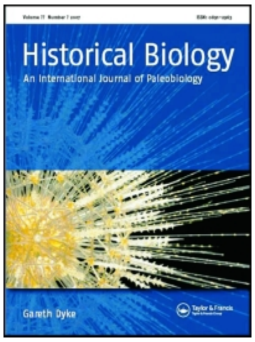

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Historical Biology
An International Journal of Paleobiology

ISSN: 0891-2963 (Print) 1029-2381 (Online) Journal homepage: http://www.tandfonline.com/loi/ghbi20

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To cite this article: Lida Xing , Guangzhao Peng, Hendrik Klein, Yong Ye, Shan Jiang , Michael E Burns & Hao Ran (2017) Middle Jurassic tetrapod burrows preserved in association with the large sauropod Omeisaurus jiaoi from the Sichuan Basin, China, Historical Biology, 29:7, 931-936, DOI: 10.1080/08912963.2016.1263627

To link to this article: http://dx.doi.org/10.1080/08912963.2016.1263627

HISTORICAL BIOLOGY, 2017
VOL. 29, NO. 7, 931–936
https://doi.org/10.1080/08912963.2016.1263627

Middle Jurassic tetrapod burrows preserved in association with the large sauropod *Omeisaurus jiaoi* from the Sichuan Basin, China

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ABSTRACT

Here we report a Jurassic tetrapod burrow preserved in association with the partial skeleton of a large sauropod specimen of *Omeisaurus jiaoi* from Zigong, Sichuan Province, China. The ichnofossil can be divided into two parts, which may indicate two individual trace makers and some social behavior, although the possibility that they are two portions of one trace by a single trace maker cannot be ruled out. The burrow trace was examined via petrographic thin sections and carbonate analysis. Considering the spatial relationship of the burrows and the skeleton, it is likely that decomposition of the sauropod carcass preceded the formation of the burrows. It is possible that the process of decomposition improved the humus level of the soil, which would have attracted more soil-dwelling invertebrates and, by consequence, tetrapod predators thereof. The discovery of ZDM5051 has increased our understanding of global ichnofossil diversity.

ARTICLE HISTORY
Received 18 November 2016
Accepted 18 November 2016

KEYWORDS
Tetrapod burrows; sauropod; Sichuan Basin; China

Introduction

Burrowing behavior is common in modern animals, and can be found in, among other groups, crustaceans, insects, worms, fishes, and tetrapods (Bishop & Williams 2005; Krapovickas et al. 2013; Xing et al. 2013; Catena & Hembree 2014). Burrows can conceal the activities of the burrower, hide offspring from predators (Talanda et al. 2011; Xing et al. 2013), and can also provide climatic shelters or act as sites of food storage (Reichman & Smith 1990; Varricchio et al. 2007; Krapovickas et al. 2013).

Burrowing behavior evolved independently several times in different animal groups (Talanda et al. 2011). In vertebrates, this behavior may have evolved by the Early Devonian according to trace fossil records (Allen & Williams 1981; Graham & Pollard 1982; Catena & Hembree 2014), while the earliest known tetrapod burrows are dated to the Early Carboniferous (Storm et al. 2010). Stratigraphically younger records come, for example, from the Permian (Smith 1987; Liu & Li 2013), Triassic (Miller et al. 2001; Hasiotis et al. 2004; Bordy et al. 2010; Talanda et al. 2011; Voigt et al. 2011), Jurassic and Cretaceous (Loope 2006; Paik et al. 2015). Extant and fossil records of burrowing tetrapods are known from amphibians, therapsids, mammals, parareptiles and eureptiles, including dinosaurs and birds (Smith 1987; Damiani et al. 2003; Varricchio et al. 2007; Martin 2009; Krapovickas et al. 2013).

