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Rapid riparian ecosystem recovery in low-latitudinal North China following the end-Permian mass extinction

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eLife Assessment

This is a well-written **important** paper on the recovery of fauna and flora following the end-Permian extinction event in several continental sites in northern China. The **convincing** conclusion, a rapid recovery in tropical riparian ecosystems following a short phase of hostile environments and depauperate biota, is supported by an impressive amount of data from sedimentology, body fossils of animals and plants, and especially trace fossils.

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Abstract

The greatest mass extinction at the end-Permian, 252 million years ago (Ma), led to a tropical dead zone on land and sea. The speed of recovery of life has been debated, whether fast or slow, and terrestrial ecosystems are much less understood than marine. Here, we show fast reestablished riparian ecosystems in low-latitude North China within as little as ~2 million years (Myr) after the end-Permian extinction. The initial ichnoassemblages in shallow lacustrine and fluvial facies of late Smithian age are monospecific, devoid of infaunalization, with apparent size reduction. In the following Spathian, newly identified medium-sized carnivores, plant stems, root traces, coupled with improved ichnological criteria and significantly increased infaunalization, suggesting a relatively complex, multi-level trophic structured riverain ecosystem had been rebuilt. Specifically, burrowing behavior had re-emerged as a key life strategy not only to minimize stressful climatic conditions, but possible to escape predation.

Introduction

The end-Permian mass extinction (EPME) is one of the most devastating bio-crises in the history of life, destroying both marine and terrestrial ecosystems (Wignall, 2015; Fan et al., 2020). A key feature of the EPME is the clearing of life from tropical ecosystems (e.g., Sun et al., 2012). The environmental extremes, especially lethal heat, have largely flattened the tropical biodiversity peak, and marine animals were forced to migrated poleward or into deeper water (Liu et al., 2020; Song et al., 2020). Such effects are more brutal on land. A tropical "tetrapod gap", spanning between 15°N and ~31°S, prevailed through the Early Triassic, or at least during particular interval of intense global warming (Bernardi et al., 2018; Allen et al., 2020; Romano et al., 2020; Liu et al., 2022).

It has been demonstrated that long-term environmental perturbations after the EPME resulted in the delayed recovery until to the Middle Triassic in the sea (Chen and Benton, 2012), although several fast evolvers would bounce back fast before being killed by further repeat hyperthermal events through the Early Triassic, as evidenced by the Guiyang Biota found ~1 Myr after the EPME (Dai et al., 2023). However, the post-extinction recovery on land remained largely unclear. The taxonomic diversity of vertebrates may have re-flourished soon after the extinction in European Russia (Tverdokhlebov et al., 2003), but it apparently took longer, until the latest Early Triassic, in the Central European Basin (e.g., Mujal et al., 2017). Model results of the tetrapod-dominated paleocommunities from the Karoo also displayed a short lived, unstable ecosystem during the Early Triassic *Lystrosaurus* Assemblage Zone, before being replaced by a globally stable ecological structure established in the Middle Triassic (Roopnarinev et al., 2019; Viglietti et al., 2022). It seemed that plants showed a quick return in Australia (Vajda and Kear, 2024), yet reorganization of floral communities were hindered by repeated climatic stressors, such as the Smithian–Spathian warming event (Mays et al., 2020; Vajda et al., 2020). Likewise, the initial construction of the mesophytic flora was in the earliest Middle Triassic in North China (Shu et al., 2022).

Other body fossils, especially non-marine invertebrates, are relatively scarce in the post-extinction interval. The earliest Middle Triassic riverine community, consisting of insects, rare fishes and trace fossils in equatorial western peri-Tethys (Baucon et al., 2014; Mujal et al., 2020; Matamales-Andreu et al., 2021) and the Anisian–Ladinian deep lake biota, comprising of diverse insects, fishes, fish coprolites and plants in tropical North China (Zhao et al., 2020), were thought representative of the recovered terrestrial ecosystems after the EPME. However, recently studies revealed that the biodiversity would be not as low as expected in North China from the ichnological point of view, relatively diversified trace fossils have been found during the late Early Triassic with moderate bioturbations (Guo et al., 2019; Xing et al., 2021; Zheng et al., 2021). Here, we report the unexpectedly fast recovered ecosystem from the tropical dead zone after the EPME, based on compiled data of vertebrates, invertebrate trace fossils, and plant remains from Lower Triassic successions and outcrops in North China, to show how animal behaved to survive in harsh conditions and finally recovered from the mass extinction event.

Materials and Methods

Abundant trace fossils have been identified from the uppermost Permian–Lower Triassic of the Shichuanhe, Dayulin, Liulin sections and Hongyatou, Tuncun, Mafang outcrops in the Central North China Basin (**Fig. 1**). During the early Mesozoic, the North China Block was located at about 20°N based on paleomagnetic reconstruction (Huang et al., 2018; Guo et al., 2022). The Permo-Triassic strata, typically terrestrial red-beds, comprising the Sunjiagou, Liujiagou,

Heshanggou (HSG) and Ermaying formations in ascending order, display varied depositional environments from fluvial to lacustrine facies (See **Figure S1** and **Table S1** in the Supporting Information). The Sunjiagou Formation mainly consists of red massive siltstone and intercalated sandstone of varied thickness, and paleosols and trace fossils were locally developed, demonstrating floodplain to lakeshore facies (Ji et al., 2022; Yu et al., 2022). The Liujiagou Formation is characterized by thick cross-bedded sandstone and intraclast conglomerate. Lenticular sand bodies and erosive bases of sandstones were common in the lower part, indicating fluvial channel facies under braided river systems (Zhu et al., 2019; Ji et al., 2022). Interlayered thick siltstone of lakeshore facies increased upwards, accompanied by weak biological activities. The HSG is dominated by massive siltstones, with multi-layered paleosols, diverse trace fossils and some plant remains, belonging to alluvial plain and lakeshore facies, with periodic aerial exposure (Zhu et al., 2020; Ji et al., 2022).

Recently, a U-Pb CA-ID-TIMS age calibrated magnetostratigraphy from the Shichuanhe section provided a basic geochronological timescale for the fossil-poor strata in North China (Guo et al., 2022; **Figure S2**). Accordingly, the Permian–Triasssic Boundary is constrained in the upper part of the Sunjiagou Formation based on the age of 252.21 ± 0.15 Ma, with the base of Smithian and Spathian being roughly located in the lower and upper Liujiagou Formation respectively. However, loss of several magnetozones due to regional hiatus made it difficult to precisely place the Lower–Middle Triassic Boundary, which was tentatively put at the lithological contact of HSG and the overlying Ermaying Formation (Guo et al., 2022). The 245–247 Ma ages from tuff layers at the base of the Ermaying Formation roughly supported this correlation (Zhu et al., 2022).

In order to discriminate the recovery stages, several ichno-ecological criteria were incorporated. Both bioturbation index (BI) and ichnofabric index (ii), which have been critically reviewed by Luo et al. (2020), are used to quantify bioturbation intensity. Values of ii and BI, ranging from 1–6 and 0– 6, respectively, co-indicate the gradual increase of biotic disturbance from no bioturbation to total homogenization of sediments. Ichnodiversity represents the number of ichnotaxa, but it is not strictly equivalent to biodiversity, as a certain trace can be made by different animals and multiple trace types can originate from a single taxon (Luo et al., 2019). Ichnodisparity emphasizes the variability of architectural designs of trace fossils (Buatois et al., 2017). Therefore, both ichnodiversity and ichnodisparity are employed to assess the behavioural responses of animals and the stage of infaunal biotic recovery (**Table S2**–**4**). Size and penetration depth were also measured in place that can represent average level of each burrow. Tiering, referring to the life position of an animal vertically in the sediment, is divided into surficial, semi-infaunal (0–0.5 cm), shallow (0.5–6 cm), intermediate (6–12 cm) and deep infaunal tiers (> 12 cm), adopted from Minter et al. (2017).

Thin sections of plant stem specimens were prepared to examine vertical and cross-sectional microstructures. Meanwhile, Micro-CT scanning (SkyScan 1172 X-ray; State Key Laboratory of Biogeology and Environmental Geology) was employed to reconstruct the internal structures of stems.

Results and Discussion

Infaunal crisis and living strategy after the EPME in North China

An infaunal crisis, marked by the disappearance of the moderately diversified pre-extinction ichnofauna and the absence of biogenic structures, was identified during the late Changhsingian–early Smithian. The latest Permian floodplain facies mainly occupied by shallow–intermediate tiers of freely motile non-specialized deposit-feeding animals (**Figure 1**), akin to the Paleozoic suites reported before (Minter et al., 2017). Both the ichnodiversity and ichnodisparity declined abruptly in the middle Sunjiagou Formation (near the 252.21 Ma aged tuff layer), following a

