

## A revision of the Cretaceous ant genus *Zigrasimecia* Barden & Grimaldi, 2013 (Hymenoptera: Formicidae: †Zigrasimeciinae)

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### ABSTRACT

The extinct Cretaceous ant genus *Zigrasimecia* Barden & Grimaldi, the “iron maiden ants” from Myanmar, is revised, and five new species are described: †*Z. boudinoti* **sp. nov.**, †*Z. caohuijiae* **sp. nov.**, †*Z. chuyangsui* **sp. nov.**, †*Z. perrichoti* **sp. nov.**, and †*Z. thate* **sp. nov.** *Zigrasimecia hoelldobleri* paratype (CNU-HYM-MA2019054) is removed from the type series. New diagnoses for all species are provided and species boundaries are discussed. Studied specimens that are not ideally preserved are presented and discussed, some of them are putative new species. Two identification keys for the genus are provided, a traditional, dichotomous key and an interactive, multi-entry key hosted online at the website [www.Xper3.fr](http://www.Xper3.fr). I briefly discuss the unlikeliness of the genus *Boltonimecia* to belong to the subfamily Zigrasimeciinae, and also the taxonomic problem caused by the description of species based on alates and poorly preserved fossils.

**Key words:** Palaeoentomology, Burmese amber, Cenomanian Age, Stem ants

### 1. INTRODUCTION

Cretaceous ants preserved in amber have been found in deposits in Myanmar (Kachin State and Magway Region), U.S.A (New Jersey State), Russia (Taimyr Peninsula), France (Charentes), and Canada (Alberta Province) (Lapolla *et al.*, 2013; Zheng *et al.*, 2018). The first described species of this period was *Sphecomyrma freyi* Wilson & Brown, 1967. However, most Cretaceous ant diversity has only recently been described (Boudinot *et al.*, 2020a; Bolton, 2023). These species comprise, particularly those found in the Burmese amber deposits from northern Myanmar, an assemblage of stem Formicidae which are key to the understanding of the origins of the family (Lapolla *et al.*, 2013; Barden, 2017; Barden *et al.*, 2020; Boudinot *et al.*, 2020; Boudinot *et al.*, 2022a). Most of them belong to ant stem lineages of three subfamilies, Sphecomyrminae Wilson & Brown, 1967, Haidomyrmecinae Bolton, 2003, and Zigrasimeciinae Borysenko, 2017. A few are enigmatic and remain as Incertae Sedis in Formicidae (Boudinot *et al.*, 2022a).

The sphecomyrmines do not possess conspicuous aberrant morphological features (Barden & Grimaldi, 2014) and can be considered as “regular” ants among the Cretaceous fauna. The haidomyrmecines have spectacular cephalic features, including elongate, scythe-like mandibles, small to huge clypeal “horns”, and numerous types of odd chaetae, which are unparalleled both among extinct and extant ants (Perrichot *et al.*, 2020). Not as flagrantly bizarre as the haidomyrmecines, but still quite peculiar, are the zigrasimeciines, which possess a set of morphological traits, such as extreme fusion of mesosomal sclerites in most species and a unique combination of types of chaetae on the mouthparts and anterior cephalic capsule, which makes them unique (Cao *et al.*, 2020a, but see discussion on *Boltonimecia* in Section 3.4).

The Zigrasimeciinae currently comprises two Burmese genera, *Zigrasimecia* Barden & Grimaldi, 2013 and *Protozigrasimecia* Cao, Boudinot & Gao, 2020 and one Canadian genus, *Boltonimecia* Borysenko, 2017 (Cao *et al.*, 2020a). The genus *Zigrasimecia* and its first species, *Zigrasimecia tonsora* Barden & Grimaldi, 2013, was described based on a dealate queen. Shortly thereafter, a second species, *Zigrasimecia ferox* Perrichot, 2014, was described based on three well-preserved workers. Recently, *Zigrasimecia hoelldobleri* Cao, Boudinot & Gao, 2020

and *Zigrasimecia goldingot* Zhuang, Ran, Li, Feng & Liu, 2022 were added to the genus, the first based on workers and the latter based on a winged queen.

Modern ants have pronounced sexual dimorphism and, between female castes, morphological variation can vary from undetectable or mild (*Dinoponera* Roger, 1861, *Pachycondyla* Smith, 1858) to strong or very strong (*Iridomyrmex* Mayr, 1862, *Crematogaster* Lund, 1831, *Atta* Fabricius, 1804, *Dorylus* Fabricius, 1793). Finding these forms together within the colony or using genetic techniques to pair them allows us to determine the morphological variation between males and females, and between female castes of any given species. In the case of fossils, there is great difficulty in making that match, as the individuals are fossilized outside the colony and genetics cannot help. In *Zigrasimecia*, the existence of two out of four species described based on queens imposes to its taxonomy the following challenge: new species described based on workers, such as those described in this paper, could always potentially be synonyms of *Z. tonsora* or *Z. goldingot*, save when significant differences in pilosity, or in the shape of the head or metasoma occur, rule out chances of conspecificity. For example, any unidentified worker specimen having the pilosity similar to that of *Z. hoelldobleri* is unlikely to belong to *Z. tonsora* or *Z. goldingot*, because both queens lack the typical thick, erect, and clubbed setae of *Z. hoelldobleri*. On the other hand, if a specimen has similar pilosity to either *Z. tonsora* or *Z. goldingot*, it can be really hard to discard it as a possible worker caste for those species, because when pilosity is similar, there remain only a few traits to be considered as evidence to judge whether a match is correct or not; the shape of the head and the metasoma (especially the petiole) being the main things, but even in those respects, queens and their workers sometimes naturally vary considerably (so a non-match does not necessarily indicate non-conspecificity).

*Zigrasimecia* specimens from the Hukawng Valley, Myanmar, were made physically available for study. Here, I revise the genus based on those specimens, images of all specimens from the literature, and a few images of specimens maintained in private collections. A revised genus diagnosis is given, five new species are described, and identification keys are provided, including an interactive, multi-entry key. I briefly discuss the placement of the genus *Boltonimecia* as a member of the Zigrasimeciinae and the taxonomic difficulty created when species are described based on queens, males, or poorly preserved fossils.

## 2. MATERIALS AND METHODS

**2. 1. Repository institution and databank.** Specimens physically studied and described were donated from the author's private collection to the Entomological Collection of the Coleoptera Systematics Laboratory (CELC), at the Universidade Federal de Viçosa, Minas Gerais, Brazil (Evenhuis, 2023). The specimens physically examined, discussed as morphospecies, and not described are deposited in the author's private collection (JCMCC, Júlio C. M. Chaul, personal collection). Images of some specimens deposited at the Yunnan Key Laboratory for Palaeobiology (YKLP), Institute of Palaeontology, Yunnan University, Kunming, China, were made available by Yuhui Zhuang (studied, but not presented in this paper, except in the multi-entry key and all uploaded to Antweb). Images of other specimens from the private collections of Michele Baldi, from Vicenza, Italy (MBC, Michele Baldi, private collection) and José Gómez Durán, Madrid, Spain (JGDC, José G. Durán, private collection) were also studied (a few images presented in this paper, all included in the multi-entry key and all uploaded to Antweb).

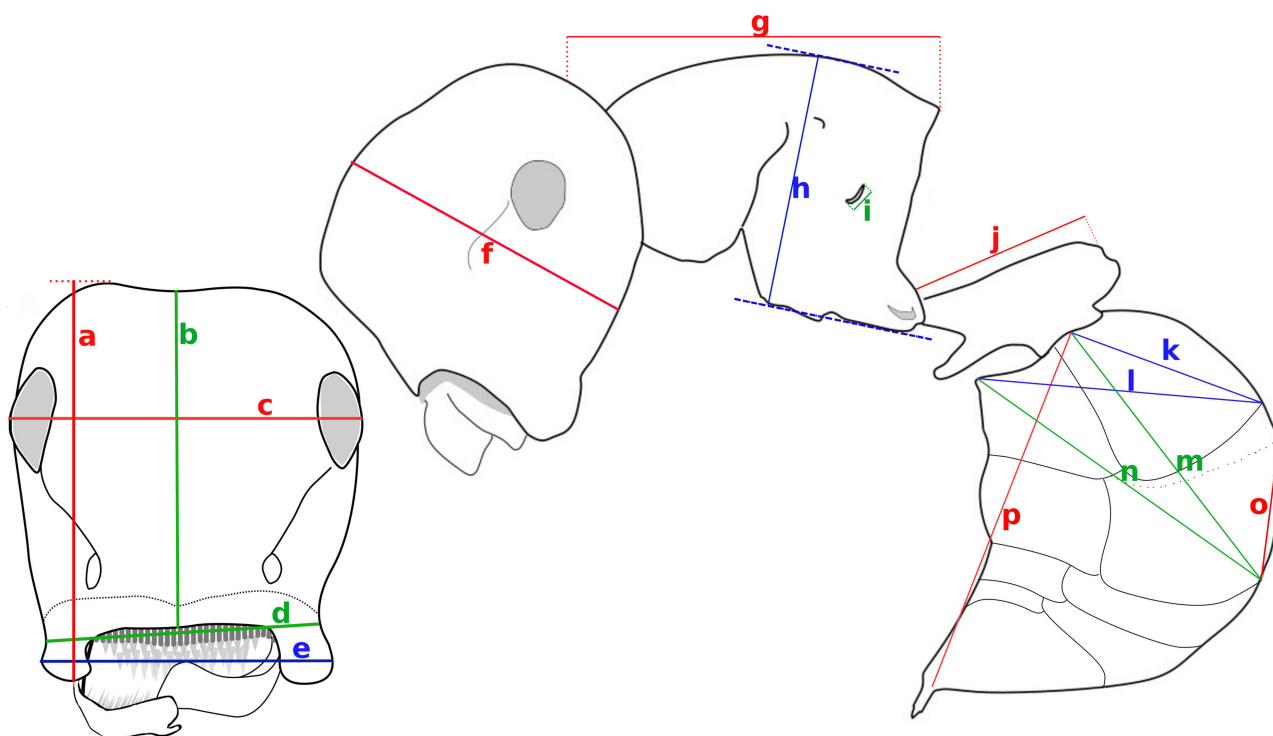
The study of specimens deposited in private collections does not meet the standards recommended by the Society of Vertebrate Paleontology (SVP) (Rayfield *et al.*, 2020), although none of the described species in this paper are in private collections (only specimens discussed as morphospecies). A critical response to the SVP recommendation was given by Haug, C. *et al.* (2020) to which I here concur. Partnerships between amateurs and scientists are beneficial in the study of amber: on the one hand, scientists gain by having access to specimens (sometimes physically, sometimes through images); on the other hand, amateurs are guided into the scientific practice, in the case of paleontology, by receiving curating tips from scientists. Additionally, during this exchange, there is an opportunity to discuss the importance of ultimately depositing their specimens in public institutions. Moreover, among burmite private collectors, some are experienced photographers who produce high-quality images, often as good as or better than those made by scientists.

**2. 2. Studied specimens.** Specimens studied were bought from Chinese Ebay sellers who confirmed their source being the Hukawng Valley, in Kachin State, northern Myanmar. I was able to confirm that part of the specimens were bought by one of the sellers in Tanai township, Myitkyina District (a locality where amber mined in the Hukawng

Valley is first traded). Other specimens were bought from a seller who directly mined, processed, and traded the stones (personal communication by Cunte, or “Terry Su”, a burmite miner and trader). Ambers from this locality are suggested to be early Cenomanian in age ( $98.79 \pm 0.62$  Ma, Shi *et al.* 2012).

Stones, received from the sellers usually as roughly polished pebbles, were cut and faceted to allow inspection in desirable views and to bring the specimen closer to the surface, since flat surfaces and less amber matrix between the specimen and facet increase visibility and resolution. Facets were made with a series of increasingly finer sandpapers (100 to 3000 grit) and then polishing paste was applied. Facets revealing the dorsal, profile and the full-face views were preferred. In specimens for which, for any reason, these views would not be informative (either for the presence of bubbles, debris, or for the position of the ant itself) or hard to achieve (due to the conditions of the stone), facets with alternative angulation were made. Prepared specimens were glued to a small piece of plastic sheet, and then pinned and labeled, as regular dry-mounted entomological collections specimens. All specimens studied were purchased from 2018 onwards. Due to the political and military conflicts that occurred in Myanmar, the SVP, in the same letter cited above, requested/recommended to editors of peer-reviewed journals a moratorium on publication for any fossil specimens purchased from sources in Myanmar after June 2017 (Rayfield *et al.*, 2020; Theodor *et al.*, 2021). A response to the 2020 SVP letter in disagreement with their position was given by Haug, J. *et al.* (2020), to which I concur. The CELC manifested in favor of housing the holotypes here designed.

**2.3. Imaging.** Images were acquired using a Canon 1100D mounted either on a Leica APO S8 stereomicroscope (with 2x auxiliary objective), an Olympus CX41 compound microscope, or an Olympus BX60 epifluorescence microscope. Raw images were processed in Zerene, Gimp (Kimball & Mattis, 1996) and ImageJ (Schneider *et al.*, 2012) softwares for stacking, enhancing, and scaling, respectively. Specimens in amber are often hard to illuminate satisfactorily, so multiple (up to four) strong LED illuminators and various layers of tracing paper (used as light diffusers in between the lights and the specimens) were oriented around the specimen before each series of photos were taken to maximize the penetration of diffused light in the amber matrix. All images, including some not shown in the figures, are deposited in high resolution on Antweb.org.



**FIGURE 1.** Schematic drawings of most of the measurements taken from the specimens (presented in the species descriptions or in Appendix 1). See Materials and Methods or Appendix 1 for a detailed explanation of the measurements. Codes: **a**, head length; **b**, head length 2; **c**, head width; **d**, head width 2; **e**, head width 3; **f**, head maximum depth; **g**, mesosoma length (see also Fig.6); **h**, mesosoma height; **i**, propodeal spiracle length; **j**, petiole anterior face length; **k**, posttergite 3 length; **o**, posttergite 4 length. Measurements **a**, **g**, **j**, **k**, and **o** summed equal total length (TL). Gaster measurements **l**, **m**, **n**, and **p** are additional metasomal measurements that are useful if the measurements **k** and **o** are blocked (see Appendix 1).

**2. 4. Terminology.** I followed Bolton (2003) and Keller (2011) for most terms. The term “chaetae” (Boudinot *et al.*, 2020; Boudinot *et al.*, 2022a; Boudinot *et al.*, 2022b) was used to describe the clypeal, labral, and mandibular armature in place of denticles or spicules (Perrichot, 2013). For the mesosomal sclerites of the gynes I followed Boudinot (2015); specifically for the pleural regions of workers and gynes I followed Aibekova *et al.* (2022).

**2. 5. Measurements.** Various measurements were made additionally to the ones presented under each species (Fig. 1). All such measurements and their detailed descriptions are given in Appendix 1 and are replicated in the following online spreadsheet for ease of data prospection:

[https://docs.google.com/spreadsheets/d/1svFwd3IEKKgWVCCcpDpxa3I1kPWkxtWWHva0t8M2cAw/edit?usp=share\\_link](https://docs.google.com/spreadsheets/d/1svFwd3IEKKgWVCCcpDpxa3I1kPWkxtWWHva0t8M2cAw/edit?usp=share_link)

They are intended to serve as a database for standardized future work on the genus and can also help in the identification of fragmentary specimens which commonly have only one or a few measurable parts preserved in the body. Such measurements, if not helping for precise identification of a species, will at least narrow down the possibilities in the identification process.

In the main text, under each description, the following measurements are given:

**HL**—In full-face view, the straight line from anteriormost point of clypeal lobe to posteriormost point of vertex (Fig. 1, a).

**HW**—Maximum width of posterior half of the head in full-face view. Usually the widest portion of head and at the eye level. Measurement captures the bulging eyes, if eyes are like so (Fig. 1, c).

**EL**—Maximum diameter of compound eye, preferably taken in lateral view.

**ON**—Ommatidia number approximate count.

**MesL**—Measured in dorsal or lateral views, from anteriormost point of pronotal neck to posteriormost point of propodeum (Fig. 1, g and Fig. 6, F). If propodeum has a concave posterior surface (in dorsal view forming a concave posterior margin), then the measurement posterior end is at the midpoint of an imaginary line that touches the apex of the posterolateral propodeal protruberances (Fig. 1, g, although it is preferably taken in dorsal view as depicted in Fig. 6, F). This is an alternative measurement to Weber's length which is usually difficult to be extracted from fossils that lack a side view and even harder in *Zigrasimecia*, since the head normally blocks part of the pronotal anterior section in lateral view.

**MesH**—Height of mesosoma measured in profile as the distance between the "mesosoma floor line" and the "mesosoma peak line". The "mesosoma floor" being a horizontal imaginary line where meso- and metathorax lower margins sit and the "mesosoma peak" being an imaginary line parallel to the mesosoma floor line and touching the uppermost mesosomal point (Fig. 1, h).

**PetAFL**—Length of the anterior face of the petiole, measured either in lateral or full view of the anterior surface of the petiole (Fig. 1, j).

**Ptg3L**—Length measured in lateral view from anteriormost point of third posttergite (at mid-height of petiolar insertion) to its posteriormost point (Fig. 1, k).

**Ptg4L**—Length of fourth posttergite in dorsal or lateral view (Fig. 1, o). It can be hard to differentiate between pre- and posttergites (to detect when pretergite is exposed); pilosity helps in such cases, as they are present on posttergite, but not in pretergite.

**TL**—Total length of the body is the sum of HL, MesL, PetAFL, Ptg3L, and Ptg4L. This incomplete "total length" is an attempt to rule out errors caused by the distention of the gaster. The error consists of the fact that abdominal segments V to VII length vary a lot from specimen to specimen due to what degree pre- and postsclerites are inserted into each other. This can, therefore, artificially and significantly change the variation of total length of a species. To use only measurements of the posttergites III and IV in the sum is ideal as they are the greatest in the gaster, therefore accurately reflecting the species size. Mandible length is also excluded from TL, as in *Zigrasimecia* the mandible anteriormost point is at about the same level as the anteriormost point of the clypeal lobes when mandible is closed.

**2. 6. Identification.** Apart from the dichotomous key below, an interactive, multi-entry key was also constructed and is hosted in the Xper<sup>3</sup> platform (Ung *et al.*, 2010; Vignes-Lebbe *et al.*, 2017, Kerner *et al.*, 2021). It works online, in the web browser, and does not require any software installation. Different from the dichotomous key, in the multi-entry key some important specimens or morphospecies are included together with the formally described species (only *Zigrasimecia* ufv-11 included in the dichotomous key). It works by the user choosing any of the

characters in the list, preferably one that is clearly seen in the specimen at hand. Upon choosing the character, character states are presented and the user chooses the one that matches better the keyed specimen. As this process repeats the list of possible species gets shorter each time until, ideally, only one species remain. The user must then click on that species to see its various images, measurements, and diagnosis to confer if the result makes sense as an identification for the specimen.

### 3. RESULTS

I studied physically eleven specimens. Through images, I studied five specimens of the private collections of José Gonzalez (Madrid, Spain) and Michele Baldi (Vicenza, Italy), and all published images of specimens so far (Barden & Grimaldi, 2013; Perrichot, 2014; Cao *et al.*, 2020; Zhuang *et al.* 2022a; Zhuang *et al.* 2022b; Antweb, 2023). Five new species are described below, totaling nine species for the genus. Some of the studied specimens might represent other new species but are not described due to the overall poor preservation of the fossils which prevents visualization of a number of key features; they are instead discussed after the Taxonomy section.

#### 3. 1. Identification.

Multi-entry keys have the advantage of allowing the identification of poorly preserved specimens that have only a few recognizable characters, a common situation in paleontology. Such specimens would easily get "stuck" in couplets of a traditional dichotomous key and the identification process would fail. This interactive, multi-entry key will be constantly updated to include new species, morphospecies, or variations described/reported in future publications. Considering the current rate of description of burmite inclusions (Guo *et al.*, 2017), the genus is expected to grow in diversity soon. The multi-entry key can be accessed through the following link:

<http://www.xper3.fr/xper3GeneratedFiles/publish/identification/-680003750967095397/mkey.html>

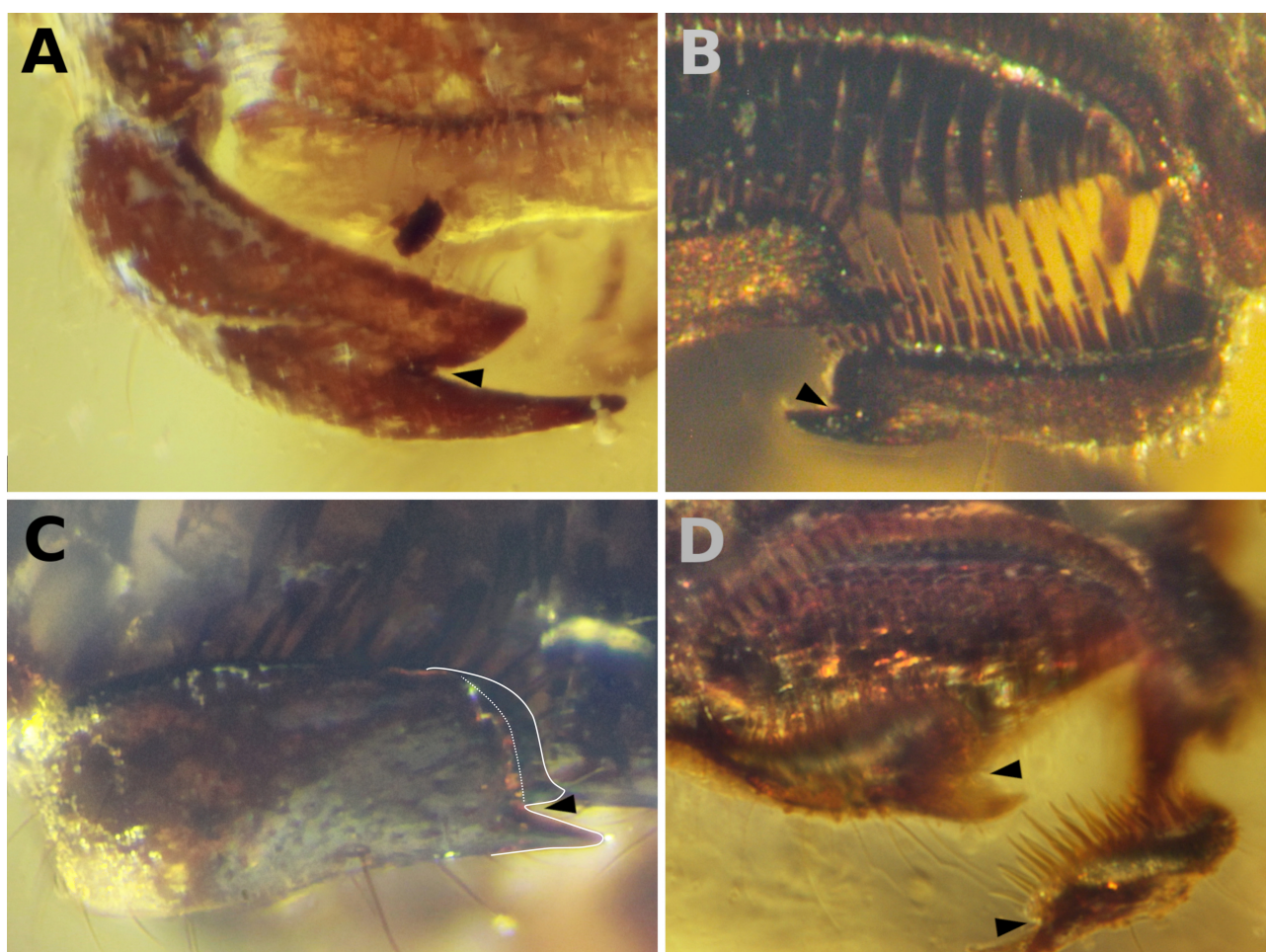
Nevertheless, a traditional dichotomous key, including all described species and the morphospecies *Zigrasimecia* ufv-11 (see below under section 3. 3), was also made and is presented below.

#### Key to the females of *Zigrasimecia*

Notes: *Z. tonsora* and *Z. goldingot*, described based on queens, are tentatively included in the key based on their head and metasomal characters. Any mesosomal character mentioned in the key must not be considered if the keyed specimen is a queen.

