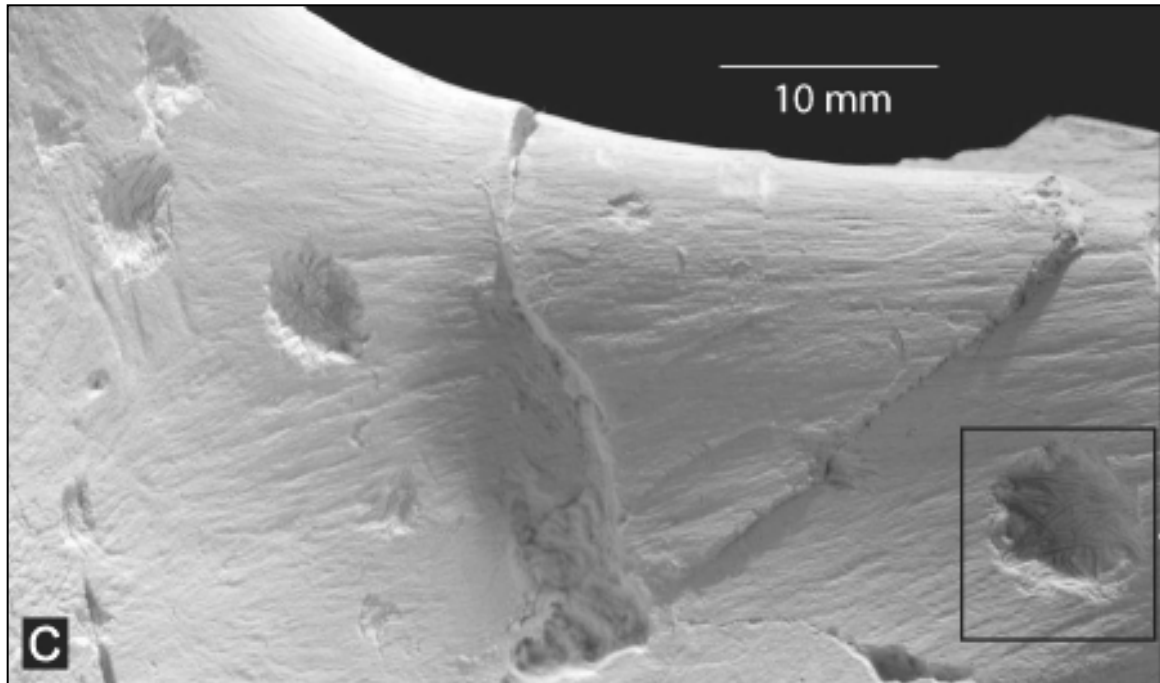


Paleoecology of Mesozoic terrestrial habitats using non-marine borings in dinosaur bones



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Cover artwork from Britt et al. (2008), fig. 1C.

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Abstract

Several borings in bone have been discovered in Jurassic and Cretaceous Period vertebrate deposits. The use of non-marine borings within studies on paleoclimatic conditions of terrestrial habitats has become popular in the literature recently. Based on lithology of the bone units and taphonomic data, these borings occurred in subaerial environments. Review of several common bone borers, including mayflies, termites, and tineid moths, compared to the borings seen in the various studies, conclude dermestid beetles as those responsible. Often dermestid beetle traces show shallow pits with parallel-grooved mandible marks. Adult dermestid beetles bore into decaying carcasses above the water table, create pupate chambers, and proceed to lay eggs. Once the larvae hatch, the dermestids consume the carcass. Preferably, adult dermestid beetles occupy carcasses contained in dry terrestrial environments in order to prevent competition between various other insects. Thus, the presence of dermestid beetle borings provide evidence towards a subaerial, dry paleoclimate. Furthermore, non-marine borings can be used to describe plausible soil moisture, water-table levels, and various other climatic variables of ancient terrestrial habitats.

Introduction

The use of invertebrate ichnofossils to interpret past environments is a vital tool for paleontologists. Many have studied traces of marine life throughout the Mesozoic Era in order to obtain a good sense of the aquatic realms occupied by organisms during this time. These same techniques can be applied when analyzing invertebrate ichnofossils found within a terrestrial environment. Recently, paleontologists have reported findings

of non-marine borings within dinosaur bones (Bader et al., 2009; Britt et al., 2008; Francis and Harland, 2006; Hasiotis, 2004; Paik, 2000; Roberts et al., 2007). Much like the methodology and analysis used on marine traces, these bone borings enhance our understanding of terrestrial habitats during the life history of dinosaurs, one of popular interest to both scientists and the general public. Much of our understanding for terrestrial ichnofossils stems from the great success of arthropods throughout geologic time. Arthropods commonly contribute to the traces preserved in terrestrial rock, often being linked to related extant species or even those still in existence. Paleontologists can thus connect the habitats of pre-existing terrestrial fauna to those found preserved in rock, leading to a wealth of knowledge (soil moisture, water-table levels, e.g.) on terrestrial habitats.

