

CONTINENTAL INSECT BORINGS IN DINOSAUR BONE: EXAMPLES FROM THE LATE CRETACEOUS OF MADAGASCAR AND UTAH

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ABSTRACT—Two new insect-related ichnogenera are reported in fossil dinosaur bones from Upper Cretaceous continental strata in Madagascar and Utah. *Cubiculum ornatus* n. igen. and isp. is described from numerous fossil bones in the Upper Cretaceous Maevarano Formation of northwestern Madagascar, and consists of hollow, ovoid chambers with concave flanks excavated into both spongy and compact bone. Traces similar in morphology to *Cubiculum ornatus* have been reported elsewhere in North America, Asia, Europe, and Africa in bones ranging in age from Jurassic to Pleistocene, and have been interpreted as pupal chambers constructed by carrion beetle larvae. *Osteocallis mandibulus* n. igen. and isp. is described in dinosaur bones from continental deposits of the Upper Cretaceous Maevarano Formation of Madagascar and the Upper Cretaceous Kaiparowits Formation of southern Utah. *O. mandibulus* consists of shallow, meandering surface trails, composed of numerous arcuate grooves, bored into compact (cortical) bone surfaces, and is tentatively interpreted as a feeding trace. Based on similar patterns of bioglyph preserved in both *Cubiculum ornatus* and *Osteocallis mandibulus*, the tracemaker is interpreted to be the same or similar for both borings. Given the recurrent association with animal remains, the tracemaker is furthermore presumed to be a necrophagous or osteophagous insect that used bone as a substrate for both reproduction (*C. ornatus*) and feeding (*O. mandibulus*).

INTRODUCTION

BONE-MODIFICATION features provide critical insights into the postmortem histories of vertebrate fossil assemblages. For example, the analysis of bone-weathering states clarifies the formative history of a fossil assemblage and reveals degrees of time-averaging (e.g., Behrensmeyer, 1978; Potts, 1986; Tappen, 1994). Similarly, such biogenic modification features as trample marks and tooth marks reveal postmortem processes at burial sites, and also provide evidence of behavior and trophic interactions within ancient communities (Fiorillo, 1988, 1989; Olsen and Shipman, 1988; Behrensmeyer et al., 1989; Jacobsen, 1998; Rogers et al., 2003). Insect-generated bone modifications are particularly useful in this regard. Insects are extremely sensitive to local conditions (humidity, temperature, light), and they utilize a wide array of biological materials (soft tissues, feces, bones) for feeding, reproduction, and shelter (Tiemeier, 1939; Hinton, 1945; Reed, 1958; Payne, 1965; Payne and King, 1968).

Bone-modification features produced by insects have been recognized for decades (Tobien, 1965; Behrensmeyer, 1978; Kitching, 1980; Denys, 1986; Hill, 1987; Rogers, 1992; Tappen, 1994; Martin and West, 1995; Laws et al., 1996; Hasiotis and Fiorillo, 1997; Kirkland et al., 1998; Hasiotis et al., 1999; Schwanke and Kellner, 1999; Kaiser, 2000; West and Martin, 2002; Roberts et al., 2003; Chin and Bishop, 2004; Nolte et al., 2004; Fejfar and Kaiser, 2005). However, there is presently no ichnotaxonomy specifically designed to accommodate insect traces in bones derived from continental settings. This paper describes and names two new insect-generated trace fossils in bone, and presents a review of putative insect bone borings in the fossil record.

MATERIALS AND METHODS

Samples described in this report were discovered and collected during broader geologic and taphonomic investigations of the Maevarano Formation in northwestern Madagascar and the Kaiparowits Formation of southern Utah, between 1996 and 2004 (Fig. 1). Bored dinosaur bones were collected from eight localities in the Anembalemba Member of the Maevarano Formation, and from seven localities in the Kaiparowits Formation. Laboratory investigations included detailed measurements of the sizes (diameters, lengths) and spatial distribution of traces. Samples are deposited at the University of Antananarivo and the Utah Museum of Natural History.

GEOLOGICAL SETTING

The Maevarano Formation crops out in the central part of the Mahajanga Basin in northwestern Madagascar (Fig. 1). Bored bones were recovered from several well-documented bonebed localities (e.g., MAD93-01, MAD93-18, MAD93-33, MAD93-35) and as surface float from wide-ranging sites in the Anembalemba Member of the Maevarano Formation (Krause et al., 1999; Rogers et al., 2000). Sedimentological data indicate that the Anembalemba Member accumulated in a semiarid alluvial setting prone to sporadic fine-grained debris flows (Rogers, 2005). Correlation with biostratigraphically zoned marine facies indicates that this terrestrial unit is, at least in part, Maastrichtian in age (Rogers et al., 2000; Abramovich et al., 2002).

The Kaiparowits Formation is exceptionally well exposed within the Grand Staircase-Escalante National Monument in southern Utah (Fig. 1). Dinosaur bone borings were recovered from seven localities within the middle unit of the ~850 m thick formation (Fig. 1), which accumulated in a mosaic of channel and floodplain settings inland of the western margin of the Western Interior Seaway (Eaton, 1991; Little, 1995; Roberts et al., 2005). Thick paludal deposits, large channel bodies, and poorly developed hydro-morphic paleosols suggest deposition transpired in a relatively wet alluvial system (Roberts and Tapanila, 2006). Mammalian biostratigraphy and recent radiometric dating of ash beds indicate that the Kaiparowits Formation is late Campanian (Judithian) in age (Eaton and Cifelli, 1988; Cifelli, 1990; Eaton, 1991, 2002; Roberts et al., 2005).

