Acta Geologica Sinica (English Edition), 2022, 96(4): 1115–1135

Special Paper for 100th Anniversary

The Shishugou Fauna of the Middle–Late Jurassic Transition Period in the Junggar Basin of Western China

1922—2022

XU Xing[1, 2, *], James M. CLARK[3, *], David A. EBERTH[4, *] and Philip J. CURRIE[5]

[1] *Centre for Vertebrate Evolutionary Biology, Yunnan University, Kunming 650500, China*
[2] *Key Laboratory of Vertebrate Evolution and Human Origins, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China*
[3] *Department of Biological Sciences, George Washington University, Washington DC, 20052, USA*
[4] *Royal Tyrrell Museum of Palaeontology, Box 7500, Drumheller, Alberta T0J 0Y0, Canada*
[5] *Department of Biological Sciences, University of Alberta 116 Street and 85 Avenue, Edmonton, AB T6G 2R3, Canada*

Abstract: The Middle–Late Jurassic transition period is a critical period for the evolution of terrestrial vertebrates, but the global fossil record from this time is relatively poor. The Shishugou Fauna of this period has recently produced significant fossil remains of dinosaurs and other vertebrate groups, some representing the earliest known members of several dinosaurian groups and other vertebrate groups and some representing the best-known specimens of their group. These discoveries are significant for our understanding of the origin and evolution of several vertebrate lineages. Radiometric dating indicates that the fauna is aged approximately 159–164 Ma. Comparisons with other similarly-aged terrestrial faunas such as Shaximiao and Yanliao show both taxonomic similarities and differences between these faunas and indicate that the Junggar deposits might have preserved the most complete vertebrate fossil record for a Middle–Late Jurassic Laurasian terrestrial fauna.

Key words: Middle–Late Jurassic, Shishugou Fauna, Shishugou Formation, terrestrial ecosystem, Shaximiao, Yanliao, Junggar Basin

Citation: Xu et al., 2022. The Shishugou Fauna of the Middle–Late Jurassic Transition Period in the Junggar Basin of Western China. Acta Geologica Sinica (English Edition), 96(4): 1115–1135. DOI: 10.1111/1755-6724.14996

1 Introduction

China is home to three celebrated dinosaur faunas (Fig. 1) from the otherwise poorly known Middle-Late Jurassic transition – the Shaximiao Fauna (equivalent to the widely known Dashanpu Fauna in Zigong, Sichuan or the *Shunosaurus* + *Mamenchisaurus* fauna in Sichuan) preserved in the Shaximiao Formation (previously called Upper and Lower Shaximiao formations) in Sichuan and Chongqing (Peng et al., 2005), the Yanliao (Daohugou) Biota preserved in the Haifanggou/Longmen and Tiaojishan/Lanqi/Jiulongshan formations of Inner Mongolia, Liaoning and Hebei (Zhou et al., 2010; Sullivan et al., 2014; Xu et al., 2016), and the Shishugou Fauna preserved in the Shishugou Formation of Xinjiang (Clark and Xu, 2009b; He et al., 2013). The Shishugou Formation was the source of the first dinosaur collected for scientific study from any of these formations, in 1930, but due to its remote location in the far western reaches of the Gobi Desert the initial discovery was not followed up until the 1980s when oil exploration made travel to the area easier (Zhao et al., 1987a). The Shaximiao Formation was the first of these to be systematically developed starting in the 1950s, producing the *Mamenchisaurus* sauropod fauna and culminating in the construction of the world-renowned Zigong Dinosaur Museum in Dashanpu (Peng et al., 2005). The Yanliao Biota is famous for the preservation of theropod dinosaurs with feathers, and has been exploited only relatively recently (Zhou et al., 2010; Sullivan et al., 2014; Xu et al., 2016).

The Shishugou Formation crops out in the eastern and western parts of the Junggar Basin north of the Tian Shan (the Mountains of Heaven), but significant fossil vertebrates are known only in the eastern part. Comprising 380 meters of fluvial sediments, the formation name (*shí*, rock; *shù*, tree; *gōu*, wash) derives from the abundant remains of silicified tree trunks, including some preserved vertically with roots intact, mostly of the wood form genus *Agathoxylon* (Hinz et al., 2010). The lower part of the formation has been distinguished as a separate unit, the Wucaiwan Formation (Zhao et al., 1987a), but the distinction is no longer recognized (see below). The age of the formation has long been considered to span the Middle –Upper Jurassic boundary, and radiometric dating and a revision of the time scale now place nearly all of the formation in the lower Upper Jurassic, and more specifically in the Oxfordian.

Fossils are known mainly from three areas of eastern

* These authors contribute equally to this study.

Corresponding authors. E-mail: xu.xing@ivpp.ac.cn (XU X.), jclark@gwu.edu (J. CLARK)

http://www.geojournals.cn/dzxbcn/ch/index.aspx; https://onlinelibrary.wiley.com/journal/17556724

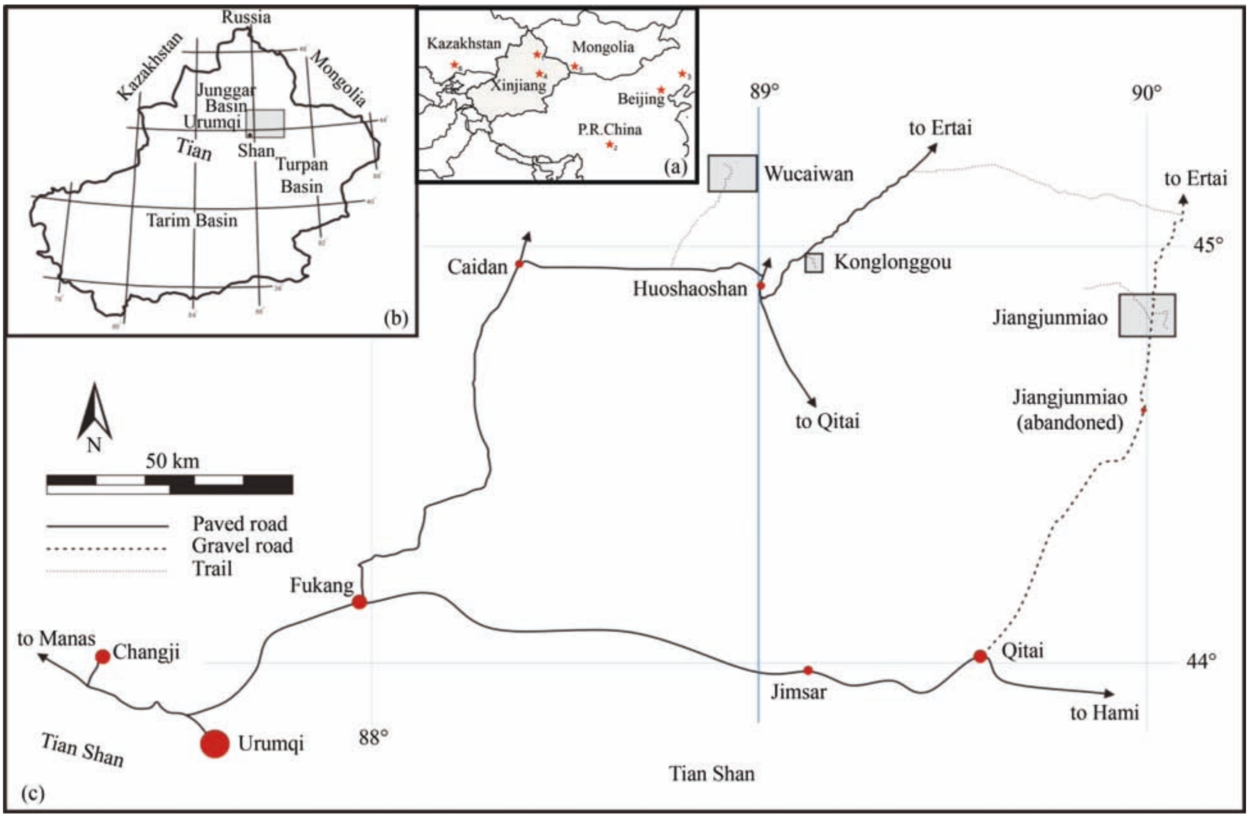

Fig. 1. Map of the three main areas that yield the Shishugou Fauna of northwestern China and some other Middle-Late-Jurassic-transition-period faunas.

(a) Map showing the location of Xinjiang (the shaded area) and several Middle–Late Jurassic Asian terrestrial faunas (1–Junggar; 2–Shaximiao; 3–Yanliao; 4–Turpan; 5–Shar Teg; 6–Karabastau); (b) Xinjiang map showing the location of Shishugou Fauna (the shaded area); (c) the shaded area in (b) enlarged and shown in detail. Wucaiwan, Jiangjunmiao, and Konglonggou areas lie along the southern flank of a Tertiary-age uplift. The Tian Shan (Heavenly Mountains) borders this portion of the Junggar Basin to the south. Numerous modern highways have been constructed, and extensive mining has begun since our fieldwork was conducted (and this map was compiled) in the 2000s. An examination of current Google Earth satellite imagery confirms that all of the sites described here remain undisturbed by those activities.

Shishugou outcrops, spanning approximately 100 km (Fig. 1). In the east, the Jiangjunmiao area consists of a set of outcrops on two sides of a valley; most fossils are from the eastern part while outcrops on the western side have been less productive but include an in situ petrified forest. The eastern area and the part of the western area with fossil trees has been designated the Qitai Silicified Wood-Dinosaur National Geopark. Further west, near the petroleum industrial town of Huoshaoshan, Konglonggou ("Dinosaur Wash") preserves a monotypic bone bed comprising disarticulated elements of the sauropod *Bellusaurus sui*. The western-most extent of the outcrops is the Wucaiwan area, known for its multi-colored outcrops of the Xishanyao Formation that are a tourist site and were used in filming *Crouching Tiger, Hidden Dragon* (2000), with outcrops of the Shishugou Formation to the west.

The first vertebrate fossil known from the formation, the sauropod *Tienshanosaurus* Young (1937), was discovered by Professor Yuan Fuli working with the Sino-Swedish expedition under the supervision of the explorer Sven Hedin (Young, 1937). An account by the leader of the expedition (Hedin, 1933), repeated in Hedin 1943) confuses Professor Yuan's discovery of Triassic vertebrates in the foothills of the Tian Shan in 1928 with the dinosaur discovery in December 1930 (Young 1937), and the confusion was compounded by Young's use of the name ascribed to the Triassic finds by Hedin (citing Yuan), "Tien Shan-saurus". Young (1937) places the locality 250 li (125 km) north of Qitai, which in a straight line is approximately 50 km NW of Jiangjunmiao and in the middle of Paleozoic rocks of the Kelamaili Shan, but it likely was at Jiangjunmiao as these outcrops are near a road and are more easily accessed than those to the west. Dinosaurs were discovered further west at Konglonggou in 1954 during exploration for petroleum, and further collections were made at that site in the early 1960s by the Regional Museum of the Uygur Autonomous Region but the specimens were lost (Dong, 1990). In 1983 and 1984 the IVPP made substantial collections at the two previously known localities and made the first collection at Wucaiwan (Zhao et al., 1987a; Dong, 1993b). The China Canada Dinosaur Project (CCDP), a joint project organized by Canadian paleontologists Phil Currie and Dale Russell and Chinese paleontologists Dong Zhiming and Zhao Xijin, returned to the areas in 1987–1990, working mainly at Jiangjunmiao (Dong, 1993b; Grady, 1993; You and Cui, 2019) but also collecting at Wucaiwan, which they referred to as Pingfengshan. From 2000 to 2011 a series of expeditions (here referred as the

Sino-American expeditions) co-led by Xu and Clark collected numerous fossil vertebrates from the Shishugou Formation, mainly at Wucaiwan but also from the two other areas. Smaller collections have been made, mainly at Jiangjunmiao, by Sino-German expeditions (Maisch et al., 2004; Tütken et al., 2004; Wings, 2015; Augustin et al., 2021) and others (e.g., Wang et al., 2019).

It should be noted that the fossil assemblages recovered from these three areas display significant differences, though they are similar to each other in the general faunal composition. For example, in general larger taxa such as sauropods are more abundant at Jiangjunmiao and small to medium sized taxa are more abundant at Wucaiwan; nearly all fossils at Konglonggou come from two sites, the monotypic *Bellusaurus* sauropod quarry (which produced evidence of more than 17 juvenile individuals) and a microvertebrate site where the mammal *Klamelia* was found, and both of these taxa are currently known only from Konglonggou. The faunal composition difference likely results from taphonomic processes, paleoecological differences or even presence of some form of geographic barrier between these areas (He et al., 2013), which need further analysis. Nevertheless, Wucaiwan and Jiangjunmiao share several taxa at the genus or species level, including tritylodontids (e.g., *Bienotheroides*), turtles (e.g., *Xinjiangchelys junggarensis* and *X. radiplacatoides*), theropods (e.g., *Sinraptor*), sauropods (e.g., *Mamenchisaurus sinocanadorum*), and ornithischians (e.g., "*Gongbusaurus*" *wucaiwanensis*), among others. For this reason, He et al. (2013) proposed the term "Shishugou Fauna" for the fossil assemblage preserved in the Shishugou Formation of the eastern Junggar Basin, which is followed by this study.

2 Geology of the Shishugou Formation

The Shishugou Formation is well exposed in shallow badlands at Wucaiwan, Jiangjunmiao, and Konglonggou (Fig. 1), a combined linear extent of about 100 km that stretches along the southern margins of the Kelameili Shan, a complex Mesozoic–Tertiary uplift belt (Vincent and Allen, 2001). Xu and Clark concentrated our geological efforts at Wucaiwan because a complete section of the formation is preserved there (including bottom and top contacts), and exposures can be continuously traced across many kilometers (Fig. 2; Eberth et al., 2010). The stratigraphic patterns and lithofacies that we documented at Wucaiwan provide a solid understanding of the formation's paleoenvironments and depositional history that is applicable throughout the region. Because the area is uniquely rich in well-preserved fossil vertebrates, the stratigraphic and sedimentological data gathered from Wucaiwan are useful in documenting recurring taphonomic patterns for the region. Ultimately, geological data from Wucaiwan provide the fundamental baseline for stratigraphic correlations, and paleoenvironmental and taphonomic interpretations among all the Shishugou Formation exposures that we have explored.

At Wucaiwan, Jurassic-age (and younger) sedimentary strata are exposed along the southern and western margins of the Kelameili Shan (bordering the South Dishuiquan Fault). Our investigations in the northern area of the Wucaiwan canyon confirmed that the South Dishuiquan Fault System sharply separates Shishugou Formation strata from these more northern Paleozoic rocks. Although Shishugou strata dip steeply (up to 55 degrees to the south) adjacent to and just south of this fault system (as a result of drag along the fault), strata typically exhibit much shallower dip angles (less than 10 degrees south) approximately 1 km south of the fault. A prominent 4-km-long synclinal fold-axis oriented WNW–ESE is present approximately 1.0–1.5 km south of the fault system (Fig. 2). Throughout the remainder of the field area, as well as at Konglonggou and Jiangjunmiao, Shishugou strata dip between 0–10 degrees in a generally westward direction, suggesting that the more easterly portions of the bordering Kelameili Shan exerted a widespread and stronger influence on the adjacent Jurassic (and Cretaceous) strata.

2.1 Stratigraphy of the Shishugou Formation

The 380-m-thick Shishugou Formation was deposited along the northeastern edge of the internally drained, Mesozoic-age, Junggar foreland basin (Eberth et al., 2001; Vincent and Allen, 2001). In all areas, the Shishugou Formation rests unconformably on the middle Jurassic Xishanyao Formation. However, the upper contact is preserved only at Wucaiwan, where eolian strata of the Lower Cretaceous Tugulu Group rest sharply and with angular unconformity on the formation (e.g., Eberth et al., 2001, 2010). At Jiangjunmiao the Shishugou Formation is truncated by Tertiary-age Gobi deposits and at least 50 m of the uppermost section that is preserved at Wucaiwan appears to be missing. At Konglonggou the top of the formation was not observed and correlations are further complicated by poor exposure and structural complexities.

