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Giant-toothed white sharks and cetacean trophic interaction from the Pliocene Caribbean Paraguaná Formation

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with 2 figures

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Abstract: The role of the extinct giant-toothed white shark *Carcharodon megalodon* (AGASSIZ) in the Caribbean Neogene is discussed based on new evidence of predation on cetaceans from the Lower Pliocene Paraguaná Formation in Venezuela. Large sharks have occupied the highest trophic level in the marine environment. However, based on the recovery of a giant white shark tooth piercing a cetacean lumbar vertebra, the predator-prey relationship is discussed under the hypothesis of initial shark attack, subsequent floating transport of the cetacean carcass, and scavenging prior to deposition on the bottom. The scarce Caribbean fossil records of both giant-toothed sharks and cetaceans suggest that these species were transients during the Pliocene on the Venezuelan coast.

Keywords: Cetaceans • sharks • predation • scavenging • Pliocene • Caribbean

Kurzfassung: Die Rolle des ausgestorbenen Riesenweißhaies *Carcharodon megalodon* (AGASSIZ) im Neogen der Karibik wird anhand eines neuen Predationsbefundes aus der unter-pliozänen Paraguaná-Formation in Venezuela diskutiert. Große Haie haben die höchste trophische Ebene im marinen Milieu besetzt. Hier wird ein Zahn eines Riesenweißhaies dokumentiert, der noch in einem Lumbarwirbel eines Wales steckt, was für ein Räuber-Beute-Verhältnis spricht. Die Befunde sprechen für einen Angriff des Räubers, gefolgt von Transport des Walkadavers, Aasfressen und schließlich Ablagerung am Boden des Meeres. Riesenweißhaie und Cetaceen waren im Pliozän in den Küstenregionen von Venezuela vorhanden.

Schlüsselwörter: Cetacea • Haie • Räuber • Aasfresser • Pliozän • Karibik

Introduction

The published literature reflects a close relationship between cetacean and pinniped abundance, cold and temperate waters, and presence of the giant white shark, *Carcharodon megalodon* (PURDY 1996, 1998, 2001). KRUCKOW & THIES (1990) made an early report of *C. megalodon* from the Caribbean, with additional records by AGUILERA (2004), AGUILERA & RODRIGUES DE AGUILERA (2001, 2004), DONOVAN & GUNTER (2001), FLEMMING & MACFARLANE (1998), ITURRALDE-VINENT et al. (1996), LAURITO (1999), and NIEVES-RIVERA et al. (2003). AGUILERA & RODRIGUES DE AGUILERA (2004) interpreted the scarcity of giant white sharks in the Caribbean sedimentary basin as an artifact of sampling, and regarded their presence as an indicator of coastal upwelling.

Preliminary research in the Paraguaná Península (Venezuela) has revealed cetacean and sirenian skeletal remains that exhibit giant white shark bite marks, suggesting predator-prey relationships (AGUILERA & RODRIGUES DE AGUILERA 2004). CIGALA-FULGOSI (1990) described similar bite marks, attributed to the great white shark (*Carcharodon carcharias*), on cetacean bones from the European Pliocene, and BIANUCCI et al. (2000) described trophic interactions between white sharks and cetaceans from the Pliocene and Recent central Mediterranean Sea. PURDY (1996) also described

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bite marks attributed to the giant-toothed white shark on cetacean remains from the North Atlantic Ocean. Today young white sharks are primarily piscivores and adults feed mostly on mammals (McCosker 1985).

Fossil cetaceans from Venezuela are rare. A few previous publications mention the presence of *Prosqualodon australis* and Platanistoidea incertae sedis in the Lower Miocene Castillo Formation (Sánchez-Villagra et al. 2000, 2001; but see Cozzuol & Aguilera, this volume), Iniidae in the Upper Miocene Urumaco Formation (Aguilera 2004) and the Middle Miocene Socorro Formation (Linares 2004), a *Notocetus*-like odontocete in the Lower Miocene Castillo Formation (O'Leary 2004), ?Squalodelphinidae in the Lower Miocene Cantaure Formation, and indeterminate Mysticeti in the Lower Pliocene Punta Gavilán Formation (Cozzuol & Aguilera, this volume).

