



## Novel insect traces on a dinosaur skeleton from the Lower Jurassic Lufeng Formation of China



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### ABSTRACT

Dense networks of burrow-like traces on the surfaces of bones are preserved on a partial skeleton of a prosauropod dinosaur (cf. *Yunnanosaurus*) from the Lower Jurassic Lufeng Formation in Yunnan, China. The traces, which gently meander across and, in places, shallowly excavate the surfaces of several axial and appendicular skeletal elements (total cumulative length over 29 m) consist of simple burrows, Y-shaped branches, overlapping intersections, and chambers. This unusual network is morphologically most similar to foraging traces of eusocial insects, particularly termites. Comparisons of known continental ichnofossils, demonstrate the novelty of this trace, which thus pertains to a new ichnotaxon, *Taotieichnus orientalis* ichnogen. et ichnosp. nov. *T. orientalis* most closely resembles subaerial foraging galleries constructed of mud or carton (saliva and faecal material mixed with soil or partially digested wood particles) and produced by a range of subterranean termites. Periodic, possibly seasonal, use of carrion as a nutrient source, and the construction of carton foraging galleries over decomposing vertebrate carcasses, is a known, but little documented, dietary supplement for some xylophagus, neotropical termite species. These Early Jurassic traces constitute the earliest evidence of eusocial insect foraging behavior, and suggest that a possible adaptive radiation of stem- or crown-group termites as foragers—or, at least, opportunistic decomposers—of animal carcasses had already occurred by the Early Jurassic.

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### 1. Introduction

Ichnofossils are traces formed by the behavior of an organism in the process of interacting with a substrate. Examples of such behaviors include walking, digging, nesting, foraging, and dwelling (Yang, 1990; Buatois and Mángano, 2011). Ichnofossils reflect the behaviors and/or morphologies of the trace maker, often providing information about the lifestyles of extinct organisms that cannot readily be inferred from body fossils, such as velocity, foraging style, and social behavior (Yang, 1990; Seilacher, 2007). Borings are relatively common ichnofossils, primarily in the marine realm where micro- and macro-boring invertebrates, such as some worms, sponges, bivalves, and echinoids, routinely bore into substrates, including bones (e.g., Tapanila et al., 2004; Kiel et al., 2010, 2011). In most instances, the trace maker is not fossilized along with the trace, making associating the trace with a particular organism difficult, a problem compounded because morphologically

indistinguishable traces can sometimes be made by different organisms (Buatois and Mángano, 2011). In many instances, inferring the identity of a trace maker requires comparing its trace with those made by extant organisms (Yang, 1990; Seilacher, 2007).

The study of insect traces, usually in continental settings, is a relatively new branch of ichnology (Genise et al., 2005). In addition to feeding traces left on leaves (Wilf, 2008), insect ichnofossils include dwelling traces constructed in sediments (e.g., Hasiotis, 2003, 2004; Genise, 2004) and wood (e.g., Moran et al., 2010; Tapanila and Roberts, 2012), but a growing record documents interactions between insects and vertebrate bones. Fossil borings in bone made by insects have been reported from various continental paleoenvironments from the Middle or Late Triassic through the Pleistocene (e.g., Rogers, 1992; Hasiotis et al., 1999; Schwanke and Kellner, 1999; Kaiser, 2000; Paik, 2000; Dangerfield et al., 2005; Fejfar and Kaiser, 2005; Roberts et al., 2007; West and Hasiotis, 2007; Britt et al., 2008; Bader et al., 2009; Kirkland and Bader, 2010; Cabral et al., 2011; Saneyoshi et al., 2011). However, compared to other trace fossils, few insect trace fossils made in (or on) bone have been formally named (Roberts et al., 2007). Here we describe a new trace fossil, composed of a complex network of burrows that form

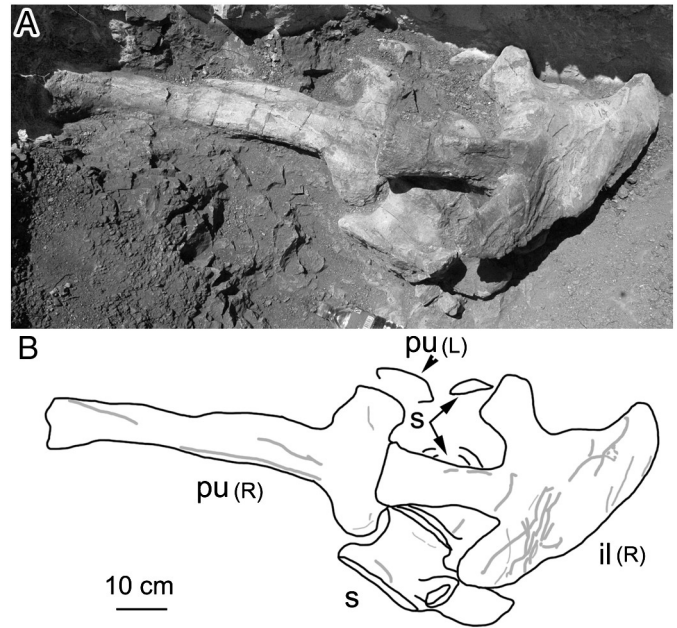
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a gallery system around numerous elements of an incomplete, partially articulated skeleton of an Early Jurassic prosauropod dinosaur from the Lufeng Formation in Dalishu Village, Konglongshan Town, Lufeng County, Yunnan Province, China.

**2. Geologic setting**

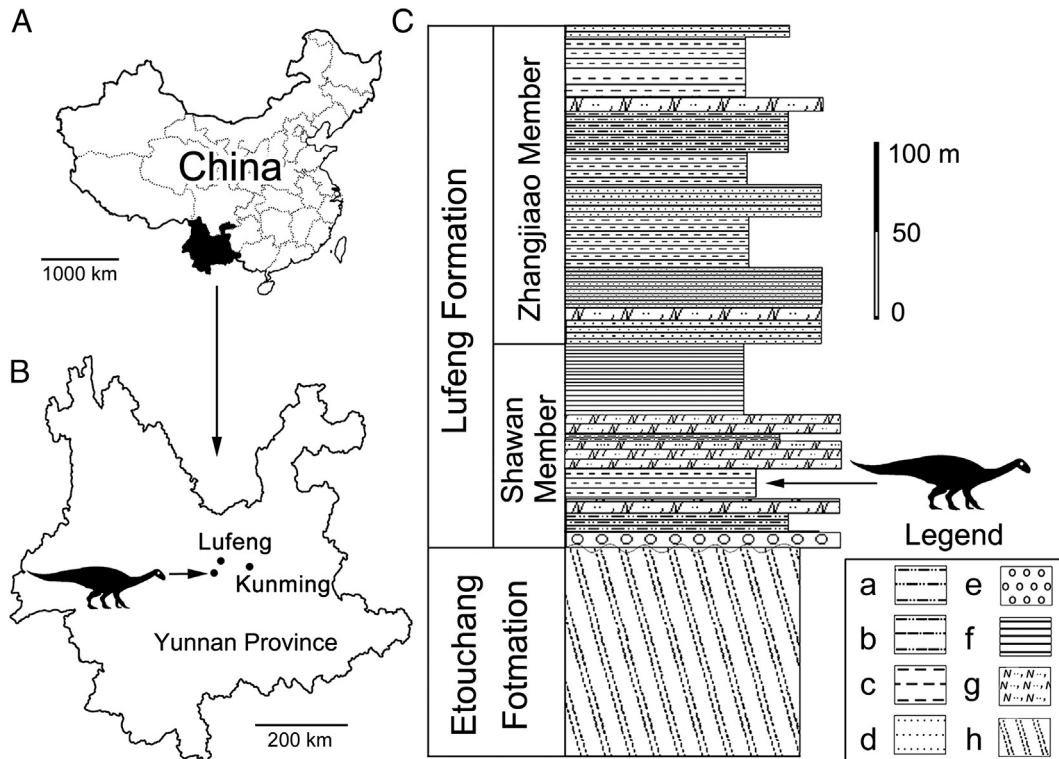
An extensive succession of Lower Jurassic through Cretaceous continental strata is exposed across much of southwestern Yunnan Province in China. These deposits are preserved in a number of small basins across the region and were part of a large, low-relief alluvial plain during the Mesozoic. The most famous and fossiliferous unit in this succession is the Lower Jurassic Lufeng Formation, which has produced a rich vertebrate fauna that includes early dinosaurs, early mammals and derived, late-surviving, non-mammalian eucynodonts, basal crocodylomorphs, and sphenodontians. Fang et al. (2000) studied the stratigraphic section at Laochangqing–Dajianfeng in the Chuanjie Basin and restricted the name “Lufeng Formation” to what was previously known as the Lower Lufeng Formation. They divided their redefined Lufeng Formation into the Shawan and Zhangjia’ao members, a stratigraphic nomenclature we follow herein (Fig. 1). Based on a combination of invertebrate (bivalves: *Sibireconcha*; ostracodes: *Gomphocythere?*–*Darwinula* association [Zhang, 1995]) and vertebrate (Luo and Wu, 1995; Luo et al., 2001; Irmis, 2004) biostratigraphy, this unit has been widely accepted as Early Jurassic in age.