Eberth et al. (2001) proposed that the use of megasequence patterns allow broad chronostratigraphic correlations of stratigraphic units across the Junggar Basin. Using a megasequence approach, they correlated the Shishugou Formation of the northeastern Junggar Basin with the combined Toutunhe and Qigu formations to the south and west near Urumqi and Urho, respectively. However, whereas Eberth et al. (2001) suggested an age range of 154–169 Ma for this megasequence, more recent refinement of the GTS (e.g., Gradstein et al., 2012) and our dating of three tuffs at Wucaiwan using Ar^{40}/Ar^{39} single-crystal laser ablation techniques suggests a Late Jurassic (Oxfordian age) for the entire section at Wucaiwan. Our original results were obtained in 2005 using the Fish Canyon Sanidine (FCS) monitor mineral dated at 28.02 Ma. Subsequently, we recalibrated the original data using a revised age of 28.201 Ma for the FCS (Kuiper et al., 2008). This resulted in a readjustment in the ages of the Wucaiwan tuffs to approximately 0.6% older (e.g., Choiniere et al., 2014). The revised ages of the three tuffs (T-4, T-BW, and T-1) are presented in Figure 3. In 2010 and 2011, we attempted to use U-Pb LA-ICP dating of zircons from these tuffs with only marginal success. An imprecise age of 154.03 ± 5.0 Ma was calculated for T-4, again suggesting a Late Jurassic, Oxfordian age for the section. More recently, we initiated U-Pb TIMS dating of

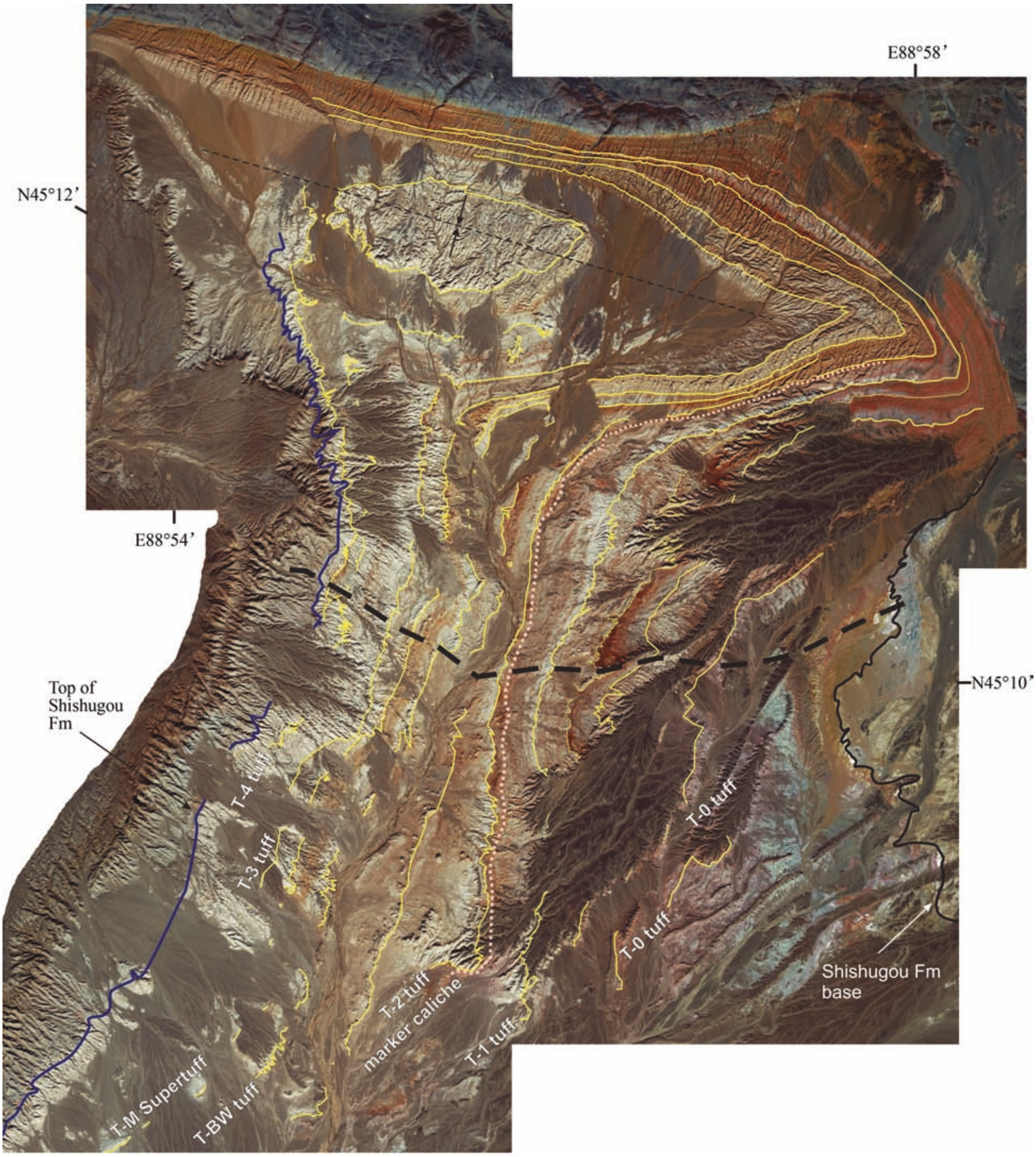

Fig. 2. Continuous marker beds (tuffs in yellow; caliche pink dotted) at Wucaiwan overlain on QuickBird satellite imagery. Bottom and top of Shishugou Formation indicated by black and blue lines, respectively. Approximate location of composite measured section indicated by heavy dashed black line.

zircons separated from a prominent channel sandstone at Wucaiwan. That approach also shows considerable promise.

At Wucaiwan, the Shishugou exhibits a classic, tectonically-induced two-phase megasequence pattern characterized by a lower, upward-fining phase and a subsequent, upward-coarsening phase (Fig. 3). The coarsest portions of the megasequence are at the bottom and top of the formation, where each is characterized by conglomeratic sheets and lenses. There is also a pebbly, paleochannel-rich zone in the middle of the exposures (225 m to 255 m, Fig. 3) that may represent a minor pulse of coarse-grained sedimentation. Channel-belt deposits, alluvial-to-paludal mudstones, volcanic tuffs, and sheetflood deposits characterize the remaining section. Although a fining/coarsening-upward megasequence stratigraphy suggests alternating episodes of tectonic uplift and quiescence, regional climatic variations may have also

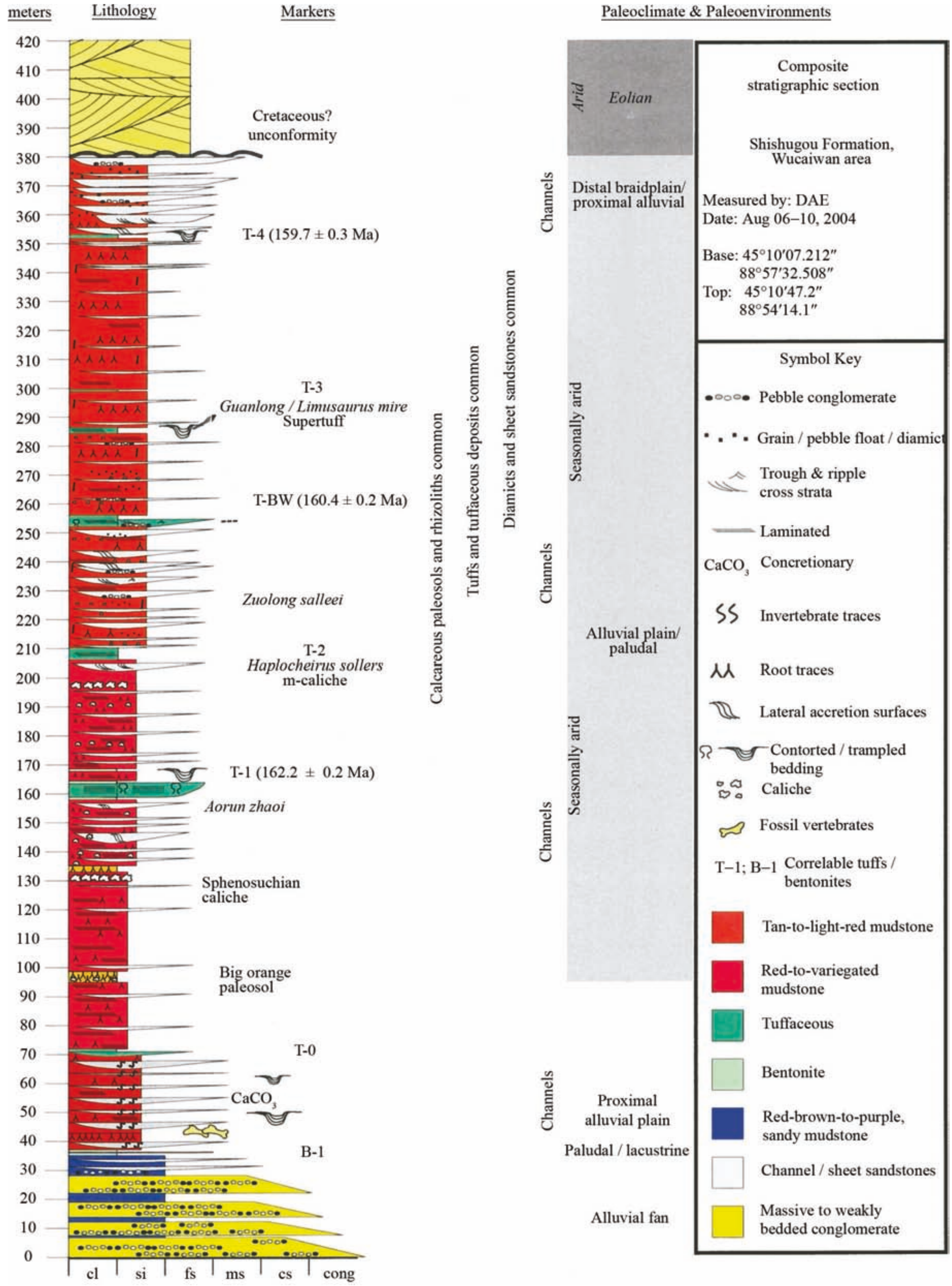

Fig. 3. Composite measured section. Stratigraphic position of tuffs (and one bentonite) indicated in green and numbered using "T-" lettering. Two prominent marker caliches and a prominent paleosol are also indicated (m-caliche, sphenosuchian caliche, big orange) at 197, 131, and 96 m, respectively. Important fossil localities in descending order: *Guanlong*/*Limusaurus* "death pits" (286 m), *Zuolong* (225 m), *Haplocheirus* (202 m), and *Aorun* (155 m). The zone of sparsely pebbly sandstones (230–255 m) likely correlates with a similar zone of pebbly to cobbly sandstone and silicified logs near the middle of the stratigraphic section at Jiangjunmiao.

influenced grain size patterns.

Laterally continuous horizons of mature caliche, other non-calcareous paleosol horizons, zones of coarse-grained sediment, and tuffaceous volcanic airfall deposits allow very precise mapping, correlation, and relative stratigraphic placement of fossil locations and other geological units of interest at Wucaiwan (Figs. 2, 3). In this context, we recognize numerous traceable horizons in the composite stratigraphic section at Wucaiwan. These are key in assembling the depositional history of the formation, documenting changes in the faunal and preservational characteristics of the unit through time, and comparing the section at Wucaiwan with exposures of the formation at Jiangjunmiao and Konglonggou.

2.2 Facies and paleoenvironments

The Shishugou Formation at Wucaiwan consists primarily of alluvial (river/floodplain) and paludal (wetland) facies deposited at the up-dip margins of the Junggar Basin, a long-standing, internally-drained basin that has persisted since the Triassic (Eberth et al., 2001). However, outcrops are exposed only in locations that were adjacent to the actively eroding source-area highlands, as indicated by conglomeratic sheets and lenses that dominate both the lower and upper 30 m of the stratigraphic section at Wucaiwan. The lower conglomerate deposits are mostly sheets and lenses (channel fills) of matrix-supported conglomerate consisting of mixtures of angular to well-rounded pebbles and cobbles of Paleozoic metamorphic rocks (up to 6 cm in diameter), separated by mixtures of sandy mudstones. This fabric suggests sheet flooding and mass-sediment flows in an alluvial fan setting, likely during major rainfall events. Although fragments of silicified fossil wood are present, vertebrate and other fossils are, as yet, unknown in these conglomerates.

The conglomerates at the top of the section are finer grained than those below. They range from rare sheets of clast-supported pebbles (no cobbles) a few cm thick to more abundant diamicts (structureless beds with ‘floating’ granules and pebbles), 10 cm or more thick. Diamicts are a common facies in modern alluvium in the Junggar Basin, as well as other badland locations across northern China and southern Mongolia. In these modern semi-arid to arid settings, adjacent coarse-grained bedrock erodes rapidly, thus allowing its constituent grains, granules and pebbles to mix with the alluvium, that is itself being eroded and reworked, typically via mass sediment flows (see discussion in Eberth, 2018; p. 38; figs. 8E, F). In general, diamicts in the Shishugou Formation section suggest the occurrence of mass sediment flows close to source area and in a rapidly eroding landscape.

From meter 30 up-section to meter 210 (a 180 m thickness), the Shishugou Formation section at Wucaiwan is dominated by a dark red calcareous overbank/floodplain mudstone succession that hosts a variety of facies (Fig. 3). These include: (1) lenticular paleochannel deposits (~10% of the section) that consist of fine-to-medium grained, cross-bedded sandstone, (2) numerous caliche horizons that range from glaebular to nodular but also include a few mature caliche hard pans, (3) shallow root-trace horizons and *Planolites* burrows (in sandstones), and (4) very rare tuffaceous mudstone/sandstone horizons that suggest the onset of volcanism. The mudstones themselves include both massive and laminated deposits suggestive of subaerially exposed floodplains and ponds/small lakes, respectively. Diamicts are noticeably rare in this interval (compared to the upper portions of the section) confirming that the setting was relatively more distant from source and beyond the reach of mass sediment flows.

Although paleochannel dimensions are variable, most are less than 5 m thick and 100 m wide, with cross-bedding that suggests a south-southwest direction of flow generally toward the basin center (typical of feeder channels). Paleochannel deposits exhibit some lateral accretion surfaces, but occurrences are minor and appear related to channel infilling and abandonment. In some rare cases – the upper portion of this interval – paleochannel deposits were as much as 10 m thick and 400 m wide, and exhibit evidence of flow toward the NW, suggestive of a larger, trunk paleochannel flowing distal to the alluvial fan but parallel to the foredeep and/or source. Trunk river systems are common beyond the toes of alluvial fans in modern seasonally wet/dry and mesic settings.

Fossils in this interval consist of wood, sauropod tracks, and a variety of skeletal occurrences of lungfish, amphibians, crocodiles, sphenosuchians, small ornithischians, turtles, tritylodonts, and small and large theropods. Fossils are associated with (1) massive red mudstones with caliche glaebules (semi-arid environment paleosols), (2) lenticular mudstones (abandoned bodies of water) and (3) sheet sandstones (alluvial splay deposits).

From ~210 m up to ~350 m (a 140 m thickness), the Shishugou Formation becomes noticeably lighter colored (grey-orange) in weathered outcrop, due to increases in the abundance and thicknesses of tuffaceous deposits, and increased abundances of sandstone and siltstone beds. This change in color above the middle of the formation was the basis for the division of the formation into the lower “Wucaiwan Formation” and the upper “Shishugou Formation” as proposed by Zhao et al. (1987b). However, this lithic dichotomy is gradual in its up-section expression, inconsistent from section to section and from location to location, and cannot be accurately mapped or used meaningfully as a detailed stratigraphic datum. Furthermore, maintaining this stratigraphic dichotomy logically requires that the lowermost and uppermost conglomeratic horizons are recognized as separate units because of their notable differences in color and lithic content. In contrast, the current “megasequence” approach to this package defines the Shishugou Formation based on its lower and upper unconformities, which are manifest across the basin. This said it might be possible in the future to consistently and meaningfully subdivide the Shishugou section into “members” or other sub-formational units using one or more of the prominent and widespread paleosols or tuffaceous beds we refer to here.

Although sandstone/mudstone ratios increase to 1:5 in this interval, paleochannels are notably smaller and less abundant than lower in section. In contrast, sheet sandstones and diamicts are more abundant in this interval, suggesting that this part of the section records seasonal flow and mass sediment flooding events, all consistent with the interpretation that an alluvial fan system was prograding into the area from the northeast. Rhizoconcretions, fossil wood, and caliche glaebules are present, but well-developed and traceable caliche horizons are rare, suggesting that depositional and erosional events occurred with increasing frequency, thus preventing the development of widespread and long-term hiatal surfaces and mature paleosol profiles.

Fossil vertebrates are abundant in this tuffaceous/diamict-rich succession with notable occurrences including mass death assemblages of small bipedal theropods that were mired and died in quickmud ‘pools’ caused by sauropod trampling and local liquefaction of wetland substrates (Eberth et al., 2010). Fully articulated to associated skeletons of small quadrupedal ornithischians and tritylodonts are frequently preserved in massive, sandy mudstones, suggestive of in-burrow death events due to flooding, burial, and suffocation.