1. The specimen is a gyne: mesosoma is complex, having discernible mesoscutum and mesoscutellum and clear divisions between the sclerites ..... 2
- The specimen is a worker: mesosoma is compact and simplified, most sclerites are fused and indiscernible ..... 3
2. [Triplet] With the following combination of characters: More than 30 clypeal chaetae. Petiole having a distinct anterior, dorsal, and posterior surfaces; dorsal surface appearing flat (Fig. 1, B of Barden & Grimaldi, 2013). Head having short, fine setae on frons and vertex which are progressively longer posterad. Frons with a V-shaped shallow groove. Propodeum dorsal surface long (Fig. 2, A and B of Barden and Grimaldi, 2013) ..... ***Z. tonsora* Barden & Grimaldi, 2013**
- With the following combination of characters: Less than 25 clypeal chaetae. Petiole node apex brief, not forming a distinct dorsal surface. In anterolateral (or posterolateral) views of the petiole, apex of node bilobed. Setation on body mostly of decumbent small setae. Frons without grooves. Propodeum dorsal surface short (micro-CT scan image by Yuhui Zhuang available at Antweb under specimen YKLP-AMB-001) ..... ***Z. goldingot* Zhuang *et al.*, 2022**
- Without the above two combinations. From now on, run your queen specimen in the key without considering mesosomal characters whenever mentioned ..... 3
3. Abundant and conspicuous standing setae on dorsum of head, mesosoma, and metasoma. Setae varying in morphology (Figs. 6, 8, 11) ..... 4
- Conspicuous standing setae on body absent or restricted to dorsum of head. Body mainly glabrous, at most covered by very small, appressed, setae (Figs. 7, 8, 12, 13) ..... 7
4. Standing setae on body thin and filiform (Figs. 6, 9) ..... 5
- Standing setae on body thick, tip of individual seta truncate and sometimes slightly clavate (Fig. 14) ..... ***Z. hoelldobleri* Cao *et al.*, 2020**

5. Setae on body sparse, relatively short, erect (not flexuous). Tip of petiolar node truncate. Cinctus on abdominal segment IV weak, but discernible (Fig. 11) ..... ***Z. ferox* Perrichot, 2014**
- Setae on body flexuous and relatively long, usually abundant. Tip of petiolar node either round and without paired protrusions (Fig. 10, D) or thin (barely forming a dorsal surface) and with a pair of protrusions (Fig. 6 D). Cinctus on abdominal segment IV vestigial to absent . . . . . 6
6. Mesosoma extremely compact, "chubby". Frontal carina vestigial, merely a soft oblique bump between the torulus and the eye. Tip of petiolar node round. Head in full-face view round, with poorly differentiated lateral and vertexal margins. Eyes with less than 100 ommatidia (Fig. 9) ..... ***Z. chuyangsui* sp. nov.**
- Mesosoma not particularly compact. Frontal carina conspicuous. Tip of petiolar node with a pair of protrusions. Head in full-face view subrectangular, having distinct lateral and vertexal margins. Eyes with more than 150 ommatidia (Fig. 6) . . . . . ***Z. boudinoti* sp. nov.**
7. Dorsum of head, at the frontal and vertexal areas, with a conspicuous patch of setae which can be raised and long, and flagellate or short, decumbent and curved . . . . . 8
- Dorsum of head without a patch of specialized setae . . . . . 9
8. Long, subflagellate, looped setae on dorsum of head. Head in full-face view almost as long as broad (Fig.13) . . . . . ***Z. thate* sp. nov.**
- Short, curved, and decumbent setae on dorsum of head. Head in full-face view slightly longer than wide (Fig. 20). . . . . ***Zigrasimecia* ufv-11**
9. Head in full-face view subrectangular. In profile, propodeal dorsal and posterior (descending) margins distinct. Medium-sized species (TL 2.86) (Fig. 12) . . . . . ***Z. perrichoti* sp. nov.**
- Head in full-face view round. In profile, propodeal dorsal and posterior (descending) margins softly merge into each other. Small species (TL 2.25) (Fig. 7) . . . . . ***Z. caohuijiae* sp. nov.**



**FIGURE 2.** Masticatory margin of mandible in *Gerontoformica* and *Zigrasimecia*. **A**, *Gerontoformica* sp. (ANTWEB1032629); **B**, *Z. ferox* (ANTWEB1008126); **C**, *Z. chuyangsui* (ANTWEB1032660); **D**, *Z. tonsora* (ANTWEB11008098). Black triangles indicate incision between apical and basal teeth (or basal lamella). Image of *Z. tonsora* by Philip Barden and image of *Z. ferox* by Vincent Perrichot, courtesy of Antweb.org.

### 3. 2. Taxonomy

#### Synopsis of the genus †*Zigrasimecia* Barden & Grimaldi, 2013

- †*Zigrasimecia* Barden & Grimaldi, 2013: 407. Type-species: †*Zigrasimecia tonsora*, by original designation.  
†*Zigrasimecia incertae sedis* in Formicidae: Barden & Grimaldi, 2013;  
†*Zigrasimecia* in †Sphecomyrminae: †Sphecomyrmini: Perrichot, 2014;  
†*Zigrasimecia* in †Sphecomyrminae: †*Zigrasimeciini*: Borysenko, 2017;  
†*Zigrasimecia* in †*Zigrasimeciinae*: Boudinot *et al.*, 2020

#### Species list

- †*Zigrasimecia boudinoti* Chaul, **sp. nov.** Myanmar (Burmese amber, early Cenomanian).  
†*Zigrasimecia caohuijiae* Chaul, **sp. nov.** Myanmar (Burmese amber, early Cenomanian).  
†*Zigrasimecia chuyangsui* Chaul, **sp. nov.** Myanmar (Burmese amber, early Cenomanian).  
†*Zigrasimecia ferox* Perrichot, 2014. Myanmar (Burmese amber, early Cenomanian).  
†*Zigrasimecia goldingot* Zhuang, Ran, Li, Feng & Liu, 2022. Myanmar (Burmese amber, early Cenomanian).  
†*Zigrasimecia hoelldobleri* Cao, Boudinot & Gao, 2020. Myanmar (Burmese amber, early Cenomanian).  
†*Zigrasimecia perrichoti* Chaul, **sp. nov.** Myanmar (Burmese amber, early Cenomanian).  
†*Zigrasimecia thate* Chaul, **sp. nov.** Myanmar (Burmese amber, early Cenomanian).  
†*Zigrasimecia tonsora* Barden & Grimaldi, 2013. Myanmar (Burmese amber, early Cenomanian).

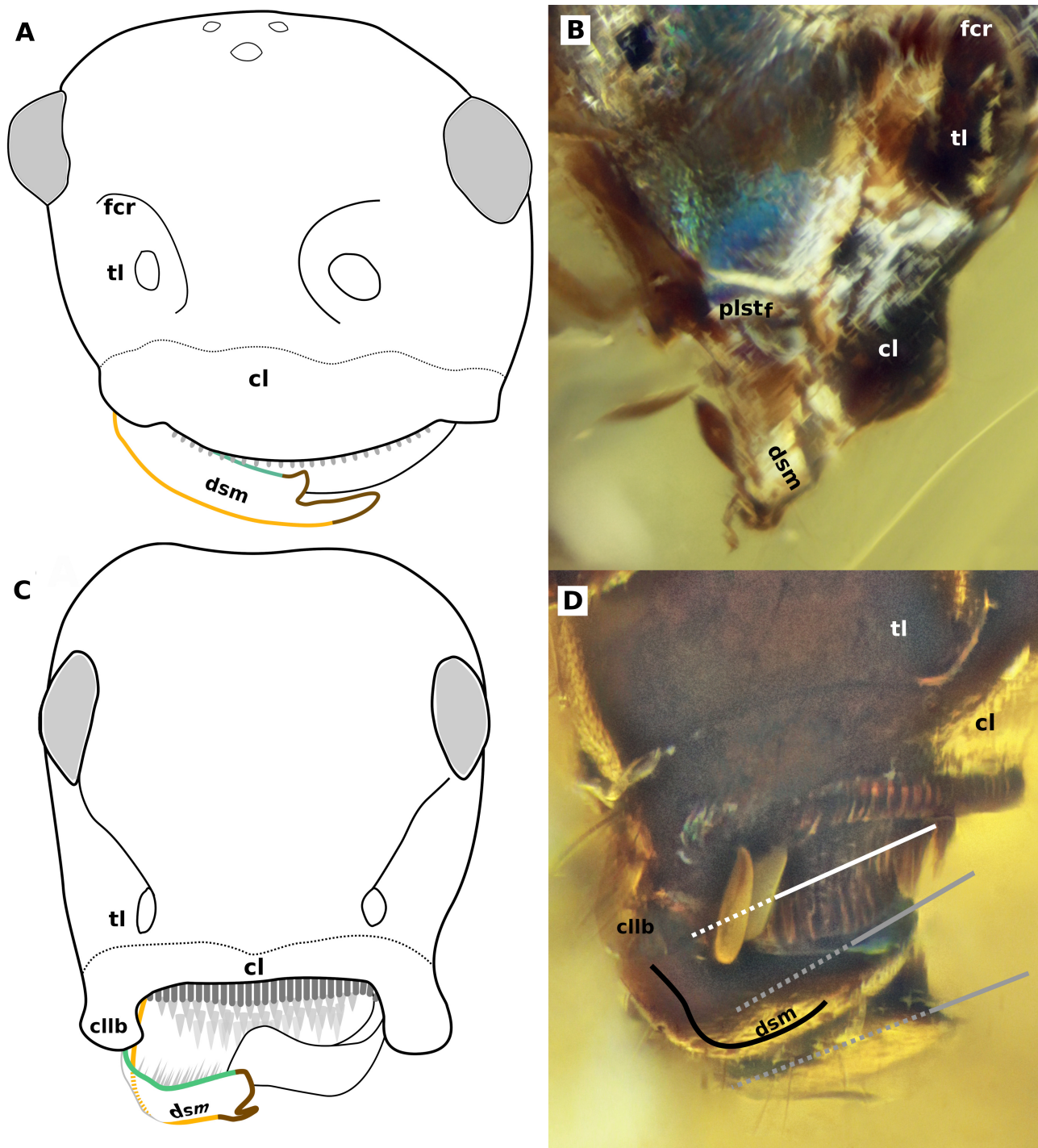
#### †*Zigrasimecia* emended diagnosis (females).

Note: all traits are observed in workers and queens, except when noted.

Masticatory margin of mandible formed by a developed apical tooth and a low, long, rectangular lamella which spans most the masticatory margin posterad the apical tooth; the lamella often ends apically in a marked angle or even an indented point; the apical margin of the lamella and the basal margin of the apical tooth form a small V-shaped groove (Note 1; Fig. 2). Inner surface of mandible densely covered with thin, spiny chaetae (Note 2). Body of mandible strongly torqued approximately in between its first and second thirds and mandibular insertion shifted ventrolaterally (Note 3; Fig. 3 and 4). Apical portion of body of mandible spatulate (Note 3; Fig. 7, F; Fig. 10, A). Labrum large, having stout, spiny chaetae basally and medially, distal margin medially with a pair of low lobes (Note 4 and 5; Fig. 7, D and F; Fig. 10, A). Palp formula variable, either 5, 3 or 6, 4 (Note 6). Cross-section of cephalic capsule bean-shaped or omega-shaped (Note 7). Pleurostomal fossa lateroventrally migrated (Note 3, Fig. 4, B). Clypeus transverse, mildly arched. Clypeal lobes strongly developed and anteriorly projected over mandibular insertions (Note 8). Clypeal chaetae blunt, relatively long, and densely arranged across anterior clypeal margin (Note 9). In full-face view, anterior clypeal margin strongly concave. Frons strongly protruded dorsally (Note 10). Frontal carina originating somewhere at the posterior (upper) or medial (inner) torular edge and reaching the perimeter of the compound eyes anteromedially; sometimes poorly marked (Note 11). Ocelli absent in workers. Antenna of worker and alate gyne 12-merous. Scape at least twice the length of pedicel. Mesosoma compact, most sclerites fused; dorsal sutures and lines absent; dorsal margin of mesosoma in profile without abrupt breaks, varying from mildly to strongly convex; mesosomal spiracles (metanotal and propodeal) without hood-shaped protrusions over their openings; metanotal spiracle facing laterally; propodeal spiracle slit-shaped and large; mesonotal and metanotal spiracles very approximated (workers only, Note 12, Fig. 5, but see *Zigrasimecia* ufv-10, Fig. 19). Calcar with or without a bifid tip (Note 13). Tibial spur formula 2s, 2 (1p, 1s) (Note 14). Tibiae either anteroposteriorly flattened or being approximately cylindrical. Pretarsal claws inner margins toothed. Petiole sessile or subsessile, in most species roughly pyramidal; anterior surface oblique, the longest; dorsal surface sometimes brief (only a curved or sharpened transition to the posterior surface), sometimes properly forming a flattened or round surface; posterior surface descending, shorter than the anterior; subpetiolar process conspicuous, anteriorly inclined (Note 15). Helcium (= articulatory sclerites of abdominal segment III) axial, situated at segment III midheight. Poststernite III having a keel-shaped or acute V-shaped anterior process (the "prora"). Abdominal segment IV lacking or having a soft constriction between its pre- and postsclerites, the cinctus (Note 16). Gyne: most head and metasomal characters similar to workers. Mesoscutum and mesoscutellum demarcated by sulcus; mesosoma muscled for

flight; forewing with seven closed cells: the costal, two submarginal, one marginal, the basal, subbasal, and first discal.

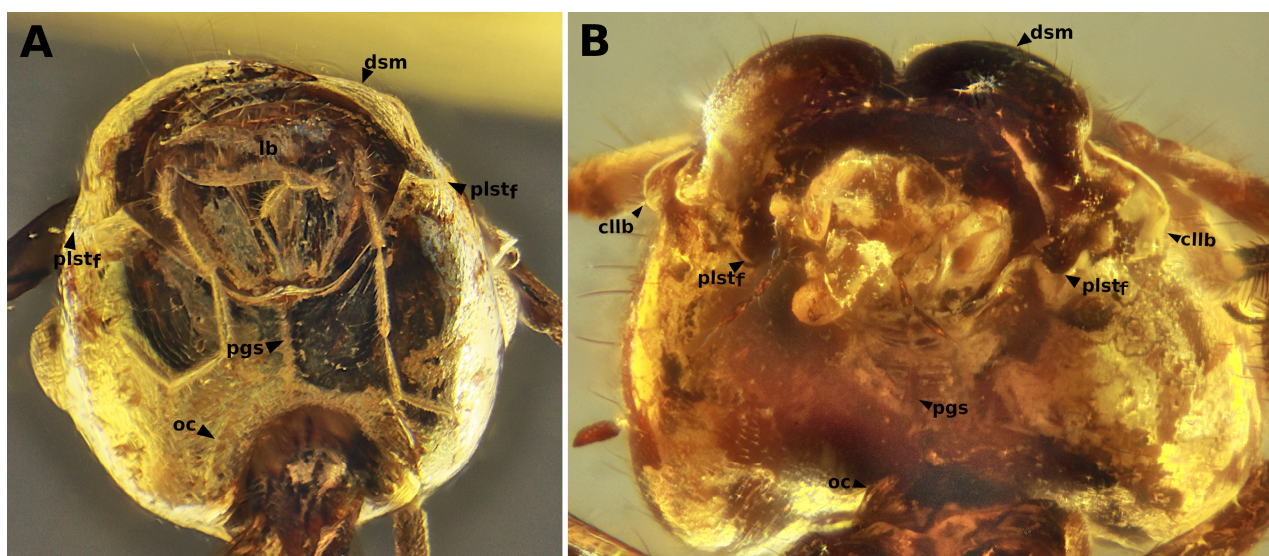
**Note 1.** This character varies slightly among the species in terms of how tall the lamella is and how sharply defined its apical angle is.



**FIGURE 3.** Comparison between *Gerontoformica* and *Zigrasimecia* cephalic and mandibular morphology (see genus diagnosis above for detailed explanation). A and C, schematic drawing of full-face view of *Gerontoformica* and *Zigrasimecia*, respectively. B and D, lateral view of anterior head of *Gerontoformica* (ANTWEB1032649) and *Zigrasimecia* (ANTWEB1032623), respectively. Abbreviations: **cl**, clypeus; **cllb**, clypeal lobe; **dsm**, dorsal surface of mandible; **fcr**, frontal carina; **plstf**, pleurostomal fossa; **tl**, torulus. In D, white line indicates plane (as seen laterally) of labrum; gray line is the plane (as seen laterally) of the apical half surface of the mandible; and black line shows the strong mandible curvature.

**Note 2.** Somewhat similar mandibular chaetae on the oral surface are found in *Camelomecia* Barden & Grimaldi, 2016 (apparently thinner than those of *Zigrasimecia*), and *Brownimecia* Grimaldi *et al.*, 1997 (relatively smaller than in *Zigrasimecia*); among extant ants, in *Tatuidris* Brown & Kempf, 1968 (very similar to *Zigrasimecia*) and in some leptanillines, such as *Protanilla izanagi* Terayama, 2013 (strikingly similar).

**Note 3.** The ventral mandibular articulation, and the corresponding pleurostomal fossa, in *Zigrasimecia* is strongly ventrally shifted when compared to *Gerontoformica* and, in fact, most other ants (Fig. 4, see also Fig. 3 of Richter *et al.*, 2022). Because of that shift, the expected plane of movement for the closing mandibles if they were not torqued would be from an anterolateral to posteromedial, similar to what is understood for the Haidomyrmecinae (Barden & Grimaldi, 2012; Barden *et al.*, 2017), instead of a regular lateral to medial plane. The torsion of the body of the mandible, however, prevents its flat apical portion to rise posterad during the shutting movement and makes the apical torqued portion to stay parallel and beneath the labrum when both are in full adduction. This generates an increase in the contact zone between the mandible inner surface and the dorsum of labrum, both surfaces covered on spiny chaetae (Fig. 3, D). The flat, expanded, apical portion of the mandible further increases this contact surface between mandibles and labrum. This mechanism presumably allowed *Zigrasimecia* to have a strong grip, which could be an adaptation for hunting arthropods, maybe prey much larger than the ants itself, as do the amblyoponines, which prey on centipedes much larger than the individual ants; or, alternatively, for hunting prey which has powerful escaping devices (e.g. the furca of springtails).



**FIGURE 4.** Ventral view of the head of *Gerontoformica* (A) and *Zigrasimecia* (B). Abbreviations: **cllb**, clypeal lobe; **dsm**, dorsal surface of mandible; **lb**, labrum; **oc**, occipital carina; **pgs**, postgenal suture; **plstf**, pleurostomal fossa.

**Note 4.** A hypertrophied labrum is unusual in Formicidae. In Sphecomyrminae it occurs in *Myanmyrma maraudera* (Barden & Grimaldi, 2016). In extant ants, robust and considerably developed labra are observed in the Dorylinae. Highly modified, but not necessarily hypertrophied, labra are seen in the closely related ants of the genus *Strumigenys*, the phalacromyrmecine genera, and the basicerotine genera, with a few species, *Eurhopalothrix spectabilis* Kempf, 1962 and *Rhopalothrix jtl015* (USNMENT00688794) having very large labra, the latter, indeed, resembling considerably that of *Zigrasimecia* in terms of shape.

**Note 5.** Although labral chaetae occur among other Cretaceous ants (e.g., *Myanmyrma* Engel & Grimaldi, 2005, some *Gerontoformica* Nel & Perrault, 2004, *Dhagnathos* Perrichot *et al.*, 2020 and *Chonidris* Perrichot *et al.*, 2020), the exact conformation seen in *Zigrasimecia*, with the chaetae forming a dense patch formed by various rows on the basal-medial portion of the labrum disc (not restricted to one or two transversal basal row) and being stout and pointy is unique to the Zigrasimeciinae. In extant genera, labral chaetae are usually disposed as a basal, transverse row and are seen in the following genera: *Protanilla* Taylor, 1990, *Anomalomyrma* Taylor, 1990, *Opamyrma* Yamane *et al.*, 2008, *Apomyrma* Brown *et al.*, 1971, *Amblyopone* Erichson, 1842 and *Onychomyrmex* Emery, 1895.

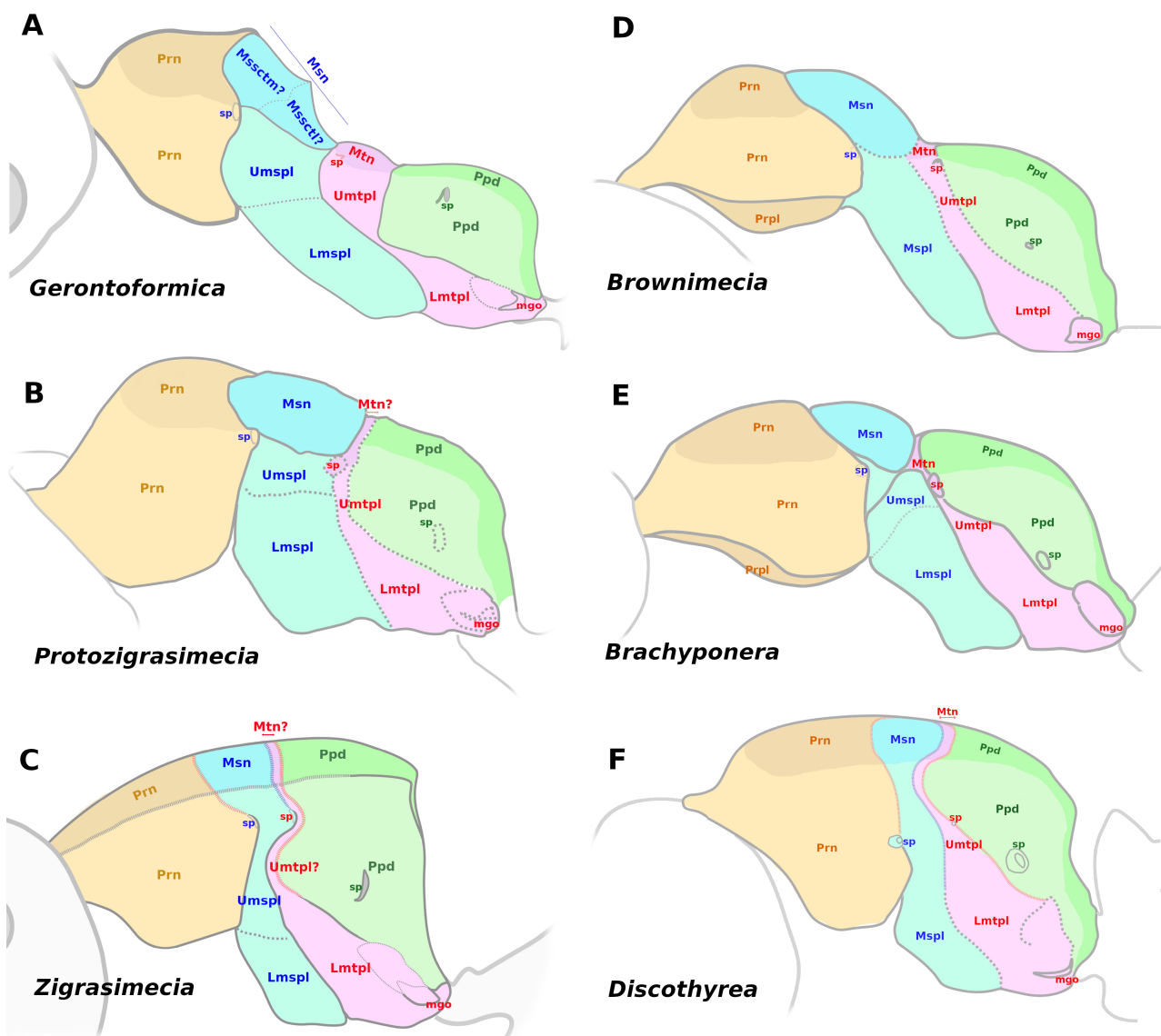
**Note 6.** The palpal formula of *Z. ferox* is 5, 3 (Perrichot, 2014). The only species which could have its palpal formula established in this paper, *Z. chuyangsui* **sp. nov.**, showed an undoubted 6, 4 count (Fig. 10, B), indicating variation in the palpal formula within the genus. The queen *Zigrasimecia* YKLP-AMB-002 also has the palpal formula 6, 4 (although presented as 4, 3 in Zhuang *et al.*, 2022b, see below).

**Note 7.** This feature is widespread in the genus, although more conspicuous in *Z. chuyangsui* **sp. nov.**, *Zigrasimecia* ufv-08, when compared to species like *Z. thate* **sp. nov.** or *Z. perrichoti* **sp. nov.**.

**Note 8.** Smaller clypeal lobes, which are only slightly projected over mandible insertions, are seen in some species of *Gerontoformica* (e.g. *Gerontoformica* ufv-01, ANTWEB1032418), *Myanmyrma*, and *Boltonimecia*.

**Note 9.** Among fossils, clypeal chaetae are seen in *Gerontoformica* and *Myanmyrma*, *Aquilomyrmex*, *Dhagnathos* and *Chonidris*. Among extant ants such setae are present in *Opamyrra*, *Apomyrra* and in most amblyoponine genera. However, the *Zigrasimecia* type of relatively elongate with subparallel sides and round/truncate apex chaetae is very rare or unseen in other stem ants or extant lineages, with a similar shape only seen in *Apomyrra*, *Opamyrra* and *Stigmatomma pluto* (Gotwald & Léviex, 1972).

**Note 10.** This feature is best seen in profile view, where anterior half of the head dorsum outline is strongly oblique from the anterior clypeal margin to the frons level (Figs. 6, E; Fig. 13, B). Despite having a prominent frons, there is no sign of an elevated platform on the frons and vertex as that of *Boltonimecia* and which was suggested as a character shared between both genera (Borysenko, 2017, see section 3. 4 below).



