To my family, Bryan, Debra, and Sydney Ehret, Alyssa, Jim, Doyle, and Cowan Fagen 
for all of their support
ACKNOWLEDGMENTS

I am grateful for the guidance of my advisor Bruce MacFadden, who has been a source of intellectual and research support. I thank my Ph.D. Committee, including Doug Jones, Karen Bjorndal, Jonathan Bloch, Greg Erickson, Dick Franz, and Gordon Hubbell, for their support with my research. I would especially like to thank Gordon and Kate Hubbell for all of their hospitality, time spent teaching me about fossil sharks, and moral support. Jonathan Bloch has contributed to my development as a researcher and has provided invaluable advice while searching and applying for jobs. Richard Hulbert has helped by teaching me curatorial and field collection techniques, offering editorial advice, and providing access to fossil materials.

My dissertation research would not have been possible without access to museum collections including: the Florida Museum of Natural History (FLMNH), Jaws International, Gainesville, Florida (GH), Museo de Historia Natural Javier Prado, Lima, Peru (MUSM), Royal Belgian Institute of Natural Sciences, Brussels, Belgium (IRSNB), Saitama Prefectural Museum, Saitama, Japan (SPM), Smithsonian Institution, Washington, D. C. (USNM), and Natural History Museum, London, England (NHM). Specifically, I thank the following persons for access to, and help with, the relevant collections under their care: Richard Hulbert, Vertebrate Paleontology, FLMNH; Gordon Hubbell, GH; Rodolfo Salas-Gismondi, Departamento de Paleontologia de Vertebrados, MUSM; Dirk Nolf, Vertebrate Paleontology, IRSNB; Osamu Sakamoto, Vertebrate Paleontology, SPM; Dave Bohaska, Department of Paleobiology, USNM; Zerina Johanson, Department of Palaeontology, NHM.

Chapter 2 is a collaborative effort with Bruce MacFadden and Gordon Hubbell. I thank Jason Curtis, Irvy Quitmyer, and David Steadman for assistance with
geochemical analyses that were performed at the FLMNH and Department of Geological Sciences at the University of Florida. Cathy Bester and Jeff Gage were instrumental in the preparation of the illustrations. Doug Jones, FLMNH, Thomas DeVries from Vashon Island, Washington, and Rodolfo Salas-Gismondi and Marcelo 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 John Maisey and the reviewers Kenshu Shimada and Michael Gottfried made constructive suggestions for the improvement of this manuscript.

Chapter 3 is a collaborative effort with Bruce MacFadden and Rodolfo Salas-Gismondi. I would like to thank Jana Miller for assistance with figures. I also offer thanks to the 2007 Peruvian field crew and two anonymous reviewers for comments and suggestions.

Chapter 4 is a collaborative effort with Bruce MacFadden, Doug Jones, Thomas DeVries, David Foster, and Rodolfo Salas-Gismondi. I especially thank Gordon Hubbell for donating UF 226255 to the Florida Museum of Natural History as well as access to his collection and his wealth of knowledge about fossil sharks. I would also like to thank Mikael Siverson from the Western Australian Museum, Welshpool, Western Australia, and James Bourdon of www.elasmo.com for discussions and constructive suggestions for this chapter. Evgeny Mavrodiev from FLMNH provided valuable assistance with Russian translations. I also thank David Ward and Jürgen Kriwet for constructive comments and suggestions to improve this manuscript.

For assistance with the research in Chapter 5, I would like to thank Sabine Wintner, Sheldon Dudley, and Geremy Cliff of the Kwazulu-Natal Sharks Board, South
Africa, for their hospitality, access to white shark specimens, and growth data. Matthew Colbert, Timothy Rowe, Christopher Bell, Kerin Claeson, and Jennifer Olori of the University of Texas, Austin, offered their hospitality, assistance, and guidance with CT scans and digital imaging. I thank Michael Warren and the staff of the C. A. Pound Human Identification Laboratory, University of Florida, for help with digital imaging. I would also like to thank Andrew Piercy, University of North Florida, Nicholas Pyenson, National Museum of Natural History, Smithsonian Institution, and Ellen Martin, University of Florida, Department of Geological Sciences for valuable discussions regarding shark growth, cetacean evolution, and paleoclimate. I thank James Colee, University of Florida, Department of Statistics, for assistance with analyses. I also thank Jonathan Bloch, Jason Bourque, Richard Hulbert, Julie Mathis, and Irvy Quitmyer, FLMNH, for discussions and technical support of this chapter.

The School of Natural Resources, the Florida Museum of Natural History, and the Department of Biology have provided logistical and financial support, including access to museum specimens, office space, staff assistance, and a teaching assistantship. My research assistantship, digital imaging, and travel were also supported by National Science Foundation grants EAR 0418042 and 0735554. Additional financial support was supplied by the Florida Museum of Natural History Lucy Dickinson Scholarship, the Jackson School of Geosciences Student Member Travel Grant provided by the Society of Vertebrate Paleontology, and travel grants supplied by the Graduate Student Council and the School of Natural Resources and Environment at the University of Florida.

I am thankful for the support of the School of Natural Resources, Department of Biology, Department of Wildlife Ecology and Conservation, Department of Geological
Sciences, Florida Museum of Natural History, and the I^3 program faculty, students, and staff. George Burgess, Stephen Humphrey, Nikki Kernaghan, Ellen Martin, Michael Moulton, Larry Page, David Reed, and Sandra Russo have provided research, educational, and/or career support. Ben Atkinson, Cathy Bester, Ashley Boggs, Jason Bourque, J. R. Cash, Stephen Chester, Lisa Marie Erickson, Alex Hastings, Larisa Grawe-Desantis, Carly Manz, Julie Mathis, Russ McCarty, Paul Morse, Catalina Pimiento, Sarah Reintjes-Tolen, Julian Resasco, Allen, Kaley, Amelie, and Ivan Shorter, and Emily Woodruff have offered a diversity of assistance from advice on research to moral support. Pam Dennis, Chris Pickles, Art Poyer, Cathy Ritchie, Meisha Wade, and Shuronna Wilson helped with logistics.

Finally, I am extremely grateful for the continued support from my family. I am thankful for my parents, Bryan and Debra Ehret for being there with not only moral, but also financial support. I thank my sister Alyssa, my brother-in-law Jim, my nephews Doyle and Cowan, my grandparents, aunts, and uncles for understanding all of the missed holidays. I appreciate the weekend visits from my Uncle Kevin and Cousins Drew and Matthew, even if they were more excited for the football games. And last but not least, I am grateful for my dog Sydney who has been there with me through it all and is always happily awaiting my return home.
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>ACKNOWLEDGMENTS</td>
<td>4</td>
</tr>
<tr>
<td>LIST OF TABLES</td>
<td>11</td>
</tr>
<tr>
<td>LIST OF FIGURES</td>
<td>12</td>
</tr>
<tr>
<td>ABSTRACT</td>
<td>14</td>
</tr>
<tr>
<td>CHAPTER</td>
<td></td>
</tr>
<tr>
<td>1 INTRODUCTION</td>
<td>16</td>
</tr>
<tr>
<td>2 EXCEPTIONAL PRESERVATION OF THE WHITE SHARK CARCHARODON</td>
<td>21</td>
</tr>
<tr>
<td>(LAMNIFORMES, LAMNIDAE) FROM THE EARLY PLIOCENE OF PERU</td>
<td></td>
</tr>
<tr>
<td>Introduction</td>
<td>21</td>
</tr>
<tr>
<td>Geological Setting and Marine Vertebrates from the Pisco Formation</td>
<td>21</td>
</tr>
<tr>
<td>Fossil Record and Origin of Carcharodon carcharias</td>
<td>23</td>
</tr>
<tr>
<td>Materials, Methods, and Abbreviations</td>
<td>25</td>
</tr>
<tr>
<td>Abbreviations</td>
<td>27</td>
</tr>
<tr>
<td>Referred Material</td>
<td>27</td>
</tr>
<tr>
<td>Occurrence</td>
<td>28</td>
</tr>
<tr>
<td>Anatomical Description</td>
<td>28</td>
</tr>
<tr>
<td>Mandibular arch</td>
<td>28</td>
</tr>
<tr>
<td>Neurocranium</td>
<td>29</td>
</tr>
<tr>
<td>Dentition</td>
<td>30</td>
</tr>
<tr>
<td>Vertebral centra</td>
<td>32</td>
</tr>
<tr>
<td>Discussion</td>
<td>32</td>
</tr>
<tr>
<td>Fossil Record and Evolution of Carcharodon carcharias</td>
<td>32</td>
</tr>
<tr>
<td>Incremental Growth of Vertebral Centra</td>
<td>34</td>
</tr>
<tr>
<td>Length Estimation of Fossil and Extant Carcharodon carcharias</td>
<td>36</td>
</tr>
<tr>
<td>Conclusions</td>
<td>38</td>
</tr>
<tr>
<td>3 CAUGHT IN THE ACT: TROPHIC INTERACTIONS BETWEEN A 4-MILLION-YEAR-OLD</td>
<td>54</td>
</tr>
<tr>
<td>WHITE SHARK (CARCHARODON) AND MYSTICETE WHALE FROM PERU</td>
<td></td>
</tr>
<tr>
<td>Introduction</td>
<td>54</td>
</tr>
<tr>
<td>Locality and Stratigraphy</td>
<td>55</td>
</tr>
<tr>
<td>Specimen Description</td>
<td>57</td>
</tr>
<tr>
<td>Discussion</td>
<td>59</td>
</tr>
<tr>
<td>Conclusions</td>
<td>61</td>
</tr>
</tbody>
</table>
4 ORIGIN OF THE WHITE SHARK, *CARCHARODON* (LAMNIFORMES: LAMNIDAE), BASED ON RECALIBRATION OF THE LATE NEOGENE, PISCO FORMATION OF PERU ................................................................. 66

Introduction ........................................................................................................... 66
Methods and Materials ...................................................................................... 69
Geological Setting and Geochronology ............................................................ 71
Overview of Taxonomy and Fossil Record of *Carcharodon*............................... 74
Systematic Palaeontology ............................................................................... 80
  Depository and Abbreviations ........................................................................ 80
  Type Species .................................................................................................. 80
  Remarks ......................................................................................................... 80
  Holotype ........................................................................................................ 81
  Other Material ............................................................................................... 81
  Type Locality, Horizon and Age .................................................................. 81
  Diagnosis ........................................................................................................ 82
  Description ................................................................................................... 82
  Remarks ......................................................................................................... 84
Discussion .......................................................................................................... 85
  Geology and Stratigraphy ............................................................................. 85
  Taxonomy and Evolution of *Carcharodon* ................................................... 87
Conclusions ....................................................................................................... 90

5 MACROEVOLUTION, AGE, AND GROWTH DETERMINATION OF THE MEGATOOTHED SHARKS (LAMNIFORMES: OTODONTIDAE) ....................... 100

Introduction ........................................................................................................... 100
Materials and Methods .................................................................................... 101
  Materials ....................................................................................................... 101
  Methods ....................................................................................................... 103
Results ................................................................................................................ 107
Discussion ......................................................................................................... 110
  Heterochrony ............................................................................................... 113
  Biotic and Abiotic Factors .......................................................................... 118
Conclusions ....................................................................................................... 124

6 CONCLUSIONS ................................................................................................. 137

APPENDIX

A OUTREACH ACTIVITIES .................................................................................. 142

B ABSTRACTS OF OTHER RESEARCH PROJECTS .......................................... 147

  Nursery Area for Giant Baby Sharks in the Miocene of Panama ................... 147
  Background ................................................................................................... 147
  Methodology/Principal Findings ................................................................... 147
  Conclusions/Significance ............................................................................. 148
Biodiversity and Paleoecology of Late Miocene Sharks (Chondrichthyes, Elasmobranchii, Selachii) from the Gatun Formation, Panama .......................... 148
An extinct map turtle *Graptemys* (Testudines: Emydidae) from the Pleistocene of Florida ........................................................................................................ 149

LIST OF REFERENCES .......................................................................................................................... 150

BIOGRAPHICAL SKETCH ..................................................................................................................... 165
**LIST OF TABLES**

<table>
<thead>
<tr>
<th>Table</th>
<th>Title</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>2-1</td>
<td>Tooth measurements for all teeth in the functional series of UF 226255</td>
<td>49</td>
</tr>
<tr>
<td>2-2</td>
<td>Stable isotope ($\delta^{13}$C and $\delta^{18}$O) results from microsampling along growth axis of vertebral centrum of <em>Carcharodon</em> sp. (UF 226255)</td>
<td>51</td>
</tr>
<tr>
<td>2-3</td>
<td>Total length (TL) estimates for UF 226255.</td>
<td>52</td>
</tr>
<tr>
<td>2-4</td>
<td>References and equations for TL regression estimates.</td>
<td>53</td>
</tr>
<tr>
<td>4-1</td>
<td>Strontium chemostratigraphic analyses of fossil marine mollusk shells from the Pisco Formation</td>
<td>99</td>
</tr>
<tr>
<td>5-1</td>
<td>Centrum radius (CR) and growth ring (GR) measurements for otodontid sharks</td>
<td>133</td>
</tr>
<tr>
<td>5-2</td>
<td>Analysis of Covariance slopes (= rates of growth) for otodontid and white sharks</td>
<td>135</td>
</tr>
<tr>
<td>5-3</td>
<td>Paired t-test comparing the slopes (rates of growth) between otodontid and white sharks</td>
<td>136</td>
</tr>
</tbody>
</table>
## LIST OF FIGURES

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>2-1</td>
<td>Location of the Pisco Formation in southwestern Peru.</td>
</tr>
<tr>
<td>2-2</td>
<td>Measured sections of Pisco Formation, Peru.</td>
</tr>
<tr>
<td>2-3</td>
<td>Hypothetical phylogenies of the possible origination of <em>Carcharodon carcharias</em>.</td>
</tr>
<tr>
<td>2-4</td>
<td>Ventral view of <em>Carcharodon</em> sp. (UF 226255).</td>
</tr>
<tr>
<td>2-5</td>
<td>Close-up view of upper teeth of <em>Carcharodon</em> sp.</td>
</tr>
<tr>
<td>2-6</td>
<td>Close-up view of lower teeth of <em>Carcharodon</em> sp.</td>
</tr>
<tr>
<td>2-7</td>
<td>Reconstruction of tooth set of UF 226255.</td>
</tr>
<tr>
<td>2-8</td>
<td>Silhouettes of A1 teeth for comparison of serration types.</td>
</tr>
<tr>
<td>2-9</td>
<td>First vertebral centrum of UF 226255.</td>
</tr>
<tr>
<td>2-10</td>
<td>X-ray image of centrum of UF 226255 analyzed for stable isotopes.</td>
</tr>
<tr>
<td>3-1</td>
<td>Location of study area, Sud-Sacaco West, along the southwestern coast of Peru.</td>
</tr>
<tr>
<td>3-2</td>
<td>Composite stratigraphic section for the upper Pisco Formation.</td>
</tr>
<tr>
<td>3-3</td>
<td>Mysticete mandible with white shark (<em>Carcharodon</em> sp.) tooth (MUSM 1470).</td>
</tr>
<tr>
<td>4-1</td>
<td>Map of Peru with localities within the Southern section of the Pisco Formation.</td>
</tr>
<tr>
<td>4-2</td>
<td>Stratigraphic map of the Pisco Formation, Peru.</td>
</tr>
<tr>
<td>4-3</td>
<td><em>Carcharocles megalodon</em> tooth, USNM 336204.</td>
</tr>
<tr>
<td>4-4</td>
<td>Comparison of serration types in lamnid and otodontid sharks.</td>
</tr>
<tr>
<td>4-5</td>
<td><em>Isurus escheri</em> from the Delden Member (Early Pliocene), the Netherlands.</td>
</tr>
<tr>
<td>4-6</td>
<td><em>Carcharodon</em> n. sp., UF 226255 (holotype).</td>
</tr>
<tr>
<td>4-7</td>
<td>Functional tooth series of <em>Carcharodon</em> n. sp., UF 226255 (holotype).</td>
</tr>
<tr>
<td>4-8</td>
<td>Vertebral centrum of <em>Carcharodon</em> n. sp., UF 226255 (holotype).</td>
</tr>
<tr>
<td>4-9</td>
<td>Individual upper teeth demonstrating the gradation of serrations from the Pisco Formation, Peru. 98</td>
</tr>
<tr>
<td>5-1</td>
<td>Images of megatoothed shark vertebral centra. 127</td>
</tr>
<tr>
<td>5-2</td>
<td>X-radiographs of vertebral centra. 128</td>
</tr>
<tr>
<td>5-3</td>
<td>Centrum radius (CR) per growth ring (GR). (A) otodontid sharks, (B) otodontid sharks compared to growth in <em>Carcharodon carcharias</em>. 129</td>
</tr>
<tr>
<td>5-4</td>
<td>Analysis of covariance, Centrum area vs. growth rings (GR) for the four megatoothed species and <em>Carcharodon carcharias</em>. 130</td>
</tr>
<tr>
<td>5-5</td>
<td>Anterior otodontid shark teeth through time. 131</td>
</tr>
<tr>
<td>5-6</td>
<td>Growth rates for otodontid sharks compared with neocete diversity through geologic time. 132</td>
</tr>
</tbody>
</table>
Abstract of Dissertation Presented to the Graduate School of the University of Florida in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy

PALEOBIOLOGY AND TAXONOMY OF EXTINCT LAMNID AND OTODONTID SHARKS (CHONDRICHTHYES, ELASMOBRANCHII, LAMNIFORMES)

By

Dana Joseph Ehret

December 2010

Chair: Bruce J. MacFadden
Cochair: Douglas S. Jones
Major: Interdisciplinary Ecology

Studies of Cenozoic lamnid and otodontid sharks are important for gaining insights into the evolution and paleoecology of ancient marine systems. These groups, including the white, mako, and megatoothed sharks, are of particular significance due to their large size and status as apex predators. However, the lack of preserved cartilages and associated specimens has resulted in taxonomic and paleobiological studies that are largely based on isolated teeth. Recent innovations in the field of lamniform paleobiology have yielded new and promising information about the growth, paleoecology, and trophic interactions of these sharks. My dissertation aims to utilize new techniques and well-preserved specimens to elucidate the taxonomy and paleobiology of these two families.

The first part of my dissertation focuses on the evolution of the white shark, *Carcharodon*, during the Late Miocene. The description of an exceptionally well-preserved species from the Pisco Formation of Peru provides direct evidence for the evolution of *Carcharodon carcharias* from *Carcharodon (Cosmopolitodus) hastalis* in the Pacific Basin. This new species exhibits characteristics of both species including weak
serrations, a symmetrical first anterior tooth, and a mesially slanted third anterior tooth. Growth analysis of this species also reveals a rate slower than that of the extant white shark. Recalibration of Sacaco Basin sediments within the Pisco Formation, Peru using zircon U-Pb dating and strontium-ratio isotopic analysis suggests that localities are older, Late Miocene (6–8 Ma) rather than previously thought. The next part of my dissertation discusses direct evidence for trophic interactions between a white shark (Carcharodon n. sp.) and a mysticete whale also from the Pisco Formation. This evidence includes a partial mandible with a partial tooth of a white shark embedded within the cortical bone.

The final part of my dissertation focuses on the growth of the megatoothed sharks. I calculate the age and growth rates for species, including Otodus obliquus, Carcharocles auriculatus, Carcharocles angustidens and Carcharocles megalodon using incremental growth bands visible in X-radiographs of fossilized vertebral centra. Species growth rates spanning the Early Eocene (~55 Ma) through Middle Miocene (~12 Ma) are compared with shifts in paleoclimate and whale evolution and diversity.
CHAPTER 1
INTRODUCTION

Studies of fossil neoselachians have traditionally focused on descriptions of species and faunal assemblages based on isolated teeth, incidences of predatory behaviors, and in rare instances, associated specimens (including tooth sets and vertebral centra). These studies tend to be descriptive in nature owing to lack of more complete specimens. The prevalence of isolated teeth and the paucity of associated skeletons in the fossil record are related to two main features of chondrichthyan anatomy: constant tooth replacement and the cartilaginous skeleton.

Constant tooth replacement in chondrichthyan species is a characteristic present in most species dating back to the Devonian (Botella et al. 2009). Replacement rates in extant taxa have been documented from one row per every 1-5 weeks depending on the species up to one tooth per every 1-2 days in the sandtiger shark, *Carcharias taurus* (Overstrom 1991; Correia 1999; Botella et al. 2009). Hubbell (1996) estimated that an individual lemon shark, *Negaprion brevirostris*, could produce more than 20,000 teeth in its lifetime. Therefore, it is no surprise that shark teeth, which have been continuously shed by shark populations through time, are the most common vertebrate fossils found today.

Conversely, the cartilaginous skeleton of neoselachians (and chondrichthyan species in general) is largely uncalcified and rarely found fossilized. The lack of skeletal materials in the fossil record has severely limited our knowledge, both taxonomic and paleobiologic, of extinct neoselachians. In these rare instances, when skeletal materials, including vertebral centra and other cartilages, are preserved they can offer a unique glimpse into the paleobiology of these sharks. This information can include but is not
limited to: body size and shape, information about growth (i.e. birth size, rate, and age), dietary requirements, and evolutionary relationships. However, the value of these specimens and their paleobiological implications has only recently been explored (Gottfried et al. 1996; Purdy 1996; Shimada 1997a; MacFadden et al. 2004; Labs-Hochstein and MacFadden 2006; Shimada 2008; Ehret, Hubbell, and MacFadden 2009).