2.3 Depositional history of the Shishugou Formation at Wucaiwan

By combining previously published paleoenvironmental interpretations with interpretations of the facies, facies assemblage, and fossil/facies associations described here, we confirm that the Shishugou Formation was deposited along the flanks of a Mesozoic uplift in an internally-drained basin during the Late Jurassic. The climate remained warm-to-hot and seasonally wet/dry during deposition of the Shishugou sedimentary succession. At Wucaiwan, both the bottom and top of the Shishugou Formation includes a total of 60 m of middle-to-distal alluvial fan sheetflood and mass-sediment flow deposits, across which largely unconstrained floodwaters would have presented periodically challenging conditions for a paleoflora/fauna.

The remaining 320 m of strata in the middle of the section reflect the presence of more stable paleoenvironments, beyond the downslope margins of alluvial fans. These comprise a mixture of fluvial/alluvial and paludal (wetland) settings. The lower 180 m of this section (meter 30 to meter 210) represents landscapes that were dominated by small, low-sinuosity rivers and rarer trunk rivers, as well as an extensive alluvial plain dotted by lakes, ephemeral ponds and wetlands that stretched southward to an inland lake that occupied the center of the basin (Eberth et al., 2001). We regard the paleoenvironmental setting at Wucaiwan during the Late Jurassic as broadly similar to that of the modern Pantanal in Paraguay (Eberth et al., 2010). Seasonally wet/dry conditions were ideal for prolonged droughts and floods, and might have been responsible for some of the vertebrate fossil occurrences in this portion of the formation.

Subsequently, the next 140 meters of this portion of the section (meter 210 to meter 350), with its increasingly numerous diamicts and granular conglomerates, reflects a time of increased flooding and progradation of distal-most alluvial fan paleoenvironments back into the Wucaiwan area. Volcanic ash deposits are also thicker and more numerous in this part of the section, indicating increased volcanism in the region at this time. The area remained seasonally wet/dry but evidence of substrate liquefaction by sauropods further suggests that boggy, spring-saturated substrates likely occurred at the distal margins of the alluvial fans, just as they do today across the modern Gobi Desert. Such locations were potential mires, trapping and killing small theropods (Eberth et al., 2010). Flooding events also appear to have been responsible for trapping and killing many small-to-medium size vertebrates in their burrows, as well as burying the partial skeletal remains of other vertebrates where they lay. Ultimately, alluvial-fan deposits continued prograding to the southwest, burying the entire Wucaiwan area.

2.4 Comparison with the Jiangjunmiao and Konglonggou Sections

Jiangjunmiao is particularly famous as a fossil forest site that yields hundreds of fossilized tree trunks and stumps (McKnight et al., 1990; Hinz et al., 2010). Fossilized stumps (all about 1 m tall) are preserved in situ at one horizon in the middle of the exposed section and appear to have been killed during volcanic ashfall events that were increasing in frequency throughout the region. At a slightly lower horizon, silicified downed tree trunks (without bark) were apparently reworked and buried in fluvial channels (McKnight et al., 1990); ~250 m in our composite measured section (Fig. 4).

A composite measured section (340 m thick) compiled by us at Jiangjunmiao in 2002 and 2005 (Fig. 4) indicates that, similar to Wucaiwan, the Shishugou Formation includes a lower conglomerate interval (48 m), and a combined redbeds and diamict/tuffaceous sediments interval (~300 m). However, the section is truncated at the top (western area of Jiangjunmiao) by a Tertiary-age unconformity and sharply overlain by gobi deposits. In this interpretation, the Jiangjunmiao section is missing the J-K unconformity as well as the uppermost conglomerate interval preserved at Wucaiwan.

Jiangjunmiao differs sedimentologically from Wucaiwan in a number of important ways. First, pebble-to-cobble conglomerates are present in numerous broad channel belt deposits that also host hundreds of silicified logs at some locations. Log-rich channel belt deposits are expressed throughout the Jiangjunmiao field area and are targets for fossil wood miners. In general, they mark the upsection transition from redbeds to orange-grey colored tuffaceous and diamict-rich sediments. Secondly, very thick and steep-wise-incised valley fills (up to 25 m thick) are abundant locally and host vertically aggraded paleochannel sandstones. Thirdly, tuffaceous deposits/intervals, although broadly identical in number and relative spacing as at Wucaiwan, are generally thicker than their counterparts at Wucaiwan. Some interbedded successions of tuff, siltstone, and sandstone are up to 15 m in thickness. Lastly, although there appear to be more occurrences of articulated to associated skeletons of large dinosaurs (*Mamenchisaurus*, *Monolophosaurus*, *Sinraptor*) in paleochannel sandstones at Jiangjunmiao, we did not observe any of the deep sauropod-trampling structures that are so abundant at Wucaiwan (Eberth et al.

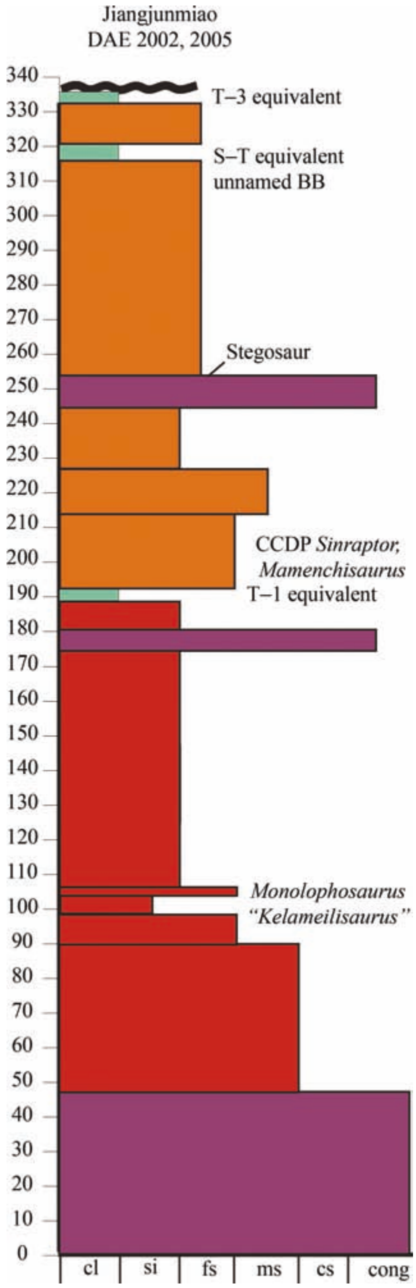

Fig. 4. Measured section at Jiangjunmiao.

2010).

Together, these differences suggest that Jiangjunmiao was positioned closer to the fluvial and volcanic source areas than Wucaiwan. Secondly, the area likely experienced localized uplift (perhaps related to volcanic events), which allowed channels to incise deeply into the landscape and become laterally stable drainages, characterized by vertical aggradation. Lastly, Jiangjunmiao hosted more and larger fluvial channels, as well as conglomeratic sheetfloods suggesting that its more proximal location relative to source made it a poor setting for groundwater seepage, thus inhibiting the development of deep sauropod trampling structures and mires in general that are common at Wucaiwan.

Regardless of the differences between the two areas, the overall similarities in stratigraphic patterns, especially the relative number and spacing of tuffaceous beds at both locations, allows us to approximate the stratigraphic positions of many of Jiangjunmiao's fossil vertebrates with respect to those at Wucaiwan. For example, CCDP and other localities east of the Qitai Fossil Forest Preserve occur in a restricted stratigraphic interval just above the first prominent tuff bed (190 m), and thus appear to correlate well with the stratigraphic interval at Wucaiwan that is bounded by T-1 and the m-caliche, 165–195 m above the base of the formation.

More specifically, we place the position of the *Monolophosaurus* quarry very low in section at Jiangjunmiao equivalent to a position midway between the base of the section and T1 at Wucaiwan. The CCDP *Sinraptor* specimen (collected from the base of a paleochannel deposit) occurs 7.5 m above the lowest prominent tuff we observed in section at Jiangjunmiao, which we regard as likely equivalent to T-1 at Wucaiwan. The CCDP *Mamenchisaurus* site occurs approximately 3 m above this same tuff and at the margin of a paleochannel deposit. This same interval at Wucaiwan is dominated by floodplain mudstones and calcareous paleosols and lacks large paleochannel deposits, which may explain the differences in fossil preservation between the two sites at this horizon.

A number of important localities occur in the western exposures at Jiangjunmiao, which are generally higher in stratigraphic section than the eastern exposures. For example, "Rene's ornithischian" JJM 02-6 and "the stegosaur [2001–2002]") JJM 02-10 occur at or slightly above the prominent conglomerate-rich sandstone broad paleochannel belt that hosts the silicified logs ~250 m above the base of the formation (Fig. 4). This position correlates well with the thick paleochannel complex and some underlying pebbly sandstones referred to as "Big White" at Wucaiwan, which occurs below the *Guanlong* and *Limusaurus* "traps" horizon and above the *Zuolong* site. Likewise, an unnamed sauropod bonebed in this western area occurs 17 m below a tuff that we infer to be reasonably equivalent to the T-3 tuff at Wucaiwan, and 6 m below another tuff that we infer to be the equivalent of the S-Tuff at Wucaiwan (Fig. 4).

In contrast to Wucaiwan and Jiangjunmiao, exposures and continuous sections are limited at Konglonggou making correlations difficult. Nonetheless, our section measurements at both the *Bellusaurus* quarry and the *Kelameili* site (separated by ~3.5 km) indicate that both occur approximately 110-120 above the base of the Shishugou Formation in that area. However, because the Konglonggou sections are missing the thick lower zone of conglomerates seen at Wucaiwan and Jiangjunmiao, these fossiliferous sites were likely deposited in a more down-dip location, where wetlands were more fully developed, and where the section was less thick. In this context, we hypothesize that the two fossil horizons are approximately equivalent to the stratigraphic interval bounded by T-1 and T-2 tuffaceous beds at Wucaiwan. Tuffaceous beds and lighter-colored outcrop dominate the remaining section above these fossil sites at Konglonggou, supporting this interpretation. Nonetheless confident correlation of these sites with Wucaiwan and Jiangjunmiao awaits a more refined stratigraphic study at Konglonggou.

We propose that careful section measurements that document a variety of lithostratigraphic features (specifically: tuffs, mature caliches and paleosol profiles) can be used in the future to continue integrating existing and future fossil discoveries into the emerging regionally coherent stratigraphic framework.

3 Fauna of the Shishugou Formation

Below we review the vertebrate fauna from the Shishugou Formation, listing only the fossils from the eastern Junggar Basin (Table 1). However, taxonomically and chronologically similar fossils are also known from several nearby areas, both within (Martin et al., 2008; Wings et al., 2012) and outside (Zhou et al., 2010; Sullivan et al., 2014; Huang, 2015; Xu et al., 2016) Xinjiang, and the fossil assemblages from these areas are possibly assignable to the same fauna as the Shishugou fossils (see discussion section). It should be noted that most articulated skeletons are preserved as mass death assemblages (Fig. 5), though in different forms (e.g., in a death pit with a mixture of different taxa or in a monospecific bed). The majority of the Shishugou fossils are housed at the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP).

3.1 Chondrichthyes

The Shishugou cartilaginous fishes are represented by

Table 1 Shishugou vertebrate fossils

Clade	Species	Distribution	Abundance	Collector (s)
Chondrichthyes	Family indet.	?USF/W, K	R	IVPP, CCDP, SA
	Family indet.	USF/J, W, K	R	SA
Osteichthyes	Actinopterygii indet.	?USF/K	R	SA
	Dipnomorpha indet.	USF/W	R	SA
Temnospondyli	Brachyopoidea indet.	?USF/W, K	R	SA
Mammaliomorpha	*Yuanotherium minor*	USF/W	R/OL	SA
	Bienotheroides zigongensis	LSF/J,W	M/ML	CCDP, SA
	Bienotheroides ultimus	USF/J	M/ML	SG
	Klamelia zhaopengi	?USF/K	R/OL	IVPP
	Dsungarodon zuoi	USF/W	R/OL	SG, SA
	Docodontidae indet.	USF/W	R/OL	SA
	Docodontidae indet.	USF/K	R/OL	SA
Testudinata	*Xinjiangchelys junggarensis*	USF/W,J	C/ML	IVPP, SA
	Xinjiangchelys radiplicatoides	USF/W,J	C/ML	CCDP, SA
	Xinjiangchelys chowi	USF/W	R/OL	SA
	Sichuanchelys palatodentata	USF/W	M/ML	SA
	Annemys sp.	?USF/W	R/ML	SA
Squamata	Paramacellodidae indet.	?LSF, USF/W	M/ML	SA
	Paramacellodidae indet.	USF/W	R/ML	SA
	Family indet.	USF/W	R/ML	SA
Crocodylomorpha	*Sunosuchus junggarensis*	USF/W	M/ML	CCDP, SA
	Junggarsuchus sloani	LSF/W	R/ML	SA
	Nominosuchus sp.	USF/W	C/ML	SA
	Shartegosuchus sp.	USF/W	R/OL	SA
Pterosauria	*Sericipterus wucaiwanensis*	USF/W	R/OL	SA
	Kryptodrakon progenitor	LSF/W	R/OL	SA
Ornithischia	*"Gongbusaurus" wucaiwanensis*	USF/W, J	M/ML	IVPP, SA
	Jiangjunosaurus junggarensis	USF/J	R/OL	SA
	Stegosauridae indet.	USF/J, W	M/ML	SA, SG
	Yinlong downsi	USF/W	C/ML	SA
	Hualianceratops wucaiwanensis	USF/W	R/OL	SA
Sauropoda	*Tienshanosaurus chitaiensis*	?USF/?J	R/OL	SS
	Mamenchisaurus sinocanadorum	USF/J, ?W	M/ML	CCDP, SA
	Bellusaurus sui	?USF/K	C/OL	IVPP, SA
	Klamelisaurus gobiensis	LSF/J	R/OL	IVPP
	Brachiosauridae indet.	LSF/W	R/OL	SA
	Fushanosaurus qitaiensis	?/J	R/OL	
Theropoda	*Monolophosaurus jiangi*	LSF/J	R/OL	IVPP
	Limusaurus inextricabilis	USF/W	C/?ML	SA
	Sinraptor dongi	USF/J	R/OL	CCDP
	Sinraptor sp.	USF/W	M/ML	SA
	Haplocheirus sollers	USF/W	R/?ML	SA
	Shishugounykus inexpectus	USF/W	R/OL	SA
	Aorun zhaoi	USF/W	R/OL	SA
	Guanlong wucaii	USF/W	M/ML	SA
	Zuolong salleei	USF/W	R/OL	SA

Abbreviations: J–Jiangjunmiao; K–Konglonggou; W–Wucaiwan (including Pingfengshan); LSF–Lower section of Shishugou Formation; USF–Upper section of Shishugou Formation; R–Rare in abundance; C–Common in abundance; M–Moderate in abundance; OL–Recovered from one layer; ML–Recovered from multiple layers; CCDP–China-Canada Dinosaur Project; IVPP–IVPP expedition; SA–Sino-American expeditions; SG–Sino-German expeditions; SS–Sino-Swedish expedition.