**FIGURE 5.** Types of mesosoma in fossil and extant ants. **A**, *Gerontoformica*; **B**, *Protozigrasimecia*; **C**, *Zigrasimecia*; **D**, *Brownimecia*; **E**, *Brachyponera* and **F**, *Discothyrea*. Among extant ants, *Discothyrea* presents a degree of mesosomal compaction similar to that of *Zigrasimecia*. Abbreviations: **Lmspl**, lower mesopleuron; **Lmtpl**, lower metapleuron; **mgo**, metapleural gland opening; **Msn**, mesonotum; **Mspl**, mesopleuron; **Mssct**, mesoscutum; **Mssctl**, mesoscutellum; **Mtn**, metanotum; **Ppd**, propodeum; **Prn**, pronotum; **Prpl**, propleuron; **sp**, spiracle; **Umspl**, upper mesopleuron; **Umtpl**, upper metapleuron.

**Note 11.** In most *Gerontoformica* the frontal carina is crescent-shaped and around the torulus. In *Myanmyrma maraudera*, the frontal carina resembles that of *Zigrasimecia*, however, it is more developed and reaches the anterior portion of the torulus. In *Zigrasimecia* the carina may be poorly marked (e.g. *Z. chuyangsui* **sp. nov.**), only represented by a wave of the cuticle which forms a somewhat shallow scrobe.

**Note 12.** The mesosomal conformation of *Zigrasimecia* sets it apart from other stem ants. Dorsally it has no signs of sutures, so that notal and propodeal limits can be only guessed (usually by the position of the spiracles on the lateral surfaces). It is particularly difficult to determine whether *Zigrasimecia* has a developed metanotum as other stem lineages or if it shrunk in between the mesonotum and the dorsum of the propodeum, resembling modern ants, where this sclerite is reduced. Mesosoma as compressed and fused as that of *Zigrasimecia* is found in some lineages of the Myrmicinae, Agroecomyrmecinae, some Dorylinae, and in the Proceratiinae, being particularly similar to *Tatuidris* and *Discothyrea* Roger, 1863.

**Note 13.** The calcar in many Cretaceous ants is considerably different from extant ants (personal observation). In many species of various genera it has a bifid tip, it does not have a well-developed comb across its length, the inner margin is most of the time concave, sometimes lamellate along the main axis (sometimes there are projections, but they are not as tidily organized, not forming a comb-like structure as in extant ants). In *Zigrasimecia*, the tip is rarely bifid.

**Note 14.** All Formicidae, including Mesozoic ones, have only 1 protibial spur, the calcar. The calcar can be associated with 1 or 2 posterior, subapical, spur-like setae (Lattke & Melo 2020; Perrichot *et al.* 2020; Cao *et al.* 2020a) (Fig. 8, G), which explains previous reports of *Zigrasimecia* having more than one protibial spur. Therefore, the formula accounts only for the meso- and metatibiae.

**Note 15.** The petiole of *Zigrasimecia* is quite unique among the stem lineages. Considering all *Zigrasimecia* specimens examined, the pedunculate state, considered as a trait shared by *Zigrasimecia* and *Boltonimecia* (Borysenko, 2017), is not likely correct (see section 3. 4 below). In *Zigrasimecia*, in profile view, the anterior petiole margin is straight and inclined posterodorsally across its length, never forming a proper anterior peduncle clearly distinct from the node. Among the species in the genus with longer petioles, this is maintained, although the impression of a pedunculate petiole is greater. Moreover, not rarely the petiole is slightly disarticulated from the mesosoma, reinforcing this impression. This petiole shape is seen in some modern species (e.g. *Eurhopalothrix bruchi* (Santschi, 1922) and related spp., see images of CASENT0173970 at Antweb).

**Note 16.** The cinctus between pre- and postsclerites of fourth abdominal segment, when present, is always mild in *Zigrasimecia* (see discussion under *Z. ferox*). Among other Cretaceous ants, the constriction goes from entirely absent to the formation of a conspicuous postpetiole (Barden & Grimaldi, 2014; Miao & Wang, 2019).

## Species Accounts

### *Zigrasimecia boudinoti* Chaul, **sp. nov.**

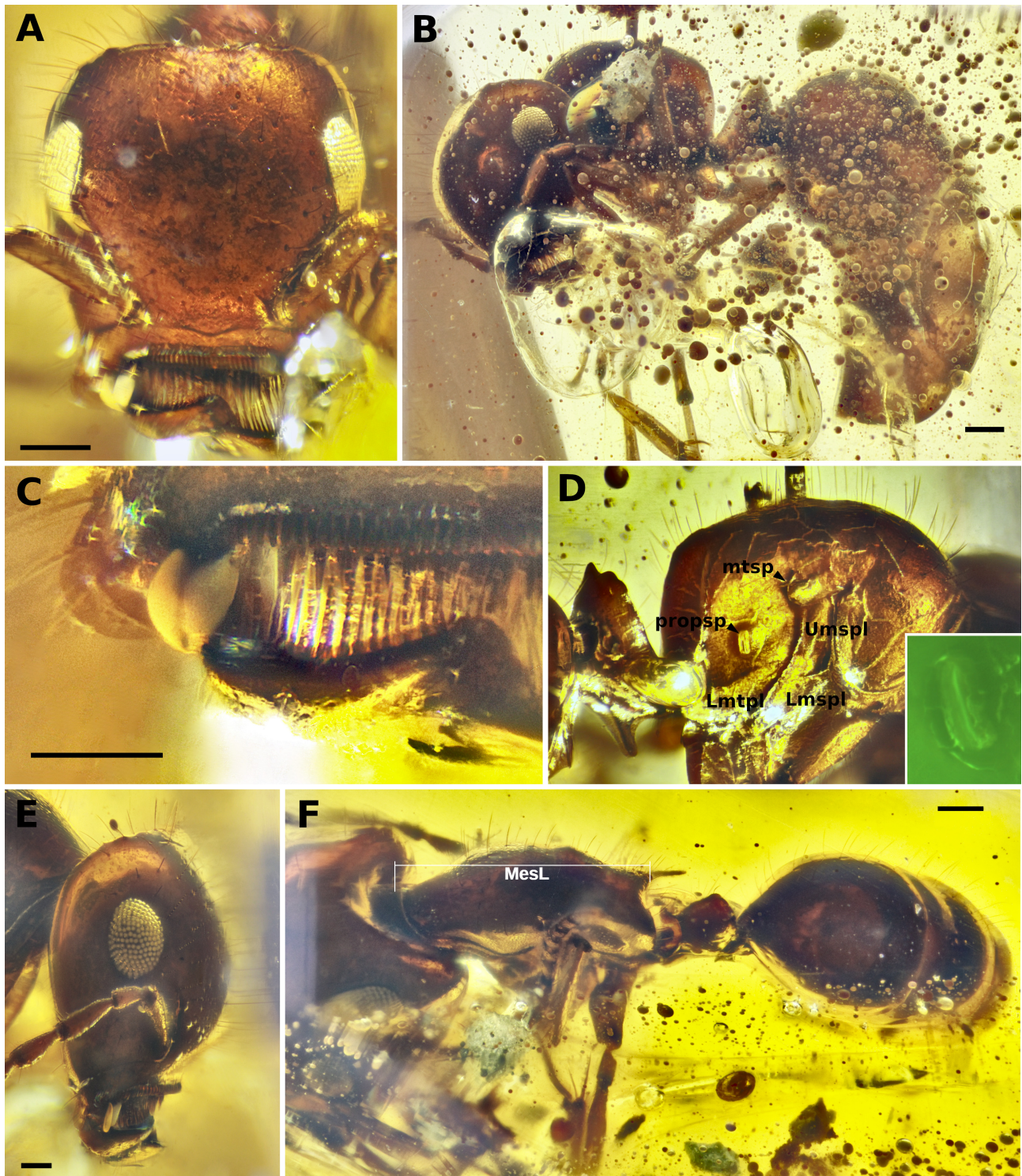
(Fig. 6)

**Diagnosis (worker).** Large species. Head roughly subrectangular (longer than wide) in full-face view. Body pilosity composed of abundant, relatively long, flexuous or erect, filiform setae. Dorsal mesosomal outline mildly convex; propodeum dorsal and posterior surfaces distinct, but not separated from one another by a strongly marked corner. In dorsal view, propodeal posterior margin pronounced laterally (medially concave). Petiolar node apex sharp, not forming a dorsal surface; transversally the apex is bilobed.

**Examined material.** Holotype worker (ANTWEB1032623). Hukawng Valley, Kachin Province, Myanmar; Lower Cenomanian (ca.98.79 ± 0.62 Ma) [CELC].

**Description.** Holotype worker. Measurements: HW 0.90, HL 0.99, EL 0.27, ON >150, MesL 1.1, MesH 0.79, PetAFL 0.45, Ptg3L 0.85, Ptg4L 0.50, TL 3.89. **Head.** In full-face view, lateral margins of head gently convex. Vertexal corners round, but well-defined, with clearly differentiated lateral and vertexal margins. Vertexal margin slightly concave (Fig. 6, A). Mandible dorsal margin apparently sinuous close to the apical tooth (difficult to confirm due to distortion of the amber piece in that position). Labrum and labio-maxillary complex including all palpomeres not visible at any angle. Clypeal anterior margin having around 34 chaetae. Clypeal lobe about twice the size of torular diameter. Clypeal middle longitudinal length smaller than lateral portions; epistomal sulcus touching the

anteriormost portion of the toruli. Scrobe well-developed, formed by a sharply delimited frontal carina. Head, including compound eye's surface, and scape covered with simple, filiform, erect setae. Compound eye relatively large, with more than 150 ommatidia. **Mesosoma.** Overall, mesosoma not as compact as most species in the genus. In profile, dorsal outline of mesosoma mildly convex, abruptly descending into a steep, concave, posterior propodeal



**FIGURE 6.** Holotype of *Zigrasimecia boudinoti* (ANTWEB1032623). **A**, full-face view of the head; **B**, profile view of left side of body; **C**, right portion of anterior head, evincing clypeal lobe, and clypeal, mandibular and labral chaetae; **D**, profile of the right side of mesosoma with metanotal and propodeal spiracles indicated (mtsp and prosp) and propodeal spiracle magnified on the bottom right corner (under epifluorescence light); **E**, profile of right side of the head; **F**, dorsal view of the body. Scale bars are 0.2 mm in A, B, and F and 0.1 mm in C and E. Abbreviations: **Umspl**, upper mesopleuron; **Lmspl**, lower mesopleuron; **Lmtpl**, lower metapleuron; **MesL**, mesosoma length.

margin. Dorsal mesosoma sclerites fused, as usual for the genus, but feeble "waves" in the lateral mesosomal margins in dorsal view apparently indicate the limits of the pronotal, the "mesometanotal", and the propodeal areas. A soft depression that goes from one metanotal spiracle to the other likely indicates the anterior propodeal limit. Pronotum width 0.44 x head width. Lower and upper mesopleura and lower metapleura at least partially delimited by carinae. Metanotal spiracle distant from mesonotal spiracle about as much as it is from propodeal spiracle. Propodeal spiracle 0.09 mm (about 11% MesH), metanotal spiracle 0.11 mm (Fig. 6. D). Metapleural and propodeal lateral surfaces separated by a carina only on the lower portion. Posterior propodeal surface concave, its lateral margins well defined, subcarinated. Dorsal propodeal area merging into the propodeal lateral and posterior surfaces through soft curved corners. Protibia having a pair of simple spur-like setae next to the calcar, the latter with a poorly defined velum and bifid apically; mesotibial and metatibial smaller (anterior) spurs simple, mesotibial larger (posterior) spur barbate apically; metatibial larger (posterior) spur pectinate. Larger metatibial spur clearly barbate. Legs, dorsum of mesosoma, and corners of propodeal posterior surface covered with filiform setae similar to those on the head, but often longer. Dorsum of metacoxae posteriorly carinated. Tiny, pubescence-like, curved setae are present on dorsum of pronotum, mesometanotal, and propodeum, denser on the latter. **Metasoma.** Tip of petiolar node bilobed and thin, not forming a clear dorsal surface. Process of petiolar sternite well-developed, digitiform and anteriorly inclined. Prora in lateral view forming a sharp angle between ventral and anterior faces of first gaster sternite; in anterior view, V-shaped. A very mild cinctus likely present on A4, indicated by a curvature at the edge of A3 tergite which articulates on A4 pretergite. Dorsum of petiole and gaster covered on setae similar to those on the head and mesosoma. Tiny, curved setae are also present, sparse on gaster, except on fourth and fifth gaster tergites (AVI and AVII) where they are abundant.

**Comments.** This species is, together with *Z. hoelldobleri*, the largest in the genus (both being larger than the species known by queens, Fig. 14). *Zigrasimecia boudinoti* cannot be confused with *Z. hoelldobleri* by the radically different body setation. It shares the same type of setae as *Z. chuyangsui*, but the latter has a chubbier appearance, with a more compact and evenly curved mesosoma, and a round petiolar node apex rather than a thin bilobed one.

The specimen itself is superbly preserved, but the surrounding amber matrix is considerably dirt, which prevents the visualization of some features. There are mild distortions on the petiole anteriorly, where it articulates with the mesosoma, and posteriorly, where it articulates with A3; the node itself appears intact.

**Etymology.** The name is in honour of the great myrmecologist and friend Brendon Elias Boudinot. The name was created by adding the singular Latin genitive case suffix -i to the last name of a male person. The orthography of an eponym is unchangeable and not dependent on the generic name in which the epithet is used.

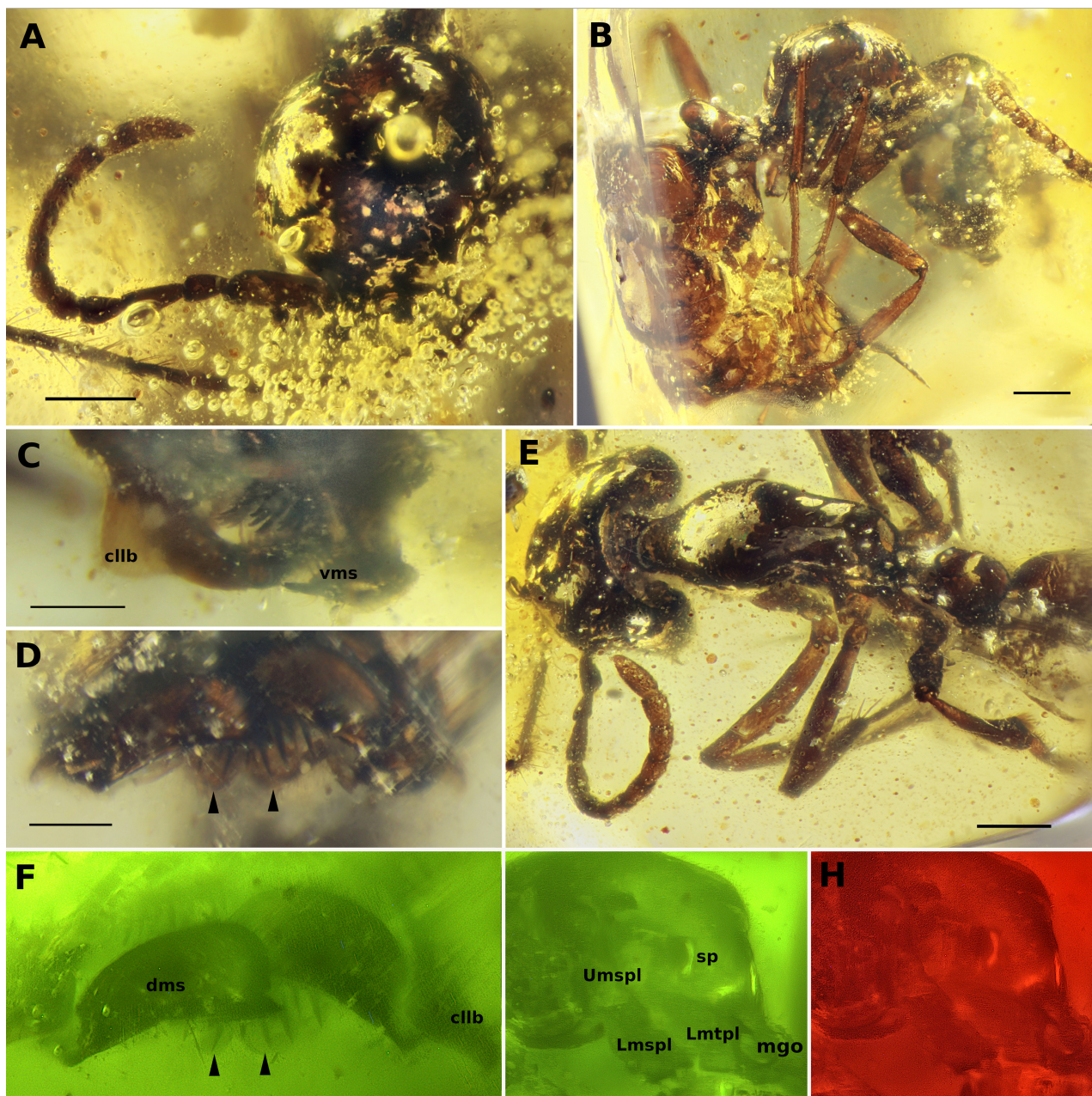
### *Zigrasimecia caohuijiae* Chaul, sp. nov.

(Figs. 7–8)

**Diagnosis (worker).** Small species. Head round in full-face view. Standing setae on body absent, except for tiny pubescence across the body. Dorsal mesosomal outline conspicuously convex; propodeal dorsal and posterior surfaces not separated from one another by a strongly marked corner. Petiolar node dorsal surface developed, round.

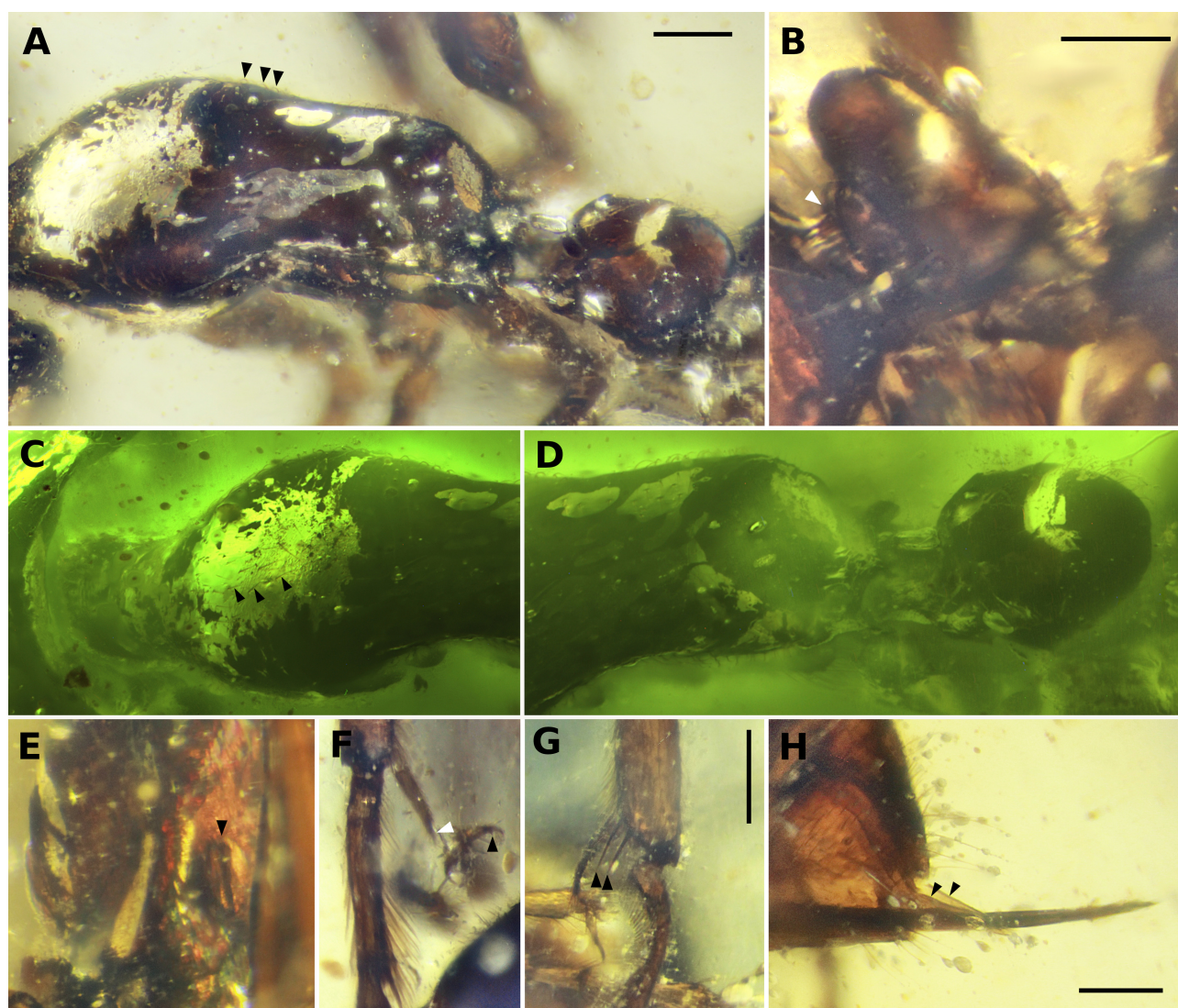
**Examined material.** Holotype worker (ANTWEB1041055). Hukawng Valley, Kachin Province, Myanmar; Lower Cenomanian (ca. 98.79 ± 0.62 Ma) [CELC].

**Description.** Holotype worker. Measurements: HW 0.58, HL 0.64, EL 0.16, ON ≈ 50, MesL 0.66, MesH 0.4, PetAFL 0.26, Ptg3L 0.31, Ptg4L 0.38, TL 2.25. **Head.** Anterior portion of full-face view of the head and mandibles mostly blocked by an insect antenna which is very close to the ant (could not be removed during specimen preparation). Lateral margins of head straight up to the eye level; from eye posterad, vertexal angles round and poorly defined, vertexal margin strongly convex (head lateral and vertexal margins without clear differentiation from one another). Both compound eyes mostly collapsed and depressed (appearing as they would only be slightly bulging in a preserved condition). Labrum distal margin with one pair of lobes; labral chaetae restricted to basad and mesad areas of labral shield, the distal fringe devoid of them. Hypostomal teeth appearing in anterior view of the head as two lobes laterad the labral lobes. Labio-maxillary complex including all palpomeres completely concealed by the labrum. Dorsal margin of mandible close to apical tooth almost straight. Antennomeres relatively thick and short. Scrobe on the right side of the head clearly visible; unlikely forming a sharp frontal carina (difficult to gauge



**FIGURE 7.** Holotype of *Zigrasimecia caohuijiae* (ANTWEB1041055). **A**, full-face view of the head (view of anterior portion blocked by an insect antenna and bubbles); **B**, profile view of right side of body; **C**, ventrolateral view of anterior portion of head; **D** and **F**, anterior view of head, with a full view of dorsal surface of mandibles, **F** is under epifluorescence; **E**, dorsal view of the body; **G** and **H**, Detail of mesosoma under different types of epifluorescence. Scale bars are 0.2 mm in **A**, **B** and **E** and 0.1 mm in **C** and **D**. Black triangles point to the labral medial lobes (laterally to the median lobes in **D** a pair of protuberances which are likely the hypostomal teeth). Abbreviations: **cllb**, clypeal lobe; **dsm**, dorsal surface of mandible; **Lmspl**, lower mesopleuron; **Lmtpl**, lower metapleuron; **sp**, spiracle; **Umspl**, upper mesopleuron; **vsm**, ventral surface of mandible.

precisely), most likely a bump on the head dividing the surface from torulus to eye in a medial raised and a lateral depressed levels. Conspicuous setae on the head apparently entirely absent, with only minute pubescence similar to that imaged for the mesosoma (Fig. 8, **A**, **C** and **D**, this decumbent pubescence much smaller than the recurved setae on the head of *Zigrasimecia ufv-11*, see below and Fig. 20, **B**). **Mesosoma**. In profile, mesosomal dorsal outline evenly convex, softly merging into the propodeal posterior margin; still, propodeal posterior surface discernible as a shallowly concave area. In dorsal view, mesosomal lateral margins convex at the pronotal level, tapering along the mesometanotal level, and subparallel along the propodeal level; sclerites on dorsum of mesosoma entirely fused, without lines or sutures to indicate their boundaries. Pronotum width 0.53 x head width. Minute pubescence on



**FIGURE 8.** Holotype of *Zigrasimecia caohuijiae* (ANTWEB1041055). **A**, dorsal view of mesosoma and petiole; **B**, detail of the right side of the petiole in profile, white triangle indicates the edge of the sclerite (posterior petiole tube or collar); **C**, zooming of pronotum in dorsal view under epifluorescent light, black triangles in **A** and **C** indicate minute decumbent setae on mesosoma (setae also clear in image **D**); **D**, zooming of propodeum and petiole under epifluorescent light; **E**, posterolateral view of propodeum, black triangle indicates hypertrophied propodeal spiracle; **F**, detail of probasitarsus, showing concentration of long, fine setae, white triangle indicates calcar with simple tip (not bifid), and black triangle indicates mesopretarsal claws with toothed inner margins; **G**, inner face of protibia and probasitarsus, showing two spur-like setae next to calcar; **H**, detail of abdominal segment VII and sting, black triangles show gonostyli. Scale bars are 0.1 mm.

dorsum of mesosoma not particularly dense, but neither sparse, without standing setae or recurved conspicuous setae. Propodeal spiracle approximately 0.07 mm, relatively large (about 18% MesH), positioned on mid-height of propodeal lateral surface. Mesosoma in lateral view with the sclerites more easily defined, upper and lower mesopleuron easily-defined and lower metapleuron poorly marked but discernible. Protibia apicoventrally with a pair of simple spur-like setae and the calcar, the latter with a bifid tip and undeveloped velum; on the mesotibia, a pair of simple, subequal spurs and a third, smaller, simple spur; on the metatibia, a simple spur plus a longer and barbulate one. Pretarsal claw with a minute tooth on inner margin; arolia small, about a third the length of the pretarsal claws, present on all pretarsi. **Metasoma.** In anterodorsal view, anterior surface of petiole node suboval, tip of node arch-shaped; node relatively thick, not anteroposteriorly compressed. In profile view, anterior margin of petiole node oblique, straight to slightly convex, curving evenly into a poorly defined dorsal margin and then to a straight posterior surface which meets a short, ring-like posterior tube. Prora and subpetiolar process interlocked, the shape of both being impossible to precisely describe, although apparently matching the genus diagnosis. Gaster

covered on tiny, curved, appressed setae similar to those of the head and mesosoma; devoid of standing setae, except around the sting. Cinctus on dorsal view of the gaster likely moderately developed, but a damage on middle of A4 and A3 tergites makes it difficult to confirm; cinctus difficult to see in lateral view due to distortion created by the corners of the facets.

