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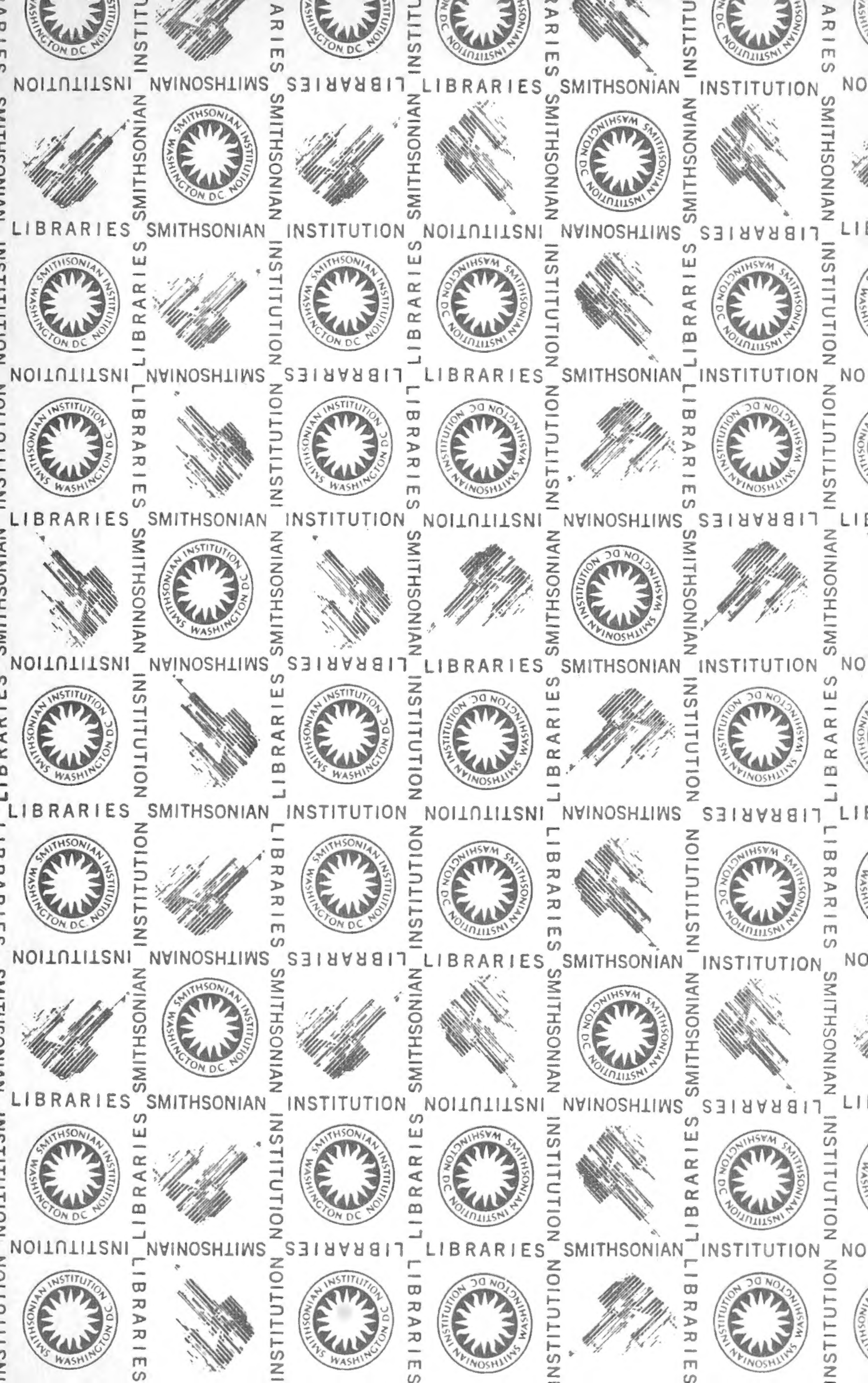
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Bulletin 23

Systematics and Morphology of American Mosasaurs

by
Dale A. Russell

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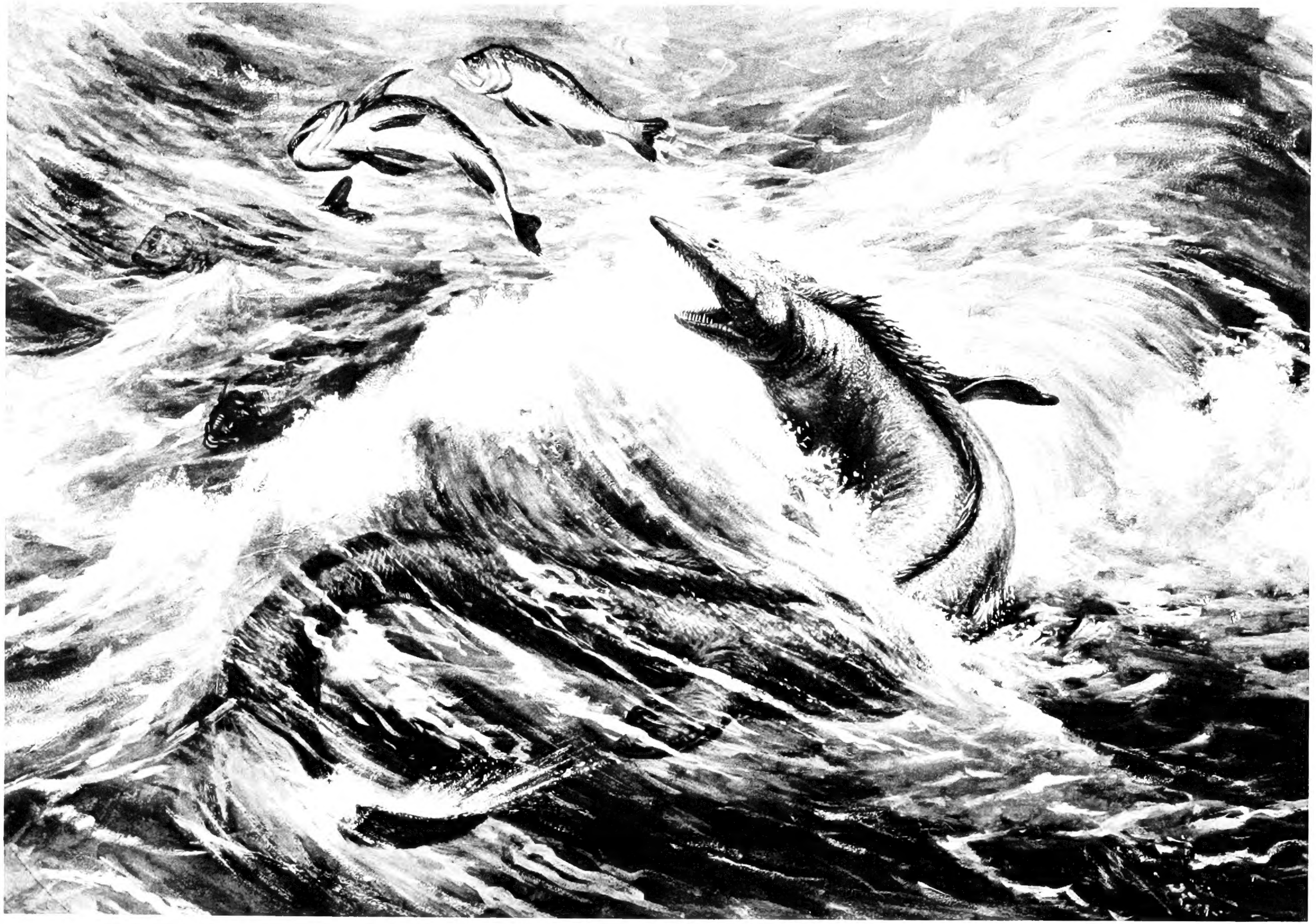

PEABODY MUSEUM OF NATURAL HISTORY
YALE UNIVERSITY
BULLETIN 23

Systematics and Morphology of American Mosasaurs (Reptilia, Sauria)

BY
DALE A. RUSSELL

Curator of Fossil Vertebrates
National Museum of Canada

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Frontispiece: Restoration of *Tylosaurus proriger*, by Charles R. Knight under the direction of Henry Fairfield Osborn (courtesy of the American Museum of Natural History).

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YALE UNIVERSITY PEABODY MUSEUM OF NATURAL HISTORY BULLETIN
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SYSTEMATICS AND MORPHOLOGY OF AMERICAN MOSASAURS
(Reptilia, Sauria)

BY DALE A. RUSSELL

ABSTRACT

Mosasaurs were large, marine platynotan lizards which became abundant and diversified during the latter half of Cretaceous time, but disappeared at the close of the period. Three subfamilies are recognized within the Family Mosasauridae: the Mosasaurinae (including the new tribes, Mosasaurini, Globidensini and Plotosaurini), the Plioplatecarpinae (including the new tribes, Plioplatecarpini and Prognathodontini), and the Tylosaurinae. At present thirteen genera and thirty species are diagnosed from the North American Cretaceous, with one new genus (*Ectenosaurus*) and one new species (*Plioplatecarpus primaevus*). Of the older names available, nineteen generic and twenty-nine specific names have been placed into synonymy, two generic and eighteen specific names are based on indeterminate material, and an additional generic and six specific names are only of dubious validity.

The osteology of mosasaurs is described in detail and with reference to the soft anatomy. Mosasaurs possessed a good sense of sight and a poor sense of smell. A calcified tympanum, present in all three subfamilies, was probably useful in transmitting waterborne sound to the middle ear and is not indicative of deep-diving habits. Streptostylic quadrates permitted anteroposterior movement of the mandibles, which in turn facilitated the underwater swallowing of prey. Mosasaurs swam by lateral undulations of the body, the flippers and relatively long neck serving as organs of equilibration. They fed on smaller mosasaurs, chelonians, fish, ammonites, belemnites, echinoderms and pelecypods, and for the most part were highly active aquatic carnivores.

Mosasaurs inhabited subtropical epicontinental seas of less than 100 fathoms (about 180 meters) depth and of variable salinity. Individual forms had a wide geographic distribution that was little affected by changes in depositional environments. The range of many species of mosasaurs inhabiting the western edge of the North Atlantic basin probably extended into western European waters. Those from the eastern edge of the Pacific basin appear to have belonged to a distinct zoogeographic province.

Mosasaurs descended from primitive middle Cretaceous varanoids (aigialosaurs) possessing many cranial characteristics of mosasaurs but with a postcranial morphology similar to that of the modern *Varanus*. Ancestral mosasaurs seem to have been of two basic types; forms with long bodies and short dilated tails giving rise to the mosasaurines, and forms with short bodies and long pointed tails giving rise to the plioplatecarpines and tylosaurines. During their relatively brief geologic existence mosasaurs exhibited a few clearly progressive trends, such as a tendency to increase in overall size, to telescope the frontals over the anterior edge of the parietals (consequently suppressing kinesis), to increase the number of pygal vertebrae, and to alter the primitive webbed paddles into long, hyperphalangic flippers.

АМЕРИКАНСКИЕ МОЗАЗАВРЫ *

ДЭЛЬ РУССЕЛЬ
КУРАТОР ОТДЕЛА ИСКОПАЕМЫХ ПОЗВОНОЧНЫХ,
НАЦИОНАЛЬНЫЙ МУЗЕЙ КАНАДЫ

АБСТРАКТ

Мозазавры были крупные морские плоскозубые ящерицы. Они изобиловали и были разнообразными во второй половине мела, но исчезли в конце его. В семействе мозазавров различают три подсемейства:
мозазаурины (включая новые трибы мозазаурини, глобиденсини и плотозаурини),
плиоплатекарпины (включая новые трибы плиоплатекарпини и прогнатодонтини),
тилозаурины.

В настоящее время в меле Северной Америки определены тринадцать родов и тридцать видов, один род (эктенозавры) и один вид (плиоплатекарпус примаевус) являются новыми. Из числа имеющихся старых вназваний девятнадцать родовых и двадцать девять видовых были помещены в синонимику, два родовых и восемнадцать видовых названий основаны на неясном материале, одно родовое название и шесть видовых вызывают сомнения в смысле их пригодности.

Дается детальное описание остеологии мозазавров со ссылками на анатомию их тела. Мозазавры обладали хорошо развитым зрением и плохо развитым обонянием. Окаменевшая барабанная полость, имеющаяся у всех трех подсемейств, повидимому была полезна для передачи в среднее ухо тех звуков, которые распространялись в воде, она не указывает на то, что животное могло нырять глубоко.

Стрептостильные крадраты позволяли движение верхних челюстей вперед и назад, что в свою очередь облегчало проглатыванию добычи под водою. Мозазавры плавали посредством волнообразных движений тела в длину, плавники и относительно длинная шея служили для равновесия. Питались они более мелкими мозазаврами, черепахами, рыбой, аммонитами, белемнитами, иглокожими, пелеципoдами; они были очень активными водными плотоядными животными.

Он населяли субтропические эпиконтинентальные моря глубиною менее чем сто морских саженей (около ста восьмидесяти метров) и имеющие различное содержание солей. Отдельные их формы имели большой географический ареал, на который мало влияли различия в окружающей среде. Ареал многих видов мозазавров, населявших западную окраину Северо-Атлантического бассейна, доходил повидимому до морей Западной Европы. Их виды из восточной окраины бассейна Тихого океана повидимому принадлежали к другой зоогеографической провинции.

Мозазавры произошли от примитивных варанов среднего мела (аигиалозавры), особенности черепа последних были похожи на те же у мозазавров, но остальная морфология была как у современных варанов. Предки мозазавров повидимому были двух основных типов; были формы, имевшие длинные тела и расширенные хвосты, от них произошли мозазаурины; были формы с короткими телами и длинными остроконечными хвостами, — это были предки плиоплатекарпинов и тилозавринов.

В течение своего короткого периода жизни в истории земли мозазавры показали несколько прогрессивных тенденций, как, например, тенденцию к увеличению общего размера, к помещению передней половины темени над передним краем задней половины темени (вследствие чего уменьшилась подвижность костей черепа), увеличение числа пигальных позвонков и изменение примитивных перепончатых плавников в длинные, с бо́льшим числом фаланг.

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* Sistematika i morfologii͡a amerikanskikh͡ mozazavrov (Reptilia, Sauria)

SYSTEMATIQUES ET MORPHOLOGIE DES MOSASAURES AMÉRICAINS

(Reptilia, Sauria)

DALE A. RUSSELL

RÉSUMÉ

Les mosasaures étaient des hydrosauriens ayant la forme de grands lézards qui se sont multipliés et diversifiés dans la seconde moitié du Crétacé pour disparaître à la fin de cette période. La famille des Mosasauridés se subdivise en trois sous-familles: les mosasaurinés, comprenant les nouvelles tribus des mosasaurins, des globidensins et des plotosaurins, les plioplatécarpinés, comprenant les nouvelles tribus des plioplatécarpins et des prognathodontins, et les tylosaurinés. On a jusqu'ici catégorisé 13 genres et 30 espèces du Crétacé en Amérique du Nord, y compris un nouveau genre *(Ectenosaurus)* et une nouvelle espèce *(Plioplatecarpus primaevus)*. Parmi les noms déjà existants, dix-neuf noms génériques et vingt-neuf noms spécifiques ont été placés en synonymie, deux noms génériques et dix-huit noms spécifiques sont basés sur des données insuffisantes, et la valeur d'un autre nom générique et de six noms spécifiques est contestable.

L'ostéologie des mosasaures est décrite en détail et en rapport avec la partie non-osseuse de leur anatomie. Les mosasaures étaient doués d'une bonne vue, mais leur odorat était faible. Un tympan calcifié, que l'on a retrouvé chez les trois sous-familles, devait servir à transmettre les sons produits dans l'eau à l'oreille médiane, et n'indique pas que ces sauriens avaient l'habitude de plonger en profondeur. Les os carrés streptostyliques permettaient le mouvement antéro-postérieur des mandibules, ce qui permettait d'avaler facilement des proies sous l'eau. Les mosasaures nageaient par mouvements ondulants latéraux, se maintenant en équilibre grâce à leurs nageoires et à leur long cou. Grands carnivores aquatiques, ils se nourrissaient de mosasaures plus petits qu'eux, de chéloniens, de poissons, d'ammonites, de bélemnites, d'échinodermes et de pélécypodes.

Les mosasaures habitaient les mers semi-tropicales d'une profondeur de moins de 100 brasses (environ 180 mètres) et d'une salinité variable. Des formes particulières de ces animaux suivaient une répartition géographique étendue qui n'était que peu influencée par les dépôts sédimentaires présents. Plusieurs espèces de mosasaures habitant la section occidentale du bassin de l'Atlantique Nord se sont probablement répandues jusque dans les eaux de l'Europe de l'Ouest. Les mosasaures de la section orientale du bassin du Pacifique semblent avoir appartenu à une province zoogéographique distincte.

Les mosasaures descendaient de varanidés primitifs (aigialosaures) du Crétacé moyen qui possédaient plusieurs caractéristiques du crâne que l'on retrouve chez les mosasaures, mais conservaient une morphologie post-crânienne semblable à celle du *Varanus* moderne. A l'orgine il semble y avoir existé deux types de base de mosasaures: un type au corps allongé et à la queue courte, mais déployée, qui a donné naissance aux mosasaurinés, et un type de plus petite taille, mais à la queue longue et effilée, qui a donné naissance aux plioplatécarpinés et aux tylosaurinés. Au cours de leur présence relativement brève dans l'histoire géologique, les mosasaures ont donné quelques signes évidents d'une évolution: leur taille a eu tendance à s'accroître, leur frontal s'est recouvert sur la section antérieure du pariétal (éliminant ainsi toute possibilité de la cinétique crânienne), le nombre de leurs vertèbres à la base de la queue a augmenté, et leurs nageoires primitives palmées se sont transformées en longues pattes-nageoires hyperphalangiques.

SYSTEMATICS AND MORPHOLOGY OF AMERICAN MOSASAURS

(Reptilia, Sauria)

Dale A. Russell*

INTRODUCTION

Surely as much has been written about mosasaurs as any other group of fossil reptiles of comparable abundance and diversity. The division of the family Mosasauridae into three major subfamilies and the close relationship to varanid lizards has been generally recognized for more than fifty years. Yet on a generic and specific level their taxonomy has been so confused that even after a careful survey of the literature it was usually impossible to be sure of the correct binomial to use in identifying a given specimen. As a consequence modern vertebrate paleontologists have by and large tended to ignore mosasaurs as a subject of research.

The present study grew out of an attempt to provide a systematic revision of the mosasaurs of the United States. The morphology of the mosasaur skull was studied in some detail in the course of preparing a doctoral dissertation for the Graduate Faculties of Columbia University. A review of the postcranial skeleton was largely completed during the tenure of a postdoctoral fellowship at Yale University. Speculations on the nature of non-ossified organs are to be found with the descriptions of the associated bones. A dissection of the head and limbs of *Varanus niloticus,* together with the assistance of various publications on the anatomy of lizards, has been a great aid in interpreting the functional significance of joints and areas of muscle attachment in the head and body of mosasaurs.

Mexican mosasaurs reported on by Mehl and Mülleried have not been seen, and information included below on Californian mosasaurs is based entirely on Camp's monograph. Undescribed mosasaur collections from the Selma Formation of Alabama in the Chicago Natural History Museum and from various localities in Canada preserved in the museums of that country are not considered here. Otherwise mosasaurian material in the collections of some nineteen North American institutions has been examined. References in the primary scientific literature (not including bibliographies, encyclopedias, textbooks, etc.) pertaining to material of American mosasaurs are listed under the proper generic and specific headings in the section on systematics. Where possible, published figures of specimens are referred to species recognized in this study. In many cases, however, when figures do not show diagnostic characters, they are placed after the generic headings or under the species as identified by the particular worker. The frontispiece was painted by Charles R. Knight in 1899, under the direction of H. F. Osborn, and plates I and II have been taken from illustrations in Williston (1898b), Osborn (1899a) and Camp (1942). Miss Linda McKnay prepared figures 46, 52 and 59, and the remaining illustrations are by the author.

A tooth and jaw fragment from the Cretaceous of New Jersey, recognized by Mitchill in 1818 as being similar to the then unnamed type of *Mosasaurus hoffmanni,* was the first mosasaur specimen described from North America. The next half-century was characterized by a steadily increasing series of short publica-

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tions on fragmentary remains from New Jersey and the southern Atlantic and Gulf states. An important exception was the discovery in about 1830 (see Simpson, 1942, p. 172) of the type of *Mosasaurus missouriensis* from the Missouri territory, which was later described by Harlan and Goldfuss. In 1865 Leidy published the first revision of American mosasaurs with excellent illustrations of the material from New Jersey. During the latter part of the 1860's Cope and Marsh described new, and in some instances relatively well-preserved, specimens from the New Jersey and Gulf Coast Cretaceous. These new taxa were listed by Cope in 1870 together with a review of all previous work.

Marsh and Cope led field parties into the Niobrara Chalk of western Kansas in 1870-1871 and soon began describing new mosasaur material. Far too many species were named; all were inadequately diagnosed; and the resulting confusion has been a serious handicap to subsequent workers. Marsh, however, correctly diagnosed the three common Niobrara genera in 1872, and Cope in his 1875, "The Vertebrata of the Cretaceous formations of the West," republished his original descriptions of Niobrara mosasaurs, figured his types and published an up-to-date summary of named mosasaur species from America. Marsh had collectors working in the Niobrara for seven consecutive field seasons between 1874-1880 and amassed the very large collection of mosasaurs in the Yale museum, which for the most part remained unstudied. Special mention is due to Prof. B. F. Mudge, who collected for Marsh during the summers of 1874-1876. The industry and thoroughness with which he worked the Niobrara Chalk, the excellence and number of his specimens, and the relative accuracy and completeness of his field journal were outstanding for his time. C. H. Sternberg collected the Niobrara for Cope in 1875 and 1877, but met with relatively little success as Yale crews had prospected the outcrops before him.