Based on the recovery of additional evidence of predator-prey relationships, the role of the extinct giant-toothed white shark *Carcharodon megalodon* (Agassiz) in the Caribbean area is discussed under the hypothesis of initial shark attack, subsequent floating transport of the cetacean carcass, and scavenging prior to deposition on the bottom.

Material and methods

The study area consists of a single locality in the northwestern Venezuelan sedimentary basin on the Paraguaná Península, near the town of El Yacural (11° 55'48" N, 70° 00'34" W) (Fig. 1). A single shark tooth in direct association with a cetacean lumbar vertebra and a dozen other *C. megalodon* teeth and cetacean remains come from surface collections. Shark classification follows Purdy et al. (2001) and continues to be a matter of controversy in published formal papers (see Gottfried & Fordyce 2001) and other media (see Lutz 2006). However, these taxonomic discrepancies only reflect the necessity to know the paleobiology, paleobiogeography, and geochronology distribution of the extinct giant-toothed white sharks. The cetacean lumbar vertebra and associated shark tooth were found in the Lower Pliocene Paraguaná Formation on the Caribbean coast of Venezuela. The Paraguaná Formation comprises two members. The lower Member (El Hato Member) is characterized by light brown marine shale. The gray limose layer alternates with fine clay and ferruginous limonite. The base of this member is not exposed. The upper Member (Amuay Member) is represented by a fossiliferous carbonate interval that forms most of the surface of the Paraguaná Península. The top of the member is eroded in some western sections, and the contact be-