SYSTEMATIC ICNOLOGY

Ichnogenus CUBICULUM new ichnogenus

Type ichnospecies.—*Cubiculum ornatus* n. isp.

Diagnosis.—Discrete ovoid borings in bone. Hollow, oval chambers with concave flanks bored into inner spongy and outer cortical bone surfaces. Chamber length three to four times greater than diameter. May be isolated, but observed more commonly in dense, sometimes overlapping concentrations. Walls roughened commonly, composed of shallow, arcuate (apparently paired) grooves.

Etymology.—*Cubiculum* (Latin), chamber, bedroom. Refers to the inferred nature of the trace as an insect pupal chamber.

Discussion.—*Cubiculum* is readily differentiated from other

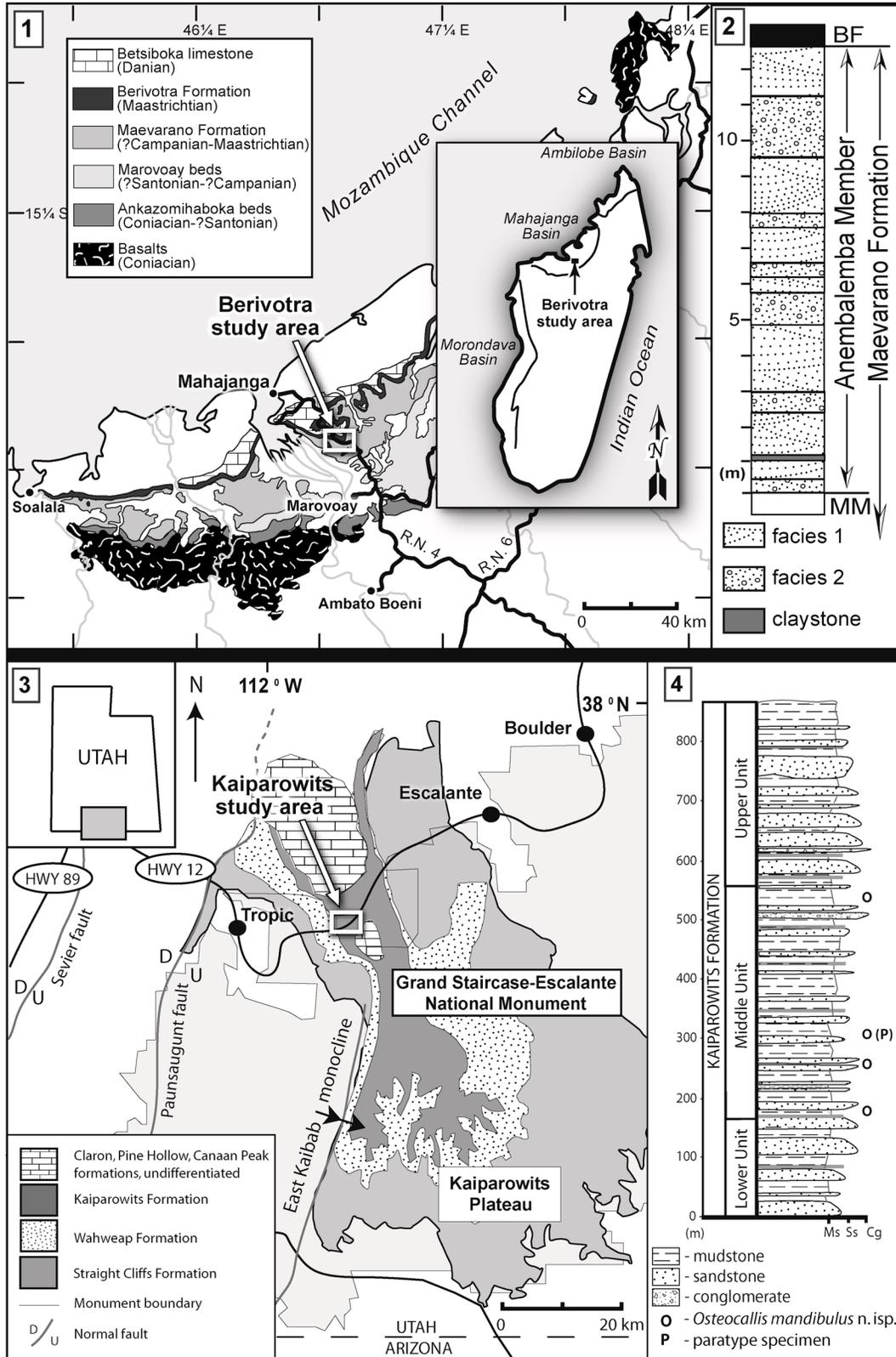


FIGURE 1—Locality maps with measured stratigraphic sections, showing general locations of specimens described in this report. 1, Maevarano Formation locality map; 2, measured section through the Anembalemba Member of the Maevarano Formation (both bone borings are distributed throughout the ~12 m thick Anembalemba Member); 3, Kaiparowits Formation locality map; 4, measured section through the Kaiparowits Formation, showing the distribution of bone borings.

