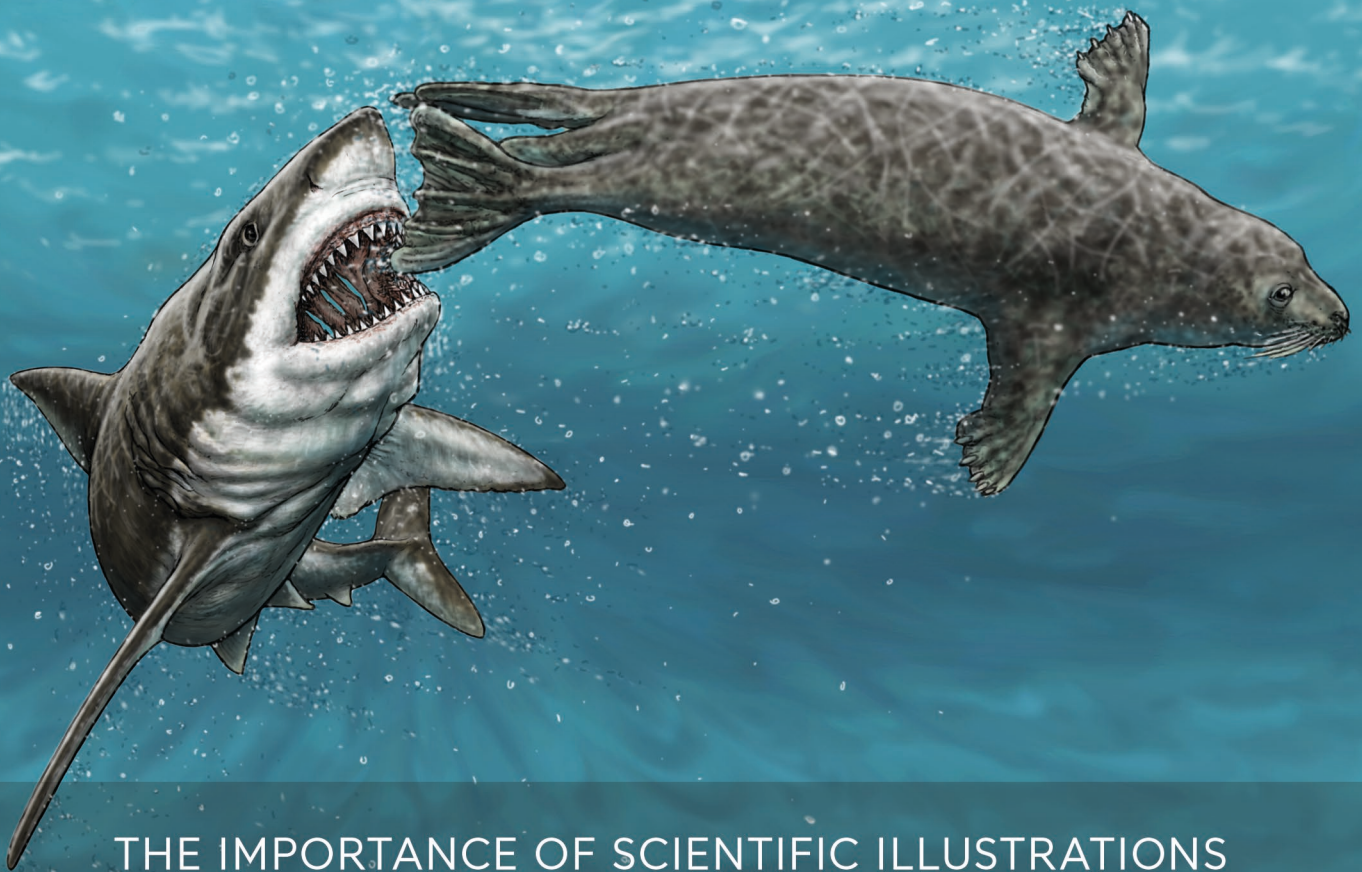


## First report in the fossil record of a shark tooth embedded in a pinniped bone

Stephen J. GODFREY, Paul MURDOCH, Leonard DEWAELE,  
Victor J. PEREZ & Clarence SCHUMAKER



## THE IMPORTANCE OF SCIENTIFIC ILLUSTRATIONS IN PALEONTOLOGY: A TRIBUTE TO DIANE SCOTT

Edited by Michel LAURIN, Sean P. MODESTO & Robert R. REISZ

DIRECTEURS DE LA PUBLICATION / PUBLICATION DIRECTORS :

Gilles Bloch, Président du Muséum national d'Histoire naturelle  
Étienne Ghys, Secrétaire perpétuel de l'Académie des sciences

RÉDACTEURS EN CHEF / EDITORS-IN-CHIEF (\*, took charge of the editorial process of the article/a pris en charge le suivi éditorial de l'article) :

**Michel Laurin\*** (CNRS), Philippe Taquet (Académie des sciences)

ASSISTANTE DE RÉDACTION / ASSISTANT EDITOR : Adenise Lopes (Académie des sciences; cr-palevol@academie-sciences.fr)

MISE EN PAGE / PAGE LAYOUT : Audrina Neveu (Muséum national d'Histoire naturelle; audrina.neveu@mnhn.fr)

RÉVISIONS LINGUISTIQUES DES TEXTES ANGLAIS / ENGLISH LANGUAGE REVISIONS : Kevin Padian (University of California at Berkeley)

RÉDACTEURS ASSOCIÉS / ASSOCIATE EDITORS :

Micropaléontologie/Micropalaeontology

Lorenzo Consorti (Institute of Marine Sciences, Italian National Research Council, Trieste)

Paléobotanique/Palaeobotany

Cyrille Prestianni (Royal Belgian Institute of Natural Sciences, Brussels)

Métazoaires/Metazoa

Annalisa Ferretti (Università di Modena e Reggio Emilia, Modena)

Paléoichthyologie/Palaeoichthyology

Philippe Janvier (Muséum national d'Histoire naturelle, Académie des sciences, Paris)

Amniotes du Mésozoïque/Mesozoic amniotes

Hans-Dieter Sues (Smithsonian National Museum of Natural History, Washington)

Tortues/Turtles

Walter Joyce (Universität Freiburg, Switzerland)

Lépidosauromorphes/Lepidosauromorphs

Hussam Zaher (Universidade de São Paulo)

Oiseaux/Birds

Eric Buffetaut (CNRS, École Normale Supérieure, Paris)

Paléomammalogie (mammifères de moyenne et grande taille)/Palaeomammalogy (large and mid-sized mammals)

Lorenzo Rook (Università degli Studi di Firenze, Firenze)

Paléomammalogie (petits mammifères sauf Euarchontoglires)/Palaeomammalogy (small mammals except for Euarchontoglires)

Robert Asher (Cambridge University, Cambridge)

Paléomammalogie (Euarchontoglires)/Palaeomammalogy (Euarchontoglires)

K. Christopher Beard (University of Kansas, Lawrence)

Paléoanthropologie/Palaeoanthropology

Aurélien Mounier (CNRS/Muséum national d'Histoire naturelle, Paris)

Archéologie préhistorique (Paléolithique et Mésolithique)/Prehistoric archaeology (Palaeolithic and Mesolithic)

Nicolas Teyssandier (CNRS/Université de Toulouse, Toulouse)

Archéologie préhistorique (Néolithique et âge du bronze)/Prehistoric archaeology (Neolithic and Bronze Age)

Marc Vander Linden (Bournemouth University, Bournemouth)

RÉFÉRÉS / REVIEWERS : <https://sciencepress.mnhn.fr/fr/periodiques/comptes-rendus-palevol/referes-du-journal>

COUVERTURE / COVER :

Illustration showing one possible way in which the tip of a Pliocene great white shark tooth became embedded in a seal heel bone. Credits: Clarence Schumaker.

*Comptes Rendus Palevol* est indexé dans / *Comptes Rendus Palevol* is indexed by:

- Cambridge Scientific Abstracts
- Current Contents® Physical
- Chemical, and Earth Sciences®
- ISI Alerting Services®
- Geoabstracts, Geobase, Georef, Inspec, Pascal
- Science Citation Index®, Science Citation Index Expanded®
- Scopus®.

Les articles ainsi que les nouveautés nomenclaturales publiés dans *Comptes Rendus Palevol* sont référencés par /  
*Articles and nomenclatural novelties published in Comptes Rendus Palevol* are registered on:

- ZooBank® (<http://zoobank.org>)

*Comptes Rendus Palevol* est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris et l'Académie des sciences, Paris  
*Comptes Rendus Palevol* is a fast track journal published by the Museum Science Press, Paris and the Académie des sciences, Paris

Les Publications scientifiques du Muséum publient aussi / The Museum Science Press also publish:

*Adansonia*, *Geodiversitas*, *Zoosystema*, *Anthropozoologica*, *European Journal of Taxonomy*, *Naturae*, *Cryptogamie* sous-sections *Algologie*, *Bryologie*, *Mycologie*.

L'Académie des sciences publie aussi / The Académie des sciences also publishes:

*Comptes Rendus Mathématique*, *Comptes Rendus Physique*, *Comptes Rendus Mécanique*, *Comptes Rendus Chimie*, *Comptes Rendus Géoscience*, *Comptes Rendus Biologies*.

Diffusion – Publications scientifiques Muséum national d'Histoire naturelle

CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)

Tél. : 33 (0)1 40 79 48 05 / Fax: 33 (0)1 40 79 38 40

diff.pub@mnhn.fr / <https://sciencepress.mnhn.fr>

Académie des sciences, Institut de France, 23 quai de Conti, 75006 Paris.