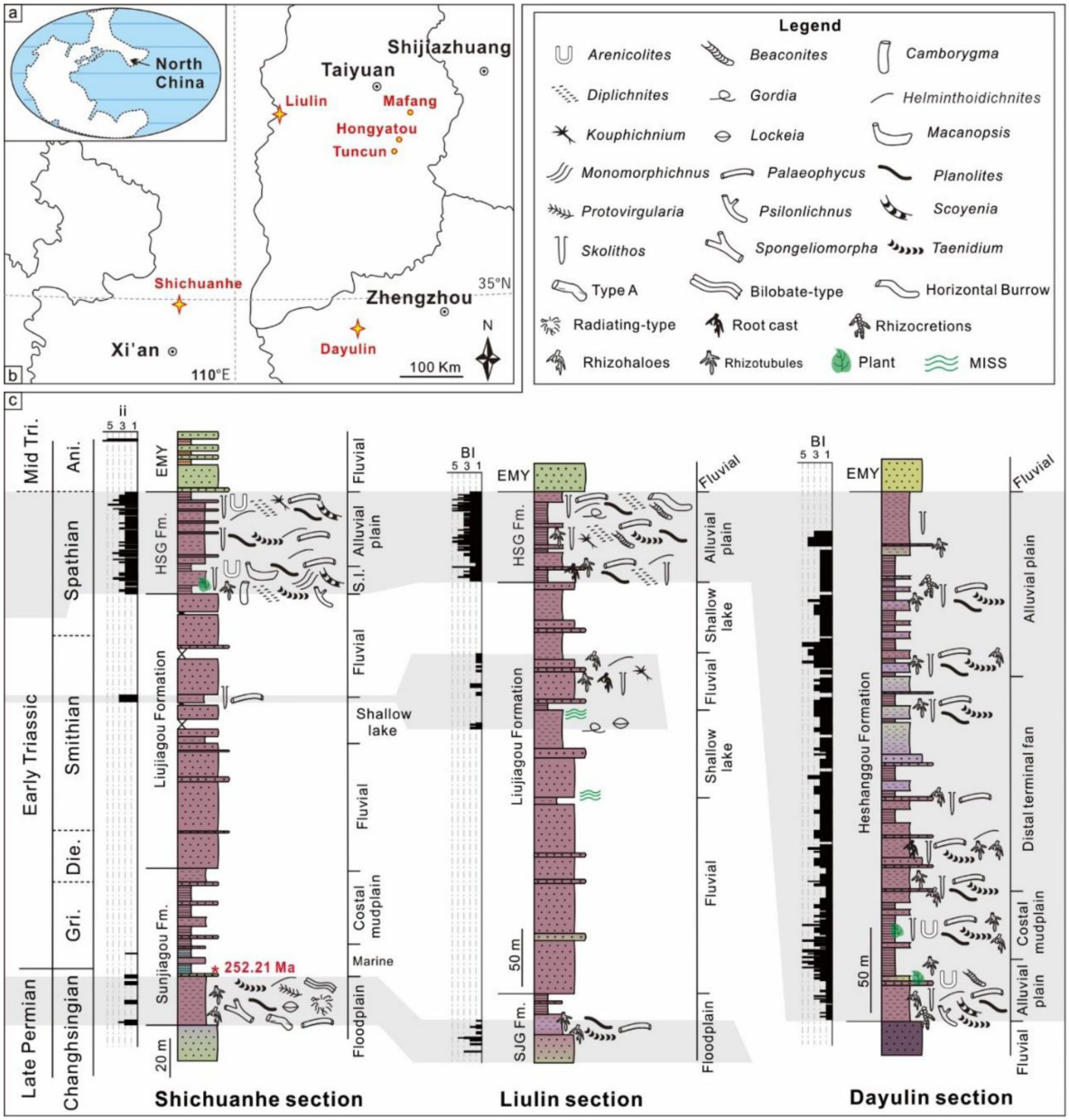

Figure 1.

Location of the studied regions and lithological columns. (a–b) Permian-Triassic paleogeographic map of North China and the studied successions (stars) and outcrops (points). Base map of a is modified from Sun et al. (2012). (c) Depositional facies and detailed distribution of trace fossils in three main successions.

prolong non-bioturbated interval in North China (Guo et al., 2019, 2022; Xing et al., 2021). The infaunal crisis was contemporary with the extirpation of the pareiasaur fauna (*Shihtienfenia*) and deforestation of the youngest Palaeozoic *Ullmannia-Pseudovoltzia-Germaropteris* assemblage in North China, representing the EPME on land (Liu et al., 2022; Shu et al., 2022).

The early resurged ichnofaunal in the upper Liujiagou Formation, about late Smithian in age, were short-lived. This lakeshore ichnofauna, including seven ichnogenera of six ichnodisparities, were characterized by surficial and semi-infaunal tiered simple burrows or trails, with rare trackways and root traces, which weakly disturbed the sediments (**Figure S3**). Dwarfism in trace makers is observed from all ichnogenera, with burrow sizes reduced from 4.06 mm before the EPME (n = 779) to 2.06 mm (n = 341) in the late Smithian (**Figure 4** and **Figure S7**), or single ichnogenus, such as *Kouphichnim* (Shu et al., 2018). The depauperate ichnofauna of the late Smithian were monospecific, representing initial recolonization of empty niches by opportunists, but the coeval thrived microbial mats indicated harsh environments, which might have inhibited the recovery of freshwater ecosystems (Tu et al., 2016; Chu et al., 2017; Mays et al., 2021).

Abundant trace fossils were identified in the Spathian HSG Formation, comprising 16 ichnogenera of nine ichnodisparities, and two informally designated types (**Figure 2** and **Figure S4**–**5**). The morphologically complex ichnofauna were dominated by actively filled burrows, with few arthropod trackways, which were probably produced by decapod crustaceous, myriapods and insects (**Table S5**). The lakeshore and alluvial plain facies were occupied multi-tiered traces, including surficial trackways (e.g., *Diplichnites*; *Kouphichnium*), semi-infaunal (e.g., *Helminthoidichnites*; *Gordia*), shallow (e.g., *Palaeophycus*; *Scoyenia*), intermediate (e.g., *Taenidium*) and deep tiers (*Camborygma*; *Skolithos*; **Figure 1c**). Trace producers colonized varied ecospace and shallower tiers are generally crosscut by deeper penetrative burrows (**Figure 2a**), resulting in moderately to substantially bioturbations, with ii 2–3 and BI 3–4 at most layers. In several horizons, the uppermost few centimeters of sediments are totally obliterated, mostly by the activity of deposit feeding animals. However, distal terminal fan facies are weakly reworked by simple traces such as *Skolithos* and *Palaeophycus* or root traces. Additionally, average burrow sizes of all ichnogenera also increased to 3.9 mm in the HSG (n = 2241, **Figure 4** and **Figure S7**–**8**).

Several large burrows in the Spthian indicate the occurrence of advanced ecosystem engineers. *Camborygma litonomos* were found in the basal HSG of the Shichuanhe section and outcrop in Hongyatou, co-occurring with *in situ* preserved *Neocalamites* plant fossils, and other traces, such as *Diplichnites*, *Monomorphichnus* and *Skolithos* (**Figure S6**). Surfaces of *C. litonomos* were occasionally intertwined with rhizotubules (**Figure 2l**), suggesting that those plants could be important constituents in the diet of crayfish or that the crayfishes may use the roots to hide among. In addition, another large burrow was identified at the Liulin section. The sub-horizontal unbranched burrow displayed probable longitudinal scratch marks on the external surface, but poor preservation and limited specimens hindered a definite designation (**Figure S5**). ? *Beaconites*, found in the lower part of the HSG at Mafang, are characterized by meniscate structures (**Figure 2o–p** and **Figure S5C–E**), akin to those of large *Beaconites* from breccia facies in the Devonian red sandstone of Britain (Brück, 1987). Although the biological nature of these large burrows cannot be confirmed, their activities increased biogenic reworking of sediment and soils, improved geochemical recycling and ecosystem complexity in the Spathian, implying key roles in ecosystem functioning.

Although climatic and environmental conditions in the early Spathian were still not cool and wet enough for thriving and abundant life, a fossorial strategy would have been useful for continental animals to avoid heat and aridity. Midday temperatures > 35°C, as occurred during peaks of global warming at the EPME and at points through the Early Triassic, cannot be tolerated for long by terrestrial (or aquatic) animals (Benton, 2018; Liu et al., 2022). The increase in tetrapod

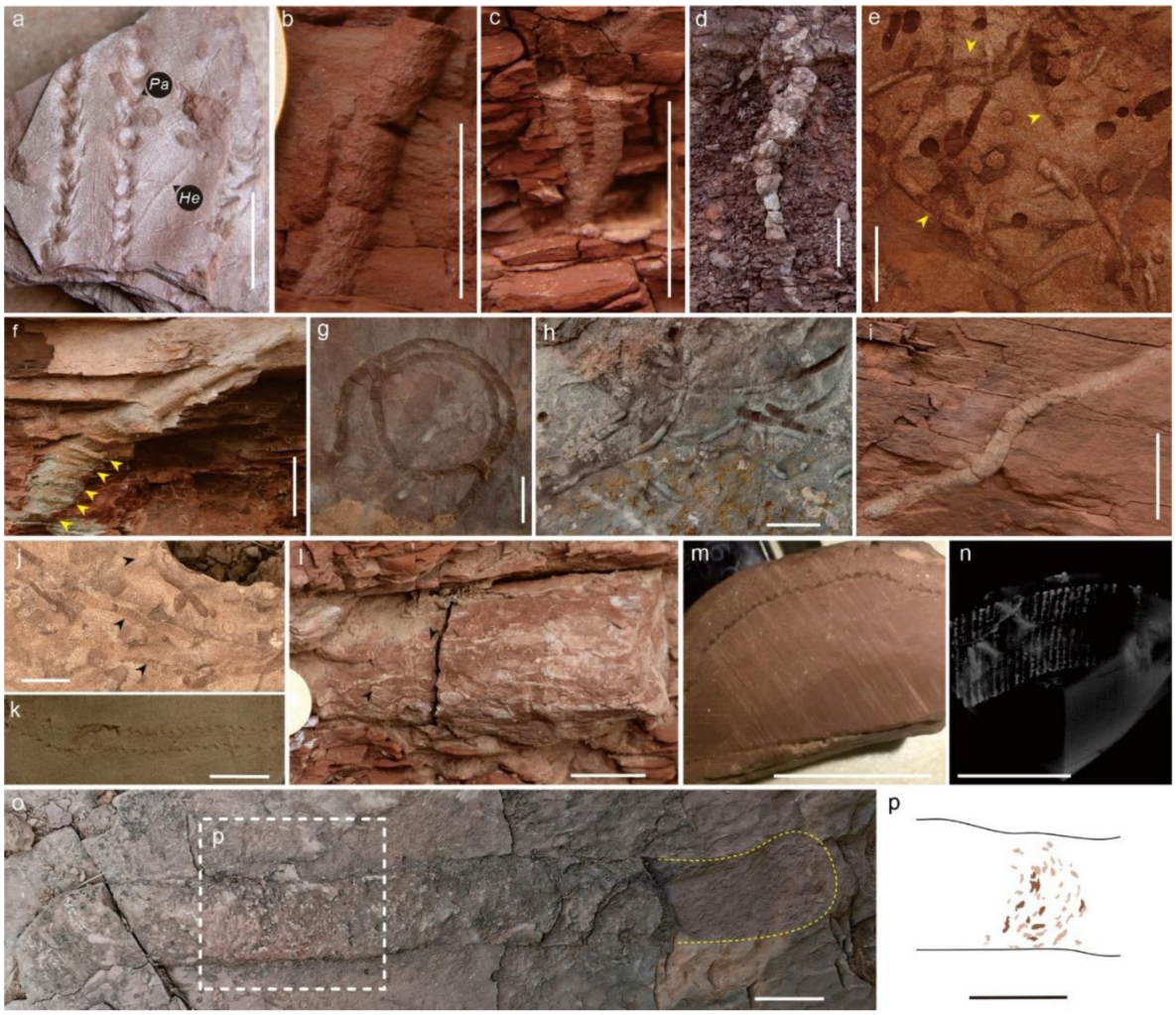

Figure 2.