Common Bone Borers

Of all the terrestrial organisms that contribute to the development of ichnofossils, only four are known to bore into bone. These four organisms include: mayflies (Ephemeroptera, Polymitarcyidae), termites (Isoptera, numerous families), moths (Lepidoptera, Tineidae), and beetles (Coleoptera, Dermestidae). All of these organisms are extant; thus much is known about the environmental conditions within their habitats and the roles they take on, contributing to the understanding of the Mesozoic terrestrial habitats (Britt et al., 2008).

Mayflies

The nymphs of polymitarcyid mayflies often produce U-shaped burrows within submerged wood or stream banks. Similar U-shaped burrows within Miocene bones have

been interpreted as mayfly nymph traces. The entry and exit points of these burrows are typically closely spaced and consist of a pair of adjacent parallel tubes. The tubes are separated by a thin wall and terminate in an unexpanded cul-de-sac. The nymph mandibles are sclerotized and asymmetrical, while some have varying numbers of incisors on opposite mandibles (Britt et al., 2008).

Termites

Termites have also been known to consume bone, both fresh and weathered, as well as wood (Francis and Harland, 2006). They typically infest a carcass once the muscles and organs have been consumed. Most of the foraging occurs by the worker termites. They consume bone within sheltered foraging tunnels, leaving trails or irregular patches of pits. The pits range from a fraction of a millimeter to greater than 15 millimeters wide and are shallow, rough-rimmed, and roughly circular in shape. Many of the pits will occur in patches and lineations, depending on whether it is a foraging or gallery site. Mandible marks are sometimes visible on smooth, little impacted bone, with the largest grooves being about 96 μm wide. The traces typically result in deep surficial bioerosion or consumption of trabecular bone. Their mandibles are asymmetrical, with an apical tooth in the middle of two to three left marginal teeth and two right teeth (Britt et al., 2008).

Tineid Moths

According to Britt et al. (2008), many tineid moth larvae have been known to consume hair and other keratinous materials of both carcasses and dung. Many taxa have also been known to damage bone, chewing elliptical holes through the horn sheath in

which the organism crawls to the core to feed (Bader et al., 2009). *Tinea deperdella* and *Cerotaphaga* leave shallow pits and canoe-shaped excavations roughly 5 mm wide and 25 mm long on horn core surfaces. Their mouthparts are small and no traces of mandible marks have been reported within their markings. The mandibles of *Tinea translucens* are symmetrical with two apical teeth roughly 27 μm apart.

Dermestid Beetles

Both larval and adult dermestids have a large variety of food sources. Britt et al. (2008) also note that several genera, including *Dermestes*, are primarily necrophagous. *Dermestes* are the only dermestid beetles that create pupal chambers in a hard substrate, and typically bore into an array of materials including cloth, cork, wood, bone, and mortar (Bader et al., 2009; Britt et al., 2008; Hasiotis, 2004). Dermestid pupal chambers are ovoid, flask-shaped pits that are 3.5-5.2 mm across. Their damage includes the destruction of smaller bones, borings through spongy bone, and furrows on articular surfaces. Their mandibles include two to three apical teeth that can often be widely spaced. For instance, the mandibles of *Dermestes maculatus* bear two apical teeth connected by a medially convex ridge spaced about 170 μm apart (Figure 1). Thus, a mandible can make one or two grooves in a single stroke depending upon the angle of the head with the substrate (Britt et al., 2008).

