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The earliest fossil evidence of bone boring by terrestrial invertebrates, examples from China and South Africa

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ABSTRACT

We report the oldest fossil evidence of osteophagia by terrestrial invertebrates on both the Asian and African continents. Bones attributable to the Middle Jurassic dinosaur *Chuanjiesaurus* (Dinosauria: Sauropoda) were found with post-mortem insect modification in the Chuanjie Formation, Yunnan Province, China. The morphology of the borings closely matches the ichnogenus *Cubiculum*. Based on the lack of bioglyphs observed in *Cubiculum ornatus*, a new ichnospecies is proposed here. The new trace fossil, *Cubiculum inornatus* isp. nov., is interpreted to have been constructed for pupation by an unknown taxon of insect. Additionally, we report even older borings from Early Jurassic dinosaur bones of the Elliott Formation in the Karoo Basin, which represent the second oldest occurrence of insect traces in bone from continental settings. Both trace fossils sites have palaeogeographic implications for the origins and dispersal of osteophagia amongst terrestrial invertebrates during the Mesozoic. These discoveries push back the antiquity of pupation in animal bones by more than 100 million years to the Middle Jurassic, indicating that this behaviour, and osteophagy more generally, originated early in the Mesozoic, roughly comparable with the origination of insect pupation in woody substrates (Late Triassic).

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1. Introduction

Insects are a highly diverse group of organisms that originated during the Early Ordovician roughly 479 million years ago (Misof et al. 2014). Yet, because of their generally limited fossil record, information about the evolution of insects and their behaviour remains limited. Recently though, significant breakthroughs in understanding the timing and relationships among, the certain insect clades have been made due to advances in molecular phylogenetics and dating (Misof et al. 2014). However, capturing evidence of the timing of major behavioural innovations and advances is more difficult. Here, the fossil and rock record plays an important role in understanding and reconstructing the timing of development of certain behaviours. In particular, the study of borings in fossil bones has proven to be a valuable new avenue of research in paleobiology; both in marine and continental ecosystems. The wealth of readily accessible vertebrate fossils housed in museum collections provides an important archive of information for investigating insect behaviours. In a similar vein study of traces of plant–insect interactions (particular trace damage to leaves) has proven to be a valuable proxy

for understanding insect evolution and behaviour. Such studies have greatly expanded our understanding of functional feeding groups, niche partitioning, and insect diversity across major extinction events (Labandeira 1997, 2005, 2006; Labandeira et al. 2002; Wilf et al. 2006). Thus, comprehensive comparative studies of insect–bone interactions can substantially contribute to our understanding of the carrion-dependent invertebrate communities through time.

Insects are the most regularly inferred macro-bioeroders of bone in continental settings. Osteophagia by modern insects was reported in the early twentieth century (Derry 1911), but this behaviour is by no means modern, as putative insect traces have been reported in bones from as far back as the Triassic (Schwanke and Kellner 1999). However, there appears to be a significant increase in the abundance of bone borings reported in fossil bones from the Late Jurassic (Hasiotis et al. 1999; Chin and Bishop 2006; Britt et al. 2008; Bader et al. 2009) and Cretaceous (Rogers 1992; Paik 2000; Nolte et al. 2004; Roberts et al. 2007; Kirkland and Bader 2010; Cabral et al. 2011; Saneyoshi et al. 2011; Pirrone, Buatois and González Riga 2014b; Gianechini and De Valais 2015).

