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An exceptionally preserved fossil assemblage from the early Jurassic of Chongqing (China) reveals a complex lacustrine ecosystem

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One of the five greatest mass extinction events in the history of life occurred at the end of the Triassic (~ 201 million years ago), as confirmed by profound loss of life in marine realm. Terrestrial ecosystems were also suffered but the extent of life loss and timing of subsequent recovery remain equivocal, largely because of scarcity of fossil record. Here we report an exceptionally-preserved fossil assemblage, Yuzhou Biota, from the Sinemurian (~ 199–193 Ma), Early Jurassic lacustrine deposits of northern Chongqing, China. The biota documents the first known trophically complex lacustrine ecosystem after the end-Triassic extinction in China, including various representative species ranging from primary consumers (e.g., ostracods, conchostracans, gastropods and bivalves) to large predators (e.g., a variety of jawed fishes and pliosauroids). The most striking feature is its diversified aquatic vertebrates; the hybodontiforms, ceratodontiforms, ptycholepiformes, ginglymodians and pliosauroids from the biota all represent their first occurrences above the Triassic-Jurassic boundary in China. As such, the discovery enriches our understanding of the faunal turnover of aquatic vertebrates following the end-Triassic mass extinction, and provides a novel window on the Early Jurassic lacustrine ecosystems.

The end of Triassic marks one of the five largest extinction episodes in the history of life with a loss of over 50% of the biota at the genus level in both marine and continental realms[1–5]. The cause of this extinction and the subsequent biotic recovery in the Early Jurassic have attracted interests of lots of geologists and palaeontologists, and much works have been done on the Triassic-Jurassic sequences, specifically those from the Newark–Hartford basins of eastern North America, the Bristol Channel Basin of the United Kingdom, the Eiberg Basin of Austria, and the Junggar and Sichuan Basins of China[6–11]. It is suggested that the principal kill mechanism was concomitant changes in climate, atmosphere, and oceans associated with the eruptions of the Central Atlantic Magmatic Province[12–14]. In the Junggar Basin, the abrupt temperature drop following the Triassic 'hothouse' potentially caused bivalves along with some other invertebrates disappeared or became extinct in the late Rhaetian (latest Triassic), and it was not until the Sinemurian (Early Jurassic, when the climate warmed) that the bivalves reappeared with their taxonomic composition distinctly changed[11]. However, because of scarcity of fossils, the faunal turnover of aquatic vertebrates during the Triassic-Jurassic transition remains poorly known in China[7].

Here, we report a new fossil assemblage, named the Yuzhou Biota, from northern Chongqi, China (Fig. 1), which provides a novel window on Early Jurassic vertebrates from the lacustrine ecosystems. Besides plant and invertebrates, a variety of articulated bony fishes, hybodontiform sharks, pliosauroids, and bromalites (coprolites and regurgitalites) have been collected in our recent fieldworks. Impressively, there are several thousands of well-preserved ray-finned fish specimens that represent at least six new species. The ceratodontiform lungfishes are exceptionally preserved, showing an unexpected diversity with detailed anatomical features on both skull and postcranium; by contrast, most of Mesozoic lungfishes were known only by their tooth plates[15–17]. Additionally, the coprolites are three-dimensionally preserved without bioturbation, providing direct evidence of tropic relationships. The rich freshwater bivalves, conchostracans and ceratodontiforms are unambiguous indicators of freshwater environments, and marine organisms (e.g., ammonoids) are lacking. The whole fossil assemblage