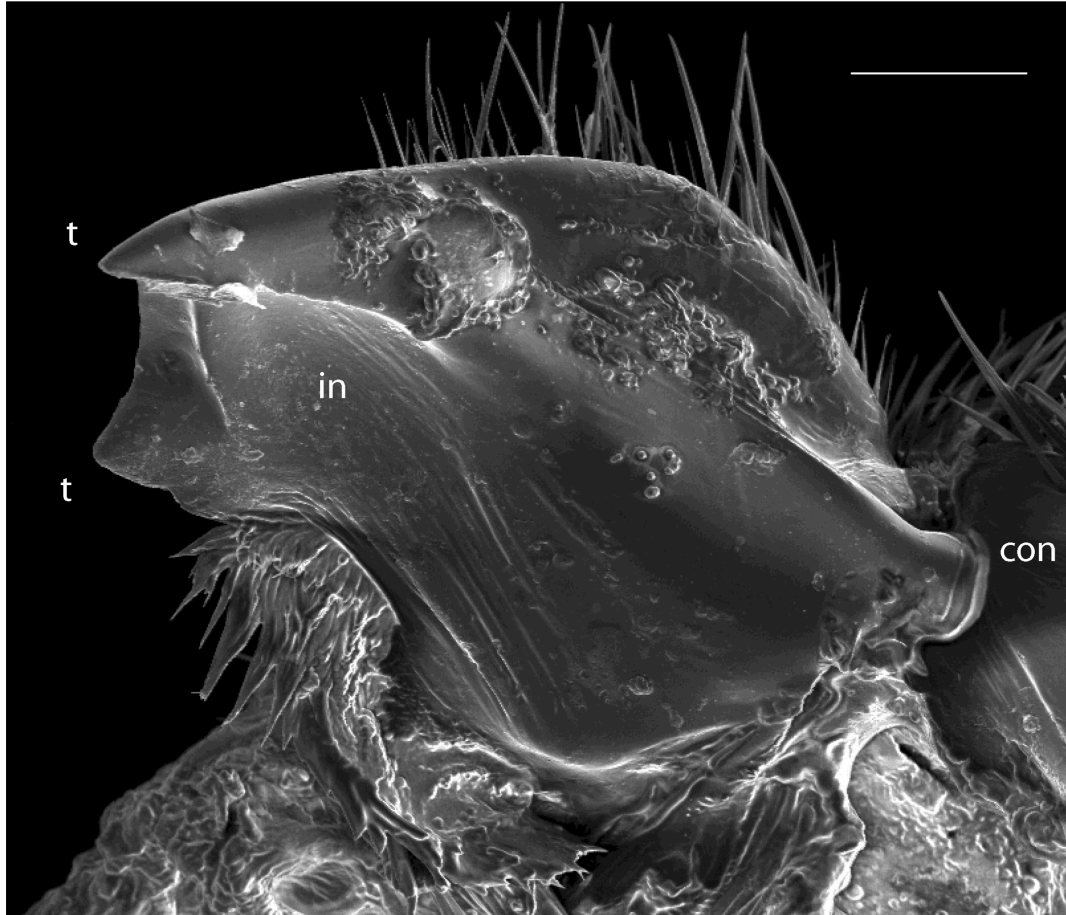


Figure 1. Adult *Dermestes maculatus* left mandible in ventromedial view. Scale bar equals 100 μm (Britt et al., 2008, fig. 3).

Methods of Classification

Many of the sources used in this study examined bones and other materials under low angle, high intensity lights in order to make note of any trace fossils. Britt et al. (2008) coated their specimens in ammonium chloride to prevent variations in surface color, and then photographed them using low-magnification stereo microscopes. They also created impression molds of specimens and studied them under SEM. All studies take detailed measurements of the sizes and spatial distribution of the traces to apply a specific organism to the boring. Britt et al. (2008) set up a table describing their traces pictorially and textually (Table 1). These terms are then used throughout their work to

describe the numerous traces found on their specimens. Similarly, Hasiotis (2004) set up a table describing the multiple moisture zones relevant to the numerous trace fossils within his study, including borings in bone (Table 2).

Term	Definition	Plan view	X-section view	Interpretation
Groove	Fine to coarse scratch marks, often paired			Mandible mark
Shallow pit	Shallow depression usually with clear grooves, depth <0.5 mm			Incipient pit-probe
Pit	Surficial, moderately deep, hemispherical excavation, sides not parallel			Incipient bore-probe
Shallow bore	Parallel sided excavation, depth <5 mm			Incipient bore-probe
Bore	Tunnel-like, deep bore, length >5 mm			Internal mining/harvesting
Furrow	Canal-like, surficial excavation, often sinuous			External mining/harvesting

Table 1. Terms used by Britt et al. (2008, table 2), including their detailed descriptions.

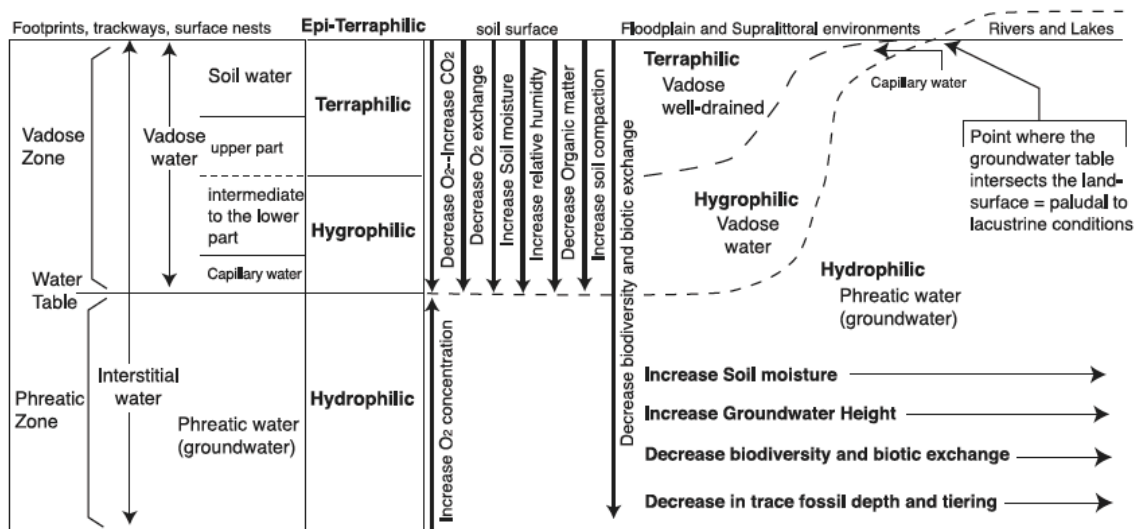


Table 2. Specific moisture zones and space/trophic resources apparent through specific ichnofossils (Hasiotis, 2004, fig. 2).