My dissertation focuses on the taxonomy and paleobiology of Cenozoic lamniform sharks, utilizing exceptionally well-preserved specimens recovered from localities in Peru, Belgium, and Morocco. Within the Lamniformes, I will focus specifically on the evolution of lamnid and otodontid sharks during this period. Species within these two families include the largest extant (*Carcharodon carcharias*) and extinct (*Carcharocles megalodon*) predatory sharks to have ever lived. The evolution of large body size within both groups and presence of numerous convergent characters has caused much confusion among paleontologists. Utilizing fossil materials from the Florida Museum of Natural History, Gordon Hubbell Collection and Royal Belgian Institute of Natural Sciences I will address these key questions:

- Is the extant *Carcharodon carcharias* more closely related to the megatoothed or mako sharks? (Chapters 2 and 4)
- How has growth in white sharks (*Carcharodon*) evolved through time? (Chapter 2)
- Is the evolution of serrations on the teeth of *Carcharodon* related to changes in diet? (Chapter 3)
- When and where did the transition from *Carcharodon (Cosmopolitodus) hastalis* to *Carcharodon carcharias* occur? (Chapter 4)
- How did *Carcharocles megalodon* grow so large? (Chapter 5)
Chapter 2 describes an exceptionally well-preserved white shark (*Carcharodon* n. sp.) fossil from the Pisco Formation of southwestern Peru. The teeth of this specimen show characters of both *Carcharodon* and *Isurus/Cosmopolitodus*. While *Carcharodon* n. sp. from the Pisco Formation shows numerous diagnostic characteristics shared with *C. carcharias* it also exhibits unique characters that represent a distinct species. The vertebral centra of the Pisco *Carcharodon* preserve distinctive dark and light incremental bands that, based on calibration with oxygen isotopes, indicate annual growth couplets. Based on tooth and vertebral centra measurements, 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*. The fossil record of lamnid sharks preserved in the Pisco Formation demonstrates that the modern white shark is more closely related to *Isurus (Cosmopolitodus hastalis)* than it is to the species *Carcharodon megalodon*, and the latter is therefore best allocated to the genus *Carcharocles*.

Chapter 3 focuses on trophic interactions between an extinct white shark and a mysticete whale. Trophic interactions captured in the fossil record are categorized as either indirect or direct evidence. Indirect evidence includes such traces as shark tooth marks and gouges on the bones of prey, including fish, reptiles, whales, dolphins, and seals. Direct evidence is represented by the presence of shark teeth in definite association with prey species. This chapter describes direct evidence for trophic interactions between a white shark (*Carcharodon* n. sp.) and a mysticete whale from the Pisco Formation of Peru. The evidence includes a partial mandible of an unidentified mysticete whale with a partial tooth of a white shark embedded within the cortical bone. Modern white sharks are known predators of many marine mammal species and both
active hunting and scavenging have been well documented. This fossil is unusual because it represents a seldom reported event that preserves direct evidence of trophic interactions.

Chapter 4 includes the formal description of the exceptionally complete fossil white shark, *Carcharodon* from the Late Miocene, Pisco Formation of Peru. Morphological evidence presented suggests the extant white shark is derived from the broad-toothed *Carcharodon* (*Cosmopolitodus*) *hastalis* based on the description of *Carcharodon* n. sp. – a taxon that demonstrates this transition. Specimens from the Pisco Formation clearly demonstrate an evolutionary mosaic of characters of both recent *Carcharodon carcharias* and fossil *Carcharodon hastalis*.

In addition to this description, I also provide a recalibration of the Pisco Formation, within the Sacaco Basin, Peru using zircon U-Pb dating and strontium-ratio isotopic analysis. The recalibration of the absolute dates suggests that *Carcharodon* n. sp. is from the Late Miocene (6–8 Ma) not the Early Pliocene (4–5 Ma) as previously reported. These new dates provide tighter constraints and elucidate the timing of white shark evolution in the Pacific Ocean during the Late Miocene.

Chapter 5 discusses the macroevolution of body size and changes to growth rates in the otodontid (megatoothed) sharks. It is hypothesized that the megatoothed sharks, including *Otodus obliquus*, *Carcharocles auriculatus*, *Carcharocles angustidens*, and *Carcharocles megalodon*, represent an extinct lineage of large predatory neoselachians that replace one another through time via phyletic evolution (Glikman 1964; Zhelezko and Kozlov 1999; Ward and Bonavia 2001; Cappetta and Cavallo 2006). Arising in the Paleocene and extending into the Pliocene, an evolutionary series of taxa have been
described that exhibit shifts in tooth structure and a general increase in size through time. To test the hypothesis that megatoothed shark species increased in size through time, I measure the incremental growth bands preserved within the vertebral centra of the four extinct species listed above. I calculate growth rates and discuss the heterochronic changes in growth for the megatoothed species and compare those with *Carcharodon carcharias*. Additionally, changes in growth rates and tooth morphology of the otodontids are compared with the evolution and diversification of marine mammals and changes in paleoclimate through time.

The aim of this dissertation is to advance the field of paleichthyology by utilizing new paleoecological techniques that have been previously ignored. The use of exceptionally preserved specimens (i.e. fossilized cartilages, associated dentitions, and evidence of trophic interactions) can provide valuable information regarding the evolution and paleobiology of extinct neoselachians. In addition to the description of a new species of *Carcharodon* and my work on the paleobiology of extinct lamniform sharks, I also discuss the outreach activities that I have participated in to disseminate my research to the general public. These activities have included: front-end evaluations and panel content for the traveling exhibit, “Megalodon: The Largest Shark That Ever Lived”, lectures delivered to amateur fossil-collecting organizations, and a two-week field camp in vertebrate paleontology for local 5th grade students. By incorporating biological principles, paleontological research, and outreach, I will continue to improve understanding of neoselachian paleobiology and share my knowledge and enthusiasm with the general public.
CHAPTER 2
EXCEPTIONAL PRESERVATION OF THE WHITE SHARK CARCHARODON (LAMNIFORMES, LAMNIDAE) FROM THE EARLY PLIOCENE OF PERU

Introduction

Isolated shark teeth are the most commonly preserved and collected vertebrate fossils from Neogene marine sediments worldwide. In contrast to the ubiquitous occurrence of shark 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 (de Muizon and DeVries 1985, Figure 2-1). 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 (Figure 2-2). 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 (de 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; de Muizon and DeVries 1985; de Muizon and McDonald 1995; de Muizon et al. 2002; de 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 (de 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).

**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 (Figure 2-3A). 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 (Figure 2-3B), including *Isurus hastalis* (Casier 1960; Glikman 1964; de 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; Glikman 1964; Cappetta 1987). Casier (1960) considered that the labiobuccal flattening in the teeth of both the fossil *Isurus* (specifically *I. xiphodon* of Purdy *et al.* 2001) and *Carcharodon carcharias* is a shared derived character (Nyberg *et al.* 2006). De 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 de 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 I use ‘lower third anterior tooth’ rather than ‘lower 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 2-1).

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™ computer interfaced automated drilling device. Thirty-one microsamples of approximately 5 mg each were collected by running the drill to a depth of 100 mm 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 H₂O₂, 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 at the University of Florida. The carbonate fraction of the hydroxylapatite was analyzed using this method and the results are presented below using the standard notation: \( \delta \) (parts per mil, ‰) = \([R_{\text{sample}}/R_{\text{standard}} - 100] \times 1,000\) where \( R \) = either \(^{13}\text{C}/^{12}\text{C}\) or \(^{18}\text{O}/^{16}\text{O}\) 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 CHORDICHTHYES Huxley 1880

Subclass ELASMOBRANCHII Bonaparte 1838

Order LAMNIFORMES Berg 1958

Family LAMNIDAE Müller and Henle 1838

Genus CARCHARODON Smith in Müller and Henle 1838

*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 (Figure 2-4).
**Occurrence**

Collected from Sud-Sacaco West, approximately 30 m above base of measured section (de 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 (Figures 2-1, 2-2).

**Anatomical Description**

**Mandibular arch**

Portions of both palatoquadrate and Meckel’s cartilages are preserved, although, the specimen is flattened dorsoventrally, making it very difficult to reconstruct the anteroposterior shape of the jaws (Figure 2-4). The palatoquadrate lacks most of the dorsal portions on both left and right sides, with preserved cartilage beginning just above where the functional 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 palatoquadrate does 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 palatoquadrate 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 (Figure 2-4). It is also flattened dorsoventrally and does not preserve much structure. The occipital hemicentrum and the anterior portion of a foramen magnum are present (Figure 2-4). 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 are present on the articulated palatoquadrates and the Meckel’s cartilages. The functional series has been removed for study (Figures 2-5, 2-6), 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 2-1). 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 (Figures 2-5 and 2-7). 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 (Figure 2-5). 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 (Figure 2-6). 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 (Figure 2-8). 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* (Figures 2-5, 2-7). 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 (Figure 2-6). 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 (Figure 2-4). 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, Figure 2-9). 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 annual 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 de Muizon and DeVries (1985) of Peru to *I. xiphodon* from the Late Miocene and dismiss an *Isurus–Carcharodon* 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). There is disagreement 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 it is designated 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.

**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 (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 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 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 1997b). 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 isotopes are used 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 (Figure 2-10, Table 2-2). For the carbon isotope data (Table 2-2), Student t (*t*<sub>observed</sub> = 0.626, *t*<sub>critical</sub> = 2.131, *P* = .540) and Mann-Whitney U (*Z*<sub>observed</sub> = 0.289, *Z*<sub>critical</sub>, *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 δ<sup>13</sup>C signal than one feeding on an herbivorous mysticete whale. Using this extant model, the lack of significant variation in the δ<sup>13</sup>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 2-2), Student t (*t*<sub>observed</sub> = 2.549, *t*<sub>critical</sub> = 2.131, *P* = .020) and Mann-Whitney U (*Z*<sub>observed</sub> = 2.502, *Z*<sub>critical</sub> = 1.960, *P* = .012) tests indicate statistically significant differences (*P* =
.05) between the dark and light bands, with the mean value for δ¹⁸O for the winter bands being more enriched, as would be expected if this indeed is accurately archiving a temperature proxy (MacFadden et al. 2004).

So far as can be determined, adjacent dark-light band ‘couplets’ (Figure 2-10) are interpreted to represent intervals of annual 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 annual 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 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); all available fossil teeth were used 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 2-3. The mean for the 42 measurements was calculated to provide an estimated TL of 5.07 m.

In addition to using CH, TL estimates are extrapolated 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 2-4. 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). Figure 2-11 shows a reconstruction of this shark, exhibiting characteristics of both *Carcharodon* and *Isurus*.

**Conclusions**

UF 226255 is an extraordinarily well-preserved fossil lamnid shark from the Early Pliocene of Peru. The presence of a nearly complete tooth series preserved with other portions of the skeleton provides new information regarding the evolutionary history of *Carcharodon carcharias*. This specimen is allocated 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).

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.
Figure 2-1. Location of the Pisco Formation in southwestern Peru. A, Geographic location; B, surface geology of Sacaco Basin. Measured sections A, B, and C correspond to those depicted in Figure 2-2 (after de Muizon and DeVries 1985).
Figure 2-2. Measured sections of Pisco Formation, Peru. (A–C) in Sacaco Basin (from de Muizon and DeVries 1985; also see Figure 2-1) and stratigraphic context (section C) of *Carcharodon* sp., UF 226255, from early Pliocene Pisco Formation of Peru.
Figure 2-3. Hypothetical phylogenies of the 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*. 
Figure 2-4. Ventral view of *Carcharodon* sp. (UF 226255). Specimen consists of an 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. Scale bar represents 10 cm.
Figure 2-5. 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 Figure 2-4. Scale bar represents 5 cm.
Figure 2-6. 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 Figure 2-4. Scale bar represents 5 cm.
Figure 2-7. Reconstruction of tooth set of UF 226255. Scale bar represents 5 cm.

Figure 2-8. Silhouettes of A1 teeth for comparison of serration types. A, *Carcharodon carcharias*; B, *Carcharodon* sp. Scale bar represents 5 cm.
Figure 2-9. First vertebral centrum of UF 226255. A, anterior view; B, dorsal view. Scale bar represents 5 cm.
Figure 2-10. X-ray image of centrum of UF 226255 analyzed for stable isotopes. Scale bar represents 1 cm.
Figure 2-11. Reconstruction of *Carcharodon* sp. from the Pisco Formation, Peru.
Table 2-1. Tooth measurements for all teeth in the functional series of UF 226255. All measurements in millimeters and abbreviations are in the text. Tooth angle 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.

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

<table>
<thead>
<tr>
<th>Tooth</th>
<th>CH</th>
<th>CW</th>
<th>Angle (°)</th>
<th>Distal Length</th>
<th>Mesial Length</th>
<th>Distal Serrations</th>
<th>Mesial Serrations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Left Side</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>I1</td>
<td>28.4</td>
<td>27.2</td>
<td>-1</td>
<td>32.3</td>
<td>29.2</td>
<td>23</td>
<td>21</td>
</tr>
<tr>
<td>I2</td>
<td>24.6</td>
<td>27.2</td>
<td>-1</td>
<td>30.6</td>
<td>27.3</td>
<td>16</td>
<td>13</td>
</tr>
<tr>
<td>I3</td>
<td>19.8</td>
<td>21.4</td>
<td>0</td>
<td>22.0</td>
<td>22.5</td>
<td>9</td>
<td>11</td>
</tr>
<tr>
<td>I4</td>
<td>15.9</td>
<td>18.6</td>
<td>0</td>
<td>17.9</td>
<td>17.6</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>I5</td>
<td>9.1</td>
<td>14.0</td>
<td>0</td>
<td>11.5</td>
<td>12.2</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>I6</td>
<td>6.8</td>
<td>11.2</td>
<td>0</td>
<td>8.2</td>
<td>9.1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>I7</td>
<td>5.0</td>
<td>9.0</td>
<td>0</td>
<td>5.6</td>
<td>6.9</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>I8</td>
<td>3.6</td>
<td>8.0</td>
<td>0</td>
<td>4.5</td>
<td>5.6</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
Table 2.2. Stable isotope ($\delta^{13}$C and $\delta^{18}$O) results from microsampling along growth axis of vertebral centrum of *Carcharodon* sp. (UF 226255). Also see Figure 2-10. 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>
<thead>
<tr>
<th>Distance from Center (mm)</th>
<th>Lab Sample Number (2007)</th>
<th>Band Interval Type</th>
<th>$\delta^{13}$C (‰ VPDB)</th>
<th>$\delta^{18}$O (‰ VPDB)</th>
</tr>
</thead>
<tbody>
<tr>
<td>14.2</td>
<td>PS 28</td>
<td>Dark</td>
<td>-7.36</td>
<td>0.63</td>
</tr>
<tr>
<td>16.5</td>
<td>PS 27</td>
<td>Dark</td>
<td>-7.65</td>
<td>0.75</td>
</tr>
<tr>
<td>21.0</td>
<td>PS 25</td>
<td>Light</td>
<td>-8.35</td>
<td>0.18</td>
</tr>
<tr>
<td>22.3</td>
<td>PS 24</td>
<td>Light</td>
<td>-8.13</td>
<td>0.05</td>
</tr>
<tr>
<td>24.5</td>
<td>PS 23</td>
<td>Dark</td>
<td>-7.76</td>
<td>0.16</td>
</tr>
<tr>
<td>27.9</td>
<td>PS 21</td>
<td>Dark</td>
<td>-7.42</td>
<td>0.01</td>
</tr>
<tr>
<td>29.7</td>
<td>PS 20</td>
<td>Light</td>
<td>-7.13</td>
<td>-0.07</td>
</tr>
<tr>
<td>31.0</td>
<td>PS 19</td>
<td>Light</td>
<td>-7.21</td>
<td>-0.27</td>
</tr>
<tr>
<td>32.0</td>
<td>PS 18</td>
<td>Light</td>
<td>-7.22</td>
<td>-0.13</td>
</tr>
<tr>
<td>33.2</td>
<td>PS 17</td>
<td>Dark</td>
<td>-7.19</td>
<td>0.10</td>
</tr>
<tr>
<td>34.5</td>
<td>PS 16</td>
<td>Dark</td>
<td>-7.04</td>
<td>0.06</td>
</tr>
<tr>
<td>37.2</td>
<td>PS 14</td>
<td>Light</td>
<td>-6.86</td>
<td>-0.07</td>
</tr>
<tr>
<td>38.3</td>
<td>PS 13</td>
<td>Dark</td>
<td>-6.77</td>
<td>-0.06</td>
</tr>
<tr>
<td>46.9</td>
<td>PS 05</td>
<td>Dark</td>
<td>-6.98</td>
<td>-0.07</td>
</tr>
<tr>
<td>47.8</td>
<td>PS 04</td>
<td>Light</td>
<td>-6.99</td>
<td>-0.19</td>
</tr>
<tr>
<td>48.9</td>
<td>PS 03</td>
<td>Light</td>
<td>-7.57</td>
<td>-0.15</td>
</tr>
<tr>
<td>50.2</td>
<td>PS 01</td>
<td>Light</td>
<td>-7.19</td>
<td>-0.21</td>
</tr>
</tbody>
</table>
Table 2-3. Total length (TL) estimates for UF 226255. Results based on the CH regressions of Shimada (2003) for each tooth position present. CH and TL given in cm.

<table>
<thead>
<tr>
<th>Tooth</th>
<th>Regression Equation (x=CH)</th>
<th>CH</th>
<th>TL</th>
</tr>
</thead>
<tbody>
<tr>
<td>Right Side</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A1</td>
<td>TL = 5.234+11.522x</td>
<td>44.63</td>
<td>519.46</td>
</tr>
<tr>
<td>A2</td>
<td>TL = -2.16+12.103x</td>
<td>42.71</td>
<td>514.76</td>
</tr>
<tr>
<td>I</td>
<td>TL = 19.162+15.738x</td>
<td>33.00</td>
<td>538.52</td>
</tr>
<tr>
<td>L1</td>
<td>TL = 5.540+14.197x</td>
<td>34.09</td>
<td>489.52</td>
</tr>
<tr>
<td>L2</td>
<td>TL = 4.911+13.433x</td>
<td>34.42</td>
<td>467.27</td>
</tr>
<tr>
<td>L3</td>
<td>TL = 0.464+14.550x</td>
<td>31.47</td>
<td>458.35</td>
</tr>
<tr>
<td>L4</td>
<td>TL = 5.569+17.658x</td>
<td>24.48</td>
<td>437.84</td>
</tr>
<tr>
<td>L5</td>
<td>TL = -5.778+26.381x</td>
<td>17.46</td>
<td>454.83</td>
</tr>
<tr>
<td>L6</td>
<td>TL = -71.915+50.205x</td>
<td>12.04</td>
<td>532.55</td>
</tr>
<tr>
<td>L7</td>
<td>TL = -48.696+69.292x</td>
<td>8.45</td>
<td>536.82</td>
</tr>
<tr>
<td>L8</td>
<td>TL = -84.781+104.968x</td>
<td>6.63</td>
<td>611.16</td>
</tr>
<tr>
<td>L9</td>
<td>TL = -62.050+142.142x</td>
<td>4.65</td>
<td>598.91</td>
</tr>
<tr>
<td>a1</td>
<td>TL = -8.216+14.895x</td>
<td>37.77</td>
<td>554.37</td>
</tr>
<tr>
<td>a2</td>
<td>TL = -7.643+13.597x</td>
<td>42.95</td>
<td>576.35</td>
</tr>
<tr>
<td>a3</td>
<td>TL = -10.765+17.616x</td>
<td>31.19</td>
<td>538.68</td>
</tr>
<tr>
<td>I1</td>
<td>TL = 9.962+17.437x</td>
<td>27.82</td>
<td>495.06</td>
</tr>
<tr>
<td>I2</td>
<td>TL = 1.131+19.204x</td>
<td>23.86</td>
<td>459.34</td>
</tr>
<tr>
<td>I3</td>
<td>TL = 30.947+25.132x</td>
<td>20.03</td>
<td>472.45</td>
</tr>
<tr>
<td>I4</td>
<td>TL = -51.765+35.210x</td>
<td>13.73</td>
<td>431.67</td>
</tr>
<tr>
<td>I5</td>
<td>TL = -73.120+55.262x</td>
<td>9.52</td>
<td>452.97</td>
</tr>
<tr>
<td>Left Side</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A1</td>
<td>TL = 5.234+11.522x</td>
<td>43.47</td>
<td>506.10</td>
</tr>
<tr>
<td>A2</td>
<td>TL = -2.16+12.103x</td>
<td>42.95</td>
<td>517.66</td>
</tr>
<tr>
<td>I</td>
<td>TL = 19.162+15.738x</td>
<td>30.30</td>
<td>492.02</td>
</tr>
<tr>
<td>L1</td>
<td>TL = 5.540+14.197x</td>
<td>33.74</td>
<td>484.55</td>
</tr>
<tr>
<td>L2</td>
<td>TL = 4.911+13.433x</td>
<td>35.27</td>
<td>478.69</td>
</tr>
<tr>
<td>L3</td>
<td>TL = 0.464+14.550x</td>
<td>32.92</td>
<td>479.45</td>
</tr>
<tr>
<td>L4</td>
<td>TL = 5.569+17.658x</td>
<td>24.80</td>
<td>443.49</td>
</tr>
<tr>
<td>L5</td>
<td>TL = -5.778+26.381x</td>
<td>17.45</td>
<td>454.57</td>
</tr>
<tr>
<td>L6</td>
<td>TL = -71.915+50.205x</td>
<td>12.80</td>
<td>570.71</td>
</tr>
<tr>
<td>L7</td>
<td>TL = -48.696+69.292x</td>
<td>9.36</td>
<td>599.88</td>
</tr>
<tr>
<td>L8</td>
<td>TL = -84.781+104.968x</td>
<td>7.62</td>
<td>715.10</td>
</tr>
<tr>
<td>a1</td>
<td>TL = -8.216+14.895x</td>
<td>37.74</td>
<td>553.92</td>
</tr>
<tr>
<td>a2</td>
<td>TL = -7.643+13.597x</td>
<td>41.69</td>
<td>559.22</td>
</tr>
<tr>
<td>a3</td>
<td>TL = -10.765+17.616x</td>
<td>31.90</td>
<td>551.19</td>
</tr>
<tr>
<td>I1</td>
<td>TL = 9.962+17.437x</td>
<td>28.39</td>
<td>505.00</td>
</tr>
<tr>
<td>I2</td>
<td>TL = 1.131+19.204x</td>
<td>24.60</td>
<td>473.55</td>
</tr>
<tr>
<td>I3</td>
<td>TL = 30.947+25.132x</td>
<td>19.82</td>
<td>467.17</td>
</tr>
<tr>
<td>I4</td>
<td>TL = -51.765+35.210x</td>
<td>15.86</td>
<td>506.67</td>
</tr>
<tr>
<td>I5</td>
<td>TL = -73.120+55.262x</td>
<td>6.81</td>
<td>303.21</td>
</tr>
<tr>
<td>I6</td>
<td>TL = -117.456+96.971x</td>
<td>5.01</td>
<td>368.37</td>
</tr>
<tr>
<td>I7</td>
<td>TL = -64.732+138.350x</td>
<td>3.55</td>
<td>426.41</td>
</tr>
<tr>
<td>I8</td>
<td>TL = -137.583+231.411x</td>
<td>3.60</td>
<td>695.50</td>
</tr>
</tbody>
</table>
Table 2-4. References and equations for TL regression estimates. Abbreviations: VD, vertebral diameter; VR, vertebral radius. TL estimates given in cm. Other abbreviations: $r^2$, correlation coefficient; n, sample size; PCL, precaudal length; Fl, fork length.