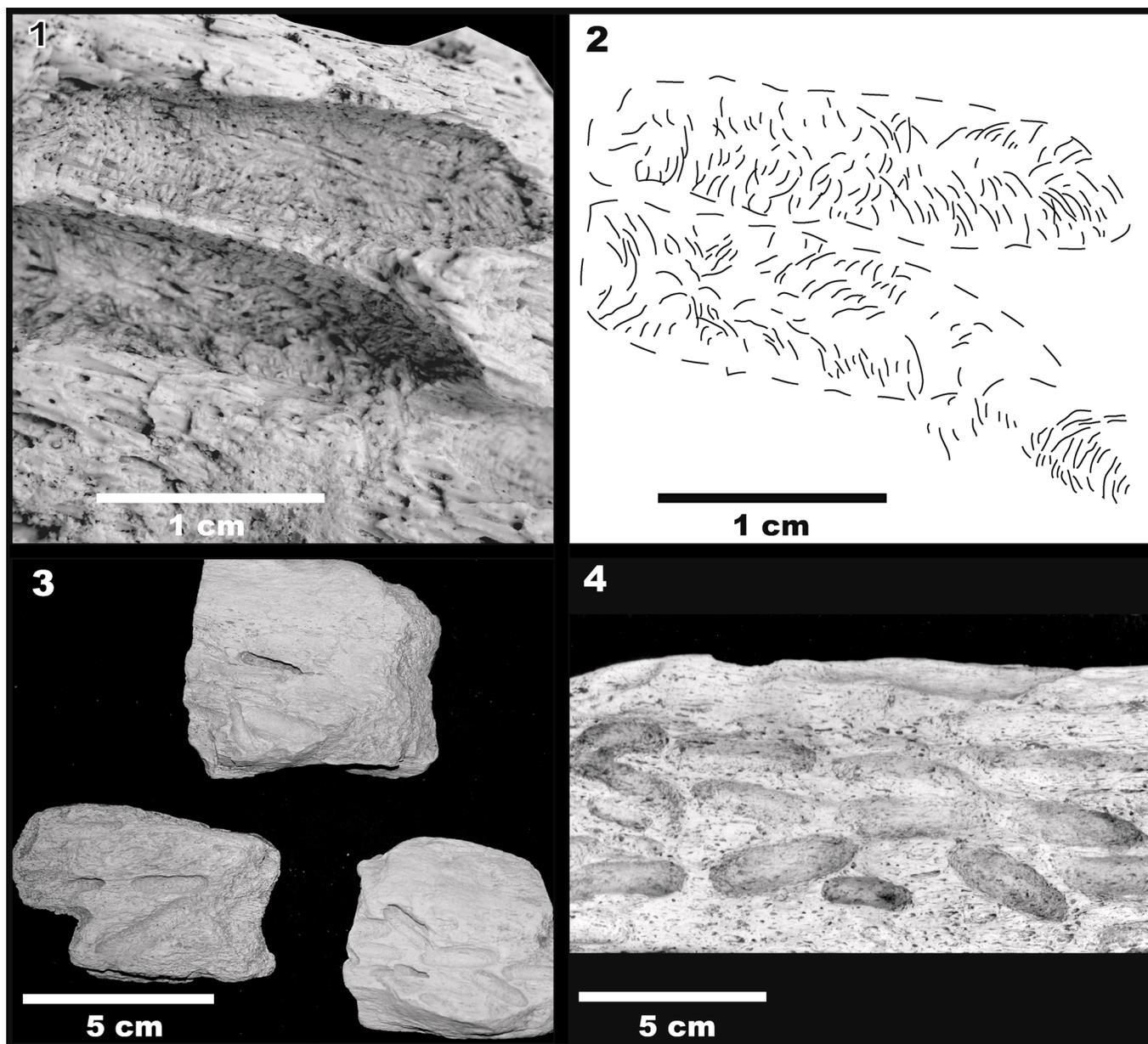


FIGURE 2—*Cubiculum ornatus* n. isp. from the Maevarano Formation, Madagascar. 1, Ovoid pupal chambers showing distinctive, arcuate scratches, likely produced by mandibles of necrophagous insects (UA 9087); 2, plan-view tracing of bioglyph preserved in 1; 3, 4, *C. ornatus* preserved in other bones.

ichnogenera that describe clavate borings (Kelly and Bromley, 1984). *Cubiculum* is presently known to be produced only in bones from continental settings, thus permitting it to be distinguished easily from borings of marine affinity, including *Gastrochaenolites* Leymerie, 1842, *Teredolites* Leymerie, 1842, *Palaeosabella* Clarke, 1921, *Rogerella* Saint-Seine, 1951, and *Petroxestes* Wilson and Palmer, 1988. Moreover, *Teredolites*, *Gastrochaenolites*, and *Palaeosabella* are clavate and often widen towards their bases. No such morphology occurs in *Cubiculum*. The bioglyph observed in *Gastrochaenolites* shows a directional arrangement of V-shaped, downshaft-spiraled grooves (Leymerie, 1842) that differs considerably from the arcuate (commonly paired) scratches in *Cubiculum*. *Petroxestes* is an elongate groove with an approximate five to one length-to-width ratio, and lacks

the ovoid shape, concave flanks, and bioglyph that are characteristic of *Cubiculum*. *Rogerella* is similar in shape to *Petroxestes*, but significantly smaller (~2 mm diameter) than either *Petroxestes* or *Cubiculum*.

