

# Evidence of shark-on-shark trophic interactions in the Miocene of Costa Rica, Southern Central America

## Evidencia de interacciones tróficas entre tiburones en el Mioceno de Costa Rica, América Central Meridional

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**Abstract:** The trophic interactions of many extant shark species are well known. When examining the fossil record, the evidence is weak, often indirect, and subject to interpretation, almost always limited to bite marks on bones. However, the record of shark teeth embedded in skeletal remains, although rare in the fossil record, constitutes direct evidence of predation and/or scavenging. Even rarer is the record of trophic interactions type Shark-on-Shark. Here, we describe the discovery of a fossil that provides direct evidence of trophic interaction between a Hemigaleid shark on Carcharhinid shark, from inner neritic sediments of the Santa Teresa Formation of Miocene age.

**Keywords:** Carcharhinidae; Hemigaleidae; scavenging; Santa Teresa Fm.; Miocene; Puntarenas province.

**Resumen:** Las interacciones tróficas de muchas especies de tiburones actuales son bien conocidas. Al examinar el registro fósil, la evidencia es débil, a menudo indirecta y sujeta a interpretación, casi siempre limitada a marcas de mordeduras en huesos. Sin embargo, el registro de dientes de tiburón incrustados en restos óseos, aunque poco frecuente en el registro fósil, constituye evidencia directa de depredación y/o carroñeo, pero aún más raro es el registro de interacciones tróficas entre tiburones. Aquí describimos el hallazgo de un fósil que aporta evidencia directa de interacción trófica entre un tiburón Hemigaleidae y un Carcharhinidae, procedente de sedimentos neríticos internos de la Formación Santa Teresa, de edad Mioceno.

**Palabras clave:** Carcharhinidae, Hemigaleidae, carroñeo, Fm. Santa Teresa, Mioceno, provincia de Puntarenas.



## Introduction

It is not uncommon to find direct or indirect evidence in the fossil record of the trophic interaction of sharks with other marine organisms (Ehret et al., 2009), and even with organisms that inhabited lake environments with a predominance of freshwater (Kriwet et al., 2008). Such evidence consists primarily of bite marks preserved in skeletal remains; loose teeth associated with fossil skeletal remains of other vertebrates; less frequently, the record of detached teeth embedded in fossilized bones; even rarer, the record of fossilized skeletal, dental, or scales remains preserved in areas associated with a shark's digestive tract, corresponding to soft-body structures that are rarely preserved; and even rarer inclusions in coprolites.

The trophic interaction of sharks in the past, as well as today, was not limited solely to the vertebrate group, but also involves many invertebrates as part of their diet. Always focusing on vertebrates, the Paleozoic fossil record highlights the predation of amphibians by batrachophagous sharks (Soler-Gijón, 1995; Kriwet et al., 2008). In the Mesozoic, we have frequent records of sharks feeding on mosasaur and plesiosaur reptiles (Dortangs et al., 2002; Everhart, 2004; Rothschild, et al., 2005; Hamm & Shimada, 2007), pterosaurs, †*Pteranodon* spp. (Hone et al., 2018; Ehret & Harrell, 2018), turtles (Shimada & Hooks, 2004; Almafitano et al., 2017), Crocodyliformes Hyposaurinae (Hill et al., 2015), Hesperornithiformes birds (Shimada & Hanks, 2020) and Dinosauria of the families Hadrosauridae (Everhart & Ewell, 2006; Shein & Poole, 2014) and Nodosaurinidae that inhabited coastal environments in the Late Cretaceous (Everhart & Hamm, 2005).

In most of the cited cases, trophic interaction, predation and/or scavenging, was caused, indirectly or directly, by Lamniformes sharks, primarily by †*Cretoxyrhina mantelli* (Agassiz), an apex predator of the food chain in the Late Cretaceous seas (Shimada, 1997a) that probably stabbed and anchored its food with large anterior teeth, and cut food primarily with its more distally located teeth (Shimada, 1997b).

