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A new Triassic insect assemblage from the southern Ordos Basin, Shaanxi, North China

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Abstract

Insects are among the most diverse and ecologically significant groups in the fossil record, providing key insights into palaeoecology and diversity evolution of terrestrial ecosystems. This study reports a new insect fossil assemblage from the Chang 6 Member of the Yanchang Formation in the Ordos Basin, Huanglong, Shaanxi Province of China. The assemblage is dominated by Hemiptera and Coleoptera, with additional taxa belonging to Blattodea, and Plecoptera. Comparative analyses of entomofaunal composition show that Mesoblattinidae and Cupedidae co-occurred in both the Huanglong and Madygen entomofaunas, whereas Zygophlebiidae and Thaumatomeropidae, characteristic taxa of Madygen, are also documented in the Tongchuan entomofauna, highlighting ecological connectivity among these insect assemblages. The occurrence of Plecoptera (stoneflies), together with lithological evidence, could have indicated stronger hydrodynamic conditions than those of the Tongchuan fauna, consistent with a palaeogeographic scenario of enhanced water mobility during the contraction phase of the Chang 6 Member lacustrine basin. Furthermore, the warm, humid climate and extensive swamp forests of the Middle–Late Triassic likely promoted cross-regional insect dispersal and radiation.

Keywords: Triassic, entomofauna, Ordos Basin, Yanchang Formation

Introduction

A handful of upper Paleozoic and lower Mesozoic terrestrial sedimentary beds within the Ordos Basin yield insect fossils of diverse morphotypes, offering critical insights into terrestrial ecosystem diversity, insect evolutionary trajectories, and paleoecological dynamics (Huang *et al*., 2024). Notably, abundant specimens of roachoids were recovered from black-gray mudstones of the Benxi Group in the Luohe section of the Weibei Coalfield, Shaanxi Province, with a total of 18 genera and species identified (including 8 new genera and 13 new species) (Feng & Shang, 1980). The earliest Jurassic insect fossil from the Ordos Basin, *Orthophlebia quadrimacula* (Mecoptera), was described by Lin (1982) based on material collected near the Qingjian River in Zichang City, Shaanxi Province. More recently, extensive fossil collections from gray shales of the Middle Jurassic Yan'an Formation near Peizhuang Village, Yan'an City, have revealed a number of insect fossils encompassing at least 12 insect orders. To date, five new genera and 11 new species from six orders: Hemiptera, Orthoptera, Mecoptera, Hymenoptera, Phasmatodea, and superorder Odonatoptera, have been formally described (Fu & Huang, 2020; Xu *et al*., 2023; Fu *et al*., 2024; Nel & Huang,

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2024; Nel *et al*., 2024; Lian *et al*., 2024; Jouault, 2024). Meanwhile, abundant insect fossils have been found in the Middle Jurassic Yan'an Formation in Qingyun Town, Yulin City, Shaanxi Province, including the order Odonata, Ephemeroptera, Phasmatodea, Coleoptera, Mecoptera, Neuroptera, Orthoptera and Hemiptera (F. Tian *et al*., 2023; Guo *et al*., 2025)

Lin (1978) described two new dictyopteran taxa, *Anusoblatta recta* and *Subioblatta tongchuanensis*, from the Triassic strata around Tongchuan City, Shaanxi Province. Further discoveries in the Tongchuan Formation of Tongchuan City led to the designation of the "Shaanxi Entomofauna", characterized by the dominance of Dictyoptera, Coleoptera, Neuroptera, and Hymenoptera, as documented in both the Longxian (Liu *et al*., 1985) and Tongchuan entomological assemblages (Hong, 1998). The term for the fauna was later refined to "Tongchuan Entomofauna" due to their shared stratigraphic origin as systematic taxonomic investigation of over one thousand insect specimens from this formation has since been conducted (Zhang *et al*., 2015), resulting in the documentation of 79 species across 11 orders and 35 families (Zheng *et al*., 2018; Zhang *et al*., 2022). This study reports a new Triassic insect fossil assemblage from the Chang 6 Member of the Yanchang Formation in Huanglong Country, Shaanxi Province.

