A Toothy Tale of Evolution:

Convergence in Tooth Morphology among Marine Mesozoic – Cenozoic Sharks, Reptiles, and Mammals

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ABSTRACT

Although mechanisms of niche replacement are discussed thoroughly in the evolutionary paleontological literature (i.e., extinctions, competition, evolution of new adaptive morphologies), actual studies involving quantitative analyses are not common. In this study, morphological features of dentition in Late Cretaceous and Cenozoic marine vertebrate predators were analyzed. The analysis included species of Late Cretaceous and Cenozoic sharks, Late Cretaceous marine reptiles, and Cenozoic marine mammals. Dental characters used in the study were both discrete and continuous. Species included in the analysis were originally collected from Late Cretaceous and Cenozoic rocks from the south-central, southeastern, and the mid-Atlantic regions of the United States, as well as Europe and the Pacific Rim.

A morphometric "tooth space" was constructed using the eigenvectors generated from Principal Component Analysis of the dental character data. The results of the analysis show that Mesozoic marine reptiles occupied a small, discrete region of the tooth morphospace, whereas Cretaceous sharks occupied a much larger, diffuse region of the morphospace. During the Paleogene a profusion of shark tooth morphologies occurred and then expanded into new areas of tooth morphospace. Yet, no overlap with the morphospace previously occupied by Mesozoic marine reptiles occurred. A large number of novel tooth morphologies evolved with the evolution of marine mammals during the Cenozoic. Remarkably, many of the tooth forms converged on the Mesozoic marine reptile designs, and hence a major overlap of marine mammal tooth morphospace with the previously occupied Mesozoic marine reptile morphospace occurred. Additionally, the shift from heterodonty (teeth of different types) to homodonty (teeth of similar types) occurred in several members of both the Mesozoic marine reptiles and the Cenozoic marine mammals.

Based on dental morphology, this study indicates that following the extinction of the Mesozoic marine reptiles during the Late Cretaceous, Cenozoic sharks failed to occupy the vacated niches, yet Cenozoic marine mammal dentition converged on the previous Mesozoic marine reptile tooth designs. Apparently, Cenozoic marine mammals occupied the vacated Mesozoic marine reptile dietary niches.

INTRODUCTION

The idea of faunal niche replacement has been discussed for well over a century. Darwin (1859) first proposed the idea by using the analogy of "wedges hammered into a log." Classic paleontological examples include the replacement of non-avian dinosaurs by mammals (Benton, 1990, 1996a,b), the replacement of brachiopods by pelecypods as the dominant post-Paleozoic benthic bivalved fauna (Gould and Calloway, 1980), and even the replacement of whole monophyletic groups of articulated brachiopods by other monophyletic articulated brachiopod groups (Ciampaglio, 2004). Less attention has been paid to morphological convergence as a direct consequence of faunal niche replacement. Although the phenomenon has been addressed, particularly within reef complexes throughout the Phanerozoic (McKerrow, 1978; Wood, 1999), studies involving quantitative analyses are rare in the paleontological literature.

Morphological convergence among Mesozoic marine reptiles and Cenozoic marine mammals is well known (Figure 1). When the fossilized remains of Eocene whales were first uncovered in Louisiana and Alabama they were originally identified as belonging to a "plesiosaur-like" reptile and named *Basilosaurus* by Harlan (1834, 1835). It was nearly five years later that Owen (1839) corrected Harlan's taxonomic mistake and properly identified the fossilized animals as marine mammals. Recently, many studies analyzing the biomechanics of swimming and feeding have used the modern cetaceans as suitable proxies for Mesozoic marine reptiles (Taylor, 1987; Massare, 1987, 1997; Budney, 2002). In addition to converging upon similar body plan, marine mammals have also converged upon the small number of tooth morphologies exhibited by Mesozoic marine reptiles (Massare, 1997).

In this study, morphological features of dentition of Late Cretaceous and Cenozoic marine vertebrate predators were analyzed using multivariate statistics. While Mesozoic marine reptiles and Cenozoic marine mammals show a surprising amount of morphological convergence, elasmobranchs (sharks and rays) display a wide, divergent array of morphological tooth types (Kent, 1994; Capetta, 1987). Although morphological tooth diversity among elasmobranchs is high during the Late Cretaceous, the greatest number of tooth designs are present throughout the Eocene.

