GEOLOGY | THE GEOLOGICAL SOCIETY OF AMERICA®

https://doi.org/10.1130/G47502.1

Manuscript received 7 January 2020
Revised manuscript received 21 February 2020
Manuscript accepted 21 February 2020

Published online 30 March 2020

Recovery of lacustrine ecosystems after the end-Permian mass extinction

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ABSTRACT

The end-Permian mass extinction (EPME; ca. 252 Ma) led to profound changes in lacustrine ecosystems. However, whether or not post-extinction recovery of lacustrine ecosystems was delayed has remained uncertain, due to the apparent rarity of Early and Middle Triassic deep perennial lakes. Here we report on mid–Middle Triassic lacustrine organic-rich shales with abundant fossils and tuff interlayers in the Ordos Basin of China, dated to ca. 242 Ma (around the Anisian-Ladinian boundary of the Middle Triassic). The organic-rich sediments record the earliest known appearance, after the mass extinction, of a deep perennial lake that developed at least 5 m.y. earlier than the globally distributed lacustrine shales and mudstones dated as Late Triassic. The fossil assemblage in the organic-rich sediments is diverse and includes plants, notostracans, ostracods, insects, fishes, and fish coprolites, and thus documents a Mesozoic-type, trophically multileveled lacustrine ecosystem. The results reveal the earliest known complex lacustrine ecosystem after the EPME and suggest that Triassic lacustrine ecosystems took at most 10 m.y. to recover fully, which is consistent with the termination of the "coal gap" that signifies substantial restoration of peat-forming forests.

INTRODUCTION

The end-Permian mass extinction (EPME; ca. 252 Ma) was the greatest biological and ecological crisis of the Phanerozoic Eon on Earth, and caused a transformation from Paleozoic to modern evolutionary fauna, which built new ecosystems that have persisted to the present day (Benton and Newell, 2014; Wignall, 2015). Ecosystem recovery after the EPME was seemingly delayed because the subsequent Early Triassic interval was characterized by recurrent, rapid global warming and harsh marine and terrestrial conditions (Algeo et al., 2011; Retallack et al., 2011; Chen and Benton, 2012; Sun et al., 2012). Marine ecosystems are thought to have recovered substantially by the middle to late Anisian, 8–10 m.y. after the EPME (Chen and Benton, 2012), and their restoration was still ongoing in the latest Triassic (Song et al., 2018).

The timing and pattern of recovery of marine ecosystems are relatively well known worldwide, but the pattern of recovery of lacustrine ecosystems is still unclear due to the highly fragmentary freshwater fossil record (Benton and Newell, 2014; Hochuli et al., 2016; Nowak et al., 2019; Vajda et al., 2020). Although occupying only a small area, lakes potentially play an important role in the global cycling of dissolved geochemical species (Cohen, 2003). Studies of post-extinction recovery of lacustrine environments can provide a better understanding of how such ecosystems have responded geologically to global warming (Mendonça et al., 2017). However, Lower Triassic and lower Middle Triassic continental records are fluvially dominated successions with only local lacustrine deposits that were shallow, ephemeral, and evaporitic in character (Gierlowski-Kordesch and Kelts, 1994; Gall and Grauvogel-Stamm, 2005; Benton and Newell, 2014; Buatois et al., 2016). Until now, the oldest known Mesozoic complex lacustrine ecosystem was dated to the latest Middle Triassic–earliest Late Triassic in China and central Asia (ca. 237 Ma) (Buatois et al., 2016; Zheng et al., 2018); older Mesozoic complex lacustrine ecosystems were unknown either because they had not yet evolved or because their sedimentary records had not been found. Here we extend the record of such systems back in time by describing mid-Triassic lacustrine organic-rich shales containing abundant tuff interlayers and fossils (ca. 242 Ma) from three outcrops in the Ordos Basin of northwestern China (Fig. 1). The fossil assemblage reveals a diverse Mesozoic-type, trophically multileveled ecosystem that represents the earliest-known such ecosystem after the EPME and suggests that such ecosystems took as long as 10 m.y. to recover fully.