**Comments.** The original specimen was a 33 mm x 23 mm x 8 mm polished piece. It contained a lot of debris, an entire mite, a well-preserved small Staphylinidae, a damaged medium-sized beetle (head and pronotum missing), and some fragments of other arthropods, one of which is a long filiform antenna passing right in front of the ant's head. The gaster of the ant was positioned at the edge, with a small portion of the first and second gastral segments damaged. It was isolated from the rest of the piece and is now within a tiny 2.5 mm x 2.2 mm x 2 mm 7-faceted amber block. The filiform insect antenna in front of the ant's head could not be removed and prevents a clear full-face view of the anterior head, blocking most of the antennal insertions, the entire clypeus, and most of the mandibles. The specimen itself has little or no distortion/ stretching and the integument appears intact, except for the compound eyes and maybe a few portions of the frontovertexal area which appear shriveled/sunken.

*Zigrasimecia caohuijiae* is unlikely the worker caste of *Z. tonsora* or *Z. goldingot*, the two species described based on queens (see below under *Z. goldingot*), and can be differentiated from *Z. boudinoti*, *Z. chuyangsui* and *Z. ferox* by the lack of standing setae on body. It differs from the most glabrous *Z. thate* in the absence of a patch of flagellate setae on the frontovertexal area and by the head and mesosoma shape (head subquadrate and propodeal dorsal and posterior surfaces in *Z. thate* marked by a strong corner and propodeal lobes). It differs from *Z. perrichoti* by its smaller size, relatively smaller compound eye with fewer ommatidia, and petiole shape.

**Etymology.** The name is in honor of myrmecologist and paleontologist Huijia Cao. The name was created by adding the singular Latin genitive case suffix -ae to the first and last names of a female person combined. The orthography of an eponym is unchangeable and not dependent on the generic name in which the epithet is used.

### *Zigrasimecia chuyangsui* Chaul, sp. nov.

(Figs. 9–10)

**Diagnosis (worker).** Medium-sized species. Head more inflated than usual for the genus, apparently subround in full-face view. Frontal carinae poorly marked to absent. Body pilosity composed of abundant, filiform, relatively long, and flexuous setae. Dorsal mesosomal outline conspicuously convex, chubby; propodeum without strongly marked corners between the dorsal and posterior surfaces. Petiolar node thick in lateral view, its dorsal surface developed, round.

**Examined material.** Holotype worker (ANTWEB1032660). Hukawng Valley, Kachin Province, Myanmar; Lower Cenomanian (ca.98.79 ± 0.62 Ma) [CELC].

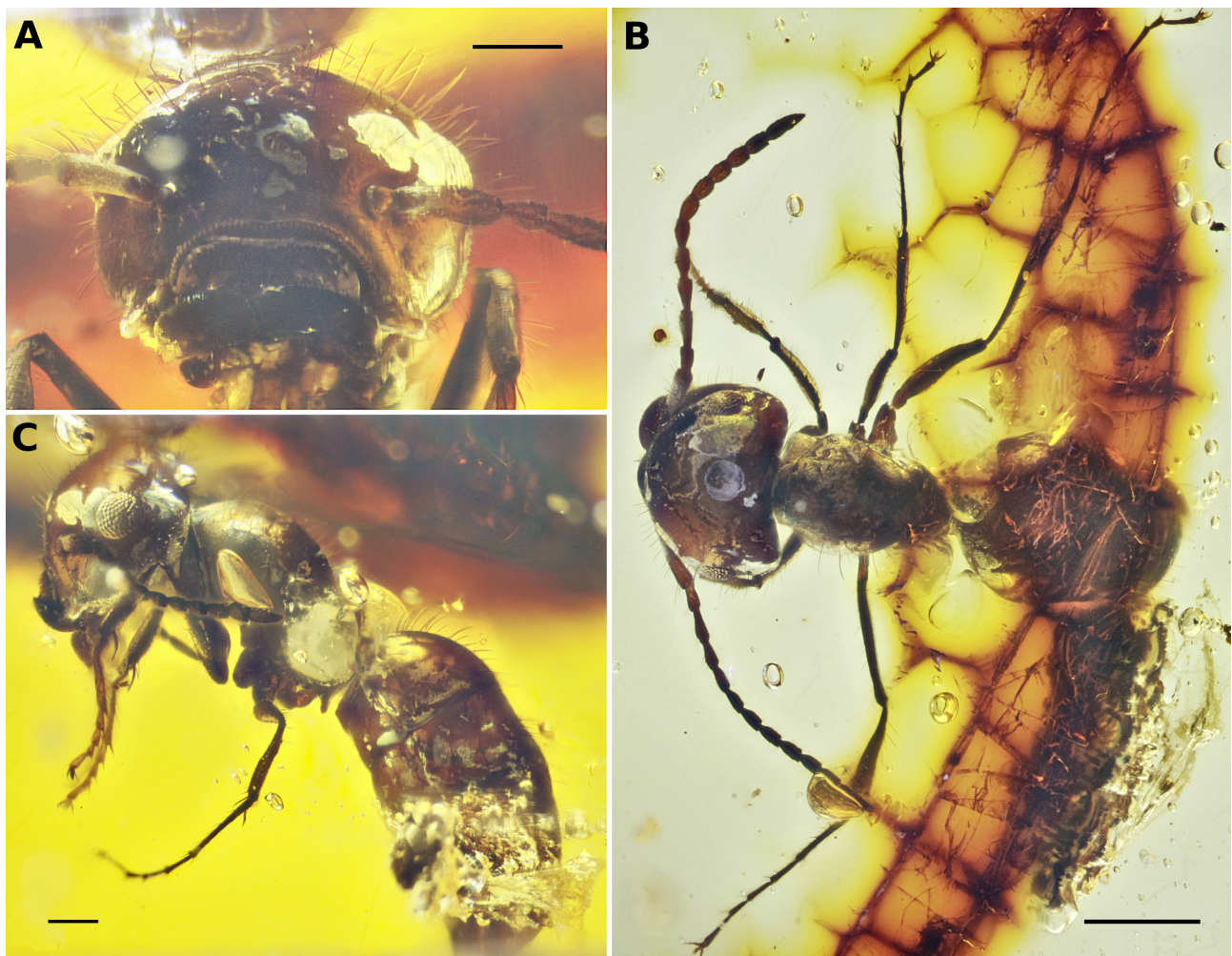
**Description.** Holotype worker. Measurements: HW 0.85, HL 0.81, EL 0.19, ON ≈90, MesL 0.71, MesH 0.60, PetAFL ≈0.25, Ptg3L 0.60, Ptg4L 0.38, TL 2.75. **Head.** Head very large, inflated. In anterodorsal view, lateral margins anterad the eyes gradually diverging and, posterad the eyes, converging and forming round vertexal corners and a mildly convex vertexal margin (head could not be examined in a perfect full-face view due to faceting of the stone). Clypeal lobe relatively poorly developed, its area subequal to torular diameter, surface of the lobe slightly laterally turned instead of facing fully dorsally. Clypeal chaetae count around 46. External surface of mandibles smooth, without any carina or swollen areas. Distinct and sharp apical tooth of the mandible; preapical tooth indistinct, fused to the lamella. Spiny chaetae on the oral surface of the mandible barely seen, as mandibles are tightly closed. Labral stout spiny chaetae increasingly thicker apicad. Palpal formula 6, 4. Anterior clypeal margin bearing 46 stout, truncate chaetae. Posterior clypeal margin (epistomal sulcus) poorly marked, but discernible. Anteriormost torular point almost reaching posterior clypeal margin. Frontal carina virtually absent, at most a very mild oblique swelling of the cuticle going from torulus to compound eye. Compound eyes well-developed, slightly bulging. Simple, filiform setae covering the dorsum of head, and antennae; the flagellum has a combination of these setae and smaller, finer, pubescence-like hairs. **Mesosoma.** Pronotum fused to mesonotum, but a shallow, inconspicuous groove indicates the promesonotal boundary. Pronotum width 0.61 x head width. Mesonotum not delimited posteriorly, nor laterally. Mesopleuron undivided in upper and lower sections, but entirely delimited anteriorly (from lateral pronotum) and posteriorly (from metapleuron), roughly boomerang-shaped. Region corresponding to upper mesopleuron much thinner than that of lower mesopleuron. Metanotal spiracle covered by round, raised cuticle, positioned at the top of

the mesopleuron posterior sulcus, and very approximated to the mesonotal spiracle. Posterior mesosoma in lateral view mostly obscured by bubbles, but propodeum appears to be without defined angles or carinae between its dorsal, lateral and posterior surfaces. Dorsum of mesosoma and legs covered on similar setae to those on the head. Protibia with a simple spur-like seta and the calcar; on the mesotibia, two simple spurs subequal in length; on the metatibia, a simple plus a longer and barbulate one. The calcar is as described for the genus, except for having a slightly more developed velum. Arolia developed on all pretarsi. All pretarsal claws with a conspicuous tooth on inner margin. Protarsomeres I-IV bearing a tiny apicoventral, medial truncate chaeta. Metanotal coxa with posterodorsal swelling. **Metasoma.** Most of the petiole obscured by a pair of bubbles on each of its sides. Top of petiolar node round. Petiolar ventral process long and digitiform. Prora in lateral view a keel-shaped protrusion, forming an angle of approximately 110° degrees between anterior and ventral margins of the gastral sternite. Cinctus residual to absent. Setae on gaster as on head and mesosoma, denser around the sting

**Comments.** The specimen has little or no distortion or stretching, and the cuticle is not damaged or desiccated, except for a small cut on vertex caused by the specimen preparation. Bubbles around the petiole, a piece of debris at the apical left side of the gaster, and a leaf remain positioned dorsad the metasoma obscure some views of the specimen.

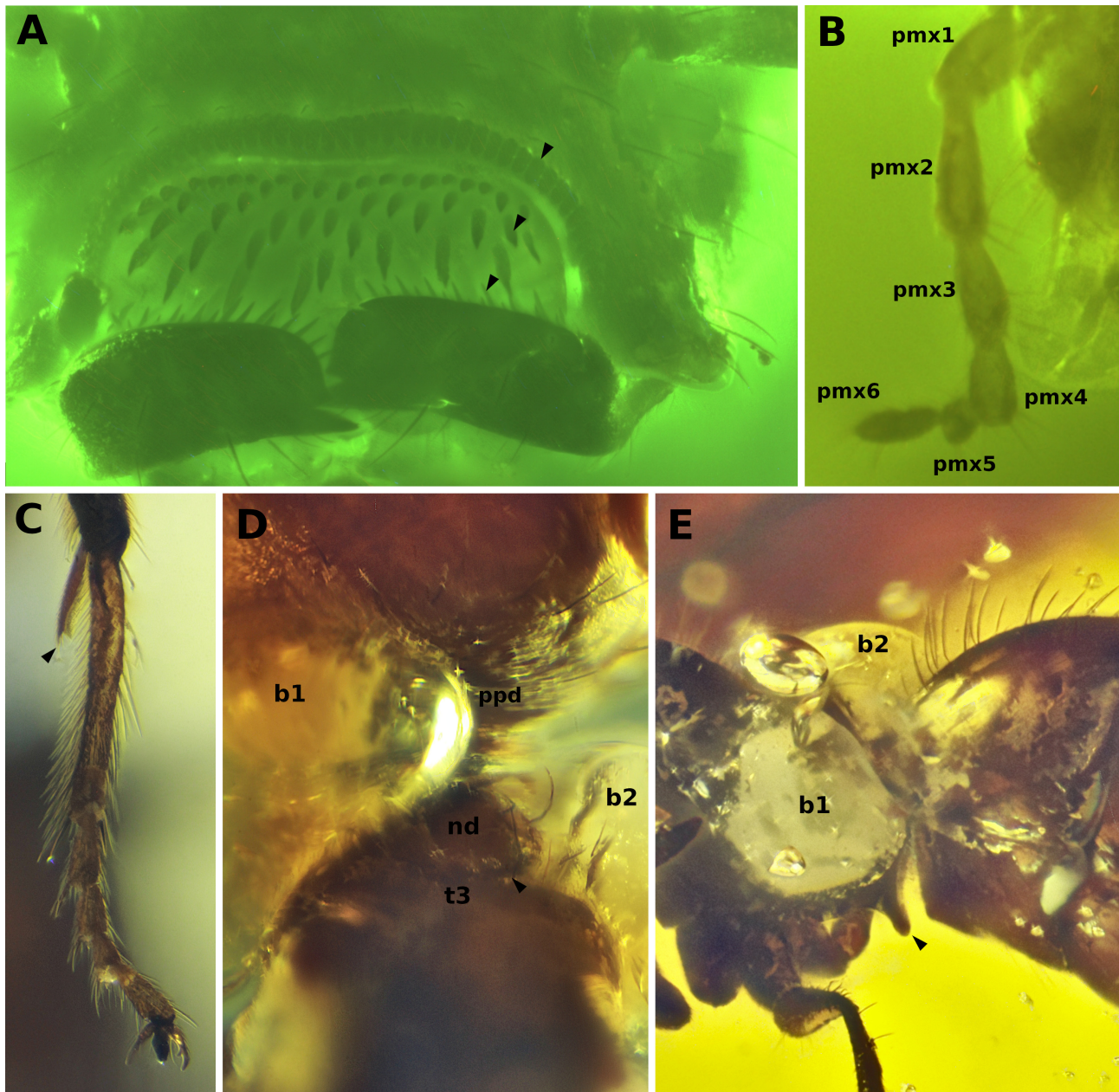
Among the species that have standing setae on most of the body, *Z. chuyangsui* can be unmistakably identified for the overall chubby appearance of the body, especially by the shape of the mesosoma, with the lateral, dorsal, and posterior surfaces softly merging into each other, rather than separated by discrete corners and borders.

The tiny ventral, apicoventral, medial, and truncate chaetae seen in the protarsomeres of the holotype of *Z. chuyangsui* are shared with *Camelosphecia* Boudinot *et al.*, 2020, although they are lobate, somewhat hypertrophied in the latter.



**FIGURE 09.** Holotype of *Zigrasimecia chuyangsui* (ANTWEB1032660). **A**, Head in anterodorsal view; **B**, dorsal view of the body; **C**, profile of left side of the body. Scale bars are 0.2 mm in A and C and 0.5 in B.

**Etymology.** The name is in honor of Chu Yang Su, the son of Cunte (or "Terry Su"), a kind Burmese/Chinese trader which sold most of the specimens which are being described in this paper. Cunte is by far the largest seller of burmite with animal inclusions on Ebay (currently the most popular platform where burmite is traded outside Myanmar and China). Cunte conducts both mining and trading activities and narrated interesting, adventurous (sometimes dangerous) stories about daily activities in the amber mining camps of northern Myanmar. When asked whether he would like to have a species named after him, he asked whether it could instead be named after his son. The name was created by adding the singular Latin genitive case suffix -i to all names of a male person combined. The orthography of an eponym is unchangeable and not dependent on the generic name in which the epithet is used.



**FIGURE 10.** Holotype of *Zigrasimecia chuyangsui* (ANTWEB1032660). **A**, zooming of anterodorsal view of head, showing mouthparts, black triangles from top to bottom point to clypeal, labral, and mandible chaetae; **B**, 6-segmented right maxillary palp; **C**, left protarsus, black triangle points to tip (bifid) of protibial calcar; **D** and **E**, dorsal and lateral zooming of petiole obscured by bubbles, black triangles in **D** indicate posterior margin of petiole node and in **E** indicates tip of subpetiolar process. Abbreviations: **b1** and **b2**, bubbles; **nd**, petiole node; **pmx1**–**pmx6**, maxillary palpomeres 1–6; **ppd**, propodeum; **t3**, tergum of abdominal segment 3 (first gaster tergite).

### *Zigrasimecia ferox* Perrichot, 2014

(Fig. 11)

**Diagnosis (worker).** Small species. Head subrectangular (longer than wide) in full-face view. Body pilosity composed of filiform, sparse, short, and erect setae. Dorsal mesosomal outline convex; propodeal dorsal and posterior surfaces separated by a strongly marked corner. Petiolar node with a distinct truncate dorsal surface. Cinctus on A4 present, mild.

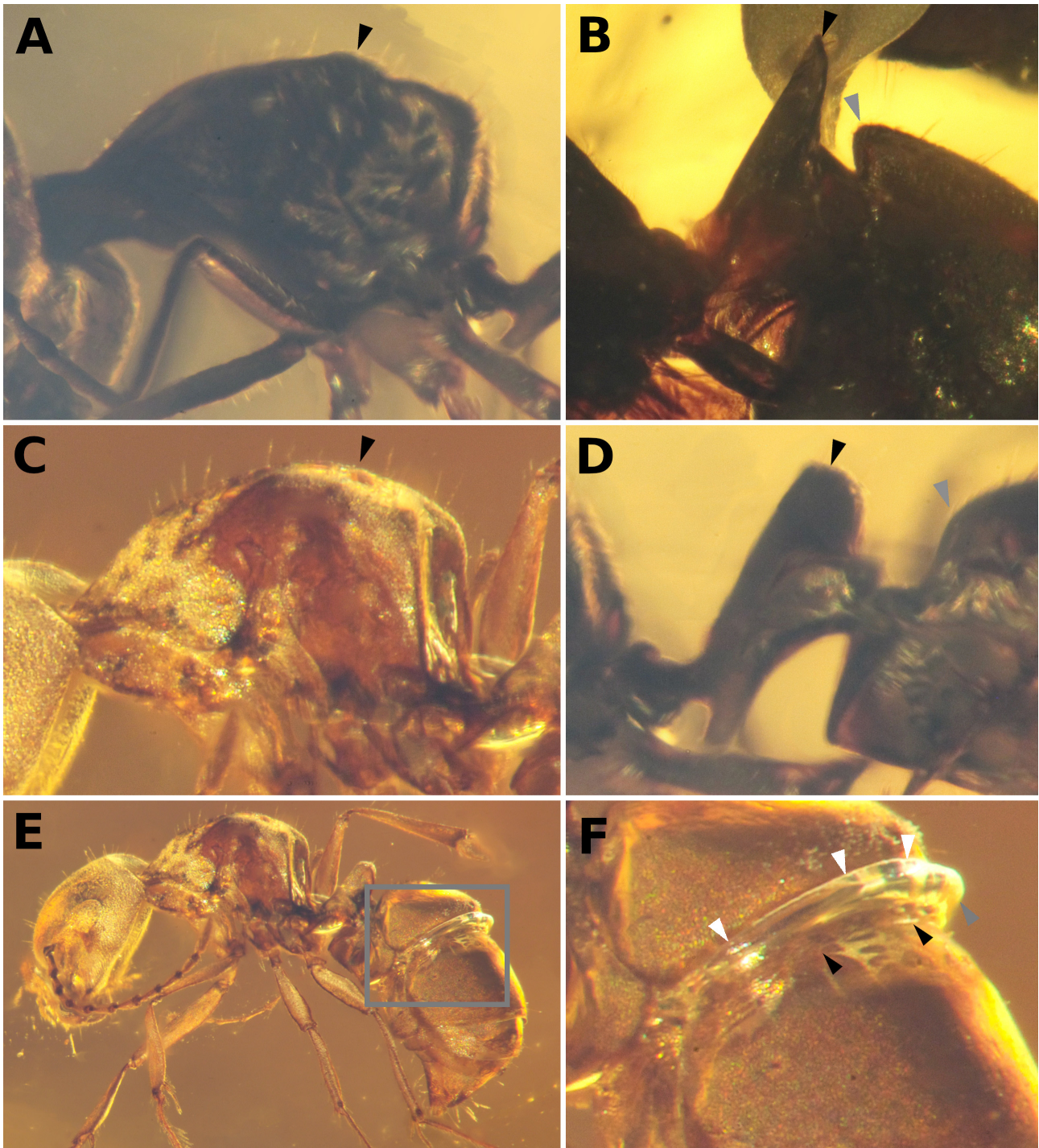
**Comments.** All complete specimens from the type series of *Z. ferox* were originally syninclusions in the same piece of amber (Perrichot, 2014). After treatment of the original piece, the holotype (JWJ-Bu18a in Perrichot, 2014, ANTWEB1008126-JWJ-hym18a on AntWeb webpage) and one paratype (JWJ-Bu18b in Perrichot, 2014, ANTWEB1008128-JWJ-hym-18b on AntWeb webpage) are still together in the same amber piece, while another paratype (JWJ-Bu17 in Perrichot, 2014, ANTWEB1008127-JWJ-hym17 on Antweb webpage) is included in another piece. Curiously, at first look, the three specimens differ enough to raise suspicion about their conspecificity; however, that is just an impression, as their differences are almost certainly a result of the preservation. The holotype has a low bump on the dorsal mesosomal outline, at about the level of the metanotum or anterior portion of the propodeum (Fig. 11, A), as opposed to a continuous dorsal outline as seen in the paratypes, and its cuticle, especially on the head, looks overall a bit desiccated. Paratype ANTWEB1008128 differs from the holotype and the other paratype by having an acute apex of the petiolar node that barely forms a dorsal margin (Fig. 11, B), as opposed to a truncate top of the node, forming a clear dorsal margin in profile (Fig. 11, D and E). It also differs by the shape of the anterior surface of the A3 tergite (first gastral tergite), which is concave and projecting over the helcium, as opposed to a flat to slightly convex anterior surface. Paratype ANTWEB1008127 appears to have the best preservation among the type series, with only a small detachment of the metasoma between A3 and A4. These differences between the types are here interpreted as taphonomic effects. The mesosomal bump in the holotype is assumed to be an artifact, the true state for the species being the shape seen in the paratypes. The cinctus on A4, initially interpreted as possibly the result of poor preservation (Perrichot, 2014), is here interpreted as a true feature of *Z. ferox*, since it is seen in the three complete specimens (although apparently weak in ANTWEB1008128), but especially because in paratype ANTWEB1008127, which has A3 disarticulating from A4, the formation of a distinct pretergite on A4, a typical result of cinctus formation in ants, is observed (Fig. 11, F). All that considered, as well as the diagnoses of the new species, *Z. ferox* can be differentiated from any other species in the genus by its new diagnosis presented above. The variation observed in the species treated in Cao *et al.* (2020b) is commented below, with some of the specimens studied in that work here considered as belonging to different species.

### *Zigrasimecia goldingot* Zhuang, Ran, Li, Feng & Liu, 2022

**Diagnosis (worker).** Head roughly subquadrate in full-face view. Pilosity on body composed of inconspicuous, decumbent, small setae; on the dorsum of head setae curving towards the midline. Compound eyes subcircular (in relation to *Z. tonsora*). Reduced number of clypeal chaetae (less than 25). Dorsal propodeal surface relatively short (in relation to *Z. tonsora*). Petiolar node apex sharp, not forming a proper dorsal surface; transversally the apex is mildly bilobed.

**Comments.** *Zigrasimecia goldingot* and *Z. tonsora* are species known only by queens. Below is summarized why the species described from workers are unlikely conspecific to them.

