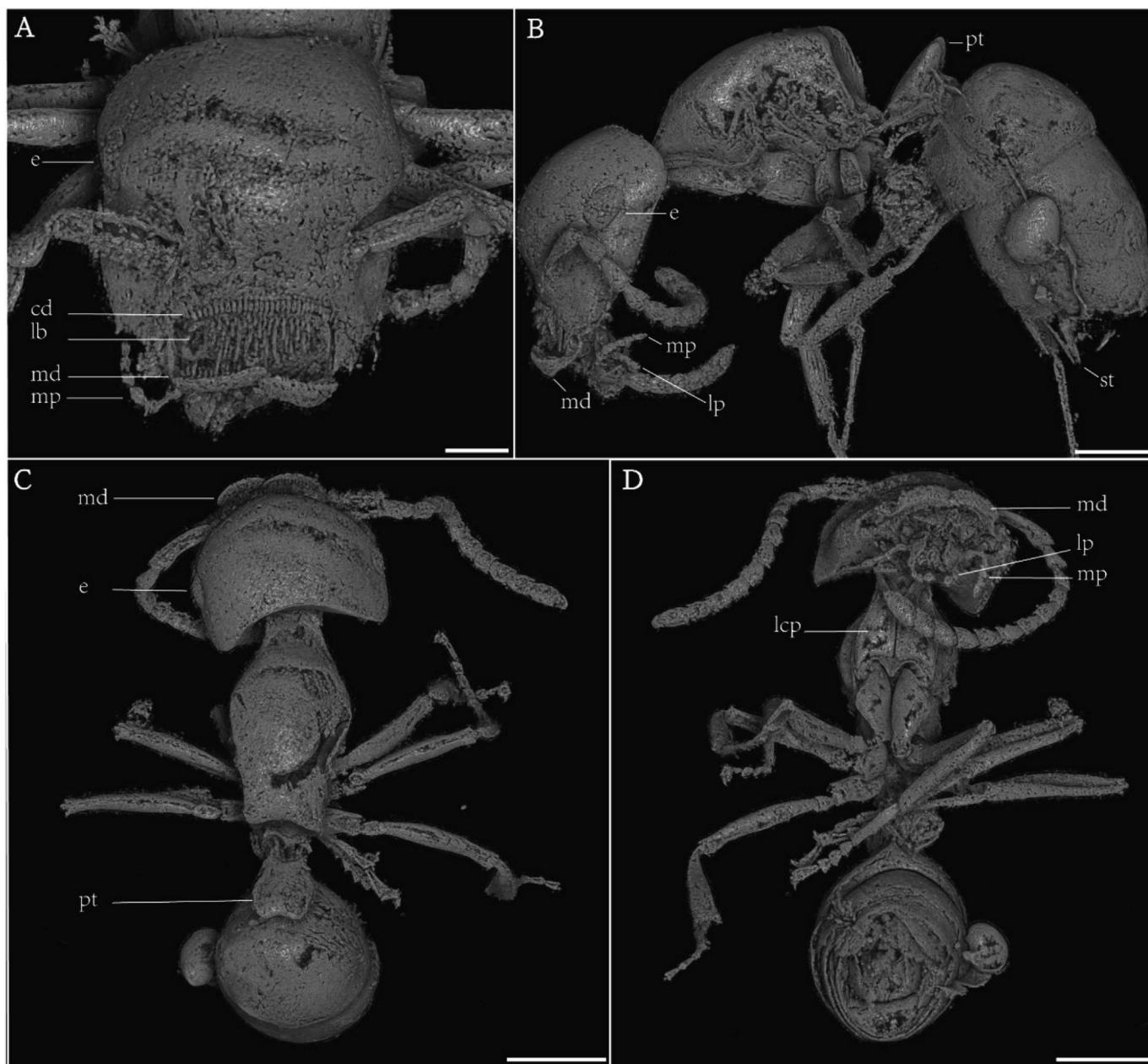


**Fig. 1.** Worker of *Zigrasimecia zui* sp. n., holotype, YKLP-AMB-005. All scale bars = 0.5 mm. (A), photograph of body lateral view. (B), interpretive drawing of YKLP-AMB-005 in lateral view. (C), photograph of head, frontal view. (D), photograph of mesosoma, dorsal view. Abbreviation: cd = clypeal denticles; e = compound eye; lb = labrum; lbs = labial setae; mp = maxillary palp; mpgo = metapleural gland opening; mds = mandibular setae; ppd = propodeum; pt = petiole; st = sting.