MATERIALS AND METHODS

The Ordos Basin is a continental basin developed on the Paleozoic North China craton whose freshwater character without marine influence has been identified on paleontological and geochemical grounds (Qiu et al., 2015;

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CITATION: Zhao, X., et al., 2020, Recovery of lacustrine ecosystems after the end-Permian mass extinction: Geology, v. 48, p. 609–613, https://doi.org/10.1130/G47502.1

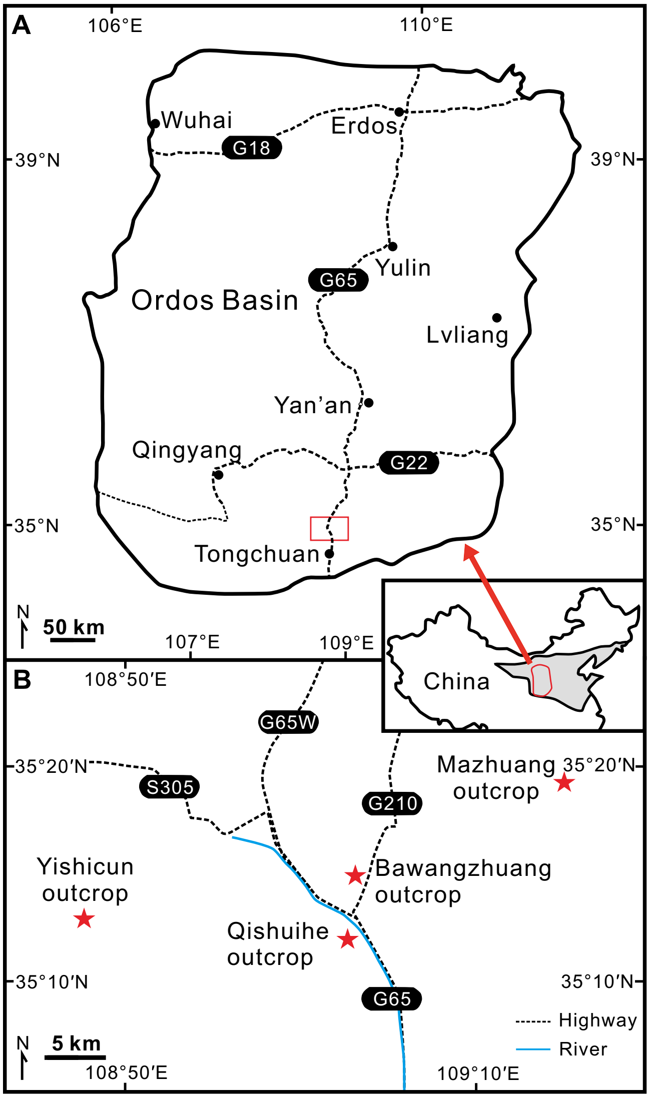

Figure 1. Geographic map of study area. (A) Location of Ordos Basin in northwestern China (modified from Sun et al., 2019). Gray area represents North China plate. (B) Locations of four outcrops, enlarged from red inset in A. Numbers represent road numbers.

Zheng et al., 2018; Du et al., 2019). The Triassic continental strata in the Ordos Basin include, from bottom to top, the Liujiagou Formation, Heshanggou Formation, Ermaying Formation, Tongchuan Formation, and Yanchang Formation (Deng et al., 2018; Zheng et al., 2018).

A well-known section, the 1980-m-thick Qishuihe outcrop (35°14′50.29″N, 109°0′45.10″E) was investigated to locate the earliest appearance of a Triassic coal seam. The organic-rich shale was documented in three sections: the 31.2-m-thick Bawangzhuang outcrop (35°14′2.83″N, 109°2′28.86″E), the 31.4-m-thick Mazhuang outcrop (35°19′19.54″N, 109°14′39.37″E), and the 38.9-m-thick Yishicun outcrop (35°11′34.21″N, 108°51′6.04″E). We analyzed the U-Pb isotopic ages of tuffaceous layers (tuff, tuffaceous sandstone, volcanic ash) in these three outcrops to constrain the age of the organic-rich shale and its associated biota (Figs. DR1D–DR1F in the GSA Data Repository[1]). Four samples were collected for dating, including one tuff sample (BW-1) from the Bawangzhuang outcrop, one tuffaceous sandstone sample (MZ-1) from the Mazhuang outcrop, and two volcanic ash samples (YQ-1 and YQ-2) from the Yishicun outcrop. U-Pb isotopic data from zircons were obtained at the Department of Earth Sciences, The University of Hong Kong, using a Nu Instruments multi-collector (MC) inductively coupled plasma mass spectrometer (ICP-MS) with a Resonetics RESOlution M-50-HR excimer laser ablation system. More laboratory details are given in the Data Repository.