CUBICULUM ORNATUS new ichnospecies
Figure 2, Table 1

Diagnosis.—Only known ichnospecies, the same as for the ichnogenus.

Description.—Trace fossil shallow, ovoid hollow bored in both compact and spongy bone. Ovoids typically range from 7 to 20 mm in length and from 2 to 6 mm in diameter (Fig. 2; Table 1). Individual ovoids discrete, usually ranging between 2 and 5 mm deep (rarely exceeding 10 mm), in shape of a hollow chamber,

TABLE 1—Summary of size data for *Cubiculum ornatus* from the Maevarano Formation (n = 244).

Measurement	Range	Median	Mean	Standard Deviation
Depth (mm)	2.0–12.3	2.9	3.1	1.4
Width (mm)	1.3–9.0	4.5	4.6	1.5
Length (mm)	5.2–41.7	15.7	15.9	5.6
Width/Length	0.08–0.76	0.29	0.31	0.1

with upper third planed-off (during boring) parallel to long axis. Bioglyph (surficial morphology) observed commonly on chamber walls, and characterized by shallow, commonly paired, and sometimes overlapping arcuate grooves between 0.5 and 1 mm wide (Fig. 2).

Etymology.—*Ornatus* (Latin), embellishment, ornament. Refers to the bioglyph or surficial morphology present on the walls of the hollow ovoid.

Type.—Holotype, UA 9087.

Occurrence.—Holotype collected from quarry MAD93-35 in the Anembalemba Member of the Maevarano Formation in northwestern Madagascar (15°54'9.5"S, 46°34'43.2"E). Dozens of dinosaur bones have been collected containing this ichnofossil. Up to 38 chambers have been observed in a single bone, and to date several hundred borings referable to *C. ornatus* have been documented in the Anembalemba Member from eight different localities.

Discussion.—The most common trace fossil observed with *Cubiculum ornatus* is *Osteocallis mandibulus* n. isp. (see below). Additionally, through-going borings (tunnels) of comparable diameter to *C. ornatus* have been observed in dinosaur bones collected in the Maevarano Formation (Fig. 3). Many of these tunnels are characterized by the same pattern of bioglyph, suggesting that this trace fossil was produced by a similar (if not the same) tracemaker that produced both *C. ornatus* and *O. mandibulus*. Carnivore tooth marks are also found on bones preserved in the Maevarano Formation (Rogers et al., 2003).

Cubiculum ornatus borings are interpreted as insect pupal chambers, based on close resemblance to modern arthropod pupae and ancient examples of bone-hosted pupal chambers (Hinton, 1945; also see Kitching, 1980; Rogers, 1992; Martin and West, 1995). Trace fossils referable to *C. ornatus* have been described previously by Tobien (1965), Kitching (1980), and Martin and

West (1995) and attributed to dermestid beetles (see Rogers [1992], Martin and West [1995], and West and Martin [2002] for a review of the dermestid beetle life cycle and the environmental and climatic conditions in which they utilize vertebrate carcasses). Given the absence of associated body fossils and the paucity of observational and experimental data on the morphology of dermestid borings (but see Roberts et al., 2003), we prefer to avoid definitively linking these traces from Cretaceous-age bones to dermestid beetles. However, given the clear and recurrent association with animal remains, we feel confident linking these traces to the activity of necrophagous or osteophagous carrion insect fauna.

Ichnogenus OSTEOCALLIS new ichnogenus

Type ichnospecies.—*Osteocallis mandibulus* n. isp.

Diagnosis.—Shallow, meandering trail of arcuate grooves (apparently paired) bored into external (cortical) bone surfaces. May be single trail or network of randomly overlapping trails.

Etymology.—*Osteo-* (Latin), bone; *Callis* (Latin), narrow track, footpath. Path across bone. Refers to the trails of grooves produced on cortical bone surfaces.

Discussion.—*Osteocallis* is observed in bone from continental settings and is readily distinguished from other ichnogenes that describe etching traces or shallow, grooves on the surface of other hard substrates. *Osteocallis* differs from etchings in shells and rocks, such as *Radulichnus* Voigt, 1977 and *Gnathichnus* Bromley, 1975, by having arcuate, paired (commonly) scratches. *Radulichnus* is composed of straight scratches, while *Gnathichnus* is composed of radially arranged scratches. *Osteocallis* is grossly similar to channels produced under bark by modern bark beetles, and to the ichnogenes *Paleoscolytus* Walker, 1938, which is described for channels under bark of fossil wood. *Paleoscolytus*, however, lacks the shallow grooves or scratches that are diagnostic of *Osteocallis*.

OSTEOCALLIS MANDIBULUS new ichnospecies

Figure 4, Tables 2, 3

Diagnosis.—Only known ichnospecies, the same as for the ichnogenus.

