Carnets Geol. 21 (17)

E-ISSN 1634-0744
DOI 10.2110/carnets.2021.2117

The ichnospecies *Linichnus bromleyi* on a Miocene baleen whale radius preserving multiple shark bite-shake traces suggests scavenging

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Abstract: An isolated Miocene baleen whale left radius was marked repeatedly by shark bite-shake traces. The radius probably derives from the Plum Point Member of the Calvert Formation, Calvert Cliffs, Calvert County, Maryland, U.S.A. At least three successive bite-shake traces marking the radius, made by multiple teeth, are attributed to the trace fossil *Linichnus bromleyi.* These bite-shake traces consisting of shallow, thin arching gouges on a radius, likely indicate scavenging rather than active predation. The most likely means of producing the bundle of *L. bromleyi* within each of the three sets of traces would be through repeated biting as the shark re-positioned the prey in its mouth or, perhaps, by a shark species with multiple functional teeth within their tooth row. If the bite traces were produced by a non-serrated tooth (as they appear to have been), then the most likely candidate would be *Carcharodon hastalis.*

Key-words:

- bite traces;
- trophic interaction;
- shark;
- Mysticeti;
- Miocene;
- Calvert Cliffs;
- Maryland

Citation: GODFREY S.J. & LOWRY A.J. (2021).- The ichnospecies *Linichnus bromleyi* on a Miocene baleen whale radius preserving multiple shark bite-shake traces suggests scavenging.- *Carnets Geol.*, Madrid, vol. 21, no. 17, p. 391-398.

Résumé : *L'ichnoespèce* Linichnus bromleyi *sur un radius de baleine à fanons miocène comportant de multiples traces de morsure- secouage de requin suggère son charognage.-* Un radius gauche isolé de baleine à fanons miocène a enregistré à plusieurs reprises des traces de morsure-secouage de requin. Le radius provient probablement du Plum Point Member de la Calvert Formation des Calvert Cliffs (Comté de Calvert, Maryland, États-Unis d'Amérique). Au moins trois ensembles de morsure-secouage successifs marquant ce radius et provenant de plusieurs dents sont attribués à la trace fossile *Linichnus bromleyi*. Ces traces de morsure-secouage se composant de gouges peu profondes, fines et arquées sur le radius indiquent vraisemblablement du charognage plutôt qu'une prédation active. L'origine la plus probable de ce regroupement de *L. bromleyi* au sein de chacun de ces trois ensembles de traces serait par le biais de morsures répétées alors que le requin repositionne sa proie dans sa gueule ou, autre possibilité, de morsures d'une espèce de requin dotée de plusieurs dents fonctionnelles au sein même de sa rangée dentaire. Si les traces de morsure sont produites par des dents non-crantées (comme cela semble être le cas), alors le candidat le plus probable serait *Carcharodon hastalis*.

Mots-clefs :

- traces de morsures ;
- interactions trophiques ;
- requin ;
- Mysticètes ;
- Miocène ;
- Calvert Cliffs;
- Maryland

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Published online in final form (pdf) on October 24, 2021
[Editor: Alberto COLLARETA; technical editor: Bruno R.C. GRANIER]

1. Introduction and setting

The Calvert Cliffs are one of the most fossiliferous regions on the east coast of the continental United States (Godfrey, 2018; Vogt *et al.*, 2018). During part of the Miocene epoch (from approximately 22-8 Ma), the Chesapeake area (*i.e.*, the Salisbury Embayment) was intermittently flooded by the Atlantic Ocean. The shallow marine sediments that now comprise the cliffs abound with marine fossils, including the tests of planktonic organisms, shelled invertebrates, shark teeth, teleosts, and marine mammals (Godfrey, 2018, and the references therein). In addition to innumerable body fossils, Calvert Cliffs preserve trace fossils including invertebrate burrows (*Thalassinoides*, *Gyrolithes* and *Ophiomorpha* Kidwell *et al.*, 2015), coprolites (Wetmore, 1943; Godfrey & Smith, 2010; Kent, 2018; Weems, 2018; Godfrey *et al.*, accepted), and shark bite traces, usually on cetacean bone (Godfrey, 2003; Godfrey *et al.*, 2018).