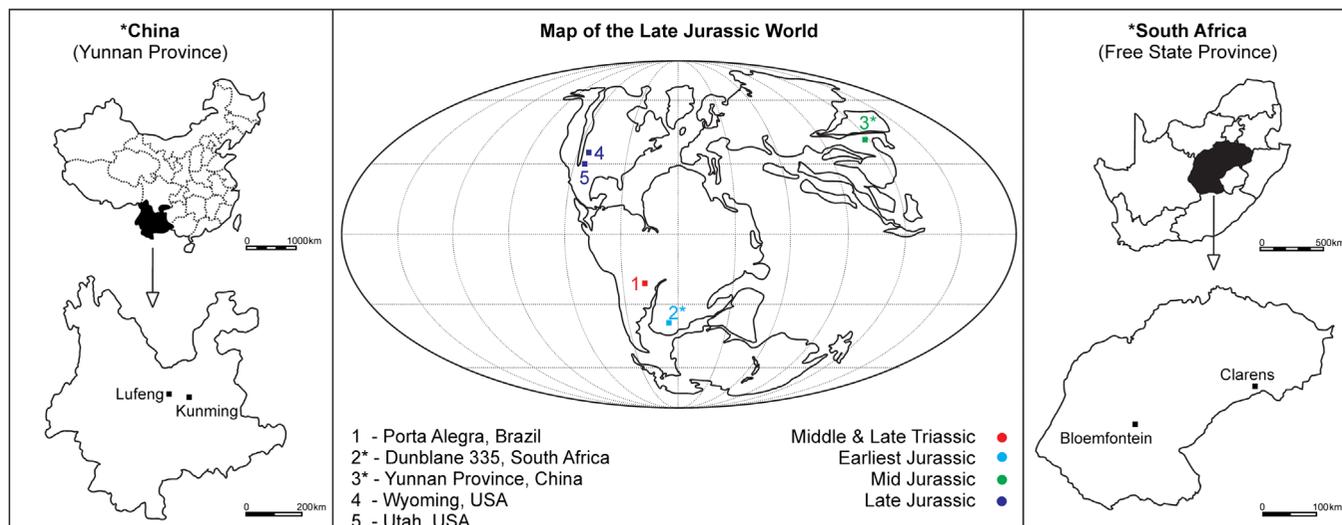


Figure 1. Geographic map showing the locations of the fossil localities described in this study, as well as a global distribution map indicating the location of reports of osteophagia by terrestrial invertebrates by the end of the Jurassic Period.

Reports from Asia are restricted to Cretaceous-aged deposits in Korea (Paik 2000) and Mongolia (Kirkland and Bader 2010; Saneyoshi et al. 2011; Fanti et al. 2012). However, Xing et al. (2013) recently reported insect-generated traces associated with dinosaur bones from the Lower Jurassic of China. Interestingly, they report only minor surface damage to the bones which appears to be incidental, associated with the construction of shelter tubes around a dinosaur carcass. Reports of insect damage to bone on the African continent are restricted to fossil localities dating from the last 3 million years (Kitching 1980; Newman 1993; Kaiser 2000; Val et al. 2015). A number of reports come from hominin-bearing sites within the Cradle of Humankind, namely Malapa Cave (Val et al. 2015), Swartkrans (Newman 1993) and Sterkfontein (Pickering 1999), whilst others from South Africa are attributed to either Late Stone Age or Middle Stone Age sites (Backwell et al. 2012) as well as the fossil sites of Florisbad and Makapansgat Member 3 (Kitching 1980, Brink 1987). A single report comes from Laetoli (Tanzania) (Kaiser 2000) and the last from Porc Epic Cave (Ethiopia) (Backwell et al. 2012).

Traces in bone produced by insects primarily fall into eight general morphological categories including grooves, striae, pits, bores, tubes, chambers, furrows or channels (Pirrone, Buatois and Bromley 2014a). An increasing number of empirical studies reveal a diversity of modern insects that modify bone including dermestids (Fernández-Jalvo and Monfort 2008; Zanetti et al. 2014), tenebrionids (Holden et al. 2013), clerids (Zanetti et al. 2015) and termites (Watson and Abbey 1986; Backwell et al. 2012). However, in a palaeontological context, the identification of the responsible agent is difficult to ascertain. Neoichnological research is critical to the identification of particular causal agents, which can provide valuable palaeoecologic, palaeoenvironment and palaeoclimatic insights (Genise et al. 2004; Seilacher 2007; Backwell et al. 2012; Huchet et al. 2013). However, beyond documenting fossil trace markers, trace fossils represent a key for establishing the timing of certain behaviours in ancient organisms. Thus, the study of bone modifications by insects has developed into an important branch of ichnology. The establishment of ichnotaxa for these traces is a relatively recent endeavour

and to date only three ichnospecies having been diagnosed – *Osteocallis mandibulus* (Roberts et al. 2007), *Cubiculum ornatus* (Roberts et al. 2007) and *Cubiculum levis* (Pirrone, Buatois and González Riga 2014b). These ichnotaxa are interpreted as being representative of either, feeding traces (*O. mandibulus*) or pupation chambers (*C. ornatus* & *C. levis*). An examination of the geographic distribution of reports of bone borings by terrestrial invertebrates suggests that by the Late Jurassic this behaviour was relatively wide spread (Figure 1). Here, we extend the temporal range of this behaviour by reporting the oldest evidence of insects pupating in bone from the Asian continent, and in doing so push back the range of *Cubiculum* to the Jurassic of China. Additionally, we provide the oldest reported evidence of insect–bone interactions from Africa.

2. Geologic settings and vertebrate fauna

2.1. Chuanjie Formation, Yunnan, China

The Red Beds of the Lufeng Series, in the Lufeng Basin, are approximately 750 m thick, and are conventionally divided into upper and lower units (Bien 1941). An Early Jurassic age was proposed for the Lower Lufeng Formation and a Middle Jurassic age for the Upper Lufeng Formation (Sheng et al. 1962). Fang et al. (2000) assigned strata that had at various times been included in the Upper Lufeng Formation to the Chuanjie, Laoluocun, Madishan and Anning formations (Fang et al. 2000). Based on stratigraphic correlation and invertebrate fossils, such as charophyta, ostracodes and bivalves, the Chuanjie Formation can be attributed to lacustrine deposition (Cheng et al. 2004). The climate of Middle Jurassic of the Sichuan–Yunnan region is estimated as subtropical warm-moist to semiarid (Wang et al. 2008; Li et al. 2011; Sekiya 2011). In the Chuanjie Formation, the Chuanjie bone bed is the only horizon that has produced skeletal material of dinosaurs. The bone bed has yielded material from at least four individuals of the large sauropod *Chuanjiesaurus anaensis* (Fang et al. 2000; Sekiya 2011), the theropod *Shidaisaurus jinae* (Currie et al. 2009) and a variety of turtles such as *Xinjiangchelys* (Tong et al. 2015).

