TOOTH MORPHOLOGY AND PREY PREFERENCE OF MESOZOIC MARINE REPTILES

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ABSTRACT—The large reptilian marine predators of the Mesozoic preyed upon pelagic animals such as bony fish, sharks, soft cephalopods, belemnoids, ammonoids, and even each other. All had undifferentiated conical teeth of one of several forms ranging from a blunt, bulbous shape to a slender, sharply pointed cone, to a robust, slightly compressed cone with two distinct cutting edges. Tooth form, along with tooth wear and occasionally preserved stomach contents, suggests the preferred prey of each species.

Seven somewhat overlapping predator types, or guilds, can be defined on the basis of tooth form and prey preference. Members of each guild have tooth morphologies which fall within a defined range, and thus they probably shared the same preferred prey. The guilds present in six well-preserved faunas of the Jurassic and Cretaceous illustrate the structure of and changes in the large marine predator adaptive zone. Six guilds co-existed for most of the Jurassic. Although the composition of some of the guilds changed in the Middle Jurassic, the kinds and number of guilds remained constant. Sometime before the Late Cretaceous, however, there was a major reorganization of the large marine predator adaptive zone resulting in a reduction in the number of reptilian guilds to three. Although the number of guilds increased in the later part of the Late Cretaceous, reptilian predators never attained their earlier diversity before the Cretaceous-Tertiary extinction ended their reign as the dominant large marine predators.

INTRODUCTION

The dominant large marine predators of the Jurassic and Cretaceous were from four reptilian orders: ichthyosaurs of the Order Ichthyosauria, the plesiosauroids and pliosauroids of the Order Sauropterygia (Suborder Plesiosauria), the metriorhynchids and teleosaurs of the Order Crocodylia, and the mosasaurs of the Order Squamata. Although they were quite distinct osteologically, there were some remarkable parallels in overall body proportions and in tooth morphologies among these groups. This paper focuses on the similarities in tooth forms and what they may reveal about the partitioning of available food resources, the prey, among the co-existing predators.

Although quite different in appearances, most of the marine reptiles probably ate pelagic prey as do most modern marine mammals, capturing their prey from the water column rather than from the sea floor. Like modern toothed whales, they had more or less homodont dentitions, and probably used their teeth to seize prey and manipulate it into the right position to be swallowed. Teeth were not used to masticate the prey, but instead, the prey was swallowed whole. Therefore, most reptiles probably ate prey much smaller than they were (Williston, 1914:90, 159). They could choose from a variety of pelagic animals: ammonoids, belemnoids and other soft cephalopods, bony fish including armored holostean fish, sharks, and, of course, other marine reptiles. Thus the marine reptiles filled a very specific adaptive zone: that of large, mobile, pelagic

predators of macroscopic prey. Today, this adaptive zone is filled by toothed whales, seals and sea lions.

The constraints on the kind of prey consumed were the size of the reptile's gullet and the kind of prey the teeth could handle. Some kinds of teeth are used for crushing, other kinds are used for piercing and still others are used for cutting or tearing. These functions are reflected in the tooth shape. The general shape of the crown suggests qualitative differences in the diets of these diverse groups of reptiles. There may have been some temporal fluctuations in the availability of specific prey in the Mesozoic, as there are today. Prey preference, therefore, cannot be thought of in terms of specific species (or even families or orders) being consumed. Nonetheless, some prey must be crushed, other kinds must be pierced, to be caught. So the tooth shape and inferred function suggest at least the broad category of prey types that the predator could handle: whether the prey had hard external armor or shell, whether it was very soft with practically no hard parts, or whether it was fleshy with large bones.

TOOTH FORM OF MODERN LARGE MARINE PREDATORS

The teeth of some modern marine predators show features similar to those found in reptile teeth, and we have a better, although by no means thorough, understanding of their prey. Thus they provide useful analogies in explaining the form and function of marine reptile teeth.
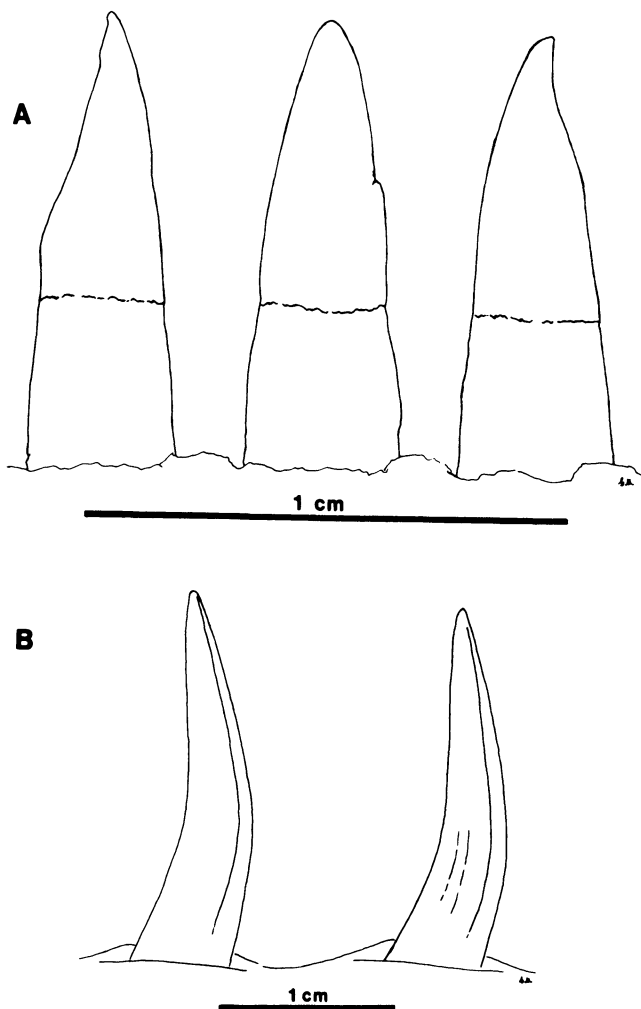
FIGURE 1. A, teeth of a spotted dolphin, *Stenella attenuata* (USNM 395332), are shown here in buccal view of the lower jaw. The teeth curve inward (out of page) slightly. Two teeth show wear, presumably from abrasion with opposing tooth in the upper jaw. The basal cross-section is circular. **B**, teeth of a gavial (*Gavialis gangeticus*) in lateral view. Note the slender shape and pointed apex. Both of these modern predators are piscivorous, and capture their prey by piercing it on a long row of pointed teeth.

The river dolphins (Family Platanistidae) are exclusively fish eaters (Slijper, 1976:93), as are many dolphins of the family Delphinidae (Gaskin, 1982:33, 37). Their tooth crowns are typically like that of the spotted dolphin (Fig. 1A). They have undifferentiated, slender, pointed teeth. A fish is caught by piercing it on the long row of sharp teeth. Commonly one side of the tooth has a wear facet from abrasion with the corresponding tooth in the opposing row. Whether by accident or design, this serves to maintain a sharp point. Another modern, exclusively piscivorous predator is the gavial (Guggisberg, 1972), a crocodile of the large rivers of the Indian subcontinent. Its teeth are also slender cones with sharply pointed apices (Fig. 1B) They differ in being slightly compressed with two dis-

tinct carinae, and in being more recurved. The recurved shape may aid in maneuvering the fish back towards the gullet. The shared features, however, suggest a specific tooth morphology for piercing fish: slender shape, moderate size and a pointed apex.

The sperm whale, which preys mainly upon squid and cuttlefish (Gaskin, 1982:35–36; Matthews, 1978: 70–71; Slijper, 1976:97), has a different tooth crown morphology. It has functional teeth only in its lower jaw. They are simple cones with acute but rounded tips (Fig. 2, left two teeth). On worn teeth, the crown apex can be very blunt and is frequently polished (Fig. 2, right two teeth). Beaked whales (Family Ziphiidae) also feed on soft prey, being exclusively squid eaters (Gaskin, 1982:35–36; Slijper, 1976:93). Most lack teeth entirely, or have only a single tooth in the lower jaw. These examples suggest that the tooth of a squid eater, if present at all, need not be sharp or long to pierce the soft prey, but need only grasp the prey to capture it.

Killer whales have yet another kind of tooth. They are at the end of the modern marine food chain, feeding on dolphins, seals, and birds (Slijper, 1976:92–94; Matthews, 1978:72), as well as fish and squid when the opportunity presents itself (Gaskin, 1982:30–32). Generally, the prey is swallowed whole, although killer whales have been known to tear flesh from larger baleen whales (Gaskin, 1982:32; Matthews, 1978:73; Slijper, 1976:92). Killer whale teeth are sharp, for cutting into fleshy prey, but robust to reduce breakage by the large bones of their prey (Fig. 3). Tooth wear is distinctive and common: the apex is frequently broken, often at an oblique angle, and the break is rounded and polished. One can speculate that the teeth break against the large bones of the prey, or from a vigorous fight with it, and then the break is smoothed by abrasion with bones. This kind of tooth form and wear is distinct from that of dolphins and sperm whales.
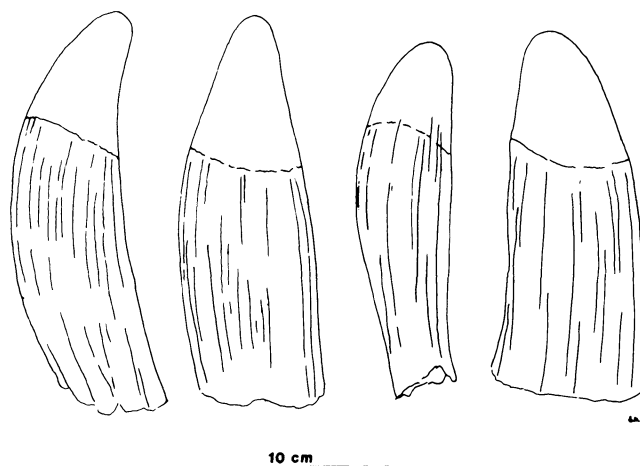
Another tooth form is found in modern walruses.