<table>
<thead>
<tr>
<th>Reference</th>
<th>Equation [(r^2); n; TL conversion (when needed)]</th>
<th>TL</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cailliet et al. (1985)</td>
<td>TL = 35.9 + 5.7 * VD [0.90; 67; -]</td>
<td>470</td>
</tr>
<tr>
<td>Gottfried et al. (1996)</td>
<td>TL = 22 + 5.8 * VD [0.97; 16; -]</td>
<td>464</td>
</tr>
<tr>
<td>Wintner and Cliff (1999)</td>
<td>PCL = (VD/10 + 0.3)/0.02 [0.96; 114; TL = 5.2 + 1.3 * PCL]</td>
<td>520</td>
</tr>
<tr>
<td>Natanson (2001)</td>
<td>FL = 21.0 + 11.8 * VR [0.94; 14; TL = (FL + 0.06)/0.94]</td>
<td>501</td>
</tr>
</tbody>
</table>
CHAPTER 3
CAUGHT IN THE ACT: TROPHIC INTERACTIONS BETWEEN A 4-MILLION-YEAR-OLD WHITE SHARK (CARCHARODON) AND MYSTICETE WHALE FROM PERU

Introduction

Neoselachian sharks are represented most commonly in the fossil record by unassociated teeth.\(^2\) In fact, shark teeth are some of the most abundant vertebrate fossils in the geologic record (Hubbell 1996). Less commonly, other fossil shark remains are recovered that include preserved cartilage, coprolites, gastric residues, and indirect evidence of predation or scavenging. The scarcity of these types of specimens corresponds to the low probability of uncalcified tissues and trace fossils being preserved. Most evidence of shark predation and scavenging from the fossil record consists of tooth scrapes and gouges on bones (Deméré and Cerutti 1982; Cigala-Fulgosi 1990; Noriega et al. 2007). Very rarely shark teeth or portions of teeth are found embedded in, or in direct association with, the prey species (Repenning and Packard 1990; Schwimmer et al. 1997; Shimada and Everhart 2004; Shimada and Hooks 2004).

This report describes a partial mysticete whale mandible that contains an embedded partial white shark (Carcharodon sp.) tooth and associated scrape marks. The specimen was collected from the Upper Miocene to Upper Pliocene Pisco Formation of southern Peru, an area well known for both its abundance of marine fossils and the exceptional preservation of articulated skeletons (de Muizon and DeVries 1985; Pilleri and Siber 1989; Bouetel and de Muizon 2006). This unique preservational environment is exceptional because we can infer more about the paleoecology of the

\(^2\) Reprinted with permission from EHRET, D. J., MACFADDEN, B. J. and SALAS-GISMONDI, R. 2009. Caught in the act: Trophic interactions between a 4-Million-Year-Old white shark (Carcharodon) and mysticete whale from Peru. Palaios, 24, 329–333.
assemblage than from many other shallow marine localities. The site where the specimen was found has produced numerous complete whale skeletons and one of the most complete specimens of a fossil white shark ever found (de Muizon and DeVries 1985; Ehret, Hubbell, and MacFadden 2009). In addition, this is the first report of a fossil white shark tooth embedded within the bone of its prey. Previous reports of fossil white shark feeding behavior include possible predation of an extinct bottle-nosed dolphin from Italy (Cigala-Fulgosi 1990), scavenging of a cetotheriid whale from California (Deméré and Cerutti 1982), and scavenging of a balaenopterid whale in Argentina (Noriega et al. 2007).

**Locality and Stratigraphy**

The Pisco Formation of southern Peru (Figure 3-1) represents a series of marine transgressive and regressive cycles deposited in a forearc basin along 350 km of coastline from Pisco to Yauca (de Muizon and DeVries 1985; Bouetel and de Muizon 2006; Ehret, Hubbell, and MacFadden 2009). These rocks range in age from Late Miocene to Late Pliocene, or ~10–4 Ma. The outcrops are discontinuous throughout the region and the formation is not fully exposed at any single site. The stratigraphy, therefore, is a composite section based on numerous separate localities (Figure 3-2). The deposits consist of tuffaceous sandy siltstone, medium- to coarse-grained sandstone, shelly sandstone with some bedded tuff, conglomerate, and coquina (de Muizon and Devries 1985). De Muizon and Devries (1985) concluded that the Pisco Formation represents nearshore, intertidal, and lagoonal depositional environments during higher sea levels in the past, based on the sequence, lithology, and structure of the deposits.
The specimen was collected on 13 August 2007 from an area known as Sud-Sacaco West (15° 34’ 21‖S, 74° 43’ 48‖W). This locality is characterized by a fossil zone, referred to as SAS by de Muizon and Devries (1985), that extends from ~21 to 43 m above the base of the local measured section and represents the interval from which this specimen was collected (Ehret, Hubbell, and MacFadden 2009). A diverse shallow-water marine invertebrate fauna also present in the SAS supports the interpretation that the deposits represent barrier bar and lagoonal settings. Sud-Sacaco West is thought to be Early Pliocene in age between 4–5 Ma old, based on correlations to an overlying section (Sacaco) with an associated K-Ar tuff date of 3.9 Ma, and younger than the Miocene based on biostratigraphy (de Muizon and DeVries 1985; DeVries and Schrader 1997; Ehret, Hubbell, and MacFadden 2009).

In addition to sharks and mysticete whales, marine vertebrate fossils in the Pisco Formation include rays, teleosts, chelonians, crocodilians, sea birds, seals, and an aquatic sloth (Hoffstetter 1968; de Muizon and DeVries 1985; de Muizon et al. 1994; de Muizon et al. 2002). The relative abundance of species, however, is difficult to deduce due to mostly nonsystematic collecting practices. Of the lamniform species, there is a good representation of lamnid and odontodid sharks. *Carcharocles megalodon* and *Isurus hastalis* are abundant in the lower part of the formation (Late Miocene), whereas *C. megalodon* and *Carcharodon* sp. occur in the upper (Early Pliocene) part of the formation (de Muizon and DeVries 1985; Ehret, Hubbell, and MacFadden 2009). The upper Pisco Formation correlates approximately to the contemporaneous, mostly shallow-water marine fauna of the Yorktown Formation of North Carolina (Purdy et al.
2001), as well as the marginal marine Palmetto fauna of the Upper Bone Valley Formation in Florida (Morgan 1994) based on the vertebrate biostratigraphy.

**Specimen Description**

The specimen, MUSM 1470, is housed in the Museo de Historia Natural (MUSM), Lima, Peru, and consists of a portion of mandible of a mysticete whale with an embedded partial tooth crown from a lamnid shark (Figure 3-3). The tooth crown can be referred to a white shark (*Carcharodon* sp.) based on overall morphology and the presence of weak serrations (Ehret, Hubbell, and MacFadden 2009).

The cetacean mandible is 183.0 mm long and slightly convex. The dorsal side of the bone has a vestigial alveolar groove present that is 111.1 mm long and 7.9 mm wide. This groove tapers off roughly three-quarters of the way down the bone. This fossil represents the left labial portion of the mandible based on the convex shape of the bone and the direction that the vestigial alveolar groove tapers. There are several small foramina parallel to this groove, the largest of which is ~2.0 mm in diameter. MUSM 1470 potentially could be referred to one of two species of mysticete whales currently recognized from Sud-Sacaco West. The first is the cetotheriid whale, *Piscobalaena nana*, which is a small, baleen-bearing mysticete (Pilleri and Siber 1989; Bouetel and de Muizon 2006). The second is an undescribed balaenopterid referred to as *Balaenoptera* sp. (Pilleri and Siber 1989; Bouetel and de Muizon 2006). There is no positive identification as to which species it represents due to the fragmentary nature of the specimen.

The crown is broken off in the cortical bone of the whale mandible. The apex, or tip, of the tooth is visible on the reverse side, within the marrow cavity. The tooth is situated ~44.0 mm from the dorsal surface and 29.4 mm from the ventral surface of the
bone. The labial side of the tooth is situated parallel to the dorsal surface of the mandible and the lingual surface of the tooth parallel to the ventral surface of the bone. The tooth fragment measures 26.4 mm from the apex to the highest portion of enameloid preserved. Weak serrations are developed on the labial side of the bone, whereas the apex of the tooth has a smooth edge, a characteristic of this white shark (de Muizon and Devries 1985; Ehret, Hubbell, and MacFadden 2009). When the tooth is removed from the bone, weak serrations are visible on both cutting surfaces (Figure 3-3). The tooth has been broken on an angle, so that the broken edge is flush with the surface of the bone. The medial edge is longer and contains 17 serrations, whereas the lateral edge is shorter and has 11 serrations. The number of serrations per millimeter is also consistent with that of the *Carcharodon* sp. specimen described from Sud-Sacaco West, Ehret, Hubbell, and MacFadden (2009). The exact tooth position in the jaws of *Carcharodon* cannot be positively identified due to the fragmentary nature of the specimen. The tooth is most likely a lateral tooth based on its size and curvature, however.

In addition to the tooth crown, there are two other tooth marks on the bone. One appears anterior, and the other posterior, to the partial crown. Both marks appear as shallow grooves across the labial surface of the bone (Figure 3-3). They are < 1 mm deep and do not have any visible serration marks. The anterior mark is 59.4 mm long and runs at an angle of 35° across the bone. The posterior mark is punctuated by a small pit, 4.5 mm long that leads into a shallow groove that extends for 42.6 mm and continues off the edge of the specimen at a 40° angle.
Discussion

There have been numerous isolated cases of predation and scavenging by sharks documented in the literature. Prey items including sea turtles, mosasaurs, bony fishes, cetaceans, a desmostylian, and even a dinosaur have been recorded (Deméré and Cerutti 1982; Cigala-Fulgosi 1990; Repenning and Packard 1990; Schwimmer et al. 1997; Shimada and Everhart 2004; Shimada and Hooks 2004; Noriega et al. 2006). These reports, however, are only a small fraction of all of the shark-bitten materials in collections that have not been identified or described. Most papers focus only on extraordinary examples of predation or ones where the shark or prey species can be identified. While these reports do give some insight into the paleoecology of fossil species, it is difficult to ascertain what would be considered normal prey items. In contrast, there are very few studies that have examined the paleoecology of sharks based on multiple lines the feeding evidence from a given locality (Purdy 1996; Aguilera and Aguilera 2004).

In MUSM 1470, the characteristics of the tooth are consistent with those of a *Carcharodon* sp. The only other shark species with large, serrated teeth found at Sud-Sacaco West is *Carcharocles megalodon*. There is no doubt, however, that this tooth represents a white shark based on the serration pattern, thickness, and size of the tooth. An articulated specimen of *Carcharodon* sp., UF 226255, was collected only a few hundred meters from MUSM 1470 in 1988, which includes a nearly complete dentition (Ehret, Hubbell, and MacFadden 2009). Documenting the co-occurrence and interactions between this species and other marine organisms in the Pisco Formation is significant to the paleoecological community.
The diet of modern white sharks (*Carcharodon carcharias*) has been studied extensively (e.g., McCosker 1985; Long and Jones 1996). A dietary shift in trophic levels has been documented from juveniles to adults that can be traced through the use of nitrogen and carbon isotopes (Kerr *et al.* 2006). Juvenile white sharks are mainly piscivorous with a shift to marine mammals as they reach maturity. This shift is most likely tied to changes in morphology, energetic requirements, and size of predator and prey (Tricas and McCosker 1984). Adult white sharks will actively pursue pinnipeds, whereas attacks on live cetaceans are extremely rare (Long and Jones 1996). When feeding on pinnipeds, behavior usually entails bite and release which usually inflicts a fatal injury known as the bite and spit strategy. The shark then waits for the individual to die before eating the carcass (Tricas and McCosker 1984; Long *et al.* 1996). In other feeding modes, white sharks typically scavenge cetacean carcasses, stripping off layers of blubber (Long and Jones 1996; Curtis *et al.* 2006; Dicken 2008).

It is extremely difficult to separate acts of predation from those of scavenging in the fossil record. Active predation could be identified by bone growth or healing around a wound (Schwimmer *et al.* 1997; Shimada and Hooks 1997). In contrast, bite marks that do not show signs of healing could be related to either predation, which resulted in death, or scavenging (Cigala-Fulgosi 1990; Shimada and Hooks 2004). As stated previously, modern white sharks very rarely attack live cetaceans. In those rare instances when predation has occurred, the sharks targeted the back or side of the body with no bite marks in the cranial region (Long and Jones 1996). In MUSM 1470, the partial tooth crown is positioned with the lingual surface parallel to the dorsal surface of the mandible and the labial surface parallel to the ventral surface of the mandible.
The shark would have bitten the mandible ventrally based on the orientation of the bite mark. The nature of the fossil record makes it difficult to discriminate if this trophic interaction was an act of predation or scavenging, but considering previous discussions, MUSM 1470 is interpreted to represent a scavenging event.

Recent observations of feeding behaviors in modern juvenile white sharks support our hypothesis. Dicken (2008) witnessed young of the year and juvenile white sharks preferentially biting and feeding around the mouth region of a deceased humpback whale (*Megaptera novaeangliae*). The whale carcass had inverted and was floating due to gas build up during decomposition (Noriega *et al.* 2007; Dicken 2008). The carcass remained in that state for over one month during which time numerous white sharks fed on the carcass. This report is the first case of juvenile white sharks feeding on a whale carcass and the first documentation of preferential feeding in and around the mouth region. While the total length of the fossil white shark in our specimen cannot be ascertained, it seems to represent a juvenile or young adult. Thus, similarities appear to exist in feeding behavior with modern white shark analogs.

**Conclusions**

MUSM 1470 represents a scavenging event by a fossil *Carcharodon* sp. on a mysticete whale based on the feeding observations of modern white sharks. Documenting the trophic interactions between this large predatory shark and a cetacean elucidates the paleoecology of southern coastal Peru during the Pliocene. Reconstructing the life histories of fossil sharks is often hampered by the incomplete preservation of their cartilaginous skeletons. Interpreting paleoecological information from isolated teeth is extremely difficult, and even with indirect evidence of feeding, the exact interactions between species can be difficult to ascertain. When such specimens
as MUSM 1470 are discovered, they provide almost unique opportunities to advance knowledge about trophic dynamics within ancient ecosystems.
Figure 3-1. Location of study area, Sud-Sacaco West, along the southwestern coast of Peru.
Figure 3-2. Composite stratigraphic section for the upper Pisco Formation. MTM = Montemar; SAO = Sacaco; SAS = Sud-Sacaco West (after de Muizon and DeVries 1985).
Figure 3-3. Mysticete mandible with white shark (*Carcharodon* sp.) tooth (MUSM 1470). The tooth is figured at center. Boxes on left and right show tooth scrapes.
INTRODUCTION

Neoselachians are well represented in the fossil record worldwide during the Neogene with most of the fossil material found consisting of isolated teeth. Shark teeth are shed by the thousands over an individual’s lifetime and have an enameloid crown that acts as a protective layer during fossilization. The cartilaginous skeleton of chondrichthians does not typically preserve except in rare instances, and calcified vertebral centra, portions of the neurocranium, and fin rays have been described (Uyeno et al. 1990; Shimada 1997b; Siverson 1999; Gottfried and Fordyce 2001; Shimada 2007; Ehret, Hubbell, and MacFadden 2009). The lack of more complete specimens of most fossil taxa has led to conflicting interpretations about the taxonomy and anatomy of many species. Such problems have caused much confusion in the nomenclature (including generic and specific names) and terminology (i.e. dental homologies) of fossil neoselachians.

One of the most debated enigmas within the neoselachians focuses on the evolution and taxonomic placement of the white shark, Carcharodon carcharias Linnaeus, 1758, within the Lamniformes. There are two distinct hypotheses regarding the evolution of C. carcharias that have been proposed in the literature. The first hypothesis places all large, serrated megatoothed sharks within the genus

---

*Carcharodon*, including *C. carcharias* as well as those species referred to as *Carcharocles*, e.g. *Carcharocles megalodon* Jordan and Hannibal, 1923 and its related taxa. Based on this taxonomy, the lineage of *C. carcharias* branched off as smaller forms of the megatoothed sharks and co-evolved alongside the truly large taxa, such as *C. megalodon* (Applegate and Espinosa-Arrubarrena 1996; Gottfried *et al.* 1996; Purdy 1996; Gottfried and Fordyce 2001; Purdy *et al.* 2001).

The second hypothesis proposes that *Carcharodon carcharias* evolved from the broad-toothed *Carcharodon hastalis* Agassiz, 1838 while the megatoothed sharks belong to a separate family, the Otodontidae, within the Lamniformes (Casier 1960; Glikman 1964; Cappetta 1987; Ward and Bonavia 2001; Nyberg *et al.* 2006; Ehret, Hubbell, and MacFadden 2009). *Carcharodon hastalis* was originally assigned to the genus *Oxyrhina* and later to *Isurus*. However, based on affinities with *C. carcharias* Glikman (1964) suggested the reassignment of all unserrated forms within the *Carcharodon* lineage to the genus *Cosmopolitodus* to reflect this relationship (Siverson 1999; Ward and Bonavia 2001). From a taxonomic standpoint, *C. hastalis* and *C. carcharias* represent chronospecies as one species is replaced by another in geological time through a stepwise gradation. Furthermore, the teeth of *C. hastalis* do not share characters with *Isurus* but instead are more similar to *C. carcharias* exhibiting triangular crowns that are labiolingually flattened, a flat labial face, a lingual face that is slightly convex, and a root that is flat and quite high (Cappetta 1987). As such, the genus *Carcharodon* Smith in Müller and Henle, 1838 is the senior synonym of *Cosmopolitodus* Glikman, 1964 the proper genus name for *C. hastalis*. Fossil materials collected from the Late Miocene and Early Pliocene of the Pacific Basin including Peru (specifically the
Pisco Formation), Chile, California, and Japan provide further evidence of this relationship (de Muizon and DeVries 1985; Long 1993; Tanaka and Mori 1996; Stewart 1999, 2002; Yabe 2000; Suarez et al. 2006; Nyberg et al. 2006; Ehret, Hubbell, and MacFadden 2009).

The shallow-water, marine Pisco Formation of southwestern Peru consists of sediments that accumulated during the Late Miocene to Early Pliocene (c.13–4 Ma) and it is a deposit that is well known for its excellently preserved fossils. In addition to the presence of complete whale, fish, bird, and aquatic sloth skeletons, the area also contains the partial remains of fossil sharks including: associated tooth sets, vertebral centra, and preserved cartilage of the jaws and neurocrania. Additionally, the Pisco Formation represents a period of time when Carcharodon hastalis disappeared and Carcharodon carcharias first appeared. Another taxon that exhibits intermediate characters between the two species, previously referred to as Carcharodon sp., is also abundant in some localities of the Pisco Formation (de Muizon and DeVries 1985; Ehret, Hubbell, and MacFadden 2009).

The recent description of an articulated specimen of this intermediate form of Carcharodon from the Pisco Formation presents important new insights into the evolutionary history and taxonomy of the genus (Ehret, Hubbell, and MacFadden 2009). In their description the specimen was referred to the Early Pliocene (c. 4.5 Ma) based on the stratigraphic framework of de Muizon and DeVries (1985). However, isotopic recalibration of some of the original localities of de Muizon and DeVries (1985) using strontium and zircon dating allows us to reassess the ages of these localities. Based on these recalibrations, this specimen is now referred to the Late Miocene rather than the
Early Pliocene. The purpose of this paper is to present a reassessment of the ages of some localities within the Pisco Formation, formally describe a new species of white shark, and relate changes in age and taxonomy to the evolution of the white shark within the Pacific Basin.

Methods and Materials

Numerous studies indicate the Miocene Epoch was characterized by rapidly increasing $^{87}\text{Sr} / ^{86}\text{Sr}$ in the global ocean; therefore, it is especially amenable to dating and correlating marine sediments using strontium isotope chemostratigraphy (e.g. Hodell et al. 1991; Miller et al. 1991; Hodell and Woodruff 1994; Oslick et al. 1994; Miller and Sugarman 1995; Martin et al. 1999; McArthur et al. 2001). Three fossil marine mollusk shells were analyzed from each of five localities within the Pisco Formation in order to determine the ratio of $^{87}\text{Sr} / ^{86}\text{Sr}$ in the shell calcium carbonate. When compared to the global seawater reference curve, these data allow us to estimate the geological age for each locality (Table 4-1).

For isotopic analyses, a portion of the surface layer of each shell specimen was ground off to reduce possible contamination. Areas showing chalkiness or other signs of diagenetic alteration were avoided. Approximately 0.01 to 0.03 g of aragonite or low-magnesium calcite powder was recovered from each fossil sample. The powdered samples were dissolved in 100 µl of 3.5 N HNO$_3$ and then loaded onto cation exchange columns packed with strontium-selective crown ether resin (Eichrom Technologies, Inc.) to separate Sr from other ions (Pin and Bassin 1992). Sr isotope analyses were performed on a Micromass Sector 54 Thermal Ionization Mass Spectrometer equipped with seven Faraday collectors and one Daly detector in the Department of Geological Sciences, University of Florida. Sr was loaded onto oxidized tungsten single filaments
and run in triple collector dynamic mode. Data were acquired at a beam intensity of about 1.5 V for $^{88}\text{Sr}$, with corrections for instrumental discrimination made assuming $^{86}\text{Sr}/^{88}\text{Sr} = 0.1194$. Errors in measured $^{87}\text{Sr}/^{86}\text{Sr}$ are better than ±0.00002 (2σ), based on long-term reproducibility of NIST 987 ($^{87}\text{Sr}/^{86}\text{Sr} = 0.71024$). Age estimates were determined using the Miocene portion of Look-Up Table Version 4:08/03 associated with the strontium isotopic age model of McArthur et al. (2001).