Jurassic Period

Morrison Formation, Wyoming, USA

General Location and Geology

Britt et al. (2008) base their study around a small *Camptosaurus* collected in 1995 within the Morrison Formation. Their paper outlines the importance of ichnofossils within vertebrate bones and how they are often overlooked or ignored, much like *Camptosaurus* bones. Their specimen was collected about 15 km northeast of Medicine Bow, Carbon County, Wyoming, on private land. Most of the bones were articulated, except for the hands and skull, and the skeleton was partially exposed. It was preserved on its right side and was found below a surface occupied by prairie grasses and in contact with modern roots. The surfaces on the bone in which the root came into contact left light colored, shallow grooves roughly 0.75 mm wide and are generally covered by a thin calcite film (Britt et al., 2008). Britt et al. (2008) believe the specimen is a half-grown juvenile, based on a humeral length of 245 mm.

The specimen was found within a tan, smectitic, clayey siltstone near the top of the Morrison Formation. The horizon is equivalent to the Salt Wash Member of the Morrison Formation in Colorado based on long-range correlation. Further sedimentological and taphonomical data were not taken upon collection (Britt et al., 2008).

A study by Hasiotis (2004) describes over seventy-five different ichnofossil types found within the Upper Jurassic Morrison Formation. He describes how the Morrison Formation was deposited throughout the Rocky Mountain region, stretching from Montana to New Mexico (Figure 2). It ranges from 0 to 300 m in thickness throughout

the Colorado Plateau and is composed of conglomerate, sandstone, siltstone, mudstone, mudrock, limestone, and evaporites. These deposits mark several environmental facies, including: alluvial, lacustrine, eolian, and continental-marine transitions. Throughout most of Hasiotis' (2004) study area, the Morrison Formation is represented by the Brushy Basin Member, composed mainly of smectitic, swelling clays. The Brushy Basin Member also contains sandstones, mudstones, mudrocks, tuffs, and limestones deposited through alternating alluvial and lacustrine environments.

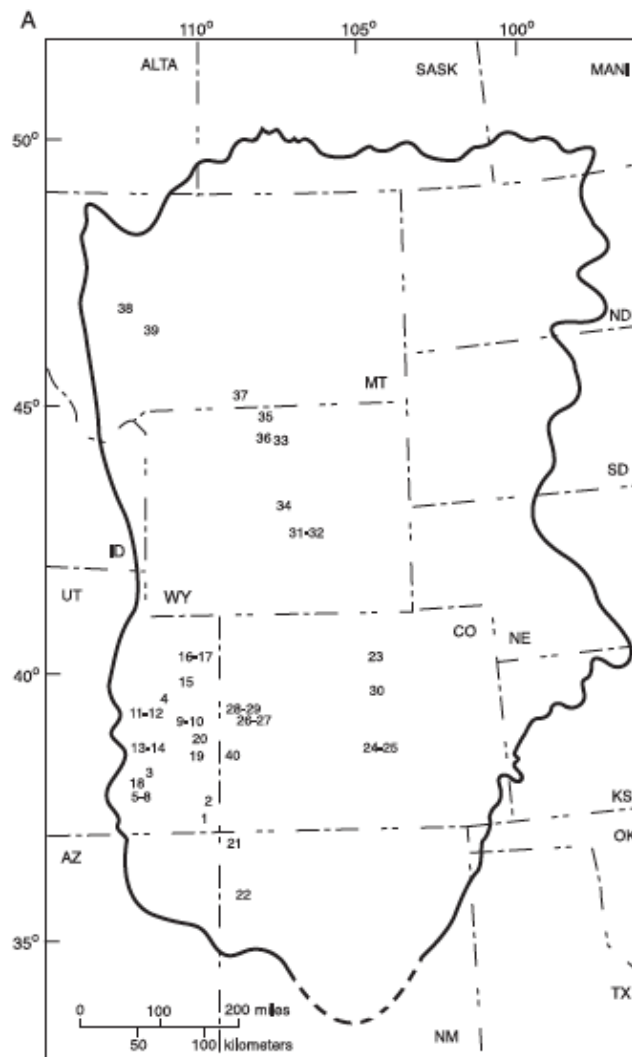


Figure 2. Localities within the Rocky Mountain region used by Hasiotis (2004, fig. 1A).

Bone Borings

Britt et al. (2008) collected nearly 120 bones belonging to *Camptosaurus*, all of which show evidence of traces except three. These traces are matrix-filled, disproving a modern origin. Britt and his colleagues (2008) classified several of the traces into the following categories: pits, shallow bores, grooves, bores, and furrows.

