Exceptional Preservation of the White Shark Carcharodon (Lamniformes, Lamnidae) from the Early Pliocene of Peru

Authors: Ehret, Dana J., Hubbell, Gordon, and MacFadden, Bruce J.

Source: Journal of Vertebrate Paleontology, 29(1) : 1-13

Published By: The Society of Vertebrate Paleontology

URL: https://doi.org/10.1671/039.029.0113

Journal of Vertebrate Paleontology 29(1):1–13, March 2009

FEATURED ARTICLE

EXCEPTIONAL PRESERVATION OF THE WHITE SHARK *CARCHARODON* (LAMNIFORMES, LAMNIDAE) FROM THE EARLY PLIOCENE OF PERU

DANA J. EHRET,[*,1] GORDON HUBBELL,[2] and BRUCE J. MACFADDEN[1]
[1]Florida Museum of Natural History, University of Florida, Gainesville, Florida 32611, dehret@flmnh.ufl.edu;
[2]Jaws International, 1703 SW 82nd Drive, Gainesville, Florida 32607

ABSTRACT—An exceptionally well-preserved white shark fossil (*Carcharodon* sp.) is described here from the early Pliocene (ca. 4 Ma) Pisco Formation of southwestern Peru. This specimen preserves 222 teeth and 45 vertebrae as well as fragmentary jaws. The teeth show characters of *Carcharodon*, including weak serrations and a symmetrical first anterior tooth that is the largest in the tooth row. This dentition also shows a character of *Isurus* with a distally inclined but mesially slanted intermediate tooth. Although the Pisco specimen demonstrates characters of both *Isurus*, also known form the Pisco Formation, and modern *Carcharodon carcharias*, it is assigned to the genus *Carcharodon* and referred to herein as *Carcharodon* sp. While *Carcharodon* sp. From the Pisco Formation shows numerous diagnostic characteristics shared with *C. carcharias*, it differs from the extant species in having a distal inclination of the intermediate tooth. The precaudal vertebral centra of the Pisco *Carcharodon* preserve distinctive dark and light incremental bands that, based on calibration with oxygen isotopes, indicate annular growth couplets. The fossil shark was at least 20 (±1) years old at the time of its death. Based on measurements of teeth and vertebral centra, this specimen is estimated to have had a minimum total body length of 4.80–5.07 m, similar to estimates for modern older individuals of *C. carcharias*. Relative to the extant *Carcharodon carcharias*, the Pisco *Carcharodon* sp. grew at a slower rate. The fossil record of lamnoid sharks preserved in the Pisco Formation demonstrates that the modern white shark is more closely related to *Isurus* (*I. hastalis*) than it is to the species *Carcharodon megalodon*, and the latter is therefore best allocated to the genus *Carcharocles*.

INTRODUCTION

Isolated sharks' teeth are the most commonly preserved and collected vertebrate fossils from Neogene marine sediments worldwide. In contrast to the ubiquitous occurrence of sharks' teeth, however, other parts of the skeleton generally are not as common in the fossil record. When exceptionally well-preserved specimens of extinct shark species are found in the fossil record, they greatly increase knowledge about both the range of dental variation exhibited within an individual (and species) and other related skeletal characters.

In 1988, an exceptionally well-preserved individual of a white shark, *Carcharodon*, was collected from approximately 4-million-year-old (early Pliocene) sediments of the Pisco Formation of southern Peru. This specimen contains 222 teeth on the upper and lower jaws, and a series of 45 vertebral centra. The purpose of this paper is to describe this specimen and to discuss its importance in elucidating the morphological variation and paleobiology of a white shark, *Carcharodon*, from the Pliocene of Peru.

Geological Setting and Marine Vertebrates from the Pisco Formation

Extending inland from the coast of southwestern Peru at low elevation (less than a few hundred meters), Neogene sediments of the Sacaco Basin preserve a rich record of marine transgressive and regressive cycles as well as fossils deposited in a forearc basin (Muizon and DeVries, 1985; Fig. 1). Of relevance to understanding the geological context of the shark fossil described here, the late Miocene through early Pliocene Pisco Formation consists of basal coarse-grained deposits along with massive intervals of tuffaceous and diatomaceous siltstone and sandstones. The stratigraphic section that includes the fossil shark is termed "Sud-Sacaco West." Within this section, a rich fossil zone, "SAS," extends from approximately 21 to 43 m above the base of the local measured section and is the interval from which the fossil shark was collected (Fig. 2). This section also contains a diverse shallow-water marine invertebrate fauna interpreted to represent a barrier bar and lagoonal facies. Sud-Sacaco West is early Pliocene in age, dating to between about 4 and 5 Ma ago, based on correlations to an overlying section (Sacaco) with an associated K-Ar age of 3.9 Ma, and younger than the Miocene based on biostratigraphy (Muizon and DeVries, 1985; DeVries and Schrader, 1997).

The rich marine vertebrate fauna has been known from the Pisco Formation for over a century. In addition to other taxa of sharks, the Pisco marine faunas contain rays and chimeras, teleosts, chelonians, crocodilians, a diversity of shore birds, seals, whales and dolphins, and an aquatic sloth (Hoffstetter, 1968; Muizon and DeVries, 1985; Muizon and McDonald, 1995; Muizon et al., 2002; Muizon et al., 2004). Of relevance to this paper, the otodontid and lamnid sharks *Carcharocles megalodon* and *Isurus hastalis* occur in the lower (late Miocene) part of the formation and *Carcharocles megalodon* and *Carcharodon* sp. occur in the upper (early Pliocene) part of the Pisco Formation (Muizon and DeVries, 1985). The vertebrate biostratigraphy of the upper Pisco Formation indicates a correlation with the approximately contemporaneous, shallow-water, primarily marine fauna of the Yorktown Formation of North Carolina (Purdy et al., 2001) as well as with the marginal marine Palmetto faunas of the Upper Bone Valley Formation in Florida (Morgan, 1994).

*Corresponding author.

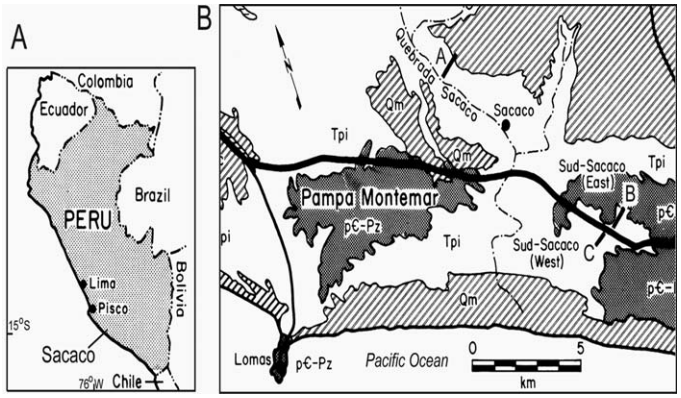

FIGURE 1. **A**, Geographic location; **B**, surface geology of Sacaco Basin in coastal southwestern Peru. Measured sections A, B, and C correspond to those depicted in Figure 2 (taken from Muizon and DeVries 1985).

Fossil Record and Origin of *Carcharodon carcharias*

The evolutionary history and taxonomic placement of the white shark, *Carcharodon carcharias*, within the Lamnidae remains a controversial issue. Two hypotheses have been proposed for the evolutionary history of the modern white shark. The first contends that *Carcharodon carcharias* is more closely related to the megatoothed sharks, including *C. megalodon* (Applegate and Espinosa-Arrubarrena, 1996; Gottfried et al., 1996; Martin, 1996; Gottfried and Fordyce 2001; Purdy et al., 2001). In this scenario, *C. carcharias* shares diagnostic characters with *C. megalodon* and the other megatoothed sharks to place them within the same genus (Fig. 3A). This phylogeny is based on characters of tooth morphology in the fossil and modern species which include: (1) an ontogenetic gradation, whereby the teeth of *C. carcharias* shift from having coarse serrations as a juvenile to fine serrations as an adult, the latter resemble those of *C. megalodon*; (2) morphological similarity of teeth of young *C. megalodon* to those of *C. carcharias*; (3) a symmetrical second anterior tooth; (4) large intermediate tooth that is inclined mesially; and (5) upper anterior teeth that have a chevron-shaped neck area on the lingual surface (Gottfried et al., 1996; Gottfried and Fordyce, 2001; Purdy et al., 2001). Following this hypothesis, the white shark evolved as a result of dwarfism from a larger ancestor. However, the neck that lacks enameloid seen in *C. megalodon* and other megatoothed sharks is not seen in *C. carcharias*. In addition, serrations are much finer in the megatoothed sharks than in *C. carcharias* (Nyberg et al., 2006). Proponents of this hypothesis (e.g., Gottfried et al., 1996; Purdy et al., 2001) assess a case of heterochrony in which large teeth of *C. carcharias* and equal-sized teeth of *C. megalodon* look very similar (Nyberg et al., 2006).

The second hypothesis contends that the megatoothed sharks are in a separate family (the Otodontidae) and that *C. carcharias* shares a more recent common ancestor with the mako sharks (Fig. 3B), including *Isurus hastalis* (Casier, 1960; Glickman, 1964; Muizon and DeVries, 1985; Cappetta, 1987; Nyberg et al., 2006). In this scenario, the species *C. megalodon* and the other megatoothed sharks are allocated to the genus *Carcharocles* and placed within the Otodontidae with *Otodus* and *Parotodus* (sensu Casier, 1960; Glickman, 1964; Capetta, 1987). Casier (1960) considered that the labiolingual flattening in the teeth of both the fossil *Isurus* (specifically *I. xiphidon* of Purdy et al., 2001) and *Carcharodon carcharias* is a shared derived character (Nyberg et al., 2006). Muizon and DeVries (1985) also suggested a possible *Isurus–Carcharodon* relationship when they described weakly serrated teeth from the early Pliocene Pisco Formation of Peru that they believed show characters of both *Isurus* and *Carcharodon carcharias*. It should be noted that their interpretation was challenged by Purdy (1996) and Purdy et al. (2001) because the fossil record for *Carcharodon* has been reported to extend into the middle Miocene elsewhere, pre-dating the Peruvian specimens. These other specimens of *Carcharodon* have been described from the middle to late Miocene of Maryland (Gottfried and Fordyce, 2001), California (Stewart, 1999, 2000, 2002), and Japan (Hatai et al., 1974; Tanaka and Mori, 1996; Yabe, 2000). In addition, molecular-clock dating on the origins of *Carcharodon* has shown a divergence time close to 60 Ma (Martin, 1996; Martin et al., 2002). Nyberg et al. (2006) used morphometric analysis to compare geometrically the teeth of *I. hastalis*, *I. xiphodon*, *Carcharodon carcharias*, *Carcharocles megalodon*, and the "Sacaco sp.," the latter representing the transitional species of Muizon and DeVries (1985) and *Carcharodon* sp. of this paper. Based on tooth and serration shape, they concluded that *Carcharodon carcharias* and *Isurus* are more closely related than are *Carcharodon carcharias* and the megatoothed sharks.