The trace fossils reported herein occur in direct association with a prosauropod (sensu Upchurch et al., 2007) dinosaur skeleton (ZLJ 0035; Figs. 2–6) that was found in the Dalishu bonebed. The specimen was preserved in a dull purplish, silty mudstone layer within the lower Shawan Member of the Lufeng Formation. The Lufeng Formation is interpreted as having been deposited in piedmont plain, lake, and fluvial environments (Luo and Wu, 1995); the lower part of Lufeng Formation includes shallow lacustrine strata (Tan, 1997).

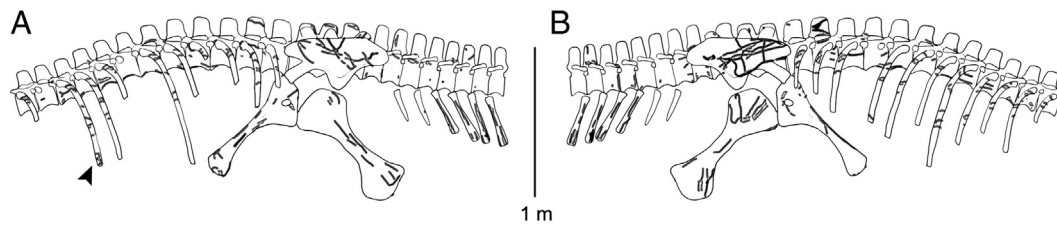


**Fig. 2.** A) Photograph, and B) schematic diagram of an exposed portion of the pelvis of ZLJ 0035 during excavation. The dorsal and caudal vertebrae were collected prior to the time at which this photograph was taken. *Taotieichnus orientalis* burrows highlighted in grey in B. Abbreviations: il = ilium, L = left, pu = pubis, R = right, s = sacral vertebrae.

The skeleton (ZLJ 0035) was discovered and excavated in 2005. Unfortunately, few details of the discovery and excavation are available, though photographs taken of the site provide some important details. Reconstructing the precise geologic context of the skeleton is therefore



**Fig. 1.** Map (A and B) showing the location (dinosaur silhouette) of the Dalishu bonebed locality in Yunnan Province, China. Stratigraphic section (C) of Lower Jurassic–Cretaceous strata in the Lufeng Basin. Legend: a) Pelitic siltstone, b) Sandy mudstone, c) Mudstone, d) Sandstone, e) Conglomerate, f) Shale, g) Orthomicrite, h) Fossiliferous orthomicrite.



**Fig. 3.** Positions of burrow traces on the preserved portions of prosauropod dinosaur skeleton ZLJ 0035 in A) right lateral and B) left lateral views. *Taotieichnus orientalis* burrow trace fossils marked as grey lines. Arrow points to area from which petrographic sections shown in Fig. 6 were taken.

difficult. Based on the available photographs, the skeleton was partially articulated, indicating that the specimen was not transported far, if at all, postmortem, and interred prior to complete decomposition of connective soft tissues. The skeleton comprises cervical vertebrae 1–5, dorsal vertebrae 2–14, sacral vertebrae 1–3, caudal vertebrae 1–8, several ribs, haemal arches 1–6, both ilia, ischia, and pubes, and the distal one-third of the right femur. The vertebrae and ilia are typical of a prosauropod (Galton and Upchurch, 2004). The most common Lufeng prosauropods are *Lufengosaurus* and *Yunnanosaurus*, although various other basal sauropodomorphs, such as “*Pachysuchus*” (Barrett and Xu, 2012) and *Xixiposaurus* (Sekiya, 2010), as well as the basal sauropod (sensu Upchurch et al., 2007) *Jingshanosaurus* (Zhang and Yang, 1995), are also present. With its elongate, cranially squared-off preacetabular portion and generally collinear dorsal margin, the ilium of ZLJ 0035 bears greater similarity to that of *Yunnanosaurus* (Young, 1942) than *Lufengosaurus* (Young, 1941); an ilium of *Xixiposaurus* has not been described, so we refer the specimen to cf. *Yunnanosaurus*.

### 3. Materials and methods

The bone borings and galleries adorning the skeleton were identified by the lead author in the collections at the World Dinosaur Valley Park (Lufeng Dinosaurian Museum). Samples of cement-infilled burrow traces selected for petrographic analysis were stabilized via resin impregnation using Buehler EpoThin Low Viscosity Resin and Hardener.

Thin sections were prepared to a thickness of 60–80  $\mu\text{m}$  and polished to a high gloss using  $\text{CeO}_2$  powder. Sections were examined on a Nikon Eclipse E600POL trinocular, polarizing microscope with an attached Nikon DXM 1200 F digital camera. Scans of the slides were taken with a Nikon Super Coolscan 5000 ED using polarized film. Using the field photographs and previously published restorations of prosauropod dinosaurs, such as *Lufengosaurus* (Young, 1941, 1951) and *Plateosaurus* (Mallison, 2010), a schematic restoration of the skeleton of ZLJ 0035 and the encasing burrows was made using Adobe Photoshop CS4.

### 4. Systematic paleontology

**Ichnogenus:** *Taotieichnus* ichnogen. nov.

Etymology: ‘Taotie’ (Chinese), meaning a glutton, a greedy person, or a ferocious man-eating animal from a Chinese legend; ‘ichnus’ (Latin), meaning ‘trace’.