© This article is licensed under the Creative Commons Attribution 4.0 International License (<https://creativecommons.org/licenses/by/4.0/>)  
ISSN (imprimé / print) : 1631-0683/ ISSN (électronique / electronic) : 1777-571X

# First report in the fossil record of a shark tooth embedded in a pinniped bone

**Stephen J. GODFREY**

Department of Paleontology, Calvert Marine Museum,  
P.O. Box 97, Solomons, Maryland 20688 (United States)  
and Research Associate, Department of Paleobiology, National Museum  
of Natural History, Smithsonian Institution, 10th Street & Constitution Avenue NW,  
Washington, DC 20013-7012 (United States)  
stephen.godfrey@calvertcountymd.gov (corresponding author)

**Paul MURDOCH**

6080 Fir Road, St. Leonard, Maryland 20685 (United States)  
paul.r.murdoch@gmail.com

**Leonard DEWAELE**

Chef de travaux Directorate of Earth and History of Life, Royal Belgian Institute  
of Natural Sciences, 29 rue Vautier, Brussels 1000 (Belgium)  
and Senior researcher, FunMorph Lab, Department of Biology, Antwerp University,  
Campus Drie Eiken, 1 Universiteitsplein, Antwerp 2610 (Belgium)  
and Research affiliate, EDDy Lab, Department of Geology, Liège University,  
Quartier Agora, 14 Allée du six Août, Liège 4000 (Belgium)  
ldewaele@naturalsciences.be

**Victor J. PEREZ**

Visiting Assistant Professor, Environmental Studies Department,  
St. Mary's College of Maryland, St. Mary's City, 47645 College Drive,  
St. Mary's City, Maryland 20686-3001 (United States)  
vjperez@smcm.edu

**Clarence SCHUMAKER**

Daybreak Studios 4022 15th Street, Chesapeake Beach, Maryland 20732 (United States)  
inquiries@daybreakstudios.com

Submitted on 20 December 2022 | Accepted on 25 May 2023 | Published on 15 February 2024

---

urn:lsid:zoobank.org:pub:7A61764A-8EFA-4FBA-A1D8-C024E92193B6

---

Godfrey S. J., Murdoch P., Dewaele L., Perez V. J. & Schumaker C. 2024. — First report in the fossil record of a shark tooth embedded in a pinniped bone, *in* Laurin M., Modesto S. P. & Reisz R. R. (eds), The importance of scientific illustrations in paleontology: a tribute to Diane Scott. *Comptes Rendus Palevol* 23 (8): 107–118. <https://doi.org/10.5852/cr-palevol2024v23a8>

## ABSTRACT

There are now many examples in the fossil record of shark bite marks preserved on biogenic materials including coprolites, ammonoids, sea star ossicles, an echinoid, and bone and calcified cartilage. These exceptional fossils document evidence of exploratory behavior, active predation, and/or scavenging.

**KEY WORDS**  
Seal calcaneum,  
white shark tooth,  
trophic interaction,  
bite marks,  
morderolite,  
Neogene.

However, only a small subset report on the presence of shark teeth embedded in fossilized bone or cartilage. Although a few shark tooth-marked seal bones are known from the fossil record, no direct evidence of predation or scavenging in the form of a shark tooth embedded in a fossil seal bone has yet been documented. Herein, we describe the first shark tooth embedded in a seal (*Phocidae* Gray, 1821) bone, a calcaneum (CMM-V-6964), that was surface collected in Mosaic's South Fort Meade Mine, Hardee County, Fort Meade, Florida, United States. The isolated bone originated from within the Bone Valley Member of the Peace River Formation (Hawthorn Group). The partial tooth is identified as having come from an Early Pliocene great white shark, *Carcharodon carcharias* (Linnaeus, 1758). This discovery also represents the first *C. carcharias* tooth ever found embedded in a fossil bone. The embedded tooth may have come about as a result of active predation or scavenging. The extant macropredatory sharks, *Carcharodon carcharias* (great white shark), *Notorynchus cepedianus* (Péron, 1807) (sevendill shark), *Somniosus microcephalus* (Bloch & Schneider, 1801) (the Greenland shark), and *Somniosus antarcticus* Whitley, 1939 (sleeper shark), are known to actively prey upon seals (*Pinnipedia* Illiger, 1811). If this peculiar fossil association resulted from active predation, the seal did not survive the encounter because there is no evidence of healing in the area around the embedded shark tooth.

## RÉSUMÉ

*Premier rapport dans le registre fossile d'une dent de requin enchâssée dans un os de Pinnipède.*

Il existe aujourd'hui de nombreux signalements fossiles portant des marques de morsures de requins préservées sur des matériaux biogènes, notamment des coprolithes, des ammonioïdes, des osselets d'étoiles de mer, un échinoïde, des os et du cartilage calcifié. Ces fossiles exceptionnels témoignent d'un comportement explorateur, d'une prédation active et/ou d'une activité de charognage. Cependant, seul un petit sous-ensemble rapporte la présence de dents de requins incrustées dans de l'os ou du cartilage fossilisé. Bien que quelques os de phoques marqués par des dents de requins soient connus dans les archives fossiles, aucune preuve directe de prédation ou de charognage sous la forme d'une dent de requin incrustée dans un os de phoque fossile n'a encore été documentée. Nous décrivons ici la première dent de requin incrustée dans un os de phoque (*Phocidae* Gray, 1821), un calcanéum (CMM-V-6964), qui a été prélevé en surface dans la mine de Mosaic South Fort Meade, dans le comté de Hardee, à Fort Meade, en Floride, aux États-Unis. La dent partielle a été identifiée comme provenant d'un grand requin blanc du Pliocène précoce, *Carcharodon carcharias* (Linnaeus, 1758). Cette découverte représente également la première dent de *C. carcharias* jamais trouvée intégrée dans un os fossile. La dent incrustée pourrait être le résultat d'une prédation active ou d'une fouille. Les requins macropredateurs existants, *Carcharodon carcharias* (Linnaeus, 1758) (grand requin blanc), *Notorynchus cepedianus* (Péron, 1807) (requin septgill), *Somniosus microcephalus* (Bloch & Schneider, 1801) (requin du Groenland) et *Somniosus antarcticus* Whitley, 1939 (requin dormeur), sont connus pour s'attaquer activement aux phoques (*Pinnipedia* Illiger, 1811). Si cette association fossile particulière résulte d'une prédation active, le phoque n'a pas survécu à la rencontre car il n'y a aucun signe de guérison dans la zone entourant la dent de requin incrustée.

**MOTS CLÉS**  
Calcanéum de phoque,  
dent de requin blanc,  
interaction trophique,  
morsures,  
morderolite,  
Néogène.

## INTRODUCTION

There are now many examples in the fossil record of shark bite marks preserved on biogenic materials (Hunt & Lucas 2021: table A.3). These morderolites (Godfrey & Collareta 2022) document evidence of successful or failed predation, scavenging and/or exploratory behavior. However, of these numerous examples that evidence shark trophic interaction, only a subset report on the presence of shark teeth embedded in cartilage or bone (Williston 1898: 214; Everhart *et al.* 1995; Shimada 1997; Schwimmer *et al.* 1997; Klimley *et al.* 2001; Everhart 2004; Shimada & Everhart 2004; Shimada & Hooks 2004; Rothschild *et al.* 2005; Shimada & Fielitz 2006; Lambert & Gigase 2007; Aguilera *et al.* 2008; Cicimurri & Knight 2009; Ehret *et al.* 2009; Govender & Chinsamy 2013; Perez *et al.* 2021; Collareta *et al.* 2022). The occurrence of teeth embed-

ded in prey substrate offers unequivocal evidence of trophic interactions and, generally, allow one to more confidently identify the predator than bite marks alone.

Extant great white sharks (*Carcharodon carcharias* (Linnaeus, 1758)), sevengill sharks (*Notorynchus cepedianus* (Péron, 1807)), and Greenland and sleeper sharks (*Somniosus microcephalus* (Bloch & Schneider, 1801) and *S. antarcticus* Whitley, 1939) are known to actively prey upon seals, although there is strategic diversity in the ways in which they go about it (Ebert 1991: fig. 3; Klimley *et al.* 1996; Martin *et al.* 2005; Hammerschlag *et al.* 2006; Hoff & Morrice 2008; Laroche *et al.* 2008; Lucas & Natanson 2010; Martin & Hammerschlag 2012; Watanabea *et al.* 2012; Fallows *et al.* 2013). Sluggish-slow swimming Greenland and sleeper sharks simply latch onto sleeping seals (Hoff & Morrice 2008; Watanabea *et al.* 2012), whereas great white sharks stalk and strike their phocid prey

from below or behind at speed (Martin & Hammerschlag 2012). Sevengill sharks employ a range of predatory strategies including burst speed, ambush, stealth, and social facilitation (Ebert 1991). While a few shark-bitten pinniped bones are known from the fossil record (Bigelow 1994; Govender & Chinsamy 2013; Boessenecker *et al.* 2014; Collareta *et al.* 2017; Govender 2021), no direct evidence of predation or scavenging in the form of a shark tooth embedded in a fossil seal bone has yet been reported. Herein, we describe the first shark tooth embedded in a seal (Phocidae Gray, 1821) bone, a calcaneum. Furthermore, the partial tooth is identified as that of a great white shark, *Carcharodon carcharias*, the first report in the fossil record of a tooth from this species of shark embedded in bone. Ames & Morejohn (1980) reported on the presence of an extant white shark tooth embedded in the skull of the sea otter, *Enhydra lutris* (Linnaeus, 1758), and Ehret *et al.* (2009, 2012) described a *Carcharodon hubbelli* Ehret, MacFadden, Jones, DeVries, Foster & Salas-Gismondi, 2012 partial tooth crown embedded in a mysticete mandible (MUSM 1470) from the Pisco Formation of Peru. Fallows *et al.* (2013) also reported the presence of two modern white shark teeth in the head of another white shark, the result of an apparently unintentional bite during a concerted whale carcass scavenging event. The current study provides a description of this exceptional direct evidence of a marine trophic interaction in the fossil record, with comments on its paleoecological and biomechanical significance.