FIGURE 2. The two left figures show different views of two sperm whale teeth, *Physeter macrocephalus* (USNM 234358). Note the rounded, not pointed, apices. The two right figures show the same views of worn teeth, with more blunt and polished apices.

Although walruses are best known for their long tusks, their other teeth, used for processing food, are equally distinctive. They are short cylindrical pegs, wider than they are high, and are used for crushing oysters and clams (Walker, 1975). Thus, as one would expect, teeth used on prey with hard external shells (or skeletons) are very blunt and robust to avoid breakage.

These modern pelagic predators illustrate four types of teeth that have counterparts in the Mesozoic marine reptiles: (1) pointed, slender teeth for piercing fish, (2) somewhat blunt teeth for grasping squid and other soft cephalopods, (3) pointed, robust cutting teeth for feeding on large marine vertebrates, and (4) blunt, robust teeth for crushing prey with a hard exterior. These forms suggest several features of tooth morphology that may be of functional significance.

Apex shape: The apices of teeth used to pierce fish are pointed. The pointed apex probably facilitates penetration and might also, coupled with a slender shape, permit teeth to slide in between bones thus reducing resistance and tooth breakage. Teeth used to seize squid, on the other hand, are not pointed, and some squid eaters lack teeth entirely. The latter suggests that the force of the closing jaw kills the prey, not the penetration by the teeth. The internal pen of a squid or shell of a cuttlefish may provide enough resistance to penetration that sharply pointed teeth would become dull. Thus the apex shape may distinguish between piercing teeth, where the prey is killed by the penetration of the teeth, and grasping teeth, where the prey is killed by being squashed between the jaws.

Tooth wear: The tooth wear of killer whales may characterize higher order, opportunistic predators. The oblique break and subsequent abrasion, and the frequency of such wear, may be related to the ability to seize large, active marine vertebrates whose large bones could cause tooth breakage and abrasion. Worn sperm whale teeth show rounding of the apex rather than breakage. Perhaps the internal pen or shell of soft cephalopods presents enough resistance to dull the teeth, but not enough to break them.

Tooth size: The absence of teeth among the beaked whales suggests that squid eaters need not have large teeth, probably related to squashing the prey rather than piercing it. Teeth used to penetrate the prey, on the other hand, are moderate to large relative to the gullet size. If gullet width is measured as the distance between the jaw articulations, the crown height/gullet width ratio ranges from 0.14 (spotted dolphin) to 0.18 (gavial) to 0.30 (killer whale).

With these features in mind, the tooth forms of Mesozoic marine reptiles will be examined.

TOOTH FORM IN MESOZOIC MARINE REPTILES

The range of tooth crown morphologies among Mesozoic marine reptiles was at least as great as that of
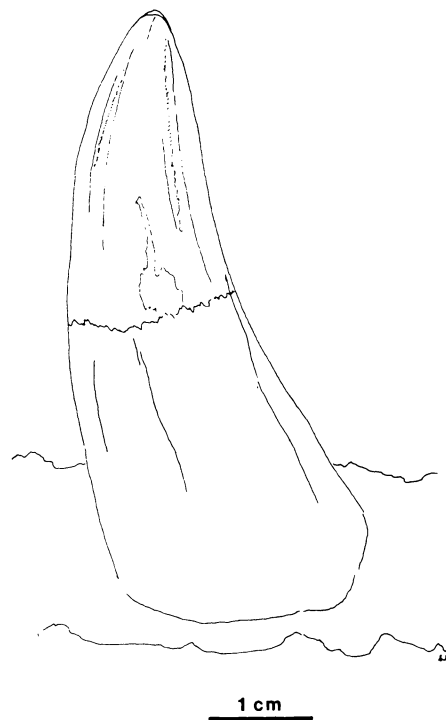

FIGURE 3. Tooth of a killer whale, *Orcinus orca* (USNM 16625), showing a fairly sharp apex and a robust shape. Teeth are often broken: 6 of 14 examined on one side of the jaw of USNM 11980 were broken, and the breaks were rounded and polished.

modern marine mammals. Eight distinct tooth forms are present in the ichthyosaurs, plesiosaurs, marine crocodiles, and mosasaurs that shared Jurassic and Cretaceous seas. These forms transcend taxonomic boundaries for the most part. Many tooth forms are found in two or more reptilian groups, and each group contains representatives of more than a single tooth morphology. The descriptions that follow refer to characteristic teeth of the anterior and middle jaw, used for seizing and manipulating the prey. Many reptiles have smaller, more robust teeth in the posterior region of the jaw.

The teeth of many plesiosauroids, such as *Plesiosaurus dolichodierus, P. brachypterygius, Muraenosaurus leedsi,* and *Cryptoclidus eurymerus,* are very long, slender cones with sharply pointed apices (Fig. 4; Brown, 1981, figs. 5, 19, 24, 39; Andrews, 1910; Owen, 1840–45). The ratio of the crown height to the basal diameter is usually greater than 3.5, and never less than 3.0. In many Jurassic plesiosauroid teeth, the apex of the crown is slightly compressed, resulting in two distinct, fairly sharp carinae at the tip. The cross-section is circular for most of the length of the tooth, however. Often there are thin, sharp, low longitudinal ridges, the exact pattern of which can be used for genus or species identification (Brown, 1981). These teeth are very large with respect to the size of the gullet, with
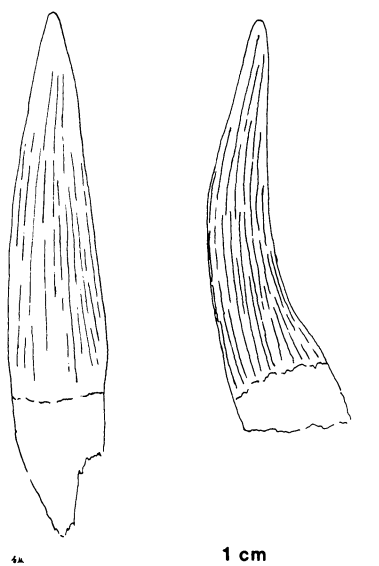
FIGURE 4. Piercing tooth of a Lower Liassic plesiosauroid, *Plesiosaurus dolichodeirus,* teeth drawn from BMNH 39490 in ?lingual and lateral views. The tip is slightly compressed in a lingual-buccal direction, but most of the crown has a circular cross-section. The thin longitudinal ridges are sharp.

ratios of tooth height to skull width greater than 0.3. These teeth rarely show wear (Brown, 1981; and pers. obs.). This, coupled with the pointed apex, suggests that they were probably used to pierce soft prey. This type of tooth is also found in ichthyosaurs, in which it is not quite as large and lacks the compressed tip, but is still sharply pointed and slender. Unlike the plesiosauroid teeth, ichthyosaur teeth are usually smooth, although the roots are frequently fluted. This form is found in many of the large, long-snouted ichthyosaurs such as *Eurhinosaurus longirostris* and *Ichthyosaurus tenuirostris.*

A second tooth type is found in the metriorhynchids (Fig. 5), some teleosaurs, and a few slender-toothed mosasaurs (e.g. *Ectenosaurus*). It is a smooth, slender, buccal-lingually compressed cone with two distinct carinae, which can form sharp cutting edges. The carinae are oriented parallel to the length of the jaw, unlike those of the modern gavial. The apex is pointed. The crown height/skull width ratio ranges from 0.15 to 0.25. Longitudinal sculpture is frequently present, especially in the crocodiles, in the form of low, rounded, irregular ridges that are very subdued and produce a rough surface texture, rather than distinct longitudinal ridges as in the previous tooth form. The height/diameter ratio of the crown varies from 2.0 to 3.0. This is also probably a piercing tooth, although it would have made an incision rather than a simple puncture. A similar form occurs in some teleosaurs, but the carinae are absent. These forms probably pierced slightly harder or bonier prey than the previous one because they are not as delicate or slender. Occasionally the tip of the tooth is broken (perpendicular to the long axis)

and smoothed. Again this suggests slightly harder or bonier prey than that of the previous form.

The third type of tooth crown is found in many ichthyosaurs, especially those of the genus *Stenopterygius,* and is probably the most common tooth form among the small (<3 m) ichthyosaurs. I have not seen it in any other marine reptile group. It is a fairly straight, simple cone with an acute but rounded apex (Fig. 6). The cross-section is circular. Usually, there are narrow grooves that extend from the base of the crown to about $\frac{2}{3}$ to $\frac{3}{4}$ of the way to the apex and delineate low, rounded ridges that get narrower towards the apex. These grooves often continue into the roots as major infolding producing the fluting on the root. The height/diameter ratio of the crown ranges from 2.0 to 3.0. Keller (1976) described the preserved stomach contents of a number of *Stenopterygius* species as consisting of cephalopod hooklets, although a few fish remains and even bits of wood were found in rare cases. Pollard's (1968) examination of some small *Ichthyosaurus* specimens indicates that they fed on dibranchiate cephalopods, probably phragmoteuthids. Previously, some gut content material had been identified as belemnoid hooklets, but this was based on forged specimens: phragmoteuthids to which belemnite guards had been attached (Donovan, 1977; Reigraf and Reitner, 1979). No belemnoid material has yet been found in ichthyosaurs, although if the rostra had been bitten off and had fallen to the bottom, there would be no hard
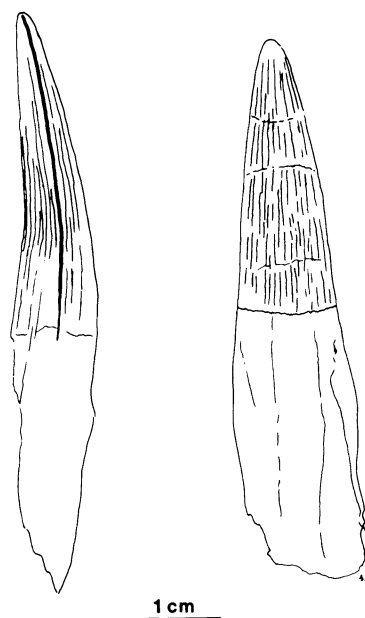

FIGURE 5. Two teeth of a Callovian metriorhynchid, *Metiorhynchus cultridens* (BMNH 3804), drawn in lateral and buccal views, show a typical piercing tooth. The very sharp carinae form cutting edges that are oriented along the jaw line. Longitudinal striations are low, irregular, and rounded, producing a rough surface texture, but not producing distinct ridges as in the previous tooth form (Fig. 4). The tooth is slightly compressed in a lingual-buccal direction.