*Zigrasimecia goldingot* differs strikingly in pilosity from the species *Z. boudinoti*, *Z. chuyangsui*, *Z. ferox*, and *Z. hoelldobleri* as it has small and decumbent setae while those four species have conspicuous standing setae on the body. It differs from *Z. thate* and *Z. perrichoti* in the low number of clypeal chaetae (less than 25, rather than more than 30); from *Z. thate* alone, for not having the flagellate, hook-shaped setae on the frons and vertex; and from *Z. perrichoti* alone in the subquadrate, rather than subrectangular, head (although different shape of the head is common between queens and workers in many ant species), and for having many small, recurved, decumbent setae on the head, rather than a mostly glabrous head (or maybe with very thin and inconspicuous setae, see description of *Z. perrichoti*). Finally, *Z. goldingot* is unlikely conspecific to *Z. caohuijiae* for its petiole with a short and bilobed apex, rather than having the broad and round dorsal surface of the node seen in *Z. caohuijiae*.



**FIGURE 11.** Type series of *Zigrasimecia ferox*. Putative taphonomic effects (A and B) and the corresponding states assumed to be true for the species (C and D). Black triangles in A and C point to the metanotum (or anterior propodeal) level, with holotype in A having a bump which could be an artifact of preservation. Black triangles in B and D indicate the apex of the petiole node, possibly artificially reduced by compression in B. Gray triangles in B and D indicate the anterior surface of A3 tergite, with the shelf-like projection in B being probably the result of folding of the sclerite in the taphonomic process. Cinctus on A4 (E and zoomed in F) is interpreted as a true feature of *Z. ferox*, not an artifact of preservation. In F, the white triangles show posterior edge of A3, black triangles indicate constriction on A4 (cinctus), which separates pre- and posttergites 4, and gray triangle shows swollen intersegmental membrane or internal liquid overflow.

*Zigrasimecia tonsora* can be differentiated from *Z. boudinoti*, *Z. chuyangsui*, and *Z. hoelldobleri* for the type of its standing pilosity, which is shorter, thinner and not as homogeneously distributed on the dorsal surfaces of

the head, mesosoma and metasoma as in those species. Also due to pilosity, *Z. tonsora* is unlikely conspecific to *Z. caohuijiae*, *Z. perrichoti*, and *Z. thate*, as the three are mostly glabrous, except that *Z. thate* has a patch of hook-shaped, flagellate standing setae on the head (setae on the head of *Z. tonsora* being simple, thin, and suberect). The type of the pilosity in *Z. ferox* is similar to *Z. tonsora* for being short and suberect to erect, however, in *Z. ferox* the setae appears more sparse and evenly distributed, while it is patchy and denser in *Z. tonsora*. *Z. tonsora* differs from most species by having the apical tooth strongly offset (outer margin sinuous distally, Fig. 2, D). Finally, there are two unique traits that isolate *Z. tonsora*, a V-shaped groove on the frons, and a pair of vertexal ridges (see comment on that last character under *Z. tonsora*).

### *Zigrasimecia hoelldobleri* Cao, Boudinot & Gao, 2020

**Diagnosis (worker).** Large species. Head subquadrate in full-face view. Body pilosity composed of long, flexuous, mildly clavate, and apically truncate setae. Labral distal margin fringed with soft setae. Dorsal mesosomal outline conspicuously convex; propodeum without strongly marked corners between the dorsal and posterior surfaces. Petiolar node apex brief, but not sharp, the transition from the anterior to the posterior surfaces being a short, curved surface.

**Comments.** The holotype of this species is very distinct for its pilosity and large size (Fig. 14), being easily separated from all remaining species of *Zigrasimecia* by those respects. Two morphospecies are similar to *Z. hoelldobleri*, however their poor preservation prevents any conclusive identification. See comments under morphospecies *Zigrasimecia* ufv-04 about a possible complex of species formed by it, *Z. hoelldobleri* and *Zigrasimecia* ufv-06.

The paratype CNU-HYM-MA2019054 of *Z. hoelldobleri*, differs considerably from the holotype and is here taken out of the type series of the species for not sharing the same type of setation with the holotype. Moreover, CNU-HYM-MA2019054 propodeum appears to have better-defined faces and the petiolar node with better defined top and posterior faces. The specimen is probably conspecific to specimen CNU-HYM-MA2019065, both are likely members of a new species similar to *Z. ferox*, but differing from the latter by having somewhat longer and more abundant pilosity on the body, the apex of the node oblique rather than flat, and a slightly different shape of the head, with the anterior section just posterad the clypeal lobes a bit more constricted (see comments about specimen CNU-HYM-MA2019065 below). Alternatively, the limits of *Z. ferox* could be broadened to include specimens CNU-HYM-MA2019065 and CNU-HYM-MA2019054, something that should preferably be done when more specimens are available and/or can be physically examined.

The distalmost row of very thin, crooked setae on the labrum of *Z. hoelldobleri* holotype is an odd and unique trait of the species; however, it is difficult to check in specimens with a retracted labrum (most of the known specimens so far); therefore, it could be, in fact, a more common trait in the genus.

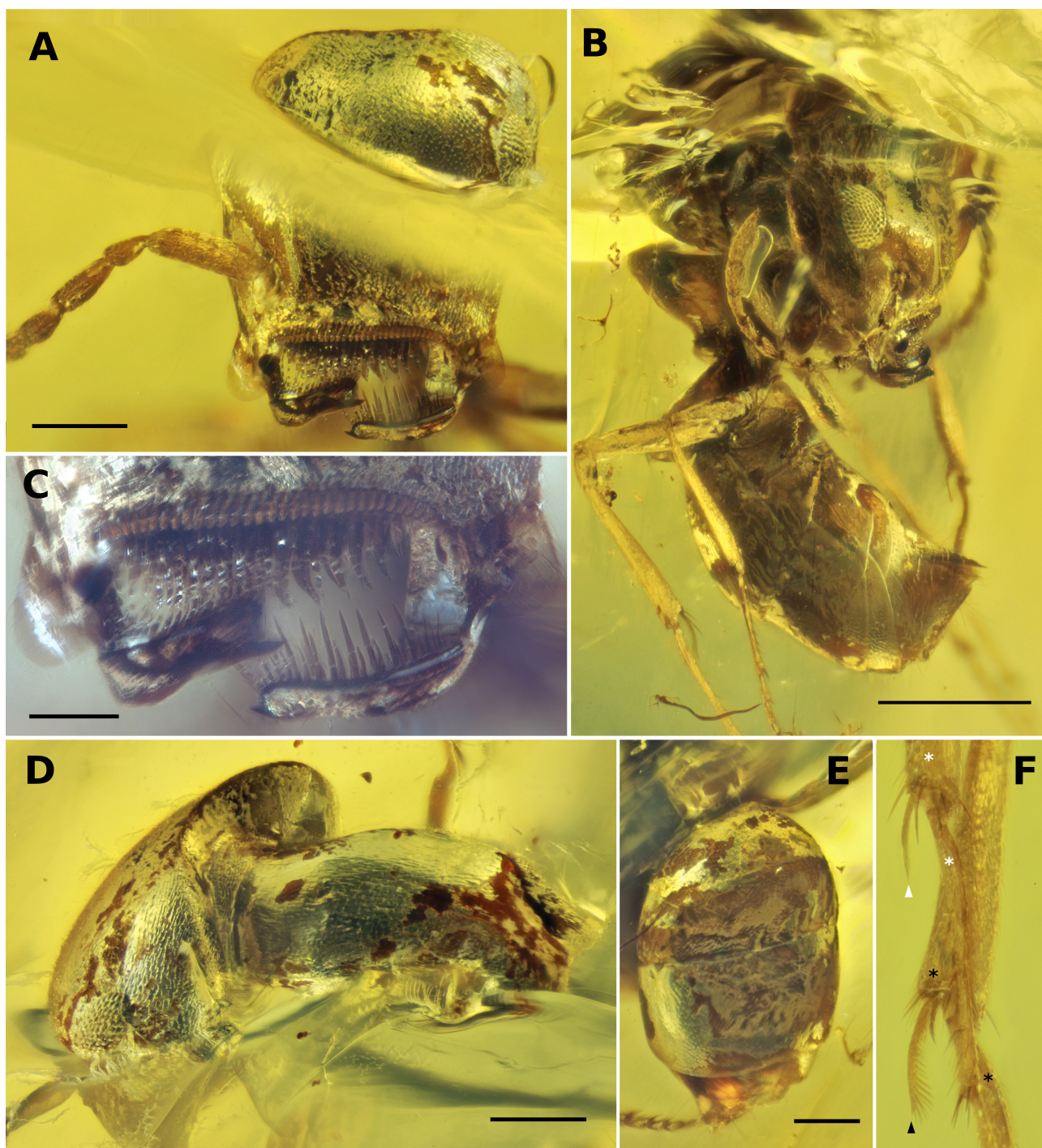
### *Zigrasimecia perrichoti* Chaul, sp. nov.

(Fig. 12)

**Diagnosis (worker).** Medium-sized species. Head subrectangular in full-face view. Standing or conspicuous decumbent setae absent on dorsum of head, mesosoma and most of metasoma (except on apex of gaster, A5–A7); minute pubescence likely present. Petiolar node without a well-formed dorsal surface; apex transversally not bilobed.

**Examined material.** Holotype worker (UFV-LABECOL-010301). Hukawng Valley, Kachin Province, Myanmar; Lower Cenomanian (ca. 98.79 ± 0.62 Ma) [CELC].

**Description.** Holotype worker. Measurements: HW 0.73, HL 0.81, EL 0.21, ON ≈ 90, MesL 0.75, MesH 0.50, PetAFL 0.34, Ptg3L 0.60, Ptg4L 0.36, TL 2.86. **Head.** In full-face view, head subrectangular, lateral margins mildly diverging posteriorly from the most constricted level (just posterad the clypeal lobes) to the compound eyes level; vertexal margin mildly concave and vertexal corners neither too weakly, nor too strongly marked. Clypeal lobe well-developed, its width much larger than torular diameter. Clypeal chaetae count around 34. Portion of dorsal surface of mandible, which is ventrally turned, with a filiform, erect seta on its middle. Teeth on masticatory margin



**FIGURE 12.** Holotype of *Zigrasimecia perrichoti* (UFV-LABECOL-010301). **A**, full-face view of the head; **B**, profile view of right side of body (crack in the amber on the upper mesosoma and upper head level creating a mirror effect in the image); **C**, detail of anterior head showing clypeal lobes, and clypeal, mandibular and labral chaetae; **D**, dorsal view of head and mesosoma; **E**, dorsal view of gaster; **F**, meso- and metatibia and meso- and metabasitarsus, white asterisks at distal mesotibia and basal mesobasitarsus, white triangle points to tip of mesotibial spur; black asterisks and triangle the same positions in the hind leg. Scale bars are 0.2 mm in A, D, and E; 0.1 mm in C; and 0.5 mm in B.

of mandible as for the genus, but apical tooth relatively large. Spiny chaetae on ventral surface of mandible and stout labral chaetae as for the genus, the distribution of chaetae on labral disc is not visible. Labral distal margin not visible. Labio-maxillary complex including all palpomeres not visible. Posterior clypeal margin (epistomal sulcus) weakly marked. Frontal carinae well-impressed. Dorsal surface of the head with abundant piligerous marks, but no setae visible. This punctuation is likely the marks of very fine head pubescence (difficult to confirm). Antennae

without standing setae. **Mesosoma.** In profile, dorsal mesosomal outline gently convex, meeting an oblique posterior propodeal margin at a marked angle. In dorsal view, mesosomal outline subrectangular, lateral margins flat to mildly convex, region corresponding to promesonotum slightly wider than that corresponding to propodeum. Propodeum in dorsal view with a flat to mild concave posterior margin. Propodeal spiracle slit-shaped, relatively small (0.05 mm, about 10% mesosoma height). Protibia having a pair of simple spur-like next to the calcar; calcar velum poorly-developed, tip of calcar frayed; mesotibial spurs subequal, the posterior one with inconspicuous barbulation; metatibial smaller (anterior) spur simple, larger (posterior) spur pectinate. **Metasoma.** In lateral view, anterior petiolar margin convex, apex only a brief curvature which leads to posterior descending margin which is also convex, especially on the lower portion. Petiole in anterior view subrectangular, the apical transverse margin almost straight. Although not forming a conspicuous dorsal surface, petiole is relatively thickened, not sharpened on the apex or lateral edges. Gaster large. A mild cinctus present on A4, indicated by a soft curvature at the edge of A3 tergite which articulates on A4 pretergite. Metasoma glabrous, except for A5–7, which bears several curved, long, simple setae on its edge. Sting tip exposed.

**Comments.** The specimen has little or no distortion or stretching, the cuticle is not damaged or desiccated. The matrix is very clear, but has a fracture that crosses the specimen from side to side, passing in the head posteriorly and upper mesosoma. The fracture causes a mirroring effect which does interfere significantly with the visualization of the ant, however, multiple facets and different illumination might reveal parts that are obscured by that artifact.

*Zigrasimecia perrichoti* cannot be mistaken for its congeners as the almost entirely glabrous body differentiates it from *Z. ferox*, *Z. hoelldobleri*, *Z. boudinoti*, and *Z. chuyangsui*. *Zigrasimecia thate* and *Zigrasimecia ufv-11*, which are mostly glabrous, have patches of conspicuous setae on the dorsum of the head. In fact, *Z. perrichoti* is overall very similar to *Zigrasimecia ufv-11*, having a very similar head shape, differing mainly on head pilosity and compound eye size. *Zigrasimecia caohuijiae* shares with *Z. perrichoti* the lack of standing setae on the body, but it is much smaller, with relatively smaller compound eyes, and a differently shaped mesosoma and head. Regarding the two species described based on queens, *Z. perrichoti* is unlikely the worker caste of *Z. goldingot* for having more clypeal chaetae and a more rectangular rather than quadrate and unlikely the worker caste of *Z. tonsora* for lacking standing body pilosity.

**Etymology.** The name is in honour of the great paleontologist Vincent Perrichot. The name was created by adding the singular Latin genitive case suffix -i to the last name of a male person. The orthography of an eponym is unchangeable and not dependent on the generic name in which the epithet is used.

### *Zigrasimecia thate* Chaul sp. nov.

(Fig. 13)

**Diagnosis (worker).** Small species. Head subquadrate in full-face view. Standing setae on body almost entirely absent, except for a patch of long, subflagellate or hook-shaped setae on the frontovertexal region. Small compound eyes. Dorsal mesosomal outline mildly convex; propodeum strongly angled between the dorsal and posterior surfaces. Petiolar node not forming a distinct dorsal surface, the transition from the anterior to the posterior surfaces being a short, curved surface in lateral view; apex of node transversally mildly bilobed.

**Examined material.** Holotype worker (ANTWEB1038912). Hukawng Valley, Kachin Province, Myanmar; Lower Cenomanian (ca.98.79 ± 0.62 Ma) [CELC].

**Description.** Holotype worker. Measurements: HW 0.58, HL 0.62, EL 0.11, ON 32, MesL 0.67, MesH 0.39, PetAFL 0.325, Ptg3L 0.48, Ptg4L 0.20, TL 2.29. **Head.** In full-face view, head subquadrate, the lateral margins not diverging posteriorly, slightly convex along most of their length (except just posterior to the clypeal lobes where they are slightly concave), and vertexal margin roughly straight. Clypeal lobes well-developed, their width 0.9x the compound eye diameter. Clypeal chaetae count around 30. When mandibles are fully closed, the anteriormost point of the mandible is slightly posterior to the anteriormost point of clypeal lobe (seen in holotype's left mandible). Portion of dorsal surface of mandible, which is ventrally turned, with a filiform, erect seta on its middle. Teeth on masticatory margin of mandible not discernible, but visualization is difficult, as masticatory margin of left mandible entirely occluded by right mandible and basal portion of masticatory margin of right mandible occluded by clypeal teeth. Spiny chaetae on ventral surface of mandible only seen through a gap on the right mandible in full-face view. Labral stout, spiny chaetae only present on the basal-medial area of the labral disc; distal margin wavy, forming two

pairs of low, blunt lobes. Labio-maxillary complex including all palpomeres completely concealed by the labrum. Labral distal margin notched medially. Posterior clypeal margin (epistomal sulcus) vestigial, only discernible by a weak angulation on the anterior portion of the head. Frontal carinae small, but well-marked, forming a shallow diagonal scrobe. Numerous, long, equally-spaced, subflagellate or hook-shaped setae on frontovertexal region, their tips (apical quarters) curved medially. **Mesosoma.** In profile, dorsal mesosoma outline gently convex, meeting an almost straight posterior propodeal margin in a strongly marked angle. Mesosomal dorsum, pleura, and posterior propodeal surface separated by marked, non-carinated, angles. In dorsal view, region likely corresponding to promesonotum gradually tapering to propodeum, the latter about 0.7 times as wide as the former. Propodeum in dorsal view having a concave posterior margin, which descends into a concave posterior surface (not appearing concave in lateral view). Pronotum width 0.5 x head width. Mesopleuron divided into upper and lower sections. Propodeal spiracle slit-shaped, relatively small (0.05 mm, about 0.125 x mesosomal height), mid-height positioned. Metanotal spiracle half the size of propodeal spiracle, positioned at the upper end of the third quarter of mesosomal height. Metanotal spiracle closer to mesonotal spiracle than to propodeal spiracle. Metapleuro-propodeal suture vestigial. Metapleural gland opening subequal in size to propodeal spiracle, with at least a few thin setae around it. Likely only a single spur-like seta present next to the calcar, but difficult to ascertain due to an internal fracture at the level of the apex of left tibiae (confirmation on the right legs difficult due to the positioning of the legs on that side of the body). **Metasoma.** In anterodorsal view, petiolar node anterior surface subrectangular, its spiracles slightly protruding lower on the lateral margins, and top of node slightly concave. In lateral view the apex of the node being short and curved, barely forming a proper dorsal surface. First gastral tergite roughly convex, not forming conspicuous anterior and dorsal surfaces on the sclerite. No cinctus on A4. Metasoma glabrous, except for A7, which has several curved, long, simple setae on its edge. Sting tip exposed.

**Comments.** The specimen has little or no distortion or stretching, the cuticle is not damaged or desiccated. The matrix is very clear, but has a fracture that crosses the specimen from side to side, passing in the head at mid-height, in the legs more or less at the tibial level (on the left side), and across the gaster. The fracture does not interfere substantially on the visualization of the ant.

The subflagellate setae on the frontovertexal area are immediately diagnostic of *Z. thate*. The hook-shaped appearance of the setae could be thought of as preservational, formed by the resistance the resin while the ant was trapped, but since all the setae on the right side are curved opposite to those on the left side, the condition is thus interpreted as a true feature of the species. *Zigrasimecia* ufv-11, discussed below, have similarly curved setae on the dorsum of head, however, in that morphospecies, the setae are much smaller, appressed, and appear to be thicker.

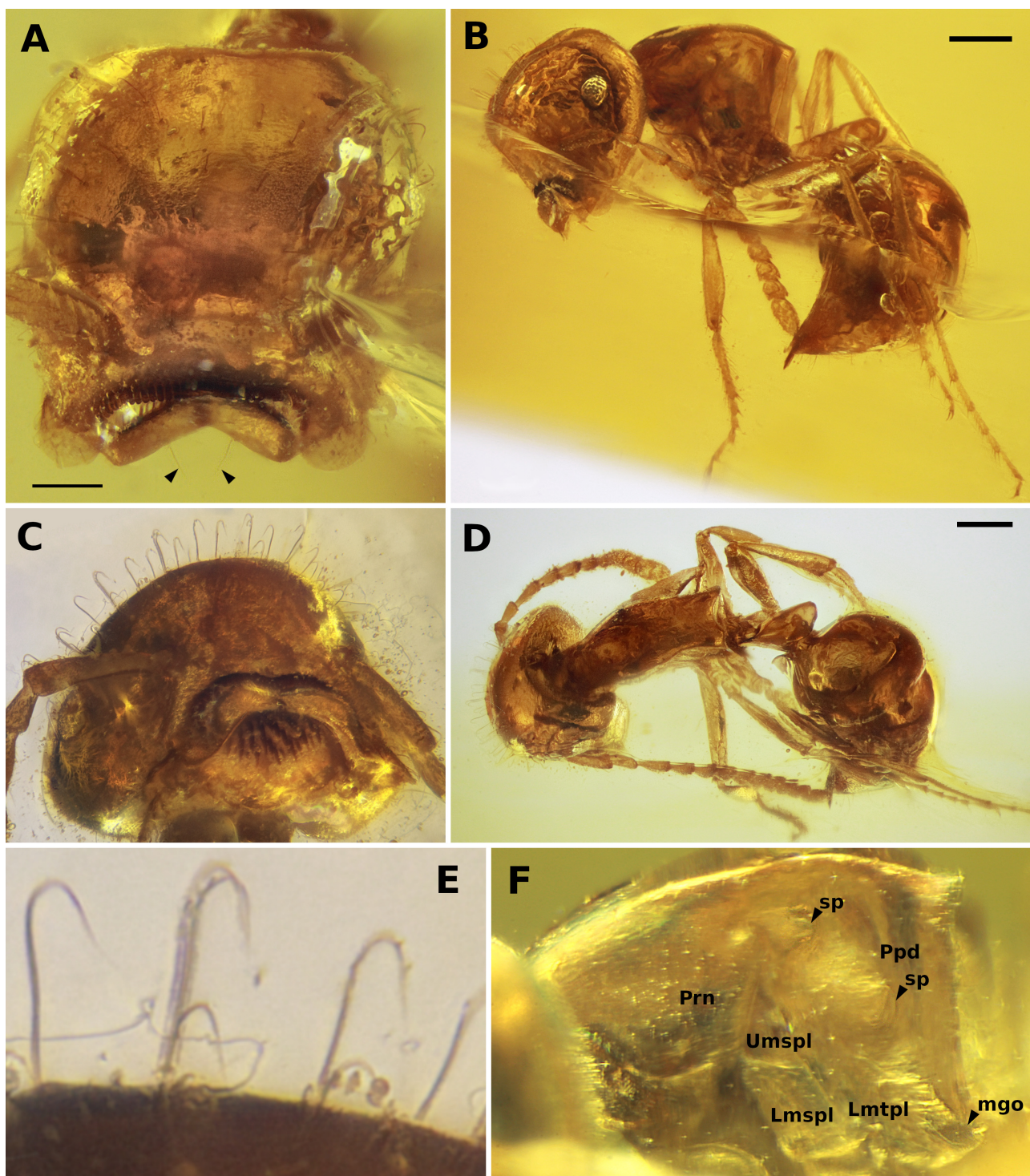
The pair of setae on the dorsal surfaces of the mandibles (Fig. 13, A, black triangles) is clearly seen in *Z. perrichoti* and *Zigrasimecia* ufv-11, and might well be common to all *Zigrasimecia* species although not detected in most specimens due to the difficulties to prospect information inherent of amber specimens.

**Etymology.** The specific epithet is a non-Latinized portmanteau of part of the names of Thaís Merij Mário and Maria Tereza Mário Chaul, mother and sister of the author, respectively. Thaís and Tereza have financed the studies of the author through the years, including the acquisition of numerous amber specimens such as the ones described in this work.

### *Zigrasimecia tonsora* Barden & Grimaldi, 2013

**Diagnosis (queen).** Frons with a shallow V-shaped groove; vertex with a pair of cuticular ridges or protuberances (see comment below). Mandible apical tooth strongly offset from mandible's outer margin. Compound eyes ovoid (in relation to *Z. goldingot*). Pilosity on dorsum of head composed of abundant, thin, flexuous setae (Fig. 1, E of Barden & Grimaldi, 2013, better observed in Antweb's high-resolution version than in the article's figure in the pdf), similar setae also present on dorsum of pronotum, mesothorax and propodeum. Dorsal propodeal surface relatively long (in relation to *Z. goldingot*). Petiolar node forming a distinct, truncate dorsal surface, apex transversally apparently without lateral protuberances (or apparently not bilobed).

**Comments.** The holotype of *Z. tonsora*, *Zigrasimecia* genotype, is not a perfectly preserved specimen and, for this reason, and for being a queen rather than a worker, creates a taxonomical challenge in ascertaining conspecificity between it and any worker specimen. The reasons why the new species described here do not belong to *Z. tonsora* are presented above (see above in *Z. goldingot* Comments).