Ichnofossils from the Heshanggou Formation of North China. (a) Shallow tiers *Kouphichnium* and *Helminthoidichnites* (He) are crosscut by immediate tier *Palaeophycus* (Pa). (b) *Skolithos* cf. *serratus* with faint oblique striations. (c) Y-shaped *Psilonichnus* isp. (d) Downward unbranched and tapered rhizocretion. (e) Shallow tiers *Beaconites coronus*, arrows show tightly stacked arcuate meniscus. (f) *Camborygma* isp. shows enlarged terminal chamber and possible transverse scratches (arrows). (g) *Gordia* isp. with darker and finer infills. (h) High density *Palaeophycus tubularis* preserved on the sole of thick sandstone. (i) Inclined *Planolites beverleyensis* within siltstone. (j) *Taenidium barretti* (arrows) pass through the rippled surface. (k) Horizontal *Camborygma*, the outer surface is intertwined with tinny root traces (arrows). (l) Biserial *Diplichnites gouldi*. (m-n) Internode cross-section of *Neocalamites* stem and micro-CT structure, showing the clear ribs and grooves. (o-p) Large ?*Beaconites* on top of rippled sandstone, rectangle in (p) shows meniscus-like portions comprising of gritty infillings. Scale bar of (d, f, h, o-p) are 40 mm, the rest are all 20 mm.

burrow abundance and complexity in the Lower Triassic suggest that a fossorial lifestyle allowed tetrapods to endure harsh post-extinction environmental conditions (Marchettti et al., 2024). Likewise, we envisaged that infaunalization could also have been a vital strategy for invertebrates to survive and thrive. More intensively occupied ecospace in the late Spathian, characterized by increased burrowing and complicated crosscutting relationships among ichnogenera, may indicate an adaptive response to heightened predation pressure or competition for available resources.

Fast recovered terrestrial ecosystem in low-latitudinal region

Newly discovered tetrapods from the HSG provide crucial insight into the post-EPME ecosystem. Historically, vertebrates found in this lithological unit were exclusively from its middle– upper portions (Li et al., 2008; **Fig. 3**). The presence of Archosauromorpha (e.g., *Fugusuchus*; **Fig. 3c**) and Procolophonomorpha (e.g., *Eumetabolodon*; **Fig. 3d**) could reflect their tolerance to hot and arid condition, while the initial diversification of archosauromorphs in the Olenekian was interpreted as a response to empty ecological space after the EPME (McLoughlin et al., 2020; Romano et al., 2020). Herein, a cluster of tetrapod skeletons, includes a few articulated bones, were found near the base of HSG (early Spathian; **Figure 3i**). The body trunk lengths are estimated at 30–40 cm for the well exposed vertebrates, and the postcranial skeleton suggests a carnivorous feeding strategy. Although the specimens are not yet fully prepared for taxonomic description, they clearly show the existence of tetrapod at this level.

Plants, as key components of the ecosystem, were patchy distributed in the Early Triassic (Shu et al., 2022). However, root traces (rhizoliths) are quite abundant, especially at the Dayulin section (**Figure 2d** and **Figure S6**). The different styles of preservation and various morphologies of rhizoliths provide information about the moderately to relatively well-drained red paleosols in alluvial plain facies in North China (Kraus and Hasiotis, 2006). Specifically, *in situ* preserved vertical *Neocalamites* stems and *Pleuromeia* found in the lower HSG of the Shichuanhe and Hongyatou sections, both emerged in tandem with crayfish trace fossils and other burrows.

Delayed terrestrial recovery was proposed based on the Tongchuan fauna from North China, which consisted of diverse insects, ostracods, fishes, etc, signalling a fully recovered deep lake ecosystem in the middle Triassic, i.e., ~8–12 Myr after the EPME (Zheng et al., 2018; Zhao et al., 2020). However, compiled paleontological data herein show the reconstruction of ecosystem on land in tropical region was as early as in the Spathian, ~2 Myr after the EPME (**Figure S9**). The enhanced floral coverages, attributed to different types of roots and plant fossils, have great impacts to the initiation of post-EPME ecosystem, especially cooccurred stems and trace fossils, which suggest that riverain realms may be refugia for the survival and evolution of the Spahtian biota. Increased abundance and quantity of faunal communities can be inferred from ichnodiversity, with possible candidate of trace-producers including limuloids, crayfishes, spinicaudatan, insects and even small-sized vertebrates (**Table S5**), and moderate bioturbations made by high-density resting traces, respectively. Coeval tetrapods, despite rare, do show the existence of carnivores and further improved the local ecological structures. Reconstruction of freshwater ecosystems in the Spathian was also facilitated by amelioration of the climate (**Fig. 4**). Paleosol-based paleoclimatic reconstructions suggest that precipitation was ~520–680 mm/y in the late Spathian, with pCO_2 estimated from paleosols at 1523 ± 417 ppm (Joachimski et al., 2022; Yu et al., 2022), indicating mitigation of hyperthermal conditions. Geochemical proxies of weathering intensity, salinity and clayiness, along with increased hygrophyte/xerophyte ratio, also demonstrate the transition to wetter conditions (Shu et al., 2022; Zhu et al., 2022).

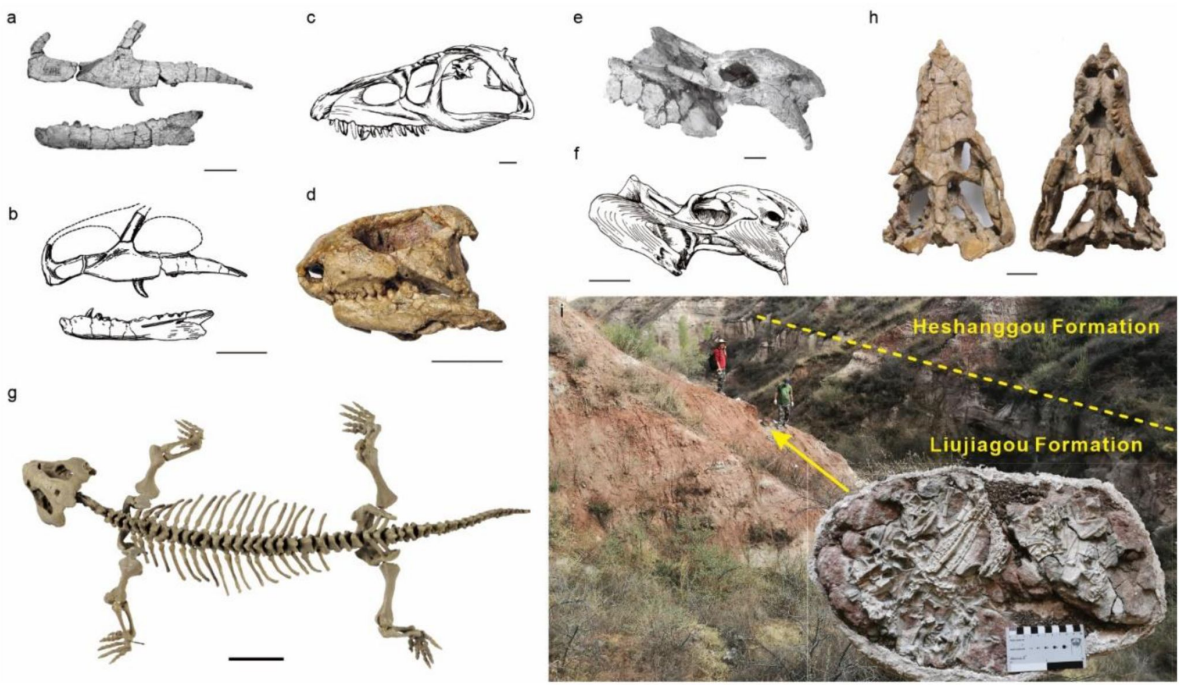

Figure 3.

Vertebrates from the Heshanggou Formation of North China. (a–b) Skull elements of *Xilousuchus sapingensis* and drawings. (c) *Fugusuchus hejiapanensis*. (d) *Eumetabolodon bathycephalus*. (e–f) *Shaanbeikannemeyeria xilouensis* and drawing. (g) *Pentaedrusaurus ordosianus*. (h) *Hazhenia concava*, (i) Dashed line shows the boundary between the Liujiagou and Heshanggou formations. Arrow displays fossil horizon of the inserted picture at the base of the Heshanggou Formation. (b, c, f) are from Li et al. (2008). Scale bars are 40 mm.