MATERIALS, METHODS, AND ABBREVIATIONS

Tooth nomenclature follows that of Shimada (2002), except that we use 'lower third anterior tooth' rather than 'lower

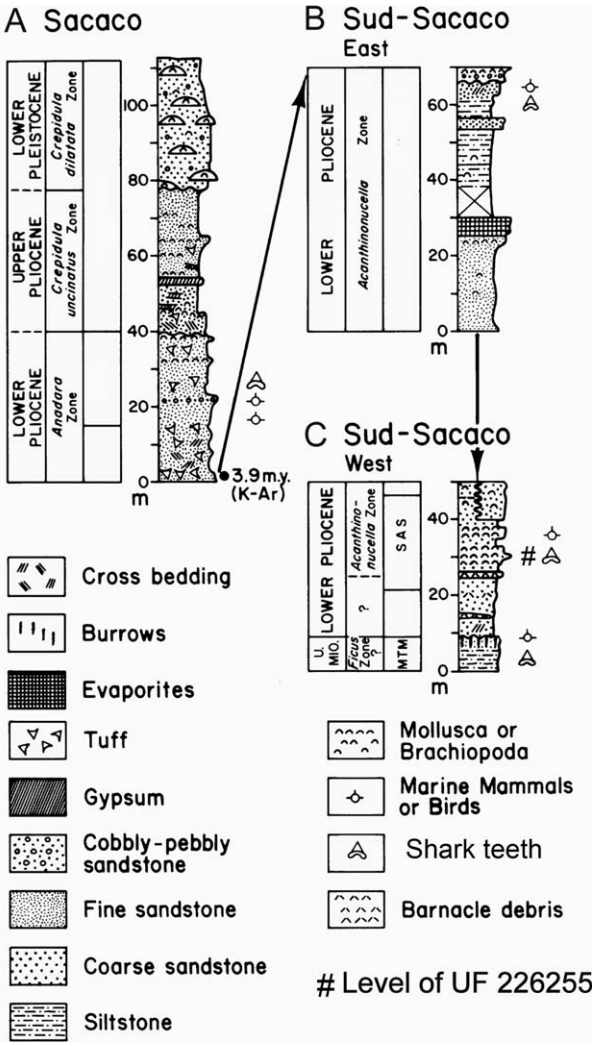

FIGURE 2. Measured sections of Pisco Formation (A–C) in Sacaco basin (from Muizon and DeVries 1985; also see Figure 1) and stratigraphic context (section C) of *Carcharodon* sp., UF 226255, from early Pliocene Pisco Formation of Peru.

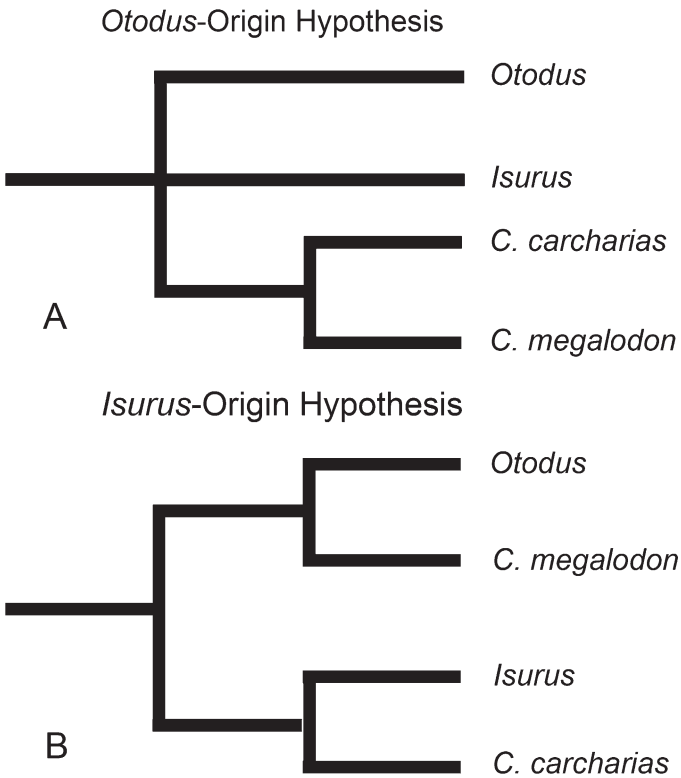

FIGURE 3. Phylogenies of possible origination of *Carcharodon carcharias*. **A**, *Otodus*-origin hypothesis proposes that *C. carcharias* descends from megatoothed sharks. **B**, *Isurus*-origin hypothesis proposes that *C. carcharias* descends from *I. hastalis*.

intermediate tooth' as proposed and used by Shimada (2002, 2007) in order to retain the most commonly used terminology. Five measurements were taken on the labial side of each tooth in the functional series, following Hubbell (1996) and Shimada (2002): (1) crown height: the vertical distance between a line, drawn across the lowest reaches where the tooth enamel touches the root, and the apex of the crown; (2) basal crown width: the widest region of the enamel, located where the enamel and root meet; (3) mesial crown edge length: the number of serrations along the edge of the tooth facing the jaw midline; (4) distal crown edge length: the number of serrations along the edge of the tooth facing the outer edge of the jaw; and (5) degree of slant: the angle between a perpendicular line that bisects a line drawn across the lowest reaches where the tooth enamel touches the root and another line drawn from that point that runs through the apex of the tooth (i.e., inclination). The angle is positive if the tooth is slanted toward the distal side of the mouth and negative if the tooth is slanted toward the mesial side of the mouth (Table 1).

The vertebral centra were measured, imaged using X-radiography, and subjected to incremental growth and isotopic analyses. The diameter of each prepared centrum was taken using the longer (dorsoventral) measurement. It should be noted that in the anterior-most vertebrae, the anterior and posterior articular surfaces have different diameters (the posterior surface being larger than the anterior surface). The posterior, or larger, diameters are recorded here. Anteroposterior length measurements were also taken along the dorsal side of the centra.

To differentiate density differences between light and dark bands, X-rays were taken at the C. A. Pound Human Identification Laboratory at the University of Florida. The X-rays were set at 78 kV for 2 minutes following MacFadden et al. (2004). Using this technique, X-ray images are the reverse of those seen in the actual specimen (i.e., dark bands appear as light bands and light bands appear as dark bands). Using Adobe Photoshop, the X-ray images were then reversed to show light and dark banding for age and isotopic analysis.

To interpret incremental growth bands preserved, one precaudal vertebral centrum was sampled for carbon and oxygen isotopic analysis. The centrum was mounted to a petri dish for stability and sampled using a MicroMill^{TM} computer interfaced automated drilling device. Thirty-one microsamples of approximately 5 mg each were collected by running the drill to a depth of 100 μm across the centrum. Samples were taken consecutively across the growth axis from the center to the outer margin, using a method similar to that described in MacFadden et al. (2004). The goal was to sample the light and dark bands across the centrum. Sample powders were treated using established isotope preparation techniques for fossil hydroxylapatite (e.g., Koch et al., 1997). This includes successive treatments with H_20_2, weak (0.1 M) acetic acid, and then a methanol rinse. About 1–2 mg of the resulting treated powder was analyzed in the VG Prism stable isotope ratio mass spectrometer using an automated carousel introduction device for each sample at the Center for Isotope Geoscience, Department of Geological Sciences, University of Florida. The carbonate fraction of the hydroxylapatite was analyzed using this method and the results are presented below using the standard notation:

$$\delta \text{ (parts per mil, ‰)} = [R_{sample}/R_{standard}\text{-}100] \times 1{,}000$$

where R = either $^{13}C/^{12}C$ or $^{18}O/^{16}O$ of the sample being analyzed, as compared to the "Vienna" PDB (Pee Dee Belemnite) standard (Coplen, 1994).

Abbreviations—The following abbreviations are used in the text: **A1**, first upper anterior tooth; **a1**, first lower anterior tooth; **A2**, second upper anterior tooth; **a2**, second lower anterior tooth; **a3**, third lower anterior tooth; **CH**, crown height; **BCW**, basal crown width; **I**, intermediate tooth; **L**, upper lateral teeth; **l**, lower lateral teeth; **PCL**, pre-caudal length; **TL**, total body length; **UF**, Vertebrate Paleontology Collection, Florida Museum of Natural History, Gainesville, Florida; **VD**, vertebral diameter; **VR**, vertebral radius.

SYSTEMATIC PALEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880
Subclass ELASMOBRANCHII Bonaparte, 1838
Order LAMNIFORMES Berg, 1958
Family LAMNIDAE Müller and Henle, 1838
Genus *CARCHARODON* Linnaeus, 1758
CARCHARODON sp.

Referred Material—UF 226255, exceptionally well-preserved, articulated individual consisting of upper and lower jaws with 222 teeth and 45 associated precaudal vertebral centra (Fig. 4).

Occurrence—Collected from Sud-Sacaco West, approximately 30 m above base of measured section (Muizon and DeVries, 1985), Upper Pisco Formation; approximately 5 km east of Lomas (Punta Lomas), coastal Peru, 15° 33' S, 74° 46' W; early Pliocene, more than 3.9 Ma (Figs. 1, 2).