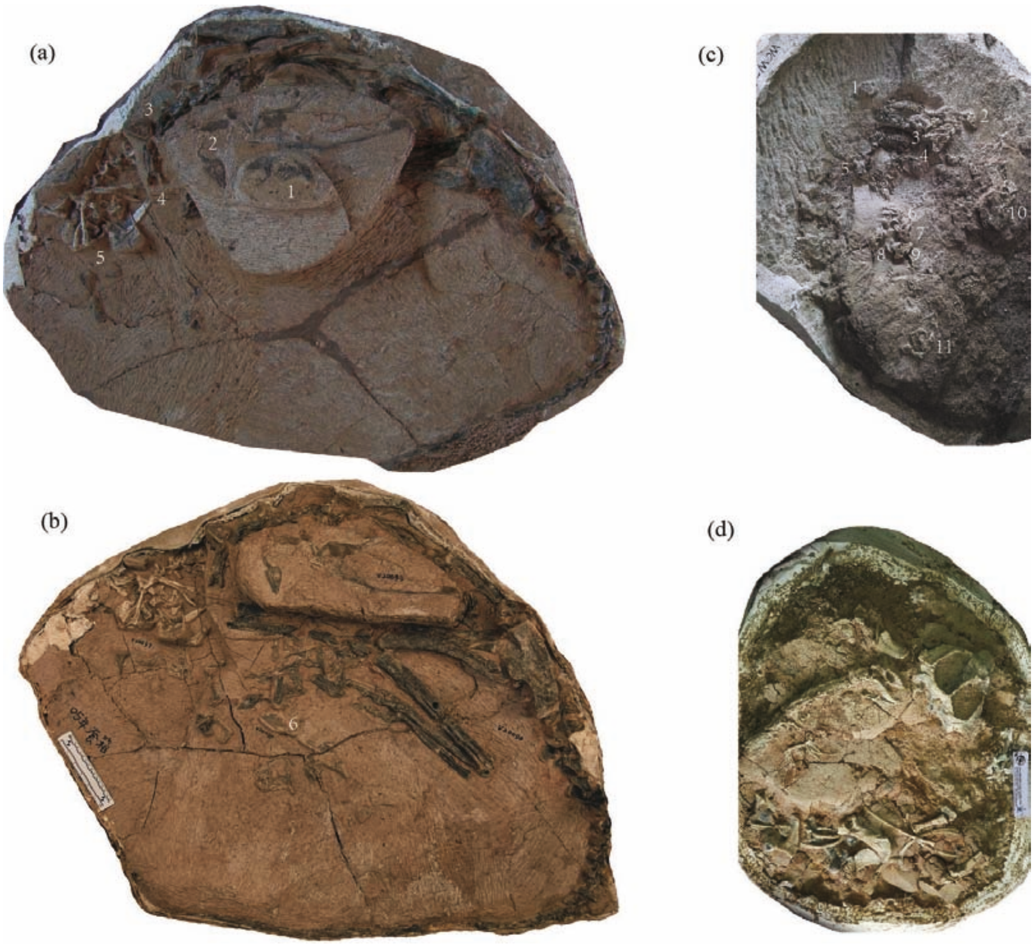

Fig. 5. Photographs of selected Shishugou vertebrate mass death assemblages.
(a) A large block preserving multiple articulated theropod and mammaliomorphan skeletons in different sedimentary layers. From top to the bottom level: 1, a docodont mammaliomorphan; 2, a juvenile *Limusaurus*; 3 and 4, a juvenile and a subadult *Limusaurus*; 5, a subadult *Limusaurus*. (b) The same block with additional matrix including the one preserving the docodont skeleton removed. Additional fossil including one more juvenile *Limusaurus* (6) exposed in lower layer. (c) Multiple semi-articulated shartegosuchid skeletons cf. *Nominosuch* preserved in one sedimentary layer. 1–11 refer to skulls of 11 different-sized shartegosuchids. (d) An articulated lizard skeleton and a semi-articulated tritylodont skeleton preserved in one block.

hybodont sharks, which is an extinct clade known from Late Devonian to the Late Cretaceous. To date, only isolated teeth of this group have been recovered, and although they are rare occurrences in the formation, they are known in all three major fossil-producing areas of eastern Junggar.

3.2 Osteichthyes

Bony fishes are represented by both ray-finned and lobe-finned fishes in the Shishugou Fauna. Isolated vertebrae, ganoid scales and teeth referred to Actinopterygii are abundant at the *Klamelia* site at Konglonggou but are otherwise rare in the formation.

The lobe-finned fishes are represented by lungfishes, a clade of freshwater creatures that represent the closest living relative of tetrapods. Lungfishes are abundant in the Devonian, but they are rare afterwards (Clack et al., 2016). Most lungfish fossils are represented by tooth plates at Wucaiwan, and among the collection, only one specimen (IVPP V 28943), from the upper part of the formation, preserves associated cranial bones besides tooth plates (Fig. 6a). In general, lungfishes are rare in the formation.

3.3 Brachyopoid Temnospondyli

Early-diverging tetrapods are represented by brachyopoids. Brachyopoidea is a clade of temnospondyls that are mostly known from the Triassic with only a few species from the Jurassic and Early Cretaceous (Ruta et al., 2007). Isolated vertebral segments referred to Brachyopoidea have been recovered from the formation in both Wucaiwan and Konglonggou, but in general they are rare in the formation. The only known non-vertebral material is a single dentary (IVPP V 18141, Fig. 6b) that displays the broad curvature typical of brachyopoid dentaries, and similar material is also known in the lower Shaximiao Formation (Dong, 1985).

3.4 Mammaliamorpha

The Mammaliamorpha is represented by

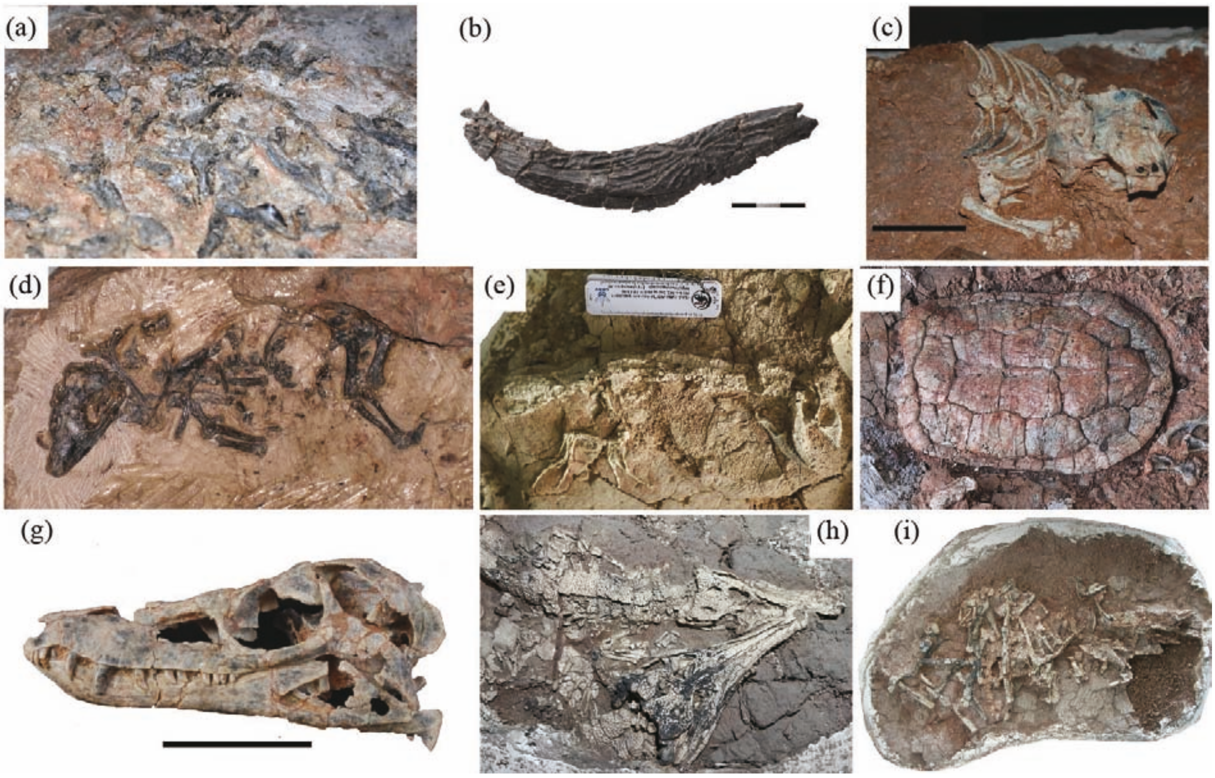

Fig. 6. Photographs of selected Shishugou non-dinosaur vertebrate fossils.
(a) A partial associated lungfish skeleton; (b) a brachyopoid amphibian dentary; (c) a partial articulated tritylodont skeleton; (d) a nearly complete docodont skeleton; (e) a nearly complete articulated lizard skeleton; (f) a complete turtle carapace; (g) the crocodylomorphan *Junggarsuchus sloani* holotype skull; (h) two skeletons of the goniopholidid crocodylomorph *Sunosuchus*; (i) the pterosaur *Sericipterus wucaiwanensis* holotype.

Tritylodontidae, Docodonta, and Eutriconodonta in the Shishugou Fauna.

Tritylodontids are a group of dominantly herbivorous cynodonts with a nearly global distribution from Late Triassic through Early Cretaceous, and they are considered among the closest relatives of the Mammaliaformes (Liu and Olsen, 2010; Ruta et al., 2013). The Shishugou tritylodontids are represented by a large collection of fossils, including several complete skulls and articulated skeletons (e.g., Fig. 6c).

Bienotheroides zigongensis Sun 1986 is a tritylodont represented by a skull from the “Wucaiwan” (i.e., lower Shishugou) Formation at Jiangjunmiao. It was described by Sun and Cui (1989) as indistinguishable from a *Bienotheroides zigongensis* fossil from the lower Shaximiao Formation of Sichuan (Sun, 1986).

B. ultimus Maisch et al. 2004 is a second species of *Bienotheroides* that was described from the upper Shishugou at Jiangjunmiao. It differs from *B. zigongensis* mainly in features of the quadrate and postcranial skeleton. Maisch et al. (2004) described a difference in orientation of the stapedial process of the quadrate that implied they consider the specimen described by Sun and Cui (1989) to be *B. zigongensis,* and that both species of this genus are present at Jiangjunmiao (Maisch et al., 2004).

Yuanotherium minor Hu et al. 2009 is represented by a small maxilla with three teeth from Wucaiwan. It is distinguished from other tritylodontids by details of its tooth cusps (Hu et al., 2009). It is similar to some other tritylodontids, such as *Bienotheroides*, in having a highly reduced maxilla (Clark and Hopson, 1985). Velazco et al. (2017) found it to be closest to two new genera – *Shartegodon* and *Nuurtherium* – from the Ulan Malgait Svita of Mongolia.

Docodonts are a group of mammaliaforms known from the Middle Jurassic to Early Cretaceous of Laurasia. They are among the closest relatives of the Mammalia and display a high ecological diversity, including forms considered to be burrowing, semiaquatic, and arboreal (Ji et al., 2006; Luo et al., 2015; Meng et al., 2015; Meng, 2017).

Dsungarodon zuoi Pfretzschner et al. 2005 is a docodont dentary from the upper Shishugou Formation at Wucaiwan. It was described as *Acuodulodon suni* Hu et al. 2007 – a new taxon – but is considered a subjective junior synonym of *D. zuoi* (Pfretschner et al., 2005) by Martin et al. (2010). Hu et al. (2007) distinguished it from the described dental morphology of *D. zuoi,* known only from isolated teeth from the Qigu Formation of Xinjiang, but Martin et al. (2010) noted that the original description of *D. zuoi* had misinterpreted important aspects of the dentition, and with new material and interpretations there were no significant differences between the two taxa.

A second docodontid taxon is known from a mostly complete articulated skeleton (IVPP V31407, Fig. 6d) found with the *Limusaurus inextricabilis* holotype in the upper Shishugou Formation at Wucaiwan, currently under study by Meng Jin. An isolated docodont tooth was also recovered from the *Klamelia* site at Konglonggou.

Eutriconodonts are a group of mammalians with a nearly global distribution during the Jurassic and Cretaceous. They are widely accepted as an early-diverging lineage of therian mammals, though one study considers eutriconodonts as a paraphyletic group outside the crown group Mammalia (Celik and Phillips, 2020). Eutriconodonts display a high ecological diversity: mostly carnivorous including scavenging and piscivorous forms, and some insectivorous, and display adaptations to aquatic, fossorial, arboreal, and aerial locomotion (Hu et al., 2005; Jin et al., 2006; Meng et al., 2006; Luo et al., 2007).

Klamelia zhaopengi Chow and Rich 1984 is represented by a single dentary of *K. zhaopengi* that was described by Chow and Rich (1984). No further specimens have been found in spite of screen washing the original site by the Sino-American expeditions. Chow and Rich (1984) considered it to be a gobiconodontan, but the interpretation of the tooth positions by Chow and Rich (1984) was questioned by Rougier et al. (2001), who considered it to be of uncertain position within Mammaliaformes. In their description of *Ferganodon* from the Middle Jurassic Balaban Svita of Kyrgyzstan, Martin and Averianov (2007) supported the tooth position interpretation of Chow and Rich (1984) and erected the Klameliidae within Eutriconodonta for the two sister taxa.

3.5 Squamata

The Shishugou squamates are represented by at least two taxa. The larger of the two is represented by many isolated vertebrae and one incomplete associated skeleton. Some vertebral features such as platynotan vertebrae are suggestive of its reference to the Paramacellodidae, an early squamate clade with a global distribution from Middle Jurassic through the end of the Cretaceous. It is either referrable to scincomorphs or cordyloids. The other taxon is heavily armored and is represented by two articulated skeletons with skulls (IVPP V17916; IVPP V 31401, Fig. 6e). These specimens are currently under study by Hongyu Yi.

3.6 Testudinata

Shishugou has yielded abundant turtle fossils (e.g., Fig. 6f), and they are in general similar to those from the Shaximiao Fauna, but they also display some differences. Sichuanchelyidae is a stem turtle clade ranging from Middle Jurassic to late Paleocene of Laurasia and it is closely related to the crown group Testudines (Adán, 2020).

Several skeletons of *Sichuanchelys palatodentata* Joyce et al. 2016 were described by Joyce et al. (2016) from the upper Shishugou Formation at Wucaiwan. They have palatal teeth. *Sichuanchelys* is otherwise known from *S. chowi* in the lower Shaximiao Formation of Sichuan (Ye and Pi, 1997). However, Joyce (2017) found *S. palatodentata* to be closer to *Mongolochelys* from the Late Cretaceous of Mongolia than to *S. chowi*, the genotypic species, indicating that "*S.*" *palatodentata* may belong in a different genus.

Xinjiangchelyidae is a turtle lineage that diverged later than Sichuanchelyidae, and it is widely accepted to be a stem group of the hidden-necked turtles (Cryptodira), one major lineage of Testudines. However, it has also been hypothesized to be the sister group to the Testudines (Evers and Benson, 2019).

Xinjiangchelys junggarensis Ye 1986 was originally recovered from Jiangjunmiao (Ye, 1986). The Sino-American expeditions collected thirteen specimens from the upper part of the Shishugou at Wucaiwan Brinkman et al. (2012).

X. radiplacatoides Brinkman et al. 2013 is based on numerous specimens that the Sino-American expeditions collected from Wucaiwan and the CCDP collected from Jiangjunmiao. It is very similar to *X. radiplacatus* from the upper Shaximiao Formation in Sichuan. Joyce et al. (2016) found it to be closest to *X. wusu* from the Qigu Formation of Turpan, Xinjiang and *Annemys levensis* from the Ulan Malgait Svita of Mongolia but did not include *X. radiplacatus* in the analysis.

X. chowi Matzke et al. 2005 is from the Toutunhe Formation near Urumchi, Xinjiang and is present in the upper Shishugou at Wucaiwan (Brinkman et al., 2012).

The genus *Annemys* Sukhanov and Narmandakh 2006 was described on the basis of two species from the Ulan Malgait Svita at Shar Teg, Mongolia (Rabi et al., 2014). It is also known from the Qigu Formation of Xinjiang (Wings et al., 2012), the Itat Formation of Russia (Danilov et al., 2018), the Tiaojishan Formation of Hebei (Tong et al., 2021) and from two specimens including a skull from Wucaiwan described by Brinkman et al. (2012). The skull differs from that of *A. levensis,* but because the skull of *A. latiens* is not known, it is not clear whether this is *A. latiens* or a new species.

3.7 Crocodylomorpha

Shishugou crocodylomorphans are represented by the early-diverging crocodylomorphan *Junggarsuchus sloani*, the shartegosuchids *Nominosuchus* and *Shartegosuchus*, and the goniopholidid *Sunosuchus*.

Junggarsuchus sloani Clark et al. 2004 is known mainly from the holotype skull (Fig. 6g) and anterior skeleton from the middle of the formation at Wucaiwan (Clark et al., 2004), as well as a few isolated vertebrae from the lower part of the formation there. The posterior part of a skeleton in the neck of the *Haplocheirus sollers* holotype may belong to this species but requires preparation. A detailed description by Ruebenstahl et al. (2022) found it to be part of a group including crocodyliforms, *Macelognathus* from the Kimmeridgian Morrison Formation, and *Almadasuchus* from the Late Jurassic part of the Cañadon Asfalto Formation of Argentina, all sharing a firmer articulation of the quadrate to the braincase than in more basal crocodylomorphs. The poorly known *Phyllodontosuchus* from the Lower Jurassic Lufeng Formation of Yunnan is placed with *Junggarsuchus* in some analyses. An undescribed taxon very similar to *J. sloani* has been reported from the Yanliao (Daohugou) Fauna of Hebei (Xu et al., 2015).