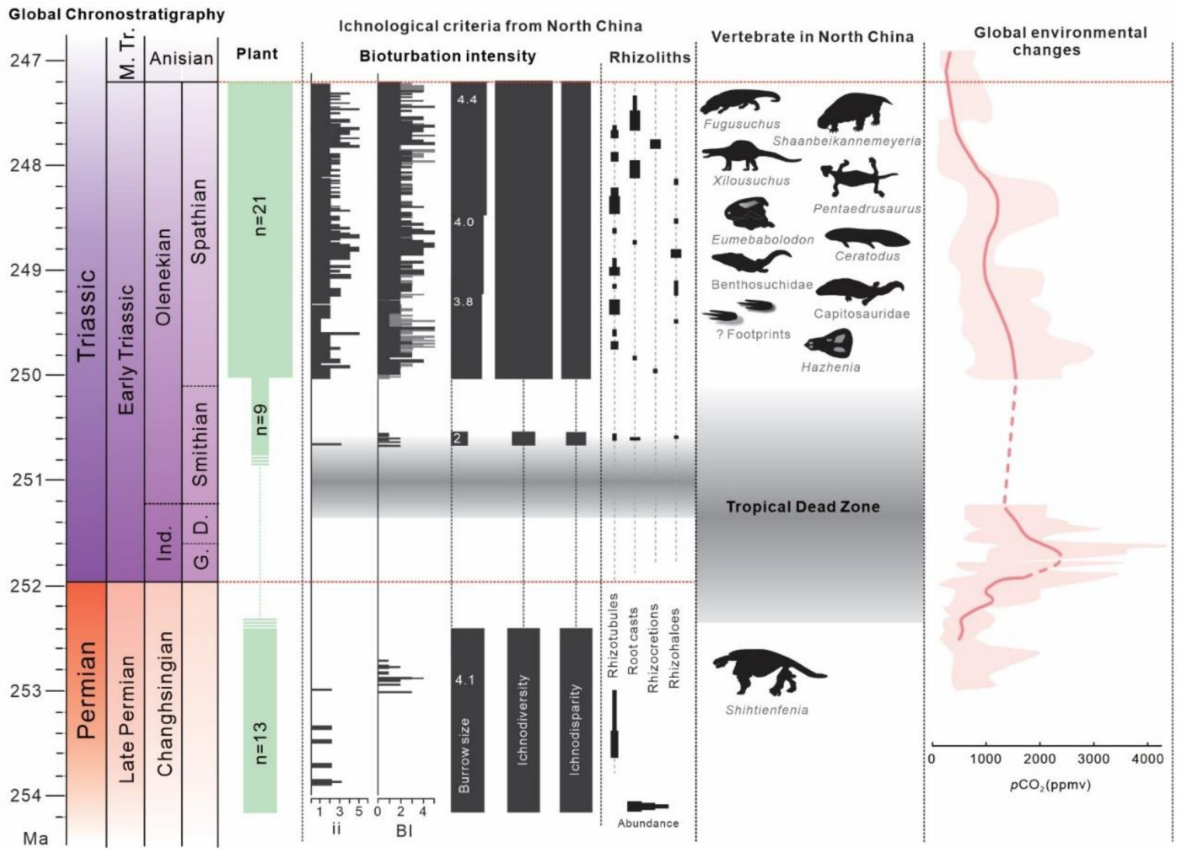

Figure 4.

Ichnofossil criteria in North China and global terrestrial ecosystem changes from latest Permian to earliest Middle Triassic. Geochronological timescale is based on the latest version of the International Chronostratigraphic Chart (*https://stratigraphy.org/*). Plant richness from Shu et al. (2022). Numbers in Burrow size column represent the mean trace fossil sizes from the investigated interval. Drainage conditions of paleosols are inferred from preservation of rhizoliths and their relative depths. Ranges of microbially induced sedimentary structures (MISS) are from Chu et al. (2017). Atmospheric CO_2 curves are modified from Joachimski et al. (2022). Abbreviations: Ind. = Induan; G. = Griesbachian; D. = Dienerian.

Conclusions

The diverse community of the HSG Formation, consisting of tetrapods, plant stems, rhizoliths, and diverse ichnofossils suggests a rapid recovery of life in low-latitude terrestrial environments in the Spathian, as little as ~2 Myr after the end-Permian biotic crisis. The newly discovered vertebrate fossils are medium-sized carnivores of approximately early Spathian age, representing the earliest tetrapod found in North China. High ichnodiversity and ichnodisparity, and three types of large burrows, not only results in intensified bioturbation, but provide additional information about the enriched local biota. Furthermore, enhanced burrowing behavior is considered a key survival-recovery strategy to adapt to harsh climatic and environmental conditions on land. The cooccurred trace fossils and stems, and coeval tetrapod in alluvial plain facies, suggesting that the riverain regions could be refugia for the reorganization of post-EPME ecosystem.

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Supplementary files

Introduction

The Supplementary files include: (1) file 1: Early Triassic chronostratigraphic timescale in North China (**Figures S1**-**2**) and brief description of facies associations of the studied sections (**Table S1**); file 2: detailed description of traces fossils (**Fig S3**-**6**), fossil size variations (**Figures S7**-**8**), reconstruction of the late Early Triassic (Heshanggou Formation) coastal mudplain to alluvial ecosystem (**Figure S9**), designations of ichnodiversity and tiering level (**Tables S2**-**4**) and possible trace producers on land (**Table S5**).

File 1. Integrated stratigraphic timescale and depositional environment

Detailed sedimentological investigations at the three studied sections have been undertaken by Ji et al. (2022) and Yu et al., (2022). Therefore, we primarily summarize the lithofacies and facies associations, and add more information about trace fossils (**Figure S1** and **Table S1**).

Body fossil records in the red bed predominated Permian–Triassic transitional successions were too limited to establish a high-resolution timescale for global correlation. Based on the U-Pb CA-ID-TIMS age calibrated magnetostratigraphy from the Shichuanhe section (Guo et al., 2022), we complied other detrital zircon U-Pb ages during the Early Triassic, to provide a better constrained chronostratigraphy in North China (Zhu et al., 2019; 2022; Lu et al., 2022).

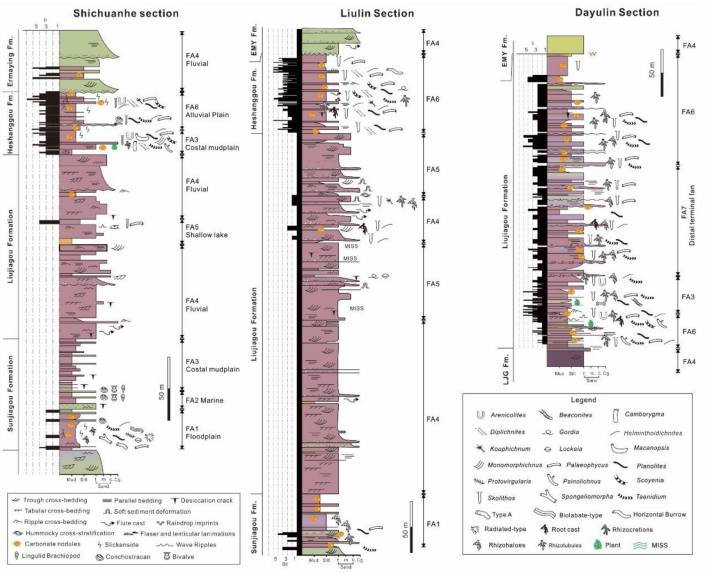

Figure S1.

Lithology, sedimentology and ichnology of the studied sections.

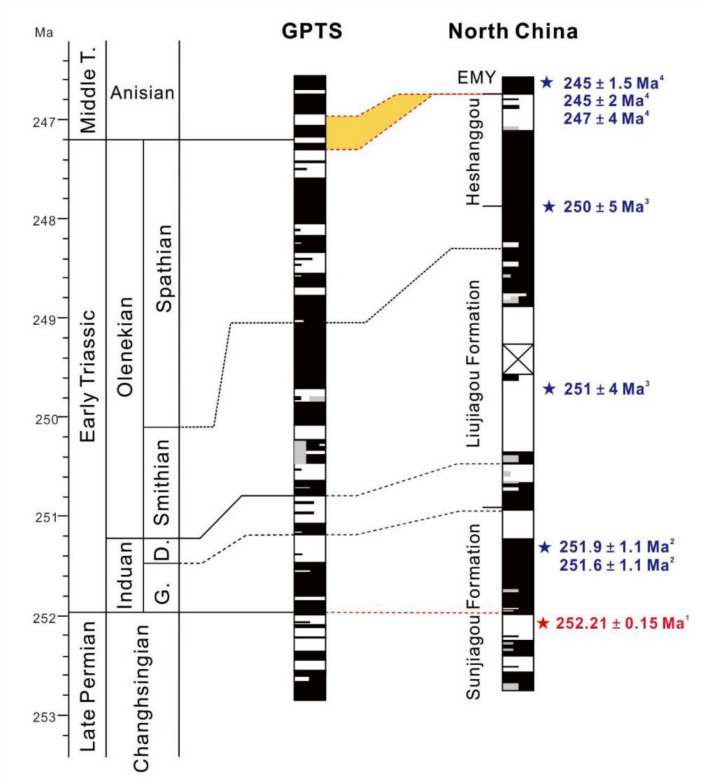

Figure S2.

Early Triassic geochronological scale in North China.

The Geo-magnetic polarity timescale (GPTS) is from Hounslow and Muttoni (2010) and Hounslow and Balabanov (2018). Magnetostratigraphy and the CA-ID-TIMS age of [1] are from Guo et al. (2022). Detrital zircon U-Pb ages are based on: [2] = tuffaceous claystones sampled from the uppermost part of the Sunjiagou Formation (Lu et al., 2022), [2] = around middle part of the Liujiagou Formation (Zhu et al., 2019), [3] = sandstone from the base of the Heshanggou Formation and tuffs from the bottom Ermaying Formation (EMY; Zhu et al., 2022). G. = Griesbachian, D. = Dienerian.

Table S1.

Brief description of lithofacies, facies associations (FA) and trace fossils at the studied sections.

