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AN UPPER CRETACEOUS AMMONITE
BITTEN BY A MOSASAUR

BY

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CONTRIBUTIONS FROM THE MUSEUM OF PALEONTOLOGY

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INTRODUCTION

AN UPPER CRETACEOUS ammonite of the genus *Placenticer* has been found bearing numerous perforations and impressions made by the teeth of a mosasaur. Although the specimen was previously illustrated (Fenton and Fenton, 1958, color photograph opposite p. 19), it has not been described. The shell was bitten repeatedly, and bears dramatic evidence of the fatal encounter. From a composite of the patterns of tooth marks we have reconstructed the dentition, and from the relationships of the upper and lower jaws in inflicting the bites we offer certain inferences on the shape of the head, the structure and action of the jaws, and the diet of the mosasaur.

Although ammonites are abundant in Upper Cretaceous deposits in many parts of the world, this is the only specimen known with tooth marks. That it was bitten by a mosasaur is firmly established by distinct marks of pterygoid teeth, which are unknown in other marine animals of that time. Two of the bites crushed the living chamber of the ammonite, and, we presume, ruptured the membrane and disengaged the muscles by which the body of the ammonite was held in the shell. Probably, thereupon, the soft parts of the ammonite were devoured by the mosasaur, and

the mutilated shell settled to the bottom, where it was buried by accumulating sediment.

We are very grateful to Mr. Irving G. Reimann, of the Exhibit Museum of the University of Michigan, who found the specimen, partly prepared it, and presented it to the Museum of Paleontology. Dr. Claude W. Hibbard, of the Museum of Paleontology, identified the tooth marks as those of a mosasaur, started the study, and gave us helpful suggestions and guidance. Our comparison of the tooth marks on the ammonite with the dentition of *Platecarpus brachycephalus* Loomis was made possible through the very helpful co-operation of Dr. George W. Bain, of the Department of Geology at Amherst College, who sent excellent photographs of the type specimen, and Dr. Albert E. Wood, of the Department of Biology at Amherst, who sent an informative description of the type material. Dr. G. M. Ehlers and Dr. C. A. Arnold read and criticized the manuscript. To all who have assisted in our study we are sincerely grateful.

The specimen is deposited and cataloged in the Museum of Paleontology of the University of Michigan.

DISCOVERY OF SPECIMEN

In the summer of 1947, while on a vacation trip, Irving G. Reimann, now Director of the Exhibit Museum of the University of Michigan, stopped at Scenic, South Dakota. In company with Ed Curtin, a local fossil collector, he visited an outcrop of upper strata of the Pierre shale along a small north-flowing tributary of the Cheyenne River. This exposure was well known to Curtin and to other collectors in the region, who obtained numerous large ammonites there. It was north of Scenic, in Pennington County, on the ranch operated at the time by Mr. and Mrs. Habinck.

Among the specimens of *Placenticerus* brought back by Reimann from this locality was the one described here. Although most of it was still embedded in a gray concretion, he selected this specimen because small exposed areas showed well-preserved mother-of-pearl, and he hoped to remove the matrix. That night Reimann started cleaning the specimen. He soon uncovered a puncture surrounded by a crushed area.

"My first reaction," Reimann recalls, "was that the ammonite had somehow been badly crushed at spots inside the concretion and was not worth cleaning up. But as I took off more matrix, I found a second puncture and a third. Instead of being disappointed, I suddenly realized that these punctures, which lined up like tooth marks, might make the specimen of exceptional interest." He then abandoned further removal of the matrix and coated the exposed part of the conch with preservative.

Later, he presented the specimen to the Museum of Paleontology, where it is now cataloged as No. 35484.

We tried to find a more exact location of the fossil's occurrence. Our letter to Curtin came back marked "Addressee deceased." We then wrote to Tom Friet, another local collector who had known the locality, but that letter was also returned "Addressee deceased."

We also wrote to Mrs. G. W. Laudenslager in Scenic. After the manuscript of this paper was submitted, we received her reply (on April 12, 1960). She inquired about the locality from Mr. and Mrs. Habinck, and learned that "the fossils you were referring to were taken from what is known as Hay Draw, 14 miles north of Scenic in the Cheyenne River Brakes." We are sincerely grateful to Mrs. Laudenslager for her efforts in tracing down the exact locality.

From the proximity of the outcrop to the Badlands National Monument, where early Tertiary formations are exposed, we adjudge the strata that yielded the specimen to be in the upper part of the Pierre shale. Further, from the occurrence of numerous specimens of *Placenticer*s, we are led to believe that they are in the Virgin Creek member. Reeside stated (1957, pp. 534-35): "The highly fossiliferous concretions in the dark shales, particularly in the Virgin Creek member, contain a variety of species and testify to the favorable conditions for life. . . . The ammonite *Placenticer*s was for the first time abundant in association with mud bottoms."

DESCRIPTION OF AMMONITE

The specimen, a moderately large *Placenticer*s, appears, by its compressed shell, small umbilicus, slightly concave venter, and weakly ornamented, non-nodose flanks, to be *P. whitfieldi* Hyatt or a very closely related species. Specific identification cannot be confirmed without removing the external shell wall, which obscures all sutures. Because the specimen is of unusual interest we have declined such action.

The conch is nearly complete. Only the apertural one-fourth of the living chamber is crushed. The specimen is generally free of matrix except the apertural one-third of the right side of the living chamber, which retains a thin layer of the enclosing argillaceous limestone concretion. Inasmuch as the specimen is crushed and fractured in this region we did not risk seriously damaging the conch by attempting removal of this part of the matrix. The aperture seems to be filled with the same material, as are the perforations, but the interior of the conch has not been seen.

The shell walls bear numerous subround perforations, crushed areas, and dents of several sizes which were made by teeth of a mosasaur. These

marks are present on both sides of the shell, but are best developed on the left side (Pl. I), which shows an almost complete set of maxillary impressions. A dorsal sector of the conch has been fractured and slightly displaced, and the living chamber, which makes up about half of the outer whorl in *Placenticerus*, has been severely crushed and slightly torn at its apertural margin.

The dimensions of the specimen, UMMP No. 35484, are as follows: height, 28.9 cm.; length, 23.1 cm.; and greatest width at the base of the aperture, 8.1 cm.

GENERAL FEATURES OF MOSASAURS

Mosasaurs were large predaceous marine lizards. From their structure, they have been adjudged the most vicious, rapacious creatures of the warm epicontinental seas during the epoch of their existence. They were evidently numerous, for many remarkably complete skeletons have been discovered. Mosasaurs were also widespread; specimens have been described from England, France, Morocco, Egypt, Palestine, Nigeria, South Africa, Siberia, Timor, New Zealand, South America, Mexico, and many places in the United States, chiefly in the regions of the Gulf Coast, the Great Plains, and California (Camp, 1924, p. 1).

From a study of excellently preserved skeletons, vertebrate paleontologists have inferred the appearance and mode of life of the mosasaurs. Detailed interpretations have been written by Williston (1898, pp. 209-16; 1904, pp. 43-51; 1914, pp. 152-67), Osborn (1899, p. 6), Raymond (1939, pp. 158-59), Camp (1942, pp. 1, 47-48), and Hoffstetter (1955, pp. 630-37), of which the following is a digest.

Although mosasaurs lived only during the Upper Cretaceous epoch, they evolved rapidly. Four adaptive types, on which the subfamilies are based, have been recognized. As will be discussed later, each of these types had more or less distinctive jaws and teeth.

Mosasaurs were elongate, round-bodied, short-limbed reptiles completely adapted to marine life and well constructed for agility and rapid swimming. Adults varied in length according to species; one was only 8 feet, but a complete specimen of another was over 30 feet; and incomplete skeletons of some indicate a maximum of about 40 feet. The head was flat and narrow, anteriorly produced as a long, tapering snout. Upper and lower jaws were equipped with numerous teeth, and each of the paired pterygoid bones in the roof of the mouth had a row of sharp teeth. The lower jaw was hinged near the middle. The neck was short and strong, the trunk long and slender, and the tail very long, in some species as long as the rest of the body. Near the end, the tail in some was expanded

in a kind of caudal fin. The short limbs were reduced to paddles; in some mosasaurs the digits were spread apart and connected by a smooth membrane to form a flexible fin, but in others the hands and feet developed numerous additional bones and became tapering and less flexible. The pelvic girdle, reflecting the adaptation to marine life, was loosely suspended in the abdomen and useless to support the animal's weight. Impressions of the skin reveal that, except for the membranes between the fingers and toes, the mosasaurs were covered with relatively small overlapping scales and provided with a nuchal crest, probably like that of the iguana. Fossilized stomach contents contain fish bones and scales.

Mosasaurs spent most, perhaps all, of their lives in water. It seems certain that at least some could dive deeply, for one genus, *Plioplatecarpus*, developed a thick osseous tympanic operculum, capable of withstanding great pressure on the inner ear. Williston (1914, p. 163) was of the opinion that mosasaurs did not achieve extraordinary speed, but captured their prey by sudden lateral darting movements, for which they were adapted by their powerful and flexible paddles. Raymond (1939, p. 159) conjectured that they swam with a "wriggling, eel-like" motion.

Their legs were so completely modified for swimming and their pelvic girdle so weakly attached, that mosasaurs must have been nearly helpless on land. According to Williston (1914, p. 156), they were "able perhaps to move about in a serpentine way when accidentally stranded upon the beaches, but probably never seeking the land voluntarily."

The females, however, may have come ashore to lay their eggs. Strangely, skeletons of very young mosasaurs have never been found. As suggested by Williston (1914, pp. 163-64), the young may have lived in a different environment than the adults. Furthermore, no skeleton of an adult has been discovered containing fetal bones, from which it has been assumed that mosasaurs laid eggs. If so, the eggs were probably deposited on land, inasmuch as no living reptile lays its eggs in water. Perhaps the females ascended into rivers and spawned on the banks, and the young hatched there, not venturing into the sea until they were nearly full grown. Such an explanation was proposed by Williston (1904, p. 50), who stated that "It is, of course, possible that the shallow waters of the bays and estuaries may have afforded sufficient protection for the young mosasaurs, but this is doubtful, in the entire absence of all remains of such animals in marine deposits. It seems more probable that the mosasaurs were brought forth, perhaps alive, in fresh water, that the females ascended the rivers to breed, and that the young remained in such protected places until fairly able to care for themselves."

The pugnacious nature of mosasaurs is attested by many scars and

mutilations, which have been noted by Williston (1914, p. 161) on lower jaws, vertebrae of the tail, and bones of the paddles. Undoubtedly, these huge marine lizards did not hesitate to attack any animal in the offshore waters of the Cretaceous seas.

MOSASAUR TEETH

Inasmuch as this study is concerned with marks left by mosasaur teeth, it is important to consider what is known of the structure and development of teeth from their occurrence in mosasaur skeletons. The marginal teeth of upper and lower jaws were strongly constructed but rather loosely attached to the bone of the jaw. Their expanded osseous bases were set into shallow pits or sockets. As a result, the teeth were easily dislodged. In all mosasaur jaws that have been described, the teeth are unequal; some are fully developed, but others are just erupting, and one or more may be represented by empty sockets.

In addition to loss through use, mosasaur teeth were replaced by successional teeth growing outward. As Gregory (1951, p. 351) remarked: ". . . the osseous base of the functional tooth was eroded until it fell out and was replaced." Frequent loss of teeth and continued rapid replacement are characteristic of all living predaceous reptiles.

Williston (1914, p. 161) explained that, "The constant renewal of the sharply pointed teeth, thereby preventing deterioration by use or accident, preserved, even in the oldest animals, the effectiveness of the youthful structure." It is presumed that mosasaurs, like their nearest living relatives, the varanid lizards, retained the same number of teeth throughout life. Because of irregularities in the cycle of replacement, however, the teeth of one side were not invariably directly opposite the corresponding teeth of the other side. The marginal teeth of both upper and lower jaws were generally curved backward, but the degree of curvature varied, even within the same specimen (Fig. 1). The pterygoid teeth, on the other hand show very little variation in each skull and, insofar as known, did not develop irregularities in cyclical replacement. Evidently, they did not normally function in biting, but in holding the prey in the rear of the mouth while it was being engorged.

For convenience, the position of any tooth can be designated by letters and numbers. In the text, each tooth on the right side is identified by R, and each on the left side by L. Each half of the upper jaw, from front to back, contains two premaxillary teeth, Pmx1 and Pmx2, and several maxillary teeth, Mx1, Mx2, and so on. The premaxillary teeth are somewhat smaller than the maxillary, but do not differ from them significantly. All teeth of each lower jaw are attached to the dentary bone; from front

to back, they are designated as D1, D2, and so on. In this system, the third maxillary tooth on the right side would be referred to as RMx3, and the fifth dentary tooth on the left side as LD5.

The marginal or jaw teeth are set in the marginal areas of the tapering snout and lower jaws. In all described mosasaur skulls, the maxillary rows flare outward at the rear, so that the intermaxillary angle is much greater in the posterior half of the upper jaws than in the anterior. From a comparison of the illustrations given by Williston (1898, Pls. 10–21), we suspect that the degree of flare, which can be measured as intermaxillary angle at the rear of the jaws, is generically significant. In the present classification of mosasaurs, however, this feature has not been considered. The lower jaws are parallel to the upper, but slightly narrower and less curved.

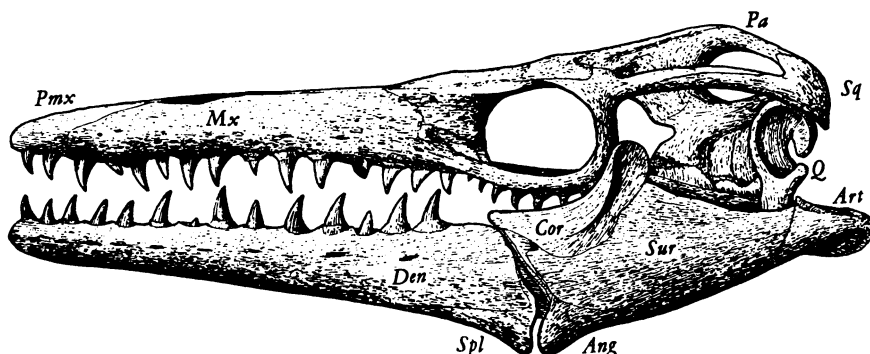


FIG. 1. *Mosasaurus horridus* Williston. Left lateral view of head, with certain bones designated by the following abbreviations: *Ang*—angular; *Art*—articular; *Cor*—coronoid; *Den*—dentary; *Mx*—maxillary; *Pa*—parietal; *Pmx*—premaxillary; *Q*—quadrate; *Spl*—splenial; *Sq*—squamosal; *Sur*—surangular. $\times 1/9$. (After Williston, 1898, Pl. 19)

The pterygoid teeth on each side are arranged in a row, either an outwardly convex arc, as in *Mosasaurus*, or a sigmoid curve with the anterior half outwardly convex, as in *Platecarpus*. The front pterygoid tooth is nearly aligned with the rear maxillary tooth; in some species it is slightly ahead, and in others slightly behind. It lies about half way between the rear maxillary tooth and the midplane of the skull, its exact position more or less constant in each genus.

The spacing of the marginal teeth in a particular part of the jaw is not the same in one genus as in another. This character might well be con-

sidered in generic comparisons. Various ratios, such as that between the average separation of pterygoid teeth in each row and the distance between the rear maxillary teeth, could also be used.

Each tooth exhibits certain features that have been regarded as taxonomically important. For example, the cross section of the tooth varies from elongate in *Mosasaurus* to round or broadly ovate in *Platecarpus*. The width of the base compared to total length differentiates the "stout" tooth of *Mosasaurus* from the "delicate" tooth of *Clidastes*. Teeth of some mosasaurs are grooved, or striated, whereas those of others are smooth. Such surface features would not likely be recorded in perforations made by the teeth.

The marks left on the ammonite described in this paper reveal the number, size, shape, and spacing of the teeth, as well as the shape of the jaws of the mosasaur that attacked it. Thus, this unusual fossil preserves several clues to the nature of the mosasaur.

PATTERNS OF TOOTH MARKS

Only a casual glance at the left side of the ammonite (Pl. I) is needed to select one set of tooth marks. These marks are conspicuous because the force of the bite not only drove the shafts of the teeth through the shell, but also pressed the expanded bases of the larger teeth inward to crush areas around the perforations. They are arranged in two nearly straight lines which converge toward the edge of the shell. Certain adjacent crushed areas are nearly tangent to each other, eliminating any possibility that smaller teeth were interspersed with those making the perforations. Because of this there is tangible evidence of the size and spacing of some of the teeth and the angle of convergence of the jaws (Fig. 2).

The opposite side of the ammonite (Pl. II) shows other tooth marks deeply impressed and aligned in two converging lines, more or less parallel to those on the left side (Fig. 4*e*). In these rows, however, some marks are spaced so far apart that it seems highly possible that, between the teeth that produced them, there were either shorter teeth which left no marks or empty sockets representing missing teeth (Fig. 3).