Since tooth morphologies reflect dietary preferences, convergence among functionally homologous tooth types most likely indicates dietary convergences as well. Thus, by analyzing the species content of the occupied regions of the tooth morphospace we propose that it is possible to unravel guild structures, investigate cases of tooth convergence, and determine the overall expansion or contraction of feeding strategies among the marine vertebrate predators from the Late Cretaceous Period through the Cenozoic Era.

DENTITION IN MARINE VERTEBRATES

Late Cretaceous marine reptiles – Marine reptiles were the dominant predators of the Jurassic and Cretaceous seas. Large, mobile, fully pelagic, predatory groups include the orders Ichthyosauria, Sauropterygia (plesiosaurids and pliosaurids), and the family Mosasauridae. Although the basic dental crown design is a simple cone, many complex morphologies have arisen, including modified designs for piercing, crushing, cutting, and tearing (Peyer, 1968; Pollard, 1968; Massare, 1987). Most Mesozoic

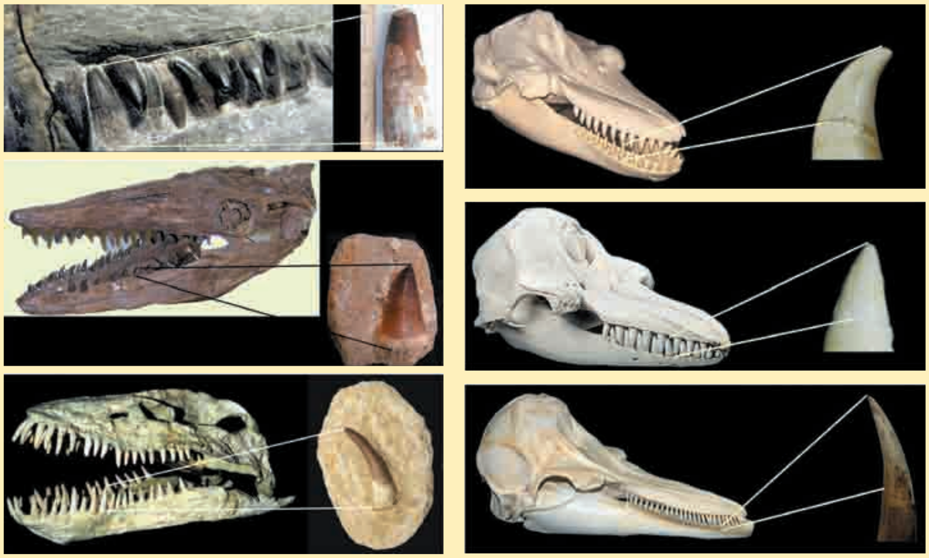

Figure 1: Selected skulls and dentitions of Late Cretaceous marine reptiles and Cenozoic marine mammals. Clockwise from upper-left: Ichthyosaurus; Killer Whale; False Killer Whale; Pacific White Sided Dolphin; the plesiosaur Thalassomedon*; the mosasaur* Tylosaurus.

marine reptiles have a homodont dentition (teeth of similar types), but in many cases, e.g., ichthyosaurs, homodonty is a derived character (Massare and Calloway, 1990).

Cetaceans and pinnipeds (Cenozoic marine mammals) – The predominant Cenozoic vertebrate predators belong to the mammalian orders Cetacea (whales, dolphins, and porpoises) and Pinnipedia (seals, sea-lions, and walruses). The first known cetaceans date to the early Eocene (Gingerich et al., 1983). Early whales, the protocetids and basilosaurids, had a heterodont dentition (teeth of different types). Molars are generally multi-cusped and have a more complicated form than premolars. The early cetaceans could use their dentition to shear and grind, as well as pierce and secure their prey (Fordyce, 1982). Later cetaceans, including the modern odontocetes (toothed whales, dolphins, and porpoises) have a homodont dentition. Some delphinids (oceanic whales and dolphins) have sharp, pointed, slender teeth that are used to pierce and secure their prey, while killer whales have sharp, robust teeth used not only for cutting flesh, but also for chopping and breaking bones (Massare, 1987).

