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Fossil insects from the Ordos Basin

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The Ordos Basin, located in northwestern China, is a major sedimentary basin known for its extensive deposits of late Paleozoic and Mesozoic strata. Situated in the western part of the North China Craton (NCC) or potentially a sub-craton, the basin is bordered by highlands and mountainous regions, with outcrops widely distributed around its periphery. The Ordos Basin is a superimposed basin that developed during the Mesoproterozoic on NCC. Its basement is primarily composed of Precambrian metamorphic crystalline rocks of the craton, along with middle Palaeozoic marine tuffs interbedded with clastic rocks (Zhang *et al.* 2021; Hai *et al.* 2022). These deposits predominantly consist of well-developed clastic continental sediments, spanning geological ages from the Carboniferous to the Early Cretaceous (Chou & Hong 1989; Wang *et al.* 2022). The strata are gently folded, providing an exceptional opportunity for stratigraphic studies and palaeontological studies. The southeastern margin of the Ordos Basin, particularly around the regions of Hancheng and Tongchuan, features notable Triassic sedimentary sequences. Among these, the Middle-Upper Triassic Yanchang Formation stands out as a significant geological unit.

Insect fossils from the Ordos Basin span a wide range from the Carboniferous to the Cretaceous, but are primarily found in three key biotas: the late Middle Triassic Tongchuan biota, the Early to Middle Jurassic Yan'an biota, and the Middle Jurassic Jiyuan biota, which are the focus of this paper. The Mesozoic lithostratigraphy of the Ordos Basin refers to recent studies (e.g., Huang 2019; Lian *et al.* 2024).

The Yanchang Formation, located in the Ordos Basin in northwestern China, is a significant source of Middle Triassic insect fossils. These fossils are predominantly found in lacustrine sediments, reflecting the lake-dominated depositional environment of the formation. The Tongchuan Entomofauna represents one of the most important Middle Triassic insect assemblages in China, contributing significantly to the understanding of Triassic insect diversity and distribution. The Tongchuan entomofauna, dated to approximately 238-237 million years ago (Ladinian), addresses a critical gap in the fossil record of early to middle Triassic insects. The fossil evidence confirms the rapid diversification of Holometabola, a clade that includes most modern insect species, during the middle to late Triassic. The discovery of early aquatic insects, such as caddisfly cases (Trichoptera) and water boatmen (Hemiptera), suggests that the diversification of aquatic insects, a hallmark of the Mesozoic Lacustrine Revolution, had already commenced by the Middle Triassic (Zheng et al. 2018). The formation captures the interplay between terrestrial and freshwater ecosystems during a critical period of ecological diversification, providing data for reconstructing the evolutionary trajectory of insects and highlights their role in the diversification of terrestrial and aquatic ecosystems during the Middle Triassic. The Tongchuan entomofauna has yielded numerous insect fossils, mainly from Hemiptera, Mecoptera, and Coleoptera, the dominant orders in the Chinese Triassic entomofauna (Fu & Huang 2022; Fu et al. 2022a,b). Research into the Tongchuan insect fossils began in the mid-20th century, with early studies marking a shift in understanding China's Triassic entomofauna. Of over 50 Middle Triassic insect species known from China, a considerable number are known from this formation (Zhang et al. 2022). The Tongchuan entomofauna is integral to reconstructing the evolutionary trajectory of insects during the Triassic, offering insights into their diversification and ecological roles within the broader paleoenvironments of the time (Zheng et al. 2018). The rapid recovery of lacustrine ecosystems after the end-Permian mass extinction (EPME) sheds light on the resilience of these systems. Insects, as a critical component of these ecosystems, provide valuable evidence for understanding the establishment of ecological networks. Their diversity and ecological roles during the Triassic suggest that Triassic lacustrine ecosystems took at most 10 myr. to fully recover after the EPME (Zhao et al. 2020).