The pits and shallow traces occur largely in dense, cortical bone and often in clusters. The pits are elliptical to round and range in size from 1.1-5.2 mm wide. Fifty-five percent of the pits occur on the stratigraphically upward portions of the bones. The shallow pits contain fine grooves and often consist of a smaller pit within a larger, shallow, flat-bottomed depression marked with radiating grooves (Figure 3; Britt et al., 2008).

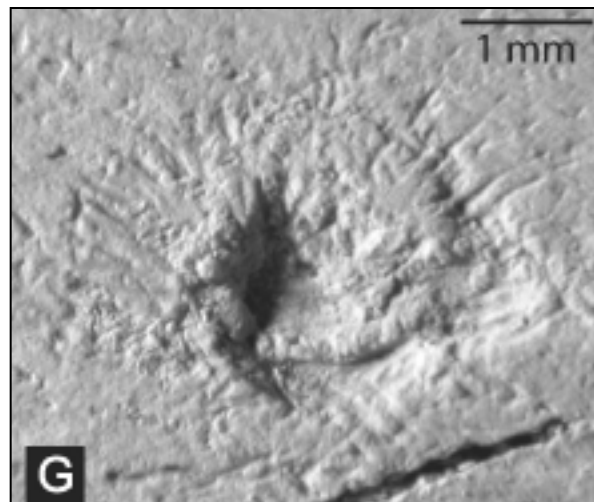


Figure 3. Incipient pit with grooved (mandible mark) terrace (Britt et al., 2008, fig. 1G).

The grooves described by Britt et al. (2008) are typically found near pitting locations. An area on the left femur, roughly 7 by 20 mm, is significantly incised by grooves. Their widths range from 36 to 211 μm and some occur in parallel sets (Figure 4).

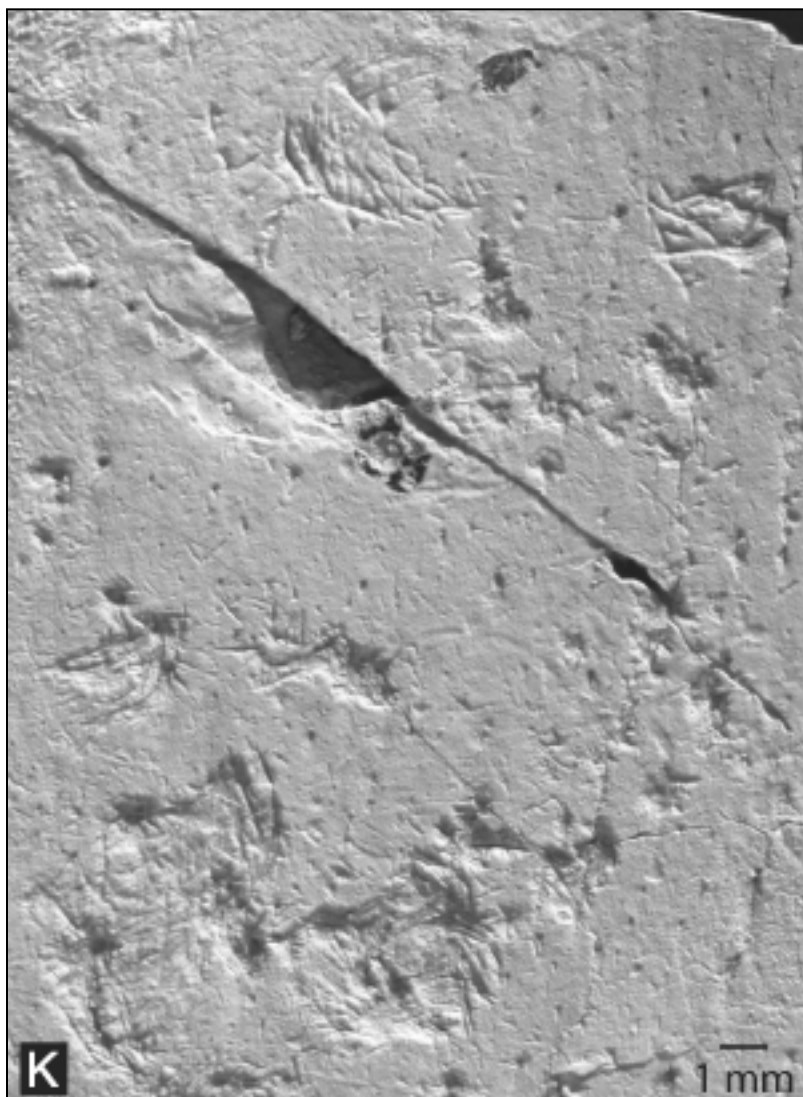


Figure 4. Several grouped mandible marks (Britt et al., 2008, fig. 1K).

Britt et al. (2008) also describe multiple borings that penetrate deep into the bone, often destroying most of the trabecular bone (Figure 5). Many of these borings are filled with fine, matrix-supported bone fragments that range in size from micrometers to millimeters. Britt et al. (2008) also make note of an interesting boring that extends the length of the 45-mm-long dorsal centrum.

