

PALEONTOLOGY

Middle-Late Triassic insect radiation revealed by diverse fossils and isotopic ages from China

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The Triassic represented an important period that witnessed the diversification of marine and terrestrial ecosystems. The radiations of terrestrial plants and vertebrates during this period have been widely investigated; however, the Triassic history of insects, the most diverse group of organisms on Earth, remains enigmatic because of the rarity of Early-Middle Triassic fossils. We report new insect fossils from a Ladinian deposit (Tongchuan entomofauna) dated to approximately 238 to 237 million years ago and a Carnian deposit (Karamay entomofauna) in northwestern China, including the earliest definite caddisfly cases (Trichoptera), water boatmen (Hemiptera), diverse polyphagan beetles (Coleoptera), and scorpionflies (Mecoptera). The Tongchuan entomofauna is near the Ladinian-Carnian boundary in age, providing a calibration date for correlation to contemporaneous biotas. Our findings confirm that the clade Holometabola, comprising most of the modern-day insect species, experienced extraordinary diversification in the Middle-Late Triassic. Moreover, our results suggest that the diversification of aquatic insects (a key event of the “Mesozoic Lacustrine Revolution”) had already begun by the Middle Triassic, providing new insights into the early evolution of freshwater ecosystems.

INTRODUCTION

The end-Permian mass extinction (EPME) caused a severe crisis in terrestrial ecosystems, possibly due to global wildfires at the Permian-Triassic boundary, long-term aridification, and short-term warming and acid rain during the Early Triassic (1, 2). After the EPME, the Triassic is a period for the radiation of organisms in both marine and terrestrial ecosystems (2, 3); it marks the first major step in the origin of modern ecosystems and is thus frequently known as the “Dawn of the Modern World” (4, 5). For terrestrial ecosystems, many key modern vertebrates appeared during the Triassic (2), including two of the most important events: the origin and rise of the dinosaurs (6) and mammaliaforms (7). Plants experienced an especially important development during this period. Following the domination of the lycopsid plants during the Early Triassic, conifers, cycadophytes, and pteridosperms all radiated during the Middle Triassic, subsequently evolving into their modern forms (8, 9).

The EPME led to changes in insect fauna at high taxonomic levels: a drop in abundance and overall diversity (10–12) and probably a severe extinction (13, 14). After the EPME, Triassic insects probably kept pace with the megafloal development: Modern insects feeding on the pteridophytes and gymnosperms replaced ancient insects feeding on the pteridophytes and basal gymnosperms (15); plant-insect associations became significantly diverse during the Late Triassic (16–18). However, the scarcity of Early-Middle Triassic entomofaunas constrains our knowledge on the radiation of insects (19–21). In contrast to terrestrial plants and vertebrates, the evolutionary history of Triassic insects is still poorly understood. Little is known about the

Triassic evolution of holometabolous and aquatic insects. These groups have the potential to provide insights into the early evolution of terrestrial (including freshwater) ecosystems (22, 23) because the former is the most species-rich group of extant animals (24) and the latter is a key element of the “Mesozoic Lacustrine Revolution” (25).

Here, we report a late Ladinian Tongchuan entomofauna, with radioisotopically determined ages, and a Carnian Karamay entomofauna from northwestern China. Our results provide not only the earliest records of several modern insect elements but also a calibration point for correlation with contemporaneous biotas. These findings confirm that holometabolous and aquatic insects experienced extraordinary diversification during the Middle-Late Triassic.

RESULTS

Insect fossils

More than 800 insect fossils were collected from the upper part of the Karamay Formation in the Huayangou outcrop (45°40′24″N, 84°55′57″E), Karamay City, Xinjiang (Fig. 1, A, C, and E), and the top of the lower part of the Tongchuan Formation in the Qishuihe outcrop (28°17′24″N, 117°52′32″E), Hejiafang Village, Jinsuoguan Town, Tongchuan City, Shaanxi Province (Fig. 1, B, D, and E, and fig. S1), Northwest China. The insect-bearing layer of the Tongchuan Formation is considered to be from the latest Ladinian stage [~238 to 237 million years (Ma) ago] and that of the Karamay Formation is regarded as Carnian in age. For detailed stratigraphic information, see the Supplementary Materials.