2.2. Elliot Formation, Karoo Basin, South Africa

The Elliot Formation is a package of predominantly fluvially derived sedimentary rocks that crop out in Lesotho, Free State and Eastern Cape Provinces of South Africa (Haughton 1921; Kitching and Raath 1984; Smith and Kitching 1997; Bordy et al. 2004). The Elliot Formation was deposited during the last interval of development of the Karoo Basin (Catuneanu et al. 1998; Catuneanu et al. 2005), and estimates of its age range between latest Triassic and Early Jurassic (Kitching and Raath 1984; Olsen and Galton 1984; Smith and Kitching 1997). Aeolian sandstones and lacustrine shales can also be found within these typical terrestrial red beds, which are renowned for their preservation of dinosaur fossils, as well as other Mesozoic terrestrial vertebrates (Haughton 1921; Olsen and Galton 1984; Yates and Kitching 2003; Yates 2005; Yates et al. 2010). The 'middle Elliot Formation' does not have a formal lithostratigraphic definition, but it was recognised by Kitching & Raath (1984) as being deposited in a fluvial channel and floodplain environment, with the upper portions of the section having extensive pedogenic horizons with occasional subaerial depositional environments. The middle Elliot was extensively reviewed by Smith and Kitching (1997), who found widespread pedogenic nodule conglomerates in middle Elliot Strata, which they interpreted as evidence for a large-scale deflation surface in the north-western part of the Karoo Basin in the Early Jurassic. They reported a rich fauna of vertebrates from these middle Elliot layers, typified by the derived therapsid *Tritylodon*, and they proposed a formally defined 'Tritylodon Acme Zone' to biostratigraphically recognise the specificity of the middle Elliot Fauna. However, Bordy et al. (2004) was unable to find widespread evidence of a lithologically characteristic *Tritylodon* Acme Zone in their work in the southern part of the basin and in Lesotho, and they considered the middle Elliot strata to be part of the upper Elliot Formation.

3. Materials and methods

Institutional abbreviations and acronyms. ZLJ = Lufeng Dinosaur Museum of World Dinosaur Valley Park, China. BPI = Bernhard Price Institute for Palaeontological Research now referred to as the ESI (Evolutionary Studies Institute, University of the Witwatersrand, South Africa).

In 1995, the skeleton ZLJ0121 was discovered and collected by Lufeng Dinosaur Museum from the Chuanjie Formation in Lufeng County (GPS: 24°58'20.84"N, 102° 4'34.31"E), Yunnan Province, China (Figure 1). ZLJ0121 belongs to *Chuanjiesaurus anaensis* (Fang et al. 2000; Sekiya 2011). *Chuanjiesaurus anaensis* was originally considered a member of Cetiosauridae (Fang et al. 2000), but was later moved into Mamenchisauridea (Sekiya 2011). The ZLJ0121 materials included six articulated caudal vertebrae, catalogued as ZLJ0121-1-6. All the caudal vertebrae of ZLJ0121 are procoelous. There are no pleurocoels in the proximal caudal centra. The ventral surface of the proximal caudal centra is convex transversely. Their morphology is consistent with the description for the first to tenth caudal centra of *C. anaensis* (Sekiya 2011). Therefore, the ZLJ0121 materials are interpreted as belonging to the anterior caudal vertebrae. The caudal vertebrae (ZLJ0121) do not display pathology. Traces were only recorded on two of the six caudal vertebrae (ZLJ0121-3 and ZLJ0121-4) (Figure 2).

BPI-1-4268 is an isolated prosauropodomorph fibula collected in 1971 by James Kitching in the Caledon Park area, Dunblane 335. Dunblane 335 is approximately 1–2 km SW of the town of Clarens in the Eastern Free State, South Africa (Figure 1). The farm consists mainly of Drakensberg volcanic or Clarens sandstone, with only a thin strip of Elliot Formation in the southern half of the farm. The collections record for BPI-1-4268 states that the specimen is from the 'Middle Elliot Formation'. Thus BPI-1-4268 is associated to the Triassic-Jurassic boundary and is Rhaetian-Hettangian in age (Olsen and Galton 1984).

The following measurements were taken for all traces described in this study: length, width and depth. Length and width measurements were obtained using calipers, whilst depth was measured from the deepest to most superficial point on the cast of the traces also using digital caliper. All measurements are presented in mm.

4. Results

4.1. Systematic ichnology

Ichnogenus *Cubiculum* Roberts et al. 2007.

Type Ichnospecies: Cubiculum ornatus Roberts et al. 2007.

Emended diagnosis: Discrete ellipsoidal borings in bone. Hollow, oval borings bored into inner spongy and outer cortical bone surfaces. Boring length two to five times greater than its diameter. Structures may be isolated but may form dense, locally overlapping concentrations.