There are now many examples of shark bite traces on bone, either from active predation or scavenging (Deméré & Cerutti, 1982; Cigala Fulgosi, 1990; Purdy, 1996; Schwimmer *et al.*, 1997; Bianucci *et al.*, 2000, 2009, 2010, 2018; Purdy *et al.*, 2001; Hanks & Shimada, 2002; Renz, 2002; Godfrey, 2003; Corral *et al.*, 2004; Godfrey & Altman, 2005; Noriega *et al.*, 2007; Aguilera *et al.*, 2008; Diedrich, 2008; Cicimurri & Knight, 2009; Ehret *et al.*, 2009; Bianucci & Gingerich, 2011; Kallal *et al.*, 2012; Govender & Chinsamy, 2013; Takakuwa, 2014; Govender, 2015, 2021; Carrillo-Briceño *et al.*, 2016; Collareta *et al.*, 2017, 2019; Godfrey *et al.*, 2018, 2021; Kent, 2018; Cortés *et al.*, 2019; Mierzwiak & Godfrey, 2019; Muñiz *et al.*, 2020; Bosio *et al.*, 2021; Feichtinger *et al.*, 2021; Perez *et al.*, accepted). The authors of some of these case studies have been able to determine the species of shark that left the bite trace, either by finding shark teeth imbedded in the fossil bone, or by comparing the morphology of the tooth traces to shark teeth found in the same formation (Everhart *et al.*, 1995; Schwimmer *et al.*, 1997; Shimada, 1997; Shimada *et al.*, 2002; Corral *et al.*, 2004; Shimada & Everhart, 2004; Shimada & Hooks, 2004; Rothschild *et al.*, 2005; Noriega *et al.*, 2007; Bianucci *et al.*, 2009; Cicimurri & Knight, 2009; Ehret *et al.*, 2009; Govender & Chinsamy, 2013; Govender, 2015; Godfrey *et al.*, 2018, 2021; Kent, 2018; Cortés *et al.*, 2019; Feichtinger *et al.*, 2021).

Location and nature of bite traces can indicate the context of the interaction, as deep bites on bones near vital organs might be indicative of predation by a large shark (Kent, 2018). In contrast, small, thin tooth traces on appendages suggest scavenging, as smaller sharks will feed leisurely on a whale carcass at the water line (Dudley *et al.*, 2000; Govender & Chinsamy, 2013; Bisconti *et al.*, 2020).

Here we describe an isolated Miocene baleen whale radius from Calvert Cliffs that preserves signs of a unique trophic interaction with a single shark. The bite traces are exceptional in that they preserve three successive shark bite-shake behaviors that left arching traces on both the dorsal (external) and ventral (internal) sides of the bone. Although the species of the shark and whale are yet undetermined, these bite traces are superb examples of the recently named trace fossil *Linichnus bromleyi* (Muñiz *et al.*, 2020) and worthy of being described here.

2. Materials and methods

- CMM-V = the fossil vertebrate collection at the Calvert Marine Museum in Solomons, Maryland, U.S.A.
- USNM PAL, Department of Paleobiology collections, National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A.

To measure the depth and width of the shark tooth traces on the radius (CMM-V-3979), a silicone rubber mold was prepared of both upper and lower sides of the bone. Depth and width of the bite traces were measured from the positive mold using digital calipers.

In its natural state, CMM-V-3979 is very dark, so to improve contrast and visibility in Figure 1, the bone was lightly dusted with sublimed ammonium chloride, *i.e.*, a whitening technique described by Cooper (1935) and Feldman (1989). After the specimen was photographed with a Nikon CoolPix P510 camera under fluorescent light, the ammonium chloride was removed by holding CMM-V-3979 under running water (Shelburne & Thompson, 2016).

3. Systematic ichnology

***Linichnus* Jacobsen & Bromley, 2009**

***Linichnus bromleyi* Muñiz *et al.*, 2020**

Horizon and locality: CMM-V-3979, Figure 1, was collected by William (Douggie) Douglass, as float on the beach south of Parkers Creek along Calvert Cliffs in Calvert County, Maryland, U.S.A. When found, the specimen was devoid of entombing sediment. Even though it was not found *in situ*, there is no reason to think that it was not locally derived from the adjacent cliffs at Warrior's Rest Wildlife Sanctuary. At the point where CMM-V-3979 was found, Shattuck Zones 11-19 are exposed, which includes the upper portion of the Plum Point Member (Shattuck Zones 11-16A) of the Calvert Formation along with the Drumcliff (Shattuck Zones 16B-17), St. Leonard (Shattuck Zone 18), and Boston Cliff (Shattuck Zone 19) members of the Choptank Formation (Kidwell *et al.*, 2015). The sediments comprising this section of the cliffs range in age from approximately 16.5-12.5 Ma (Perez *et al.*, 2019, Fig. 1).