The first known pinnipeds date to the latest Oligocene (Mitchell and Tedford, 1973; Barnes, 1979). Early members retain the dental features of their terrestrial carnivoran ancestors, namely well-defined carnassial teeth used to shear meat. Many later families have a modified dentition similar to that of the cetaceans; distal curving cusps, widely spaced cheek teeth, and similar molar and pre-molars. In some cases homodonty is present (Peyer, 1968; Hillson, 1986; Carroll, 1988).

Elasmobranchs (sharks and rays) – While the fossil record of sharks extends back into the Late Silurian, it was during the Late Devonian that a burst of evolutionary diversification occurred (Zangerl, 1981; Carroll, 1988). Paleozoic tooth forms are generally sharply pointed, with one or more cusps. This form of dentition provides an effective means for grasping and holding prey. During the later part of the Mesozoic and early Cenozoic, neoselachian (modern sharks, rays, and skates) squaliform, lamniform, and carchariniform shark groups developed a highly effective jaw mechanism that allowed these sharks to gouge and wrench large pieces from prey. Additionally, many neoselachians evolved sharp, blade-like teeth, often with serrated edges, which served to slice deep into the flesh of large fish and marine mammals. This allowed for predation on prey larger than the sharks themselves and opened up new feeding niches (Moss, 1977; Capetta, 1987; Vermeij, 1987).

While some groups of neoselachians developed formidable serrated blade-like teeth, other tooth morphologies also evolved, including teeth designed for tearing, clutching, and crushing. In general, neoselachian anterior teeth are sharper and narrower than the lateral teeth, upper teeth are relatively wide and slanted posteriorly, lower teeth are relatively narrow and straight (Moss, 1977; Capetta, 1987; Kent, 1994).

General vertebrate tooth types – Several schemes have been used to classify basic tooth designs in sharks (Peyer, 1968; Moss, 1977; Capetta, 1987; Kent, 1994), Mesozoic marine reptiles (Peyer, 1968; Massare, 1987, 1997), and marine mammals (Peyer, 1968; Hillson, 1986; Massare, 1987). Since this study involves all three vertebrate groups, a comprehensive classification scheme that accommodates each major tooth type was required. What follows is a hybrid tooth scheme based on the previous classifications referenced above (Figure 2).

Clutching – Teeth are generally small, with a low profile crown, typically surrounded by small cusplets. The enamaloid is frequently folded or ridged longitudinally, increasing the strength of the crown. Clutching dentition is used to restrain prey, as well as crush weakly armored prey.

Crushing/Grinding – Teeth generally have a high crown with a polygonal outline, or are robust with a bulging crown that is transversely streamlined. Typically individual teeth form a dental plate with a nearly planar surface, or functional rows. This form of dentition is used to fragment or smash open hard-shelled prey that typically inhabit benthic or near bottom settings.

Grasp/Crush/Chop – Teeth are usually conical and robust. Sometimes teeth bear fine longitudinal ridges. This type of dentition is used to puncture and restrain prey, as well as to smash and chop bones.

Pierce/Gouge – Teeth are smooth and pointed. Sometimes teeth are recurved. Teeth may be delicate and slender, or relatively robust. This dentition is used to pierce and grasp prey, or used to wrench out pieces of flesh.

Slicing/Gouge – Teeth are generally flattened labio-lingually or ellipsoid in cross-section. The crown may be serrated, or have cutting edges. Teeth function to slice and/or gouge the flesh of relatively large prey.

MATERIALS AND METHODS

Dental character data collected from Late

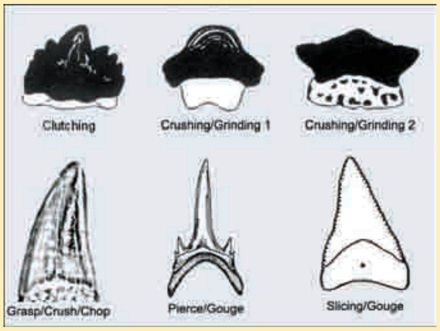

Figure 2: Representative tooth types found among predatory marine vertebrates. Note that there are two types of Crushing/Grinding teeth. Type 1 teeth have a robust, semi-rounded dental crown, while type 2 teeth have a polygonal outline and a relatively high dental crown.