Remarks: Emendation of the ichnogenetic diagnosis is considered necessary to extend the size range whilst disassociating the wall (flank) profiles from the ichnogenus. The proportions of length two to five times greater than its diameter will allow for broader inclusion of chamber-shaped morphologies. Wall (flank) profiles are considered an ichnotaxobase at the ichnospecies level. The occurrence of bioglyphs as well as their pattern of occurrence (Pirrone, Buatois and Bromley 2014a) are also considered an ichnotaxobase at an ichnospecies level.

Cubiculum inornatus isp nov.

Holotype: Specimen ZLJ0121-T1 on the caudal vertebrae ZLJ0121-4 of *Chuanjiesaurus anaensis* from Middle Jurassic Chuanjie Formation of Yunnan, China (Figure 3(A)).

Referred specimens: One complete (T1) and three partially completed (T2, T3, T4) specimens (ZLJ0121-T-1-4) on two caudal vertebrae (ZLJ0121-3 and ZLJ0121-4) of *Chuanjiesaurus anaensis* from Middle Jurassic Chuanjie Formation of Yunnan, China (Figure 3(A)–(C)).

Etymology: Latin 'in' meaning 'not', 'ornatus' meaning 'decorated'.

Diagnosis: Ellipsoidal borings embedded in cortical bone penetrating into trabecular bone. The borings display a length width ratio ranging from 2:1 and 5:1 and slightly tapers towards one end. The walls run perpendicular to the bone surface, whilst the base of the boring is rounded. No filling or bioglyphs are present.

Description: All of the specimens are borings embedded in cortical and trabecular bone with a length 2–5 times that of its associated width. All the chambers have a rounded bottom (not flat), and the interior walls of the trace are smooth and do not record bioglyphs. The holotype (T1) measures 47.6 mm long and is 9.6 mm wide and displays a near perfect ellipsoidal morphology.

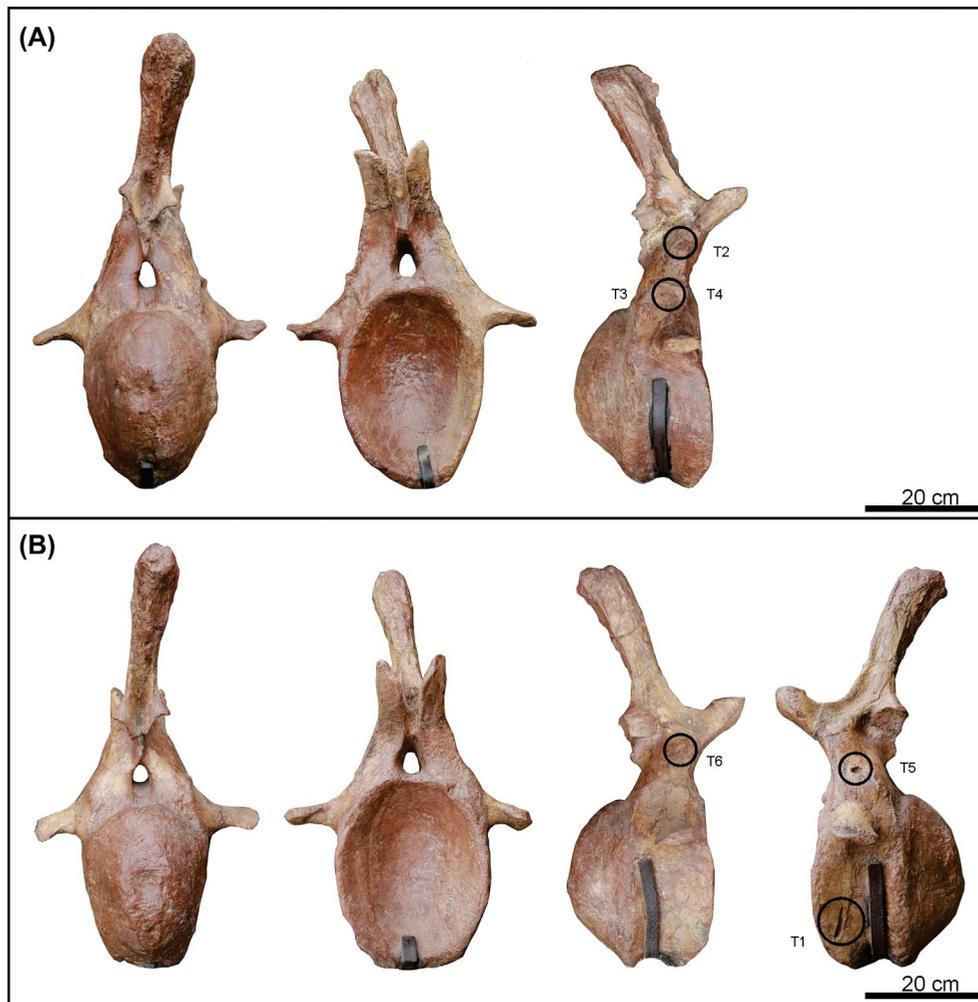


Figure 2. Photographs of two caudal vertebrae (ZLJ0121-3 and ZLJ0121-4) of *Chuanjiesaurus anaensis* recovered from World Dinosaur Valley Park, Chuanjie Formation, Yunnan, China. Circles indicate the position of the traces identified on the two vertebra. T1 is the holotype of *Cubiculum inornatus* isp. nov. T2, T3, T4 incomplete specimens of *C. inornatus*, and T5, T6 are interpreted as feeding traces.