Most of the mosasaur specimens in the museum of the University of Kansas were obtained by H. T. Martin, C. H. Sternberg, E. P. West, and S. W. Williston from the Niobrara Chalk during 1890-1895. These specimens formed the basis of Williston's 1898 revision of the Kansas mosasaurs, an excellent work which was unfortunately limited because Williston was unable to examine Cope's and Marsh's types. Other important papers published during this time were Baur's detailed description of the skull of *Platecarpus* (1892) and Merriam's doctoral dissertation on Kansas mosasaurs in the collections of the University of Munich (1894).

Since the 1880's C. H. Sternberg and his sons have collected many excellent mosasaur specimens from the Niobrara and sent them to museums all over the United States and Canada, as well as to China, England, Germany and Sweden. The writings of the elder Sternberg present a very interesting account of his collecting experiences in the Niobrara Chalk and give a unique and vivid impression of mosasaurs as living animals. For a more detailed history of early collecting in the Niobrara see Williston, 1898a, pp. 28-32.

After 1910 the literature has been mainly restricted to the documentation of sporadic new occurrences, with the description of a few obviously distinct forms. In 1942 Camp published detailed descriptions and figures of the unusual mosasaurs from the latest Cretaceous of California, and Zangerl during 1945-1946 collected many new specimens from the Mooreville Member of the Selma Chalk in Alabama.

Although the imagination and industry of the individual researcher lies at the base of progress in our understanding of vertebrate evolution, this progress

is certainly greatly facilitated by mutual co-operation between workers. The present study could not have been sustained without the generous assistance of many vertebrate paleontologists throughout the United States and Canada. Above all, I am deeply grateful to Dr. Edwin H. Colbert, of the American Museum of Natural History and Columbia University, for his sponsorship of this project, for his critical reading of much of the manuscript and for making the collections of the American Museum available to me for study. His wise guidance and patient counsel were invaluable and have made being his student a pleasure. I would especially like to thank Dr. Bobb Schaeffer and Dr. Malcolm McKenna, both of the American Museum of Natural History and Columbia University, for their encouragement, their review of much of the manuscript, and for their many valuable and instructive suggestions on its organization and content. I am indebted to Dr. Donald Baird, of Princeton University, for many stimulating conversations and for the interest he has shown in this work. I have also profited greatly from discussions on the kinetics of the sauropsid skull with my fellow student at Columbia, Georg Zappler.

I was fortunate to receive a grant from the American Museum of Natural History to visit several important collections in the United States and Canada east of the Rocky Mountains. Of the numerous people who have aided me in the course of these travels I would like to acknowledge the following who freely gave much of their time to acquaint me with mosasaur specimens in the collections of their respective institutions: Dr. Theodore Eaton of the University of Kansas, Dr. William Fox of Williams College, Dr. Nicholas Hotton III and Dr. C. Lewis Gazin of the United States National Museum, Dr. John H. Ostrom of Yale University, Dr. Horace Richards of the Academy of Natural Sciences of Philadelphia, Dr. Alfred S. Romer of Harvard University, Dr. L. S. Russell, formerly of the National Museum of Canada, now of the Royal Ontario Museum, Mr. Myrl Walker of Fort Hays Kansas State College, Dr. Robert W. Wilson of the South Dakota School of Mines and Technology, Dr. Albert Wood of Amherst College, and Dr. Ranier Zangerl of the Chicago Natural History Museum. I am particularly grateful to Dr. and Mrs. William A. Clemens of the University of Kansas for inviting me to stay in their home during the time spent studying mosasaurs in the extensive Kansas collections.

I would like to express my sincerest thanks to Dr. Elwyn L. Simons of Yale University for making his home available to me over a two month period in 1963 and again for a month in 1964, enabling me to study the collections there without financial difficulty. I then entered on the tenure of a National Science Foundation Postdoctoral Fellowship generously granted to me to complete the review of the postcranial skeleton based for the most part on the great collection of mosasaurs assembled at the Peabody Museum of Yale by Prof. Marsh. Discussions of the functional anatomy, particularly that of the head, have been greatly improved by the detailed constructive criticism of Dr. John H. Ostrom and Dr. James A. Hopson of Yale University. Dr. Wann Langston, Jr. of the Texas Memorial Museum has supplied much information on the skull and skeleton of a *Mosasaurus maximus* from the Cretaceous of Texas. Dr. Karl Waage of Yale University and Dr. J. A. Jeletzky of the Geological Survey of Canada have very kindly proofread the section on stratigraphy.

Finally I would like to thank my brother and sister, Dr. Donald E. Russell of the Muséum National d'Histoire Naturelle, Paris, and Mrs. John E. Mawby and especially my wife, Janice A. Russell, whose assistance and encouragement during various phases of this work have been very much appreciated.

The following abbreviations of institutional names precede the specimen numbers referred to in the text and identify the place of storage of the specimens:

A.C.—Museum of Amherst College.
A.M.N.H.—American Museum of Natural History.
A.N.S.P.—Academy of Natural Sciences of Philadelphia.
C.I.T.—California Institute of Technology, collections are now in the Los Angeles County Museum.
C.M.—Carnegie Museum.
C.N.H.M.—Chicago Natural History Museum.
F.H.M.—Museum of Fort Hays Kansas State College.
K.U.—University of Kansas Museum of Natural History.
M.C.Z.—Museum of Comparative Zoology, Harvard University.
M.S.S.C.—Museum of Southern State College, Arkansas (casts of specimens given to the A.M.N.H. by Dr. J. Chapman).
Museum of Williams College (not abbreviated).
N.J.G.S.—New Jersey Geological Survey.
N.J.S.M.—New Jersey State Museum.
N.M.C.—National Museum of Canada.
P.U.—Museum of Princeton University.
S.D.S.M.—Museum of the South Dakota School of Mines and Technology
T.M.M.—Texas Memorial Museum.
U.S.N.M.—United States National Museum.
Y.P.M.—Yale University, Peabody Museum of Natural History.

HISTORY OF CLASSIFICATION

General Relations of Mosasaurs

The history of the first mosasaur specimen to attract the attention of the scientific world is most unusual and has been repeated often. Its discovery antedates that of the first dinosaur by some 42 years. The fossil was found in 1780 by quarrymen working in a shaft 90 feet below the surface of St. Peters Mount at Maestricht, Holland, in rocks of latest Cretaceous age. Dr. Hoffman, a surgeon of Maestricht, was called to examine the remains of what proved to be a fine skull and vertebral column and proceeded to direct their excavation. However the specimen was found beneath ground owned by a clergyman named Goddin who laid claim to it and forced Hoffman to yield the specimen as well as pay the costs of the resulting lawsuit. In 1795 the troops of the French Republic repulsed the Austrians, laid siege to the city of Maestricht and bombarded Fort St. Peter. The commanding general of the French army ordered his artillerymen to avoid Goddin's country house where the now-famous fossil was kept. Goddin guessed the reason behind this apparent act of benevolence and had the specimen removed and hidden in the city. After Maestricht fell a reward of 600 bottles of wine was offered for its recovery and the following day the specimen was borne into French hands by a dozen grenadiers and sent to Paris, where it remains in the collections of the Muséum National d'Histoire Naturelle (see Faujas Saint Fond, 1799, quoted in Williston, 1898b, pp. 84-85; and Cuvier, 1808).

The first general review of the "grand animal fossile de Maestricht" was that of Cuvier (1808) in which the remains were redescribed and refigured, and the speculations of four earlier authors were discussed. Pierre Camper and Van Marum are stated to have thought the animal was a cetacean, though Faujas Saint Fond firmly believed that it was a crocodile. Adrien Camper recognized that the animal was indeed a lizard, showing resemblances to iguanas on one hand and to varanids on the other, a conclusion which Cuvier (1808, pp. 175-176) endorsed. Forty-two years after its discovery the fossil was named *Mosasaurus* by Conybeare (1822, p. 298). The trivial names *belgicus, camperi, giganteus* and *hoffmanni* have all been applied to this specimen. Camp (1942, pp. 44-45) after a careful perusal of the literature found that *Mosasaurus hoffmanni* Mantell (1829, p. 207) is probably the earliest name available, with the famous Maestricht fossil as its designated type.

For the next eighty years European workers continued to regard mosasaurs as large marine lizards closely allied to varanids. Goldfuss (1845, pp. 179, 188) in describing an American species of *Mosasaurus* supported this view. Owen (1840-1845, p. 258) agreed that the true relations of *Mosasaurus* lay between the iguanids and varanids. He noted that the teeth of his newly-named *Liodon* resembled those of *Mosasaurus* more closely than those of any other reptile known at that time. Later (1849-1884, pp. 29-45) Owen placed *Mosasaurus* and *Liodon* together in the undiagnosed tribe Natantia of the Lacertilia. In 1853 (p. 471) Gervais proposed the family Mosasauridae and included it in the Lacertilia, although provisionally in a distinct suborder along with the Megalosauridae and Iguanodontidae, both of the latter being families of dinosaurs. Within the Mosasauridae were ranged *Mosasaurus, Liodon, Onchosaurus* (a batoid shark, see Romer, 1945, p. 577), *Oplosaurus* (= *Pelorosaurus,* a sauropod, see Romer, 1956, p. 621), *Macrosaurus* and *Geosaurus* (a thalattosuchian crocodile, see Romer, 1956, p. 607). Owen made a detailed comparison of the skulls of chelonians, lizards (*Amblyrhynchus, Varanus,* etc.), snakes (*Python*) and mosasaurs (*Clidastes, Mosasaurus, Platecarpus*) and concluded (1877, p. 715) in response to Cope's (1875, pp. 113-127) assertion that mosasaurs belonged to a separate order allied to snakes, ". . . that the fossil evidences of the mosasaurians hitherto made known do not yield a single character peculiar to and characteristic of the ophidian order." Owen implied that mosasaurs should be classed within the Lacertilia as a distinct suborder, taking the assignment of the Pinnipedia under the Carnivora as an analogous example.

Cope (1869b, p. 254) had erected a new order of reptiles, the Pythonomorpha, solely for the inclusion of the mosasaurs. These animals were postulated to combine lacertilian and ophidian characters and were diagnosed by Cope (1869b, p. 254) as follows: "Opisthotic distinct, not, or scarcely in contact with parietal arc, embraced at one end by the prootic and exoccipital, and supporting squamosal and quadratum." Later Cope (1875, p. 126) stated that, "As a conclusion, it may be derived that (mosasaurs) are not nearly related to the Varanidae as has been supposed, but constitute a distinct order of the streptostylate group (which also includes the orders Lacertilia and Ophidia); that they are primarily related to the Lacertilia, secondarily to the Ophidia, and thirdly to the Sauropterygia; that they present more points of affinity to the serpents than does any other order; and their nearest point of relationship in the Lacertilia is the Varanidae or Thecaglossa." Throughout his life this remained his opinion in the face of much opposition (see Cope, 1869-1870, 1878, 1895a, 1895b, 1896; for summaries see Baur, 1892; and Williston, 1898b, pp. 94-99).

Marsh (1872b, p. 448) initially followed Cope in regarding mosasaurs as a separate order of reptiles. Leidy (1873, p. 271) preferred not to use Cope's term "Pythonomorpha" but separated the mosasaurs on an ordinal level from the lizards. By 1880 (p. 87) Marsh referred the suborder Mosasauria (also abandoning the term "Pythonomorpha") to the Lacertilia because of the presence of a sternum, fore and hind limbs, and the absence of palatine teeth. Merriam (1894, p. 14), after a critical appraisal of Cope's (1878) list of characters of pythonomorphs, likewise concluded that they could not be separated from lizards. The polemic between Cope (1895a, 1895b, 1896) and Baur (1892, 1895, 1896) on mosasaur relationships is particularly hard to follow because of their differing views on the homologies of the bones of the quadratic suspensorium (see Camp, 1923, p. 347). Cope's position was that the element here termed the supratemporal was actually a separate paroccipital ossification. Irrespective of the nomenclature involved, precisely the same bony elements bearing almost exactly the same mutual relations exist in the suspensorium of *Varanus,* as Baur (1896, p. 146) pointed out, and Cope's key distinction for his concept of the Pythonomorpha cannot be vindicated.

Beginning with the last decade of the nineteenth century speculation on mosasaur-lizard affinities took on a new dimension. Two groups of amphibious lizards had been discovered in rocks of early late Cretaceous age in Yugoslavia and England (Aigialosauridae and Dolichosauridae). These lizards are clearly varanoid, with well-developed limbs, but also possess many characteristics of mosasaurs.

Some authors thought the mosasaurs were a lacertilian derivation that branched off the main phylum far back in Mesozoic time. Osborn (1899a, p. 172) did not mention the aigialosaurs, but stated that mosasaurs could not have descended from the dolichosaurs because of the greater number of cervical vertebrae in the latter group. He concluded (1899a, p. 188), "The Mosasaurs are a very ancient marine offshoot of the Lacertilia, retaining certain primitive and generalized Lacertilian characters and presenting a few resemblances in the skull to the Varanoids; they are very highly specialized throughout for marine predaceous life, and constitute a distinct subdivision of the order Lacertilia." Fürbringer (1900, pp. 616-622) followed Osborn's conclusions and separated the varanids, aigialosaurs and dolichosaurs from the mosasaurs on a subordinal level. Fejérváry (1918, p. 435) held that it would have been impossible for the aigialosaurs to acquire all the specializations of mosasaurs by late Cretaceous time and instead derived mosasaurs from hypothetical Jurassic platynotans.

Another school of thought, represented by Boulenger, Dollo, Gadow, Kornhuber, Kramberger, and Nopcsa, probably influenced by the analogy drawn by Owen between the Lacertilia and Mosasauria, and the Fissipeda and Pinnipedia, considered the former two groups to be of equal taxonomic rank. Boulenger (1891, p. 118; 1893, p. 205) regarded dolichosaurs as the common ancestors of mosasaurs, lizards and snakes. Kramberger (1892, pp. 102-105) was the first to point out that aigialosaurs were intermediate in morphology between lizards and mosasaurs and were probably ancestral to both. Dollo (1894, pp. 252-258; 1903, pp. 137-139; 1904b, pp. 217-222) and Nopcsa (1903a, p. 41; 1903b; 1923, p. 144) agreed in deriving the mosasaurs from the aigialosaurs, but maintained that varanids and aigialosaurs descended from primitive terrestrial varanoids ("Proplatynota") that resembled modern varanids in many respects. Kornhuber (1901, pp. 20-22) believed his *Opetiosaurus* (an aigialosaur) was the best available ancestor for mosasaurs and did not distinguish aigialosaurs from varanids, combining both within the family Varanidae. Nopcsa (1908, p. 61) suggested that snakes descended from the dolichosaurs, a possibility that was opposed by Janensch (1906, p. 32), Fejérváry (1918, p. 441), Camp (1923, p. 332), and others. Gadow (1901, p. 489) considered mosasaurs to be the marine collateral branch of the Lacertilia.

The contemporary view of the relations of mosasaurs finds its roots in the publications of Baur (1890, p. 262; 1892, p. 21) who insisted that mosasaurs be considered as true lacertilians and classed them with the varanids in the superfamily Varanoidea. Williston (1904) found Baur's arrangement to be somewhat extreme, yet largely substantiated by the discovery of the aigialosaurs. Williston (1904, p. 48; 1914, pp. 146-148; 1925, pp. 269-273) grouped the varanids, dolichosaurs and aigialosaurs in the superfamily Platynota, included the mosasaurs in the superfamily Mosasauria, and listed both superfamilies under the Lacertilia. He stated (1904, p. 47) that he knew of ". . . no more striking examples of evolution presented in all vertebrate paleontology than that of the aquatic mosasaurs of the Upper Cretaceous, through the semiaquatic aigialosaurs of the Lower Cretaceous, from the (hypothetical) terrestrial varanoids of the lowermost Cretaceous or Upper Jura." Versluys (1907) noted that an intermandibular joint was already present in varanids and aigialosaurs and was well-developed in mosasaurs. In his classification of lizards Camp (1923, pp. 321-322) ". . . consider[ed] the aigialosaurs as derived from true lizards near the Varanidae and as ancestral to both Dolichosauridae and Mosasauridae . . . and regard[ed] the presence of the annectant Aigialosauridae as grounds for denying rank higher than that of a superfamily to the mosasaurs." This last work also contains a summary of the history of classification of mosasaurs (1923, pp. 322-325).

In 1942 (p. 44) Camp reinforced his earlier conclusions on the systematic position of mosasaurs: "Altogether, the inner ear, skull elements, and cranial foramina of *Platecarpus* have so many of the peculiarities of *Varanus* that we must admit a close relationship of the two forms. It may be correct to say that the skull differences are much less than those between the fissiped and pinniped Carnivora, and are also less than those between *Varanus* and the Iguanidae, Agamidae, Amphisbaenidae, and Gekkonidae. Manifestly there are good morphological and paleontological grounds for considering the mosasaurs to be derived from early Cretaceous varanoid lizards. Retention of so many close similarities in the skull elements, brain case, cranial foramina, inner ear, extracolumella, and lower jaw, as well as the presence in the lower Cretaceous of the annectant Aigialosaurinae, should be recognized in the classification. This should permit the mosasaurs to be included in the suborder Sauria as a superfamily of the subsection Platynota."

Camp has been followed by Gilmore (1928), Nopcsa (1928), and Hoffstetter (1962), but not by McDowell and Bogert (1954, pp. 131-133) who combine the Mosasauridae, Aigialosauridae, Dolichosauridae and Lanthanotidae in an " 'aigialosaurian' group" and thus separate them from the Varanidae and Helodermatidae, also in the superfamily Platynota. Hoffstetter (1955, p. 611) and Romer (1956, pp. 557-563) do not allow more than a familial distinction between mosasaurs and other platynotans.

Subdivisions of Mosasaurs

The separation of mosasaurs into subordinate groups has had a rather complicated history. Cope (1869b, p. 258) originally divided his Pythonomorpha into two families, the Mosasauridae and the Clidastidae. The former were diagnosed as lacking a zygosphenal articulation on the vertebrae and having the pterygoids fused along their medial surfaces. The last character was based on Goldfuss' (1845, pl. 8) erroneous figure of the palate of *Mosasaurus missouriensis* in which the pterygoids were drawn as co-ossified. Included genera were *Macrosaurus, Mosasaurus* and *Platecarpus.* The Clidastidae, including only *Clidastes,* were characterized by the presence of a vertebral zygosphenal articulation and separate pterygoids. In his 1869-1870 synopsis Cope added *Halisaurus, Liodon, Polygonodon* (a fish tooth, not mosasaurian) and *Tylosaurus* to his Mosasauridae. The first indication of a modern type of classification is seen in a semi-popular paper by Marsh (1876, p. 59) where the families Edestosauridae (based on *Edestosaurus* = *Clidastes*) and Tylosauridae were mentioned in passing but not characterized.

Following Owen and Marsh, in 1884 (p. 653) and 1885b (p. 335) Dollo classed the mosasaurs as a suborder of the Lacertilia and separated them into two families. The Plioplatecarpidae were defined as possessing a sacrum, an interclavicle and a canal through the basioccipital-basisphenoid, all three characters presumably being absent in the Mosasauridae. *Clidastes, Mosasaurus, Liodon, Platecarpus, Halisaurus* and *Tylosaurus* were placed in the latter family, while the former was monotypic, including only the genus *Plioplatecarpus.* In 1890 (pp. 162-163) Dollo divided his Mosasauridae into three groups, based on the degree of development of a rostrum on the premaxilla, the size of the suprastapedial process of the quadrate, and whether or not the haemal arches were fused to the centra of the caudal vertebrae. A "microrhynchous" group contained *Platecarpus* and *Prognathodon;* a "mesorhynchous" group, *Clidastes* and *Mosasaurus;* and a "megarhynchous" group, *Tylosaurus* and *Hainosaurus.* Dollo noted (1890, p. 169) that *Plioplatecarpus* had the characteristics of the microrhynchous group. In 1894 (p. 221) Dollo realized that the "sacral" vertebrae of his original two specimens of *Plioplatecarpus* were pathologically fused "lumbars" (pygals), and that an interclavicle was also present in *Mosasaurus.* He therefore synonymized his Plioplatecarpidae with the Mosasauridae and recognized but one family of mosasaurs. Evidently abandoning his own Clidastidae, Cope (1889, p. 866; 1891, p. 50; 1898, p. 79) continued to subdivide the mosasaurs into the two families used earlier by Dollo.

Williston (1895, p. 169; 1897b, p. 102) included *Clidastes* and *Mosasaurus* in the Mosasauridae and named the Tylosauridae for *Tylosaurus* and *Platecarpus,* diagnosing both families on postcranial characters. Soon after, he (Williston, 1897d, pp. 176-177) formally replaced Dollo's microrhynchous, mesorhynchous and megarhynchous groups of mosasaurs with the subfamily names Platecarpinae, Mosasaurinae and Tylosaurinae. These subfamilies were well-defined (1897d, pp. 180-181) and correspond to the three subfamilies used in the present work, after reducing the rank of Dollo's older Plioplatecarpidae and substituting it for Williston's Platecarpinae. It should be noted that Dollo redefined his Plioplatecarpidae again in 1924 (p. 188) for the genus *Plioplatecarpus* and named the Globidensidae for *Globidens* and *Compressidens.* The latter family name has been accepted in modified form by Williston (1925, p. 273), Gilmore (1928, p. 8), Romer (1956, p. 562), and others, but is probably best considered a synonym of the Mosasaurinae.