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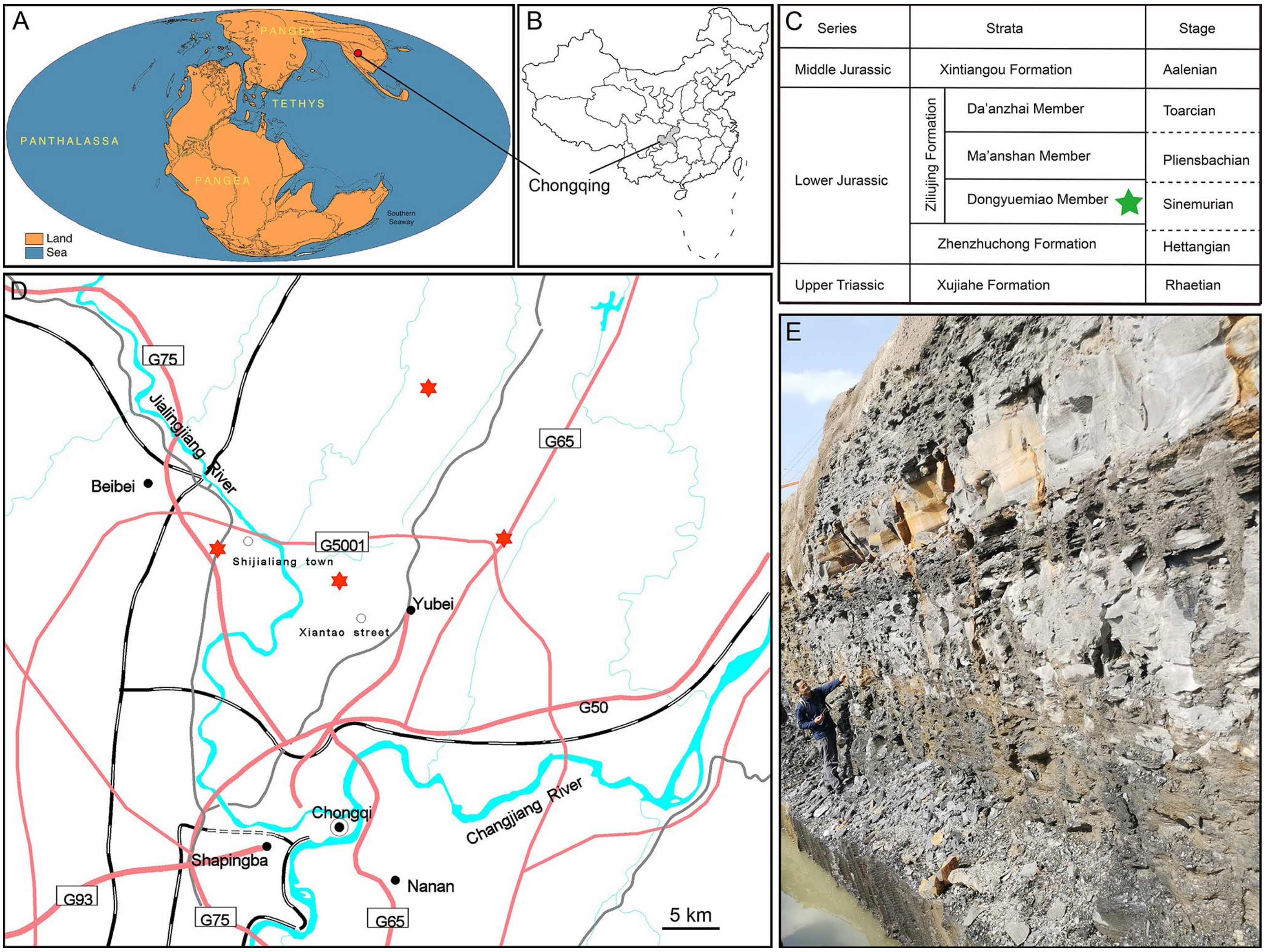

Fig. 1. Geological context and outcrop of the Yuzhou Biota. (**A**-**C**), Early Jurassic and present-day locations of the studied exposures. The Early Jurassic palaeogeographic map (**A**) was modified from ref.[19] (https://www.earthbyte.org/). The fossil localities are indicated by red stars. The maps B and C are created using Baidu Map (https://map.baidu.com) and Adobe CS (https://www.adobe.com/). (**D**), Stratigraphic division of Late Triassic-Middle Jurassic deposits in Chongqing with a green star indicating the position of the Yuzhou Biota. (**E**), The outcrop yielding the Yuzhou Biota at the Huashigou locality in Chongqing, China. Figure created by G.-H. Xu and Q.-D. Wang.

represents a diverse and trophically complex lacustrine ecosystem rarely known in the Sinemurian (Early Jurassic).

Geologic setting and age of the Yuzhou Biota

The fossil localities were located at the eastern margin of the Sichuan Basin, which was a large craton basin of about 260,000 km^2 on the western Upper Yangtze Platform[18,19]. Coal-swamp to lacustrine-fluvial deposits were developed on the basin during the Triassic-Jurassic transition, including the Late Triassic Xujiahe Formation and the Early Jurassic Zhenzhuchong and Ziliujing Formations[10]. Specimens of the Yuzhou Biota were found from the basal unit (Dongyuemiao Member) of the Ziliujing Formation (Fig. 1D), characterized by gray–black shales intercalated shell limestones and argillaceous limestones. The fossil beds are interpreted to have been deposited in semi-deep to deep lakes, where oxygen-depleted environments frequently occurred[18]. The upper two units of the Ziliujing Formation, Ma'anshan and Da'anzai Members, are well constrained to Pliensbachian–Toarcian, according to palynological and ostracod data and Re-Os dating[20,21]. The Sinemurian-Pliensbachian boundary event (192.9 Ma), a global perturbation of the carbon cycle, has been recorded near the top of the Dongyuemiao Member, as evidenced by a prominent (8‰) negative carbon-isotope excursion[21]. Below this boundary, the main part of the Dongyuemiao Member is pointed to the Sinemurian, supported by palynological data[21] and an electron spin resonance dating (~ 199 Ma[22]). The underlying Zhenzhuchong Formation, originally referred to as the bottom unit of the Ziliujing Formation, represents the earliest Jurassic (Hettangian to earliest Sinemurian) sequences that overly the Late Triassic Xujiahe Formation[10]. The fossil assemblage of the Yuzhou Biota was collected from shell limestones and argillaceous limestones at the lower and middle parts of the

Dongyuemiao Member, and is consequently constrained to Sinemurian. The biota represents one of the oldest known trophically complexed lacustrine ecosystems following the end-Triassic mass extinction.