Unfortunately, these clearly associated marks do not form a complete set for either upper or lower jaws, because the snout of the mosasaur projected beyond the edge of the ammonite. Our first objective, then, was to establish the complete dentition of the mosasaur from a composite of the numerous marks. In the deep bite, a few perforations are much larger than others, indicating that they were made by larger, and presumably longer teeth. On the left side of the specimen (Pl. VII, Fig. 1), the larger perforations are those labeled LMx4, LMx5, LMx6, LMx8, RMx4, RMx5,

and RMx6; on the right side (Pl. VII, Fig. 2), they are LD6, LD7, LD9, RD3, RD4, and RD6.

If the other tooth marks on the cephalopod were made by the same mosasaur, we reasoned, they should be distributed in sets representing various bites. In addition, the teeth which made the larger perforations in the strongest bite would leave a record in the weak bites in the form of small perforations or dents. The immediate problem was to discover repetitions of the basic tooth pattern, and thereby divide the remaining numerous marks into sets. As a practical approach, holes were cut in one sheet of cardboard at the positions of the major tooth marks on the left side of the shell, and in another sheet at the positions of those on the right side. Equipped with these punched cards, representing parts of the dentition in the mosasaur's upper and lower jaws, we examined the spacing of other tooth marks on the shell by direct comparison. Each pattern was found to be repeated several times. For nearly every set of marks by the upper teeth there was found a set by the lower teeth more or less directly opposed, by its position and orientation indicating that the two sets resulted from one bite.

Certain sets disclosed the relative locations of additional teeth, which were added to the punched-card overlays and used in further study of all sets. The front teeth of upper and lower jaws left marks in one bite, revealing that the jaws tapered evenly throughout their length. The association of pterygoid teeth was used to establish the rear maxillary teeth. The front pterygoid tooth of each side lies proximal and nearly in line with the rear maxillary tooth in known mosasaurs, and we assume that the same relationship in tooth marks on the specimen can be utilized to tell which maxillary tooth was inserted beside the front pterygoid. In several of the bites (Pl. VII, Figs. 1, 3; Pl. VIII, Figs. 4-6), the ammonite extended into the mosasaur's mouth well behind the last teeth which left marks, and which, from their location, intermaxillary angle, and the relation to the pterygoid teeth, we feel certain were the rear teeth. Of the numbered dental positions of premaxillary, maxillary, and dentary teeth, each is represented by a tooth mark from the left jaw, the right jaw, or both (Tables I and II). Of the 22 marginal teeth of the upper jaws, only 3 left no record; and of the 20 teeth of the lower jaws, only 5 failed to hit the specimen. In the superimposed white-line prints shown in Plates IV through IX, the positions of each unrecorded tooth have been filled in symmetrically to the corresponding tooth of the opposite jaw.

The marks produced by shallow, intermediate, and deep penetrations yield reliable cross sections of the teeth at several levels. When the marks representing several bites are superimposed in sequence from the largest

perforations to the smallest dents, they reveal the form of the teeth. From their study it is possible to determine the relative length and curvature of many teeth.

In the upper jaw, the largest teeth were LMx5-6, LMx9, and RMx5. They were nearly straight. LMx4, LMx8, RMx2-4, and RMx6 were somewhat shorter, but they were also major components of the dentition. Of these teeth, only LMx8 was straight; RMx3-4 and RMx6 were slightly

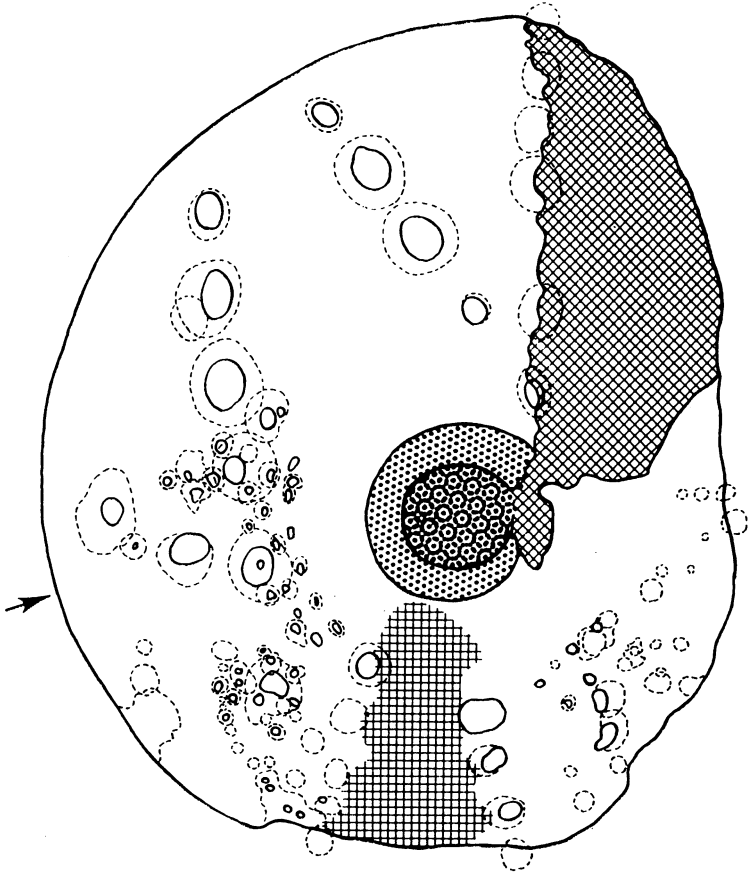


FIG. 2. *Placenticeris* sp. cf. *P. whitfieldi* Hyatt. Left side of specimen with tooth marks of a mosasaur. Compare with Plate I. KEY: vertical and horizontal crosshatching—area covered by matrix; 45-degree crosshatching—crushed zone of shell; dotted patterns—umbilical region; solid lines—outlines of perforations; dashed lines—outlines of crushed zones and dents; arrow—adapical limit of the living chamber (approximate). $\times 3/8$.

curved posteriorly; and LMx4 and RMx2 were moderately curved backward. RMx7 and LMx7 were of medium length; the former was nearly straight, whereas the latter had moderate posterior curvature.

Several maxillaries and premaxillaries left impressions of very small diameter, even in deep bites. These were probably fully developed small teeth at the front of the mouth, rather than incompletely grown replacements. It seems doubtful that all front teeth would have been broken out

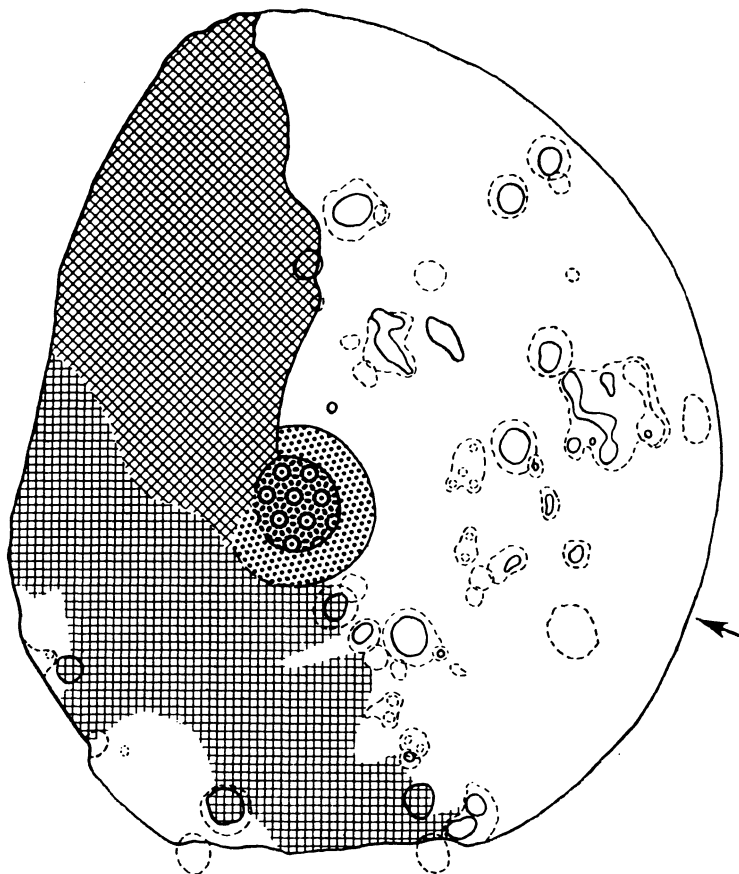


FIG. 3. *Placenticerus* sp. cf. *P. whitfieldi* Hyatt. Right side of specimen with tooth marks of a mosasaur. Compare with Plate II. KEY: vertical and horizontal crosshatching—area covered by matrix; 45-degree crosshatching—crushed zone of shell; dotted patterns—umbilical region; solid lines—outlines of perforations; dashed lines—outlines of crushed zones and dents; arrow—adapical limit of the living chamber (approximate). $\times 3/8$.

at one time and replaced at the same rate. These impressions represent the four premaxillaries, LMx1-2, and RMx1. With the exception of LMx2, which is inclined slightly toward the front, all of these teeth curve backward slightly to moderately.

No marks were found corresponding to LMx3 and RMx8-9. Either these teeth were so small or underdeveloped that they failed to mar the shell in even the most deeply incised bites, or they were missing. Empty tooth sockets are common in many mosasaur skulls, and, considering the loose mode of tooth attachment, there is no reason to doubt that these teeth were temporarily missing at the time of the encounter with the ammonite.

Although marks of the dentary teeth are not as well represented as those of the maxillaries, it was possible to conduct a study similar to that on the maxillaries and premaxillaries. RD5, LD6, and LD9 appear to have been the longest and largest dentary teeth. RD3-4, although known from fewer bites, seem to have been nearly as large. With the exception of RD3, which was straight, all these teeth were recurved posteriorly—LD9 slightly, LD6 moderately, and RD4-5 rather sharply.

RD6 and LD7 were also large teeth, but slightly shorter than those mentioned above. The former was moderately recurved and the latter nearly straight. Dentary teeth of medium length include RD7 and LD10, which were slightly curved backward, and RD2, which was moderately curved.

Several teeth in the lower jaw were small. LD1-3, LD5, and LD8 left only minor dents, even in well-developed bites. These teeth were nearly straight; only LD1 and LD5 displayed a slight posterior curvature. RD1, RD8-10, and LD4 left no record.

The bites offer some evidence on the ease with which larger teeth could be torn out or dislodged. RD5, perhaps the largest dentary tooth, left large dents and perforations whenever it hit the shell until after bite 4. In bites 2 and 4 (Table II) it left larger and deeper marks than RD6. In bite 7, however, it made no impression, although the adjacent teeth perforated the shell. We can only conclude that this tooth was dislodged and lost. A similar fate is postulated for RD7. In bites 2 and 4 (Table II), it produced a record comparable to that of RD6, the tooth immediately in front of it; but in bite 7 and later bites it made no mark whatever, although RD6 perforated the conch in bite 7 and dented it in bite 8.

In summary, the maxillaries were straight or slightly curved and most of them were large, whereas the dentaries were mostly curved, some rather sharply, and smaller than the maxillaries. It is plausible that the size and shape were related to function; the teeth of the upper jaw were used to

stab and to hold the prey, but the teeth of the lower jaw were used to rake the prey and to pull it farther back toward the throat.

After deciding the size, shape, and spacing of the teeth, insofar as we were able, we tried to establish the sequence of the bites. To determine the order in which bites were inflicted, the relationship of each bite to others was investigated. The following considerations were used:

1. When two or more tooth impressions occur in the same area, or overlap, the one which has been modified preceded the other. If a dent is found in the crushed area around the perforation of a tooth in another bite, the dent was made later; otherwise, the crushing around the perforation would have altered or obliterated the dent.

By this criterion, it can be demonstrated that four bites occurred after bite 7. In bite 8 (Pl. VII, Fig. 3) LMx6 made a dent within the crushed zone produced by LMx5 in bite 7. Additional evidence for this sequence can be seen on the other side of the ammonite, where the dent of RD6 in bite 8 (Pl. VII, Fig. 4) is impressed in the crushed zone of RD3 in bite 7 (Pl. VII, Fig. 2). The relationship of marks of pterygoid teeth to crushed zones associated with bite 7 are shown in Pl. III, Fig. 2. In bite 12 (Pl. VIII, Fig. 4) the first and second pterygoids fall within the zone of LMx7, and the fifth pterygoid within the zone of LMx8 in bite 7 (Pl. VII, Fig. 1). The third pterygoid in bite 13 (Pl. VIII, Fig. 5) left its scar in the crushed zone of LMx8 in bite 7. Bites 15 and 16 were subsequent to bite 7, as shown by the fact that in crushing the living chamber they bent down one side of the conch containing the perforation of RMx7 in bite 7 (compare Pl. IX, Figs. 2-3 with Pl. VII, Fig. 1).

2. The coincidence of two or more tooth marks of one bite with those produced by an earlier bite should not be regarded as unusual. The exterior of the ammonite shell was a hard, smooth surface, difficult to seize. In addition, the ammonite was undoubtedly seeking to escape during most of the encounter. As the mosasaur sought to grip this moving, hard discoidal object, it is to be expected that one or more of its teeth would slip into previously made punctures. In bite 8 (Pl. VII, Fig. 3) the right maxillary teeth came into holes made by the previous bite (Pl. VII, Fig. 1), although the jaw had been thrust forward so that RMx4 fitted into the perforation made by RMx3, RMx5 into that of RMx4, and so on. This confirms the sequence of bites 7 and 8, as postulated by the first consideration above. Figures 2 and 3 and Plates I and II show readily that the tendency of the teeth to find purchase in previously made depressions resulted in complexes of closely spaced dents, perforations, and crushed areas in several parts of the shell.

3. When sets of marks by two or more bites occur in the same region

and when the bites were made from the same direction and overlap, the set which projects inward the greatest distance is considered the youngest. This is based on the assumption that mosasaurs fed in a manner similar to that of lizards, their living relatives. A lizard grabs its prey and shifts it farther back in the mouth by a series of bites, in which it momentarily opens the jaws, lunges forward with the head, and grasps again.

There is direct evidence already presented that bite 8 was made after bite 7. Obviously, between these bites (Pl. VII, Figs. 1 and 3) the mosasaur thrust its jaws forward. If one assumes that this sequence represents the habitual feeding behavior of the mosasaur, then bite 1 (Pl. IV, Figs. 1-2) was succeeded by bite 2 (Pl. IV, Figs. 3-4), bite 5 (Pl. VI, Figs. 1-2) initiated a series of bites that ended with bite 8 (Pl. VII, Figs. 3-4), bites 9-11 (Pl. VIII, Figs. 1-3) were followed by bites 12-14 (Pl. VIII, Figs. 4-6), and bite 15 (Pl. IX, Fig. 2) by bite 16 (Pl. IX, Fig. 3).

4. When marks of pterygoid teeth are arranged in nearly parallel rows, as in bites 9-11 and bites 12-14, the row nearest the margin of the shell is presumed to precede the others. Modern lizards tend to center their prey in the mouth to facilitate swallowing. It is logical to assume that the mosasaur also shifted the ammonite toward the center of its mouth. At least one factor supports this theory. Associated with the marks of the left pterygoid teeth and LMx9, there are, on the opposite side of the specimen, curved grooves made by LD10 (Pl. IX, Fig. 1) when the lower jaw was drawn back with great force, tearing and crushing its way through the outer layer of shell. The result of such action would be to center a discoidal object held in the rear region of the mouth.

5. The bites which crushed the outer part of the living chamber are regarded as the last made on the ammonite shell. Undoubtedly, the force of these bites broke the soft parts free from their attachment to the shell. Inasmuch as the crushed fragments of the apertural region caved in, it would seem that the mosasaur concluded its successful attack by seizing the ammonite's arms, jerking the body out of the living chamber, and devouring it. Apparently, the shell was abandoned immediately after the soft parts were removed.

6. During the attack, the cephalopod turned over or the mosasaur changed its approach. In most bites the maxillary and premaxillary teeth struck the left side of the conch and the dentaries the right side, but this orientation was reversed in the first two bites (numbered 1 and 2). These bites, in which the dentaries left impressions on the left side of the ammonite, are closely related, came from the same direction, and overlap, indicating that they were inflicted in succession. Because the final series of

bites show maxillary impressions on the left side, we assume that, after the first two bites, the mosasaur flipped the ammonite over or the ammonite, whose soft parts were as yet uninjured, momentarily escaped and turned around.