The major classification adopted here is that of Camp (1961, p. 522) and the arrangement of subfamilies is similar to that of Williston. Tribal categories within the Mosasauridae are new.

Class REPTILIA

Superorder SQUAMATA
Order SAURIA (= LACERTILIA)
Suborder ANGUIMORPHA
Infraorder PLATYNOTA

- Superfamily VARANOIDEA
  - Family AIGIALOSAURIDAE
  - Family DOLICHOSAURIDAE
  - Family HELODERMATIDAE
  - Family LANTHANOTIDAE
  - Family VARANIDAE

- Superfamily MOSASAUROIDEA
  - Family MOSASAURIDAE
    - Subfamily MOSASAURINAE
      - Tribe MOSASAURINI
      - Tribe GLOBIDENSINI
      - Tribe PLOTOSAURINI
    - Subfamily PLIOPLATECARPINAE (= PLATECARPINAE)
      - Tribe PLIOPLATECARPINI
      - Tribe PROGNATHODONTINI
    - Subfamily TYLOSAURINAE

GENERAL DESCRIPTION OF MOSASAUR SKULL

The general shape of the skull is quite constant among the different genera of mosasaurs and suggests a closely-knit group of reptiles related to, but distinctly separated from, the varanid lizards. Although the range of form within the Mosasauridae is greater than that in the Varanidae, it is interesting to observe parallel variations occurring within both families; for example, the convergence of the margins of the parietal "table" at the center of the dorsal surface of the bone in *Platecarpus* and *Varanus grayi,* the unusually broad parietal of *Clidastes sternbergi* and *Varanus* subgenus *Tectovaranus,* and the powerfully built jaws and crushing dentitions of *Globidens* and *Varanus* subgenus *Empagusia* (see Mertens, 1942, pls. 22-26 for figures of the above-mentioned varanids).

The mosasaur skull grossly resembles an elongate, laterally compressed and bluntly terminated cone, the posteroventral corner of which has been horizontally transected. The muzzle forms the anterior half or more of the skull and lies in front of the antorbital wall and the splenio-angular joint of the lower jaw. Except for the slender bilobate external narial opening and the space between the ventral margin of the dentary, the muzzle is completely surfaced with bone. The large orbits are located behind the anteroposterior midpoint of the skull and open laterally and slightly dorsoanteriorly. The supratemporal fenestra is located above and behind the orbit and is widely separated from its opposite by the broad dorsal surface of the parietal. The large infratemporal opening is separated from the above fenestra by a slender arcade of bone that connects the dorsoposterior rim of the orbit with the quadratic suspensorium. The quadrate is streptostylic, articulating with the distal end of the suspensorium above and the mandible below, and was presumably bound ventroanteriorly to the posteroventral corner of the jugal by a long ligament. The lateral surface of the lower jaw narrows posteriorly and terminates in a rounded retroarticular process which projects behind the occipital condyle. The roof of the oral cavity is broken by five major fenestrae: two anterior openings between the vomero-palatines and the maxillae for the internal nares; two suborbital vacuities bounded by the palatines, pterygoids, ectopterygoids and jugals; and a slender lenticular opening (incisura piriformis) between the anterior portions of the pterygoids. Behind the ectopterygoidal processes the pterygoids are constricted to allow the passage of the temporal musculature to the lower jaws. The pterygoids then diverge posteriorly to meet the quadrates. On either side of the supraoccipital the posttemporal fenestrae pierce the occipital face of the skull between the suspensorial bridge from the parietal above and the paroccipital process below. The foramen magnum is relatively smaller than in *Varanus.*

In *Clidastes* the skull is slender with relatively long jaws and a shortened temporal region. The skull is similar but larger in *Mosasaurus,* where the jaws are more powerfully constructed. In *Plotosaurus* (Camp, 1942, fig. 1) the skull is remarkably ichthyosaurian in lateral outline, with large orbits and dorsally convex, gently posterior-inclined, alveolar margins. The skull in *Platecarpus* is short and deep, with a relatively large temporal region. *Prognathodon* generally resembles *Mosasaurus* in the shape of the head, although the anterior portion of the muzzle is deeper and more bluntly terminated. Except for its very elongated rostrum, the skull of *Ectenosaurus* seems to be close to that of *Platecarpus.* In

Tylosaurus the head is more perfectly conical than in the above genera, and the muzzle is proportionally longer than in any of them, with the exclusion of *Ectenosaurus.*

The mosasaur skull can be divided into nine structural components, each primitively articulating with at least one other such unit through a moveable joint, although later in the phylogeny of mosasaurs some of these articulations lost their mobility. These components are the muzzle unit, the parietal unit, the occipital unit, pterygoid units, epipterygoid units, stapes units, quadrate units, the anterior division of the mandible and the posterior divison of the mandible. In the following section each individual bony element in the mosasaur head is described under the structural unit of which it is a part. The variations of that particular element among the different genera are noted. A survey of the literature on varanids together with a dissection of the head of *Varanus niloticus* has greatly facilitated speculation on the interrelationships between the bones and soft anatomy of the head, for the mosasaur skull is generally quite comparable to that of varanids. The terminology of musculature is after Lakjer (1926), that of the cranial nerves is after Watkinson (1906) and Bahl (1937).

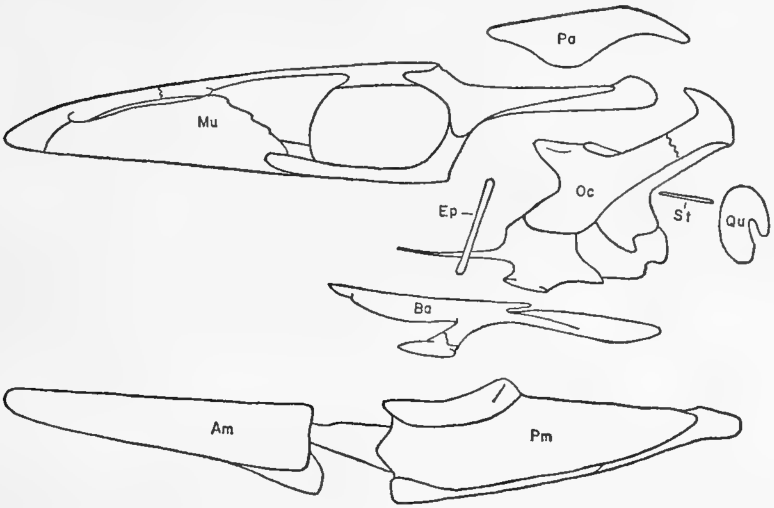
For additional descriptions of the cranial morphology of American mosasaurs the reader is referred to the works of Camp (1942), Williston (1898b), Huene (1910, 1911), Merriam (1894), Baur (1892), and Osborn (1899a), listed in order of decreasing importance. The California material has not been examined and the information included below relating to these forms has been taken from Camp's (1942) monograph.

Muzzle Unit

The largest of the nine structural units in the mosasaur cranium is the muzzle unit. This forms the anterior two-thirds of the skull and includes 24 bones (fused premaxillae, maxillae, nasals, fused frontals, lacrymals, prefrontals, supraciliaries, postorbitofrontals, jugals, squamosals, palatine-vomers, septomaxillae and orbitosphenoids) united together to form a half-cone with the vaulted surface above and two arms (supratemporal arcades) projecting posteriorly to the quadratic suspensoria. The muzzle unit meets the parietal dorsoposteriorly in a broad transverse hinge (mesokinetic axis) and the pterygoids (pterygoid units) ventroposteriorly on either side of the incisura piriformis through flexible overlapping sheets of bone (hypokinetic axis). The jugal contacts the lateral face of the ectopterygoid (pterygoid unit) through a flat vertical sliding surface. On the posterior termination of the supratemporal arcade the expanded end of the squamosal forms a rotating joint (metakinetic axis) with the lateral face of the supratemporal (occipital unit). The anterior and posterior portions of the muzzle unit are then raised or lowered about the mesokinetic axis. The unit is supported below by two flexible struts (pterygoid units) and posteriorly by the connection of the supratemporal arcades with the distal end of the quadratic suspensoria.

PREMAXILLAE

The mosasaur premaxillae differ markedly from those of *Varanus* because their anterior rostral surfaces are always smoothly continuous with the rostral surface of the skull, instead of being depressed posteriorly to form a part of the floor of the nasal capsule. They possess alveoli for only two teeth instead of four as in *Varanus.* Like *Varanus,* however, the premaxillae are co-ossified with no indication of a suture and are described below as one bone.



Text-fig. 1. Diagram of the functional units of a mosasaur skull. Abbreviations for this and all cranial figures are as follows.

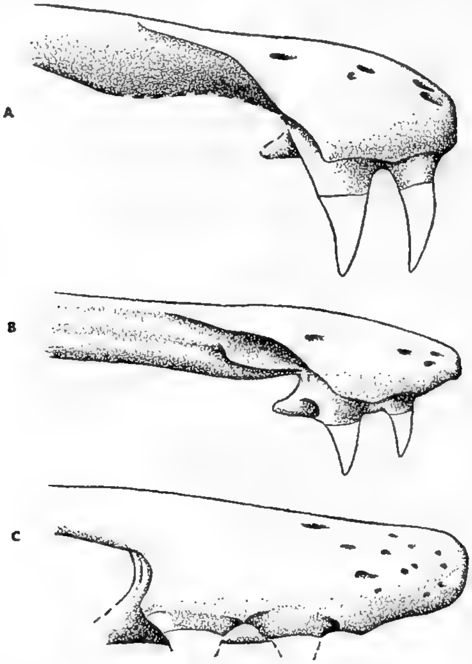
Kinetic units: Am, anterior mandibular unit; Ba, basal unit; Ep, epipterygoid unit; max, mesokinetic axis; mtj, metakinetic joint; mtx, metakinetic axis; Mu, muzzle unit; Oc, occipital segment; Pa, parietal unit; Pm, posterior mandibular unit; Qu, quadrate unit; St, stapes unit.

Cranial structures: a, angular; ah, ampulla of horizontal and anterior vertical semicircular canals; ala, alar process of basisphenoid; ap, ampulla of posterior vertical semicircular canal; ar, articular; ba, basilar artery; bab, branch of basilar artery; bo, basioccipital; bs, basisphenoid; bt, basipterygoid process of basisphenoid; c, coronoid; ca, anterior vertical semicircular canal; ch, horizontal semicircular canal; che, cerebral hemisphere; cp, posterior vertical semicircular canal; ct, foramen for corda tympani; d, dentary; ds, dorsum sellae; e, epipterygoid; ec, ectopterygoid; en, external naris; end, endolymphatic duct; ens, endolymphatic sacculus; f, frontal or frontal suture; fo, fenestra ovalis; gl, intermandibular articulation; IAM, internal auditory meatus; ic, internal carotid artery; icb, branch of internal carotid artery; in, internal naris; inc, incisura piriformis; ios, interorbital septum; j, jugal; jo, aperture for Jacobson's organ; l, lacrymal; la, lagena; m, maxilla or maxillary suture; o, opisthotic; of, olfactory lobe; or, orbit; os, orbitosphenoid; ot, otosphenoidal crest of basisphenoid; p, parietal or suture for parietal; paf, parietal foramen; pl, palatatine; pld, perilymphatic duct; pls, perilymphatic sacculus; pm, premaxilla; pof, postorbitofrontal or suture for postorbitofrontal; popr, paroccipital process of opisthotic; pr, prootic; pra, prearticular; prf, prefrontal or suture for prefrontal; ps, parasphenoid; pt, pterygoid; q, quadrate; sa, surangular; set, sella turcica; soc, supraoccipital; sp, splenial; sq, squamosal; st, supratemporal; sta, stapes; tym, calcified tympanum; u, utriculus; v, vomer; vc, vidian canal; vcl, vena capitis lateralis.

Cranial nerves: I, olfactory nerve; II, optic nerve; V, trigeminal nerve; VI, abducens nerve; VII, facial nerve; VIII, acoustic nerve, -a, anterior branch, -p, posterior branch; IX, glossopharyngeal nerve; X, vagus nerve; XI, accessory nerve; XII, hypoglossal nerve.

Muscles inserting on cranium: AEMS, Mm. adductor mandibulae externus medialis et superficialis; AEP, M. adductor mandibulae externus profundus, -pp, posterior head, -pq, quadrate head; AM, M. adductor mandibulae, undivided; AMP, M. adductor mandibulae posterior; B, bodenaponeurosis; CM, M. cervicomandibularis; DM, M. depressor mandibulae; ICC, M. iliocostalis capitis; LAO, M. levator angularis oris; LCap, pars articulo-parietalis of M. longissimus capitis; LCtc, pars transversalis capitis of M. longissimus capitis; LCtce, pars transversalis cervicis of M. longissimus capitis; LPt, M. levator pterygoid; OCM, M. obliquus capitis magnus; PPt, M. protractor pterygoid; PQ, M. protractor quadrati; Ps, M. pseudotemporalis, -pr, profundus, -sup, superficialis; Pt, M. pterygoideus, undivided; PtP, M. pterygoideus profundus; PtS, M. pterygoideus superficialis; RCA, M. rectus capitis anterior; RCP, M. rectus capitis posterior, -d, dorsal portion, -v, ventral portion; SC, M. spinalis capitis.

For descriptive purposes the mosasaur premaxilla may be divided into two major portions, a broad anterior tooth-bearing apex and a slender internarial bar. A large cylindrical "prow" projects in front of the premaxillary teeth in *Tylosaurus,* and a smaller, more conical one is present in *Clidastes, Mosasaurus, Ectenosaurus* and to some extent in *Plotosaurus.* The premaxilla terminates directly in front of the most anterior tooth in *Platecarpus, Plioplatecarpus* (Dollo, 1889b, p. 275), *Prognathodon* and *Plesiotylosaurus.* The dorsal midline of the bone may be smooth (*Clidastes, Mosasaurus missouriensis, Ectenosaurus* and *Tylosaurus*), with a slight dorsal crest (*Mosasaurus maximus* and *Plotosaurus*) or slightly sulcate (*Platecarpus* and *Prognathodon*). Paralleling the dorsal midline on either side is an irregular row of foramina in *Clidastes, Mosasaurus, Plotosaurus, Platecarpus* and *Prognathodon.* In *Tylosaurus* they are distributed randomly over the sides of the "prow." These foramina mark the exits of the ophthalmic ramus of the fifth nerve which in *Varanus* enters the premaxilla near the top of the premaxillo-maxillary sutural surface. In lateral trace this suture varies among the species of mosasaurs, but generally is parabolic in form, rising steeply from the alveolar margin and sweeping posteriorly to merge with the outer edge of the internarial bar. Ventrally the roots of the premaxillary teeth are separated from those of the opposite side by a grooved median ridge (*Clidastes, Platecarpus* and also in *Tylosaurus,* according to Williston, 1898b, p. 104). A nubbin on the center of the ventral surface of the "prow" in *Tylosaurus* is connected by weak ridges to the lateral margin of the dental alveoli and probably marked the anterior limit of the gum line.



Text-fig. 2. Mosasaur premaxillae. A. *Platecarpus ictericus* (AMNH 1820, × ½). B. ***Clidastes propython*** (YPM 1319, × ½). C. *Tylosaurus proriger* (AMNH 1592, × ½).

The internarial bar arises from a triangular base enclosed between the anterior wings of the maxilla on the dorsal surface of the skull in two species of *Clidastes,* in *Mosasaurus, Plotosaurus, Platecarpus, Ectenosaurus* and *Prog-*

nathodon. It arises from a broad rectangular base in a similar position in *Tylosaurus* and a narrower rectangular one in *Clidastes sternbergi.* In cross-section the bar exhibits the shape of a "T" or an inverted triangle, the descending keel of which probably supported a cartilaginous internasal septum posteroventrally, as in *Varanus* (Bahl, 1937, p. 163). The internarial bar is laterally constricted between the dilated anterior portion of the external narial opening and re-expands behind this region just before being wedged into the median cleft in the anterior end of the frontals in *Clidastes, Mosasaurus, Plotosaurus, Platecarpus, Ectenosaurus,* and *Plesiotylosaurus.* The internarial bar is nearly unconstricted and is relatively wide throughout its length in *Tylosaurus,* and penetrates the frontal to a point far behind the posterior termination of the narial opening, unlike in any of the foregoing genera. In *Varanus* the fused nasals link the internarial bar of the premaxilla with the frontals, although the premaxilla and frontals may contact beneath this bone. In mosasaurs the nasals are vestigial and separated by the premaxillary bar and frontals (Camp, 1942, pp. 27-28, fig. 14).

MAXILLA

The maxilla is rather constant in form in mosasaurs. Ventrally there is a longitudinally flattened buttress supporting the tooth bases and housing the conduit for the maxillary artery and the maxillary division of the fifth nerve. Out of the lateral edge of this buttress a vertical lamina of bone ascends to form a squamose suture with the prefrontal posteriorly. It is emarginated above by the opening for the external nares and re-expands anteriorly to be cut off by the obliquely descending premaxillary suture. The ventral outline of the buttress is slightly concave upwards in *Platecarpus, Ectenosaurus* and *Plotosaurus,* but is straight in *Clidastes, Globidens, Mosasaurus, Prognathodon* and *Tylosaurus.* As would be expected the buttress is much wider and heavier posteriorly in *Globidens* to support the powerful dentition. There is a medially projecting keel on its posterointernal edge that contacts the palatine in *Clidastes, Platecarpus* and *Tylosaurus.* Terminal branches of the maxillary nerve emerge through a row of foramina just above the gum line on the lateral surface of the maxilla and through smaller foramina scattered over the anterior surface of the bone.

In lateral aspect the suture for the premaxilla rises steeply from the alveolar margin, then slopes posteriorly at a geometrically decreasing angle with the horizontal axis of the skull in *Clidastes, Globidens* and *Mosasaurus.* In *Plotosaurus, Platecarpus, Ectenosaurus, Prognathodon* and *Tylosaurus,* the suture usually rises vertically from the alveolar border, makes an abrupt turn after reaching a position lateral to the top of the maxillary buttress, and continues posterodorsally in a straight line. The sutural surface appears triangular in dorsal outline, with the base of the triangle at the transversely truncated ventral maxillary buttress and the apex pointing posteriorly along the anterior ascending lamina. In *Platecarpus* and *Tylosaurus* the apex of the triangle coincides with the posterodorsal termination the suture; its surface is longitudinally ribbed and grooved and is bounded externally by a large crest. In *Clidastes, Globidens* and *Mosasaurus* the triangular area is small and lies far anteriorly on the suture; its surface is smooth and continues posteriorly into an even crest, shaped like an inverted "V" in cross-section, that extends back to meet the anterior end of the narial emargination. The ante-narial portion of the maxilla is never bent medially to form a floor beneath the nasal capsule, as it is in *Varanus.*

The external nares are bounded laterally by the maxilla, medially by the internarial bar of the premaxilla, and posterolaterally by the prefrontal in

Clidastes, Mosasaurus, Platecarpus, Prognathodon and *Plesiotylosaurus,* but not in *Plotosaurus, Ectenosaurus* and *Tylosaurus* where the prefrontal is excluded from the narial margin by a tongue of the maxilla. They terminate posteriorly in a "V"-shaped notch formed by the frontal and prefrontals meeting at an acute angle in *Clidastes, Mosasaurus, Prognathodon* and *Plesiotylosaurus,* but not in *Platecarpus, Plotosaurus* and *Tylosaurus* where the narial opening ends in a rounded notch in the anterior margin of the frontal. The lateral swelling of the internarial bar before it reaches the frontal and a gentle convexity on the dorsal rim of the narial margin of the maxilla indistinctly divide the narial opening into a large anterior lobe, presumably occupied by the external naris, and a smaller posterior one *(Clidastes, Mosasaurus, Plotosaurus, Platecarpus, Ectenosaurus, Prognathodon* and *Tylosaurus).* In *Plesiotylosaurus* the lobes are subequal in size. The external narial fenestra is relatively long in *Plotosaurus bennisoni* (amounting to 39% of skull length), intermediate in *Prognathodon overtoni, Plotosaurus tuckeri, Mosasaurus missouriensis* (Williston, 1898b, pl. 20; Goldfuss, 1845, pl. 6), *Platecarpus ictericus* and *Clidastes liodontus* (amounting to 26-34% of skull length) and short in *Tylosaurus proriger* and *Plesiotylosaurus crassidens* (amounting to 20-24% of skull length).

Behind the premaxillary suture and from a point dorsal to the second maxillary tooth back to the seventh (eleventh in *Clidastes sternbergi)* the upper rim of the maxilla is sharply emarginated from above for the anterior lobe of the external narial opening. It re-ascends posteriorly in a smooth curve to be emarginated again, but to a lesser extent, forming the ventral border of the posterior lobe of the narial fenestra. In some genera *Plotosaurus, Ectenosaurus* and *Tylosaurus,* the maxilla may send a tongue posteromedially over the prefrontal to contact the lateral edge of the frontal, but usually this tongue is small and the maxilla forms a squamose suture directly with the lateral lamina of the prefrontal. This suture descends in a straight line to the posterior end of the maxilla. The maxilla overlaps the prefrontal anterolaterally and is in turn overlapped posteriorly by the spatulate anterior end of the horizontal ramus of the jugal.