In the Cenozoic, the fossil remains of cetaceans among all marine mammals, constitute the group of vertebrates that provides the greatest evidence of trophic activity attributed to sharks, due to their remarkable size, high diversity and cosmopolitan distribution (Aguilera et al. 2008; Bianucci et al., 2000; Cicimurri & Knight, 2009; Cigala Fulgosi, 1990; Cortés et al., 2019; Cozzuol & Aguilera, 2008; Collareta et al., 2017; Freschi, 2017; Freschi & Cau, 2020; Govender & Chinsamy, 2013; Govender, 2015; Noriega et al. 2007; Takakuwua, 2014). It is striking that attacks on cetaceans by predation or possible scavenging during the Miocene and Pliocene, due to the size and configuration of the bite marks and shark teeth associated with the bone remains, are attributed or are directly related to sharks of the Otodontoidea family, such as †*Otodus (Megaselachus) chubutensis* and †*Otodus (Megaselachus) megalodon* (Godfrey et al., 2021); while during the later Pliocene and until the Recent, sharks of the Lamnidae family, particularly the genus *Carcharodon* and the species *Carcharodon carcharias*, are attributed most of the trophic activity towards cetaceans (Deméré and Cerutti, 1982; Cigala-Fulgosi, 1990; Bianucci et al., 2000; Freschi, 2017; Freschi and Cau, 2020), all species of sharks corresponding to apex predators.

In addition to the cetacean record, there is fossil evidence of trophic interactions between sharks and other marine mammals. This is particularly true of Sirenia, where dugongs provide the most significant evidence of shark predation or scavenging (Benites-Palomino et al., 2023; Merella et al., 2021; Feichtinger et al., 2021; Rateau et al., 2009), followed by the record of Pinnipedia (Bigelow, 1994; Collareta et al., 2017; Govender, 2021; Godfrey et al., 2018; Godfrey et al., 2024a).

On the other hand, fossil evidence of trophic interaction between sharks and bony fish is even scarcer; one notable example is a specimen of †*Xiphactinus audax* from the Niobrara Chalk (Upper Cretaceous) of western Kansas that contains an embedded tooth of †*Cretoxyrhina mantelli* (Shimada & Everhart, 2004).

Shark-on-shark trophic interactions have existed for hundreds of millions of years (Perez et al., 2021), despite this, their fossil record is extremely rare, for example Shark remains present within the gut contents of the Devonian shark *Cladoselache* represent the oldest documented evidence of shark-on-shark predation (Williams, 1990). In the Cretaceous, the discovery of †*Pseudocorax* and †*Squalicorax* teeth associated with a semi-articulated skeleton of †*Cretoxyrhina mantelli* is a remarkable fact, which was interpreted by Shimada, 1997b, as evidence of scavenging.

In addition to evidence of predation or scavenging, resulting from trophic interactions between sharks and other vertebrates, including other sharks, there is evidence in the fossil record of teeth bearing marks that may have been involuntarily self-inflicted, resulting from one tooth striking another in the opposing jaw during forced occlusion, collateral damage from feeding, or aggressive behavior (Godfrey et al., 2024b; Perez, 2020; Purdy et al., 2001).

Among the Neogene records of shark-on-shark trophic interactions, the following stand out: the discovery of several vertebral centra from the Atlantic Coastal Plain, collected in Miocene sediments of North Carolina and Maryland, which present bite marks attributed to *Galeocerdo cuvier* (Péron & Lesueur, 1822); an incomplete vertebral centrum of an indeterminate carcharhinid was described from the Calvert Formation in Chesapeake Beach, Maryland, which contains two embedded shark teeth of Carcharhinidae indet. (both cases reported by Perez et al., 2021); and the record of two shark vertebral centra associated with a *Carcharodon carcharias* tooth from the Pliocene of the Po Basin, Italy, considered a case of trophic interaction between sharks (Rondelli et al., 2024). Here we report the first fossil record of a Shark-on-shark trophic interactions found in Central America and the Caribbean Region.

## Geological setting

The vertebral centra presented here, was collected on the surface of Santa Teresa beach at coordinates 9°38'42.85"N and 85°10'18.04"W, south of the Nicoya Peninsula in the Province of Puntarenas, Costa Rica (Fig. 1). From the natural color of this concretion it most likely comes from sediments of the Santa Teresa Formation of Miocene to Early Pliocene age. The sedimentology of the Santa Teresa Formation suggests shallow marine, sublittoral and proximal neritic paleo-environments (Calvo, 1987).

## Material

A concretion containing four articulated shark vertebral centra, and associated with the vertebrae are the remains of three shark teeth. The material is housed at the rocks, minerals and fossils collection of the National Museum of Costa Rica under the code CFM-5496. It was collected with the collaboration of Manú Salom Araya and Lucas Pérez Rojas, students from the CATIE Inter-American School.

