

# Cretaceous ants shed new light on the origins of worker polymorphism

Huijia Cao<sup>1†</sup>, Brendon E. Boudinot<sup>2†</sup>, Chungkun Shih<sup>1,3</sup>, Dong Ren<sup>1\*</sup> & Taiping Gao<sup>1\*</sup>

<sup>1</sup>College of Life Sciences and Academy for Multidisciplinary Studies, Capital Normal University, Beijing 100048, China;

<sup>2</sup>The Evergreen State College, Washington 98505, USA;

<sup>3</sup>Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013-7012, USA

Received September 28, 2019; accepted December 17, 2019; published online March 6, 2020

**Citation:** Cao, H., Boudinot, B.E., Shih, C., Ren, D., and Gao, T. (2020). Cretaceous ants shed new light on the origins of worker polymorphism. *Sci China Life Sci* 63, <https://doi.org/10.1007/s11427-019-1617-4>

Dear editor,

Polymorphism refers to two or more clearly different phenotypes coexisting in the population of a species. It has been observed and studied among ants, bees, wasps, termites, dung beetles and stag beetles (Trible and Kronauer, 2017; Zhao et al., 2019). Size and shape variation of these holometabolic insects, especially ants, usually happen in larval development rather than adult stage. Worker polymorphism, continuous variation of body sizes, is considered as a significant feature of advanced insect societies and the reason of castes differentiation in ant eusociality. Variation in individual sizes influences not only the behavioral repertoire of individuals, but also the trophic ecology, energetic efficiency of the colony (Peeters and Ito, 2015). Size-variable worker polymorphism is also associated with increased behavioral specialization and caste determination in colony (Trible and Kronauer, 2017). For example, major workers having larger body and mandibles usually take charge of defense or food transportation; but dwarf workers having smaller body usually take care of eggs and trophallaxis. However, it is hard to elucidate early polymorphism within worker caste due to sparse fossil evidence because of difficulties to identify workers to be co-species or to confirm whether they are co-

colony. Engel and Grimaldi supposed that *Haidomyrmex* Dlussky, 1996 should be a kind of “major” worker as a subcaste of workers for its special mandibles (Engel and Grimaldi, 2005). But subsequent studies suggested that workers with such unique cranio-mandibular were common in all castes rather than “major” workers (Perrichot et al., 2008). Thus, polymorphism of worker ants has never been described in fossils hitherto.

The earliest confirmed fossil ants can be dated to the late Albian (ca. 100 Mya). Several taxa of stem-group ants reported from mid-Cretaceous Burmese amber (ca. 99 Mya) suggest that the eusociality appeared at least in the mid-Cretaceous. For example, the type species of *Zigrasimecia* (Barden and Grimaldi, 2013), *Z. tonsora* is a dealate gyne, while all specimens, reported as the other species in *Zigrasimecia* (Perrichot, 2014), *Z. ferox* are workers. Herein, we provide further characters for *Z. ferox* based on additional two alate specimens from Kachin (Hukawng Valley) of Northern Myanmar, ca. 99 Mya. (Figure 1A and B, Figure S1A and B in Supporting Information). We assign these two alate gynes within *Zigrasimecia* based on typical dense mandibular brush and clypeal combs. They differ from *Z. tonsora* in that *Z. tonsora* has a concavity on the external surface of the mandible near the apex, while these two alate gynes and workers of *Z. ferox* without concavity. They also conform with *Z. ferox* in having a steep posterior margin of the propodeum and the right angle of ventral surface of gastral segment I. Moreover, referring to venational no-