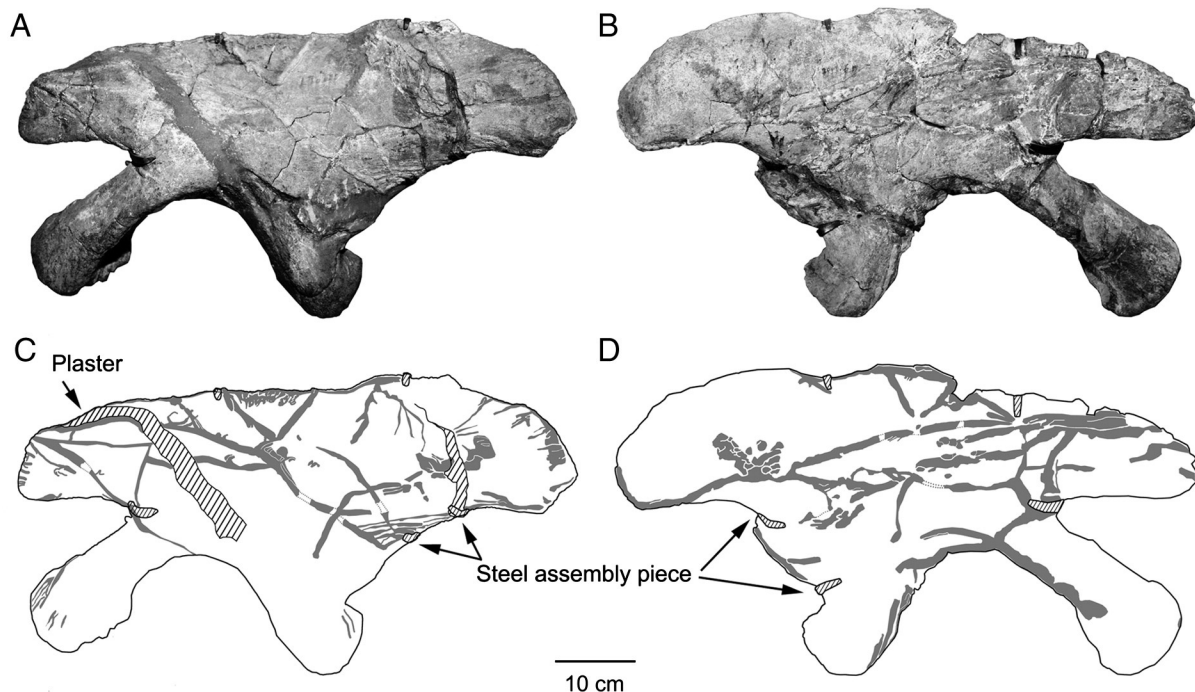
Pronunciation: TAO-tee-eh-IHK-nuss.

Diagnosis: Same as for ichnospecies.

Ichnospecies: *Taotieichnus orientalis* ichnosp. nov. (Figs. 2–6; Supplementary Information)

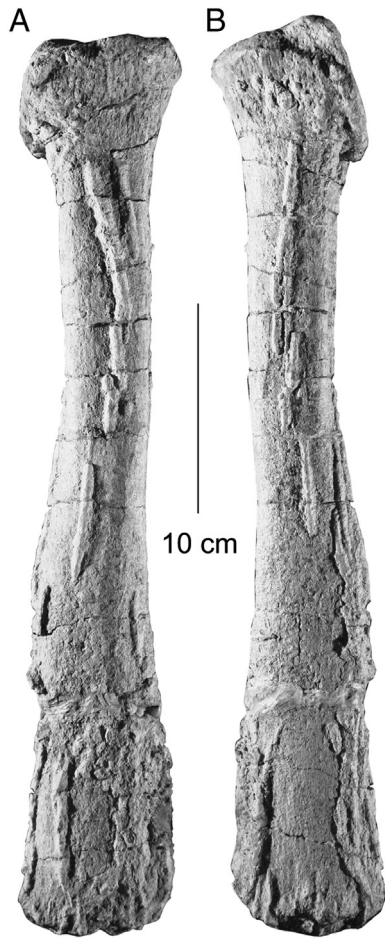
Etymology: ‘Orientalis’ (Latin), meaning ‘eastern’.

Holotype: ZLJ 0035: insect traces preserved on elements of a prosauropod dinosaur skeleton that is housed at World Dinosaur Valley Park, Yunnan Province, China.



**Fig. 4.** Photographs and outline drawings of the A, C) left ilium and B, D) right ilium of prosauropod dinosaur skeleton ZLJ 0035 in lateral view, highlighting the positions and patterns of *Taotieichnus orientalis* burrow traces (solid grey lines in B and D).





**Fig. 5.** Photographs of the fifth haemal arch of prosauropod dinosaur skeleton ZLJ 0035 in A) left and B) right lateral views. At the distal end of the bone (bottom), *Taotieichnus orientalis* traces form enclosed chamber shelters, especially on the right surface.

Type locality and horizon: Dalishu bonebed, Shawan Member, Lufeng Formation, Early Jurassic. Dalishu Village, Konglongshan Town, Lufeng County, Yunnan Province, China.

Diagnosis: Epichnia, convex burrows (Fig. 7A) with dilated parts considered to be chambers (Fig. 7B). Traces columnar, branching, convex, with Y-shaped branches (Fig. 7C). Traces wind around the surfaces of the bones. At junctions other than Y-shaped branches, traces overlap rather than intersect directly (Fig. 7D). Surface texture rough. Traces hollow with thin mud constructed walls and cement infilled.

#### 4.1. Description

##### 4.1.1. Trace morphology

Traces preserved directly on bones of vertebrate specimen ZLJ0035 total 29.83 m in length. They form complex gallery systems in convex topographic relief on and around the bone surfaces, and lack any extensions into the surrounding matrix. No bone fragments are found within the burrows or tunnels. The traces consist of 436 simple burrows, 40 chambers, 89 Y-shaped branches, and 27 overlapping intersections (Fig. 3).

The simple burrows are flush with the bone surfaces and straight to gently arcuate, often with ovate ends (Fig. 7A). Tunnel heights range from 0.1 to 1.2 cm (based on measurements of 66 tunnels), and widths range from 0.2 to 2.2 cm, making the traces wider than tall, but in any one simple burrow, dimensions vary a little.

Irregularly shaped expansions of the galleries are frequently observed and termed 'chambers' (Fig. 7B). Additionally, 'Y-shaped' branches occur at intervals where the galleries branch at  $\sim 45^\circ$  angles from stem into branch burrows (Fig. 7C). Overlapping intersections occur when burrows cross over or under one another in different planes—burrows of similar diameters do not intersect with one another in the same plane (Fig. 7D). No other forms of the branches, intersections, or chambers are found in *Taotieichnus*. Small, shallow grooves appear to be excavated into the outer surfaces of the bones, but this has only been observed in a few places where the convex traces have detached from the bone.

All preserved bones except the cervical vertebrae of ZLJ 0035 preserve *Taotieichnus* traces, though the structures are most densely concentrated on the ilia (Fig. 4), ischia, and haemal arches (Fig. 5). The majority of the burrows (92% total burrow length [TTL], 8% distributed on ischia and pubes) cover the surfaces of the axial skeleton and the ilia.

On the axial skeleton, traces can be found on the dorsal, sacral, and caudal vertebrae. There are 218 simple burrows (widths: 0.19–2.21 cm; lengths: 1.14–21.60 cm), 13 chambers (widths: 0.34–3.18 cm; lengths: 0.65–6.73 cm), 29 Y-shaped branches, and nine overlapping intersections. The traces occur along the vertebrae and continue across several vertebrae in places. Some traces on transverse processes and neural spines are wind around the surfaces of the bones.