#### ABBREVIATIONS

|        |                                                                                  |
|--------|----------------------------------------------------------------------------------|
| CMM-V- | Calvert Marine Museum vertebrate paleontology collection, Solomons, Maryland;    |
| Ma     | mega annum;                                                                      |
| MUSM   | Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima;  |
| NALMA  | North American land mammal ages;                                                 |
| UF-VP- | University of Florida, vertebrate paleontology collection, Gainesville, Florida. |

#### MATERIAL AND METHODS

Herein, we describe a single seal calcaneum (CMM-V-6964), bearing the partial crown of an embedded shark tooth and possible shark bite marks. The specimen is housed in the Calvert Marine Museum (CMM).

The specimen was photographed on black velvet under fluorescent light with a Nikon Coolpix P510 camera. The individual images were edited in Adobe Photoshop® and Figures 1-3 were assembled in Adobe Illustrator®.

#### GEOLOGIC SETTING

The shark-bitten seal calcaneum, CMM-V-6964 (Fig. 1), was collected in April 2008 by author P. M. in Hardee County, Fort Meade, Florida, United States, at Mosaic's South Fort Meade Mine, presumably from the Bone Valley Member of the Peace River Formation (Hawthorn Group). CMM-V-6964 was not collected *in situ*, but rather from a spoil pile within the mine at approximately 27°29'58.52"N, 82°06'05.93"W. Consequently, the precise stratigraphic provenance within the

mine is not known. The Bone Valley Member was formerly the Bone Valley Formation of Matson & Clapp (1909), but was redefined as a member of the Peace River Formation by Scott (1988) due to the limited areal extent of the unit. The Peace River Formation comprises two subunits (both within the Bone Valley Member), an Upper Miocene unit (*c.* 11-8.5 Ma) and a Lower Pliocene unit (*c.* 5.2-4.3 Ma) based on biostratigraphy, magnetostratigraphy, and strontium isotopes (Guertin 1998; Guertin *et al.* 1999, 2000). The vertebrate assemblage within the younger Pliocene unit has been described as the Bone Valley Fauna or the Palmetto Fauna and is assigned to the Hemphillian North American Land Mammal Age (Sellards 1916; Simpson 1930; MacFadden & Webb 1982; Webb & Crissinger 1983; Hulbert 2001; Webb *et al.* 2008). There are two specimens of *Carcharodon carcharias* known from the Pliocene Palmetto Fauna that are cataloged in the Florida Museum vertebrate paleontology collection (UF-VP-17916 and UF-VP-93661). There are no known definitive occurrences of *C. carcharias* from Florida prior to the Hemphillian (Perez 2022a, b); therefore, the seal calcaneum and embedded tooth most likely originated from the Lower Pliocene unit (Hemphillian NALMA/Zanclean Stage) of the Bone Valley Member within the Peace River Formation.

#### DESCRIPTION

CMM-V-6964 is an almost complete, isolated right calcaneum with a maximum length of 78 mm (Fig. 1). Major anatomical features including the calcaneal tubercle, the cuboid articular facet, the sulcus for *m. peroneus longus* and the troclear sulcus confirm its identity as a calcaneum. The taxonomic identity of the calcaneum is discussed below.

Only a small portion of the tip of the shark tooth remains embedded in the calcaneum. The crown is embedded in the lateral surface of the bone immediately distal to the sulcus for *m. peroneus longus* (Fig. 1B). The broken enameloid edge of the tooth is fractured and ragged (Fig. 2), measuring 6.12 mm wide. The crown is infilled with osteodentine (Fig. 2B), with no evidence of a pulp cavity. Six serrations are visible along the cutting edge above the point where the tip of the tooth is embedded in the bone. The apex of each serration is very nearly evenly rounded and differing only slightly in size (Fig. 2B). The identification of this tooth as belonging to a great white shark is discussed below.

In addition to the anatomical features, and the embedded shark tooth shown in Figure 1, the outer surface of the calcaneum also preserves at least seven small roughly circular breaks/shallow depressions in the compact (i.e., cortical) bone (some of which are indicated by the black arrows in Figure 1).

#### DISCUSSION

##### IDENTITY OF THE PREY

A distinguishing characteristic of the calcaneum of Phocidae is the proportionally short medial and lateral tubercles (Fig. 1). Among Carnivora, this characteristic is shared only with *Allodesmus* Kellogg, 1922 and Odobenidae Allen, 1880

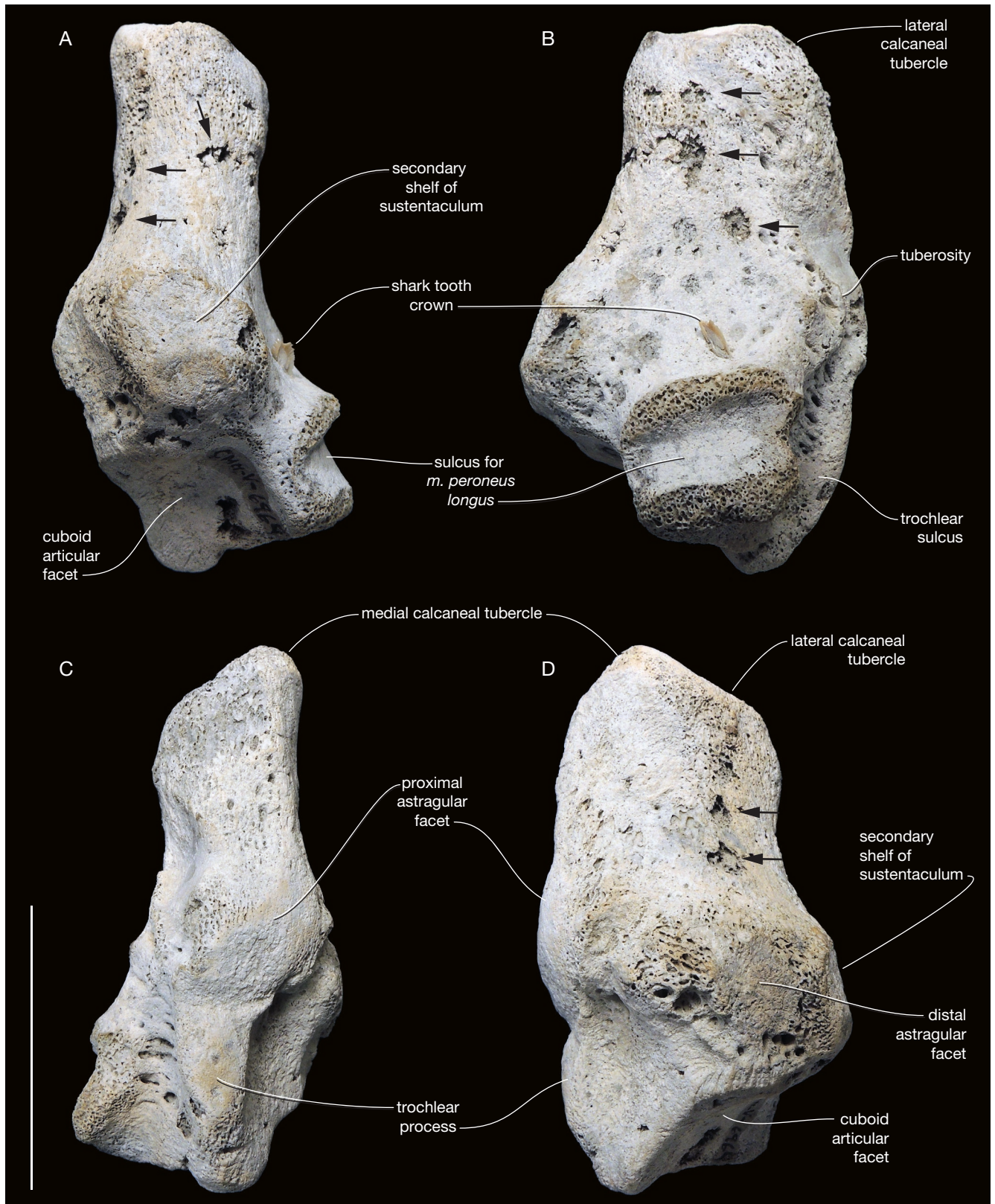


FIG. 1. — CMM-V-6964, phocid right calcaneum found in the Bone Valley Member of the Peace River Formation (Hawthorn Group), Mosaic South Fort Meade Mine (Hardee County, Fort Meade, Florida, United States): **A**, ventral view; **B**, lateral view; **C**, dorsal view; **D**, medial view. The embedded *Carcharodon carcharias* (Linnaeus, 1758) partial tooth is visible in **A** and **B**. The **black arrows** point out some of the possible biogenic traces. Scale bar: 50 mm.