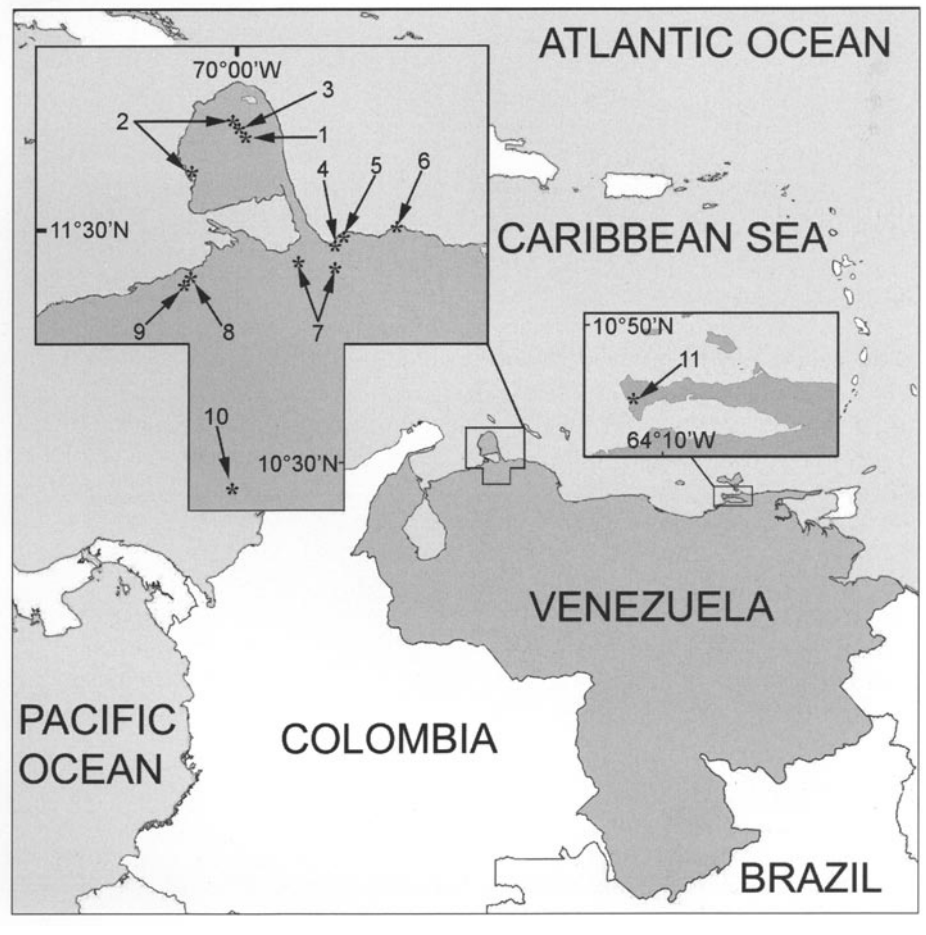

Fig. 1. Location map of main Venezuelan *Carcharodon* localities. – 1–2, Lower Pliocene Paraguaná Formation (1, sampling site discussed in the text); 3, Lower Miocene Cantaure Formation; 4, Lower Pliocene La Vela Formation; 5, Upper Miocene Caujarao Formation; 6, Pliocene Punta Gavilán Formation; 7, Middle Miocene Socorro Formation; 8, Upper Miocene to Lower Pliocene Codore Formation; 9, Upper Miocene Urumaco Formation; 10, Upper Oligocene to Lower Miocene Castillo Formation; 11, Upper Miocene to Lower Pliocene Cubagua Formation.

tween the lower El Hato and the upper Amuay members is concordant and bioturbated (HUNTER & BARTOK 1974; REY 1996; RODRÍGUEZ 1968). The paleoenvironmental associations reflect near-shore tropical marine environments, shallow bays and litoral lagoons (FEO-CODECIDO 1971; REY 1996; RODRÍGUEZ 1968). For additional information about the geology of these units, see MINISTERIO DE ENERGÍA Y MINAS (1997).

The fossil was collected from the El Hato Member and consists of a three-dimensionally preserved, partially broken cetacean lumbar vertebra (vertebra length: 144 mm, anterior diameter of centrum: 105 mm, posterior diameter of centrum: 110 mm) with a partial shark tooth broken at the root (crown length: 55 mm, crown width: 49 mm, total tooth length including the broken root: 74 mm) embedded in the spongy bone of the vertebra. Fine, loose sand matrix surrounding the specimen was removed with brushes, requiring softening with water, and manual cleaning with fine-tipped dental tools. The cetacean vertebra is not diagnostic at a lower taxonomic level than that reported here.

Repository: The specimen is deposited at the Universidad Nacional Experimental Francisco de Miranda (UNEFM).