124

parts in the ichthyosaur's stomach to be preserved! On worn teeth, the apex is more rounded and polished, suggestive of the kind of wear seen on sperm whale teeth. These teeth are small, with a height/skull width ratio always less than 0.15, and often less than 0.10. In fact, at least one ichthyosaur species, *Stenopterygius quadriscissus,* had reduced dentition or was edentulous as an adult (McGowan, 1979). The small size is in keeping with the general trend in modern predators on squid and cuttlefish. The size, kind of wear, and the apex shape suggest a grasping rather than a piercing function for this tooth form.

A fourth tooth form is found in some moderately large ichthyosaur species (*Ichthyosaurus communis, Temnodontosaurus risor,* and *Leptopterygius disinteger*), as well as some teleosaurs (*Steneosaurus obtusidens* and *Machimosaurus hugii*) and metriorhynchids (*Metriorhynchus superciliosum*). It is a straight, robust cone with a blunt tip and a circular cross-section (Fig. 7). The crown height/diameter ratio varies from 2.0 to 3.0. The apex of the crown has a rough surface of very small raised bumps. This roughness can continue for the whole tooth, or there may be longitudinal grooves or rounded ridges for up to ¾ of the crown length. One or more ridges may be more prominent than the rest,
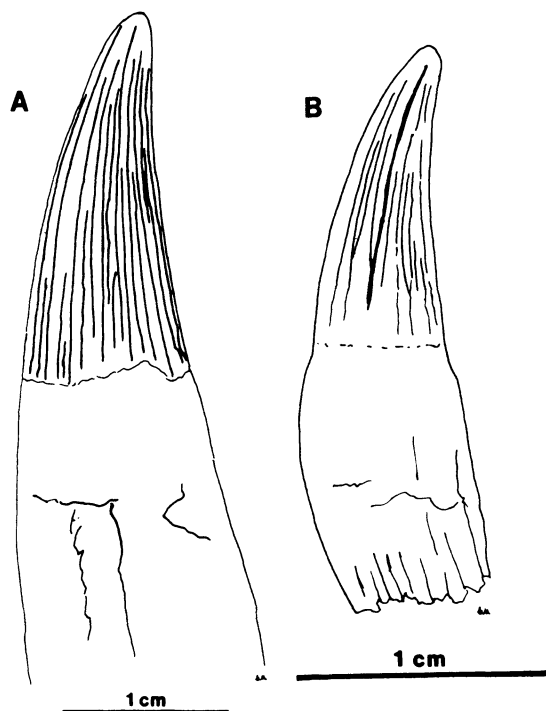
FIGURE 6. A, *Platypterygius campylodon* (Early Cretaceous ichthyosaur); the tooth (BMNH 47235) is small, with an acute, but rounded apex. Longitudinal grooves (dark lines) delininate low, rounded ridges which extend almost to the apex. The cross-section is circular. B, this tooth of *Ophthalmosaurus icenicus* (BMNH R2150), a Callovian ichthyosaur, gives another example of a smashing tooth morphology. The longitudinal sculpture is less continuous and the grooves are less pronounced. The cross-section is circular.
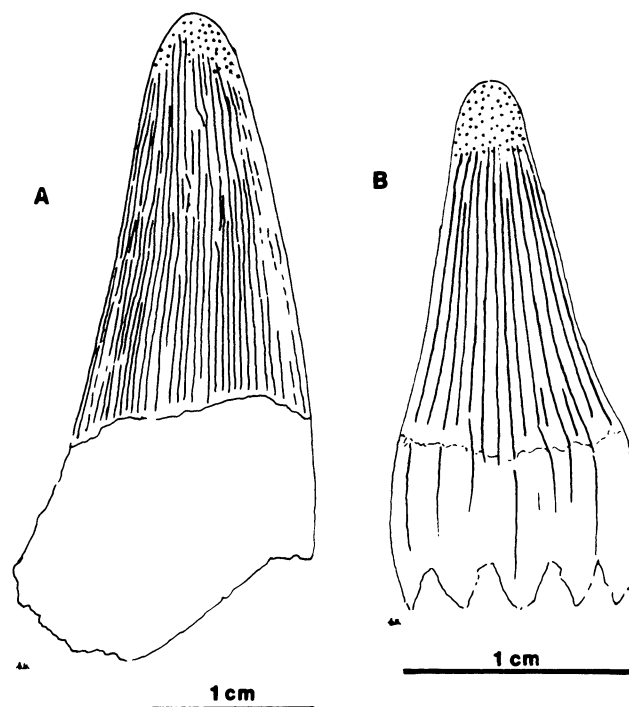
FIGURE 7. A, the crunching tooth of *Steneosaurus obtusidens* (BMNH R3168), a Callovian teleosaur, is fairly robust with a blunt tip. The apex has a rough surface of raised bumps. Fine longitudinal ridges extend from the base of the crown almost to the apex, often becoming more discontinuous towards the apex. B, a similar morphology occurs in YPM 1656, an upper Liassic ichthyosaur. The longitudinal sculpture is produced by longitudinal grooves (dark lines), which delineate low, rounded ridges that become narrower towards the apex. Again, the blunt apex has a rough surface on unworn teeth.

but they never form sharp cutting edges. Worn teeth on the ichthyosaurs tend to have a polished or pitted apex rather than the rough surface, suggesting abrasion with hard prey. The tooth crown height relative to the skull width is usually less than 0.15, suggesting a grasping rather than a piercing function. Stomach contents of two *Ichthyosaurus communis* specimens consist of a mass of *Pholidophorus* fish scales (Buckland, 1858: 188–190) and a sparse scattering of cephalopod hooklets (Pollard, 1968). Two other small *I. communis* specimens have densely packed cephalopod hooklets preserved within the rib cage (Pollard, 1968). The latter two specimens are likely juveniles, because of their small size, and probably have more slender, pointed teeth than the adults of the species. The blunt apex and tooth wear suggest that this tooth form was used for grasping prey with a hard exterior, possibly armored holostean fish or even thin-shelled ammonites.

The fifth tooth form is found in Early Jurassic pliosauroids such as *Rhomaleosaurus victor,* and in some Cretaceous plesiosauroids and pliosauroids. It is a recurved cone with fine longitudinal ridges and a circular cross-section (Fig. 8). The longitudinal ridges are folds

FIGURE 8. The tooth crowns of the Lower Liassic plio-sauroid, *Rhomaleosaurus victor* (BMNH 40094?) were fairly pointed and strongly curved (inward). The fine longitudinal ridges were fairly continuous and sharp, but did not reach all the way to the apex. The basal and apical cross-sections were approximately circular.
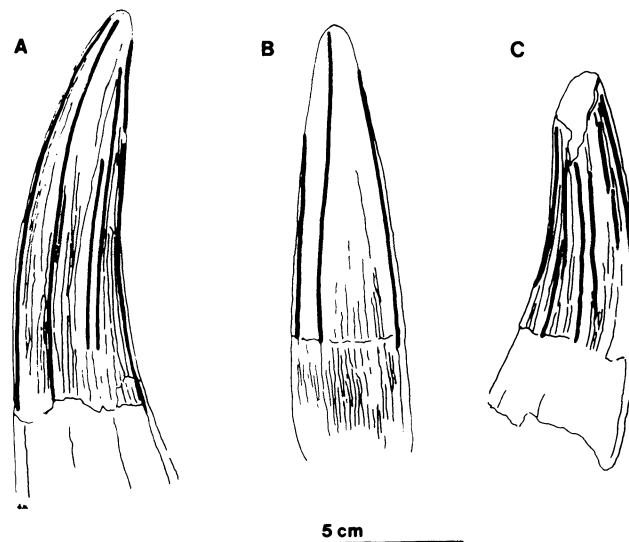

FIGURE 9. The tooth of *Liopleurodon ferox*, a Callovian pliosauroid, is shown here in lateral (A) and lingual (B) views (drawn from BMNH 3536). It has coarse longitudinal ridges (heavy lines), triangular in cross-section and very sharp. The ridges are more closely spaced on the buccal (concave) side of the tooth. The less prominent longitudinal striations give the surface between the ridges a rough texture but they are not sharp ridges themselves. C, (BMNH 5796) shows the characterisic wear; a large part of the apex is broken, and the edges and top surface of this break are rounded and polished.
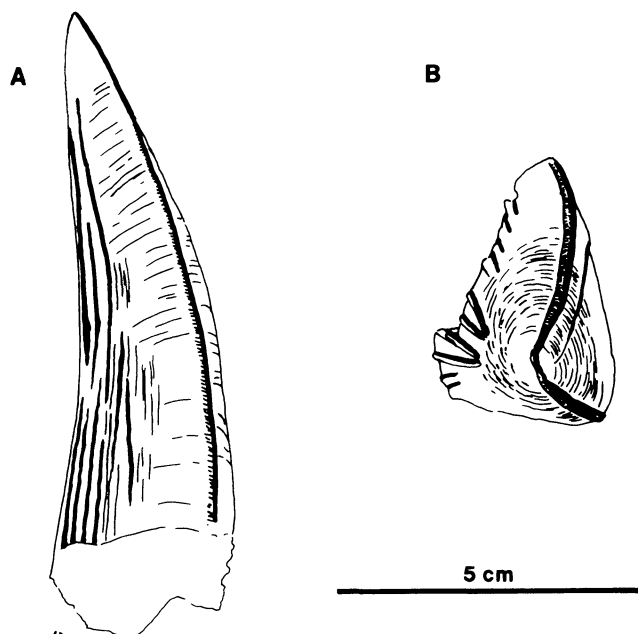
in the enamel that do not extend into the dentine as seems to be characteristic of teeth of the Plesiosauria (Owen, 1840–45). They are not coarse enough to serve as cutting edges. The tip is fairly pointed, but is round-ed on worn teeth. This form is of moderate size (crown height/skull width of 0.15–0.25), and neither particu-larly slender nor really robust (height/diameter usually 2.0–3.0, rarely as high as 3.5). The size suggests a pierc-ing function, but the wear is more like that seen on sperm whale teeth. It perhaps indicates a somewhat generalized diet of fish, soft cephalopods, and/or bel-emnoids.