Description.—Trace fossil a shallow trail of grooves or scratches bored into outer surface of bone, from 1.1 to 12.9 mm wide and may extend for many tens of mm in length (Fig. 4; Tables 2, 3). Trail width between 1.0 and 3.5 mm most commonly (Tables 2, 3). Penetration of these borings extremely shallow, from 0.5 to

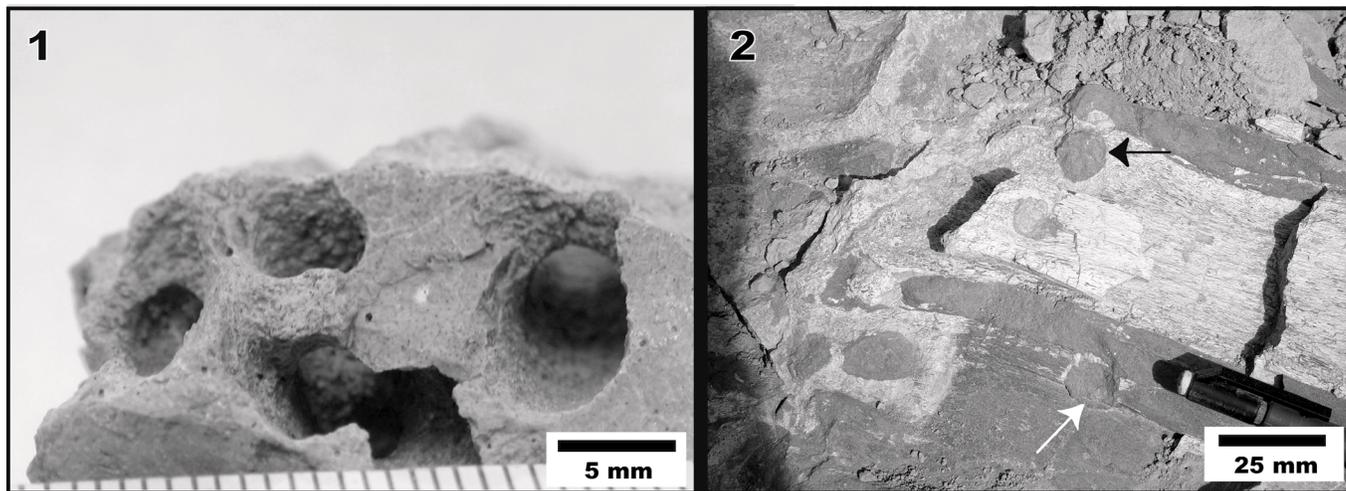


FIGURE 3—Photographs of through-penetrating bone borings (“tunnels”) observed in dinosaur bones from the Maevarano and Kaiparowits Formations. 1, Maevarano Formation; 2, Kaiparowits Formation.