U-Pb geochronology

Two tuffaceous sandstone samples (TC-01 and TC-02), each weighing about 5 kg, were collected between insect fossil-bearing strata of the Qishuihe outcrop (Fig. 1D) and separated for LA-MC-ICP-MS (laser ablation–multi-collector–inductively coupled plasma mass spectrometry) U-Pb dating. The zircon grain sizes of sample TC-01 (Fig. 2, A and B) ranged from 80 to 120 μm . Most grains exhibited euhedral morphologies and oscillatory zoning patterns, indicating an igneous origin (Fig. 2B). Angular grain facets also suggest minimal abrasion during

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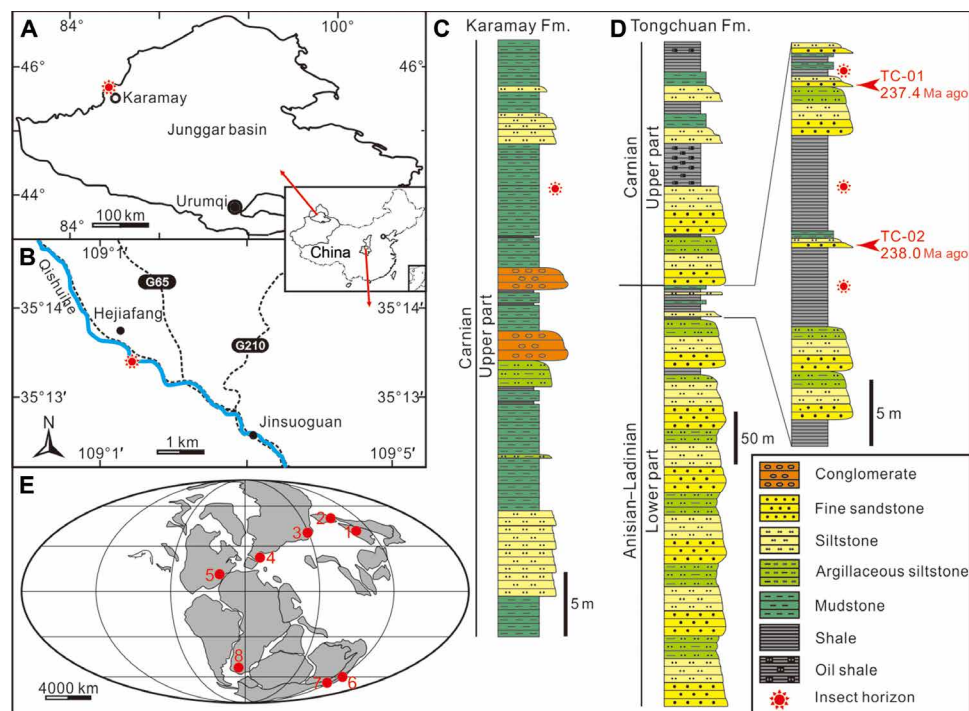


Fig. 1. Geology of Tongchuan and Karamay entomofaunas. Geological map showing the location of entomofauna in Karamay City in (A) Xinjiang and (B) Tongchuan City in Shaanxi, Northwest China. (C and D) Stratigraphic column showing lithologies, sample points, and age results. Global paleogeographic reconstructions [Carnian; after Rasnitsyn and Quicke (33) and Golonka (62)], highlighting main coeval insect-bearing localities (E): (1) Tongchuan, China (Ladinian); (2) Karamay, China (Carnian); (3) Madygen, Kyrgyzstan (Ladinian-Carnian); (4) Vosges, France (early Anisian); (5) Solite, USA (late Carnian); (6) Ipswich, Australia (Carnian); (7) Brookvale, Australia (Anisian); and (8) Molteno, South Africa (Carnian).