Table 1. Measurements of insect traces from Chuanjie bone bed, Yunnan Province, China (ZLJ) and Elliot Formation, South Africa (BPI).

Trace type	Specimen number	Maximum diameter (mm)	Minimum diameter (mm)	Maximum depth (mm)	Figure reference
<i>Cubiculum inornatus</i>	ZLJ0121-T1	47.6	9.6	7.4	3A
	ZLJ0121-T2	29.1	7.8	8.2	3B
	ZLJ0121-T3	12	4.9	7.2	3C
	ZLJ0121-T4	16.4	5.7	7.2	3C
Hole	ZLJ0121-T5	15.1	12.1	9.2	3D
Hole	ZLJ0121-T6	20.3	8.8	7.5	3E
Hole	BPI-1-4268-T1	13.12	11.45	12.5	4B
Hole	BPI-1-4268-T2	10.6	–	–	4B
Tube – entrance	BPI-1-4268-T3.1	6.7	7.1	12.8	4C
Tube – exit	BPI-1-4268-T3.2	9.8	9.3	19.4	4C

Trace 2 (Figure 3(B)) measures 29.1 mm long and 7.8 mm wide, Trace 3 measures 12 mm long and 4.9 mm wide. Lastly, Trace 4 measures (Figure 3(C)) 16.4 mm long and 5.7 mm wide (Table 1). Their extremes intersect, so their major axis form a 45° angle.

4.2. Other trace descriptions

4.2.1. China

Two other traces (T5 and T6) were identified in association with *Cubiculum inornatus* but their unique morphology enables differentiation from *C. inornatus*. The maximum and minimum

diameters of T5 (Figure 3(D)) are similar but the resultant morphology is irregular, whilst the minimum diameter of the trace well exceeds the minimum diameter of *C. inornatus*. Neither the walls nor the bottom of this trace are smooth (unlike that of *C. inornatus*). This trace can be differentiated from other Mesozoic- and Cenozoic-aged bite traces as reported in the literature (Mikuláš et al. 2006; Hone and Tanke 2015). Trace 6 has a lens-shaped morphology, marked constriction on both ends and a maximum diameter of close to 9 mm at its centre (Figure 3(E)). Lastly, the base of T6 is flat and runs near parallel to the bone surface which is unlike the well-rounded bottom of *C. inornatus*.

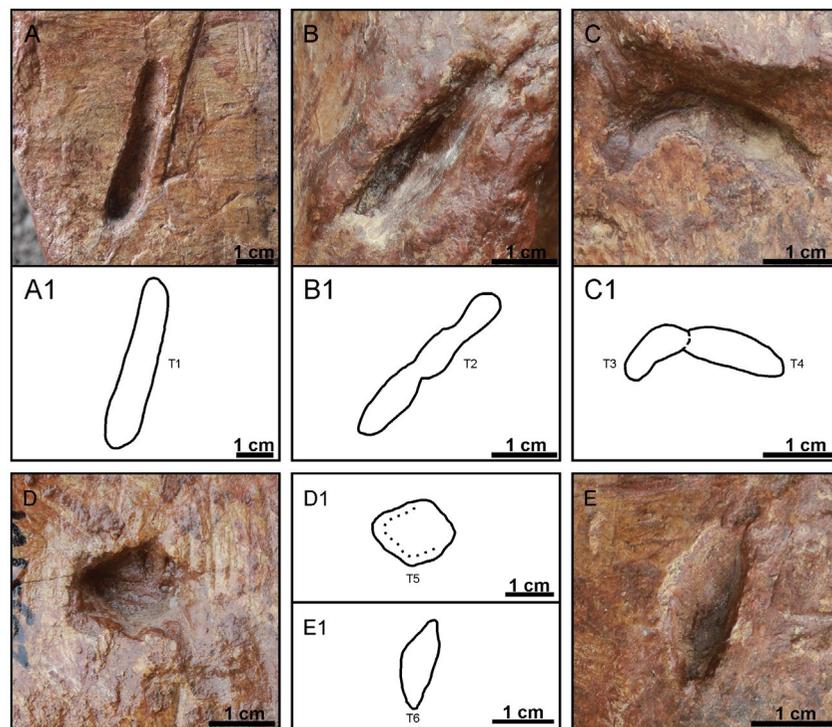


Figure 3. Photographs and schematics of invertebrate traces from World Dinosaur Valley Park, Chuanjie Formation, Yunnan Province, China (A and A1) Holotype of *Cubiculum inornatus* isp. nov. (B, B1, C, and C1) incomplete specimens of *C. inornatus* isp. nov. (D, D1, E, and E1) Feedings traces found in association with *C. inornatus* isp. nov.