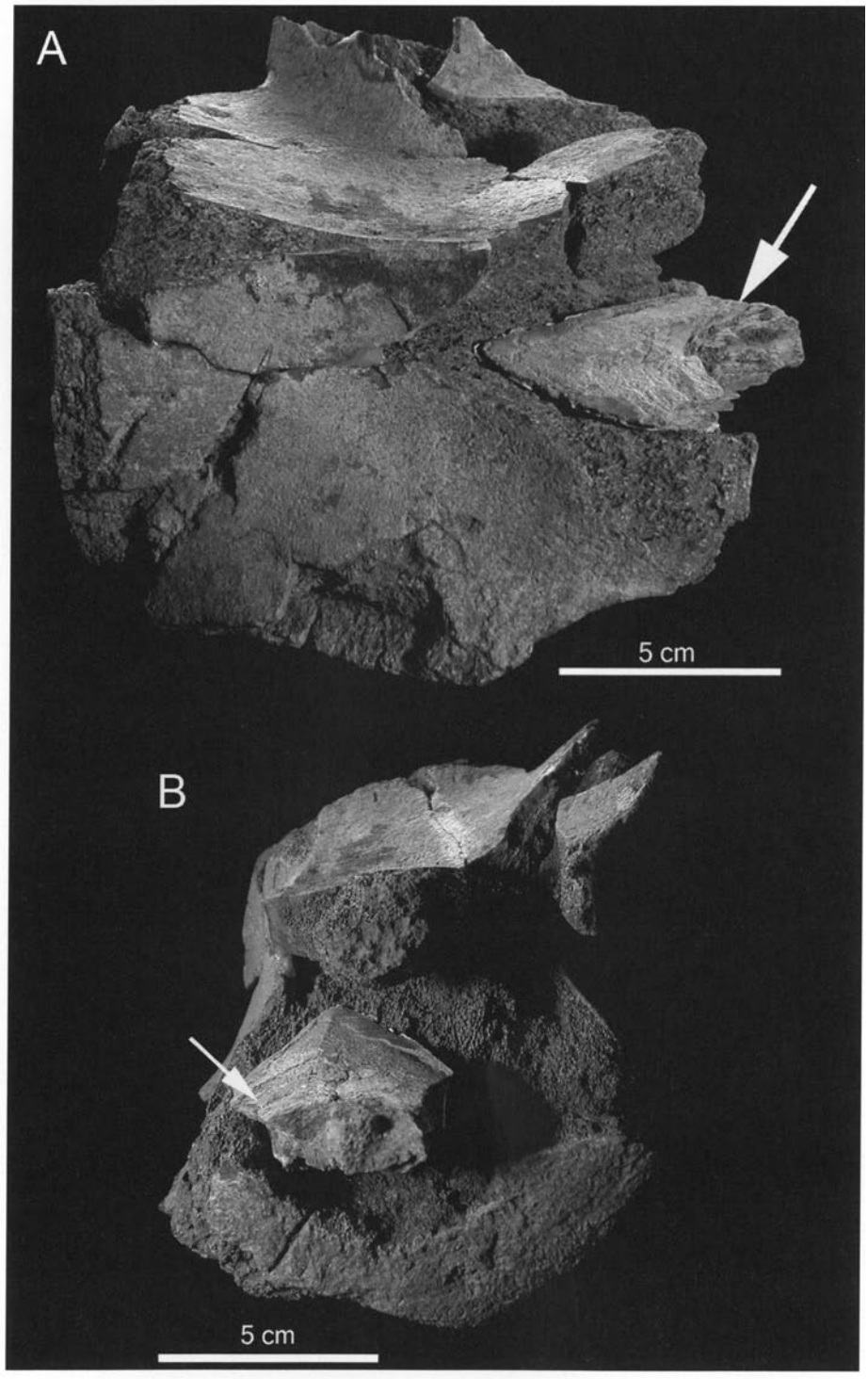

Fig. 2. Cetacean lumbar vertebra with associated tooth of *Carcharodon megalodon* (AGASSIZ), UNEFM-VF-38. El Yacural (11° 55' 48" N, 70° 00' 34" W), Lower Pliocene Paraguaná Formation, Paraguaná Península, Venezuela. **A**: Lateral view; **B**: Posterior view. – Black arrow points to the cemented shark tooth.

Results

The shark tooth embedded in the cetacean vertebra is characterized by a triangular, broad, high and slightly curved crown, a cutting edge incised by numerous, small, and regular serrations, a marked neck, which is strongly curved toward the top, and the labial boundary of the enamel with a median obtuse angle directed toward the top (Fig. 2). This description matches the tooth morphology of *C. megalodon* following PURDY et al. (2001).

The warm and cold water preferences of *C. megalodon* noted by PURDY (1996) suggest that a coastal upwelling environment occurred in this area in the Early Pliocene, as it does today around the Paraguaná Peninsula in Venezuela (GINÉS 1982; MONENTE & ASTOR 1987; AKL et al. 1997) or in the Araya Peninsula area (AGUILERA & RODRIGUES DE AGUILERA 2004). The *C. megalodon* specimens collected in the Venezuelan Caribbean deposits probably fed mainly on small cetaceans, sirenians, turtles, and large fishes.

In Venezuelan Neogene deposits, *Carcharodon megalodon* has previously been recorded in a continuous geochronological sequence, from the Lower Miocene Castillo, Lower Miocene Cantaure, Middle Miocene Socorro, Upper Miocene Urumaco, Upper Miocene Caujarao, Upper Miocene to Lower Pliocene Codore and Cubagua, Lower Pliocene Paraguaná and La Vela, and Pliocene Punta Gavilán formations (LERICHE 1938; AGUILERA & RODRIGUES DE AGUILERA 2001, 2004).

Discussion

According to BIANUCCI et al. (2000), the presence of bite marks on cetacean skeletal remains, the direct association of teeth and cetacean bones, and the coexistence of shark teeth and cetacean remains in the same deposit were the basic criteria to hypothesize interactions between the giant-toothed white shark and cetaceans. The exceptional discovery of the giant-tooth white shark tooth embedded in a cetacean lumbar vertebra, together with the bite marks and the predator-prey assemblages previously reported by AGUILERA & RODRIGUES DE AGUILERA (2004), suggest the hypothesis of initial shark attack, subsequent floating transport of the cetacean carcass, and scavenging of the carcass prior to deposition on the bottom (see BIANUCCI et al. 2000).

The unusual Caribbean fossil association of giant-toothed white shark and cetacean as predator and prey suggests their fortuitous presence as transient species during the Pliocene on the Venezuelan coast.

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