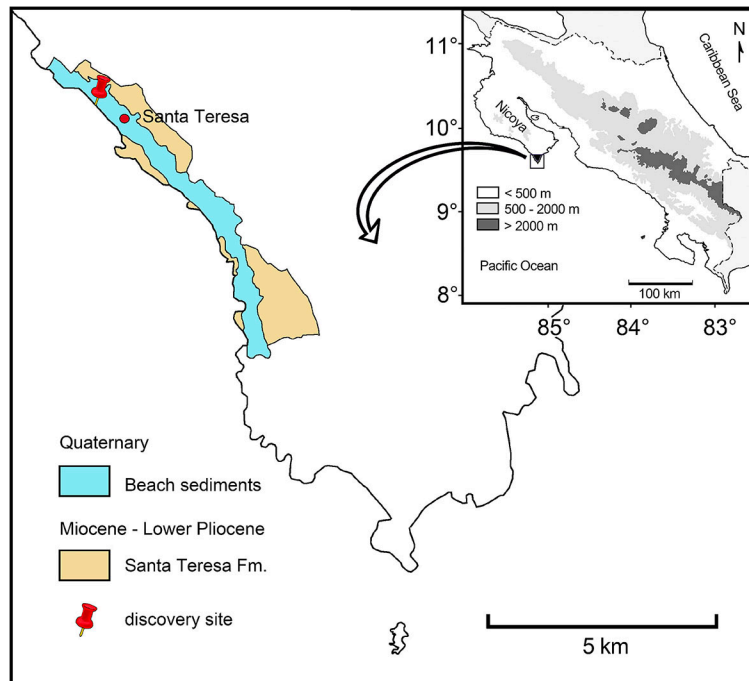


Fig. 1: The southern Nicoya Peninsula shows the extent of the Santa Teresa Formation, Puntarenas Province. The red dot along the coastline marks the location where the vertebral centra concretion was collected. The geological information was taken from the geological map of the Cabuya Sheet (3144-I) scale 1:50000 (Denyer et al., 2013).

## Description

The vertebral centra measure approximately 48 mm at their widest point, 45 mm high, and 20 mm thick. Both the anterior and posterior surfaces of the exposed vertebrae are broken, and their phosphate corpus is missing. However, the central point of the birth ring can be seen on both surfaces, as well as its internal structures, such as the basidorsal and basiventral attachments of the neural and hemal arches. Both the neural and hemal arches were not preserved, as is natural due to their lack of ossification. In the inner vertebrae, the rim of the external growth ring is well preserved. The cavities or foramina for the basiventral insertions are also visible, although they are filled with cemented material precipitated during diagenesis, the oval and slightly elongated outline of the foramina can be seen. The vertebrae exhibit structural characteristics such as well-defined vertebral centra aseptate. The overall width of the vertebral centrum is greater than its thickness. The vertebral centrum has a well-defined and spacious phosphated nucleus, and the intermediate zone is surrounded by a mineralized band.

On the other hand, the vertebrae carry three fossilized dental fragments belonging to sharks. Two of the three preserved crowns are characterized by a high triangular outline, measuring 18 mm and 20 mm in height, with a prominent apex inclined toward the commissure, and edges with prominent serrations, the commissural serrations being thicker than the mesial ones. The serrations increase in size toward the apex. Both crowns have a wide triangular groove on their lower half.

The third crown fragment is very small, its observable length reaches 5.5 mm, and it has a slightly inflated concave labial surface with smooth edges on the sides.

## Discussion and conclusions

Vertebral centra are among the most commonly preserved shark remains in the fossil record, after oral and dermal teeth. This is because neural and hemal arches are less mineralized than vertebral centra, so they are not usually preserved. The vertebral centra also allow differentiation between different lineages, which makes them of taxonomic value (Burris, 2004; Ehret et al., 2009; Kozuch & Fitzgerald, 1989; Medeiros et al., 2024; Welton & Farish, 1993).