A sixth tooth form is found in the large pliosauroids of the late Middle and Late Jurassic, such as *Liopleu-rodon ferox* and *Pliosaurus andrewsi*. It has a height/diameter ratio of 2.0–3.0, and is slightly recurved with coarse longitudinal ridges (Fig. 9). A few of these ridges reach the crown apex, giving the tooth a carinate tip which is quite sharp even though it does not look very pointed. The ridges themselves are triangular in cross-section and are sharp. On *Liopleurodon ferox* there are fine, transverse ribs on the ridges, producing an essen-tially serrated edge. These longitudinal ridges are prob-ably cutting edges, presumably used for tearing fleshy prey. The cross-section of the tooth is roughly circular for the length of the crown. Tooth wear is common in some species (Andrews, 1913; and pers. obs.). The teeth are frequently broken, and the break is rounded and polished (Fig. 9C; Andrews, 1913). Often the break cuts obliquely across the tooth, and removes a consid-erable portion of it. This wear is similar to that seen

FIGURE 10. Tooth of a Kimmeridgian pliosaur, *Pliosau-rus brachydeirus* (BMNH 1681), shown here in lateral view (A). A slightly off-center top view (B) shows the two prom-inent ridges that served as cutting edges (drawn from YPM 537). Coarse longitudinal ridges are confined to the buccal (concave) side. The cross-section is sub-triangular.

126

in killer whale teeth, further suggesting a diet of fleshy prey with fairly large bones, such as very large fish and other reptiles. In the Late Jurassic pliosauroids, this tooth form was modified (Fig. 10); the circular cross-section became sub-triangular, with the planar face of the crown towards the outside of the mouth. The planar face lacks most longitudinal sculpture, except for a single ridge at each end of the face. This makes two cutting edges more pronounced. The inner part of the tooth still has longitudinal ridges and is convex. This form approaches that of the seventh type. The only stomach contents are known from a Late Jurassic plio-sauroid, *Pliosaurus brachyspondylus,* consisting of some cephalopod hooklets (Tarlo, 1959a). This is not consistent with the form and wear of the tooth crown, and perhaps indicates that these pliosauroids were opportunistic predators like modern killer whales.

The seventh tooth form is found in the large ich-thyosaurs *Temnodontosaurus platyodon, T. eury-cephalus,* and *Leptopterygius acutirostris.* It is a slightly compressed, robust cone with two distinct, sharp ca-rinae that probably served as cutting edges (Fig. 11). These edges were aligned parallel to the length of the jaw. Unlike most ichthyosaur teeth, the crown surface is fairly smooth in spite of the strongly fluted root. There are slightly developed low ridges that divide the crown into flattened facets (Owen, 1840–45). These are most distinct towards the base of the crown. The height/diameter ratio of the crown ranges from 1.5 to 2.5. Ichthyosaurs with this type of tooth frequently show tooth breakage. The apex is broken and the break is rounded and polished. A specimen of *Leptopterygius acutirostris* has been found with the remains of another ichthyosaur in its stomach (R. Wild, pers. comm.). Most mosasaurs also have this tooth form (Fig. 12),
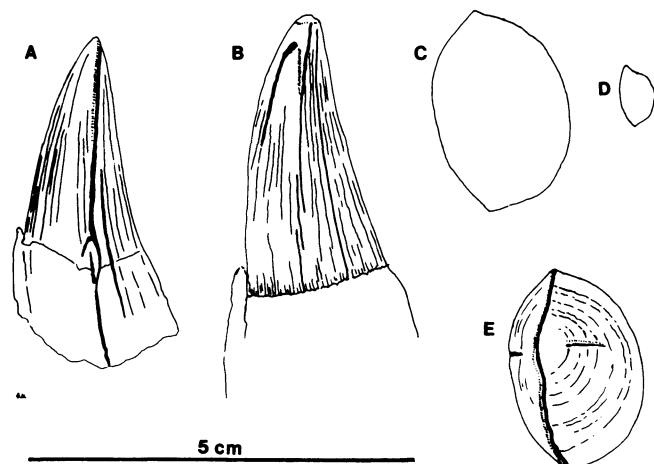

FIGURE 12. A tooth of *Mosasaurus maximus* (YPM 430), a Late Cretaceous mosasaur, is shown in lingual (**A**) and frontal (**B**) views, and obliquely from above (**C**). It differs from that in Figure 11 only in the greater inward and backward curvature. It is also more buccal-lingually compressed.

although the amount of curvature of the tooth varies. In species of *Mosasaurus,* each tooth is curved backwards and inwards. In other mosasaur species, the tooth is almost straight, or only curved backwards. In *Mosasaurus maximus* (and perhaps all *Mosasaurus* species) and *Prognathodon overtoni,* the two carinae have transverse ribs on them, resulting in serrated cutting edges. A specimen of *Tylosaurus proriger* has been found with preserved stomach contents consisting of mosasaur, fish, shark, and bird fragments (Bjork, 1981). Other mosasaurs have been found with fish, belemnites, and turtle bones in their stomach region (Table 1). Thus the tooth form, tooth wear and some of the preserved stomach contents suggest that the preferred prey were large, fleshy animals such as reptiles and large fish, although the stomach contents of the mosasaurs suggest that some of these predators were capable of eating just about anything that they encountered.

The last tooth form is found in the mosasaur genus *Globidens* (Fig. 13). It is a bulbous, acorn-shaped tooth (Gilmore, 1912), with a height/diameter ratio of 1.0 or less. The apex of the crown is very blunt, and the top surface sometimes shows abrasion. The tooth is small, with a height/skull width ratio of 0.10 to 0.15. This form is unique among the marine reptiles, although it was functionally similar to the more plate-like teeth of the placodonts of the Triassic. The skull of *Globidens* was more massive than that of other mo-sasaurs (Russell, 1975). This, and the tooth morphology, suggests a probable diet of very hard prey such as clams and other shelled mollusks (Russell, 1975; Williston, 1914).

Table 2 summarizes the eight tooth forms described, the kind of wear exhibited, and stomach contents associated with each form. The tooth function is inferred from the tooth shape, the apex shape, tooth size as well

FIGURE 11. The cutting teeth of a Lower Liassic ichthyo-saur, *Temnodontosaurus platyodon,* are shown (**A**) in lateral view (BMNH 28283-4), (**B**) in ?buccal view (BMNH 28283-4), (**C**) outline of basal cross-section of crown (BMNH R215), (**D**) outline of cross-section of apex (BMNH 28283a), and (**E**) in top view (BMNH 28283a). Low broad longitudinal ridges define somewhat planar facets on the crown. There is a rough surface texture.
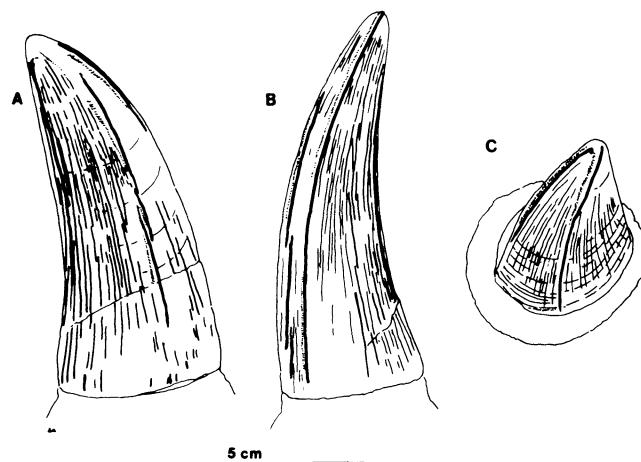
TABLE 1. Preserved stomach contents of Mesozoic marine reptiles.