Anatomical Description

Mandibular Arch—Portions of both palatoquadrates and Meckel's cartilages are preserved, although, the specimen is flattened dorsoventrally, making it very difficult to reconstruct the anteroposterior shape of the jaws (Fig. 4). The palatoquadrates lack most of the dorsal portions on both left and right sides, with preserved cartilage beginning just above where the functional

TABLE 1. Tooth measurements for all teeth in the functional series of UF 226255.

Tooth	CH	CW	Angle (°)	Distal Length	Mesial Length	Distal Serrations	Mesial Serrations
Right Side							
A1	44.6	34.7	1	48.9	47.7	39	32
A2	42.7	36.8	1	46.7	50.2	34	38
I	33.0	31.8	3	35.9	38.5	28	29
L1	34.1	35.1	4	34.1	45.3	28	30
L2	24.4	34.9	3	37.4	42.7	32	27
L3	31.5	34.3	6	33.8	41.6	29	26
L4	24.5	26.1	2	25.7	30.2	22	26
L5	17.5	22.9	2	19.4	24.8	16	17
L6	12.0	17.7	1	13.0	16.2	7	8
L7	8.5	12.2	1	9.4	11.5	2	1
L8	6.6	10.2	1	7.3	8.2	1	0
L9	4.7	8.7	1	5.0	7.0	0	0
L10	3.0	7.6	0	5.0	4.4	0	0
a1	37.8	28.5	0	40.4	39.4	31	26
a2	43.0	31.4	0	46.1	46.4	32	33
a3	31.2	27.8	–1	34.0	32.5	18	23
l1	27.8	27.7	–1	31.7	29.6	26	24
l2	23.9	22.1	–1	27.2	24.4	20	15
l3	20.0	21.0	0	21.9	21.9	10	17
l4	13.7	16.7	–1	16.2	15.9	1	1
l5	9.5	14.0	–1	10.9	12.7	1	1
Left Side							
A1	43.5	34.0	2	46.4	48.8	37	39
A2	43.0	36.2	2	46.0	51.1	38	39
I	30.3	30.7	3	33.2	38.2	26	23
L1	33.7	34.6	6	33.6	44.2	29	33
L2	35.3	35.0	2	36.8	44.6	27	28
L3	32.9	34.5*	2	35.0*	43.8*	23	26
L4	24.8	28.3	2	26.2	33.4	20	18
L5	17.5	17.6*	1	18.3	17.6*	12	8
L6	12.8	16.5	2	13.3	16.7	8	10
L7	9.4	12.6	1	10.5	11.9	1	1
L8	7.6	11.4	1	8.1	9.9	1	1
a1	37.7	29.3	0	41.0	39.7	30	28
a2	41.7	31.4	0	44.2	44.9	31	23
a3	31.9	28.1	–1	36.9	36.5	26	22
l1	28.4	27.2	–1	32.3	29.2	23	21
l2	24.6	27.2	–1	30.6	27.3	16	13
l3	19.8	21.4	0	22.0	22.5	9	11
l4	15.9	18.6	0	17.9	17.6	1	1
l5	9.1	14.0	0	11.5	12.2	1	1
l6	6.8	11.2	0	8.2	9.1	0	0
l7	5.0	9.0	0	5.6	6.9	0	0
l8	3.6	8.0	0	4.5	5.6	0	0

All measurements in millimeters and abbreviations are in the text. Tooth angle is given in degrees; teeth are inclined distally unless denoted with (-), then they are inclined mesially. Measurements denoted with (*) are teeth that are damaged or have missing pieces.

tooth series was present and arcing laterally. The left palatoquadrate is not preserved distally, resulting in the loss of several lateral tooth rows. The upper dental bullae are present and contain both the anterior and intermediate tooth rows. There is a defined intermediate bar on each palatoquadrate that appears as a labiolingual constriction in the cartilage of the jaw (Siverson, 1999). The intermediate bar is preceded distally by the lateral teeth, which are not situated in the upper dental bullae. The symphysis of each palatoquadrate is square and relatively deep. The palatoquadrates do connect distally with the Meckel's cartilages; however, the medial and lateral quadratomandibular joints are not discernable due to the dorsoventral flattening of the specimen. Although the mouth is preserved agape, the palatoquadrates protrude farther than the Meckel's cartilages, suggesting a subterminal mouth. Length measurements were taken from the symphysis to the distal edge of the seventh lateral tooth position. This landmark was chosen because the seventh lateral tooth is the distal-most tooth preserved in both palatoquadrates. The left palatoquadrate measures 33.4 cm while the right palatoquadrate measures 32 cm for the same distance. The lateral gape of the palatoquadrates was also measured, also using the distal edges of the seventh lateral teeth as landmarks, and is 48 cm across. The absence of the distal portion of the left palatoquadrate makes it impossible to assess the true gape of the specimen.

The Meckel's cartilage is significantly deeper than the palatoquadrate. However, the posterior portions of both cartilages are highly fragmented and their exact shape is not distinguishable. There is significantly less arcing seen in the lower jaws in comparison to the palatoquadrates. The lower symphysis of the Meckel's cartilages appears to be shallower than that of the palatoquadrates, suggesting a weaker connection (Shimada and Cicimurri 2005). Due to the better preservation of the lower jaws, lengths were taken of both Meckel's cartilages from the symphysis to the lateral edges of the cartilage. The left Meckel's cartilage measures 28.5 cm while the right measures 25.5 cm.

Neurocranium—The posterior portion of the neurocranium is the only part preserved in UF 226255 (Fig. 4). It is also flattened dorsoventrally and does not preserve much structure. The occipital hemicentrum and the anterior portion of a foramen magnum are present (Fig. 4). Other fragments of sheet-like preserved cartilage within the jaws are most likely attributable to the basal plate of the neurocranium. While some perforations are visible in this preserved cartilage, some appear to be areas of erosion

and not true foramina. No other defined structures are visibly identifiable.

Dentition—A total of 222 teeth is present on the articulated palatoquadrates and the Meckel's cartilages. The functional series has been removed for study (Figs. 5 and 6), leaving four to five replacement series visible, depending on the tooth row. The teeth are flattened labiolingually, with a slight convex curve on the lingual surface. CH of individual teeth within the functional tooth series ranges from 44.6 mm for the largest anterior tooth to 2.9 mm for the smallest lateral tooth (Table 1). The enameloid shows some post-mortem cracking and peeling on a few teeth, but is otherwise well preserved.

Although UF 226255 is most similar to *C. carcharias*, the morphology of the tooth series is not entirely diagnostic of the modern white shark, showing a distal inclination of the intermediate tooth (Figs. 5 and 7). Each palatoquadrate contains two anterior and one intermediate tooth. The upper right side contains ten lateral teeth, whereas the upper left side contains eight lateral teeth (Fig. 5). In the lower jaw there are three anterior teeth in each side of the Meckel's cartilage. There are five lateral teeth on the right side while the left side contains eight laterals (Fig. 6). The discrepancy in the number of lateral teeth in the palatoquadrates and Meckel's cartilages is a result of preservation, with the loss of some teeth on the left side during fossilization. The serrations are weaker than those seen in extant white sharks. Anterior teeth average more than 30 serrations per side, while lateral teeth vary from more than 30 serrations per side for the larger laterals to no serrations for the distal-most laterals. There is no consistent differentiation in the number of serrations per centimeter between the anterior and lateral teeth. All teeth that have serrations average 8–12 serrations per centimeter on both mesial and distal sides (Fig. 8). The most basal serration on most of the teeth is larger than the other serrations. This larger, basal serration is very similar to the lateral cusplets seen in juvenile teeth of *Carcharodon carcharias* (Uyeno and Matsushima, 1979; Hubbell, 1996). The teeth in the lower jaw are smaller than the corresponding upper teeth in both CH and BCW.

In the palatoquadrate, the two anterior teeth are the largest in the series. The intermediate tooth has a distal inclination, which is atypical for *Carcharodon* (Figs. 5, 7). The first two lateral teeth are larger than the intermediate tooth and become progressively smaller distally. The lateral teeth also have a distal inclination, with the first lateral tooth having the strongest asymmetry. In the lower jaw, the second anterior tooth is larger than the first. The lateral teeth become progressively smaller distally, as seen in the palatoquadrate. There is very little inclination of the teeth in the lower jaw. The roots of the upper teeth are rectangular, with a weak basal concavity (Fig. 6). The roots of the lower teeth have a deep basal concavity and are somewhat thicker than those of the upper teeth, giving them a relatively bulbous appearance. The concavity is most prominent in the anterior teeth, and becomes less so in the lateral series. Central foramina are also present labially in some roots, primarily in the first several laterals in both the upper and lower jaws.

Replacement tooth series are also present in UF 226255. The replacement teeth are identical in morphology and appearance to those of the functional series. These series consist of both fully formed teeth labially and enameloid shells that represent teeth that have not fully formed lingually. There are three series of fully developed upper and lower anterior teeth and two series of enameloid shells in labio-lingual succession. This differs from the number of series of lateral teeth, for which there are two series of fully developed upper and lower lateral teeth and two series of enameloid shells present.

Vertebral Centra—UF 226255 contains 45 vertebrae including the first seven centra in situ and connected to the occipital hemicentrum (Fig. 4). The *remaining* preserved vertebrae are in small numbered blocks of two to five centra that have not been prepared.

The centra are laterally compressed, with concave articular surfaces that show clear, concentric, calcified lamellae (Ridewood, 1921; Fig. 9). Sunken pits present in the center of the articular surfaces indicate the position of a notochordal constriction (Gottfried and Fordyce, 2001). Centra are composed of two calcified cones supported by radiating calcified lamellae within the intermedialia, with paired pits for the insertion of both the haemal and neural arches. Lamellae vary in number and size around the circumference of each centrum. Lateral compression of the centra gives them an oblong appearance and results in a larger dorso-ventral diameter. The measurements of dorso-ventral diameters for the first 17 centra range from 47.2 to 76.2 mm. These diameters are based on the posterior articular surface, which is larger than the anterior surface in the first several centra. Antero-posterior length measurements range from 19.4 to 38.6 mm. The articular surfaces show well-marked dark-light incremental couplet rings that are interpreted to represent annular growth cycles (Cailliet et al., 1985), as is also discussed below.