Fossil burrows provide information about the trace maker and are important sources of paleoenvironmental information (Catena & Hembree 2014). Apart from Liu and Li (2013) who reported two fossilized tetrapod burrows from the Permian of Nei Mongol, the record of these particular ichnofossils in China is sparse. Here we report the first Jurassic tetrapod burrow material from China, discovered in Zigong, Sichuan Province (Figure 1) and preserved in association with a partial skeleton of the large-bodied sauropod *Omeisaurs jiaoi* (Jiang et al. 2011).

Geologic settings

The burrow material was found in deposits of the Xiashaximiao Formation of Zigong, Sichuan Province, China (Figure 1). In the Sichuan Basin, the Jurassic outcrop is divided into the Middle Jurassic Xiashaximiao Formation and the Upper Jurassic Shangshaximiao Formation (Peng et al. 2005; Xing et al. 2014). The Xiashaximiao Formation also yields the *Shunosaurus* fauna, whereas the overlying Shangshaximiao Formation yields the *Mamenchisaurus* fauna (Peng et al. 2005; Li et al. 2011). The Xiashaximiao Formation of Zigong City area comprises two sedimentary rhythms formed by dark purple or red purple mudstone interbedded with two to three layers of gray or yellow gray thick massive fine-medium grained feldspathic quartz sandstone or lithic feldspar sandstone. The thickness of the zone is 90–217 m. Mudstones in this formation are relatively stable, whereas sandstones are variable, usually interbedded with one to two sand lenses. There are abundant vertebrate fossils, exemplified by the famous Dashanpu *Shunosaurus* fauna from sandstone layers in the lower part of this formaiton (Gu et al. 1997; Peng et al. 2005; Li et al. 2011). The sedimentary facies of the Xiashaximiao Formation are an alternation of fluvial and lacustrine in Zigong,

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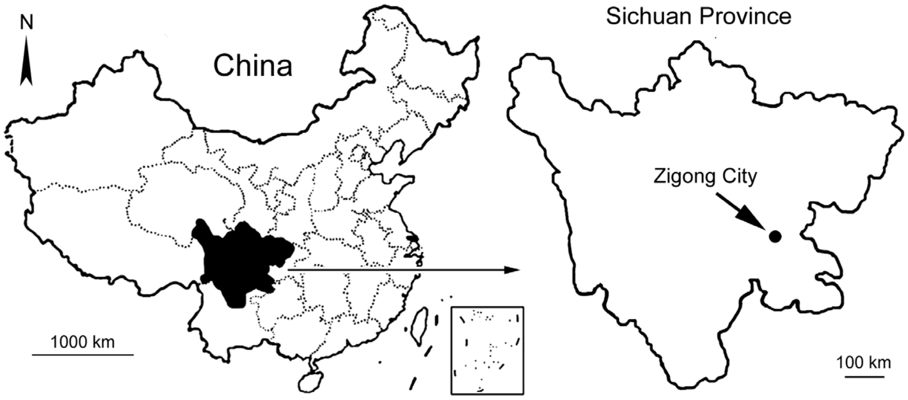

Figure 1. Map showing the position of Middle Jurassic tetrapod burrows localities in Sichuan Province, China.

and might have been deposited within a relatively short space of time (Peng et al. 2005; Wang et al. 2007).

The Xiashaximiao Formation contains many vertebrate fossils, and abundant dinosaur remains have been discovered from both the Saurischia and Ornithischia, in addition to representatives of Pterosauria, Testudines, Crocodyliformes, Sauropterygia, Therapsida, Chondrichthyes, Pahwonisciformes, Semionotiformes, Dipnoi, and Amphibia (Peng et al. 2005; Wang et al. 2008; Li et al. 2011). In the 2800 m^2 excavated area now housed by the Zigong Dinosaur Museum, 130 dinosaur individuals were found, including adults and juveniles, together with some skin impressions (Peng et al. 2005; Wang et al. 2008). The dinosaurian fauna and the ichnofossils are preserved in fine-grain feldspathic litharenite. Ripple marks and tabular cross-bedding suggest a low-energy lakeshore environment (Xia et al. 1988). Wang et al. (2007) analyzed a new section, and considered the area of the Zigong Dinosaur Museum as belonging to a delta-lacustrine depositional system, with the dinosaur remains being allochthonous and washed in after death. Some of the fossil material, however, has a high arsenic content, which indicates a possible heavy metal poisoning event. This has been hypothesized as a possible reason for the animals' deaths and the accumulation of skeletons in the locality (Xia et al. 1988).