Zircons were extracted from samples using standard crushing, density separation, and magnetic separation techniques. The zircons were hand picked, mounted in epoxy plugs along with the reference zircon FC-1 (Paces and Miller 1993), and analyzed using laser ablation multi-collector inductively coupled plasma mass spectrometry (LA-MC-ICP-MS). A Nu-Plasma mass spectrometer fitted with a U-Pb collector array was used for analysis at the Department of Geological Sciences, University of Florida. $^{238}\text{U}$ and $^{235}\text{U}$ abundances were measured on Faraday collectors and $^{207}\text{Pb}$, $^{206}\text{Pb}$, and $^{204}\text{Pb}$ abundances on ion counters. The Nu Plasma mass spectrometer is coupled with a New Wave 213 nm ultraviolet laser for ablating 30–60 µm spots within zircon grains. Laser ablation was carried out in the presence of a helium carrier gas, which was mixed with argon gas just prior to introduction to the plasma torch. Isotopic data were acquired during the analyses using Time Resolved Analysis software from Nu-Instruments. Before the ablation of each zircon a 30 s peak zero was determined on the blank He and Ar gases with closed laser shutter. This zero was used for on-line correction for isobaric interferences, particularly from $^{204}\text{Hg}$. Following blank acquisitions individual zircons underwent ablation and analysis for c. 30–60 seconds. The analyses of unknown zircons were bracketed by analyzing an FC-1 standard zircon.


**Geological Setting and Geochronology**

The Pisco Formation crops out on the coastal plain of southern Peru from the town of Pisco south to Yauca (Figure 4-1). Its sediments, which include tuffaceous and diatomaceous sandstone and siltstone, ash horizons, bioclastic conglomerates and phosphorite, representing shallow marine environments preserve cyclic marine transgressive and regressive periods spanning the mid Miocene (c. 13 Ma) through the Pliocene (c. 4 Ma) (de Muizon and DeVries 1985; Dunbar 1990; DeVries 1998; Amiot et al. 2008). This formation is well known for its wealth of vertebrate fossils including elasmobranchs, teleosts, chelonians, shore birds, seals, dolphins, whales, and aquatic sloths (Hoffstetter 1968; de Muizon and DeVries 1985; de Muizon and McDonald 1995; de Muizon et al. 2002; Amiot et al. 2008; Ehret, Hubbell, and MacFadden 2009).

Around the Sacaco area, de Muizon and DeVries (1985) recognized 5 vertebrate fossil layers within the Pisco Formation: El Jahuay (Alto Grande) (ELJ), Aguada de Lomas (AGL), Montemar (MTM), Sud Sacaco (West) (SAS), and Sacaco (SAO) (Figure 4-2). These layers are distinguished by a high diversity of species. The ELJ level contains layers of mollusks, as well as a tuff bed that has been assigned an age of 9.5 Ma based on K-Ar dating (de Muizon and DeVries 1985; de Muizon and Bellon 1986). This layer is also marked by the presence of *Carcharodon hastalis* and *Carcharocles megalodon*. AGL is similar in stratigraphy and it might be contemporaneous with ELJ. Two tuff beds dated using K-Ar were assigned ages of 8 Ma and 8.8 Ma respectively (de Muizon and DeVries 1985; de Muizon and Bellon 1986). Montemar was considered to be latest Miocene (c. 6 Ma) in age based partially on the occurrence of transitional *Carcharodon* teeth and several molluscan species. The Sud Sacaco vertebrate layer is marked by a series of barnacle and shell beds that that contains a diverse assemblage.
of mollusks and vertebrates. These beds are capped by thick vertebrate-bearing tuffs, fining upward cycles of brachiopod-bearing sandstones which contain more strongly serrated *Carcharodon carcharias*-like teeth (de Muizon and DeVries 1985). Based on the stratigraphy and palaeontology, it was believed that these beds were older than the 3.9 Ma tuff bed of de Muizon and Bellon (1980), but younger than the Miocene (de Muizon and DeVries 1985). Finally, the SAO level is found above a tuff bed that was dated at 3.9 Ma, indicating an Early Pliocene age (de Muizon and Bellon 1980; de Muizon and DeVries 1985).

Additional sampling of invertebrate fossils and the tuff beds taken from ELJ, MTM, SAS, and SAO during the summer of 2007 were analyzed for $^{87}\text{Sr}/^{86}\text{Sr}$ isotopes and zircon U-Pb. At Alto Grande, within the ELJ vertebrate layer, $^{87}\text{Sr}/^{86}\text{Sr}$ ages of the invertebrates gave an age range of 9.03–6.51 Ma with a mean of 7.46 Ma. Analysis of 55 zircon grains collected from the tuff bed at Alto Grande yielded 54 that gave ages that were Neoproterozoic through Cretaceous, which are obviously inherited or mixed detritus. One grain gave a concordant crystallization age of 10±1 Ma, which could also be inherited and should be treated as an upper limit for the locality.

Mollusk samples analyzed from MTM yield $^{87}\text{Sr}/^{86}\text{Sr}$ dates of 8.70–6.45 Ma with a mean of 7.30 Ma. These ages are congruent with the estimation of de Muizon and DeVries (1985) based on the vertebrate and invertebrate faunas. While the resolution of the strontium data is not more precise than the estimate based on the molluscan fauna, it does confirm a Late Miocene age for the locality.

At Sud Sacaco (West) (SAS) *Dosinia* Scopoli, 1777 beds that graded into gastropod layer were sampled for strontium. $^{87}\text{Sr}/^{86}\text{Sr}$ dates for the layer ranged from
10.77–2.50 Ma with a mean of 6.59 Ma. Additionally, the vertebrate-bearing tuff bed was located and sampled for zircon data. In total, 35 zircon grains were analyzed with a majority being inherited or mixed detrital grains. Of the Oligocene and Miocene zircons identified, the youngest grain is 7±1 Ma and is probably the upper limit of the depositional range. An in situ Carcharodon specimen (UF 226255) was recovered 20–40 cm above the base of this ash layer and will be discussed in detail below (Ehret, Hubbell, and MacFadden 2009). Diatom analysis of the SAS (West) (Hans Schrader, University of Bergen, Norway, 1986, unpublished data) ash bed (locality DV 432-1) recovered the following species: Rossiella tatsunokuchiensis Koizumi, 1972, FAD (first appearance datum) 7 Ma, LAD (last appearance datum) 3 Ma; Shionodiscus oestrupii Alverson et al., 2006 FAD 6 Ma, LAD 0 Ma, which are consistent with both ash and Sr data. On the east side of SAS (West), approximately 10 m above the ash layer, a shell bed containing abundant Ophiomorpha Lundgren, 1891 burrows was sampled for strontium and yielded an age range of 6.35–5.47 Ma, with a mean of 5.93 Ma. These new dates for the SAS are older than those previously recorded for the locality and suggest a Late Miocene rather than Early Pliocene age (de Muizon and DeVries 1985).

At the youngest locality, Sacaco (SAO), mollusk samples were collected near the Museo de Sacaco and yielded $^{87}\text{Sr}/^{86}\text{Sr}$ dates of 6.76–4.86 Ma, with a mean of 5.89 Ma. This age is much older than the underlying tuff bed dated at 3.9 Ma by de Muizon and Bellon (1980). Additional unpublished Ar-Ar data from the SAO ash bed located on the floor of eastern side of Quebrada Sacaco (locality DV 514-2Snee) below the unconformity that separates Sacaco shell beds from upper portion of sequence on the hillsides of Sacaco yielded an age of 5.75±0.05 Ma (Lawrence Snee, USGS, sample
collected 1987). This new Sr and Ar data makes the 3.9 Ma age of de Muizon and Bellon (1980) suspect. The Sacaco section appears to be older than previously recorded while the angular unconformity on the hillside of Sacaco represents more time than originally thought.

Overview of Taxonomy and Fossil Record of *Carcharodon*

As previously discussed, the evolutionary history of *Carcharodon* has been a contentious subject. In order to elucidate our current knowledge of the subject, it is important to review the hypotheses that have been previously proposed. Next, material from Peru will be compared and incorporated into these paradigms. The taxonomy of the megatoothed sharks (including *Otodus* Agassiz, 1838 and *Carcharocles* Jordan and Hannibal, 1923) beyond their relationship to *Carcharodon carcharias* is not within the scope of this paper and will only be addressed to the extent necessary.

The first hypothesis places the megatoothed sharks (*Otodus* and *Carcharocles*) and *Carcharodon carcharias* within the Lamnidae. The serrated-toothed forms of the megatoothed sharks are assigned to the genus *Carcharodon* (referred to as *Carcharocles* here), while the unserrated form is recognized as being related and has been given a separate generic name, *Otodus* (Applegate and Espinosa-Arrubarrena 1996; Gottfried *et al.* 1996; Purdy 1996; Purdy *et al.* 2001). It should be noted that a recent shift in paradigm recognizes *Otodus* as a chronospecies, thereby placing all species of *Carcharocles* into the genus *Otodus*, with the exception of *megalodon*, which has been referred to the genus *Megaselachus* Glikman, 1964 (Casier 1960; Zhelezko and Kozlov 1999; Ward and Bonavia 2001, Cappetta and Cavallo 2006). For the purpose of this discussion, however, all serrated megatoothed sharks are referred to *Carcharocles* based on the accepted taxonomy in the literature at the present time.
The grouping of megatoothed sharks with *Carcharodon carcharias* was based on a number of dental characters including: (1) a symmetrical second anterior tooth; (2) large third anterior (intermediate) tooth that is inclined mesially; (3) upper anterior teeth that have a chevron shaped neck on the lingual surface; (4) an ontogenetic gradation whereby the coarse serrations of a juvenile *C. carcharias* shift to fine serrations in the adult, the latter serrations resembling those of *Carcharocles megalodon*; (5) morphological similarity between the teeth of young *C. megalodon* and adult *C. carcharias* (Gottfried *et al.* 1996; Gottfried and Fordyce 2001; Purdy *et al.* 2001; Ehret, Hubbell, and MacFadden 2009). Following this hypothesis, *C. carcharias* is either the result of dwarfism from a larger megatoothed taxon or evolved via cladogenesis from a large megatoothed shark species sometime during the Paleocene and coevolved alongside the other species (Gottfried 1996; Martin 1996; Purdy 1996; Purdy *et al.* 2001).

This taxonomy, however, does not truly reflect the fossil record. The characters listed above as diagnostic, uniting the megatoothed sharks and *Carcharodon carcharias*, are a result of a combination of individual variation, interpretation, and homoplasy (Hubbell 1996; Shimada 2005). Variation and pathologic abnormalities within individual teeth can lead to the incorrect interpretation and identification of specimens. As an example, USNM 336204 has been described as lateral tooth of *Carcharodon* sp. (Purdy 1996) or *C. carcharias* (Gottfried and Fordyce 2001) from the Middle Miocene of the Calvert Formation of Maryland (Figure 4-3). However, re-analysis of this specimen reveals that it is a small *Carcharocles megalodon*, based on the presence of a chevron-shaped neck, the thickness of the crown, and the serration type.
While the serrations are somewhat coarse for *C. megalodon* and could be misleading, the presence of the other characters listed above make this identification more plausible. Furthermore, the reconstruction of dental patterns of extinct sharks based on isolated teeth or disarticulated tooth sets are misleading when extant taxa are used as a template for interpretations (Shimada 2006, 2007). Finally, the presence of serrations in both the megatoothed and white sharks is a result of homoplasy rather than a diagnostic character uniting the two taxa. A comparison of the serrations shows that they are in fact very different, with the *Carcharocles* exhibiting very fine and regular serrations while those of *Carcharodon* are coarse and irregular (Figure 4-4).

The second hypothesis keeps *Carcharodon carcharias* and the broad-toothed ‘makos’ within the Lamnidae while the megatoothed sharks are reclassified into their own family, the Otodontidae within the Lamniformes. This hypothesis proposes that *Carcharodon hastalis* gave rise to the serrated-toothed *C. carcharias* during the Late Miocene or Early Pliocene (Casier 1960; Glikman 1964; de Muizon and DeVries 1985; Cappetta 1987; Ward and Bonavia 2001; Nyberg et al. 2006; Ehret, Hubbell, and MacFadden 2009). This hypothesis would suggest that the lamnid and otodontid sharks last shared a common taxon in the Cretaceous (Casier 1960). Casier (1960) proposed that *C. hastalis* is ancestral to *C. carcharias* citing characters of dentition (although he did not list these characters) and offering as a possible transition between the taxa *Isurus escheri* Agassiz, 1838, which exhibits weak, fine crenulations (not true serrations) on the cutting edges of its teeth.

It should be noted that Agassiz (1833-1843) separated the broad-toothed ‘makos’ into numerous separate morphotypes, two of the most prominent were originally
referred to *Carcharodon (Oxyrhina) hastalis* and *Isurus (Oxyrhina) xiphodon* (Agassiz 1838). His differentiation of the two taxa was based on *C. hastalis* having a noticeable flattening of the lingual crown foot and narrower tooth crowns than *I. xiphodon* but conceded that the latter was too weak of a character for identification (Agassiz 1833-1843; Purdy *et al.* 2001). Leriche (1926) included *I. xiphodon* in the synonymy of *C. hastalis* and noted the uncertainty of the origin of the types, which have since been lost (Ward and Bonavia 2001). The species was recognized by Glikman (1964) and Purdy *et al.* (2001), who attributed specimens of *C. hastalis* from Peru, North Carolina, and Belgium; the new species from Peru described herein; and *Isurus escheri* from Belgium to *I. xiphodon* based solely on the broadness of their crowns. Ward and Bonavia (2001) regarded *I. xiphodon* as a *nomen dubium* based on the arguments of Leriche (1926) the absence of any type specimens, and an unlikely provenance. Recent morphometric analysis of broad-toothed ‘mako’ specimens by Whitenack and Gottfried (2010) supports a morphological difference based on the broadness of the crown in broad-toothed ‘makos’. While this study might accurately separate these species, this could also represent sexual dimorphism or ontogenetic changes in tooth morphology in one taxon. There may be a true delineation between broad and narrow crowned broad-toothed ‘makos’ however, based on the arguments of Leriche (1926) and Ward and Bonavia (2001), the name *I. xiphodon* is inappropriate and use *C. hastalis* for all forms of broad-toothed ‘makos’ at the present time.

The species *Isurus escheri* was originally placed in the genus *Oxyrhina* and later *Isurus* as a variant of *Carcharodon hastalis* (Agassiz 1833-1843; Leriche 1926; Casier 1960). Specimens have been reported from the Late Middle Miocene through the Early
to Middle Pliocene (c.14 – 4 Ma) of the northern Atlantic (including Germany, Belgium, the Netherlands, and Denmark) with materials ranging from isolated teeth to an associated set of teeth and vertebrae from northern Germany (Agassiz 1833-1843; Leriche 1926; van den Bosch et al. 1975; Nolf 1988; Mewis and Klug 2006; Mewis 2008). The crenulations on the cutting edges of the teeth are much finer than the serrations of *Carcharodon carcharias* and specimens found in the Pacific Basin and tend to be along the entire cutting edge of the tooth (Leriche 1926; van den Bosch et al. 1975; Nolf 1988). In addition to crenulations, some specimens may exhibit 1–3 pairs of lateral cusplets, which are more pronounced in the lower teeth (Mewis 2008).

The crown shape of *Isurus escheri* is less dorso-ventrally flattened and thinner antero-dorsally with a stronger distal inclination than either *Carcharodon hastalis* or *Carcharodon carcharias* (Figure 4-5). This inclination is a result of a marked change in direction of the distal cutting edge of the tooth crown and appears to be more pronounced in lateral teeth. The roots of the upper teeth also appear to be more lobate and angular than either *C. hastalis* or *C. carcharias*, which have very square, rectangular roots (Ehret, Hubell, and MacFadden 2009). The teeth of *I. escheri* appear to have stronger affinities with a more narrow-toothed form of *C. hastalis*. Whereas the vertebral centra reported from Germany appear to have the typical amphicoelous lamniform morphology, that is not diagnostic for refined taxonomic assessment above the ordinal level (Mewis and Klug 2006; Mewis 2008).

While the latter hypothesis more accurately portrays the evolutionary history of *Carcharodon*, the designation of *Isurus escheri* as a sister taxon to *Carcharodon carcharias* based on cladistic analysis of dental characters by Mewis (2008) could be
misleading. Shimada (2005) has shown that cladistic analysis combining both dental and non-dental characters of extant and fossil shark taxa generates considerable phylogenetic noise. Comparisons of consensus trees using dental characters versus trees combining dental and all other morphological characters result in different topologies. Tree statistics for the cladogram just using non-dental characters were better than those combining dental and non-dental characters (Shimada 2005). Shimada did acknowledge, however, that patterns indicated that dental characters are important for at least some phylogenetic signal. A review of the analysis by Mewis (2008) reveals that 3 of the synapomorphies uniting _I. escheri_ and _C. carcharias_ relate to the presence of serrations, which have evolved numerous times in the Lamniformes while 2 others are dependent on correct tooth position assignment of disarticulated specimens. Additionally, the restricted fossil distribution of _I. escheri_ to the northern Atlantic and Mediterranean does not support the earliest Pliocene occurrences of _C. carcharias_ in the Pacific, while appearances of the white shark are slightly later in the Atlantic.

In contrast to _Isurus escheri_, the evolution of the white shark in the Pacific during the Late Miocene and Early Pliocene (c. 10–4 Ma) is well documented in the fossil records of Peru, Japan, California, Australia and Chile (de Muizon and DeVries 1985; Kemp 1991; Long 1993; Tanaka and Mori 1996; Stewart 1999, 2002; Yabe 2000; Nyberg _et al._ 2006; Ehret, Hubbell, and MacFadden 2009). Based on the rich fossil record and the rejection of _I. escheri_ as a sister taxon to _Carcharodon carcharias_, the second origin hypothesis outlined above is more agreeable if it is amended to include a Pacific Basin origin for the genus _Carcharodon_. Furthermore, this chapter designates a
new species of *Carcharodon* from the Pacific Basin that represents an intermediate form between *Carcharodon hastalis* and *C. carcharias*.

**Systematic Palaeontology**

**Depository and Abbreviations**

The holotype and most of the specimens figured in this manuscript are deposited in the Department of Vertebrate Paleontology, Florida Museum of Natural History, Gainesville, Florida (UF). Other specimens discussed and figured in this study are deposited in the United States National Museum, Washington, D.C. (USNM) and the Museo de Historia Natural Javier Prado, Universidad Nacional Mayor de San Marcos, Lima, Peru (MUSM) respectively. Terminology follows Cappetta (1987) and Siverson (1999), specifically intermediate teeth are defined as those that form on the intermediate bar, vary in number, and are less than one half the crown heights of the anterior teeth.

Order LAMNIFORMES Berg 1958

Family LAMNIDAE Müller and Henle 1838

Genus CARCHARODON Smith *in* Müller and Henle 1838

**Type Species**

*Squalus carcharias* Linnaeus, 1758, by subsequent monotypy through *Carcharias lamia* Rafinesque, 1810.

**Remarks**

Glikman (1964, p. 104) placed the genera *Carcharodon* and *Cosmopolitodus* within the Carcharodontidae (Gill, 1893) (mis-cited as 1892 *in* Glikman) based on the following characters: teeth broad and blade-like, crowns of upper lateral teeth dorsoventrally flattened, neck very small, roots short, base of the tail with keels. The idea of the Carcharodontidae was also raised separately by Whitley (1940) and
supported by Applegate and Espinosa-Arrubarrena (1996), who cited anatomical
evidence including fin positions (but did not explicitly list the characters) and the
presence of serrations and lateral denticles as synapomorphies. However, the
characters of the Carcharodontidae listed by Glikman (1964) are not synapomorphies
specific to Carcharodon. Furthermore, the separation of the Otodontidae from the
Lamnidae and the presence of a weakly crenulated Isurus escheri do not restrict
serrations and lateral cusplets to the Carcharodontidae and therefore, the family is not
supported. Glikman (1964) also differentiated the genus Cosmopolitodus from
Carcharodon based on the absence of serrations and lateral cusplets. However, some
Late Miocene Carcharodon hastalis teeth may exhibit basal serrations.

CARCHARODON n. sp.

Figures 4-6, 4-7, 4-8

Holotype

UF 226255 (Figure 4-6), articulated dentition including 222 teeth, 45 vertebral
centra, portions of the left and right Meckel’s cartilages and palatoquadrates, and
neurocranium.

Other Material

Upper teeth (UF 245052–245057) (Figure 4-9) from type locality and horizon.

Type Locality, Horizon and Age

Sud-Sacaco West (SAS), 5 km east of Lomas, Arequipa Region, Peru. Pisco
Formation, Late Miocene c. 6.5 Ma, based on the calibrations presented in this paper,
Geographic coordinates: 15° 33’S, 74° 46’W.
Diagnosis

Large lamniform shark; teeth labio-lingually flattened, triangular in shape with one central cusp, weak serrations present but not fully developed along medial and distal cutting edges, larger serrations present basally, root flat and rectangular; A1 tooth symmetrical and largest in the dentition, A3 tooth distally inclined, A2 tooth larger than a2 tooth.

Description

The mandibular arch of UF 226255 is partially preserved, making it not possible to distinguish some features of the jaws. The left and right palatoquadrates are preserved anteriorly along with the symphysis. The symphysis of both palatoquadrates is square and deep. The upper dental bullae are also preserved in both palatoquadrates. Within these bullae the upper anterior teeth are found within a hollow, with an intermediate bar, or a labiolingual constriction of the cartilage, present between the third anterior tooth and the first lateral tooth. The distal portions of both palatoquadrates are not preserved, and the medial and lateral quadratomandibular joints are not discernable due to the dorso-ventral flattening of the specimen.

The Meckel’s cartilages are much deeper than the palatoquadrates. The posterior portions of both are highly fragmented, making the original shape impossible to discern. The lower symphysis is preserved, and appears to be much weaker than that of the palatoquadrates. The Meckel’s cartilages are situated much lower than the palatoquadrates, suggesting a subterminal mouth.

Portions of the neurocranium are preserved, however the structure is not discernable due to the dorso-ventral flattening of the specimen. The occipital hemicentrum consists of the posterior half of a calcified double-cone vertebral centrum.
which articulates with the anteriormost centrum of the vertebral column. The anterior portion of the occipital hemicentrum is separated from the basal plate of the neurocranium, which is preserved as portions of sheet-like cartilage present within the gape of the jaws. Openings present within these fragments of cartilage could represent foramina, however due to the preservation they probably represent areas of weathering.

The dentition of *Carcharodon* n. sp. is represented by 222 teeth located on the palatoquadrates and Meckel’s cartilages. The teeth are flattened labio-lingually, and triangular in shape (Figure 4-7). The crowns have a slight convex curve lingually. There are five to six tooth series present for each tooth position. The teeth are weakly serrated, with anterior teeth averaging more than 30 serrations per side for anterior to no serrations for the distal-most laterals. Of the teeth that do have serrations, there is an average of 8–12 serrations per centimeter on both edges of each tooth. Basal serrations on the teeth are larger than the other serrations on the edges.