Species	Age	Stomach contents	Source
Plesiosauroids			
Elasmosaurus platyurus	U. Cret.	vertebrae, scales, and teeth of 6 species of fish	Cope, 1871:47
?Styxosaurus browni	U. Cret.	fish vertebrae, pterodactyl bones and scaphites (thin-shelled ammonites less than 5 cm long)	Brown, 1904, and K. Carpenter, pers. comm.
Pliosauroids			
Pliosaurus brachyspondylus	Kimmer.	cephalopod hooklets	Tarlo, 1959a
pliosaur	L. Lias	*Pholidophorus bechei* (small fish)	Patterson, 1975
Ichthyosaurs			
Leptopterygius acutirostris	U. Lias	fragments of smaller ichthyosaur	R. Wild, pers. comm.
Stenopterygius crassicostatus	U. Lias	cephalopod hooklets	pers. obs.
Stenopterygius megalorhinus	U. Lias	cephalopod hooklets	pers. obs.
Stenopterygius quadriscissus (50 cm long skull)	U. Lias	fish fragments and cephalopod hooklets	Wurstemburger, 1876, cited in Pollard, 1968
Various *Stenopterygius* species	U. Lias	densely packed cephalopod hooklets; rare wood fragments and fish remains	Keller, 1976
Ichthyosaurus communis (small specimens OUM J13587 and J13593)	L. Lias	*Pholidophorus* scales and spines; cephalopod hooklets scattered throughout matrix around ribs	Buckland, 1858; Pollard, 1968
Ichthyosaurus communis (small specimens BMNH 26256 and R1072, and UM SF-1)	L. Lias	dibranchiate cephalopod hooklets	Pollard, 1968
Ichthyosaurus conybeari (BMNH 38523)	L. Lias	dibranchiate cephalopod hooklets	Pollard, 1968
Ichthyosaurus breviceps (BMNH 43006)	L. Lias	dibranchiate cephalopod hooklets	Pollard, 1968
Various ichthyosaurs (OUM J12125, J13592, J10348; BMNH R1896, R1614)	L. Lias	dibranchiate cephalopod hooklets	Pollard, 1968
Crocodiles			
Metriorhynchus sp. (large)	Call.	cephalopod hooklets	Martill, 1985a
Mosasaurs			
Tylosaurus proriger	U. Cret.	shark, teleost, *Platecarpus*, *Hesperornis* (flightless bird)	Bjork, 1981
Plotosaurus tuckeri	U. Cret.	small fish	Camp, 1942, cited in Russell, 1967:68
Compressidens fraasi	U. Cret.	echinoid test found between teeth	Dollo, 1913, cited in Russell, 1967:68
Platecarpus sp.	U. Cret.	fish bones—largest from one 4 ft long	Williston, 1899, cited in Russell, 1967:68
Platecarpus sp.	U. Cret.	tooth marks on ammonite shell	Kauffmann and Kesling, 1960
Plioplatecarpus sp.	U. Cret.	two belemnites	Dollo, 1913, cited in Russell, 1967:68
Hainosaurus sp.	U. Cret.	turtle bones	Dollo, 1887, cited in Russell, 1967:68
mosasaurs	U. Cret.	fishes 2–3 ft in length	Williston, 1914:159
?mosasaur	U. Cret.	tooth mark on giant squid pen	K. Carpenter, pers. comm.
?mosasaur	U. Cret.	tooth marks on *Tylosaurus* skull	SMM 13094
?mosasaur	U. Cret.	tooth marks on numerous ammonites	P. Currie, pers. comm.

as the kind of wear. The preserved stomach contents generally support the inference. Thus there are two kinds of cutting teeth, distinguished by their robust shape, the presence of cutting edges (often serrated), and the kind of wear. The two kinds of piercing teeth are distinguished from each other by their shape, one form being much more slender and longer than the other. The general tooth form has many characteristics

128

of a piercing tooth, but the wear is different. This distinction may not be important, and this form may just be another variation of a piercing morphology. The remaining three forms are grasping teeth, and differ from the others in having blunter apices and usually a small size. The grasping teeth are distinguished from each other by the apex shape and the kind of wear exhibited. Forms with a rounded but acute apex were probably used for fairly soft prey, and will be referred to as the "Smash" morphology. Slightly more robust forms with blunt, rough apices that become blunter and smoothed with wear were probably used to grasp prey with a somewhat hard exterior, and will be referred to as the "Crunch" morphology. The last form is distinguished by its extremely blunt apex and bulbous shape, and was probably used on prey with a very hard exterior. This is termed the "Crush" morphology.

FIGURE 13. A crushing tooth of the mosasaur *Globidens* is shown here from the side and slightly above (from Williston, 1914). The tooth is approximately 1 cm high.

TOOTH FORM AND PREY PREFERENCE

The eight forms described above display intergradation, so they can be viewed along a continuous spectrum of tooth form. The triangular diagram in Figure 14A illustrates the range of possible tooth crown morphologies of the marine reptiles. Slightly overlapping fields can be defined, representing the major tooth types. There are fields for pierce, cut, smash, crunch, and crush, reflecting the inferred primary function of the teeth. Each corner of the triangle represents a distinct, "end member" tooth form and function: at the top a very slender, pointed piercing tooth; at the lower left a blunt, robust crushing tooth; and at the lower right, a sharp, robust cutting tooth. The sides of the triangle mark paths of transformation of tooth form from one end member to another. The tooth form becomes more robust and the apex more blunt from the top corner to the lower left corner. The tooth form becomes more robust and two cutting edges develop from the top corner to the lower right corner. A third path moves down the middle of the diagram, towards the lower right corner: the tooth apex stays pointed, the tooth becomes more robust, and the longitudinal sculpture becomes coarser and sharper until these coarse longitudinal ridges function as several cutting edges. All of the observed tooth forms can be plotted on this diagram.

Predators with very delicate, slender teeth (apex of triangle), the very long-snouted ichthyosaurs and many of the plesiosauroids, tended to take small prey items (predator skull width < 10 cm). Predators with robust teeth with cutting edges (lower right corner) tended to be very large (skull width > 30 cm or more). Ichthyosaurs and teleosaurs with fairly robust crunching teeth tended to be fairly large as well (skull width > 20 cm). There is not, however, a consistent increase in the size of the predator or the prey from the top of the triangle to the bottom.

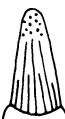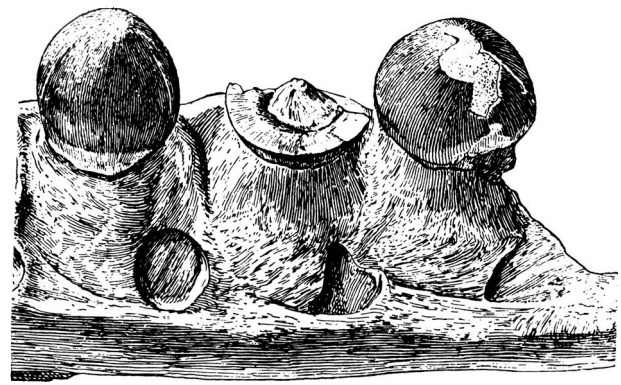Specific prey can be associated with specific tooth forms for some reptiles with preserved stomach contents (Tables 1 and 2). For many forms, however, similarities in morphology or wear with modern marine mammals suggest the types of prey that were consumed. Thus a second triangular diagram can be constructed to reflect the preferred prey for species having a particular tooth form (Fig. 14B). Again, this is a relative scale, and broad, overlapping fields can be defined. Proceeding from the apex to the lower left, successive prey items have harder external structures (thick ganoid scales or shell), and the corresponding tooth form becomes more robust and blunt. Proceeding from the apex to the lower right, the successive prey items are bonier and larger, and the corresponding tooth form is more robust with better developed cutting edges.

There is a lack of precision in correlating tooth type and preferred prey. The general category of preferred prey, however, is more important than the specific kinds of prey listed. The preferred prey was not necessarily the only prey consumed; the tooth form reflects an optimal morphology for each kind of prey. Reptiles with cutting teeth may have been best suited for seizing large fish and reptiles, but they could also eat smaller fish or squid. Similarly, reptiles with crunching teeth may have been best suited for catching prey with a fairly hard exterior, but could have eaten softer prey as well. So as one moves from the apex of the triangle to the base, successive tooth forms have additional food options open to them.

Root (1967) defined a guild as "a group of species that exploit the same class of environmental resources in a similar way", and the term groups together species without regard to their taxonomic positions. This concept is applicable here, where a number of species seem to be sharing the same kinds of prey. Thus feeding types, or guilds, can be identified on the basis of tooth morphologies (Fig. 15). The limits that define guild membership are somewhat arbitrary, as was the case in Root's analysis, because guilds can overlap or intergrade as a result of the complexity of real ecosystems. Important features in determining the feeding guilds of marine reptiles are the shape of the apex, type

TABLE 2. Tooth crown morphologies found in Mesozoic marine reptiles.

FORM	KINDS OF REPTILES WITH THIS FORM	STOMACH CONTENTS	TYPE OF WEAR	INFERRED FUNCTION
	Plesiosauroids Ichthyosaurs	none	usually none	PIERCE
	Metriorhynchids Teleosaurs	none	very tip broken and smoothed	PIERCE
	Plesiosauroids Pliosauroids	small fish mainly; pterodactyl bone, small scaphites	apex rounded	GENERAL
	Pliosauroids	cephalopod hooklets	tooth broken and break rounded and polished	CUT
	Ichthyosaurs Mosasaurs	ichthyosaur, bird, mosasaur, shark, fish, turtle, etc.	tooth broken and break rounded and polished	CUT
	Ichthyosaurs	dibranchiate cephalopods; few fish remains	apex rounded and polished	GRASP (Smash)
	Metriorhynchids Teleosaurs Ichthyosaurs	fish scales and scattered cephalopod hooklets	apex polished	GRASP (Crunch)
	Mosasaur	none	top surface shows abrasion	GRASP (Crush)

of tooth wear, presence/absence of cutting edges, shape of the crown (crown height/basal diameter), and size of the crown (crown height/skull width) (Table 3). Each guild is composed of predators the teeth of which fall within a certain range of morphology and who thus presumably shared the same preferred prey. These guilds are:

1. *Crush guild:* reptiles with very robust, crushing teeth (Fig. 13) for eating clams and other thick-shelled mollusks. The most important features of the tooth are the apex shape and the crown shape.

2. *Crunch guild:* reptiles with fairly robust, blunt teeth (Fig. 7) for eating somewhat hard prey such as armored fish, crustaceans and possibly thin-shelled ammonites. Important features of the tooth are the apex shape and the kind of wear.

3. *Smash guild:* reptiles with small teeth bearing rounded points (Fig. 6), used for grasping fairly soft prey such as belemnoids and soft cephalopods. The

most important tooth characteristics are the relative size and the kind of wear.

4. *Pierce I guild:* reptiles with long, delicate, sharply pointed teeth (Fig. 4) used for piercing soft prey items such as small fish and soft cephalopods. The diagnostic tooth features are the tooth shape and relative size. This guild probably included the species with the fewest options open to them.

