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Short communication

Ontogeny and life history of a large lamniform shark from the Early Cretaceous of North America

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ABSTRACT

Due to an incomplete fossil record, little is known about lamniform shark life history from the Early Cretaceous of North America. Recent discoveries have shown that during this time, some lamniformes reached gigantic sizes (>6–8 m in total length) not seen in earlier species. Given the importance of life history to understand how organisms reach such sizes, we conducted an ontogenetic analysis on three very large shark vertebrae, representing a single individual from the Lower Cretaceous (Albian) Duck Creek Formation of Texas. Using three different techniques (computed tomography, histological sectioning, and surface texture analysis), we were able to show that this individual was born at a relatively small size and subsequently grew at rapid rate, achieving a total length of over 6.3 m in approximately 18 years; a rate not observed in any other Cretaceous species. Comparison of the different aging techniques yielded complementary results; however, surface texture analysis produced the most complete ontogenetic record for this specimen. More work is needed to determine broad patterns in the life history evolution of giant Early Cretaceous lamniform sharks.

1. Introduction

Lamniform sharks represent some of the largest pelagic predators in modern oceans, but their trophic dominance was only established during the last 100 Ma, when large body sizes evolved in multiple lineages (Underwood, 2006). These Early Cretaceous sharks never reached the sizes of some Cenozoic species (>10 m in *Carcharocles megalodon*; Gottfried et al., 1996), but nonetheless achieved impressive lengths (>6–8 m; Shimada, 1997; Frederickson et al., 2015) that hypothetically allowed them to occupy the same ecological position that they hold today. Thus it stands to reason that understanding the growth dynamics of these early giants would greatly benefit our broader knowledge regarding shark ontogeny and evolution.

Little is currently known about how these Early Cretaceous sharks became so large. A poor fossil record has, until now, hindered determining whether their size can be attributed to an increased growth rate or a longer duration of growth than their ancestors. Species from the Upper Cretaceous of North America, however, have a more robust fossil record which has allowed these questions to be investigated in the form of multiple growth studies (Shimada, 2008; Cook et al., 2011; Newbrey et al., in press). For example, *Cretoxyrhina mantelli* had a growth rate, maximum longevity, and total length comparable to those of the modern great white shark (*Carcharodon carcharias*; Shimada, 2008). This means that, by the Late Cretaceous, lamniform sharks had already established themselves as dominant pelagic macropredators.

Our knowledge of giant Early Cretaceous sharks from North America has recently increased with the description of three very large vertebrae from Albian-aged deposits of Texas (OMNH 68860; Frederickson et al., 2015). These new specimens compare closely to another large specimen, from contemporaneous deposits in Kansas (KUVP 16343; Shimada, 1997), which is hypothesized to represent the same species of shark (Fig. 1). This specimen, however, is currently under study (Newbrey, personal communication) and thus was not available for the present analyses. Here, we determine the ontogenetic status of the Texas specimens, in order to contrast the life history strategies of this Early Cretaceous giant

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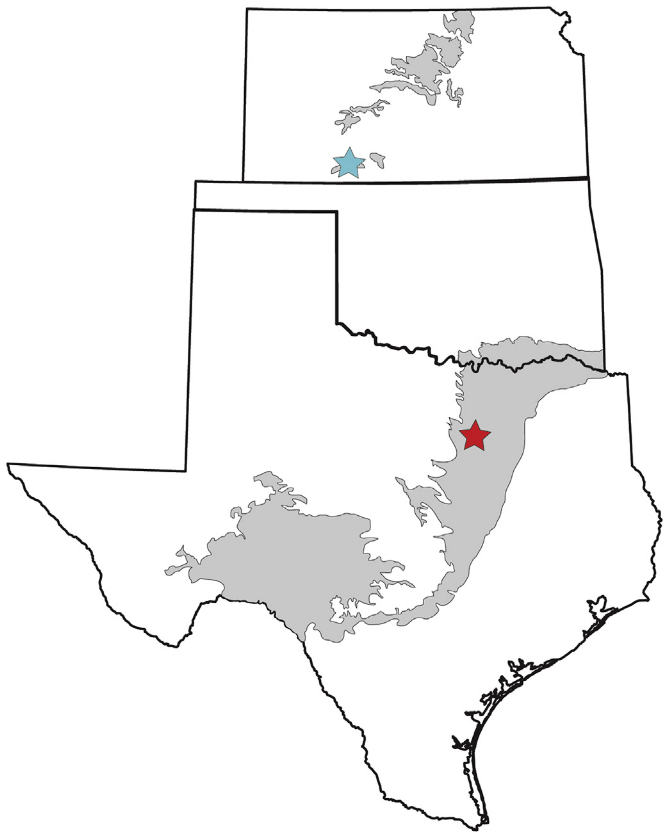

Fig. 1. A map showing the distribution of middle Cretaceous rocks in Kansas, Oklahoma, and Texas, with the approximate locations of discovery of OMNH 68860 (red star) and KUVP 16343 (blue star). Map modified from Kansas Geological Survey (2008), Miser (1954), and The Bureau of Economic Geology (1992). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

shark with later occurring species from the Cretaceous and Cenozoic.