There are three anterior teeth present in each palatoquadrate. The A1 is symmetrical and it is the largest in the tooth in the dentition. The A2 is also symmetrical and is slightly larger than the a2. The A3 is distally inclined. The upper lateral teeth are also inclined distally (with L1 having the greatest inclination), and get progressively smaller towards the distal edge of the jaw. The roots of the teeth are relatively flat and rectangular in shape.

In the Meckel’s cartilages, there are three anterior teeth present. Overall, the lower teeth have crowns that are more slender than those of the uppers. There is very little inclination seen in any of the lower teeth. As in the uppers, the teeth of the Meckel’s
cartilages are progressively reduced distally. The roots of the lower teeth have a deep basal concavity and are thicker than those of the upper teeth, being somewhat lobate.

There are 45 vertebral centra of UF 226255 preserved in the holotype. The centra are asterospondylic, laterally compressed, and are composed of two calcified cones connected by radiating calcified lamellae within the intermedalia (Figure 4-8). The articular surfaces are concave and show clear, calcified lamellae as well as pits in the center that represent the notochordal constrictures (Ridewood 1921; Gottfried and Fordyce 2001). In UF 226255, the occipital hemicentrum followed by the first 45 centra which get larger in size in ascending order.

Remarks

*Carcharodon* n. sp. is an intermediate form between *Carcharodon hastalis* and *Carcharodon carcharias* and demonstrates a mosaic of dental characters of both *C. hastalis* and *C. carcharias*. Tooth crowns of *Carcharodon* n. sp. are convex and curve lingually similar to the crowns of *C. hastalis*. The serrations of *Carcharodon* n. sp. are enlarged basally and progressively get weaker towards the apex of the crown. This unique serration pattern represents an intermediate between the unserrated *C. hastalis* and the coarsely serrated *C. carcharias* (Figures 4-4, 4-9). Additionally, the enlarged basal serrations of *Carcharodon* n. sp. are very similar to the lateral cusplets seen in juvenile *C. carcharias* (Ueno and Matsushima 1979; Hubbell 1996). Other characters that unite *Carcharodon* n. sp. with *C. carcharias* include an A2 that is symmetrical and slightly larger than the a2 (Compagno 2001). Whereas, the A3 of *Carcharodon* n. sp. is inclined distally a feature shared with *C. hastalis*.

*Carcharodon hastalis*, *Carcharodon* n. sp., and *Carcharodon carcharias* are chronospecies, with *Carcharodon* n. sp. representing a morphological intermediate
between *C. hastalis* and *C. carcharias*. Specimens collected in Late Miocene deposits throughout the Pacific Basin exhibit a morphologic gradation from *C. hastalis* to *Carcharodon* n. sp. and later to *C. carcharias* in the Early Pliocene. The observable transition of species through time is denoted here by the designation of *C. hastalis* and *Carcharodon* n. sp. to the genus *Carcharodon* (Smith in Muller and Henle, 1838) which is given precedence over *Cosmopolitodus* (Glikman, 1964). Furthermore, the diagnosis of *Cosmopolitodus* by Glikman (1964) is misleading since some Late Miocene *C. hastalis* teeth may present basal serrations.

**Discussion**

**Geology and Stratigraphy**

The new absolute ages obtained from many of the localities of the Pisco Fm. suggest that the deposits are older than previously published. These results have direct bearing on the age of the holotype for *Carcharodon* n. sp. and the evolution of white sharks in the Pacific Basin. The changes to the ages of the localities within the Pisco Fm. require a reassessment of the stratigraphy and palaeontology of those areas affected.

Previous dating of the tuff bed at Alto Grande within the ELJ vertebrate level resulted in an age of 9.5 Ma based on K-Ar dating (de Muizon and DeVries 1985; de Muizon and Bellon 1986). This date is consistent with the non-inherited zircon grain (10±1 Ma) analyzed in this study. The strontium data collected from shell layers overlying the tuff bed yielded ages that are younger than those for the ash layer. However, the upper limits of these ages are within the range for the other dating methods making these age estimates congruent with previously published dates.

The original age of the MTM level is consistent with the new dates from the strontium data. A Late Miocene (c. 6 Ma) age based on the correlation of gypsum beds
with AGL, fossiliferous sandy siltstone with SAS (West), and calibration of the molluscan fauna was posited by de Muizon and DeVries (1985). The range of dates between 8.70–6.45 Ma with a mean of 7.30 Ma is consistent with the resolution of mollusk calibration method (±2 Ma).

Both geochemical methods, zircon U-Pb and strontium isotopic data, yield ages for the SAS level that are older than previous reported by 1–2 million years (de Muizon and DeVries 1985; Tsuchi et al. 1988). Analysis of diatoms from this locality supports this interpretation (H. Schrader, pers. comm. 1986). This difference changes the age of the SAS (West) from the Early Pliocene to the Late Miocene (Gibbard et al. 2010). Previous methods of calibrating the SAS level include correlation of mollusks with white shark (Carcharodon carcharias) fossils. The reassignment of the shark fossils from C. carcharias (Early/Middle Pliocene) to Carcharodon n. sp. (Late Miocene/Early Pliocene) supports an older age for the locality. This change would also suggest that an unconformity (i.e. buried erosional surface) above Sacaco may represent more time than previously thought (3–5 million years). Interestingly, the youngest horizons within the Ica Valley section of the Pisco Fm. to the North of Sacaco are dated at 7–5 Ma, raising the possibility of a basin wide erosional event (i.e. sea level regression) during this time.

Ages from the east side of Sud Sacaco (West) and Sacaco, while both older than previously reported, were very similar in age to one another. The average age of 5.93 Ma for the east side of Sud Sacaco (West) supports the reinterpretation of Sud Sacaco being Late Miocene. However, the stratigraphy at SAS (West) and SAO suggests that the beds are not at the same level especially when taking into account regional tilt (de
Muizon and DeVries 1985). The older ages from SAO may actually represent an area of faulting where older sediments, presumably those that correlate to SAS, are exposed within the section. In that case, the new median ages of 5.89 Ma from strontium and 5.75±0.5 Ma from argon isotopes has more bearing on the age of SAS than on the SAO level itself.

**Taxonomy and Evolution of Carcharodon**

The taxonomic evolution and placement of *Carcharodon* is a complex subject that has been compounded by the lack of more complete specimens and high levels of homoplasy in the tooth morphology of many species. While a *Carcharodon hastalis*-origin hypothesis has gained popularity in recent years, the timing and transition from one taxon to the other has remained unresolved. It is generally accepted that *Carcharodon carcharias* is directly related to *C. hastalis* and not the megatoothed sharks as previously discussed.

*Isurus escheri* from the Middle Miocene through Early Pliocene of the northern Atlantic has been suggested as a possible sister taxon to *Carcharodon carcharias*, based mainly on the presence of crenulations on the cutting edges of the teeth (Figure 4-4). However, these fossils are restricted to the northern Atlantic and Mediterranean and become extinct just prior to or as a result of the appearance of *C. carcharias* in the Atlantic by the mid Pliocene. This species likely evolved from an Atlantic population of slim-toothed *Carcharodon hastalis* or *hastalis*-like taxon in the Early Miocene. Meanwhile, materials from the Miocene Pacific Basin clearly demonstrate an intermediate form between *C. hastalis* and *C. carcharias* that is significantly different from *I. escheri*. The discovery and description of *Carcharodon* n. sp. from the Late Miocene of Peru, and the recalibration of the Pisco Formation demonstrate the
presence of serrated forms in the Miocene and Early Pliocene of the Pacific, while there is general lack of specimens from the Atlantic at the same period.

The distinction of *Carcharodon* n. sp. from *Isurus escheri* is validated by the morphological differences exhibited in UF 226255 and specimens of *I. escheri* examined from the Delden Member (Early Pliocene), the Netherlands (UF 245058 and UF 245059) and the description of an associated specimen from Germany (Mewis and Klug 2006; Mewis 2008). *I. escheri* has been identified from the Middle Miocene (c. 14 Ma) to at least the Early Pliocene (c. 5–4 Ma) throughout northern Europe. Van den Bosch (1978, 1980) differentiates *I. escheri* from the Late Miocene as weakly crenulate and Early Pliocene teeth as strongly crenulate types. However, this difference was not quantified or figured in either of the studies and is inconsistent with our Early Pliocene samples that demonstrate weak crenulations (Figure 4-5). *Carcharodon* n. sp. teeth show a progressive increase in the number and overall coarseness of serrations on their cutting edges from the Late Miocene to the Early Pliocene that are distinctively different and appear to evolve separately from *I. escheri* (Figure 4-9). Additionally, the *in situ* dentition of UF 226255 demonstrates a mixture of characters expressed in both *Carcharodon hastalis* and *Carcharodon carcharias*, supporting our revised *C. hastalis* origin hypothesis.

*Isurus escheri*, on the other hand, appears to be a separate taxon more closely related to a narrow-crowned *Carcharodon hastalis* or *hastalis*-like taxon. Tooth serrations (or in this case crenulations) have evolved independently numerous times throughout the evolution of the selachians (Casier 1960; Cappetta 1987; Frazzetta 1988). Based on the living mako sharks, their tooth shape, and overall body size, it is
hypothesized that species within the genus *Isurus* were piscivorous (Applegate and Espinosa-Arrubarrena 1996; Purdy *et al*. 2001; Aguilera and de Aguilera 2004). The evolution of serrations or crenulations would be advantageous for competition with other piscivorous shark taxa (*C. hastalis*, *Galeocerdo* Müller and Henle, 1837, *Hemipristis* Agassiz, 1835, and *Carcharhinus* de Blainville, 1816). Therefore, it is not surprising that more than one form would acquire serrations.

The evolution of the white shark in the Pacific Basin is validated by the presence of weakly to moderately serrated teeth in the fossil deposits from the Late Miocene and Early Pliocene of North and South America, Asia, and Australia (de Muizon and DeVries 1985; Kemp 1991; Long 1993; Tanaka and Mori 1996; Stewart 1999, 2002; Yabe 2000; Nyberg *et al*. 2006; Ehret, Hubbell, and MacFadden 2009). While many of these specimens from the Pacific represent different degrees of evolution between *Carcharodon hastalis* and *Carcharodon carcharias* it is not possible to separate these based on isolated teeth. A complete tooth set, exhibiting more definitive characters would be required to differentiate potentially different forms. Therefore, these teeth are assigned to the species *Carcharodon* n. sp.; previous identifications as *Isurus escheri* (Kemp 1991) *Carcharodon* sp. (Nyberg *et al*. 2006; Ehret, Hubbell, and MacFadden 2009), or *C. carcharias* (de Muizon and DeVries 1985; Long 1993; Tanaka and Mori 1996) should be amended to reflect this new assignment.

Additional research on *Carcharodon* n. sp. has shed light on the palaeobiology of this species (Ehret, Hubbell, and MacFadden 2009; Ehret, MacFadden, and Salas-Gismondi 2009). Incremental growth analyses of the vertebral centra of UF 226255 have revealed annual growth patterns that relate to the life history of this specimen. Growth rings
visible using X-radiography appear to represent annual periodicity based on the calibration of oxygen and carbon isotope analysis within the rings. Counts of the growth rings using the X-radiographs provide an age estimate of at least 20 years. The overall length of the specimen was estimated using the averages of both crown height and vertebral centrum diameter regressions from previously published studies of *Carcharodon carcharias*. Resulting data provides total length estimates between 4.89 and 5.09 m. for the specimen. Based on growth curves of modern *C. carcharias*, UF 226255 appears to have been growing at a slower rate than white sharks today.

Further palaeobiological information about *Carcharodon* n. sp. includes a partial mysticete whale mandible from the SAS layer containing a partial tooth crown MUSM 1470, housed in the collection of the Museo de Historia Natural Javier Prado, Universidad Nacional Mayor de San Marcos, Lima, Peru (MUSM) described by Ehret, MacFadden, and Salas-Gismondi (2009). This specimen represents direct evidence of feeding behavior of the species in the Late Miocene. The presence of tooth serrations and MUSM 1470 provide definitive proof that *Carcharodon* n. sp. was adapted for taking marine mammals as prey as early as c. 6.5 Ma.

**Conclusions**

The recalibration of localities within the Pisco Formation indicates ages that are older than previously published (de Muizon and Bellon 1980; de Muizon and DeVries 1985; de Muizon and Bellon 1986). While these changes are not exceptionally large, it does directly relate to the evolutionary history of the genus *Carcharodon*. Previous accounts of shark material from the Pisco Formation exhibiting characteristics of both *Carcharodon hastalis* and *Carcharodon carcharias* were referred to the Early Pliocene (c. 5–4 Ma) (de Muizon and DeVries 1985; Nyberg *et al.* 2006; Ehret, Hubbell, and
MacFadden 2009; Ehret, MacFadden, and Salas-Gismondi 2009). However, the geological age of these specimens was not consistent with the first records of *C. carcharias* in the Early to Middle Pliocene. New ages for the SAS (West) layer placing it in the Late Miocene (c. 6.5 Ma) accord better with the evolutionary history of the white shark.

The discovery and description of an outstanding specimen from the Pisco Formation further elucidates the taxonomy and paleobiology of the white sharks. The hypothesis that *Isurus escheri* is a sister taxon of *Carcharodon carcharias* is refuted based on the Miocene and Pliocene distribution of *Carcharodon* fossils from the Pacific Basin and tooth morphology. The genus *Carcharodon* should be amended to include the species *hastalis*, n. sp., and *carcharias* based on tooth characters shared between the taxa discussed above, and our interpretation of the *C. hastalis*-n. sp.-*carcharias* transition as an example of chronospecies. Palaeobiological information from UF 226255 reveals that this specimen grew at a rate comparatively slower than modern white sharks. MUSM 1470 confirms that the diet of *Carcharodon* n. sp. was at least partially comprised of marine mammals as early as the Late Miocene. Continued research on these specimens and others will only further advance our knowledge of the fossil lamnid sharks.
Figure 4.1. Map of Peru with localities within the Southern section of the Pisco Formation.
Figure 4-2. Stratigraphic map of the Pisco Formation, Peru. After de Muizon and DeVries 1985.
Figure 4-3. *Carcharocles megalodon* tooth, USNM 336204. Scale bar represents 10 mm.

Figure 4-4. Comparison of serration types in the lamnid and otodontid sharks. (A) *Carcharodon hastalis* (UF 57267), (B) *Carcharodon* n. sp. (UF 226255), (C) *Isurus escheri* (UF 245058), (D) *Carcharocles megalodon* (UF 217225), (E) *Carcharodon carcharias* (G. Hubbell collection). Scale bar represents 10 mm.
Figure 4-5. *Isurus escheri* from the Delden Member (Early Pliocene), the Netherlands. Upper Anterior tooth, UF 245058 (A) Labial view, (B) Lingual view; Upper Lateral tooth, UF 245059 (C) Labial view, (D) Lingual view. Scale bar represents 10 mm.
Figure 4-6. *Carcharodon* n. sp., UF 226255 (holotype). Scale bar represents 10 cm.
Figure 4-7. Functional tooth series of *Carcharodon* n. sp., UF 226255 (holotype). Scale bar represents 5 cm.
Figure 4-8. Vertebral centrum of *Carcharodon* n. sp., UF 226255 (holotype). Scale bar represents 10 mm.

Figure 4-9. Individual upper teeth demonstrating the gradation of serrations from the Pisco Formation, Peru. Upper teeth from left to right, UF 245052–245057. A–F, labial view; G–L, lingual view. Scale bar represents 10 mm.
Table 4-1. Strontium chemostratigraphic analyses of fossil marine mollusk shells from the Pisco Formation. Ages and confidence intervals (CI) determined from McArthur et al. (2001).

<table>
<thead>
<tr>
<th>Locality</th>
<th>Mean $^{87}\text{Sr}/^{86}\text{Sr}$</th>
<th>Sr Age estimate (Ma)</th>
<th>95% CI (Ma)</th>
</tr>
</thead>
<tbody>
<tr>
<td>ELJ</td>
<td>0.7089424</td>
<td>7.46</td>
<td>9.03-6.51</td>
</tr>
<tr>
<td>MTM</td>
<td>0.7089468</td>
<td>7.30</td>
<td>8.70-6.45</td>
</tr>
<tr>
<td>SAS (West)</td>
<td>0.7089659</td>
<td>6.59</td>
<td>10.77-2.50</td>
</tr>
<tr>
<td>SAS (West)</td>
<td>0.7089978</td>
<td>5.93</td>
<td>6.35-5.47</td>
</tr>
<tr>
<td>SAO</td>
<td>0.7090005</td>
<td>5.89</td>
<td>6.76-4.86</td>
</tr>
</tbody>
</table>
CHAPTER 5
MACROEVOLUTION, AGE, AND GROWTH DETERMINATION OF THE MEGATOOTHED SHARKS (LAMNIFORMES: OTODONTIDAE)

Introduction

The extinct otodontid (or megatoothed) shark species in the genera *Otodus* and *Carcharocles* include some of the largest predatory sharks to have ever lived. The species *Otodus obliquus* first appears in the Late Paleocene, becoming more predominant in the Early Eocene, and is replaced by a series of species belonging to the genus *Carcharocles* through time by what some believe is phyletic evolution (Zhelezko and Kozlov 1999; Cappetta and Cavallo 2006). The otodontid shark lineage ends with the extinction of the largest species of the family, *Carcharocles megalodon*, in the Pliocene. These sharks were large, apex predators that were likely filling the top trophic levels in the world’s oceans (Aguilera and Aguilera 2004).

The fragmentary nature of chondrichthyan fossils, due mainly to their cartilaginous skeletons, has made taxonomic and paleobiological studies very difficult. In particular, a majority of the fossil record for neoselachian sharks is comprised solely of isolated teeth. The lack of bony structures in paleontological studies of sharks can be clearly demonstrated by the discrepancies in generic and species assignments for the megatoothed sharks (see Jordan and Hannibal 1923; Leriche 1926; Casier 1960; Glikman 1964; Applegate and Espinosa-Arrubarrena 1996; Gottfried and Fordyce 2001; Purdy *et al.* 2001; Zhelezko and Kozlov 1999; Cappetta and Cavallo 2006) where multiple taxonomic combinations are recognized for most species. Furthermore, paleobiological studies of the megatoothed sharks are relatively limited considering the overwhelming public interest in this group. Previously published research includes studies on skeletal anatomy and sizing, paleoecology, trophic interactions, diagenesis...
and growth, and nursery areas (Gottfried et al. 1996; Purdy 1996; Aguilera and Aguilera 2004; MacFadden et al. 2004; Pimiento et al. 2010).

The study of growth in fossil sharks and how it relates to their paleobiology is a relatively new field because it focuses on the rarely preserved vertebral centra. Previous studies of incremental growth include: documentation of incremental bands in fossil lamniform centra (Shimada 1997a), growth and diagenesis of Early Eocene *O. obliquus* (MacFadden et al. 2004; Labs-Hochstein and MacFadden 2006), ontogenetic parameters and life history of Late Cretaceous *Cretoxyrhina mantelli* (Shimada 2008), and incremental growth of Late Miocene *Carcharodon* n. sp. (Ehret, Hubbell, and MacFadden 2009; Ehret et al. In Press). In this chapter, I present research on the growth rates of four megatoothed shark species in order to compare heterochronic change in size through time. Additionally, I investigate two factors, one biotic and one abiotic, that are thought to have contributed to these changes. The otodontid sharks were chosen because of their extremely large size, their perceived increase in overall length, and the corresponding changes to their growth through time (Gottfried and Fordyce 2001).

**Materials and Methods**

**Materials**

Vertebral centra from four megatoothed shark taxa: *Otodus obliquus*, *Carcharocles auriculatus*, *Carcharocles angustidens*, and *Carcharocles megalodon*, were analyzed for incremental growth bands using digital X-radiography (Figure 5-1). *Otodus obliquus* specimens are from the Florida Museum of Natural History (UF) (UF 162732; UF 256397) and were collected in the Ouled Abdoun Basin of Morocco and are Ypresian (55.8–48.6 Ma) in age (Arambourg, 1952; MacFadden et al. 2004).
Carcharocles specimens (including *C. auriculatus*, *C. angustidens*, and *C. megalodon*) are on loan from the collections of the Royal Belgian Institute of Natural Sciences (IRSNB). The *Carcharocles auriculatus* specimen (IRSNB P809) was collected in the Brussels Formation of Belgium and is Lutetian in age (48.6–40.4 Ma) (Nolf 1988). The *C. angustidens* specimen (IRSNB P929) was collected from the Argile de Boom, Belgium and is Rupelian in age (33.9–28.4 Ma) (Nolf 1988). Finally, the *C. megalodon* specimen (IRSNB 3121) is from an associated vertebral column which was collected in Antwerp, Belgium in the 1860s and is designated only as Miocene (23.3–5.3 Ma) in age but likely represents the Middle to Late Miocene (~14–5.3 Ma) (Leriche 1926; Gottfried et al. 1996).

Although the taxonomy of the megatoothed sharks is beyond the scope of this study, the nomenclature I will follow should be justified. While it is widely accepted that the megatoothed sharks are lamniforms, their placement within the Lamniformes has been a contentious subject. In his original descriptions of the megatoothed shark species, Agassiz (1835) placed all serrated-toothed taxa within the genus *Carcharodon*, which also includes the modern white shark (*Carcharodon carcharias*). Thus megatoothed sharks were assigned to the Lamnidae with close interrelationships with *C. carcharias*, *Isurus*, and *Lamna*. In 1923, Jordan and Hannibal erected the genus *Carcharocles* for the serrated megatoothed sharks, thereby implying that they did not share close affinities with *C. carcharias*. Casier (1960) separately drew the same conclusion renamed these species *Procarcharodon*, which was accepted by many authors before being considered a junior synonym of *Carcharocles*. In 1964, Glikman erected the family Otodontidae for the megatoothed sharks, including the genera
Otodus, Carcharocles, and Parotodus. He placed the species C. auriculatus and C. angustidens within the genus Otodus based on the hypothesis that these species evolved directly from O. obliquus and erected the genus Megaselachus for Carcharocles chubutensis and C. megalodon citing the reduction/loss of lateral cusplets on the tooth crowns as a diagnostic character. Recent literature (1990s-present) has been divided into three separate ideologies with regards to nomenclature. A small minority of researchers still refers the serrated megatoothed sharks to the genus Carcharodon and places them within the Lamnidae (Applegate and Espinosa-Arrubarrena 1996; Purdy 1996, Gottfried et al. 1996; Gottfried and Fordyce 2001; Purdy 2001). However, although entrenched in the popular literature, this idea is no longer widely accepted. A second group follows the designations of Glikman (1964) and refers the serrated-toothed species ‘auriculatus’ and ‘angustidens’ to the genus Otodus and ‘megalodon’ to the genus Megaselachus based on the idea that the lineage represents a series of chronospecies (Zhelezko and Kozlov 1999; Cappetta and Cavallo 2006; Adnet et al. 2010). The third view, which I follow here, accepts Casier’s (1960) assignment of the megatoothed sharks to the family Otodontidae, but separates Otodus obliquus, which has smooth-edged teeth, from the serrated forms, Carcharocles, following Jordan and Hannibal (1923) (Ward and Bonavia 2001; Ehret, Hubbell, MacFadden 2009; Pimiento et al. 2010, Ehret et al. In Press).