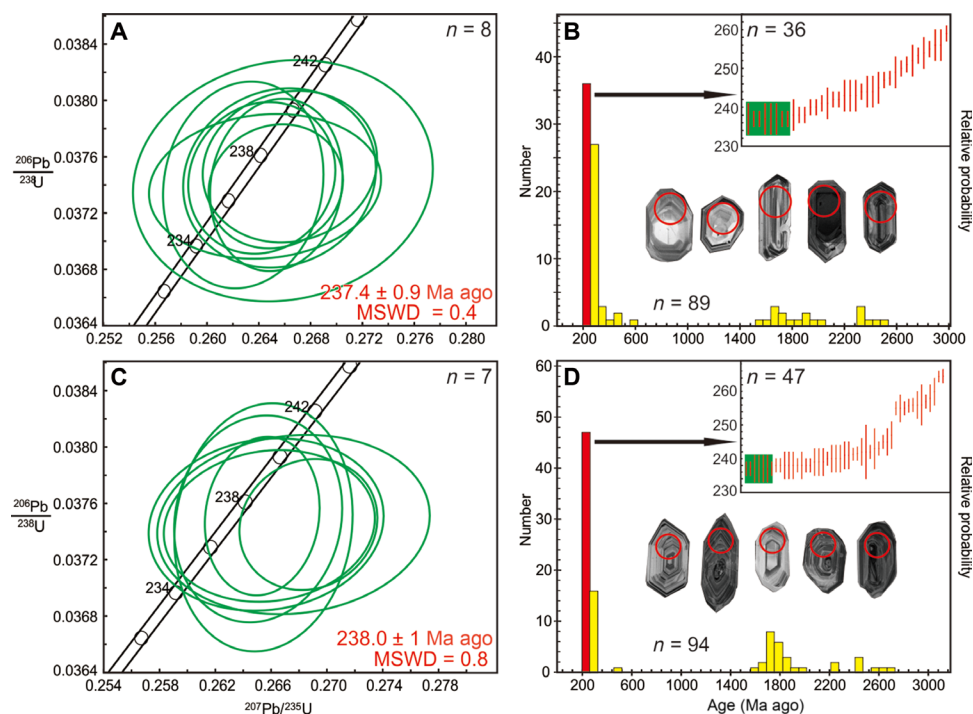


Fig. 2. U-Pb geochronology for samples from layers bearing Tongchuan entomofauna. U-Pb concordia plots for zircons in youngest ages (left) and frequency histograms (right) of detrital age populations from sample TC-01 (A and B) and sample TC-02 (C and D). Black arrows showing rank order plots (green bars represent youngest ages). Select cathodoluminescence (CL) images of zircons are in frequency histograms (age, 237 Ma ago; red circle diameter, 40 μ m).



Fig. 3. Representative fossils from Tongchuan and Karamay entomofaunas. Tongchuan entomofauna (A to C, E to J, and L to O), and Karamay entomofauna (D and K). (A) *Zygophlebia* (Odonatoptera: Zygophlebiidae), NIGP163160; (B) Locustavidae (Orthoptera), NIGP162042; (C) *Prochoristella* (Mecoptera: Permochoristidae), NIGP162043; (D) Corixidae, NIGP162044; (E) *Boreocixius* (Hemiptera: Surijokociiidae), NIGP162045; (F) Dunstaniidae (Hemiptera), NIGP162046; (G) Aphidoidea (Hemiptera), NIGP162047; (H) *Chauliodites* (Grylloblattida: Chaulioditidae), NIGP162048; (I) Cicadocorinae (Hemiptera: Progonocimicidae), NIGP162049; (J) Ichneumon *Folindusia* (Trichoptera), NIGP162050; (K) Ichneumon *Terrindusia* (Trichoptera), NIGP162051; (L) Myxophaga (Coleoptera), NIGP162052; (M) Elateriformia (Coleoptera), NIGP162053; (N) Dytiscoida (Coleoptera), NIGP162054; (O) Cicadocorinae (Hemiptera: Progonocimicidae), NIGP162055. Scale bars, 5 mm (white), and 1 mm (black).