Materials and methods

The fossilized burrow (Zigong Dinosaur Museum (ZDM) 5051) was preserved in light gray-green sandstone, together with a partially articulated sauropod skeleton (Figure 2). The specimen can be divided into two sections: ZDM5051-1 representing the shorter segment and ZDM5051-2 the longer segment (Figure 3), both of which are roughly oriented in the same direction.

The associated sauropod skeleton represents the holotype specimen of *Omeisaurs jiaoi* Jiang et al. 2011, and includes dorsal, sacral, and caudal vertebrae, ribs, chevrons, and near-complete pectoral and pelvic girdles and limbs. The skeleton and ichnofossils were photographed using a Canon EOS 5D Mark III, and measured with a flexible tape measure and Vernier calipers.

Petrographic thin sections (thickness: 0.04–0.05 mm) of the burrows were made for microscopic examination. The sections were observed with plane- and cross-polarized transmitted light microscopy on an Olympus BX51 and photographed with 100× magnification.

Six samples (Analysis sample Nos. 06119001-06119006) were used for chemical composition analysis, which included one sample of ZDM5051 (No. 06119001), one dinosaur rib sample (No. 06119003), one sample of matrix encrusting the sauropod fossils (No. 06119004), one common globular nodule sample (No. 06119005) (see Section 'Description'), one uncommon globular nodule sample (No. 06119002), and one sandstone sample (No. 06119006) from the same site. Colorimetry was used with UV-VIS8500 to analyze P_2O_5 content under Chinese national standard GB/T14506-93. Flame emission spectrometry with Hitachi 180-80 was done to analyze the content of K_2O and Na_2O, also under GB/T14506-93. Volumetry with a BS124S electronic balance was done to determine the content of Al_2O_3 and CaO under GB/T14506-93. Gravimetry was performed with a BS124S electronic balance to analyze the SiO_2 content under GB/T14506-93. And CO_2 was measured by Jena EA2000 under the DZG9000 standard.

Description

As preserved, from the exposed upper side (Figure 3), ZDM5051-1 is 930 mm long and has a minimum width of 66 mm, whereas ZDM5051-2 is 1510 mm long with a minimum width of 70 mm (Table 1). One end of ZDM5051-1, which is in contact or overlapping with ZDM5051-2 is curved downward by about 45°, whereas ZDM5051-2 is almost horizontally oriented. The exact relationship of both tunnels is uncertain, and it cannot be decided, if they are separated from each other or not. They show a horizontal sinuous curvature with central angles less than 118° for ZDM5051-1 and less than 128° for ZDM5051-2. Both are expanded at their distal portions, finally tapering then terminating in blunt ends. No true branches are visible, however two blind diverticula are present laterally in ZDM 5051-1. The surface texture of both is rough and not well preserved, with no obvious transverse striations. Although there are several irregular flaws on the surface, they cannot be reliably identified as scratch marks or other structures related to the burrows. Some evidence may have been lost by earlier preparatory work on the specimens.

In cross-sectional view, ZDM5051-1 is roughly heart-shaped with a convex protrusion characterizing the upper surface and a concave furrow preserved on the lower surface (Figure 4). The cross-sectional area is 46.5 cm^2. The cross-sectional shape of ZDM5051-2 is elliptical with horizontal long axis. There was no