Using these considerations, we worked out the following sequence of bites:

Bite 1.—The initial bite (Fig. 4*a*; Pl. IV, Figs. 1–2) resulted in eight impressions on the shell. Teeth of the upper jaw struck the right side of the conch, leaving marks of four maxillary teeth (Table I); LMx5 pro-

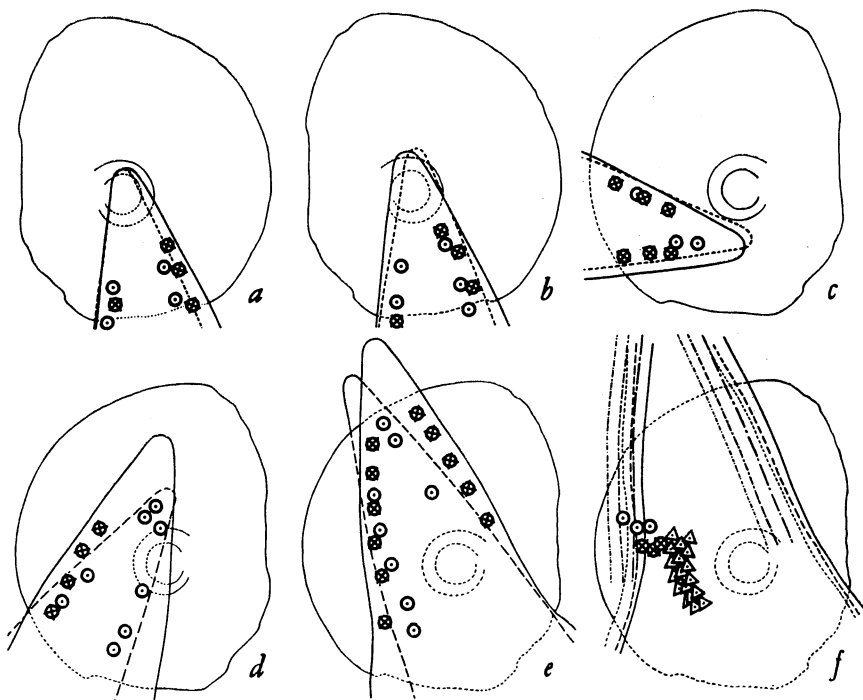


FIG. 4. *Placenticerus* sp. cf. *P. whitfieldi* Hyatt. Six views showing the tooth marks associated in several bites. In each view, the marks of the upper teeth are seen from above and are designated by circles with crosses; positions of the marks of the lower teeth (on the opposite side of the specimen) are designated by circles with dots; marks of pterygoid teeth are designated by triangles around dots. *a*.—Bite 1; compare with Pl. IV, Figs. 1–2. *b*.—Bite 2; compare with Pl. IV, Figs. 3–4. *c*.—Bite 3; compare with Pl. V, Figs. 1–2. *d*.—Bite 4; compare with Pl. V, Figs. 3–4. *e*.—Bite 7; compare with Pl. VII, Figs. 1–2. *f*.—Bites 12–14; compare with Pl. VIII, Figs. 4–6 and Pl. IX, Fig. 1. “Scissors”-type bites are shown in *a*–*c*, “nutcracker”-type bites in *d*–*e*, and “gulp”-type bites in *f*. $\times 0.14$.

duced a perforation, RMx3-4 shallow dents, and RMx5 a deep dent. Four dentary teeth made impressions on the left side of the shell; LD6 and RD6 left perforations, and LD7 and RD5 deep dents. According to our reconstruction of the mosasaur's dentition, based on a composite of all bites, all teeth represented in bite 1 are strongly developed. Since only three perforated the shell, the mosasaur did not exert much pressure in this bite. Teeth anterior to those listed above left no marks because they were over the umbilical region and were not long enough to reach the shell material there.

Each mark is nearly symmetrical, indicating that contact of the teeth was normal to the surface of the shell. Since the bite was directed from the anterodorsal side of the ammonite, above its aperture, the animal may have been picked up from the bottom or attacked while swimming at some distance below the surface.

Bite 2.—This bite (Fig. 4*b*; Pl. IV, Figs. 3-4), more or less superimposed on the first, was inflicted from the same direction and involves about the same teeth. Because it extended farther over the shell, however, it is considered to have followed bite 1. On the right side of the conch, RMx5 made a perforation, RMx2-3 and LMx6 deep dents, and RMx4 a shallow dent. On the left side, LD6-7 and RD5 perforated the shell and RD6-7 dented it deeply. LD6 and RD5 penetrated so far that their expanded bases left concentric crushed zones around the perforations.

As in bite 1, the symmetry of impressions indicates biting normal to the shell surface, and the anterior teeth were over the umbilicus, so that they left no marks. The two jaws were slightly offset in this bite (Fig. 4*b*).

At some time between bites 2 and 3 the position of the ammonite was reversed, so that the maxillary teeth were thereafter on the left side of the conch. There is little evidence as to whether this was caused by the efforts of the ammonite to escape or by the mosasaur forcefully flipping it to secure a better hold. That reversal may have been due to the latter is suggested by the tearing of a triangular piece of shell that was lying between the dentaries, probably sheared by sudden and great force. This could have been done by the mosasaur as he shook the ammonite violently while disengaging his dentary teeth. It seems extremely doubtful that the ammonite, while held in this position, was powerful enough to grasp the mosasaur and wrench itself free by tearing its shell.

Bite 3.—This bite (Fig. 4*c*; Pl. V, Figs. 1-2) was inflicted from the posterodorsal part of the conch in the region of the last septum, and was directed anteriorly. On the left side of the shell, the bite consists of perforations with crushed zones by LMx5 and RMx4 and perforations by LMx4 and RMx2-3; on the right side, it has a perforation by LD6 and

shallow dents by LD5 and RD3-4. All maxillaries that came in contact with the shell perforated it. Teeth anterior to those mentioned were in a region covered by matrix or within the torn triangular sector made after bite 2.

Just after bite 4, the mosasaur probably released the ammonite briefly before grabbing it from another direction.

Bite 4.—This set of tooth marks (Fig. 4*d*; Pl. V, Figs 3-4) was made by a bite from a dorsal and slightly posterior position on the conch. It represents the most extensive bite made to that time. Twelve teeth left distinct impressions: on the left side, LMx5-6 left perforations with crushed areas, LMx4 a perforation, and LMx7 a small dent, and on the right side, LD6 left a perforation, LD7 and RD5 deep dents, and LD1-2, RD2, and RD6-7 small dents. Evidently, this bite was slightly weaker than bite 2, since several teeth did not penetrate as far as before. For example (Table II), LD7 made a deep dent (formerly made a perforation), LD6 a perforation (formerly a perforation with crushed area), RD5 a deep dent (formerly a perforation with crushed area), and RD6-7 small dents (formerly deep dents). Note, however, that the relative lengths of the teeth, based on depths of impressions, agree in both bites. In this bite, the long maxillary teeth crushed in so deeply that they left marks of their expanded osseous bases, whereas only one dentary tooth made a perforation. Perhaps this seeming anomaly is the result of a downward stabbing action, coupled with biting, by the mosasaur.

After bite 4, the cephalopod was again turned before bite 5, which came from still another direction and initiated a series of ten related bites.

Bite 5.—This set of impressions (Pl. VI, Figs. 1-2) is located just above the aperture on the apical part of the outer whorl. It consists of the marks of three maxillaries, four premaxillaries, and one dentary. This is the only record of the premaxillaries. LMx1, LPmx1-2, and RPmx1 left small perforations, and the other teeth produced dents. Presumably, the front teeth of the upper jaw maintained sharp points.

Bite 6.—This bite (Pl. VI, Figs. 3-4) straddles marks of bite 5 and extends inward almost to the umbilicus. Little pressure was applied, and the resulting impressions are poorly developed. Four shallow dents represent LMx2, LMx4, and RMx2-3 on the left side of the shell. Two dents were made by LD5 and RD4 on the right side. By the shallow impressions, we adjudge this bite to be a temporary hold on the ammonite.

Bite 7.—This study was started to investigate the possibility that this set of tooth impressions was inflicted by some marine reptile. Nineteen clear, deep marks form the most dramatic set found on the shell, and from their spacing and penetration, much of the information on the mosasaur's dentition was derived.

On the left side of the conch (Pl. I; Pl. VII, Figs. 1-2), eleven maxillaries, LMx4-9 and RMx3-7, pierced the shell wall. Nearly all teeth penetrated as far as their bases, producing crushed areas up to 10 mm. wide around the perforations; only RMx7 failed to form a crushed area, from which it is inferred that this tooth was a replacement that had not attained full growth. Most crushed zones are nearly tangent one to another, indicating that the teeth had crushed in to about the full extent of their bases.

On the right side, eight dentaries left marks. All except LD8, which is represented by a small dent, perforated the shell wall. Five of these (RD3-4, LD6-7, and LD9) were driven in as far as the bases, crushing the shell around the perforations. As in previous bites, the position of the lower jaw is slightly offset from that of the upper (Fig. 4e), which, from the loose articulation of the lower jaw with the rest of the skull, one might expect.

This was the best hold the mosasaur procured in the entire series of bites. Strong pressure was applied by the jaws, with the tips of the upper and lower teeth penetrating past the center of the conch. The ammonite was held firmly in this position, but it is doubtful that it was killed by the bite. Five right maxillaries and four, perhaps five, left maxillaries stabbed through the living chamber from the left side, and four or five dentaries from the right side. The animal would have been mortally hurt only if one of these teeth had hit its heart or one of the main arteries or veins.

As already pointed out, it is of particular interest that RD5 and RD7, although well represented in bites 2 and 4, leave no mark in this or in succeeding bites. Presumably, these teeth were dislodged during the encounter, at some time after bite 4 and before bite 7. They were not left in the shell during bite 4, since they produced only dents. This bite, the third in a series starting on the dorsal margin with bite 5, was the first bite in which the jaws extended across and beyond the entire ammonite conch. It was also the first bite in which the posterior teeth of both upper and lower jaws came in contact with the shell.

Bite 8.—This bite (Pl. VII, Figs. 3-4) is superimposed on bite 7. Each of the right maxillary teeth involved in the bite utilized the perforation made previously (in bite 7) by the maxillary tooth immediately in front of it. Some of the right maxillaries seem to have distorted the previous punctures, evidence to the dual role of each hole along this line. The left maxillary teeth, however, formed a new line of marks distal to those of bite 7. Apart from the right maxillaries, which occupied or modified perforations of bite 7, the bite includes dents made by LMx6, LMx8, LD6-7, and RD6 and a perforation by LD9. This was a much weaker bite than bite 7.

Each successive bite in this series represents a forward lunge and quick grab by the mosasaur, by which it further engulfed the prey between the jaws, much in the manner of many modern lizards. It is not, in our opinion, a chewing action, but rather successive attempts to gulp down the prey. As can be seen in the photograph and white overlay in Plate VII, the ammonite was too large for the mosasaur to swallow whole.

Bites 9-14.—These six sets of impressions (Fig. 4*f*; Pl. VIII, Figs. 1-6; Pl. IX, Fig. 1) are discussed together because they involve the same teeth and were made by similar biting actions. They differ significantly only in position.

These bites are especially interesting because they include impressions of the pterygoid teeth, and firmly establish that they were made by a mosasaur. Six teeth of the left pterygoid are represented in each of these bites, and we suppose that this was the total number of pterygoid teeth on each side. In each bite, there was ample exposed shell surface in front of the first pterygoid and behind the rear one for any other pterygoids to have left impressions, had they been present. There are no other marks, even in bite 14, in which the left pterygoids were driven far into the shell.

In each bite, LMx9 also pierced the shell. In addition, LD10 left marks on the right side of the shell in bites 12-14 (Pl. IX, Fig. 1). The right pterygoid teeth left no record because, in each of these bites, they were over either the umbilicus or the area torn during bites 1 and 2. Due to the position of the ammonite, far back in the jaws, and the angle of the jaws in biting, only the last marginal teeth in both jaws contacted the shell. The jaws were open so wide that only D10 and Mx9, aligned with the front pterygoid teeth, reached the ammonite.

The marks of the pterygoids occur in two groups of three parallel rows each, one group near the posterodorsal edge and the other near the posterior part of the umbilicus, just inside and superimposed on the left rear maxillary impressions made in bite 7. The distal group, bites 9-11 (Pl. VIII, Figs. 1-3), are made up of three sets of small parallel dents and a few small perforations. Several other little dents are associated with these but do not form complete sets, although as many as three dents in each of several incomplete sets have the proper spacing and orientation. Perhaps these represent additional bites in the series. We did not include them in this numbered sequence and mention them only to indicate that the sequence of events was even more complex than we have outlined.

The proximal group, bites 12-14 (Pl. VIII, Figs. 4-6), is better developed than the distal. In it, most pterygoids perforated the shell wall, leaving well-defined impressions. Bite 14, the best set of pterygoid marks, shows perforations nearly rectangular; apparently, this was the shape of

each pterygoid tooth in cross section near its base. None of the pterygoid impressions has an associated crushed zone around its margins. One may conclude that the teeth did not pierce as far as their bases.

The marks of the pterygoid teeth are small and very closely set. The spacing is unusually close as compared with that in skulls of known mosasaurs. Each group of pterygoid impressions is accompanied by a crushed complex in the position of LMx9, formed when that tooth hit the shell at least three times within a small area. In the distal group the area is so complexly crushed that the position of LMx9 in each bite cannot be determined. In the proximal group, however, the position is better defined (Fig. 4f), and the distance between the marks of LMx9 and the front pterygoid is the same for each bite.

The nature of the impressions made by LD10 on the right side of the conch in bites 12–14 yields information on the specialized movement of the lower jaw. As did the rear maxillary on the opposite side of the shell, LD10 struck the conch at least three times, producing a small complex area of crushing. The position of the tooth in each bite is indicated by a perforation with crushed area, but the perforations are posteriorly drawn out into deep narrow grooves leading to other perforations (Pl. IX, Fig. 1). Evidently, the lower jaw was drawn back with great force during each of these bites in an effort to bring the shell farther back toward the throat. Because the ammonite already abutted against the rear of the mouth, this action succeeded only in raking the teeth through the outer layers of shell wall, forming the grooves. It would seem that after bite 14 the mosasaur discovered the ammonite was too large to swallow whole, for it changed tactics, released the shell, and attacked the soft parts of the animal.

Bite 15.—This bite (Pl. IX, Fig. 2) and the following one were close together and parallel. Because they completely crushed the outer part of the living chamber, only those teeth that came in contact at the inner edge of this area left distinct impressions, although others may have been involved.

Bite 15 is represented by two distinct marks, large crushed areas attributed to LMx5–6. The size of these areas indicates that they were made by expanded tooth bases, and, therefore, that the teeth must certainly have perforated the shell. Except for a small area made by LMx6, these perforations are obliterated by the crushing. Any impressions which may have been made by the dentaries on the right side of the shell are now covered by matrix. The right sides of both jaws were off the margin of the shell. A few shallow dents in front of the aperture could have been made by the pterygoids at this time, but this is uncertain.

Bite 16.—The only definite impressions in this bite (Pl. IX, Fig. 3) are those of LMx5-6 and LMx8, which alternate with those made in bite 15. They are set along the inner edge of the crushed zone. Each is a large, incomplete crushed zone made by the base of the tooth, in which the perforation is more or less obscured by crushed fragments of the living chamber. As in bite 15, marks anterior to the aperture may have been made by pterygoid teeth, but could not be positively identified.

The net result of bites 15 and 16 was to completely crush the outer one-fourth of the living chamber. Undoubtedly, the force of these bites ruptured the membranous band of tissue around the outer edge of the living chamber and disengaged the muscles holding and controlling the position of the body. Presumably, the mosasaur dislodged the soft parts and ate them, because the crushed area of the conch collapsed. That numerous fragments of shell within the crushed area are still in nearly their original relationships can be explained by the presence of a thin membrane lining the living chamber. Although it ruptured along the outer border, this membrane evidently adhered to the crushed fragments and held them in place. Burial must have been rapid, because otherwise bacterial action and scavengers would have destroyed the membrane and released the fragments.

STRUCTURE AND ACTION OF MOSASAUR JAWS

Much has been written and postulated about the action of mosasaur jaws based on relationships of the bones of the head, particularly the articulations of the jaws, but the ammonite described here presents the first available evidence on how mosasaur jaws actually fitted in biting.

Movement of each lower jaw was controlled by the free movement of the quadrate bone at the rear, the hinge developed near its middle, and its junction with the opposite lower jaw at the front. According to Camp's study (1942, pp. 34-35) of mosasaur streptostyly, other parts of the skull also had movable joints; their action may conceivably have played a part in mechanics of the jaws, but we believe it was a minor one.

Independent movement of the quadrate is now firmly established, but it was once thought to be of small amplitude because of the pterygoquadrate junction. In 1898 (p. 102) Williston wrote: "The long, flattened, involute posterior process [of the pterygoid] is curved outward and downward to articulate with the inferior angle of the quadrate. Its roughened end fits closely to a corresponding surface of the quadrate, and, while the union may not be rigid, it cannot admit of much motion."

Later (1914, p. 154) Williston changed his interpretation drastically, and stated: "The quadrates were loosely attached at the upper end,

permitting great freedom of movement in all directions, more even than the land lizards have."