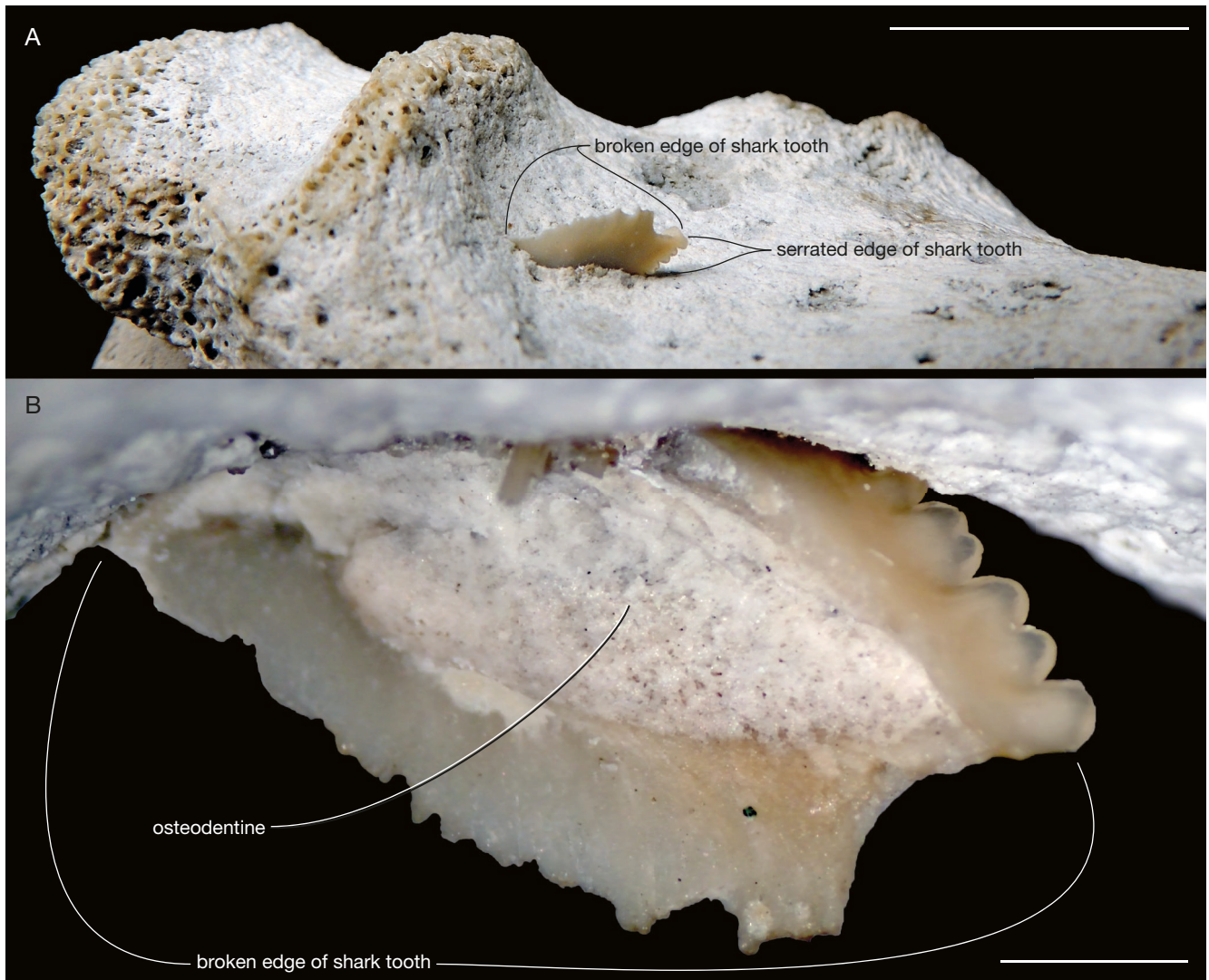


FIG. 2. — CMM-V-6964: **A**, phocid right calcaneum looking proximally along the lateral surface of the bone showing the sulcus for *m. peroneus longus* in the left half of the image with, in the foreground, a view of the embedded *Carcharodon carcharias* (Linnaeus, 1758) partial tooth showing both its broken and serrated edges; **B**, an enlarged view of the shark tooth in **A** looking distally, i.e., 180° from the side shown in **A**. Notice that the interior of the tooth comprises osteodentine. Scale bars: **A**, 10 mm; **B**, 1 mm.

(Berta & Wyss 1994; and references therein). However, e.g. the medial calcaneal tubercle is only weakly developed in the present specimen (contra *Allodesmus* and Odobenidae) (Repenning & Tedford 1977; Tonomori *et al.* 2018). In addition, whereas Phocidae have widely been reported from the North Atlantic during the Neogene, to the best of our knowledge, *Allodesmus* lived exclusively in the North Pacific Ocean during the Early and Middle Miocene (Berta *et al.* 2018; and references therein). Furthermore, Late Miocene and geologically younger odobenids from the North Atlantic are too large for this calcaneum to have come from one of them. Consequently, CMM-V-6469 is positively identified as phocid in origin.

The height/length ratio of the calcaneum is approximately 48 mm/78 mm = 0.615. This groups with ratios observed among extant Lobodontini Gray, 1869 (0.583-0.633; notice that this ratio refers to extant Lobodontini), but exceeds the

ratios observed in other extant and extinct Monachinae Gray, 1869 (0.509-0.541; the latter referring to *Mirounga* Gray, 1827 and Monachini Trouessart, 1897) and certainly Phocinae (0.444-0.500), in which the calcaneum is comparatively longer and less high (Muizon 1981: table 8). Furthermore, the sulcus for *m. peroneus longus* and the trochlear sulcus are well outlined in CMM-V-6469, a feature shared among Monachinae. Consequently, CMM-V-6469 is tentatively identified as a calcaneum from a monachine phocid.

Moreover, with a total length of 78 mm, the calcaneum is large for a monachine. Comparing it to the measurements presented by de Muizon (1981), this calcaneum is notably smaller than the exceptionally large elephant seals of the genus *Mirounga*, but slightly larger than the length of the calcaneum of the leopard seal *Hydrurga leptonyx* (de Blainville, 1820) as presented by de Muizon (1981): 76 mm. With a body length between 2.9 and 3.6 m, *H. leptonyx*

is considered the largest extant phocid after the elephant seals *Mirounga angustirostris* (Gill, 1866) and *Mirounga leonina* (Linnaeus, 1758). Thus, with a length exceeding that of the calcaneum of the extant leopard seal *Hydrurga leptonyx*, CMM-V-6469 likely originated from a large seal, apparently exceeding 3 m in total body length.

Koretsky & Ray (2008) identified *Platyphoca vulgaris* (Van Beneden, 1876), *Phocanella pumila* (Van Beneden, 1876), *Gryphoca similis* (Van Beneden, 1876), *Callophoca obscura* (Van Beneden, 1876), *Pliophoca etrusca* Tavani, 1941 and *Homiphoca capensis* (Hendey & Repenning, 1972) from the Pliocene of the Atlantic Coastal Plain. More recently, Rahmat *et al.* (2017, 2021), Dewaele *et al.* (2018), and Rule *et al.* (2020) described new species of Monachinae from this area: *Auroraphoca atlantica* Dewaele, Peredo, Meyvisch & Louwye, 2018, *Magnotherium johnsii* Rahmat, Hamed, Godfrey, Nance & Koretsky, 2021, *Sarcodectes magnus* Rule, Adams, Rovinsky, Hocking, Evans & Fitzgerald, 2020, *Terranectes magnus* Rahmat, Koretsky, Osborne & Alford, 2017, *Terranectes parvus* Rahmat, Koretsky, Osborne & Alford, 2017, and *Virginiaphoca magurai* Dewaele, Peredo, Meyvisch & Louwye, 2018. However, considering that most extinct Monachinae are known from isolated single bones, no calcanea can unequivocally be assigned to any of these, pending the discovery of more complete specimens including associated and articulated bones. Based on the size of the type specimens alone, *S. magnus* is the most likely candidate, estimated by Rule *et al.* (2020) to have had a body length of 2.83 m. Unfortunately, the incompleteness of the fossil record for these species makes identifying the most likely candidate uncertain.

CMM-V-6964 compares favorably to two calcanea (USNM PAL 205850 and 529247) from the Pliocene, Yorktown Formation, both found in the Aurora Phosphate Mine, Aurora, North Carolina, United States (Fig. 3). USNM PAL 205850 (Fig. 3A, D) is a right calcaneum from a partial but associated pes that Koretsky & Ray (2008: fig. 38) attributed to *Callophoca obscura*. USNM PAL 529247 (Fig. 3C, F) is a taxonomically unassigned and isolated left calcaneum (reflected in Figure 3) that is larger, more complete and better preserved than CMM-V-6964. Other than differing in size (one smaller and the other larger), both of the Yorktown Formation phocid calcanea are virtually identical to that of CMM-V-6964 (Fig. 3B, E). Despite their overall morphological similarity, an isolated calcaneum hardly seems to be sufficient to confirm the identity of a phocid to the specific level. Furthermore, given the historical and taxonomic uncertainties surrounding *Callophoca obscura* (see Rule *et al.* 2020), we do not think it prudent to assign CMM-V-6964 to that binomen, even though they may be conspecific (whatever USNM PAL 205850 turns out to be, *Callophoca obscura* or otherwise). Therefore, we will content ourselves with identifying the great white shark partial tooth-embedded seal calcaneum as monachine phocid in origin.

#### IDENTITY OF THE PREDATOR

A total of 29 chondrichthyan genera, belonging to eight different orders, have been recognized from the Bone Valley Member of the Peace River Formation (Perez 2022a, b). Among these

genera, only nine include taxa with serrated teeth. Assuming the tooth is broken close to the crown tip, the symmetry and size of the tooth fragment (6.12 mm wide) embedded in CMM-V-6964 further reduces the potential contenders to three possible taxa: *Carcharodon carcharias*, *Hemipristis serra* Agassiz, 1843 and *Otodus megalodon* (Agassiz, 1835). While all three taxa have large, serrated teeth, the size, shape and spacing of the serrations varies widely between them. Both *Otodus megalodon* and *Hemipristis serra* have serrations that are relatively uniformly spaced, whereas *Carcharodon carcharias* has more irregularly spaced serrations similar to the tooth fragment embedded in CMM-V-6964.