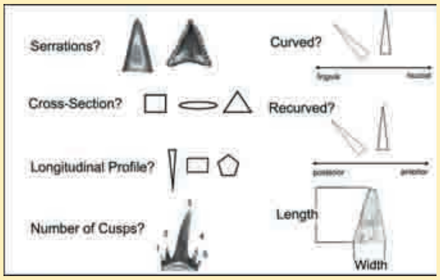

Figure 3: Examples of the characters used in the morphological analysis. In the figure all characters are discrete except length and width.

Cretaceous marine reptiles, Cenozoic marine mammals, and Late Cretaceous - Cenozoic elasmobranchs was were analyzed using PCA (Principal Component Analysis) because of the wide variety of tooth morphologies among marine vertebrate predators, morphological convergence and divergence. The eigenvectors generated from the analysis were used to construct a morphometric "tooth space." Analysis revealed that semi-discrete regions of the tooth morphospace are occupied predominantly by single tooth types. Since tooth morphology can be reasonably correlated to diet, the semi-discrete regions of occupied tooth morphospace can be used as proxies for feeding guilds (Moss, 1977; Capetta, 1987; Massare, 1987, 1997; Taylor, 1987).

Data Collection – The analysis included 39 species of Late Cretaceous sharks, 20 species of Paleocene sharks, 40 species of Eocene and Oligocene sharks, 20 species of Late Cretaceous marine reptiles, and 29 species of Cenozoic marine mammals (which represents all major Cenozoic tooth types). While the number of species used in the analysis is large, it is not comprehensive. However, all major tooth types for each major group were included.

The lack of homologous tooth morphology among the major groups analyzed required a combination of discrete as well as simple dimensional measurements. Dental characters utilized in the study included tooth length, width, cross-sectional outline, and longitudinal outline, the presence of serrations, number of lateral cusps, the presence of curvature and/or the presence of recurvature (Figure 3). Species included in the analysis were originally collected from Late Cretaceous and Cenozoic rocks located in the south-central, southeastern, and the mid-Atlantic United States, as well as Europe and the Pacific Rim. Specimens used in the study were obtained from the National Museum of Natural History and the North Carolina Museum of Natural Sciences.

Analysis of measurement data – A correlational PCA was performed using the program PC-ORD (McCune and Mefford, 1999). All characters were included in the PCA analyses, as were all species included in the study. A morphometric tooth space was constructed using the eigenvectors generated from the PCA of the dental data.

RESULTS

The first two eigenvectors of the analysis capture over 50% of the variance. The resulting morphometric tooth space is divided into semi-discrete regions defined by the resulting clusters of the following tooth types; clutching, piercing/gouge, crushing/grinding, slicing/gouge, and grasp/crush/chop (Figure 4). Figure 4 shows a sub-sample of the total number of species that occupy each semi-discrete region. In the figure, and the entire analysis, each tooth represents a single species, except in the case of the early whales. Here, due to heterodonty, both the canines and molars are used in the analysis.

Figure 5 shows occupation of the dental morphospace during the Late Cretaceous, Paleocene, Eocene, and Oligocene – Neogene. Color-shaded polygons represent the occupied region of the tooth morphospace by each group under analysis. In each case, the shaded polygons represent more-or-less evenly filled regions (i.e., the data points are not patchily distributed within the polygon). In each panel the region of morphospace occupied by Late Cretaceous marine reptiles is shown for comparison.

During the Late Cretaceous marine reptiles occupy a small, discrete region of morphospace. With the exception of a small region of the crushing/grinding morphospace, the Late Cretaceous marine reptiles solely occupy the grasp/crush/chop portion of morphospace. Conversely, Late Cretaceous sharks occupy a much greater portion of the tooth morphospace, nearly filling the crushing/grinding and piercing/gouging regions and substantially filling the clutching region. Only a few species occupy the slicing/gouge region, while none occupy the grasp/crush/chop region of morphospace.