Shartegosuchidae is an early-diverging crocodyliform lineage restricted in distribution to the Late Jurassic to

Early Cretaceous of Laurasia. At least two shartegosuchid taxa are known from the Shishugou Fauna.

Nominosuchus Efimov 1996 is represented by numerous specimens, many nearly complete, from the upper Shishugou at Wucaiwan. It is a crocodyliform that is very similar to *Nominosuchus matutinus* (Efimov, 1996) from the Ulan Malgait Svita at Shar Teg, Mongolia (Clark and Xu, 2009a; Clark and Xu, 2009b). Some of the known specimens occur in concentrations of multiple individuals at small localities. Study of these specimens is currently under way by James Clark.

A nearly complete, articulated skeleton of a small crocodyliform from the upper Shishugou at Wucaiwan is tentatively identified as *Shartegosuchus* Efimov 1988, a taxon otherwise known only from the Upper Jurassic Ulan Malgait Svita at Shar Teg, Mongolia (Dollman et al., 2018). It shares with *Shartegosuchus* the lack of an antorbital fenestra and ornamentation around the occipital margin of the parietal and squamosal, similar also to the shartegosuchid *Fruitachampsa* from the Morrison Formation of Colorado (Clark, 2011).

Goniopholididae is a neosuchian clade with a distribution from the Early Jurassic to the Late Cretaceous of Laurasia, and the members of this group are superficially similar to living crocodilians in many semi-aquatic adaptations but also display significant differences.

Sunosuchus junggarensis Wu et al. 1996 was described by Wu and Sues (1996) on the basis of six specimens collected by the CCDP from Wucaiwan, and Sino-American expeditions collected a few additional specimens (e.g., WCW-16-A-40, Fig. 6h). Its relationships within Goniopholididae are poorly understood; Andrade et al. (2011) found it closest to *Eutretauranosuchus* from the Upper Jurassic Morrison Formation of North America within a clade including the type species of *Sunosuchus* (*S. miaoi*), Pritchard et al. (2013) found it closest to *Calsoyasuchus* from the Lower Jurassic Kayenta Formation of Arizona, and Groh et al. (2020) found it closest to the type species of *Sunosuchus* but did not include *Calsoyasuchus*.

3.8 Pterosauria

Pterosaurs are represented by at least two taxa in the Shishugou Fauna, including a rhamphorhynchid and a pterodactyloid. The Rhamphorhynchidae is an early-diverging pterosaur lineage restricted in Jurassic temporally. One specimen of this group was collected from the upper Shishugou Formation. The Pterodactyloidea is the largest pterosaur clade, including most of pterosaur species diversity. One earliest-diverging pterodactyloid species has been found in the lower Shishugou Formation.

Sericipterus wucaiwanensis Andres et al. 2010 is known from a single crushed skeleton (Fig. 6i) from the upper Shishugou Formation at Wucaiwan. Andres et al. (2010) found it closest to *Angustinaripterus longicephalus* from the lower Shaximiao Formation of Sichuan, and in an analysis accompanying the description of the new species *Dearc sgiathanach* from the Middle Jurassic of Scotland, Jagielska et al. (2022) found *Dearc* in an unresolved trichotomy with the two Chinese species.

Kryptodrakon progenitor Andres et al. 2014 is the oldest known pterodactyloid, and is known from a single fragmentary specimen from the lower part of the Shishugou at Wucaiwan. Andres et al. (2014) found it as the earliest diverging pterodactyloid.

3.9 Sauropoda

Shishugou sauropods are represented by numerous fossils, mostly fragmentary ones (Tütken et al., 2004). Most of the fossils are identified as mamenchisaurids, some as turiasaurians or early-diverging macronarian sauropods, and some as titanosauriforms. Titanosauriformes is the largest clade within the Macronaria, the sister group to the Diplodocoidea; Turiasauria is an early-diverging eusauropod clade mostly known from the Middle Jurassic to the Early Cretaceous of Europe, North America, and Africa; Mamenchisauridae is an early-diverging eusauropod clade mostly restricted in distribution to the Early Jurassic to the Early Cretaceous of Asia, though one species has also been found in Africa (Mannion et al., 2019). Shishugou mamenchisaurids include three reported species.

Mamenchisaurus sinocanadorum Russell and Zheng 1994 is based on a neck and associated skull (Fig. 7a) remains from the upper Shishugou Formation at Jiangjunmiao (Russell and Zheng, 1993). A recent phylogenetic analysis places it closer to *Qijianglong* from the Lower Cretaceous Suiling Formation of Sichuan rather than to other named species of *Mamenchisaurus* (Moore et al., 2020). A series of cervicodorsal vertebrae from Wucaiwan, IVPP field number WCW-05-35 (Moore et al., 2020, fig. 33D), is very similar to *M. sinocanadorum* but distinguishable from it.

Klamelisaurus gobiensis Zhao 1993 is known from a single, moderately complete skeleton lacking a skull (Fig. 7b) from the lower Shishugou at Jiangjunmiao (Zhao, 1993). A recent redescription of *K. gobiensis* by Moore et al. (2020) found it to be closely related to *Mamenchisaurus hochuanensis* from the upper Shaximiao Formation.

Tienshanosaurus chitaiensis Young 1937 needs a detailed redescription, but its current position seems to be near mamenchisaurids (Moore et al., 2020). It was the first dinosaur described from the Shishugou Formation, apparently from the Jiangjunmiao area (Young, 1937). Dong (1990) identified a specimen from Wucaiwan comprising articulated cervical and caudal vertebrae (IVPP V8301) as *Tienshanosaurus* sp.

Bellusaurus sui Dong 1990 is represented by relatively abundant (scapulae suggest at least 17 individuals) disarticulated remains of sub-adult individuals, from a single site at Konglonggou (Dong, 1990). Sino-American expeditions re-opened the quarry and recovered important new skull material, described by Moore et al. (2018). A recent analysis found it to be an early diverging macronarian sauropod (Moore et al., 2020).

Fushanosaurus qitaiensis Wang et al. 2019 is known from a single large femur from Jiangjunmiao. It was referred to the Titanosauriformes (Wang et al., 2019), but the characters cited have a broader distribution, including more basal taxa such as *Jobaria* and *Chuanjiesaurus* (A.

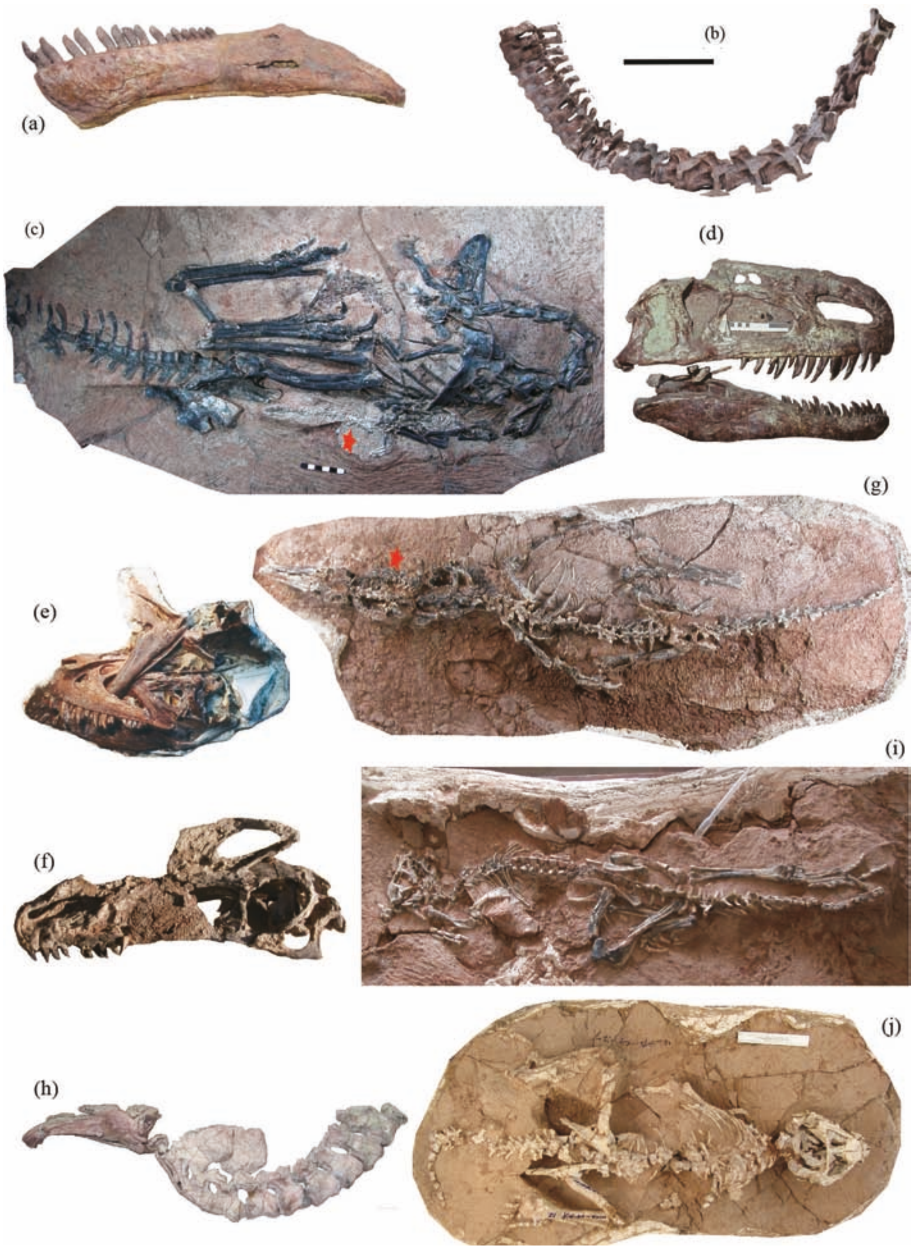

Fig. 7. Photographs of selected Shishugou dinosaur fossils.
(a) The mandible of the sauropod *Mamenchisaurus sinocanadorum*; (b) the sauropod *Klamelisaurus gobiensis* presacral vertebral series; (c) the holotype of the ceratosaur *Limusaurus inextricabilis* preserved together with a shartegosuchid crocodylomorphan skeleton (as indicated by a red star); (d) the skull and mandible of the early-diverging tetanuran *Monolophosaurus jiangi* holotype; (e) the skull and mandible of the allosauroid *Sinraptor dongi* holotype; (f) the tyrannosauroid *Guanlong wucaii* holotype skull; (g) the alvarezsaur *Haplocherius sollers* holotype preserved together with a partial crocodylomorphan skeleton (as indicated by a red star); (h) the stegosaur *Jiangjunosaurus junggarensis* holotype; (i) an early-diverging ornithischian skeleton; (j) the ceratopsian *Yinlong downsi* holotype.

Moore, pers. comm.).

A small cervical vertebra from the lower Shishugou at Wucaiwan was identified as a brachiosaurid (Hone et al., 2009), but the characters cited have a broader distribution than Brachiosauridae and it shares features with Mamenchisauridae, especially *Klamelisaurus* (A. Moore, pers. comm.).

3.10 Theropoda

Theropoda is represented by one noasaurid ceratosaur species, several species covering a few tetanuran subclades including Alvarezsauroidea, Metriacanthosauridae, and Tyrannosauroidea, and possible dromaeosaurids and troodontids represented by dental fossils in the Shishugou Fauna.

The Noasauridae is a subgroup of the ceratosaurian theropods, mostly known from the Cretaceous of Gondwana and some from Europe and Asia. *Limusaurus* represents the only known Asian noasaurid, but some theropod fossils (e.g., the paratype of

Chuandongocoelurus primitivus; Stiegler, 2019) from the Shaximiao fossil assemblage are probably referable to the Ceratosauria and possibly even to the Noasauridae.

Limusaurus inextricabilis Xu et al. 2009 is an unusual species that is the first ceratosaur known from Asia (Xu et al., 2009). It is represented by 19 partial to nearly complete neonate to adult skeletons (Fig. 7c). They occur in three assemblages in the upper Shishugou that was deposited as mire pits (Eberth et al., 2010). The postcranial skeleton was described by Stiegler (2019). The unusual occurrence of teeth in the youngest specimens and their loss in juveniles and adults has received particular attention (Wang et al., 2017a, b). A phylogenetic analysis by J. Stiegler (in Wang et al., 2017a) places *Limusaurus* with *Elaphrosaurus* (Upper Jurassic Tendaguru Formation of Tanzania) and *Spinostropheus* (Middle Jurassic Tiouraren Formation of Niger).

The Tetanurae is a species-rich clade that includes birds. The Shishugou tetanurans include one early-diverging tetanuran species, possibly two or three species of metriacanthosaurid tetanurans, and several species of coelurosaurian tetanurans that represent at least the Alvarezsauroidea and Tyrannosauroidea.

Monolophosaurus jiangi Zhao and Currie 1994 is known from a single partial skeleton with skull (Fig. 7d) from Jiangjunmiao (Zhao and Currie, 1993). The postcranial skeleton was re-described by Zhao et al. (2009). Carrano et al. (2012) found it to be an early branching tetanuran. Isolated teeth possibly referable to *Monolophosaurus* were found at Wucaiwan (Han et al., 2011).

Metriacanthosauridae is a subgroup of allosauroid theropods from the Middle Jurassic to the Early Cretaceous of Europe and Asia. This group seems to represent the dominant predatory animals in the Shishugou Fauna.

Sinraptor dongi Currie and Zhao 1994 is known from a single partial skeleton with skull (Fig. 7e) from Jiangjunmiao. Its anatomy was described by Currie and Zhao (1993), Currie (2006), and Hendrickx et al. (2020). It is closely related to *Sinraptor heipingensis* Gao (1992) from the upper Shaximiao Formation of Sichuan (Gao, 1992), originally placed in the genus *Yangchuanosaurus* (Dong, 1978). Carrano et al. (2012) found *S. dongi* to be most closely related to *Siamotyrannus isanensis*, from the Lower Cretaceous Sao Khua Formation of Thailand. An isolated left metatarsal IV from the upper Shishugou at Wucaiwan is similar to that of *S. dongi* but differs in some respects, such as being more robust, and may represent a different species of *Sinraptor* (He et al., 2013). Isolated teeth possibly referable to *Sinraptor* were found at Wucaiwan (Han et al., 2011), and an extremely large tooth from the upper Shishugou at Wucaiwan–the largest of any Jurassic theropod – may be from an unusually large *Sinraptor* or a related form (Xu and Clark, 2008). The presence of a metriacanthosaurid in the Qigu Formation of Liuhuanggou, southern Junggar Basin is inferred from bitemarks in sauropod bones (Augustin et al., 2020).

The Coelurosauria is a tetanuran theropod clade whose fossil record is relatively poor in Jurassic sediments. However, the Shisugou Formation has produced relatively abundant coelurosaurian fossils, including the early-diverging coelurosaurian *Zuolong*, one tyrannosauroid species, three alvarezsauroid species, and some isolated teeth from Wucaiwan that are possibly referable to Dromaeosauridae and Troodontidae (Han et al., 2011).

Zuolong salleei Choiniere et al. 2010 is an associated partial skeleton from the upper Shishugou at Wucaiwan that represents an early branching coelurosaur (Choiniere et al., 2010a).

Tyrannosauroidea is mostly known from the Cretaceous of Laurasia, but several species are also known from the Jurassic.

Guanlong wucai Xu et al. 2006 is the best known early tyrannosauroid, represented by adult and juvenile skeletons with nearly all elements known except the end of the tail (Xu et al., 2006a). A third specimen was collected after the original description and possesses a more complete cranial crest than the holotype (Fig. 7f). It is a member of an early branching tyrannosauroid clade, the Proceratosauridae (Rauhut et al., 2010), including *Protoceratosaurus bradleyi* (Middle Jurassic Great Oolite of England) and *Kileskus aristotocus* (Middle Jurassic Itat Formation of Russia). A detailed description of its osteology was presented in the dissertation of J. Choiniere (2010) and a publication is in preparation.

Alvarezsauroidea is a maniraptoran coelurosaurian clade, late-diverging members of which were once considered as secondarily flightless birds. The three Shishugou alvarezsauroids represent the only Jurassic members of the group, and the remaining species are all known from the Cretaceous.

Haplocheirus sollers Choiniere et al. 2010a is known from a nearly complete skeleton (Fig. 7g), and is the best known alvarezsauroid from before the Late Cretaceous (Choiniere et al., 2010). The skull was described by Choiniere et al. (2014), and the postcranial skeleton was described in Choiniere's 2010 dissertation. It is more closely related to later alvarezsauroids than are the other two Shishugou alvarezsauroids (Qin et al., 2019).