In addition to the tooth size and shape, we can also consider the tooth histology. Shark teeth can be categorized into three histotypes: orthodont, pseudoosteodont, and osteodont (Jambura *et al.* 2020). These histotypes correspond with the dentine patterns that underlie the enameloid crown and are reflective of the evolutionary history of different taxonomic groups. The tooth fragment in CMM-V-6964 lacks evidence of a pulp cavity and would consequently be assigned to the osteodont histotype (Kent 1994). The osteodont histotype is exclusively exhibited by lamniform sharks, which provides further evidence that the tooth could not have come from a carcharhiniform shark (e.g. *Hemipristis serra*) and supports the assignment to a lamniform shark (e.g. *Carcharodon carcharias* or *Otodus megalodon*). The serration morphology and spacing indicate that this tooth belonged to the great white shark, *Carcharodon carcharias*, given that teeth of *Otodus megalodon* are characterized by finer serrae (Nyberg *et al.* 2006: fig. 8).

Variation in the size and shape of the serrations in extant *Carcharodon carcharias* encompasses the size and shape of the serrations preserved in CMM-V-6964. The tips of proximal serrations on the teeth of *C. carcharias* are generally more pointed than those preserved on the embedded partially tooth in CMM-V-6964. However, the serrations on the tips of the teeth of *C. carcharias* are not as pointed as are more proximal ones; they are instead more comparable to those preserved in CMM-V-6964 (Fig. 2), indicating not unreasonably, that the embedded section of the tooth represents its tip. Unfortunately, from the limited preservation of the embedded crown, it is not possible to estimate the original size of the tooth, nor the size of the great white shark.

#### PALEOECOLOGICAL AND BIOMECHANICAL INSIGHTS

Teeth attributed to *Carcharodon carcharias* are known from the Bone Valley Member of the Peace River Formation (Perez 2022a, b). Although uncommon, *C. carcharias* was obviously in the same place at the same time as was the shark-bitten phocid. Great white sharks are known to prey upon seals at seal rookeries worldwide (Hammerschlag *et al.* 2006; Johnson *et al.* 2009; Diedrich 2013; Fallows *et al.* 2013; de Vos *et al.* 2015). Therefore, the presence of the tip of a broken tooth embedded in a calcaneum is unsurprising. What is surprising is that no comparable seal bone or any vertebrate bone (or shark cartilage) preserving an embedded *C. carcharias* tooth has yet been described from the fossil record. Thus, despite

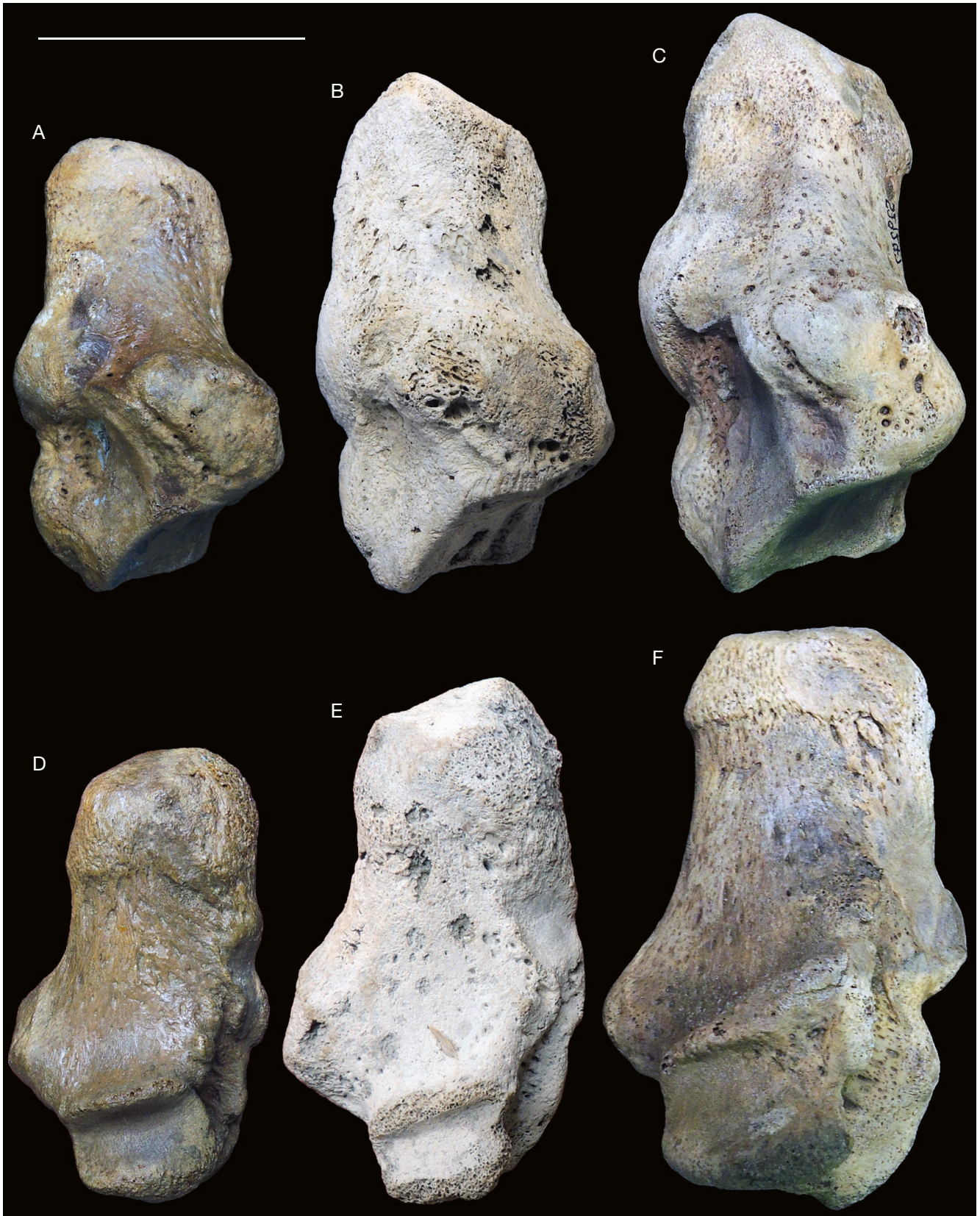


FIG. 3. — **A, D**, USNM PAL 205850, right calcaneum of *Callophoca obscura* (Van Beneden, 1876) (*sensu* Koretsky & Ray 2008) in medial and lateral views respectively from an associated partial right pes; **B, E**, CMM-V-6964, right calcaneum in medial and lateral views respectively with embedded shark tooth visible in **E**; **C, F**, USNM PAL 529247, left calcaneum (reflected vertically 180° in both) of an unnamed phocid in medial and lateral views respectively. Scale bar: 50 mm.

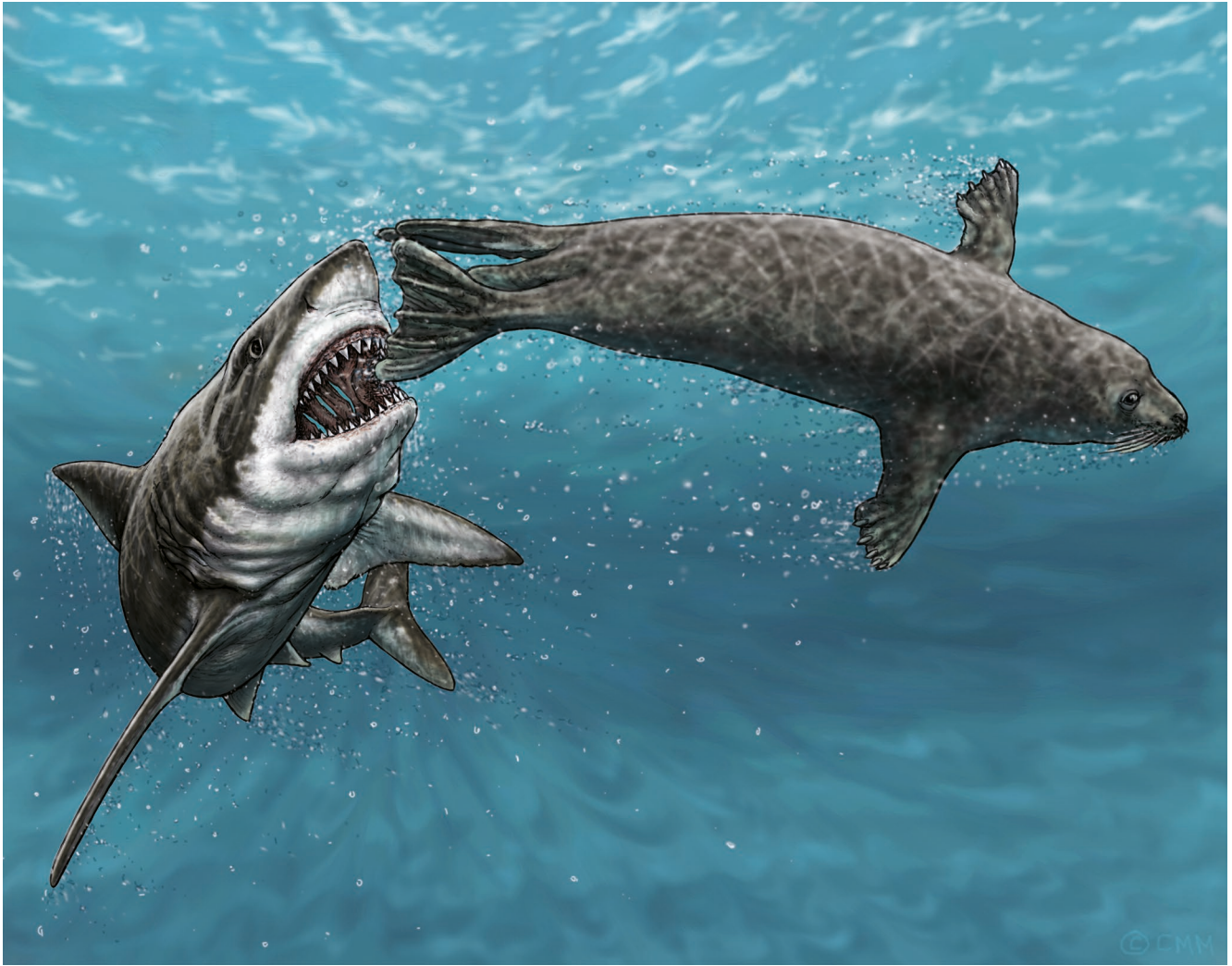


FIG. 4. — Rendering of one of the ways in which the seal calcaneum may have been bitten by the great white shark, *Carcharodon carcharias* (Linnaeus, 1758). This illustration depicts an active predatory encounter between the seal and the great white, although it may have come about as a result of scavenging. Notes: the exact size of the predator and prey represented by CMM-V-6964 are not known. The life-restoration of the pinniped is based mostly on the extant Leopard seal. Credits: Clarence Schumaker.