**Fig. 2.** YKLP-AMB-006, Alate female (gyne) and interpretive drawing. All scale bars = 0.5 mm. (A), photograph of body dorsal view. (B), photograph of head frontal view. (C), photograph of head lateral view. Interpretive drawing (D), body in dorsal view. (E) and (F), venation diagram of forewing, where (E) indicates cells and (F) indicates veins. (G) venation diagram of hindwing. Abbreviation: cd = clypeal denticles; e = compound eye; md = mandible; mn = mesonotum; oc = ocelli; pn = pronotum; ppd = propodeum; sl = scutellum; ts = tibial spur.



**Fig. 3.** 3D-reconstruction of YKLP-AMB-005. Scale bars for (A), (B) = 0.1 mm, for (C), (D) = 0.2 mm. (A), head in frontal view. (B), body in lateral view. (C), body in dorsal view. (D), body in ventral view. Abbreviation: cd = clypeal denticles; e = compound eye; lcp = laterocervical plate; lb = labrum; md = mandible; lp = labial palp; mn = mesonotum; mp = maxillary palp; oc = ocelli; pn = pronotum; ppd = propodeum; pt = petiole; sl = scutellum; ts = tibial spur; st = sting.

dorsal view, slightly concave, not distinct from mesotergum. Meta-pleural gland opening broad, towards abdomen. Legs: trochantellus present on all legs and well developed; foreleg and middle-leg basis dorsoventrally flattened; hindleg basis, femur and (longer) tibia with heights and widths basically equal; tibial spur formula 1–2; all tibiae with few short setae developed towards tibial spur; protibial and mesotibial spur short; metatibial spur long; tarsomeres slender, 5-segmented, basitarsus twice length of tarsomere V, pretarsal claws dentate. Petiole large, slightly concave in middle of apex and lean back.

Gaster: five visible segments. Abdominal segment III apparently large, length over one-third of gaster. Surface of gaster sparsely covered with tiny setae. Gaster apparently narrower than head in dorsal view. Sting short. Gonostyli absent.

Measurements (in millimetres) for holotype (YKLP-AMB-005): body length 1.76; head length 0.52, width (excluding eyes) 0.50; eye diameter 0.10, width 0.07; length of antennomeres: total 0.87, scape 0.22, pedicel 0.08, flagellomeres I–X 0.07 0.06 0.04 0.04 0.06 0.06 0.05 0.05 0.05 0.09; mandible (base to apex) 0.17; length thorax 0.53, petiole 0.13, gaster 0.58; length foreleg 0.97, trochantellus 0.06, femur 0.29, tibia 0.28, tarsomeres I–V 0.15 0.05 0.04 0.04 0.06; length middle leg 0.93, trochantellus 0.04, femur 0.22, tibia 0.26, tarsomeres I–V 0.17 0.06 0.05 0.05 0.08; length hindleg 1.16, trochantellus 0.06, femur 0.34, tibia 0.23, tarsomeres I–V 0.21 0.08 0.08 0.06 0.10.

**Zigrasimecia** sp. (gyne)

*Material.* YKLP-AMB-006, gyne.

**Type locality and stratigraphy.** Hukawng Valley, Kachin Province, northern Myanmar. Upper Albian–lower Cenomanian (ca.  $98.79 \pm 0.62$  Ma).