Results

Taxonomic composition

The Yuzhou Biota showed a diversified fossil assemblage, including ray-finned fishes (actinopterygians), lungfishes (ceratodontiform dipnoans), hybodontiform sharks, pliosauroid plesiosaurians, ornithischians, bivalves, ostracods, gastropods, plants, and bromalites (Figs. 2 and 3). Among them, the most common

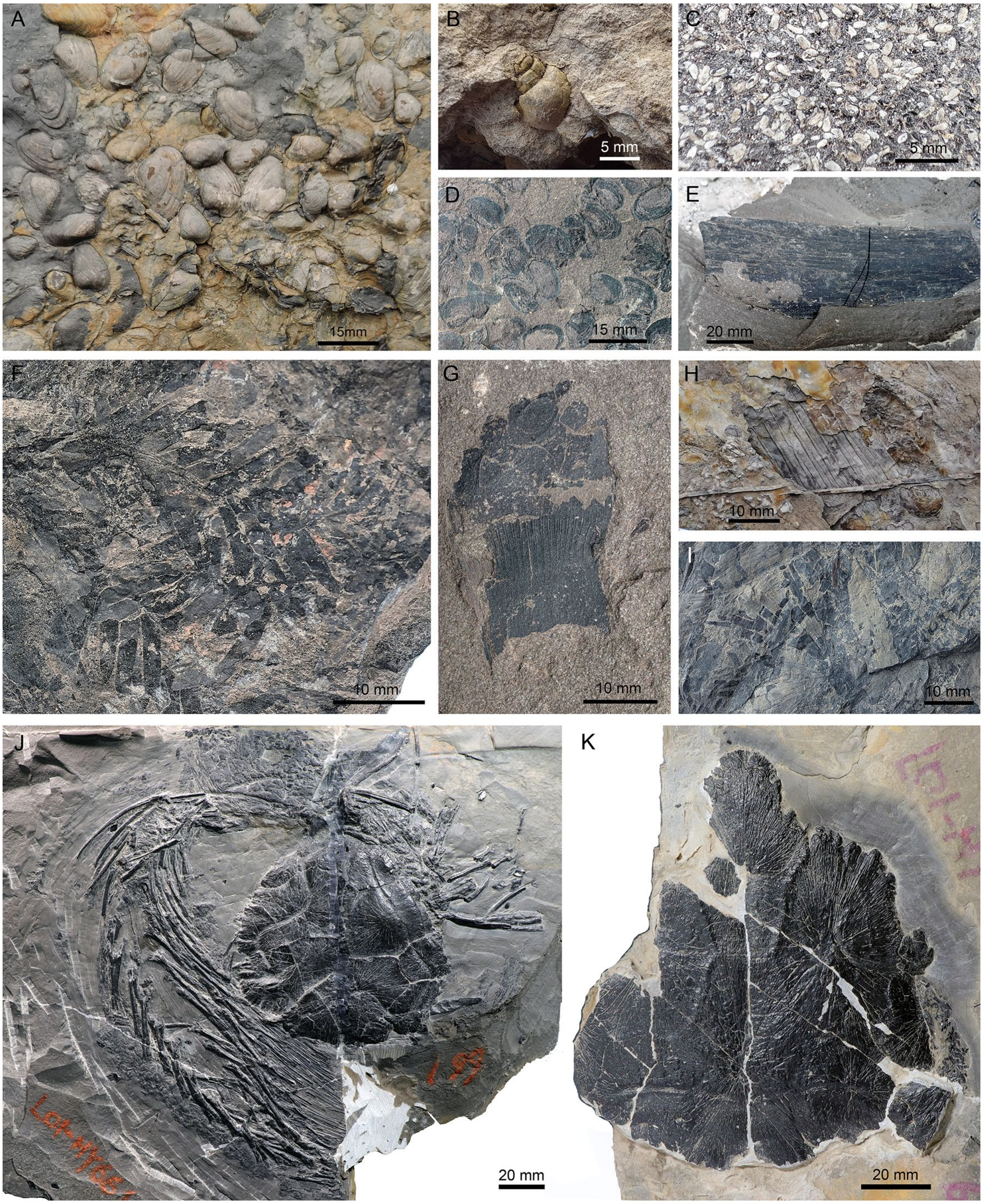

Fig. 2. Invertebrates, plants and lungfishes from the Yuzhou Biota. (**A**), Bivalves, SSGT L03-133. (**B**), Gastropod *Lioplacodes orientalis*, SSGT L03-134. (**C**), Conchostracans, SSGT JXH259. (**D**), Ostracods, SSGT JXH258. (**E**–**I**), Plants. (**E**), SSGT HSZ03. (**F**), Bennettitales (*Nilssonia*), SSGT L01-HY1367. (**G**), Equisetites, SSGT CHS2331. (**H**), SSGT L01-HY108. (**I**), Ginkgoales (*Baiera*), SSGT L01-HY1368. (**J**, **K**), Ceratodontiform indet. (**J**), SSGT L01-HY-661. (**K**), SSGT L01-HY-654.