sedimentary transport and support the interpretation that the tuffaceous sandstone depocenter lays near the magmatic source of the zircons. Eighty-nine analyses provided concordant ages ranging from 2480 to 237 Ma ago (Fig. 2B). Eight youngest analyses gave a weighted mean of 237.4 ± 0.9 Ma ago [mean square weighted deviation (MSWD), 0.4; uncertainties are given at the 2σ level] as the maximum depositional age for sample TC-01. The major subpopulation of ages generally fell between 237 and 362 Ma ago, with some between 1538 and 2480 Ma ago. Several sporadic ages fell in the Devonian (404 Ma ago), Ordovician (472 Ma ago), and Cambrian (492 Ma ago). The zircon grain sizes of sample TC-02 (Fig. 2, C and D) were similar to those from sample TC-01. While some grains were intact, most exhibited fractured morphologies. Euhedral facets and oscillatory zoning patterns indicate an igneous origin and limited exposure to sedimentary processes (Fig. 2D). Ninety-four zircon grains gave concordant ages ranging from 2703 to 237 Ma ago (Fig. 2D). The seven youngest, with equivalent $^{206}\text{Pb}/^{238}\text{U}$ dates, gave a weighted mean of 238.0 ± 1 Ma ago (MSWD, 0.8; uncertainties are given at the 2σ level) as the maximum depositional age for sample TC-02. The largest subpopulation of ages generally fell between 237 and 307 Ma ago, and the second one fell between 1611 and 2703 Ma ago. The age distribution also included one outlier age of 503 Ma ago (Cambrian). The two youngest age

populations with weighted means of 237.4 ± 0.9 Ma ago and 238.0 ± 1 Ma ago suggest a latest Ladinian age (26) for the top of the lower part of the Tongchuan Formation. For detrital zircons, the youngest age populations may not represent the most accurate depositional age (27), since the deposition should be later than youngest magmatic events (28, 29), but may offer approximate constraints on deposition (6). The latest Ladinian age agrees with the previous isotopic age results (~ 236 to 234 Ma ago) (30) for the upper part of the Tongchuan Formation and the biostratigraphic correlation (Middle Triassic) for this formation and can approximately represent the depositional age (for detailed age discussions, see the Supplementary Materials).

DISCUSSION

Characters of two entomofaunas

The Tongchuan entomofauna contains at least 28 insect families in 11 orders, viz. Blattodea, Coleoptera, Diptera, Grylloblattida, Glosselytrodea, Hemiptera, Mecoptera, Miomoptera, Odonatoptera, Orthoptera, and Trichoptera (table S1), making it among the most diverse Triassic entomofaunas (typical coeval insect-bearing sites; see Fig. 1E). This entomofauna includes more than 14 families of holometabolous

insects, which also distinctly outnumber other insects with respect to specimen numbers (approximately 65% of 520 specimens). The Tongchuan entomofauna has many typical Triassic elements, such as Zygophlebiidae (Odonoptera), Locustavidae (Orthoptera), and Curvicutitidae (Hemiptera), which were widespread in the Ladinian-Carnian of Kyrgyzstan and the Carnian of Ipswich, Australia (31). It yields some Late Permian and Early Triassic components, such as Chaulioditidae (Grylloblattida: *Chauliodites*) (21), Surijokociidae (Hemiptera), Dunstaniidae (Hemiptera), and primitive Aphidoidea (Hemiptera), and the Aphidoidea is related to a Permian aphid from France (32). In addition, it yields the earliest Cicadocorinae (Hemiptera) (Fig. 3I), which are common moss bugs in the Jurassic and Early Cretaceous (33). The Karamay entomofauna yields 10 insect families in six orders, including caddisfly cases and the earliest known water boatmen. Aquatic beetles and bugs (Permosynidae, Schizocoleidae, and Corixidae) are quite abundant in this entomofauna, in which the diversity is dominated by beetles (five families). The complete and detailed descriptions of these fossils from the two entomofaunas will be published elsewhere.