More recently, Camp (1942, p. 35) concluded that "The movement of the head of the quadrate on the squamoso-tabulo-paroccipital border is another joint in the mosasaur cranium which remains loose in the adult skull. This joint allowed the lower jaws to move anteriorly and posteriorly when they were partly or wholly opened."

As can be seen in the lateral view of the head of *Mosasaurus horridus* (Fig. 1), the head of the quadrate possessed a large, strongly curved surface which articulated with the bones of the skull above. Its distal margin fitted into a concavity in the squamosal bone, and its inner part into concavities in the tabular and paroccipital bones (hidden by the squamosal in lateral view). Thus the quadrate was free to rock back and forth in a modified trough.

The base of the quadrate, smaller and less convex than the head, articulated with the rear part of the lower jaw. It fitted into the cotylar cavity, which was shared by the articular and surangular bones. Since each mandible was hinged to the quadrate, and the quadrate was movable at its articulation with the skull, the mosasaur was able to open the lower jaws and to shift them forward and back. This structure enabled the mosasaur to bite in several ways, utilizing at will the movement of the hinge at the base of the quadrate, shifting of the quadrate on the skull, or various combinations of the two.

The unusual hinge in the lower jaw has been known for many years. Cope (1872, pp. 319-20) explained it in great detail; his account, in part, was as follows:

"... and here we have to consider a peculiarity of these creatures, in which they are unique among animals. Swallowing their prey entire like snakes, they were without that wonderful expansibility of throat due in the latter to an arrangement of levers supporting the lower jaw. Instead of this each half of that jaw was articulated or jointed at a point nearly midway between the ear and the chin. This was of the ball-and-socket type, and enabled the jaw to make an angle outward, and so widen by much the space enclosed between it and its fellow The ends of these bones were in the Pythonomorpha [mosasaurs] as independent as in the serpents, being only bound by flexible ligaments The outward movement of the basal half of the jaw necessarily twists in the same direction the column-like bone to which it is suspended. The peculiar shape of the joint by which the last bone is attached to the skull depends on the degree of twist to be permitted, and therefore to the degree of expansion of which the jaws were capable."

Three years later (1875, pp. 113-30) Cope wrote further on mosasaur osteology, and gave essentially the same analysis of the hinge in the lower jaw.

Owen (1877) strongly criticized Cope's work on mosasaurs, denying, among other particulars, that the lower jaw possessed an articulation. According to his explanation, the bones on both outer and inner sides of the mandible overlapped, preventing flexure.

In his equally strong rebuttal, Cope (1878, p. 301) gave the following lucid report on the structure of bones above the ball-and-socket joint: "The anterior extremities of the surangular and coronoid are contracted to an obtuse edge, which fits into a groove or rabbet of the dentary and splenial elements, so as to form a movable joint, the two segments of the ramus being held together by a lamina of bone which in life was doubtless perfectly flexible." [As pointed out by Gregory (1951, p. 350), this "lamina" is the prearticular bone.] Cope's analysis of the osteology was correct, in contrast to those of several later writers.

Williston (1898, pp. 212-13) offered another interpretation of the use of the hinged lower jaws in eating. After postulating that the quadrate was rather firmly united to the pterygoid, he wrote:

"... the remarkable, though incomplete, ball-and-socket joint back of the middle of the jaw is conspicuous, differing in this respect from all other reptiles, ancient or modern.* That there was any degree of vertical motion here is scarcely possible, since the union of the jaw above was too close. As has been described, a thin plate of bone passed across the joint and was ensheathed within the presplenial [splenial], permitting probably a small amount of lateral bending, but little or none of the vertical. The animals living in the water, with no solid objects to aid in deglutition, the body not serpentine enough to coil about the prey and hold while being forced down the gullet, and the limbs non-prehensile and small, it is seen that, without some peculiar modification of the jaws, food would have been swallowed with difficulty. This peculiar modification is seen in the structure of the joint in the jaws. It has been supposed that the prey, after seizure, was pulled down the throat by the alternate protrusion and fixing of the separated jaws. This, however, could not have been true. The mandibles in front, while not rigidly connected, yet show ligamentous union, and, as we have seen, the quadrates were largely fixed by the pterygoids posteriorly. The jaws, acting together, pulled the prey backward by the lateral bending at the articulation, and the nboth were disengaged after the upper jaw teeth and the pterygoid teeth had been inserted."

This supposed action of mosasaur jaws was based entirely on the mechanics of the joints and the freedom which could be assumed for them. Now that the ammonite showing marks of mosasaur bites has been found, it is possible to study how the jaws must have fitted together to produce such bites. Our conclusions differ somewhat from earlier theories.

From a study of the association of marks produced by upper and lower jaw teeth, we have distinguished three types of bites produced by the

* Williston later (1904, p. 47) discovered the same kind of hinged lower jaw in aigialosaurs, the Lower Cretaceous ancestors of the mosasaurs.

mosasaur. The first two resemble those described by Colbert (1954) to point out the different jaw actions in two orders of dinosaurs. He wrote (p. 88): "In the Saurischia . . . the hinge of the jaw is approximately on a line with the tooth sockets. The jaws were closed by a scissors action, with the upper and lower teeth sliding past each other;" and (p. 89): "In the Ornithischia . . . the hinge of the jaw is below the line of the tooth sockets, and the jaws are closed by a 'nutcracker' action, with the teeth clamping together almost all at the same time."

The third type involves the pterygoid teeth, and is similar to the advanced stage in engorgement which Williston (1898, p. 213) envisaged.

The three distinctive bites are designated as follows:

1. "*Scissors*" type.—In this action, the whole of each lower jaw operated as a unit and pivoted at the rear joint formed by its cotylar cavity and the base of the quadrate. The jaws closed with a shearing action, in which the rear teeth first engaged the prey, and successively anterior teeth penetrated only as the jaws were drawn together. When the bite was completed and the jaws fully closed, the dentary teeth came into their normal relationship to the premaxillary and maxillary teeth above. The lower jaws remained rigid in all phases of the bite.

The bites numbered 1 to 3 (Fig. 4*a-c*; Pl. IV, Figs. 1-4; Pl. V, Figs. 1-2) are clearly of this type, as are those numbered 5 and 6 (Pl. VI, Figs. 1-4). In each, the mosasaur struck the ammonite no farther than the umbilicus. Bites 1 and 2 show especially strong shearing action, nearly tearing out a segment of the ammonite. Bites 15 and 16 (Pl. IX, Figs. 2-3), which extend across one side of the ammonite and are responsible for crushing the living chamber, also seem to be scissors type, but the marks of the dentary teeth are covered by matrix and their exact positions cannot be determined.

2. "*Nutcracker*" type.—In this bite, the upper and lower jaws were parallel when they struck the prey. Inasmuch as many teeth engaged simultaneously, they crushed rather than sheared. As shown in bites 4 (Fig. 4*d*; Pl. V, Figs. 3-4), 7 (Fig. 4*e*; Pl. VII, Figs. 1-2), and 8 (Pl. VII, Figs. 3-4), the ammonite was held between the parallel jaws while the teeth perforated. The dentary teeth could be brought into position parallel to those of the upper jaw only when the front half of each mandible was drawn backward, and they could penetrate evenly only when the pivots of the lower jaws were not aligned with the upper jaw. In this type of bite, therefore, each mandible bent at its splenioangular joint and, as a unit, pivoted with the quadrate at its proximal articulation with the skull (see Fig. 1).

The nutcracker type of bite developed differently in dinosaurs and in mosasaurs, but the action of the teeth was very similar. In the ornithischian dinosaurs, the pivot was below the level of the mandibular teeth, at the base of the fixed quadrate, whereas in the mosasaurs it was well above this level, at the head of the movable quadrate.

Contrary to the opinion expressed by Cope (1872, pp. 319–20) and repeated by later paleontologists working on mosasaur skeletons, the front half of each mandible could bend upward at the splenioangular joint without splaying outward. The lower jaws maintained the same intermandibular angle in the nutcracker type of bite as in the scissors type; they did not spread apart laterally to a discernible degree. Compare the locations of dentary teeth in a definite “nutcracker” bite (Pl. VII, Fig. 2) with those in a scissors bite (Pl. V, Fig. 2).

The discovery of this type of bite does not, of course, prove that the lower jaws of other mosasaurs operated in the same way, or even that the jaws of this mosasaur would not have spread apart, had it been able to swallow the ammonite. It does establish that the unique hinge in the lower jaw of mosasaurs did not always function as had been conjectured.

3. “*Gulp*” type.—A distinct type of bite involved only the pterygoid and the rear maxillary teeth above and the rear dentary teeth below. Apparently, when the prey was in the rear part of the mouth, pressure was applied from the upper surfaces of the coronoid bones (Fig. 1). Because only the rear maxillary and dentary teeth left any marks, the bite probably began as a scissors type. There is no evidence that the lower jaw was flexed at its splenioangular joint.

As shown by the elongate sigmoid grooves produced by the rear dentary tooth (Pl. IX, Fig. 1), the lower jaw was pulled back by the quadrate. This action was repeated three times, in bites 12 to 14. The mosasaur attempted thus to pull the ammonite farther toward the throat, and only the large size of the ammonite seems to have prevented its being swallowed. In bite 12 (Pl. VIII, Fig. 4), the ammonite was evidently as far back in the mouth as it could be engulfed, so that, despite the raking action of the rear dentary teeth, it was not forced backward any farther before bites 13 and 14 (Pl. VIII, Figs. 5–6) followed.

It would seem that a smaller ammonite or a soft-bodied animal would have been alternately held by the pterygoid teeth and drawn backward by the action imparted to the rear dentary teeth by the rocking of the quadrates, until finally it was swallowed. Cope’s (1872, p. 319) comparison of the jaw action of mosasaurs to that of snakes, which engorge large prey by a succession of holding and pulling movements, was not entirely inappropriate. From the evidence presented here, however, we conclude that,

in gulping, the mandibles of mosasaurs acted in unison, rather than independently, like those of snakes.

How did the mosasaur bend the mandibles at the splenioangular joints? As pointed out above, the nutcracker type of bite, such as bite 7 (Fig. 4e; Pl. VII, Figs. 1-2), was made when the lower jaw was drawn backward and the tooth-bearing front half was bent upward to bring the mandibular teeth parallel to those of the upper jaw. It is easy to determine that the lower jaw bent at the splenioangular joint, but much more difficult to explain how it bent.

The jaws of modern reptiles have no muscles to lift the front half of the mandible. In living lizards, none of the adductors of the mandible are attached to the dentary or splenial bones; all are attached to the rear part of the jaw. It is highly probable that the jaw muscles in mosasaurs conformed to the general pattern in living reptiles, and that no adductors were developed to elevate the front half of the mandible independent of the rear half.

There is, however, a logical explanation of the bending, based on the kinematic relationships of the joints in the lower jaw. The front half of each mandible, which contained the dentary and splenial bones (Fig. 1), was controlled by the nature of symphysis with the opposite jaw, the splenioangular joint, and the articulations of the quadrate with the mandible and with the skull. The splenioangular joint played a particularly important role in the bending action, but the other structures also contributed. Each has been restudied from published descriptions and from mosasaur specimens in the collection of the Museum of Paleontology at the University of Michigan. From the following analysis we conclude that the bending was a mechanical response to torques created by rotation of the rear half of each jaw as it was drawn back, and that this rotation resulted from the shape and action of the quadrate bone.

1. *The symphysis of the mandibles.*—As Williston pointed out (1898, p. 213) the mandibles “while not rigidly connected, yet show ligamentous union.” Of the seven bites showing marks by dentary teeth of both sides (Table II), all show the same relationship of the two jaws. In none of the bites is one jaw drawn back behind the other. We assume the juncture permitted a small amount of turning of the mandibles but prevented independent movement of one mandible. Apparently, both front halves of the mandibles acted together, so that when one mandible bent at the splenioangular joint, the other bent at its joint by the same amount.

2. *The splenioangular joint.*—The manner in which this joint functioned was strongly influenced by the juncture of the two halves of each mandible, the ball-and-socket device, and the inclination of this part of the jaw to the median plane of the head.

First, although the front and rear halves were not independent, they were not rigidly joined together. The juncture was spanned by a thin lamina of bone extending from the rear half, as described by Cope (1878, p. 301). This is the anterior projection of the prearticular bone (Gregory, 1951, p. 350). The two parts of each mandible were held in position by a scabbard-and-blade arrangement, in which the dentary and splenial bones formed the scabbard and the prearticular bone the blade. As illustrated by Gregory (1951, Fig. 5), in *Platecarpus* the extension of the prearticular bone from the rear part of the jaw was broad but very thin, whereas the scabbard formed by the front half of the jaw was very spacious. In life, however, much of the cavity was occupied by Meckel's cartilage and by cartilage associated with the bones. The prearticular bone undoubtedly did not fit as loosely within the front part of the mandible as the fossilized bones would suggest.

Cope (1878, p. 301) and Williston (1898, p. 212) supposed that the jaws expanded outward at the splenioangular joints and that the extensions of the prearticular bones served as springs to restore the jaws to their normal shape. This analysis now appears to be unacceptable, particularly because the intermandibular angle does not perceptibly change from the scissors bite, in which the mandibles are straight (Fig. 4*b*), to the nut-cracker bite, in which they are drawn back and bent (Fig. 4*e*).

The extension of the prearticular bone probably served primarily as a control for movement of the joint below, sliding freely back and forth when the front half of the jaw was bent up or down but resisting, by its rigidity, any appreciable lateral bending of the jaw. As Cope recognized (1878, p. 301), the rear half of the jaw tapers forward to an obtuse edge and the front half is rabbetted posteriorly. When the front half was bent upward, we believe, the narrow edges of the surangular and coronoid bones were accommodated in the recess of the dentary and splenial bones, in a tongue-and-groove structure.

Second, the ball-and-socket shape of the joint at the lower edge of the jaw did *not* insure that "great freedom of movement in all directions . . ." was possible, as Williston stated (p. 154). With the limitations imposed by the sheathing around the prearticular bone above, it is much more likely that the splenioangular joint was functionally a hinge, rather than a true ball-and-socket joint. In other words, the joint was ginglymoid rather than enarthrodial. Movement was restricted to a plane essentially parallel to the side of the mandible and passing through the joint and the extension of the prearticular bone.

Third, the sides of the mandible at the joint are not vertical, as some have assumed. A specimen of *Plotosaurus bennisoni* (Camp), described

and illustrated by Camp (1942, pp. 2-8, Fig. 1, Pl. 1) and here shown in Fig. 5, has the mandibles preserved in place. As can be readily seen, the side of each mandible slants upward and outward from the splenioangular joint at an angle of about 45 degrees to the median plane of the head. This inclination becomes significant when one considers the operation of the jaws. For the front halves of the two mandibles to bend upward, it was necessary either that the front tips of the mandibles were drawn a considerable distance apart or that the mandibles were rotated about their long

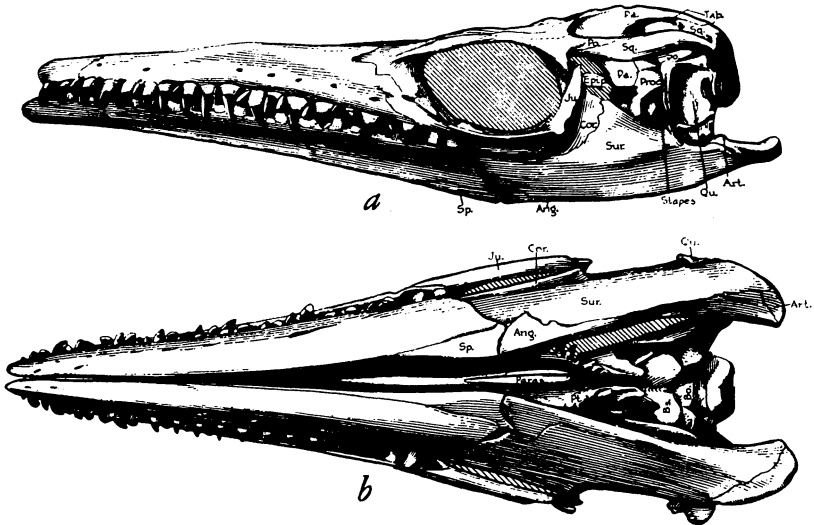


FIG. 5. *Plotosaurus bennisoni* (Camp). *a, b*. Left lateral and ventral views of an excellently preserved mosasaur head in which the mandibles occur in their natural positions. Note the proximity of the left and right splenioangular joints. $\times 1/5$. (After Camp, 1942, Fig. 1).

axes. Inasmuch as the former seems impossible, we assume that the upward bending was accompanied by a rotation or twisting of the mandibles. Rotation of the rear halves of the mandibles, such that the upper edges were turned inward and the lower edges outward, would produce a torque forcing the front halves of the mandibles upward.