Aorun zhaoi Choiniere et al. 2013 is known only from a partial skeleton with a skull, and died at less than a year old (Qin et al., 2021). However, it possesses unique features that are not thought to be ontogenetically labile. The original analysis placed it as an early branching coelurosaurian (Choiniere et al., 2013), but Xu et al. (2018) and Qin et al. (2019) found it to be an early branching alvarezsauroid.

Shishugounykus inexpectus Qin et al. 2019 is the third alvarezsauroid from the upper Shishugou at Wucaiwan, and is known from a partial postcranial skeleton (Qin et al., 2019). Qin et al. (2019) found it in an unresolved trichotomy with *Aorun* and *Haplocheirus* + later alvarezsauroids.

3.11 Ornithischia

The Shishugou ornithischians are represent by stegosaurs, early-diverging neoornithischians, and ceratopsians.

Jiangjunosaurus junggarensis Jia et al. 2007 was the first stegosaur discovered in the formation, at Jiangjunmiao (Jia et al., 2007). It is known from a partial skull and neck (Fig. 7h). Raven and Maidment (2017) found it to be the sister-taxon to the remaining members of the Stegosauridae, just outside of *Gigantspinosaurus sichuanensis* Ouyang (1992) from the upper Shaximiao Formation of Sichuan.

A stegosaur pelvis collected from the cliffs west of Jiangjunmiao and a disarticulated partial skeleton from the upper beds at Wucaiwan have not been studied, but an isolated stegosaur tooth from Jiangjunmiao was described by Wings et al. (2015).

The holotype of "*Gongbusaurus*" *wucaiwanensis* Dong 1989 is a fragmentary skeleton from the upper Shishugou at Wucaiwan (Dong, 1989) that cannot be located. The genus is based on a species from the upper Shaximiao Formation of Sichuan that is a nomen dubium (Norman et al., 2004). Several articulated skeletons with skulls from the upper Shishugou at Wucaiwan (e.g., IVPP 14559) and an incomplete skeleton from the cliffs west of Jiangjunmiao likely represent "*G.*" *wucaiwanensis* (Fig. 7i) and are currently being studied by C. Forster and others; a photograph of one skull was published by Li et al. (2018). The new material is similar to basal neornithischians such as *Hexinlusaurus* from the lower Shaximiao Formation of Sichuan but its relationships are not yet resolved.

Ceratopsia is a neoornithischian clade with members that are mostly known from the Cretaceous. The Shishugou ceratopsian fossils represent the best fossil record of the group in Jurassic sediments.

Multiple skeletons of *Yinlong downsi* Xu et al. 2006a, an early branching ceratopsian, are known from the upper Shishugou at Wucaiwan (Fig. 7j). The skull was described by Han et al. (2016), the dentition by Tanoue et al. (2009) and the postcranial skeleton by Han et al. (2018). Originally believed to be the earliest-diverging ceratopsian (Xu et al., 2006b), an analysis by Han et al. (2018) found it to be a member of a clade with *Chaoyangsaurus* (Upper Jurassic-Lower Cretaceous Tuchengzi Formation of Liaoning) within which it is closest to *Stenopelix valdensis* (Lower Cretaceous Obernkirchen Sandstein Formation of Germany).

Hualianceratops wucaiwanensis Han et al. 2015 from the upper Shishugou at Wucaiwan is known from a fragmentary skull and postcranial skeleton (Han et al., 2015). It is similar to *Y. downsi* but differs in several respects. Han et al. (2018) found it to be closest to *Xuanhuaceratops niei* (Upper Jurassic–Lower Cretaceous Houcheng Formation of Hebei).

4 Discussion

The Shishugou Fauna is largely a typical Middle–Late Jurassic Laurasian terrestrial fauna. It contains many types of animals that are common in the Jurassic of Laurasia, including tritylodontid, docodont, and eutriconodont mammaliamorphs, xinjiangchelyid and sichuanchelyid turtles, paramacellodid lizards, shartegosuchid and goniopholidid crocodylomorphs, rhamphorhynchid pterosaurs, mamenchisaurid sauropods, metriacanthosaurid theropods, and stegosaurid ornithischians. Some of these taxa have relatively restricted geographical distributions and have been considered as evidence for the presence of an endemic dinosaur fauna in central Asia during the Middle–Late Jurassic (Russell, 1993). However, the Shishugou Fauna also contains several relatively rare taxa for a Jurassic fauna, such as lungfishes and brachyopoid temnospondyls, and particularly, early representatives of several archosaurian taxa, such as the earliest known alvarezsauroid and ceratopsian dinosaurs, the earliest known pterodactyloid species, and early noasaurid and tyrannosauroid theropods. The Shishugou fauna is thus significant for understanding Jurassic terrestrial vertebrate biogeography and temporal distribution of several vertebrate groups.

It should be noted that fossil vertebrates similar in age and taxonomy to those from the Shishugou Formation in the eastern Junggar Basin are also known from several nearby areas, such as the southern edge of the Junggar Basin and the adjacent Turpan-Hami Basin on the south side of the Tian Shan (Martin et al., 2008; Wings et al., 2012). The southern Junggar, best represented by the Liuhuanggou site approximately 200 km southwest of Wucaiwan, has produced (mainly using screen washing) a diverse vertebrate fauna collected from the Qigu Formation. The fauna includes a phylogenetically wide range of vertebrate taxa, including hybodont sharks, actinopterygians, both non-lissamphibian and lissamphibian temnospondyls, squamates, turtles, crocodylomorphs, and mammals (Maisch et al., 2003; Martin et al., 2008, 2010; Skutschas et al., 2009; Richter et al., 2010). Comparatively, only a few dinosaur fossils are known from the southern Junggar, including one fragmentary specimen of the ankylosaur *Tianchiasaurus* (Dong, 1993a) and some stegosaur teeth (Wings et al., 2015) and a possible mamenchisaurid (Maisch and Matzke, 2019). Nevertheless, the southern Junggar is similar to the eastern Junggar Shishugou Fauna in the general composition of vertebrate fossils, and the two areas even share some vertebrates at the species level, such as the turtle *Xinjiangchelys chowi* and the mammaliaform *Dsungarodon zuoi*. The Jurassic vertebrate fossils from the Turpan–Hami Basin are mainly recovered from the Qiketai area, where a number of dinosaur and other vertebrate fossils, including mamenchisaurid sauropods (Upchurch et al., 2021) and xinjiangchelyid turtles (e.g., *Annemys*) (Wings et al., 2012), have been recovered from the Middle to Late Jurassic deposits that have been assigned to different formations, including the Toutunhe/Qiketai, Qigu, and Kalaza formations (Maisch and Matzke, 2019; Upchurch et al., 2021). Although the stratigraphic assignments and correlations of fossil-bearing-beds in the southern Junggar and Turpan–Hami Basins are not yet in agreement (Maisch and Matzke, 2019; Upchurch et al., 2021), the fossil assemblages recovered from these areas are closely related, or even referable to the Shishugou Fauna.

On a larger geographic scale, several fossil assemblages similar to the Shishugou Fauna are known from other parts of China and nearby countries. They include the Shaximiao Fauna in Sichuan Province, southwestern China, the Shar Teg fossil assemblage in western

Mongolia, the Karabastau fossil assemblage in southern Kazakhstan, and the Yanliao/Daohugou Biota of northeastern China (Dzik et al., 2010; Zhou et al., 2010; Sullivan et al., 2014; Huang, 2015; Xu et al., 2016; Liu et al., 2021). One study emphasizes the similarities between these faunas/biotas, which considers these faunas/biotas as the same in a broad sense (Huang, 2015). Among these faunas, the Shishugou Fauna is most similar to the Shaximiao Fauna and the Shar Teg fossil assemblage.

The Shishugou and the Shaximiao faunas not only are nearly identical to each other in faunal composition at a relatively high level (Russell, 1993), and also share low-ranked taxa (e.g., *Mamenchisaurus, Sichuanchelys*, and *Sinraptor*) and some Shishugou fossils have even referred to the Shaximiao species (e.g., *Bienotheroides zigongensis*) (Sun and Cui, 1989). The Shar Teg fossil assemblage found at Shar Teg, Mongolia, approximately 450 km E–SE of Jiangjunmiao, is preserved in the Shar Teg and overlying Ulan Malgait Svitas (the Russian svita is somewhat comparable to a formation). Dinosaur fossils are rare in the Ulan Malgait Svita, which preserves a diversity of small vertebrates, plants and invertebrates while the Shar Teg Svita is notable for its insect fauna (Ponomarenko et al., 2014). Similar to the Shaximiao Fauna, the Ulan Malgait fossils are similar to those of the Shishugou not only in many high-ranked taxa, but also in some taxa at the genus (e.g., the crocodylomorph *Shartegosuchus* and the turtle *Annemys*) or even species level (e.g., probably *Nominosuchus matutinus*) (Efimov, 1996; Clark and Xu, 2009a, b).

Several studies have compared these Middle-Late Jurassic terrestrial faunas from several different perspectives, including faunal composition, paleoecology, biogeography, taphonomy and sedimentology (He et al., 2013; Sullivan et al., 2014; Huang, 2015; Xu et al., 2016; Liu et al., 2021). Some of these studies have revealed some significant differences between these faunas. In terms of high-ranked taxa, the Junggar deposits have produced the most diverse vertebrate fossils and the Yanliao Biota the least diverse ones (Fig. 8). The former cover nearly all major vertebrate groups, including several fish, both non-lissamphibian and lissamphibian temnospondyls, tritylodontid and mammalian mammaliomorphans, squamates, turtles, several crocodylomorphan groups, pterosaurs, sauropods, several ornithischian groups, multiple theropod groups, and even possibly choristoderes. The Yanliao Biota lacks some common elements typical of a Middle-Late Jurassic Laurasian terrestrial ecosystem, including sauropods, relatively large theropods, some ornithischian taxa, turtles, and tritylodontids, and is relatively poor in fish and crocodylomorphan fossil records. There are several different factors leading to these differences. Some apparent taxonomic differences are probably related to taphonomy. For example, the alluvial Junggar deposits are likely to favor the preservation of robust terrestrial animals (e.g., abundant tritylodontid, crocodylomorph and turtle material) but not the delicate caudates and pterosaurs that are common in Yanliao Biota (Sullivan et al., 2014). The preservation of relatively large-sized animals in the Shishugou and Shaximiao such as sauropods, stegosaurs and early-diverging tetanurans all of which are absent in Yanliao Biota is also likely to be taphonomy-related. Size-biased preservation is even seen within the Shishugou Fauna (e.g., relatively abundant small fossils in Wucaiwan but few in Jiangjunmiao of small-sized fossils). Other taxonomic differences likely reflect genuine ecologic or biogeographic patterns (He et al., 2013; Sullivan et al., 2014; Liu et al., 2021). For example, the absence of several coelurosaurian groups such as alvarezsauroids and tyrannosauroids from the Shaximiao, the absence of heterodontosaurid and paravian dinosaurs from the Junggar and Shaximiao, and the absence of ceratopsian dinosaurs from Yaoliao Biota likely reflect real biogeographic differences. In other words, at least some of these taxa may have had only limited geographical

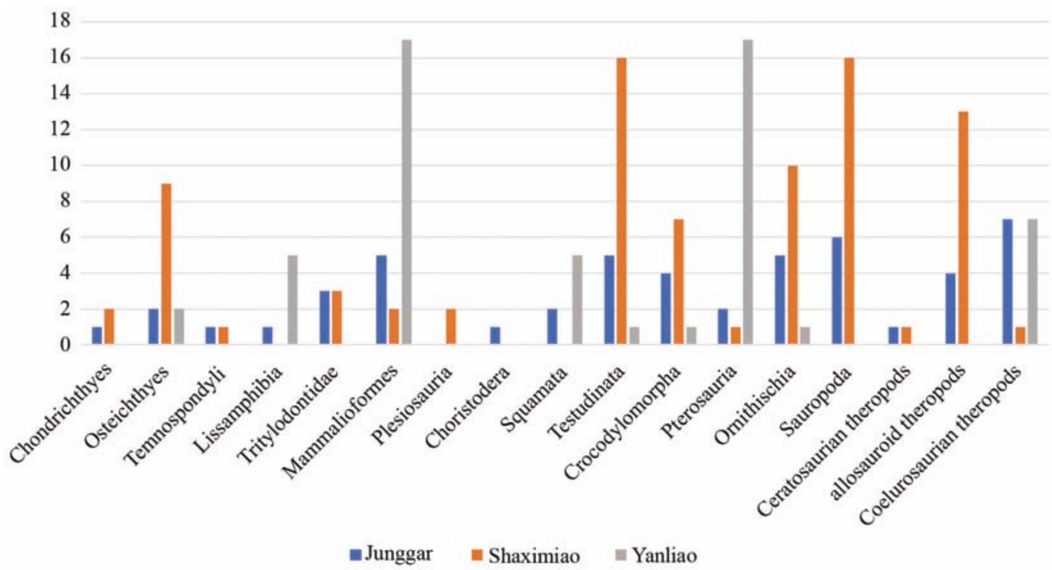

Fig. 8. Comparison of vertebrate taxonomical composition of the Shishugou, Shaximiao, and Yanliao faunas.

distributions between the Middle to Late Jurassic transition. The absence of gliding and aquatic mammaliomorphans from the Junggar and Shaximiao, and their presence in Yanliao Biota likely can be attributed to ecological differences. There is evidence suggesting relatively open environments (e.g., floodplains) for the Shishugou Fauna but relatively closed environment (e.g., forests) for the Yanliao Biota. The Junggar deposits seem to have preserved the most complete vertebrate fossil record for a Middle–Late Jurassic Laurasian terrestrial fauna.

Acknowledgements

The authors thank Wang Haijun and other members of the Sino-American expedition team for collecting fossils and other geological samples, D. Ward for screen washing at Konglonggou, A. Moore for discussion, Ren Minghui for editing the figures, and the Smithsonian Freer Gallery Library. The work was supported by the National Natural Science Foundation of China (42288201, 41688103, 40830210, 41120124002), the National Science Foundation Division of Earth Sciences (NSF EAR 0310217, 0922187, 1636753) and the National Geographic Society.

Manuscript accepted Aug. 8, 2022
edited by FEI Hongcai

References

Adán, P.-G., 2020. Surviving the Cretaceous-Paleogene mass extinction event: A terrestrial stem turtle in the Cenozoic of Laurasia. Scientific Reports, 10: 1489.

Andrade, M.B., Edmonds, R., Benton, M.J., and Schouten, R., 2011. A new Berriasian species of *Goniopholis* (Mesoeucrocodylia, Neosuchia) from England, and a review of the genus. Zoological Journal of the Linnean Society, 163 (s1): S66–S108.

Andres, B., Clark, J., and Xu, X., 2014. The earliest pterodactyloid and the origin of the group. Current Biology, 24(9): 1011–1016.

Andres, B., Clark, J.M., and Xu, X., 2010. A new rhamphorhynchid pterosaur from the Upper Jurassic of Xinjiang, China, and the phylogenetic relationships of basal pterosaurs. Journal of Vertebrate Paleontology, 30(1): 163–187.

Augustin, F.J., Matzke, A.T., Maisch, M.W., and Pfretzschner, H.-U., 2020. A theropod dinosaur feeding site from the Upper Jurassic of the Junggar Basin, NW China. Palaeogeography, Palaeoclimatology, Palaeoecology, 560: 109999.

Augustin, F.J., Matzke, A.T., Maisch, M.W., and Pfretzschner, H.-U., 2021. Dinosaur taphonomy of the Jurassic Shishugou Formation (Northern Junggar Basin, NW China) – insights from bioerosional trace fossils on bone. Ichnos, 28(2): 87–96.

Brinkman, D.B., Eberth, D.A., Xu, X., Clark, J.M., and Wu, X.C., 2012. Turtles from the Jurassic Shishugou Formation of the Junggar Basin, People's Republic of China, with comments on the basicranial region of basal eucryptodires. In: Brinkman, D.B., Holroyd, P.A., and Gardner, J.D., (eds.), Morphology and Evolution of Turtles. Dordrecht: Springer Science+Business Media, 147–172.

Carrano, M.T., Benson, R.B.J., and Sampson, S.D., 2012. The phylogeny of Tetanurae (Dinosauria: Theropoda). Journal of Systematic Palaeontology, 10(2): 211–300.

Celik, M.A., and Phillips, M.J., 2020. Conflict resolution for Mesozoic mammals: Reconciling phylogenetic incongruence among anatomical regions. Frontiers in Genetics, 11: 0651.

Choiniere, J., 2010. Anatomy and systematics of coelurosaurian theropods from the Late Jurassic of Xinjiang, China, with comments on forelimb evolution in Theropoda (Ph.D. dissertation), George Washington University.