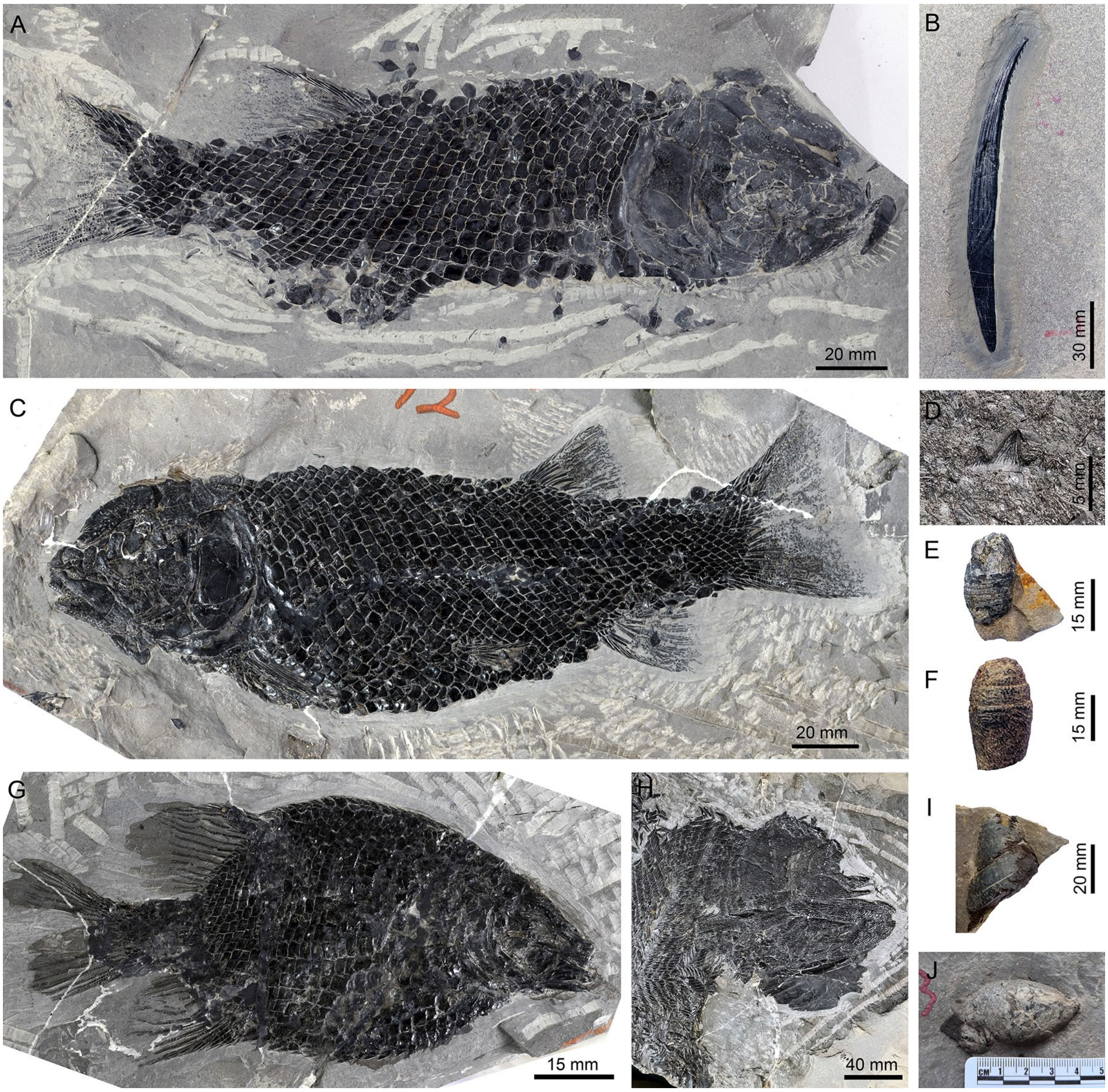

Fig. 3. Actinopterygii, Hybodontiformes and coprolites from the Yuzhou Biota. (**A**), Ginglymodi indet., SSGT JK062. (**B**), Hybodontiform dorsal fin-spine, SSGT L01-HY224. (**C**), Ginglymodi indet., SSGT L01-HY892. (**D**), Hybodontiform tooth, SSGT TX01. (**E**, **F**, **I**, **J**), Coprolites. (**E**), SSGT CQ-YF02. (**F**), SSGT CQ-YF04. (**I**), SSGT L01-HY1011. (**J**), SSGT L01-HY283. (**G**) Ginglymodi indet., SSGT JK004. (**H**) Ptycholepiformes indet., SSGT JK029.

