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# Borings in early Eocene turtle shell from the Wasatch Formation, South Pass, Wyoming

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**Abstract.**—Borings in fossil turtle shells collected from the lowermost beds of the early Eocene Cathedral Bluffs Tongue of the Wasatch Formation in the northwestern part of the Green River Basin near South Pass, Wyoming, are herein described. Individual turtle shells in the study area are characterized by as few as one or two and as many as >100 borings. The borings include both non-penetrative forms (those which do not pass fully though the shell) as well as penetrative forms (those which pass fully from the exterior to the interior surface of the shell). All non-penetrative forms occur on external surfaces of the carapace and plastron (i.e. those that would have been accessible while the host taxon was alive). Two new ichnogenera and four new ichnospecies are established to describe these borings. *Karethraichnus* (new ichnogenus) includes three ichnospecies: *K. lakkos* (new ichnospecies), *K. kulindros* (new ichnospecies), and *K. fiale* (new ichnospecies). *Karethraichnus lakkos* are shallow (non-penetrating), hemispherical pits with rounded, to flattened bases. *Karethraichnus kulindros* are deep, non-penetrative traces with a cylindrical profile, an axis approximately perpendicular to the substrate surface and with rounded to flattened, hemispherical termini. *Karethraichnus fiale* are penetrative traces with a cylindrical to bi-convex or flask-shaped profile, and an axis approximately perpendicular to the substrate surface. *Thatchtelithichnus* (new ichnogenus) *Thatchtelithichnus holmani* (new ichnospecies) consist of non-penetrative borings into a bone substrate. They consist of a ring-shaped trace, with a central pedestal or platform. The position of the borings on the shells, and evidence of syn-emplacement healing of the borings in several of the turtles, indicates that these borings were emplacement by ectoparasites/mesoparasites while the animals were living. Similar traces in modern emydid turtles are attributed to ticks, leeches, or spirorchid liver flukes.

## Introduction

Bioerosional structures on fossil bone are common in the rock record. Scratch marks, tooth marks, and other evidence of predation and scavenging occur on fossil bone material from a variety of successions (e.g., Behrensmeyer, 1978; Fiorillo, 1987, 1990; Tappan, 1994; Hasiotis, 2004; Tapanila et al., 2004). In the past couple of decades, the influence that invertebrate borings have on bone preservation and modification has become evident (e.g., Rogers, 1992; Paik, 2000; Kaiser, 2000; Britt et al., 2006; Cabral et al., 2011).

In marine settings, a variety of organisms have been shown to be involved in bone boring activities including amoebae (Ascenzi and Silvestrini, 1984), annelid worms (Kiel et al., 2010; Higgs et al., 2011), and bivalves (Tapanila et al., 2004; Belaústegui et al., 2012). Some organisms such as the annelid worm *Osedax* have recently been shown to be significant biodegraders of whale bones in marine settings (Kiel et al., 2010; Higgs et al., 2011).

In continental settings, microbial bioerosion, via fungi, bacteria, and cyanobacteria is a primary means of bone degradation (Jans, 2008). Bone macroborings in continental settings are generally attributed to the activity of insects and their larvae. Silphid beetles, dermestid beetles, and termites have all been shown to bore into the bones of a variety of vertebrates (Tappan, 1994; Kaiser, 2000; Britt et al., 2006; Roberts et al., 2007; Cabral et al., 2011; Pirrone et al., 2014). In all of these studies, however, the borings were emplaced in the bones of dead organisms. The borings occurred to the animals after necrosis and were not demonstrably involved in the death of the organisms involved. For most parasites, and for most host taxa, boring is only likely to occur after death. Elaterid beetles prey upon, and kill, living land snails but have not been known to bore into vertebrate material (Baalbergen et al., 2014).

Herein we describe a suite of borings emplaced in the plastron and carapace of fossil geoemydid turtles. The turtles were collected from the lowermost beds of the early Eocene Cathedral Bluffs Tongue of the Wasatch Formation in the northeastern part of the Green River Basin near South Pass, Wyoming (Figs. 1 and 2). Individual turtle shells are characterized by as few as one or two borings but may have over 100 borings. The position of the borings on the shells, and evidence of syn-emplacement healing of the borings in several of the specimens, indicates that these borings were usually if not always emplaced by ectoparasites/mesoparasites while the animals were living.



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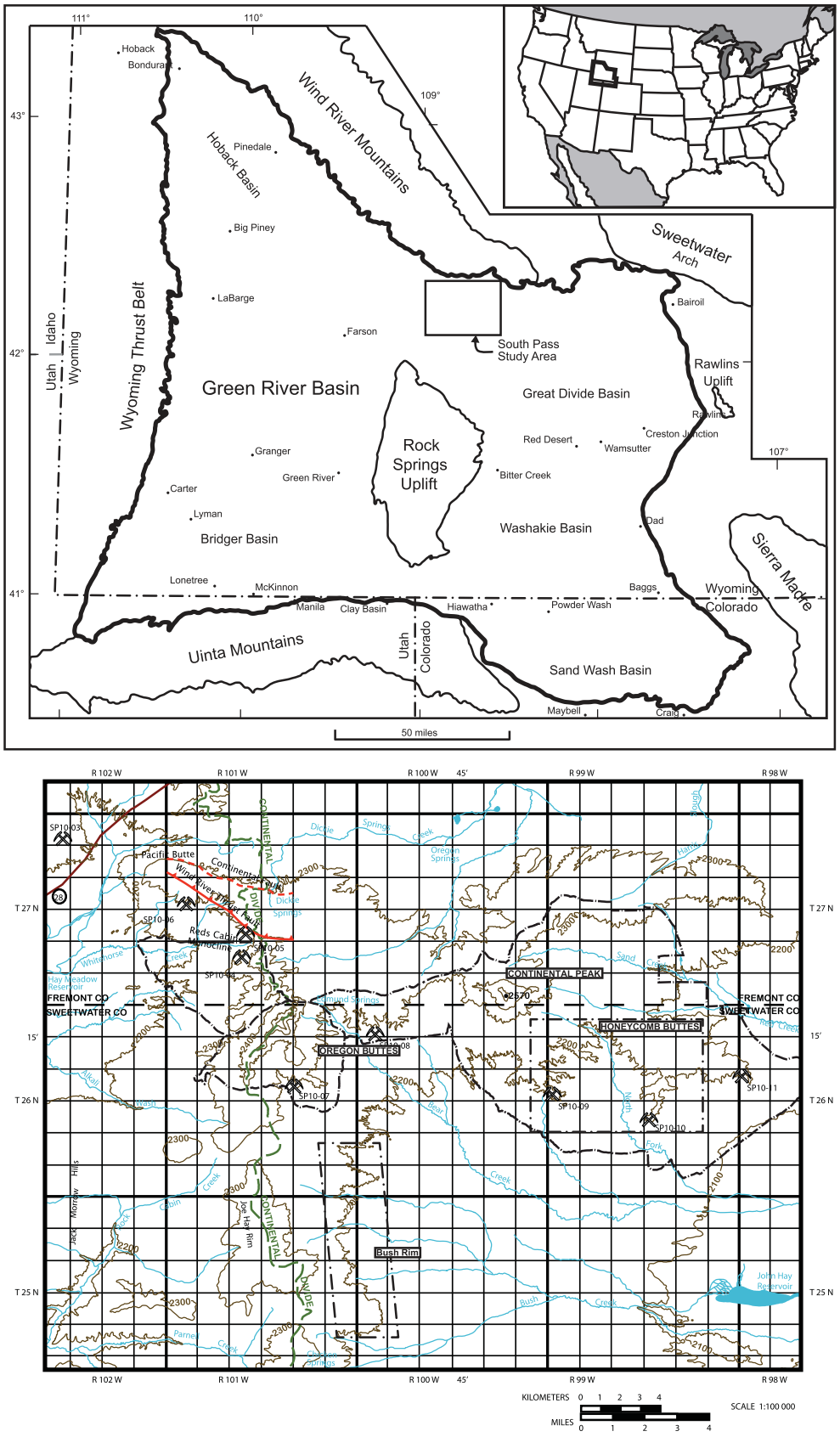



**Figure 1.** Location map of the study area.

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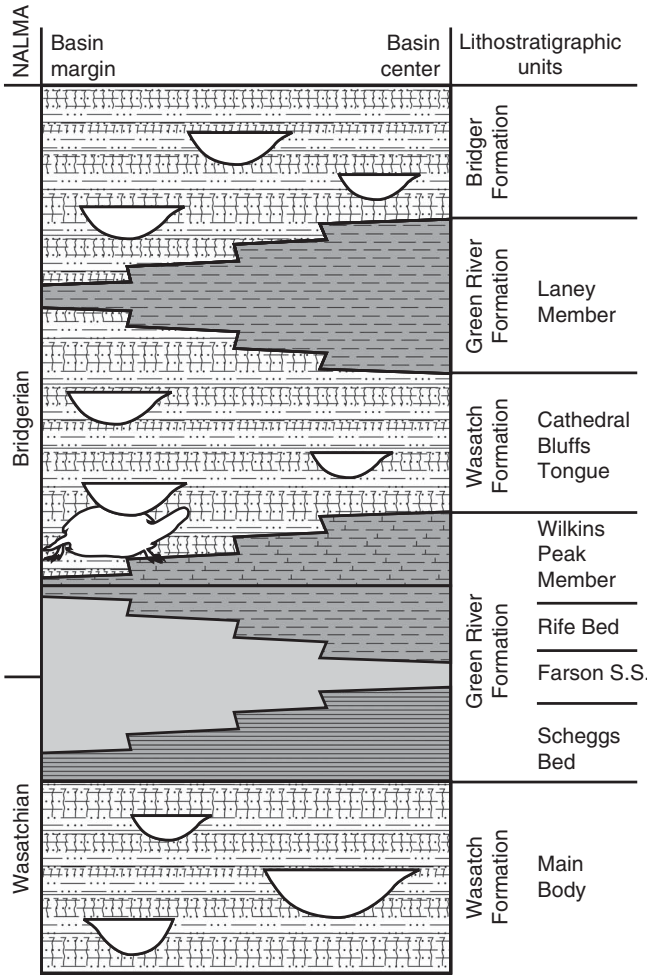



**Figure 2.** Eocene stratigraphic units at South Pass, Wyoming.

## Geological setting

The study area occurs on the northeastern margin of the Green River Basin in the southwestern corner of Wyoming (Fig. 1.1). The Green River Basin formed a major depocenter during the Cretaceous and Paleogene. Subsidence in the northeastern Green River Basin, and concomitant creation of accommodation space and sediment preservation in the study area, was a flexural response to uplift of the Wind River Mountains to the northeast (Shuster and Steidtmann, 1988; Steidtmann and Middleton, 1991).

The sedimentary history of the Eocene succession in the Green River Basin records multiple regressions and transgressions of Eocene Lake Gosiute, a large shallow lake that occupied the center of the basin (Roehler, 1991, 1992). During periods of maximum transgression, the lake lapped at the foot of the Laramide uplifts that surround the basin (Roehler, 1991, 1992; Zonneveld et al., 2003). During periods of maximum regression, the lake was limited to the center of the basin and fluvial deposition dominated in the basin (Zonneveld et al., 2003).