NASAL

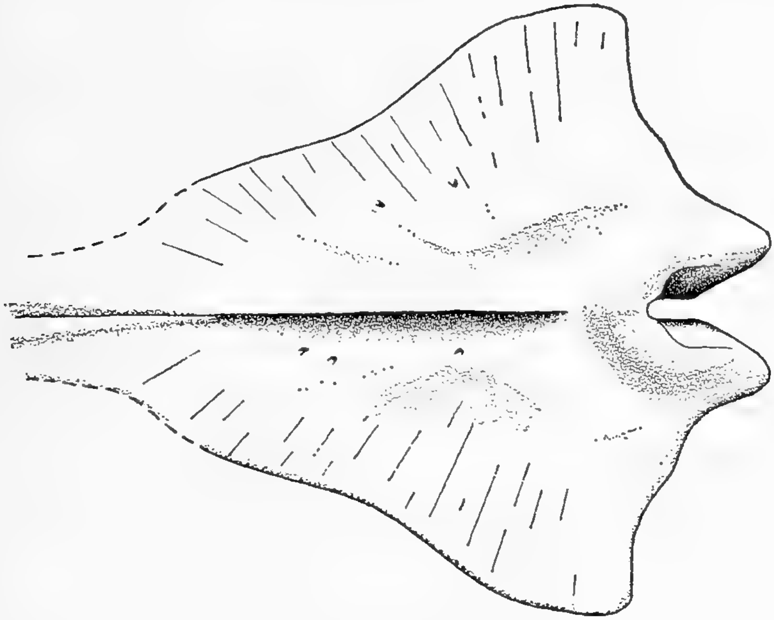
The nasal is known in only three specimens of American mosasaurs. The nasal in the type of *Plotosaurus bennisoni* ". . . is a vestigial bone only 60 mm. in length which lies at the junction of the premaxillary and frontal under the broadened posterior fourth of the internarial bar. Its anterior tip loosely occupies a hollow in the side of the premaxillary bar and its thin posterior end articulates with the lateral side of the internarial process of the frontal on a squamous suture. One-third of the way forward is a small, rounded vertical ridge which may mark an attachment to the outer wall of the nasal membrane. The loose articulation of the nasals with the internarial bar and their frequent loss may indicate that the nasals were closely united to the saclike integuments of the narial chamber." (Camp, 1942, pp. 27-28, fig. 14)

The nasals in *Tylosaurus* ". . . sind schmale längliche Knöchelchen an dem Medialrand jeder Nasenöffnung. Sie kommen beinahe, aber nicht ganz mit dem spitzen des Frontale zusammen." (Huene, 1910, p. 303, fig. 5) Separate nasals were reported by Wiman (1920, p. 15, fig. 4) in *Clidastes sternbergi.*

FRONTALS

The frontals are solidly fused along the midline of the skull, forming a flat triangular plate linking the internarial process from the premaxilla with the median dorsal axis of the parietal. The frontal is narrow anteriorly and forms the posteriormost portion of the internarial bar, enclosing the premaxillary shaft in a tight "V"-shaped notch (*Clidastes, Plotosaurus, Platecarpus, Ectenosaurus* and *Plesiotylosaurus*). In *Tylosaurus* the internarial bar is formed almost entirely of the premaxilla which penetrates deeply into the anterior end of the frontal.

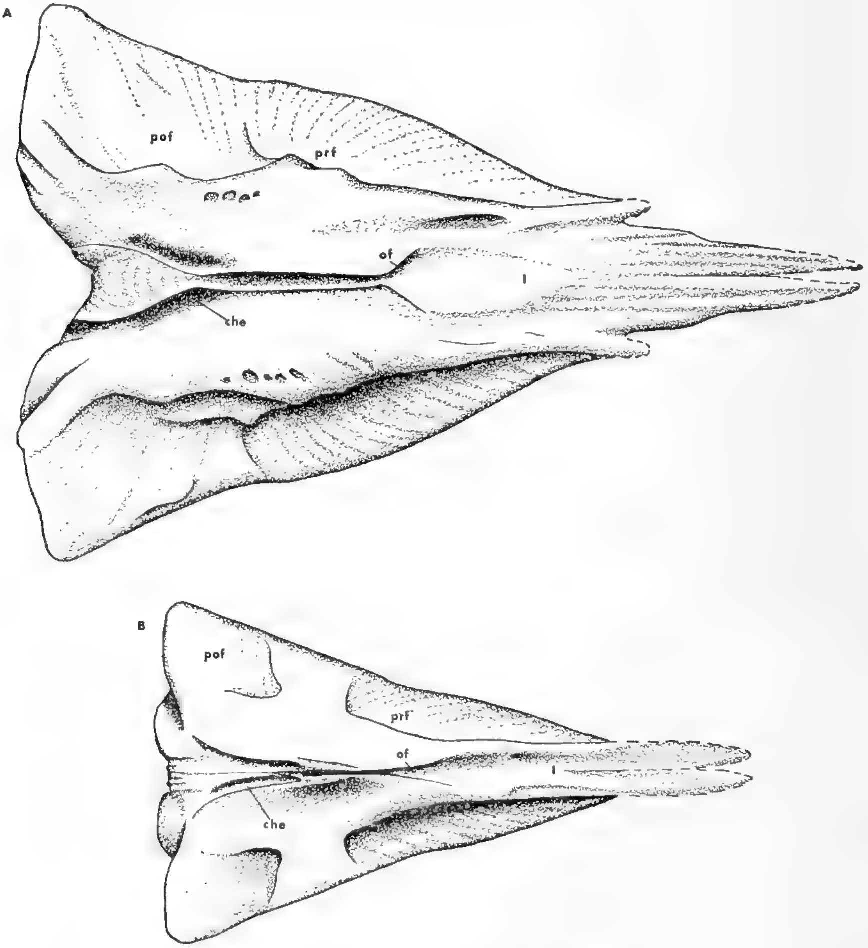
The frontal dilates behind the external narial opening, in some instances forming a rounded posterior boundary for the narial fenestrae (*Plotosaurus, Platecarpus* and *Tylosaurus*), in others the anterolateral margins diverge posteriorly in a more regular manner (*Clidastes, Plesiotylosaurus*). In *Mosasaurus* the anterior edges of the frontal parallel the cranial midline behind the pointed posterior ends of the external nares, then in front of the antorbital wall diverge at a nearly 180° angle for a short distance, and finally turn posteriorly and a little laterally to continue in a straight line back to the posterior base of the bone. In *Platecarpus* and *Ectenosaurus* the lateral margins of the frontal curve outwardly back to a point above the antorbital wall. Here they turn gently medially and then diverge again, forming a shallow sulcus over the orbits. The frontal is similar in *Clidastes* but is relatively narrower and has straighter margins. In *Prognathodon* the frontal is shorter and broader than in *Platecarpus*. Its anterior margins diverge in straight lines back to the prominence above the antorbital wall and from here posteriorly parallel the longitudinal axis of the skull, showing no signs of a supraorbital emargination. In *Tylosaurus, Plesiotylosaurus* and *Plotosaurus* the frontal margins are more regular than in the foregoing genera and not so strongly divergent posteriorly. In the former two genera the margins are slightly convex; in the latter one they are slightly concave. A median dorsal ridge is present on the frontal of *Clidastes* (weakly developed), *Globidens* (present but not sharply defined), *Mosasaurus, Platecarpus, Ectenosaurus* and *Prognatho-*



Text-fig. 3. Frontal of *Mosasaurus maximus* (NJSM 11052, × 2/7).

don. It may be either well-developed or absent in *Tylosaurus* and is absent in *Plotosaurus*.

On the undersurface of the frontals a triangular excavation, representing the suture for the prefrontals, lies anterior to the center of the orbit and lateral to the impressions of the olfactory tract along the ventral midline. In forms where the prefrontal and postorbitofrontal are separate (*Clidastes* and *Globidens*?) the posterior boundary of the suture is clearly marked by a laterally directed buttress. In other mosasaurs (*Platecarpus* and *Tylosaurus*) where these two bones meet beneath the frontal, the posterior boundary of the suture is obscured by that of the postorbitofrontal. The postorbitofrontal suture proper is located on the ventral surface of the posterolateral corner of the frontal. It extends medially about one-half of the distance from the edge of the frontal to its midline in *Clidastes*, *Platecarpus* and *Tylosaurus*, less than this distance in *Globidens*,



Text-fig. 4. Undersurface of frontal. A. *Platecarpus ictericus* (AMNH 1820, × ½). B. *Clidastes propython* (YPM 1368, × ½).

and only one-fourth of this distance in *Clidastes sternbergi* where it ends against a buttress that approximately parallels the longitudinal axis of the skull. Both of the above sutural surfaces are relatively smooth in *Clidastes*, but are marked with ridges and grooves radiating from the center of the bone in *Globidens, Platecarpus* and *Tylosaurus.* The suture with the parietal is long and transversely oriented (see description of parietal). Ridges and grooves on its surface dip more steeply as the center of the frontal is approached, becoming vertical in the middle of the bone. Tongue-like extensions from the frontal overlap the mesokinetic axis on either side of the cranial midline to cover the anteromedial surface of the parietal in several genera (see description of parietal).

The outline of the cerebral hemispheres is not clearly defined over the posterior undersurface of the frontal but, as Camp (1942, p. 40, fig. 24) has indicated, the hemispheres themselves must have been smaller than in *Varanus.* Impressions in the frontal suggest that the cerebral hemispheres partly roofed the posterior base of the olfactory tract. In front of the hemispheres this tract expands slightly to form the olfactory bulbs which were sheathed ventrally by wings from the frontal much as in *Varanus.* Fibers of the first cranial nerve then probably spread out anteriorly under the frontal portion of the internarial bar. In *Clidastes* and *Globidens* the olfactory tracts arise on a level with the dorsal surface of the cerebral hemispheres, but in *Platecarpus* and *Tylosaurus* they arise more ventrally. In *Mosasaurus* the flanges beneath the olfactory bulbs may have been absent and the first nerve seems to have been more divergent anteriorly than in the above genera.

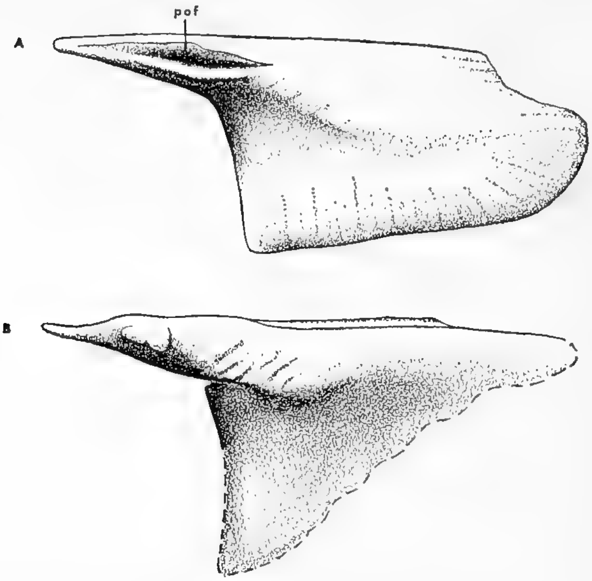
LACRYMAL

The lacrymal is a small bone located between the prefrontal and maxilla, dorsal to the jugal on the anteroexternal edge of the orbit. It is rarely preserved and, when present, is usually badly crushed. The lacrymal in *Plotosaurus* lies almost entirely within the ventroanterior wall of the orbit. There is a small foramen between the prefrontal, maxilla and lacrymal which may be homologous with the much larger foramen between the lacrymal and prefrontal in *Varanus.* Merriam (1894, pp. 28-29) states that in *Platecarpus* the lacrymal is a four-sided plate with a small, deep notch appearing on one border.

In *Tylosaurus* the roughened lenticular outer surface of the lacrymal separates the maxilla and prefrontal posterolaterally (see Osborn, 1899a, pl. 21; Huene, 1910, fig. 5; Merriam, 1894, p. 22). The apparently well-exposed lateral surface of the lacrymal seems to have had a quadrilateral outline in *Clidastes.* According to Williston (1898b, p. 109) its outer side is also slightly roughened. The element figured by Goldfuss (1845, pl. 7) is probably a fragment of the jugal instead of the lacrymal as stated.

PREFRONTAL

The prefrontal in mosasaurs consists essentially of a flat dorsal plate of bone that roofs the anterior half of the orbit, is in turn overlain by the frontal above, and extends anteriorly out onto the face of the rostrum as far as the posterior border of the external nares. The prefrontal is excluded from the narial margins in *Plotosaurus, Ectenosaurus* and *Tylosaurus* by a tongue of the maxilla. A thin lateral lamina descends vertically from the rostrally exposed portion of this dorsal plate to be overlapped ventroanteriorly by a thin sheet of bone from the maxilla. Another heavier lamina that is vertically-convex posteriorly descends perpendicularly from a point one-third of the way from the posterior end of the dorsal plate, forms the anterior border of the orbit, meets the lateral plate at right angles, and contacts a similar rising wall from the palatines below. The connections with the palatine seem to have been cartilaginous. Thus the prefrontal may be divided into: 1) a supraorbital plate or process continuing



Text-fig. 5. Prefrontal. A. *Tylosaurus proriger* (AMNH 4909, × ½). B. *Platecarpus ictericus* (AMNH 1820, × ½).

anteromedially into an exposed diamond-shaped surface; 2) a triangular lateral plate bounded by the maxilla anteroventrally, by the orbit posteriorly, and by the dorsal surface of the skull above; 3) a vertical wall of bone descending from the anterior limit of the supraorbital process.

The supraorbital process of the prefrontal is quite variable in mosasaurs. In *Clidastes* and to a lesser extent in *Mosasaurus, Prognathodon, Plotosaurus* and *Plesiotylosaurus,* there is a broad triangular ala projecting laterally from the supraorbital process. This ala is present only as a small nubbin in *Platecarpus* and *Plioplatecarpus* (Dollo, 1889b, pl. 9, fig. 6) and is entirely absent in *Ectenosaurus* and *Tylosaurus.* In *Clidastes* and possibly also *Globidens* the prefrontal and postorbitofrontal do not come in contact beneath the frontal. In *Prognathodon* these bones contact, and in *Platecarpus* and *Mosasaurus* the postorbitofrontal underlies a small portion of the posterior tip of the prefrontal. In *Tylosaurus* the supraorbital process of the prefrontal receives a tongue from the postorbitofrontal in a posteriorly deepening groove in its lateral margin. These two elements are nearly fused in *Plotosaurus.*

SUPERCILIARY

There is an element infrequently associated with *Platecarpus* skulls that can only be identified as the superciliary. It is, like the ectopterygoid, an "L"-shaped bone with a broad short wing possessing an oblique sutural surface on its dorsal (?) face and a longer and slenderer wing whose lateral edge is beveled off. There is no sharp, anteriorly projecting point at the anterior apex of the "L" as is usually the case in *Varanus.* What is here taken as the ventral surface is smooth and longitudinally concave. Both Baur (1892, p. 15) and Camp (1942, p. 32) have noted a roughened area on the lateral rim of the supraorbital wing of the prefrontal in *Platecarpus* (present also in *Plioplatecarpus,* see Dollo, 1889b, pl. 9 fig. 6) that may have marked the point of attachment of the superciliary bone.

Baur (1892, pl. 1 fig. 1) has illustrated the element under consideration and identified it as the superciliary, while Camp's (1942, fig. 18) superciliary is here believed to be an orbitosphenoid.

Osborn (1899a, p. 171, pl. 21 upper figure, element marked "x") tentatively identified a small bone as a superciliary in *Tylosaurus.* It has not been seen in exceptionally well-preserved skulls of *Clidastes* and *Plotosaurus.*

POSTORBITOFRONTAL

The postorbitals and postfrontals are co-ossified in mosasaurs to form a single four-pronged element, much as in *Varanus* (Camp, 1942, p. 5, reports that a trace of a suture remains between these bones in *Plotosaurus).* The main body of the postorbitofrontal consists of the dorsally exposed surface of a process that extends anteriorly along the lateral edge of the frontal and bounds the orbit posterodorsally. From this central body another process passes along the posterior border of the frontal to contact the parietal medially, a third descends to the jugal, and a final long and slender process fits into a deep groove in the dorsal edge of the squamosal. The first two processes are connected underneath the frontal by a thin sheet of bone and are separated from the other more ventrally located rami by a groove in some genera *(Platecarpus* and *Tylosaurus)* but are smoothly continuous with these rami in *Clidastes, Globidens, Plotosaurus, Mosasaurus* and *Prognathodon.*

The main body of the postorbitofrontal is expanded laterally into a broad triangular ala in *Clidastes,* comparable to the one developed on the prefrontal in this genus. A similar but smaller and heavier ala exists in *Globidens.* In *Mosasaurus, Plotosaurus* and *Prognathodon* the ala is not so well developed, and in *Platecarpus* and *Tylosaurus* the anterolateral edge of the postorbitofrontal is only narrowly exposed. The external apex of the ala is curved ventrally in *Clidastes, Globidens, Mosasaurus, Plotosaurus* and *Prognathodon* to form a suture with the dorsolateral surface of the jugal. The process to the jugal is larger in *Platecarpus* and *Tylosaurus* and in the former genus is distally expanded, overlapping the jugal anteriorly and externally.

The medial process to the parietal is short in *Platecarpus* and loosely articulated with the parietal. In *Mosasaurus* and especially *Clidastes* the process is largely covered by and apparently firmly sutured to a lateral wing from the parietal. In *Clidastes, Globidens, Mosasaurus, Plotosaurus, Platecarpus, Prognathodon* and *Tylosaurus* the long process to the squamosal forms the anterolateral boundary of the supratemporal fenestra and bears a sharply defined keel along the entire length of its ventral surface which fits into a groove on the squamosal. This process is exceedingly broad in *Globidens,* indicating the insertion of a powerful M. adductor mandibulae externus on the ventral surface of the underlying squamosal.

The face of the postorbitofrontal lying beneath the posterolateral corner of the frontal is smooth in *Platecarpus* and *Tylosaurus.* There is a ventral ridge trending transversely and somewhat posteriorly across this surface in *Clidastes* and *Globidens* which in *Mosasaurus* is less clearly developed. In *Mosasaurus, Plotosaurus* and *Platecarpus* all four processes of the postorbitofrontal lie in the same curved plane within the dorsolateral margin of the skull; in *Clidastes* and *Globidens* the broad ala must have projected beyond this plane. In *Tylosaurus* the parietal and jugal processes and a third antero-posterior axis formed by the processes to the prefrontal and squamosal meet each other at right angles. The prefrontal and parietal processes never enclose a lateral lobe from the parietal between them in mosasaurs as they do in *Varanus.*

JUGAL

The mosasaur jugal in an "L"-shaped bone with a broad ascending ramus forming the posterior boundary of the orbit and a narrower anterior horizontal ramus forming its ventral boundary. There is a well-marked posteroventral tuberosity at the crux of the "L" in *Platecarpus, Mosasaurus* and *Ectenosaurus,* which is weaker in *Prognathodon, Tylosaurus* and *Plotosaurus,* and absent in *Clidastes.* This tuberosity represents the anterior point of attachment of the "quadratomaxillary" ligament which in *Varanus* arises partly on a lateral prominence of the ectopterygoid and partly on the adjacent posteriormost tip of the maxilla.

The vertical ramus of the jugal in *Platecarpus* and *Plotosaurus* is overlapped dorsally by the postorbitofrontal but does not form an interlocking suture with this element. Anteriorly, the horizontal ramus becomes laterally compressed and is loosely applied to the posterior surface of the maxilla in *Clidastes, Platecarpus, Ectenosaurus, Prognathodon* and *Tylosaurus.* Medially the horizontal ramus contacts the ectopterygoid but there is no indication of a suture and the joint was probably a sliding one.

SQUAMOSAL

The squamosal is a comma-shaped bone in mosasaurs that connects the upper temporal arcade with the quadratic suspensorium. For the insertion of the postorbitofrontal the anterior shaft of the squamosal is deeply grooved dorsally from its slender anterior termination next to the jugular process of the postorbitofrontal back to a point opposite the posterolateral corner of the supratemporal fenestra in *Clidastes, Mosasaurus missouriensis* (Williston, 1898b, pl. 20), *Plotosaurus tuckeri, Platecarpus, Prognathodon, Plesiotylosaurus* and *Tylosaurus,* and somewhat behind this point in *Mosasaurus maximus, Plotosaurus bennisoni* and *Ectenosaurus.*

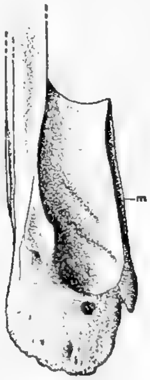
Posteriorly, the squamosal is expanded into an arrowhead-shaped body, whose median axis is more ventrally inclined than the anterior shaft of the bone. The suture for the supratemporal covers all of the internal face of the head of the squamosal and contains a shallow excavation that parallels its median axis anterodorsally to the posterior end of the squamosal shaft *(Mosasaurus, Platecarpus)* or extends for a short distance over the posteromedial surface of the shaft *(Clidastes, Tylosaurus*). A small wing of bone extends from the triangular body of the squamosal dorsomedially to contact the suspensorial ramus of the parietal in *Clidastes, Mosasaurus* (where it is very small), *Plotosaurus, Platecarpus, Prognathodon, Plesiotylosaurus* and *Tylosaurus.* The squamosal has a horizontal facet at its ventroposterior margin for articulation with the quadrate in *Clidastes, Platecarpus* and *Tylosaurus.* In *Mosasaurus maximus* the surface of the facet is vertical and located on the ventral face of the body of the squamosal.

The upper temporal arcade is bowed somewhat dorsally in *Platecarpus* and *Clidastes* but is approximately straight in *Mosasaurus, Plotosaurus, Prognathodon* and *Tylosaurus.* Its ventral border is sheathed entirely by the squamosal and it must have been on this bone that the pars superficialis and medialis of the M. adductor mandibulae externus originated.