During the Paleocene, sharks partly occupy the piercing/gouging, crushing/grinding, and slicing/gouge regions of the tooth morphospace. Throughout the remainder of the Paleogene and during the Neogene a profusion of shark tooth morphologies evolved. Partial occupation of the clutching, pierce/gouge, and crushing/grinding regions occurred, while the slicing/gouge region of morphospace was nearly totally occupied. As in the Late Cretaceous, Paleogene and Neogene sharks failed to occupy the grasp/crush/chop region of morphospace.

Eocene marine mammals consist solely of two groups of cetaceans, basilosaurids and protocetids. Together the two groups occupy the grasp/crush/chop and slicing/gouge region of morphospace. These early cetaceans essentially had a dual dentition, posterior teeth designed to slice and shear, anterior teeth capable of grasping and restraining prey. From the Oligocene onward through the Neogene a burst of marine mammal evolution occurred. In addition to the first odontocetes, pinnipeds also appeared. A significant shift occurred in the occupied regions of the tooth morpho-

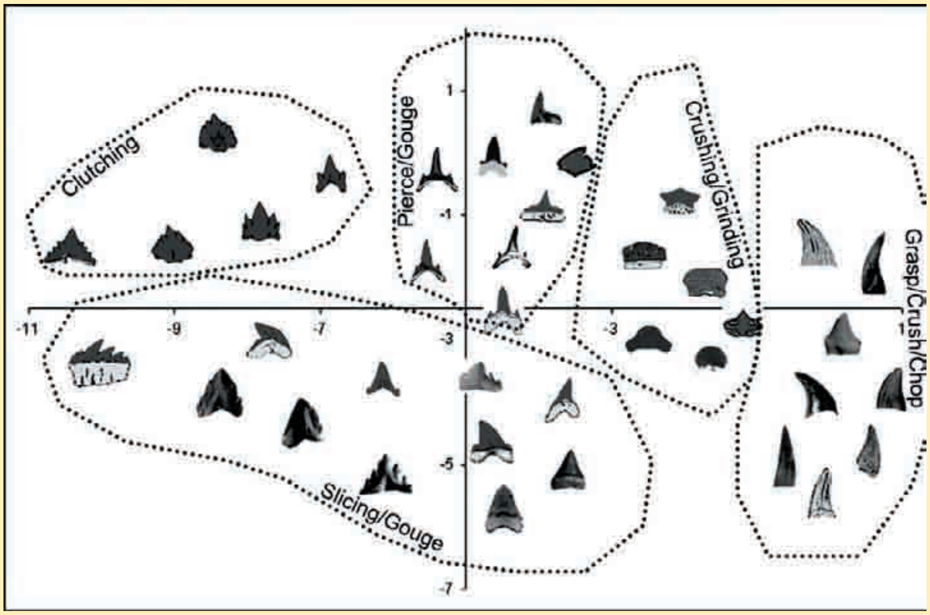

Figure 4: The "tooth" morphospace based on the first two principal eigenvectors generated from the PCA analysis. Semi-discrete regions occupied by specific tooth types are labeled. A sub-sample of the total number of species that occupy each semi-discrete region is shown (each tooth shown represents a single species).