The deposits of Paleolake Gosiute, consisting of calcareous and dolomitic mudstone, sandstone, bioclastic packstone and grainstone, micrite, oomicrite, gypsum, trona, oil shale, stromatolitic biolithite, and organic-rich shale are primarily included within the Green River Formation (Roehler, 1991, 1992). Brightly variegated mudstone and siltstone with laterally restricted sandstone and conglomerate beds have been interpreted as alluvial and fluvial sediments overprinted with paleosols and are included in the Wasatch Formation (Roehler, 1991, 1992; Zonneveld et al., 2003). The Wasatch Formation intertongues with the Green River Formation along most of the margin of the Green River Basin (Fig. 2) (Roehler, 1991, 1992).

The fossils discussed herein were collected from the lower beds of the Cathedral Bluffs Tongue of the Wasatch Formation (Fig. 2) in the Honeycomb Buttes area near South Pass (Fig. 1.2). Although highly variegated and brightly colored, similar to paleosol successions higher in the section, the presence of wave-rippled sandstone beds, stromatolite-covered branches and logs, as well as lacustrine vertebrate fossils such as gars, bowfins, aquatic turtles, alligators, and crocodilids supports the interpretation that the basal Cathedral Bluffs Tongue at Honeycomb Buttes represents lake margin to shallow lacustrine deposition with pedogenic overprinting. Supporting this interpretation as well is the presence of several specimens of the shorebird *Presbyornis* in association with eggshell fragments (suggesting a possible nesting site) and abundant fossils of emydid turtles (*Echmatemys* and a closely related form). The trace fossils that are the focus of this contribution occur on carapace and plastron elements of these turtles.

## Terminology and acronyms

The specimens discussed herein occur on turtles that are housed in the paleontology collections at The University of Michigan Museum of Paleontology (UMMP) and the collections of The University of Alberta, Department of Earth and Atmospheric Sciences (UA-TF). Where possible, the precise shell element upon which the borings occurred is identified. Individual bones of the carapace and plastron and acronyms used to identify them are identified in Figure 3.1–3.3. The external surface refers to the surface of the shell covered by keratinized layers of the epidermal epithelium (epidermal scutes). The visceral surface of the shell refers to the surface of the plastron or carapace against which the soft tissue of the turtle would occur during life (Fig. 3.1). 'Internal surface' is used for the internal parts of outlying bones (such as the eipiplastrons, xiphiplastrons, nuchals, pygals, and some peripherals) which would have had distal components not covered by soft tissue but rather covered by epidermal scutes (Fig. 3.2 and 3.3).

The boundaries between the scutes form seams or 'sulci' (Fig. 3.2 and 3.3). Although the epidermal scutes are not preserved in any of the fossil material discussed herein, each sulcus is represented by a groove preserved on the underlying dermal bone and thus the shapes of the original scutes can be elucidated. It is worth noting that the epidermal sulci and the sutures between individual dermal bones in the plastron and carapace do not overlap (Fig. 3.2 and 3.3).

Following the precedence set by previous workers (eg. Bromley, 1981, 1993; Brett, 1985; Nielsen and Nielsen, 2001), 'hole' is used to identify a perforation that penetrates all the way through a shell bone, whereas 'pits' terminate within the bone and do not fully penetrate from the external to the internal

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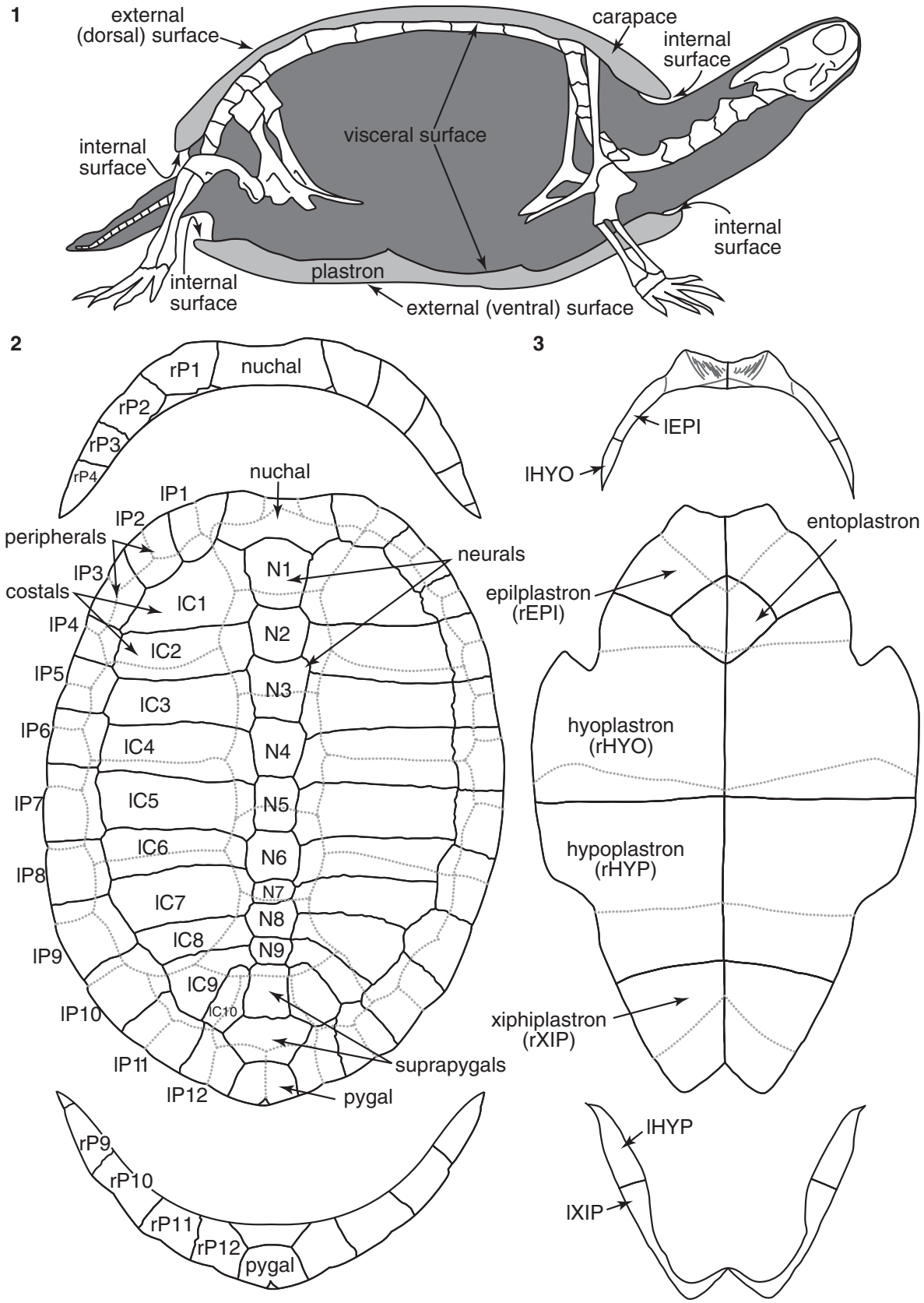



**Figure 3.** Summary of osteological terminology used in the South Pass vertebrate boring study. (**1**) Cross-section through a generalized emydid turtle showing the surfaces of bones. 'Visceral surface' denotes bone surfaces that would have been covered by animal's soft tissue during life. 'Dorsal surface,' 'ventral surface,' 'external surface,' and 'internal surface' denote surfaces of the bone that were covered in a thin layer of epidural scute and were prone to parasite colonization during the animal's life span. (**2**) Identification of carapace elements including, at top and base, those portions of the carapace not covered by viscera. 'l' and 'r' denote left and right, respectively. (**3**) Identification of plastron elements including, at top and base, those portions of the plastron not covered by viscera.

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surface. This differs slightly from the use of these terms in Pirrone and others (2014), wherein both pit and hole are used for non-penetrative borings.

## Systematic paleontology

The focus of this paper is the ichnology of borings in turtle plastron and carapace bones. A formal taxonomic treatment of the host taxa is not provided herein. Several taxa are present in the turtle fauna of the Wasatch Formation at South Pass including at least two trionychids, one baenid, one dermatemydid, and several emydids (*sensu lato*). Overwhelmingly ($n \geq 99\%$) the borings discussed herein occur on the shells of a new taxon of small emydid turtle closely related to *Echmatemys*, referred to herein as cf. *Echmatemys* sp. A few rare specimens were also noted on baenid and dermatemydid shell bones.

At several localities in the lower Wasatch Formation at South Pass, both in the Honeycomb Buttes area and along Bush Rim (Fig. 1.2), bored turtle bone is exceptionally abundant. Thus, although measurements were made of many specimens in the field, only representative samples were obtained and incorporated into collections.

Ichnogenus *Karethraichnus* new ichnogenus

*Type ichnospecies*.—*Karethraichus lakkos* new ichnospecies.

*Other ichnospecies*.—*Karethraichus fiale* new ichnospecies; *Karethraichus kulindros* new ichnospecies.

*Diagnosis*.—Circular to subcircular holes bored into a bone substrate. Holes may penetrate fully though the substrate or terminate within the bone. Penetrative holes may have straight or convex vertical margins. Non-penetrative pits terminate within the substrate as a shallow, bowl-shaped pit or as a deeper shaft with a rounded, blunt, or pointed terminus.

*Etymology*.—From the greek 'karethra' (romanization of κηρήθρα) meaning 'honeycomb,' referring to the type locality of the type species in the Honeycomb Buttes area of South Pass, Wyoming, and 'ichnus' meaning trace.

*Occurrence*.—Eocene of the Green River Basin, Wyoming.

*Remarks*.—The observed diameter of *Karethraichnus* ranges from 0.5 to 8.0 mm with 1 to 5 mm being typical. *Karethraichnus* bears morphological and size similarities to the ichnogenera *Sedilichnus* (Müller, 1977), *Oichnus* (Bromley, 1981), *Tremichnus* (Brett, 1985), and *Fossichnus* (Nielsen et al., 2001), which occurs in marine and freshwater invertebrates. Recent taxonomic reassessments have suggested that *Tremichnus* is a junior synonym of *Oichnus* (Pickerill and Donovan, 1998) and that *Oichnus*, *Tremichnus*, and *Fossichnus* are junior synonyms of *Sedilichnus* (Zonneveld and Gingras, 2014). *Karethraichnus* differs in the plasticity of its overall morphology and the nature of the substrate in which the trace occurs.

The morphological variability exhibited by specimens of *Karethraichnus* is considerably wider than that displayed by *Sedilichnus*. Individual ichnospecies of *Sedilichnus* may show considerable variance in size, however, they are remarkably consistent in the circularity of the external burrow opening although this may not be true for the internal burrow opening (i.e., circularity ~0.95–1.0; Fig. 4) and, to a lesser extent, in the evenness/symmetry of their cross-sectional profile. *Karethraichnus* are considerably more variable in both these criteria. Many specimens, although rounded, have irregular external boundaries (i.e. circularity 0.75–0.95; Fig. 4).