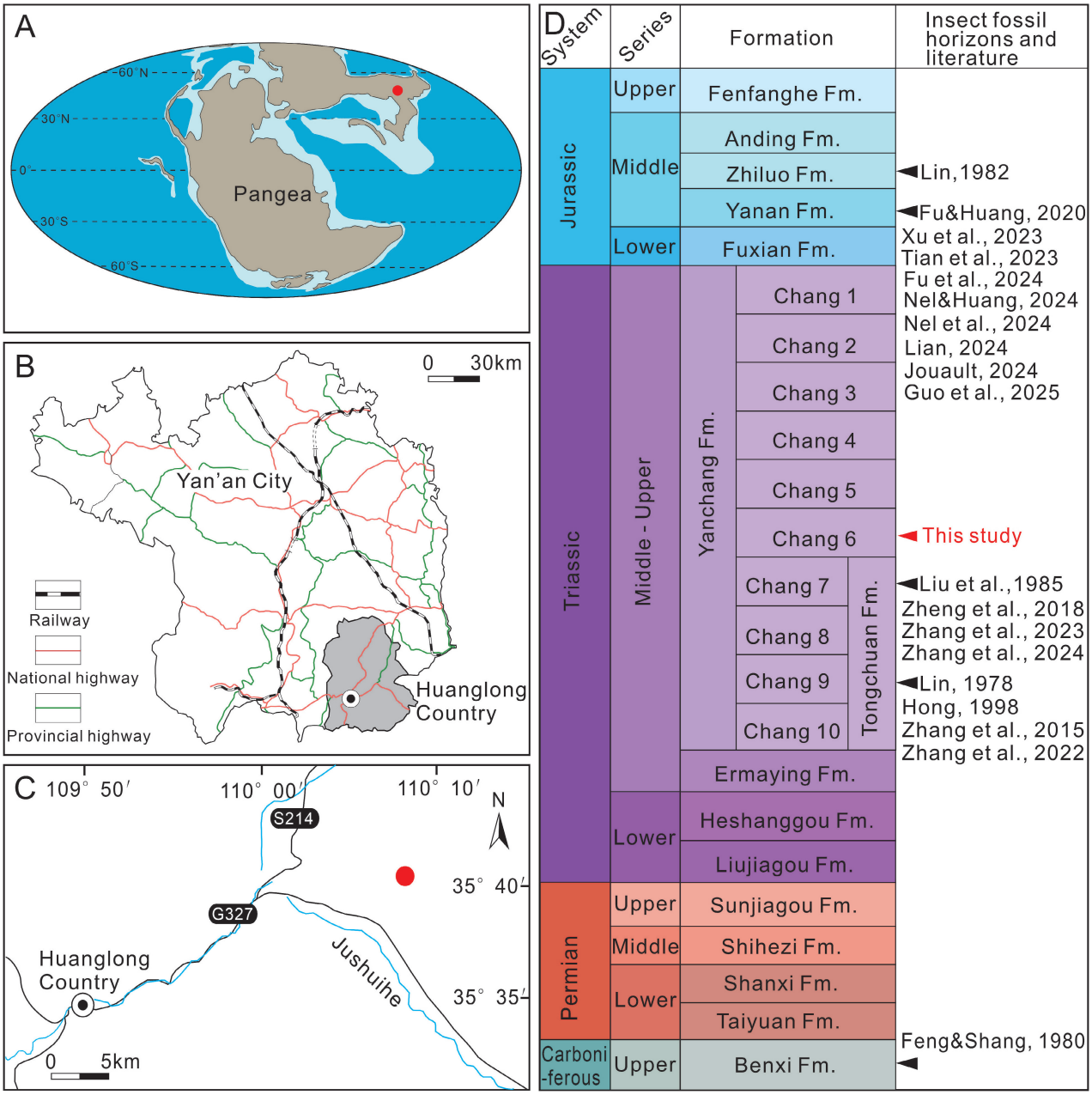

FIGURE 1. Geology of Huanglong County in Yan'an City, Shaanxi Province, NW China and strata in the Ordos Basin. **A**–**C**, Late Triassic and present-day locations of the studied exposures. Late Triassic paleogeographic map was modified from Scotese (2014). **D**, Carboniferous to Jurassic strata in Ordos Basin and insect-bearing horizons.