Most of Triassic beetles are preserved as isolated elytra (33–36). However, there are diverse beetles with bodies in the Tongchuan entomofauna, including the earliest putative Myxophaga (characterized by an elongate body with short elytra and widely separated mesocoxae and metacoxae; Fig. 3L), Elateriformia (characterized by a robust body with a distinct prosternal intercoxal process and produced hind pronotal angles; Fig. 2M), and Dytiscoidea (characterized by a streamlined body with two eyes, smooth elytra, and second abdominal sternite divided by metacoxae; Fig. 2N). These fossils, therefore, are potential key calibration points for the molecular phylogenetic analysis of beetle phylogeny.

Another interesting discovery is the earliest caddisfly cases (Trichoptera) in both entomofaunas (Fig. 3, J and K). Larval caddisflies construct cases using sand grains, shells, fish scales, coprolites, or vegetation cemented with the silk they secrete (23). The order Trichoptera is the sister to the Lepidoptera, of which the earliest record was near the Triassic-Jurassic boundary (37). The true Trichoptera was thought to have diverged from Amphiesmenoptera in the earliest Jurassic, and the earliest previously identified caddisfly case fossil was from the Early Jurassic of Siberia (Fig. 4) (23, 38). The Permian and Triassic “trichopteran” most probably belongs to the stem group of Amphiesmenoptera (39). The Permian marine “caddisfly” cases (40) were probably incorrectly identified since the caddisfly larva cannot build these cases with short, thick silk bundles (maximum, 1 mm diameter) arranged in an overlapping manner and not transversely circular. These marine cases were probably constructed by worms. The ichnogenus *Folindusia* (narrow-long, straight case built mainly of densely packed plant fragments, with some transverse arranged; Fig. 3J) from the Tongchuan entomofauna and the ichnogenus *Terrendusia* (narrow-long, straight case built of small densely and irregularly packed sand grains; Fig. 3K) from the Karamay entomofauna suggest an unexpected Middle Triassic origin of the construction behavior, much earlier than previously proposed from molecular studies (41, 42).

Middle-Late Triassic insect radiation

The Holometabola are the most diverse insects in the Tongchuan and Karamay entomofaunas, which are represented by diverse beetles and scorpionflies. Nowadays, holometabolous insects have the highest number of species of any clade and greatly contribute to the animal species biodiversity (43). Although they are already known from the Early Carboniferous (41, 43) and diversified during the Early-Middle