†Contributed equally to this work

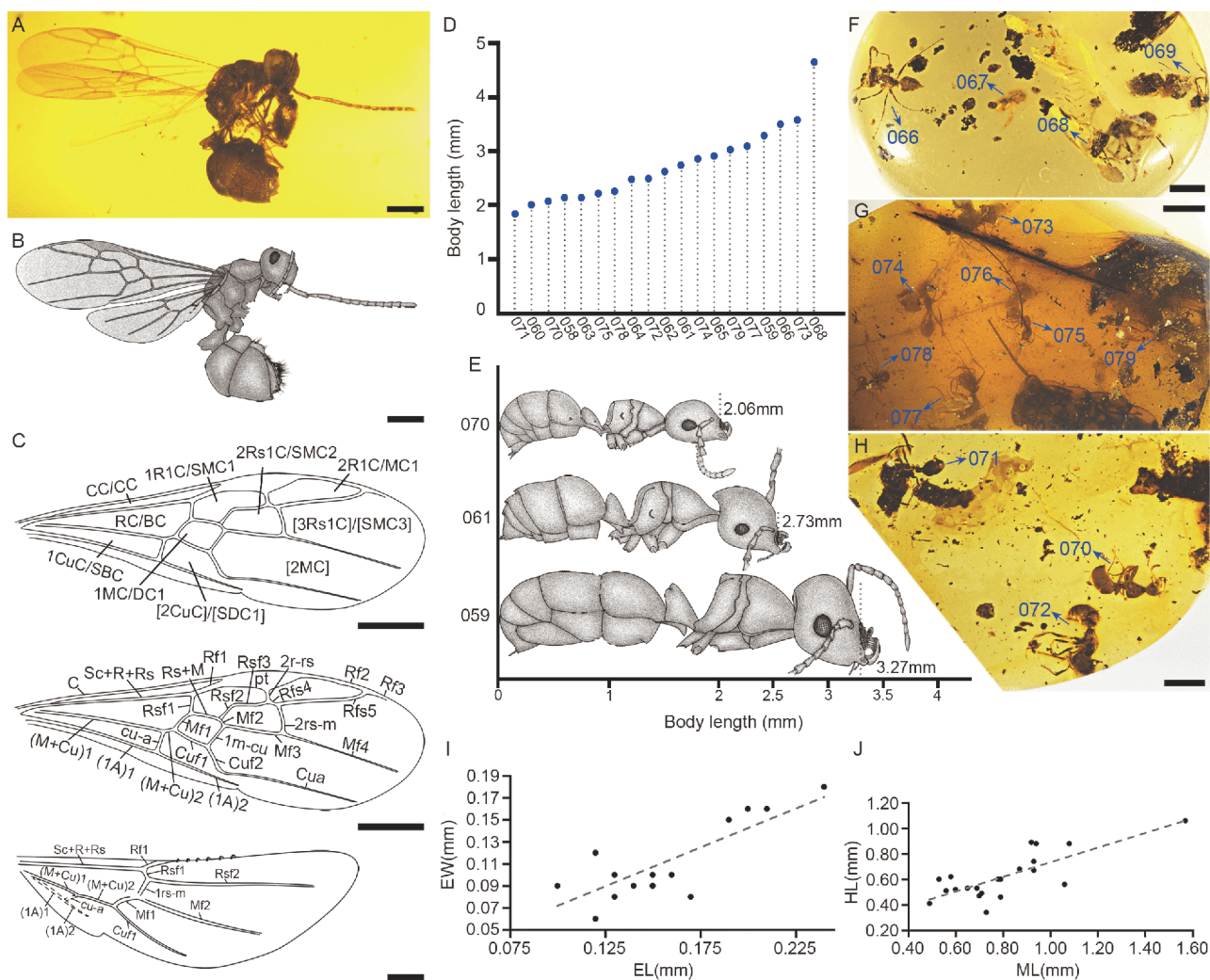
\*Corresponding authors (Dong Ren, email: [rendong@mail.cnu.edu.cn](mailto:rendong@mail.cnu.edu.cn); Taiping Gao, email: [tpgao@cnu.edu.cn](mailto:tpgao@cnu.edu.cn))

menclature of [Brown and Nutting \(1949\)](#), venations of *Z. ferox* are emended ([Figure 1C](#)): forewing (M+Cu)<sub>1</sub> branched into (M+Cu)<sub>2</sub> and cu-a; Rsf2 and Rsf3 distinguished; cell 2Rs1C/SMC2 6 sided; Mf2 short, nearly as long as Rsf4. Hind wing Mf1 bent and inclined, the length equal to cross-vein 1rs-m and longer than twice of Rsf1.