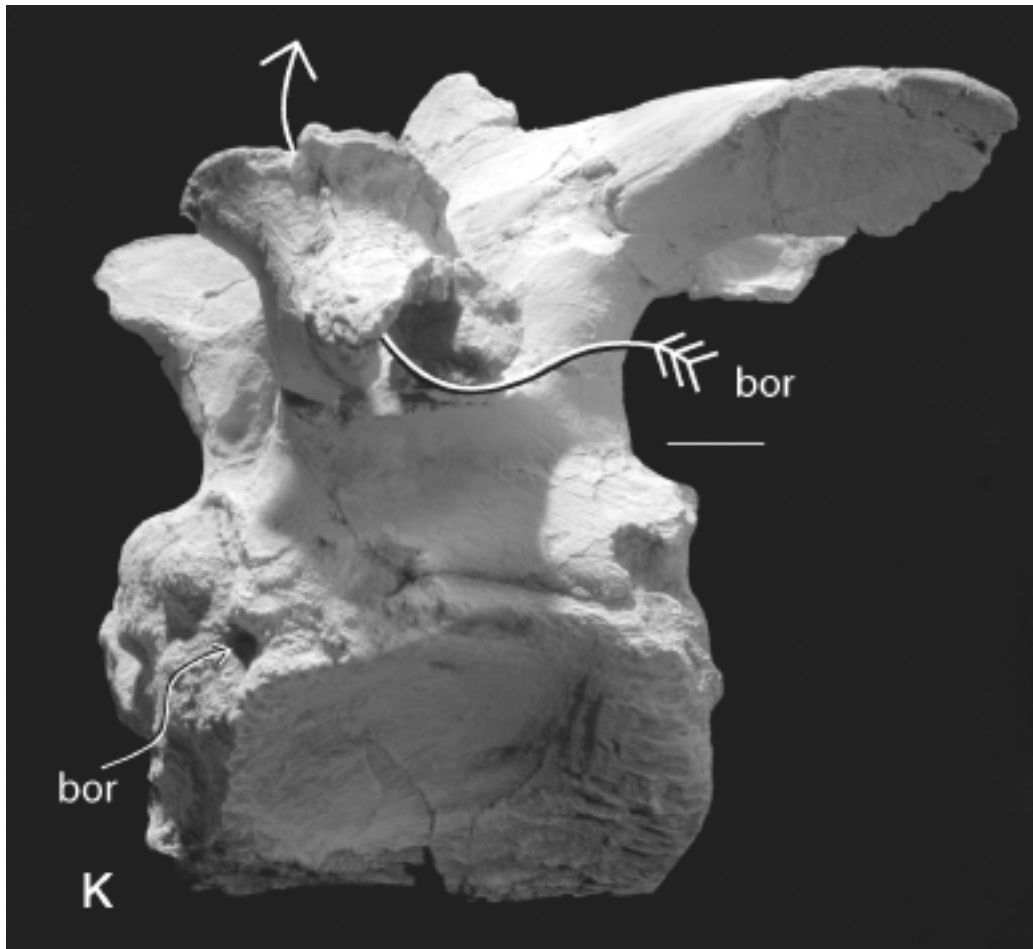


Figure 5. Borings in and around the eighth cervical vertebra (Britt et al., 2008, fig. 2K).

Lastly, Britt et al. (2008) describe a set of furrows that are mainly destructive around the articular surfaces of appendicular elements. Their furrows consist of sinuous canals roughly 1.8-8 mm wide. Some of the cervical vertebrae contain laterally extended furrows from the cotyle to the parapophyses.

The borings in the study by Hasiotis (2004) are predominately circular to elliptical, preserved by molds and casts within the bones (Figure 6). They consist of shallow hemispheres 0.01-4.0 mm deep, some appearing to be incomplete borings. They range from 0.5-5.0 mm in diameter and appear to be randomly distributed. None of Hasiotis' (2004) specimens contain deep holes or trails.