Methods

Vertebral centra were imaged using traditional x-radiographic (X-rays) photography. In studies of extant sharks, it is recommended to choose a centrum anterior to the first dorsal fin (precaudal) from individuals (Wintner and Cliff 1999). However, due to the rarity of megatoothed shark centra, all available specimens were
sampled. Digital X-rays were taken at the C. A. Pound Human Identification Laboratory at the University of Florida. The X-rays reveal differences in bone density and produce reversed images in DICOM and JPEG formats (Figure 5-2). X-ray settings followed those used by MacFadden et al. (2004) and Ehret, Hubbell, and MacFadden (2009), approximately 78 kV for 1 ½ to 2 minutes. However, depending on differences in preservation and mineralization of individual centra (which is related to age, locality, and sedimentology) settings were adjusted accordingly.

Digital X-rays were set to the actual specimen diameter, converted to TIFF files, and examined using Adobe Photoshop. This included adjustments to the contrast and brightness of the X-rays in order to fully view all growth bands. Centra were oriented with the insertions for the neural arches and basopophyses (following Walker 1975) in life-position (i.e. the dorsal neural arch insertions are positioned along the top edge of the image and the ventral basopophyses insertions positioned along the bottom edge) (Natanson and Cailliet 1990; Natanson et al. 2008). Diameter and growth ring measurements for the centra were taken along the midlateral axis following Cailliet et al. (1985) and Wintner and Cliff (1999) (Figure 5-2).

Incremental growth pattern terminology follows that recommended by Cailliet et al. (2006). The term growth band is used for seasonal periods (i.e. opaque bands that tend to deposited in summer months and translucent bands that tend to be deposited in winter months in modern chondrichthyans). While the term growth ring (GR) is used for patterns that are demonstrated or assumed to represent a period of a year. Therefore, one opaque and one translucent growth band pair represent one growth ring. Incomplete or finer, narrow bands were observed but not used for ageing purposes
(Cailliet et al. 1985; Officer et al. 1997; Wintner and Cliff 1999). The birth mark is defined as the angle change on the centrum face, which marks the difference between fast intrauterine and slower postnatal growth (Wintner and Cliff 1999).

The annual periodicity of growth rings in megatoothed sharks is assumed based on studies of extant and isotopic work of extinct lamniforms (MacFadden et al. 2004; Kerr et al. 2006; Labs-Hochstein and MacFadden 2006; Ehret, Hubbell, and MacFadden 2009). Using methods including oxytetracycline (OTC)-injected markers, known-age individuals, bomb radiocarbon dating, and marginal increment analysis (MIA), researchers have shown that numerous lamniform sharks: the shortfin mako, Isurus oxyrinchus, porbeagle, Lamna nasus, salmon, Lamna ditropis, sand tiger, Carcharias taurus, and white, Carcharodon carcharias all deposit annual growth rings (Cailliet et al. 1985; Wintner and Cliff 1999; Natanson 2001; Campana et al. 2002; Natanson et al. 2002; Goldman and Musick 2003; Ribot-Carballal et al. 2005; Ardizzone et al. 2006; Goldman et al. 2006; Kerr et al. 2006; Natanson et al. 2006). The only lamniform species that does not follow this rule is the basking shark, Cetorhinus maximus, which produces growth rings that are neither periodic nor associated with age (Parker and Stott 1965; Natanson et al. 2008). Instead, growth ring counts in C. maximus change with centrum position within the vertebral column and numbers are related to structural morphology rather than age (Natanson et al. 2008). It should be noted that basking sharks are atypical lamniforms for numerous reasons: (1) their centra are less calcified than other species; (2) the number of lamellae in centra becomes reduced posteriorly in the vertebral column, and (3) the vertebral morphology changes with age (Ridewood 1921; Natanson et al. 2008).
Growth rings were identified and marked using Adobe Photoshop (Figure 5-2). The image files were then imported into the program Image J®, where the radius of each growth ring and the birth mark were measured for analysis. X-radiographs for each fossil specimen were counted and measured on four separate occasions by the author. The average number of rings and centrum radii for each growth ring from the four separate counts were used for the final analysis. Analyses compare centrum radius (CR) as a measure of size and growth ring count as a measure of age. Centrum radius is used because total length (TL) of these sharks is not known. Previous studies of fossil lamniforms (Gottfried et al. 1996; Shimada 1997b; Shimada 2008; Ehret, Hubbell, and MacFadden 2009; Pimiento et al. 2010) have estimated TL of extinct species based on CR or centrum diameter of the extant *C. carcharias*. While TL regressions may be acceptable for establishing general estimated body lengths, I caution the use of this information in growth studies without a reasonable justification. Furthermore, this study compares growth in fossil megatoothed sharks to *C. carcharias* specimens from the Indian Ocean previously reported by Wintner and Cliff (1999). Comparisons of growth in megatoothed and white sharks, based solely on TL or precaudal length (PCL) of *Carcharodon* could misrepresent the fossil data.

Growth data of fossil megatoothed sharks was compared with growth data from extant *C. carcharias* specimens from the Indian Ocean, Wintner and Cliff (1999), to provide a baseline growth rate and a modern analog. Data from white sharks include CR and age information for 109 individuals ranging from 0–13 years. Unlike fossil specimens, extant data represent the maximum age and CR for each specimen.
However, when all extant specimens are plotted together, the resulting data represent a hypothetical growth rate for the species.

To determine if the growth rates of megatoothed and white sharks differed statistically from one another, an analysis of covariance (ANCOVA) was performed using SAS® software. Linear regressions based on the area of each centrum were calculated for each of the shark species, which included pooled data for the two *O. obliquus* specimens. The slopes of the linear regressions (i.e. growth rates) were then compared to one another using a t-test with probability (P) values > 0.05 representing statistically different rates using JMP® software (Natanson and Cailliet 1990).

**Results**

Annual growth rings were observed in X-rays of all fossil megatoothed shark vertebral centra. Growth rings in the three *Carcharocles* species (*C. auriculatus*, *C. angustidens*, and *C. megalodon*) were more clearly visible than those seen in *O. obliquus*, which is likely related to the mineralization, diagenesis, and preservation of the specimens (Figure 5-2). The four individual readings of each X-ray were consistent in most cases, but differed by a maximum of 3 GR in one observation. This difference was observed in one of the *Otodus* specimens (UF 162732), and relates to the visibility of GRs. The averages of the GR counts, the radii per GR, and the area of the centrum at each GR for each specimen were used for comparisons (Table 5-1).

Birth marks (BM) were observed in all X-radiographs. While the change in angle is not directly observable in X-rays, the presence of the first opaque band distal to the focus was defined as the BM (Natanson *et al.* 2006). The perceived BMs in the X-rays were compared with physical BMs present on corpus calcareum of the specimens using landmarks also visible in the digital images. In every observation, BMs in X-rays
matched the actual specimens correctly. BM radii for *O. obliquus* (UF 162732, UF 256397) and *C. auriculatus* (IRSNB P809) specimens were smaller than the CR for the one South African white shark (1.11 cm) that recorded an age of 0 (Table 5-1). *C. angustidens* (IRSNB P929) had a BM radius that was slightly larger, but comparable in size to the extant *C. carcharias*. The radius of the BM for *C. megalodon* (IRSNB 3121), meanwhile, was significantly larger (1.66 cm) than all other species, and corresponded to extant *C. carcharias* specimens that were at least 2 years old.

Growth of the megatoothed and white shark species was compared in terms of centrum area vs. number of growth rings (GR; i.e. age in years) (Figure 5-3). Total length (TL) and/or precaudal length (PCL), which is commonly measured and reported in modern studies, was not available for fossil species. Previous studies estimating megatoothed shark lengths are based on measurements for extant *Carcharodon carcharias* (Gottfried *et al.* 1996, Pimiento *et al.* 2010). Since white shark growth data were used for comparison to give a baseline for growth of modern lamniforms, using data from *Carcharodon* to estimate megatoothed TLs would be biased.

The overall numbers of growth rings counted in the megatoothed shark specimens fall within the range of published counts for modern chondrichthyan taxa (Table 5-1). However, megatoothed GR numbers are higher, ranging from 18–30 years for fossil specimens, than many modern studies (Cailliet *et al.* 1985; Wintner and Cliff, 1999; Natanson *et al.* 2002). Relatively high counts for extant species have been documented and include: 31 and 32 GRs for *Isurus oxyrinchus* (Ardizzone *et al.* 2006; Natanson *et al.* 2006), 35 GRs for *Lamna nasus* (Francis *et al.* 2007), and 41 GRs for *Galeorhinus galeus* (Francis and Mulligan 1998). Total age limits (potential longevity) for
chondrichthyans have been estimated to approach 60 years or more (Francis et al. 2007). The lack of older extant specimens might be related to over-fishing of shark species (Goldman et al. 2006; Francis et al. 2007). However, Francis et al. (2007) also discussed the potential for age underestimation of L. nasus specimens over 20 years in age (GRs), as somatic growth slows in adult individuals. Results showed that GRs become more tightly compacted, making them more difficult to accurately differentiate and count in cross-section.

Plotted growth data for all fossil species depicts a decrease in slope angle (i.e. decreasing somatic growth) with increasing GR (i.e. age) (Figure 5-3). Shimada (2008) also observed this pattern in the Cretaceous lamniform shark, Cretoxyrhina mantelli, and similar patterns are also visible in length/mass vs. GR data for modern lamniforms including C. carcharias, I. oxyrinchus, L. nasus, L. ditropis, and C. taurus (Cailliet et al. 1985; Wintner and Cliff 1999; Campana et al. 2002; Natanson et al. 2002; Goldman and Musick 2003; Ribot-Carballal et al. 2005; Ardizzone et al. 2006; Goldman et al. 2006; Natanson et al. 2006). While the visual decrease in slope angles is comparable for most species, it should be noted that C. megalodon is well above and outside the range of all others both in overall growth and the delay in growth decrease.

Growth rates for the fossil and modern species were calculated comparing the area of centrum surface based on the measurement of GR radii to the number of GRs. The results of the analysis of covariance (ANCOVA) can be seen in Figure 5-4. For the purpose of this study, growth rates are reported and compared in terms of the slope of the covariance analysis (Table 5-2). Data for fossil megatoothed specimens are compared to a population of extant white sharks (Wintner and Cliff 1999) to set a
baseline growth parameter that is tangible. As observed with BM CR, the overall growth rates for *C. auriculatus* and *C. angustidens* are comparable to *C. carcharias*, while *O. obliquus* and *C. megalodon* are significantly higher than the other species.

To accurately assess the growth rates between the different fossil species and how their rates compare to *C. carcharias*, the slopes from each taxon were analyzed using a t-test. Growth rates were considered statistically different from one another if the P-value > 0.05 (Table 5-3). The growth rate for the Early Eocene *Otodus obliquus*, which is recognized as the first otodontid taxon, was determined to be faster (i.e. having a steeper slope) and significantly different than that of *C. carcharias*.

The general growth rates for the genus *Carcharocles* are characterized by an overall increase in rate through time. In the Middle Eocene, *C. auriculatus* had a growth rate statistically similar to that of *C. carcharias* and significantly slower than *O. obliquus* (Table 5-2; 5-3). Therefore, the transition from *Otodus* to *Carcharocles* is marked by a significant decrease in growth rates between the Early and Middle Eocene. *Carcharocles angustidens*, in the Early Oligocene, evolved a growth rate that is statistically similar to the fossils *O. obliquus* and *C. auriculatus*, as well as *C. carcharias*. Comparison of their actual slopes (Table 5-2; 5-3) reveals that the growth rate of *C. angustidens* is intermediate between *C. auriculatus* and *O. obliquus* and therefore, faster (i.e. has a steeper slope) than *Carcharodon carcharias*. In the Middle to Late Miocene *C. megalodon*, the final otodontid species before their extinction in the Pliocene grew at a much faster rate than any other species in this study.

**Discussion**

Fossilized vertebral centra from four species of megatoothed shark were analyzed for annual growth rings using X-radiography. Growth rings were observed in all
specimens, although some exhibited more visible GRs than others (Figure 5-2). Four GR counts and radius measurements were taken and averaged for all fossil specimens. Growth rates were calculated for *O. obliquus, C. auriculatus, C. angustidens*, and *C. megalodon* through time and compared to each other and the extant white shark, *Carcharodon carcharias*.

In the Early Eocene (Ypresian), *Otodus obliquus* exhibited growth rates that were comparatively faster than *C. carcharias*. However, the overall size of the vertebral centra at birth was comparable to, or slightly smaller than, the extant white shark. Annual growth ring counts for the two specimens (UF 162732, UF 256397) were calculated at 24 and 18 years, respectively (Table 5-1). Based on rates for *C. carcharias* (Wintner and Cliff 1999), and age estimates for attaining sexual maturity (~9–10 years), *O. obliquus* also appears to have prolonged a faster growth rate (i.e. somatic growth) during its lifetime (Cailliet *et al.* 1985). While it is tempting to associate this prolonged rate with age at maturation, it is not possible to glean this information from the X-rays (Araya and Cubillos 2006).

Growth trends for the genus *Carcharocles* are characterized by an increase in both rate and overall size through time. The earliest species of the genus, *Carcharocles auriculatus* from the Middle Eocene (Lutetian), has a growth rate that is comparatively slower than *O. obliquus* and statistically similar to *C. carcharias* (Figure 5-3; Table 5-2; 5-3). If *Carcharocles* did arise from *Otodus* during the Eocene via phyletic evolution (Glikman 1964; Zhelezko and Kozlov 1999; Cappetta and Cavallo 2006), growth rates slowed significantly across this transition. However, size at birth (based on the radius of BM), overall lifespan, and the duration of somatic growth appears to remain relatively
consistent. Interestingly, this period of time also corresponds to the appearance of serrations on the cutting edges of tooth crowns. Hypotheses related to the cause of this growth rate change and evolution of serrations, including temperature fluctuations and diet, will be discussed below.

The calculated growth rate for the Early Oligocene (Rupelian) *C. angustidens* is statistically similar to three species: *C. auriculatus, O. obliquus*, and *C. carcharias*. Upon comparison of the slopes (i.e. growth rates) of plotted data, the rate for *C. angustidens* was slightly faster than *C. auriculatus* and *C. carcharias* and slower than *O. obliquus* (Table 5-2; 5-3). Size at birth, based on the radius of the BM for IRSNB P929, is larger than that of *O. obliquus, C. auriculatus*, and *C. carcharias*. However, other growth and age parameters are well within the range of the other species.

The Middle-Late Miocene *Carcharocles megalodon* specimen exhibits a growth strategy that is significantly different from other megatoothed sharks. Previously discussed (and geologically older) species had relatively similar sizes at birth and comparable growth rates. In contrast, *C. megalodon* exhibits a larger size at birth and a substantially faster growth rate. A comparison of BM radius between *C. megalodon* and *C. angustidens*, the next largest specimen, reveals that the former was 1.3 times larger at birth. Furthermore, the growth rate for *C. megalodon*, when compared with *O. obliquus*, which had the second fastest calculated rate, was found to be 1.5 times greater.

In addition to both birth size and growth rate increases, the overall number of GRs for *C. megalodon* (30) is also greater than all other specimens (Table 5-1). This count is within the range of modern chondrichthyans and not significantly higher than other fossil
species however, it is important for comparisons of somatic growth duration. Plotted data of growth for the megatoothed sharks (Figure 5-3) reveal that *C. megalodon* prolonged somatic growth for a longer duration of its lifetime compared to other species. In *C. megalodon*, cessation or slowing of somatic growth, appears to occur at or around 25 years of age. This prolonged growth rate would have been advantageous for attaining larger sizes however, if this feature is related to sexual maturity, this extremely slow maturation (compared to *C. carcharias*) might have been detrimental to the species (Cailliet *et al.* 1985; Wintner and Cliff 1999).

**Heterochrony**

Heterochrony is defined as a documented change in rate of growth and timing of developmental processes between species (typically with an ancestor-descendant relationship; Gould 1977; Alberch *et al.* 1979; Stanley 1979; McKinney and McNamara 1991; Rice 1996; Klingenberg 1998; McNamara and McKinney 2005). Although the literature on this subject is quite confusing, the two main forms of heterochrony are: paedomorphosis or the retention of juvenile traits in an adult stage, and peramorphosis, or the delaying of sexual maturity beyond the adult stage. Within each of these subdivisions, there are three further divisions which are related to the onset and offset of development as well as the duration of somatic growth (see McKinney and McNamara 1991). In recent years, the use of heterochrony to describe changes in the rate and timing of developmental events across taxonomic groups through time and space has come under scrutiny due to its broad definitions and application on many different levels (i.e. molecular, individual characters, species, etc.) (Rice 1997; Klingenberg 1998; McNamara and McKinney 2005). However, I describe changes in
megatoothed shark growth through time using published terminology of McKinney and McNamara (1991) and Klingenberg (1998) but acknowledge these arguments.

As discussed previously, the change in overall growth rates between *Otodus* and *C. auriculatus* decrease during the Late to Middle Eocene. The offset time (i.e., the slowing or cessation of somatic growth) does not appear to change through time (Figure 5-3; Alberch *et al.* 1979). If we consider *O. obliquus* to be directly related to *Carcharocles*, this decreased growth rate, without a change in offset time, corresponds to the heterochronic mechanism known as neoteny (Alberch *et al.* 1979; Klingenberg 1998). Neoteny is defined as a type of paedomorphosis whereby somatic development is slowed with regards to maturation when comparing ancestral-descendant species (Gould 1977; Stanley 1979).

In addition to changes in growth, characteristics of its dental morphology separate *C. auriculatus* from *Otodus* and other *Carcharocles* species. The most obvious differentiation from *Otodus* being presence of fine serrations along the cutting edges of the tooth crowns. Applegate and Espinosa-Arrubarrena (1996) also noted that the crowns and lateral cusplets of *O. obliquus* are proportionally longer than those of *Carcharocles auriculatus*. Additionally, they hypothesized that *C. auriculatus* was the smallest species of the genus *Carcharocles* based on comparisons of upper anterior teeth between megatoothed species and with the extant *C. carcharias*. These observations are consistent with a reduction in overall growth rate and size between *Otodus* and *C. auriculatus* in the Early-Middle Eocene.

The growth rate and offset timing for *Carcharocles angustidens* is not statistically different from either *C. auriculatus* or *O. obliquus*, meaning that cessation or slowing of
somatic growth remains relatively constant in megatoothed shark species throughout the Eocene and Early-Middle Oligocene (Figure 5-3; Table 5-2; 5-3). It should be noted, however, that the actual growth rate of *C. angustidens* falls in between the two species. This increase, without a change in offset can be categorized as a type of peramorphosis known as acceleration (Alberch *et al.* 1979; Klingenberg 1998).

A comparison of tooth morphology between *C. angustidens* and earlier *Carcharocles* species reveals changes consistent with the growth analysis. The teeth are larger than *C. auriculatus* with finer, more regular serrations. Tooth crowns of *C. angustidens* have also been described as being proportionately narrower than those of earlier species (Applegate and Espinosa-Arrubarrena 1996; Gottfried and Fordyce 2001). However, the general trend for *Carcharocles* is a widening of tooth crowns through time. Lateral cusplets are present in *C. angustidens* although they vary in morphology amongst different tooth positions, being more pronounced in the anterior teeth and reduced in the posterior laterals (Gottfried and Fordyce 2001).

The final species analyzed in this study, *Carcharocles megalodon*, exhibits a growth pattern very different from all other taxa. The combination of an increased rate of growth and a delayed offset timing, compared to other megatoothed species, results in one of the largest predatory sharks to have ever lived, with estimated lengths up to 17 m (Gottfried *et al.* 1996; Pimiento *et al.* 2010). *C. megalodon* exhibits two different types of peramorphosis: (1) acceleration of growth rate similar to, but at a much greater level than, *C. angustidens* and (2) hypermorphosis, which is the delay in the offset timing of somatic growth (Alberch *et al.* 1979; Klingenberg 1998).
The analysis of growth patterns in *C. megalodon* is reinforced by its tooth morphology. Tooth sizes for *C. megalodon* are the largest of all known chondrichthians, with published measurements of anterior teeth over 16 cm in total height (Gottfried *et al.* 1996; Purdy *et al.* 2001). Upper tooth crowns are broad and triangular in shape, ranging from equilateral to isosceles, with lowers being somewhat narrower. One of the most notable characters of *C. megalodon* teeth are the lateral cusplets, which are not present in subadult and adult teeth and may or may not be present in juveniles (Leriche 1926; Casier 1960; Glikman 1964; Menesini 1974; Applegate and Espinosa-Arrubarrera 1996; Gottfried and Fordyce 2001; Purdy *et al.* 2001; Ward and Bonavia 2001; Pimiento *et al.* 2010). The size of lateral cusplets in megatoothed sharks becomes reduced through geological time and are functionally absent in *C. megalodon*. This reduction and eventual loss of cusplets has been cited as an evolutionary trend in *Carcharocles* related to an ontogenetic shift in morphology (Menesini 1974; Applegate and Espinosa-Arrubarrera 1996; Ward and Bonavia 2001). This hypothesis is supported by the growth data presented in this study.