FA	Lithology	Trace fossils	Depositional environments
FA1	• Dominated by red mud-siltstone with paleosols (Msp) and interbedded with cross-bedded sandstone (Scb). • Well-developed paleosols in Msp, of moderate to very high maturity, contained layered calcareous nodules up to 10 cm in diameter, which were assigned to Aridisols and Vertisols.	• Root traces (Rh) and burrows (e.g., *Planolites* (*Pl*, *Taenidium* (*Ta*)) are common in Msp. • Scb is also bioturbated, especially at the Shichuanhe section. Diverse traces, including *Lockeia* (*Lo*), *Protovirgularis*, *Pa*, *Ta*, *Spongeliomorpha*, and several informally designated types have been identified. • Generally, animal traces are crosscut by roots.	• Distributed in the middle and upper Sunjiagou Formation. • **Arid floodplain.**
FA2	• Comprised of grayish-green silty mudstone (Ms), marine marls and calcareous sandstone. • A mixed continental-marine fauna, including conchostracans, bivalves, brachiopods and plant debris, have been identified, indicative of **terrestrial facies with periodical marine flooding events** (Chu et al., 2019).	No trace fossil found.	• Exclusively distributed in the lower Sunjiagou Formation of Shichuanhe section.
FA3	• Comprise red Ms and Sandstone (S). • In upper Sunjiagou Formation, gypsum crystals, blocky calcite cements, Fe-oxide hypocoating occasionally occurred.	• Bioturbation is absent. • Strata in the lower Heshanggou Formation are moderately reworked, several ichnogenera (e.g., *Pl*, *Palaeophycus* (*Pa*), *Beaconites* (*Be*), *Ta*), plant debris, root traces, and vertebrate remains, have been identified.	• Distributed in upper Sunjiagou and lower Heshanggou formations. • **Costal mudplain facies.**
FA4	• Dominated by Pale red to grey purple Scb, planar-laminated sandstone (Sp), interbedded with thin dark red siltstone (Si), where Inceptisols are weakly- developed.	• *Kouphichnium* (*Kou*) (Shu et al., 2018) and tiny *Helminthoidichnites* have been found in Si. • Vertical burrows of *Skolithos* (*Sk*) and Rh, occurred occasionally in Scb, but the sediments were weakly bioturbated.	• Distributed in the Liujiagou and Ermaying formations. • **Low sinuosity fluvial system.**
FA5	• Consists of Scb, planar-laminated sandstone (Sp), hummocky and swaley cross-stratified sandstone (Sh), current and wave-rippled sandstone (Scr, Swr), interbedded with Intraformational conglomerate (Ci), which • Microbially induced sedimentary structures (MISS) are quite common, especially at Liulin Section (Chu et al., 2015, 2017).	• Depauperated ichnofauna, dominated by monospecific ichnoassemblage, i.e., *Sk*, *Lo*, *Gordia*. • Bioturbation in this interval is weak.	• Distributed in the middle-upper Liujiagou Formation. • **Shallow lake and lake margin facies, with influence of major storm events.**
FA6	• Consists of dark red massive Msp, Scb, and Sp. • Sheetlike sandy bodies display lightly erosive bases.	• Msp contain diverse trace fossils, including *Kou*, *Diplichnites*, *Be*, *Ta*, *Camborygma*, *Psinolichnus* and various types of root traces, which moderately disturbed the sediments. • Trace fossils in sandstones are mainly *Sk*, *Pl* and Rh. • In several horizons, the top of several centimeters of the strata is strongly reworked.	• Heshanggou Formation. • **Alluvial plain with shallow lakes facies.**
FA7	• Dominated by massive sandstone with sharp base and trough cross-bedded or planar lamination, interlayered with dark red Msp and intraclast conglomerates, constituting several fining-upward sequences. • Vertisols and calcic Inceptisols, of low maturity, are well-developed in Msp.	• Relatively simple ichnoassemblage, dominated by *Sk*, *Pa*, *Ta* and Rh • Root traces generally crosscut animal traces.	• In the Heshanggou Formation of Dayulin section. • **Distal terminal fan facies**

File 2. Ichnological information

In this section, all trace fossils encountered (**Figures S2**–**5**) and their size variations **Figures S6**–**7**) are provided herein. Ichnodisparity designation (**Tables S2**–**4**) follows Buatois et al. (2017). Traces from the Shichuanhe section have been documented by Guo et al. (2019), but several new ichnogenera have been found during the ongoing field seasons and are described here (**Figure S3**). Additionally, possible trace maker(s) on land are also discussed, based on paleontological and neoichnological evidence (**Table S5**). Accordingly, an artistic illustration of the early recovered ecosystem on land in North China have been reconstructed (**Figure S8**).

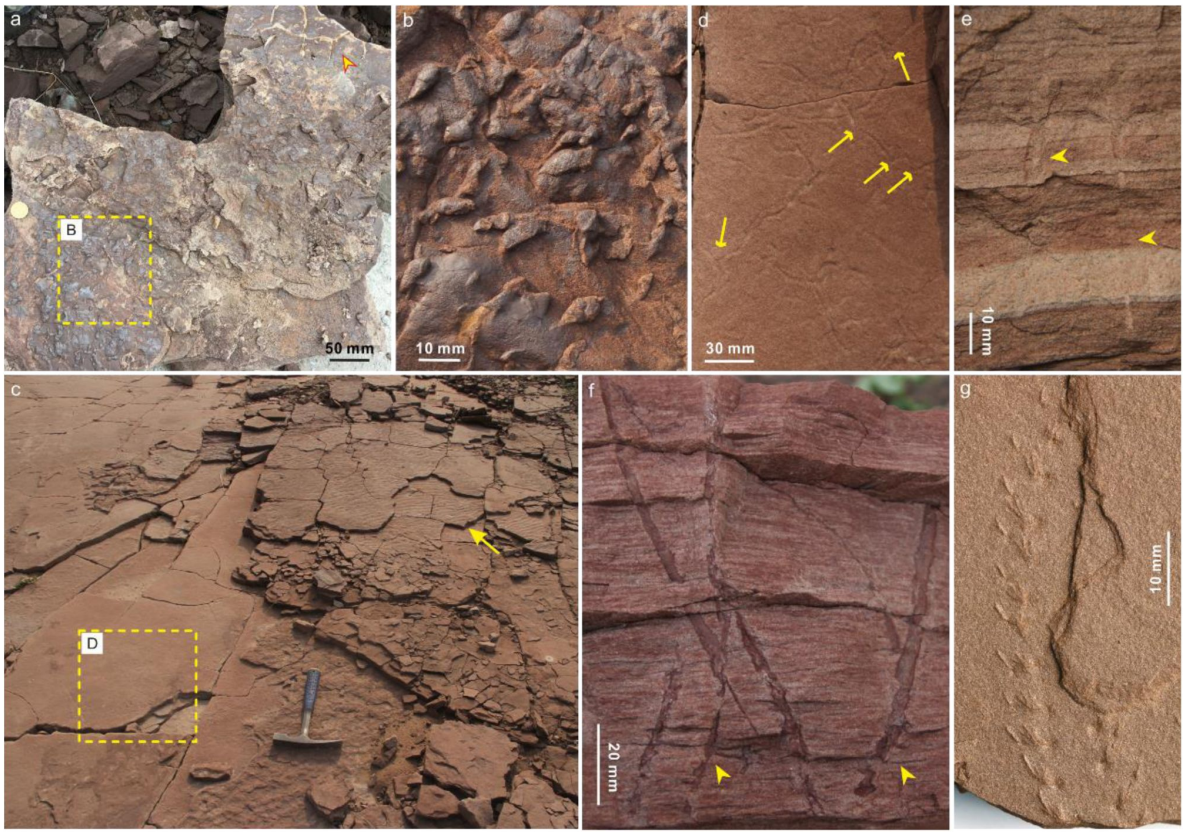

Figure S3.

Ichnofauna from the Liujiagou Formation at Liulin section.

(a-b) Ovate to elongated almond-shaped *Lockeia siliquaria* roughly arranged along a similar direction, fossils were preserved as convex hypichia in sandstone with desiccation cracks (arrow in a). (c-dd) Simple unbranched surficial burrows with sharp turns (arrows in d), self-overcrossing occasionally seen, traces are identified as *Gordia indianaensis* and preserved in rippled sandstone (arrow in c). (e) Vertical *Skolithos linearis* in sandstone. (f) Vertical root traces, showing inconsistent burrow sizes and tiny bifurcations (arrows). (g) *Kouphichnium didactylum* with simple foot imprints and a pusher imprint.