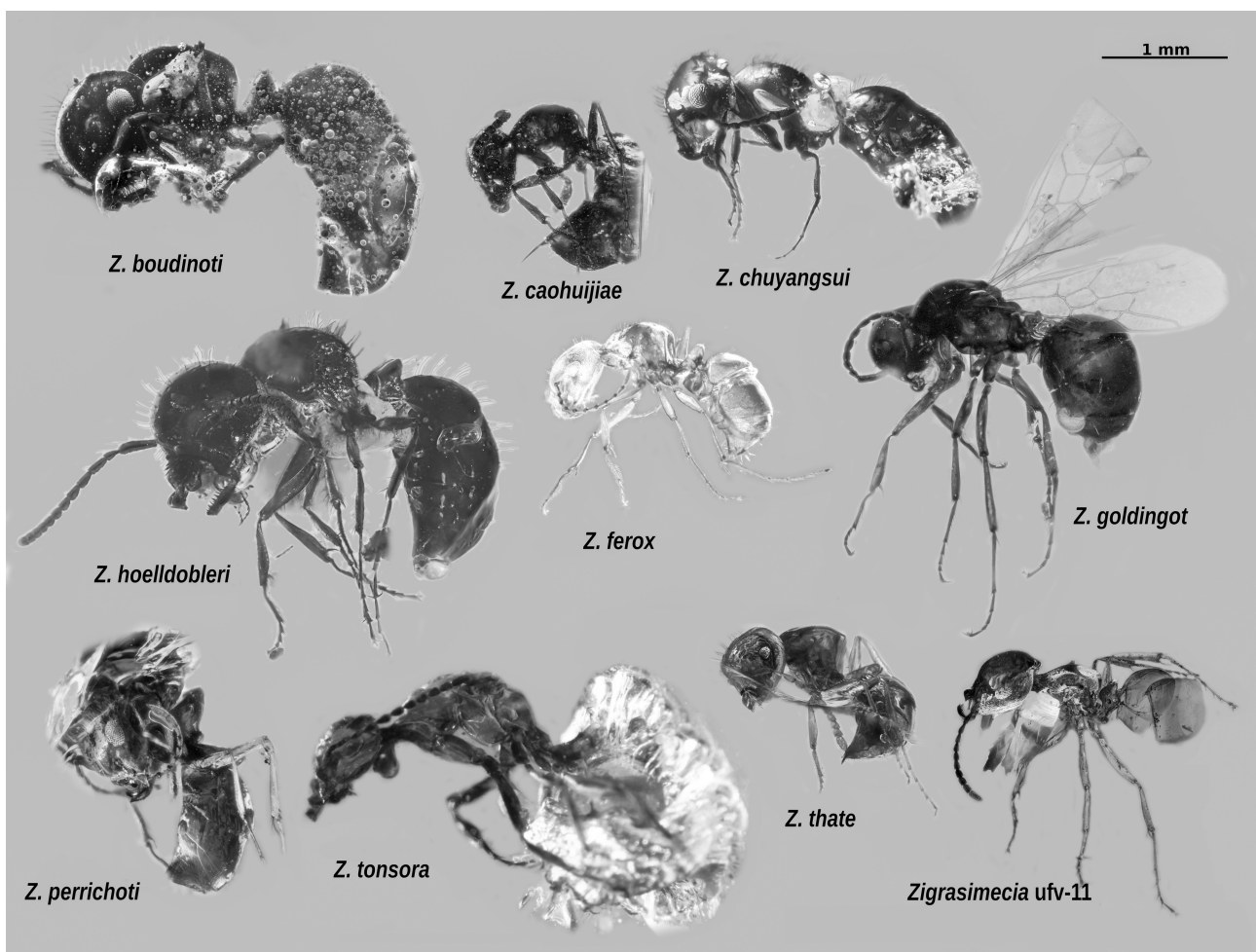


**FIGURE 13.** Holotype of *Zigrasimecia thate* (ANTWEB1038912). **A**, full-face view of the head, black triangles indicate mandible dorsal setae; **B**, profile view of left side of body; **C**, anterior view of the head; **D**, dorsal view of the body; **E**, zoom of flagelliform setae on frons and vertex (same view as C); **F**, detail of mesosomal profile. Abbreviations: **Lmspl**, lower mesopleuron; **Lmtpl**, lower metapleuron; **mgo**, metapleural gland opening; **Ppd**, propodeum; **Prn**, pronotum; **sp**, spiracles (metanotal and propodeal); **Umspl**, upper mesopleuron. Scale bars are 0.2 mm in B and D, and 0.1 mm in A.

The holotype head appears slightly desiccated and wrinkled; the "coronal rugosities", a pair of vertexal cuticular ridges, could be a preservational feature (Cao *et al.*, 2020a: note 7), although an anonymous reviewer called attention to the note by these authors claiming the paired structure is, in fact, symmetrical. By the illustration in the original publication the ridges are not perfectly mirrored, but considering how much compression and stretching forces

the fossils are subjected to, that degree of displacement of one ridge in relation to the other is still acceptable to account for them as a symmetrical paired structure, if they are a natural trait of the specimen. Indeed, most burmite ants observed by the author are not free from at least a minimal amount of asymmetry due to preservation in at least one part of the body. So, whether the vertexal ridges are a natural trait of *Z. tonsora* is an open question that might be solved as more specimens are discovered. In addition, a drawing of the toruli (Fig. 2, C of Barden & Grimaldi, 2013) is not in perfect accordance with the image presented (Fig. 1, C of Barden & Grimaldi, 2013), so the tubular shape of the illustration is here considered a misinterpretation. Instead, the toruli appear to have a regular ring-like shape, as in most ants, being, at most, slightly raised. The mesosoma is well-preserved. In the metasoma, only the petiole is preserved, the gaster being entirely covered by an internal fracture of the amber; the shape of the petiole, especially the flat dorsal surface of the node, is better seen in photo of Fig.1, B than in drawing of Fig.2, A of Barden & Grimaldi (2013).

All characters of the diagnosis, except the ones compared to *Z. goldingot* (eye shape and propodeum shape), are expected to be shared between the queen and worker.



**FIGURE 14.** Relative body size comparison of all described species of *Zigrasimecia* (with morphospecies *Zigrasimecia ufv-11* included, see Section 3.3 of text).

### 3. 3. Important specimens not fitting into the described species

Below, I discuss various specimens from the literature or morphospecies, which, for many reasons, have not been formally described. The specimens are either unsatisfactorily preserved, have not been physically examined, or, in one case, are currently under study by other researchers. Presenting these specimens here is crucial, as there is a paucity of specimens for each species of Cretaceous ants (species are often described based on a single specimen). Therefore, proper characterization might help future taxonomic studies on *Zigrasimecia*.

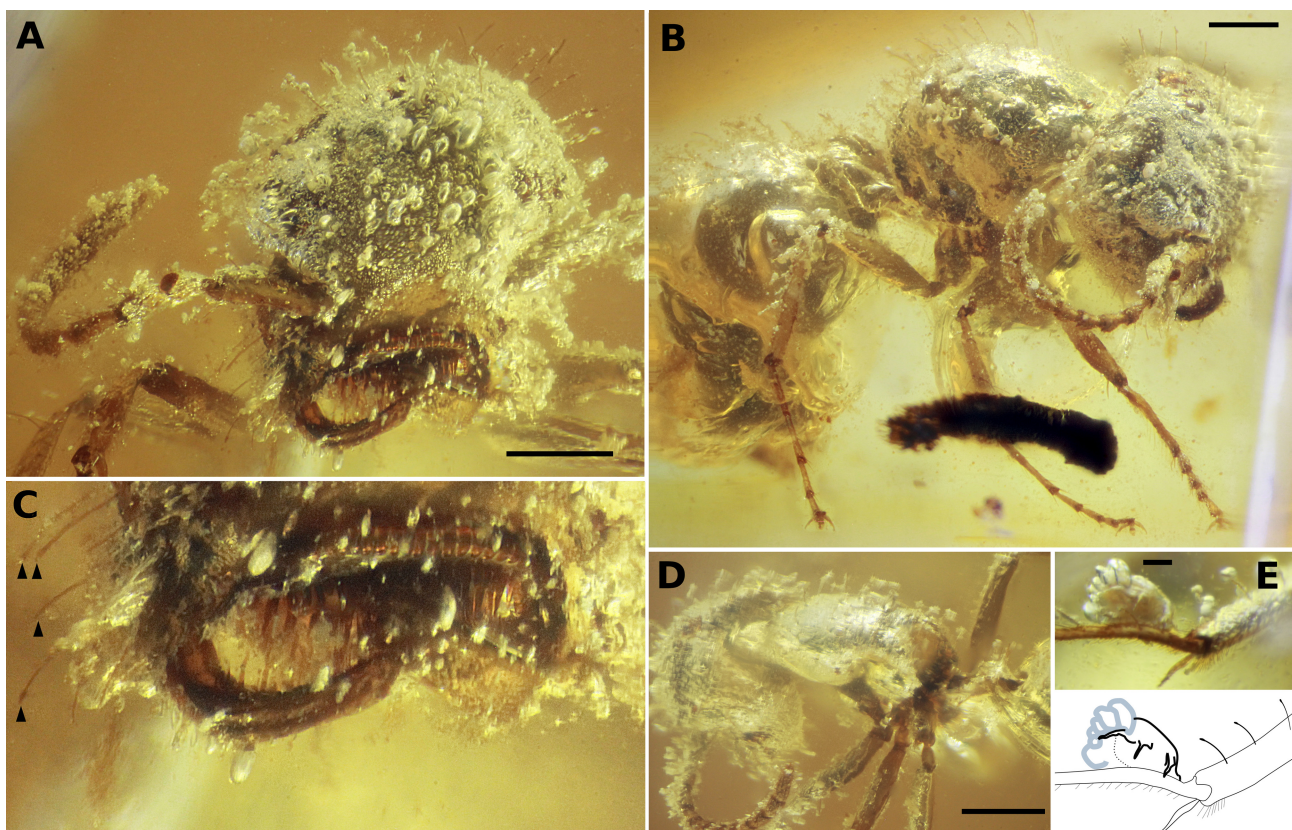
### *Zigrasimecia* ufv-04

(Fig. 15)

This morphospecies is most likely related to *Z. hoelldobleri*, but the unique specimen representing it is covered by hundreds of small bubbles which make impossible a proper examination and an unambiguous identification. *Zigrasimecia* ufv-04 is relatively small (HW 0.66). It has 32–36 clypeal chaetae. Frontal carina is strongly marked, forming a mildly sinuous margin from torulus to compound eye. Compound eye has around 50 ommatidia. Standing setae on body thick, clubbed and truncate. Petiolar node bilobed, node not particularly anteroposteriorly compressed. The peculiar clubbed setae (Fig. 15, C) and the petiole shape are the main characters suggesting the morphospecies *Zigrasimecia* ufv-04, *Zigrasimecia* ufv-06, and *Z. hoelldobleri* are a small group of related species within the genus. It is possible that *Zigrasimecia* ufv-04 and/or *Zigrasimecia* ufv-06 could belong to *Z. hoelldobleri* itself, but confirming that would likely require a better characterization of both morphospecies, which would be possible only through micro-CT scanning or with additional, better-preserved specimens. This morphospecies was excluded to all identification keys due to insufficient characters to differentiate it from *Z. hoelldobleri*; in the dichotomous key, it would easily key out as the latter.

A mite is attached to the metabasitarsus of the specimen (Fig. 15, e).

**Examined material.** Worker (ANTWEB1038932). Hukawng Valley, Kachin Province, Myanmar; Lower Cenomanian (ca.98.79 ± 0.62 Ma) [JCMCC].



**FIGURE 15.** Morphospecies *Zigrasimecia* ufv-04 (specimen ANTWEB1038932). **A**, head in full-face view; **B**, profile of right side of body; **C**, detail of mandibles and clypeus, black triangles indicate clubbed setae on gena; **D**, posterodorsolateral view of mesosoma and head; **E**, phoretic mite on mesotibia, with a simplified scheme below the image. Scale bars are 0.2 mm in A, B and D and 0.05 mm in E.

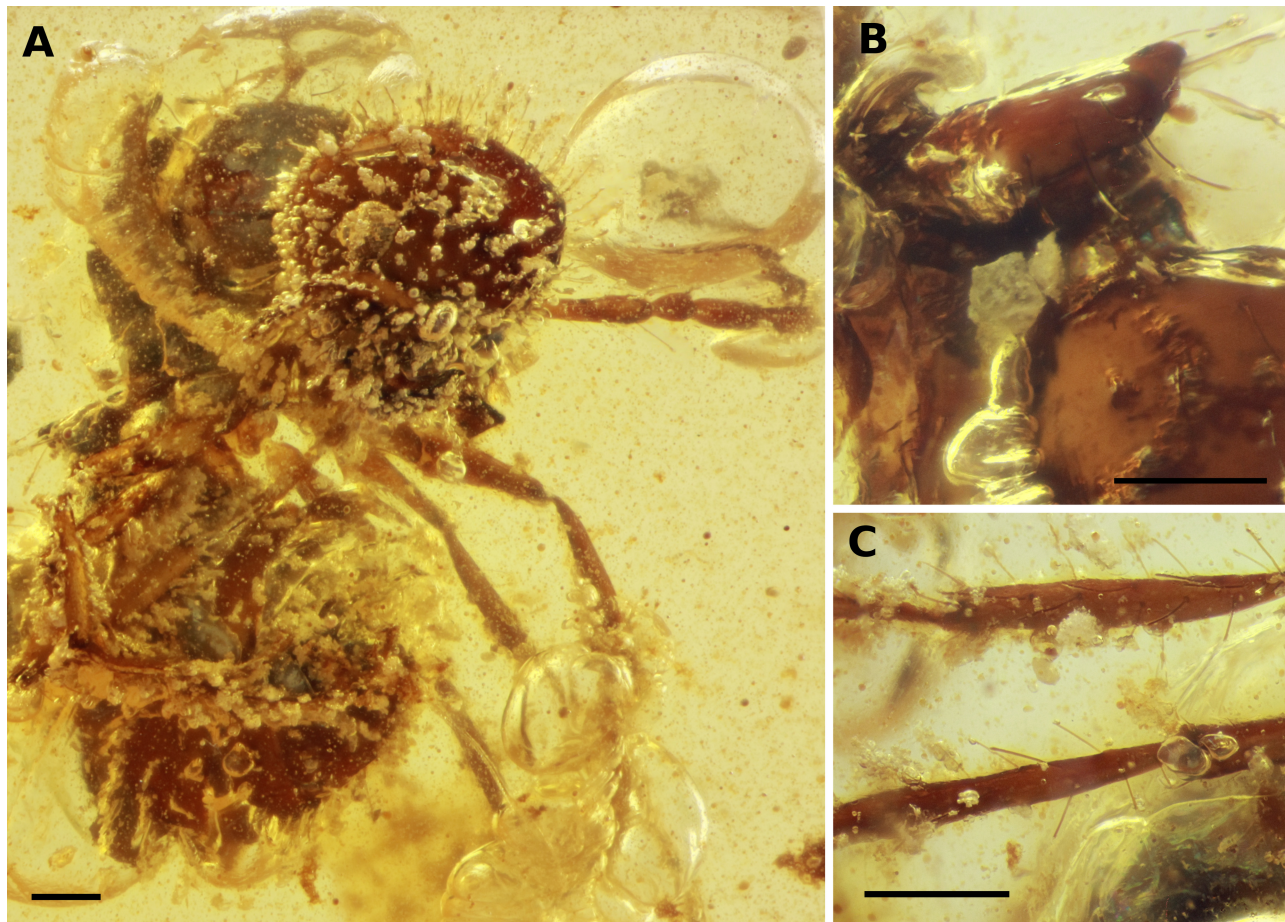
### *Zigrasimecia* ufv-06

(Fig. 16)

The specimen is covered by hundreds of bubbles in the amber matrix, which makes it difficult to achieve satisfactory characterization. This morphospecies is overall very similar to *Zigrasimecia* ufv-04, sharing with it

the abovementioned traits, except for being larger (HW 0.8, ML 0.72) and with the compound eye formed by more ommatidia, at least 90. It has approximately 34 clypeal chaetae. See above a discussion on the possible relatedness of the two morphospecies to *Z. hoelldobleri*. This morphospecies was excluded from all identification keys due to insufficient characters to differentiate it from *Z. hoelldobleri*; in the dichotomous key it would easily key out as the latter.

**Examined material.** Worker (ANTWEB1032645). Hukawng Valley, Kachin Province, Myanmar; Lower Cenomanian (ca.98.79 ± 0.62 Ma) [JCMCC].



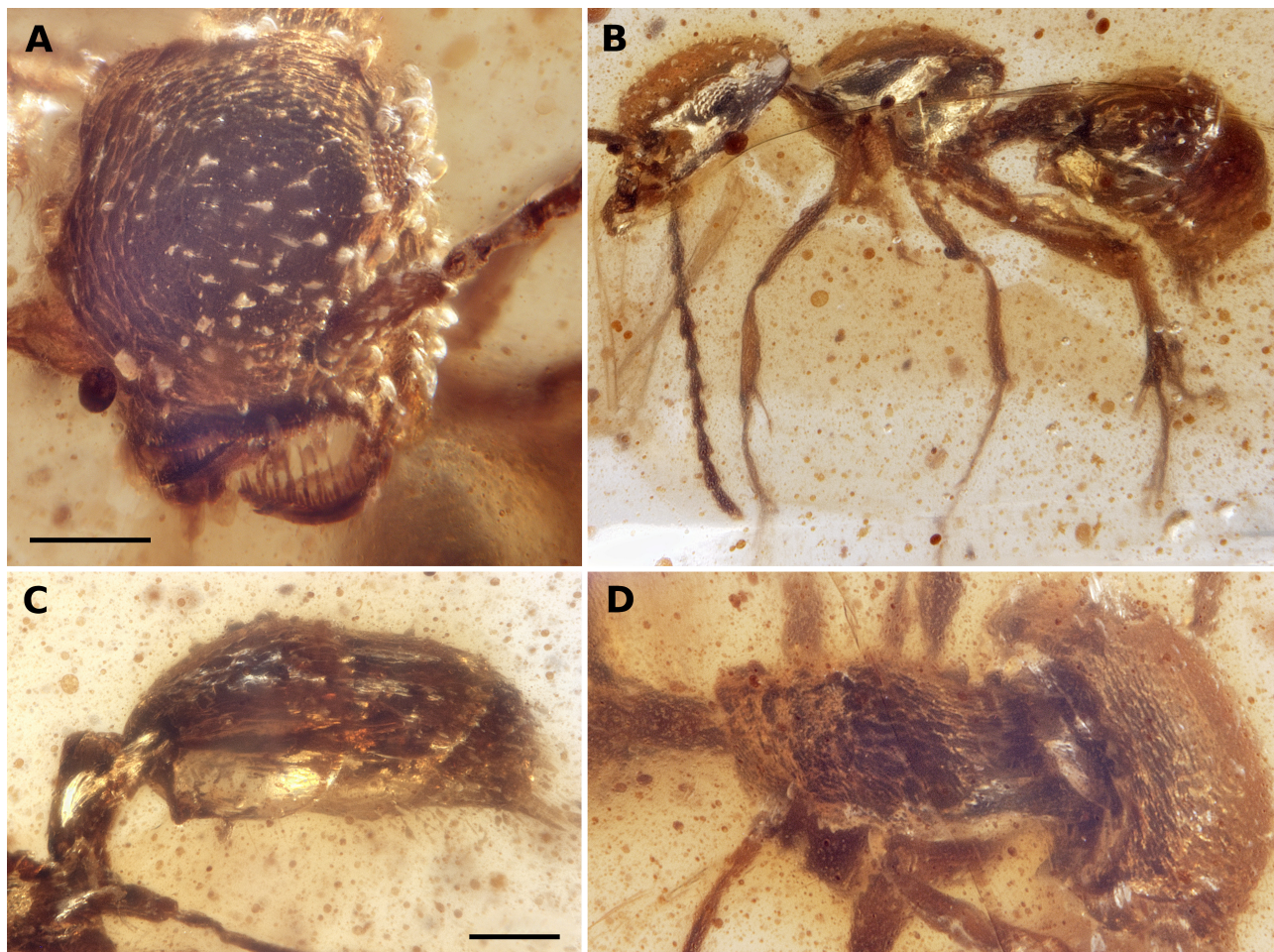
**FIGURE 16.** Morphospecies *Zigrasimecia* ufv-06 (specimen ANTWEB1032645). **A**, profile of right side of body; **B**, left side of petiole in dorsolateral view; **C**, meso- and metatibiae (upper and lower portions of image, respectively), evincing thickened, truncate pilosity. Scale bars are 0.2 mm.

### *Zigrasimecia* ufv-08

(Fig. 17)

This morphospecies is composed of two specimens that were originally in one single piece (separated for study). The amber matrix is extremely dirty and both specimens appear desiccated (the entire body "sculpturing" appears to be an artifact). The specimens do not have conspicuous standing setae, instead, they have a curved small pilosity on the head which is similar to *Zigrasimecia* ufv-11 (see below). They have a subrectangular head. Compound eye has around 50 ommatidia. The frontal carina is poorly developed. The propodeal dorsal and descending surfaces are separated by a strong angle. The petiole is somewhat long and low, the node top surface is round, not bilobed (very distinct from any shape seen in other species or morphospecies). If better-preserved specimens confirm that the traits attributed to this morphospecies are not artifactual (some sclerite shapes could be a result of stretching), it will certainly belong to a new species, as this combination of traits is unique in the genus. This morphospecies was excluded from the dichotomous identification key.

**Examined material.** Workers (UFV-LABECOL-010579 and UFV-LABECOL-010580). Hukawng Valley, Kachin Province, Myanmar; Lower Cenomanian (ca.98.79 ± 0.62 Ma) [JCMCC].



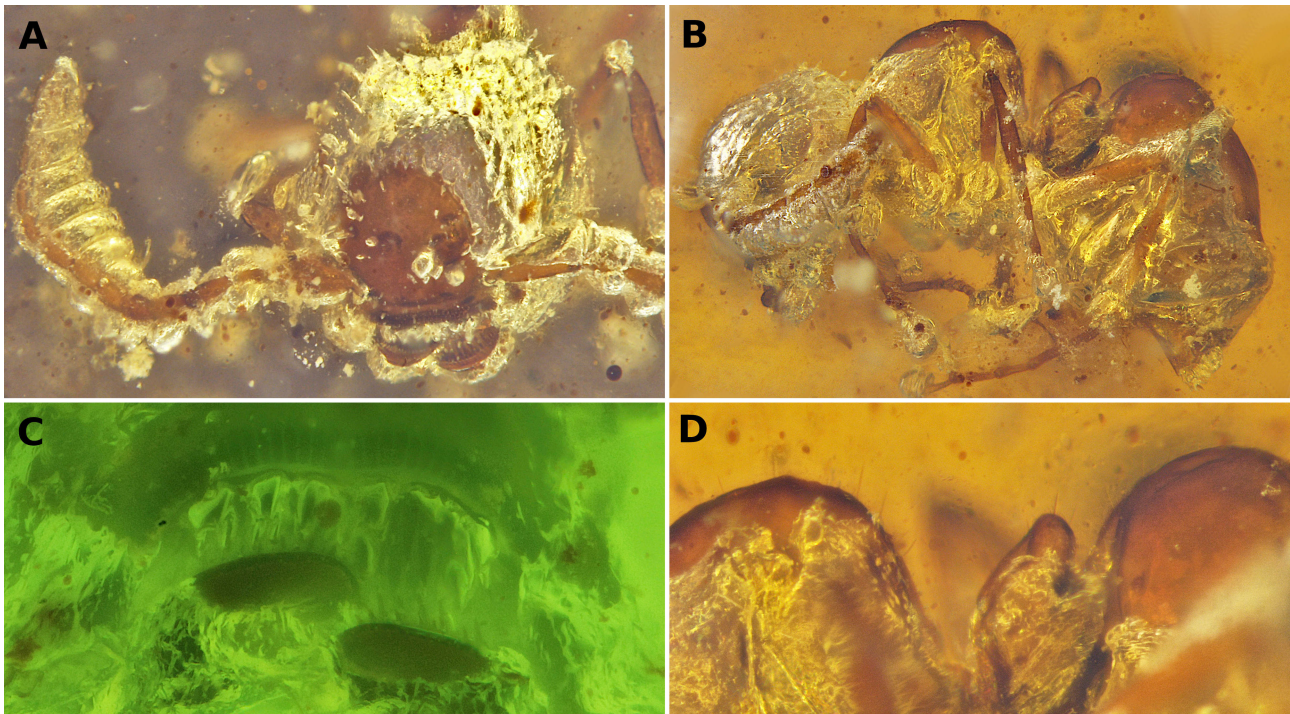
**FIGURE 17.** Morphospecies *Zigrasimecia* ufv-08, two specimens originally in the same piece (separated for study). Specimen UFV-LABECOL-010580 in A, C and D and specimen UFV-LABECOL-010579 in B. **A**, full-face view of head; **B**, profile of left side of body; **C**, zooming of left side of metasoma in profile; **D**, detail of mesosoma in dorsal view. Scale bars are 0.2 mm.