5. *Pierce II guild:* reptiles with smooth, pointed teeth (Fig. 5) used for piercing prey. The important tooth features are the apex shape and the relative tooth size. These teeth differ from those of the previous guild in their shape and kind of wear.

6. *General guild:* reptiles with fairly pointed teeth bearing fine longitudinal ridges (Fig. 8), which may have been used for both piercing and smashing. These teeth differ from Pierce II teeth in the presence of fine longitudinal ridges and in the type of wear displayed. These were probably primarily piercing teeth, and the
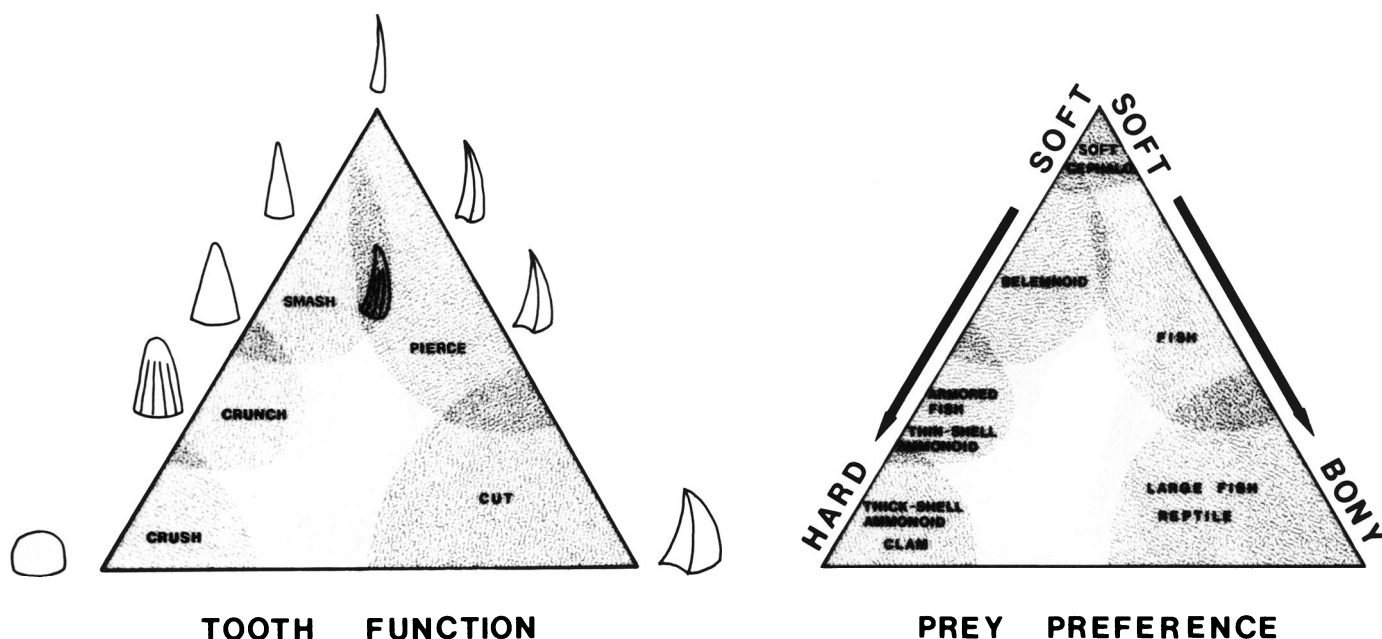
TOOTH FUNCTION

PREY PREFERENCE

FIGURE 14. **A**, the range of tooth crown morphology can be illustrated on a triangular diagram. Tooth function can be inferred by observations of tooth wear and by some general comparisons with modern toothed whales. **B**, fields of preferred prey, corresponding to various tooth forms, can be inferred on the basis of preserved stomach contents (Table 1) and by comparisons with modern toothed whales. This is illustrated on a similar triangular diagram. See text for further explanations.

distinction between this guild and the previous one may not be significant.

7. *Cut guild:* reptiles with fairly robust, pointed teeth with two more more cutting edges (Figs. 9–12) used for seizing large marine vertebrates. The diagnostic features are the presence of cutting edges and the type of wear. The largest reptiles in a particular fauna characteristically had this kind of tooth. These were probably the highest order predators and, because of the many options open to them, may have included many opportunistic species.

PREDATOR GUILD STRUCTURE IN THE JURASSIC AND CRETACEOUS

The guilds represented in a particular fauna can be plotted on a triangular diagram similar to Figure 15. An analysis of the feeding guilds present in six faunal assemblages in the Jurassic and Cretaceous provides a picture of the structure of and changes in the large marine predator adaptive zone during much of the Mesozoic. These faunas were selected because each is the best preserved marine reptile fauna of a particular age. Each assemblage encompasses a different duration of time. Furthermore, these faunas do not represent identical environments, so relative proportions of various kinds of predators cannot be considered, at least not at the scale at which this study was done. Instead, the assemblages were analyzed in terms of the diversity of predator types (the number of guilds), and the taxonomic composition of each guild. The horizons se-

lected were: the Lower Liassic (Hettangian-Sinemurian) fauna of Lyme Regis, England; the Upper Liassic (Toarcian) fauna of Holzmaden, Germany; the Callovian fauna of the Oxford Clay, Peterborough area,
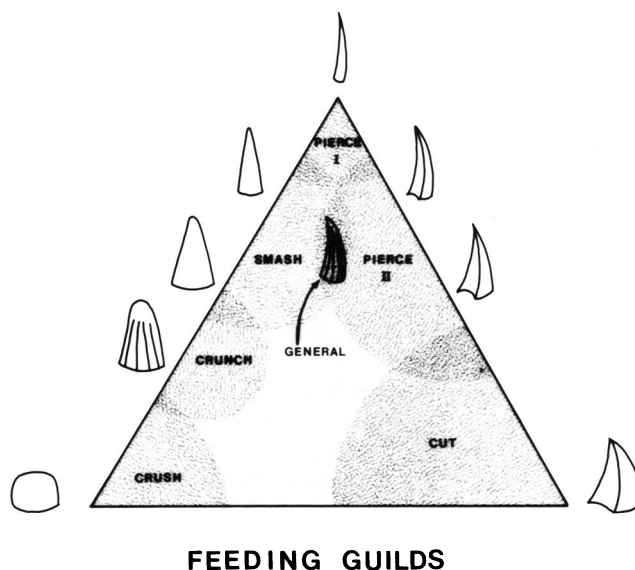

FEEDING GUILDS

FIGURE 15. The seven guilds defined on the basis of tooth crown morphology criteria of Table 3 can be illustrated on another triangular diagram. Each guild includes a range of tooth crown morphologies, and is gradational or overlapping with other guilds.

TABLE 3. Characteristics of tooth crown morphology used in determining guild assignment.

Guild	Shape of apex	Type of wear	Cutting edges	Relative tooth size*	Shape of largest tooth**
Cut	pointed	breakage is common; break is rounded and polished	2 or more; sometimes serrated	usually <0.20 but varies	1.5–2.5
Pierce II	pointed	apex sometimes broken and polished	usually 2, not serrated	0.15–0.25	usually 2.0–3.0
Pierce I	pointed	rare	none or just at the tip	>0.30, usually higher	usually >3.5, never <3.0
General	fairly pointed	apex is rounded	none	0.15–0.25	usually 2.0–3.0, rarely as high as 3.5
Smash	rounded but acute	apex is rounded and polished	none	≤0.15, usually <0.10	2.0–3.0
Crunch	blunt with rough surface	rough apex is smooth and polished	none	≤0.15	1.5–2.5
Crush	very blunt	top surface shows abrasion	none	0.10–0.15	<1.0

*The relative tooth size is the crown height/skull width. Skull width was measured as the distance between the quadrates. Where preservation prevented that measurement, skull width was estimated by the distance between the jaw articulation or as the maximum width across the top of the skull at the temporal fossa.

**The tooth shape is the height/basal diameter of the largest tooth crown. For laterally compressed teeth, the average of the two basal widths was used for the diameter.

England; a composite fauna for the Kimmeridgian of Europe; the Coniacian to Campanian fauna of the Niobrara Chalk of the Western Interior of the U.S.; and the Campanian to Maestrichtian fauna of the Pierre Shale of the Western Interior of the U.S.

Figure 16 plots the distribution of predator guilds on triangular diagrams, based on the criteria for guild assignments summarized in Table 3. For each species, the largest teeth in the middle to anterior portion of the jaw were examined. The appendix lists the exact specimens used in the plots in Figure 16. Within each guild, species are plotted relative to each other rather subjectively, with more robust tooth forms towards the base of the triangle. Plotting a species as a point is not biologically accurate since the ranges of tooth form for species within a guild often overlap. Nonetheless, it will serve to illustrate the pattern of diversity of predator types in these faunas.

The Lower Liassic Lyme Regis fauna contains representatives of at least five guilds (Fig. 16). The ichthyosaurs dominate the fauna, composing four guilds: Cut, Crunch, Smash, and Pierce I. Plesiosauroids composed the Pierce I guild, and, with the pliosauroids, constituted the General guild. There was a fairly high diversity of predator types, with almost every guild represented. The pattern is much the same for the Up-

per Liassic Holzmaden fauna (Fig. 16). There was a very high diversity of predator types, with six guilds represented. The ichthyosaurs still composed four guilds. The pliosauroids still formed the General guild. The plesiosauroids still constituted the Pierce I guild, but were no longer a part of the General guild. Because of some taxonomic problems in distinguishing Early Liassic plesiosauroids from pliosauroids, this latter change may not be real. The main differences beween the Holzmaden and the Lyme Regis faunas was the addition of the teleosaurs, which formed the Pierce II guild. Thus the Early Jurassic can be characterized as a diverse, ichthyosaur-dominated fauna that saw a slight increase in diversity with the appearance of the teleosaurs towards the end of the Early Jurassic. The number of guilds and their order-level taxonomic composition was fairly constant.