**Description (Fig. 2).**

**Head:** broad and flattened. Forehead smooth. Head strongly concave on posterior margin (omega-shaped in dorsal view). Ocelli small, inverted triangle on top of forehead. Frontal carinae present, shallow. Antennal fossa flat, developed with shallow ring-like toruli. Antenna with 12 flagellomeres; scape about 2.7 times longer than pedicel (pedicel length = flagellomere X length); each antennal segment developed with dense setae. In frontal view, clypeus flattened and slightly concave, developing outwards both sides, till wrapping base of mandibles; clypeal upper margin shallow; anterior margin of clypeus developed, >48 clypeal denticles, closely arranged; clypeal denticles becoming gradually shorter and taper from the middle to sides of clypeus. Labrum covered with dense, robust, spine-like setae arranged in 3–5 rows. Mandibles overlap each other; mandibular apex developed with two teeth, anterior teeth stout; dense, straight setae developed on outer side of mandibles; mandibular inner side covered with two rows of sharp, needle-like setae (inner labial setae are approximately twice length of outer ones).

**Mesosoma:** thorax well-developed, width equivalent to head. Neck short, almost completely covered by pronotum. Junctions and grooves distinct on thoracic nota. Pronotum very broad. Propodeum narrower in dorsal view. Metapleural gland opening obscured by forewing, cannot be observed. Legs: trochantellus present. Femur, tibia and basitarsomere of each leg of equal length; tarsomere V of each leg twice as long as tarsomere IV; excluding trochantellus, dense setae developed on each leg; tibial spur formula 2–2; protibia with simple long spur, about one-third length of foreleg tibia; mesotibia spur short; metatibia spur long. Petiole slender and elongated, its dorsoventral axis roughly perpendicular to body axis.

**Gaster:** five visible segments, well developed. Abdominal segments III and IV covered with long setae; short setae developed on abdominal segments V–VII. Sting stout.

**Wings:** fore- and hindwings outstretched and venation almost complete, 8 closed cells. Cell SMC1 pentagonal; cell SMC2 quadrilateral; cell SMC3 irregularly triangular; cell MC1 wedge-shaped; cell DC almost regular quadrilateral; Rs + M almost as long as Mf1, slightly shorter than Cuf1; cross-vein Rsf5 curved towards wing cell

MC1; Mf3 linearly developed, almost as long as 2rs–m. Hindwing anterior margin with 7 hamuli, cross-vein Rsf1 about twice as long as Rs + M.

Measurements (in millimetres) for YKLP-AMB-006: body length 3.50; head length 0.45, width (excluding eyes) 0.50; eye diameter 0.19, width 0.15; length of antennomeres: total 1.69, scape 0.27, pedicel 0.10, flagellomeres I–X 0.17 0.14 0.11 0.11 0.11 0.11 0.11 0.12 0.23; length of mandible (base to apex) 0.24; length of thorax 1.20, petiole 0.37, gaster 1.48; length of foreleg 2.18, trochantellus 0.15, femur 0.58, tibia 0.53, tarsomeres I–V 0.41 0.15 0.12 0.08 0.16; length of middle leg 2.14, trochantellus 0.14, femur 0.53, tibia 0.55, tarsomeres I–V 0.41 0.15 0.12 0.08 0.16; hindleg length 2.46, trochantellus 0.15, femur 0.68, tibia 0.63, tarsomeres I–V 0.50 0.15 0.10 0.09 0.16.

**4. Discussion**

**4.1. Species establishment based on worker specimens within Zigrasimecia**

In myrmecological research, the establishment of new species usually includes detailed descriptions of worker, queen (including wing type) and male (Bolton, 1994) which undoubtedly facilitates the identification and comparison of specimens and is biologically helpful. Because workers are the largest and most readily available specimens in the group, however, they are usually considered as the type specimens, especially holotypes. Only a handful of species in a few genera use reproductive ants as the type specimens due to prior failure to obtain workers, e. g. in *Aenictus* (Shattuck, 2008).