[1]GSA Data Repository item 2020179, supplementary figures and data tables, is available online at http://www.geosociety.org/datarepository/2020/, or on request from editing@geosociety.org.

RESULTS AND DISCUSSION

Sedimentology and Paleontology

The Ordos Basin is the second-largest sedimentary basin in China (Fig. 1; Qiu et al., 2015). The upper part of the Tongchuan Formation and Yanchang Formation are particularly rich in organic matter (Du et al., 2019). The lower part of the Tongchuan Formation was long thought to be dominated by sandstone (Zheng et al., 2018). However, 20–30-m-thick organic-rich shales with abundant tuff and less-fissile mudstone interlayers were recently found in the lower part of this formation in three outcrops (Bawangzhuang, Mazhuang, and Yishicun) in the southern Ordos Basin (Fig. 2; Fig. DR1). The shales have yielded abundant fossils, including microalgae (Yang et al., 2016), macroalgae (Yang et al., 2016), notostracans (tadpole shrimps; Fig. 3J), ostracods (seed shrimps; Fig. 3I), insects (Figs. 3F and 3G), fishes (Fig. 3H; Fig. DR2), and fish coprolites (Figs. 3A–3E). These fossils show conclusively that the organic-rich shales are lacustrine, consistent with previous interpretations based on paleontological and geochemical evidence (Qiu et al., 2015; Zheng et al., 2018; Du et al., 2019). Tuffs are extremely abundant in the studied sections, especially in the Bawangzhuang outcrop where there are >30 such layers (Fig. DR1).

The insect assemblage is dominated by aquatic beetles (Figs. 3F and 3G), which typically have a particularly hard chitinous exoskeleton that gives them a high preservation potential within the sediment. Spirally coiled coprolites are also abundant in the organic-rich shale and display a well-defined heteropolar structure (Figs. 3A–3C). The chitinous mandibles of predatory dipteran larvae are found in phosphatized coprolites. These mandibles are ~0.1 mm long, have dark-colored tips (Figs. 3D and 3E), and are broad, strong spines that are very weakly bent in lateral view, similar to those of chaoborid larvae (Richter and Baszio, 2001). The fish coprolites range from 55.6 mm to 77.7 mm in length, suggesting that the fish were large. However, the largest skeletal fragment found so far is estimated to derive from a fish no longer than 250 mm (Fig. DR2). By contrast, the coiled coprolites probably belonged to larger cartilaginous fish predators that have a spiral valve. Importantly, because they occupy the higher trophic guilds in lake food chains, top predators such as large fish are important indicators of the presence of complex food webs.

Our U-Pb isotopic ages of tuffaceous layers in three outcrops extend the oldest age of the Triassic organic-rich shale to 242 Ma (Fig. 2), near the Anisian-Ladinian boundary (Cohen et al., 2013), which is consistent with the thermal ionization mass spectrometry (TIMS) zircon U-Pb dating age (241.558 Ma) of the lower part of the Tongchuan Formation near Yishicun (Zhu et al., 2019; Chu et al., 2020). In addition, the result is also supported by the presence of the notostracan *Xinjiangiops*, which is restricted to the lower part of the Tongchuan Formation (Xie et al., 2015). The age of this Triassic organic-rich shale in the Ordos Basin has been widely thought to lie within the Late Triassic Epoch (Du et al., 2019; Sun et al., 2019). However, our findings reveal that Middle Triassic