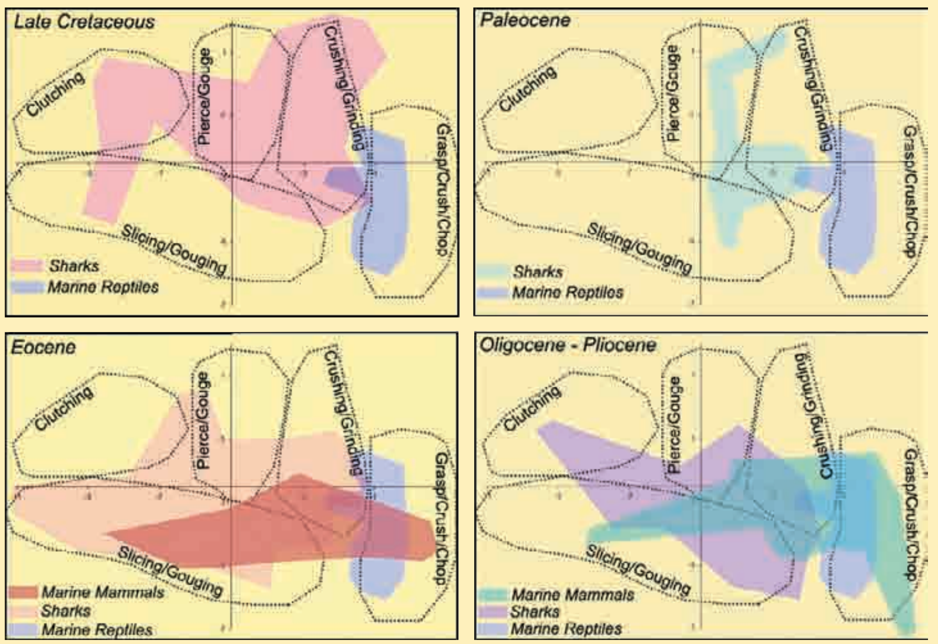

Figure 5: Occupation of the tooth morphospace during the Late Cretaceous, Paleocene, Eocene, Oligocene – Pliocene. Color shaded polygons represent the amount of morphospace occupied by each indicated group. In each panel the shaded portion of tooth morphospace occupied by the Late Cretaceous marine reptiles is shown for comparison.

space. During the Neogene marine mammals nearly fill the grasp/crush/chop region of morphospace, and almost completely overlap the region of space previously occupied by the Late Cretaceous marine reptiles.

DISCUSSION

Analysis of the tooth morphospace points to two phenomena. First, during the Cenozoic a profusion of shark tooth morphologies evolved, yet there is little overlap with the vacated Late Cretaceous marine reptile tooth morphospace. Second, with the evolution of marine mammals in the Cenozoic many tooth forms converged on the previously occupied Late Cretaceous marine reptile tooth morphospace. If dental morphologies are an indicator of dietary niches, than Cenozoic sharks failed to occupy the niches vacated by the marine reptiles, while Cenozoic marine mammals nearly completely occupied the vacated niches. This is clearly not a case of competitive exclusion. There is nearly a 10 million year gap between the extinction of the Late Cretaceous and the evolution of the Cenozoic marine mammals.

Jaw morphology and anatomy may partially explain the failure of sharks to occupy the grasp/crush/chop dietary niche. Paleozoic shark feeding mechanisms featured terminal mouths coupled with a grasping cladodont dentition characterized by a wide tooth base, a large central cusp and a variable number of lateral cusps. Subsequent modification of the jaw and dentition throughout the late Paleozoic and Mesozoic included a relative shortening of the jaws, a modification of the braincase and jaw structure allowing the upper jaw to move freely, and a modified hyomandibular bone which allowed the upper and lower jaws to be raised and lowered relative to the braincase resulting in movement fore and aft (Moss, 1977; Carroll, 1988). Sharks were able to feed on large prey by forcing their jaws into the body and gouging out pieces. Accompanying this new jaw design were blade-like teeth modified to slice. Many of the large sharks also developed serrated dentition, which became much more common during the Cenozoic, perhaps in response to the evolution of marine mammals. Flexible jaws, serrated blade-like, or sharply pointed teeth, allowed sharks to feed by wrenching and gouging the flesh of their "fleshy" marine mammalian prey. Thus, the dentition of many Cenozoic sharks, particularly the squaliform, lamniform, and carchariniform groups, may have been shaped more by anatomy than by ecology.

Morphological innovation among Cenozoic marine mammals was undoubtedly constrained by fluid mechanics, as were their distant reptilian "cousins." The shape of the head determines the drag exerted by surrounding water during sideways sweep. In order to minimize resistance, the cross-sectional area of the head must kept to a minimum, especially near the anterior end. This yields a slender profile that is dorso-ventrally compressed. Yet, the jaws must be robust enough to capture and restrain prey. Together this trade-off leads to the familiar shape of both the Cenozoic marine mammal and Late Cretaceous marine reptile head profile (Figure 1) (Moss, 1977; Massare, 1987; Taylor, 1987).