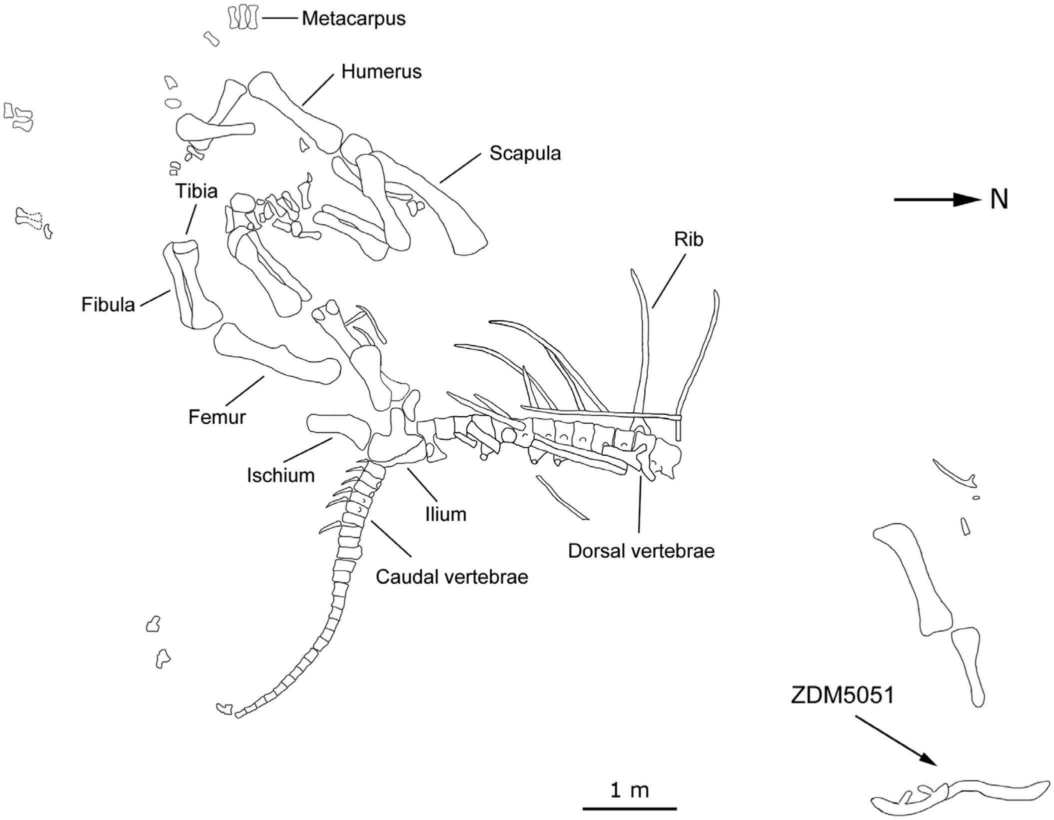

Figure 2. The holotype of *Omeisaurs jiaoi* (Jiang et al. 2011) and ZDM5051 were preserved associated with each other.
Note: The arrow show the place of ZDM5051.

distinct bulge or hollow on the surface of ZDM5051-2. There were no natural breaks so a direct view of the cross section of this part of the specimen was not possible without employing destructive techniques.

In thin section, the fossils reveal a calcareous coarse siltstone or silty limestone with a non-uniform distribution of grains. ZDM5051 consists mainly of quartz with some feldspar, mica, rock debris, and sparse heavy metallic mineral inclusions like zircon (Figure 5). No micro vegetable fiber or vertebrate fossil fragments were found.

The relative abundances of seven compounds (SiO_2, Al_2O_3, CaO, K_2O, Na_2O, P_2O_5, and CO_2) were analyzed from the ZDM5051 burrow material, as well as from associated dinosaur rib fossils, globular nodules, and sandstone from the same site (Table 2). The major component of ZDM5051 is silica, followed by calcium and aluminum, with a low concentration of phosphorus. The compound ratios constituting the make-up of the sandstone, globular nodules, and dinosaur rib fossils are different (Table 2). The sandstone, as expected, is mainly composed of silica. The skeletal body fossils themselves have a distinctly low silica content relative to the surrounding rock, but high calcium and phosphorus content. The globular nodules show an intermediate silica and calcium content contents but a relative abundance of carbon.