Geological setting

The Ordos Basin, located in the western part of the North China Craton, underwent a transition from fluvial-deltaic facies to an inland lacustrine environment during the Late Paleozoic to Mesozoic, driven by the Hercynian-Indosinian orogeny (Ruan *et al*., 2021). This basin was characterized by extensive areal coverage, shallow water depths, and far-reaching deltaic systems during the Triassic (Liu, 2019). As the major Middle-Late Triassic strata unit of the area, the Yanchang Formation is subdivided into ten members enumerated from upper to lower, and the Chang 10 to Chang 7 members (from bottom to top) equivalent to the Tongchuan Formation (Deng *et al*., 2018; Fig. 1D). Sediments of the Chang 1–10 members are indicative of shallow-water environments, with well-developed fluvial, deltaic, and shore-shallow lacustrine facies, whilst the Chang 7 Member is distinguished by extensive deep-water sedimentation, featuring a widespread distribution of semi-deep to deep lacustrine facies. The deposition of the Chang 7 Member represents the peak period of the basin evolution, marked by the attainment of the maximum flooding surface (Fu *et al*., 2020). However, there are controversial views regarding the chronostratigraphic age of the Chang 7 Member. Some researchers, utilizing distinct fossil assemblages, absolute age data, have assigned the lower part of the Chang 7 Member to the Ladinian Stage and its upper part to the Carnian Stage (Zhang *et al*., 2019; Lu *et al*., 2022). Whereas, based on integrated biostratigraphic, regional correlation studies and geochemical dating research, some researchers propose that the Chang 7 Member should be assigned to the Ladinian Stage of the Middle Triassic, with ages of 241.06 ± 0.12 Ma and 241.558 ± 0.093 Ma from top and bottom, respectively (Zhu *et al*., 2019; Cui *et al*., 2023; K. Tian *et al*., 2023). Hence, the Huanglong Entomofauna, hosted by the overlying Chang 6 Member, likely dates to the Ladinian.

The insect fossils reported in this study were collected from grayish green mudstones in the Chang 6 Member of the Yanchang Formation. The Chang 6 Member is predominantly composed of grayish-green coarse-grained sandstone, grayish green fine-grained sandstone, siltstone, and interbedded yellowish green/grayish black mudstone with coal seams. Combined with its characteristic sedimentary cyclicity of coarse-grained sandstone-fine-grained sandstone-siltstone-mudstone, these features collectively indicate a transitional sedimentary trend from fluvial facies to swamp facies depositional environments. The newly discovered fossil collection comprises over fifty specimens, among which 22 well-preserved fossils are suitable for detailed taxonomic study. In addition to the insect fossils, plant fossils, bivalves, and fish debris have also been identified in the same horizon (Fig. 2). Collectively, this fossil assemblage indicates a depositional setting characterized by waning hydrodynamic energy during sedimentary regression of the basin.

All the collected fossil specimens are deposited in China University of Geosciences (Wuhan). After numbering the collected fossil specimens and cleaning the surface impurities, some fossils were repaired and the