the likely prevalence of predation on seals by *C. carcharias* throughout their *c.* 6-million-year coexistence, the likelihood of a comparable find is evidently exceedingly low, perhaps because bitten bones are, more often than not, consumed, leaving no possibility for the preservation of a bone with an embedded tooth. Or bitten bones are taphonomically destroyed (or almost so) so that they are no longer recognizable. The bone shows no obvious signs of having been ingested; there are no signs of bone dissolution (like gastric pitting) from digestive acids, therefore, the calcaneum was probably not swallowed by the shark. However, Boessenecker *et al.* (2014: fig. 29K-M) figured a distal femur from a fur seal (*Pinnipedia* Illiger, 1811: Otariidae Gray, 1825: *Thalassoleon* sp., cf. *T. macnallyae*) with gastric acid pitting and linear scrape marks. There are two seemingly, equally likely scenarios to account for the presence of the partial shark tooth crown embedded in the calcaneum: successful active predation or scavenging. There is no osteological evidence of healing

(i.e., no evidence of new bone growth around the embedded partial crown, there is no evidence of periosteal reaction [as in Kallal *et al.* 2012]), so if the encounter came about as a result of active predation, the seal did not survive for long.

Although great white sharks actively prey upon small marine mammals, they have only infrequently been reported to scavenge seals or diminutive odontocetes, thus seemingly preferring large, fat-rich whale carcasses (Fallows *et al.* 2013; Collareta *et al.* 2017). Although, these purported scavenging preferences may have resulted from observer lack of opportunity: it would be easier to observe a great white shark scavenging a large baleen whale carcass than to observe the same behavior on small marine mammal carcasses. However, if in fact great white sharks only rarely scavenge the carcasses of seals, then this find would tilt the balance towards active predation. Furthermore, one could argue that there is not much flesh on the foot of a seal. In terms of return on effort, a powerful bite to the foot might more strongly

suggest active pursuit for the purpose of immobilizing the seal, versus scavenging. Furthermore, Long *et al.* (1996) pointed out that seals use hind flipper propulsion and are not as able (as sea lions) to escape from a posterior attack by a great white shark. At this point, although we favor active predation, there does not appear to be any definitive evidence pointing conclusively to one or the other.

Although the surface of the bone is marked by at least seven small areas of broken/perforated bone, it is not known if these represent postmortem taphonomic damage to the exterior surface of the bone or if they are shark bite marks, collateral damage from the same attack during which the tooth became embedded, or a subsequent scavenging encounter. If they are shark bite marks in origin, they most closely conform to the trace fossil *Nihilichnus nihilicus* Mikuláš, Kadlecová, Fejfar & Dvořák, 2006 (Mikuláš *et al.* 2006). However, the aforementioned identification is not compelling and the surface markings on the calcaneum could also be interpreted as evidence for the activity of the osteophagous worms *Osedax* Rouse, Goffredi & Vrijenhoek, 2004 (Annelida Lamarck, 1809: Siboglinidae Caullery, 1914); their galleries that collapsed under burial compaction (Boessenecker & Fordyce 2015). To complicate matters, it is within the realm of possibility that they represent biogenic markings made by ectoparasites (i.e., *Karethraichnus lakkos* Zonneveld, Bartels, Gunnell & McHugh, 2015-like trace fossils or *Thatchtelithichnus* Zonneveld, Bartels, Gunnell & McHugh, 2015 scars (Collareta *et al.* 2021)).

Only a few publications implicate *C. carcharias* in preying or scavenging on Neogene marine mammals (Bianucci *et al.* 2002; Govender 2015; Cortés *et al.* 2019; Govender 2021). No publications to date have described an embedded *C. carcharias* tooth in a prey item from the fossil record. Therefore, CMM-V-6964 is a unique morderolite in the fossil record. However, Ames & Morejohn (1980) did describe an embedded *C. carcharias* tooth in a modern sea otter skull. Interestingly, there are publications that document evidence of great white sharks off the California coast attacking, but not consuming, sea otters (e.g. Moxley *et al.* 2019; and references therein). These shark attacks are due to mistaken identity (mistargeted prey) with their preferred prey, juvenile elephant seals (*Mirounga angustirostris* (Gill, 1866)) at coastal rookeries (Moxley *et al.* 2019).

Although we cannot say with certainty, we think that the embedded tooth broke at the time when it became embedded in the calcaneum (Fig. 4). The fact that this bite was concentrated on an area of the body with minimal fat may have led to tooth failure, as it punctured the hard bone. Broadly triangular, serrated teeth, like those of *Carcharodon carcharias*, are regarded as representative of the cutting functional type and are thought to be adapted for feeding on large, fleshy prey (Frazzetta 1988; Kent 1994; Perez 2022a). Having a dentition equipped with cutting-type teeth allows predators to dismember their prey more effectively than other tooth morphologies. However, even with these cutting-type teeth, CMM-V-6964 demonstrates that tooth failure is possible when the bite force is concentrated on bone and even cartilage.

This is also evident by more recent examples, including partial teeth of great white sharks found embedded in the skull of a sea otter (Ames & Morejohn 1980) and within another great white (Fallows *et al.* 2013).

### Acknowledgements

This work is dedicated to Ms Diane Scott, whose infectious exuberance permeated Dr Robert Reisz's paleo lab during S.J.G.'s postdoctoral tenure there and doubtless during the entirety of her amazingly productive career as an exceedingly gifted fossil preparator and artist. Obviously, this publication would not have been possible without access to Mosaic's South Fort Meade Mine (Mosaic Fertilizer, LLC). Consequently, we thank the management of the mine for granting access to the spoil piles so that scientifically important fossils, like the one described herein, could be collected. We gratefully and specifically acknowledge the following mine employees who worked at the mine when the seal calcaneum was collected: Howie Stoughton (Mine Manager), Diana Youmans (Mine Sr. Public Relations), and Bonnie Dodson (Mine Geologist).

We would like to express our thanks to CMM Paleontology Collections Manager, John R. Nance for encouraging access to specimens in his care. We are also grateful to the constructive reviews given by Dr Robert W. Boessenecker (Mace Brown Museum of Natural History, College of Charleston), Dr Alberto Collareta (Museo di Storia Naturale, Università di Pisa), and Dr Olivier Lambert (Institut royal des Sciences naturelles de Belgique, Belgium), which improved upon our initial effort, and Dr Michel Laurin who kept the manuscript moving through the publication process. We are grateful that Dr Robert R. Reisz invited us to contribute to this issue. 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.

### REFERENCES

- AGUILERA O. A., GARCÍA L. & COZZUOL M. A. 2008. — Giant-toothed white sharks and cetacean trophic interaction from the Pliocene Caribbean Paraguaná Formation. *Paläontologische Zeitschrift* 82: 204–208. <https://doi.org/10.1007/BF02988410>
- AMES J. A. & MOREJOHN G. V. 1980. — Evidence of white shark, *Carcharodon carcharias*, attacks on sea otters, *Enhydra lutris*. *California Fish and Game* 66: 196–209.
- BERTA A. & WYSS A. R. 1994. — Pinniped phylogeny. *Proceedings of the San Diego Society of Natural History* 29: 33–56.
- BERTA A., CHURCHILL M. & BOESSENECKER R. W. 2018. — The origin and evolutionary biology of Pinnipeds: seals, sea lions, and walruses. *Annual Review of Earth and Planetary Sciences* 46: 203–228. <https://doi.org/10.1146/annurev-earth-082517-010009>
- BIANUCCI G., BISCONTI M., LANDINI W., STORAI T., ZUFFA M., GIULIANI S. & MOJETTA A. 2002. — Trophic interactions between white sharks (*Carcharodon carcharias*) and cetaceans: a comparison between Pliocene and recent data, in VACCHI M., LA MESA G., SERENA F. & SÈRET B. (eds), Proceedings 4th meeting of the European Elasmobranch Association, Livorno (Italy) 27–30 September 2000. Imprimerie F. Paillart, Abbeville: 33–48.