PALATINE-VOMER

The palatine is a rectangular plate of bone wedged between the pterygoids posteriorly, the maxilla laterally, and the vomer anteriorly. The posterodorsal surface of the palatine slopes up from its posterior termination to form a "J"-

shaped ridge, which surrounds a basin in the superior surface of the bone posteriorly and medially and contacts the descending antorbital wall from the prefrontal above. In *Platecarpus* and *Tylosaurus* there are two small crests which trend anteromedially over the surface of this basin. The ventral surface of the palatine is ridged posteromedially to receive an anteromedial process from the pterygoid. Laterally the palatine expands somewhat to enclose an elongated elliptical cavity which fits over a longitudinal ridge on the posteromedial side of the maxilla. The bone thins anteriorly to end in a shallow sulcus forming the posterior border of the internal naris. In *Varanus* the palatine foramen lies just medial to the maxillary suture on the posterior rim of the palatine and transmits the maxillary branch of nerve V, the inferior orbital artery, and the maxillary vein into the alveolar canal of the maxilla (Bahl, 1937, p. 161). This foramen has not been seen in *Clidastes, Platecarpus* or *Tylosaurus*; it may have been destroyed by crushing or the blood vessels and nerve may have passed through a gap between the palatine and prefrontal in the lateral portion of the antorbital wall. The palatines are relatively longer in *Clidastes* than in *Plotosaurus* or *Tylosaurus* and are shortest in *Platecarpus*. They do not meet along the midline.



Text-fig. 6. Dorsal view of right palatine of *Platecarpus ictericus* (AMNH 1820 × ½).

In *Plotosaurus* the vomerine process of the palatine arises medial to the posterior border of the internal naris, gently curves medially and then laterally to complete the boundary of the naris internally and obliquely overlap the vomer laterodorsally. The vomers cannot surely be distinguished from the vomerine processes in *Clidastes, Platecarpus* and *Tylosaurus*. The vomers are much longer and more closely appressed along the midline of the skull in all of these genera than in *Varanus*. In *Platecarpus* one anterointernally trending crest crosses the posterior portion of the undersurface of the vomer and another similar but smaller crest crosses just behind the aperture for the Jacobson's organ, very reminiscent of the ventral appearance of this bone in *Varanus*. In *Tylosaurus* a single heavy crest extends from the lateral edge of the center of the vomer past the aperture for Jacobson's organ to contact the premaxilla far anteriorly. There is a longitudinal crest along the ventrolateral edge of the ventral shaft of the vomer in *Clidastes*.

The bony opening for the internal naris lies medial to the posterior half of the maxilla in mosasaurs. It is wide and triangular in *Platecarpus*, less wide but also triangular in *Clidastes*, teardrop-shaped in *Plotosaurus*, and with the form of a compressed teardrop in *Tylosaurus*. The aperture for Jacobson's organ lies between the maxilla and vomer, making a shallow groove in the side of the latter element opposite the second maxillary tooth in *Platecarpus* and the fourth in *Tylosaurus*. Immediately anterior to this aperture the vomer is sutured to the medial wall of the maxilla. The foramen for the vein to the medial palatine sinus emerges in front of the aperture for Jacobson's organ, instead of behind it as in *Varanus* (Bahl, 1937, p. 163). In *Platecarpus* the exit for this vein lies wholly within the vomer; in *Tylosaurus* it is bounded laterally by the maxilla. The most anterior portion of the vomer is quite slender and drawn-out in *Tylosaurus* compared to *Platecarpus*.

SEPTOMAXILLA

"In the type skull of *Kolposaurus (=Plotosaurus) bennisoni* there is a long, thin, bladelike bone, the septomaxillary, lying beneath the internarial bar and spreading out anteriorly above the prevomers. Posteriorly it continues to a point beneath the frontal notches of the external nares. There it gives rise to a pair of small, hooked, dorsal processes which curve backward toward the borders of the palatine conchae. The thin dorsal margin of the septomaxillary contains a longitudinal groove in its posterior half and this marks the midline fusion. The deepest part of the internarial premaxillary bar lies in the forward continuation of this groove. Near the anterior limit of the narial chamber, the bone becomes depressed and enwraps a canal which passes forward and downward, evidently to continue into the cavity where the Jacobson's organ was lodged. Parts of the septomaxillary have evidently been seen in *Tylosaurus* by Merriam (1894, p. 21, pl. 1 fig. 3) and by Huene (1910, p. 303, fig. 5). . . ." (Camp, 1942, p. 28)

In a *Tylosaurus* skull in the Yale museum (YPM 4002) the septomaxillary bones are clearly not fused, one appearing on the medial side of each narial opening.

ORBITOSPHENOID

According to Camp (1942, p. 32, fig. 15) the orbitosphenoid in *Plotosaurus* ". . . supported the ventrolateral wall of the cerebrum and half enclosed the fenestra for the optic chiasma which it half encircled above and posteriorly. It extends obliquely forward and upward. Two small bony points extend upward from its dorsal curved border. The general shape and position of the element is much like that of *Varanus* and *Gerrhonotus*. The orbitosphenoid of *Kolposaurus (=Plotosaurus)* displays another interesting feature which is not found, so far as known, in recent lizards. From near its anteroventral border, a thin, bony process extends forward and downward. The tip of this process adjoins its fellow from the opposite side. A brownish stain, accompanying granules of bone in the matrix, runs from these tips obliquely forward and downward. This stain and the granules seem to indicate the presence of a calcified cartilage in the interorbital septum. The stain merges ventrally with a thick nodule of true bone lying on the midline 12 mm. above the parasphenoid. This nodule was evidently an ossified part of the ventral margin of the interorbital septum."

Elements associated with several *Platecarpus* skulls in various museums have the same general form as the orbitosphenoid in *Plotosaurus*. The dorsal portion of the bone is flattened and fan-shaped and curves posteroventrally into a smaller, vertical column that ends abruptly below in a rounded cap. Similar bones from *Platecarpus* have been figured by Williston (1898b, pl. 29 fig. 5) and Camp (1942, fig. 18). Williston (1902, pp. 250-251) also identified the orbitosphenoids in the specimen here referred to *Mosasaurus ivoensis*, subsequently lost, and in another specimen of *Platecarpus* in which the expanded dorsal portion

Text-fig. 7. Lateral view of left orbitosphenoid of *Platecarpus* (AMNH 122, × 1).

of each bone was lying directly beneath an elliptical excavation for the cerebral hemispheres located on either side of the olfactory groove on the posteroventral face of the frontal.

Parietal Unit

In mosasaurs the parietal unit is formed of only one element, the parietal itself, but relations with other units in the skull are complicated. Ventrally a descending flange loosely overlaps the prootics (occipital unit) and epipterygoids (epipterygoid units). Further back on its posteroventral midline the parietal articulates with the supraoccipital (occipital unit) by a narrow, interdigitating hinge (metakinetic joint). The parietal is connected with the frontal (muzzle unit) by the mesokinetic axis on the dorsal surface of the skull. Posterolaterally each suspensorial ramus of the parietal slides over the dorsal surface of a long medially-directed process of the supratemporal (occipital unit). Thus the parietal unit is rocked up and down about the metakinetic joint through rotation of the occipital unit below. It partially supports the occipital and epipterygoid units anterodorsally through the hinge with the muzzle unit.

PARIETAL

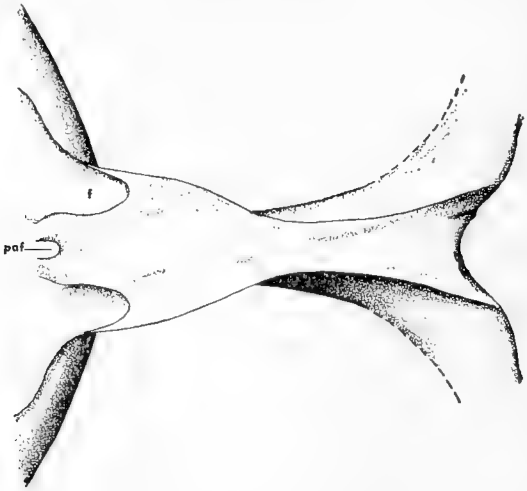
The parietals are fused in mosasaurs without a trace of a suture and are here considered as a unit. The parietal is broad anteriorly forming the anteromedian margins of the supratemporal fenestrae, narrows posteriorly, and then branches into two laterally diverging suspensorial rami which close the posterior boundaries of the fenestrae. In most mosasaurs the median dorsal surface of the parietal is in the form of a rectangular "table" with the long axis oriented in the anteroposterior direction. It is bounded on each side by an overhanging crest, beneath which the M. pseudotemporalis superficialis presumably originated on the dorsolateral wall of the parietal. These crests usually extend caudally across to the posterior edge of the suspensorial rami and may indicate a more extensive posterior area of origin for the M. pseudotemporalis superficialis than in *Varanus*. In a few mosasaurs, *Platecarpus*, *Plioplatecarpus* (Dollo, 1889b, pl. 9 fig. 6), and *Ectenosaurus* to a degree, these overhanging crests converge posteriorly and meet in the midline of the parietal, forming a triangular "table" dorsally on the parietal. In these forms the M. pseudotemporalis superficialis may have been concentrated in the anterior region of the supratemporal fenestra.

The parietal foramen is always present close to or rarely, as in *Platecarpus*, is bordered anteriorly by the frontal and is quite large in some forms, *Platecarpus*, *Clidastes sternbergi*, *Plotosaurus* and *Plioplatecarpus* (Dollo, 1889b, pl. 9 fig. 6).

In *Prognathodon* the parietal foramen is located in the center of a small rectangular prominence in the anterior end of the parietal "field."

The suspensorial rami of the parietal are horizontal in cross-section instead of vertical as in *Varanus* and are covered ventrally by long flat extensions from the supratemporal. In *Plotosaurus, Tylosaurus* (Huene, 1910, fig. 7) and *Prognathodon* a second posterolateral wing from the parietal covers the ventromedial termination of the supratemporal, a condition that is incipient in *Clidastes* (Camp, 1942, p. 35). In *Varanus* the suspensorial ramus of the parietal forms the entire posteromedial surface of the suspensorial arcade, sheathing the supratemporal posteriorly and providing a major point of origin for the M. adductor mandibulae externus profundus distally. If the latter muscle occupied the same general area of the skull in mosasaurs as in *Varanus* it must have originated instead largely from the flat ventral surface of the supratemporal. The suspensorial ramus abuts against a short, anteromedially extending wing from the squamosal in mosasaurs. As in *Varanus,* the M. spinalis capitis and dorsal portion of the M. rectus capitis posterior probably inserted next to the cranial midline between the diverging bases of the suspensorial rami. The pars articuloparietalis of the M. longissimus capitis, and fibers of the M. depressor mandibulae originated further laterally on the posterior surface of the rami.

In *Platecarpus* the parietal broadly invades the posterior dorsal surface of the frontal medially and forms a relatively loose suture with that element. In *Clidastes* and *Tylosaurus* this suture was probably less moveable, for the keels and grooves on the sutural surfaces are finer and more tightly interlocking. The suture meets the dorsal surface of the skull in the latter two genera in a nearly straight transverse line, although the parietal may invade the frontal slightly on either side of the dorsal cranial midline. In *Mosasaurus, Plotosaurus, Prognathodon, Plesiotylosaurus* and to a slight degree in *Ectenosaurus* the parietal is overlapped on either side of the midline anteriorly by posteriorly projecting wings from the frontal. This overlapping must have inhibited movement about the mesokinetic axis.



Text-fig. 8. Dorsal surface of parietal of *Mosasaurus maximus* (NJSM 11052, × ¼).

The parietal meets the medial wing from the postorbitofrontal loosely just lateral to the center of the anterior wall of the supratemporal fenestra in *Plate-*

carpus and *Tylosaurus*. In *Clidastes* and *Mosasaurus* the parietal has a much broader contact with the medial wing from the postorbitofrontal and overlaps its posterior surface extensively. The suture between these two bones lies in the center of the anterior border of the supratemporal fenestra in *Plotosaurus tuckeri*; in *Mosasaurus* and *Plotosaurus bennisoni* it is more laterally situated. The suture is located in the anteroexternal corner of the supratemporal fenestra in *Prognathodon* as in *Clidastes* and the parietal probably also covers much of the medial wing of the postorbitofrontal. The parietal meets the postorbitofrontal in the anteromedial corner of the supratemporal fenestra in *Plesiotylosaurus*.

In *Tylosaurus, Clidastes* and *Platecarpus* there are two longitudinally-grooved, knuckle-like projections that fit onto similar projections on the dorsal apex of the supraoccipital, forming a sliding joint. In *Mosasaurus* these projections are apparently absent and a cartilaginous processus ascendens tecti synotici presumably fit into a longitudinal sulcus along the ventral surface of the posterior parietal midline. Though almost absent in *Varanus,* in all mosasaurs there are flattened descending alae from the parietal forming part of the medial wall of the supratemporal fenestra. These alae are crescentric in lateral profile, except in *Plotosaurus* and *Mosasaurus missouriensis* (Goldfuss, 1845, pl. 7) where they are especially large and fused to the prootic and supraoccipital.

As in *Varanus,* the cerebral hemispheres of *Platecarpus* were centered directly beneath the mesokinetic axis. Ventrally, on each side of the parietal foramen, a ridge converges posteriorly, nearly meets its opposite across the midline and then diverges to terminate at the condylar articulation for the supraoccipital. A shallow sulcus, which must have roofed the optic lobes of the mesencephalon, lies between this ridge and the medial surface of the braincase wall. In *Clidastes propython* and *C. liodontus* the region behind the parietal foramen and between the converging ridges is flat or convex, but in *Platecarpus* and *Tylosaurus* it is concave. In *C. sternbergi* the ridges extend in a straight line back to the condylar articulations for the supraoccipital and the region between them is flat. The two ridges fuse into a single median crest behind the ventral opening for the parietal foramen in *Tylosaurus*.

Occipital Unit

The occipital unit is a key element in the structure of the mosasaur skull. In it are included the basioccipital, basisphenoid, parasphenoid, prootics, opisthotic-exoccipitals, supraoccipital and supratemporals. The entire unit rotates in a vertical longitudinal plane on the anterior end of the vertebral column. This motion causes the quadratic suspensoria to turn relative to the posterior ends of the supratemporal arcades (muzzle unit), the dorsal portion of the supraoccipital to slide through the metakinetic joint and the anterior ascending ramus of the prootics to slide between the descending flanges of the parietal unit. Longitudinal motion is imparted to the pterygoid units ventrally via the basipterygoid processes of the basisphenoid.

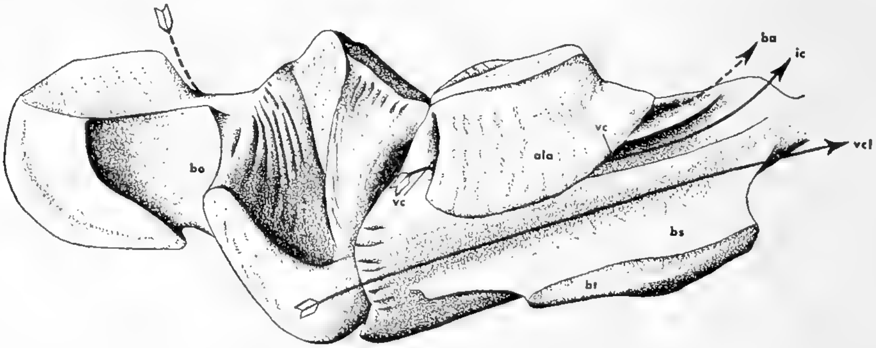
BASIOCCIPITAL

The basioccipital is a stout, triradiate bone in mosasaurs. Anteriorly, there is a very heavy, ventrolaterally directed basal tuber on each side of the cranial midline. Posteriorly, the main shaft of the bone expands laterally, then terminates abruptly in a rounded crescent-shaped occipital condyle whose dorsolateral corners extend out onto the exoccipitals. The dorsal surface of the basioccipital is hollowed longitudinally to support the medulla from below. The short, heavy wall bounding the medullary cavity meets the opisthotic-exoccipital above and the prootic on an anteriorly inclined facet, through a flat cartilaginous surface which is overlapped laterally by a tongue of the opisthotic firmly sutured to the posterolateral corner of the basal tuber below. Anteriorly the basioccipital abuts against the basisphenoid to which it is anchored by the interdigitating contact of the anterior face of the basal tubera with the posteroexternal processes from the ventral surface of the basisphenoid.

The basal tubera are very large in *Mosasaurus,* large and ventrally connected by a transverse swelling of bone in *Clidastes,* intermediately developed in *Tylosaurus,* and small and more anteromedially rotated in *Platecarpus.* The distal end of the tuber is pitted and ridged and was probably capped by a meniscus of cartilage. The floor of the medullary cavity is smooth in *Clidastes,* but in *Platecarpus* it is interrupted posteriorly by a large bilobate foramen through which the basilar artery entered the basioccipital. The tunnel for this artery curves ventrally and then anteriorly to pass into the basisphenoid. The floor of the medullary cavity in *Prognathodon* seems to have been deeply grooved, but there is no tunnel as such for the basilar artery. In *Tylosaurus* a broad sheet of bone from the basisphenoid floors the medullary cavity over the basioccipital all the way back to the foramen magnum. A slender "ear" of this sheet extends laterally out over the anterior portion of the exoccipital suture. The M. rectus capitus anterior must have inserted on the broad posterior face of the basal tuber, and the M. ilio-costalis capitis together with the pars transversalis cervicis of the M. longissimus capitis inserted on the roughened distal surface of the tuber, as they do in *Varanus.*

BASISPHENOID

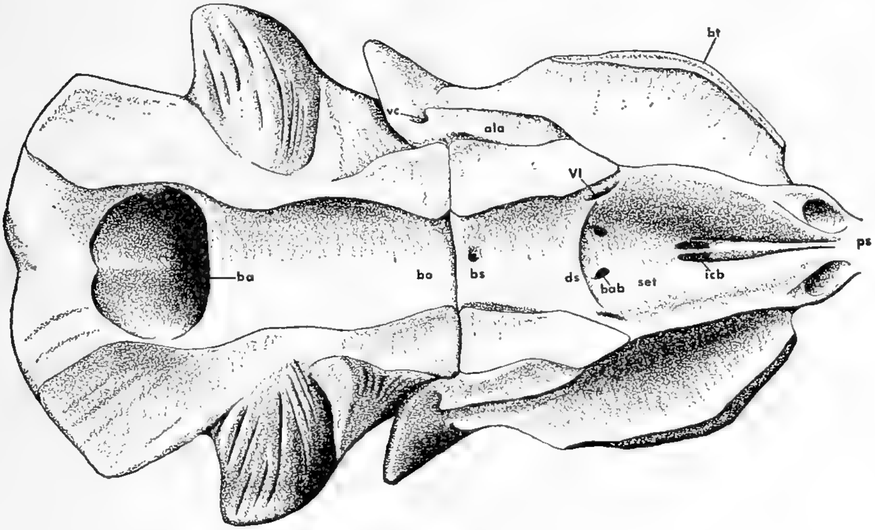
The basisphenoid is a square block of bone with a long parasphenoid rostrum extending forward ventromedially from the dorsum sellae to floor the sella turcica. Ventrally it is tetraradiate with a basipterygoid process projecting anteroexternally from each side of the parasphenoid rostrum and a wide, ventrally convex tongue of bone spread posteroexternally on either side of the midline over the anteroventral face of the basal tuber of the basioccipital. Behind the dorsum sellae the dorsal surface of the bone is shallowly concave and expanded dorsolaterally into a heavy alar process which overhangs the lateral wall of the basisphenoid below and is sutured to the basisphenoid ramus of the prootic above. The basisphenoid meets the basioccipital through a vertically transverse cartilaginous suture which is strengthened below by the interdigitating suture between the ventroposterior tongues of the basisphenoid and the basal tubera.



Text-fig. 9. Lateral view of basioccipital-basisphenoid of *Platecarpus* (YPM 4025, × 1).

The lateral wall of the basisphenoid is smoothly sulcate inwardly from the ventral wall of the alar process down over the thin sheet of bone covering the vidian canal and out across the base of the basipterygoid process. The internal jugular vein must have passed along this sulcus. The vidian canal transported the internal carotid artery and the palatine branch of the seventh nerve into the basisphenoid beneath the posterior end of the alar process and out again onto the anterolateral surface of the parasphenoid rostrum. A small branch of the internal carotid artery left the vidian canal and passed through the basisphenoid medially to the posterior end of the sella turcica as in *Varanus* (see Bahl, 1937, pp. 145-146). The basipterygoid process is wide and separated anteriorly by a small vertical notch from the parasphenoid rostrum. Its elliptical distal surface trends posterolaterally and was capped by a cartilaginous meniscus connecting it to the sides of the notch between the basisphenoid and quadrate processes of the pterygoid below. Fibers of the M. protractor pterygoid may have originated on the dorsal surface of the basipterygoid process as they do in *Varanus.*

The parasphenoid rostrum is long and laterally compressed, terminating anteriorly in a vertical transverse surface for attachment of the presphenoid cartilage. The parasphenoid arises beneath this surface. Two sharp crests extend longitudinally over the entire dorsal length of the rostrum, enclosing a broad medial groove between them. Externally, a narrower groove between these crests and a ridge from the lateral wall of the vidian canal conducts the internal carotid artery anteriorly into the ventral region of the orbit. The vertical anterior wall of the alar processes is formed by the dorsum sellae which rises behind the sella turcica and curves around it somewhat anterolaterally. The foramen for the sixth nerve enters the anterolateral corner of the dorsal surface of the alar process and emerges from the dorsolateral corner of the dorsum sellae. Between the prootic above and the deep sulcus for the internal jugular vein below, the vertical external surface of the alar process is approximately rectangular in shape and is roughened, probably for the insertion of part of the M. protractor pterygoid. The suture for the prootic is transversely horizontal and slopes pos-



Text-fig. 10. Dorsal view of basioccipital-basisphenoid of *Platecarpus* (YPM 4025, × 1).

teromedially to the posterior edge of the bone. The center of the suture is cartilaginous but this area is bounded internally by a dentate ridge and externally by a posterolaterally descending dentate sutural area. There is a small "U"-shaped trough located along the posterior half of the dorsal surface of the basisphenoid.