DISCUSSION

Fossil Record and Evolution of *Carcharodon carcharias*

Carcharodon is a monotypic genus belonging to the order Lamniformes. Within the Lamniformes, the genus is placed in the Family Lamnidae (the mackerel sharks) along with *Isurus* and *Lamna*. Based on molecular data and morphological analyses, *Isurus* and *Carcharodon* are considered to be sister taxa (Compagno, 1990; Martin, 1996; Naylor et al., 1997; Martin et al., 2002; Shimada, 2005). The similarities in tooth morphology between the two taxa are consistent with this interpretation. However, the origination time for the genus *Carcharodon* based on molecular clock analyses has yielded a divergence time close to 60 Ma (Martin 1996; Martin et al., 2002).

Purdy et al. (2001) allocate the weakly serrated teeth described by Muizon and DeVries (1985) of Peru to *I. xiphidon* from the late Miocene and dismiss an *Isurus–Carcharias* transition based on the presence of *Carcharodon* fossils from the middle to late Miocene. The oldest fossil specimen attributed to the species *Carcharodon carcharias* appears to be a single tooth from the late Miocene of Maryland (Gottfried and Fordyce 2001). We disagree with the conclusions of Purdy et al. (2001) for two reasons: (1) the complete tooth set described here does not match the characters of *I. xiphodon* based on their artificially assembled composite tooth set; and (2) the temporal range of the specimens alone cannot discount an *Isurus* origin for *C. carcharias* (Nyberg et al., 2006).

The associated specimen described here from the early Pliocene of Peru shows morphological characters that are present in *Carcharodon carcharias* and *Isurus hastalis*. The A1 tooth, is the largest in the dentition and it is symmetrical, as seen in *C. carcharias* (Uyeno and Matsushima, 1979; Purdy et al., 2001). In UF 226255, the A2 tooth is slightly larger than the a2, another character of *C. carcharias* (Compagno, 2001). There are also weak serrations found on a majority of the teeth in the dentition; however, the use of this character has been debated for use in phylogenetic analysis (Purdy et al., 2001; Nyberg et al., 2006). Alternatively, the intermediate tooth (I) in this specimen is inclined distally, a feature characteristic of the genus *Isurus* (Compagno, 2001). UF 226255 has more characters in common with *Carcharodon*, and that is why we designate it as such. UF 226255 may be considered a new species; however, at the present time, the correct specific name is unclear and thus UF 226255 is designated as *Carcharodon* sp.

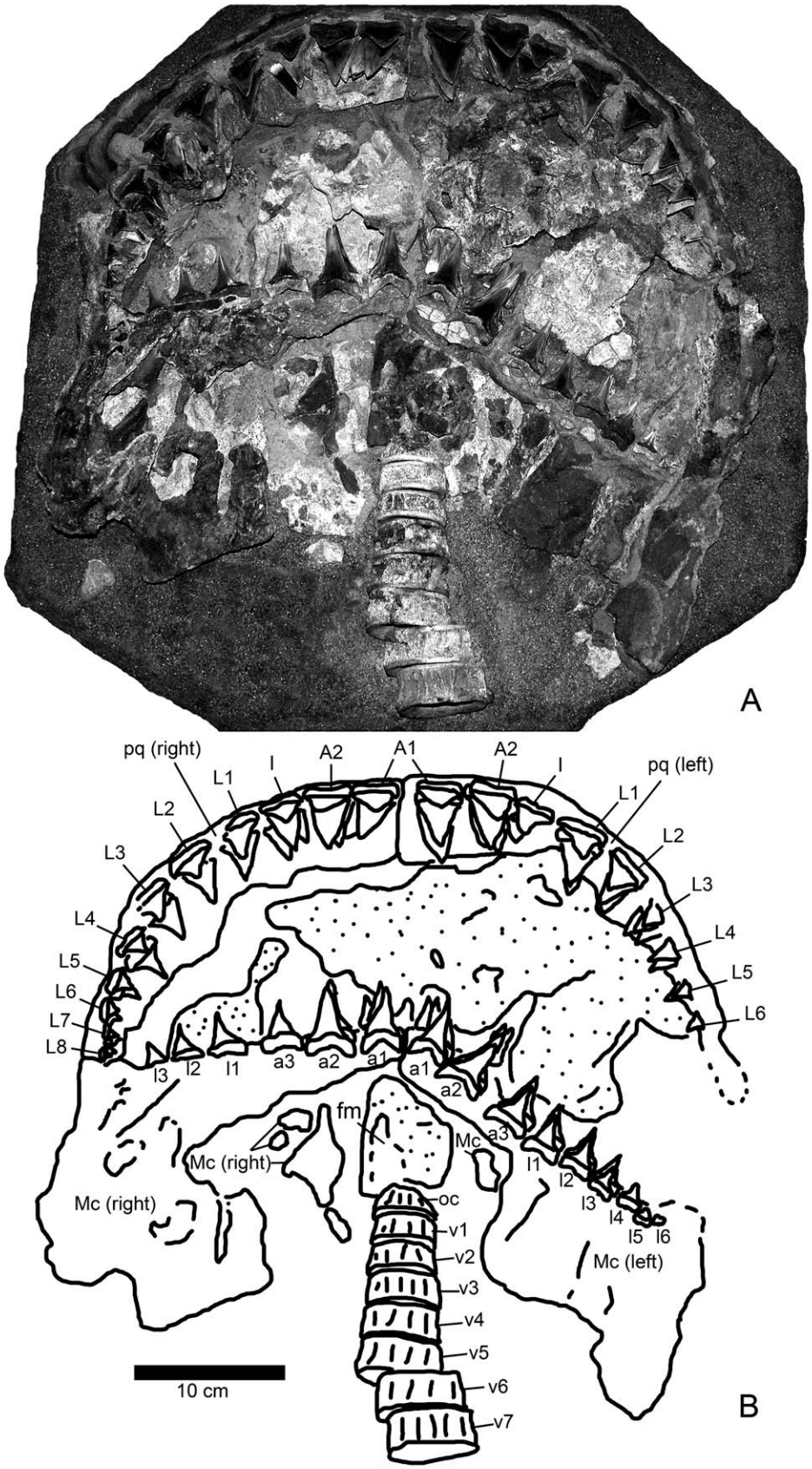

FIGURE 4. Ventral view of UF 226255, consisting of associated dentition, preserved cartilage of the jaws, and seven of the associated vertebral centra. **A**, photograph; **B**, line-drawing (stippled areas represent cartilage of the neurocranium). Note: not all tooth positions present are represented in the line-drawing because some teeth have been removed from the specimen. **Abbreviations**: **A**, upper anterior tooth; **a**, lower anterior tooth; **fm**, foramen magnum; **I**, intermediate tooth; **L**, upper lateral tooth; **l**, lower anterior tooth; **Mc**, Meckel's cartilage; **pq**, palatoquadrate; **oc**, occipital hemicentrum; **v**, vertebra.

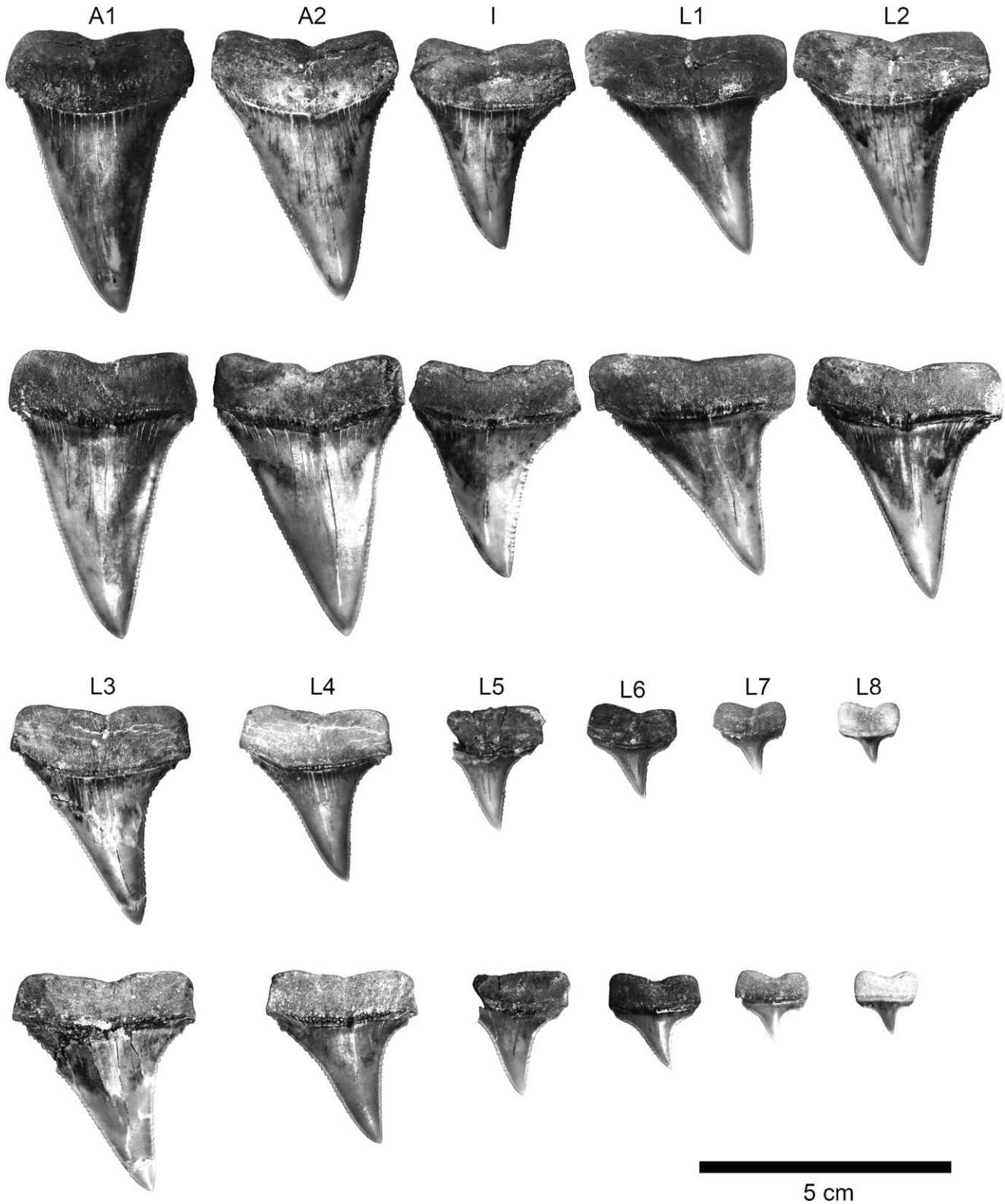

FIGURE 5. Close-up view of upper teeth of *Carcharodon* sp. Top row shows lingual view (depicting upper right dentition); bottom row shows labial view (images reversed to depict upper left dentition). **Abbreviations**: as for Fig. 4.