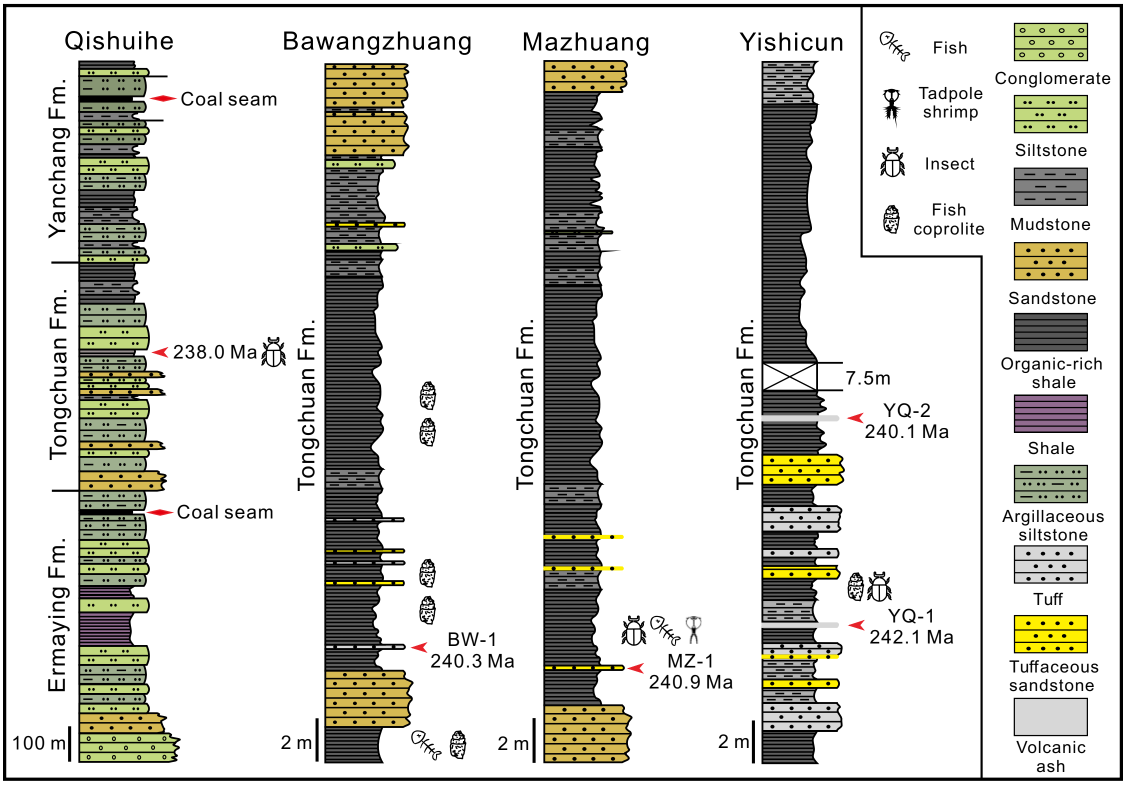

Figure 2. Stratigraphic columns showing lithologies, fossiliferous horizons, sample points, and age results (see Fig. 1 for locations). Lower Ladinian organic-rich shale is absent from the Qishuihe outcrop, but is well developed in other three outcrops.

organic-rich shale is present in three discrete outcrops extending over a lateral distance of 40 km. Its absence in the Qishuihe section is probably due to local facies variation, which is common in this area near the southern margin of the basin (Fig. 1). Combined with the results from the southwestern Ordos Basin (Deng et al., 2018), our findings suggest that this distinctive facies may have been widespread in the southern Ordos Basin during the early–middle Ladinian and provide new insight into the Triassic sedimentary history of the area.

Recovery of Lacustrine Ecosystems after the EPME

This account details the oldest record of lacustrine organic-rich shales after the EPME. Despite the presence of suitable tectonic settings for deep perennial lakes (e.g., linear rift basins), Early Triassic and early Middle Triassic lacustrine deposits are shallow, ephemeral, and evaporitic, probably due to the high global temperatures and rates of evaporation relative to water input (Benton and Newell, 2014); continental records are fluvially dominated successions. This pattern of sedimentation was also characteristic of the Ordos Basin, with lowest Middle Triassic deposits (Ermaying Formation) being purple-colored fluvially dominated facies (Yang et al., 2016). Post-dating the purple-colored fluvially dominated successions, the organic-rich shale in the lower part of the Tongchuan Formation represents the first known appearance of a deep perennial lake after the EPME, which developed at least 5 m.y. earlier than the worldwide occurrence of deepwater, organic-rich lacustrine shales and mudstones of the Late Triassic (Smith, 1990; Gierlowski-Kordesch and Kelts, 1994).