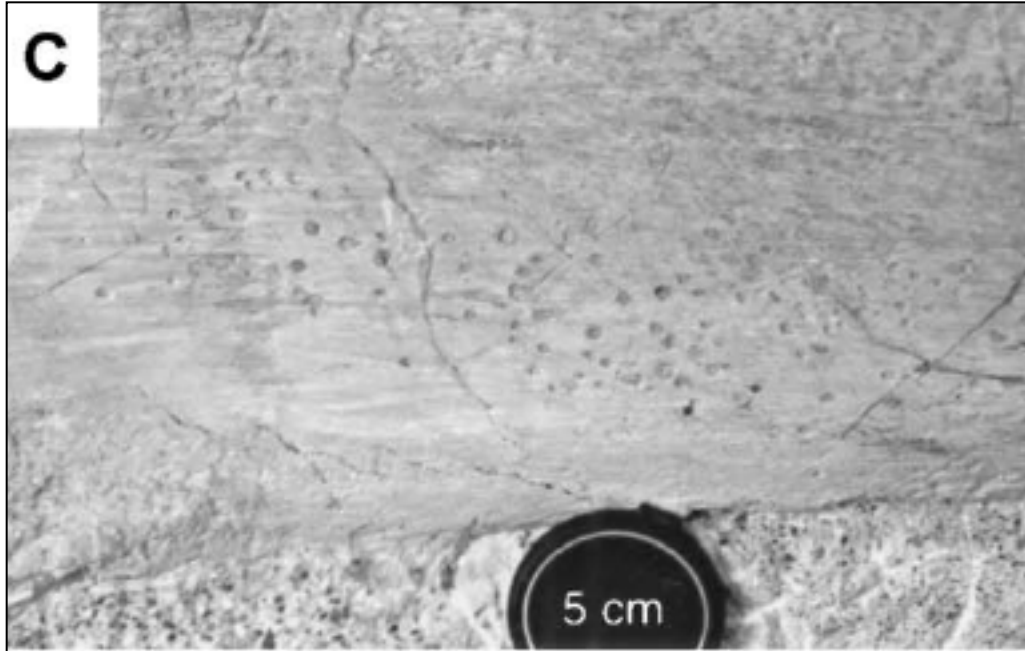


Figure 6. Several borings within bone that preserve bite marks of the insect larvae (Hasiotis, 2004, fig. 13C).

Discussion

The star-like pattern seen in Britt et al. (2008) opposed grooves is consistent with mandibular traces. The insect digs into the substrate in an arc and then pulls up and out towards the mouth. The parallel grooves within these traces show evidence that the insect contained two teeth on symmetrical mandibles. The elliptical pits shown by Britt et al. (2008) indicate the insect's range of motion and that the body remained relatively fixed. The growth of their larvae is evident within the varying widths of furrows, whose sinuous paths indicate mining/harvesting traces. Much of this evidence better supports the dermestid beetle as the probable culprit, compared to the other common bone borers listed within this study (Britt et al., 2008).

The morphologies evident in the study by Hasiotis (2004) also indicate larval dermestid beetles as the trace-maker. Hasiotis (2004) notes their similar appearance to borings made by modern dermestid beetles. The borings within his samples resulted from

the formation of cocoons during their transitional phases from larva to adult. Thus, the bones had to adhere to several environmental conditions in order to support such a community of dermestids. The presence of the pupal chambers implies: (1) the skeletons were partially covered by flesh; (2) the carcasses were dry/above water; and (3) the carcasses were in the sediment long enough for dermestid infestation (Hasiotis, 2004).

Hasiotis (2004) describes how the dermestid beetles must have occupied the carcasses during a dry season, noting various other fossils that indicate a wet season with fluvial processes during the deposition of the Morrison Formation. Modern dermestid beetles occupy areas with moderate, seasonal, wet-dry climates. Hasiotis' (2004) traces also indicate well-drained substrates with weakly developed paleosols near alluvial and supralittoral lacustrine settings.

Cretaceous Period

Two Medicine Formation, Montana, USA

General Location and Geology

The Two Medicine Formation in northwestern Montana crops out east of the Rocky Mountain Overthrust Belt (Figure 7). During the Campanian, much of the sediment comprising the Two Medicine Formation was derived from the western shore of the Western Interior Seaway. The formation is made up of fine to medium-grained sand interbedded with silty and muddy interchannel deposits, suggesting an alluvial origin. Lorenz (1981) states that the bone-bearing horizon is about 50 m below the contact with the overlying Bearpaw Formation. Based on taphonomic and sedimentological evidence, the bonebed represents a monospecific fossil drought assemblage (Rogers, 1990; 1992).