- BIGELOW P. K. 1994. — Occurrence of a squaloid shark (Chondrichthyes: Squaliformes) with the pinniped *Allodemus* from the Upper Miocene of Washington. *Journal of Paleontology* 68 (3): 680-684. <https://doi.org/10.1017/s0022336000026032>
- BOESSENECKER R. W. & FORDYCE R. E. 2015. — Trace fossil evidence of predation upon bone-eating worms on a baleen whale skeleton from the Oligocene of New Zealand. *Lethaia* 48 (3): 326-331. <https://doi.org/10.1111/let.12108>
- BOESSENECKER R. W., PERRY F. A. & SCHMITT J. G. 2014. — Comparative taphonomy, taphofacies, and bonebeds of the Mio-Pliocene Purisima Formation, Central California: strong physical control on marine vertebrate preservation in shallow marine settings. *PLoS ONE* 9 (3): e91419. <https://doi.org/10.1371/journal.pone.0091419>
- CICIMURRI D. J. & KNIGHT J. L. 2009. — Two shark-bitten whale skeletons from Coastal Plain deposits of South Carolina. *Southeastern Naturalist* 8 (1): 71-82. <https://www.jstor.org/stable/25599297>
- COLLARETA A., LAMBERT O., LANDINI W., DI CELMA C., MALINVERNO E., VARAS-MALCA R., URBINA M. & BIANUCCI G. 2017. — Did the giant extinct shark *Carcharocles megalodon* target small prey? Bite marks on marine mammal remains from the late Miocene of Peru. *Palaeogeography, Palaeoclimatology, Palaeoecology* 469: 84-91. <https://doi.org/10.1016/j.palaeo.2017.01.001>
- COLLARETA A., TSAI C. H., COLETTI G. & BOSSELAERS M. 2021. — *Thachtelithichnus* on a Pliocene grey whale mandible and barnacles as possible tracemakers. *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen* 302: 53-61. <https://doi.org/10.1127/njgpa/2021/1018>
- COLLARETA A., MERELLA M., CASATI S., DI CENCIO A. & BIANUCCI G. 2022. — Smoking guns for cold cases: the find of a *Carcharhinus* tooth piercing a fossil cetacean rib, with notes on the feeding ecology of some Mediterranean Pliocene requiem sharks. *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen* 305: 145-152. <https://doi.org/10.1127/njgpa/2022/1082>
- CORTÉS D., DE GRACIA C., CARRILLO-BRICEÑO J. D., AGUIRRE-FERNÁNDEZ G., JARAMILLO C., BENITES-PALOMINO A. & ATENCIO-ARAÚZ J. E. 2019. — Shark-cetacean trophic interactions during the late Pliocene in the Central Eastern Pacific (Panama). *Palaeontologia Electronica* 22 (2): 49A 1-13. <https://doi.org/10.26879/953>
- DE VOS A., O'RIAIN M. J., MEYER M. A., KOTZE P. G. & KOCK A. A. 2015. — Behavior of Cape fur seals (*Arctocephalus pusillus pusillus*) in relation to temporal variation in predation risk by white sharks (*Carcharodon carcharias*) around a seal rookery in False Bay, South Africa. *Marine Mammal Science* 31 (3): 1118-1131. <https://doi.org/10.1111/mms.12208>
- DEWAELE L., PEREDO C. M., MEYVISCH P. & LOUWY S. 2018. — Diversity of late Neogene Monachinae (Carnivora, Phocidae) from the North Atlantic, with the description of two new species. *Royal Society Open Science* 5 (3): 172437. <https://doi.org/10.1098/rsos.172437>
- DIEDRICH C. G. 2013. — Evolution of white and megatooth sharks, and evidence for early predation on seals, sirenia, and whales. *Natural Science* 5 (11): 1203-1218. <https://doi.org/10.4236/ns.2013.511148>
- EBERT D. A. 1991. — Observations on the predatory behaviour of the sevengill shark *Notorynchus cepedianus*. *South African Journal of Marine Science* 11 (1): 455-465. <https://doi.org/10.2989/025776191784287637>
- EHRET D. J., MACFADDEN B. J., JONES D. S., DEVRIES T. J. & SALAS-GISMONDI R. 2009. — Caught in the act: trophic interactions between a 4-million-year-old white shark (*Carcharodon*) and mysticete whale from Peru. *Palaio* 24: 329-333. <https://doi.org/10.2110/palo.2008.p08-077r>
- EHRET D. J., MACFADDEN B. J., JONES D. S., DEVRIES T. J., FOSTER D. A. & SALAS-GISMONDI R. 2012. — Origin of the white shark *Carcharodon* (Lamniformes: Lamnidae) based on recalibration of the Upper Neogene Pisco Formation of Peru. *Palaeontology* 55 (6): 1139-1153. <https://doi.org/10.1111/j.1475-4983.2012.01201.x>
- EVERHART M. J., EVERHART P. A. & SHIMADA K. 1995. — *A New Specimen of Shark Bitten Mosasaur Vertebrae from the Smoky Hill Chalk (Upper Cretaceous) in Western Kansas*. Abstracts, 127th Annual Meeting, Kansas Academy of Science 14: 19.
- EVERHART M. J. 2004. — Late Cretaceous interaction between predators and prey. Evidence of feeding by two species of shark on a mosasaur. *PalArch, Vertebrate Palaeontology* 1 (1): 1-7.
- FALLOWS C., GALLAGHER A. J. & HAMMERSCHLAG N. 2013. — White Sharks (*Carcharodon carcharias*) scavenging on whales and its potential role in further shaping the ecology of an apex predator. *PLoS ONE* 8 (4): e60797. <https://doi.org/10.1371/journal.pone.0060797>
- FRAZZETTA T. H. 1988. — The mechanics of cutting and the form of shark teeth (Chondrichthyes, Elasmobranchii). *Zoomorphology* 108: 93-107. <https://doi.org/10.1007/BF00539785>
- FRESCHI A. 2017. — New *Carcharodon* scavenging evidence on Pliocene whale bones remains from Northern Apennines. *Quaderni del Museo Civico di Storia Naturale di Ferrara* 5: 33-36.
- FRESCHI A. & CAU S. 2021. — Nuovi segni d'interazione trofica tra *Carcharodon carcharias* ed un odontoceto dal bacino plio-pleistocenico di Castell'Arquato (Piacenza, Appennino Settentrionale). *Parva Naturalia* 15: 133-156.
- GODFREY S. J. & COLLARETA A. 2022. — Suggested names for major classes of fossils. *The Ecphora* 37 (2): 25.
- GOVENDER R. 2015. — Shark-cetacean trophic interaction, Duinefontein, Koeberg, (5 Ma), South Africa. *South African Journal of Science* 111 (11-12): 1-7. <https://doi.org/10.17159/sajs.2015/20140453>
- GOVENDER R. 2021. — Shark-seal interaction off South Africa's west coast during the early Pliocene (5 Ma). *South African Journal of Science* 117 (3/4): #8837. <https://doi.org/10.17159/sajs.2021/8837>
- GOVENDER R. & CHINSAMY A. 2013. — Early Pliocene (5 Ma) shark-cetacean trophic interaction from Langebaanweg, Western Coast of South Africa. *PALAIOS* 28 (5): 270-277. <https://doi.org/10.2110/palo.2012.p12-058r>
- GUERTIN L. A. 1998. — *A Late Cenozoic Mixed Carbonate/Siliciclastic System, South Florida: Lithostratigraphy, Chronostratigraphy, and Sea-Level Record*. PhD dissertation, University of Miami, Coral Gables, Florida, 424 p.
- GUERTIN L. A., MCNEILL D. F., LIDZ B. H. & CUNNINGHAM K. J. 1999. — Chronologic model and transgressive-regressive signatures in the late Neogene siliciclastic foundation (Long Key Formation) of the Florida Keys. *Journal of Sedimentary Research* 69: 653-666. <https://doi.org/10.2110/jsr.69.653>
- GUERTIN L. A., MISSIMER T. M. & MCNEILL D. F. 2000. — Hiatal duration of correlative sequence boundaries from Oligocene-Pliocene mixed carbonate/siliciclastic sediments of the south Florida Platform. *Sedimentary Geology* 134 (1-2): 1-6. [https://doi.org/10.1016/S0037-0738\(00\)00011-7](https://doi.org/10.1016/S0037-0738(00)00011-7)
- HAMMERSCHLAG N., MARTIN R. A. & FALLOWS C. 2006. — Effects of environmental conditions on predator-prey interactions between white sharks (*Carcharodon carcharias*) and Cape fur seals (*Arctocephalus pusillus pusillus*) at Seal Island, South Africa. *Environmental Biology of Fishes* 76: 341-350. <https://doi.org/10.1007/s10641-006-9038-z>
- HOFF J. VAN DEN & MORRICE M. G. 2008. — Sleeper shark (*Somniosus antarcticus*) and other bite wounds observed on southern elephant seals (*Mirounga leonina*) at Macquarie Island. *Marine Mammal Science* 24 (1): 239-247. <https://doi.org/10.1111/j.1748-7692.2007.00181.x>
- HULBERT JR. R. C. 2001. — *The Fossil Vertebrates of Florida*. University Press of Florida, Gainesville, 384 p.
- HUNT A. P. & LUCAS S. G. 2021. — The ichnology of vertebrate consumption: Dentalites, gastroliths and bromalites. *New Mexico Museum of Natural History & Science Bulletin* 87: 1-226.