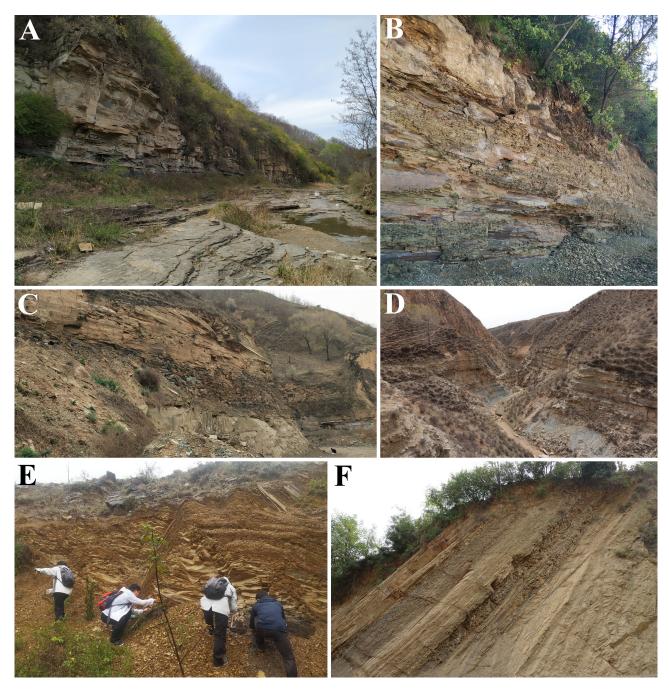


Figure 1. Representative fossiliferous sections from the Ordos Basin. **A**, The Qishuihe Section of the Yanchang Formation yielded the Middle Triassic Tongchuan biota in Tongchuan City, Shaanxi Province; **B**, The fossil layers of the Tongchuan biota; **C**, Fossil locality of the Middle Jurassic Yan'an Formation near Peizhuang Village, Yan'an City, yielded fossil insects; **D**, Fossil locality of the Yan'an Formation at the Huangjiagou locality in Yulin City, Shaanxi Province; **E**, Fossil insects-bearing layers of the Tanzhuang Formation in Jiyuan City, Henan Province; **F**, The Middle Jurassic Yangshuzhuang Formation in Jiyuan City yielded fossil insects.

The Yan'an Formation, located on the southwestern margin of the Ordos Basin, is a major Jurassic coal reservoir in China and a key focus for oil and gas exploration. It is characterized by the widespread development of coal and organic-rich shale, with plant debris commonly found in the associated mudstone and coal, indicative of swampy environments. Sandstones within the formation exhibit features typical of fluvial deposits, such as parallel laminations, interlaminated structures, and scour surfaces. The Yan'an Formation represents a significant coal-forming interval in Earth's history, contributing to the extensive mid-latitude coal reserves of that era (Deng *et al.* 2003). Zhang *et al.* (2021) recently established a high-resolution chronological framework for the Yan'an Formation using integrated methods. High-precision U-Pb zircon geochronology was conducted on interstratified ash beds utilizing chemical abrasion-isotope dilution-thermal ionization mass spectrometry (CA-ID-TIMS), complemented by cyclostratigraphy based on centimeter-scale magnetic susceptibility. Their results indicate that the primary coal-forming interval of this formation occurred between approximately 174.0 Ma and <171.7 Ma, aligning with the onset of the Middle Jurassic (Zhang *et al.* 2021; Chen *et al.* 2022). The Yan'an Formation is unconformably overlain by the Pliocene Baode Formation and conformably underlies the Lower Jurassic Fuxian Formation at Yulin. Recently, fossil insects have been discovered in grayish shale from the middle to upper sections of the Middle Jurassic Yan'an Formation near Peizhuang Village, Yan'an City, Shaanxi Province, North China. These fossil insects exhibit remarkable diversity, representing at least 13 orders: Ephemeroptera, Odonata, Orthoptera, Blattodea, Dermaptera, Phasmatodea, Hemiptera, Thysanoptera, Neuroptera, Coleoptera, Mecoptera, Diptera, and Hymenoptera (Zheng *et al.* 2017; Fu & Huang 2020, 2021; Huang 2023; Xu *et al.* 2023).