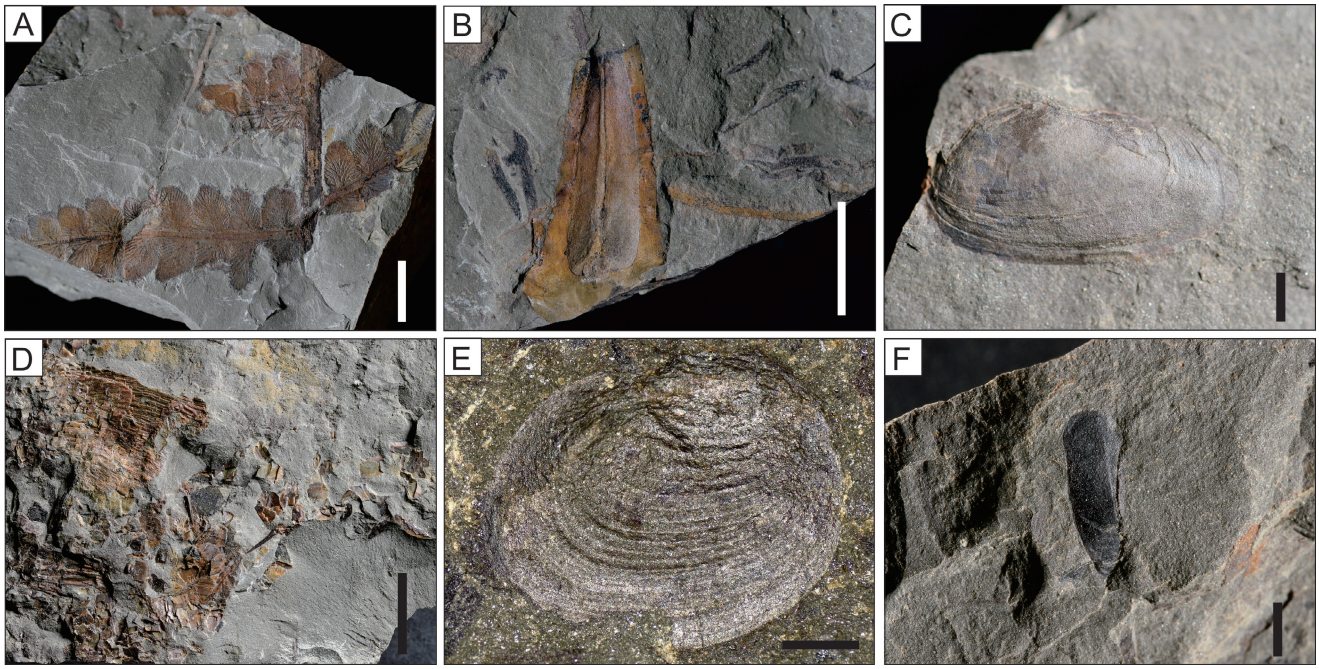

FIGURE 2. Biological fossils from Member 6 of Yanchang Formation. **A**, *Todites* sp. **B**, *Annalepis* sp. **C**, Bivalve. **D**, Fish remains. **E**, Conchostracan. **F**, Beetle elytron. Scale bars: 1 cm in **A**, **D**; 5 mm in **B**; 2 mm in **C** and **F**; 1 mm in **E**.