1.1. Institutional abbreviations

KUVP, Kansas University Vertebrate Paleontology Laboratory, Kansas Museum of Natural History, Lawrence, Kansas, USA; OMNH, Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma, USA.

2. Materials and methods

The specimens analyzed consist of three large vertebrae from a single individual (OMNH 68860), herein referred to as A, B, and C following fig. 4 of Frederickson et al. (2015), where specimens A and B represent the two fully prepared and largest (most-rostral) specimens. These specimens come from OMNH V1727 in the upper Albian Duck Creek Formation of Tarrant County, Texas. The largest vertebra (vertebra A) measures approximately 110 mm in centrum diameter, giving the shark a minimum reconstructed total length of 6.3 m (Frederickson et al., 2015). This specimen was not discovered with associated teeth, making taxonomic identification difficult beyond Lamniformes; however, it is likely that this specimen belongs to the basal lamniform *Leptostyrax macrorhiza* (family Eoptolamnidae [Kriwet, Klug, Canudo, & Cuenca-Bescos, 2008]) (Frederickson et al., 2015), the largest lamniform shark known from the Duck Creek Formation (Welton and Farish, 1993). In order to determine its growth rate, we followed the protocol established by Shimada (2008), where counts and measurements of yearly growth bands were extrapolated for total length.

In many shark species, growth rates can be determined by measuring concentric bands found within the corpus calcareum of the vertebrae. These bands of translucent and opaque tissue are hypothesized to represent seasonal, slow-fast deposition. In fossil lamniform sharks, it is often assumed that the preserved band pairs (a neighboring dense translucent and thin opaque band; Cailliet et al., 2006) are annually deposited, as is the case typically seen in most extant lamniform sharks (e.g., *Alopias* spp. [Cailliet, Martin, Harvey, Kusher, & Welden, 1983; Liu, Chiang, & Chen, 1998; Liu, Chen, & Liao, 1999], *Carcharias taurus* [Goldman, Branstetter, & Musick, 2006], *Carcharodon carcharias* [Wintner & Cliff, 1999], and *Isurus oxyrinchus* [Campana, Marks, & Joyce, 2005; Ardizzone et al., 2006; Bishop, Francis, Duffy, & Montgomery, 2006]); with the basking shark (*Cetorhinus maximus*) being one of the only notable exceptions (Parker and Stott, 1965; Natanson et al., 2008).

Band counts for OMNH 68860 were taken using three different approaches: computed tomography, histology, and surface texture analysis. Specimens were chosen for each analysis based on their level of preparation, degree of deformation, and relative completeness, ensuring to subject at least one vertebra to all three methods. In this case, specimen B was chosen for destructive sampling (thus all three methods), because it is the smaller and less complete of the two prepared vertebrae. CT scans for the prepared vertebrae (A and B) were conducted at the University of Oklahoma Health Sciences Center using a Philips Brilliance 16 slice CT. We produced our dataset using overlapping 0.6 mm slices with 140 kV and 300 mA. We made our acquisition scan in an axial orientation and produced planar reconstructions in sagittal and coronal planes as well. Data were exported as DICOM files representing a 139.0 mm field of view. Data are on file at the OMNH Vertebrate Paleontology Collection and are available by request. A polished thick histological section was then taken directly from vertebra B, following a natural crack in the fossil. The slice was taken using a standard 10-inch rock saw at the OMNH Invertebrate Paleontology Laboratory, and was then polished using a dry grinding wheel to remove any inconsistencies in the cut surface. Finally, all three vertebrae were analyzed using counts of the furrows on the rostral and caudal articular surfaces, following the procedure of Newbrey et al. (in press). Surface furrows were recognized as continuous circumferential grooves observed through unaided observation. Counts for both surface furrows and the histological section were confirmed using a Nikon SMZ-10A dissecting microscope.

Direct measurements of annular growth bands were taken using calipers; for measurements of CT scans, images were measured directly using ImageJ software (version 1.48v; Rasband, 2014). Measurements were taken where the growth banding (or furrows) was most pronounced, and thus was not constrained to the same area for comparison. This could have potentially yielded differential counts between specimens; however, since the growth bands are circumferential features, they should hypothetically be present in equal counts throughout the entire corpus calcareum on a single side. In order to compare growth curves for multiple species, we transformed the radius measurements into area, using the standard formula for area of a circle, $A = \pi r^2$ (Ehret, 2010). This technique transformed the asymptotic growth curve into a linear growth rate, allowing us to measure the slope (i.e. growth rate) using the linear regression function in Microsoft Excel. In addition, centrum radius measurements were plotted as a growth curve, that were then transformed into total length reconstructions using the surface texture measurements following the procedure and algorithm of Shimada (2008), where total length (TL in cm) is calculated using