invertebrates, bivalves (Fig. 2A), are particularly abundant from the shell limestones at the lower part of the Dongyuemiao Member with 24 species of *Pesudocardinia* and several species of *Tutuella*, *Sibireconcha*, *Cuneopsis*, *Kijja* and *Acyrena* recognized[23]. Other invertebrates (Fig. 2B–D) include three species of ostracods (*Darwinula incurve*, *D. sarytirmenensis*, *Metacypris* sp.), some conchostracans (*Palaeolimnadia* sp.) and at least a gastropod (*Lioplacodes orientalis*). Additionally, 20 species in 14 genera of plant fossils have been found[24,25], including mainly ferns, cycads, sphenopsids, ginkgoales and conifers (Fig. 2E–I). The vertebrates, highlights of our recent findings, are introduced specially below.

Actinopterygians are the main component of vertebrates in the biota, represented by several thousand articulated specimens. They are taxonomically rich, including basal actinopterygians (e.g., Ptycholepiformes; Fig. 3H)) and crown neopterygians (e.g., Ginglymodi). There are two species of ptycholepiforms, showing differences on shapes of cranial bones. The largest specimen reaches a body length of ~ 0.7 m, documenting the largest bony fish known so far from the biota. Three ginglymodian species have been identified with differences on cranial bones, jaws, body shape and pterygial formula (Fig. 3A, C, G). From their body shape, the ginglymodians show two ecomorphological types resembling the conditions in Triassic kyphosichthyids and semionotids[26,27]: one with an elongated and fusiform body (Fig. 3A, C), and the other a short and deep body (Fig. 3G). The fusiform-bodied form has a maximal body length of ~ 0.5 m, and the deep-bodied form a maximal body length of ~ 0.2 m. Additionally, at least a stem teleost has been found (Fig. 4A, B, E), resembling the Early Jurassic *Dorsetichthys* from Europe[28] in several aspects, such as a frontal acutely tapering anteriorly,