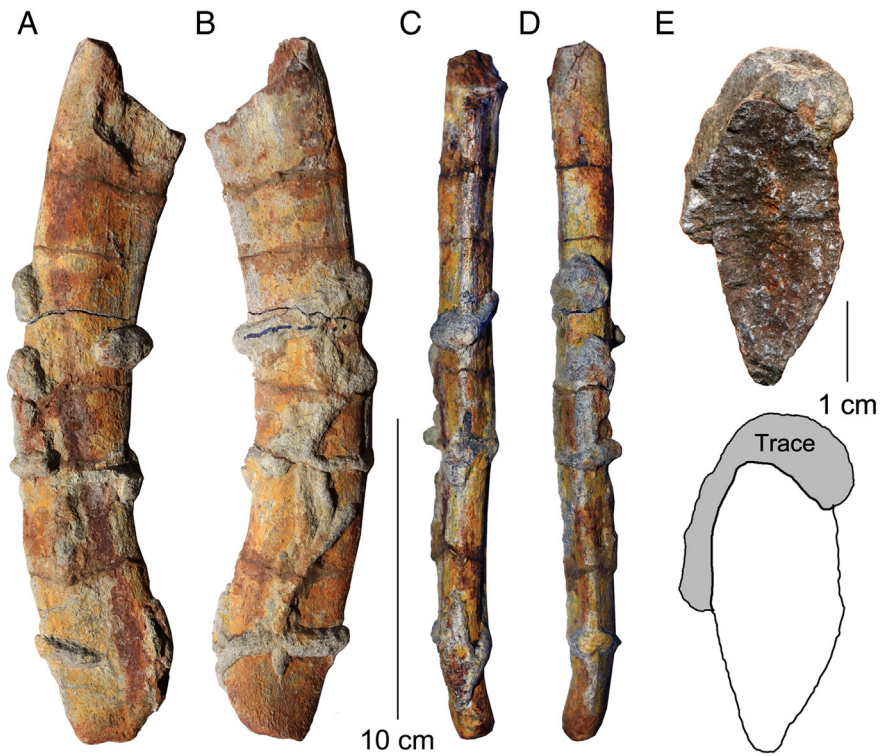
On the ilia, there are 89 simple burrows, 15 chambers, 40 Y-shaped branches, and six overlapping burrows (Fig. 4). Traces adorn both sides of the bones, but more densely on the medial surfaces. The right ilium bears 31 simple burrows (widths: 0.23–1.76 cm; lengths: 2.41–54.55 cm), seven chambers (widths: 0.40–2.77 cm; lengths: 1.36–5.79 cm), 15 Y-shaped branches, and two overlapping intersections. The burrows extend along the anteroposterior axis of the bone; the single longest (54.55 cm) individual burrow is on the lateral surface of the right ilium. The left ilium bears 58 simple burrows (widths: 0.17–1.39 cm; lengths: 0.68–49.02 cm), eight chambers (widths: 0.35–2.32 cm; lengths: 1.38–3.23 cm), 25 Y-shaped branches, and four overlapping intersections. Unlike on the right ilium, the burrows lie predominantly at a  $45^\circ$  angle to the anteroposterior axis of the bone. Three prominent burrows wind from the lateral surface onto the medial surface; these also form three overlapping intersections with a large burrow found along the top border of the ilium in lateral view. In some places on the lateral surface of the left ilium, the traces are densely packed and piled onto one another.

The haemal arches collectively bear 80 simple burrows (widths: 0.81–1.16 cm; lengths: 1.13–24.67 cm), eight chambers (widths: 0.39–4.02 cm; lengths: 0.98–8.77 cm), 12 Y-shaped branches, and five overlapping intersections. Most traces parallel the long axes of the bones, some spanning the entire length. An overlapping intersection formed by two main burrows can be seen on the left surface of the third haemal arch; a similar intersection can be seen on the fourth haemal arch. On the right side of the fifth haemal arch, two elongate chambers are preserved (Fig. 5).

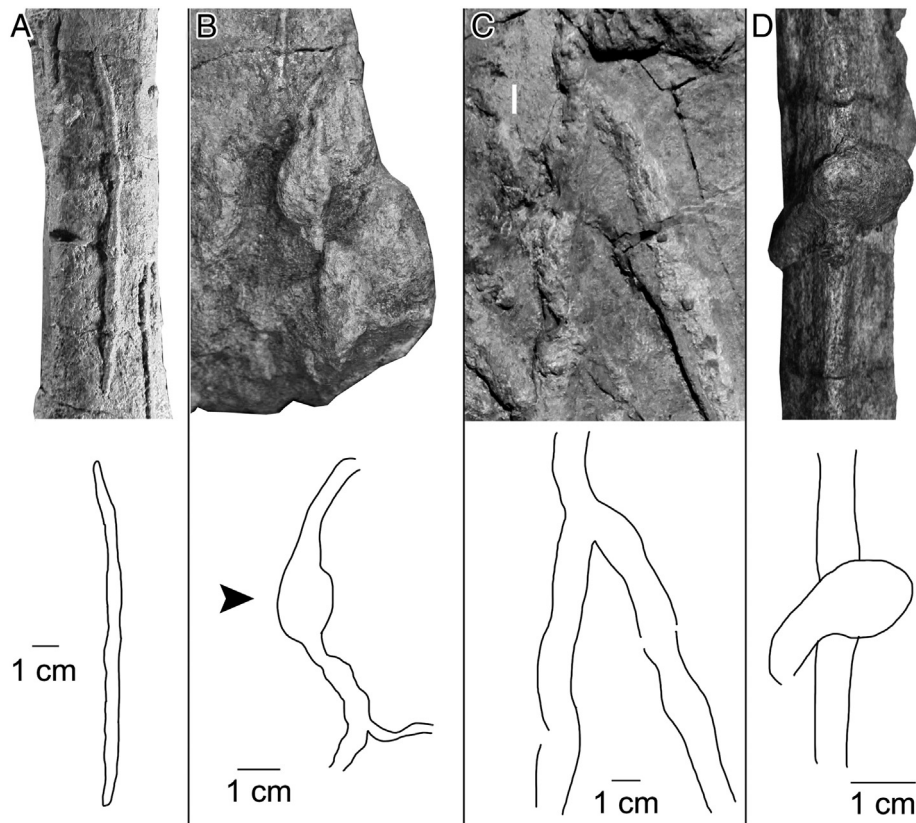
The pubes bear 20 simple burrows (widths: 0.22–1.31 cm; lengths: 2.62–22.70 cm), one chamber (width: 1.40–2.77 cm; length: 5.06 cm), four Y-shaped branches, and no overlapping intersections. Most traces are oriented along the long axis of the bones. On the right pubis, traces encircle, but do not travel through, the obturator foramen.

On the ischia, the traces are poorly preserved. They bear 18 simple burrows (widths: 0.28–1.73 cm; lengths: 2.40–15.75 cm), three chambers (widths: 0.49–1.45 cm; lengths: 1.78–3.18 cm), no Y-shaped branches, and no overlapping intersections. Most traces are oriented along the long axes of the bones. Near the distal end of the right ischium, a chamber is preserved (Fig. 7B).

Traces are preserved on two rib fragments. One fragment bears only one simple trace (width: 0.22–0.61 cm; length: 9.09 cm) along its long axis. However, the other fragment bears 11 simple burrows (widths:



**Fig. 6.** Photographs of a rib fragment from prosauropod dinosaur skeleton ZLJ 0035 in A) medial, B) lateral, C) anterior, D) posterior, and E) cross-sectional views showing extensive *Taotieichnus orientalis* trace fossil modification.



**Fig. 7.** Photographs and schematic drawings demonstrating the variability of the morphologies of *Taotieichnus orientalis* burrows on prosauropod dinosaur skeleton ZLJ 0035. A) Simple burrow, B) chamber, C) Y-shaped branch, and D) overlapping intersection.



0.17–1.90 cm; lengths: 1.81–13.37 cm) along its long axis and seven overlapping intersections, four Y-shaped branches, and no chambers along its short axis. The burrows along the short axis wind around the circumference of the bone (Fig. 6).