Another important distinction between *Karethraichnus* and *Sedilichnus* is the differing substrate in which they occur. *Karethraichnus* occurs within vertebrate bone, whereas *Sedilichnus* and its junior synonyms occur within invertebrate skeletal tests such as bivalve shells. Bone provides a unique substrate that is both mineralogically and compositionally distinct from invertebrate shells. Turtle shell, the substrate in which all of the borings discussed herein occur, consists of an external keratinous epidermal layer with a tripartite inner layer of bone (Achrai and Wagner, 2013; Fig. 5). The epidermal scutes consist of external layer of dead, cornified cells in a keratin matrix, overlying layers of keratinocytes in an amorphous keratin matrix that includes melanocytes, pigments, and lipids (Alibardi and Thompson, 2006). The sandwich-like structure of the bone layer consists of dense outer and inner

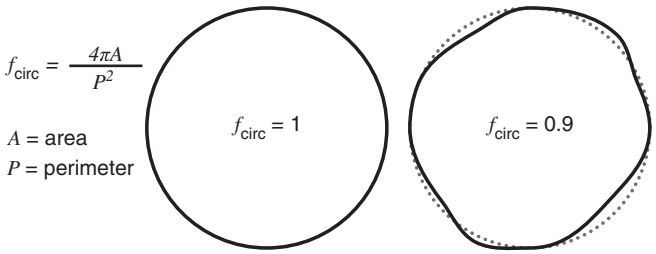



**Figure 4.** Circularity in trace fossils. Traces with perfect, equidimensional horizontal symmetry have circularities of 1. Trace fossils with imperfect equidimensional horizontal symmetry have circularities less than 1. Most *Sedilichnus* species have regular outlines and thus a circularity approximating 1. *Karethraichnus* have more variance within their horizontal profiles and may have circularities ranging from ~0.75 to 1.

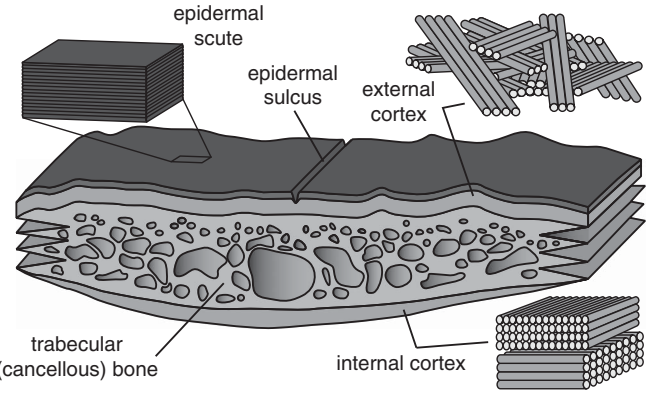



**Figure 5.** Layers in living turtle and plastron bone. Adapted from Achrai and Wagner (2013). Note that the boundaries (sulci) between epidermal scutes are not generally coincident with the sutures between individual carapace and plastron elements. The compact outer bone is considerably denser than the inner cancellous bone. All four layers were penetrated by borings in the study interval.

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cortex layers and an internal cancellous layer (Achrai and Wagner, 2013; Fig. 5). The bone consists of both organic (collagen helices) and inorganic (hydroxyapatite nanocrystals) components (Weiner and Wagner, 1998; Achrai and Wagner, 2013). This differs significantly from borings in gastropod or bivalve shells wherein the borer had to penetrate through a thin periostracum layer and one or more layers of calcite or aragonite ($CaCO_3$).

There is considerable precedence in distinguishing ichnogenera by the substrate in which they occur (Bertling et al., 2006). Borings in wood, rock, and unconsolidated sediment form distinct ichnotaxonomic groups. Clavate borings emplaced in rock are typically referred to the ichnogenus *Gastrochaenolites*, those emplaced in wood are referred to *Teredolites*, and those excavated in firm, unconsolidated sediment are referred to *Amphorichnus*. It has been suggested that bone be considered 'lithic' in ichnological analyses (Bertling et al., 2006; Pirrone et al., 2014). We disagree. These authors specifically considered dead, predated, or scavenged bone in their analyses. Evidence of bone healing at the site of many borings as well as the location on the carapace and plastron of many other borings indicates that many, if not all, of the turtle bone borings discussed herein were emplaced while the host animals were alive. The borers had to penetrate through the epidermal scute to penetrate into or through the dermal bone. In addition to the keratin of the epidermal layer and the hydroxyapatite ($3Ca_3(PO_4)2\text{-}Ca(OH)_2$) in the bone, blood vessels, cartilage, and collagen would have formed part of the substrate. Bone, particularly living bone, is clearly not a typical lithic substrate and should be considered differently.

*Karethraichnus lakkos* new ichnospecies

*Diagnosis*.—Shallow (non-penetrating) *Karethraichnus* having a simple hemispherical profile with a rounded to flattened, hemispherical terminus.

*Description*.—The holotype (Fig. 6.1) and associated material (Figs. 6, 7) of *Karethraichnus lakkos* occur in the carapaces and plastrons of the geoemydid turtle cf. *Echmatemys* sp. (Fig. 3). In the material analyzed, trace diameter ranges from 0.6 to 9.0 mm and depth ranges from 0.3 mm to 5.5 mm. The width-to-depth ratio of specimens of *K. lakkos* ranges from >2 to approximately 1 (i.e., specimens range from half spheres to pits that are much wider than deep). Specimens commonly form imperfect circles with circularities typically less than 1 and greater than 0.75 (Fig. 4). The bases are typically rounded although flattened bases were also observed (Fig. 6.1–6.8, 6.12, 6.16–6.21).

*Etymology*.—From the greek 'lakkos' (romanization of λάκκος) meaning pit referring to the shape of the traces.

*Holotype*.—The holotype (UA-TF140-1) consists of a small pit on the ventral surface of a peripheral (Fig. 6.1). Paratypes are herein identified as other shallow pits on this, and other, peripheral carapace bones (UA-TF140; Fig. 6.1–6.7). The type locality consists of a low relief badland hill consisting of interstratified pedogenically altered siltstone and mudstone, and sheet-like to channelized sandstone and conglomerate of the Cathedral Bluffs Tongue of the Wasatch Formation at Bush Rim, South Pass, Wyoming (Fig. 1.2).

*Occurrence*.—Early Eocene (Ypresian-Lutetian/Wasatchian-Bridgerian) of southwestern Wyoming, USA.

*Remarks*.—*Karethraichnus lakkos* are the most common bone boring ichnotaxon encountered in the study area. They occur on the dorsal surface of the carapace, the ventral surface of the plastron or on the internal lip of the epiplastra, xiphiplastra, nuchal, and foremost peripherals. Numerous examples were noted in lines on or adjacent to epidermal sulci (Figs. 6.12 and 7.3). *Karethraichnus lakkos* range in abundance on individual turtle specimens from single borings to over 100 occurrences. The size range of this ichnospecies, even on individual turtle fossils, is highly variable (Figs. 6 and 7). This may indicate that the size range of the infesting parasite was highly variable or that infection/colonization by the parasites was ongoing throughout the turtle's lifespan. The shallow penetration of this ichnotaxon means that these traces penetrate through the external cortical layer of the bone, but seldom penetrate deeply into the cancellous bone layer.

*Karethraichnus kulindros* new ichnospecies

*Diagnosis*.—Deep, non-penetrative *Karethraichnus* having a cylindrical profile, axis approximately perpendicular to the substrate surface, with rounded to flattened, hemispherical terminus.

*Description*.—The holotype (Fig. 6.13–6.15) and associated material of *Karethraichnus kulindros* (Fig. 6.9–6.11) occur in the carapaces and plastrons of the geoemydid turtle cf. *Echmatemys* sp. In the material analyzed, trace diameter ranges from 0.6 to 5.5 mm and depth ranges from 0.5 to 6 mm. *Karethraichnus kulindros* commonly co-occurs with *K. lakkos* and *K. fiale* on individual turtle fossils.

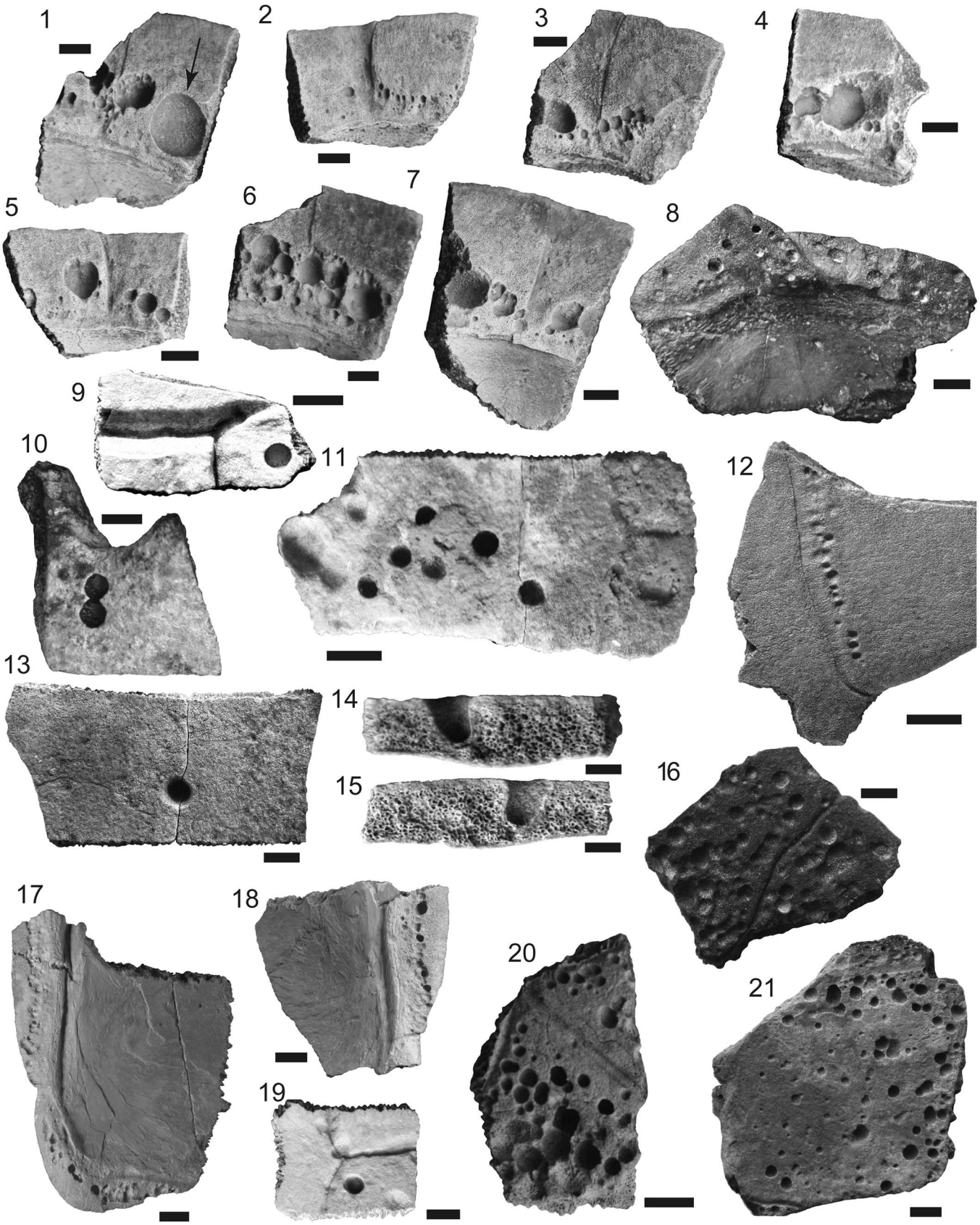
*Etymology*.—From the greek 'kulindros' (romanization of κύλινδρος) meaning cylinder, referring to the shape of the traces.

