

# Advanced Research on Fossil Insects

Haichun Zhang <sup>1,\*</sup>  and Mathias Harzhauser <sup>2</sup> 

<sup>1</sup> State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China

<sup>2</sup> Geological-Paleontological Department, Natural History Museum Vienna, Burgring 7, 1010 Vienna, Austria

\* Correspondence: hczhang@nigpas.ac.cn

Fossils provide the only direct evidence we have of ancient life, and fossil insects are a window into the evolutionary history of insects. Recent work on taxonomy, palaeobiology, phylogenetics, taphonomy, and other related fields has facilitated the novel understanding of important evolutionary events in palaeoentomology and opened up new perspectives.

- (1) Insects have been living on Earth for approximately 480 million years [1], developing wings around 410 million years ago [1,2], about 180 million years before the pterosaurs [3], the next animals to take to the skies.
- (2) As the most diverse extant insect clade, Holometabola comprises more than 95% of the total species diversity of the entirety of Insecta, and complete metamorphosis is widely accepted to be a key innovation responsible for the success of insects [4]. Although already known from the Late Carboniferous, holometabolans experienced a distinct radiation during the Early-Middle Triassic and came to dominate insect diversity by the Middle Triassic [5].
- (3) Eusociality is perhaps the most striking and sophisticated innovation by insects. Termites are considered the oldest eusocial organisms, with the earliest known representatives being from the Early Cretaceous [6]. Ants are deduced to appear in the Late Jurassic or Early Cretaceous by molecular phylogenetic estimates, with the oldest fossil record dating back to 100 million years ago [7], whereas the fossil record of eusocial bees and wasps dates back to the Late Cretaceous [8].
- (4) The Mid-Mesozoic Parasitoid Revolution is a dramatic radiation of parasitoid lineages during the Middle Jurassic to Early Cretaceous, and is therefore proposed as a major biological event in terrestrial food-web history [9]. It is closely related to a shift from bottom-up regulation of terrestrial food webs to top-down trophic regulation, which is explained by the trophic cascade hypothesis and the trophic efficiency of parasitoids compared with predators [9]. Furthermore, it also increased total insect diversity by occupying new niches and by initiating an evolutionary arms race that would have increased the diversification rates of the lineages they targeted [10].
- (5) Insects were pollinating a variety of gymnosperm groups throughout the Mesozoic, a feature that originated during the Permian [11], with six insect pollinator lineages (within Coleoptera, Diptera, Mecoptera, Neuroptera, Thysanoptera, and Alienoptera) showing direct evidence of gymnosperm associations documented in the fossil record [12]. Insect pollination is also a key contributor to the Early Cretaceous radiation of angiosperms. During the mid-Cretaceous, four major evolutionary patterns occurred in pollinating insect lineages: some lineages transferred from their gymnosperm hosts to angiosperms; others, failing to adapt to their changing world, went extinct; some persisted on their gymnosperm hosts but were greatly reduced in diversity; and new insect lineages with angiosperm associations originated during this interval [12,13]. Early angiosperm pollination systems were generally less specialized and were composed of small pollinating insects. During the mid-Cretaceous, these pollinators were only beginning their association with flowering plants [12].



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- (6) Complicated mimesis and camouflage behavior depicted by fossils suggest that mimicry and camouflage among insects must have originated before the Mesozoic [12]. The varied fossil record indicates that complex mimesis was emerging in the Jurassic [14]. During the Cretaceous, mimicry among insects was distinctly more developed. From the unrecorded Triassic to the diverse Cretaceous, mimicry and camouflage among insects went through an increasingly sophisticated evolution, with most extant debris-carrying insects (groups with direct camouflage) independently evolving debris-carrying camouflage in the mid-Cretaceous ecosystems [12].
- (7) Two evolutionary entomofaunas have been identified in the history of insects: the Palaeozoic Insect Fauna and the Modern Insect Fauna [15]. The end-Permian mass extinction is regarded as the approximate midpoint of the gradual turnover between these two faunas [15], and altered insect diversity at ordinal levels, removing from the fauna the Palaeodictyoptera and stem-group orders to the palaeopterous and polyneopterous insects [16]. The Mesozoic was a key era for the rise of the modern insect fauna.

The fossil record of insects obviously contains larger geographic, temporal, and taxonomic gaps than that of vertebrates and of some marine invertebrates. Due to this condition, the estimation of insect palaeodiversity is mainly restricted to higher-level taxa, and the detailed ecological response of insects to several key environmental events is still unclear [12]. In particular, there are two insect fossil gaps: a 60-million-year gap spanning from the middle Devonian to the middle Carboniferous, and a 24-million-year gap from the latest Cretaceous to the early Paleocene, which markedly hinder our understanding of the early evolution of insects, and the impact of the Cretaceous-Palaeogene Extinction Event on the evolution of insects. Additionally, there is a preservation and research bias toward medium-sized insects [15], reminding us that the currently known evolutionary history of insects and some insect interactions may be incomplete [12].