Incremental Growth of Vertebral Centra

The cartilaginous centra of sharks progressively calcify (Ridewood, 1921), being mineralized with hydroxylapatite, thus providing a potentially preservable record of incremental growth during ontogeny. MacFadden et al. (2004) found that even though early Eocene centra of the lamnoid *Otodus obliquus* from Morocco were highly altered by diagenesis

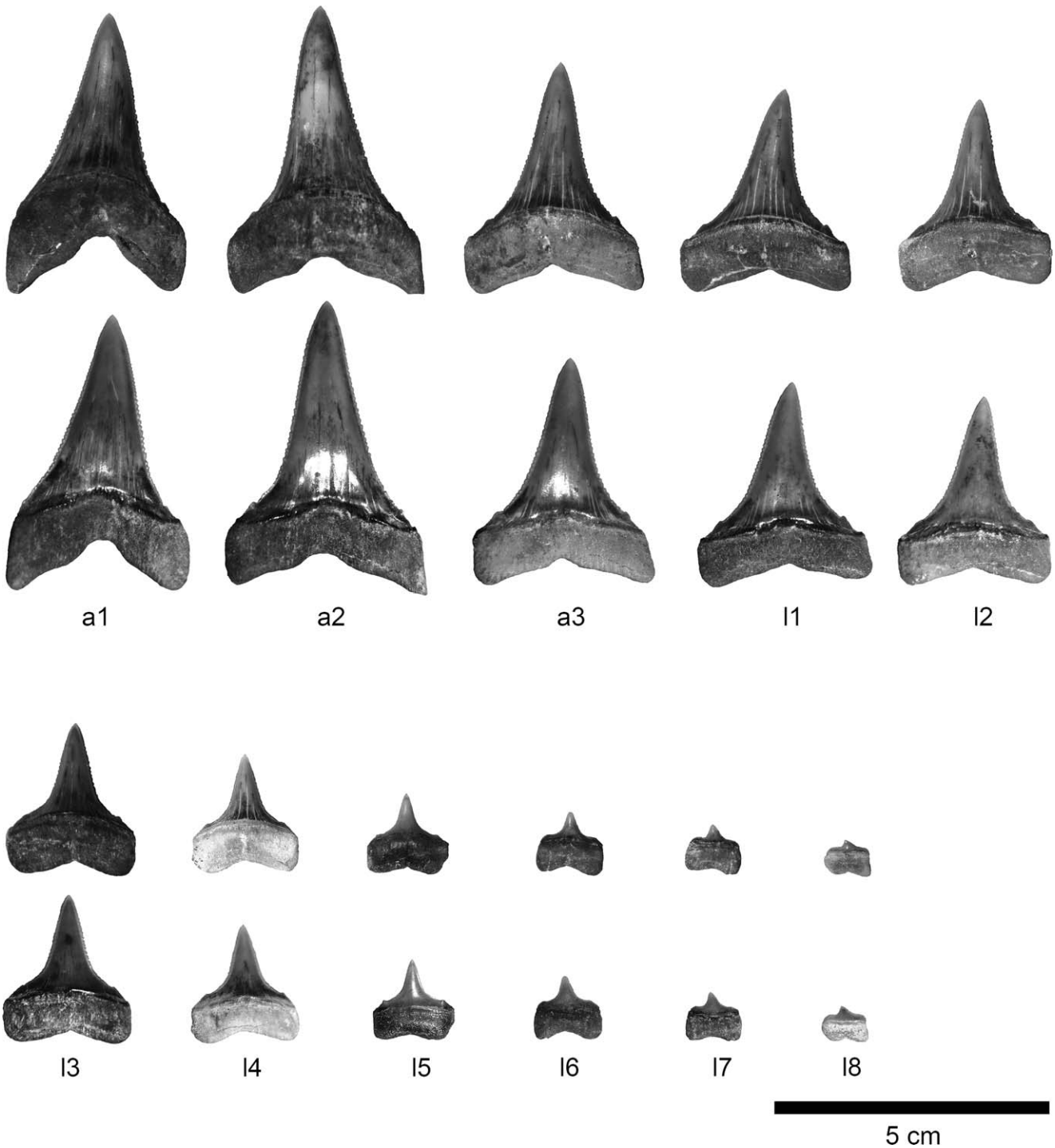

FIGURE 6. Close-up view of lower teeth of *Carcharodon* sp. Top rows shows lingual view (depicting lower right dentition); bottom row shows labial view (images reversed to depict lower left dentition). **Abbreviations**: as for Fig. 4.

(Labs-Hochstein and MacFadden, 2006), they nevertheless archived a predictable pattern of $\delta^{18}O$ across the growth axis. This pattern was interpreted to represent seasonal differences in environmental temperature experienced by the sharks, although we recognize that this is not necessarily the case for all elasmobranchs (Cailliet et al., 1986; Branstetter, 1987; Natanson and Cailliet, 1990). Similar signals are also found in modern lamnoid sharks (Labs Hochstein and MacFadden, 2006), which likewise preserve growth couplets (Cailliet et al., 1986; Wintner and Cliff, 1999; Cailliet and Goldman, 2004; Cailliet et al., 2006), with the darker bands representing times of relatively slower growth during colder seasons (as confirmed by increased $\delta^{18}O$) and the lighter bands correspondingly representing periods of more rapid growth during warmer seasons (also confirmed by more negative $\delta^{18}O$ values). These dark-light band couplets are therefore interpreted to represent 'annuli,' i.e., annular growth cycles of

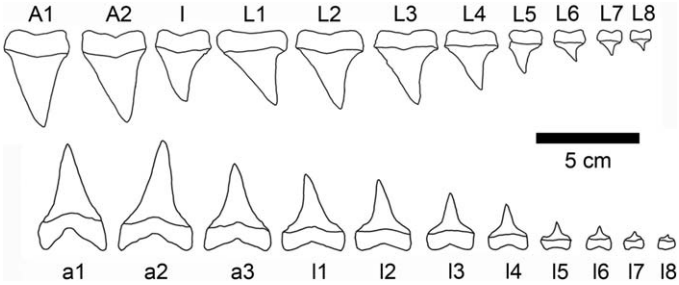

FIGURE 7. Reconstruction of tooth set of UF 226255 with teeth labeled.

progressive mineralization. In addition to those of *O. obliquus*, similar physical incremental growth, interpreted as annuli, has been described for other fossil lamnoids, including the exceptionally well-preserved Oligocene *Carcharocles angustidens* from the late Oligocene of New Zealand (Gottfried and Fordyce, 2001) and *Cretoxyrhina mantelli* from the late Cretaceous of Kansas (Shimada, 1997). It should be noted, however, that although annuli characteristically correspond to annual growth cycles, they sometimes can represent other, non-annual periodicities. Thus, in this paper we use isotopes as an independent proxy to elucidate and calibrate the incremental growth pattern of UF 226255.

Isotopic analyses of microsamples from eight dark and nine light bands, interpreted to represent, respectively, increments of slower winter and faster summer growth, were sampled along the growth axis of one of the associated centra of UF 226255 (Fig. 10; Table 2). For the carbon isotope data (Table 2), Student t ($t_{observed} = 0.626$, $t_{critical} = 2.131$, $P = .540$) and Mann-Whitney U ($Z_{observed} = 0.289$, $Z_{critical}$, $P = .773$) tests indicate that there are no significant differences ($P = .05$) for the microsamples of the dark versus light bands. In modern sharks, including the white, carbon isotope data vary with the trophic level of the prey species eaten (Estrada et al., 2006). Thus, a shark feeding on predatory marine mammals such as carnivorous seals would have a relatively higher $\delta^{13}C$ signal than one feeding on an herbivorous mysticete whale. Using this extant model, the lack of significant variation in the $\delta^{13}C$ signal for UF 226255 is interpreted to indicate that there are no seasonal or ontogenetic differences in the trophic level of the diet of this shark. In contrast, for the oxygen isotope data (Table 2), Student t ($t_{observed} = 2.549$, $t_{critical} = 2.131$, $P = .020$) and Mann-Whitney U ($Z_{observed} = 2.502$, $Z_{critical} = 1.960$, $P = .012$) tests indicate statistically significant differences ($P = .05$) between the dark and light bands, with the mean value for $\delta^{18}O$ for the winter bands being more enriched, as would be expected if this indeed is accurately archiving a temperature proxy (MacFadden et al., 2004).