*Holotype*.—The holotype (UA-TF140-8) consists of a subvertical cylindrical pit on the dorsal surface of costal bone (Fig. 6.13–6.15). The type locality consists of a low relief badland hill consisting of interstratified pedogenically altered siltstone and mudstone, and sheet-like to channelized sandstone and conglomerate of the Cathedral Bluffs Tongue of the Wasatch Formation at Bush Rim, South Pass, Wyoming (Fig. 1.2).

*Occurrence*.—Early Eocene, Cathedral Bluffs Tongue, Wasatch Formation, South Pass, Wyoming.

*Remarks*.—The depth of *Karethraichnus kulindros* means that these traces invariably penetrate through the external cortex, and typically terminate deeply within the cancellous layer, commonly bottoming out at or near the inner surface of the internal cortex. Note that this trace does not penetrate fully through the bone. *Karethraichnus kulindros* differs from

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*K. lakkos* in its cylindrical versus hemispherical morphology and from *K. fiale* in its straight walls and lack of complete penetration. *Karethraichnus kulindros* are overall much rarer than *K. fiale* and approximately as common as *K. fiale*.

*Karethraichnus fiale* new ichnospecies

*Diagnosis*.—Penetrative *Karethraichnus* having a cylindrical to bi-convex or flask-shaped profile, axis approximately perpendicular to the substrate surface.

*Description*.—*Karethraichnus fiale* penetrate fully through individual shell elements (Figs. 7.1–7.4, 7.9–7.11). Where they penetrate through thick cortical bone and minimal trabecular (cancellous) bone, the shaft of this trace is typically straight and is oriented approximately perpendicular to the shell surface (Fig 8.2). In-shell elements with thin cortical bone and a thicker cancellous bone layer these trace are typically biconvex, with the thickest portion of the trace occurring in the center of the bone (Fig. 8.2).

*Etymology*.—From the greek '*fiale*' (romanization of φιάλη) meaning flask, referring to the bi-convex shape of the traces.

*Types*.—The holotype (UA-TF148-1) consists of a circular bi-convex hole through the medial portion of a costal bone (Fig. 7.1, 7.2, and 7.9). Paratypes are designated as other penetrative holes on the same specimen (Figs 7.3, 7.4; 7.9–7.11), including a penetrative hole capped by a hemispherical bone patch (Fig. 7.6–7.8) The type locality consists of badland hills below Continental Peak, consisting of interstratified pedogenically altered siltstone and mudstone, and sheet-like to channelized sandstone and conglomerate of the Cathedral Bluffs Tongue of the Wasatch Formation in the Honeycomb Buttes area, South Pass, Wyoming (Fig. 1.2).

*Occurrence*.—Early Eocene, Cathedral Bluffs Tongue, Wasatch Formation, South Pass, Wyoming.

*Remarks*.—The clavate or flask-shape of trace fossils such as *Teredolites* in woodground substrates and *Gastrochaenolites* in hardground settings reflects the gradual, in situ growth of the trace maker (Kelly and Bromley, 1984). In contrast, the flask shape of *K. fiale* is interpreted to reflect penetration through several different bone types, including the hard, dense external and internal cortex bone and the softer, more coelous internal trabecular bone (Fig. 5).

Many, although not all, *Karethraichnus fiale* are characterized by a raised lip, bone spur, or bone patch that may narrow, or completely cover the hole. This bone growth is not considered a diagnostic component of the ichnospecies. This ichnospecies differs from *K. kulindros* in their biconvex morphology and penetration depths that equals or (in examples with secondary bony healings or patches) exceeds the primary thickness of the bone. *Karethraichnus fiale* represents a breach through the external bone armor of the host organism. The bone growth indicates that, despite the presence of the parasite, negative affects to the host taxon were insufficient to kill it immediately (if at all).

Ichnogenus *Thatchtelithichnus* new ichnogenus

*Type ichnospecies*.—*Thatchtelithichnus holmani* new ichnospecies.

*Other ichnospecies*.—*Thatchtelithichnus bagginsi* new ichnospecies.

*Diagnosis*.—Circular to subcircular grooves with a central boss or platform, bored into a bone substrate. Grooves penetrate into the cortical layer of the bone. The central platform may consist of an unmodified platform or a rounded nubbin. Burrow walls rounded, convex. or sharp and perpendicular to the external substrate surface.

*Etymology*.—From the greek 'thachtelithi' (latinization of δαχτυλίδι) meaning 'ring,' referring to the shape of the specimen and 'ichnus' meaning trace.

*Occurrence*.—Eocene of the Green River Basin, Wyoming.

*Remarks*.—*Thatchtelithichnus* bears morphological and size similarities to the ichnogenus *Oichnus* Bromley, specifically to the taxon *Oichnus excavatus* Donovan and Jagt, 2002, which occurs in marine and freshwater invertebrates. Recent taxonomic reassessments have suggested that *Oichnus* is a junior synonym of *Sedilichnus* (Zonneveld and Gingras, 2014). *Thatchtelithichnus* differs in the nature of the substrate in which the trace occurs (discussed above).

Only a single species of *Thatchtelithichnus* is identified. Similar to *Oichnus excavatus*, *Thatchtelithichnus* ranges in morphology between end-members in which the central platform remains unmodified by the tracemaker and those in which it is modified. Because only a single specimen with an unmodified central platform was identified in the study material, at this time the two morphotypes are included within a single ichnogenus.

*Thatchtelithichnus holmani* new ichnospecies

**Figure 6.** *Karethraichnus* on cf. *Echmatemys* sp. bones. All scale bars are 5 mm. (**1–7**) *Karethraichnus lakkos* on the ventral surface of peripherals from a single turtle specimen (UA-TF140). The holotype of *K. lakkos* (UA-TF140-1) is identified by an arrow in (**1**). Note the variability in size of individual borings on this single turtle specimen. (**8**) *Karethraichnus lakkos* on the dorsal surface of the margin of a right epiplastron (UA-TF141). (**9**) Solitary *K. kulindros* on the dorsal surface of a peripheral (UM1032831). (**J**) Two touching *K. kulindros* on the dorsal surface of a hyoplastron fragment (UA-TF142). (**11**) Several *K. kulindros* and two *K. lakkos* on a costal fragment, likely of a C3, C4 or a C5 (UA-TF143). (**12**) Abundant *K. lakkos* on a hypoplastron fragment (UM102792). Note that the borings follow the edge of the epidermal suture line, a natural access point to the shell through the epidermal layer. (**13**) The holotype of the deeply penetrating trace fossil *K. kulindros* on the dorsal surface of a central costal bone (UA-TF140-8). (**14, 15**) Vertical sections through the holotype of *K. kulindros*. Note that the boring nearly penetrates through the entire bone and that, although slightly curved, is overall cylindrical. (**16**) A highly bored costal fragment covered in abundant *K. lakkos* (UA-TF144). (**17, 18**). Bored xiphiplastra from the same specimen (UM103361). Note that the borings occur on the ventral surface of the periphery of the bone. S. Single *K. lakkos* on the dorsal surface of a central costal (UA-TF145). (**20, 21**) Highly bored plastron fragments with abundant *K. kulindros* (UA-TF146 and UA-TF147).

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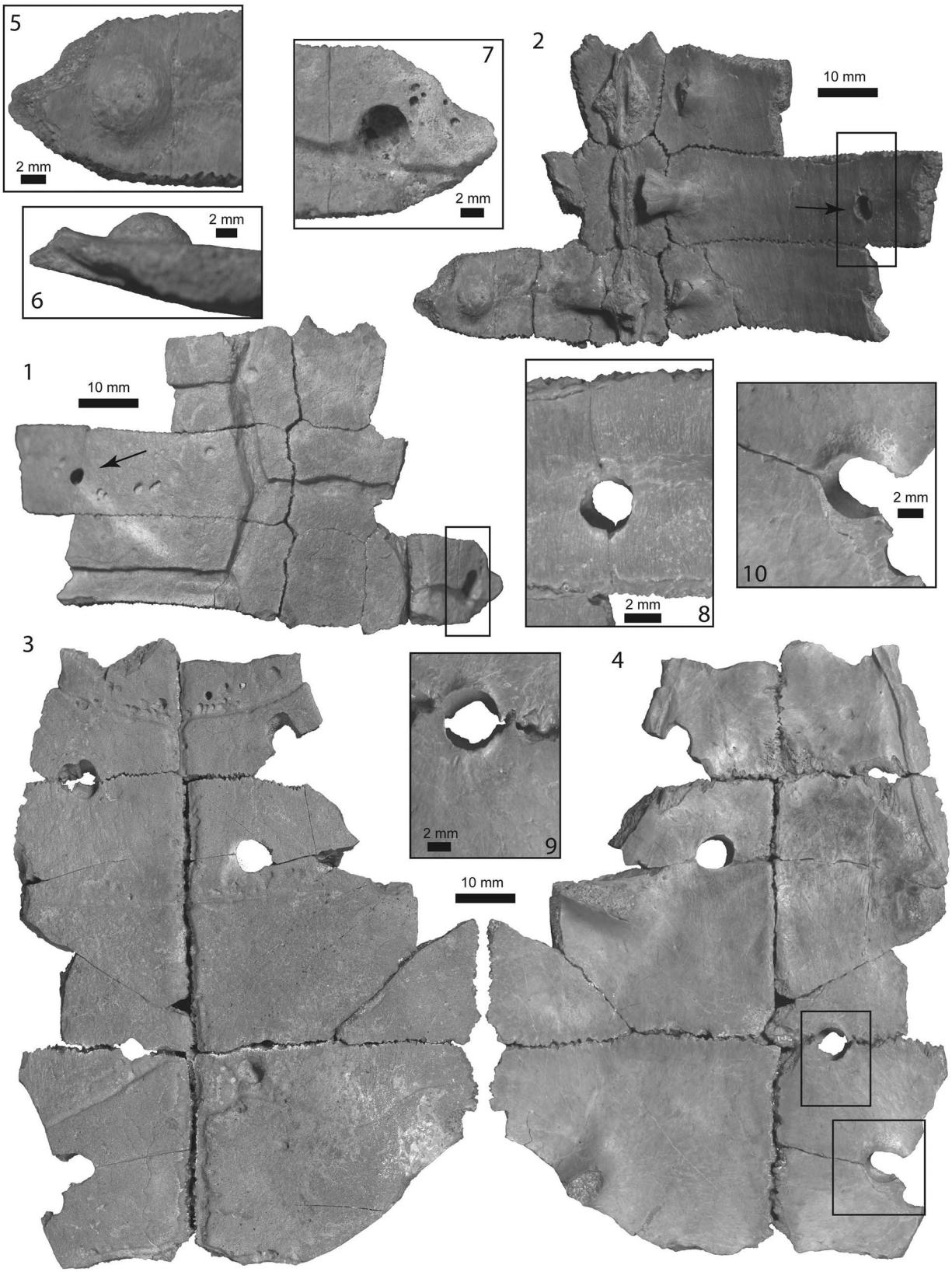



**Figure 7.** Borings on a single specimen of cf. *Echmatemys* sp. (UAAES14009). Note that the borings occur on both the plastron and carapace. (**1, 2**) External (**1**) and internal (**2**) views of carapace. The box in 1 denotes the location of the healed boring in (**7**), (**8**), and (**9**). The box in B identifies the holotype of *Karethraichnus fiale* (also shown in **8**). (**3**, **4**) External (**3**) and internal (**4**) views of plastron. Note how the small borings follow the sulcus on the xiphiplastra. (**E**) Close-up of the internal surface of the healed boring in (**2**). (**6**) Cross-sectional view of the healed boring in (**2**). (**7**) External view of the pit that terminates in the bone healing, identified in the box in (**2**). (**8**) The holotype of *K. fiale*. (**9**) Close-up of internal view of large boring on left hypoplastron/hyoplastron suture (upper box in **4**). Note the raised lip surrounding the hole. (**10**) Close-up of the penetrative borings with enraised lips shown in the lower box of (**4**).