#### 4.2. Trace infills

Thin sections cut perpendicular to the long axes of several burrows reveal that they were originally hollow tubes or burrows with thin, mud-constructed outer walls. The outermost margins of the tubes (Fig. 8A) consist of a 1–2 mm-thick rind or outer wall that is composed largely of silt-sized quartz and feldspar grains held together by a cement and clay matrix. The tunnels are almost completely infilled by coarse, diagenetic cement that has grown inward from the margins of the burrow towards the bone surface. The pore-filling cement is fibrous and shows a distinctive, swallow-tail-like twinning pattern. These features, plus the relatively low-order interference colors, indicate that the cement is predominantly gypsum; however, when powdered, the infill reacts with 5% HCl, suggesting that carbonate—probably dolomite since the infill does not effervesce when unpowdered—is also present. Due to overambitious fossil preparation, the softer outer walls of many tunnels were removed, leaving only the cement-filled, internal molds of the tunnels (Figs. 7–8).

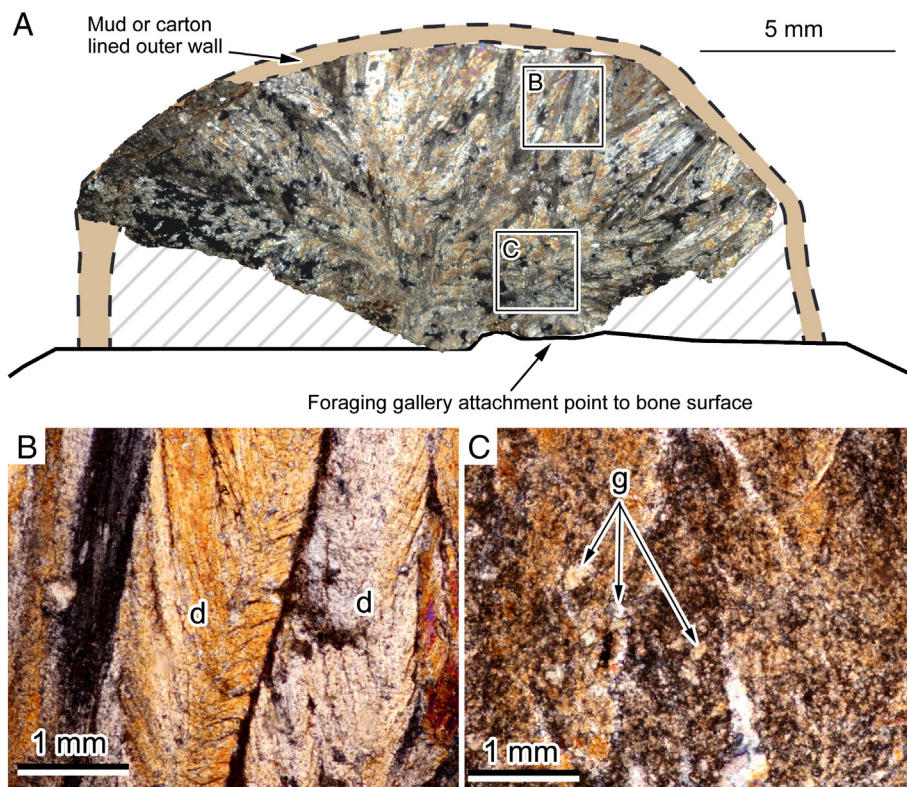
### 5. Discussion

#### 5.1. Analysis of the infills and trace morphology

No bone, bone chips, or bone-like fabrics were found in cement-infilled tunnels of *Taotieichnus* that would indicate that they are either pathological outgrowths of bone or re-healed/remodeled bone. Similarly, the absence of healed-bone indicators in or around the structures

demonstrates that the traces were produced after the prosauropod individual died (Tanke and Rothschild, 1997). The superposition of *Taotieichnus* directly on the bone surfaces, plus the shallow scratches into the outermost bone surfaces where the burrows have been removed, implies that the trace producer may have specifically targeted the decaying flesh on the bones. The coarse, crystalline gypsum cement infilling indicates that the traces originally were open burrows or galleries, rather than backfilled burrow systems, as are commonly produced by infaunal, detritivorous soil organisms. The burrows must have been either lined or constructed with very competent materials (e.g., moist, clay-rich mud) in order not to have collapsed prior to diagenetic infilling of cement. The most likely scenario is that the burrows were produced subaerially on bone surfaces as ‘shelter tubes’ or mud- or carton-construction galleries similar to those produced today by various insect groups. Carton is a saliva plus faecal or mud material commonly produced by subterranean termites, mud wasps, and other insects during foraging to help avoid desiccation and provide protection during foraging or nest production. Regardless of whether the traces were produced subaerially prior to burial or within the soil after burial of the skeleton, the tunnels were clearly lined and remained largely free of debris until coarse gypsum cement precipitated within the chambers and galleries on the bone surfaces, which enabled their three-dimensional preservation.

The traces protrude in convex topographic relief from the bone surfaces and form a complex gallery system (Figs. 2–6) unlike any previously reported from the fossil record on or in bone (Fisher, 1995; Roberts et al., 2007; Britt et al., 2008; Bader et al., 2009; Kirkland and Bader, 2010; Saneyoshi et al., 2011). The winding, random distribution of the burrows and the gloves on bones implies that the trace makers were, at least in part, using the bone and/or decaying flesh around the carcass as a nutrient resource (Seilacher, 2007; Britt et al., 2008; Bader et al., 2009; Backwell et al., 2012). If so, then the traces are best referred



**Fig. 8.** Petrographic sections of *Taotieichnus orientalis* tunnel infills on prosauropod dinosaur skeleton ZLJ 0035. In all photographs, the top (outer) surface of the burrow is towards the top of the image. A) Cross-sectional thin section through a tunnel on a rib (arrows on Fig. 4A, B) in cross-polarized light showing compositional differences in regions distal (B) and adjacent to (C) the bone. B) Large dolomite crystals in the distal region grade into smaller, rounded grains adjacent to the bone (C). Abbreviations: d = dolomite crystals; g = quartz sand grains.

to as fodichnia. However, the shallow excavations into the bone surfaces may have been purely incidental, and the trace makers were simply utilizing the bone surfaces as a substrate to which to attach their dwellings; alternatively, the trace makers incidentally encountered the bones as they produced foraging tunnels in the surrounding sediment. In either case, the traces would then constitute domicinia.

The small range in diameters of the burrows suggests a correspondingly small body size of the trace making taxon. The changing diameters of simple burrows and branches are a notable character. Burrows excavated by solitary animals, such as worms, crustaceans (other than thalassinid shrimp), and most mammals, have roughly fixed diameters that are only large enough to permit the burrowers to pass (Laundré, 1989; Reichman and Smith, 1990; Turner, 2000; Hansell, 2007). Even the burrows (though not the nest chambers) of communal burrowing mammals (e.g., *Heterocephalus*; Hill et al., 1957) are likewise of relatively constant diameters. Variations in the diameters of tunnels, such as in ZLJ 0035, indicate a social structure because they denote a flow of traffic of multiple individuals inhabiting the same space, corresponding to social organisation (Tschinkel, 2003; Chowdhury et al., 2004; Genise et al., 2005; Lee et al., 2008; Burd et al., 2010; Tschinkel, 2010).