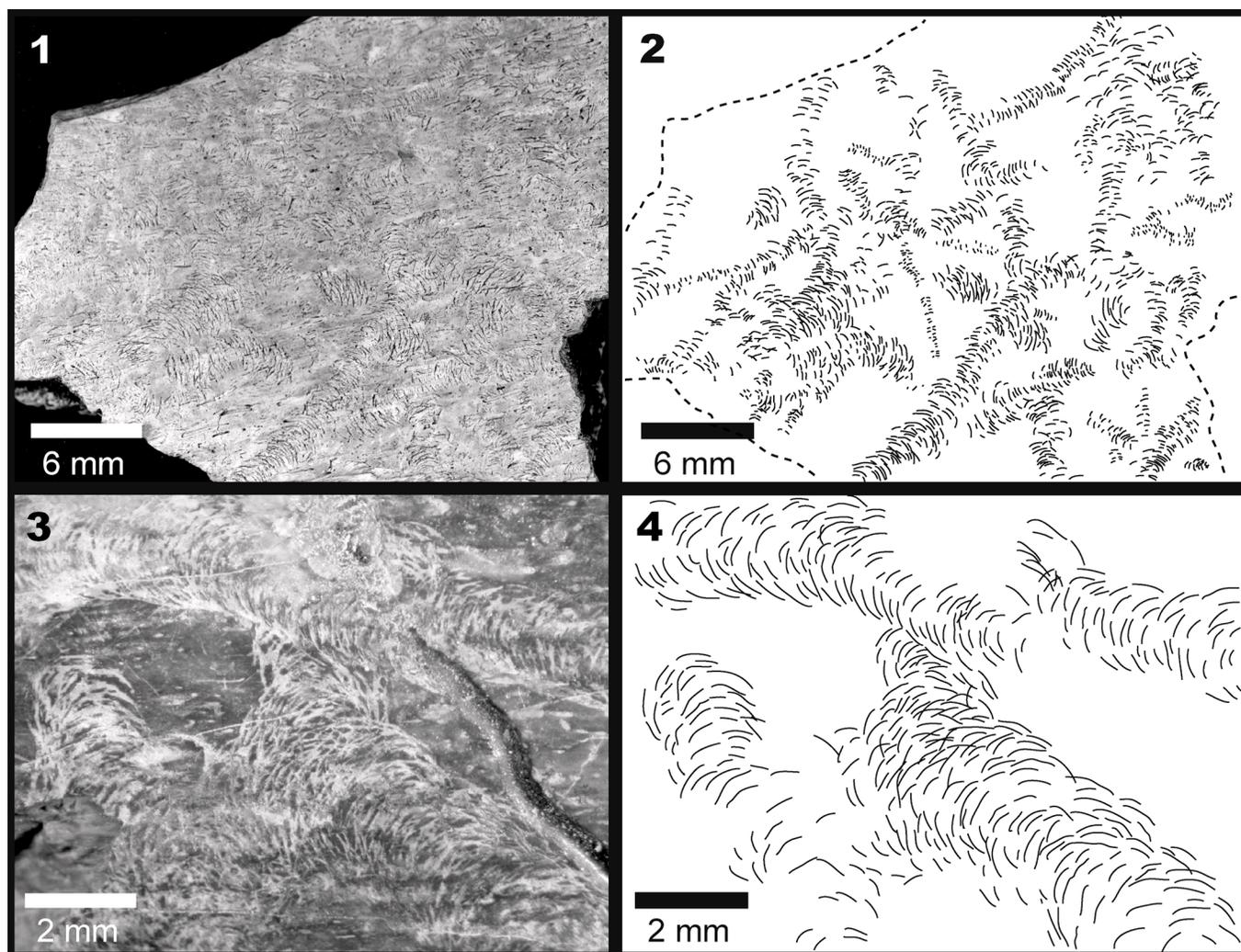


FIGURE 4—*Osteocallis mandibulus* n. isp., characterized by randomly oriented surface borings with distinct arcuate (commonly paired) scratches in dinosaur bone from the Late Cretaceous of Madagascar and Utah. 1, UA 9088, from the Maevarano Formation; 2, plan-view tracing of bioglyph preserved in 1; 3, UMNH VP-16028, from the Kaiparowits Formation; 4, plan-view tracing of bioglyph preserved in 3.

1.9 mm deep, and composed of commonly paired, arcuate scratches <1 mm wide (Fig. 4). Locally develops into deeper excavations, pits, or furrows.

Etymology.—*Mandibula* (French), any of various invertebrate mouthparts serving to hold or bite food materials. Refers to the interpreted creation of this trace by robust insect mandibles.

Type.—One holotype: UA 9088.

Other material examined.—One paratype: UMNH VP-16028.

Occurrence.—Holotype was collected in the Anembalemba Member of the Maevarano Formation in northwestern Madagascar (15°54'9.5"S, 46°34'43.2"E). Four fragmentary dinosaur bones have been collected from three different localities in the

Maevarano Formation that exhibit this trace fossil, and all contain numerous examples. At least 26 individual trails occur on the holotype specimen (UA 9088).

O. mandibulus has been documented at seven different localities in the Kaiparowits Formation. The paratype specimen occurs on a ceratopsian rib fragment collected from the Kaiparowits Blues Ceratopsian Quarry, which was found approximately 320 m above the base to the formation (37°37'45"N, 111°51'37"W) within the Grand Staircase-Escalante National Monument (Fig. 1; Getty et al., 2003).

Discussion.—In the Maevarano Formation, the most common trace fossils observed with *O. mandibulus* are *C. ornatus* n. igen.

TABLE 2—Summary of size data for *Osteocallis mandibulus* from the Maevarano Formation (n = 25).

Measurement	Range	Median	Mean	Standard Deviation
Depth (mm)	<1.0–1.9	<1.0	<1.0	0.3
Width (mm)	1.1–12.9	2.2	2.6	2.2
Length (mm)	Limited by bone breakage D 36.5 mm longest recorded			

TABLE 3—Summary of size data for *Osteocallis mandibulus* from the Kaiparowits Formation (n = 15).

Measurement	Range	Median	Mean	Standard Deviation
Depth (mm)	0.5–1.0	0.5	0.5	0.1
Width (mm)	1.1–3.5	2.0	2.2	0.6
Length (mm)	5.3–22.1	2.1	12.5	5.5