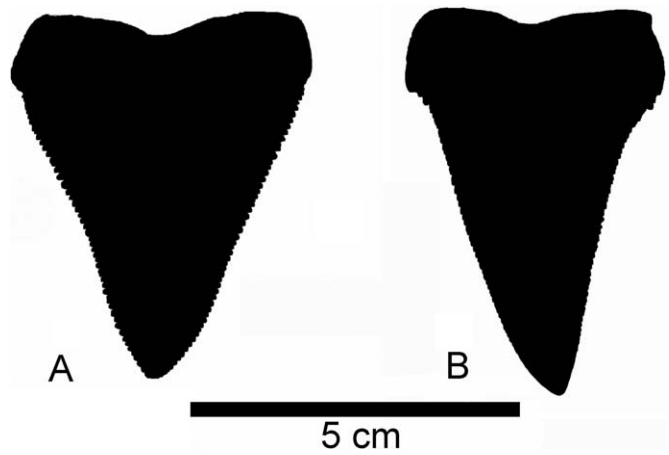

FIGURE 8. Silhouettes of A1 teeth for comparison of serration types. **A**, *Carcharodon carcharias*; **B**, *Carcharodon* sp.

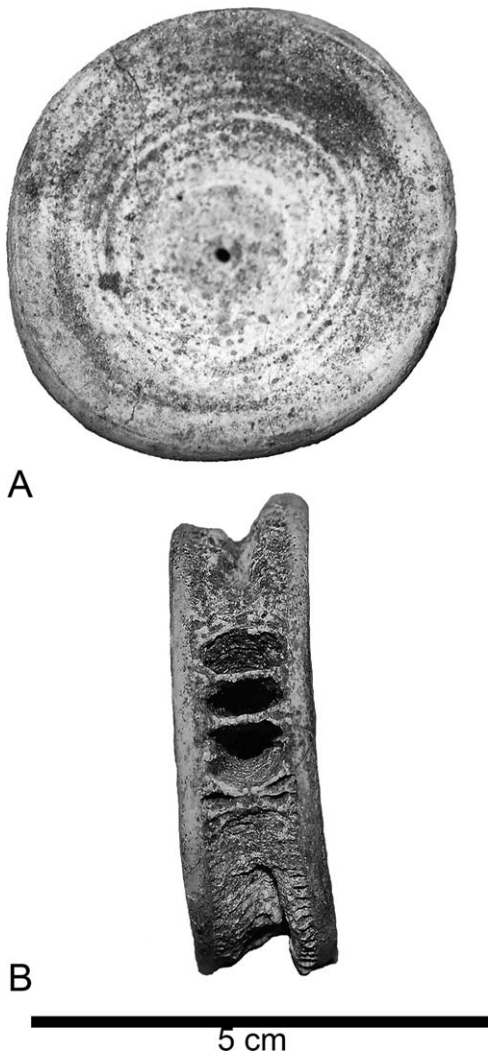

FIGURE 9. First vertebral centrum of UF 226255. **A**, anterior view; **B**, dorsal view.

So far as can be determined, adjacent dark-light band 'couplets' (Fig. 10) are interpreted to represent annuli, or intervals of annular growth similar to those seen in modern sharks, including white sharks (Francis, 1996; Wintner and Cliff, 1999). Using this assumption, approximately 20 (±1) dark-light band couplets can be counted. It is concluded, therefore, that UF 226255 was at least 20 years old when it died. Most vertebrates follow a Von Bertalanffy growth curve (Von Bertalanffy, 1960), where incremental growth decreases through later ontogeny, particularly from the time that individuals reach sexual maturity until later years during their lifetime. Decreased annular growth is correlated with onset of sexual reproduction. For example, a 5.36 m-long modern pregnant white shark caught off the coast of New Zealand was estimated from incremental growth of its centrum to have been 22 years old. Growth rate during the later years had decreased (Francis, 1996). Comparing UF 226255 with published growth curves for *Carcharodon carcharias*, the fossil

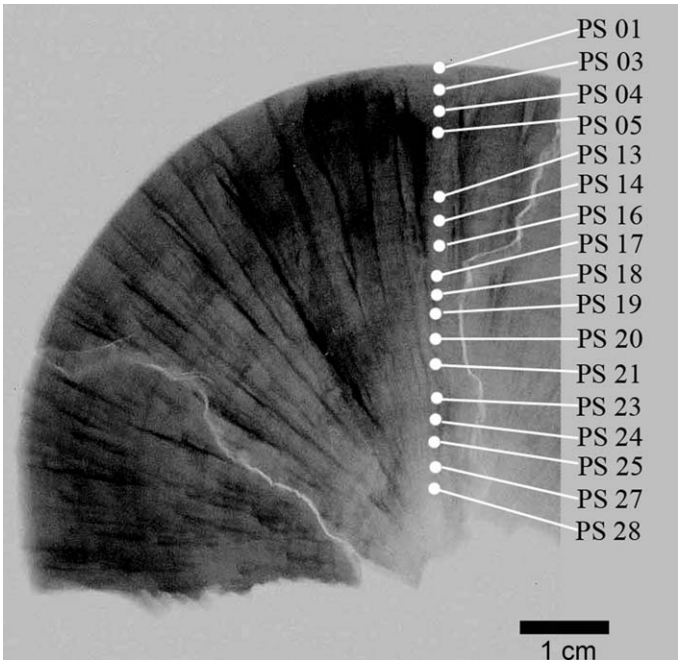

FIGURE 10. X-ray image of centrum of UF 226255 analyzed for stable isotopes. Image was manipulated using Adobe Photoshop™.

appears to have been growing at a slower rate than extant white sharks (Cailliet et al., 1985; Francis, 1996; Kerr et al., 2006).

Length Estimation of Fossil and Extant *Carcharodon carcharias*

The exaggeration of total length (TL) estimates for modern shark species occurs commonly due to the difficult nature of measuring a large shark. Distortion that occurs while the shark individual is being brought out of the water and the lack of a trained scientist at the time of capture can oftentimes lead to a mismeasurement (Mollet et al., 1996). TL estimates for modern white sharks are also exaggerated because of their fearsome reputation, and have included specimens reported to be 7 to 11.1 m long (Randall, 1973, 1987; Mollet et al., 1996). Most of these TLs have been refuted and even individuals more than 6.4 m in length are somewhat rare (Randall, 1987; Mollet et al., 1996). Two previous papers have published TL estimates for fossil *C. carcharias*, one from the Pliocene (Goto et al., 1984) and one from the Pleistocene (Uyeno and Matsushima, 1979) based on the tooth size regression of Randall (1973). The use of morphometrics has been proven to be a reasonable method for estimating TL (Mollet et al., 1996). When using teeth, CH is used rather than tooth height because: (1) the growth rate between the crown and the root is not isometric; and (2) fossil teeth do not necessarily preserve the entire root, making TL estimates inaccurate (Shimada 2002).

The growth regressions of Shimada (2003) were used to correlate CH with TL in the fossil specimen. Regressions were published for all tooth positions in Shimada (2003); we used all available fossil teeth to determine an average TL for UF 226255. TL estimates were obtained for all 42 tooth positions present in the specimens and can be seen in Table 3. The mean for the 42 measurements was calculated to provide an estimated TL of 5.07 m.

In addition to using CH, we also extrapolated an estimated TL based on the vertebral diameter (VD) or vertebral radius (VR) as proposed by Cailliet et al. (1985), Gottfried et al. (1996), Wintner and Cliff (1999), and Natanson (2001) following the work of Shimada (2007). The largest measurable vertebral centrum (17th) with a diameter of 76.2 mm was used for these calculations; however, it is not necessarily the largest in the vertebral column. The published regression equations and TL estimates can be seen in Table 4. The mean of the four TL estimates is 4.89 m, which corresponds very closely with the estimate of 5.07 m based on CH measurements. Based on the vertebral annuli, UF 226255 may not have been sexually mature, but using our TL estimates, this individual falls within the range of an extant mature white shark based on Gottfried et al. (1996) and Compagno (2001).

CONCLUSIONS

UF 226255 is an extraordinarily well-preserved fossil lamnid shark from the early Pliocene of Peru. The presence of a nearly

TABLE 2. Stable isotope ($\delta^{13}C$ and $\delta^{18}O$) results from microsampling along growth axis of vertebral centrum of *Carcharodon* sp., UF 226255, from the early Pliocene Pisco Formation, Peru.

Distance from Center (mm)	Lab sample Number (2007)	Band interval Type	$\delta^{13}C$ (‰ VPDB)	$\delta^{18}O$ (‰ VPDB)
14.2	PS 28	Dark	–7.36	0.63
16.5	PS 27	Dark	–7.65	0.75
21.0	PS 25	Light	–8.35	0.18
22.3	PS 24	Light	–8.13	0.05
24.5	PS 23	Dark	–7.76	0.16
27.9	PS 21	Dark	–7.42	0.01
29.7	PS 20	Light	–7.13	–0.07
31.0	PS 19	Light	–7.21	–0.27
32.0	PS 18	Light	–7.22	–0.13
33.2	PS 17	Dark	–7.19	0.10
34.5	PS 16	Dark	–7.04	0.06
37.2	PS 14	Light	–6.86	–0.07
38.3	PS 13	Dark	–6.77	–0.06
46.9	PS 05	Dark	–6.98	–0.07
47.8	PS 04	Light	–6.99	–0.19
48.9	PS 03	Light	–7.57	–0.15
50.2	PS 01	Light	–7.19	–0.21

Pooled mean sample statistics
Dark bands (N = 8): Mean $\delta^{13}C$ = –7.27 ‰ (s = 0.40, min = –7.76, max = –6.78)
Mean $\delta^{18}O$ = 0.20 ‰ (s = 0.32, min = –0.07, max = 0.75)
Light bands (N = 9): Mean $\delta^{13}C$ = –7.41 ‰ (s = 0.51, min = –8.35, max = –6.86)
Mean $\delta^{18}O$ = –0.10 ‰ (s = 0.14, min = –0.27, max = 0.18)

TABLE 3. Total length (TL) estimates based on the CH regressions of Shimada (2003) for each tooth position present.