By Callovian time, represented by the Oxford Clay fauna, a number of changes occurred. The same guilds were present, but the reptiles constituting some guilds changed (Fig. 16). Plesiosauroids still formed the Pierce I guild, and ichthyosaurs still composed the Smash guild. The teleosaurs increased in their diversity of predator types and, with the metriorhynchids, shared the Pierce II and Crunch guilds. The pliosauroids diversified as well, sharing the Pierce II guild with the

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FIGURE 16. Guild composition of six Mesozoic faunas are illustrated here. Species are plotted on a triangular diagram, with the shaded areas denoting the fields for the guilds defined in Table 3 and Figure 14. The numbers at the sides of the triangles indicate the individual species plotted and the specimens on which it is based (see appendix). Note the decrease in diversity of predator types after the Kimmeridgian.
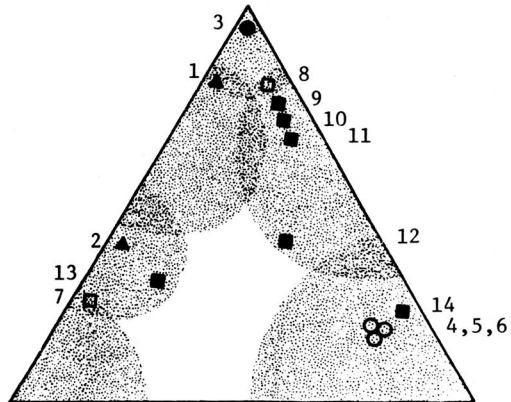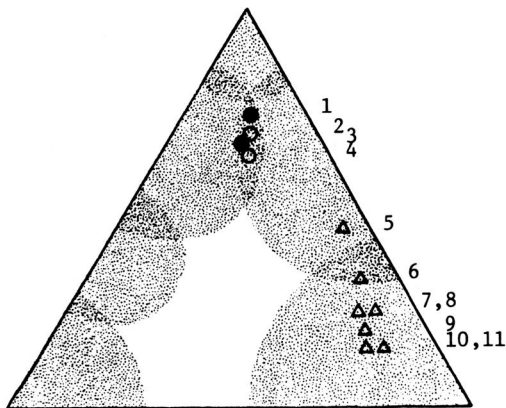
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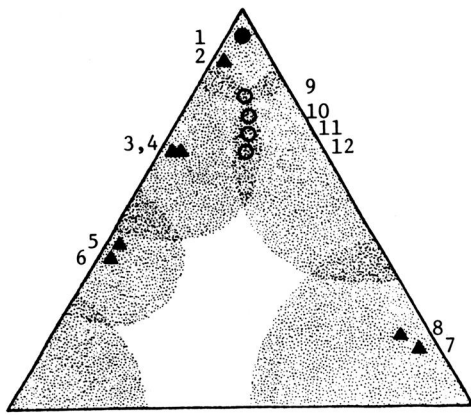
LYME REGIS FAUNA
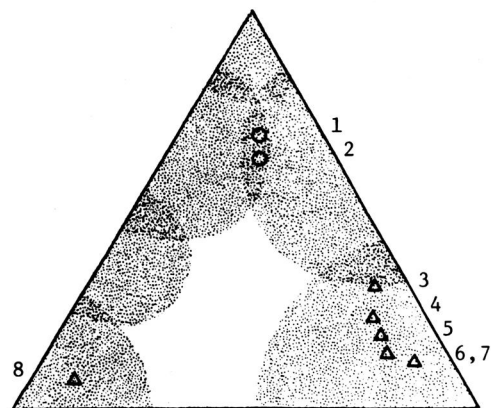LOWER LIASSIC
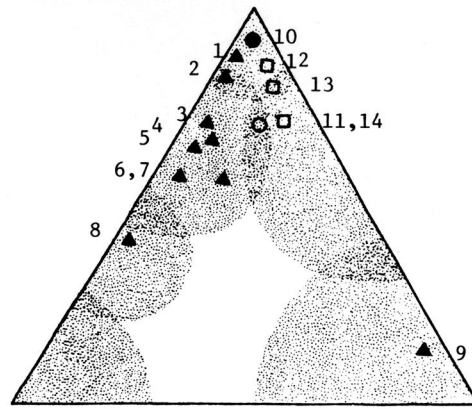
HOLZMADEN FAUNA
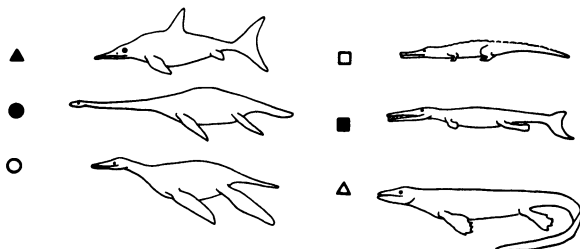UPPER LIASSIC
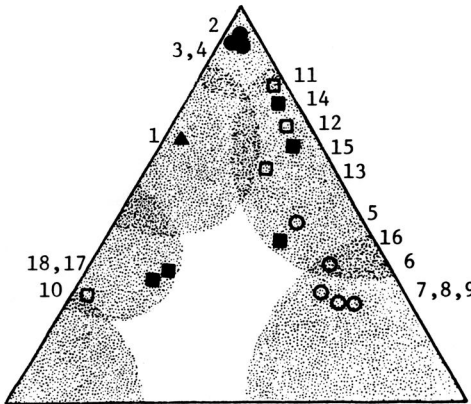
OXFORD CLAY FAUNA
CALLOVIAN

EUROPEAN COMPOSITE
KIMMERIDGIAN

NIOBRARA CHALK
CONIACIAN-CAMPANIAN

PIERRE SHALE
CAMPANIAN-MAESTRICHTIAN

crocodiles, and replacing the ichthyosaurs as the highest order predator in the Cut guild. This pattern persisted at least through the Kimmeridgian (Fig. 16D). The main differences are a slight increase in diversity of ichthyosaurs and metriorhynchids, each represented in an additional guild, and a slight decrease in the diversity of pliosauroids and teleosaurs, each occupying one less guild. Thus the late Middle and Late Jurassic is characterized by very diverse assemblages dominated by pliosauroids and crocodiles. The kinds and distribution of predator guilds, however, did not change from that of the Early Jurassic. The reorganization that occurred some time in the Middle Jurassic was a within-guild one.

By the Late Cretaceous, a second, larger reorganization occurred. In the Niobrara Chalk, only three guilds are represented (Fig. 16). Mosasaurs replaced the metriorhynchids and pliosauroids in the Cut and Pierce II guilds. The plesiosauroids and pliosauroids composed the General guild, as they did in the Early Liassic. This placement is somewhat tentative since only a few specimens of elasmosaurs have been examined. Welles' (1943, 1952, 1962) reconstructions suggest that the teeth of the Cretaceous elasmosaurs were very long and slender as in the Late Jurassic species. Specimens of *Styxosaurus snowi* (UK 1301 from the Niobrara Chalk), *Elasmosaurus morgani* (SMU type specimen from the Eagle Ford Shale), and an unidentified elasmosaurid (UNSM 50132 from the Graneros Shale) suggest that the teeth of these Cretaceous plesiosauroids are not as delicate and pointed as those of the Jurassic ones. Elasmosaur teeth, although large with respect to the gullet size, are more robust than the teeth of Jurassic plesiosauroids. Except for their larger size, they are very similar to the teeth of Liassic pliosauroids, having fine longitudinal ridges, a somewhat rounded apex, a circular cross-section, and not a particularly slender shape. The largest complete teeth of *Elasmosaurus morgani* have height/diameter ratios of 2.3 to 3.2. The aforementioned elasmosaurid (UNSM 50132) has ratios ranging from 2.5 to 3.2. Because the teeth are not as delicate as those of Jurassic plesiosauroids, I tend to place the Cretaceous species in the General guild. This is, however, based on very few specimens, and reconstructions do suggest a more delicate tooth. Some species may very well belong to the Pierce I guild. This, of course, would argue for less of a decrease in diversity of predator types in the Late Cretaceous, but a decrease nevertheless. Regardless of whether the elasmosaurs belonged to one or two guilds, there was a major reorganization at some time between the Kimmeridgian and the Late Cretaceous. The pliosauroid/crocodile dominated fauna was replaced by a mosasaur dominated fauna, and this pattern continued through the Late Cretaceous. The Pierre Shale fauna (Fig. 16) contains representatives of the same three guilds. The biggest difference was the appearance of a mollusk-crushing mosasaur, *Globidens,* constituting the Crush guild. This was the first occurrence of this type of predator among the marine reptiles since the pla-

codonts of the Triassic, and may have marked the beginning of a radiation by the mosasaurs. Events at the Cretaceous-Tertiary boundary, however, ended the reign of reptiles as the large marine predators.

The dramatic decrease in diversity of predator types in the Late Cretaceous is probably not a result of collecting biases. The Oxford Clay fauna is largely from one ammonite zone in the Callovian (Adams-Tresman, 1980; Martill, 1985a), and collection of material centered around Peterborough, England. The diversity of predator types is very high in the Oxford Clay fauna in spite of the limited geographical and stratigraphical sampling. On the other hand, the Pierre Shale and the Niobrara Chalk together represent almost four stages of the Late Cretaceous and a fairly large geographic area (western Kansas, southwestern South Dakota, eastern Wyoming and eastern Colorado). Their combined diversity of predator types, however, is very low, suggesting that the difference observed between the Late Jurassic and Late Cretaceous faunas is real. Although there were many mosasaur species in the Late Cretaceous, they all had similar tooth forms (Fig. 16).