4.2.2. South Africa

BPI-1-4268 is an isolated fibula displaying damage on both the proximal and distal ends (Figure 4(A)). Two borings have been excavated into the proximal end of the long bone (Figure 4(B)). The first boring (T1) has a maximum diameter of 13 mm with a minimum diameter of 11.45 mm. In surface view, the hole has an almost circular morphology and penetrates the bone at a slightly oblique angle relative to the bone surface, to a depth of 12.5 mm. The walls of the boring are smooth and straight, whilst the base is slightly rounded. The boring has been extended by excavating a channel in the wall of the boring towards the most distal margin of the fibula. The boring does not penetrate through the bone. The second boring (T2) on the proximal end of the fibula penetrates the bone (Figure 4(B)), has a maximum diameter of 10.6 mm and a near circular morphology. The most proximal margin of the boring has not been preserved and during preparation a small amount of infill was left *in situ*. The distal portion of the fibula shows a higher degree of modification in comparison with the proximal end. A tube entrance visible on the bone surface (Figure 4(C), T3.2), travels into the bone for close to 20 mm, then changes direction and travels a further 13 mm, then terminates at the contact region with the area where the bone has been completely destroyed (Figure 4(C), T3.1). A schematic drawing of this tube is presented in Figure 4(C)1. Measurement data is presented in Table 1.

5. Discussion

Cubiculum inornatus displays marked differences when compared to all other diagnosed *Cubiculum* ichnospecies including *C. ornatus* (Roberts et al. 2007) and *C. levis* (Pirrone, Buatois

and González Riga 2014b): *Cubiculum inornatus* may fall within the reported size range of *C. ornatus* (Roberts et al. 2007); however, the absence of concave walls (flanks) and bioglyphs is what differentiates the species. Similarly, *Cubiculum inornatus* is distinguishable from *C. levis* (Pirrone, Buatois and González Riga 2014b) due to the lack of pronounced concavity of the walls (flanks) and constriction of the entrance which gives this species its characteristic bowl-shaped morphology.

The four specimens of *C. inornatus* display both size and minor morphological variation which is common for other *Cubiculum* ichnospecies (Roberts et al. 2007; Pirrone, Buatois and González Riga, 2014b). However, all specimens of *C. inornatus* maintain a gross ellipsoidal morphology. Generally, size variation is most regularly attributed to the variable presence of soft/desiccated tissue during construction (Martin and West 1995; Hasiotis et al. 1999; Bader et al. 2009; Kirkland and Bader 2010; Huchet et al. 2013), but morphological variation has previously been explained in terms of incipient stages of construction (Britt et al. 2008). We propose that *C. inornatus* holotype (Figure 3(A)) is reflective of the final stage of construction, whilst the remaining specimens (Figure 3(B)–(C)) are merely representative of incipient stages of construction. Minimal exposure to the trace makers would account for the limited number of traces on the two vertebra and the absence of traces on the four remaining vertebrae. The vertebrae were isolated but articulated when recovered from the lacustrine sediments (Cheng et al. 2004) of the Chuanjie Formation. It is hypothesised that the *Chuanjiesaurus anaensis* skeleton had reached the early dry stage of decomposition and that subsequent transportation is the most likely process which resulted in the disassociation of the rest of the skeleton from the recovered vertebrae. However, remnant ligaments and desiccated

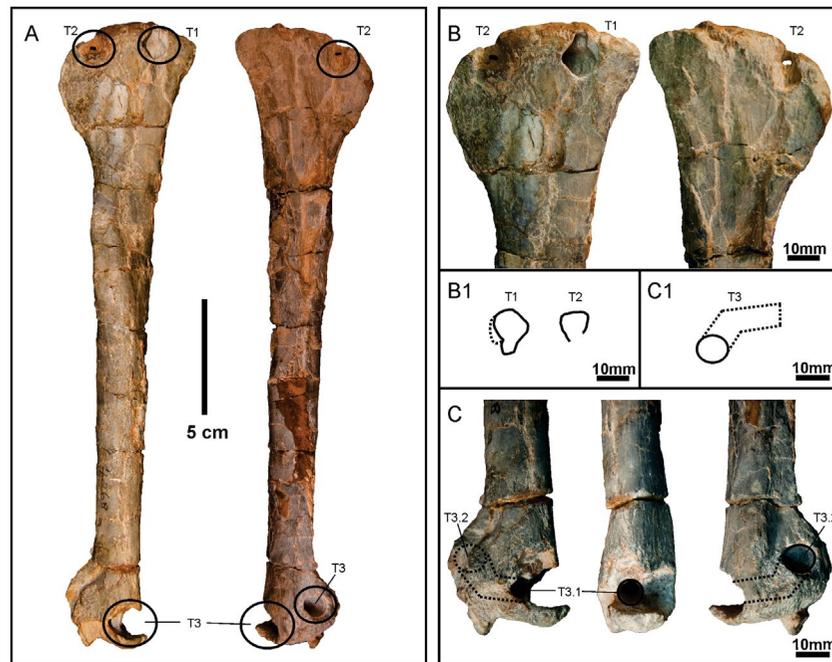


Figure 4. Photographs and schematics of the traces identified on the fibula of a prosauropodomorph from the Elliot Formation of South Africa. Note: (A) Macro view of the fibula indicating the position of the traces (B and B1) Holes identified on the proximal end (C and C1) Tube identified on the distal end.

tissue kept the six vertebrae in articulation prior to burial. The *C. anaensis* could have either been washed down stream then deposited in the paleo-lake, else may have died along the lake shore. Unfortunately, there is insufficient evidence to support either hypothesis.