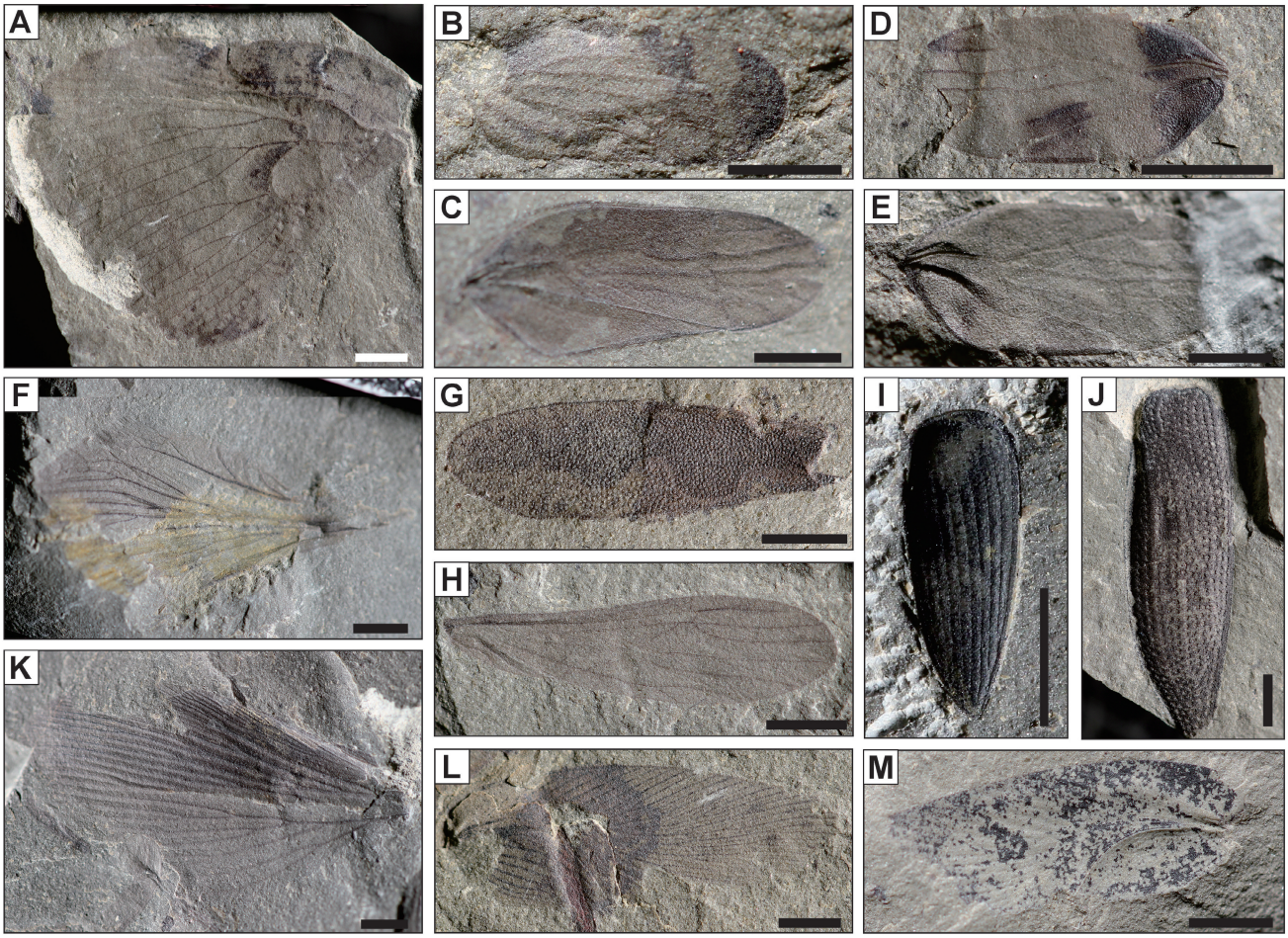

FIGURE 3. Representative fossils from the Huanglong entomofauna. **A**, Ignotalidae (Hemiptera: Cicadomorpha), BYC1812025. **B**, Surijokocixiidae (Hemiptera: Fulgoromorpha), BYC1812008. **C**, Unidentified cicadomorphan specimen, BYC1812016. **D**, Unidentified cicadomorphan specimen, BYC1812024-a. **E**, Unidentified cicadomorphan specimen, BYC1812024-b. **F**, Dictyoptera, BYC1885014. **G**, Granulidae (Hemiptera), BYC1812037. **H**, Plecoptera, BYC1812027. **I**, Coleoptera, BYC1885009. **J**, Possible Tricoleidae (Coleoptera), BYC1812007. **K**, Dictyoptera, BYC1885012. **L**, Dictyoptera, BYC1812020. **M**, Dictyoptera, BYC1812018. Scale bars: 2 mm.

surrounding rocks were removed using pneumatic pens to ensure their structure exposure. The specimens were uniformly photographed with the Canon EOS7D. In this process, the specimens with insect wing vein features were photographed by the ethanol immersion method (Zheng *et al*., 2018).

Results

The discovered insect fossil assemblage reported herein is predominantly composed of Coleoptera, Hemiptera and Dictyoptera, with Plecoptera (Fig. 3). The Hemiptera are represented by six preserved specimens and show the highest family diversity in the assemblage. Excluding three specimens of uncertain taxonomic affinity, the remaining three are definitively assigned to the families Surijokocixiidae, Granulidae, and Ignotalidae of the infaorders Fulgoromorpha and Cicadomorpha. Eight specimens of Coleoptera were preserved by isolated elytra, lacking critical diagnostic features such as body parts, preventing detailed taxonomic identification. Only two very well preserved Coleoptera specimens could be tentatively assigned to Cupedidae and Tricoleidae, based on the available material. Five specimens of Dictyoptera (three specimens assigned to the extinct family Mesoblattinidae with two unidentified specimens), have been recovered. In addition, one specimen of Plecoptera was discovered.