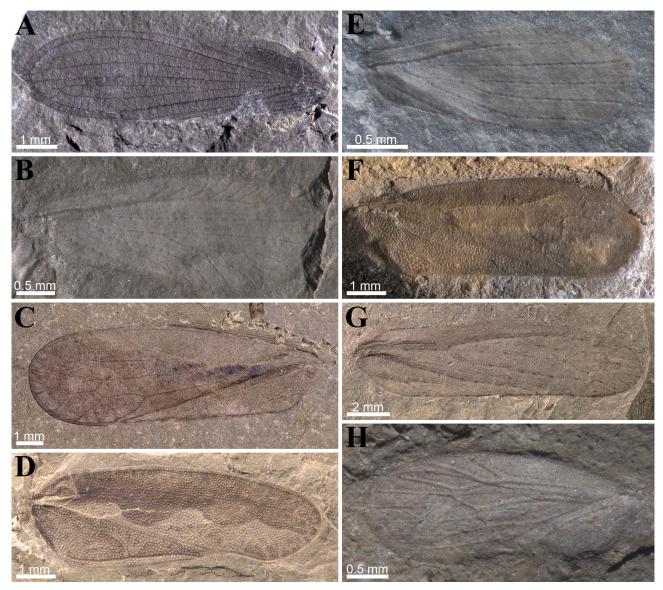


Figure 2. Fossil insects from the Ordos Basin of China. **A**, *Sinoglosselytron qishuiheenesis* from the Middle Triassic Tongchuan biota; **B**, *Triassopsyllidiida pectinata* from the Middle Triassic Tongchuan biota; **C**, *Eocicadellium grimaldii* from the Middle Triassic Tongchuan biota; **D**, *Sinogranulus jinsuoguanensis* from the Middle Triassic Tongchuan biota; **E**, *Sinopsocus yananensis* from the Middle Jurassic Yan'an biota; **F**, *Kisa fasciata* from the Middle Jurassic Jiyuan biota; **G**, *Qibinius maculatus* from the Middle Jurassic Jiyuan biota; **H**, *Cicadocoris henanensis* from the Middle Jurassic Jiyuan biota.

The Jiyuan Basin is considered to be connected to or a part of the Ordos Basin. Insect fossils from the Jiyuan Basin are primarily found in the Yangshuzhuang Formation. Abundant elytra have also been reported from the Upper Triassic Tanzhuang Formation (Xu *et al.* 2023). Additionally, a few unpublished insect specimens have been collected from the Early Jurassic Anyao Formation. The Yangshuzhuang Formation is located in the Upper Jurassic strata near Anyao Village, Chengliu Township, Jiyuan City, Henan Province, China. The studied outcrop is positioned at the top of the Yangshuzhuang Formation, near its boundary with the overlying Ma'ao Formation. Traditionally, both

formations were regarded as Middle Jurassic in age (Deng *et al.* 2003). Recent studies (Huang 2019) suggest that the Yangshuzhuang Formation correlates to the Haifanggou Formation, known for its abundant and exceptional fossils, particularly diverse insect assemblages (Huang 2016). The Ma'ao Formation is considered equivalent to the Tiaojishan Formation in northern China. Thus, the Yangshuzhuang Formation is assigned to the Middle Jurassic, with its uppermost layers potentially dating to the earliest Late Jurassic. To date, the fossil insect record from this locality remains relatively sparse, with only a few studies contributing to our understanding of its palaeobiodiversity. The first formally described fossil insect from this site was *Jurathemis incompletus* Huang *et al.*, 2018, a member of the small Jurassic family Selenothemistidae. Subsequent investigations have revealed a broader diversity of fossil taxa, including several species of Odonata, Hemiptera, Diptera, and Spinicaudata (Huang *et al.* 2018, 2023; Fu & Huang 2020, 2021; Liu & Huang 2020, 2021; Liao *et al.* 2023; Fu *et al.* 2024). Together, these studies highlight the potential of this site to yield significant palaeoentomological discoveries, enriching our understanding of the Jurassic terrestrial ecosystems in this region.

Moreover, Carboniferous insect fossils from the Ordos Basin are mainly roaches discovered in the Weibei Coal Mine (Feng & Shang 1980). A species of Paraplecoptera was described from the Upper Carboniferous-Lower Permian Taiyuan Formation in Chengcheng County, Shaanxi Province, and another species was described from Hejin City, Shanxi Province (Hong 1983). The Lower Cretaceous Huanchi-Huahe Formation has been also yielded some fossil insects (e.g., Chou & Hong 1989).

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