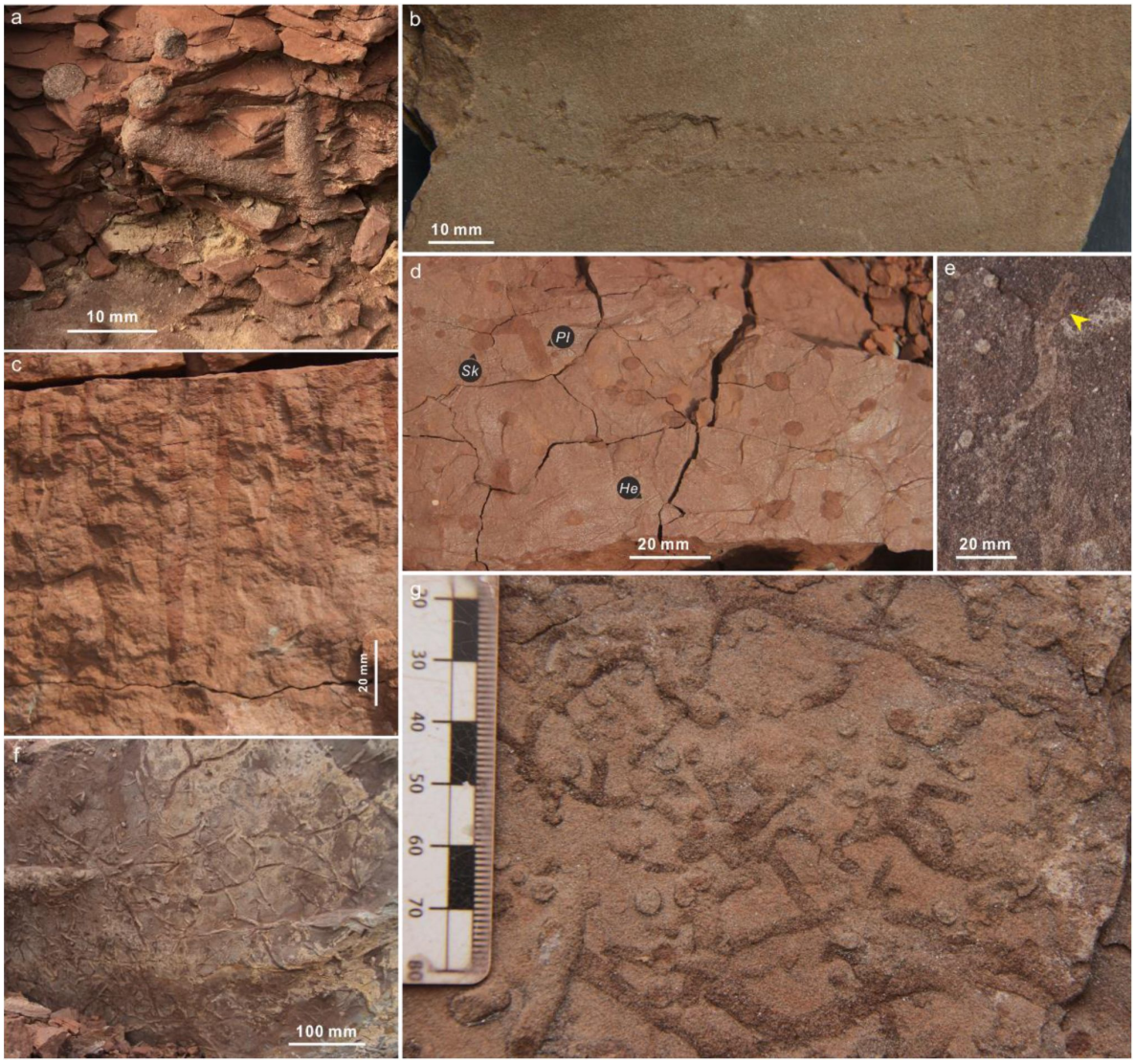

Figure S4.

Ichnofauna from the Heshanggou Formation.

(a) Y-shaped *Psilonichnus* cf. *upsilon*, the branch portion displays similar size with the main tube. FA3 costal mudplain facies at Shichuanhe section. (b) *Diplichnites gouldi*, evenly spaced imprints are comma or elongated and incline to the midline. Fossils preserved in FA3 at Shichuanhe section. (c) High-density simple vertical *Skolithos linearis* at Dayunlin section. (d) Actively filled *Planolites beverleyensis* (*Pl*) pass through surficial Helminthoidichnites tenuis (*He*), which in turn, crosscut by *Skolithos* (*Sk*). Dayunlin section. (e) Horizontal *Taenidium serpentinum*, distance between menisci (arrow) is roughly equal to the burrow width. Dayunlin section. (f) Crowded *Palaeophycus tubularis* preserved on the sole of thick sandstone. Liulin section. (g) Horizontal to inclined, straight to curve, lined *Beaconites coronus* with moderately arcuate menisci. Liulin section.

Figure S5.

Large burrows from the Heshanggou Formation.

(a-b) Horizontal but inclined unlined burrow with elliptical cross sections, branching and terminal chamber were no found. Possible lateral scratches could be seen on the side (Arrows in b). trace fossil is informally assigned to undesigned burrow. Liuin section. (c-e) Large*Beaconites* and other relatively small traces (e.g., *Palaeophycus*) on the rippled siltstone (ripple marks can be seen at the top-right of c). Burrows display meniscus-like portions, comprising of gritty infillings (Arrow in e), akin to *Beaconites* reported from breccia facies in the Devonian (Brück, 1987). Mafang outcrops. (f-h) Vertical to subhorizontal burrows with circular cross sections, filled with calcareous sand. Trace fossils are similar to crayfish burrows (*Camborygma*), although branches, terminal chamber or scratch marks were no found. Hongyatou outcrop. (i-j) In situ preserved *Neocalamites* stems in the lower part of the Heshanggou Formation at Shichuanhe section and Hongyatou outcrop, respectively. Typically, all the stems are associated with *Camborygma* and other burrows and trackways.

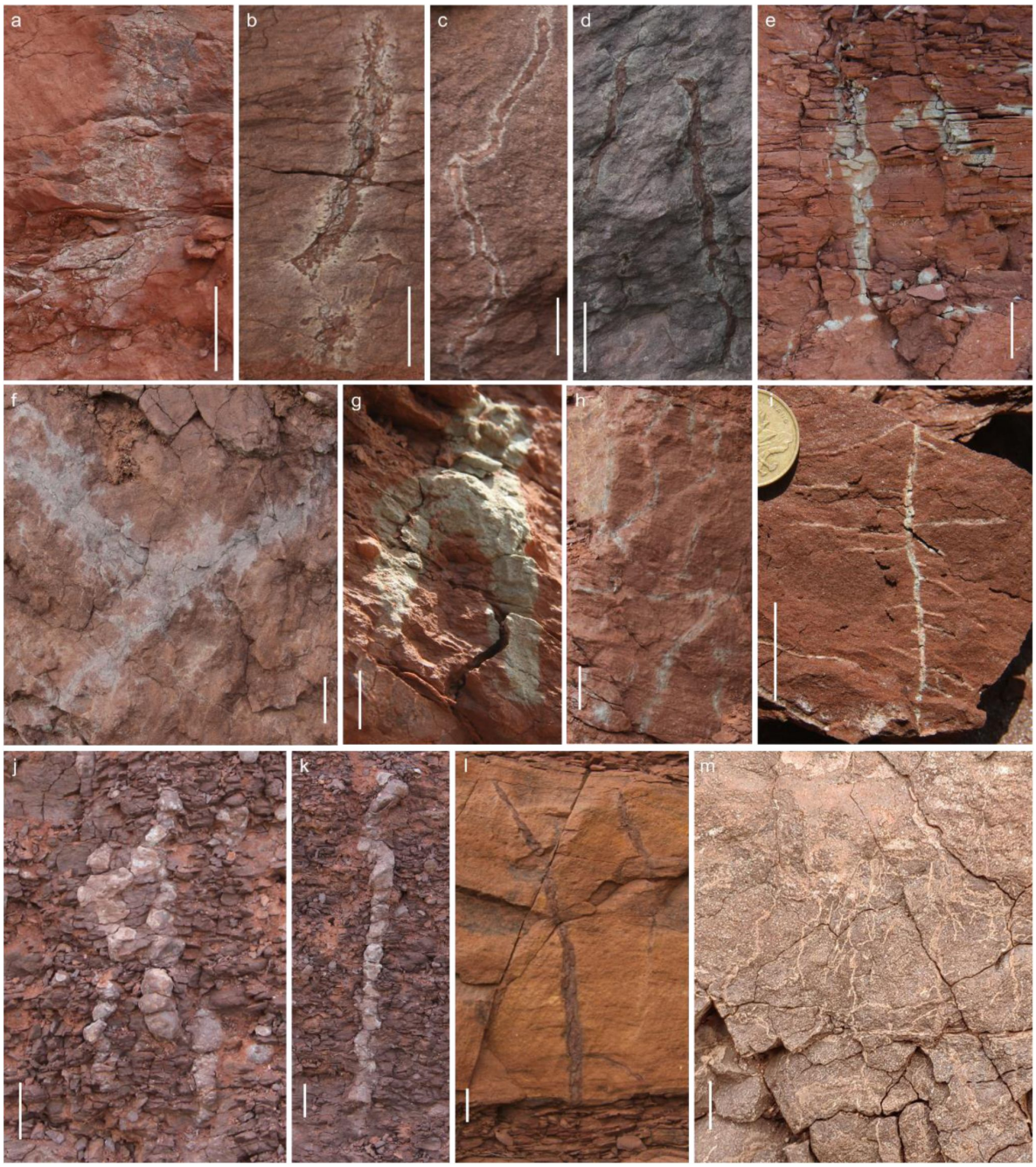

Figure S6.

Root traces from the Heshanggou Formation in studied sections and outcrops.

(a-h) Vertical branched rhizolith with green or pale purple haloes, showing irregular burrow sizes and lateral small rootlets (d, f), Yiyang section. (i) Herringbone-like branched rhizotubules, Yiyang section. (j-k) Vertical tapered unbranched or bifurcated rhiozocretions, Yiyang section. (l) Simple vertical branched roots, Tuncun outcrops. (m) Horizontal small rootlets, Yiyang section. Classification of root traces are based on Klappa (1980) and Kraus and Hasiotis (2006). All scale bars are 20 mm.