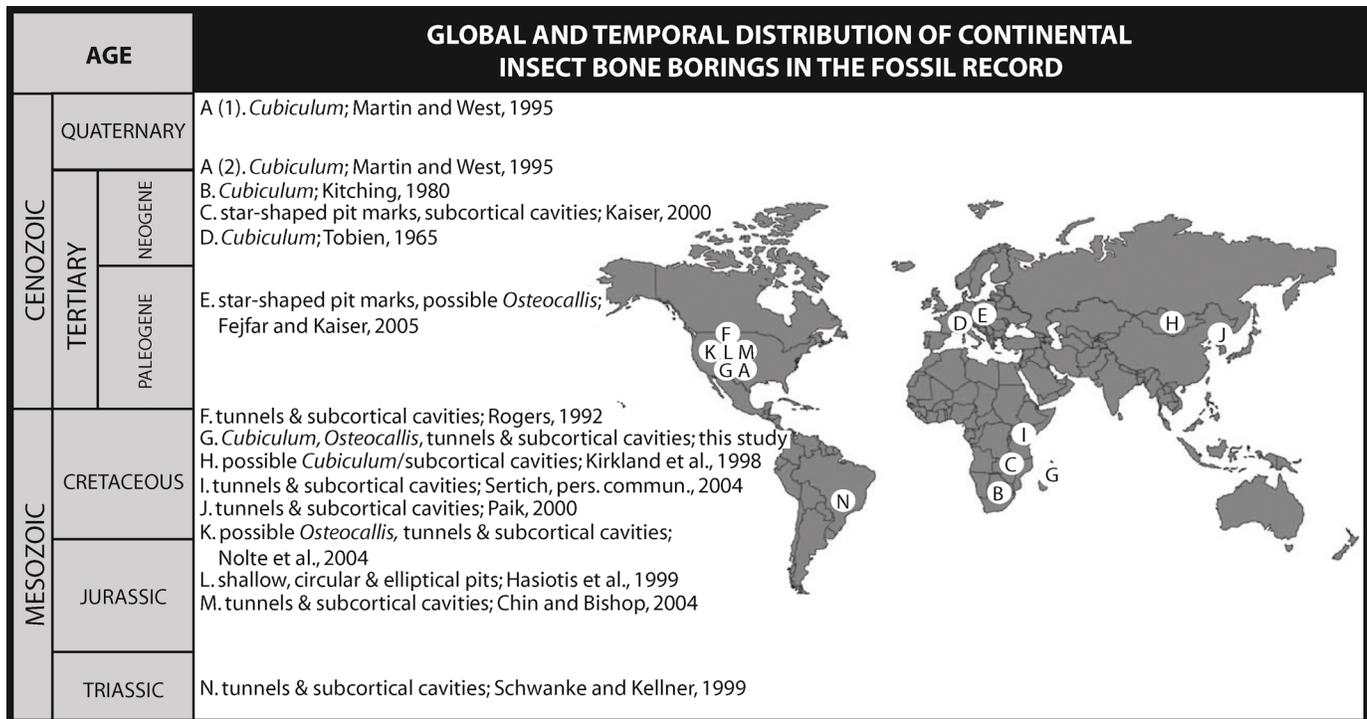


FIGURE 5—Map and geologic timescale, showing the global and temporal distribution of insect bone borings in the continental fossil record.

and isp., through-penetrating borings (tunnels) of roughly the same diameter as *C. ornatus* (Fig. 3), and carnivore tooth marks. In the Kaiparowits Formation, *O. mandibulus* is found in association with carnivore tooth marks on bones and other insect traces, including meniscate back-filled burrows, 10–18 mm diameter borings through dinosaur bones (Fig. 3), and the social insect nest trace fossil *Socialites tumulus* Roberts and Tapanila (2006).

In the Madagascar bones, multiple overlapping trails of *O. mandibulus* of slightly different widths occur commonly on the same bone. These width variations suggest that *O. mandibulus* may be produced by individuals of different sizes feeding at varying stages of larval development. Based on similar patterns of bioglyph preserved in *Cubiculum* and *Osteocallis mandibulus*, the tracemaker, likely a taxon of necrophagous or osteophagous insect(s), is interpreted to be similar (possibly the same) for both borings.

A REVIEW OF INSECT-RELATED BONE BORINGS IN CONTINENTAL SETTINGS

Continental vertebrate-fossil assemblages containing putative insect borings have been reported for nearly four decades from deposits ranging in age from Triassic to Pleistocene. In recent years, the number of such reports has increased significantly, and a record of insect-bone borings now exists from terrestrial deposits on every continent except Antarctica and Australia (Fig. 5). Hypothesized tracemakers most commonly include carrion insects such as dermestid, silphid, and histereid beetles, tineid moths, and a variety of neotropical termite species (e.g., Behrensmeier, 1978; Rogers, 1992; Tappen, 1994; Martin and West, 1995; Kaiser, 2000).

The most commonly cited trace fossil morphologies can be grouped into five general categories: 1) *Cubiculum* n. igen. (i.e., ovoid chambers); 2) shallow circular to elliptical pits; 3) star-shaped pit marks; 4) *Osteocallis* n. igen. (i.e., surface trails); and 5) tunnels and subcortical cavities. A variety of other bone borings that do not readily fit into these categories have also been

reported (e.g., surface erosion; Roberts et al., 2003), but due to their indistinct morphologies and anecdotal descriptions, they are not discussed here.

Cubiculum (ovoid chambers).—Bone borings referable to *Cubiculum* have been reported from continental deposits in Idaho, Kansas, South Africa, and Germany (Fig. 5; Tobien, 1965; Kitching, 1980; Martin and West, 1995). Tobien (1965) first recognized Neogene mammal bones from Germany that contained distinctive ovoid chambers (2–7 mm in diameter), which he interpreted as dermestid beetle pupal chambers. Similar borings were described in Plio–Pleistocene mammal bones from South Africa by Kitching (1980), who also associated them with dermestid beetles. Martin and West (1995) described slightly smaller (2–4 mm) ovoid bone borings from the late Pliocene of Idaho and the middle-late Pleistocene of Kansas. They followed earlier workers and also attributed these traces to dermestid beetles.

Other workers have briefly described insect borings which may also be referable to *Cubiculum*. Schwanke and Kellner (1999) noted a similarity between certain cylindrical borings observed in Triassic vertebrate bones from Brazil and purported dermestid pupation chambers. Less clear, but possibly referable to *Cubiculum*, are large (1 cm × 2.5 cm), circular (in cross section) borings documented in dinosaur bones from the Upper Cretaceous of Mongolia (Kirkland et al., 1998).

Shallow, circular and elliptical pits.—Laws et al. (1996), Hasiotis and Fiorillo (1997), and Hasiotis et al. (1999) observed borings in dinosaur bones from Jurassic continental deposits in Wyoming and Utah (Fig. 5). They identified a variety of different skeletal elements with moderate to dense concentrations of very shallow circular to elliptical pits (0.5–5.0 mm in diameter). Laws et al. (1996) interpreted these traces to have been produced during cocoon construction (for pupation) by dermestid beetle larvae.