Figure 1: CMM-V-3979, a Miocene baleen whale radius preserving several specimens of the ichnospecies *Linichnus bromleyi.* **A**. Dorsal (external) view. **B**. Ventral (internal) view. Top of the image is proximal. Numbers 1-3 mark the locations where the shark teeth raked the surface of the radius. Numbers 1-1, 2-2, 3-3 correspond to bite traces made on the radius by teeth in opposing jaws. To improve contrast and highlight detail, CMM-V-3979 was whitened with sublimed ammonium chloride.

4. Description of the substrate and the trace fossils

From its size and gently curving shape, CMM-V-3979 can only be a mysticete radius (Fig. 1). CMM-V-3979 measures 275 mm in length and 68 mm at its widest point (*i.e.*, at approximately 53 mm along the shaft of the bone from its proximal articular surface). The maximum dorsoventral thickness of the bone is 45 mm through the proximal articular condyle. Both epiphyses are fully fused to the diaphysis and articular surfaces are well defined, indicating that the radius came from a mature individual. The proximal condyle is gently concave anteriorly. The distal condyle is bifurcated into two concave surfaces that articulated with the carpals. It is not known what damaged both the proximal and distal ends of the bone; if this was the result of shark-feeding damage or modern damage from the time the bone fell out of the cliffs until it was found. Furthermore, the anterior and posterior faces of the bone are also missing the outer smooth compact cortical bony layer.

Both dorsal (external) and ventral (internal) surfaces show three repeating patterns of bite-shake traces lying at nearly right angles to the curved longitudinal axis of the bone (Fig. 1). The bite traces reach a maximum depth of 1.47 mm (although most are less than 1 mm deep) and a maximum width of 1.33 mm (although these measurements did not coincide on the same trace). No serration marks were observed along the edges of the gouges, but because only the tips of the teeth cut into the bone, it is not surprising that serration traces are absent (if the originating teeth were serrated at all). Furthermore, the cut bone is coarsely textured, further obscuring any possibility of preserving serration traces.

5. Remarks

A. Identity of the whale

There are a number of basal thalassotherians (Mysticeti) known from the Calvert and Choptank formations along Calvert Cliffs for which their radius is also known. The radius of the Calvert Formation mysticete *Pelocetus calvertensis* (USNM PAL 11976) is 397 mm long (Kellogg, 1965), 122 mm longer than CMM-V-3979. The radius in "*Eschrichtius*" *pusillus* was even longer than in *Pelocetus* (Kellogg, 1968). The radius of the Choptank Formation mysticete *Thinocetus arthritis* (USNM PAL 23794) is 385 mm long (Kellogg, 1969), 110 mm longer than CMM-V-3979, and it is not even from a fully mature individual. The best match is an isolated radius (USNM PAL 23019, Kellogg, 1968, Fig. 73), questionably assigned to the Calvert Formation mysticete, *Diorocetus hiatus*, which is exactly the same length as the radius of CMM-V-3979. Although they are not a perfect match morphologically, they are very close. Both the type specimen of *Diorocetus* (USNM PAL 16738) and CMM-V-3979 were found just south of Parkers Creek, along Calvert Cliffs.

B. Identity of the shark

From the sharks that are known from along Calvert Cliffs (Visaggi & Godfrey, 2010; Kent, 2018), we think that the bite traces on CMM-V-3979 could have been made by any one of the following sharks (listed here alphabetically: *Alopias grandis*, *Alopias palatasi*, *Carcharhinus* spp., *Carcharodon hastalis*, *Galeocerdo aduncus*, *Hemipristis serra*, a juvenile *Otodus megalodon*, *Physogaleus contortus*, or *Sphyrna laevissima.* The most likely means of producing the bundle of *L. bromleyi* specimens within each of the three sets of traces would be through repeated biting as the shark re-positioned the prey in its mouth or, perhaps, by a shark species with multiple functional teeth within their tooth row. A similar interpretation in a different situation was discussed by Bianucci *et al.* (2018, Fig. 13B-E & G). If the bite traces were produced by a non-serrated tooth (as they appear to have been), then the most likely candidate would be *Carcharodon hastalis* (V. Perez, pers. comm. July 26, 2021).