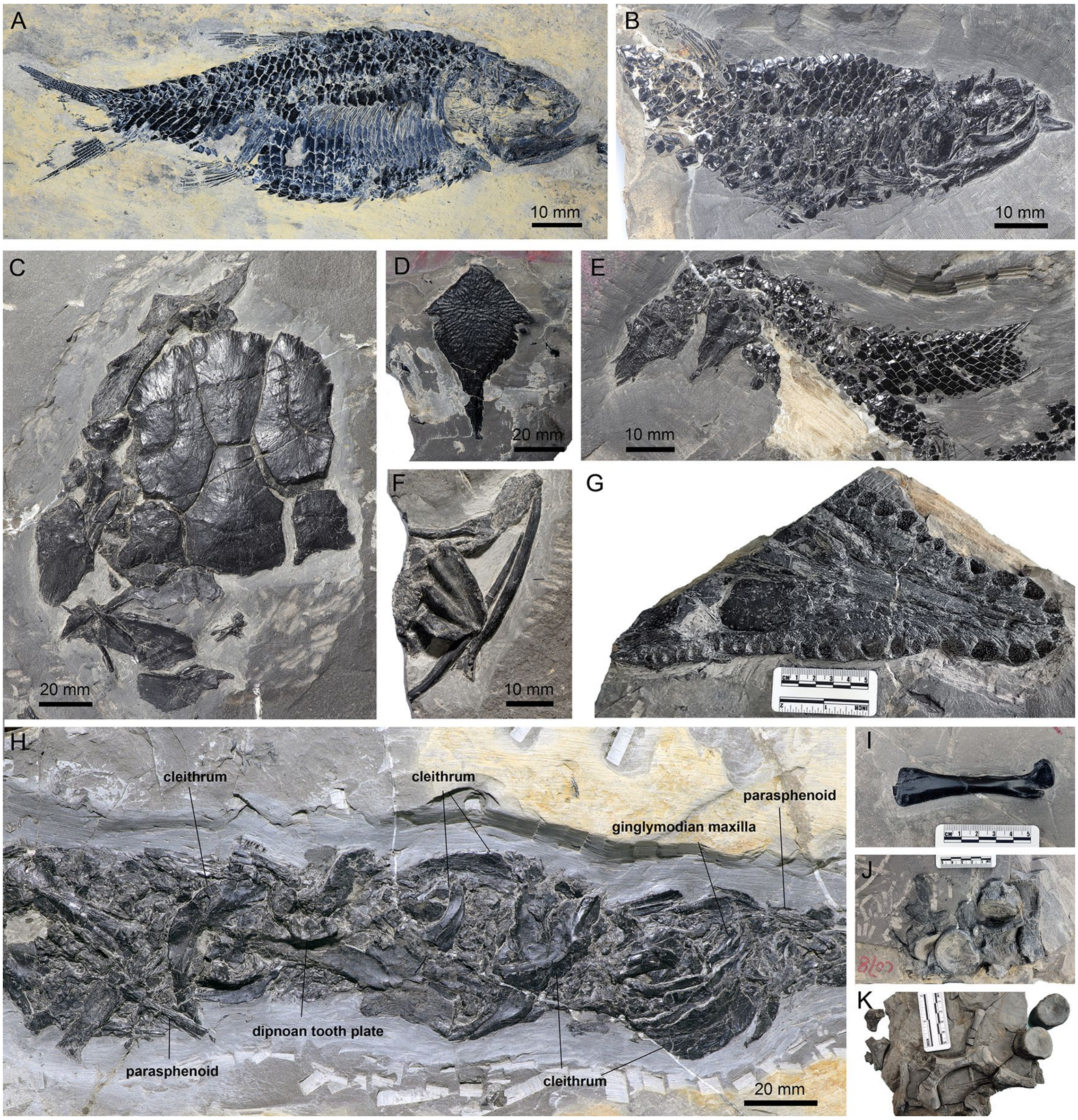

Fig. 4. Bony fishes, reptiles and regurgitalites from the Yuzhou Biota. (**A**, **B**, **E**), Teleostei indet. (**A**), SSGT L01-HY269-2. (**B**), SSGT L01-HY749. (**E**), SSGT JXL1062. (**C**, **D**, **F**), Ceratodontiform indet. (**C**), SSGT THS2715. (**D**), SSGT TXH132. (**F**), SSGT THS2716. (**G**, **J**, **K**), Pliosauroid *Bishanopliosaurus youngi*. (**G**), SSGT T035. (**J**), SSGT C078. (**K**), SSGT JHSY60. (**H**), Regurgitalite, SSGT L01-HY709. (**I**), Ornithischia indet., SSGT L01-HY999.

a triangular and mobile premaxilla, and ganoid scales of lepisosteoid type with smooth surface and posterior margin. It is the smallest ray-finned fish from the biota with a body length of ~ 0.13 m.

Lungfishes are another important component of the biota (Figs. 2J and K and 4C, D and F). Besides isolated tooth plates, there are several articulated specimens. They show an unexpected diversity of at least three species of ceratodontiforms that differ in skull roofing bones. With an estimated body length of ~ 0.5 m, one specimen (Fig. 2J) even shows morphologic details on both skull and postcranium (including pectoral girdle, axial skeletons, fins and scales), which documents the most complete lungfish fossil known in the Jurassic. In Asia, non-dental cranial materials of Mesozoic lungfishes were previously reported from the Late Triassic and Middle Jurassic of Kyrgyzstan[29] and latest Jurassic (or Early Cretaceous) of Thailand[17], and little information was presented by them on the postcranium.

Hybodontiform sharks are the only known chondrichthyans from the Yuzhou Biota, represented by some dorsal fin-spines and teeth (Fig. 3B, D). The fin-spine shows a distal curvature in lateral view with more than 20 denticles on its posterior wall. The outer surface of the spine is striated with 4 or 5 longitudinal ridges on each side. The fin-spines have a maximal depth of 0.17 m in completely preserved specimens. Deduced from the ratio of fin-spine to body length of the Late Jurassic hybodontiform *Asteracanthus ornatissimus* based on articulated specimens from Europe[30], the new hybodontiforms likely have a maximal body length of ~ 1 m. The tooth has a large central cusp and one or two pairs of shorter cusplets with many ridges extending from crown root to the cutting ridge of the cusp and cusplets (Fig. 3D).

The freshwater plesiosaurian remains, including part of skull, upper jaw, vertebrae, rids, girdles have been found (Fig. 4G, J, K). They are tentatively referred to the pliosauroid *Bishanopliosaurus youngi* from the same fossiliferous level in Chongqing[31]. The holotype is an incomplete postcranial skeleton collected at the Bishan locality, and the individual was estimated to have a body length of 4 m[32]. The new discovery provides addition materials for studying this poorly known taxon.

A small-sized ornithischianan dinosaur, represented by a nearly complete left femur (Fig. 4I), has been found. The femur, 93 mm in total length, was probably derived from an individual that was serendipitously washed into the lake from nearby terrestrial habitats. Two morphological characters, a broad, wing-like anterior trochanter and a pendent fourth trochanter, allow an unambiguous assignment of the taxon into ornithischian dinosaurs (taxonomic identification given by X. Yao and X. Xu). The femur of the new ornithischianan is reminiscent of that of the Late Triassic *Eocursor parvus* from South Africa; the latter taxon is estimated to be a fast runner with a body length of ~ 1 m[33]. Given the potentially close relationships between them, the discovery likely represents a south to north dispersal event of this ornithischian lineage on the Pangea.