In addition to the cusplet loss, generalized changes in tooth morphology of otodontid sharks through time includes: (1) overall increase in size, (2) development of serrations, (3) broadening of tooth crowns (Figure 5-5). As discussed previously, this evidence is the basis for the hypothesis that otodontid sharks represent a series of chronospecies, which replace one another through time (Glikman 1964; Zhelezko and Kozlov 1999; Ward and Bonavia 2001, Cappetta and Cavallo 2006). These morphological shifts are continuous, making clear delineations between the species/genera difficult. This issue is evident when reviewing the overwhelming number
of nominal species that have been published in the literature (Agassiz, 1833/1843; Jordan and Hannibal 1923; Leriche 1926; Casier 1960; Glikman 1964; Applegate and Espinosa-Arrubarrena 1996; Purdy 1996; Zhelezko and Kozlov 1999; Gottfried and Fordyce 2001; Purdy et al. 2001; Ward and Bonavia 2001). Growth data presented in this study corroborate the documented morphological shifts in tooth shape and structure. The increase in overall tooth size and the reduction and loss of lateral cusplets could be related to the increase in birth size through time. However, increased birth size does not necessarily translate to a change of onset timing with regards to growth. In contrast, it is more logical to assume the relationship between these morphological changes is a result of increased growth rates through time.

While ontogenetic shifts in growth rate and/or the onset or offset timing of somatic growth might be able to explain some of the morphological changes of otodontid teeth by, it cannot explain all of these features. The evolution of serrations along the cutting edges of teeth in the transition from *O. obliquus* to *Carcharocles* is likely related to a shift in diet through time (Purdy 1996). The smooth edged teeth of *O. obliquus* and the presence of lateral cusplets are somewhat similar in general tooth shape to the genus *Carcharias* (Applegate and Espinosa-Arrubarrena 1996). However, this superficial convergence is likely related to their diet preferences rather than an actual taxonomic affinity. Frazzetta (1988) has shown these tooth types are ideal for the rapid penetration and puncture of prey items, and is common in piscivorous sharks. Furthermore, Frazzetta (1988) hypothesized that lateral cusplets might fill in gaps between the narrow tooth crowns and trap food that might otherwise be lost. The evolution of serrations in the Late Paleocene/Early Eocene otodontids coincides to the evolution of cetaceans at
this same period of time (Purdy 1996; Thewissen and Williams 2002; Uhen 2010). Tooth serrations are well adapted for slicing flesh and are present in most actively predaceous extant sharks including *C. carcharias*, *Carcharhinus leucas*, and *Galeocerdo cuvier* (Frazzetta 1988). Perhaps most notably, *Carcharodon* is well known for using its serrated teeth for predation of pinnipeds and other cetaceans (Long and Jones 1996; Compagno 2001; Kerr *et al.* 2006; Ehret, MacFadden, and Salas-Gismondi 2009). Furthermore, the loss of lateral cusplets might also correspond to the widening of the tooth crowns during the Late Oligocene and Miocene.

**Biotic and Abiotic Factors**

The causation for the evolution of large body size and the eventual extinction of the otodontids has been an unresolved issue for many years (Gottfried *et al.* 1996; Purdy 1996). The two major hypotheses that have been proposed for both focus on the evolution and diversification of cetaceans and climate change throughout the Cenozoic. The data presented in this study can be used to make correlations with both the evolution and diversity of cetaceans and change in temperatures through time.

The earliest cetacean, *Himalayacetus*, has been described from the Early Eocene (~52 Ma) of India (Bajpai and Gingerich 1998; Uhen 2010). These first whales are characterized as being semi-aquatic, freshwater, and confined almost exclusively to the Indo-Pakistan region (Bajpai and Gingerich 1998; Thewissen and Williams 2002). The widespread invasion of marine ecosystems by cetaceans does not occur until the Middle Eocene. This initial, and cosmopolitan, diversification of archaeocetes is documented in the fossil record throughout Europe, North Africa, North America, and parts of South America (Steeman *et al.* 2009; Uhen 2010).
This diversification of archaeocete whales also coincides with a number of changes within the otodontid sharks. The first evidence of serrations in *Otodus/Carcharocles* is found in the fossil record during this transition between the latest Paleocene and Early-Middle Eocene. Teeth from this period are formally referred to as *Carcharocles (Otodus) aksuaticus* and have been described from Kazakhstan (Zhelezko and Kozlov 1999). Additionally, the transition from the Middle to Late Eocene is marked by the reduction of growth rate in *C. auriculatus* (this study). While there are little data on the feeding habits of either *C. auriculatus* or archaeocete whales, fossil materials of both have been recovered in the same localities and it can be surmised that either interspecies competition, predator/prey relationships, or both occurred (Purdy 1996; Thewissen and Williams 2002).

The origin of the Neoceti (including the mysticete and odontocete whales) in the Late Eocene (~ 36 Ma) and their rapid diversification coincides with the initial increase of growth in *Carcharocles angustidens* (Steeman et al. 2009; Uhen 2010). Sperm (Physeteroidea) and beaked whales (Ziphiidae) and dolphins and their relatives (Delphinidae) appear ~30 Ma, while the baleen whales (Mysticeti) closely follow at 29-26 Ma (Steeman et al. 2009). Hypotheses for this rapid diversification include: the restructuring of the ocean basins, the origination of currents (i.e. the Antarctic Circumpolar Current), changes in sea temperatures, and increases to and diversification of diatoms (Steeman et al. 2009; Marx and Uhen 2010). Although the growth rate change of *C. angustidens* in the Early Oligocene does not differ significantly from the Middle Eocene *C. auriculatus*, the origination of neocetes appears to be concurrent. Therefore, *C. angustidens* (IRSNB P929) is recording the earliest stages of a long-term
growth pattern shift in *Carcharocles* which might be related to this initial diversification of neocetes.

The pattern of increased growth and size in *Carcharocles* through time can also be correlated with a peak in neocete diversity during the Late Middle to Early Late Miocene (~12–8 Ma) (Steeman *et al.* 2009; Marx and Uhen 2010; Uhen 2010). This peak has been calibrated using all published taxa listed in the Paleobiology Database separately by Steeman *et al.* (2009) and Marx and Uhen (2010). Much like the origination of the neocetes across the Eocene-Oligocene transition, this peak has been linked to diatom diversity (i.e. food resources) and temperature shifts (Marx and Uhen 2010). This period also coincides with the first occurrence of *Carcharocles megalodon* in the fossil record. The increased growth rates recorded in the *C. megalodon* specimen in this study coincides with this peak in neocete diversity (Figure 5-6). It should be noted, however, that this diversity drops severely during the Late Miocene while records for *C. megalodon* continue into the Middle to Late Pliocene before going extinct. Further sampling of Late Miocene and Pliocene samples of *C. megalodon* centra may reveal a decrease in growth. Additionally, this drop in resource diversity and availability may be a driving factor in the extinction of the megatoothed sharks.

A second hypothesis related to overall body size and the eventual extinction of the megatoothed sharks is based on global climate change during the Cenozoic. Previous studies have posited that the movements of large whales to higher latitudes and the cooling of ocean temperatures in the Pliocene may have led to the extinction of *Carcharocles* (Gottfried *et al.* 1996; Purdy 1996). This hypothesis is partially based on the ectothermic physiology of most chondrichthyan species (Carlson *et al.* 2004). Based
on this assumption, these large sharks would not have been able to follow food resources into colder waters during the Pliocene. Extant lamnid sharks (white, mako, porbeagle, and salmon sharks) however, do exhibit endothermy and maintain constant, elevated body temperatures regardless of water temperatures (Goldman et al. 1996; Goldman 1997; Carlson et al. 2004). If these sharks were ectothermic, climatic changes through the Cenozoic should impact their growth rates (i.e. warmer temperatures would lead to faster rates, and colder temperatures would result in slower rates). To test this hypothesis, we can compare calculated rates for otodontids through time with previously published literature on climatic change through the Cenozoic.

Global temperature trends during the Cenozoic track patterns of general warming and cooling events driven by plate tectonics, orbital processes, and other aberrant events (Zachos et al. 2001). Comparing evolutionary trends in otodontid growth and ocean temperatures is a difficult task, considering that the distribution and migratory pathways of these sharks is relatively unknown (Purdy 1996). Therefore, the localities of fossil specimens might not necessarily be indicative of the environment where the sharks lived.

As discussed previously, Otodus obliquus first appears in the Late Paleocene and becomes relatively common in the Early Eocene (Ypresian) (Cappetta 1987). The timing of O. obliquus is also characterized by having the warmest temperatures of the Cenozoic. There are two major spikes in temperature during this period: the Paleocene-Eocene Thermal Maximum (PETM) at ~55 Ma, and the Early Eocene Climactic Optimum (EECO) at 51–53 Ma (Zachos et al. 2001; Zachos et al. 2008). The PETM is characterized by a rise in sea surface temperatures (SST) by as much as 8°C in higher
latitudes and less closer to the equator (Zachos et al. 2001). Zachos et al. (2006) calculated mid-latitude Atlantic SSTs in excess of 30°C and possibly as high as 35°C across the PETM and EECO. As discussed previously, calculated growth rates for *O. obliquus* during this period are greater than other megatoothed sharks, except for *C. megalodon* in the Middle-Late Miocene. These increased ocean temperatures during the PETM and EECO might have influenced the rate of growth in *Otodus* during the Early Eocene. However, samples from the Late Paleocene would provide more relevant data for meaningful comparisons.

Eocene ocean temperatures, following the PETM and EECO, decline over the next 17 Ma and are punctuated by an extreme cooling event at the Eocene-Oligocene transition (~ 34 Ma) (Zachos et al. 2001; Lear et al. 2008; Lui et al. 2009). Temperature declines across the Eocene have been estimated at ~ 7°C for deep-sea cooling (Zachos et al. 2001). In addition to this general decline, temperatures at the Eocene-Oligocene transition were an additional 2.5–5°C cooler, creating the first significant glaciation event in the Antarctic during the Cenozoic (Lear et al. 2008; Lui et al. 2009). The general cooling trend in the Middle Eocene coincides with a reduction in growth rate found in the transition from *O. obliquus* to *C. auriculatus*. However, as discussed previously other physical, and presumably physiological, changes were also occurring in the otodontids during this period (i.e. evolution of serrations and its dietary implications). The cooling event at the Eocene-Oligocene transition does not appear to have impacted growth in *C. angustidens* during the Early Oligocene. If *C. angustidens* was ectothermic, observed growth rates would presumably decline during this period. However, the opposite effect
is documented suggesting that either: (1) otodontids were able to regulate their body temperatures, or (2) other factors had a greater influence on growth.

Climatic conditions across the Oligocene and Early Miocene is marked by a series of warmer and cooler oscillations with periods of both glaciation and ice-free or reduced ice conditions (Zachos et al. 2001). Temperature variations across this period are cooler than those seen in the Eocene. As discussed earlier, this time period also coincides with the evolution of most modern groups of marine mammals. A significant warming event during the Middle Miocene, the Middle Miocene Climate Optimum (MMCO), occurs at ~15–12 Ma and coincides with the first records of *C. megalodon* in the fossil record (Cappetta, 1987; Applegate and Espinosa-Arrubarrena 1996; Gottfried et al. 1996). The estimated global average SST during this period has been calculated to be ~18.4°C or ~3°C above average modern-day ocean temperatures (You et al. 2009). Based on the increased growth rates of *C. angustidens* in the Oligocene, and the size of otodontid teeth (*Carcharocles chubutensis*) in the Late Oligocene/Early Miocene it does not appear that the significantly advanced growth patterns seen in *C. megalodon* could have evolved concurrently with the MMCO. Additionally, generally cooler temperatures during the Oligocene should have reduced the growth rate of an ectothermic species. The pattern of increased growth in *Carcharocles* appears to be a long-term trend that begins in the Early Oligocene and continues at least into the Middle-Late Miocene and possibly the Pliocene. The MMCO might have had a localized affect on the growth of *C. megalodon* during the Middle Miocene but likely did not drive growth in genus. The lack of overall correlation between long-term climate trends and increased growth rates in *Carcharocles* suggests that the otodontid sharks might have exhibited endothermy.
Conclusions

Vertebral centra from four species of megatoothed sharks (*Otodus obliquus*, *Carcharocles auriculatus*, *Carcharocles angustidens*, and *Carcharocles megalodon*) were analyzed for annual growth rings using X-radiography and compared to the extant *Carcharodon carcharias*. Based on data involving both modern and fossil shark species, growth rings (GR) observed within the X-rays are assumed to represent annual increments. Counts of GRs in the fossil specimens were used to reconstruct growth rates for the species that were then compared to the extant white shark, *Carcharodon carcharias*. Overall growth patterns for *O. obliquus* in the Early Eocene reveals a relatively fast growing species when compared to early *Carcharocles* taxa and the extant *C. carcharias*. The transition from *O. obliquus* to *Carcharocles auriculatus* in the Early-Middle Eocene is not only characterized by a physical change in tooth morphology (i.e. acquisition of serrations) but also a decrease in growth to rates comparable to *C. carcharias*. Growth rates for the Early Oligocene *C. angustidens* are not statistically different from *C. auriculatus* but do reveal a moderate increase. Analysis of *C. megalodon* in the Middle-Late Miocene provides evidence for a substantial increase in growth rates and delay of offset timing for *Carcharocles* through time. *Carcharocles megalodon* was found to have a growth rate 1.5 times faster than the next comparable species, *O. obliquus*. Comparisons of BM radius reveal that *C. megalodon* was also significantly (1.3 times) larger at birth than the next largest species, *C. angustidens*. Finally, its age at offset timing was also found to be significantly older than all other species examined.

The overall trends of growth in *Carcharocles* can be explained by an increase in the rate, size at birth, and age at offset of species across the Early-Middle Eocene
through the Mio-Pliocene. Morphological changes in tooth structure including: a widening of the tooth crowns, the reduction and eventual loss of lateral cusplets in adults, and an overall increase in tooth size track these changes in growth patterns. While the evolution and refinement of serrations along the cutting edges of the tooth crowns likely reflects a shift in dietary preference that is correlated with the evolution of whales in the Eocene (Applegate and Espinosa-Arrubarrena 1996; Gottfried et al. 1996; Purdy 1996; Bajpai and Gingerich 1998; Purdy et al. 2001; Thewissen and Williams 2002; Uhen 2010).

Proposed biotic and abiotic factors that likely influenced the increased rates of growth and overall size include the evolution and diversification of cetaceans and overall climate change. The appearance of whales in the Early Eocene corresponds to the evolution of serrations on the tooth crowns in *Carcharocles*. While the evolution of neocetes in the Oligocene and their increased diversity up until a peak in the Middle Miocene tracks the increased growth patterns observed in *Carcharocles* during the same period of time. A significant reduction in diversity in the Late Miocene and Early Pliocene may correspond to the eventual extinction of *Carcharocles* in the Pliocene.

Trends in climate and SSTs through time correspond to some, but not all of the changes in otodontid growth patterns if we assume ectothermy. Rapid growth rates in *O. obliquus* during the Paleocene/Eocene correspond with increased temperatures during the PETM and EECO. However, the general trend of increased growth in *Carcharocles* through the Eocene-Miocene does not track climate changes during the same period. In particular, a glaciation event at the Eocene-Oligocene transition and the relatively cooler temperatures across the Oligocene and Early Miocene do not agree
with the increased growth rates seen in *Carcharocles angustidens* and *C. megalodon*. Therefore, otodontid sharks may have exhibited endothermy or other factors (including whale diversity) might have had a larger impact on overall growth.

The study of the otodontid sharks has been mired in confusion due to the lack of fossilization of skeletal remains and convergent evolution in tooth morphology with *Carcharodon carcharias* (Ehret *et al.* 2010). Paleobiological studies of well-preserved specimens, including this chapter, yield valuable data that can further our knowledge of these taxa and their interrelationships. Furthermore, research in the fields of global climate change, plate tectonics, oceanography, neocete evolution, etc, as evidenced here, should be correlated with fossil chondrichthyan research to reveal new and exciting trends in evolution.
Figure 5-1. Images of megatoothed shark vertebral centra. (A) Otodus obliquus, UF 162732, (B) Otodus obliquus, UF 256397, (C) Carcharocles auriculatus, IRSNB P809, (D) Carcharocles angustidens, IRSNB P929, (E) Carcharocles megalodon, IRSNM 3121. Scale bar represents 5 cm.
Figure 5-2. X-radiographs of vertebral centra. (A) *Otodus obliquus*, UF 162732, (B) *Otodus obliquus*, UF 256397, (C) *Carcharocles auriculatus*, IRSNB P809, (D) *Carcharocles angustidens*, IRSNB P929, (E) *Carcharocles megalodon*, IRSNB 3121. Scale bar represents 5 cm.
Figure 5-3. Centrum radius (CR) per growth ring (GR). (A) otodontid sharks, (B) otodontid sharks compared to growth in *Carcharodon carcharias* (after Wintner and Cliff 1999).
Figure 5-4. Analysis of covariance, Centrum area vs. growth rings (GR) for the four megatoothed species and *Carcharodon carcharias*. 
Figure 5-5. Anterior otodontid shark teeth through time. Lingual views on top row, labial views on bottom row. A) *Otodus obliquus*, B) *Carcharocles auriculatus*, C) *Carcharocles angustidens*, D) *Carcharocles chubutensis* and E) *Carcharocles megalodon*. All specimens are part of the G. Hubbell Collection. Scale bar represents 5 cm.
Figure 5-6. Growth rates for otodontid sharks compared with neocete diversity through geologic time (Neocete diversity data from Marx and Uhen, 2010). Data points for otodontid sharks represent time-averaged dates for the species included in this study.
Table 5-1. Centrum radius (CR) and growth ring (GR) measurements for otodontid sharks. CR measurements in cm, GR counts in years.

<table>
<thead>
<tr>
<th>Growth Ring (GR)</th>
<th><em>Otodus obliquus</em> Centrum Radius (CR)</th>
<th><em>Otodus obliquus</em> Centrum Radius (CR)</th>
<th><em>Carcharocles auriculatus</em> Centrum Radius (CR)</th>
<th><em>Carcharocles angustidens</em> Centrum Radius (CR)</th>
<th><em>Carcharocles megalodon</em> Centrum Radius (CR)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>1.04</td>
<td>0.84</td>
<td>1.00</td>
<td>1.24</td>
<td>1.66</td>
</tr>
<tr>
<td>1</td>
<td>1.48</td>
<td>1.28</td>
<td>1.21</td>
<td>1.57</td>
<td>1.99</td>
</tr>
<tr>
<td>2</td>
<td>1.74</td>
<td>1.60</td>
<td>1.39</td>
<td>1.89</td>
<td>2.24</td>
</tr>
<tr>
<td>3</td>
<td>1.95</td>
<td>1.89</td>
<td>1.58</td>
<td>2.09</td>
<td>2.47</td>
</tr>
<tr>
<td>4</td>
<td>2.14</td>
<td>2.11</td>
<td>1.77</td>
<td>2.33</td>
<td>2.68</td>
</tr>
<tr>
<td>5</td>
<td>2.35</td>
<td>2.37</td>
<td>2.00</td>
<td>2.52</td>
<td>2.91</td>
</tr>
<tr>
<td>6</td>
<td>2.58</td>
<td>2.57</td>
<td>2.23</td>
<td>2.66</td>
<td>3.11</td>
</tr>
<tr>
<td>7</td>
<td>2.75</td>
<td>2.77</td>
<td>2.42</td>
<td>2.78</td>
<td>3.36</td>
</tr>
<tr>
<td>8</td>
<td>2.91</td>
<td>2.93</td>
<td>2.61</td>
<td>2.91</td>
<td>3.54</td>
</tr>
<tr>
<td>9</td>
<td>3.15</td>
<td>3.11</td>
<td>2.80</td>
<td>3.05</td>
<td>3.73</td>
</tr>
<tr>
<td>10</td>
<td>3.28</td>
<td>3.25</td>
<td>2.96</td>
<td>3.22</td>
<td>3.91</td>
</tr>
<tr>
<td>12</td>
<td>3.60</td>
<td>3.53</td>
<td>3.27</td>
<td>3.55</td>
<td>4.37</td>
</tr>
<tr>
<td>13</td>
<td>3.76</td>
<td>3.67</td>
<td>3.41</td>
<td>3.70</td>
<td>4.66</td>
</tr>
<tr>
<td>14</td>
<td>3.93</td>
<td>3.80</td>
<td>3.52</td>
<td>3.85</td>
<td>4.85</td>
</tr>
<tr>
<td>15</td>
<td>4.09</td>
<td>3.93</td>
<td>3.65</td>
<td>3.97</td>
<td>5.01</td>
</tr>
<tr>
<td>16</td>
<td>4.27</td>
<td>4.04</td>
<td>3.83</td>
<td>4.13</td>
<td>5.21</td>
</tr>
<tr>
<td>17</td>
<td>4.46</td>
<td>4.14</td>
<td>4.01</td>
<td>4.28</td>
<td>5.42</td>
</tr>
<tr>
<td>18</td>
<td>4.65</td>
<td>4.25</td>
<td>4.15</td>
<td>4.43</td>
<td>5.59</td>
</tr>
<tr>
<td>19</td>
<td>4.82</td>
<td>4.25</td>
<td>4.56</td>
<td>5.81</td>
<td></td>
</tr>
<tr>
<td>20</td>
<td>4.96</td>
<td>4.35</td>
<td>4.67</td>
<td>6.00</td>
<td></td>
</tr>
<tr>
<td>21</td>
<td>5.12</td>
<td>4.46</td>
<td>4.72</td>
<td>6.17</td>
<td></td>
</tr>
<tr>
<td>22</td>
<td>5.26</td>
<td>4.57</td>
<td>4.80</td>
<td>6.34</td>
<td></td>
</tr>
<tr>
<td>23</td>
<td>5.41</td>
<td>4.66</td>
<td>5.51</td>
<td></td>
<td></td>
</tr>
<tr>
<td>24</td>
<td>5.50</td>
<td>4.72</td>
<td>6.64</td>
<td></td>
<td></td>
</tr>
<tr>
<td>25</td>
<td></td>
<td></td>
<td>6.79</td>
<td></td>
<td></td>
</tr>
<tr>
<td>26</td>
<td></td>
<td></td>
<td>6.95</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Growth Ring (GR)</td>
<td><em>Otodus obliquus</em> Centrum Radius (CR)</td>
<td><em>Otodus obliquus</em> Centrum Radius (CR)</td>
<td><em>Carcharocles auriculatus</em> Centrum Radius (CR)</td>
<td><em>Carcharocles angustidens</em> Centrum Radius (CR)</td>
<td><em>Carcharocles megalodon</em> Centrum Radius (CR)</td>
</tr>
<tr>
<td>-----------------</td>
<td>------------------------------------------</td>
<td>------------------------------------------</td>
<td>-----------------------------------------------</td>
<td>-----------------------------------------------</td>
<td>-----------------------------------------------</td>
</tr>
<tr>
<td>29</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>7.29</td>
</tr>
<tr>
<td>30</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>7.37</td>
</tr>
</tbody>
</table>
Table 5-2. Analysis of Covariance slopes (= rates of growth) for otodontid and white sharks.