Choiniere, J.N., Clark, J.M., Forster, C.A., Norell, M.A., Eberth, D.A., Erickson, G.M., Chu, H.J., and Xu, X., 2013. A juvenile specimen of a new coelurosaur (Dinosauria: Theropoda) from the Middle–Late Jurassic Shishugou Formation of Xinjiang, People's Republic of China. Journal of Systematic Palaeontology, 12(2): 177–215.

Choiniere, J.N., Clark, J.M., Forster, C.A., and Xu, X., 2010a. A basal coelurosaur (Dinosauria: Theropoda) from the Late Jurassic (Oxfordian) of the Shishugou Formation in Wucaiwan, People's Republic of China. Journal of Vertebrate Paleontology, 30(6): 1773–1796.

Choiniere, J.N., Clark, J.M., Norell, M.A., and Xu, X., 2014. Cranial Osteology of *Haplocheirus sollers* Choiniere et al., 2010 (Theropoda: Alvarezsauroidea). American Museum Novitates, 51(5): 1–44.

Choiniere, J.N., Xu, X., Clark, J.M., Forster, C.A., Guo, Y., and Han, F.L., 2010. A basal alvarezsauroid theropod from the early Late Jurassic of Xinjiang, China. Science, 327(5965): 571–574.

Chow, M.C., and Rich, T.H.V., 1984. A new triconodontan (Mammalia) from the Jurassic of China. Journal of Vertebrate Paleontology 3(4): 226–231.

Clack, J.A., Sharp, E.L., and Long, J.A., 2016. The fossil record of lungfishes. In: Jørgensen, J., Kemp, A., and Wang, T. (eds.), The Biology of Lungfish. Enfield, New Hampshire: Science Publishers Inc.

Clark, J., and Xu, X., 2009a. Shartegosuchid crocodyliforms from the Late Jurassic of Asia and North America. Journal of Vertebrate Paleontology, 29: 79A.

Clark, J.M., 2011. A new shartegosuchid crocodyliform from the Upper Jurassic Morrison Formation of western Colorado. Zoological Journal of the Linnean Society, 163(s1): S152–S172.

Clark, J.M., and Hopson, J.A., 1985. Distinctive mammal-like reptile from Mexico and its bearing on the phylogeny of the Tritylodontidae. Nature, 315: 398–400.

Clark, J.M., and Xu, X., 2009b. Evolutionary transitions among dinosaurs: examples from the Jurassic of China. Evo Edu Outreach, 2: 236–247.

Clark, J.M., Xu, X., F,orster, C.A., and Wang, Y., 2004. A Middle Jurassic 'sphenosuchian' from China and the origin of the crocodylian skull. Nature, 430: 1021–1025.

Currie, P.J., 2006. On the quadrate of *Sinraptor dongi* (Theropoda: Allosauroidea) from the Late Jurassic of China. In: Cziki, Z. (ed.), Mesozoic and Cenozoic vertebrates and paleoenvironments. Tributes to the career of Prof. Dan Grigorescu. Buchaest: Editura Ars Docendi:111–115.

Currie, P.J., and Zhao, X.J., 1993. A new carnosaur (Dinosauria, Theropoda) from the Jurassic of Xinjiang, People's Republic of China. Canadian Journal of Earth Sciences, 30(10–11): 2037–2081.

Danilov, I.G., Obraztsova, E.M., Boitsova, E.A., and Skutchas, P.P., 2018. Diversity of Middle Jurassic turtles from the Berezovsk Quarry locality, Krasnoyarsk Region, Russia: morphology and histological Study. Paleontological Journal, 52(1): 58–70.

Dollman, K.N., Clark, J.M., Norell, M.A., Xu, X., and Choiniere, J.N., 2018. Convergent evolution of a eusuchian-type secondary palate within Shartegosuchidae. American Museum Novitates, 3901: 1–23.

Dong, Z.M., 1978. A new carnosaur from Yongchuan County, Sichuan Province. 23(5): 302–304.

Dong, Z.M., 1985. The Dashanpu dinosaur fauna of Zigong Sichuan, short report V-labyrinthodont Amphibia. Vertebrata PalAsiatica, 23(4): 301–305.

Dong, Z.M., 1989. On a small ornithopod (*Gongbusaurus wucaiwanensis* sp. nov.) from Kelamaili, Junggar Basin, Xinjiang, China. Vertebrata PalAsiatica, 27(2): 140–147.

Dong, Z.M., 1990. Sauropoda from the Kelameili Region of the Junggar Basin, Xinjiang Autonomous Region. Vertebrata PalAsiatica, 28: 43–58.

Dong, Z.M., 1993a. An ankylosaur (Ornithischian dinosaur) from the Middle Jurassic of the Junggar Basin, China. Vertebrata PalAsiatica, 31(4): 257–266.

Dong, Z.M., 1993b. The field activities of the Sino-Canadian Dinosaur Project in China, 1987–1990. *Canadian* Journal of Earth Sciences, 30: 1997–2001.

Dzik, J., Sulej, T., and Niedzwiedzki, G., 2010. Possible link connecting reptilian scales with avian feathers from the early Late Jurassic of Kazakhstan. Historical Biology, 22: 394–402.

Eberth, D.A., 2018. Stratigraphy and paleoenvironmental evolution of the dinosaur-rich Baruungoyot-Nemegt succession (Upper Cretaceous), Nemegt Basin, southern Mongolia. *P*alaeogeography, Palaeoclimatology, Palaeoecology, 494: 29–50.

Eberth, D.A., Brinkman, D.B., Chen, P.J., Yuan, F.T., Wu, S.Z., Li, G., and Cheng, X.S., 2001. Sequence stratigraphy, paleoclimate patterns, and vertebrate fossil preservation in Jurassic Cretaceous strata of the Junggar Basin, Xinjiang Autonomous Region, People's Republic of China. Canadian Journal of Earth Sciences, 38(12): 1627–1644.

Eberth, D.A., Xing, X., and Clark, J.M., 2010. Dinosaur death pits from the Jurassic of China. Palaios, 25(1–2): 112–125.

Efimov, M.B., 1996. The Jurassic crocodylomorphs of Inner Asia. In: Morales, M. (ed.), The Continental Jurassic. Flagstaff: Museum of Northern Arizona Press, 305–310.

Evers, S.W., and Benson, R.B.J., 2019. A new phylogenetic hypothesis of turtles with implications for the timing and number of evolutionary transitions to marine lifestyles in the group. Palaeontology, 62(1): 93–134.

Gao, Y.H., 1992. *Yangchuanosaurus hepingensis*-a new species of carnosaur from Zigong, Sichuan. Vertebara Palasiatica, 30 (4): 313–324.

Gradstein, F.M., Ogg, J.G., Schmitz, M.D., Ogg, G.M., Agterberg, F.P., Anthonissen, D.E., Becker, T.R., Catt, J.A., Cooper, R.A., Davydov, V.I., Gradstein, S.R., Henderson, C.M., Hilgen, F.J., Hinnov, L.A., McArthur, J.M., Melchin, M.J., Narbonne, G.M., Paytan, A., Peng, S., Peucker-Ehrenbrink, B., Pillans, B., Saltzman, M.R., Simmons, M.D., Shields, G.A., Tanaka, K.L., Vandenberghe, N., Van Kranendonk, M.J., Zalasiewicz, J., Altermann, W., Babcock, L.E., Beard, B.L., Beu, A.G., Boyes, A.F., Cramer, B.D., Crutzen, P.J., van Dam, J.A., Gehling, J.G., Gibbard, P.L., Gray, E.T., Hammer, O., Hartmann, W.K., Hill, A.C., Hoffman, P.F., Hollis, C.J., Hooker, J.J., Howarth, R.J., Huang, C., Johnson, C.M., Kasting, J.F., Kerp, H., Korn, D., Krijgsman, W., Lourens, L.J., MacGabhann, B.A., Maslin, M.A., Melezhik, V.A., Nutman, A.P., Papineau, D., Piller, W.E., Pirajno, F., Ravizza, G.E., Sadler, P.M., Speijer, R.P., Steffen, W., Thomas, E., Wardlaw, B.R., Wilson, D.S., and Xiao, S., 2012. The geologic time scale. Boston: Elsevier, 1144.

Grady, W., 1993. The Dinosaur Project: The Story of the Greatest Dinosaur Expedition Ever Mounted. Toronto: Macfarlane Walter and Ross.

Groh, S.S., Upchurch, P., Barrett, P.M., and Day, J.J., 2020. The phylogenetic relationships of neosuchian crocodiles and their implications for the convergent evolution of the longirostrine condition. Zoological Journal of the Linnean Society, 188(2): 473–506.

Han, F.-L., Forster, C.A., Clark, J.M., and Xu, X., 2016. Cranial anatomy of Yinlong downsi (Ornithischia: Ceratopsia) from the Upper Jurassic Shishugou Formation of Xinjiang, China. Journal of Vertebrate Paleontology, 36(1): e1029579.

Han, F., Clark, J.M., Xu, X., Sullivan, C., Choiniere, J., and Hone, D.W.E., 2011. Theropod teeth from the Middle-Upper Jurassic Shishugou Formation of northwest Xinjiang, China. Journal of Vertebrate Paleontology, 31(1): 111–126.

Han, F., Forster, C.A., Clark, J.M., and Xu, X., 2015. A new taxon of basal ceratopsian from China and the early evolution of Ceratopsia. PLoS ONE, 10(12): e0143369.

Han, F., Forster, C.A., Xu, X., and Clark, J.M., 2018. Postcranial anatomy of *Yinlong downsi* (Dinosauria: Ceratopsia) from the Upper Jurassic Shishugou Formation of China and the phylogeny of basal ornithischians. Journal of Systematic Palaeontology, 16(14): 1159–1187.

He, Y.M., Clark, J.M., and Xu, X., 2013. A large theropod metatarsal from the upper part of Jurassic Shishugou Formation in Junggar Basin, Xinjiang, China. Vertebrata PalAsiatica, 51(1): 29–42.

Hedin, S., 1933. *Riddles of Gobi*. New York: E.P. Dutton and Company.

Hendrickx, C., Stiegler, J., Currie, P.J., Han, F., Xu, X., Choiniere, J., and Wu, X.C., 2020. Dental anatomy of the apex predator Sinraptor dongi (Theropoda: Allosauroidea) from the Late Jurassic of China. Canadian Journal of Earth Sciences, 57(9): 1127–1147.

Hinz, J., Smith, I., Pfretzschner, H.-U., Wings, O., and Sun, G., 2010. A high-resolution three-dimensional reconstruction of a fossil forest (Upper Jurassic Shishugou Formation, Junggar Basin, Northwest China). Palaeobiodiversity and Palaeoenvironments, 90(3): 215–240.

Hone, D., Wedel, M., Xu, X., and Clark, J.M., 2009. A small Asian brachiosaurid sauropod dinosaur from the Late Middle Jurassic of China. Journal of Vertebrate Paleontology, 29 (suppl): 116A.

Hu, Y.-M., Meng, J., and Clark, J.M., 2007. A new Late Jurassic docodont (Mammalia) from northeastern Xinjiang, China. *Vertebrata PalAsiatica,* 45: 173–194.

Hu, Y.M., Meng, J., and Clark, J.M., 2009. A new tritylodontid from the Upper Jurassic of Xinjiang, China. Acta Paleontologica Polonica 54(3): 385–391.

Hu, Y.M., Meng, J., Wang, Y.Q., and Li, C.K., 2005. Large Mesozoic mammals fed on young dinosaurs. Nature, 433 (7022): 149–152.

Huang, D.Y., 2015. Yanliao Biota and Yanshan Movement. Acta Palaeontologica Sinica, 54(4): 501–546.

Jagielska, N., Sullivan, M.O., Funston, G.F., Butler, I.B., Challands, T.J., Clark, N.D.L., Fraser, N.C., Penny, A., Ross, D.A., Wilkinson, M., and Brusatte, S.L., 2022. A skeleton from the Middle Jurassic of Scotland illuminates an earlier origin of large pterosaurs. Current Biology, 32: 1–8.

Ji, Q., Luo, Z. X., Yuan, C. X., and Tabrum, A.R., 2006. A swimming mammaliaform from the Middle Jurassic and ecomorphological diversification of early mammals. Science, 311: 1123–1127.

Jia, C., Forster, C.A., Xu, X., and Clark, J.M., 2007. The first stegosaur (Dinosauria, Ornithischia) from the Upper Jurassic Shishugou Formation of Xinjiang, China. Acta Geologica Sinica (English Edition), 81(3): 351–356.

Jin, M., Hu, Y.M., Li, C.K., and Wang, Y.Q., 2006. The mammal fauna in the Early Cretaceous Jehol Biota: implications for diversity and biology of Mesozoic mammals. Geological Journal, 41(3–4): 439–463.

Joyce, W., Rabi, M., Clark, J., and Xu, X., 2016. A toothed turtle from the Late Jurassic of China and the global biogeographic history of turtles. BMC Evolutionary Biology, 16(1): 236.

Joyce, W.G., 2017. A review of the fossil record of basal Mesozoic turtles. Bulletin of the Peabody Museum of Natural History, 58: 65–113.

Kuiper, K.F., Deino, A., Hilgen, F.J., Krijgsman, W., Renne, P.R., and Wijbrans, J.R., 2008. Synchronizing rock clocks of Earth history. Science, 320(5875): 500–504.

Li, Z., Zhou, Z., and Clarke, J.A., 2018. Convergent evolution of a mobile bony tongue in flighted dinosaurs and pterosaurs. PLoS ONE, 13(6): e0198078.

Liu, F., Wu, R., and Han, F.L., 2021. Vertebrate diversity of the Yanliao Biota and comparison with other biotas. Acta Palaeontologica Sinica, 60(4): 2020027.

Liu, J., and Olsen, P., 2010. The Phylogenetic Relationships of Eucynodontia (Amniota: Synapsida). Journal of Mammalian Evolution, 17: 151–176.

Luo, Z.X., Chen, P.J., Li, G., and Chen, M., 2007. A new eutriconodont mammal and evolutionary development in early mammals. Nature, 446: 288–293.

Luo, Z.X., Meng, Q.J., Ji, Q., Liu, D., Zhang, Y.G., and Neander, A.I., 2015. Evolutionary development in basal mammaliaforms as revealed by a docodontan. Science, 347: 760–764.