Our study of skull bones of *Platecarpus* in the collection of the Museum of Paleontology of the University of Michigan indicates that peculiarities of the quadrate bones and their articulation to the rest of the skull caused the rotation of the mandibles. Not all of the long, curved head of each quadrate was in contact with the articulating surface at one time. The part of the head that articulated at a particular time determined the angle

which the quadrate bone assumed in reference to the midplane of the skull. As seen from the rear, the head of each quadrate is slightly twisted and curves back at an angle to the shaft. In addition, the articulating surfaces on the squamosal, tabular, and paroccipital bones, which fit against the quadrate, are not quite parallel to the midplane of the skull; instead, they are set at a slight angle. As a result, each quadrate bone hung nearly vertical when the front part of its head was involved in the articulation, but its base swung outward when the lower jaw was drawn back, bringing the twisted rear part of the quadrate head into the region of articulation. Since the cotylar cavity was a trough extending across the rear part of the mandible, outward movement of the base of the quadrate rotated the mandible. The amplitude of the rotation, although small, created enough torque, in our opinion, to force the front half of the jaw upward.

Briefly, we postulate that the following factors were responsible for maintaining the mandibles straight in the scissors bite, but bending them at the splenioangular joint in the nutcracker bite. When the jaws were closed or used in a scissors bite, the front part of the head of each quadrate articulated with the skull. The quadrate hung vertical, and the mandible hinged on the base of the quadrate. Since no stress was applied at the splenioangular joint, the lower jaw could open or close while remaining straight. When the jaws were used in a nutcracker bite, however, the lower jaw was drawn back, rocking the rear part of the quadrate head forward to the place of articulation. This caused the base of the quadrate to swing out, imparting rotation to the mandible at the cotylus; thereupon, the resulting torque pressed the front end of the dentary against the opposite one at the symphysis. Because the splenioangular joints acted essentially as oblique ginglymi (rather than as enarthroses or ball-and-socket joints), the only resolution of forces possible to the torques on the mandibles and the pressure of one dentary against the other was upward movement at the front of the jaws, bending them at the splenioangular joints.

RELATIONSHIPS OF THE MOSASAUR

Although the individual that left the tooth marks on the ammonite appears to belong to an undescribed species, comparison of the patterns of the marks with those of teeth in known mosasaurs indicates that the animal in question was a member of the subfamily Platecarpinae and closely related to *Platecarpus brachycephalus* Loomis and *Ancylocentrum overtoni* (Williston).

Mosasaurs have been divided into the Globidentinae, Tylosaurinae, Mosasaurinae, and Platecarpinae. These four subfamilies are compared in Table III, which shows that nine genera have been found in Upper

TABLE III
COMPARISON OF SUBFAMILIES OF MOSASAURS*

	Globidentinae	Tylosaurinae	Mososaurinae	Platecarpinae
Genera known from Upper Cretaceous deposits in North America	<i>Globidens</i> Gilmore 1912	<i>Tylosaurus</i> Marsh 1872 <i>Macrosaurus</i> Owen 1849 <i>Plesiotylosaurus</i> Camp 1942	<i>Mosaurus</i> Conybeare 1882 <i>Chidastes</i> Cope 1868 <i>Plotosaurus</i> Camp 1951	<i>Platecarpus</i> Cope 1869 <i>Ancylacentrum</i> Schmidt 1927
Genera known from Pierre shale			<i>Mosaurus</i> , <i>Chidastes</i>	<i>Platecarpus</i> , <i>Ancylacentrum</i>
Presumed habitat of animal	shelf-feeders	divers	surface forms, shallow water	high seas, some divers
Premaxillary, maxillary, and dentary teeth	mushroom-shaped terminating in knoblike processes	relatively smaller than in other genera	well developed, faceted on outer side and smooth on inner, or smooth throughout	long, slender, recurved, faceted on outer side, striate on inner
Body size	medium	medium to large	<i>Mosaurus</i> the largest known; <i>Chidastes</i> very small to medium	medium
Skull	unknown width	very slender	intermediate	broad
Trunk	unknown	short	relatively long	short
Leg bones	unknown	radius and ulna slender	short and expanded	short and expanded
Carpus and tarsus	unknown	almost wholly ossified	fully ossified	imperfectly ossified
Flippers	unknown	modified into elongate paddles of equal size	relatively small, digits distinct, rear ones smaller than front	relatively large, digits distinct
Phalanges	unknown	very numerous, supernumerary bones	few, not more than 6 to any digit	few, resembling those of Mososaurinae
Tail	unknown	proportionally long, not dilated	compressed, distally dilated to form a fin	proportionally long, not dilated
Premaxillary	unknown	projecting as a long rostrum	rostrum short, obtusely conical	short, very obtuse
Pterygoid teeth	unknown	large	intermediate	small in <i>Platecarpus</i>
Quadrate bone	unknown	short, broad suprastapedial process, more like that of <i>Chidastes</i> than <i>Platecarpus</i>	relatively small with suprastapedial process reaching about to middle of bone	large, suprastapedial process extending below middle of bone

* Based on Williston (1898, 1925), Hay (1930), and Romer (1956).

Cretaceous deposits of North America. Only four of these are known from the Pierre shale or stratigraphic equivalents.

Many excellent specimens of *Mosasaurus horridus*, *Clidastes velox*, *Platecarpus coryphaeus*, and *Tylosaurus proriger* have been discovered in the Upper Cretaceous beds of Kansas, Colorado, South Dakota, and Wyoming. Restorations of the skulls and complete skeletons by Williston (1897, Pl. 13; 1898, Pls. 10–21, 72) and Osborn (1899, Fig. 2) have very little about them that is conjectural. However, published descriptions of mosasaurs contain no extensive lists of measurements of size and spacing of the premaxillary, maxillary, dentary, and pterygoid teeth. Fortunately, restorations, particularly those of Williston (1898), have been based on exceptional specimens of each species available at that time and are reliable within very narrow limits. From his plates, therefore, reasonably accurate details of dentition can be secured. In addition, some measurements have been made on specimens at the University of Michigan. Selected characteristics and measurements of the species mentioned above are compared with the tooth marks on the ammonite in Tables IV and V.

Globidentinae.—The *Globidentinae*, represented by only the type genus, have unusual teeth. Each tooth is more or less mushroom-shaped, consisting of a cylindrical base, a short shaft or constriction, and a terminal knob-like process. In the two species known, the diameter of the knoblike process is greater than the base. Obviously, the dents, small perforations, deep perforations, and impressions of broad bases on the ammonite were not made by teeth of this type. It may be pointed out that Dollo (1913, p. 620) believed *Globidens* fed on echinoids. Probably, as suggested by Williston (1914, p. 167) and others, the teeth were adapted for feeding on any shelled invertebrates.

Tylosaurinae.—This is a better known subfamily. Many nearly complete skeletons have been discovered. The tylosaurs are medium to large mosasaurs with very slender skulls, short trunks, and long tails. Their extremities are much more modified than those of other mosasaurs, having been converted into elongate paddles around numerous supernumerary phalanges. The carpus and tarsus in these mosasaurs are nearly all cartilage. The premaxillary bone projects in front of the teeth as a long rostrum. The marginal teeth are comparatively small, but the pterygoid teeth are unusually large. The tylosaurs are thought to have been divers.

As shown in Table IV, the upper jaw of *Tylosaurus proriger* tapers rapidly from a large intermaxillary angle at the rear to a very narrow angle at the front, so that the snout has concave sides (Fig. 6*d*). In contrast, the pattern of marks of upper teeth on the conch shows that the intermaxillary angle is slightly less at the rear than at the front, so that the snout of the

TABLE IV
CHARACTERISTICS OF CERTAIN MOSASAURS
COMPARED WITH TOOTH MARKS ON AMMONITE*

	<i>Tylosaurus proriger</i>	<i>Mosasaurus horridus</i>	<i>Clidastes velox</i>	<i>Platecarpus coryphaeus</i>	Tooth marks on ammonite
Number of pre-maxillary and maxillary teeth	15	16	17, or 18 with last one small	14	11
Pterygoid teeth	10, teeth beginning farther forward, as in <i>Clidastes</i> , and not back of palatines	8 in single curve, reaching from before the posterior end of palatine, and opposite last maxillary tooth	12, greatest number known, anterior ones larger than posterior, all crowded together, moderately flattened with distinct carina	10 in reverse curve, small, much curved, somewhat flattened and striate	At least 6 in single curve, small and much flattened, about equal, evenly spaced
Position of front pterygoid tooth	ahead of rear Mx tooth	aligned with rear Mx tooth	aligned with rear Mx tooth	well behind rear Mx tooth	aligned with rear Mx tooth
Tips of pterygoid teeth	extend to level of longest Mx teeth	extend to general level of Mx tooth	front tooth at level of rear Mx, other pterygoids to level of last two Mx	all Mx teeth except rear one extending below level of the pterygoids	extend only to level of rear Mx, or slightly less
Intermaxillary angle (anterior third of upper jaw)	15°	16.5°	23°	24.5°	29°
Intermaxillary angle (posterior third of upper jaw)	32.5°	31°	22°	27°	23°

* Characteristics of mosasaurs based on descriptions and plates (restorations) of Williston (1898).

TABLE V
 VARIOUS MEASUREMENTS (IN MILLIMETERS) OF FIVE MOSASAURS
 COMPARED WITH TOOTH MARKS ON AMMONITE

	<i>Tylosaurus proriger</i> (Cope)	<i>Mosasaurus horridus</i> Williston	<i>Clidastes velox</i> (Marsh)	<i>Ancylocentrum overtoni</i> (Williston)	<i>Platecarpus coryphaeus</i> Cope	<i>Platecarpus brachycephalus</i> Loomis	Toothmarks on ammonite
Distance between rear Mx teeth	200	232	112	258*	138	145‡	133
Width frontal bone	195	239	104	270	145	156‡	...
Each Pmx and Mx tooth row	477	557	265	546†	302	292‡	257
Each pterygoid tooth row	160	175	118	...	126	...	At least 61
Distance between front pterygoid teeth	75	132	50	...	69	...	69
Diameter base largest Mx	30 x 40	36 x 42	13 x 20	27 x 34	21 x 25	23 x 24‡	27 x 32
Diameter shaft largest Mx	13 x 18	19 x 27	5 x 8	19 x 23½	9 x 13	13 x 19‡	14½ x 16½
Diameter shaft largest pterygoid tooth	12½ x 16	11 x 13	3 x 5	...	4 x 6	...	At least 2 x 4
Average spacing Pmx and Mx teeth	34.1	37.1	15.1	45.5†	23.2	24.3‡	25.7
Average spacing six front pterygoid teeth	11	26	11	...	16	...	13
Number of Pmx and Mx teeth	15	16	17 or 18	12 or 13	14	13	11
Number of dentary teeth	13	14	18	12 or 13	11	11	10
Total length of mandible	948	1013	460	1050	557	603	...
Total length of mosasaur	6341	...	3466	...	4257	4485	...

* Estimated from width of frontal bone.

† Estimated from spacing of dentary teeth.

‡ Estimated from figures and photographs of the two type specimens.

mosasaur had convex sides. *T. proriger* also has a proportionally longer row of upper teeth than the mosasaur which bit the ammonite; in *T. proriger* the tooth row is about 2.4 times the distance between the rear maxillaries, whereas the marks on the ammonite indicate a tooth row only about 1.9 times the distance between rear maxillaries (Table VI). Furthermore, *T. proriger* has 15 marginal teeth in each upper jaw, but the ammonite bears marks of only 11 (we believe the full set is represented in this number).

The pterygoid teeth also show significant differences. In *Tylosaurus* they extend down to the level of the tips of the longest maxillary teeth, but on the ammonite shell these teeth left marks only when the rear maxillaries struck the shell at an inclined angle (in what we have called the "gulp" type of bite), and hence they probably did not extend quite to the level of the rear maxillary teeth (Table IV). The front pterygoid teeth of *T. proriger* lie ahead of the rear maxillaries and are set rather closely together (Table VI; Fig. 6*d*); but the tooth marks show that the front pterygoids were aligned with the rear maxillaries and set proportionally much farther apart (Pl. VIII, Fig. 6). We conclude that the ammonite was not bitten by a mosasaur of the Tylosaurinae.

Mososaurinae.—The Mososaurinae include individuals ranging in length from 2 to 12 meters or more. The subfamily is best known from skeletons of *Mosasaurus* and *Clidastes*. These two genera differ considerably, but both have skulls intermediate in width, rather long trunks, and tails that are expanded near the end to form a caudal fin. Front and rear leg bones are short and stout, the wrists and ankles completely ossified, and the paddles relatively small, with distinct digits. In contrast to the tylosaurs, these mosasaurs do not have the upper jaws projecting as a rostrum. The marginal teeth are strong, and the pterygoid teeth intermediate in size between those in the Platecarpinae and those in the Tylosaurinae. The quadrate is rather small, with the suprastapedial process curved down only to the middle of the bone. Mosasaurs of this subfamily are presumed to have been swimmers in shallow water.

The upper tooth rows revealed on the specimen of *Placenticeras* do not taper forward as in *Mosasaurus horridus* nor do they form as narrow an angle as in *Clidastes velox*; instead, they make an average intermaxillary angle of approximately 26 degrees with slightly convex sides. As deduced from their perforations, the pterygoid teeth of the unknown mosasaur did not attain the level of any except, perhaps, the rear maxillary teeth; in this, they differ from those of *Mosasaurus horridus* or *Clidastes velox*, which project farther (Table IV). The length of each row of upper teeth was proportionally much less than that in *Mosasaurus* or *Clidastes* (Table VI).

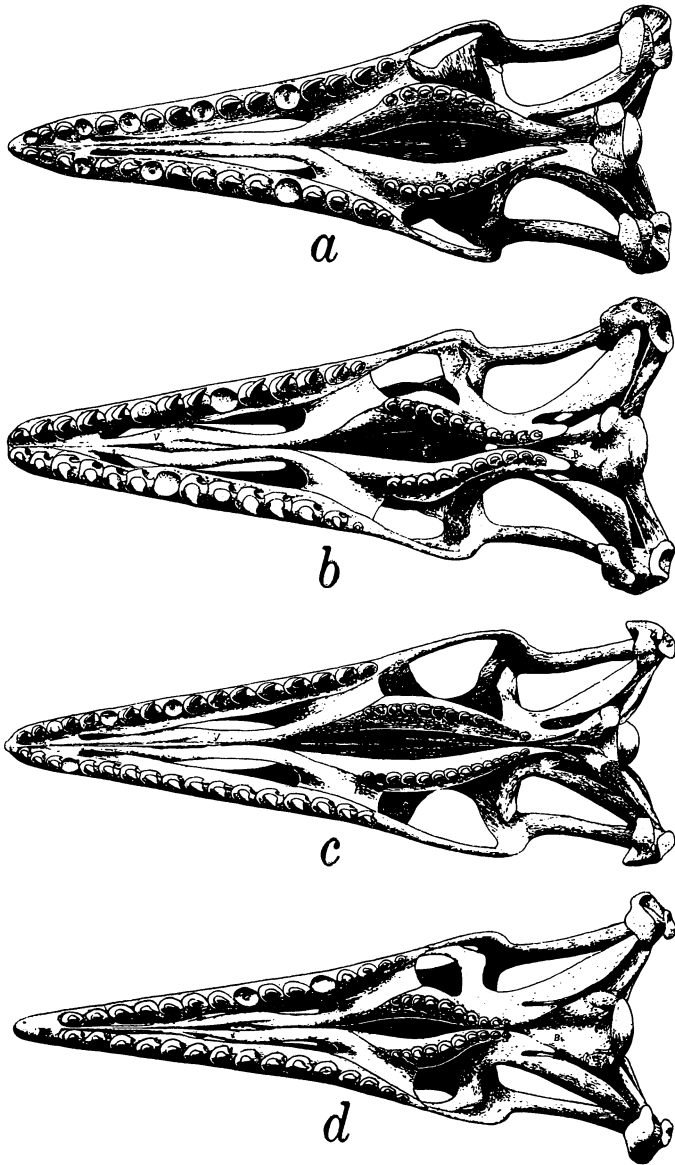


FIG. 6. Ventral views of four mosasaur skulls. *a*.—*Mosasaurus horridus* Williston, $\times 0.085$. *b*.—*Platecarpus coryphaeus* Cope, $\times 0.154$. *c*.—*Clidastes velox* Marsh, $\times 0.175$. *d*.—*Tylosaurus proriger* Cope, $\times 0.154$. All figures after Williston, 1898, Pls. 21, 15, 12, and 18.