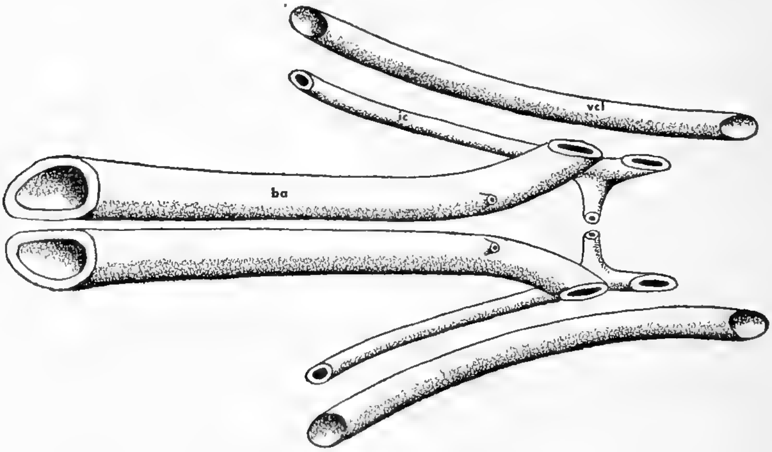
The foregoing description is based on the basisphenoid of *Clidastes*. The basisphenoid of the following genera is described only as it is known to differ from the condition of the element in *Clidastes*.

1. *Globidens*. Only the dorsal half of the basisphenoid is known but this portion of the bone, although more massive, is practically identical to that of *Clidastes*. The dorsum sellae is short and heavy and the sixth nerve emerged from a foramen near its ventrolateral corner. There is no "U"-shaped trough on the posterior half of the dorsal surface of the basisphenoid.

2. *Mosasaurus*. The basisphenoid is generally similar to that of *Clidastes*. However, the parasphenoid rostrum is less elongated, has a broader groove along its dorsal midline, and is fused anteroventrally to the parasphenoid bone. The lateral wall of the vidian canal may be incompletely developed.

3. *Plotosaurus*. Camp's (1942, fig. 15) illustration of the lateral aspect of the basisphenoid of *Plotosaurus* resembles that of *Mosasaurus*. The vertical external face of the alar process is deeper and the base of the basipterygoid process appears to be heavier.

4. *Platecarpus*. The basisphenoid is superficially like that of *Clidastes* but differs greatly from this genus in detail. The vertical external face of the alar process is larger and projects posteriorly to form the lateral wall of the vidian canal. The basipterygoid processes are wider and terminate anteriorly behind the anterior end of the parasphenoid rostrum. The distal cartilage-capped extremity of the process is larger, dorsoventrally compressed, and more strongly posteriorly inclined than in *Clidastes*. The parasphenoid bone is fused to the anteroventral end of the parasphenoid rostrum. A significant difference from the Mosasaurinae and Tylosaurinae lies in the penetration of the basisphenoid posteriorly by a bilobate tunnel, which branches beneath the sella turcica, each branch emerging through a smaller canal on either side of the parasphenoid rostrum below and anterior to the anterior opening of the vidian canal. This tunnel contained the basilar artery. Behind its anterior forking, two tiny fora-



Text-fig. 11. Reconstructed basicranial circulation of *Platecarpus*.

mina rise from the dorsal surface of the tunnel to the dorsal surface of the bone behind the central portion of the dorsum sellae.

5. *Tylosaurus.* The basisphenoid is more elongated than in *Clidastes.* The basipterygoid processes are similar to but somewhat narrower than those of *Platecarpus.* The vertical external face of the alar process is very small and overhangs a shallow groove between it and the vidian canal below, which may have contained the internal jugular vein.

Two reconstructions of cranial circulation remain to be discussed. DeVillers (1943) described in detail the braincase of *Plioplatecarpus* and his identifications of the cranial nerve foramina agree with those given here for the very similar braincase of *Platecarpus.* However, it appears that the anterior portion of the basisphenoid of DeVillers' *Plioplatecarpus* has been abraded and the basipterygoid processes as well as the lateral wall of the vidian canal have been lost. His "gouttière latérale inférieure du basisphenoide" is believed to be the vidian canal and to have housed the palatine ramus of the facial nerve and the internal carotid artery, not the internal jugular vein (vena capitis lateralis) which was probably more laterally located along the concave external wall of the basisphenoid.

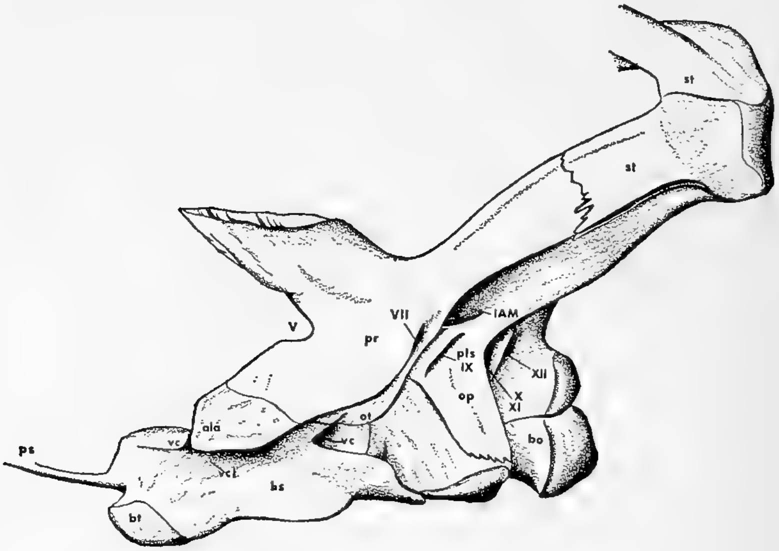
A basisphenoid of *Platecarpus* in the Yale museum (YPM 4025) exhibits the following differences from that illustrated by Camp (1942, figs. 19, 20): 1.) There is no opening for the internal jugular vein on the lateral surface of the basisphenoid dorsal to the basipterygoid processes. The internal jugular vein is therefore assumed to have lain along the lateral wall of the braincase instead of entering the basisphenoid and basioccipital along with the basilar artery. 2.) The channel for the internal carotid artery does not connect with that of the basilar artery anywhere within the basisphenoid. 3.) The internal carotid does not bifurcate into two major lateral branches below the sella turcica. In the Yale specimen, Camp's foramen for the "dorsal branch of the internal carotid" is the outlet for the anterolateral branch of the basilar artery.

PARASPHENOID

The parasphenoid in *Plotosaurus, Platecarpus* (Camp, 1942, figs. 15, 19), and *Ectenosaurus* is a long, dorsoventrally flattened, bayonet-like process of bone, fused posteriorly to the center of the anteroventral edge of the basisphenoid. It extends anteriorly, curves slightly dorsally, and ends in a point along the midline of the skull ventral to the orbits. The parasphenoid is shorter and straighter in *Tylosaurus.*

PROOTIC

As in *Varanus* the prootic is a triradiate bone in *Clidastes.* One ramus descends anteriorly to meet the dorsolateral edge of the basisphenoid just behind the sella turcica, forming a posteriorly inclined suture with a flat cartilaginous center and internally and externally dentate borders. Another ramus of somewhat greater proportions ascends anteriorly to meet the parietal anterodorsally in a broad cartilaginous inner, and a narrower digitate outer, suture. The ramus is bounded dorsoposteriorly by a similar, but longer suture for the supraoccipital. The exit for the fifth nerve is enclosed within the apex of a "V"-shaped prootic incisure between these two rami. A longer and narrower third ramus covers the lateral wall of the suspensorium, projecting posteriorly, dorsally and externally over the oposthotic, back to meet the supratemporal in a digitate suture that is oriented at right angles to the main suspensorial axis. The prootic and opisthotic meet internally in a flat cartilage-surfaced vertical suture that bisects the otic

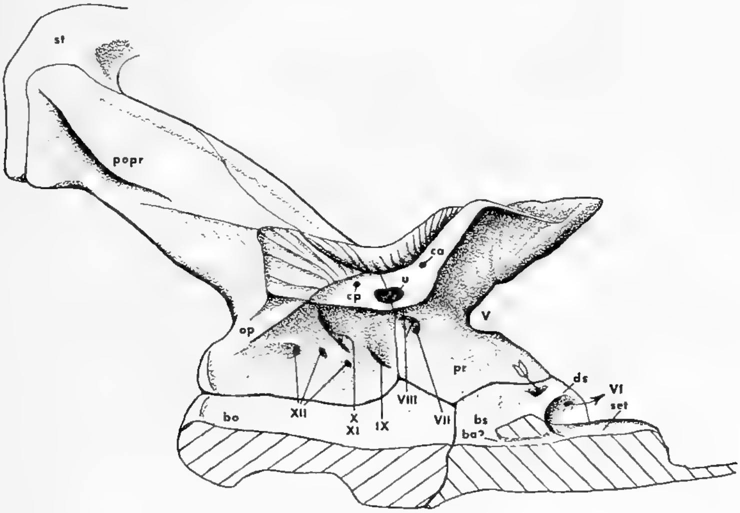


Text-fig. 12. Lateral view of braincase of *Clidastes propython* (YPM 1368, × 1).

labyrinth transversely. Lateral to this the bones are more firmly interconnected by longitudinal ridges and grooves lying in a plane coinciding with a vertical surface drawn through the central axis of the suspensorium.

By analogy with *Varanus,* the M. protractor pterygoid must have originated in part on the rectangular surface of the basisphenoid ramus of the prootic, between the ventral edge of the prootic incisure anteriorly and the otosphenoidal crest posteriorly. On the ventroanterior portion of the parietal ramus and just above the dorsal edge of the prootic incisure, there is a small ridge upon which the M. levator pterygoid may have originated. It is likely that the M. pseudotemporalis profundus was attached dorsally to a gentle convexity that parallels the axis of the parietal ramus, located above this ridge. In *Clidastes* the otosphenoidal crest has developed a thin, posteroventral-projecting ala which overhangs the channel for the internal jugular vein from above (see Bahl, 1937, p. 151). The seventh nerve emerged through a single opening from the dorsal wall of the channel, medial to the central portion of the otosphenoidal crest, and divided into the palatine and hyomandibular rami after reaching the lateral surface of the prootic. In *Varanus* there are separate exits for these two branches of the facial nerve. The tunnel transmitting the proximal end of the stapes to the fenestra ovalis passes anteroventrally through the ventral portion of the lateral prootic-opisthotic suture, above and behind the exit for the seventh nerve. Behind the internal auditory meatus the ventral border of the suspensorium is shallowly sulcate and probably housed the internal carotid artery (see Bahl, 1937, fig. 13) and internal jugular vein. Fibers of the pars posterior of the M. adductor mandibulae externus profundus may have originated on the dorsal edge of the prootic suspensorial ramus, but there is no indication of this on the surface of the bone.

The lateral face of the prootic is vertical, though the internal side curves dorsomedially, giving the bone the outline of an inverted triangle in cross-section. The labyrinth occupys the upper portion of the triangle. Only the parietal and basisphenoid rami of the prootic are visible on its longitudinally concave medial surface. The ventral suture slopes slightly posteriorly on the basisphenoid over the anterior two-thirds of its length, then rises at an angle of 45° to the vertical posterior end of the bone, and abuts posteroventrally against the basioccipital. A rounded pit located at the posterodorsal corner of the internal surface of the



Text-fig. 13. Medial view of braincase of *Clidastes propython* (YPM 1368, × 1).

prootic contains the exits for the undivided stem of the seventh nerve anteroventrally and those for the two branches of the eighth nerve dorsally. A slight prominence descends anteroventrally from the top of the bone in front of this pit, then curves posteriorly to merge with the inner wall of the prootic. The anterior vertical semicircular canal intersects the cartilaginous surface of the supraoccipital suture above and somewhat behind the posterior apex of the prootic incisure. The posterior edge of this suture is strongly emarginated near its center for the ascending sinus utriculus. Camp (1942, fig. 19) illustrates a tiny foramen for the endolymphatic duct lying in front of and medial to this emargination in *Platecarpus*.

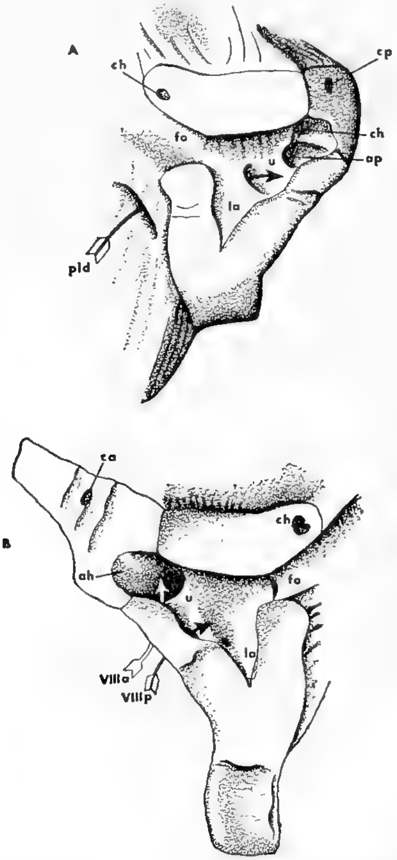
The anterior part of the vestibular cavity itself is very similar to that of *Varanus* (see Bahl, 1937, fig. 10). The posterior branch of the acoustic nerve opens into the utriculus just above the cochlear crest and anterior to the prootic-opisthotic suture. The anterior branch of this nerve enters the anterior ampullary recess which contains the horizontal and anterior ampullae. The horizontal and anterior vertical semicircular canals diverge from their respective ampullae, the former laterally and the latter anteriorly. The cochlear lagena is divided into equal halves by the prootic-opisthotic suture; it is conical in form with a pointed ventral terminus. A slight ridge separates the internal auditory meatus from the utricular cavity and marks the site of the fenestra ovalis.

The prootic of the following forms is described only as it is known to differ from the condition of the element in *Clidastes*.

1. *Clidastes sternbergi*. This species exhibits the very peculiar feature of having the medial entrance of the foramen for the seventh nerve located in the center of the prootic incisure.

2. *Mosasaurus*. In lateral aspect, the prootic of *Mosasaurus* closely resembles that of *Clidastes*, one comparatively minor difference being the heavier and larger otosphenoidal crest in the former genus. Medially the pit enclosing the

foramina for the seventh and eighth nerves is larger and less well-defined. The lagena seems to lie wholly within the prootic.

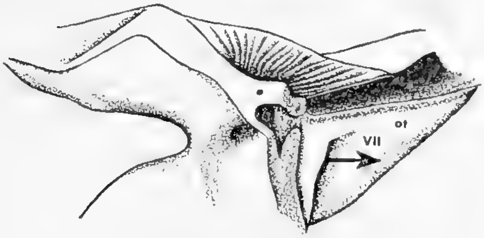


Text-fig. 14. Periotic labyrinth of *Clidastes propython* (YPM 1368, × 2). A. Anterior view of opisthotic. B. Posterior view of prootic.

3. *Plotosaurus.* According to Camp's (1942, pp. 5, 35, fig. 15) description and figure of the lateral wall of the braincase, the parietal ramus of the prootic is extensively overlapped by and firmly sutured to the descending wing of the parietal, a condition very different from that found in *Clidastes.*

4. *Platecarpus.* Both the basisphenoidal and parietal rami of the prootic are distally expanded and much larger than in *Clidastes.* The otosphenoidal ala is usually small and poorly developed. The pit enclosing the foramina for the seventh and eighth nerves is small and deep and borders directly on the prootic-opisthotic suture. The medial wall of the prootic is anteroposteriorly shortened and the prootic incisure contacts the ventroanteriorly descending prominence lying in front of the above-mentioned pit; the incisure and pit are widely separated in *Clidastes.* The labyrinth is, however, identical to that of *Clidastes* (see Camp, 1942, fig. 25).

5. *Tylosaurus.* The most striking peculiarity of the lateral surface of the prootic in this genus is the enormous development of the otosphenoidal ala which broadly connects the basisphenoidal and suspensorial rami and covers the whole ventroposterior face of the prootic, including even the anterodorsal



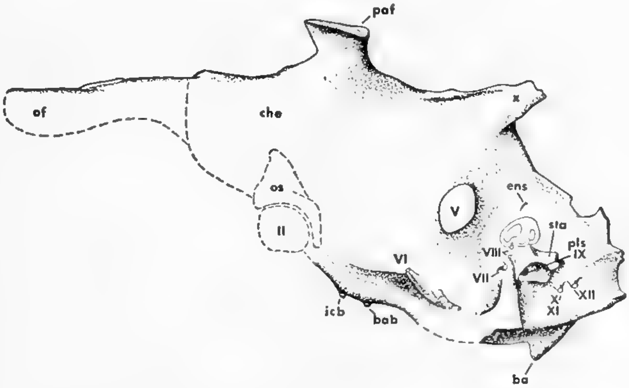
Text-fig. 15. Medial view of prootic of *Tylosaurus nepaeolicus* (AMNH 124, × ½), showing the otosphenoidal crest and exit for cranial nerve VII.

portion of that of the opisthotic. The labyrinth is again very similar to that of *Clidastes,* except that the anterior vertical semicircular canal is located much closer to the sinus utriculus on the supraoccipital suture.

OPISTHOTIC-EXOCCIPITAL

The opisthotic and exoccipital are fused in *Clidastes,* as well as in mosasaurs in general, and are considered here as one element. This ossification is composed of a rectangular block anteriorly, lying on the basioccipital behind the prootic, and a long distally expanded paroccipital process that supports the suspensorial ramus of the prootic and the supratemporal posteromedially. Laterally the anterodorsal quarter of the opisthotic-exoccipital block is overlapped by that portion of the prootic that forms the medial wall of the groove for the internal jugular vein and covers the proximal end of the internal auditory meatus. Part of the articular surface of the occipital condyle extends onto the posteroventral corner of the exoccipital region of the bone.

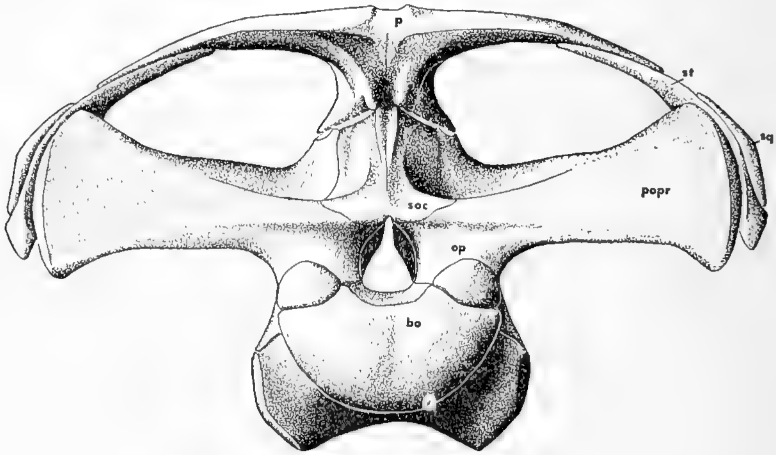
The exposed lateral surface of the opisthotic-exoccipital is triangular in outline. The ventral margin of the paroccipital process, narrowly visible under the prootic and supratemporal, rises less steeply posterodorsally from the anterior edge of the triangle. The opening for the internal auditory meatus is large and lens-shaped and situated beneath a shallow sulcus near the base of the suspensorial process of the prootic. Lying ventroanteriorly to the internal auditory meatus and separated from it by a rounded bar of bone is another



Text-fig. 16. Endocranial cast of *Platecarpus* (after Camp, 1942, fig. 24A, × ½, with slight modifications). X, cartilage between parietal and supraoccipital.

slightly smaller elliptical opening, whose long axis parallels the otosphenoidal crest. This is the fenestra rotunda, which in life was covered over by a heavy membrane that closed off the perilymphatic sac from the exterior (see Bahl, 1937, p. 140). Within the fenestra near its ventral corner is a tiny foramen marking the exit of the ninth nerve. A rounded crest from the ventral edge of the paroccipital process continues ventroanteriorly to form the posteroventral border of the internal auditory meatus. It then descends vertically behind the fenestra rotunda, forming the posterior boundary of a thin superficial tongue of bone firmly sutured below to the posterolateral corner of the basal tuber of the basioccipital. Beneath and behind this crest and paralleling its dorsal margin are two lenticular foramina, separated from each other by a thin sheet of bone. The larger dorsal foramen (jugular foramen) transmitted the vagus and accessory nerves, the posterior cerebral branch of the internal jugular vein, and the occipital branch of the internal carotid artery to the lateral surface of the braincase. The smaller ventral foramen (condylar foramen) transmitted the hypoglossal nerve to the exterior (see Bahl, 1937, p. 139). In *Clidastes* these two foramina are located on the lateral face of the braincase, though in *Varanus* the above-described crest is greatly enlarged and the single composite foramen has been shifted around to the occipital face.