The results provide data on the earliest known Triassic complex lacustrine ecosystem. Primary producers included various micro- and macroalgae, together with some notostracans, ostracods, and insects that fed on algae as primary consumers. Second-level consumers included some predatory insects (such as chaoborid larvae), with higher-order trophic levels being represented by predatory fish. Such an ecosystem is a key character of Mesozoic lakes (Ponomarenko, 1996), which were different from pre-Mesozoic lakes in which dipteran larvae were absent and aquatic beetles were rare (Cohen, 2003). We regard the occurrence of a Mesozoic-type, trophically multileveled lacustrine ecosystem as the hallmark of freshwater ecosystem recovery following the EPME. This transition from pre-Mesozoic to Mesozoic lacustrine ecosystems was partly driven by the radiation of aquatic insects (Zheng et al., 2018), which is thought to have been part of the so-called Mesozoic lacustrine revolution (Buatois et al., 2016).

The restoration of a complex lacustrine ecosystem (at ca. 242 Ma) was coincident with the termination of the "coal gap", which was an interval of ~10 m.y. when no coals were deposited worldwide (Retallack et al., 1996, 2011). In the Ordos Basin, the oldest known Triassic coal seam occurs in the uppermost part of the Ermaying Formation (Fig. 1; Fig. DR1C), the age of which is slightly greater than that of the organic-rich shale described herein (Yang et al., 2016). The appearance of Triassic coal seams is generally considered to represent the substantial recovery of peat-forming forests following the mass extinction (Retallack et al., 2011; Benton and Newell, 2014; but see McElwain and Punyasena, 2007; Vajda et al., 2020). Therefore, both lake and peat-forming forest ecosystems probably took as long as 10 m.y. to recover, much longer than the period of recovery of plant communities inferred from palynological data (Hermann et al., 2011; Vajda et al., 2020).

The hot Early Triassic climate would have limited dissolved oxygen in lakes, potentially hindering ecosystem recovery. A subsequent major increase in marine carbon burial in the Anisian could, however, have caused CO_2 drawdown and global cooling, improving lacustrine conditions (Chen and Benton, 2012; Sun et al., 2012; Grasby et al., 2016, 2019). In addition, the abundant volcanic ash likely transferred nutrients into the water and probably significantly increased the efficiency of primary productivity in the Ordos Basin (Zeng et al., 2018). Therefore, both the climate cooling and high volcanic nutrient input most likely facilitated development of this complex lake community. The near-coeval recovery of both aquatic and non-aquatic terrestrial ecosystems may suggest that they were tightly linked through biological, physical, and chemical interactions.