Tooth	Regression Equation (x = CH)	CH	TL
Right Side			
A1	TL = 5.234+11.522x	44.63	519.46
A2	TL = –2.16+12.103x	42.71	514.76
I	TL = 19.162+15.738x	33.00	538.52
L1	TL = 5.540+14.197x	34.09	489.52
L2	TL = 4.911+13.433x	34.42	467.27
L3	TL = 0.464+14.550x	31.47	458.35
L4	TL = 5.569+17.658x	24.48	437.84
L5	TL = –5.778+26.381x	17.46	454.83
L6	TL = –71.915+50.205x	12.04	532.55
L7	TL = –48.696+69.292x	8.45	536.82
L8	TL = –84.781+104.968x	6.63	611.16
L9	TL = –62.050+142.142x	4.65	598.91
a1	TL = –8.216+14.895x	37.77	554.37
a2	TL = –7.643+13.597x	42.95	576.35
a3	TL = –10.765+17.616x	31.19	538.68
l1	TL = 9.962+17.437x	27.82	495.06
l2	TL = 1.131+19.204x	23.86	459.34
l3	TL = –30.947+25.132x	20.03	472.45
l4	TL = –51.765+35.210x	13.73	431.67
l5	TL = –73.120+55.262x	9.52	452.97
Left Side			
A1	TL = 5.234+11.522x	43.47	506.10
A2	TL = –2.16+12.103x	42.95	517.66
I	TL = 19.162+15.738x	30.30	492.02
L1	TL = 5.540+14.197x	33.74	484.55
L2	TL = 4.911+13.433x	35.27	478.69
L3	TL = 0.464+14.550x	32.92	479.45
L4	TL = 5.569+17.658x	24.80	443.49
L5	TL = –5.778+26.381x	17.45	454.57
L6	TL = –71.915+50.205x	12.80	570.71
L7	TL = –48.696+69.292x	9.36	599.88
L8	TL = –84.781+104.968x	7.62	715.10
a1	TL = –8.216+14.895x	37.74	553.92
a2	TL = –7.643+13.597x	41.69	559.22
a3	TL = –10.765+17.616x	31.90	551.19
l1	TL = 9.962+17.437x	28.39	505.00
l2	TL = 1.131+19.204x	24.60	473.55
l3	TL = –30.947+25.132x	19.82	467.17
l4	TL = –51.765+35.210x	15.86	506.67
l5	TL = –73.120+55.262x	6.81	303.21
l6	TL = –117.456+96.971x	5.01	368.37
l7	TL = –64.732+138.350x	3.55	426.41
l8	TL = –137.583+231.411x	3.60	695.50

complete tooth series preserved with other portions of the skeleton provides new information regarding the evolutionary history of *Carcharodon carcharias*. We allocate this specimen to *Carcharodon,* but without identifying it to species. However, it does retain an important character linking it to the *Isurus* clade. UF 226255 exhibits an intermediate tooth inclination that is diagnostic of *Isurus*, while the presence of serrations, small side lateral cusplets, and an a2 tooth lower than its A2 is diagnostic of *Carcharodon* (Uyeno and Matsushima 1979; Compagno 2001).

TABLE 4. References for TL regressions with the equations.

Reference	Equation [r^2; n; TL conversion (when needed)]	TL
Cailliet et al. (1985)	TL = 35.9 + 5.7 * VD [.90; 67; -]	470
Gottfried et al. (1996)	TL = 22 + 5.8 * VD [.97; 16; -]	464
Wintner and Cliff (1999)	PCL = (VD/10 + 0.3)/0.02 [.96; 114; TL = 5.2 + 1.3 * PCL]	520
Natanson (2001)	FL = 21.0 + 11.8 * VR [.94; 14; TL = (FL + 0.06)/0.94]	501

Abbreviations: **Fl**, fork length; **n**, sample size; **PCL**, pre-caudal length; r^2, correlation coefficient; **TL**, total length; **VD**, vertebral diameter; **VR**, vertebral radius.
TL estimates given in centimeters.

Isotopic analysis of annuli within the centra of this specimen leads to inferences about growth and seasonality during the lifetime of this individual. This specimen grew at a presumably slower rate than modern white sharks based on TL estimates and counts of annuli (Cailliet et al., 1985; Francis, 1996; Kerr et al., 2006). Exceptionally well-preserved specimens, like UF 225266 from the Pisco Formation of Peru, advance our knowledge of the systematics and paleobiology of fossil and extant lamnoid sharks and elucidate their evolutionary history.

ACKNOWLEDGMENTS

This research is supported by National Science Foundation grants EAR 0418042 and 0735554. From the University of Florida we thank J. Curtis, I. Quitmyer, and D. Steadman for assistance with geochemical analyses, and C. Bester and J. Gage for assistance in the preparation of the illustrations. Thomas DeVries from Vashon Island, Washington, and R. Salas-Gismondi and M. Stucchi from the Museo de Historia Natural of Lima, Peru, provided critical assistance in the field in 2007 to relocate the exact site of excavation of UF 226255. Editor J. Maisey and the reviewers K. Shimada and M. Gottfried made constructive suggestions for the improvement of this manuscript. This is University of Florida Contribution to Paleobiology 601.

LITERATURE CITED

Applegate, S. P. and L. Espinosa-Arrubarrena. 1996. The fossil history of *Carcharodon* and its possible ancestor, *Cretolamna*: a study in tooth identification; pp. 19–36 in A. Kimley, and D. Ainley (eds.), Great White Sharks: the Biology of *Carcharodon carcharias*. San Diego, California: Academic Press.

Berg, L. S. 1958. System der rezenten und fossilen Fischartigen und Fische. Berlin, Germany: Deutsche Verlag Wissenschaften, 310 pp.

Bonaparte, C. L. 1838. Selachorum tabula analytica. Nuovi Annali della Science Naturali, Bologna 2:195–214.

Branstetter, S. 1987. Age and growth validation in newborn sharks held in laboratory aquaria, with comments on the life history of the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*. Copeia 1987:291–300.

Cailliet, G. M., and K. J. Goldman. 2004. Age determination and validation in chondrichthyan fishes; pp. 299–447 in J. Carrier, A. Musick, and M. R. Hiethaus (eds.), Biology of Sharks and their Relatives. Boca Raton, Florida: CRC Press.

Cailliet, G. M., R. L. Radke, and B. A. Welden. 1986. Elasmobranch age determination and verification: a review; pp. 345–359 in T. Uyeno, R. Arai, T. Taniuchi, and K. Masuura (eds.), Indo-Pacific Fish Biology. Proceedings of the Second International Conference on Indo-Pacific Fishes. Ichthyological Society of Japan, Tokyo.

Cailliet, G. M., L. J. Natanson, B. A. Welden, and D. A. Ebert. 1985. Preliminary studies on the age and growth of the white shark, *Carcharodon carcharias*, using vertebral bands. Memoirs of the Southern California Academy of Science 9:49–60.

Cailliet, G. M., W. D. Smith, H. F. Mollet, and K. J. Goldman. 2006. Age and growth studies of chondrichthyan fishes: the need for consistency in terminology, verification, validation, and growth function fitting. Environmental Biology of Fishes 77:211–228.

Cappetta, H. 1987. Chondrichthyes II. Mesozoic and Cenozoic Elasmobranchii; in H.-P. Schultze (ed.), Handbook of Paleoichthyology. Volume 3B. New York, NYVerlag Dr. Gustav Fischer193 pp.

Casier, E. 1960. Note sur la collection des poisons Paléocènes et Eocènes de l'Enclave de Cabinda (Congo). Annales du Musée Royal du Congo Belge (A.3) 1, 2:1–48.

Compagno, L. J. V. 1990. Relationships of the megamouth shark, *Megachasma pelagios* (Lamniformes: Megachasmidae), with comments on its feeding habits; pp. 357–379 in H. L. Pratt Jr., S. H. Gruber, and T. Taniuchi (eds.), Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of Fisheries. NOAA Technical Report 90.

Compagno, L. J. V. 2001. Sharks of the world: an annotated and illustrated catalogue of shark species known to date. Volume 2.

Bullhead, mackerel, and carpet sharks (Heterodontiformes, Lamniformes, and Orectolobiformes). Food and Agriculture Organization Species Catalogue for Fishery Purposes 1:1–269.

Coplen, T. B. 1994. Reporting of stable hydrogen, carbon, and oxygen isotopic abundances. Pure and Applied Chemistry 66: 273–276.

DeVries, T. J., and H. Schrader. 1997. Middle Miocene marine sediments in the Pisco basin (Peru). Boletín de la Sociedad Geológica del Perú 87:1–13.

Estrada, J. A., A. N. Rice, L. J. Natanson, and G. B. Skomal. 2006. Use of isotopic analysis of vertebrae in reconstructing ontogenetic feeding ecology in white sharks. Ecology 87:829–834.

Francis, M. P. 1996. Observations on a pregnant white shark with a review of reproductive biology; pp. 157–172 in A. Kimley and D. Ainley (eds.), Great White Sharks: the Biology of *Carcharodon carcharias*. San Diego, California: Academic Press.

Glickman, L. S. 1964. [Sharks of the Paleogene and their Stratigraphic Significance] . Nauka Press, Moscow: , 229 pp. [Russian].

Goto, M., T. Kikuchi, S. Sekimoto, and T. Noma. 1984. Fossil teeth of the great white shark, *Carcharodon carcharias*, from the Kazusa and Shimosa Groups (Pliocene to Pleistocene) in Boso Peninsula and Shimosa Upland, Central Japan. Earth Science [Chikyu Kagaku], 38(6):420–426.

Gottfried, M. D., and R. E. Fordyce. 2001. An associated specimen of *Carcharodon angustidens* (Chondrichthyes, Lamnidae) from the late Oligocene of New Zealand, with comments on *Carcharodon* interrelationships. Journal of Vertebrate Paleontology 21:730–739.

Gottfried, M. D., L. J. V. Compagno, and S. C. Bowman. 1996. Size and skeletal anatomy of the giant "megatooth" shark *Carcharodon megalodon*; pp. 55–89 in A. Kimley, and D. Ainley (eds.), Great White Sharks: the Biology of *Carcharodon carcharias*. San Diego, California: Academic Press.