### *Zigrasimecia* ufv-09

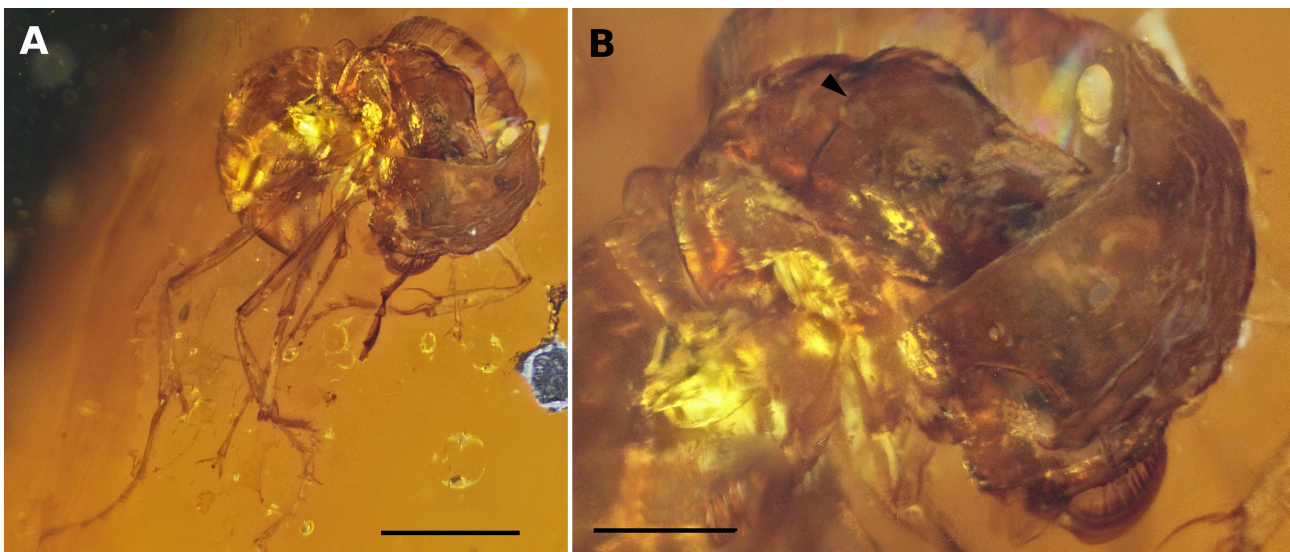
(Fig. 18)

The specimen has many bubbles around it which prevents an ascertained identification. It has similar head shape, in full-face view, to *Z. caohuijiae*. It also resembles that species by its mesosomal and petiolar shape, in profile view. There are, however, standing setae on the body which makes conspecificity to *Z. caohuijiae* unlikely. The standing setae are thin, filiform, and apparently sparse, resembling that of *Z. ferox*. The shape of the mesosoma and petiole, though, do not indicate *Zigrasimecia* ufv-09 belongs to *Z. ferox*. Additional specimens, when found, might allow a more complete characterization and help in deciding whether it is worthy of receiving a formal description. This morphospecies was excluded to all identification keys due to the small number of characters that could be extracted from the specimen.

**Examined material.** Worker (ANTWEB1047064). Hukawng Valley, Kachin Province, Myanmar; Lower Cenomanian (ca.98.79 ± 0.62 Ma) [JCMCC].



**FIGURE 18.** Morphospecies *Zigrasimecia* ufv-09 (specimen ANTWEB1047064). **A**, head in full-face view; **B**, profile of left side of body; **C**, anterior (slightly dorsal) view of mouthparts; **D**, zoom of propodeum, petiole and first gastral tergite, evincing filiform setae on body.



**FIGURE 19.** Morphospecies *Zigrasimecia* ufv-10 (specimen ANTWEB1047051). **A**, anterolateral view of right side of body; **B**, Zoom of head and mesosoma of same view of **A**, black triangle indicates putative promesonotal suture. Scale bar is 0.5 mm in **A** and 0.2 mm in **B**.

### *Zigrasimecia* ufv-10

(Fig. 19)

The specimen has the entire cuticle wrinkled. It was originally so close to the edge of the amber piece that a few polishing and faceting was possible, so there are not too many views available and the specimen could not be fully studied. It apparently lacks any conspicuous standing pilosity on body, which excludes the possibility of it being *Z. boudinoti*, *Z. chuyansui*, *Z. ferox*, *Z. hoelldobleri* or *Z. thate*. The petiole in *Zigrasimecia* ufv-10 has a bilobed

node. The specimen presents an interesting, potentially important trait, which is a visible promesonotal suture. The poor preservation conditions of the specimen, however, do not allow to exclude that some sort of folding could have resulted in a fake "promesonotal suture". If further specimens confirm the presence of a promesonotal suture in *Zigrasimecia* ufv-10, not only the morphospecies would be confirmed as a new species but it would also make the generic diagnosis outdated, as all *Zigrasimecia* workers known to date have the mesosoma fused to an almost maximum degree, without signs of a promesonotal suture whatsoever. This morphospecies was excluded from all identification keys due to uncertainty about most of its traits.

**Examined material.** Worker (ANTWEB1047051). Hukawng Valley, Kachin Province, Myanmar; Lower Cenomanian (ca.98.79 ± 0.62 Ma) [JCMCC].

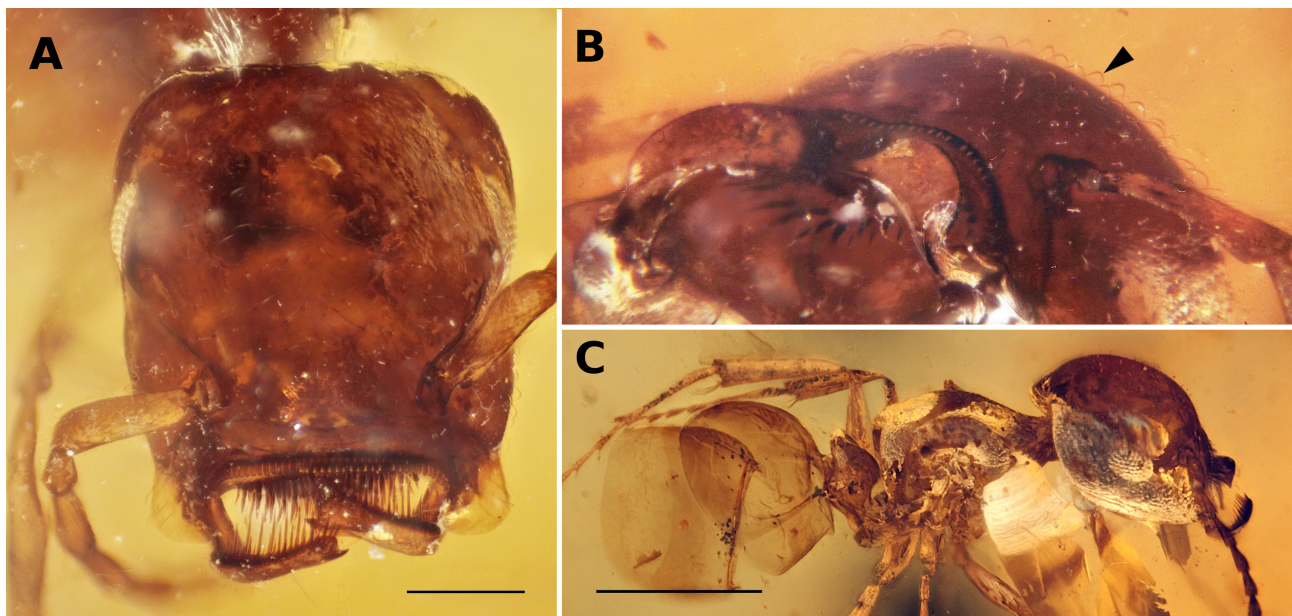
### *Zigrasimecia* ufv-11 and *Zigrasimecia* JGD-09

(Fig. 20)

Five worker specimens are likely conspecifics and compose morphospecies *Zigrasimecia* ufv-11. Images for all specimens are uploaded on Antweb. The specimens share similar shapes of the head, mesosoma, and petiole (petiole apparently badly damaged in ANTWEB1047907), and all have small, curved, decumbent setae on the head. Currently, a species based on a worker specimen and deposited in the Yunnan Key Laboratory for Palaeobiology, Institute of Palaeontology, Yunnan University, Kunming, China, is being described and images were presented to one of the authors (Yuhui Zhuang, personal communication). The species is similar to *Zigrasimecia* ufv-11 and could be conspecific or very close to it, for that reason, I refrain from describing the morphospecies here. *Zigrasimecia* ufv-11 was added to both dichotomous and the multi-entry keys, as it will soon be described and is satisfactorily characterized.

One specimen (ANTWEB1047052) deposited at JGDC (added to Antweb as morphospecies "JGD-09"), could possibly belong to morphospecies *Zigrasimecia* ufv-11, but the available images were not sufficient to ascertain that.

**Examined material.** Hukawng Valley, Kachin Province, Myanmar; Lower Cenomanian (ca.98.79 ± 0.62 Ma). Four workers (ANTWEB104703, ANTWEB104710, ANTWEB104709, and ANTWEB1047907) [MBC]. One worker (ANTWEB1047053) [JCMCC].



**FIGURE 20.** Morphospecies *Zigrasimecia* ufv-11. A and B, head in full-face and anterior views, respectively, of specimen ANTWEB1047053, black triangle indicates curved, decumbent setae on frons and vertex; C, profile view of right side of body of specimen ANTWEB1047903. Scale bar 0.2 mm in A, and 0.5 mm in C.

### ***Zigrasimecia* JGD-10 (“*Z. caohuijiae\_nr*”)**

This worker specimen is similar to *Z. caohuijiae*, except for the petiolar shape which is more antero-posteriorly compressed, therefore, without the evenly round top of the node in lateral view, and by the mesosomal dorsal surface in dorsal view, which is apparently slightly more compact than in *Z. caohuijiae*. They share a similar head shape, to a great extent the mesosomal shape, and the petiolar shape in anterior view (petiole with a curved dorsal outline in anterior view rather than flat or bilobed). It was added to multientry key but excluded from the dichotomous; the images are by José Gómez Durán, reproduced with permission.

**Examined material.** One worker (ANTWEB1047077). Hukawng Valley, Kachin Province, Myanmar; Lower Cenomanian (ca.98.79 ± 0.62 Ma) [JGDC].

### ***Zigrasimecia* YKLP-AMB-002**

This queen specimen was studied in astonishing detail through micro-CT scanning and had its external morphology described, as well as its internal organs in a work that demonstrate the power of this technique to help in the understanding of the morphology of the amber fossil ants (Zhuang *et al.*, 2022b). In their description, the palpal formula is given as 4, 3, however, it can be seen to be in fact 6, 4 (Additional file 9, Video S8, 19”).

The queen is surely not conspecific to *Z. goldingot* (one of the two species described based on queens), differing from it by the head rather subrectangular instead of subquadrate, by having 36 clypeal chaetae instead of 22, and by the shape of the mesoscutellum, which is about as long as wide while clearly wider than long in *Z. goldingot*. When compared to *Z. tonsora* (the other species described based on a queen), significant differences are not that apparent, in fact, both have similar clypeal chaetae numbers and similar mandibular shapes. Specimen YKLP-AMB-002 is better preserved than *Z. tonsora* holotype and has been better imaged due to the micro-CT scanning technique, so a detailed comparison between the two is difficult until we have a better characterization of *Z. tonsora*. Pilosity might be a main difference between the two, but chances of conspecificity should not be ruled out and direct comparison between them and/or further imaging of *Z. tonsora* should be attempted in the future.

Queen YKLP-AMB-002 was tentatively added to the multientry but not to the dichotomous key. The images in the multientry key are by Yuhui Zhuang, reproduced with permission.

**Examined material.** One alate queen (YKLP-AMB-002). Hukawng Valley, Kachin Province, Myanmar; Lower Cenomanian (ca.98.79 ± 0.62 Ma) [YKLP].

### **The specimens of Cao *et al.*, 2020b**

The species boundaries reinterpretation proposed in this paper demanded a reevaluation of what was prior described as variation of *Z. ferox* in the work of Cao *et al.* (2020b). Most of the specimens studied there, attributed as variants of *Z. ferox*, could not be satisfactorily examined, as many of the images presented in the supplementary material do not allow the visualization of key features. Below are comments for each of the ones I could attempt an identification.

***Zigrasimecia* CNU-HYM-MA2019065.** This was the closest to *Z. ferox*. It differs by the greater abundance of setae, especially on the head, and by setae size, appearing longer than in *Z. ferox*. Also, the dorsal node of the petiole appears to be oblique rather than almost flat as in *Z. ferox*. Specimen CNU-HYM-MA2019054, formerly the paratype of *Z. hoelldobleri*, is likely conspecific to this specimen (see comments under *Z. hoelldobleri*).

***Zigrasimecia* CNU-HYM-MA2019061.** The setation on the body of this specimen is denser than what would be expected for *Z. ferox* and the setae are long flexuous rather than erect and relatively short. The petiole node in profile view does not form a straight dorsal margin; instead, it is rounded and very mildly bilobed. Considering these and that the specimen is overall chubby, it matches better the diagnosis of *Z. chuyangsui*.

***Zigrasimecia* CNU-HYM-MA2019059.** The bilobed, anteroposteriorly compressed petiolar node indicates this specimen is unlikely *Z. ferox*, and a proper identification of it depends on the confirmation of how its setation is. The image has an overexposed background, which might be outshining the body pilosity. If the specimen is confirmed to be mostly glabrous, as it looks, then it could belong to *Z. perrichoti*.

***Zigrasimecia* CNU-HYM-MA2018070.** This astonishing specimen appears to be mostly glabrous and has an

evenly round top of the petiolar node. Both traits are not indicative of conspecificity to *Z. ferox*; instead, they indicate a similarity to *Z. caohuijiae*. Further images and characterization of the specimen could help confirm it as a member of *Z. caohuijiae* and its impeccable state of preservation would surely enhance the description of that species, which is currently not ideal due to a partially obscured full-face view.

**TABLE 1.** Approximate count of clypeal chaetae and ommatidia for *Zigrasimecia* species and morphospecies. *Zigrasimecia tonsora* is a queen, therefore, fewer ommatidia are expected for the worker caste when found.

Species	Clypeal chaetae	Ommatidia number	Morphospecies	Clypeal chaetae	Ommatidia number
<i>Z. boudinoti</i>	34	>150	<i>Zigrasimecia</i> ufv-04	34	50
<i>Z. caohuijiae</i>	—	50	<i>Zigrasimecia</i> ufv-06	34	70*
<i>Z. chuyangsui</i>	46	90	<i>Zigrasimecia</i> ufv-08	40	45
<i>Z. ferox</i>	30	100	<i>Zigrasimecia</i> ufv-09	36-40*	40-45*
<i>Z. goldingot</i>	22	—	<i>Zigrasimecia</i> ufv-10	—	—
<i>Z. perrichoti</i>	33	89	<i>Zigrasimecia</i> ufv-11 (ANTWEB1047953)	40	50
<i>Z. thate</i>	30	32	<i>Zigrasimecia</i> ufv-11 (ANTWEB1047903)	36	55
<i>Z. tonsora</i>	35	>150*			

\*Highly dubious, as part of the eye is obscured by debris.

### 3. 4. The subfamily *Zigrasimeciinae* Borysenko, 2017

*Boltonimecia*, a Canadian, Campanian elusive stem-ant genus, shares the subfamily with *Zigrasimecia* and *Protozigrasimecia* (Borysenko, 2017; Cao *et al.* 2022b). Prior to the erection of the subfamily, the three genera were treated as a tribe, the *Zigrasimeciini* Borysenko, 2017. Borysenko's *Zigrasimeciini* diagnosis was "(1) head capsule specialized: shield-like, with dorsal part thick and raised (putative apomorphy); (2) anterolateral clypeal margins produced over mandibular bases in rounded lobes (putative apomorphy); (3) peg-like setae on anterior clypeal margin present; (4) ocelli absent; (5) relative length of antennomeres variable; (6) neck long; (7) protibia with three spurs: one pectinate and two simple; (8) petiole pedunculate; (9) gastral constriction absent". Based on the diagnosis of *Zigrasimecia* established by Barden and Grimaldi (2013), expanded in Perrichot (2014), in Cao *et al.* (2020a), and in this paper, several important differences between *Boltonimecia* and *Zigrasimecia* must be stressed (often differences also hold true between *Boltonimecia* and *Zigrasimecia* + *Protozigrasimecia*).

Although the head capsule in *Zigrasimecia* is swollen at the frons level, it does not raise abruptly and does not form a shield-like, thick cuticle as in *Boltonimecia*. Moreover, the raised portion of the head in *Zigrasimecia* is confined to the frontal carinae, thus two linear areas between the toruli and anteromedial points of the compound eye perimeter, while in *Boltonimecia*, the raised cuticle is a single block of cuticle starting anterad the torulus, on the central portion of the clypeus, and diverging posteriorly past the "stick-like" processes, thus occupying a much larger area of the head and in a shape that is considerably different (roughly resembling that of the modern Neotropical genus *Procryptocerus* Emery, 1887). The rounded clypeal lobes of *Boltonimecia* are poorly developed in comparison to those of *Zigrasimecia* and *Protozigrasimecia* and are more similar to the ones seen in some *Gerontoformica* species, (e.g., morphospecies *Gerontoformica* ufv-01, ANTWEB1032418). The presence of clypeal chaetae ("peg-like") is not a feature shared exclusively by the three genera of *Zigrasimeciinae* and is widespread among other Sphecomyrminae and Haidomyrmecinae genera. In fact, the very reduced and pointy chaetae of *Boltonimecia*, rather than the thick, densely arranged, and truncate chaetae of *Zigrasimecia* and *Protozigrasimecia*, and their origin from a convex rather than concave anterior clypeal margin (Fig. 1, C and Fig. 2, B of Borysenko, 2017) resemble more the *Gerontoformica* conformation of clypeal chaetae. The entire mandibular structure of *Boltonimecia* does not show the various modifications of *Zigrasimecia*, many of which are shared between *Zigrasimecia* and *Protozigrasimecia* (see diagnosis above). Although the mandible of *Boltonimecia* is somewhat similar to that of *Protozigrasimecia*, it does

not seem to be more than the similarities observed between *Boltonimecia* and *Gerontoformica* or *Sphecomyrma*. There is no evidence of mandibular and labral chaetae in *Boltonimecia*, both shared traits of *Zigrasimecia* and *Protozigrasimecia*. Other Cretaceous ants, and not only *Zigrasimecia*, have the ocelli absent. The mesosoma of *Boltonimecia* has the dorsal outline with different levels, as opposed to having it strongly fused and continuous, as in *Zigrasimecia* workers. The tall pronotal middle section, very expanded mesosomal middle section (which could be the mesoscutum and mesoscutellum) followed posteriorly by a darkened transversal structure (the metanotum?) of *Boltonimecia* could even be interpreted as being the developed mesothorax of a queen; however, the images of the specimen do not allow for a definitive conclusion. In *Protozigrasimecia* the mesosomal sclerites are distinct and this is a big difference between it and *Zigrasimecia*, however, that condition is not only shared between *Protozigrasimecia* and *Boltonimecia*, as the discontinuous dorsal outline of the mesosoma is found in most Cretaceous genera. A pair of spur-like protibial setae are indeed shared by *Boltonimecia* and some species of *Zigrasimecia*. The pedunculate petiole of *Boltonimecia* is distinct, while all *Zigrasimecia* have, in fact, an oblique anterior surface which, in profile, gradually and evenly diverges from the ventral margin, thickening the petiole posterad, but the anterior section of the petiole never develops into an anterior cylindrical or tubular portion (*Z. ferox* holotype has an almost disarticulated petiole, giving the impression of a developed peduncle). In the holotype of *Protozigrasimecia chauli* Cao, Boudinot & Gao, 2020, the peduncle is long, but the right hindleg is disarticulated at the trochanter level, right next to the "peduncle", so it is possible that the petiole of *P. chauli* is not that much, or maybe not at all, pedunculate, the stretched condition observed being a result of a taphonomic effect. The cinctus in *Zigrasimecia* varies from absent to mild, *Protozigrasimecia* has a strong cinctus, and among the Sphecomyrminae and Haidomyrmecinae, it varies from absent to extreme, up to the point of forming a postpetiole in some species (e.g. *Myanmyrma gracilis* Engel & Gimaldi, 2005), so this character is therefore not useful to infer relatedness between the three genera. Moreover, *Boltonimecia* is geographically and temporally separated from *Zigrasimecia* and *Protozigrasimecia*. This *per se* does not impede a relationship between them, as related ants do occur in different deposits, as seen in the Haidomyrmecinae, which has the genus *Haidoterminus* McKellar *et al.*, 2013 occurring in Canadian, early Cretaceous amber, *Haidomyrmodes* Perrichot *et al.*, 2008 from French, mid-Cretaceous amber, and the various Burmese genera from mid-Cretaceous amber (Perrichot *et al.*, 2020). A true relationship between *Boltonimecia* and the other two Zigrasimeciinae genera is unlikely when all these differences are considered. Despite this, I maintain Borysenko's proposition until better-preserved *Boltonimecia* fossils are found and add information to the species description. A re-evaluation of *Boltonimecia canadensis* holotype using different techniques or the finding of new specimens is critical to solve these issues and better infer its affinities among the stem ants.

The eyelessness of *Boltonimecia canadensis* (Wilson, 1985), an exclusive state among stem ants, is an odd feature and the presence of the "stick-like" processes at the exact place where the eyes are expected to be makes it questionable whether the processes are not, in fact, very deformed eyes. In the original description of the species, there is no mention of an eyeless condition; however, neither have eyes been described (Wilson, 1985). It is unusual, but not nonexistent, that compound eyes are heavily deformed in Burmese amber specimens, sometimes even when the rest of the body is not that damaged (personal observation). Borysenko argues that there is no sign of ommatidia and the processes have pilosity similar to those in other areas of the head, which are important notes in favor of his hypothesis. One possibility is that compound eyes really are the "stick-like" processes, but their ommatidia limits have completely disappeared by the deformed cuticle in an unexpected manner and the compound eyes of the species have setae in between the ommatidia, a condition not so unusual in ants, although the absence of setae is more common. Conversely, if eyelessness is confirmed and considering the long legs of *B. canadensis*, it could be indicative of troglomorphic, as in the case of the newly described ant *Yavnella laventa* Griebenow, 2022. In this case, the issue becomes how could a troglomorphic species be trapped in tree resin. *Myanmyrma gracilis*, also a very long-legged ant, was described as having "eyes and ocelli not apparent". Eyelessness in this species would be just as puzzling as in *Boltonimecia*, however, in this case the holotype has strong cephalic deformations and no conclusion can be taken.

### 3. 5. Taxonomy of fossil ants

Ant species described based on alate females or, worst, males, have historically been thorns on the side of ant taxonomists. An example was the case of the enigmatic "dolichoderine" *Amyrmex golbachii* Kusnezov, 1953, which

remained a mystery for decades and after molecular studies turned out to be a member of the Dorylinae instead (Ward & Brady, 2009; Borowiec, 2016). Molecular data, however, cannot help paleontology as it does to the taxonomy of living species.

Although the descriptions of the first and fourth species of *Zigrasimecia* were based on queens (Barden & Grimaldi, 2013; Zhuang *et al.*, 2022), those acts were justified, considering the oddness of the *taxon* as well as, in the case of the first species, the uncertainty of whether a worker caste would ever be found. The same occurred with the species of *Camelosphecia*, which has one species described based on an alate female, *C. fossor* Boudinot *et al.*, 2020, and one based on a male, *C. venator* Boudinot *et al.*, 2020. With the development of the knowledge about *Zigrasimecia* though, including the results of this revision, we now know that the worker caste is not only present but relatively abundant. In fact, following online traders who sell large amounts of Burmese amber, confirms that *Zigrasimecia* workers are more common than queens and, despite being an uncommon genus, they are by no means rare, with one or a couple of specimens being auctioned monthly (personal observation). The worker caste of *Zigrasimecia* also represents the first case of extreme mesosomal simplification in ants (Boudinot *et al.*, 2022b). Given the state of the art and considering the prolific period of the taxonomy of Burmese insects, with an ever-increasing rate of descriptions (Guo *et al.*, 2017), we can be almost sure that *Zigrasimecia* species will grow significantly, and thus, descriptions should be based primarily on the worker caste to avoid the development of a parallel taxonomy. If specific epithets continue to be given to queens and workers indiscriminately, many will fatally be, at some point, spurious names that would artificially inflate the genus diversity. Once a parallel taxonomy is established, any correction attempt is impeded as side-by-side comparisons between types deposited in different institutions are difficult to make, and, even if made, the inherent morphological differences between the female castes and the fact that amber ants of different castes are found unassociated (as they are trapped outside the nest) necessarily impede the certainty of a caste match.

Species described based on fragmentary or poorly preserved specimens generate the same problems, as better preserved conspecifics will likely not be recognized as such when eventually found. For example, *Myanmyrma gracilis* was described based on a poorly preserved specimen. When well-preserved specimens of *M. gracilis* are found, it is doubtful whether anyone will be able to assign them to *M. gracilis* or if they will be described as a morphologically similar new species. Despite that, and just like the case of *Z. tonsora*, the description of *M. gracilis* was fully justified, considering how bizarre that species is; nevertheless, it does represent a taxonomic problem (perhaps an unavoidable one). An additional problem with descriptions based on poorly preserved specimens is that they can falsely augment the known morphological heterogeneity of their lineage as they can be artificially aberrant. In order not to make the publications on amber-preserved ants an obstacle for future taxonomic development, whenever possible, descriptions based on sexuals or poorly-preserved specimens should be avoided.