Maisch, M.W., and Matzke, A.T., 2019. First record of a eusauropod (Dinosauria: Sauropoda) from the Upper Jurassic Qigu-Formation (southern Junggar Basin, China), and a reconsideration of Late Jurassic sauropod diversity in Xinjiang. Neues Jahrbuch für Geologie und Paläontologie -

Abhandlungen, 291: 109–117.
Maisch, M.W., Matzke, A.T., Pfretzschner, H. U., Sun, G., Stöhr, H., and Grossmann, F., 2003. Fossil vertebrates from the Middle and Upper Jurassic of the southern Junggar Basin (NW-China)—results of the Sino-German expeditions 1999–2000. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, 2003: 297–313.
Maisch, M.W., Matzke, A.T., and Sun, G., 2004. A new tritylodontid from the Upper Jurassic Shishugou Formation of the Junggar Basin (Xinjiang, NW china). Journal of Vertebrate Paleontology, 24(3): 649–656.
Mannion, P.D., Upchurch, P., Schwarz, D., and Wings, O., 2019. Taxonomic affinities of the putative titanosaurs from the Late Jurassic Tendaguru Formation of Tanzania: Phylogenetic and biogeographic implications for eusauropod dinosaur evolution. Zoological Journal of the Linnean Society, 185(3): 784–909.
Martin, T., and Averianov, A.O., 2007. A previously unrecognized group of Middle Jurassic triconodontan mammals from Central Asia. Naturwissenschaften, 94: 43–48.
Martin, T., Averianov, A.O., and Pfretzschner, H. U., 2010. Mammals from the Late Jurassic Qigu Formation in the southern Junggar Basin, Xinjiang, Northwest China. Palaeodiversity and Palaeoenvironment, 90: 295–319.
Martin, T., Averianov, A.O., Pfretzschner, H. U., Wings, O., and Sun, G., 2008. A Late Jurassic (Oxfordian) vertebrate assemblage from the southwestern Junggar Basin (Xinjiang Autonomous Region, NW China. Mid-Mesozoic life and environments. Doc Lab Géol Lyon, 164: 62–64.
Matzke, A.T., Maisch, M.W., Sun, G., Pfretzschner, H. U., and Stöhr, H., 2005. A new Middle Jurassic xinjiangchelyid turtle (Testudines; Eucryptodira). Journal of Vertebrate Palaeontology, 25: 63–70.
McKnight, C.L., Graham, S.A., Carroll, A.R., Gan, Q., Dilcher, D.L., Zhao, M., and Liang, Y. H., 1990. Fluvial sedimentology of an Upper Jurassic petrified forest assemblage, Shishu Formation, Junggar Basin, Xinjiang, China. Palaeogeography, Palaeoclimatology, Palaeoecology, 79: 1–9.
Meng, J., Hu, Y. M., Wang, Y. Q., Wang, X. L., and Li, C. K., 2006. A Mesozoic gliding mammal from northeastern China. Nature, 444: 889–893.
Meng, Q.J., Grossnickle, D.M., Liu, D., Zhang, Y.G., Neander, A.I., Ji, Q., and Luo, Z.X., 2017. New gliding mammaliaforms from the Jurassic. Nature, 548: 291–296.
Meng, Q.J., Ji, Q., Zhang, Y.G., Liu, D., Grossnickle, D.M., and Luo, Z.X., 2015. An arboreal docodont from the Jurassic and mammaliaform ecological diversification. Science, 347: 764–768.
Moore, A.J., Mo, J., Clark, J.M., and Xu, X., 2018. Cranial anatomy of *Bellusaurus sui* (Dinosauria: Eusauropoda) from the Middle-Late Jurassic Shishugou Formation of northwest China and a review of sauropod cranial ontogeny. PeerJ, 6(2): e4881.
Moore, A.J., Upchurch, P., Barrett, P.M., Clark, J.M., and Xu, X., 2020. Osteology of *Klamelisaurus gobiensis* (Dinosauria, Eusauropoda) and the evolutionary history of Middle–Late Jurassic Chinese sauropods. Journal of Systematic Palaeontology, 18(16): 1299–1393.
Norman, D.B., Sues, H. D., Witmer, L.M., and Coria, R.A., 2004. Basal Ornithopoda. In: Weishampel, D.B., Dodson, P., and Osmolska, H. (eds.), The Dinosauria (Second Edition). Berkeley: University of California Press: 393–412.
Ouyang, H., 1992. Discovery of G*igantspinosaurus sichanensis* and its scapular spine orientation. Youth Academic Symposium on New Discoveries and Ideas in Stratigraphic Paleontology, 47–49.
Peng, G. Z., Ye, Y., Gao, Y. H., Shu, C. K., and Jiang, S., 2005. Jurassic dinosaur faunas in Zigong. Chengdu: Sichuan Press Group Sichuan People Press House, 1–236.
Pfretzschner, H. U., Martin, T., Maisch, M.W., Matzke, A.T., and Sun, G., 2005. A new docodont mammal from the Late Jurassic of the Junggar Basin in Northwest China. Acta Palaeontologica Polonica, 50 (4): 799–808.
Ponomarenko, A.D., Aristov, D.S., Bashkuev, A.S., Yu, M.G., Khramov, A.V., Lukashevich, E.D., Popov, Y.A., Pritykina, L.N., Sinitsa, S.M., Sinitshenkova, N.D., Sukatsheva, I.D., Vassilenko, D.V., and Yan, E.V., 2014. Upper Jurassic Lagerstätte Shar Teg, southwestern Mongolia. Paleontological Journal, 48(14): 1573–1682.
Pritchard, A.C., Turner, A.H., Allen, E.R., and Norell, M.A., 2013. Osteology of a North American goniopholidid (*Eutretauranosuchus delfsi*) and palate evolution in Neosuchia. American Museum Novitates, 3783: 1–56.
Qin, Z., Clark, J., Choiniere, J.N., and Xu, X., 2019. A new alvarezsaurian theropod from the Upper Jurassic Shishugou Formation of western China. Scientific Reports, 9: 11727.
Qin, Z.C., Qi, Z., Choiniere, J.N., Clark, J.M., Benton, M.J., and Xu, X., 2021. Growth and miniaturization among alvarezsauroid dinosaurs. Current Biology, 31: 3705–3706.
Rabi, M., Sukhanov, V.B., Egorova, V.N., Danilov, I., and Joyce, W.G., 2014. Osteology, relationships, and ecology of *Annemys* (Testudines, Eucryptodira) from the Late Jurassic of Shar Teg, Mongolia, and phylogenetic definitions for Xinjiangchelyidae, Sinemydidae, and Macrobaenidae. Journal of Vertebrate Paleontology, 34(2): 327–352.
Rauhut, O.W.M., Milner, A.C., and Moore-Fay, S., 2010. Cranial osteology and phylogenetic position of the theropod dinosaur *Proceratosaurus bradleyi* (Woodward, 1910) from the Middle Jurassic of England. Zoological Journal of the Linnean Society, 158: 155–195.
Raven, T.J., and Maidment, S.C.R., 2017. A new phylogeny of Stegosauria (Dinosauria, Ornithischia). Palaeontology, 60(3): 401–408.
Richter, A., Wings, O., Pfretzschner, H.-U., and Martin, T., 2010. Late Jurassic Squamata nd possible Choristodera from the Junggar Basin, Xinjiang, Northwest China. Palaeobiodiversity and Palaeoenvironments, 90: 275–282.
Rougier, G.W., Novacek, M.J., McKenna, M.C., and Wible, J.R., 2001. Gobiconodonts from the Early Cretaceous of Oshih (Ashile), Mongolia. American Museum Novitates, 3348: 1–30.
Ruebenstahl, A.A., Klein, M.D., Yi, H., Xu, X., and Clark, J.M., 2022. Anatomy and relationships of the early diverging Crocodylomorphs *Junggarsuchus sloani* and *Dibothrosuchus elaphros*. Anatomical Record.
Russell, D.A., 1993. The role of Central Asia in dinosaurian biogeography. Canadian Journal of Earth Sciences, 30: 2002–2012.
Russell, D.A., and Zheng, Z., 1993. A large mamenchisaurid from the Junggar Basin, Xinjiang, Peoples Republic of China. Canadian Journal of Earth Sciences, 30(10–11): 2082–2095.
Ruta, M., Botha-Brink, J., Mitchell, S.A., and Benton, M.J., 2013. The radiation of cynodontis and ground plan of mammalian morphological diversity. Proceedings of the Royal Society: Biological Science, 280: 201–1865.
Ruta, M., Pisani, D., Lloyd, G.T., and Benton, M.J., 2007. A supertree of Temnospondyli: Cladogenetic patterns in the most species-rich group of early tetrapods. Proceedings of the Royal Society B, 274(1629): 3087–3095.
Skutschas, P.P., Martin, T., and Sun, G., 2009. The co-occurrence of non-lissamphibian temnospondyls and salamanders in the Late Jurassic of the Southern Junggar Basin (Xinjiang Autonomous Region, NW China). Proceedings of the Zoological Institute RAS, 313(2): 143–148.
Stiegler, J.B., 2019. Anatomy, systematics, and paleobiology of noasaurid ceratosaurs from the Late Jurassic of China. (Dissertation): The George Washington University.
Sullivan, C., Wang, Y., Hone, D.W.E., Wang, Y., Xu, X., and Zhang, F., 2014. The vertebrates of the Jurassic Daohugou Biota of northeastern China. Journal of Vertebrate Paleontology, 34(2): 243–280.
Sun, A., 1986. New material of Bienotheroides (tritylodont reptile) from Shaximiao Formation of Sichuan. Vertebrata PalAsiatica, 24(3): 165–170.
Sun, A.L., and Cui, G.H., 1989. Tritylodont reptile from Xinjiang. Vertebrata PalAsiatica, 27(1): 1–8.
Tanoue, K., You, H.L., and Dodson, P., 2009. Comparative anatomy of selected basal ceratopsian dentitions. Canadian Journal of Earth Sciences, 46(6): 425–439.
Tong, H.Y., Li, L., Wang, X.L., Wang, Y., and Zhang, J.L., 2021.

First turtle remains from the Middle-Late Jurassic Yanliao Biota, NE China. Science Technology and Engineering Journal (STEJ), 7(1): 1–11.

Tütken, T., Pfretzschner, H.U., Vennemann, T.W., Sun, G., and Wang, Y.D., 2004. Paleobiology and skeletochronology of Jurassic dinosaurs: implications from the histology and oxygen isotope compositions of bones. Palaeogeography, Palaeoclimatology, Palaeoecology, 206(3–4): 217–238.

Upchurch, P., Mannion, P.D., Xu, X., and Barrett, P.M., 2021. Re-assessment of the Late Jurassic eusauropod dinosaur *Hudiesaurus sinojapanorum* Dong, 1997, from the Turpan Basin, China, and the evolution of hyper-robust antebrachia in sauropods. Journal of Vertebrate Paleontology, 41: e199441.

Velazco, P.M., Buczek, A.J., and Novacek, M.J., 2017. Two new tritylodontids (Synapsida, Cynodontia, Mammaliamorpha) from the Upper Jurassic, southwestern Mongolia. American Museum Novitates, 3874: 1–35.

Vincent, S.J., and Allen, M.B., 2001. Sedimentary record of Mesozoic intracontinental deformation in eastern Junggar Basin, northwestern China: Response to orogeny at the Asian margin. In: Hendrix, M.S., and Davis, G.A. (eds.), Paleozoic and Mesozoic tectonic evolution of central and eastern Asia – from continental assembly to intracontinental deformation. Geological Society of America. Memoir 194.

Wang, S., Stiegler, J., Amiot, R., Wang, X., Du, G. H., Clark, J.M., and Xu, X., 2017a. Extreme ontogenetic changes in a ceratosaurian theropod. Current Biology, 27(1): 144–148.

Wang, S., Stiegler, J., Wu, P., Chuong, C.M., Hu, D., Balanoff, A., Zhou, Y.C., and Xu, X., 2017b. Heterochronic truncation of odontogenesis in theropod dinosaurs provides insight into the macroevolution of avian beaks. Proceedings of the National Academy of Science of the America of United States, 114: 10930–10935.

Wang, X.R., Wu, W.H., Li, T., Ji, Q., Li, Y.X., and Guo, J.F., 2019. A new titanosauriform dinosaur (Dinosauria: Sauropoda) from Late Jurassic of Junggar Basin, Xinjiang. Global Geology, 38(3): 581–588.

Wings, O., 2015. The rarity of gastroliths in sauropod dinosaurs - a case study in the Late Jurassic Morrison Formation, western USA. Fossil Record, 18(1): 1–16.

Wings, O., Rabi, M., Schneider, J.W., Schwermann, L., Sun, G., Zhou, C.F., and Joyce, W.G., 2012. An enormous Jurassic turtle bone bed from the Turpan Basin of Xinjiang, China. Naturwissenschaften, 99(11): 925–935.

Wings, O., Tütken, T., Fowler, D.W., Martin, T., Pfretzschner, H. U., and Sun, G., 2015. Dinosaur teeth from the Jurassic Qigu and Shishugou formations of the Junggar Basin (Xinjiang/China) and their paleoecologic implications. Paläontologische Zeitschrift, 89: 485–502.

Wu, X. C., and Sues, H. D., 1996. Anatomy and phylogenetic relationships of Chimaerasuchus paradoxus, an unusual crocodyliform reptile from the Lower Cretaceous of Hubei, China. Journal of Vertebrate Paleontology, 16(4): 688–702.

Xu, X., Choiniere, J., Tan, Q., Benson, R.B.J., Clark, J., Sullivan, C., Zhao, Q., Han, F., Ma, Q., He, Y., Wang, S., Xing, H., and Tan, L., 2018. Two Early Cretaceous fossils document transitional stages in alvarezsaurian dinosaur evolution. Current Biology, 28: 2853–2860.

Xu, X., and Clark, J.M., 2008. The presence of a gigantic theropod in the Jurassic Shishugou Formation, Junggar Basin, Western China. Vertebrata PalAsiatica, 46(2): 157–160.

Xu, X., Clark, J.M., Forster, C.A., Norell, M.A., Erickson, G.M., Eberth, D.A., Jia, C., and Zhao, Q., 2006a. A basal tyrannosauroid dinosaur from the Late Jurassic of China. Nature, 439(7077): 715–718.

Xu, X., Clark, J.M., Mo, J., Choiniere, J., Forster, C.A., Erickson, G.M., Hone, D.W., Sullivan, C., Eberth, D.A., Nesbitt, S., Zhao, Q., Hernandez, R., Jia, C.K., Han, F.L., and Guo, Y., 2009. A Jurassic ceratosaur from China helps clarify avian digital homologies. Nature, 459(7249): 940–944.

Xu, X., Forster, C.A., Clark, J.M., and Mo, J., 2006b. A basal ceratopsian with transitional features from the Late Jurassic of northwestern China. Proceedings of the Royal Society B: Biological Sciences, 273(1598): 2135–2140.

Xu, X., Zheng, X.T., Sullivan, C., Wang, X.L., Xing, L.D., Wang, Y., Zhang, X.M., Connor, J.K.O., Zhang, F.C., and Pan, Y.H., 2015. A bizarre Jurassic maniraptoran theropod with preserved evidence of membranous wings. Nature, 521: 70–73.

Xu, X., Zhou, Z.H., Sullivan, C., Wang, Y., and Ren, D., 2016. An updated review of the Middle-Late Jurassic Yanliao Biota: Chronology, Taphonomy, Paleontology, and Paleoecology. Acta Geologica Sinica (English Edition), 90(6): 1801–1840.

Ye, H.K., 1986. A Jurassic turtle from Junggar, Xinjiang. Vertebrata PalAsiatica, 24(3): 171–181.

Ye, Y., and Pi, X.Z., 1997. A new genus of Chengyuchelyidae from Dashanpu, Zigong, Sichuan. Vertebrata PalAsiatica, 35 (3): 182–188.

You, H.L., and Cui, G.H., 2019. Exploring Chinese Dinosaurs. China-Canada Dinosaur Project: 1987–1990. Beijing: Institute of Vertebrate Paleontology and Paleoanthropology.

Young, C. C., 1937. A new dinosaurian from Sinkiang. Palaeontologica Sinica Series C, 2: 1–25.

Zhao, X. J., Su, Z. D., Sun, A. L., Ye, X. K., Dong, Z. M., Hou, L. H., Zhang, F. K., and Li, J. L., 1987a. Evolution of the Junggar Basi and the formation of oil and gas: Vertebrate fossils and stratigraphy of Xinjiang. Beijing: Institute of Vertebrate Paleontology and Paleoanthropology.

Zhao, X., 1993. A new Middle Jurassic sauropod subfamily (Klamelisaurinae subfam. nov.) from Xinjiang Autonomous Region, China. Vertebrata PalAsiatica, 31(2): 132–138.

Zhao, X.J., Benson, R.B.J., Brusatte, S.L., and Currie, P.J., 2009. The postcranial skeleton of Monolophosaurus jiangi (Dinosauria: Theropoda) from the Middle Jurassic of Xinjiang, China, and a review of Middle Jurassic Chinese theropods. Geological Magazine, 147: 13–27.

Zhao, X.J., and Currie, P.C., 1993. A large crested theropod from the Jurassic of Xinjiang, People's Republic of China. Canadian Journal of Earth Sciences, 30(10–11): 2027–2036.

Zhao, X.J., Sun, Z.D., Sun, A.L., Ye, X.K., Dong, Z.M., Hou, L.H., Zhang, F.K., and Li, J.L., 1987b. Evolution of the Junggar Basin and the formation of oil and gas: Vertebrate fossils and stratigraphy of Xinjiang. Beijing: Institute of Vertebrate Paleontology and Paleoanthropology.

Zhou, Z.H., Jin, F., and Wang, Y., 2010. Vertebrate assemblages from the Middle-Late Jurassic Yanliao Biota in northeast China. Earth Science Frontiers, 17: 252–254.

About the first and corresponding authors

XU Xing, male, born in 1969 in Xingyuan, Xingjiang, PR China; Ph.D.; graduated from the Chinese Academy of Sciences; Donglu Professor of Life Sciences at the Yunnan University and Distinguished Professor of the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences. He is interested in Mesozoic fossil reptiles and their evolution, especially dinosaurs. E-mail: xingxu@vip.sina. com.

James CLARK, male, born in 1956 in Long Beach, California USA; Ph.D.; graduated from the University of Chicago; Ronald Weintraub Professor of Biology, The George Washington University. He is interested in fossil reptiles and their evolution, especially crocodylomorphs. E-mail: jclark@ gwu.edu.

David EBERTH, M.A. (UCBerkeley), Ph.D. (UToronto), born in 1953, is an Emeritus Research Scientist at the Royal Tyrrell Museum in Drumheller, Alberta, Canada. His specialties are stratigraphy and sedimentology of fossiliferous non-marine rocks. He has worked on projects around the world. E-mail: david.eberth @gov.ab. ca.