Discussion

Similar sinuous burrows have been described in previous studies (Krapovickas et al. 2013; Liu & Li 2013; Xing et al. 2013), and the trace makers are considered to have used the burrows as passageways leading to an exit, a branch or a chamber. On the whole, with the sub-circular cross section and the long, slender extension with rounded ends, ZDM5051 is similar in morphology to burrows found in Lower Jurassic deposits of southeastern Utah, United States (Lucas et al. 2005), Permian deposits of Nei Mongol, China (Liu & Li 2013), and Middle Triassic deposits of Argentina (Krapovickas et al. 2013). The absence of transverse striations makes ZDM5051 different from Beaconites-type ichnofossils (Allen & Williams 1981; Graham & Pollard 1982). The possible separation of ZDM5051-1 and ZDM5051-2, and their different cross sections, suggest that they may belong to two different burrows, each constructed by a different individual. However there is still the possibility that the specimen represents two parts of a single burrow, and that the morphological differences could be attributed to distortion by geological and taphonomic processes. Although there are some detailed differences between ZDM5051-1 and ZDM5051-2 in cross-sectional view, the diameters of both are similar and if we accept a reasonable degree of variation, essentially they are of similar shapes. This suggests that if two trace makers were involved they were probably of the same species.

However, the absence of *in situ* body fossils makes the identification of the trace maker of ZDM5051 difficult (Lucas et al. 2005; Talanda et al. 2011). The blind-ending diverticula of ZDM5051-1 are also found in an Upper Triassic (Norian) burrow complex from the Wyszyna Machorowska site (Talanda et al. 2011). The expanded, rounded ends may have been used by the borrower to turn around. In continental settings, both invertebrates and vertebrates evolved burrowing behavior, and produced ichnofossils as early as the Paleozoic (Liu & Li 2013; Xing et al. 2013). In Jurassic and stratigraphically younger sediments, invertebrate burrows are typically 2–5 cm in width (Krapovickas et al. 2013; Xing et al. 2013). Those attributed to tetrapods are commonly more than 10 cm wide (Krapovickas et al. 2013). Therefore, the gross width of ZDM5051, 6.6–14.4 cm, suggests a tetrapod trace maker.

Lungfish burrows are well known and can date back to Palaeozoic (Olson & Bolles1975; Gobetz et al. 2005; Lucas et al. 2010). Surlyk et al. (2008) described possible lungfish burrows preserved together with dinosaur tracks in a shallow coastal lake environment from the Lower Cretaceous. Lungfish from the species *Ceratodus zigongensis* have also been recorded from the Xiashaximiao Formation in Zigong (Li et al. 2011). However the sub-vertical lungfish constructions (Gobetz et al. 2005; Lucas et al. 2010; Krapovickas et al. 2013) differ from the sub-horizontal orientations of ZDM5051, which are more characteristic of tetrapod burrows (Varricchio et al. 2007; Talanda et al. 2011). The heart-shaped cross section of ZDM5051-1 is also against this being a lungfish burrow because the inwardly concave ridge on the bottom does not match the burrow morphology of a limbless vertebrate, but rather suggests a tetrapod holding its belly up above the floor of the tunnel when walking (Damiani et al. 2003; Sidor et al. 2008; Krapovickas et al. 2013).

Furthermore, similar burrows with heart-shaped cross sections have been described by Damiani et al. (2003) from the Permian-Triassic of South Africa, and Sidor et al. (2008) from the Triassic of Antarctica. Both were burrowed by tetrapods (Damiani et al. 2003; Sidor et al. 2008). A body fossil of a cynodont trace maker was found in the South African sample, and the relationship between the heart-shaped cross section and this tetrapod trace maker was described (Damiani et al. 2003). The morphological similarity of ZDM5051 makes it most likely that a tetrapod was also the trace maker in this case. The burrow diameter should reflect the size of the trace maker as it couldn't be smaller than the animal and generally for economy of effort burrowers do not construct channels much larger than themselves (White 2005; Xing et al. 2013). By comparing the cross-sectional area with modern tetrapods (White 2005), the trace maker can be estimated to have weighed from 80 to 410 g, probably around 200 g.