Hatai, K., K. Masuda, and H. Noda. 1974. Marine fossils from the Moniwa Formation, distributed along the Natori River, Sendai, Northeast Honshu, Japan. Part 3. Shark teeth from the Moniwa Formation. Saito Ho-on Kai Museum Research Bulletin 43:9–25.

Hoffstetter, R. 1968. Un gisement de vertébrés tertiaires à Sacaco (Sud-Pérou), témoin néogène d'une migration de faunes australes au long de la côte occidentale sud-américaine. Comptes Rendus de l'Académie des Sciences, Paris, France 267:1273–1276.

Hubbell, G. 1996. Using tooth structure to determine the evolutionary history of the white shark; pp. 9–18 in A. Kimley and D. Ainley (eds.), Great White Sharks: the Biology of *Carcharodon carcharias*. San Diego, California: Academic Press.

Huxley, T. H. 1880. A Manual of the Anatomy of Vertebrated Animals. D. New York, NY: Appleton, 431 pp.

Kerr, L. A., A. H. Andrews, G. M. Cailliet, T. A. Brown, and K. H. Coale. 2006. Investigations of $\Delta^{14}C$, $\delta^{13}C$, and $\delta^{15}N$ in vertebrae of white shark (*Carcharodon carcharias*) from the eastern North Pacific Ocean. Environmental Biology of Fishes 77:337–353.

Koch, P. L., N. Tuross, and M. L. Fogel. 1997. The effects of sample treatment and diagenesis on the isotopic integrity of carbonate in biogenic hydroxylapatite. Journal of Archaeological Science 24:417–429.

Labs-Hochstein, J., and B. J. MacFadden. 2006. Quantification of diagenesis in Cenozoic sharks: elemental and mineralogical changes. Geochimica et Cosmochimica Acta 70:4921–4932.

Linnæus, C. 1758. Systema Naturae. 10th EditionLaurentii Salvii, Holmiæ, 824 pp.

MacFadden, B. J., J. Labs-Hochstein, I. Quitmyer, and D. Jones. 2004. Incremental growth and diagenesis of skeletal parts of the lamnoid shark *Otodus obliquus* from the early Eocene (Ypresian) of Morocco. Palaeogeography, Palaeoclimatology, Palaeoecology 206:179–192.

Martin, A. F. 1996. Systematics of the Lamnidae and origination time of *Carcharodon carcharias* inferred from the comparative analysis of mitochondrial DNA sequences; pp. 49–53 in A. Kimley and D. Ainley (eds.), Great White Sharks: the Biology of *Carcharodon carcharias*. San Diego, California: Academic Press.

Martin, A. F., A. T. Pardini, L. F. Noble, and C. S. Jones. 2002. Conservation of a dinucleotide simple sequence repeat locus in sharks. Molecular Phylogenetics and Evolution 23:205–213.

Mollett, H. F., G. M Cailliet, A. P. Kimley, D. A. Ebert, A. D. Testi, and L. J. V. Compagno. 1996. A review of length validation methods and protocols to measure large white sharks; pp. 91–108 in A. Kimley and D. Ainley (eds.), Great White Sharks: the Biology of *Carcharodon carcharias*. San Diego, California: Academic Press.

Morgan, G. S. 1994. Miocene and Pliocene marine mammal faunas from the Bone Valley Formation of central Florida; pp. 239–268 in A. Berta, and T. A. Deméré (eds.), Contributions in Marine Mammal Paleontology Honoring Frank C. Whitmore, Jr. Proceedings of the San Diego Society of Natural History, San Diego, California.

Muizon, C. de, and H. G. McDonald. 1995. An aquatic sloth from the Pliocene of Peru. Nature 375:224–227.

Muizon, C. de, and T. J. DeVries. 1985. Geology and paleontology of late Cenozoic marine deposits in the Sacaco area (Peru). Geologische Rundschau 74:547–563.

Muizon, C. de, Domning, D. P., and D. R. Ketten. 2002. *Odobenocetops peruvianus*, the walrus-convergent delphinoid (Mammalia: Cetacea) from the early Pliocene of Peru; pp. 223–262 in R. J. Emry (ed.), Cenozoic Mammals of Land and Sea: Tributes to the Career of Clayton E. Ray. Smithsonian Contributions to Paleobiology no. 93.

Muizon, C. de, McDonald, H. G., Salas, R., and M. Urbina. 2004. The youngest species of the aquatic sloth *Thalassocnus* and a reassessment of the relationships of the nothrothere sloths (Mammalia: Xenarthra). Journal of Vertebrate Paleontology 24:387–397.

Müller, J., and J. Henle. 1838. On the generic characters of cartilaginous fishes. Magazine of Natural History 2:33–37, 88–91.

Natanson, L. J. 2001. Preliminary investigations into the age and growth of the shortfin mako, *Isurus oxyrinchus*, white shark, *Carcharodon carcharias*, and thresher shark, *Alopias vulpinus*, in the Western North Atlantic Ocean. International Commission for the Conservation of Atlantic Tunas Working Document, Standing Committee on Research and Statistics 01/66.

Natanson, L. J., and G. M. Cailliet. 1990. Vertebral growth zone deposition in angel sharks. Copeia 1990:1133–1145.

Naylor, G. J. P., Martin, A. P., E. G. Mattison, and W. M. Brown. 1997. Interrelationships of lamniform sharks: testing phylogenetic hypotheses with sequence data; pp. 199–218 in T. D. Kocher and C. A. Stepien (eds.), Molecular Systematics of Fishes. San Diego, California: Academic Press.

Nyberg, K. G., Ciampaglio, C. N., and G. A. Wray. 2006. Tracing the ancestry of the great white shark, *Carcharodon carcharias*, using morphometric analyses of fossil teeth. Journal of Vertebrate Paleontology 26:806–814.

Purdy, R. 1996. Paleoecology of fossil white sharks; pp. 67–78 in A. Kimley, and D. Ainley (eds.), Great White Sharks: the Biology of *Carcharodon carcharias*. San Diego, California: Academic Press.

Purdy, R., Schneider, V. P., Applegate, S. P., McLellan, J. H., Meyer, R. L., and B. H. Slaughter. 2001. The Neogene sharks, rays, and bony fishes from Lee Creek Mine, Aurora, North Carolina; pp. 71–202 in C. E. Ray, and D. J. Bohaska (eds.), Geology and Paleontology of the Lee Creek Mine, North Carolina, III. Smithsonian Contributions to Paleobiology no. 90.

Randall, J. E. 1973. Size of the great white shark (*Carcharodon*). Science 181:169–170.

Randall, J. E. 1987. Refutation of lengths of 11.3, 9.0, and 6.4 m attributed to the white shark, *Carcharodon carcharias*. California Fish and Game 73:169–174.

Ridewood, W. G. 1921. On the calcification of the vertebral centra in sharks and rays. Philosophical transactions of the Royal Society of London. Series B 210:311–407.

Shimada, K. 1997. Periodic marker bands in vertebral centra of the Late Cretaceous lamniform shark, *Cretoxyrhina mantelli*. Copeia 1997:233–235.

Shimada, K. 2002. Dental homologies in lamniform sharks (Chondrichthyes: Elasmobranchii). Journal of Morphology 251:3–72.

Shimada, K. 2003. The relationship between the tooth size and total body length in the white shark, *Carcharodon carcharias* (Lamniformes: Lamnidae). Journal of Fossil Research 35:28–33.

Shimada, K. 2005. Phylogeny of lamniform sharks (Chondrichthyes: Elasmobranchii) and the contribution of dental characters to lamniform systematics. Paleontological Research 9:55–72.

Shimada, K. 2007. Skeletal and dental anatomy of lamniform shark, *Cretalamna appendiculata*, from Upper Cretaceous Niobrara chalk of Kansas. Journal of Vertebrate Paleontology 27:584–602.

Shimada, K., and D. J. Cicimurri. 2005. Skeletal anatomy of the Late Cretaceous shark, *Squalicorax* (Neoselachii: Anacoracidae). Palaeontoligische Zeitschrift 79:241–261.

Siverson, M. 1999. A new large lamniform shark from the uppermost Gearle Siltstone (Cenomanian, Late Cretaceous) of Western Australia. Transactions of the Royal Society of Edinburgh: Earth Sciences 90:49–66.

Stewart, J. D. 1999. Correlation of stratigraphic position with *Isurus-Carcharodon* tooth serration size in the Capistrano Formation, and its implications for the ancestry of *Carcharodon carcharias*. Journal of Vertebrate Paleontology 19(3, Supplement):78A.

Stewart, J. D. 2000. Late Miocene ontogenetic series of true *Carcharodon* teeth. Journal of Vertebrate Paleontology 20(3, Supplement):71A.

Stewart, J. D. 2002. The first paleomagnetic framework for the *Isurus hastalis-Carcharodon* transition in the Pacific Basin: The Purisama Formation, Central California. Journal of Vertebrate Paleontology 22(3, Supplement):111A.

Tanaka, T., and S. Mori. 1996. Fossil elasmobranchs from the Oiso Formation (late Miocene) in the western part of Kanagawa Prefecture. Bulletin of the Hiratsuka City Museum, 19:67–81.

Uyeno, T., and Y. Matsushima. 1979. Comparative study of teeth from Naganuma Formation of Middle Pleistocene and Recent specimens of the great white shark, *Carcharodon carcharias* from Japan. Bulletin of Kanagawa Prefectural Museum 11:11–30.

Von Bertalanffy, L. 1960. Principles and theory of growth; pp. 137–259 in W. W. Nowinski (ed.), Fundamental Aspects of Normal and Malignant Growth. Amsterdam, The Netherlands: Elsevier.

Wintner, S. P., and G. Cliff. 1999. Age and growth determination of the white shark, *Carcharodon carcharias*, from the east coast of South Africa. Fisheries Bulletin 97:153–169.

Yabe, H. 2000. Teeth of an extinct great white shark, *Carcharodon* sp., from the Neogene Senhata Formation, Miura Group, Chiba Prefecture, Japan. Tertiary Research 20:95–105.

Submitted October 23, 2007; accepted July 13, 2008.