Due to the incompleteness of the fossil record, finding associations that contain both queen and worker ants as well as males is almost impossible. The only example is the co-occurrence of *Zigrasimecia ferox* queen and worker ants in one piece of amber (Cao et al., 2020a). When the genus *Zigrasimecia* was first established, it was relatively reasonable to identify a dealate queen as the type of a new species in order to take advantage of the scientific value of the fossils (Barden and Grimaldi, 2013). And, in the mid-Cretaceous, it was not possible to assess a decade ago whether there was caste differentiation in this genus. The type specimen of *Zigrasimecia goldingot* was based on a winged female ant (Zhuang et al., 2022a), at a time when *Zigrasimecia* was still in its “taxonomic infancy”, so that the establishment of a new species based on the alate queen (gyne) was also suitable at that time. The unique clypeal denticles and head setae of *Z. goldingot* did not create problems for future comparison and recognition? of worker ants within the species; moreover, the new wing type provided a reference for comparing reproductive ants of the genus. Thus, in consequence, the establishment of new species within the genus *Zigrasimecia* ought to be based now on worker ants as type specimens and the matching of all winged reproductive ants with existing taxonomic categories. For example, in the case of the alate female *Zigrasimecia* sp. described in this paper, and the alate female which was reported to have a complete internal structure (Zhuang et al., 2022b), new taxa should be established based on morphological comparison with the queen and finding worker ants that can be matched.

**4.2. New wing type of Zigrasimecia**

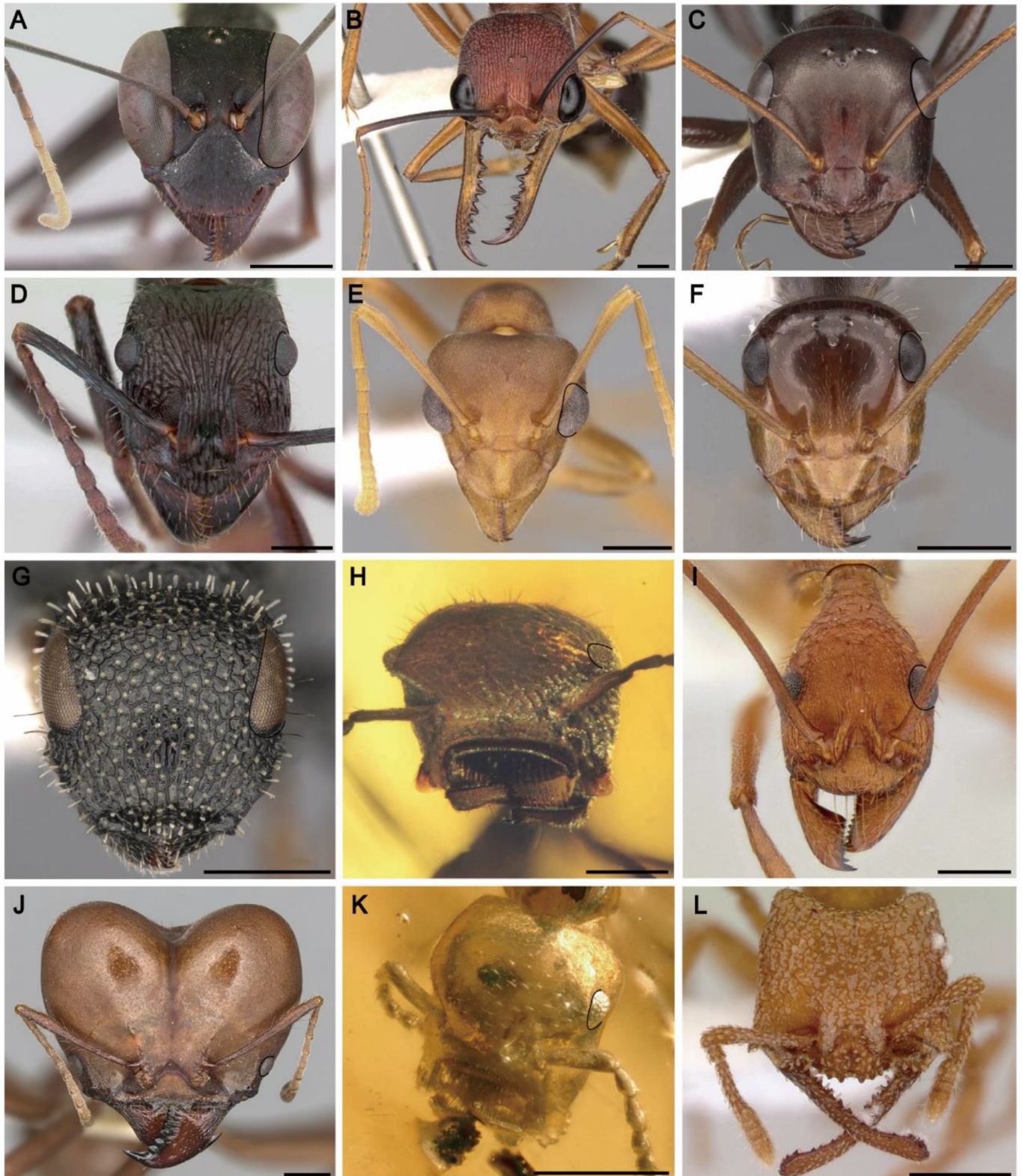
Alate female ant specimens have been found more and more frequently in recent years in the Cretaceous System (Guo et al., 2021; Zhuang et al., 2022a, 2022b). Based on the former records of *Zigrasimecia* alate female wing types, they are *Z. ferox* (Cao et al., 2020a), *Zigrasimecia* sp.1 (Cao et al., 2020b); [here we mark the undefined species as sp.1 to distinguish it from the specimen in this