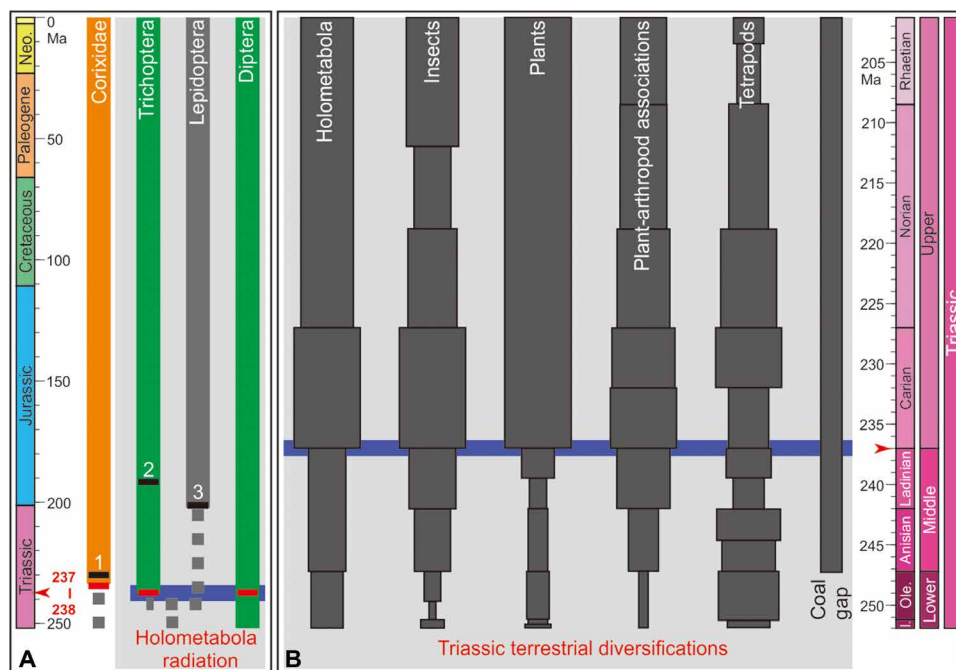


Fig. 4. Triassic terrestrial biodiversifications. (A) Middle Triassic Holometabola radiation and (B) Triassic terrestrial diversifications. The previously earliest records of (1) Corixidae (45), (2) Trichoptera (38), and (3) Lepidoptera (37) are marked by black rectangular bars, and the new records reported in the present study are marked by red rectangular bars. The Triassic terrestrial diversifications are based on the data of holometabola [family richness; (63)], insects [family richness; (14)], plants [generic richness; (9, 64)], plant-arthropod associations [relative richness; (15)], tetrapods [generic richness; (65)], and coal gap (66). I., Induan; Ole., Olenekian; Neo., Neogene.

Triassic (34), Holometabola were thought to have become dominant in the global entomofauna starting in the mid-Mesozoic (24, 44). Thus, its high diversity and abundance in Tongchuan and Karamay are relatively unexpected, revealing a radiation of Holometabola during the Middle Triassic, in correspondence to the results found from the Triassic of the Vosges (France) (34).

Aquatic insects also experienced substantial expansions in the Middle Triassic. Some key aquatic holometabolous clades, now comprising the bulk of modern freshwater biodiversity, can also be tracked back to the Middle Triassic origins, such as caddisflies and aquatic beetles (including Myxophaga and Dytiscoidea) found in both entomofaunas. In addition, water boatmen (characterized by fully sclerotized forewings with a distinct claval suture and no veins) are abundant in the Karamay entomofauna, and they are the earliest record of aquatic bugs (Fig. 3D). This finding is slightly earlier than those found from the Upper Triassic Huangshanjie Formation of Xinjiang (see the Supplementary Materials) (45) and the Cow Branch Formation of United States (22) and is earlier than the divergence times predicted on the basis of molecular studies (estimated to have occurred in the earliest Jurassic) (Fig. 4) (46). Together with true flies from other Early and Middle Triassic entomofaunas, these aquatic insects developed new herbivore and carnivore guilds that persist to the present day (47). The diversification of aquatic insects (mainly belonging to holometabolous insects) is thought to be part of the Mesozoic Lacustrine Revolution, which was dated as “Middle Mesozoic” (25, 48). However, our results suggest that this diversification has already begun by the Middle Triassic, thus providing new insights into the early evolution of freshwater ecosystems.

In summary, our findings confirm that holometabolous and aquatic insects experienced a radiation event in the Middle Triassic. Compared to other insects, Holometabola (including some aquatic insects) were probably more resilient to Early Triassic environmental disturbances because their development would have allowed greater buffering from environmental variability [analogous to modern species with a protective pupal stage, faster development, higher population sizes, and reduced intraspecific competition between the adult and offspring (49)]. After the Early Triassic, various plants (including aquatic plants) started to appear during the Middle Triassic and spread later (1), probably further contributing to the radiation of holometabolous and aquatic insects (Fig. 4).