Of the known tetrapods found in the Xiashaximiao Formation, two species of Therapsida, *Bienotheroides zigongensis* and *Polistodon chuannanensis*, deserve further attention. The cranial width of the holotype of *Bienotheroides zigongensis* is approximately 8 cm (Sun 1986) and that of *Polistodon chuannanensis* about 7 cm (He & Cai 1984). Not only are the cranial widths of these tritylodonts close to the diameter of ZDM5051, but they also might have lifted their bellies up when walking (He & Cai 1984; Sun 1986), making these kind of animals compelling candidates for the identity of the trace maker.

If ZDM5051-1 and ZDM5051-2 were made by different individuals, the contact of the two burrows would be an unusual feature, although not unique in the literature. A similar contact was found associated with tetrapod burrows in the Lower Jurassic of Utah (USA) that form more complex networks than those described here (Lucas et al. 2005). Commonly, solitary burrowers prefer to construct tunnels separate from and not too close to each other

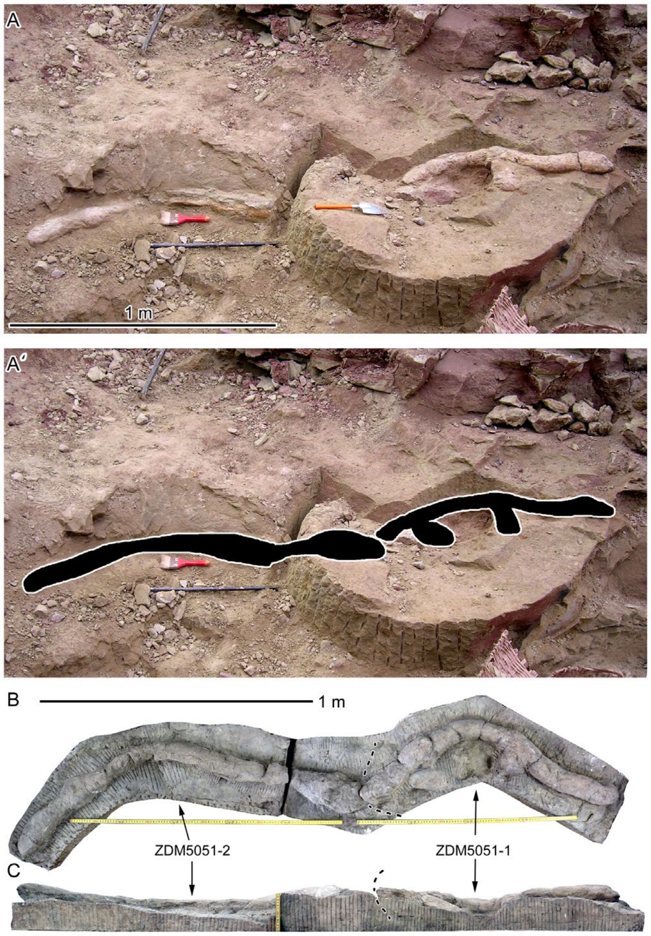

Figure 3. Photographs of tetrapod burrows ZDM5051: oblique view with superimposed drawings showing their shape (A), with angle of inclination along distal end of ZDM5051-1 (A′), dorsal view (B) and lateral view (C).

Notes: The figures A and A′ share one scale bar and figures B and C share one scale bar. The dashed lines saperate ZDM5051-1 and -2.

Table 1. The measured data (mm) of ZDM5051.

	Length	Diameter
ZDM5051-1	930	66–100
ZDM5051-2	1510	70–144

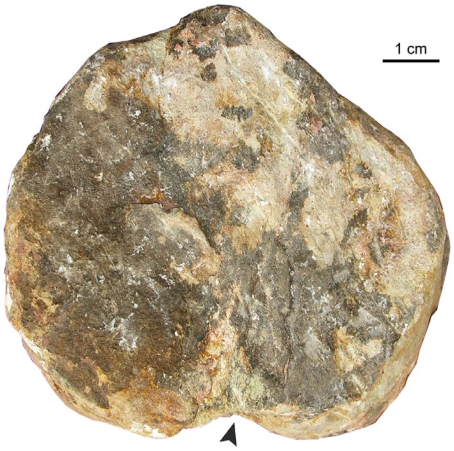

Figure 4. Photograph of cross section of ZDM5051-1.