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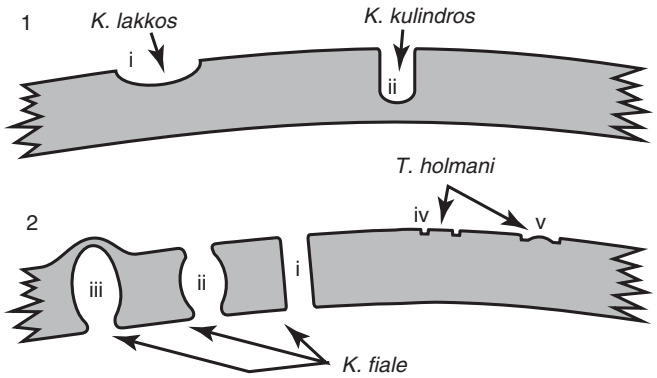



**Figure 8.** Cross-sectional shape of *Karethraichnus* and *Thatchtelithichnus* species. (**1**) *Karethraichnus lakkos* (i) comprise shallow, non-penetrative pits with margins oriented obliquely to the external surface of the trace; *Karethraichnus kulindros* (ii) are deep, non-penetrative pits with rounded to flattened bases. (**2**) *Karethraichnus fiale* (i and ii) are penetrative cylinders that pass fully from the outside surface of the shell to the inside surface. The boring walls may be straight (i) or, more commonly, convex outwards (ii), a morphology that likely results penetration through the dense outer cortex, the porous interior cancellous layer and the dense inner cortex. Rare examples penetrate fully through the primary bone and continue into the secondary bone patch (iii). *Thatchtelithichnus holmani* consists of a circular to subcircular groove in the outer layer of the turtle bone. These grooves may have sharp (iv) or curved (v) margins.

*Diagnosis*.—As for the genus. Non-penetrative borings into a bone substrate, having a ring-like profile, and a central raised boss or pedestal.

*Description*.—*Thatchtelithichnus holmani* is a shallowly penetrating boring that rarely penetrates more than 0.25–1.5 mm into the bone substrate. Most *T. holmani* penetrate only into the cortical bone without reaching the cancellous bone beneath. The outside wall of the trace is unaffected by the borers activities. The external margin of the trace is sharp. The central enraised portion may consist either of a partially raised, rounded central boss or nubbin (Figs. 9.1–9.5, 9.7–9.9) or, more rarely, a pedestal of unaltered bone in the center of the trace (Fig. 9.6).

*Etymology*.—After the late Dr. J. Alan Holman, paleontologist and herpetologist who contributed much to our understanding of recent and fossil pathology in reptiles.

*Holotype*.—The holotype (UA-TF149-1) consists of a circular bi-convex hole through the medial portion of a costal bone (Fig. 9.1). Paratypes designated herein include other specimens on the same turtle plastron (Fig. 9.1–9.5). The type locality consists of low badland hills at the base of Bush Rim, consisting of interstratified pedogenically altered siltstone and mudstone, and sheet-like to channelized sandstone and conglomerate of the Cathedral Bluffs Tongue of the Wasatch Formation, South Pass, Wyoming (Fig. 1.2).

*Occurrence*.—Early Eocene Cathedral Bluffs Tongue, Wasatch Formation, South Pass, Wyoming.

*Remarks*.—*Thatchtelithichnus holmani* is the rarest bone boring taxon observed in the study area. It has, thus far, only been observed on the ventral surface of plastron fragments. No consistent relationship between position on the plastron and the location of the trace fossil was identified. Of the 33 specimens identified, 28 occur on the ventral surface of the plastron of a single cf. *Echmatemys* sp. individual.

Similar traces were illustrated on dinosaur long bones and ribs from the Jurassic Morrison Formation (Bader et al., 2009). The Morrison material (~1–3mm in diameter) was interpreted as the pupation chambers of dermestid-type beetles (Bader et al., 2009). Dermestids typically feed on desiccated vertebrate carcasses (Timm, 1982). Although the larvae prefer soft tissue, they will bore into bone if other resources are unavailable (Hefti et al., 1980). Ring-shaped or 'rosette' traces were interpreted to be intermediate forms with hemispherical pits (Bader et al., 2009).

An analogous ichnotaxon, *Sedilichnus excavatus* occurs on invertebrate skeletal tests (holasteroid echinoids and bivalves) from marine successions (Donovan and Jagt, 2002; Thomas, 1976; Zonneveld and Gingras, 2014). *Sedilichnus excavatus* had been interpreted to be attachment or embedment structures of a sessile, filter-feeding animal (Donovan and Jagt, 2002) and has been identified as failed naticid gastropod borings (Thomas, 1976; Zonneveld and Gingras, 2014). As discussed above, ring-shaped traces are rare in the study area and are not interpreted to be a common intermediate or precursor form for species of *Karethraichnus*.

## Discussion

*Taxonomic differentiation*.—Trace fossil taxa differ from zoological taxa, both fossil and extant in that individual ichnotaxa (particularly ichnospecies) are commonly morphological end-members within a spectrum. We name the clearly differentiated states. For example, *Ophiomorpha*, *Thalassinoides*, and *Spongeliomorpha* are ichnogenera named for branching, three-dimensional networks of cylindrical burrows. They differ primarily in the nature of their linings: external pelleted lining in *Ophiomorpha*, smooth unlined to lightly lined walls in *Thalassinoides*, and ridged to scratch-marked in *Spongeliomorpha* (Häntzchel. 1962; 1965; Kennedy, 1967; Müller, 1970). Although they commonly co-occur within a single specimen attempts to lump these ichnotaxa into one or two ichnogenera (e.g. Fürsich, 1973; Bromley and Frey, 1974) have failed and all three ichnotaxa remain in common usage.

Similarly, *Sedilichnus*, a ichnotaxon used for borings in invertebrate shells, possesses 10 ichnospecies, several of which are clearly end-members on a morphological spectrum (e.g., *S. spongiophilus* and *S. paraboloides)* yet all of which have clearly definable and differentiable morphological characteristics (Zonneveld and Gingras, 2014).

Thus, although an argument could be made that gradations exist between the three *Karethraichnus* ichnospecies named herein we contend that sufficient morphological distinctions occur to warrant retention of all three names; one for shallow, surficial pits (*K. lakkos*), one for deep, narrow pits (*K. kulindros*) and the last for penetrative holes (*K. fiale*). It is worth noting that some turtles are exemplified by all three forms; however, many turtles are limited to one form or another. More commonly, *K. lakkos* co-occurs with either *K. kulindros* or *K. fiale* on single

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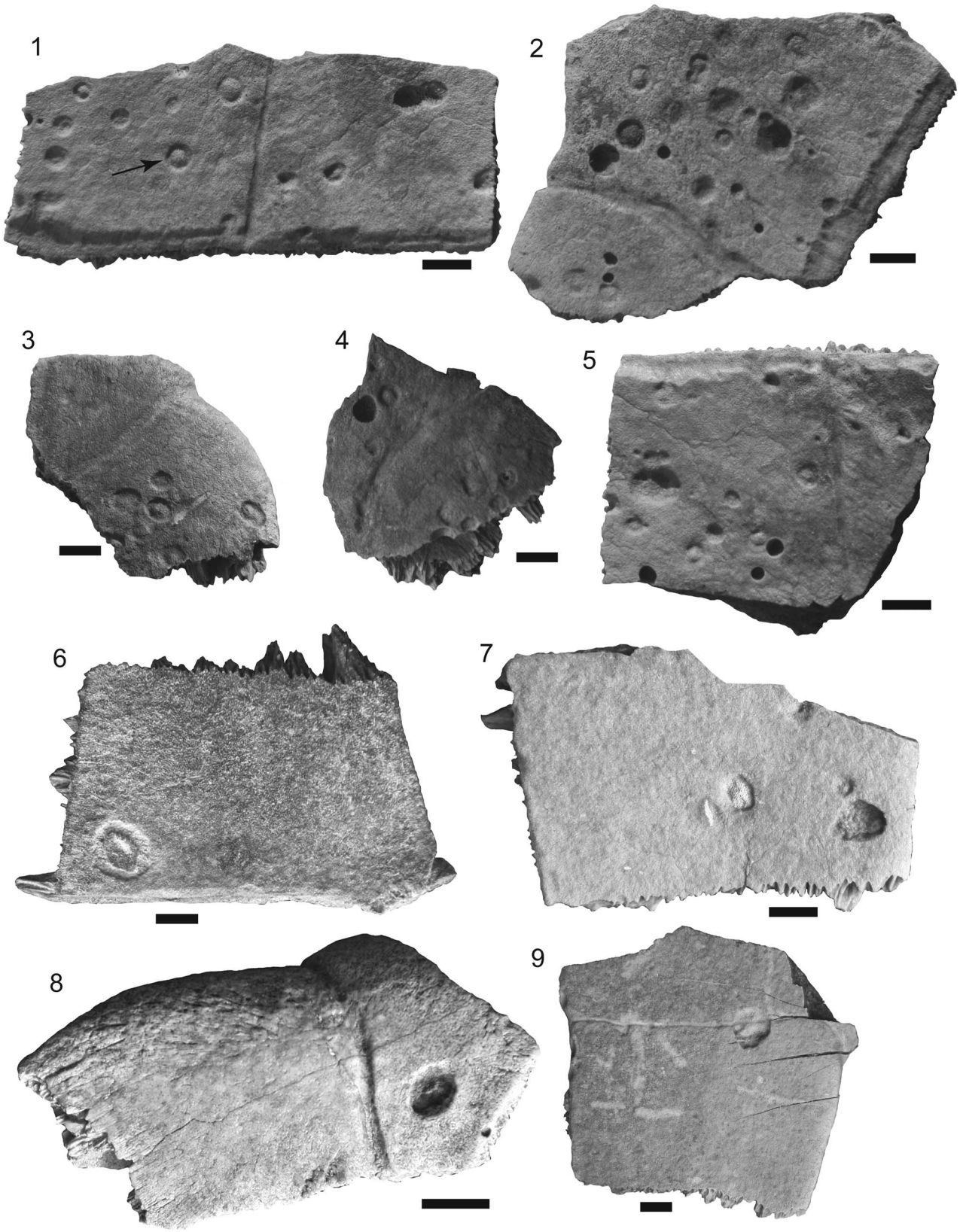



**Figure 9.** *Thatchtelithichnus holmani*. All scale bars are 5 mm. Photographs (**1**) through (**5**) are all from a single cf. *Echmatemys* sp. specimen (UA-TF149). Note the occurrence of both *Karethraichnus* taxa and *Thatchtelithichnus* on these bone fragments. (**1**) Central part of *T. holmani* on central portion of hypoplastron. The holotype of *Thatchtelithichnus holmani* is identified with an arrow. (**2**) Peripheral fragment of hypoplastron showing several *T. holmani* as well as pit-like *K. lakkos* and deep, cylindrical *K. kulindros*. (**3, 4**) Left epiplastra with several *T. holmani*. (**5**) Hyoplastron fragment with several *T. holmani*. (**6**) Hyoplastron fragment with single, large *T. holmani* (UA-TF150). (**7**) Hyoplastron fragment with several *T. holmani* (UA-TF151). (**8**) Left epiplastron with single *T. holmani* (UM102773). (**9**) Hyoplastron fragment with single *T. holmani* (UA-TF152). (**8**) and (**9**) have only slightly enraised central platforms and may be an intermediate form between *T. holmani* and *K. lakkos*. All scale bars 5 mm.