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## REFERENCES

- Aibekova, L., Boudinot, B., Beutel, R., Richter, A., Keller, R., Hita-Garcia, F. & Economo, E. (2022) The skeletomuscular system of the mesosoma of *Formica rufa* workers (Hymenoptera: Formicidae). *Insect Systematics and Diversity*, 6 (2), 1–26.  
<https://doi.org/10.1093/isd/ixac002>  
AntWeb (2023) AntWeb. Version 8.86.2. California Academy of Science. Available from: <https://www.antweb.org> (accessed 9

February 2023)

- Barden, P. (2017) Fossil ants (Hymenoptera: Formicidae): ancient diversity and the rise of modern lineages. *Myrmecological News*, 24, 1–30.  
[https://doi.org/10.25849/myrmecol.news\\_024:001](https://doi.org/10.25849/myrmecol.news_024:001)
- Barden, P. & Grimaldi, D.A. (2012) Rediscovery of the bizarre Cretaceous ant *Haidomyrmex* Dlussky (Hymenoptera: Formicidae), with two new species. *American Museum Novitates*, 3755, 1–16.  
<https://doi.org/10.1206/3755.2>
- Barden, P. & Grimaldi, D.A. (2013) A new genus of highly specialized ants in Cretaceous Burmese amber (Hymenoptera: Formicidae). *Zootaxa*, 3681 (4), 405–412.  
<https://doi.org/10.11646/zootaxa.3681.4.5>
- Barden, P. & Grimaldi, D.A. (2014) A diverse ant fauna from the mid-Cretaceous of Myanmar (Hymenoptera: Formicidae). *PLoS ONE*, 9 (4), e93627.  
<https://doi.org/10.1371/journal.pone.0093627>
- Barden, P. & Grimaldi, D.A. (2016) Adaptive radiation in socially advanced stem-group ants from the Cretaceous. *Current Biology*, 26, 515–521.  
<https://doi.org/10.1016/j.cub.2015.12.060>
- Barden, P., Herhold H.W. & Grimaldi, D.A. (2017) A new genus of hell ants from the Cretaceous (Hymenoptera: Formicidae: Haidomyrmecini) with a novel head structure. *Systematic Entomology*, 42, 837–846.  
<https://doi.org/10.1111/syen.12253>
- Bolton, B. (2003) Synopsis and classification of Formicidae. *Memoirs of the American Entomological Institute*, 71, 1–370.
- Bolton, B. (2023) *An online catalog of the ants of the world*. Available from: <https://antcat.org> (accessed 1 March 2023).
- Borowiec, M.L. (2016) Generic revision of the ant subfamily Dorylinae (Hymenoptera, Formicidae). *ZooKeys*, 608, 1–280.  
<https://doi.org/10.3897/zookeys.608.9427>
- Borysenko, L.H. (2017) Description of a new genus of primitive ants from Canadian amber, with the study of relationships between stem- and crown-group ants (Hymenoptera: Formicidae). *Insecta Mundi*, 570, 1–57.  
<https://doi.org/10.1101/051367>
- Boudinot, B.E. (2015) Contributions to the knowledge of Formicidae (Hymenoptera, Aculeata): a new diagnosis of the family, the first global male-based key to subfamilies, and a treatment of early branching lineages. *European Journal of Taxonomy*, 120, 1–62.  
<https://doi.org/10.5852/ejt.2015.120>
- Boudinot, B.E., Perrichot, V. & Chaul, J.C.M. (2020) †*Camelosphracia* gen. nov., lost ant-wasp intermediates from the mid-Cretaceous (Hymenoptera, Formicoidea). *ZooKeys*, 1005, 21–55.  
<https://doi.org/10.3897/zookeys.1005.57629>
- Boudinot, B.E., Khouri, Z., Richter, A., Griebenow, Z.H., van de Kamp, T., Perrichot, V. & Barden, P. (2022a) Evolution and systematics of the Aculeata and kin (Hymenoptera), with emphasis on the ants (Formicoidea: †@@@idae fam. nov., Formicidae). *bioRxiv*. [published online]  
<https://doi.org/10.1101/2022.02.20.480183>
- Boudinot, B.E., Richter, A., Katzke, J., Chaul, J.C.M., Keller, R.A., Economo, E.P., Beutel, R.G. & Yamamoto, S. (2022b) Evidence for the evolution of eusociality in stem ants and a systematic revision of †*Gerontoformica* (Hymenoptera: Formicidae). *Zoological Journal of the Linnean Society*, 195, 1355–1389.  
<https://doi.org/10.1093/zoolinnean/zlab097>
- Brown, W.L. Jr. & Kempf, W.W. (1968 [apparent year 1967]) *Tatuidris*, a remarkable new genus of Formicidae (Hymenoptera). *Psyche, Cambridge*, 74, 183–190.  
<https://doi.org/10.1155/1967/868759>
- Cao, H., Boudinot, B.E., Wang, Z., Miao, X., Shih, C., Ren, D. & Gao, T. (2020a). Two new iron maiden ants from Burmese amber (Hymenoptera: Formicidae: †Zigrasimeciini). *Myrmecological News*, 30, 161–173.  
[https://doi.org/10.25849/myrmecol.news\\_030:161](https://doi.org/10.25849/myrmecol.news_030:161)
- Cao, H., Boudinot, B.E., Shih, C., Ren, D. & Gao, T. (2020b) Cretaceous ants shed new light on the origins of worker polymorphism. *Science China Life Sciences*, 63, 1085–1088.  
<https://doi.org/10.1007/s11427-019-1617-4>
- Engel, M.S. & Grimaldi, D.A. (2005) Primitive new ants in Cretaceous amber from Myanmar, New Jersey, and Canada (Hymenoptera: Formicidae). *American Museum Novitates*, 3485, 1–23.  
[https://doi.org/10.1206/0003-0082\(2005\)485\[0001:PNAICA\]2.0.CO;2](https://doi.org/10.1206/0003-0082(2005)485[0001:PNAICA]2.0.CO;2)
- Evenhuis, N.L. The insect and spider collections of the world website. Available online: <http://hbs.bishopmuseum.org/codens/> (accessed 9 February 2023)
- Griebenow, Z.H., Isaia, M. & Moradmand, M. (2022) A remarkable troglomorphic ant, *Yavnella laventa* sp. nov. (Hymenoptera: Formicidae: Leptanillinae), identified as the first known worker of *Yavnella* Kugler by phylogenomic inference. *Invertebrate Systematics*, 36 (12), 1118–1138.  
<https://doi.org/10.1071/IS22035>
- Guo M., Xing, L., Wang, B., Zhang, W., Wang, S., Shi, A. & Bai, M. (2017) A catalogue of Burmite inclusions. *Zoological Systematics*, 42 (3), 249–379.

<https://doi.org/10.1186/zs.201715>

- Grimaldi, D., Agosti, D. & Carpenter, J.M. (1997) New and rediscovered primitive ants (Hymenoptera: Formicidae) in Cretaceous amber from New Jersey, and their phylogenetic relationships. *American Museum Novitates*, 3208, 1–43.
- Haug, C., Reumer, J.W.F., Haug, J.T., Arillo, A., Audou, D., Azar, D., Baranov, V., Beutel, R., Charbonnier, S., Feldmann, R., Foth, C., Fraaije, R.H.B., Frenzel, P., Gašparič, R., Greenwalt, D.E., Hyžný, M., Jagt, J.W.M., Jagt-Yazykova, E.A., Jarzembowski, E., Kerp, H., Kirejtshuk, A.G., Klug, C., Kopylov, D.S., Kotthoff, U., Kriwet, J., Kunzmann, L., McKellar, R.C., Nel, A., Neumann, C., Nützel, A., Perrichot, V., Pint, A., Rauhut, O., Schneider, J.W., Schram, F.R., Schweigert, G., Selden, P., Szewo, J., van Bakel, B.W.M., van Eldijk, T., Vega, F.J., Wang, B. & Reich, M. (2020) Comment on the letter of the Society of Vertebrate Paleontology (SVP) dated April 21, 2020 regarding “Fossils from conflict zones and reproducibility of fossil-based scientific data”: the importance of private collections. *PalZ*, 94, 413–429.  
<https://doi.org/10.1007/s12542-020-00522-x>
- Haug, J.T., Azar, D., Ross, A., Szewo, J., Wang, B., Arillo, A., Baranov, V., Bechteler, J., Beutel, R., Blagoderov, V., Delclòs, X., Dunlop, J., Feldberg, K., Feldmann, R., Foth, C., Fraaije, R.H.B., Gehler, A., Harms, D., Hedenäs, L., Hyžný, M., Jagt, J.H.M., Jagt-Yazykova, E.A., Jarzembowski, E., Kerp, H., Khine, P.K., Kirejtshuk, A.G., Klug, C., Kopylov, D.S., Kotthoff, U., Kriwet, J., McKellar, R.C., Nel, A., Neumann, C., Nützel, A., Peñalver, E., Perrichot, V., Pint, A., Ragazzi, E., Regalado, L., Reich, M., Rikinen, J., Sadowski E.M., Schmidt, A.R., Schneider, H., Schram, F.R., Schweigert, G., Selden, P., Seyfullah, L.J., Solórzano-Kraemer, M.M., Stilwell, J.D., van Bakel, B.W.M., Vega, F.J., Wang, Y., Xing, L. & Haug, C. (2020) Comment on the letter of the Society of Vertebrate Paleontology (SVP) dated April 21, 2020 regarding “Fossils from conflict zones and reproducibility of fossil-based scientific data”: Myanmar amber. *PalZ*, 94, 431–437.  
<https://doi.org/10.1007/s12542-020-00524-9>
- Keller, R.A. (2011) A phylogenetic analysis of ant morphology (Hymenoptera: Formicidae) with special reference to the poneromorph subfamilies. *Bulletin of the American Museum of Natural History*, 355, 1–90.  
<https://doi.org/10.1206/355.1>
- Kempf, W.W. (1962) Miscellaneous studies on neotropical ants. II. (Hymenoptera, Formicidae). *Studia Entomologica*, 5, 1–38.
- Kerner A., Bouquin S., Portier R. & Vignes-Lebbe R. (2021) The 8 Years of Existence of Xper3: State of the art and future developments of the platform. *Biodiversity Information Science and Standards*, 5, e74250.  
<https://doi.org/10.3897/biss.5.74250>
- Kimball, S. & Mattis, P. (1996) GIMP—The GNU Image Manipulation Program. Available from: <https://www.gimp.org> (accessed 30 May 2021)
- LaPolla, J.S., Dlussky, G.M. & Perrichot, V. (2013) Ants and the fossil record. *Annual Review of Entomology*, 58, 609–630.  
<https://doi.org/10.1146/annurev-ento-120710-100600>
- Lattke, J.E. & Melo, G.A.R. (2020) New haidomyrmecine ants (Hymenoptera: Formicidae) from mid-Cretaceous amber of northern Myanmar. *Cretaceous Research*, 114, 104502.  
<https://doi.org/10.1016/j.cretres.2020.104502>
- McKellar, R.C., Glasier, J.R.N. & Engel, M.S. (2013) A new trap-jawed ant (Hymenoptera: Formicidae: Haidomyrmecini) from Canadian Late Cretaceous amber. *Canadian Entomologist*, 145, 454–465.  
<https://doi.org/10.4039/tce.2013.23>
- Miao, Z. & Wang, M. (2019) A new species of hell ants (Hymenoptera: Formicidae: Haidomyrmecini) from the Cretaceous Burmese amber. *Journal of the Guangxi Normal University (Natural Science Edition)*, 37 (2), 139–142.  
<https://doi.org/10.16088/j.issn.1001-6600.2019.02.017>
- Nel, A., Perrault, G., Perrichot, V. & Néraudeau, D. (2004) The oldest ant in the Lower Cretaceous amber of Charente-Maritime (SW France) (Insecta: Hymenoptera: Formicidae). *Geologica Acta*, 2, 23–29.  
<https://doi.org/10.1344/105.000001630>
- Perrichot, V. (2014) A new species of the Cretaceous ant *Zigrasimecia* based on the worker caste reveals placement of the genus in the Sphecomyrminae (Hymenoptera: Formicidae). *Myrmecological News*, 19, 165–169.  
[https://doi.org/10.25849/myrmecol.news\\_019:165](https://doi.org/10.25849/myrmecol.news_019:165)
- Perrichot, V., Nel, A., Néraudeau, D., Lacau, S. & Guyot, T. (2008) New fossil ants in French Cretaceous amber (Hymenoptera: Formicidae). *Naturwissenschaften*, 95, 91–97.  
<https://doi.org/10.1007/s00114-007-0302-7>
- Perrichot, V., Wang, B. & Barden, P. (2020) New remarkable hell ants (Formicidae: Haidomyrmecinae stat. nov.) from mid-Cretaceous amber of northern Myanmar. *Cretaceous Research*, 109 (104381), 1–18.  
<https://doi.org/10.1016/j.cretres.2020.104381>
- Rayfield, E.J., Theodor, J.M. & Polly, P.D. (2020) Fossils from conflict zones and reproducibility of fossil-based scientific data. Society of Vertebrate Paleontology (SVP), letter, 21 April 2020. Available from: <https://vertpaleo.org/wp-content/uploads/2021/01/SVP-Letter-to-Editors-FINAL.pdf> (accessed 20 June 2023)
- Richter, A., Boudinot, B., Yamamoto, S., Katzke, J. & Beutel, R.G. (2022) The first reconstruction of the head anatomy of a Cretaceous insect, †*Gerontoformica gracilis* (Hymenoptera: Formicidae), and the early evolution of ants. *Insect Systematics and Diversity*, 6 (5), 1–80.  
<https://doi.org/10.1093/isd/ixac013>
- Schneider, C.A., Rasband, W.S. & Eliceiri, K.W. (2012) NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, 9,

671–675.

<https://doi.org/10.1038/nmeth.2089>

Shi, G., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Yang, M., Lei, W., Li, Q. & Li, X. (2012) Age constraint on Burmese amber based on UePb dating of zircons. *Cretaceous Research*, 37, 155e163.

<https://doi.org/10.1016/j.cretres.2012.03.014>

Terayama, M. (2013) Additions to knowledge of the ant fauna of Japan (Hymenoptera; Formicidae). *Memoirs of the Myrmecological Society of Japan*, 3, 1–24.

Theodor, J.M., Lewis, M.E. & Rayfield, E.J. (2021) Amber specimens acquired from Myanmar following military coup. Society of Vertebrate Paleontology (SVP), letter, 14 June 2021. Available from: [https://vertpaleo.org/wp-content/uploads/2021/06/SVP-Letter-to-paleontological-community-on-Myanmar-Amber\\_FINAL.pdf](https://vertpaleo.org/wp-content/uploads/2021/06/SVP-Letter-to-paleontological-community-on-Myanmar-Amber_FINAL.pdf) (accessed 24 July 2023)

Ung, V., Dubus, G., Zaragüeta-Bagils, R. & Vignes-Lebbe, R. (2010) Xper2: introducing e-taxonomy. *Bioinformatics*, 26 (5), 703–704.

<https://doi.org/10.1093/bioinformatics/btp715>

Vignes-Lebbe, R., Bouquin, S., Kerner, A. & Bourdon, E. (2017) Desktop or remote knowledge base management systems for taxonomic data and identification keys: Xper2 and Xper3. *Proceedings of TDWG*, 1, e19911.

<https://doi.org/10.3897/tdwgproceedings.1.19911>

Ward, P.S. & Brady, S.G. (2009) Rediscovery of the ant genus *Amyrmex* Kusnezov (Hymenoptera: Formicidae) and its transfer from Dolichoderinae to Leptanilloidinae. *Zootaxa*, 2063 (1), 46–54.

<https://doi.org/10.11646/zootaxa.2063.1.2>

Wilson, E.O., Carpenter, F.M. & Brown, W.L. Jr. (1967) The first Mesozoic ants, with the description of a new subfamily. *Psyche, Cambridge*, 74, 1–19.

<https://doi.org/10.1155/1967/89604>

Wilson, E.O. (1985) Ants from the Cretaceous and Eocene amber of North America. *Psyche, Cambridge*, 92, 205–216.

<https://doi.org/10.1155/1985/57604>

Zheng, D., Chang, S.C., Perrichot, V., Dutta, S., Rudra, A., Mu, L., Kelly, R.S., Li, S., Zhang, Q., Zhang, Q., Wong, J., Wang, J., Wang, H., Fang, Y., Zhang, H. & Wang, B. (2018) A Late Cretaceous amber biota from central Myanmar. *Nature Communications*, 9, 3170.

<https://doi.org/10.1038/s41467-018-05650-2>

Zhuang, Y., Ran, H., Li, X., Feng, C. & Liu, Y. (2022a) A new species of the iron maiden ant based on an alate female from mid-Cretaceous Burmese amber (Hymenoptera: Formicidae: †*Zigrasimecia*). *Cretaceous Research*, 130 (105056), 1–5.

<https://doi.org/10.1016/j.cretres.2021.105056>

Zhuang, Y., Xu, W., Zhang, G., Mai, H., Li, X., He, H., Ran, H. & Liu, Y. (2022b) Unparalleled details of soft tissues in a Cretaceous ant. *BMC Ecology and Evolution*, 22 (146), 1–10.

<https://doi.org/10.1186/s12862-022-02099-2>

## APPENDIX 1

Entire set of measurements taken from specimens examined physically. These additional measurements will help identification of specimens which have few measurable parts as well as give support to the evaluation of species boundaries.

**HW2**—In full-face view, width just posterior to the clypeal lobes, the most constricted part on the anterior portion of the head (Fig. 1, d).

**HW3**—In full-face view, maximum width at the clypeal lobe level (Fig. 1, e).

**HD**—The widest line measured in profile view of the head, normally at the level of the frons and gena (Fig. 1, f).

**HL2**—In full-face view, straight line from middle point of anterior clypeal margin (including clypeal stout setae) to posteriormost point of vertex (Fig. 1, b).

**AntL** and **AntW**—Antennomere length and width, respectively, from II to XII. Presented in Table 2 and here, but not under species descriptions.

**PropspL**—Maximum length of the propodeal spiracle measured in profile view (Fig. 1, i).

**A3L**—Diagonal length of AIII from ventral anteriormost point (the corner of the keel-shaped anterior process, or prora, of postero-sternite III) to dorsal posteriormost point of posttergite III (Fig. 1, l)

**ptg3L+ptg4L**—Diagonal measurement starting at the midpoint of the line which separates pre- from postsclerites III and ending at the posteriormost point of posttergite IV (Fig. 1, m)

**A3+A4L**—A diagonal length of AIII + AIV from ventral anteriormost point (the corner of the keel-shaped anterior process, or prora, of poststernite III) to dorsal posteriormost point of posttergite IV (Fig. 1, n).

**A3W**—Maximum width of A3 in dorsal view

**PrnW**—Maximum width of pronotum in dorsal view.

**PetW**—Metafemur maximum length, trochanter included. Ideally taken in anterior or posterior view, but depending on faceting and position of the legs it can be measured in other views provided sclerite is not seen too obliquely.

**Prfm+trochL**—Maximum length of profemur with trochanter included. Ideally taken in lateral view, but depending on faceting and position of the legs it can be measured in other views provided sclerite is not seen too obliquely.

**Prtb**—protibial maximum length.

**Prbt**—probasitarsus maximum length.

**Msfm+trochL**—Mesofemur maximum length, trochanter included. Ideally taken in anterior or posterior view, but depending on faceting and position of the legs it can be measured in other views provided sclerite is not seen too obliquely.

**Mstb**—Mesotibial maximum length. Ideally taken in dorsal view of the tibia, but depending on faceting and position of the legs it can be measured in other views provided sclerite is not seen too obliquely.

**MsbT**—Mesobasitarsus maximum length. Ideally taken in dorsal view of the tibia, but depending on faceting and position of the legs it can be measured in other views provided sclerite is not seen too obliquely.

**Mtfm+trochL**—Metafemur maximum length, trochanter included. Ideally taken in anterior or posterior view, but depending on faceting and position of the legs it can be measured in other views provided sclerite is not seen too obliquely.

**MttbL**—Metatibial maximum length. Ideally taken in dorsal view of the tibia, but depending on faceting and position of the legs it can be measured in other views provided sclerite is not seen too obliquely.

**MtbtL**—Metabasitarsus maximum length. Ideally taken in dorsal view of the tibia, but depending on faceting and position of the legs it can be measured in other views provided sclerite is not seen too obliquely.

Species or morphospecies	<i>Zigrasimecia boudinoti</i>	<i>Zigrasimecia caohuijiae</i>	<i>Zigrasimecia chuyangsui</i>	<i>Zigrasimecia perrichoti</i>	<i>Zigrasimecia thate</i>
type	holotype	holotype	holotype	holotype	holotype
code	ANTWEB 1032623	ANTWEB 1041055	ANTWEB 1032660	UFV- LABECOL- 010301	ANTWEB 1038912
HW	0.900	0.580	0.850	0.725	0.576
HW2	0.750		0.660	0.590	0.460
HW3	0.800		0.680	0.640	0.470
HD	0.530	0.410	0.530	0.490	0.480
HL	0.990	0.638	0.813	0.813	0.619
HL2	0.880	/		0.720	0.490
EL	0.270	0.160	0.190	0.210	0.110
SL	0.300	0.190	0.250	0.250	0.210
ant II L	0.100	0.090	0.100	0.100	0.100
ant III L	0.210	0.131	0.155	0.150	0.120
ant IV L	0.160	0.098	0.140	0.100	0.085
ant V L	0.140	0.090	0.125		0.080
ant VI L	0.150	0.090	0.110		0.080
ant VII L	0.140	0.082	0.100		0.070
ant VIII L	0.140	0.080	0.090		0.070
ant IX L	0.140	0.070	0.095		0.070
ant X L	0.160	0.082	0.090		0.060
ant XI L	0.130	0.090	0.100	0.090	0.060
ant XII L	0.270	0.180	0.180	0.185	0.120

.....Continued on the next page

APPENDIX 1 (Continued)

Species or morphospecies	<i>Zigrasimecia boudinoti</i>	<i>Zigrasimecia caohuijiae</i>	<i>Zigrasimecia chuyangsui</i>	<i>Zigrasimecia perrichoti</i>	<i>Zigrasimecia thate</i>
ant II W	0.060	0.053	0.060	0.050	0.045
ant III W	0.070	0.049	0.060	0.060	0.055
ant IV W	0.070	0.053	0.060	0.060	0.050
ant V W	0.080	0.062	0.070		0.045
ant VI W	0.070	0.065	0.070		0.040
ant VII W	0.070	0.066	0.070		0.050
ant VIII W	0.070	0.066	0.070		0.060
ant IX W	0.070	0.066	0.070		0.065
ant X W	0.070	0.066	0.070		0.070
ant XI W	0.075	0.066	0.070	0.065	0.075
ant XII W	0.080	0.062	0.065	0.070	0.070
WL		0.620	0.790		
MesL	1.100	0.663	0.713	0.750	0.670
MesH	0.790	0.400	0.600	0.500	0.390
PropspL	0.096	0.070		0.080	0.050
PetAFL	0.450	0.262	0.250	0.337	0.325
GL	1.500	0.990	1.040	0.880	0.650
Ptg3L: postero-tergite 3 L	0.850	0.313	0.600	0.600	0.475
AIIIL	0.988		0.700	0.787	0.580
ptgiiiL+ptgivL	1.250	0.720	0.930	0.820	
A3-A4L	1.175			0.960	
Ptg4L: postero-tergite 4 L	0.500	0.375	0.375	0.363	0.200
AIIIW	0.660		0.750		
PrnW	0.400	0.310	0.520		0.290
PetW	0.140	0.190			0.140
mtfm+troch L	0.910	0.530	0.700	0.750	0.437
mttb L	0.880	0.500	0.575	0.600	0.395
mtbt L	0.750	0.330	0.500	0.500	0.350
prfm+troch L				0.510	
prtb L				0.480	0.350
prbt L				0.320	0.210
msfm+troch L				0.590	
mstb L	0.740			0.520	
msbt L				0.310	
<b>INDEXES AND SUMS</b>					
OI: EL / HW x 100	30.00	27.59	22.35	28.97	19.11
CI: HW/HL x 100	90.91	90.91	104.55	89.18	92.98
SI: SL / HW x 100		32.76			
Metaleg L (mtfm+trochL+mttb)	2.54	1.36	1.78	1.85	1.18

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APPENDIX 1 (Continued)

Species or morphospecies	<i>Zigrasimecia boudinoti</i>	<i>Zigrasimecia caohuijiae</i>	<i>Zigrasimecia chuyangsui</i>	<i>Zigrasimecia perrichoti</i>	<i>Zigrasimecia thate</i>
Leg Index (HW /metaleg L * 100)	35.43	42.65	47.89	39.19	48.70
Leg index2 (MesL/ metalegL * 100)	43.31	48.75	40.17	40.54	56.68
PrnW/HW	0.44	0.53	0.61		0.50
<b>Total length</b> (HL+MesL+PetAFL+ Ptg3L+Ptg4L)	<b>3.89</b>	<b>2.25</b>	<b>2.75</b>	<b>2.86</b>	<b>2.29</b>