Prey acquisition is another important aspect of living in a fully marine environment. Plesiosaurs, ichthyosaurs, mosasaurs, cetaceans, and most pinnipeds fed on pelagic prey. In order to capture, restrain, and reduce prey to edible pieces, caniniform (conical, and usually recurved) dentition is optimal (Taylor, 1987). Size and girth of the caniniform tooth depends on the prey preference of the predator. Many dolphins and plesiosaurs have slender, pointed teeth suitable for piercing fish, while killer whales, some ichthyosaurs, and mosasaurs have robust, sharp teeth for seizing and chopping the bones of there marine tetrapod prey (Massare, 1987).

Perhaps the most remarkable aspect of tooth convergence among marine reptiles and marine mammals is the "switch" from heterodonty to homodonty. Many Early Triassic ichthyosaurs, such as *Mixosaurus*, *Grippia*, and *Phalarodon* had heterodont dentitions. By the Middle Triassic many ichthyosaurs had homodont dentitions, a trend that continued throughout the Jurassic and Cretaceous. Likewise, protocetid and basilosaurid whales during the Paleogene had heterodont dentitions. By the Miocene most toothed cetaceans had homodont dentitions (Massare, 1987, 1997).

CONCLUSIONS

While this study represents a preliminary look at the functional and dietary convergence among major marine vertebrate predators, several results stand out. For the most part, the dentition of Late Cretaceous sharks failed to converge on the tooth morphologies exhibited by Mesozoic marine reptiles. Following the extinction of the Late Cretaceous marine reptiles, Cenozoic sharks once again failed to converge on the reptilian tooth morphologies, despite a considerable evolutionary radiation. Conversely, the evolutionary radiation of marine mammals produced numerous cases of dentition that converged on the Mesozoic marine reptile tooth morphologies.

The failure of shark dentition to converge on the tooth morphologies exhibited by Late Cretaceous marine reptiles may be due more to anatomical constraints imposed by jaw structure than by ecological considerations. Alternatively, the convergence of marine mammal dentition on that of Late Cretaceous marine reptile tooth morphologies may be due to selective pressures involving ecological and biomechanical constraints.

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DIRECTOR'S CHAIR

Society Records

Along with the usual content in The Sedimentary Record this month, you will also find an Appendix. The appendix is a copy of the official Society Records and Annual Report for 2005. This information has previously been printed in the *Journal of Sedimentary Research* but will from now on be part of The Sedimentary Record, where it is a much better content fit and where we can make sure that it is received by all of our members, rather than only those that take JSR. The Society Records will also be posted online along with the digital version of The Sedimentary Record.

The Society Records include a summary report on the activities of the Society for 2005, including notes from the Annual Meeting, new publications, research conferences and miscellaneous information pertinent to 2005. We also include the full biographies and responses of the SEPM Awardees for 2005 along with their pictures. The audited financial statements are also there, although they come from the prior year due to the time it takes to complete the audit. Also included are the basic statistics on membership. As we continue to modify The Sedimentary Record to the membership needs, please do not hesitate to contact me with your thoughts about it.

Online Journal Tips

The Society has given all of its members online access to both journals for the last part of this year so that everyone can become better acquainted with the ins and outs of online searching and browsing at the GSW supplied member access sites for PALAIOS and Journal of Sedimentary Research. In 2006, everyone will have online access as part of the basic subscription to either of the journals or both as you have chosen. With this access now setup, I wanted to share some tips on how you can maximize it to your benefit.

The first tip is to how to setup email Alerts. These alerts will notify you at an email address of your choice when a new issue of a journal has been loaded and its Table of Contents is now available or when articles that meet your search criteria have been uploaded. First go to www.geoscienceworld.org. Setting up alerts is an open access process, you do not have to login through your SEPM member access link. Next click on the "Register" link in the upper right hand area (if you have not previously registered – not the same as your member user id and password). Here you can set up a name and password and then you are registered. GSW will assign you a registration number such as REG#### in case you need to correspond with them online. Once registered, go to "My GSW Alerts", there you can follow the directions to set up alerts for tables of contents, awareness and journal announcements. You can also set up CiteTract Alerts, which will send you email when new papers with certain search criteria (authors, key words, etc.) arrive at JSR or PALAIOS or any of the other GSW journals (if indicated).

I hope that these couple of tips will help you get more out of your online experience with JSR and PALAIOS.

Howard E. Harper, Executive Director