The approximate Y-shapes of all branches of *Taotieichnus* suggest a habitual nature of the constructions. Y-shaped, branching searching patterns are specifically structured to improve food-searching efficiency in social insects and are employed by ants and termites (Jackson et al., 2004; Lee et al., 2007). In ZLJ 0035, burrows cross over or under one another in different planes, but burrows of similar diameters do not intersect with one another in the same plane (Fig. 7D), indicating that the traces were convex, solid-walled structures when originally manufactured and that the trace makers did not disturb or modify existing structures while constructing new ones.

### 5.2. Known bone-modifying organisms as possible trace makers

Few animals construct gallery systems as complex as those observed on the Lufeng specimen. Examples of relatively complex gallery-producing organisms include derived eucynodonts (including mammals) (Hansell, 2007), burrowing shrimps (Genise, 2004; Hansell, 2007; Seilacher, 2007), termites, ants, and some beetles (Wilson, 1971). The smallest diameter (0.1 cm) gallery/burrow on ZLJ 0035 is too small to have been made by any known derived eucynodonts, including mammals (Laundré, 1989; Reichman and Smith, 1990; Chinsamy-Turan, 2012). Given the general similarity of all the traces on ZLJ 0035, the probability that they were manufactured by different trace makers is low.

The gallery system of *Taotieichnus* does not resemble those made by thalassinid shrimp (Coelho et al., 2000; Genise, 2004; Hansell, 2007; Seilacher, 2007), nor are such crustaceans known to bore into bones (Genise, 2004; Hansell, 2007; Seilacher, 2007; Bader et al., 2009). Thalassinid burrows commonly branch regularly or form boxworks of horizontal (or helical) burrows (Myrow, 1995; Coelho et al., 2000; Seilacher, 2007), unlike *Taotieichnus*. Moreover, although thalassinid shrimp burrow diameters may increase at branching points with the presence of turning chambers, adjoining burrows are almost always of equal diameter (Coelho et al., 2000; Genise, 2004; Seilacher, 2007), also unlike *Taotieichnus*. *Taotieichnus* is preserved in terrestrial sediments, but all known thalassinid shrimp species are marine (Seilacher, 2007).

Several trace fossil types indicative of post-mortem organismal activity have been documented on bones, including tooth marks (Fisher, 1995; Niedźwiedzki et al., 2010), trample marks (Fiorillo, 1984), digestive dissolution (Fisher, 1995), plant-root and fungal etching (Bader et al., 2009), and insect modification (Rogers, 1992; Roberts et al., 2007; Britt et al., 2008; Bader et al., 2009; Kirkland and Bader, 2010). The traces on ZLJ 0035 do not match the morphologies of known tooth, digestion, or etching marks.

Insects today are important decomposers in terrestrial ecosystems (Labandeira, 1998) and arose in the Late Silurian (~420 Mya) (Grimaldi and Engel, 2005). The major clades of modern insects mostly originated in the Triassic, after the end-Permian extinction (Labandeira, 1998; Grimaldi and Engel, 2005), and began to diversify in the Jurassic (Grimaldi and Engel, 2005). Insect traces on bone commonly include mandible marks, depressions, grooves, burrows, and/or chambers (Roberts et al., 2007; Britt et al., 2008; Bader et al., 2009). Shallow scratches are evident between the tunnels and bone surfaces on ZLH 0035; however because of coarse preservation, and damage caused during preparation of the dinosaur remains by trying to pry the tunnels off of the bone, the nature and presence of fine-scale features, such as mandible marks, on the fossils are difficult to identify and characterize. However, what can be observed between the traces and the bone surface in *Taotieichnus* match the general morphologies of insect traces (Roberts et al., 2007; Britt et al., 2008; Bader et al., 2009; Kirkland and Bader, 2010).

Known insect bone modifiers include mayflies (Ephemeroptera), tineid moths (Lepidoptera), some species of ants (Hymenoptera), some beetles (Coleoptera), and termites (Isoptera) (Roberts et al., 2007; Britt et al., 2008; Bader et al., 2009; Kirkland and Bader, 2010; Backwell et al., 2012). Of these possibilities, the following can be readily dismissed as candidates for the *Taotieichnus* trace maker.

Mayfly larvae live in water and create simple, U-shaped borings as shelter and filter-feeding sites in wood, occasionally boring into bones (Brittain, 1982; Charbonneau and Hare, 1998; Britt et al., 2008; Moran et al., 2010). Such burrows in Miocene wood and bone are thought to be made by mayflies (Britt et al., 2008). Mayfly larvae burrows characteristically consist of two parallel tubes adjacent to each other (Brittain, 1982; Charbonneau and Hare, 1998; Britt et al., 2008), which is dissimilar to *Taotieichnus*.

Tineid moth caterpillars can construct compound silk, earth, and keratinous tubes (Davis and Rorbinson, 1999; Deyrup et al., 2005; Britt et al., 2008). They have been reported to damage dead tortoise shell by feeding on the keratin scales (Deyrup et al., 2005) and excavate on or into animal horns (Davis and Rorbinson, 1999; Britt et al., 2008). The walls of their burrows consist of two layers: an inner, silky layer and an outer layer constructed of adhered earth pellets and food crumbs (Davis and Rorbinson, 1999; Deyrup et al., 2005). This differs from the single-layered walls in *Taotieichnus*. They have also been known to dig simple pupation chambers into bone (Hill, 1987), a feature not seen in *Taotieichnus*.

Beetles—particularly their larvae—are the most common bone modifiers. Coleoptera originated in the Early Permian (Grimaldi and Engel, 2005) and thus beetles were present in the Early Jurassic. Known coleopteran bone modifiers include silphids (Silphidae), dermestids (Dermestidae), histerids (Histeridae), scarabs (Scarabaeidae), and tenebrionids (Tenebrionidae) (Rogers, 1992; Roberts et al., 2007; Britt et al., 2008; Bader et al., 2009; Kirkland and Bader, 2010; Backwell et al., 2012). Some extant beetle species display simple social behaviors (Wilson, 1971; Hamilton et al., 1976; Costa et al., 2004). For example, *Monarthrum mali*, a bark beetle (Scolytidae), excavates comb-like social nests in wood (Wilson, 1971), although not into bone. Beetles cannot be completely discounted as possible *Taotieichnus* trace makers because an extinct beetle species may have evolved complex social behavior and convergently evolved the ability to construct complex galleries. But this is a less parsimonious conclusion than that presented below because despite being the most diverse insect (and animal) clade, no known extant or extinct beetle is known to exhibit such behavior (Wilson, 1971; Genise, 2004; Grimaldi and Engel, 2005; Hansell, 2007), and no similar complex gallery constructions or burrow systems attributable to beetles have been recorded on or in bones. As holometabolan insects, beetle larvae dig round or oval pupation chambers at feed sites (Hasiotis et al., 1999; Roberts et al., 2007; Britt et al., 2008), but as with tineid moths, no such structures are found in *Taotieichnus*.



Beetles are not known to construct burrows on or in bones, and their larvae are only capable of creating superficial structures of silk combined with soil pellets and fragments of bone (Sutherland et al., 2010) similar to those of mayfly and tineid moth larvae (Brittain, 1982; Charbonneau and Hare, 1998; Deyrup et al., 2005; Britt et al., 2008; Sutherland et al., 2010). The petrographic sections of the *Taotieichnus* structures do not support a coleopteran interpretation.