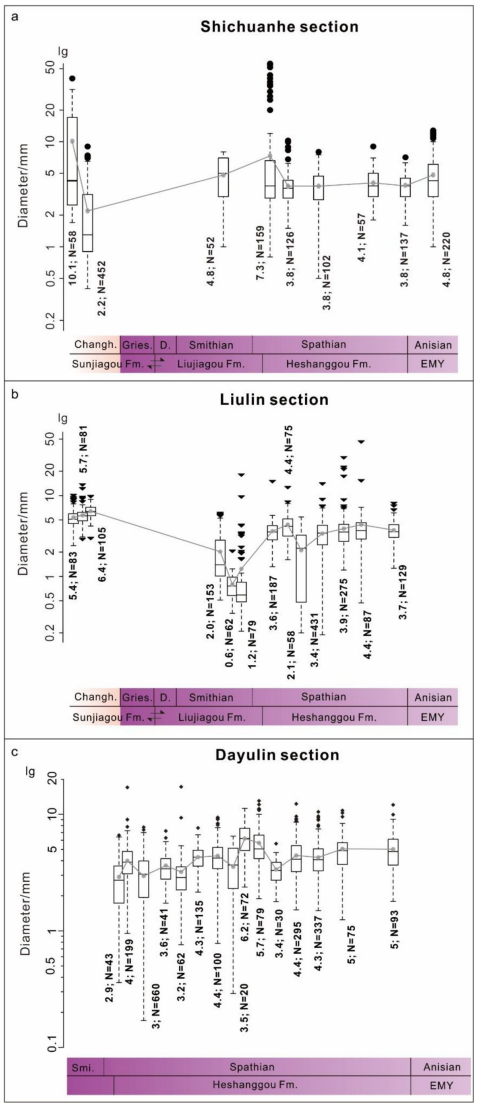

Figure S7.

Size variation of all ichnogenera from there sections.

EMY = Ermaying Formation.

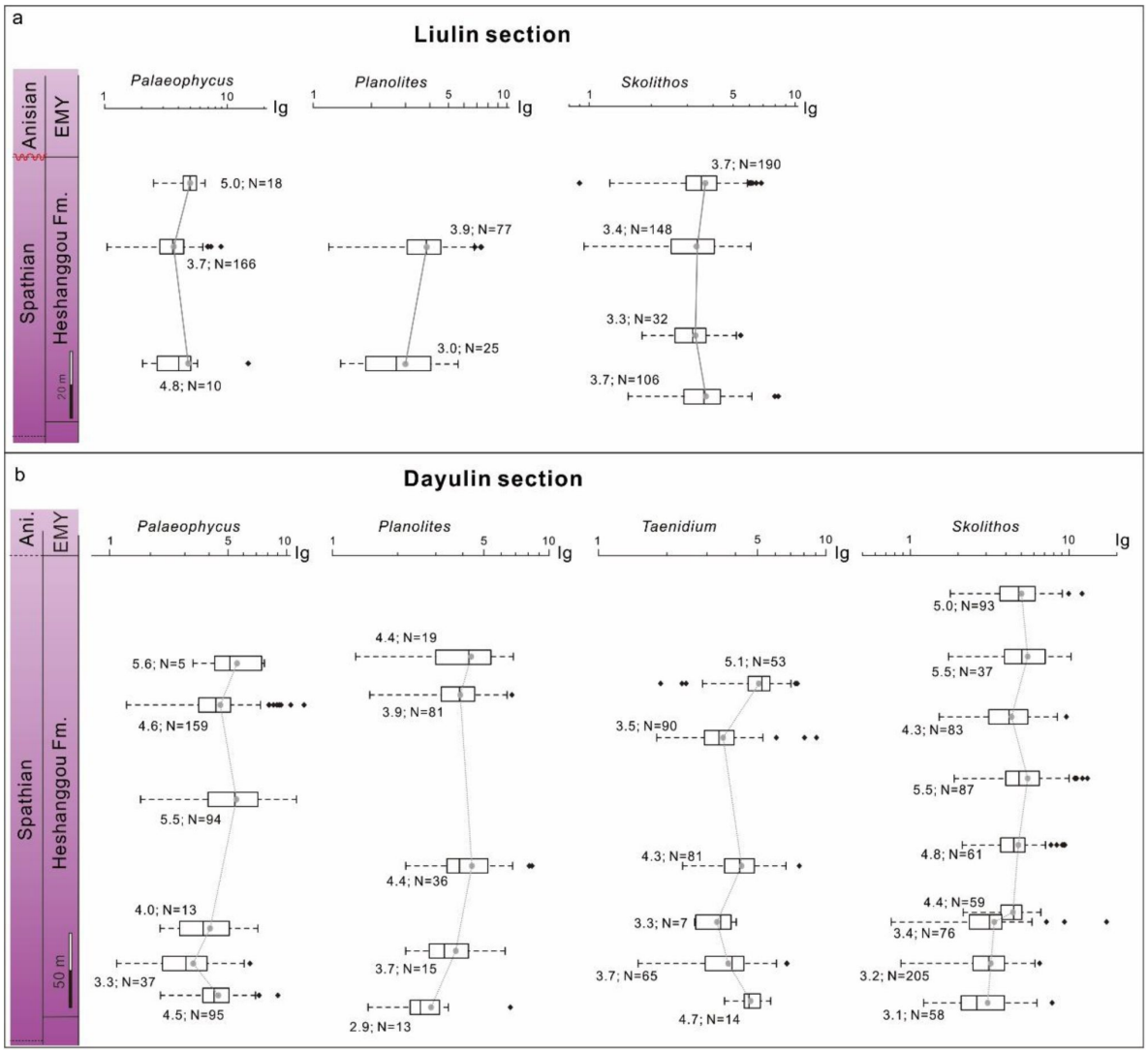

Figure S8.

Size variation of sing ichnogenus from Liulin and Dayulin sections during the Spathian.

EMY = Ermaying Formation.

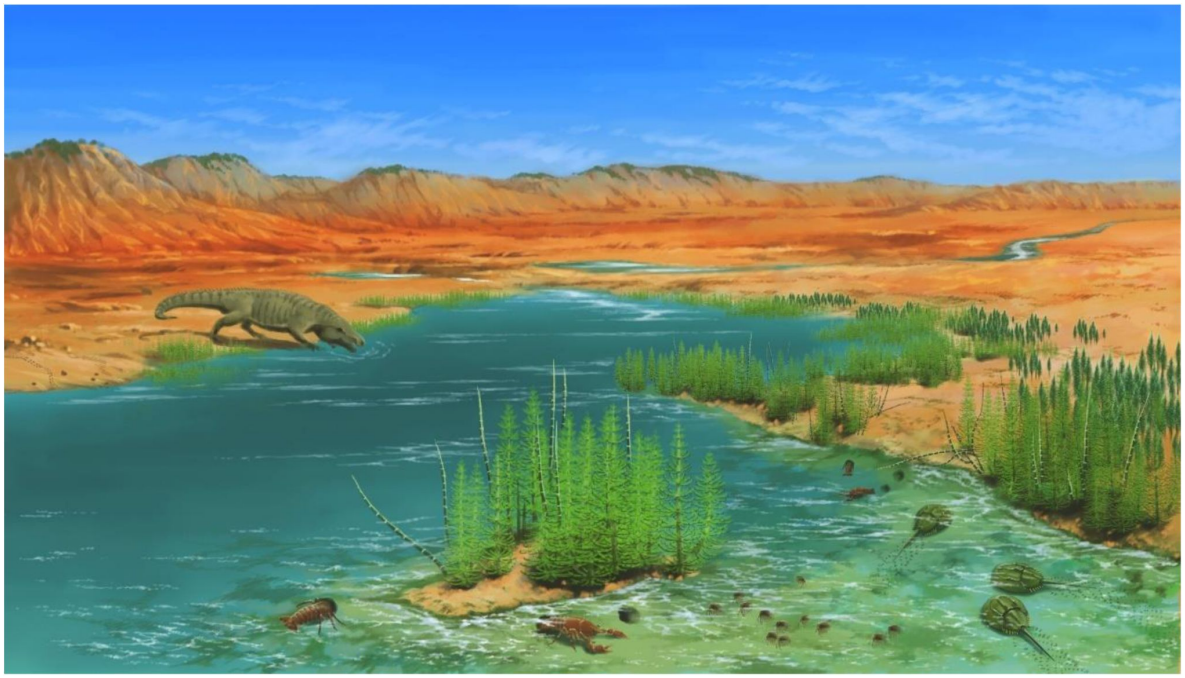

Figure S9.

Reconstruction of the Spathian (Heshanggou Formation) coastal mudplain to alluvial ecosystem in North China.

Plant communities in the coastal mudplain and alluvial facies are depauperated, dominated by *Neocalamites* and *Pleuromeia*, and only diversified at the top of the Heshanggou Formation (late Spathian; Shu et al., 2022). Reoccurrence of plants and tetrapods, coupled with diverse invertebrate, including limuloid, crayfish, spinicaudatan, and insect, etc., reveal reorganization of a relatively complex ecosystem in riverain regions during the Spathian.

Table S2.

List of ichnogenera from the Shichuanhe section, Ichnodisparity designations and Tiering level.

	Ichnodisparity	Ichnogenus	Tier
Sunjiagou Formation	10-Passively filled horizontal burrows	*Palaeophycus*	Shallow-infaunal
	35-Vertical unbranched burrows	*Skolithos*	Deep -infaunal
	50-Maze and boxwork burrows	*Spongeliomorpha*	Shallow-infaunal
	12-Simple actively filled (meniscate) horizontal to oblique	*Taenidium*	Intermediate-infaunal
	1-Simple horizontal trails	*Helminthoidichnites*	Semi-infaunal
	3-Chevronate trails	*Protovirgularia*	Shallow-infaunal
	30-Isolated and serial oval to almond-shaped burrows	*Lockeia*	Semi-infaunal
	Rhizoliths	Rhizoliths	Deep-infaunal
Liujiagou Formation	10-Passively filled horizontal burrows	*Palaeophycus*	Shallow-infaunal
	35-Vertical unbranched burrows	*Skolithos*	Deep-infaunal
	36-Vertical single U- and Y-shaped burrows	*Arenicolites*	Deep-infaunal
		Psilonichnus	Intermediate-infaunal
	52-Simple to complex burrows with terminal chambers	*Camborygma*	Deep-infaunal
		Macanopsis	Intermediate-infaunal
	1-Simple horizontal trails	*Helminthoidichnites*	Semi-infaunal
Heshanggou Formation	6-Trackways and scratch imprints	*Diplichnites*	Surficial
		Monomorphichnus	Surficial
		Kouphichnium	Surficial
	10-Passively filled horizontal burrows	*Palaeophycus*	Shallow to Intermediate-infaunal
	11-Simple actively filled (massive) horizontal to oblique	*Planolites*	Intermediate-infaunal
	12-Simple actively filled (meniscate) horizontal to oblique	*Scoyenia*	Intermediate-infaunal
		Taenidium	Shallow-infaunal
	35-Vertical unbranched burrows	*Skolithos*	Deep-infaunal
	Rhizoliths	Rhizoliths	Deep-infaunal

	Ichnodisparity	Ichnogenus	Tier
Heshanggou Formation	1-Simple horizontal trails	*Helminthoidichnites*	Semi-infaunal
	10-Passively filled horizontal burrows	*Palaeophycus*	Shallow to Intermediate-infaunal
	11-Simple actively filled (massive) horizontal to oblique	*Planolites*	Intermediate to deep- infaunal
	12-Simple actively filled (meniscate) horizontal to oblique	*Taenidium*	Intermediate-infaunal
		Beaconites	Intermediate-infaunal
		Scoyenia	Intermediate-infaunal
	35-Vertical unbranched burrows	*Skolithos*	Deep-infaunal
	36-Vertical single U- and Y-shaped burrows	*Arenicolites*	Deep-infaunal
		Psilonichnus	Intermediate to deep- infaunal
	Rhizoliths	Rhizoliths	Deep-infaunal

Table S3.