The gross morphology of *C. inornatus* is consistent with other traces that have been interpreted as pupal chambers (Laudet and Antoine 2004; Roberts et al. 2007; Britt et al. 2008; Bader et al. 2009; Huchet et al. 2013; Xing et al. 2013; Pirrone, Buatois and González Riga, 2014b). *Cubiculum inornatus* is also interpreted as pupal chambers and thus its inclusion in the *Cubiculum* ichnogenus. The description of *C. inornatus* from the Middle Jurassic of Asia represents the oldest evidence of this behaviour by terrestrial invertebrates suggesting that this behaviour first originated very early in the evolutionary history of insects and possibly in Asia. Currently, all the representatives of *Cubiculum* fall to traces in bone produced by terrestrial invertebrates.

The disassociation of bioglyphs from the diagnosis for the ichnogenus is well motivated as the presence of bioglyphs and their associated pattern of occurrence may be a key diagnostic feature which could enable differentiation of *Cubiculum* ichnospecies and/or trace markers. It has been suggested that mouth part morphology is relatively consistent within the same species of insects at the varying stages of development (Labandeira 1997; Grimaldi and Engel 2005; Britt et al. 2008), with some exceptions (Eggleton 2011; Gotoh et al. 2011), and that the boring behaviour is consistent between multiple individual of the same species (Matthews and Matthews 2009). Therefore, consistency in behaviour and mouth part morphology could then be used as a basis for differentiation of different species or groups of trace makers. Additionally, the pattern of occurrence and placement of bioglyphs could further elucidate the behavioural process of

construction. For example, the presence of bioglyphs only at the bottom of a chamber would suggest a vertical approach to excavation, whilst bioglyphs on both the side walls and bottom would suggest a vertical approach followed by a horizontal expansion of the chamber. In the case of *C. inornatus*, the absence of bioglyphs is equally as informative as this suggests that the mouth parts of the agent were capable of excavating bone, but perhaps not hard enough to leave sufficiently deep bioglyphs to enable their preservation. However other factors such as the nature of the bone as well as preservation bias also need to be considered, as experimentation has shown that bioglyphs are infrequently discernable when insects modify cancellous bone (Backwell et al. 2012; Parkinson 2013) and shallow bioglyphs could easily be destroyed by a diversity of other taphonomic processes, such as sedimentary abrasion, or natural bone deterioration due to burial conditions.

The traces identified on the South Africa specimen are interpreted as feeding traces, which is the behaviour best supported by experimental data (Watson and Abbey 1986; Fernández-Jalvo and Monfort 2008; Backwell et al. 2012; Holden et al. 2013). On the distal portion of the fibula, it is unclear which modification event took place first, but the entrance of the tunnel in the area of bone destruction is well preserved, which could suggest that bone removal took place first, followed by the invertebrate boring into the bone. The abrupt change in direction of the tube supports the involvement of a biological agent as this would not be expected if the damage was pathological. Additionally, it is unclear whether the tube changes direction or records false branching as a result of accidental intersection (D'alessandro and Bromley 1987; Pirrone, Buatois and Bromley 2014a). However, the involvement of different individuals is consistent with the size difference between the two entrances. The entrance on the bone

surface is the largest measuring 9.8×9.3 mm, whilst the entrance inside the area of destroyed bone measures only 6.7×7.1 mm. These traces appear broadly similar to those described from the Two Medicines Formation from the Upper Cretaceous deposits in north-western Montana (Rogers 1992). However, the South African borings have smaller diameters in comparison, whilst the small sample sizes from both localities and the morphological simplicity of the traces limit comprehensive comparison.

5.1. Potential causal agents

At present, known insect–bone modifiers include termites (Isoptera), some species of ants (Hymenoptera), tineid moths (Lepidoptera), beetles of the families Dermestidae and Cleridae (Coleoptera) and mayflies (Ephemeroptera) (Watson and Abbey 1986; Deyrup et al. 2005; Freymann et al. 2007; Fernández-Jalvo and Monfort 2008; Abdel-Maksoud et al. 2011; Backwell et al. 2012; Holden et al. 2013; Parkinson 2013; Zanetti et al. 2014; Zanetti et al. 2015). Ants and termites are social insects that construct complex nest systems without isolated pupal chambers (Wilson 1971; Ran 2014), whilst may fly larvae live in water and create U-shaped borings (Britt et al. 2008; Xing et al. 2013). Tineid moths utilise the keratin sheath of horns for the purposes of pupation, thus associated bone damage is primarily restricted to the inner boney horn core (Mccorquodale 1898; Walsingham 1898; Hill 1975; Hill et al. 1987; Deyrup et al. 2005). None of these match the morphology of the traces described in this study.