More importantly, workers of *Zigrasimecia ferox* ([Perrihot, 2014](#)), with continuously various body sizes and obvious features, have been identified, enabling us to study ancient polymorphism in the mid-Cretaceous. Three amber pieces, containing 4, 3 and 7 workers of *Z. ferox* with dif-

ferent body sizes and other 8 amber pieces each with an individually-preserved worker, demonstrate the earliest known continuous polymorphism in ants and imply that within-caste allometry might have appeared about the same time of the ant eusociality ([Figure 1D–J](#)). Thus, we infer that worker polymorphism appeared concomitantly with caste differentiation.

We examined 22 workers including 14 aggregated workers in three pieces of amber ([Figure 1F–H](#), [Figures S2, S3 and S4A and B](#) in Supporting Information) and 8 individually-preserved workers ([Figures S1C–H and S4C–F](#) in Support-



**Figure 1** Alate gyne and polymorphism of workers of *Zigrasimecia ferox* [Perrichot, 2014](#). A–C, Specimen of the alate gyne, No. CNU-HYM-MA2019056. D–H, Polymorphism of workers of *Z. ferox*; all the sequence numbers of specimens are abridged in the figure, the omitted part is No. CNU-HYM-MA2018 or No. CNU-HYM-MA2019. I and J, Single regression lines described all measurements plotted of *Z. ferox* workers against each other document isometry. A, Photograph of the CNU-HYM-MA2019056 in lateral view. B, Reconstructive drawing of the CNU-HYM-MA2019056. C, Reconstructions of venations of *Z. ferox* alate gyne, top: indication of cells; middle: indication of veins of forewing; bottom: indication of veins of hind wing. D, Scatter diagram of different body lengths of 19 workers of *Z. ferox* (listed in Table S1 in Supporting Information). E, Reconstructions in different lengths of tree *Z. ferox* workers, top: No. CNU-HYM-MA2018070, 2.06 mm in length; middle: No. CNU-HYM-MA2019061, 2.73 mm; bottom: No. CNU-HYM-MA2019059, 3.27 mm; see also [Figure S4](#) in Supporting Information. F, Photomicrograph of Amber No. 1, containing 4 workers, details see also [Figure S2](#) in Supporting Information. G, Photomicrograph of Amber No. 3, containing 7 workers, details see also [Figure S3](#) in Supporting Information. H, Photomicrograph of Amber No. 2, containing 3 workers, see also [Figure S2](#) in Supporting Information. I, Relationship between eye lengths and widths. J, Relationship between mesosoma lengths and head lengths. (Scale bars for A and B=0.5 mm, scale bars for forewings of C=0.5 mm, scale bar for hind wing of C=0.2 mm, scale bars for F and G=2 mm, scale bar for H=1 mm).

ing Information) from the collection of Capital Normal University. Posterior margin of propodeum of all 8 individually-preserved workers dropped steeply and nearly formed a right angle with dorsal surface. Their sub-petiole processes are strong, and the anterior edge of gastral I formed a right angle. All these characters indicated their affiliations with *Z. ferox* (Figure 1E). Additionally, we found three pieces of amber, Amber No. 1 embedded with 4 workers (Figure 1F, Figure S2 A–D in Supporting Information), Amber No. 2 with 3 workers (Figure 1H, Figure S2E–G in Supporting Information) and Amber No. 3 with 7 workers (Figure 1G, Figure S3 in Supporting Information) respectively, these workers also possess key characters of *Z. ferox*.

All of these workers show linearly continuous variation in body lengths (Figure 1D). The largest worker is 4.6 mm long, nearly 2.5 times as long as the smallest one with 1.8 mm (Figure 1D, Table S1 in Supporting Information). To further verify relationships among these individuals with various lengths of body and body structures, we measure and account other data like eye lengths, eye widths, head lengths, mesosomal lengths, etc. (Table S1 in Supporting Information). We found that these measurements plotted against each other show linear regression lines (Figure 1I and J). These results illustrate continuity in the size of conspecific workers, and the isometry of workers that we consider to derive from the same colony. Such size variation (isometry) is a sub-category of polymorphism, and is related to polyphenism, or having multiple tasks carried out by individuals. Due to preservation, some data of these *Z. ferox* worker ants in our study are not available, the numbers of points in these two linear regression analyses are different (details see Table S1 in Supporting Information).