The fossil vertebral centra here analyzed are characterized by thick basidorsal and basihemal insertions, surrounded by dense intermedialia (see figures 2c, d and d'), without the lamellar structures of Lamniformes. These characteristics are typical of the vertebral centra of Carcharhiniformes (*sensu* Welton & Farish, 1993 and Burris 2004). Additionally, the basidorsal insertion foramen is slightly elongated and oval in shape (see Fig. 2b), condition that is also observed into the family Carcharhinidae. Beyond this, it is not possible to determine the genus.

The occurrence of teeth embedded in prey substrate offers unequivocal evidence of trophic interactions and, generally, allow one to more confidently identify the predator than bite marks alone (cf. Godfrey et al., 2024a). In this case the triangular tooth crowns embedded between the vertebrae are typical of sharks of the species †*Hemipristis serra* of the Hemigaleidae family. These crowns correspond to two upper consecutive left lateral teeth that, in our case, became detached when trying to cut the soft tissue surrounding the vertebrae. Something that commonly happens to sharks, because the teeth are anchored by connective tissue fibers in the mucosa covering the jaws (Cappetta, 2012).

There is evidence of a change in the upper teeth of †*Hemipristis serra* during the Miocene: they increased in size and their edges became almost completely serrated (Chandler et al., 2006). Also, adults of †*Hemipristis serra* in the Miocene are estimated to have reached dimensions of up to 6 m, typical of a giant (Pimiento et al., 2019).

These two preserved teeth of †*Hemipristis serra* are relatively small and slender, corresponding to mesial rather than commissural lateral teeth (compare with figures 1 and 7 of Jambura et al., 2018). Another important feature is that the mesial and commissural edges are completely serrated and the cusplets of the commissural edges are well developed, confirming that this was an adult individual. Although the roots were not preserved, it can be speculated that the total length of the teeth was around 20 and 22 mm and that the commissural edge was composed of 9 to 11 cusplets.

These dental dimensions are 25 % larger than those recorded for adult individuals of the current species *Hemipristis elongata*, 196 cm long and with teeth lengths of 15.10 mm (Baranes & Ben-Tuvia, 1979), so it can be speculated that the teeth embedded in the vertebrae centra corresponded to a specimen of around 2 m in length, even slightly larger.