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## References

1. Misof, B.; Liu, S.-L.; Meusemann, K.; Peters, R.S.; Donath, A.; Mayer, C.; Frandsen, P.B.; Ware, J.; Flouri, T.; Beutel, R.G.; et al. Phylogenomics resolves the timing and pattern of insect evolution. *Science* **2014**, *346*, 763–767. [[CrossRef](#)] [[PubMed](#)]
2. Engel, M.S.; Grimaldi, D.A. New light shed on the oldest insect. *Nature* **2004**, *427*, 627–630. [[CrossRef](#)] [[PubMed](#)]
3. Baron, M.G. The origin of Pterosaurs. *Earth-Sci. Rev.* **2021**, *221*, 103777. [[CrossRef](#)]
4. Rainford, J.L.; Hofreiter, M.; Nicholson, D.B.; Mayhew, P.J. Phylogenetic distribution of extant richness suggests metamorphosis is a key innovation driving diversification in insects. *PLoS ONE* **2014**, *9*, e109085. [[CrossRef](#)] [[PubMed](#)]
5. Zheng, D.; Chang, S.-C.; Wang, H.; Fang, Y.; Wang, J.; Feng, C.-Q.; Xie, G.W.; Jarzembowski, E.A.; Zhang, H.-C.; Wang, B. Middle-Late Triassic insect radiation revealed by diverse fossils. *Sci. Adv.* **2018**, *4*, eaat1380. [[CrossRef](#)] [[PubMed](#)]
6. Engel, M.S.; Barden, P.; Riccio, M.L.; Grimaldi, D.A. Morphologically specialized termite castes and advanced sociality in the Early Cretaceous. *Curr. Biol.* **2016**, *26*, 522–530. [[CrossRef](#)] [[PubMed](#)]
7. Barden, P.; Perrichot, V.; Wang, B. Specialized predation drives aberrant morphological integration and diversity in the earliest ants. *Curr. Biol.* **2020**, *30*, 3818–3824. [[CrossRef](#)] [[PubMed](#)]
8. Barden, P.; Engel, M.S. Fossil social insects. In *Encyclopedia of Social Insects*; Starr, C.K., Ed.; Springer Nature: Cham, Switzerland, 2020; pp. 1–21. [[CrossRef](#)]
9. Labandeira, C.C.; Li, L.-F. The history of insect parasitism and the Mid-Mesozoic Parasitoid Revolution. In *The Evolution and Fossil Record of Parasitism: Identification and Macroevolution of Parasites*; De Baets, K., Huntley, J.W., Eds.; Springer Nature: Cham, Switzerland, 2021; pp. 377–533.
10. Schachat, S.R.; Labandeira, C.C.; Clapham, M.E.; Payne, J.L. A Cretaceous peak in family-level insect diversity estimated with mark-recapture methodology. *Proc. R. Soc. B Biol. Sci.* **2019**, *286*, 20192054. [[CrossRef](#)] [[PubMed](#)]
11. Labandeira, C.C. The pollination of mid Mesozoic seed plants and the early history of long-proboscid insects. *Ann. Mo. Bot. Gard.* **2010**, *97*, 469–513. [[CrossRef](#)]

12. Wang, B.; Xu, C.-P.; Jarzembowski, E.A. Ecological radiations of insects in the Mesozoic. *Trends Ecol. Evol.* **2022**, *37*, 529–540. [[CrossRef](#)] [[PubMed](#)]
13. Peris, D.; Ricardo, P.F.; Peñalver, E.; Delclòs, X.; Barrón, E.; Labandeira, C.C. False blister beetles and the expansion of gymnosperm-insect pollination modes before angiosperm dominance. *Curr. Biol.* **2017**, *27*, 897–904. [[CrossRef](#)] [[PubMed](#)]
14. Wang, Y.-J.; Liu, Z.-Q.; Wang, X.; Shih, C.-K.; Zhao, Y.-Y.; Engel, M.S.; Ren, D. Ancient pinnate leaf mimesis among lacewings. *Proc. Natl. Acad. Sci. USA* **2010**, *107*, 16212–16215. [[CrossRef](#)] [[PubMed](#)]
15. Schachat, S.R.; Labandeira, C.C. Are insects heading toward their first mass extinction? Distinguishing turnover from crises in their fossil record. *Ann. Entomol. Soc. Am.* **2021**, *114*, 99–118. [[CrossRef](#)]
16. Engel, M.S. Insect evolution. *Curr. Biol.* **2015**, *25*, R845–R875. [[CrossRef](#)] [[PubMed](#)]