The most likely trace maker would be a member of the order of Coleoptera. The most common beetle trace maker proposed is members of the dermestidae (Rogers 1992; Chin and Bishop 2006; Roberts et al. 2007; Britt et al. 2008; Bader et al. 2009). However, this inference is always approached with a degree of caution, with only one report proposing a particular species (*Dermestes maculatus*) (Britt et al. 2008). Dermestids body fossils have been reported from the Late Triassic (Dunstan 1923), but their dating is controversial (Kiselyova and Mchugh 2006; Kadej and Háva 2011). It is more widely accepted that the earliest body fossil of a basal dermestid appears only during the Late Cretaceous. In light of the body fossil record, it is thus unlikely that a member of the dermestidae family is responsible for the modifications identified in the Jurassic of China and South Africa. Furthermore, there is a paucity of experimental/observational data which would support dermestids as a potential agent of pupation chambers in bone (Haynes 1993; Fernández-Jalvo and Monfort 2008; Holden et al. 2013; Parkinson 2013).

The trace maker would have been long and thin based on the morphology and size of the chamber (Huchet et al. 2013). The occurrence of the traces clearly indicates that the trace maker was able to modify bone, but the lack of bioglyphs may suggest an inability to producing sufficiently deep bioglyphs which would enable their preservation. In a modern context, many scavenger insects are involved at the onset of decomposition of a carcass, but they are less likely to pupate in or on the dead body due to other insects preying on them during this stage (Kulshrestha and Satpathy 2001; Amendt et al. 2010; Byrd and Castner 2010). During the later stages of decomposition, the abundance of scavenger beetles greatly diminishes (Kulshrestha and Satpathy 2001; Amendt et al. 2010; Byrd and Castner 2010), which may then

prompt insects to pupate on the remaining carcass and possibly excavate bone. A lack of associated feeding traces suggests that the agent was not feeding on the bone but merely explored the bone as a protective pupation substrate (Haynes 1993; Holden et al. 2013).

Unfortunately, due to the sample size and morphological simplicity of the traces on the South African specimen, any attempt to infer a causal agent would merely be speculative. Nonetheless, what is clear is that in Southern Africa by the earliest Jurassic, an invertebrate agent had developed mouth parts which were capable of modifying bone. The restriction of modifications to the proximal and distal ends of the long bones suggests that the agent was able to modify less dense areas of long bones but was perhaps unable to modify thicker cortical bone, but this requires further testing.

5.2. Palaeogeographic implications

The earliest report of osteophagia by insects in a continental setting date from the Middle and Upper Triassic aged deposits of Brazil (Schwanke and Kellner 1999), whilst previous to this study other Mesozoic reports were restricted to the Upper Jurassic deposits of North America (Hasiotis et al. 1999; Britt et al. 2008; Bader et al. 2009) and by the Cretaceous reach a more global distribution (Rogers 1992; Paik 2000; Kirkland and Bader 2010; Cabral et al. 2011; Fanti et al. 2012; Pirrone, Buatois and González Riga, 2014b; Gianechini and De Valais, 2015). South Africa and China now have the second and third oldest reported cases of osteophagia by terrestrial invertebrates. Evidence indicates that this behavioural tendency had already evolved in South Africa by the Earliest Jurassic and in Asia by the Middle Jurassic (Figure 1). The description of *Cubiculum inornatus* demonstrates that the behavioural tendency of constructing pupal chambers in bone possibly first evolved in Asia but was more widespread by the end of the Cretaceous as *Cubiculum* sp. have been described from Western Argentina (Pirrone, Buatois and González Riga, 2014b), Utah, and Madagascar (Roberts et al. 2007). The morphological disparity across the described species of *Cubiculum* likely demonstrates convergent evolution of the necessary mechanisms to facilitate bone modification, as well as the associated behaviour of pupating in bone. Unfortunately, little is known about the carrion dependency of invertebrate communities during the Mesozoic and evidence of this dynamic niche specialisation will likely remain elusive.

6. Conclusions

Cubiculum inornatus represents the oldest evidence of pupation in bone by insects in a continental setting and represents some of the oldest examples of osteophagy from the fossil record. The traces identified on the South African specimen shows that insect–bone interactions on the modern African continent are not restricted to the last 4 million years, but in fact have ancient roots dating back some 190 million years. Our research demonstrates that insects were key players in carrion-dependent invertebrate communities during the Mesozoic, and that within a relatively short period of time after the origins of this behaviour, this niche was occupied by multiple species across several continents. The associated ages of the modifications draws into

question which particular insect produced the traces, as the most regularly inferred agents in existing literature only appear during the Late Cretaceous. To elucidate the origins of bone boring, a systematic approach to examining fossil collections is necessary to further our understanding of the origins and dispersal patterns of this behaviour, and the number of causal agents associated with decomposition during the Mesozoic.

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