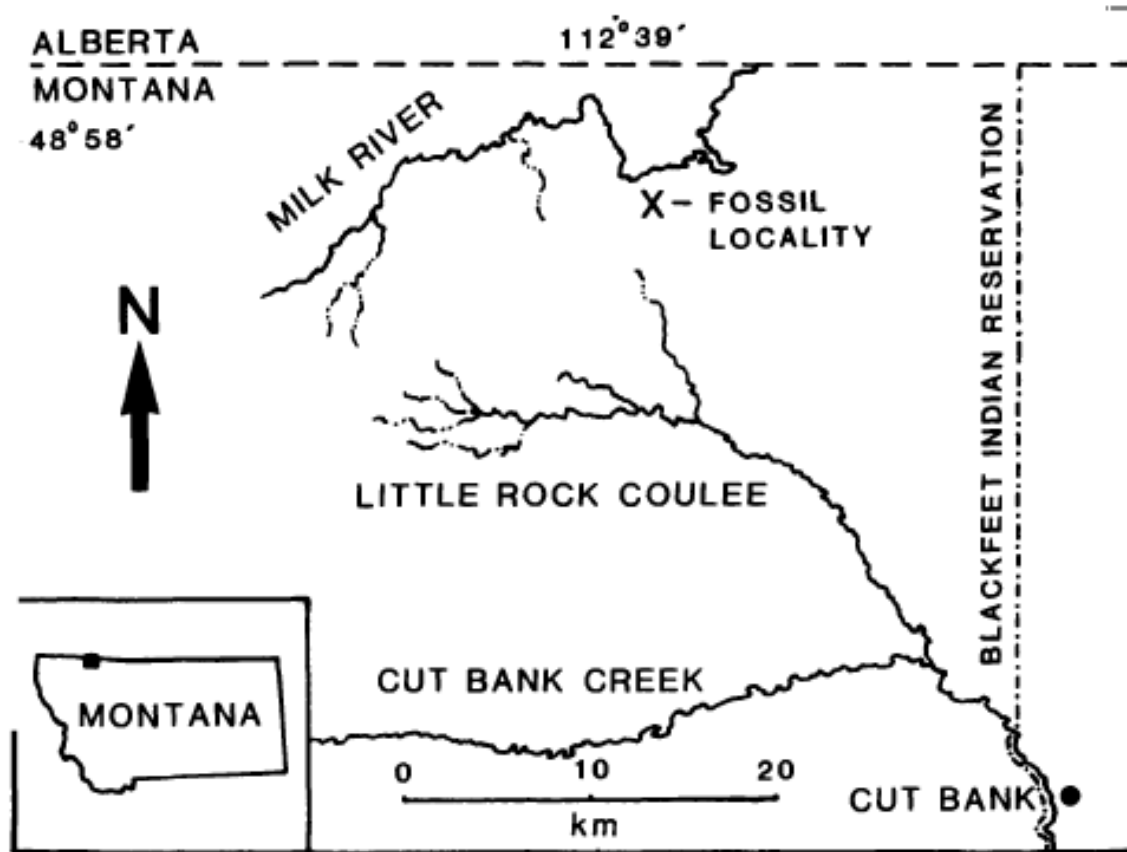


Figure 7. Locality of bonebed containing bored bones within the Two Medicine Formation (Rogers, 1992, fig. 1).

Bone Borings

The study by Rogers (1992) yielded nearly 400 bones and bone fragments belonging to *Prosaurolophus*. Within this large sampling, a left humerus and right prefrontal bone contained significant bone borings (Figure 8). The borings are described as solitary, non-tapering shafts with a diameter of 13.2-16.6 mm (humerus) and 8.7-10.1 mm (prefrontal). The longest boring within the humerus is about 76.1 mm long, while the prefrontal boring is about 28.0 mm long. The borings were filled with sediment matching the matrix of the surrounding bonebed. After making latex casts of the borings, Rogers (1992) saw no signs of scratches or grooves on the walls of the borings.



Figure 8. Boring in medial epicondyle of humerus. Scale bar = 1 cm (Rogers, 1992, fig. 2A).

Discussion

Rogers (1992) describes how the drought-related history of the bonebed suggests a subaerial origin of the bone-boring organism. The overall size/dimensions of the borings themselves rule out micro-borers, termites, and tinacid moths. The likely candidates are dermestid beetles, which are known to create elongate, shallow pits for pupate chambers. Rogers (1992) further supports this claim by describing ellipsoidal,

carbonate “concretions” that seem to represent “egg cases”. Necrophagous beetles seek out decaying carcasses, bore into the bone to create pupate chambers, and lay their eggs. Once the larvae hatch, they consume the decaying carcass (Rogers, 1992).

Typically, terrestrial beetles will seek out carcasses in which their larvae will not drown. In other words, dermestids will migrate vertically in the soil to remain above the water table. Thus, the presence of dermestid beetle borings also helps support the claim of a subaerial bonebed. Several studies on dermestid beetles show they typically infest a carcass during the “dry-stage” in order to prevent competition between other infesting organisms. This habit suggests a drier climate in which the borings were found, consistent with the drought-related history shown in the Two Medicine Formation (Rogers, 1992).

Conclusion

Both the Jurassic and Cretaceous Period show evidence of dermestid beetle bone borings comparable to modern dermestids, specifically the Morrison Formation and Two Medicine Formation described here. However, bone borings are not limited to these two formations. Several studies have found evidence of dermestid bone borings in other parts of the U.S., Madagascar, and Korea during the Mesozoic (Paik, 2000; Roberts et al., 2007).

Evidence of dermestid beetle bone borings helps provide paleoclimatic information due to the typical conditions needed for adult beetles to begin infesting a carcass. Hasiotis (2004) describes the wet-dry climatic evidence of the Morrison Formation and how the bone borings support the drier conditions preferred by dermestids. Similarly, Rogers (1992) concludes a subaerial, drought-related environment

evident in the Two Medicine Formation. In general, non-marine bone borings provide more detail towards plausible paleoclimatic conditions in terrestrial habitats. Specifically, they add to the reconstruction of dinosaur terrestrial habitats, one shown to have popular interest to both scientists and the general public.

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