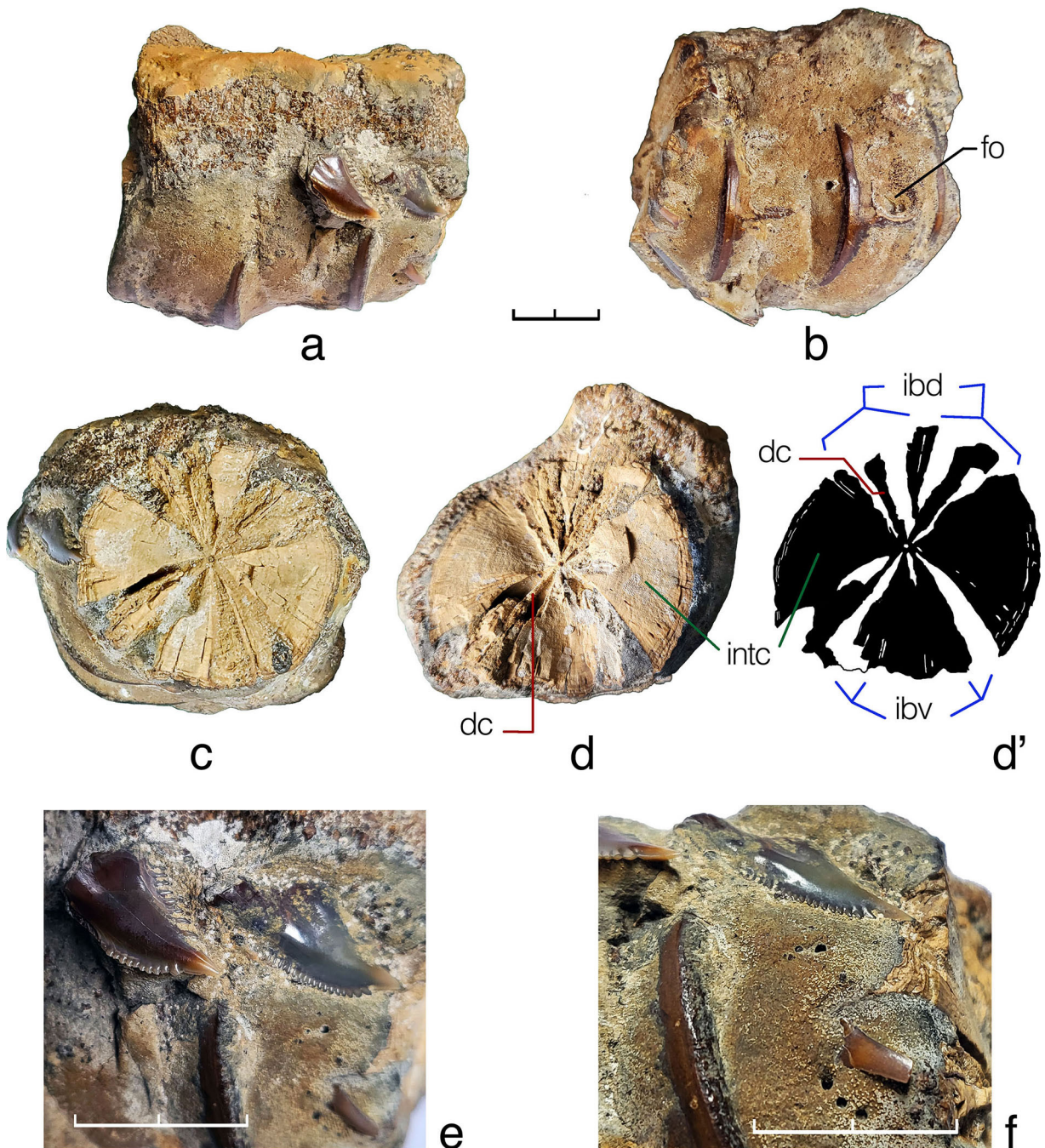


Fig. 2: Calcareous concretion containing four articulated Carcharhinidae shark vertebral centra. a. View showing the crowns of two upper left lateral teeth of †*Hemipristis serra* and part of a crown of a presumed carcharhinid. b. in basal view, showing the fo foramen for insertion of the hemal arch. c y d. front views of the vertebral centra, both fragmented, showing the cavities for the ibd basidorsal and ibv basiventral insertions of the neural and hemal arches respectively, surrounded by dense intc calcified intermedialia. d'. Schematic detail of the internal structure of the vertebral center corresponding to figure d. Detailed view of e. the teeth of †*H. serra* and f. an indeterminate Carcharhinidae. The concretion is covered by bryozoans and some modern polychaeta tubes, graphic scale 2 cm.

All the characteristics described above allow us to conclude that the morpho-dental development corresponds to forms of †*Hemipristis serra* from the Middle Miocene. This age coincides with ages suggested for the Santa Teresa Formation. This is consistent with the temporal range of †*Hemipristis serra*, which spanned the Miocene to the early Pleistocene and had a nearly global distribution (Cappetta, 2012).

Laurito (1999) considered †*Hemipristis serra*, based on its fossil record, as a shark with nektonic and epipelagic habits, which inhabited insular and continental platforms in warm seas during the Neogene. This paleobiogeographic distribution pattern is also consistent with the sedimentology of the Santa Teresa Formation.

There is no doubt that this shark was an important predator, although stating with certainty what its diet was, given that it is a fossil species, is debatable. One way to resolve this is to turn to what is known about the trophic interactions of extant species with fossil representatives from the Neogene or, as in the case analyzed, to consider direct evidence from the fossil record as a snapshot of trophic interactions. The genus *Hemipristis* is currently represented by the species *Hemipristis elongata*, whose biogeographic distribution is limited to the western Pacific, the Indian Ocean and the Red Sea (Carpenter et al., 1997; Compagno, 1998; Ebert et al., 2021). With maximum corporal dimensions of 2.40 m (Compagno, 1984), its diet does not differ from that of other sharks of the same size that share its habitat. This diet includes bony fish, cartilaginous fish such as *Carcharhinus* spp. and *Gymnura* sp., as well as cephalopods (Compagno, 1984, 1998; Ebert et al., 2021; Chappell & Serét, 2020).

Fossil CFM-5496 provides compelling evidence that Carcharhinidae sharks were part of the diet of †*Hemipristis serra* in the Miocene.

Whether the trophic interaction evidenced by the fossil clearly corresponds to predation or scavenging is difficult to determine. However, given that †*Hemipristis serra* was a significant predator, we could assume that the trophic interaction occurred “perimortem,” that is, during a predation event.

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