- JAMBURA P. L., TÜRTERSCHER J., KINDLIMANN R., METSCHER B., PFAFF C., STUMPF S., WEBER G. W. & KRIWET J. 2020. — Evolutionary trajectories of tooth histology patterns in modern sharks (Chondrichthyes, Elasmobranchii). *Journal of Anatomy* 236 (5): 753-771. <https://doi.org/10.1111/joa.13145>
- JOHNSON R. L., KESWICK T., BESTER M. N. & OOSTHUIZEN W. H. 2009. — Encounters between white sharks and Cape fur seals in a shallow channel. *Marine Biodiversity Records* 1 (2): 1-5. <https://doi.org/10.1017/s1755267209000682>
- KALLAL R. J., GODFREY S. J. & ORTNER D. J. 2012. — Bone reactions on a Pliocene cetacean rib indicate short-term survival of predation event. *International Journal of Osteoarchaeology* 22 (3): 253-260. <https://doi.org/10.1002/oa.1199>
- KENT B. W. 1994. — *Fossil Sharks of the Chesapeake Bay Region*. Egan Rees & Boyer, Inc., Columbia, MD, 146 p.
- KLIMLEY P. A., PYLE P. & ANDERSON S. D. 1996. — The behavior of white sharks and their pinniped prey during predatory attacks, in KLIMLEY A. P. & AINLEY D. G. (eds), *Great White Sharks, the Biology of Carcharodon carcharias*. Chapter 16. Academic Press, San Diego: 175-191.
- KLIMLEY A., LE BOEUF B., CANTARA K. M., RICHERT J. E., DAVIS S. F., VAN SOMMERAN S. & KELLY J. T. 2001. — The hunting strategy of white sharks (*Carcharodon carcharias*) near a seal colony. *Marine Biology* 138: 617-636. <https://doi.org/10.1007/s002270000489>
- KORETSKY I. A. & RAY C. E. 2008. — Phocidae of the Pliocene of eastern USA. *Virginia Museum of Natural History Special Publication* 14: 81-140.
- LAMBERT O. & GIGASE P. 2007. — A monodontid cetacean from the Early Pliocene of the North Sea. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* 77: 197-210.
- LAROCHE R. K., KOCK A. A., DILL L. M. & OOSTHUIZEN W. 2008. — Running the gauntlet: a predator-prey game between sharks and two age classes of seals. *Animal Behaviour* 76 (6): 1901-1917. <https://doi.org/10.1016/j.anbehav.2008.06.025>
- LONG D. J., HANNI K. D., PYLE P., ROLETT J., JONES R. & R. 1996. — White shark predation on four pinniped species in central California waters: geographic and temporal patterns inferred from wounded carcasses, in KLIMLEY A. P. & AINLEY D. G. (eds), *Great White Sharks: the Biology of Carcharodon carcharias*. Academic Press, San Diego: 263-274. <https://doi.org/10.1016/b978-012415031-7/50025-2>
- LUCAS Z. N. & NATANSON L. J. 2010. — Two shark species involved in predation on seals at Sable Island, Nova Scotia, Canada. *Proceedings of the Nova Scotian Institute of Science* 45 (2): 64-88.
- MARTIN R. A. & HAMMERSCHLAG N. 2012. — Marine predator-prey contests: Ambush and speed versus vigilance and agility. *Marine Biology Research* 8 (1): 90-94. <https://doi.org/10.1080/17451000.2011.614255>
- MARTIN R. A., HAMMERSCHLAG N., COLLIER R. S. & FALLOWS C. 2005. — Predatory behavior of white sharks (*Carcharodon carcharias*) at Seal Island, South Africa. *Journal of Marine Biology* 85 (5): 1121-1135. <https://doi.org/10.1017/S002531540501218X>
- MACFADDEN B. J. & WEBB S. D. 1982. — The succession of Miocene (Arikarean through Hemphillian) mammal localities and faunas in Florida, in SCOTT T. M. & UPCHURCH S. B. (eds), *Miocene of the southeastern United States*. *Florida Geological Survey Special Publication* 25: 186-199.
- MATSON G. C. & CLAPP F. G. 1909. — A preliminary report on the geology of Florida. *Florida Geological Survey Second Annual Report*: 23-173.
- MIKULÁŠ R., KADLECOVÁ E., FEJFAR O. & DVOŘÁK, Z. 2006. — Three new ichnogenes of biting and gnawing traces on reptilian and mammalian bones: a case study from the Miocene of the Czech Republic. *Ichnos* 13 (3): 113-127. <https://doi.org/10.1080/104209406000850729>
- MOXLEY J. H., NICHOLSON T. E., VAN HOUTAN K. S. & JORGENSEN S. J. 2019. — Non-trophic impacts from white sharks complicate population recovery for sea otters. *Ecology and Evolution* 9 (11): 6378-6388. <https://doi.org/10.1002/ece3.5209>
- MUIZON C. DE 1981. — Les vertébrés fossils de la Formation Pisco (Pérou) première partie: deux nouveaux Monachinae (Phocidae: Mammalia) du Pliocène de Sud Sacaco. *Institut Français d'Etudes Andines, Mémoire* 6: 20-161.
- NYBERG K. G., CIAMPAGLIO C. N. & WRAY G. A. 2006. — Tracing the ancestry of the great white shark, *Carcharodon carcharias*, using morphometric analyses of fossil teeth. *Journal of Vertebrate Paleontology* 26 (4): 806-814. <https://doi.org/cnd4xh>
- PEREZ V. 2022a. — The chondrichthyan fossil record of the Florida Platform (Eocene-Pleistocene). *Paleobiology* 48 (4): 622-654. <https://doi.org/10.1017/pab.2021.47>
- PEREZ V. 2022b. — *Chondrichthyan specimen data from the Florida fossil record*. Dryad, Dataset. <https://doi.org/10.5061/dryad.1zcrjdfm>
- PEREZ V. J., GODFREY S. J. & CHAPMAN P. F. 2021. — Rare evidence of shark-on-shark trophic interactions in the fossil record. *Acta Palaeontologica Polonica* 66 (4): 847-856. <https://doi.org/10.4202/app.00911.2021>
- RAHMAT S. J., KORETSKY I. A., OSBORNE J. E. & ALFORD A. A. 2017. — New Miocene Monachinae from the Western shore of the Chesapeake Bay (Maryland, USA). *Vestnik zoologii* 51 (3): 221-242.
- RAHMAT S. J., HAFED A. B., GODFREY S. J., NANCE J. R. & KORETSKY I. A. 2021. — A new unusual Monachinae from the Neogene of the Atlantic Coastal Plain (Maryland, USA). *Historical Biology* 5 (1): 1-10. <https://doi.org/10.1080/08912963.2021.1933469>
- RENNING C. A. & TEDFORD R. H. 1977. — Otarioid seals of the Neogene. *United States Geological Survey Professional Paper* 992: 1-93; pls 1-24.
- ROTHSCHILD B. M., MARTIN L. D. & SCHULP A. S. 2005. — Sharks eating mosasaurs, dead or alive? *Netherlands Journal of Geosciences* 84 (3): 335-340. <https://doi.org/10.1017/S0016774600021119>
- RULE J. P., ADAMS J. W., ROVINSKY D. S., HOCKING D. P., EVANS A. R. & FITZGERALD E. M. G. 2020. — A new large-bodied Pliocene seal with unusual cutting teeth. *Royal Society Open Science* 7 (11): 201591. <https://doi.org/10.1098/rsos.201591>
- SCHWIMMER D. R., STEWART J. D. & WILLIAMS G. D. 1997. — Scavenging by sharks of the genus *Squalicorax* in the late Cretaceous of North America. *Palaaios* 12: 71-83. <https://doi.org/10.2307/3515295>
- SCOTT T. M. 1988. — The lithostratigraphy of the Hawthorn Group (Miocene) of Florida. *Florida Geological Survey Bulletin* 59, 148 p.
- SELLARDS E. H. 1916. — Fossil vertebrates from Florida: A new Miocene fauna; new Pliocene species; the Pleistocene fauna. *Florida Geological Survey Annual Report* 8: 77-119.
- SHIMADA K. 1997. — Paleogeological relationships of the Late Cretaceous lamniform shark, *Cretoxyrhina mantelli* (Agassiz). *Journal of Paleontology* 71 (5): 926-933. <https://doi.org/10.1017/S002233600003585X>
- SHIMADA K. & EVERHART M. J. 2004. — Shark-bitten *Xiphactinus audax* (Teleostei: Ichthyodectiformes) from the Niobrara Chalk (Upper Cretaceous) of Kansas. *The Mosasaur* 7: 35-39.
- SHIMADA K. & HOOKS G. E. III. 2004. — Shark-bitten protostegid turtles from the Upper Cretaceous Mooreville Chalk, Alabama. *Journal of Paleontology* 78 (1): 205-210. <https://www.jstor.org/stable/4094849>
- SHIMADA K. & FIELTZ C. 2006. — Annotated checklist of fossil fishes from the Smoky Hill Chalk of the Niobrara Chalk (Upper Cretaceous) in Kansas, in LUCAS S. G. & SULLIVAN R. M. (eds), *Late Cretaceous vertebrates from the Western Interior*. *New Mexico Museum of Natural History and Science Bulletin* 35: 193-213.
- SIMPSON G. G. 1930. — Tertiary land mammals of Florida. *Bulletin of the American Museum of Natural History* 59: 149-211.

- TONOMORI W., SAWAMURA H., SATO T. & KOHNO N. 2018. — A new Miocene pinniped *Allodesmus* (Mammalia: Carnivora) from Hokkaido, northern Japan. *Royal Society Open Science* 5 (5): 172440. <https://doi.org/10.1098/rsos.172440>
- WATANABE Y., LYDERSEN C., FISK A., KOVACS K. 2012. — The slowest fish: swim speed and tail-beat frequency of Greenland sharks *Journal of Experimental Marine Biology and Ecology* 426-427: 5-11. <https://doi.org/10.1016/j.jembe.2012.04.021>
- WEBB S. D. & CRISSINGER D. B. 1983. — *Stratigraphy and vertebrate paleontology of the central and southern phosphate districts of Florida. Central Florida Phosphate District Field Trip Guidebook*. Geological Society of America (Southeastern Section): 28-72.
- WEBB S. D., HULBERT JR R. C., MORGAN G. S. & EVANS H. F. 2008. — Terrestrial mammals of the Palmetto Fauna (early Pliocene, latest Hemphillian) from the central Florida phosphate district. *Natural History Museum Los Angeles County Science Series* 41: 293-312.
- WILLISTON S. W. 1898. — Mosasaurs, in WILLISTON S. W. (ed.), *The University Geological Survey of Kansas*. Part V. 4. University of Kansas, Lawrence: 81-347.

*Submitted on 20 December 2022;  
accepted on 25 May 2023;  
published on 15 February 2024.*