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turtle specimens in which case the two taxa are commonly of markedly different sizes. This likely indicates that either the parasite colonization occurred at two distinct times (our preferred interpretation) or that two different parasites were involved.

*Timing of emplacement*.—Numerous examples have been discussed in the literature wherein invertebrate taxa have bored into the bones of dead continental organisms (e.g., Tappan, 1994; Kaiser, 2000; Britt et al., 2006; Roberts et al., 2007; Cabral et al., 2011; Pirrone et al., 2014). Borings into long bones and ribs by invertebrate macrobiota such as silphid and dermestid beetles or termites can only occur after the death, and at least some level of decay of the host organism. In some cases, necrophagic invertebrates, such as silphid and dermestid beetles, are attracted to the carcass by decaying soft tissues and only attack the bone when the soft tissue biomass is insufficient to support the colonizing population of beetles (Britt et al., 2008). In other cases, the organisms colonize the relatively clean bone, either as a means of constructing a domicile in a rigid, protective substrate, or to access residual organics and/or minerals within the bone (Roberts et al., 2007; Britt et al., 2008; Cabral et al., 2010; Pirrone et al., 2014).

Several lines of evidence support the contention that *Karethraichnus* ichnospecies discussed here were emplaced on the shells of living turtles. Non-penetrative forms (*K. lakkos*, *K. kulindros*) occur on both the plastron and carapace, solely in positions that would have been accessible to a parasite while the animal was alive (i.e., external surfaces; lip areas of epiplastra, xiphiplastra, nuchal, and cranial peripherals; Fig. 3). *Karethraichnus fiale*, the sole ichnotaxon described herein which penetrates fully through the shell elements, are less common than other ichnospecies. These traces commonly exhibit evidence of a physiological response to parasite penetrations. Although many traces do not penetrate through the outer layer (Fig. 10.1, 10.3, and 10.6) where they do, the bone is often altered (Fig. 10.8, 10.4, and 10.6), forming a smooth inner wall compositionally identical to the rest of the turtle bone. In some cases this consists of a raised lip surrounding the burrow that stands out from less than 1.0 mm to several mm from the surface of the surrounding bone (Figs. 7.4, 7.10, and 7.11; 10.3; 11.2–11.4; and 12.2). In other cases, the host organism formed a bone patch that completely covered over the penetration of the bone (Figs. 7.1, 7.6, and 7.7; 11.1, 11.5, and 11.6; and 12.1). In the case of the latter, the depth of the boring typically exceeded the average thickness of the shell in the area of the boring (Fig. 7.1, 7.6, and 7.7), indicating that the parasite's activities occurred simultaneously with the bone-healing response of the host organism. The bone material that forms the healed patch is typically dense and laminar, similar to the external and internal cortical bone that forms the outer surfaces of the turtle shell (Fig. 12). Traces that penetrate fully

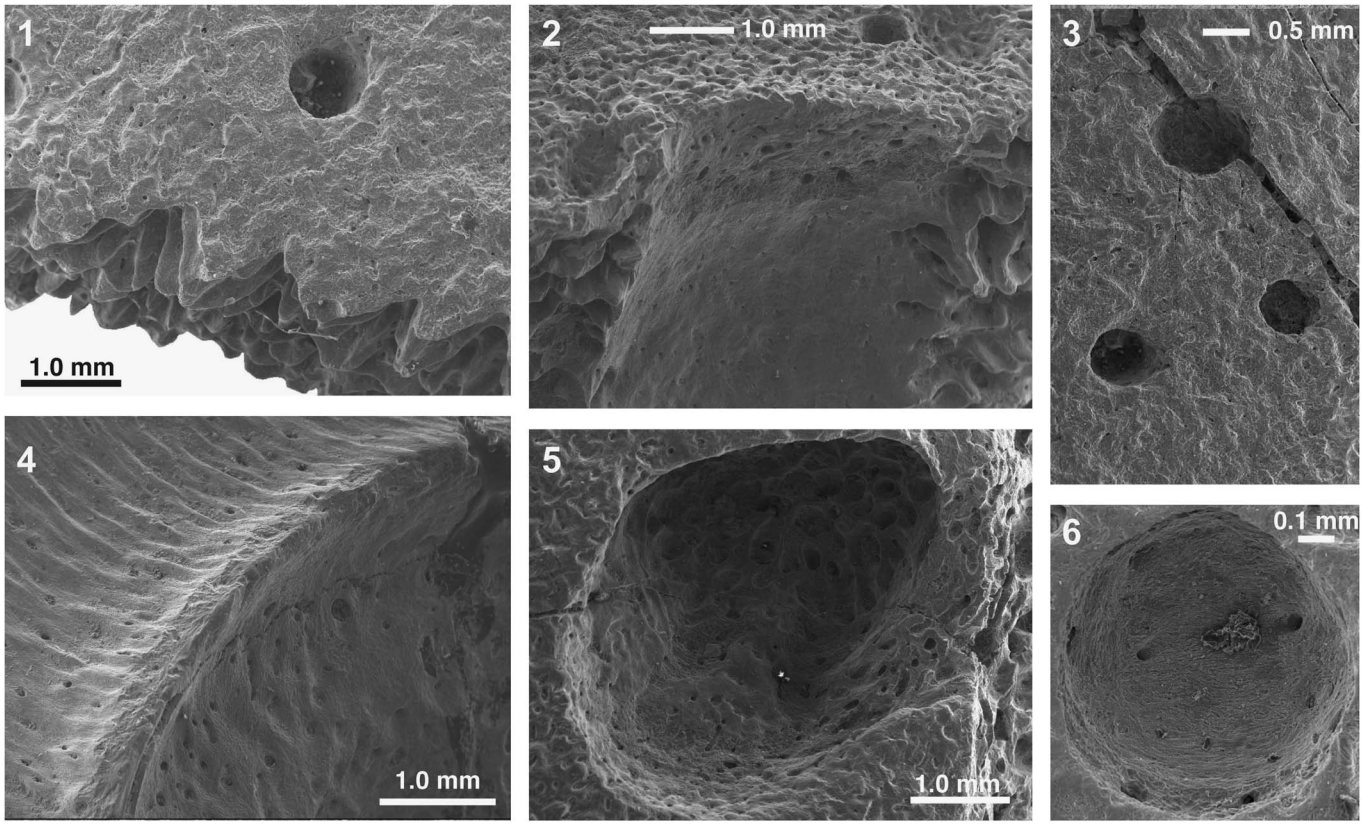



**Figure 10.** SEM images of *Karethraichnus* (UA-TF148). (**1**) Tiny *K. kulindros* at the terminus of a costal bone. The jagged edge at bottom right is the suture at the distal end of the bone. (**2**) Close-up of the edge of a *K. kulindros*. Note the smooth wall of the boring and the coelous nature of the bone to the left and right of the boring. (**3**) Three tiny *K. kulindros*. (**4**) Healed margin on the edge of a penetrative *K. kulindros*. (**5**) Elongate *K. lakkos* with latitudinal ridges near the base of the pit. (**6**) Shallow circular *K. lakkos* with possible scratch marks at bottom centre of photograph.

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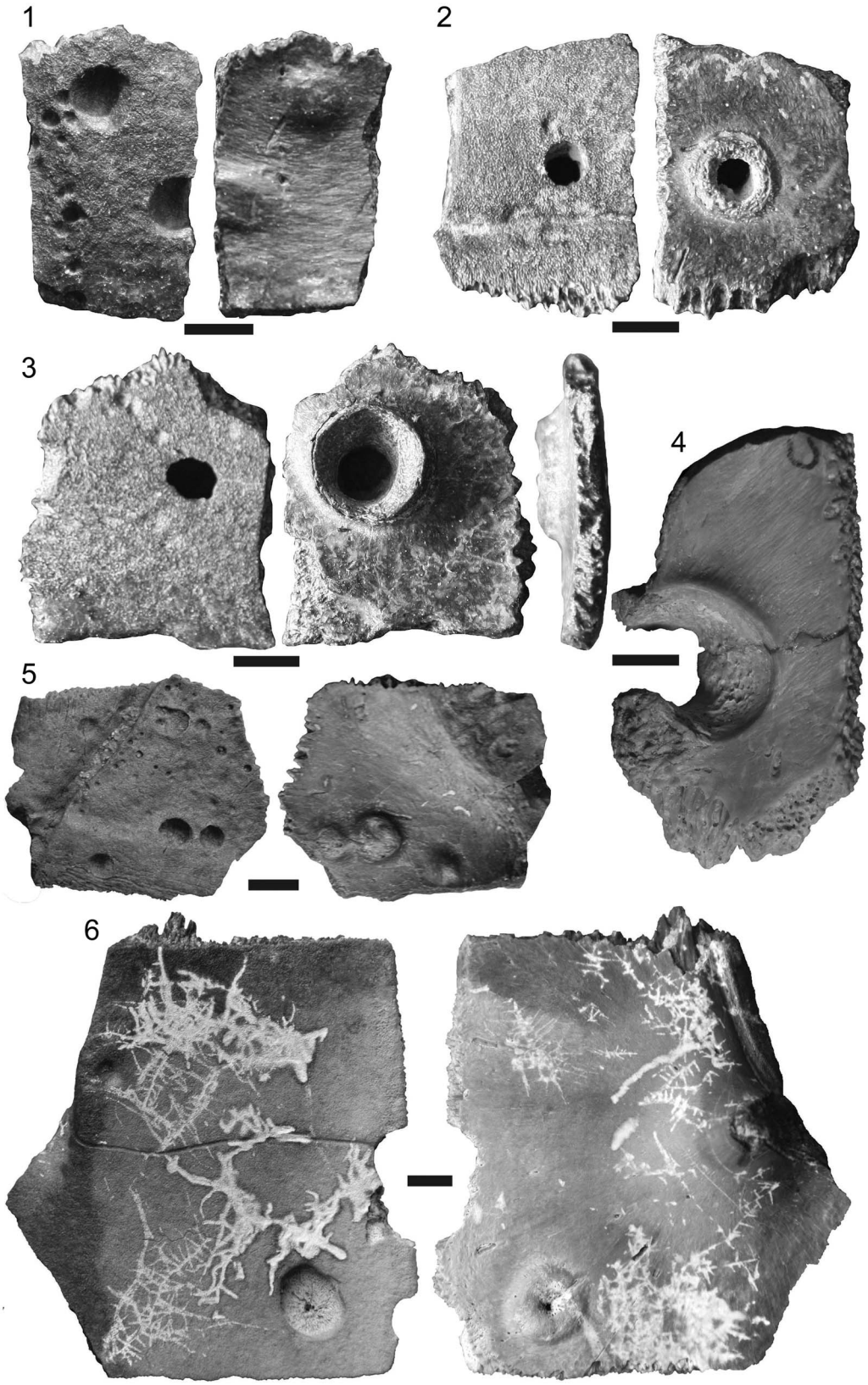



**Figure 11.** Healed penetrative *Karethraichnus* borings in cf. *Echmatemys* sp. shells. All scale bars are 5 mm. In all pairs, the left image shows the external surface and the right images shows the internal (visceral) surface. (**1**) *Karethraichnus* on a costal fragment of which the largest two have complete internal healings (UA-TF153). (**2**) Hypoplastron fragment with a single *Karethraichnus* (UA-TF154). The internal healing in this specimen is incomplete. (**3**) Costal fragments with a single *Karethraichnus* shown in external, visceral and cross-sectional views (UA-TF155). (**4**) Costal fragment with a large *Karethraichnus* penetrating through the shell (UA-TF156). The size of the healing in both (**3**) and (**4**) is larger than the external opening suggesting that the parasite continued to grow after penetrating through the shell (UA-TF157). (**5**) Three healed *Karethraichnus* borings on a costal fragment (right iC1). (**6**) A single healed *Karethraichnus* on a left hypoplastron (UA-TF158). All scale bars 5 mm.