C. Scavenging the whale

When a whale dies, it inverts and floats at the surface of the water due to the buildup of abdominal gases from decomposition. Scavenging sharks habitually feed at the water line, occasionally lifting their heads out of the water (Dudley *et al.*, 2000; Tucker *et al.*, 2019). The flippers of the whale lie at the water line and extend outward from the body, providing an easy target for scavengers. Indeed, of previous literature documenting shark-bitten cetacean flippers, all posit scavenging as the context of feeding (Noriega *et al.*, 2007; Cicimurri & Knight, 2009; Govender & Chinsamy, 2013). The shark tooth markings on Pliocene balaenopterid flippers bones from Panama described by Cortés *et al.* (2019, Fig. 3) are here attributed to *Linichnus bromleyi.*

From the similarity of the three bite traces on the dorsal side of the radius, we think that they were made by the same teeth during successive bite-shake events. Teeth in the same position in different files (rows of teeth) of the shark's mouth marked both the upper and lower surface of the radius. The shark would have clenched down on the flipper firmly and then shaken its head vigorously in an attempt to cut through the bone (unsuccessfully) or to simply remove flesh.

The existence of aligned bite-shake traces on both the upper and lower surface of the radius is due to the shark teeth marking the bone with upper and lower teeth simultaneously. It is not known which teeth in the dental arcade created the bite traces. Neither do we know if the whale was inverted during the scavenging event.

Furthermore, we do not know the order in which the three bite traces were made, distal to proximal - proximal to distal - or some other order. We assume distal to proximal because the most distal bite (number 1 in Fig. 1) would likely have resulted in the removal of some flesh covering the flipper. Following that, the shark might have re-bitten the radius at site 2, shaken its head and successfully removed more flesh before proceeding to biting and head shaking at site 3. Notice that for site number three, there are fewer bite traces on the ventral surface of the radius. Presumably, those teeth only just barely penetrated the soft tissue to contact the bone. Notice also that those bite traces are not aligned as in bite traces 1 and 2. Perhaps those shallow grooves on the ventral (internal) surface of the radius represent markings made during another head-thrashing event.

Figure 2: One possible view of the origin of the bitten Miocene whale radius. The whale could also have been bloated and floating belly up at the time the shark bite traces were made. Furthermore, the distal limb elements below the radius and ulna may already have been missing and/or eaten. Original artwork by Tim SCHEIRER and Clarence (Shoe) SHUMAKER. © Calvert Marine Museum.

There is no evidence of healing (*i.e.*, no bony callus formations as a result of the originating trauma). The whale (if it was alive at the time of the trophic encounter, which is doubtful) did not survive the biting by the shark.

Amongst extant sharks, head thrashing is employed when removing chunks from a large food source (CURTIS *et al.*, 2006). Apparently, tiger sharks use a method of head movement much like head shaking during feeding bouts; however, movement is a slower side-to-side motion (CURTIS *et al.*, 2006). Saw-biting is the term coined by LEA *et al.* (2018) to describe this behavior. It seems to be specific to tiger sharks whose serrated teeth have evolved to saw through prey too large to swallow whole (FRAZZETTA, 1988; CURTIS *et al.*, 2006).

6. Concluding remarks

Linichnus bromleyi describes vertebrate tooth bite traces raking the surface of biogenic material, in straight lines or arching curves. Head shaking/thrashing, or saw-biting behavior would account for the formation of this kind of trace fossil. *Linichnus bromleyi* can occur either as a result of exploration, predation, or scavenging. However, in CMM-V-3979, the shallow thin arching gouges on the radius indicate scavenging rather than active predation.

Acknowledgements

We would like to thank William (Douggie) DOUGLASS for having collected the radius described herein, and for having donated it to the Calvert Marine Museum. CMM artists Tim SCHEIRER and Clarence (Shoe) SHUMAKER very skillfully created Figure 2. CMM Paleontology Collections Manager, John R. NANCE is also gratefully acknowledged for encouraging the study of specimens under his care. Victor PEREZ (CMM) graciously reviewed an early version of this paper. We are very grateful for the constructive reviews by Bretton W. KENT and one anonymous reviewer. Alberto COLLARETA edited this paper for the journal, many thanks! This research was funded in part by the citizens of Calvert County Maryland, the County Board of Calvert County Commissioners, and the Clarissa and Lincoln DRYDEN Endowment for paleontology at the Calvert Marine Museum.

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