Star-shaped pit marks.—A variety of workers have described a distinct boring morphology characterized by shallow, radiating grooves, for which Kaiser (2000) coined the term “star-shaped

pit marks.” Denys (1986), Hill (1987), and Kaiser (2000) all observed the presence of star-shaped pit marks on Plio–Pleistocene mammal bones from Laetoli in northern Tanzania (Fig. 5). Kaiser (2000) described them as shallow grooves with a U-shaped profile, arranged in clusters of radially arranged incisions. They range in size from 3 to 8 mm in diameter and randomly cover bone surfaces and line cavities in compact bone. Many show paired arrangement of single grooves forming clusters. Kaiser (2000) tentatively suggested an unknown taxon of a carrion-feeding termite as a possible tracemaker. Similar bone-modification features were observed in early Oligocene mammalian bones and teeth from Bohemia (see figs. 9c, 10c, 11b in Fejfar and Kaiser, 2005).

Behrensmeyer (1978) observed perforations and grooves in modern bones from Amboseli National Park in Kenya that appear somewhat similar to the star-shaped pit marks of Kaiser (2000). She proposed that these traces may have been constructed by termites and larvae of tineid moths. Tappen (1994) also cited termites as the tracemakers of shallow pits and linear trails observed in modern bones during an empirical taphonomic investigation of bone weathering in tropical rainforests.

Osteocallis (shallow surface trails).—Nolte et al. (2004) recently described numerous bored dinosaur bones from the Dalton Wells Quarry in the Lower Cretaceous Cedar Mountain Formation of Utah (Fig. 5). The morphology of some of the borings (“burrows”) reported in their study appears similar to that of *O. mandibulus* n. isp., although they attain somewhat greater widths (0.5–18 mm). For example, as in *O. mandibulus*, paired grooves (<11 mm long) line some of the borings. Based on aspects of the depositional setting, Nolte et al. (2004) suggested that the borings were likely produced by silphid or histereid beetles. Fejfar and Kaiser (2005) reported on a variety of insect bone-modification from the Oligocene of Bohemia. While some of the traces are quite similar to the star-shaped pit marks from the Pliocene of Tanzania, others are more linear, composed of a series of shallow grooves, resembling *Osteocallis* (see figs. 8, 10a, c in Fejfar and Kaiser, 2005).

Tunnels and subcortical cavities.—Rounded gouges and tunnels are reported in fossil bones commonly and are attributed to insects generally (Fig. 3; e.g., Rogers, 1992; Kaiser, 2000; Paik, 2000). Traces of this type were first recognized by Rogers (1992) in dinosaur bones recovered from overbank deposits in the Upper Cretaceous Two Medicine Formation of Montana. These 9–17 mm-diameter borings were interpreted as incidental traces produced by carrion insects constructing pupal chambers. During this study, borings similar to those reported by Rogers (1992) were observed in both the Maevarano and Kaiparowits Formations (Fig. 5). Comparable bone borings also have been reported from paleosols in the Lower Cretaceous Hasandong Formation of South Korea (Paik, 2000). The 2–10 mm diameter Korean borings are subadjacent to bone chip-filled burrows, which provide strong evidence for bone utilization by carrion insects. Kaiser (2000) also described another class of boring from the Laetoli fossil assemblage that resembles a gallery system. These traces were referred to as “subcortical cavities.” More recently, Chin and Bishop (2004) reported the unique occurrence of bored bone within a theropod dinosaur coprolite in the Jurassic Morrison Formation. They observed nine borings that terminated in rounded ends, 3–28 mm in diameter, which they interpreted as invertebrate brood or pupal chambers. Nolte et al. (2004) noted the occurrence of 0.5–18 mm wide borings that form galleries with lateral chambers in bones from the Lower Cretaceous Cedar Mountain Formation in Utah. Additionally, as yet undescribed U-shaped borings and other bone modifications have been observed in Cretaceous dinosaur bones from Tanzania and Kenya (J. Sertich, personal commun., 2004).

CONCLUSION

Borings in fossil bones have been reported from continental settings ranging in age from Triassic to Pleistocene, and from all continents except Antarctica and Australia. The most commonly cited producers of these bone borings are carrion insects that possess robust mouthparts, such as dermestid, silphid and histereid beetles, a variety of neotropical termites, and teneid moths. Recognition of insect-modified bone in the fossil record provides a novel glimpse into the biocomplexity of ancient terrestrial ecosystems, and in some cases, can provide valuable information pertaining to paleoenvironment and paleoclimate. For instance, many insects are highly sensitive to temperature, humidity, and resource availability, and hence, can provide a valuable data source. Several workers have presented excellent reviews regarding the paleoenvironmental application of insect-generated traces in fossil bone (see Rogers, 1992; Martin and West, 1995; Hasiotis et al., 1999; West and Martin, 2002).

In this report we describe and formally name two new trace fossils, *Cubiculum ornatus* n. isp. and *Osteocallis mandibulus* n. isp., which: 1) occur in considerable abundance in Late Cretaceous dinosaur bones from Madagascar and Utah; 2) have similar patterns of bioglyph linking them to a similar (possibly the same) tracemaker; and 3) are presumed to have been constructed for purposes of reproduction (*C. ornatus*) and feeding (*O. mandibulus*) by necrophagous or osteophagous insects.

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