New findings suggest that polymorphism within worker caste appeared during or before the mid-Cretaceous. Such isometric size variation supports the hypothesis that the individuals observed are conspecific, suggesting size-based polymorphism among these stem ants, and size variation were probably ancestral in eusocial Formicidae, as predicted by Tribble and Kronauer (2017). It was an optimum across a colony to achieve efficiency in the mid-Cretaceous.

In the studies of ant polymorphism, phylogenetic analysis showed that polymorphism is an evolutionarily labile trait and repeated, but quantitative data regarding the variation within and among species are limited (Wills et al., 2018). It

was supposed that worker polymorphism is a primary trait of the formicoid clade (Peeters, 1997). However, the worker polymorphism in *Z. ferox* here provides new evidence, because *Zigrasimecia* is a stem group, independent of any crown clades.

**Compliance and ethics** The author(s) declare that they have no conflict of interest.

**Acknowledgements** This work was supported by the National Natural Science Foundation of China (31730087, 41688103 and 31872277), the Program for Changjiang Scholars and Innovative Research Team in University (IRT-17R75), and the Support Project of High-level Teachers in Beijing Municipal Universities in the Period of 13th Five-year Plan (IDHT20180518), and the Beijing Natural Science Foundation (5182004). We are grateful to Dr. Vincent Perrichot (Univ Rennes, CNRS, Géosciences Rennes) who contributed to identification of some specimens and suggestion of polymorphism; and to Dr. Elijah J. Talamas (Systematic Entomology Laboratory, USDA/ARS c/o USNM, Smithsonian Institution, Washington, D. C. U.S.A.) for assistance in part of specimen classification. We also appreciate help from Ms. Yimo Wang during paper writing.

## References

- Barden, P., and Grimaldi, D. (2013). A new genus of highly specialized ants in Cretaceous Burmese amber (Hymenoptera: Formicidae). *Zootaxa* 3681, 405–412.
- Brown, W.L., and Nutting, W.L. (1949). Wing venation and the phylogeny of the Formicidae. *Trans Am Entomol Soc* 75, 113–132.
- Engel, M.S., and Grimaldi, D.A. (2005). Primitive new ants in Cretaceous amber from Myanmar, New Jersey, and Canada (Hymenoptera: Formicidae). *Am Mus Novit* 3485, 1–24.
- Peeters, C. (1997). Morphologically “primitive” ants: Comparative review of social characters, and the importance of queen-worker dimorphism. In: Choe, J.C., and Crespi, B.J., eds. *The Evolution of Social Behavior in Insects and Arachnids*. Cambridge: Cambridge University. 372–391.
- Peeters, C., and Ito, F. (2015). Wingless and dwarf workers underlie the ecological success of ants (Hymenoptera: Formicidae). *Myrmecol News* 21, 117–130.
- Perrichot, V., Lacau, S., Néraudeau, D., and Nel, A. (2008). Fossil evidence for the early ant evolution. *Naturwissenschaften* 95, 85–90.
- 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). *Myrmecol News* 19, 165–169.
- Tribble, W., and Kronauer, D.J.C. (2017). Caste development and evolution in ants: It’s all about size. *J Exp Biol* 220, 53–62.
- Wills, B.D., Powell, S., Rivera, M.D., and Suarez, A.V. (2018). Correlates and consequences of worker polymorphism in ants. *Annu Rev Entomol* 63, 575–598.
- Zhao, Z., Yin, X., Shih, C., Gao, T., and Ren, D. (2019). Termite colonies from mid-Cretaceous Myanmar demonstrate their early eusocial lifestyle in damp wood. *Natl Sci Rev* doi: 10.1093/nsr/nwz141.

## SUPPORTING INFORMATION

- 1 Material and methods
- 2 Supplemental figures and figure legends (Figures S1–S4)
- 3 Supplemental table about the dimension of all studied workers of *Zigrasimecia ferox* Perrichot, 2014 (Table S1)

4 Descriptions of the worker and gyne specimens individually embedded in amber

5 Descriptions of the aggregated worker specimens embedded in amber

6 Supplementary References

The supporting information is available online at <http://life.scichina.com> and <https://link.springer.com>. The supporting materials are published as submitted, without typesetting or editing. The responsibility for scientific accuracy and content remains entirely with the authors.