Discussion

Globally, Middle to Late Triassic insect fossil assemblages have been formally reported from multiple

localities, including the Vosges Mountains in France, Lower Franconia and Thuringia in Germany, Kyrgyzstan, and Queensland, Australia (Gall & Grauvogel-Stamm, 2005; Bashkuev *et al*., 2012; Shcherbakov, 2008; Jell, 2004). Among them, the Middle to Late Triassic Madygen Lagerstätte in Kyrgyzstan, represents one of the world's most prolific fossil insect biotas, yielding over 20,000 insect fossils, alongside exceptionally preserved plant remains, bivalves, crustaceans, fishes, and other taxa (Shcherbakov, 2008). Taxonomic studies show that approximate twenty orders and a hundred families are recorded in the Madygen insect assemblage (Shcherbakov, 2008). The family Surijokocixiidae of Hemiptera, the families Cupedidae and Tricoleidae of Coleoptera, and the family Mesoblattinidae of Blattodea are all recorded in both the Huanglong entomofauna and the Madygen entomofauna, indicating that the paleogeographic environments of East Asia (where the Huanglong entomofauna was located) and Central Asia (where the Madygen entomofauna was located) possessed connectivity, providing dispersal corridors for these insect groups. In recent discoveries in the Tongchuan entomofauna, the family Zygophlebiidae of Odonata (Zheng *et al*., 2017) and the family Thaumatomeropidae of Mecoptera (Lian *et al*., 2023), both of which are known only from the Madygen fauna, have been reported. This further supports the paleogeographic connectivity and the likely existence of biological dispersal pathways between these regions.

Notably, the extinct hemipteran families Surijokocixiidae and Granulidae, documented in this study, have also been recorded in the previously described Tongchuan entomofauna (Zheng *et al*., 2018). Among them, the family Granulidae was originally established by Hong Youchong (1980) based on a single, well-preserved forewing fossil. Currently, one new genus and two new species of the family Granulidae have been described from the Tongchuan entomofauna (Zhang *et al*., 2021; Fu *et al*., 2022). Meanwhile, the families Cupedidae and Tricoleidae of Coleoptera, as well as the hemipteran families Surijokocixiidae and Granulidae we discovered in Huanglong, have also been reported in the Tongchuan entomofauna (Zhang *et al*., 2022), implying a close evolutionary connection between these two entomofaunas.

Because Plecoptera fossils reflect palaeoenvironments ranging from high-altitude settings, rivers, and mountain streams to lowland lakes (Zhang & Liu, 2017), the appearance of Plecoptera in Huanglong while the Tongchuan entomofauna is absent from stonefly fossils and integrating this with the lithological characteristics of the Chang 6 Member and contrasting it with the lithology of the Tongchuan Formation (where insect fossils were collected from a 10-meter-thick shale sequence; details in Zheng *et al*., 2018) suggests that the depositional environment of the Huanglong entomofauna likely could have experienced higher hydrodynamic energy and higher flow velocity compared to the Tongchuan entomofauna.

The Mesozoic Lacustrine Revolution (MLR), as a major evolutionary event in the continental realm, refers to a trend wherein the decline in diversity at the family level in lacustrine environments that took place during the Late Paleozoic–Middle Triassic was reversed later in the Mesozoic (Cohen, 2003; Buatois *et al*., 2016). However, the Triassic history of insects, the most diverse group of organisms on Earth, remains fragmentary. Critically, research indicates that aquatic insects experienced substantial expansion in the Middle Triassic. This radiation constituted the bulk of modern freshwater biodiversity, signifying that the origins of modern entomofauna can be traced back to the Middle-Late Triassic (Zheng *et al*., 2018; Gui *et al*., 2024). The successive finding of the diversified insect assemblages in both Tongchuan Formation and its overlying Chang 6 Member of the Yanchang Formation imply that the warm and humid climate during the Middle-Late Triassic provided particularly favorable habitats and dispersal conditions for insects, organisms characterized by metamorphic development (Dal Corso *et al*., 2020). The proliferation of waterlogged forests, diverse plant communities, and complex topography in mid-to-high latitudes created abundant ecological niches and food resources, facilitating insect proliferation, evolutionary radiation, and the enhancement of biodiversity (Lara *et al*., 2017).

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