TABLE VI
RATIOS OF VARIOUS MEASUREMENTS TO DISTANCE BETWEEN REAR MAXILLARY TEETH

	<i>Tylosaurus proriger</i> (Cope)	<i>Mosasaurus horridus</i> Williston	<i>Cladastes velox</i> (Marsh)	<i>Ancylocentrum overtoni</i> (Williston)*	<i>Platycarpus coryphaeus</i> Cope	<i>Platycarpus brachycephalus</i> Loomis†	Tooth marks on ammonite
Width frontal bone	.98	1.03	.93	1.05	1.05	1.08	...
Each Pmx and Mx tooth row	2.38	2.40	2.37	2.12†	2.19	2.02	1.93
Each pterygoid tooth row	.80	.75	1.0591	...	At least .46
Distance between front pterygoid teeth	.38	.57	.455052
Diameter base largest Mx	.15 x .20	.16 x .18	.12 x .18	.10 x .13	.15 x .18	.16 x .17	.20 x .24
Diameter shaft largest Mx	.07 x .09	.08 x .12	.04 x .07	.07 x .09	.07 x .09	.09 x .13	.11 x .12
Diameter shaft largest pterygoid tooth	.06 x .08	.05 x .06	.03 x .0403 x .04	...	At least .01 x .03
Average spacing Pmx and Mx teeth	.17	.16	.13	.18†	.17	.17	.19
Average spacing six front pterygoid teeth	.06	.11	.101209
Total length of mandible	4.74	4.37	4.11	4.07	4.04	4.16	...
Total length of mosasaur	31.71	...	30.95	...	30.85	30.92	...

* Distance between rear maxillary teeth estimated from width of frontal bone.

† Estimated from spacing of dentary teeth.

‡ All measurements except total lengths of mandible and mosasaur estimated from figures and photographs of the two type specimens.

Platecarpinae.—This subfamily is very well known from specimens of *Platecarpus*, many of which are remarkably well preserved. All platecarps are of medium size, with broad skulls, short trunks, and long tapering tails. Front and rear legs are short and broad, wrists and ankles somewhat ossified, and the flippers large, with distinct digits. The extremities thus resemble those in the Mososaurinae (except for their larger size) rather than the oarlike paddles in the Tylosaurinae. The marginal teeth are long and recurved, set on broad bases. The quadrate is unusually large, with a suprapedial process curved down below the middle of the bone and, in *Ancylocentrum*, fused below with the infrapedial process on the basal part of the bone.

Platecarpinae are thought to have roamed the high seas. One genus, *Plioplatecarpus*, has calcified tympanic opercula over the ear bones, from which it has been inferred that it was a deep diver, able to withstand tremendous pressure (Dollo, 1904, p. 210; 1905, pp. 125–30). The fusion of the suprapedial and infrapedial processes in the quadrate of *Ancylocentrum* encloses an opening for the ear which could readily accommodate a calcified operculum, although none has yet been discovered. The occurrence of belemnite remains within the skeleton of *Plioplatecarpus* led Dollo (1913, p. 618) to conclude that this mosasaur fed on such cephalopods.

The pattern of dents and perforations on the conch are much more like those in the Platecarpinae than those in the Mososaurinae. Because the distance between the rear maxillary teeth is nearly the same as the width of the frontal bone in known mosasaurs (Table V), we assume that the mosasaur that attacked the ammonite had a relatively broad head. The Platecarpinae have skulls broader than those in either the Mososaurinae or the Tylosaurinae (Table III).

Two species of the subfamily, *Platecarpus brachycephalus* and *Ancylocentrum overtoni*, have teeth arranged in a pattern resembling the marks on the cephalopod. Both occur in the Pierre shale of the Western Interior region, probably in strata near or within the Virgin Creek member, from which we believe the ammonite was obtained.

The mosasaur remains from which *Ancylocentrum overtoni* was described were found in strata and at the locality which Williston (1897, p. 95) gave as: "The horizon whence the specimen was obtained is near the top of the Pierre deposits of the Cheyenne river of South Dakota, and probably a hundred or more feet above that of *Mosasaurus horridus* described by me. It thus, it is seen, represents one of the latest forms hitherto made known from North America." The *Mosasaurus horridus* specimen referred to by Williston came from a bed that he previously

(1895, p. 166) mentioned as a "hard, nodular matrix of a bluish color," with some of the bones embedded in very hard, finegrained limestone nodules, several inches thick, which were bluish-gray in the middle and weathered to ochre on the outside. This lithology is like that of the Virgin Creek member of the Pierre shale. In central South Dakota the member is 185 to 225 feet thick (Crandell, 1950, p. 2338). Hence, the type specimens of both *Mosasaurus horridus* and *Ancyllocentrum overtoni* may have come from the Virgin Creek member.

Ancyllocentrum is known only from incomplete specimens of the type species, *A. overtoni* (Williston). Williston (1895, p. 169) first mentioned this species and named it *Overtoni* without assigning it to any genus. He said (p. 169): "In the University Museum there is a large part of an individual from nearly the same horizon as that of *M. horridus*, which I am not yet able to refer to any known genus, and which I believe to be distinct. It is remarkable for the very broad head, short jaws, with only eleven teeth in the maxilla and thirteen in the mandible, stout, unfaceted teeth and peculiarities of the limb bones which distinguish it from *Platecarpus*, its nearest ally . . ."

Later (1897a, pp. 95-98), Williston set up the genus *Brachysaurus* based on this species. He described it as follows (pp. 96-97):

The mandibles are remarkably stout, and have not more than fourteen teeth implanted in them. . . . The maxillae are likewise stout, and have twelve teeth implanted in each. The teeth are remarkably stout, much more so than in the other genera, save perhaps, *Tylosaurus*. They are moderately recurved and are smooth throughout, with a weak carina fore and aft. From the shape of the maxillae, the length of the lower jaws, and the breadth of the frontal bone, it is quite evident that the rostrum was not much prolonged in front of the teeth. The frontal bone is remarkably broad and heavy. . . . Altogether, the animal possessed a remarkably stout and broad head, with short jaws and teeth, and evidently short, broad and stout paddles, and short body.

Later, Schmidt (1927, pp. 58-59) discovered that the *Brachysaurus* of Williston was a junior homonym, and renamed the genus *Ancyllocentrum*.

Unfortunately, no skull of *Ancyllocentrum overtoni* has yet been found articulated and uncrushed. The distance between the rear maxillary teeth can be estimated from the width of a well-preserved frontal bone, for which Williston (1897a, Pl. 8, Fig. 2) gave measurements and an illustration. Furthermore, the material recovered includes a nearly complete mandible, both maxillae, and the frontal bone, as well as other bones of the skull, vertebrae, and limbs (Williston, 1897a, p. 95), so that the dentition of this species can be compared with the tooth marks on the ammonite.

Of *Mosasaurus horridus*, *Clidastes velox*, *Tylosaurus proriger*, *Platecarpus coryphaeus*, *P. brachycephalus*, and *Ancyllocentrum overtoni*, the

last two most closely agree with the pattern found on the conch in regard to the ratios of the premaxillary and maxillary tooth rows and the average spacing of these teeth to the distance between the rear maxillaries (Table VI). The ammonite, however, was perforated and crushed by proportionally larger maxillary teeth than those found in any of the six species just mentioned (Table VI).

Loomis (1915) described *Platecarpus brachycephalus* from specimens obtained in eastern Wyoming, about 20 miles due west of Edgemont, South Dakota, but did not offer any details of stratigraphy. The mosasaurs were found in the same bed as invertebrate shells, including *Inoceramus barabini* Morton and *I. sagensis* Owen (Loomis, 1915, p. 555). If these identifications are correct, both of these pelecypods must have come from the DeGrey, Verendrye, or Virgin Creek members, since these are the only beds in which the higher part of the range of *I. barabini* overlaps the lower part of the range of *I. sagensis* (see Cobban and Reeside, 1952, Chart 10b). In addition, Crandell (1950, p. 2337) reports that two mosasaurs from the Verendrye member in central South Dakota were identified by Dr. David H. Dunkle, of the United States National Museum, as *Platecarpus* sp. cf. *P. brachycephalus* Loomis.

The type specimens of *Platecarpus brachycephalus* are in the Amherst College Museum. Their exact status is not clear. Loomis (1915, p. 556) wrote that "I take as the type the disassociated skull, No. 389 in the Amherst Collection, and as a cotype the complete skull No. 398." The first specimen, referred to as the "type," is treated in the original description more or less like a holotype, and No. 398 (called a "cotype") and a specimen with many vertebrae in place, No. 388, are treated like paratypes. Due to muddled numbering of the types originally, the "type" has been renumbered A.C.M. No. 404. Through the courtesy of Dr. George W. Bain, of the Department of Geology at Amherst College, we obtained excellent photographs of the head of the "type," and through the courtesy of Dr. Albert E. Wood, of the Department of Biology at Amherst, a description of this specimen and the "cotype." As Dr. Wood states (letter dated October 30, 1959): "The type . . . includes considerable parts of the skeleton and a considerably disarticulated skull. The snout is present, as far back as the vomers, and the basicranium is present, but thoroughly messed up. These are exposed from the ventral surface. . . . Certainly, no pterygoid teeth are visible. . . . The cotype, No. 389, is also mounted as a block, with only the dorsum exposed."

In the "type," the maxillaries are apparently disjointed from the premaxillaries and somewhat twisted. Each maxilla is askew, with its teeth shoved toward the right side of the head; the two maxillary bones are

distorted so that the intermaxillary angle has been decreased. In contrast, as shown in the original figure (Loomis, 1915, Fig. 1), here reproduced as Figure 7, the "cotype" has each side of the skull splayed outward, so that the intermaxillary angle has been increased. Our estimates of certain measurements (Tables V and VI) for *Platecarpus brachycephalus* are averages based on photographs and figures of the type specimens. For example, the entry for "Average spacing Pmx and Mx teeth" is based on

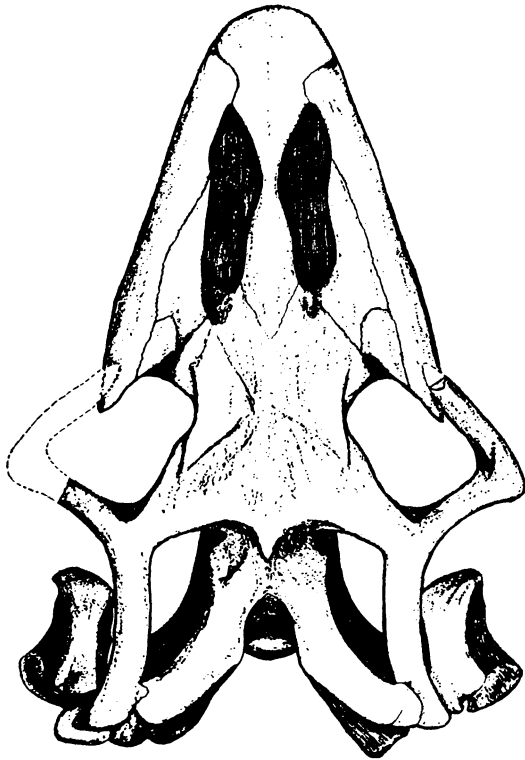


FIG. 7. *Platecarpus brachycephalus* Loomis. Top view of skull of the "cotype," Amherst College Museum No. 389. $\times 1/6$. From Loomis, 1915, Fig. 1.

the spacing of the maxillary teeth multiplied by the number of spaces in the row of premaxillary and maxillary teeth. The figures for total length of the mandible and for total length of the mosasaur are those reported by Loomis (1915, pp. 561, 563).

Although the "cotype" has been crushed and splayed outward, the convexity of its maxillary bones appears to be the natural shape and not

the result of compression. This is of particular interest because, if our interpretation is right, this is the only mosasaur with maxillaries convex like the rows of maxillary-tooth marks on the ammonite. Other mosasaurs, like those shown in Figure 6, have concave maxillary bones.

The jaws of the "type" of *Platecarpus brachycephalus* are only a little larger than those which bit the *Placenticerus* (Table V). Of the several species compared in Table VI, *P. brachycephalus* has upper teeth in a pattern most nearly like that found in the marks on the ammonite, as shown in the ratio of each Pmx-Mx tooth row to the distance between rear maxillary teeth. Differences between *P. brachycephalus* and the attacker are: (1) it has 13 premaxillary and maxillary teeth as compared to marks of 11 recorded on the ammonite; (2) it has 11 dentary teeth as compared to 10; (3) its premaxillary and maxillary teeth are slightly closer together, and (4) the bases of its teeth are a little smaller than the crushed zones on the ammonite (Pls. I and II).

In our opinion, the mosasaur that bit the *Placenticerus* is an undescribed species or, perhaps, a species known only from very fragmentary remains. It belongs to the subfamily Platecarpinae. It had a snout even blunter than that of *Ancylocentrum overtoni* and comparable to that of *Platecarpus brachycephalus*. Its marginal teeth were fewer but proportionately larger than those in described mosasaurs, and its pterygoid teeth were set rather close together in each row, but not as close as those in *Tylosaurus*. Although each pterygoid row is markedly shorter than any described (Table VI), it seems doubtful that there were any additional small pterygoid teeth at the rear which were so short they left no record. From the proportions of *Platecarpus* and *Ancylocentrum* we postulate that the mosasaur in question was about 4.1 meters long, with a mandible slightly longer than half a meter.

Was the attack opportunistic or intentional? Did the mosasaur come upon the *Placenticerus* by chance or did he seek out and pursue it? Was the kill for sport or for food? Although only one ammonite is now known with bite marks (and those made by an unknown mosasaur), we wish to point out the following:

1. The initial attack was directed at the upper side of the conch, providing the ammonite was swimming in the normal position used by its living relative, *Nautilus*. The mosasaur must have dived at it from above to seize it. The attack was pertinacious, resulting in at least sixteen bites. As shown by the marks of pterygoid teeth in the sequence of bites, the mosasaur evidently tried to swallow the entire ammonite, pulling it as far back into the throat as possible.

2. The mosasaur that bit the ammonite had large, conical, slightly curved marginal teeth mounted on exceptionally broad bases, well suited for seizing and crushing. It had only 11 upper marginal teeth and 10 lower ones (Table V)—fewer than those in any known mosasaur. In other vertebrate groups, the adaptation to crushing shellfish has been accompanied by a reduction in the number of teeth.

3. The two described mosasaurs having blunt snouts and less than 12 dentary teeth are *Platecarpus brachycephalus* and *Ancylocentrum overtoni*, both probably contemporaries of the *Placenticerus* specimen. In addition, the rows of tooth marks on the *Placenticerus* are slightly convex outward, as are the maxillary bones in the cotype of *Platecarpus brachycephalus*.

Conclusions.—From these considerations, we are of the opinion that the mosasaur was in the habit of eating ammonites. The plan of assault—seizure from above, attempt to swallow whole, and failing this, crushing the living chamber to squeeze out the soft parts—seems to indicate familiarity with the prey. The large, conical biting teeth and the wide intermaxillary angle appear to be adaptations for catching, killing, and swallowing or crushing big-shelled animals, such as ammonites.

The mosasaur was most likely a deep diver of the Platecarpinae, a close relative of *Platecarpus brachycephalus* and *Ancylocentrum overtoni*, and a feeder on large cephalopods.

PALEOECOLOGY

The finely laminated, gray calcareous shales characteristic of the Verendrye and Virgin Creek members were, according to the interpretation of Reeside (1957, pp. 532–35), deposited on a temporarily stable shelf or continental platform area. To the west, the shore line at this time extended from northwestern Montana through central Wyoming and western Colorado. The Badlands region, from which the ammonite came, was probably inundated to moderate depth, between 300 and 600 feet. The widespread and uniformly finegrained sequence of shales and the local presence, in central South Dakota, of iron-manganese layers and concretions associated with abundant reptile bones and thin-shelled pelecypods suggest slow deposition in very quiet water, probably well below wave base. The abundant fauna (especially in the Virgin Creek member) and the lack of excessive pyrite or other indications of stagnant reducing conditions are evidence of free circulation. Such an environment would be expected in the lower sublittoral zone of modern shelves.

Additional support for this interpretation has been derived from the occurrence of thinly and evenly bedded laminae and layers of volcanic ash. Rubey (1930, pp. 40–53) studied laminations in Upper Cretaceous forma-

tions in the nearby Black Hills region, concluding that "Their distinctness or degree of preservation is probably a rough measure of the quietness of the water in which the sediments accumulated. Very slight stirring would destroy thin laminations in previously deposited clay Distinct laminations would be formed and preserved only below the depth at which waves could move the very fine sediments; and therefore distinctly laminated sediments probably accumulated in deep water or at times of mild climate and gentle winds." He pointed out (pp. 41-42) that the present maximum depth of 600 feet and effective depth of about 300 feet, to which ocean waves disturb mud bottoms, might not apply to Cretaceous seas. These depths depend on many factors, such as grain size of sediment, the strength of winds, and the distance from shore, favoring strong fetch of winds and deep-wave base; but the widespread seas and moderate climates of Cretaceous time may have produced only gentle winds. Rubey was uncertain, after considering these unknown factors, about the exact depth of the Upper Cretaceous seas, although he was of the opinion that the deposits were well below the disturbances from wave action.

Recently, Crandell investigated the Pierre formation and its members in the type area of central South Dakota. Of the volcanic ash beds, he stated (1958, p. 18) that "The sharpness of contact and purity of many bentonite beds suggest that the volcanic ash fell to the water surface and settled to the bottom relatively rapidly . . . the material was not reworked after it had settled to the bottom of the sea. This leads to the inference that the volcanic ash layers accumulated in quiet water below the bottom-disturbing effect of waves."