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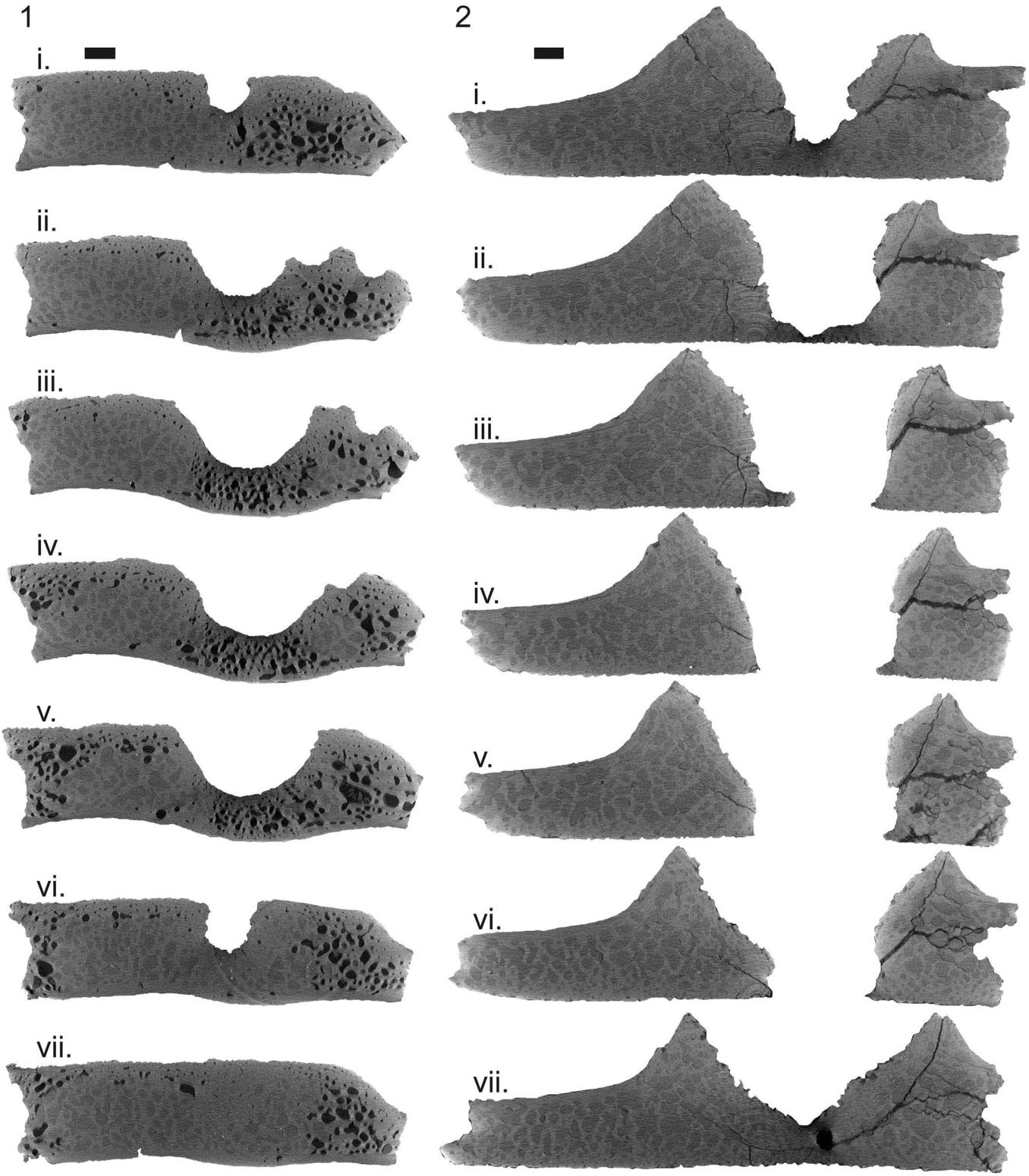



**Figure 12.** Sequential micro CT slices through penetrative and non-penetrative *Karethraichnus* on costal fragments. All scale bars are 5 mm. (**1**) *Karethraichnus* that penetrates ~80% of the bone. This boring triggered a systemic response resulting in new bone growth and thickening of the shell beneath the boring. Top of each slice is the external (dorsal) surface. Base of each slice is the outer (ventral) surface (**2**). *Karethraichnus* that penetrates fully through the bone with a spur of new bone growth in a ring surrounding the boring on the inside surface. In each slice the area above the dashed line consists of bone that grew in response to the penetration of the parasite. In this example, the hole was not fully healed such as is the case in other examples such as in Figure 11.1. All scale bars 1 mm.

through the bone and into the healed patch form compound borings/bioclaustration structures (*sensu* Palmer and Wilson, 1988) and, to our knowledge, are unique within bone-hosted trace fossils. The bioclaustration component is not part of the diagnosis or description of any ichnotaxon described herein because bioclaustration structures are pathological systemic

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responses of the affected organisms and are not trace fossils (see Bertling et al., 2006; and Donovan, 2014 for further discussion of bioclaustration features and ichnotaxobases).

These features are indeed borings and compound boring/bioclaustration structures rather than solely bioclaustrations structures that resulted from a parasite introduced during the turtle's embryonic stages. First, several of the borings were observed to preserve horizontal to subhorizontal markings that may reflect scratch marks or etch marks. Second, these traces occur on adult specimens; juvenile cf. *Echmatemys* sp. shells observed in this study did not exhibit borings. Finally, in many specimens the borings followed the sulci between epidermal scutes (a weakness in the epidermal armor), clearly indicating that the parasite colonization occurred after the animals hatched, likely as adults.

*Parasite identification*.—Modern chelonians play host to a wide variety of parasites, both internal (endoparasites) and external (ectoparasites). However, despite the diversity and prevalence of parasites on turtles and tortoises, attention has focused primarily on the affects that these parasites have on the health of the host organism (e.g., Esch and Gibbons, 1967; Ernst and Ernst, 1977; Readel et al., 2008; Bielecki et al., 2012). Minimal attention has been given to the effect that ectoparasites have on the integrity of the shells of these organisms. Below we discuss parasites that affect turtles in a myriad of settings including lake, river, terrestrial, marine, and marginal marine environments. Although the chelonian host taxa of the borings discussed herein occur in an interior fluvial-lacustrine depositional basin, isolated from any possibility of marine influences, these trace fossils are remarkably similar to borings we have observed in the shells of sea turtles and thus we include a brief discussion of marine turtle parasites.

Note also that several common boring taxa such as snails and bivalves are not considered likely candidates. Rock and wood-boring bivalves are limited to marine settings, and although there is significant size variability in bivalve borings, the shape is invariably clavate or tear-shaped (Bromley, 2004), thus differing significantly from the traces discussed herein. Shell-boring gastropods are unlikely candidates as well. Saxicavous gastropods are able to bore into carbonate lithic substrates through acid dissolution (Stanton, 1986; Quattier, 2002, 2011). Although shell-boring gastropods do occur in continental settings, typically preying upon other gastropods (Boycott, 1921, 1934; Ellis, 1969; Mordan, 1977), there is no record of these bivalves pursuing other prey types such as turtles.

*Parasites in modern sea turtles*.—Modern sea turtles play host to an wide variety of epibionts including cnidarians (hydrozoans and anthozoans), poriferans, molluscs (gastropods and bivalves), arthropods (amphipods, isopods, brachyurans, tanaids and cirripedes), platyhelminths, annelids, bryozoans, urochordates, and algae, (Caine, 1986; Frick et al., 1998, 2000; Scaravelli et al., 2001; Schärer, 2003; Pfaller et al., 2008). Of these, cirripedes (barnacles) have the most pronounced effect on the dermal bone. The attachment locales for barnacles commonly result in pitting on the surface of the carapace and plastron. These pits are approximately circular and, in our experience, have rounded bases that penetrate through the outer dense bone layer into the more coelous bone beneath. Although attachment sites may occur anywhere on the turtle, there appears to be prevalence on the sulci between epidermal scutes (when present). These parasites commonly penetrate into the bone, thus occupying an intermediate position between ectoparasites and endoparasites, and thus may be considered to be mesoparasites. Although barnacles may excavate shallow, non-penetrative pits similar to *Karethraichnus lakkos* pits observed on some specimens discussed above, they are unlikely tracemakers of the turtle shells discussed herein because the Honeycomb Buttes turtles were collected from a fluvial-lacustrine basin ~1200 km from the nearest Eocene marine setting.

*Parasites in modern marginal marine turtles*.—Several modern freshwater turtle taxa are tolerant of brackish conditions. This has allowed interactions of quintessentially freshwater vertebrate species with characteristically marine invertebrate species. Barnacles and, less commonly' oysters have been observed to colonize the shells of Diamondback Terrapins (*Malaclemys terrapin*) in coastal lagoons and estuaries (Allen and Neill, 1952; Jackson and Ross, 1971a; Ross and Jackson, 1972; Seigel, 1983). Rare examples of barnacles have also been noted on the alligator snapping turtle (*Macroclemys temminicki*; Jackson and Ross, 1971b), the red-bellied cooter (*Pseudemys alabamensis*; Jackson and Ross, 1972), and the American red-bellied turtle (*P. rubiventris*) (Ross and Jackson, 1972; Arndt, 1975; Seigel, 1983).

Barnacle infestations may be severe enough to interfere with nesting and mating behavior, cause significant shell erosion, and in rare cases death (Jackson and Ross, 1971b; Seigel, 1983). Although the carapace is the most common settling site, barnacles occur on the plastron as well (Seigel, 1983). Barnacles may cause significant shell erosion and may, in rare cases, penetrate through the shell causing development of significant scar tissue (Seigel, 1983).

*Macroparasites in modern freshwater turtles*.—Parasites, particularly leeches, are common ectoparasties on aquatic turtles in temperate and subtropical rivers, bogs, ponds, and lakes (eg. Esch and Gibbons, 1967; Hulse, 1976; McCoy et al., 2007; Oceguera-Figueroa and Siddall, 2008; Readel et al., 2008). Seasonality plays a strong role (Esch and Gibbons, 1967; MacCulloch, 1981; Readel et al., 2008) as does environmental setting. Turtles in turbid, slow-moving, or still water are also characterized by more abundant ectoparasites than those in clear or moving waters (Readel et al., 2008).

In Wintergreen Lake near Kalamazoo, Michigan, the diversity and number of parasites (nematodes and tremadodes) on the midland painted turtle (*Chrysemys picta marginata)* increased in individuals from their first to their fourth growing seasons and decrease in abundance thereafter (Esch and Gibbons, 1967). In contrast, analyses of multiple taxa from lakes and ponds in Colorado, North Carolina, and South Carolina have shown a simpler relationship, with larger turtles possessing a higher parasite load than smaller turtles both within and between taxa (McCoy et al., 2007; Readel et al., 2008).