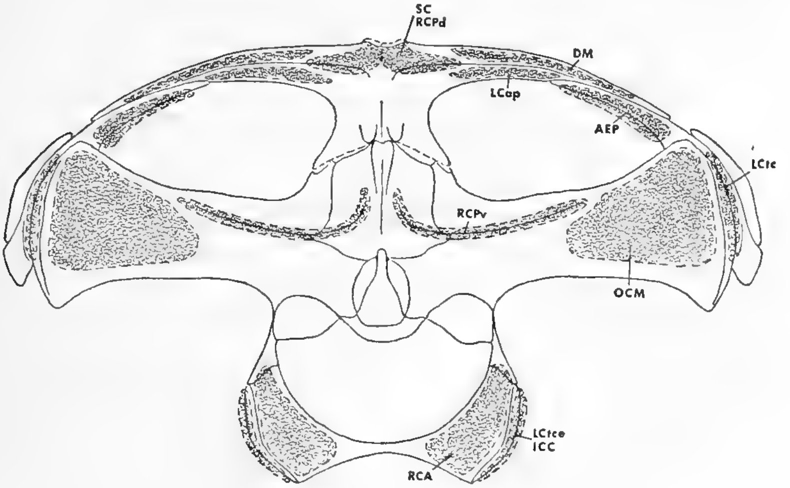
The internal surface of the opisthotic-exoccipital is longitudinally concave, the cartilaginous sutures bounding it ventrally, anteriorly, and dorsally meeting at nearly right angles. The jugular foramen, which enclosed the roots of the tenth and eleventh nerves, is large and crescentic, and extends anteroventrally across the anterior half of the medial wall. The foramen for the ninth nerve is situated midway between the ventral end of the jugular foramen and the opisthotic-prootic suture. This foramen opens externally into the floor of the perilymphatic sac, meeting it at an angle of about 60° in the center of the braincase wall. Two small anterior foramina and a larger posterior one lie in a horizontal row beneath the jugular foramen. They conducted the three roots of the twelfth nerve laterally into the single condylar foramen, which opens on the external surface of the braincase. The suture for the supraoccipital is divided into two portions of approximately equal area. Located in the medial half of the flat, transversely vertical prootic contact is the anterointernal portion consisting of a smooth "U"-shaped cartilaginous surface that has a deep notch anteriorly for the sinus utriculus. The posterior vertical semicircular canal crosses this surface near the center of its lateral margin. The posteroexternal portion is "V"-shaped,



Text-fig. 17. Occipital view of skull of *Platecarpus ictericus* (AMNH 1820, × ½).

strongly ridged and grooved longitudinally and encloses the cartilaginous surface laterally and to a slight extent posteromedially. Its posterior apex is directed out along a ventrally inclined ridge on the posterior face of the paroccipital process.

In posterior view the paroccipital process appears as an elongated rectangular bar of bone, supporting the supratemporal at its somewhat dilated distal end. A ridge crosses the posterolateral corner of the supraoccipital and continues ventrolaterally over the proximal part of the paroccipital process. The ventral part of the M. rectus capitis posterior originates from the same region in *Varanus,* though it lacks this ridge. Another crest descends ventrointernally from the center of the lateral rim of the process and turns medially to parallel its ventral margin for a short distance. The M. obliquus capitis magnus may have inserted on this crest or in the shallow sulcus lying between it and the dorsal edge of the process.



Text-fig. 18. Muscle insertions on occipital surface of skull in *Platecarpus.*

The posterior part of the vestibular cavity is also very close to that of *Varanus.* The horizontal semicircular canal passes laterally through the opisthotic just above the fenestra ovalis. Ventral to the posterior end of the horizontal canal, in the floor of the utriculus, is the ampulla for the posterior vertical semicircular canal. The perilymphatic duct leaves the lagena beneath its medial rim.

The opisthotic-exoccipital of the following genera is described only as it is known to differ from the condition of the element in *Clidastes.*

1. *Mosasaurus.* The fenestra rotunda is relatively smaller than in *Clidastes* and the foramen for the ninth nerve is located in the anterodorsal corner of the medial wall of the opisthotic instead of near the center of its anterior border.

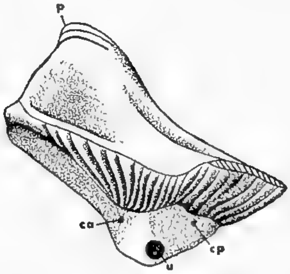
2. *Platecarpus* (see Camp, 1942, figs. 19, 25). The jugular and condylar foramina are fused into a single opening externally. On the internal wall of the braincase the foramen for the ninth nerve lies in the ventroanterior corner of the opisthotic and the three foramina for the twelfth nerve parallel the ventral border of the jugular foramen instead of the horizontal axis of the bone. The posterior vertical semicircular canal intersects the center of the anterior portion of the cartilaginous supraoccipital suture much closer to the sinus utriculus than in *Clidastes.*

3. *Tylosaurus.* The relationships between the foramina on the medial wall of

the braincase are like those of *Clidastes,* but the foramina are all confined to the anterodorsal quarter of its surface. Laterally, the jugular and condylar foramina are fused into a single opening. The labyrinth is like that of *Clidastes.*

SUPRAOCCIPITAL

In *Clidastes* the supraoccipital is a rectangular, roof-shaped element. A crest rises upward anteriorly from the foramen magnum to the parietal and forms the "ridge" of the roof. From the posterolateral corner of the bone another crest extends dorsally across the sloping side of the roof to a longitudinally grooved, knuckle-like process near the midline of the bone. This process articulates with a similar projection near the posteroventral midline of the parietal. The latter crest probably provided an area for the insertion of ventral fibers of the M. rectus capitis posterior. The ventral surface of the supraoccipital is hollowed to fit over the posterior part of the brain stem, probably originally separating the medulla oblongata from the cerebellum (see Camp, 1942, fig. 24A and B). The contacts with the prootic and opisthotic-exoccipital are the mirror images of the sutures as described above under these elements. The supraoccipital caps the otic capsule on each side of the braincase and contains the upper portions of the anterior and posterior semicircular canals and sinus utriculus (see Camp, 1942, fig. 25).



Text-fig. 19. Lateral aspect of supraoccipital of *Platecarpus* (YPM 1488, × 1).

The anterior edge of the lateral wall of the supraoccipital is truncated by a transversely vertical surface. Posteriorly the bone forms the dorsal border of the foramen magnum.

The supraoccipital of *Platecarpus* is essentially the same as that of *Clidastes.*

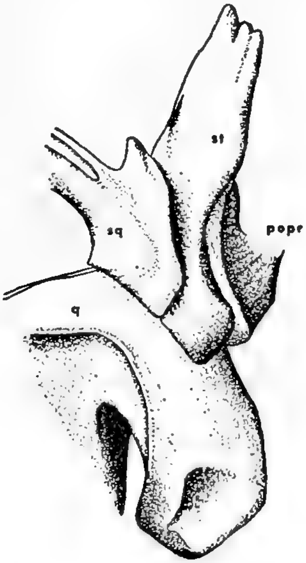
SUPRATEMPORAL

The supratemporal is a rectangular chip of bone supported posteromedially by the strong distally expanded suspensorial process of the opisthotic and loosely linked to the prootic anteromedially by a digitate suture. Its external face is faceted to receive the dorsolateral edge of the quadrate. Two processes arise from the dorsal margin of the bone; one extends anteriorly becoming sutured to the internal face of the squamosal and the other curves medially to pass under the suspensorial ramus of the parietal. In *Clidastes, Platecarpus* and *Tylosaurus* there is a gentle convexity with its long axis trending dorsoanteriorly over the sutural surface of the first process. This convexity fits into a similar-shaped concavity in the medial face of the squamosal, forming a structure that would resist rotation of the squamosal on the supratemporal. The convexity has developed into a strong crest in *Mosasaurus maximus.* The second process is long and flat and covers most of the dorsolateral surface of the posttemporal fenestra, probably providing a large part of the area of origin of the M. adductor mandibulae externus profundus. In *Plotosaurus, Tylosaurus* and *Prognathodon* it is overlapped medially by a more ventral tongue from the parietal.

Posteriorly the supratemporal is poorly exposed behind the paroccipital process and under the suspensorial ramus of the parietal in *Clidastes, Mosasaurus, Platecarpus* and *Tylosaurus.* It seems quite likely that the pars transversalis capitis of the M. longissimus capitis originated on the vertical notch lying between the distal end of the paroccipital process and the supratemporal and that fibers of the pars articuloparietalis of the M. longissimus capitis originated only along the posterior rim of the parietal, as they do in *Varanus.* The M. depressor mandibulae may have lacked an origin on the supratemporal in mosasaurs, although this is a major site of attachment of this muscle in *Varanus.*

PTERYGOID UNITS

The pterygoid units are composed of the pterygoids and ectopterygoids. They link the ventromedial corners of the quadrates (quadrate units), the basipterygoid processes (occipital unit), and the base of the epipterygoids (epipterygoid units) with a long bar of bone to brace the jugal and palatines (muzzle unit) anteriorly. Through these bones longitudinal motion from the ventral portion of the occipital unit is transmitted to the posteroventral edge of the muzzle unit.

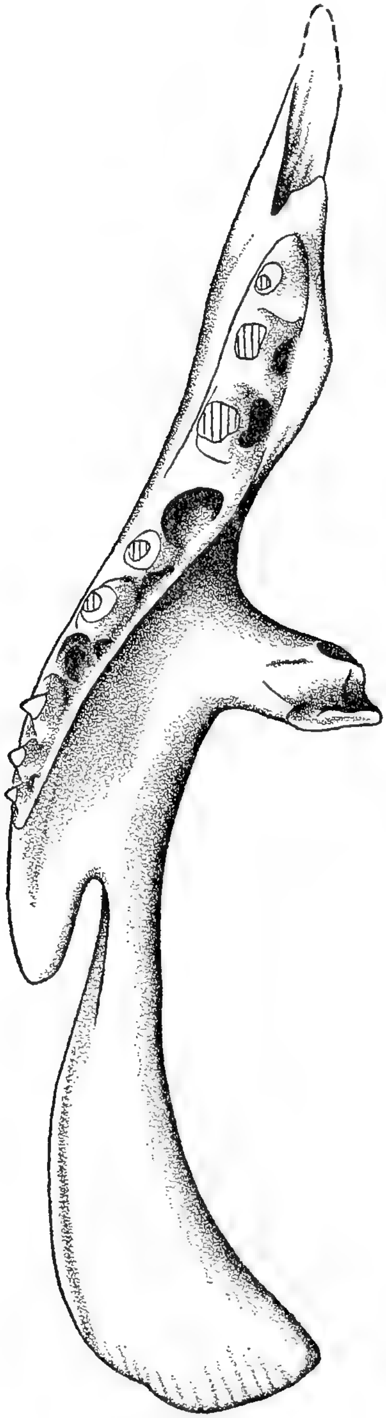


Text-fig. 20. Left quadratic suspensorium of *Platecarpus* (AMNH 1820, × ½).

PTERYGOID

The pterygoid in mosasaurs may perhaps be best considered as composed of a central, anteroposterior body with two large diverging processes, one anterolaterally to the ectopterygoid and another posterolaterally to the medial edge of the quadrate. The pterygoids do not meet along the midline of the skull, although the incisura piriformis is narrower than in *Varanus.*

The main body of the pterygoid is a short, dorsoventrally flattened column, terminating posteriorly in a tongue-shaped wing (basisphenoid process) which lies medial to the basipterygoid process of the basisphenoid. On its ventral sur-

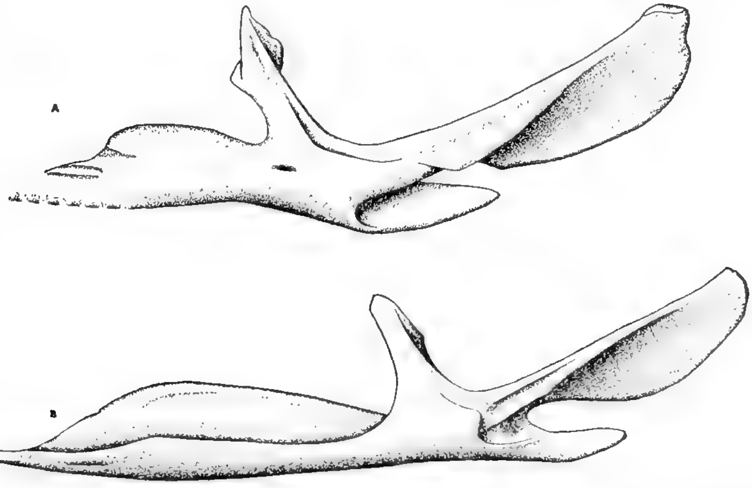


Text-fig. 21. Ventral view of left pterygoid of *Tylosaurus proriger* (AMNH 4909, × 4/7).

face is a row of teeth commonly bent in a gently recurving line extending from the medical base of the basisphenoid process to the anteroexternal termination of the bone *(Tylosaurus, Platecarpus, Prognathodon* and *Plotosaurus),* but these teeth may be oriented in a straight anteroposterior line *(Clidastes).* The pterygoid teeth are usually smaller, more strongly recurved, and more nearly circular in horizontal section than those of the mandibles (*Clidastes, Mosasaurus, Plotosaurus, Platecarpus, Ectenosaurus* and *Tylosaurus*). In *Prognathodon* and probably also *Plesiotylosaurus,* however, the pterygoid teeth are not subequal in size, as in the foregoing genera, but increase anteriorly from a very small diameter to equal the mandibular teeth in size. The number of pterygoid teeth varies from a minimum of seven in *Prognathodon* to a maximum of fifteen in *Plotosaurus.*

Although the pterygoid must have been firmly buttressed against the palatine, this contact is very rarely preserved. In *Platecarpus* the main body of the pterygoid abuts anteriorly onto the medial half of the posterior edge of the palatine and sends a long process anteriorly to cover the ventromedial surface of this bone. In ventral aspect the suture runs from the external side of the pterygo-palatine bar anteromedially in a nearly straight line to meet the internal side of the bar just behind the posterior boundary of the internal naris. Sutural indications on the ventral surface of the palatine in *Tylosaurus* and *Clidastes* suggest that the pterygo-palatine contact is probably also similar in these two genera. In *Plotosaurus* the suture is the same as in *Platecarpus,* except that it is more medially directed and reaches the medial edge of the pterygo-palatine bar far behind the internal narial opening.

The ectopterygoidal process projects from the main body of the pterygoid at a right angle in *Clidastes, Mosasaurus* and *Tylosaurus* and at an acute angle anteriorly in *Platecarpus.* Ventrally the process springs from a broad base in common with the quadratic ramus in *Clidastes, Plotosaurus* and *Tylosaurus* and from a relatively narrow base, which is more distinctly separated from that of the quadratic ramus, in *Platecarpus* and perhaps also in *Mosasaurus.* It passes smoothly into the superior surface of the main body of the pterygoid in *Platecarpus* and *Tylosaurus,* but in *Clidastes* it curves abruptly anteriorly to form a



Text-fig. 22. Dorsal view of right pterygoid of: A. *Platecarpus ictericus* (reconstructed after AMNH 1820, 5811, × ⅔). B. *Clidastes propython* (AMNH ND2, × ⅔).

long anteroposterior crest which is in turn smoothly continuous with the medial face of the pterygoid. In *Platecarpus* two distinct horizontal facets sweep around the posterolateral corner of the base of the ectopterygoidal process. Although less clearly defined, they continue posteriorly onto the lateral and ventrolateral edge of the quadratic ramus. The dorsal of these facets in *Platecarpus* is probably homologous with a lunate sulcus on the posterodorsal face of the ectopterygoidal process in *Clidastes, Mosasaurus,* and *Prognathodon* and perhaps also with a shallow groove that extends anterolaterally across the dorsal face of this process in *Tylosaurus.* The dorsal facet is here interpreted as the point of origin of the M. pterygoideus profundus and the ventral facet as that of the M. pterygoideus superficialis. These facets are not so clearly apparent on the pterygoid of *Varanus.* The ectopterygoidal process in mosasaurs is short and dorsoventrally flattened. It ends laterally in an expanded termination that is beveled off ventroexternally to form a loose, undulating suture with the ectopterygoid in *Clidastes* and *Platecarpus.* The ectopterygoidal process is broader in *Tylosaurus.* The distal suture for the ectopterygoid is more anteriorly situated and probably made a firmer connection with the latter element. In all three of these genera there is a tuberosity on the ventroposterior portion of the sutural area that would have prevented the ectopterygoid from slipping backwards.

The quadratic ramus arises from the base of the ectopterygoidal process and the side of the main body of the pterygoid and extends posterolaterally to contact the medial edge of the shaft of the quadrate. The basipterygoid process of the basisphenoid is enclosed in a "U"-shaped notch between the quadratic ramus and the much shorter basisphenoid process. Behind the anterior apex of this notch a thin wing of bone curves ventrally and medially off the base of the lateral axial portion of the quadratic ramus and expands posteromedially to give the ramus a feather-shaped appearance when viewed from below. This lamina is not present in *Varanus* and its function here is speculative. Perhaps it served as an area of attachment for fibers of the M. pterygoideus superficialis below or was partly invaded by the M. protractor pterygoid above. There is a groove along the dorsal edge of the axis of the quadratic ramus in *Clidastes* and *Tylosaurus* that probably marked the insertion of the M. protractor pterygoid. In *Platecarpus* this groove is absent and the muscle may have inserted somewhat medially onto a keel along the top of the axis of the ramus. In *Platecarpus* and *Tylosaurus* the quadratic ramus is relatively long and slender; in *Clidastes* it is much shorter and broader. There is a slight swelling for articulation with the quadrate at the posterolateral tip of the ramus in all three genera.

The epipterygoid articulates with the dorsal surface of the pterygoid in a rounded excavation that is continuous ventrally with, and immediately anterior to, the notch for the basipterygoid process of the basisphenoid in *Clidastes, Mosasaurus, Platecarpus, Prognathodon* and *Tylosaurus.* This pit is more laterally compressed in *Platecarpus* and *Tylosaurus.* In *Clidastes* its anterior border is not expanded enough posterolaterally to meet the anterior margin of the M. pterygoideus profundus facet, as it does in the other four genera. In *Varanus* the M. levator pterygoid inserts on the dorsal surface of the pterygoid just medial to the epipterygoidal pit. No indication of a scar for the muscle has been noted in the corresponding region in *Clidastes* and *Platecarpus,* although it is probably represented by a shallow anteroposterior sulcus in this position in *Tylosaurus.*

ECTOPTERYGOID

The ectopterygoid is an "L"-shaped bone, with one arm of the "L" extending laterally from the pterygoid to meet the jugal and the other more slender arm following the medial face of the jugal forward to end in a point approaching or beneath the posterior tip of the maxilla. Postero-laterally and -ventrally its suture with the ectopterygoid process of the pterygoid is ribbed and grooved; the face abutting against the jugal is smooth and vertical.

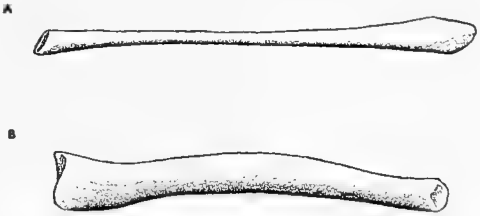
The longitudinal arm of the ectopterygoid is short in *Platecarpus* and longer in *Tylosaurus* (Williston, 1898b, pl. 18) and *Plotosaurus* where it meets the posterior rim of the palatine. The jugal contact is smooth in *Plotosaurus* and *Platecarpus,* but the posterior portion of the lateral face of the bone is medially offset from the anterior portion in *Tylosaurus.* A notch may be present or absent in the anteromedian corner of the "L" in *Platecarpus.* Such a notch is apparently lacking in *Plotosaurus, Prognathodon* and *Tylosaurus.* Only a slight trace of the transverse process of the bone is present in *Plotosaurus.*

Epipterygoid Units

The epipterygoid units include only the epipterygoids, slender rods of bone linking the center of the pterygoid units to connective tissue between the descending flanges of the parietal (parietal unit) and anterior ascending ramus of the prootics (occipital unit).

EPIPTERYGOID

In a specimen of *Platecarpus* described by Marsh (YPM 1277, Marsh, 1872b, p. 450) the epipterygoid is a simple dowel of bone with a small, rounded, ventral termination fitting into a shallow pocket on the dorsal surface of the pterygoid, anterior to the notch for the basipterygoid process. The bone swells slightly above its ventral articulation, then constricts, and finally re-expands. It is flattened dorsally, presumably lying on the lateral face of the parietal ramus of the prootic. In *Varanus* the epipterygoid both separates and provides areas of attachment for fibers of the pars anterior of the M. pseudotemporalis profundus laterally and the pars posterior medially.



Text-fig. 23. A. Stapes. B. Epipterygoid. *Platecarpus ictericus* (YPM 1277, × 1). The dorsal end of the epipterygoid is to the left.

Camp (1942, p. 30, fig. 15) describes the epipterygoid of *Plotosaurus* as being slender and more spirally curved than in *Platecarpus.* Its dorsal end is expanded into a thin blade, and a narrow groove in front of the anterior border of the descending process of the parietal evidently supported the posterior edge of this portion of the bone. Its anteromedian edge was supported in part by an ascending process of the parietal.

The epipterygoid has been reported in *Tylosaurus* by Merriam (1894, p. 21) and Huene (1910, p. 301) and is described by the latter author as "Komprimiert, leicht S-förmig geschweift, oben verschmälert, unten mit verdickter Gelenckfläche, die in eine vertiefte Stelle des Pterygoides eingreift."

Stapes Units

Properly speaking the stapes is a separate structural unit within the mosasaur skull. It had no function other than that of sound transmission.