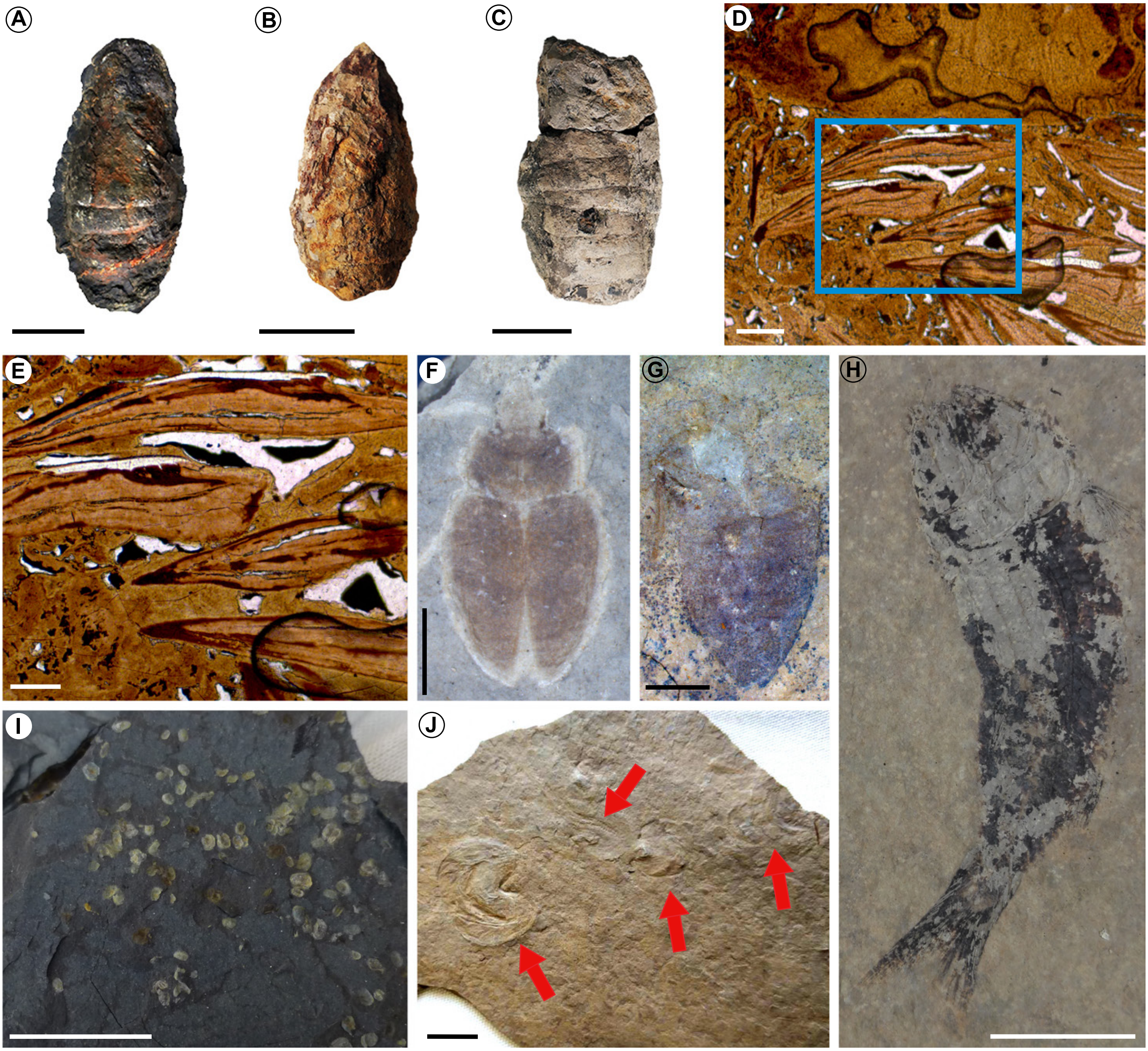

Figure 3. Representative fossils from organic-rich shale and mudstone of the Tongchuan Formation (Ordos Basin, China). (A–C) Fish coprolites from the Bawangzhuang outcrop. (D) Sliced photomicrograph showing chitinous mandibles of predatory dipteran larvae in fish coprolite. (E) Enlargement from blue inset in D. (F,G) Beetle (Insecta: Coleoptera) from the Mazhuang outcrop. (H) Fish (Neopterygii) from the Mazhuang outcrop. (I) *Tungchuania* sp. (Limnocytheridae) from the Mazhuang outcrop. (J) *Xinjiangiops* sp. (Triopsidae) from Mazhuang outcrop. Scale bars: 20 mm (A–C), 10 mm (H–J), 5 mm (G), 2 mm (F), 0.2 mm (D), and 0.1 mm (E).

ACKNOWLEDGMENTS

We thank V. Baranov, Zhikun Gai, Guanghui Xu, and Wei Wang for valuable discussions, and J. Schmitt, M. Benton, S.E. Grasby, and one anonymous reviewer for insightful comments. This work was supported by the Strategic Priority Research Program of the Chinese Academy of Sciences (XDB26000000) and the National Natural Science Foundation of China (grants 41688103 and 41730317). This is a Leverhulme Emeritus Fellowship contribution for Jarzembowski.

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