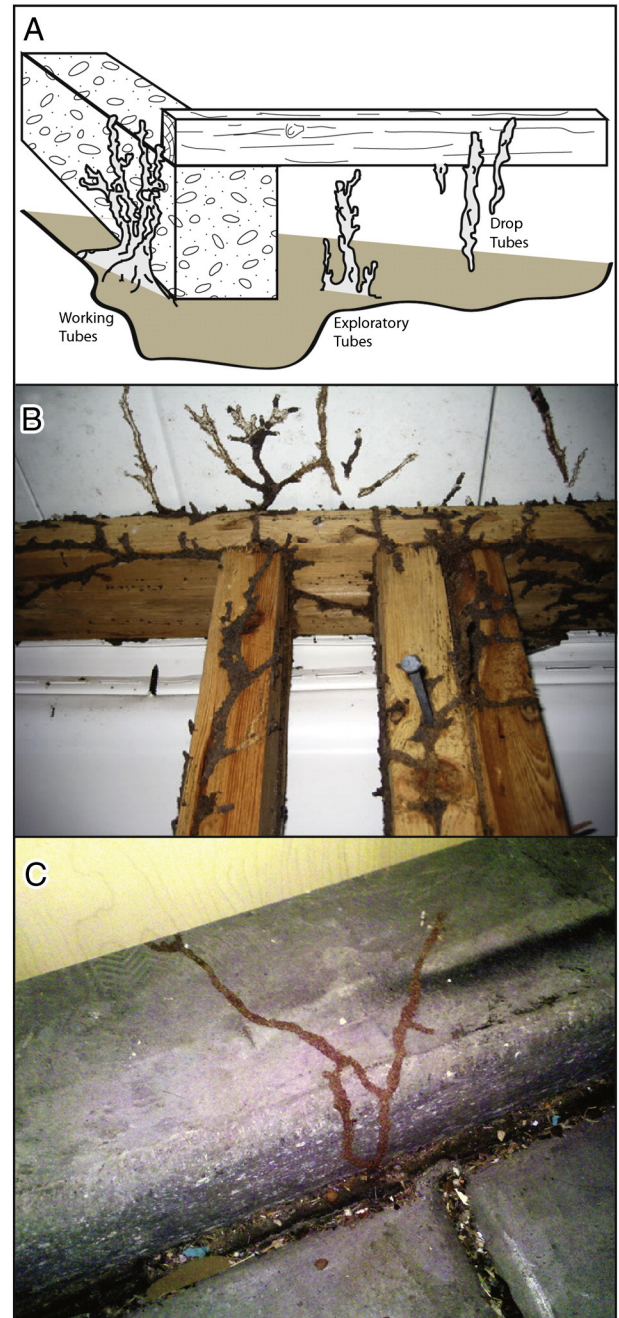
Ants and termites, as social insects, are the most characteristic constructors of complex burrow systems (Wilson, 1971; Tschinkel, 2003; Genise, 2004; Tschinkel, 2010). The diameters of the burrows on ZLJ 0035 fall within the size ranges known for those created by both ants (0.8–40 mm diameters; Wilson, 1971; Hölldobler and Wilson, 1990; Wu and Wang, 1995; Zhou, 2001; Roberts and Tapanila, 2006) and termites (1–50 mm diameters; Thorne and Kimsey, 1983; Genise, 2004; Genise et al., 2005; Tschinkel, 2010). Ants, and sometimes termites, use dead vertebrates (soft tissues and sometimes bones) as nutrient resources (Thorne and Kimsey, 1983; Hölldobler and Wilson, 1990; Gautier, 1993) and both groups can construct shelters in the open air above food sources (Wilson, 1971; Hölldobler and Wilson, 1990).

Ants cover exposed food sources with loose soil pellets and rarely construct long shelter tubes (Wilson, 1971; Hölldobler and Wilson, 1990). Although some ant species, such as *Monomorium pharaonis*, engage in branching (Y-shaped) search patterns (signaled by pheromone signposts) when foraging, no traces or shelter tubes are typically constructed that leave a record of this activity (Jackson et al., 2004). Most ant constructions consist of vertical burrows connecting horizontal to sub-horizontal chambers (Tschinkel, 2003). This is unlike the curving, irregular burrows around bone surfaces with Y-shaped branches and chambers that characterize *Taotieichnus*. Furthermore, the oldest ants likely originated no earlier than the Early Cretaceous (Grimaldi and Engel, 2005).

Although modern termites primarily feed on cellulose, they are also known to occasionally derive nutrients from both fresh and weathered bones, and can completely destroy a bone (Derry, 1911; Thorne and Kimsey, 1983; Wylie et al., 1987; Haynes, 1991; Britt et al., 2008; Bignell, 2011; Huchet et al., 2011; Backwell et al., 2012). Termite damage on modern, archeological, and fossil vertebrate bones traces in the form of scratches, star-shaped pits, and various other boring morphologies is well-documented (Fejfar and Kaiser, 2005; Huchet et al., 2011; Backwell et al., 2012); possible examples have been reported previously in Late Jurassic dinosaur bones (Dangerfield et al., 2005; Britt et al., 2008; Bader et al., 2009).

The most common termite traces reported in the literature are subterranean nests in sediment (e.g., *Termitichnus*). Termite nests usually consist of networks of simple and complex galleries that include burrows, spheres, and ramps (Bown and Genise, 1993; Genise et al., 2000; Hasiotis, 2004; Düringer et al., 2007). When foraging, subterranean (soil-nesting) termites use a mixture of saliva, faecal material, and carton to construct sheltering galleries ('shelter tubes'; Fig. 9) against unfavorable environmental conditions; these can extend into the open air from the core of a nest (Derry, 1911; Wilson, 1971; Haynes, 1991; Gilberg et al., 2003; Su et al., 2004; Grimaldi and Engel, 2005; Lee et al., 2007). Termites thus can construct three-dimensional structures similar to the convex galleries of *Taotieichnus*. Once a termite burrow is completed, it is not subsequently modified except for repairs (Su and Bardunias, 2005), which may explain why the structures on the Lufeng prosauropod overlap, rather than intersect, when crossing (Fig. 7D).

Termite galleries are often constructed around food sources—a character that is considered diagnostic of termites (Backwell et al., 2012)—fitting the occurrences of *Taotieichnus*. The Y-shaped branches of *Taotieichnus* are likewise characteristic of termite burrows (Haynes, 1991; Hasiotis, 2003; Su et al., 2004; Su and Bardunias, 2005; Perna et al., 2008). Modern termite foraging burrow systems matching this morphology have been reported on decomposing boa, turtle, sloth, and agouti skeletons on forest floors (Thorne and Kimsey, 1983), and nests and other termite



**Fig. 9.** Modern subterranean termite 'shelter tubes' or foraging galleries. A) The three general classifications of subaerial foraging galleries produced by subterranean termites, including working, exploratory, and drop tubes (after Smith and Whitman, 1992). B, C) The characteristic branching pattern and carton-construction tubes produced by termites during foraging results in a somewhat random pattern leading to and around potential food sources, morphologically similar to *Taotieichnus orientalis* traces described herein.

constructions around other tetrapod bones have been documented (Bignell, 2011; Huchet et al., 2011; Backwell et al., 2012). At least four types of termite 'shelter tubes' are recognized: working, exploratory, migratory, and drop tubes (Fig. 9A) (Smith and Whitman, 1992). Working tubes extend above ground from the subterranean nests and lead directly to woody food sources (and, in some cases, to carrion) (Fig. 9B). Exploratory and migratory tubes also exit the subterranean nest and extend subaerially, but do not directly connect to a food source (Fig. 9C). Rather, they are produced as migration pathways or as termites search for new food sources. Drop tubes do not connect to the



subterranean nest; rather, they represent new tunnels exiting the food source and moving back towards the soil surface (Fig. 9A).