The fauna of these shales consists principally of ammonites commonly associated with mud bottoms. Of these, scaphitid, baculitid, and placenticerid stocks, as well as numerous and varied loosely coiled forms, predominate. Inoceramid and ostreid pelecypods are common in the beds with the ammonites. Living conditions seem to have been favorable and food plentiful, for both invertebrates and vertebrates.

Numerous bones of mosasaurs, mainly *Platecarpinae* but also including *Mosasaurinae* and *Tylosaurinae*, have been found in the Pierre shale. In the beds of central South Dakota, the presence of high-seas forms (possibly divers) suggests that the beds were offshore outer shelf deposits. Since great numbers of large cephalopods were available on and above the mud bottoms, it is quite likely that they were included in the diet of certain mosasaurs. Although only one specimen has been found bearing authentic evidence, others probably exist.

LITERATURE CITED

- CAMP, C. L. 1942. California Mosasaurs. Mem. Univ. Calif., Vol. 13, No. 1, vi + 68 pp., 7 pls., frontispiece, 26 figs.
- COBBAN, W. A., and REESIDE, J. B., JR. 1952. Correlation of the Cretaceous Formations of the Western Interior of the United States. Bull. Geol. Soc. Amer., Vol. 63, No. 10, pp. 1011-44, 2 figs., 1 pl.
- COLBERT, E. H. 1945. The Dinosaur Book, The Ruling Reptiles and their Relatives. New York: McGraw-Hill Book Co., Inc., for the American Museum of Natural History. 156 pp., illus.
- COPE, E. D. 1872. On the Geology and Paleontology of the Cretaceous Strata of Kansas. In: Hayden, F. V., Preliminary Report of the United States Geological Survey of Montana and Portions of Adjacent Territories; being a Fifth Annual Report of Progress, Part 3. Paleontology, pp. 318-49.
- 1875. The Vertebrata of the Cretaceous Formations of the West. U. S. Geol. Surv. Territories (Hayden Reports), Vol. 2, iv + 302 pp., index, 57 pls.
- 1878. Professor Owen on the Pythonomorpha. Bull. U. S. Geol. Geograph. Surv. Territories (Hayden Survey), Vol. 4, No. 1, Art. 14, pp. 299-311.
- CRANDELL, D. R. 1950. Revision of Pierre Shale of Central South Dakota. Bull. Amer. Assoc. Petrol. Geol., Vol. 34, No. 12, pp. 2337-46, 2 figs.
- 1958. Geology of the Pierre Area, South Dakota. U. S. Geol. Survey, Prof. Paper 307, iv + 83 pp., 3 pls., 33 figs., maps.
- DOLLO, LOUIS. 1904. Les Mosasauriens de la Belgique. Bull. Soc. Belg. Géol., Vol. 18, pp. 207-16, Pl. 6.
- 1905. Un Nouvel Opercule Tympanique de Plioplatecarpus Mosasurien plongeur. Bull. Soc. Belg. Géol., Vol. 19, pp. 125-31, Pl. 3.
- 1913. *Globidens Fraasi*, Mosasurien mylodonte nouveau du Maestrichtien (Cretace superieur) du Limbourg, et l'Éthologie de la Nutrition chez les Mosasauriens. Arch. Biologie, Vol. 28, pp. 609-26, Pls. 24-25.
- FENTON, C. L., and FENTON, M. A. 1958. The Fossil Book, A Record of Prehistoric Life. Garden City, N. Y.: Doubleday & Company, Inc. xiii + 482 pp., unnumbered illus.
- GREGORY, J. T. 1951. Convergent Evolution: the Jaws of *Hesperornis* and the Mosasaurs. Evolution, Vol. 5, No. 4, pp. 345-54, 6 figs.
- LOOMIS, F. B. 1915. A New Mosasaur from the Ft. Pierre. Amer. Journ. Sci., Vol. 39, pp. 555-66, 9 figs.
- OSBORN, H. F. 1899. A Complete Mosasaur Skeleton, Osseous and Cartilaginous. Science, N. S., Vol. 10, No. 260, pp. 919-25, 3 figs.
- OWEN, RICHARD. 1877. On the Rank and Affinities in the Reptilian Class of the Mosasauridae, Gervais. Quart. Journ. Geol. Soc. London, Vol. 33, pp. 682-715, 24 figs.
- RAYMOND, P. E. 1939. Prehistoric Life. Cambridge: Harvard Univ. Press. ix + 324 pp., 156 figs.
- REESIDE, J. B., JR. 1957. Paleocology of the Cretaceous Seas of the Western Interior of the United States. In: Treatise on Marine Ecology and Paleocology, Vol. 2, Paleocology, Geol. Soc. Amer. Mem. 67, Chap. 18, pp. 505-41, 21 figs.
- ROMER, A. S. 1956. Osteology of the Reptiles. Chicago: Univ. Chicago Press. xxx + 772 pp., 248 figs.

- RUBEY, W. W. 1930. Lithologic Studies of Fine-grained Upper Cretaceous Sedimentary Rocks of the Black Hills Region. U. S. Geol. Survey, Prof. Paper 165-A, 54 pp., 5 pls., 3 figs.
- SCHMIDT, K. P. 1927. New Reptilian Generic Names. *Copeia*, Issue 163, pp. 58-9.
- WILLISTON, S. W. 1895. New or Little Known Extinct Vertebrates. *Kans. Univ. Quart.*, Vol. 3, No. 3, pp. 165-76, Pls. 14-19, unnumbered text-figs.
- 1897a. *Brachysaurus*, a New Genus of Mosasaurs. *Kans. Univ. Quart.*, Ser. A, Vol. 6, No. 2, pp. 95-8, Pl. 8.
- 1897b. Restoration of Kansas Mosasaurs. *Kans. Univ. Quart.*, Vol. 6, No. 3, pp. 107-10, Pl. 13.
- 1898. Mosasaurs. *Univ. Geol. Surv. Kans.*, Vol. 4, pp. 83-221, Pls. 8-72.
- 1904. The Relationships and Habits of the Mosasaurs. *Journ. Geol.*, Vol. 12, No. 1, pp. 43-51.
- 1914. *Water Reptiles of the Past and Present*. Chicago: Univ. Chicago Press. vi + 251 pp., 131 figs.
- 1925. *The Osteology of the Reptiles*. (Published posthumously, arranged and edited by W. K. Gregory). Cambridge: Harvard Univ. Press. xiii + 300 pp., 191 figs.

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PLATES

All figures are unretouched photographs of a specimen of *Placenticas* sp. cf. *P. whitfieldi* Hyatt which bears tooth marks of a mosasaur. It is cataloged as UMMP No. 35484. In Plates IV through IX, white overlays are superimposed on photographs of the specimen to show how the teeth fitted in each bite. This overlay is a composite based on the tooth patterns observed in sixteen bites.

The specimen was not coated with a sublimate for photographing. To reduce the reflections from the shiny, nacreous shell material, the specimen was illuminated by polarized light and photographed through a polaroid filter. Photographs by Herbert W. Wienert.

EXPLANATION OF PLATE I

(Figure $\times \frac{1}{2}$)

Placenticerus sp. cf. *P. whitfieldi* Hyatt. Left side of specimen with tooth marks of a mosasaur. See Figure 2 in text for a drawing based on this view.

PLATE I



PLATE II



EXPLANATION OF PLATE II

(Figure $\times \frac{1}{2}$)

Placenticas sp. cf. *P. whitfieldi* Hyatt. Right side of specimen with tooth marks of a mosasaur. See Figure 3 in text for a drawing based on this view.

EXPLANATION OF PLATE III

(Both figures $\times 1$)*Placenticerus* sp. cf. *P. whitfieldi* Hyatt

FIG. 1. Part of left side of specimen showing perforations and surrounding crushed zones made by the maxillary teeth of a mosasaur.

FIG. 2. Part of left side of specimen showing small perforations made by the pterygoid teeth of a mosasaur.

PLATE III

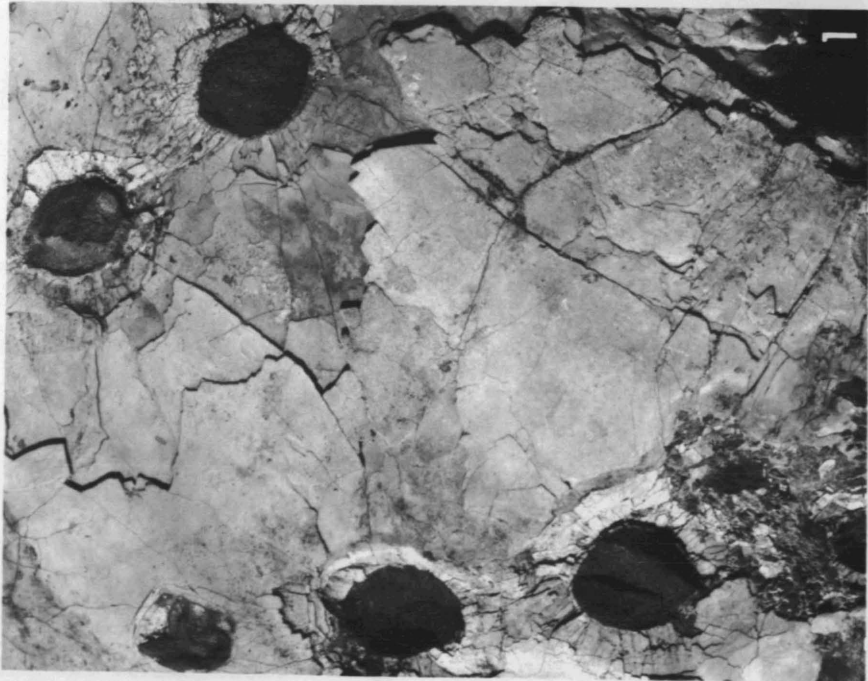
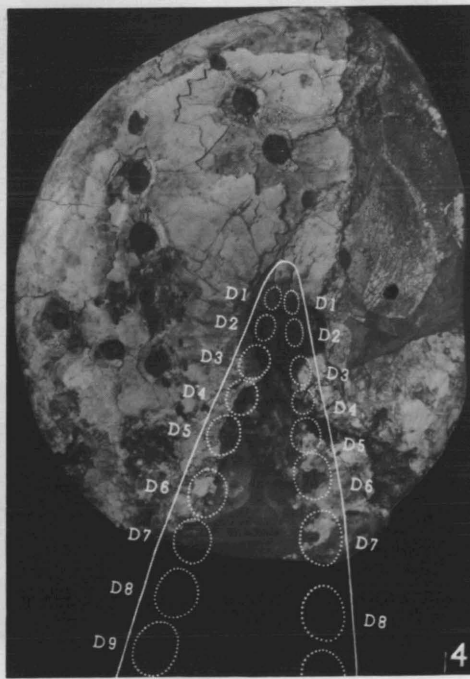
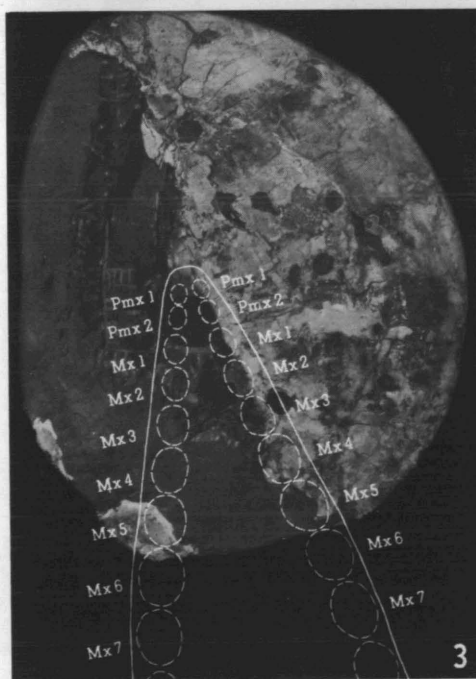
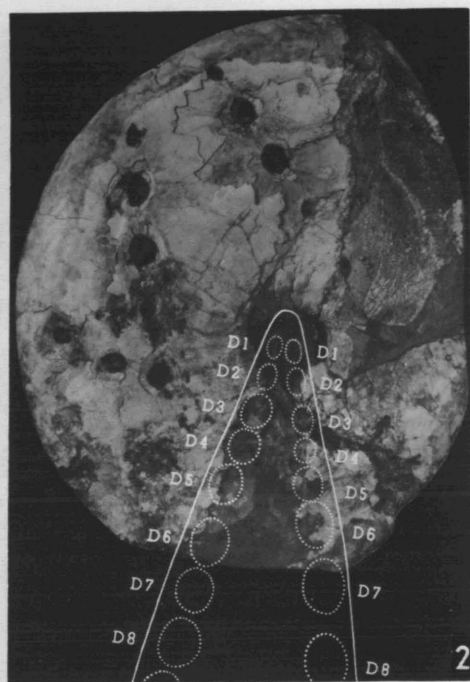
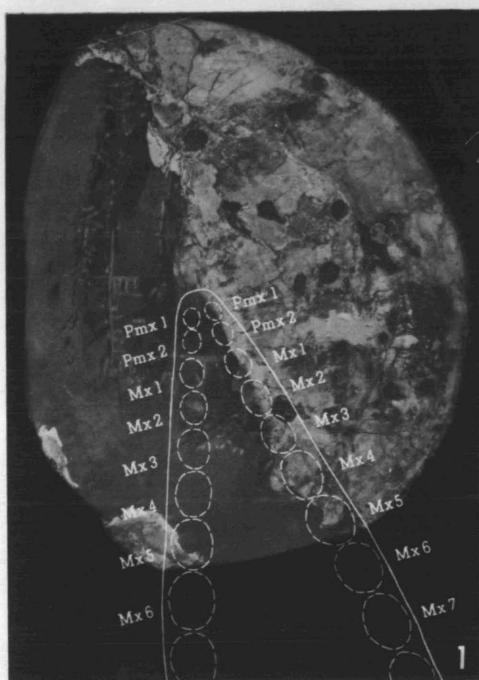


PLATE IV



EXPLANATION OF PLATE IV

(All figures $\times \frac{1}{4}$)

Placenticer sp. cf. *P. whitfieldi* Hyatt

FIGS. 1-2. Right side of specimen showing marks made by maxillary teeth and left side showing marks made by dentary teeth in bite 1. See Figure 4a in text for a drawing based on this view.

FIGS. 3-4. Right side of specimen showing marks made by maxillary teeth and left side showing marks made by dentary teeth in bite 2. See Figure 4b in text for a drawing based on this view.

EXPLANATION OF PLATE V

(All figures $\times \frac{1}{4}$)*Placenticerus* sp. cf. *P. whitfieldi* Hyatt

FIGS. 1-2. Left side of specimen showing marks made by maxillary teeth and right side showing marks made by dentary teeth in bite 3. See Figure 4c in text for a drawing based on this view.

FIGS. 3-4. Left side of specimen showing marks made by maxillary teeth and right side showing marks made by dentary teeth in bite 4. See Figure 4d in text for a drawing based on this view.