There are at least four coprolite morphotypes, including a non-spiral form and three spiral forms that differ in shape and internal structure (Fig. 3E, F, I, J). Ostracods are very common in the spiral coprolites. It was suggested that the spiral coprolites were produced by vertebrates with spiral valves, e.g., chondrichthyans, sarcopterygians, and non-teleostean primitive actinopterygians; sharks produced heteropolar spiral coprolites, non-teleostean bony fishes amphipolar spiral coprolites, and tetrapods and teleosts non-spiral coprolites[34,35]. In the Yuzhou Biota, accordingly, the heteropolar spiral coprolites were most likely produced by hybodontiform sharks, amphipolar spiral coprolites by ceratodontiforms, ptycholepiforms or ginglymodians, and non-spiral forms by plesiosaurians or stem teleosts. Additionally, regurgitalites have also been found. The longest regurgitalite (~ 0.3 m) is presented as a form of accumulations of multiple parasphenoids, jaws, hyomandibula and cleithrae of ginglymodian fishes and tooth plates of lungfishes (Fig. 4H). It likely represents orally ejected waste rather than decayed specimens or physical concentrations because of the selectivity of its composition, which consists primarily of indigestible teeth, cranial and girdle bones. Considering its large size, this would be produced by pliosauroid plesiosaurians.

Discussion

The present fossil evidences show that the Yuzhou Biota is trophically complex, including various representative species ranging from primary consumers to large predators (Fig. 5). The ostracods, conchostracans, gastropods and bivalves can be considered as primary consumers, likely feeding on algae, planktons and decaying organic matter. The primary producers, charophyte algae, have been found from the Early Jurassic (Hettangian-Sinemurian) Yimen Formation in Xichang of Sichuan[36], and their presence from the Dongyuemiao Member is highly possible but needs further microfossil analyses. The jawed fishes from the biota are likely predators. Among them, the bony fishes could generally prey small-sized invertebrates such as ostracods and conchostracans. This predator-prey relation is indicated by fish coprolites, in which ostracods are very common. Besides conchostracans and ostracods, the lungfishes could prey some hard-shelled organisms because their adults lack marginal teeth and rely on palatal dental plates for crushing food[15]. The hard-shelled preys would include gastropods and bivalves, which are very rich from the biota. The hybodontiforms from the biota have tearing-type dentition, similar to that in *Egertonodus basanus* and *Hybodus parvidens*[37]; according to Underwood and Rees[38], hybodontiforms with this type of dentition probably preyed largely on small bony fishes. The pliosauroid plesiosaurians are at the apex of trophic network of the biota. Indicated by the possible bromalites, their preys

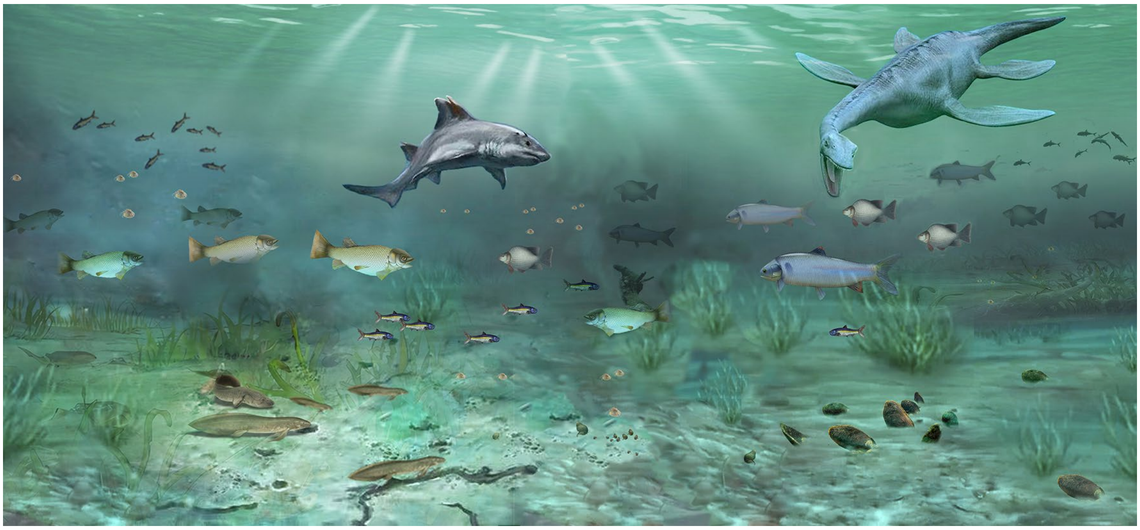

Fig. 5. Artistic reconstruction of the Yuzhou Biota.

could be mainly ginglymodians and lungfishes. Besides China, freshwater plesiosaurians were also known from England, Australia and Canada, although the majority of this clade lived in marine environments[31]. Previous studies suggested that freshwater environments might serve as refugia for these aquatic reptiles[39].