A comparison of the general morphologies and characteristics of modern, subterranean termite foraging galleries reveals close similarities to *Taotieichnus*, particularly in relation to their size, shape, branching patterns and construction around food sources (i.e., wood or carrion). Tschinkel (2010) carefully documented the morphologies and architectures of shallow subsurface foraging tubes produced by harvester termites. Morphological similarities between them and *Taotieichnus* include the following: (1) hollow sand and mud constructed gallery systems (Tschinkel, 2010: Figs. 2–3); (2) roughly equal gallery dimensions; (3) the presence of typically straight galleries that periodically inflate to form larger chambers (Tschinkel, 2010: Fig. 4); (4) somewhat similar Y-shaped branching patterns, and (5) overlapping intersections (Tschinkel, 2010: Fig. 11).

Even more striking is the morphological and situational similarities between *Taotieichnus* galleries and the subaerially constructed *Nasutitermes* galleries observed by Thorne and Kimsey (1983) on the remains of a three-toed sloth from Panama as well as variously sized, carton-encased foraging galleries over portions of several other skeletons. For example, Thorne and Kimsey (1983: fig. 1a,b) document hollow, carton-walled tunnels constructed directly over bone surfaces that expand in places to form chambers. A distinct, Y-shaped branching pattern is also observed (Thorne and Kimsey, 1983: Fig. 1b), and a general meandering pattern is noted around the skeleton. These authors noted that the classification of termites as strict xylophages may be inaccurate, following observations of Neotropical termite foraging groups associated with decomposing carcasses. Thorne and Kimsey (1983) noted small scrapes, interpreted as mandible marks, on portions of the bone over which the galleries were constructed, but absent where no galleries covered the bones, suggesting that carrion may be a part of the *Nasutitermes* diet. They followed up their observations with experiments using decaying carcasses; after several weeks, they observed foraging galleries on the forest floor that led up to the carcasses and up the leg of one carcass. They also observed that, a few days after the start of the rainy season the termites abandoned the carcass and were not seen again, implying that termites will only utilize a carcass under particular conditions. Thorne and Kimsey (1983) suggested termites may require dry weather for scouting and access to skeletons.

Modern, soil-inhabiting termites first excavate large chambers in soil and then construct complete nests within the chamber. A wall enclosing the nest is constructed and separated from the excavated chamber by a narrow space; this wall usually consists of faecal and/or regurgitated material (Genise, 2004). Fossil nests are the most common trace fossils in palaeosols because their walls increase the probability of consolidation during diagenesis (Bown and Genise, 1993). Although there is no record of subaerial termite foraging galleries or 'shelter tubes' in the fossil record, the ecological and pest-control literature contains a wealth of reports of these structures (Fig. 9), which are often hallmarks of wood-damaging, subterranean termites in buildings.

Termites are the oldest known eusocial insects (Wilson, 1971; Hölldobler and Wilson, 1990; Thorne et al., 2000; Grimaldi and Engel, 2005; Engel et al., 2009), although their actual first appearance in the fossil record is a point of contention. The oldest inarguable termite body fossils are from the Early Cretaceous of Asia, Europe, and South America (Thorne et al., 2000; Engel et al., 2007; Grimaldi et al., 2008; Engel and Delclòs, 2010). The relatively thin, soft exoskeletons of insects fossilize rarely and only under certain conditions, so the existing fossil record of early termites may not accurately reflect their time of origin (Huang et al., 1987; Thorne et al., 2000). Because the oldest known termite body fossils have a wide geographic distribution in the Early Cretaceous, termites almost certainly appeared earlier, perhaps in the Late Jurassic (Thorne et al., 2000; Engel et al., 2009; Howard and Thorne, 2011). However, based on trace fossil evidence and continental

drift, other workers have postulated even earlier origins, possibly as early as the Early Triassic (Zhu et al., 1989) or Late Permian (Emerson, 1967; Wilson, 1971; Zhu et al., 1993). Termites evolved from within the roach clade (Wilson, 1971; Thorne et al., 2000; Grimaldi and Engel, 2005; Engel et al., 2009) and are therefore considered to be a form of eusocial roaches—the traditional termite order Isoptera was reduced to an epifamily (Termitidae) in the cockroach order Blattodea (Eggleton et al., 2007; Inward et al., 2007; but see Lo et al., 2007). Blattodea first appeared in the Paleozoic (Grimaldi and Engel, 2005). If this phylogenetic position is correct, it provides a basis for predicting pre-Cretaceous termites (or stem-termites). Termite-nest-like trace fossils have been reported from the Late Triassic (Hasiotis and Dubiel, 1995) and Early Jurassic (Bordy et al., 2004; q.v. Genise et al., 2005). The fragmentary, Middle Permian wing fossil assigned to *Uralotermes* (Zalessky, 1937), while initially considered isopteran, is almost certainly not (Emerson, 1965; Wilson, 1971) and, if identifiable at all, is likely grylloblattidan (Storozhenko, 1998). The close resemblance of *Taotieichnus* to the complex nest construction that is characteristic of subterranean termites, specifically to their subaerial foraging galleries or 'shelter tubes', suggests that the trace maker may well represent an unknown termite (or stem-termite) species in the Early Jurassic.

### 5.3. Invertebrate scavengers/decomposers in the Early Jurassic

Invertebrate scavengers may use a vertebrate carcass prior to detection by vertebrate scavengers, arriving at a carcass only minutes after its death (DeVault et al., 2004; Grimaldi and Engel, 2005). They may also use remains left by such scavengers (DeVault et al., 2004). After vertebrate scavenging of a vertebrate carcass, primarily bones are left, but these remains may still serve as food resources for carnivorous insects and bone feeders, such as termites (Derry, 1911; Wylie et al., 1987; Haynes, 1991; Britt et al., 2008; Bignell, 2011; Huchet et al., 2011; Backwell et al., 2012).

*Taotieichnus* may have been constructed as foraging traces on bones of ZLJ 0035 that were left by vertebrate predators or scavengers, although no other indicators of scavenging (e.g., tooth marks) have been identified on any elements of the specimen. Other prosauropod dinosaur fossils (ZLJ LF2007-20, ZLJ LF2007-21) from the Dalishu bonebed also bear *Taotieichnus* traces, implying that osteophagous foraging of dinosaur bones was potentially common at the site. Ancient termites (or, less parsimoniously, other social insect trace makers) may have played an important role as decomposers of vertebrate remains as early as the Early Jurassic.

## 6. Conclusion

The small and variable diameters of *Taotieichnus*, combined with chambers and a complex arrangement of galleries, suggest a saprophagous, social-insect trace maker of small body size in the Early Jurassic. The cement infilling of the traces also indicates that *Taotieichnus* was initially constructed as a series of hollow, mud- or carton-lined tubes or tunnels around the cf. *Yunnanosaurus* bones post-mortem and that the tunnels walls were competent enough to remain open until they were subsequently filled in by coarse cement sometime after burial but before they could be infilled by sediments.

Coleoptera originated in the Early Permian, hence beetles cannot be completely ruled out because some extant species are some known to be social or saprophagous, although none are known to construct traces as complex as those comprising *Taotieichnus*. A termite or stem-termite is the most probable trace maker based on comparative analysis of extant termite trace morphology. In particular, this new trace fossil is strikingly similar to subterranean termite foraging galleries, or 'shelter tubes', produced above ground, commonly on existing structures, such as trees, soil, rocks, buildings, and even vertebrate carcasses, suggesting the presence of a termite or stem-termite species in the Early Jurassic.

Similar burrows on other prosauropod dinosaur fossils from the same site indicate that in the Early Jurassic, social insects may have served as important decomposers of vertebrate remains.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.palaeo.2013.07.028>.

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