PLATE V

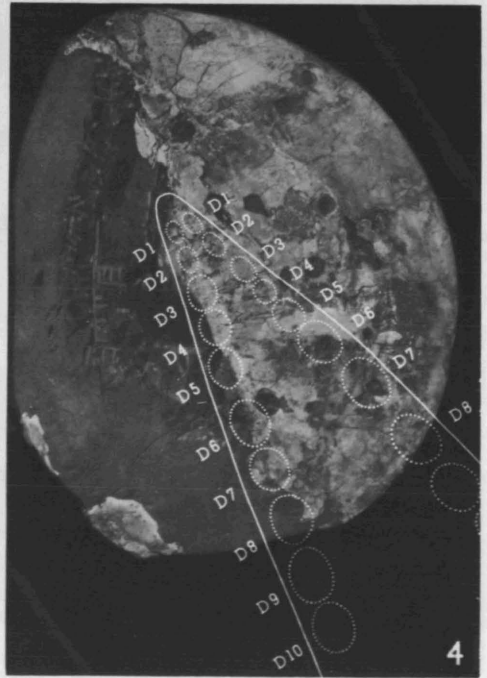
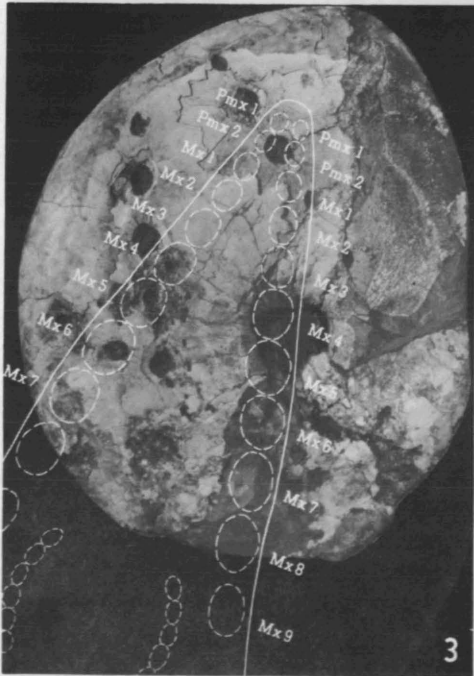
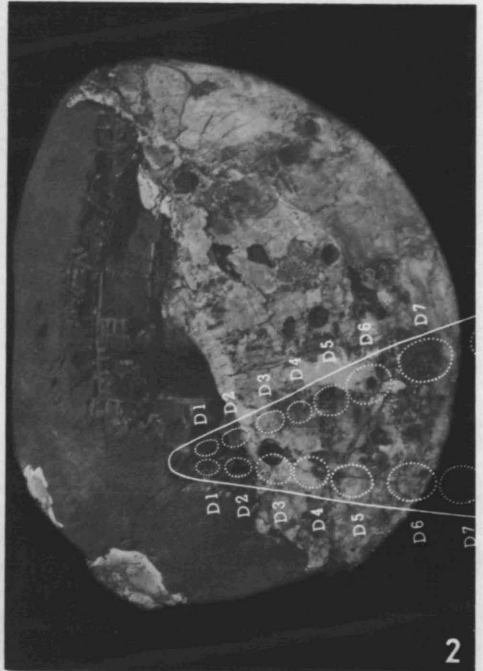
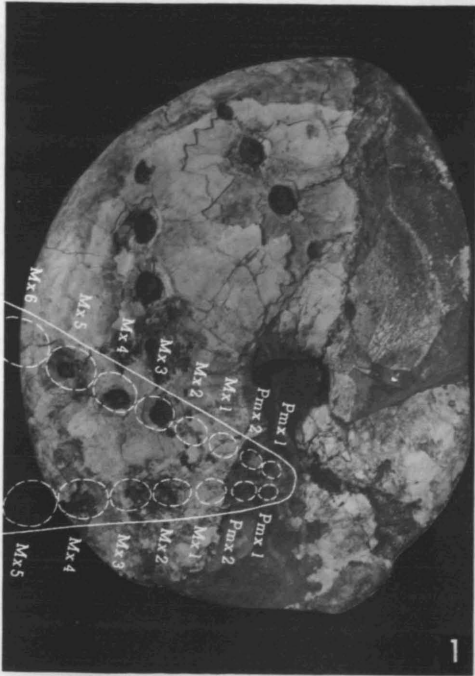
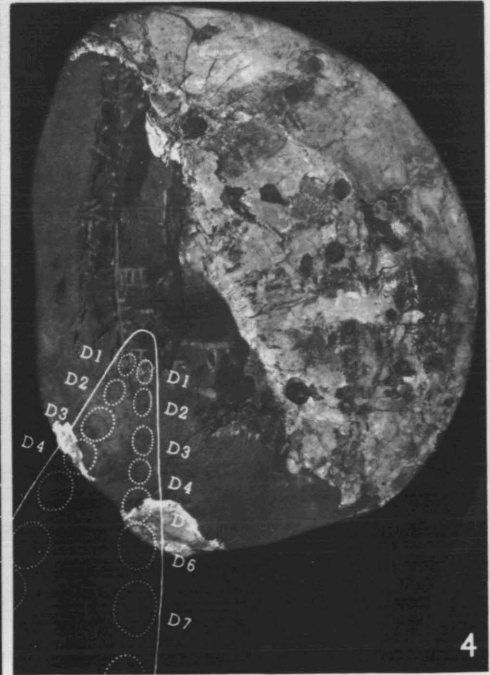
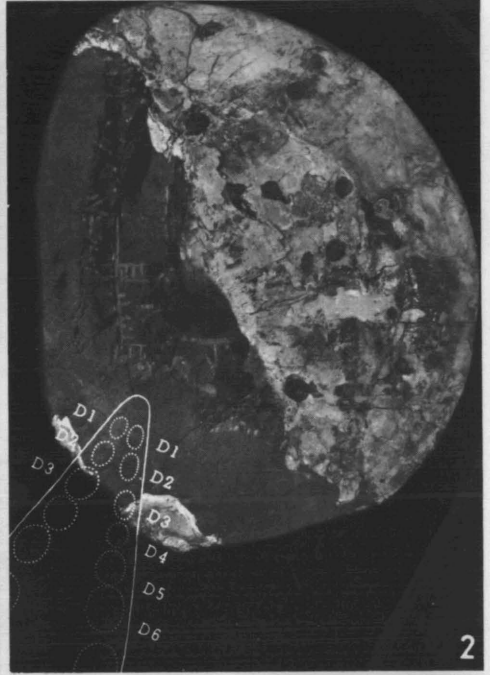


PLATE VI



EXPLANATION OF PLATE VI

(All figures $\times \frac{1}{4}$)

Placenticerus sp. cf. *P. whitfieldi* Hyatt

FIGS. 1-2. Left side of specimen showing marks made by premaxillary and maxillary teeth and right side showing marks made by dentary teeth in bite 5.

FIGS. 3-4. Left side of specimen showing marks made by maxillary teeth and right side showing marks made by dentary teeth in bite 6.

EXPLANATION OF PLATE VII

(All figures $\times \frac{1}{4}$)*Placenticerus* sp. cf. *P. whitfieldi* Hyatt

FIGS. 1-2. Left side of specimen showing marks made by maxillary teeth and right side showing marks made by dentary teeth in bite 7. The teeth were more deeply impressed in this bite than in any other. See Figure 4e in text for a drawing based on this view.

FIGS. 3-4. Left side of specimen showing marks made by maxillary teeth and right side showing marks made by dentary teeth in bite 8.

PLATE VII

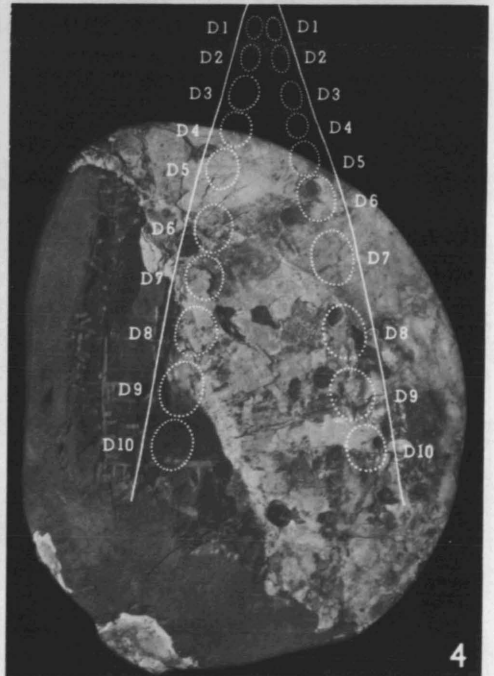
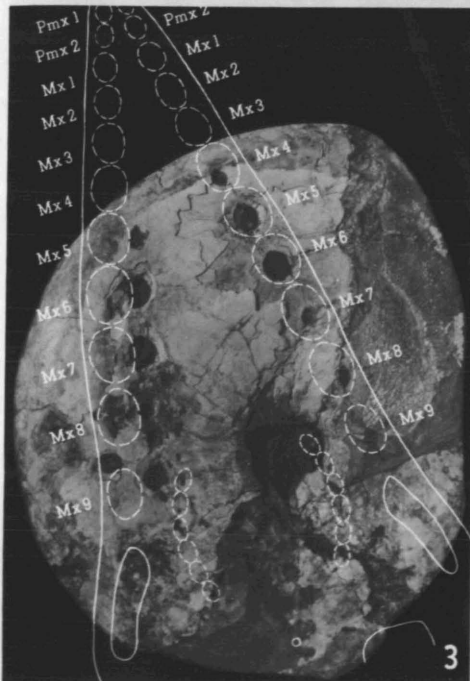
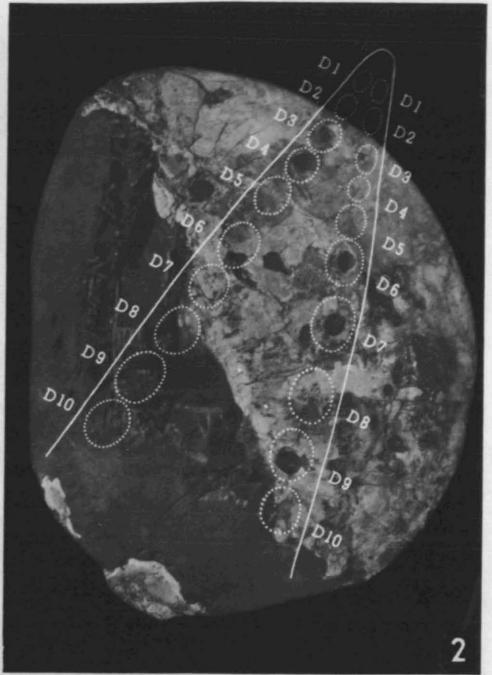
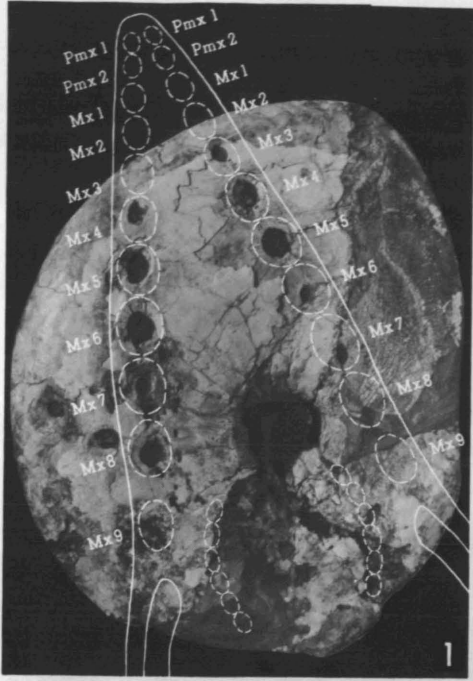
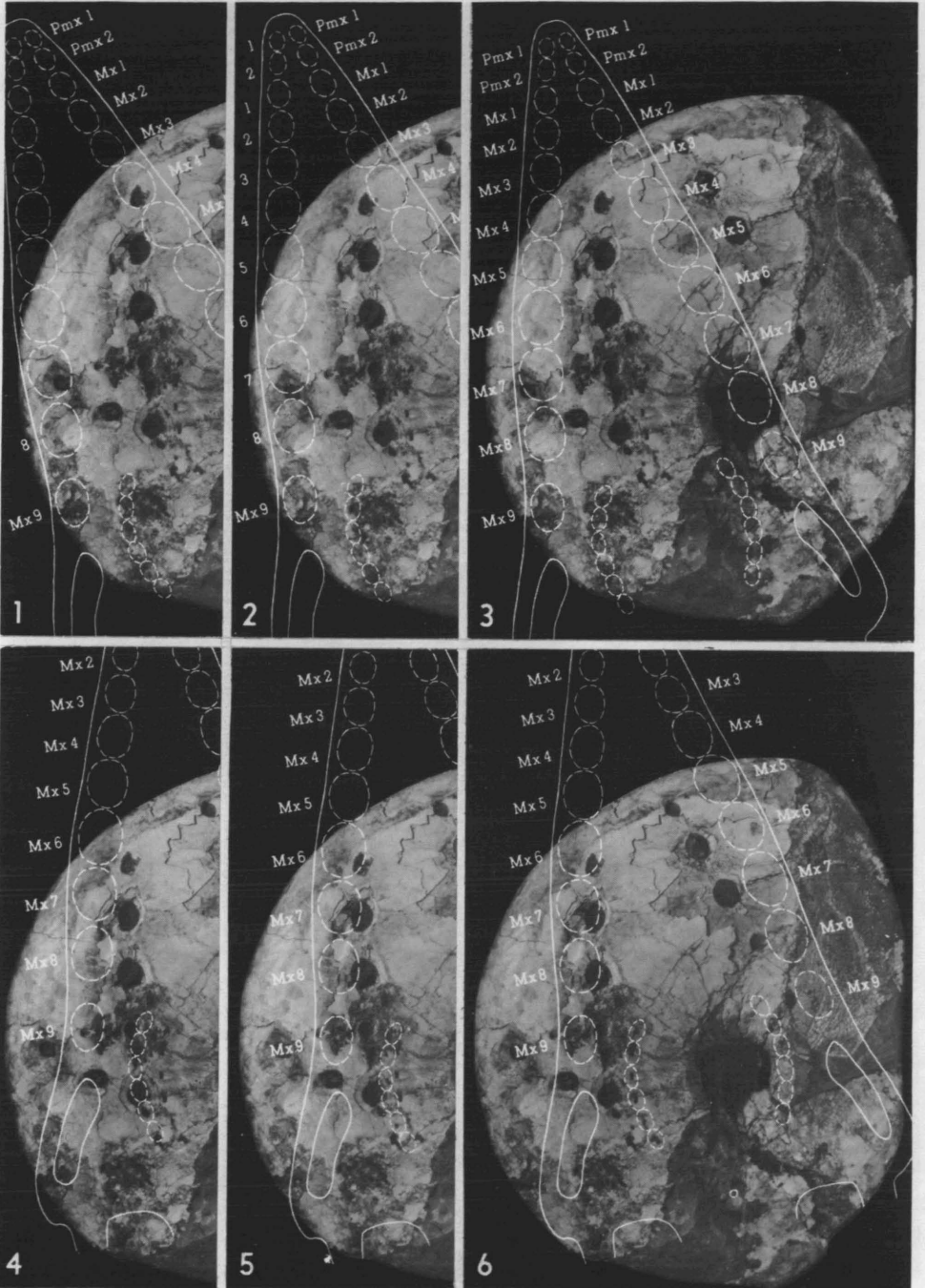


PLATE VIII



EXPLANATION OF PLATE VIII

(All figures $\times \frac{1}{4}$)

Placenticerus sp. cf. *P. whitfieldi* Hyatt

FIGS. 1-3. Left side of specimen showing marks made by the left rear maxillary and pterygoid teeth in bites 9-11.

FIGS. 4-6. Left side of specimen show marks made by the left rear maxillary and pterygoid teeth in bites 12-14. The pattern of the pterygoid teeth is particularly well illustrated in Fig. 6. See Figure 4f in text for a drawing based on this view.

EXPLANATION OF PLATE IX

(Figure 1 natural size; other figures $\times \frac{1}{4}$)*Placenticerus* sp. cf. *P. whitfieldi* Hyatt

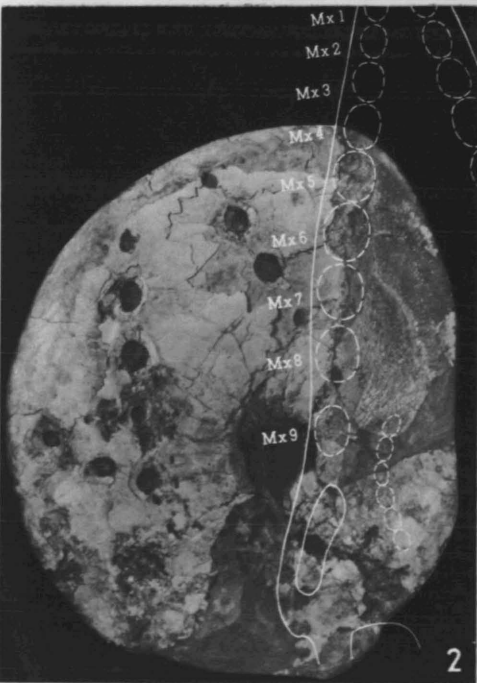
FIG. 1. Right side of specimen showing perforations and gouged grooves made by the left rear dentary tooth in bites 12-14. See Figure 4*f* in text for a drawing based on this view.

FIGS. 2-3. Left side of the specimen showing marks made by the maxillary teeth in bites 15 and 16.

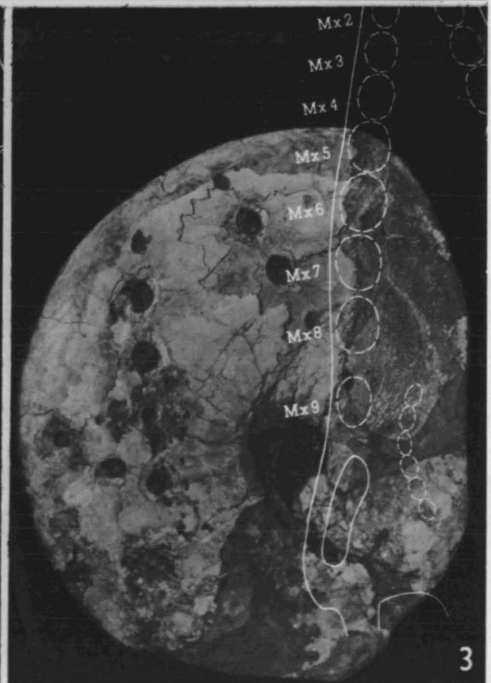
PLATE IX



1



2



3