CONCLUSIONS

Mesozoic marine reptiles showed a high diversity of tooth crown morphologies that probably reflects a high diversity of predator types. Tooth form varies within orders, within families, and even within genera, and convergence in tooth morphology is common among the reptilian orders examined in this study. Consequently, tooth form should be used with extreme caution in definitions of families or genera. The tooth form can, however, be used to infer prey preference and to define predator guilds. These guilds transcend orders, and reflect the overall effect of the marine reptilian predators on the prey.

The pattern of guild diversity throughout the Jurassic and Cretaceous was somewhat cyclic, characterized by long periods (15–20 million years) of stability punctuated by reorganizations, perhaps prompted by major extinctions. During the stable periods, there were species replacements within guilds and a slow increase in the diversity of predator types. There were two episodes of reorganization, one in the Middle Jurassic and the other in the Early Cretaceous. At these times, large scale, order-level replacements within guilds occurred. In the Middle Jurassic, a reduction in ichthyosaur diversity corresponded to the radiation of pliosauroids and crocodiles. The overall guild structure was unchanged. The second episode, however, not only changed the composition, but also reduced the number of reptilian predator guilds. Interestingly, this reorganization affected more types of reptilian predators than the terminal Cretaceous extinction, and may represent the major crisis for Mesozoic marine reptiles. The Early Cretaceous reorganization corresponds to the radiation of large teleost fish and sharks, so perhaps some of those predators constituted guilds formerly com-

134

posed of reptiles. On the other hand, perhaps this does reflect a real change in the guild structure of large marine predators. The mosasaurs, large predators in the Cut guild, may have been unusually good generalists— so good that they, in effect, occupied all of the guilds. The diversity of mosasaur prey, as seen in preserved stomach contents (Table 1), is certainly greater than for any of the other reptiles.

It is tempting to suggest competition as the cause for both of these episodes of guild reorganization: competition among reptiles causing the Jurassic reorganization, and competition with large teleost fish and sharks causing the Cretaceous reorganization. Late Jurassic pliosauroids had more robust jaws and larger temporal fossa than the large ichthyosaurs which they replaced, and so may have been more efficient predators of large fish and reptiles. Large fish (>3 m) are common in the Pierre Shale, where they outnumber reptiles by more than 3 to 1 (K. Carpenter, pers. comm.). In the Liassic Holzmaden fauna, *Chondrosteus hindenburgi* reached about 2.5 meters, but was not common. Large fish also occur in the Oxford Clay (Martill, 1985b) but seem to be uncommon compared to the reptiles. The scale on which this study was done makes the evidence for competition inconclusive.

On the other hand, the Late Cretaceous faunas may represent a period when the radiation of a new group of reptiles lagged well behind an extinction that eliminated some guilds. An accompanying change in the physical environment could have delayed a radiation. There is a similar lag in the rediversification of ammonites, which suffered an Early Cretaceous extinction (Kennedy, 1977). It is also possible that a basic lack of variability of the surviving reptile groups prevented or delayed the radiation. The Early Cretaceous extinction/reorganization was much more severe than the Middle Jurassic one. So few reptiles survived that there may have been little "raw material" for a new radiation. Perhaps turtles constituted some of the seemingly absent guilds, but since they lack teeth, they cannot be incorporated into this analysis. The Cretaceous-Tertiary extinction eliminated the possibility of the reptiles radiating and regaining their Jurassic diversity.

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APPENDIX 1. A key to the species plotted and specimens used in constructing Figure 16.

A. Lyme Regis Fauna (see Owen, 1865, 1881; McGowan, 1974a, b)
  1. *Plesiosaurus dolichodeirus* BMNH 39490, Owen (1865) pl. II, III
  2. *Ichthyosaurus tenuirostris* BMNH 24300, 2000-160X
  3. *I. breviceps* BMNH 39263
  4. *I. conybeari* as described in McGowan (1974a)
  5. *I. communis* BMNH R12, 41159, 39492, 120, R1697, 2016
  6. *Temnodontosaurus risor* BMNH R311, 43971
  7. *T. eurycephalus* BMNH 1157
  8. *T. platyodon* BMNH R312, R215, 2815, R3281
  9. "*Plesiosaurus*" *rostratus* BMNH R1371
  10. "*Plesiosaurus*" *macrocephalus* BMNH 49202
  11. *Rhomaleosaurus arcuatus* BMNH R40094, R2024, R2030

B. Holzmaden Fauna (see Fraas, 1910; Huene, 1922, 1931; Hauff, 1953; Westphal, 1962; McGowan, 1979; Urlichs et al., 1979)
  1. *Eurhinosaurus huenei* IGPT display specimen CII$_6$
  2. *Stenopterygius quadriscissus* SMNS 10460, IGPT 9532

3. *S. hauffianus* IGPT 1491/1, Ohmden CII_{4-5} and stairway display
4. *S. crassicostatus* SMNS 17500, and "Manteer 3"
5. *S. megacephalus* IGPT display specimen CII
6. *S. megalorhinus* IGPT display specimen
7. *S. zetlandicus* SMNS 14846, and IGPT CII_{10}
8. *Leptopterygius disinteger* SMNS 15390
9. *L. acutirostris* SMNS 15950, IGPT display specimens from CII_{11} and Frittingen
10. *Plesiosaurus brachypterygius* IGPT display and Museum Hauff specimens
11. *Rhomaleosaurus victor* SMNS 12478 and Museum Hauff specimen
12. *Platysaurus multiscorbiculatus* Museum Hauff specimen and Hauff (1953) pl. 26
13. *Pegalosaurus typus*
14. *Steneosaurus bollensis* SMNS 51563, IGPT 1193/2

C. Oxford Clay fauna (see Andrews, 1910–13; Adams-Tresman, 1980; Brown, 1981)
1. *Ophthalmosaurus icenicus* BMNH R2180, R2150, R3894, R3535
2. *Muraenosaurus leedsi* BMNH R2861, R2421, and Andrews (1910) figure and reconstruction
3. *Tricleidus seeleyi* BMNH R3539 and Brown (1981) figure
4. *Cryptoclidus eurymerus* BMNH R2869 and Brown (1981) fig. 23
5. *Peloneustes philarchus* BMNH R8574, R4058, R2679
6. *Simolestes vorax* BMNH R3170, R3319
7. *Pliosaurus andrewsi* from Tarlo (1960) figure
8. *Liopleurodon pachydeirus* from Andrews (1913) measurement of R2446
9. *L. ferox* BMNH R2858, R3536, R2680
10. *Steneosaurus obtusidens* BMNH R31658 and Andrews (1913) pl. VII
11. *S. leedsi* from Andrews (1913) pl. V
12. *S. durobrivense* from Andrews (1913) pl. VI and BMNH R2825
13. *Mycterosuchus nastus* from Andrews (1913) pl. VIII
14. *Metriorhynchus leedsi* BMNH R5793
15. *M. cultridens* BMNH R3804
16. *M. moreli* BMNH R2044, R2054
17. *M. durobrivensis* BMNH R1994, R2039, R2618
18. *M. superciliosum* BMNH R1521, R1530, R2030, R2053

D. Composite fauna, Kimmeridgian of western Europe (see Hulke, 1871; Fraas, 1902; Tarlo, 1959a, b, 1960; Krebs, 1968; Steel, 1973; McGowan, 1976; Brown, 1981)
1. *Nannopterygius enthekiodon* description of tooth from Hulke (1871)

2. *Grendelius mordax* description from McGowan (1976) and BMNH 45987, a tooth which is similar in morphology (A. Kirton, pers. comm.)
3. *Kimmerosaurus langhami* BMNH R4831 and Brown (1981) reconstuction
4. *Pliosaurus brachyspondylus* from Tarlo (1960) pl. 21
5. *Pliosaurus brachydeirus* BMNH R1681
6. *Stretosaurus macromerus* YPM 456
7. *Machimosaurus hugii* from Krebs (1968) and Huene (1925), Taf. XXV
8. *Aeolodon priscus* figured in Westphal (1965)
9. *Geosaurus suevicus* figured in Fraas (1902)
10. *G. gracilis* from Steel, 1973
11. *G. giganteus* BMNH 37020
12. *Metriorhynchus moreli* same as for Oxford Clay
13. *M. superciliosum* same as for Oxford Clay
14. *Dacosaurus maximus* figured in Fraas (1902) and YPM 456

E. Niobrara Chalk Fauna (see Welles, 1943, 1952, 1962; Russell, 1967)
1. *Elasmosaurus morgani* SMU type from Eagle Ford Shale, Tx
2. *Styxosaurus snowi* UK 1302
3. *Dolichorhynchops osborni* SMM 7690, UK 1300
4. "*Polycotylus*" YPM 1125
5. *Ectenosaurus clidastoides* SMM 7937
6. *Platecarpus ictericus* SMM 2913
7. *P. coryphaeus* USNM 119536, SMM 10902
8. *Tylosaurus proriger* UK 1032, 1033, and SMM VP-3
9. *Clidastes propython* KU 1000 and display specimens
10. *C. liodontus* SMM 10668
11. *Tylosaurus nepaeolicus* from Russell (1967) reconstruction
? There may be other elasmosaurs (plesiosaurs) in the Pierce I guild

F. Pierre Shale Fauna (see Welles, 1943, 1952, 1962; Russell, 1967)
1. *Dolichorhynchops osborni* UK 40001, UNSM 55810 (juvenile)
2. "*Polycotylus*" same as for Niobrara Chalk
3. *Platecarpus ictericus* CU 38-88, 38089
4. *Tylosaurus proriger* same as for Niobrara Chalk
5. *Clidastes propython* CU 20468, 20565
6. *Prognathodon overtoni* KU 950 and Russell (1967) reconstruction
7. *Mosasaurus missouriensis* from Russell reconstruction
8. *Globidens dakotaensis* USNM case 27628 (specimen unnumbered) and Russell (1975) figs. 2 and 3
? No data for the Pierre Shale elasmosaurs (plesiosaurs)—they were probably included in the General guild or the Pierce I guild, or both