**Table 1**  
Morphological features of eyes in different ant species (workers).

Ant genus /species	Rank eyes	Eye/head	Ommatidia	Eye (mm <sup>2</sup> )
<i>Gigantiops</i>	1	0.71	4137 ± 252	1.12
<i>Harpegnathos</i>	2	0.32 ± 0.02	1632 ± 241	0.77 ± 0.05
<i>Myrmecia</i>	3	0.14 ± 0.02	3237 ± 255	0.54 ± 0.12
<i>Cataglyphis</i>	4	0.11 ± 0.02	1059 ± 228	0.16 ± 0.02
<i>Ectatomma</i>	5	0.14 ± 0.02	841 ± 38	0.16 ± 0.01
<i>Oecophylla</i>	6	0.12 ± 0.02	942	0.13 ± 0.01
<i>Myrmecocystus</i>	7	0.21 ± 0.02	651 ± 42	0.21 ± 0.02
<i>Cataulacus</i>	8	0.12 ± 0.02	774 ± 226	0.14 ± 0.03
<i>Z. hoelldobleri</i>	9	0.09 ± 0.01	250 ± 30	0.06 ± 0.01
<i>Z. ferox</i>	10	0.12 ± 0.01	250 ± 30	0.04 ± 0.01
<i>Aphaenogaster</i>	11	0.08 ± 0.02	200	0.05 ± 0.01
<i>Atta</i>	12	0.02 ± 0.02	280	0.08 ± 0.04
<i>Z. zui</i>	13	0.06 ± 0.01	25 ± 1	0.02 ± 0.01
<i>Myrmium</i>	14	0.04 ± 0.02	15 ± 1	0.02 ± 0.01

**Notes:** This table is adapted from Gronenberg and Hölldobler (1999), where the data for workers are selected for comparison and their measurement methods are referenced: ants are characterized by the absolute size of their eyes (maximum cross-sectional area of the eye cup), relative eye size compared with frontal head area (eye/head ratio), and the number of ommatidia per eye. The relative eye size and the number of ommatidia are ranked and the mean of these ranks is listed as Rank eyes.





**Fig. 4.** Head comparison of †Zigrasimecia and some living ants (workers). Scale bars for (A), (B), (J) = 1 mm, for (C)–(I), (K), (L) = 0.5 mm. (A), *Gigantiops destructor*. (B), *Myrmecia fabricius*. (C), *Cataglyphis albicans*. (D), *Ectatomma edentatum*. (E), *Oecophylla longinoda*. (F), *Myrmecocystus depilis*. (G), *Cataulacus centrurus*. (H), †*Zigrasimecia ferox*. (I), *Aphaenogaster araneoides*. (J), *Atta bisphaerica*. (K), †*Zigrasimecia zui* sp. n. (L), *Myratrium camillae*. Notes: Images excluding K were downloaded from [AntWeb](https://antweb.org/) (2023).