List of ichnogenera from the Heshanggou Formation of the Dayulin section, Ichnodisparity designations and tiering level.

Table S4.

List of ichnogenera from the Liulin section, Ichnodisparity designations and tiering level.

	Ichnodisparity	Ichnogenus	Tier
Sunjiagou Formation	10-Passively filled horizontal burrows	*Palaeophycus*	semi-infaunal
	11-Simple actively filled (massive) horizontal to oblique	*Planolites*	Intermediate-infaunal
	12-Simple actively filled (meniscate) horizontal to oblique	*Taenidium*	semi-infaunal
	Rhizoliths	Rhizoliths	Deep-infaunal
Liujiagou Formation	1-Simple horizontal trails	*Helminthoidichnites*	Semi-infaunal
		Gordia	Semi-infaunal
	6-Trackways and scratch imprints	*Kouphichnium*	Surficial
	30-Isolated and serial oval to almond-shaped burrows	*Lockeia*	Shallow to Intermediate-infaunal
	Rhizoliths	Rhizoliths	Deep-infaunal
Heshanggou Formation	6-Trackways and scratch imprints	*Kouphichnium*	Surficial
		Diplichnites	Surficial
	10-Passively filled horizontal burrows	*Palaeophycus*	Shallow to Intermediate-infaunal
	11-Simple actively filled (massive) horizontal to oblique	*Planolites*	Intermediate-infaunal
	35-Vertical unbranched burrows	*Skolithos*	Deep-infaunal
	12-Simple actively filled (meniscate) horizontal to oblique	*Taenidium*	Intermediate-infaunal
		Beaconites	Intermediate-infaunal
	1-Simple horizontal trails	*Helminthoidichnites*	Semi-infaunal
		Gordia	Shallow-infaunal
	Rhizoliths	Rhizoliths	Deep-infaunal

Table S5.

Possible trace producers on land.

Morphology	Ichnogenus	Intepretation
Simple horizontal trails	*Helminthoidichnites tenuis*	• Could be made by arthropods, vermiform animals, or insect larvae (Buatois et al., 1996, 1998).
Passively or actively filled burrow	*Palaeophycus*, *Planolites*	• Probably produced by insects or arthropods (Pemberton and Frey, 1982; Buatois and Mángano, 1993; Keighley and Pickerill, 1995).
Burrows with terminal chambers	*Camborygma*	• Freshwater crayfishes (Hasiotis and Mitchell, 1993; Hasiotis et al., 1993).
Vertical unbranched, single U- or Y-shaped burrows	*Skolithos*,	• Most of the *Skolithos* are smooth, but several specimens display distinct subvertical scratches. • arachnids, coleopterans, crickets, cicadas, bees or annelids can all build such burrows (Schlirf et al., 2001; do Nascimento and Netto, 2019).
	Arenicolites,	• Deeply extended with tiny tubes and wide limb distance. • Burrowed by polychaeta worms, crustaceans or may fly larvaes (Bromley, 1996; Rindsberg and Kopaska-Merkel, 2005).
	Psilonichnus	• Display similar sizes with branches, with bifurcation angle at 15°-45°. • Generally occurred in the Cenozoic marine facies, and constructed by decapod (Frey et al., 1984; de Carvalho, 2016). • Neoichnological investigations show that terrestrial arthropod, such as scorpion, can also produce similar Y-shaped burrows as temporary shelters or permanent dwellings (Hembree, 2016).
Backfilled burrows	*Beaconites* *Scoyenia* *Taenidium*	• Could be made by insects (cicadas, beetle larvaes), millipedes, oligochetes (earthworms) or vermiform on land, based on modern observations (Keighley and Pickerill, 1994; Rodríguez-Tovar et al., 2016; Boyd and McIlroy, 2017).
	? *Beaconites*	• Could be produced by either invertebrate, like arthropods and polychaete worms, or vertebrate, such as reptiles, amphibians (Brück, 1987; Allen and Williams, 1981; Morrissey and Braddy, 2004).
Trackways and scratch imprints	*Diplichnites* *Monomorphichnus*	• Could be left by myriapods or morphological similar arthropods (Bradshaw, 1981).
	Kouphichnium	• Limuloid (i.e., Shu et al., 2018).

Data Availability Statement

All supplementary data related to this paper is available in the end of this manuscript.

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Reviewer #1 (Public review):

Summary:

This is a very well-written paper presenting interesting findings related to the recovery following the end-Permian event in continental settings, from N China. The finding is timely as the topic is actively discussed in the scientific community. The data provides additional insights into the faunal, and partly, floral global recovery following the EPE, adding to the global picture.

Strengths:

The conclusions are supported by an impressive amount of sedimentological and paleontological data (mainly trace fossils) and illustrations.

Weaknesses:

The occurrence of MISS (Microbially Induced Sedimentary Structures) could be discussed more in detail as these provide interesting information directly linked to the delayed recovery of the biota.

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Reviewer #2 (Public review):

Summary:

A rapid recovery of the ecosystems during the late Early Triassic, in the aftermath of the end-Permian mass extinction, is discussed based on different types of fossils.

Strengths:

The combined study of invertebrate trace fossils, tetrapod bones, and plant remains together with their stratigraphic distribution in different sections provides a convincing case to support a rapid recovery as the authors hypothesize.

Weaknesses:

The study is based on three regions with Triassic successions from the North China block. While a first-hand study of other localities of similar age would be ideal, this is of course a difficult task. Instead, the authors provide comparisons with other worldwide regions to build their case and support the initial hypothesis.

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Reviewer #3 (Public review):

Summary:

This manuscript by Guo and colleagues features the documentation and interpretation of three successions of continental to marginal marine deposits spanning the P/T transition and their respective ichnofaunas. Based on these new data inferences concerning end-Permian mass extinction and Triassic recovery in the tropical realm are discussed.

Strengths:

The manuscript is well-written and organized and includes a large amount of new lithological and ichnological data that illuminate ecosystem evolution in a time of large-scale transition. The lithological documentations, facies interpretations, and ichnotaxonomic assignments look okay (with a few exceptions).

Weaknesses:

Some interpretations in Table 1 could be questioned: For facies association FA2 the interpretation as „terrestrial facies with periodical flooding" should be put into the right column and, given the fossil content, other interpretations, such as "marine facies" or "lagoonal environment" with some plant debris and (terrestrial) animal remains washed in, could also be possible. For FA3 the statement "bioturbation is absent" is in conflict with the next statement "strata are moderately reworked". For FA5 the observation of a "monospecific ichnoassemblage" contradicts the listing of several ichnotaxa.

Concerning the structure of the manuscript, certain hypotheses related to the end-Permian mass extinction and the process of the P/T extinction and recovery, namely the existence of a long-persisting "tropic dead zone" are introduced as a foregone conclusion to which the new data seemingly shall be fit as corroborating evidence. Some of the data - e.g. the presence of a supposedly Smithian-age ichnofauna are interpreted as a fast recovery shortening the duration of the "tropic dead zone" episode - but these interpretations could also be interpreted as contradicting the idea of a "dead zone" sensu stricto in favour of a "normal" post-extinction environment with low diversity and occurrence of typical disaster taxa. Due to their large error bars the early Triassic radiometric ages did not put much of a constraint on the age determination of the earliest post-extinction ichnofaunas discussed here.

Considering the somewhat equivocal evidence and controversial ideas about the P/T transition, the introduction could be improved by describing how the idea of a "tropic dead zone" arose against the background of earlier ideas, alternative views, and conflicting data. In the discussion section, alternative interpretations of the extensive data presented here - e.g. proximal-distal shifts in lithofacies with respect to the sediment source, sea level changes, preservation bias, the local occurrence of hostile environments instead of a regional scale, etc. should be discussed, also to avoid the impression that the author's conclusion was driven by confirmation bias.

Contrary to the authors' claim, Figures S7 and S8 suggest that burrow size does not vary much within the studied sections. Size decreases and increases in the Shichuanhe and Liulin sections do not contemporaneously, are usually within the error-bar range, and might be driven by ichnotaxa composition, i.e. the presence or absence of larger ichnotaxa, rather than by size changes in the same ichnotaxon (and producer group). Here the measurement data would be needed as well to check the basis of the authors' interpretations.

Some arthropod tracks assigned here to Kouphichnium might not represent limulid traces but other (non-marine) arthropod taxa in accordance with their occurrence in terrestrial facies/non-marine units of the succession. More generally, the ichnotaxonomy of arthropod trackways is not yet well reserved - beyond Kouphichnium and Diplichnites various similar-looking types may occur that can have a variety of distinct insect, crustacean, millipede, etc. producers (including larval stages).

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