The Sinemurian Yuzhou Biota represents the first known trophically complex lacustrine ecosystem after the end-Triassic extinction in China. The most striking feature is its diversified aquatic vertebrates. The hybodontiforms, ceratodontiforms, ptycholepiformes, crown-neopterygians and pliosauroids from the biota all represent their first occurrences above the Triassic-Jurassic boundary in China. By contrast, the earlier, Hettangian lacustrine and fluvial deposits in China are barren of aquatic vertebrates. The vertebrate assemblages from the Hettangian continental realm are only characterized by the dinosaur fauna from the Dianzhong Basin of Yunnan[40,41], and no bony or cartilaginous fishes have been found from this interval in China. The macrofossils from the Zhenzhuchong Formation (Hettangian to earliest Sinemurian) in the Sichuan Basin are less diversified, represented by some plants and a few dinosaurs with some bivalves and ostracods from the upper part of the formation[10]. In the Hettangian to Sinemurian lacustrine and fluvial deposits (Badaowan Formation) of the southern Junggar Basin, vertebrates are only indicated by dinosaur tracks, and aquatic vertebrates are lacking; invertebrates are also scarce in the Hettangian, and bivalves and other invertebrates did not occur until the middle Sinemurian[7,11].

It is particularly worth mentioning the discovery of exceptionally preserved ceratodontiforms from the Yuzhou Biota. Previously, ceratodontiforms from the Triassic-Jurassic transition of China were represented only by isolated tooth plates sporadically from the Late Triassic, late Pliensbachian and Late Jurassic[42–45], and no record was known in the Sinemurian. The new findings fill the gap and further document the first known articulated lungfish fossils in the Early Jurassic. As far as we known, lungfishes based on articulated specimens were lacking in the Early Jurassic worldwide. Therefore, the new ceratodontiforms from the Yuzhou Biota provide valuable evidences for investigating the poorly unknown diversification of lungfishes in this epoch. Additionally, the hybodontiform fossil (an egg case of *Palaeoxyis*) from the late Pliensbachian Sangonghe Formation of the southern Junggar Basin was the previously first record of this clade in the Jurassic of China[7], and others are younger[46,47]. The new findings of hybodontiform dorsal fin-spines and teeth from the Yuzhou Biota extend the record of this clade back into the Sinemurian, documenting the first freshwater hybodontiforms known from the Jurassic of China. Moreover, the ginglymodian fossils from the Yuzhou Biota also represent the first freshwater record of this clade in China. As mentioned above, these Jurassic ginglymodians showed two ecomorphological types; it was suggested that the deep-bodied ginglymodians likely had a better performance in precise maneuvering than the fusiform-bodied forms[26,27].

In taxonomic diversity, the ichthyofauna from the Yuzhou Biota is comparable with the Early Jurassic (late Hettangian to Sinemurian) ichthyofaunas from the United States. The best-preserved Hettangian ichthyofaunas in the United States are from the Shuttle Meadow and East Berlin Formations in the Hartford basin, which have yielded ptycholepiforms, redfieldiiforms, semionotiform ginglymodians and coelacanths[48]. The Hettangian Lake Dixie ichthyofauna from the Whitmore Point Member of the Moenave Formation in Utah, southwestern United States is also taxonomically rich, including a hybodontiform, a ceratodontiform, a coelacanth, a 'palaeonisciform' and several semionotiforms[49,50]. The Sinemurian ichthyofaunas from the United States, e.g., the Kayenta ichthyofauna, are relatively less diversified; they have yielded hybodontiforms, ceratodontiforms and ginglymodians[47]. Compared with them, the Yunzhou Biota has similar taxa referred to Hybodontiformes, Ceratodontiformes, Ptycholepiformes and Ginglymodi; these four fish lineages appear cosmopolitan in the Early Jurassic lacustrine ecosystems. It resembles the Sinemurian ichthyofaunas from the United States in the absence of redfieldiiforms and coelacanths. Strikingly, the Yunzhou Biota is more diversified in having stem teleosts and plesiosaurians that are unknown from the late Hettangian to Sinemurian lacustrine ecosystems in the United States. Last, it is worth adding that the Yuzhou Biota remains incompletely sampled and hundreds of collected specimens are unprepared yet. The conducting preparations of more specimens will reveal an even higher taxonomic diversity of this biota. Further detailed studies of this fossil assemble would provide more information on the biological recovery of the Early Jurassic lacustrine ecosystems.

Methods

All specimens illustrated in this contribution are stored in the fossil collections of the Southeast Sichuan Geological Team (SSGT), Chongqing Bureau of Geology and Minerals Exploration in Chongqing, China. The specimens were mechanically prepared with pneumatic airscribe or sometimes with sharp steel needles. They were photographed with a digital camera (Canon EOS 800D).

Data availability

All data generated or analysed during this study are included in this published article.

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Author contributions

X.G.,R.T. and Wang.Q. designed the research, X.G. wrote the main manuscript text, X.G. and Wang.Q. prepared figures, and X.G. and M.X. did taxonomic classification. All authors reviewed the manuscript.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

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