paper]) and *Z. goldingot* (Zhuang et al., 2022a). It is not difficult to consider that the wing patterns of gynes in *Zigrasimecia* are highly convergent. All have seven sclerotised wing cells, similar DC1, SMC1 and MC1. The difference lies in whether the wing veins Rsf2-3 are convex to the inside of SMC1. However, *Zigrasimecia* sp. 2 is different with a new wing type: there are 8 sclerotised wing cells, 2r-rs splitting the original SMC1 into a new 'SMC1' and 'SMC2', and Rsf2-4 connected by a straight vein (Fig. 2).

Fossil ant wing types of other genera have been reported from the Cretaceous to be relatively similar to *Zigrasimecia* (viz. *Gerontoformica*, and *Camelomecia* Barden & Grimaldi, 2016; *Haidomyrmex* Guo, 2021). *Zigrasimecia* shares similar wing veins and cells with *Gerontoformica* (Ogata, 1991; Cao et al., 2020b). The wing vein development of *Zigrasimecia* sp. 2 is predictably highly uniform with other species within the genus, but there are subtle differences as described above. This may prove to be a derived condition of the general feature of 7 densely closed wing cells in most queen ant wing types in this genus.

#### 4.3. The ecological possibilities of concealed dwelling in *Zigrasimecia*

Most of the fossil ants reported in Kachin amber have strong locomotor potential or evidently good eyesight, e.g. *Haidomyrmecinae* (Barden et al., 2020) and *Sphecomyrminae* (Boudinot et al., 2022). Their developed compound eyes and elongated appendages suggest that these ants were vision-based predators in the tropical rainforest. With respect to specimens which have already been described in *Zigrasimecia*, only the gyne or queen have more developed compound eyes and elongated appendages (the ratio of forelegs to body length in this genus is female ~ 0.6, worker ~ 0.5) and these features may be related to nuptial flying habits in the mid-Cretaceous. However, the worker of *Zigrasimecia* has shorter appendages and smaller, less prominent compound eyes than either in *Haidomyrmecinae* or *Sphecomyrminae*, suggesting that these ants may have lived on the ground or within and were not particularly dependent on vision and motility for prey capture. Comparing the worker castes, *Z. zui* has the smallest body size, the fewest ommatidia, and the smallest ratio of compound eye to head area in the genus. In addition, the type specimen has some mud on the lateral side of the pygidium and around the mesosoma preserved in amber inclusions (Fig. 1). In order to extract greater morphological detail, CT scans and three-dimensional reconstructions of YKLP-AMB-005 have been undertaken (Fig. 3; Supplementary video 1).

Supplementary video related to this article can be found at <https://doi.org/10.1016/j.cretres.2023.105742>

The compound eye parameters of *Z. zui* were compared with those of *Z. ferox*, *Z. hoelldobleri*, and with those of extant ants from 11 diverse ecological niches (Table 1; Fig. 4. Note: Fig. 4 excludes *Harpegnathos* and *Z. hoelldobleri*, which appear in Table 1, as they lack salient differences compared with the others). On the basis of compound eye differentiation, the visual ability of *Z. zui* may have been similar to *Myrmica*, which now builds nests under rocks or dry logs on the ground (Molet et al., 2009; Larabee et al., 2018). Thus *Z. zui* possesses, at least in compound eye morphology, features that completely distinguish it from *Z. ferox* and *Z. hoelldobleri*. These significant differences in visual ability imply that differentiation of ecological niches already existed within this genus by the mid-Cretaceous.

#### 4.4. Conclusion

In the present study, we report *Zigrasimecia zui* sp. nov. and describe a new wing type of gyne within the genus *Zigrasimecia*.

The comparative morphological study augments our knowledge of this extinct genus and suggests, for the first time, possible ecological niche differentiation of these ants in the mid-Cretaceous. In the next step we can also extract the muds (the parts that are clearly distinct from the matrix) to further analyse the terrestrial environment at the time.

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