Terrestrial Ladinian-Carnian boundary

The marine GSSP (Global Boundary Stratotype Section and Point) of the Carnian Stage is defined by the first appearance of the ammonoid *Daxatina canadensis* in the Prati Di Stuores/Stuores Wiesen section in the Southern Alps, Northeast Italy (50). Chemical abrasion–thermal ionization mass spectrometry (CA-TIMS) gave a precise age of 237.77 ± 0.052 Ma ago for the ash bed from the Alpe di Siusi/Seiser Alm area, 24 km west of the GSSP. The ash bed is lower than the GSSP point, and the age of the boundary is estimated on the basis of sediment accumulation (50). The Ladinian-Carnian boundary, ~237 Ma ago, is also supported by previous dating work on several strata correlated with the GSSP (51–53). The insect-rich Tongchuan terrestrial biota dated to ca. 238 to 237 Ma ago (Fig. 2) is in greement with the marine Ladinian-Carnian boundary. It should be noted that the marine and land strata can be correlated not only by isotopic ages but also by similar spore-pollen compositions. The GSSP is indicated by typical Carnian spore and pollen species *Vallasporites ignacii* and *Patinasporites densus* (50), which are absent in the Tongchuan

Formation. In contrast, the appearance of some common insect elements in the Tongchuan, Madygen, and Australian entomofaunas indicates the close relationship among these Middle-Late Triassic terrestrial biotas. Therefore, our new age can provide a calibration point for marine and terrestrial correlations near the Ladinian-Carnian boundary and for the correlation of contemporaneous biotas.

MATERIALS AND METHODS

Insect fossils

The insect fossils were prepared using sharp pins. Photographs were taken using a Sony $\alpha 7$ camera and a Zeiss Discovery V16 microscope system with specimens moistened in 95% alcohol or dry. The figures were prepared with CorelDRAW X7 and Adobe Photoshop CS6.

U-Pb geochronology

The tuffaceous sandstone samples were crushed and separated to isolate the 80- to 200- μ m grain size fraction (54). A total of 200 inclusion-free zircon grains from each sample were then picked under a binocular microscope and mounted in epoxy resin. Hardened mounts were polished to expose zircon grain midsections at about two-thirds to one-half of their widths. CL imaging documented grain morphologies and internal structure for in situ analysis. U-Pb isotopic data from zircons were obtained at the Department of Earth Sciences, The University of Hong Kong, using a Nu Instruments MC-ICP-MS with a Resonetics RESolution M-50-HR Excimer Laser Ablation System. The analyses used a beam diameter of 30 μ m, a repetition rate of 4 Hz, and an energy density of 5 J/cm² on sample surface. Average ablation time was ca. 40 s, and pit depths reached about 30 μ m. The Harvard reference zircon 91500 (1065.4 ± 0.3 Ma ago) (55) and GJ-1 zircon (609 Ma ago) (56) were used for preliminary calibration and second reference, respectively. Detailed operational procedures are found by Xia *et al.* (57). We used ICPMSDataCal (58) to process the offline signal selection, quantitative calibration, and time-drift correction. We used a function given by Anderson (59) to correct for common Pb in Microsoft Excel. Isoplot v. 3.0 (60) was used to construct concordia diagrams and probability density plots. Within the overall detrital age distribution, we cited ²⁰⁶Pb/²³⁸U ages for zircon grains younger than 1000 Ma ago and ²⁰⁷Pb/²⁰⁶Pb ages for older grains. Here, 100 zircon grains were randomly selected from each sample, so the results were expected to reflect the characteristics of the age populations. Ages with a discordance degree of >10% were excluded from the analysis (61).

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/4/9/eaat1380/DC1>

Supplementary Materials and Methods

Fig. S1. Photographs showing outcrops bearing Tongchuan and Karamay entomofaunas.

Table S1. Insect list of the Tongchuan entomofauna.

Table S2. U-Pb analytical results for samples from the Tongchuan outcrop.

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