Note: Arrow indicates concave area.

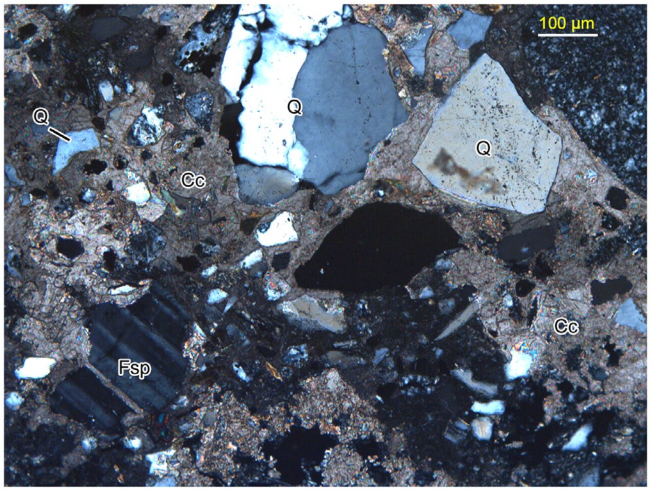

Figure 5. Petrographic sections of ZDM5051-1, Q, Quartz; Cc, Calcite; Fsp, Feldspar.

Table 2. Compound content of ZDM5051, dinosaur rib fossils, typical globular nodules, and sandstone in the same site.

	Composition and content $(\times10^{-2})$						
Specimens	SiO_2	Al_2O_3	CaO	K_2O	Na_2O	P_2O_5	CO_2
ZDM5051	43.05	10.47	19.25	1.55	1.29	0.41	15.62
Dinosaur rib	3.16	1.02	51.30	0.02	0.16	17.44	16.69
Globular nodules	27.23	5.47	32.50	1.07	0.93	0.14	24.79
Sandstone	68.42	14.56	6.58	2.31	2.17	0.16	0.30

(Krapovickas et al. 2013). In ZDM5051-1 and ZDM5051-2 if the trace makers were different individuals, the contact of the burrows could be indicative of some form of social behavior (Lucas et al. 2005; Xing et al. 2013). Also the absence of distinct chambers in ZDM5051, suggests that it was more likely used for feeding (fodinichnia), rather than as a dwelling structure (domichnia) (Reichman & Smith 1990; Krapovickas et al. 2013). If this is correct, the trace maker, like a modern mole, may have hunted within the burrows (Reichman & Smith 1990; Thomas et al. 2009).

ZDM5051 is closely associated with an area where the skeletal remains of a large sauropod are preserved. This suggests the following order of taphonomic processes and interaction with the burrower.

(1) Death of the sauropod.
(2) Transport and deposition of the sauropod carcass by water.
(3) Construction of burrows near the sauropod by the trace maker of ZDM5051.

A different scenario in which the burrows were constructed prior to the deposition of the sauropod seems unlikely because they would probably have been destroyed by the considerable hydrodynamic forces needed to move the carcass.

There is a possible relationship between these two events. The decomposition of the dinosaur carcass could have increased the organic content of the soil (Carter et al. 2007), which may have attracted insects and other invertebrates (Lavelle et al. 1997, 2006). These could have provided a rich source of food for tetrapods with the ability to construct burrows. (Reichman & Smith 1990; Krapovickas et al. 2013).

Acknowledgments

The authors thank two anonymous reviewers for their critical comments and suggestions on this paper.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This research project was supported by the 2013 and 2015 support fund for graduate student's science and technology innovation from China University of Geosciences (Beijing), China.

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