<table>
<thead>
<tr>
<th>Species</th>
<th>Slope (Rate of Growth)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Otodus obliquus</em></td>
<td>3.5259</td>
</tr>
<tr>
<td><em>Carcharocles auriculatus</em></td>
<td>2.8209</td>
</tr>
<tr>
<td><em>Carcharocles angustidens</em></td>
<td>3.1295</td>
</tr>
<tr>
<td><em>Carcharocles megalodon</em></td>
<td>5.4924</td>
</tr>
<tr>
<td><em>Carcharodon carcharias</em></td>
<td>2.8007</td>
</tr>
</tbody>
</table>
Table 5-3. Paired t-test comparing the slopes (rates of growth) between otodontid and white sharks.

<table>
<thead>
<tr>
<th>T-Scores</th>
<th>Carcharocles angustidens P-Values</th>
<th>Carcharocles auriculatus P-Values</th>
<th>Carcharocles megalodon P-Values</th>
<th>Otodus obliquus P-Values</th>
<th>Carcharodon carcharias P-Values</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carcharocles angustidens</td>
<td>0</td>
<td>1</td>
<td>1.00</td>
<td>0.32</td>
<td>-8.18</td>
</tr>
<tr>
<td>Carcharocles auriculatus</td>
<td>-1.00</td>
<td>0.32</td>
<td>0</td>
<td>1</td>
<td>-9.57</td>
</tr>
<tr>
<td>Carcharocles megalodon</td>
<td>8.18</td>
<td>&gt;0.001</td>
<td>9.57</td>
<td>&gt;0.001</td>
<td>0</td>
</tr>
<tr>
<td>Otodus obliquus</td>
<td>1.43</td>
<td>0.16</td>
<td>2.64</td>
<td>0.01</td>
<td>-8.05</td>
</tr>
<tr>
<td>Carcharodon carcharias</td>
<td>-1.41</td>
<td>0.16</td>
<td>-0.09</td>
<td>0.93</td>
<td>-13.91</td>
</tr>
</tbody>
</table>
CHAPTER 6
CONCLUSIONS

The paleobiology of extinct neoselachians can provide valuable insights into the paleoecology of ancient marine habitats. The utilization of rare, well-preserved specimens and new analyzation techniques can yield exciting new information regarding the evolution of chondrichthyan groups and their interactions with the environment. Capitalizing on the collections of Dr. Gordon Hubbell, the Florida Museum of Natural History, the Museo de Historia Natural Javier Prado, Lima, Peru, and the Royal Belgian Institute of Natural Sciences, Brussels, Belgium I have expanded our knowledge on the evolution and paleobiology of Cenozoic lamniform sharks. The focus of my research is on two of the most recognizable families, the Lamnidae (white, makos, salmon, and porbeagle) and the Otodontidae (megatoothed sharks). Their position as apex predators has directly influenced the structure of marine habitats through time and yet we know very little about their evolution and paleoecology (Purdy 1996).

The taxonomic placement of the otodontid sharks and their relationship to the extant *Carcharodon carcharias* has been a topic of debate over the past 175 years. The paucity of associated specimens and the convergent evolution of tooth structure in the otodontid, white, and mako sharks has confounded the issue, leaving the taxonomic assignment of the family open to individual interpretation (Jordan and Hannibal 1923; Casier 1960; Glikman 1964; Applegate and Espinosa-Arrubarrena 1996; Purdy 1996; Gottfried and Fordyce 2001; Purdy *et al.* 2001; Nyberg *et al.* 2006). I address this issue in Chapters 2 and 4 of my dissertation through the description and formal designation of a new species of *Carcharodon* from the Late Miocene of Peru. This specimen, collected
in 1988 and only recently made available for scientific analysis, elucidates our understanding of white shark evolution and the interrelationships of *Carcharodon* with *Isurus* and the odontids. The type specimen of *Carcharodon* n. sp. offers an unparalleled opportunity to evaluate and compare a set of unique dental and morphological characters that provide direct evidence of an evolutionary history related to *Carcharodon hastalis* and not *Carcharocles megalodon* as some have suggested. Comparisons with *Carcharocles* and *Isurus escheri* specimens suggest the convergent evolution of serrations or crenulations in multiple taxa of lamniform sharks during the Cenozoic. Additionally, the prevalence of *Carcharodon* n. sp. specimens from numerous localities within the Pacific Basin and the relative rarity of specimens elsewhere suggest a Pacific origin for the species.

I also investigated the paleobiology of extinct white sharks by incorporating studies on the growth (Chapter 2) and feeding behaviors of *Carcharodon* n. sp. in the Late Miocene of Peru. A vertebral centrum from UF 226255 was imaged using X-radiography to count and measure preserved growth increments. To verify the annual periodicity of these increments, carbon and oxygen isotope samples were collected for analysis. The resulting data validated the annual periodicity of the increments and revealed that the extinct white shark, *Carcharodon* n. sp., grew at a slower rate compared to the extant *C. carcharias* (Wintner and Cliff 1999; Ehret, Hubbell, and MacFadden 2009). This finding suggests that white sharks might have prolonged maturation, possibly in response to pressures from *Carcharocles* or other paleoenvironmental factors.

In Chapter 3, I described a partial mysticete whale mandible which included a partial tooth crown belonging to *Carcharodon* n. sp. also from the Pisco Formation. It is
well documented that extant white sharks feed on marine mammals and their coarsely serrated teeth are suited for cutting through flesh (Frazzetta 1988; Long et al. 1996; Curtis et al. 2006). Interestingly, in extant *Carcharodon*, dietary needs shift during maturation from a piscivorous diet in juveniles to one consisting primarily of marine mammals in mature adults (Estrada et al. 2006). It is hypothesized that the evolution of tooth serrations in white sharks is correlated to a dietary shift in *Carcharodon* through time from piscivory to neocetes as they diversified during the Miocene. However, there is very little fossil evidence prior to the Pleistocene for the timing of this shift in diet (Deméré and Cerutti 1982). The positive identification and description of a Late Miocene white shark preying on a mysticete whale provides some of the earliest evidence marine mammal predation by *Carcharodon*. Furthermore, the relatively weak serration pattern exhibited in *Carcharodon* n. sp. suggests that the dietary shift occurred concurrently with this morphological change.

In the final research chapter (Chapter 5) of my dissertation, I discussed the macroevolution of body size and change in the growth rates of the otodontid sharks throughout time. Based on the size of isolated teeth, it has been shown that sharks in genera *Otodus* and *Carcharocles* have increased in size through time. Causation of this change has been hypothesized to represent a response to environmental factors (i.e. increases in prey size and/or diversity and paleoclimatological shifts). I set out to examine the extent of the rate changes that led these sharks to evolve from sizes comparable to extant white sharks (∼7 m) and grow to lengths upwards of 17 m (Randall 1973, 1987; Gottfried et al. 1996; Pimiento et al. 2010). It should be noted that while this study is not the first time this question has been asked, the rarity of
megatoothed vertebral centra in the fossil record has severely limited the paleobiological studies of these sharks. Therefore, using new techniques and approaches to study the few samples available has greatly advanced our knowledge of the taxa. Additionally I examined the heterochronic mechanisms that influenced these growth changes and some potential biotic and abiotic factors that contributed to these changes in size.

Growth data taken from X-radiographs of vertebral centra were collected following the same procedures used in Chapter 2. Changes in growth rates between taxa through time were not linear as initially suspected. A distinct drop in growth rate from the Early Eocene Otodus obliquus and the Early-Middle Eocene Carcharocles auriculatus was recorded. Explanations for this shift include: climatic cooling following the PETM and EECO and a dietary shift from piscivory to feeding on marine mammals as evidenced by the evolution of tooth serrations during this period. Growth in the three species of Carcharocles (C. auriculatus, C. angustidens, and C. megalodon) examined exhibit a continued rate increase from the Middle Eocene through the Middle-Late Miocene. In particular, the growth rate of Carcharocles megalodon in the Middle-Late Miocene was found to be 1.5 times greater than the next closest species (O. obliquus). In addition to this increased rate, C. megalodon also exhibited two heterochronic changes to its growth strategy: a larger size at birth and a later offset time compared to O. obliquus, C. auriculatus, and C. angustidens which contributed to its immense size.

Hypotheses for the causation behind the increases in both growth rate and overall size within the otodontids have included: changes in paleoclimatic conditions, the initial evolution of whales in the Eocene and the diversification of neocetes during the
Oligocene and Miocene. I compared the evolution of growth rates to changes in paleotemperature through time and found very little correlation. Aside from the reduction across the Early to Middle Eocene (O. obliquus to C. auriculatus) discussed above, the general trend of increasing growth rates through the Oligocene and Miocene do not correspond with general paleoclimatological changes. This suggests that temperature was not a decisive factor in the growth of the otodontids. In contrast, comparisons of growth rates with the evolution of whales and the diversification of neocetes in the Oligocene and Miocene show some correlation. Therefore I hypothesize that dietary resources played a more important role in the macroevolution of body size and eventual extinction of the megatoothed sharks.

My dissertation presents new research on the evolution and paleobiology of extinct lamnid and otodontid sharks. I emphasize the importance of exceptionally preserved specimens in the study of extinct neoselachians. In addition to the proper collection and curation of specimens, it is imperative to acquire accurate locality and stratigraphic information. The application of new technology and techniques (including those applied to research on extant species) can offer new insights into the paleobiology of these extinct sharks. Paleoichthyologists working on chondrichthyans should move beyond interpretative papers focusing on loose teeth and start focusing on important paleobiological questions that can be addressed utilizing these new technologies.
It is the responsibility of scientists and researchers to take an active role in the dissemination of scientific information to the general public. Oftentimes there is a significant disconnect between the scientific theories and hypotheses proposed by researchers and the general public's understanding of these ideas and concepts. Such misunderstandings can be related to numerous factors including: the complex nature of the concepts, the technical language used in scientific literature and even the general mistrust of scientists by the public. Left uncorrected, these misconceptions may become ingrained in the general public's understanding of key concepts like the theory of evolution. Therefore, as a scientist I believe that it is important to use every opportunity available to convey my research and other scientific concepts to a general audience.

To become an effective communicator of scientific concepts it is important to first learn the best methods for disseminating information. I approached the subject of scientific education in a stepwise manner beginning with enrolling in a seminar course entitled “Broader Impacts of Natural Sciences on Society” taught by Bruce MacFadden in 2007. The purpose of this seminar was to provide hands-on experience for graduate students wishing to learn how to communicate science to the general public. For me, this course also served as an introduction to scientific teaching and exhibit design. One of the more important aspects of the course was to develop and administer a front-end evaluation focusing on a travelling exhibit entitled “Megalodon: The Largest Shark That Ever Lived” (www.flmnh.ufl.edu/megalodon/). The front-end evaluation was administered to visitors of the Florida Museum of Natural History (FLMNH) and was designed to the gauge the public’s existing knowledge about fossil sharks. The
evaluation also set out to determine what type of information they would want to learn in an exhibit on fossil sharks. The results were then used in the development and design of the actual exhibit. Experiences gained from this course improved my communication skills and taught me how to design evaluation tools used to gauge the public’s general understanding of scientific concepts.

Following the completion of the course, I continued to assist museum personnel in the development and design of the travelling “Megalodon” exhibit at the FLMNH in order to learn more about scientific education. My duties and responsibilities included the gathering of scientific information and materials for exhibit panels and the selection of museum specimens to be utilized in the display cases. Exhibit panels were evaluated for effectiveness by allowing visitors at FLMNH to view them. Visitors were then asked a series of questions pertaining to the material on the panels in order to gauge their understanding of the materials being presented. If overall comprehension of the panels was low, one could assume that the main themes of the panel were not being presented adequately. Once the exhibit opened, we administered summative evaluations to visitors in order to gauge the overall effectiveness of the exhibit. Evaluation results were positive and the exhibit has since travelled to several museums including: the Bishop Museum in Honolulu, Miami Science Museum, Mississippi Museum of Natural Science, and North Carolina Museum of Natural Sciences. This experience taught me how to design and test scientific information designed and written for public exhibits. From designing and executing the evaluations to working with mock-up panels, it gave me hands-on experience producing a successful museum exhibits.
Based on the experiences learned through coursework and exhibit design, I then pursued opportunities to interact directly with the public through the FLMNH. This first included a two week field camp in vertebrate paleontology for local 5th grade students. The main objective of this camp was to expose children to general concepts in paleontology and geology and to teach them basic field methods for collecting fossils. Classroom activities focused on teaching the children general geological (i.e., basic stratigraphy, the law of superposition, and mineralization) and biological (generalized taxonomy, ecology, and physiology) concepts through the use of interactive lessons. For example, large sheets (~ 4 meters in length) of paper were laid out along a sidewalk. Students dipped large sponges in water and tied them to their feet. They were then instructed to walk, run, or jog down the length of the paper at different speeds. The ‘footprints’ left by the wet sponges were then marked and the different stride lengths were measured. We then compared these stride lengths to pictures of fossilized dinosaur trackways. Students were then asked to discuss how paleontologists can determine how fast different dinosaurs could walk/run based on their footprints. The second portion of the class involved taking the students to various fossil localities around Gainesville (including Hogtown Creek and Thomas Farm) to learn the proper techniques for collecting and identifying fossils. At the end of each ‘expedition’ the students would recount the techniques they learned and their fossil finds in a ‘field notebook’. The students learned the importance of good writing skills and the need to collect and record data for scientific study. This field camp was a positive learning experience for me as the teacher, as well as the students who absorbed a substantial amount of new material in a relatively short period of time.
Given the positive feedback from the field camp, I have since committed to other outreach activities including the presentation my research to numerous amateur paleontology clubs and school groups. Presentations of my research have included numerous paleontological clubs throughout Florida, such as: the Southwest Florida Fossil Club, Lee County Fossil Club, Tampa Bay Fossil Club, and the Florida Paleontological Society. Additionally, I have also given research seminars to numerous school, college, and professional groups at many different levels including: 4th grade students at Spring Lake Heights Elementary School, New Jersey, 12th grade students at Vashon Island High School, Washington, the Biology Department at the Richard Stockton College of New Jersey, a convocation of Alachua County art teachers, and Project Shark Awareness, FLMNH. These seminars have provided me with the experience of presenting my research to groups of all different ages and backgrounds. For example, presenting fossil research to a class of 4th grade students is much different than presenting to a paleontology enthusiast group. These types of activities prepare me for a career path in paleontological research and museum outreach.

Finally, I utilized the methods acquired throughout the coursework and outreach activities discussed above to disseminate my research to a wider audience via the internet. In this technological age, the internet can be a valuable tool for reaching a large number of people on a global scale. Working in conjunction with Cathy Bester and George Burgess in the division of Ichthyology at FLMNH, we created a fossil shark research webpage through the FLMNH website (www.flmnh.ufl.edu/fish/sharks/fossils/). The website is intended to aide amateur paleontologists in the identification of their fossil shark teeth as well as present current fossil shark research at FLMNH. The initial
idea was suggested by George Burgess, who was receiving multiple requests a week to identify fossil shark teeth for amateur collectors. However, the interest and need for more readily available resources for the general public was apparent to both of us. The identification key focuses on the most common fossil species found in the southeastern United States and will eventually feature images of actual specimens. The main webpage also includes contact information which encourages visitors to contact me directly with specific questions. Based on the number of email requests I receive for identifications and additional information (~2-3 per week) and the positive feedback offered by visitors, I believe that this webpage has been successful in meeting the needs of the amateur shark collector community. In addition to the local community, email requests from other states and other countries provide evidence that our webpage is reaching a larger audience than we had initially intended.

Scientific education and public outreach are an integral part of being a scientist. By first taking pertinent coursework and then practicing outreach activities through FLMNH have supplied me with numerous opportunities to learn and refine my skills as a lecturer and teacher. As a result, these opportunities directly benefit my career goals as I work towards research in a museum and/or university setting.
Nursery Area for Giant Baby Sharks in the Miocene of Panama

Background

As we know from modern species, nursery areas are essential shark habitats for vulnerable young. Nurseries are typically highly productive, shallow-water habitats that are characterized by the presence of juveniles and neonates. It has been suggested that in these areas, sharks can find ample food resources and protection from predators. Based on the fossil record, we know that the extinct *Carcharocles megalodon* was the biggest shark that ever lived. Previous proposed paleo-nursery areas for this species were based on the anecdotal presence of juvenile fossil teeth accompanied by fossil marine mammals. We now present the first definitive evidence of ancient nurseries for *C. megalodon* from the Late Miocene of Panama, about 10 million years ago.

Methodology/Principal Findings

We collected and measured fossil shark teeth of *C. megalodon*, within the highly productive, shallow marine Gatun Formation from the Miocene of Panama. Surprisingly, and in contrast to other fossil accumulations, the majority of the teeth from Gatun are very small. Here we compare the tooth sizes from the Gatun with specimens from different, but analogous localities. In addition we calculate the total length of the individuals found in Gatun. These comparisons and estimates suggest that the small size of Gatun’s *C. megalodon* is neither related to a small population of this species nor

---

the tooth position within the jaw. Thus, the individuals from Gatun were mostly juveniles and neonates, with estimated body lengths between 2 and 10.5 meters.

**Conclusions/Significance**

We propose that the Miocene Gatun Formation represents the first documented paleo-nursery area for *C. megalodon* from the Neotropics, and one of the few recorded in the fossil record for an extinct selachian. We therefore show that sharks have used nursery areas at least for 10 millions of years as an adaptive strategy during their life histories.

**Biodiversity and Paleoecology of Late Miocene Sharks (Chondrichthyes, Elasmobranchii, Selachii) from the Gatun Formation, Panama**

The late Miocene Gatun Formation of northern Panama contains a highly diverse and well sampled neritic fossil assemblage that was located in a shallow-water strait that connected the Pacific and Atlantic (Caribbean) oceans about 10 million years ago. Although previously less well-known, the Gatun Formation likewise contains a relatively diverse selachian assemblage. Based on recent field discoveries and further analysis of existing collections, the sharks from this rich unit consist of at least 16 taxa, including four species that are extinct today. The remaining portion of the selachian biodiversity has taxonomic affinities with modern taxa and indicates relatively long-lived species. Comparisons of Gatun dental measurements with older and younger faunas suggest that many of the species have an abundance of small individuals. Based on the known habitat preferences for modern selachian analog assemblages, the Gatun sharks were primarily adapted to shallow waters (i.e., between about 20 to 40 m depth) within the neritic zone. This paleo-depth assessment is also consistent with previous interpretations based on the marine invertebrate fauna from the Gatun Formation.
Finally, even though some species are now restricted to the Caribbean, in comparison with modern species, the Gatun shark fauna has mixed Pacific-Atlantic (Caribbean) biogeographic affinities due to its location between two ancient ocean basins.

An extinct map turtle *Graptemys* (Testudines: Emydidae) from the Pleistocene of Florida

*Graptemys* n. sp., from the Suwannee River drainage of north-central Florida, represents the most southeastern occurrence of the genus. This species is morphologically and geographically most similar to the extant Barbour’s map turtle, *Graptemys barbouri*. *G. n. sp.* exhibits sexual dimorphism similar to extant *G. barbouri*, *G. ernsti*, *G. pulchra*, and *G. gibbonsi*, with females being megacephalic and attaining a much larger size than males. This new species possesses a very wide skull and mandible making it the most blunt-headed member of its clade. Specimens described here include a nearly complete skull, 6 mandibles, an epiplastron, thirteen neural bones, and an assortment of other shell fragments. Previously reported fossil material from Florida was collected in the 1960’s along the Santa Fe River and referred to both the Pliocene and Pleistocene. Rare Earth Element (REE) analysis of this material is reinterpreted here as being Rancholabrean in age.
LIST OF REFERENCES


BOUETEL, V. and MUIZON, C. de. 2006. The anatomy and relationships of *Piscobalaena nana* (Cetacea, Mysticeti), and Cetotheriidae s. s. from the early Pliocene of Peru. *Geodiversitas*, 28, 319–395.


—— MACFADDEN, B. J. and SALAS-GISMONDI, R. 2009. Caught in the act: Trophic interactions between a 4-Million-Year-Old white shark (Carcharodon) and mysticete whale from Peru. Palaios, 24, 329–333.


—— CAMPANA, S. E. and JONES, C. M. 2007. Age under-estimation in New Zealand porbeagle sharks (Lamna nasus): is there an upper limit to ages that can be determined from shark vertebrae? Marine and Freshwater Research, 58, 10–23.


GLIKMAN, L. S. 1964. Sharks of the Paleogene their stratigraphic significance. Nakua Press, Moscow-Leningrad, Russia, 229 pp. [In Russian].


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


BIOGRAPHICAL SKETCH

Dana Joseph Ehret was born in Spring Lake Heights, New Jersey. He attended Spring Lake Heights Elementary School for his primary education. During this time, his love for the natural sciences and history was fostered by two extraordinary teachers, Ardythe Wright and Richard Muhlenbruck. Dana attended Manasquan High School in Manasquan, New Jersey focusing on courses in the sciences, including marine biology. He was accepted to the Richard Stockton College of New Jersey and graduated with a Bachelor of Science degree in marine biology in 2001. While at Richard Stockton College, Dana was advised by Roger C. Wood who supported his dream of becoming a vertebrate paleontologist. In addition to coursework for his degree in marine biology, he also completed a senior thesis project entitled “Fossil turtles from the Baculum Draconis Quarry (Late Maastrichtian), Niobrara County, Wyoming”. During this period of time, he also participated in two consecutive summer internships working with diamondback terrapins at the Wetlands Institute in Stone Harbor, New Jersey under the supervision of Roger Wood. Dana enrolled in the Department of Geological Sciences at the University of Florida in 2001 under the supervision of Bruce J. MacFadden. Dana received his Master of Science degree in geological sciences during the spring of 2004. His thesis was entitled ‘Skeletochronology as a method of aging Oligocene Gopherus laticuneus and Stylemys nebrascensis, using Gopherus polyphemus as a modern analog’. Dana also received a minor in Wildlife Ecology and Conservation while working on various herpetological projects with his mentor and friend Dick Franz. In addition to his work on fossil chondrichthyans for his Doctorate of Philosophy, Dana also has a great interest in fossil and extant chelonians, particularly in the southeastern United States.