Bottom-dwelling forms, such as snapping turtles and mud turtles, commonly have higher ectoparasite loads than aerial baskers, in part because of the effects of desiccation on

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ectoparasites (Ryan and Lambert, 2005; McCoy et al., 2007; Readel et al., 2008). Seasonality plays a strong role in the presence of leeches on aerial baskers in temperate settings wherein the turtles may spend more time out of, and away from, water during warmer months (Koffler et al., 1978). Although leeches need only a single blood meal per year to survive, they require more for growth and reproduction (Sawyer, 1986). Concomitantly leeches will commonly remain attached to individual turtles for long intervals (i.e., through multiple feedings) and will commonly remain attached to an individual hibernating turtle throughout the winter (Graham et al., 1997).

Although leeches most commonly occur on the soft integument of the areas around the head and neck (Esch and Gibbons, 1967; McAucliffe, 1977; MacCulloch, 1981), in some populations leeches may be common on the carapace and plastron (Hulse, 1976; Brooks et al., 1990; Siddall and Gaffney, 2004; Bielecki et al., 2012). The leeches feed on blood sinuses within bones of the plastron and carapace with attachment sites most commonly occurring at, although not excluded to, the sulci between epidermal scutes (Siddall and Gaffney, 2004). This feeding activity was interpreted as a possible explanation for the pitting observed on some fossil turtles by Hutchison and Frye (2001). Siddall and Gaffney (2004) argued that the complex salivary secretions of the leech *Placobdella ornata* is capable of bone decalcification and digestion of connective tissue matrix although this has not be demonstrated in the laboratory and pits attributable to leeches have not been illustrated.

Freshwater turtles are also prone to numerous internal parasites including flukes (Martin, 1972; Flynn, 1973). Although most are non-pathogenic, spirorchid liver flukes cause a variety of ailments including ulcerative lesions on the carapace (Johnson et al., 1998). Spirorchid liver flukes occur in a large proportion of wild aquatic turtle populations in North America (Flynn, 1973); however, pitted ulcerations in the shell have been reported by only a few authors (Flynn, 1973; Johnson et al., 1998; Johnson, 2004). These shell imperfections are noted primarily in veterinary journals (Johnson et al., 1998; Johnson, 2004). Because the parasitic infection, if treated, does not result in death, shell damage caused by spirorchid liver flukes has not been illustrated.

*Shell disease in terrestrial and aquatic turtles*.—Freshwater turtles may be affected by a variety of shell-degrading bacterial infections including NSD (necrotizing scute disease), USD (ulcerative shell disease), and SCUD (septicemic cutaneous ulcerative disease). NSD is primarily a disease of the epidermal lamellae (i.e., scutes) but may also affect the underlying dermal bone (Rose et al., 2001). NSD is caused by a fungal infection (identified as *Fusarium semitectum*) and is only active while the host animal is alive suggesting that the fungus utilizes some substance other than the keratin (Rose et al., 2001). This disease has been reported primarily in terrestrial turtles and tortoises and appears to have only a surficial effect on the dermal bone (Jacobson et al., 2000; Rose et al., 2001).

USD is a chronic condition in many wild populations and is considered endemic in areas where environmental conditions have become degraded, either through anthropogenic or natural means (Wallach, 1975; Johnson, 2004; Bishop et al., 2007). USD has been attributed to the bacterium *Baneckea chitinovora* (Wallach, 1975; Johnson, 2004). Pitting and erosion of turtle shell are a common effect of USD, allowing invasion of other bacteria as well as macroparasites such as trematodes (Lovich et al., 1996, Garner et al., 1997; Johnson, 2004).

SCUD, also known as 'shell rot' is a common form that can result in extensive degradation of the carapace and plastron (Kaplan, 1957). SCUD is caused by the bacterium *Citrobacter freundii*, which occurs naturally in soil and water (Raphael, 2003). Turtles become infected through skin abrasions and exposure (Raphael, 2003; Johnson, 2004). Pitting and extensive erosion of the shell are common effects of SCUD in free-ranging turtle populations (Raphael, 2003; Johnson, 2004). SCUD commonly results in the death of the host organism. Although both USD and SCUD result in pitting and erosion of the dermal bone of both the plastron and carapace, SCUD degradation is commonly more extensive and more typically results in the death of the turtle (Johnson, 2004).

All three of these diseases, but particularly USD and SCUD, can result in extensive shell damage to freshwater turtles. However, the amorphous, typically extensive, etching and bone dissolution that characterize these diseases differs significantly from the discrete holes and pits that characterize the South Pass material.

*Macroparasites in modern terrestrial turtles*.—Neotropical terrestrial turtles play host to a variety of parasites, primarily ixodid arachnids (i.e., ticks) (Ernst and Ernst, 1977). Although in many cases ticks occur on soft tissue in the area around the limbs and head, ticks are also common on the carapace and plastron (Fairchild, 1943; Ernst and Ernst, 1977). A behavior and ecological study of the brown wood turtle (*Rhinoclemys annulata*) on Barro Colorado Island in Panama revealed that all specimens analyzed possessed ticks (Mittermeier, 1971). An investigation of five species of the emydid genus *Callopsis* from Central and South America revealed similar levels of tick infestation (Ernst and Ernst, 1977). In the *Callopsis* study, it was noted that the ticks (four species of genus *Ambylomma*) preferentially attached to the shell (78.5%) as opposed to the skin (Ernst and Ernst, 1977). Although most of the ticks attached to the carapace, some were also observed attached to the plastron (Ernst and Ernst, 1977). The ticks on the shell occur most commonly, although not exclusively, at epidermal scute boundaries (Ernst and Ernst, 1977).

Most notably, in both *Callopsis* and *Rhinoclemys*, ticks occupy pits within the carapace and plastron (Schmidt, 1946; Mittermeier, 1971; Ernst and Ernst, 1977). These pits are roughly circular, up to 6 mm in diameter and up to 4 mm deep (Mittermeier, 1971; Ernst and Ernst, 1977). It is unknown how the ticks bore through the epidermal scute and into the dermal bone of the carapace and plastron; however, it is thought that this is accomplished using either a histolytic secretion or through the activity of a microorganism that attacks the shell at the site of the attachment wound (Mittermeier, 1971; Ernst and Ernst, 1977). We believe that the former hypothesis is most likely since the pits do not expand significantly beyond the size of the tick and, when removed from the pits, a milk white fluid was observed in the holes (Mittermeier, 1971).

To date, we are unaware of any confirmed reports of tick-generated pits or holes in temperate taxa; however, similar pits have been observed on the carapace of North American box

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turtles (*Terrapene carolina*) in Oklahoma and Missouri (Schmidt, 1946; Carpenter, 1956; Schwartz and Schwartz, 1974; Ernst and Ernst, 1977). These pits were observed solely on the carapace, primarily on, or immediately posterior of, the suture between the second and third costal carapace epidermal scutes (Carpenter, 1956). The size of the pits is variable, from slight indentations to deep holes in the dermal bone. The pits were observed on 56% (174 out of 375) box turtles examined (Carpenter, 1956). Although ticks were not observed in association with these holes, it seems likely that they were tick-generated. They are similar in size and position to those observed from the neotropics, and significantly, occur solely on terrestrial box turtles and are absent on aquatic taxa (*Chelydra serpentina*, *Kinosternon flavescens*, *Pseudemys scripta*) collected with the same area (Carpenter, 1956).

*Significance of the South Pass borings*.—Turtle fossils are exceptionally abundant in the Eocene Wasatch, Bridger and Green River formations in the Green River Basin, Wyoming. Representatives of many chelonian groups including baenids, dermatemydids, trionychids, carettocheylids, and emydids, occur throughout the basin. Several papers have discussed the taxonomy and taphonomy of these taxa (e.g. Gunnell and Bartels, 1994; Zonneveld et al., 2000; Brand et al., 2000); however, pre-mortem bone damage was not reported in most of these manuscripts. Hutchison and Frye (2001) summarized the various types of pre-mortem bone damage they had observed on Cenozoic turtle bone, which includes predation damage (commonly from crocodilians), and damage likely attributable to fungal or bacterial infections such as USD and SCUD. Several of the forms they illustrate are similar to the borings discussed herein. These borings occur on Cenozoic specimens from the Bighorn, Wind River, and Green River Basins but are not generally very abundant (Hutchison and Frye, 2001).

Over the past two decades, we have observed several thousand turtle specimens, collected from the primarily fluvial Wasatch and Bridger formations and primarily lacustrine and marginal lacustrine Green River Formation in the Bridger Basin (western Green River Basin), Big Island/Blue Rim area (central Green River Basin), and South Pass area (northeastern Green River Basin). *Karethraichnus* occurs on rare geoemydid specimens and, even less commonly, on dermatemydid and baenid specimens throughout the basin. *Thatchtelithichnus* has, to date, only been observed on emydid specimens within the study area. Only in the study area have we observed *Karethraichnus* to be common. Indeed, essentially every single cf. *Echmatemys* sp. specimen collected or observed at South Pass is characterized by these traces. The paucity of these pre-mortem bone borings in most areas and their comparative abundance in the study area indicates some local condition that facilitated the short-term, localized spread of the parasite taxon/taxa must have been present.

## Summary

Borings, emplaced during the lifetime of the host organism, are common on the plastron and carapace of geoemydid turtles from the lowermost beds of the early Eocene Cathedral Bluffs Tongue of the Wasatch Formation in the northeastern part of the Green River Basin near South Pass, Wyoming. Individual turtle shells are characterized by a single hole to over 100 borings.

These borings are herein separated into two new ichnogenera and four new ichnospecies. *Karethraichnus lakkos* are shallow, hemispherical pits with rounded, to flattened bases. They range in size from ~1 mm to >5 mm across. *Karethraichnus kulindros* are deep, non- penetrative traces with a cylindrical profile, an axis approximately perpendicular to slightly oblique to the substrate surface and with rounded to flattened, hemispherical termini. They are commonly deeper than they are wide. They range in width from 0.5 to 5.5 mm and in depth from 0.5 to 6.0 mm. *Karethraichnus fiale* penetrate completely through the turtle shell. They are cylindrical to bi-convex or flask-shaped in profile, with an axis that runs approximately perpendicular to the substrate surfaces. *Thatchtelithichnus holmani* consist of shallow, non-penetrative ring-shaped borings, with a central pedestal or platform. Commonly the central platform consists of unmodified bone, although examples of rounded pillars or pedestals also occur.

The position of the borings on the shells, and evidence of syn-emplacement healing of the borings in several of the turtles, indicates that these borings were emplacement by ectoparasites/mesoparasites while the animals were living. The identity of the parasite remains unknown. Ticks have been known to bore into the bones of modern terrestrial turtles leaving pits that are similar to *K. lakkos* described herein. Leeches have been observed attached to blood sinuses in aquatic turtle carapaces and plastrons. They are capable of bone decalcification, although the morphology of the bone damage has not been illustrated. Similarly, some vermiform parasites, such as spirorchid liver flukes, may cause lesions on the carapace and plastron of aquatic turtles. Regardless of parasite identity, the paucity of these bone borings in other areas, and their comparative abundance in the study area indicate some local condition that facilitated the short-term, localized spread of the parasite taxon/taxa.

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