STAPES

The stapes in the *Platecarpus* specimen studied by Marsh (YPM no. 1277, Marsh, 1872b, p. 449; see also Baur, 1892, p. 12; Huene, 1911, p. 50) is a long delicate rod of bone, expanded at both ends and narrow in the middle, and is very similar to the stapes of *Varanus* (Bahl, 1937, fig. 12). In *Plotosaurus* the stapes is columnar and much more heavily constructed (Camp, 1942, figs. 7, 23).

"The extracolumella of mosasaurs is known only in the European *Plioplatecarpus* (Dollo, 1905); it is ossified and fused with [a calcified] tympanic operculum. . . In this genus the extracolumella is attached to the operculum by a Y-shaped extremity, the arms of which may be homologized with the pars superior and pars inferior of *Varanus* (Versluys, 1858, p. 65 and fig. 56). As Dollo (1888) has elsewhere shown, there is also an ossified quadratic process of the extracolumella resting in the 'suprastapedial fossette' [= 'stapedial pit'] of the quadrate in *Plioplatecarpus.* This process may be identified with the processus internus of the extracolumella as figured by Versluys."

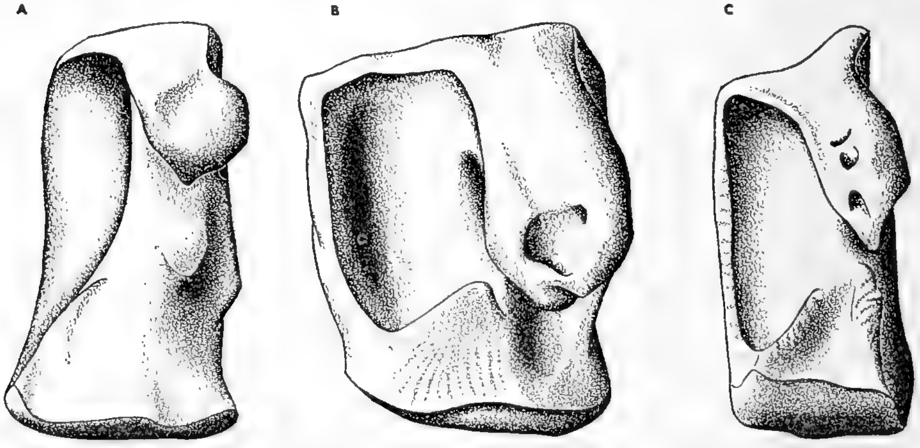
". . . there is a point, however, at which mosasaurs may agree more closely with *Varanus* than with other known lizards. The joint between the extracolumella and the stapes is set at a high angle, the stapes lying at about forty-five degrees to the body axis and the extracolumella at a right angle to it. The same condition must have obtained in mosasaurs, to allow the extracolumella to penetrate the narrow suprastapedial fossa." (Camp, 1942, p. 34)

Quadrate Units

The quadrate units (quadrates) articulate above with the quadratic suspensoria of the occipital unit and below with the posterior mandibular unit, the former joint being the less perfect of the two. The posteromedial corner of the quadrate was loosely bound by ligaments to the posterior tip of the pterygoid units.

QUADRATE

The quadrate in mosasaurs is a heavy, powerfully constructed bone and is the most frequently preserved cranial element. Its main body is a vertical shaft,

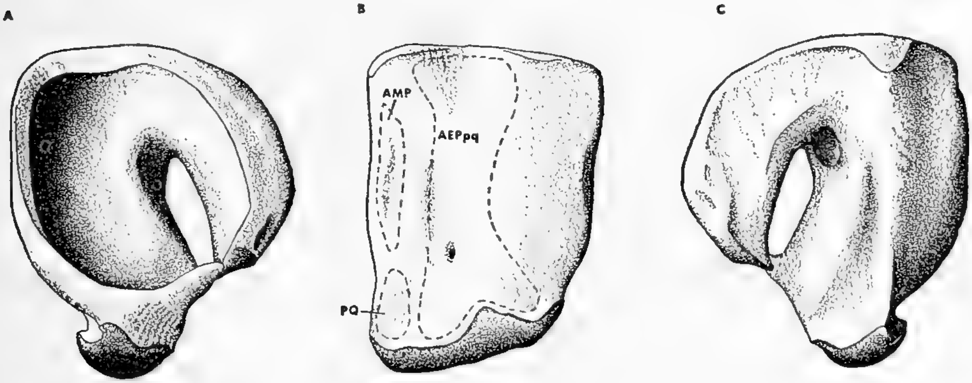


Text-fig. 24. Posterior view of quadrate. A. *Mosasaurus maximus* (YPM 430, × 5/18). B. *Platecarpus ictericus* (AMNH 1820, × 5/6). C. *Tylosaurus proriger* (reconstructed after AMNH 4909 and YPM 3990, × 5/6).

articulating above with a concavity on the lateral face of the suspensorium (composed of the supratemporal and squamosal) and ending below in a convex longitudinal condyle for articulation with the mandible. The large suprastapedial process arises from the posterodorsal surface of the quadrate shaft, curving ventrally to enclose the stapes in a notch and then ventroanteriorly towards the smaller infrastapedial process. A large crescentric tympanic ala projects out from the anteroexternal edge of the quadrate shaft.

The anterior surface of the quadrate is in the form of an upright rectangle. Its medial boundary is straight in *Mosasaurus, Plotosaurus, Platecarpus, Prognathodon* and *Tylosaurus,* but is concave laterally in *Clidastes.* There is a lenticular rugosity centered above the midline of this boundary for the origin of the M. adductor posterior in *Clidastes, Platecarpus* and *Prognathodon.* In *Tylosaurus* the muscle probably originated on an anterointernally directed facet located more ventrally on the medial boundary of the quadrate. In *Mosasaurus maximus* a small triangular medially directed crest in the same region may have served as the area of origin for this muscle. The muscle seems to have been about as well-developed in mosasaurs as it is in *Varanus.*

A large, shallow, triangular depression, whose base extends across the entire ventral edge of the anterior face of the quadrate, curving around an anterior projection of the articulating surface to reach dorsally and somewhat medially to the horizontal midline of the bone, probably marks the ventral origin of the quadrate head of the M. adductor mandibulae externus profundus. A slight rugosity is present at the dorsal apex of this triangular concavity in *Clidastes, Mosasaurus* and *Plotosaurus* which is lacking in *Platecarpus, Plioplatecarpus, Prognathodon* and *Tylosaurus.* Just beneath and lateral to this apex is a small foramen which passes through the quadrate between the main vertical shaft and the tympanic ala in *Clidastes, Mosasaurus, Platecarpus* and *Tylosaurus.* On the upper third of the anterior face of the quadrate in all seven of these genera there is a smaller shallow depression, in the form of an inverted triangle, located between the quadrate shaft and the tympanic ala. It is probable that this region provided an area of origin for dorsal fibers of the M. adductor mandibulae externus profundus, since this muscle originates over nearly the entire rostral surface of the quadrate in *Varanus.* The dorsolateral one-third to one-half of the anterior face of the quadrate is made up of the tympanic ala proper.



Text-fig. 25. Left quadrate of *Platecarpus ictericus* (AMNH 1820, × ½). A. Lateral aspect. B. Anterior aspect showing outlines of muscle attachments. C. Medial aspect.

The suprastapedial process is large in all mosasaurs, curving ventrally to enclose the stapes dorsally and posteriorly in a rounded notch. The main axis of the process is more medially directed than that of the shaft of the quadrate. The suprastapedial process is largest in members of the Plioplatecarpinae, intermediate in *Tylosaurus,* and smallest in the Mosasaurinae. The sides of the process are parallel and somewhat dilated distally in *Platecarpus, Halisaurus onchognathus* (Merriam, 1894, p. 37) and *Prognathodon overtoni,* are constricted medially in *Clidastes, Mosasaurus* and *Plotosaurus,* and strongly constricted medially in *Prognathodon rapax.* The supra- and infrastapedial processes are separate in *Clidastes propython, Mosasaurus, Plotosaurus, Platecarpus, Plioplatecarpus, Halisaurus onchognathus* (Merriam, 1894, p. 37) and *Tylosaurus,* but are fused, closing the stapedial notch posteriorly and ventrally in *Ectenosaurus, Prognathodon* and *Plesiotylosaurus.* Some of the fibers of the M. depressor mandibulae must have originated along the distal surface of the suprastapedial process, particularly in a circular depression near its end in *Clidastes, Mosasaurus, Plotosaurus, Platecarpus, Ectenosaurus* and *Prognathodon* and in a similarly placed, longitudinally elliptical depression in *Tylosaurus.* In *Plioplatecarpus* a keel between the ventral anterior border of the stapedial notch and the overhanging suprastapedial process projects posteriorly from the quadrate shaft and nearly closes off the notch from below. This keel is only incipient in *Platecarpus* and is absent in all the other known genera of mosasaurs.

The infrastapedial process is large and triangular in posterior outline with a bluntly pointed dorsal termination in *Platecarpus,* is similar but much larger in *Prognathodon, Plesiotylosaurus* and *Ectenosaurus* and covers most of the posterior base of the quadrate in these genera. The infrastapedial process is smaller in *Tylosaurus* and *Clidastes propython* where it is more clearly separated from the ventral rim for the tympanic membrane. It lies opposite and widely separated from this rim low on the posterior shaft of the quadrate in *Tylosaurus nepaeolicus,* close to the rim and higher on the shaft in *C. propython,* and above and distinctly separated from the rim in the center of the shaft in *T. proriger.* In *Mosasaurus* and *Plotosaurus* the infrastapedial process is a small rounded tuberosity situated in the center of the posterior shaft of the quadrate. It is absent in *C. liodontus* and *C. sternbergi.*

A deep pit for the processus internus of the extracolumella (stapedial pit) lies in front of and slightly above the top of the stapedial notch on the medial surface of the quadrate. The stapedial pit is elliptical in *Clidastes, Mosasaurus, Plotosaurus* and *Platecarpus,* reniform in *Plioplatecarpus,* circular in *Prognathodon,* and rectangular in *Tylosaurus.* Below the stapedial pit the medial face of the quadrate shaft possesses a heavy vertical crest dorsally and is flat ventrally in *Platecarpus* and *Plioplatecarpus,* is flat in *Tylosaurus,* is slightly concave in *Clidastes,* has a deep sulcus between the infrastapedial process and the anteromedial edge of the shaft dorsally and is flat ventrally in *Mosasaurus* and *Plotosaurus,* and has a shallow vertical sulcus that reaches ventrally almost to the condyle in *Prognathodon.* The medial surface of the quadrate is always smooth and flat just above the articular surface for the lower jaw and must have been connected ligamentously with the tip of the quadratic ramus of the pterygoid. In front of this flattened surface and beneath the area of origin of the M. adductor posterior there is a heavy ridge that descends vertically to the condyle in *Mosasaurus, Plotosaurus, Platecarpus, Prognathodon, Plesiotylosaurus* and *Tylosaurus.* In *Clidastes* it projects below the main part of the quadratomandibular joint. Possibly this ridge served as a point of attachment for a separate bundle of fibers derived from the M. protractor pterygoid (an M. protractor quadrati).

Fibers of this muscle do insert on the quadrate of *Varanus niloticus* (Lakjer, 1926, p. 14).

A delicate crest of bone curves up from the distal end of the external surface of the suprastapedial process over the dorsal part of the main shaft, projects anteroexternally from the shaft a short distance and then descends in a sweeping circle back to the ventral portion of the quadrate shaft, rising again before terminating near *(Clidastes, Mosasaurus, Plotosaurus, Tylosaurus)* or fusing with the infrastapedial process *(Platecarpus, Prognathodon, Ectenosaurus, Plioplatecarpus* (Dollo, 1904, pl. vi). This crest is grooved along its anterolateral rim in *Mosasaurus* and *Plotosaurus*. The crest is supported anteriorly by a wing of bone (tympanic ala) from the anterolateral corner of the quadrate shaft. This ala is thin and distinctly separated from the shaft of the quadrate in *Mosasaurus, Plotosaurus, Platecarpus, Plioplatecarpus, Ectenosaurus, Halisaurus onchognathus* (Merriam, 1894, p. 37) and *Tylosaurus proriger*. It is much heavier and merges imperceptibly with the quadrate shaft in *Clidastes* and *T. nepaeolicus*. A calcified tympanum has been observed in all three of the common Niobrara genera *(Clidastes, Platecarpus, Tylosaurus)* and in *Ectenosaurus* from the same formation.

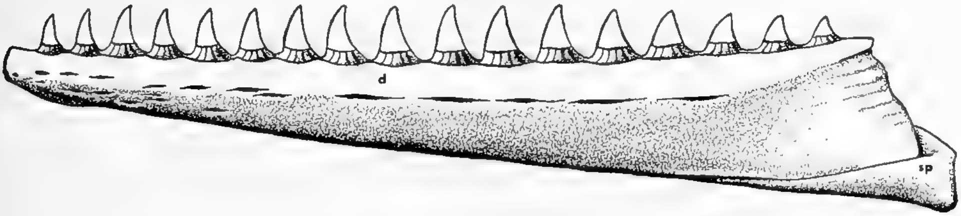
Dorsally, the quadrate shaft, the suprastapedial process, and the crest of the tympanic ala form a sharply-defined smoothly continuous surface that looks as if it had been coated with a thin veneer of cartilage in life. The transverse-oriented condyle on the lower terminus of the quadrate shaft is convex ventrally in most mosasaurs (*Mosasaurus, Plotosaurus, Platecarpus, Ectenosaurus, Prognathodon, Plesiotylosaurus)* but is flat in *Clidastes*.

ANTERIOR LOWER JAW

The anterior segment of the lower jaw is a distinct structural unit formed by the dentary and splenial. It is supported posteriorly by a well-defined joint between the splenial and angular on the ventral margin of the jaw and a blade-like extension of the prearticular into the mandibular foramen dorsal to the splenio-angular articulation. The anterior ends of these segments were ligamentously united.

DENTARY

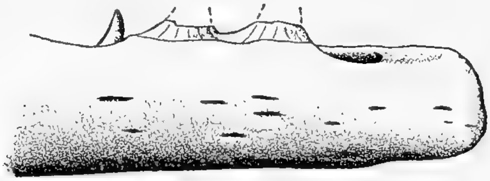
The dentary in mosasaurs is an anteriorly narrowing girder of bone that ends rather bluntly a short distance in front of the anteriormost dentary tooth. Usually the longitudinal axis of the bone is nearly straight, as are its dorsal and ventral margins. The lateral surface of the dentary is gently convex and bears a dorsal row of foramina conducting terminal branches of the mandibular division of the fifth nerve to the exterior. This dorsal row is joined anteriorly by a second more ventral row along the anterior third of the dentary. A deep groove excavated in the medial surface of the dentary opens posteriorly to form the mandibular channel. The thin anterior blade of the prearticular enters this



Text-fig. 26. Left anterior mandibular unit of *Clidastes liodontus* (YPM 1335, × ½).

channel from the posterior segment of the lower jaw and extends anteriorly between the dentary and the splenial. In *Varanus* a ligament from the M. angulari oris slides over the coronoid to insert on the tissue at the posterior end of the gum line on the dentary. In mosasaurs the dorsal surface of the dentary in this region is longitudinally grooved and may have marked the insertion of a similar tendon serving to adduct the anterior segment of the lower jaw. The segment may have been connected by an elastic ligament to the similarly grooved anterior tip of the coronoid.

The dentary is relatively powerfully built in *Mosasaurus, Prognathodon* and *Plesiotylosaurus,* is of average proportions in *Plotosaurus, Platecarpus* and *Tylosaurus,* and is more delicately constructed in *Clidastes.* The edentulous anterior terminus of the dentary is long and rectangular in outline in *Tylosaurus,* smaller in *Clidastes, Mosasaurus missouriensis, M. maximus* and *Plotosaurus,* and is absent or nearly absent in *M. ivoensis, Platecarpus, Plioplatecarpus* and *Prognathodon.* In *C. propython, C. liodontus, M. missouriensis, M. ivoensis, Platecarpus* and *Tylosaurus* the longitudinal axis of the dentary is straight; in *C. conodon, M. maximus, Prognathodon* and *Plesiotylosaurus* the axis is slightly concave upwards. In *Plotosaurus* the longitudinal axis of the dentary is convex upwards. Although unobserved in other mosasaurs, in a single fragment of a dentary referred to *Globidens* (SDSM no. 4612) there is a deep notch extending from the dorsoposterior edge of the bone anteroventrally to a point beneath the penultimate dentary tooth. There is no bony mandibular symphysis known in mosasaurs. The anteromedial tips of the dentary are roughened for the attachment of an intermandibular ligament.

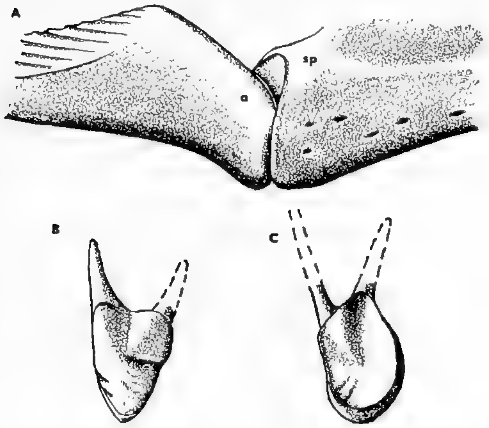


Text-fig. 27. Anterior tip of dentary of *Tylosaurus proriger* (AMNH 4909, × ½).

SPLENIAL

The main body of the splenial is a long, laterally compressed rod of bone that narrows, is increasingly overlapped anteriorly by the dentary, and finally disappears from lateral view behind the posterior third of that bone. A broad thin ala arises from the center of the medial surface of the splenial and sheaths the mandibular channel and much of the internal surface of the anterior mandibular segment. The ventral margin of this wing rises off the lower border of the jaw in front of the anterior end of the main body of the splenial. It ascends to meet the dorsal margin of the wing, which parallels the gum line, in an acute angle along the anteromedial one-third of the dentary (into the symphyseal region in *Plesiotylosaurus* fide Camp, 1942, p. 19). A foramen at the posteroventral base of the ala transmits the inferior alveolar nerve into the mandibular channel (see Bahl, 1937, p. 167). The posterior-facing surface for articulation with the angular is located behind the posterior end of the dentary at the extreme posteroventral corner of the anterior segment of the lower jaw. In outline the surface resembles a vertical ellipse, is concave, but has a perpendicular keel extending from near the center of the ellipse to its dorsal margin.

This perpendicular keel lies just medial to the center of the articulating sur-



Text-fig. 28. A. Lateral aspect of splenio-angular articulation of *Platecarpus* (YPM 1491, × ½). B. Anterior view of angular articulation. C. Posterior view of splenial articulation.

face in *Platecarpus* and *Tylosaurus* where it is of average dimensions. It is centered in *Clidastes* where it is nearly absent, in *Mosasaurus missouriensis* where it is small, and in *Globidens* where it is large. The keel lies lateral to the center of the articulating surface in *M. maximus* where it is large and in *Prognathodon* where it is small. In posterior outline the articulating surface is circular in *M. ivoensis* and *Ectenosaurus,* elliptical in *Clidastes, M. missouriensis, M. maximus, Platecarpus* and *Tylosaurus,* and laterally compressed in *Prognathodon.* A rounded prominence surrounding the ventral portion of the splenial in front of the splenio-angular joint may have marked the point of insertion of fibers of the M. cervicomandibularis, which would then have served to abduct the anterior segment of the lower jaw.

Posterior Lower Jaw

The posterior segment of the lower jaw includes the angular, surangular, coronoid and prearticular-articular. It articulates with the quadrate posteriorly and with the splenial joint (anterior unit of the lower jaw) anteroventrally. Both mandibular segments were firmly connected dorsally by a tongue of the prearticular bound into the mandibular foramen of the anterior segment.

ANGULAR

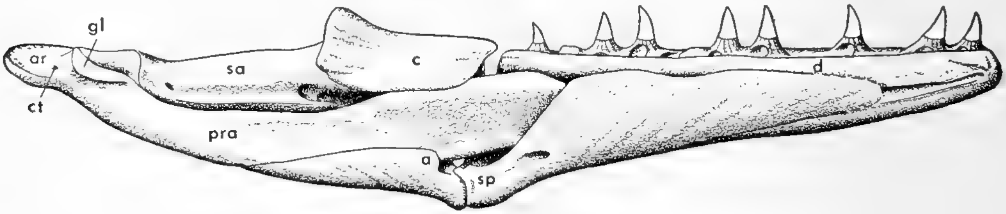
The main body of the angular is shaped like a laterally compressed cone, the anterior face of which is rounded to fit into a cup-shaped excavation in the posterior end of the splenial. This articulating surface is in the form of a rounded "V" with a median dorsal sulcus that receives a ridge from the dorsomedial portion of the articulating surface on the splenial. A short heavy wing arises laterally from the ventral margin of the posterior-directed apex of the cone and is overlapped above by the surangular. Another thinner and broader wing from the angular extends up the medial side of the posterior segment of the lower jaw and covers much of the ventrointernal face of the prearticular. The prearticular sits in the groove formed between these two alae. Posteriorly the bone usually narrows to end in a point beneath the glenoid fossa. There is a foramen or notch in the anterior base of the medial wing of the angular for the angular branch of the mandibular nerve.

The angular is very constant in shape among the different forms of mosasaurs.

Its articular face is nearly circular in *Ectenosaurus,* though in *Clidastes, Mosasaurus, Platecarpus, Halisaurus platyspondylus, Prognathodon* and *Tylosaurus* it is more laterally compressed. The internal wing of the splenial is small and widely separated from the coronoid in *Platecarpus* and *Tylosaurus.* It is larger in *Prognathodon,* but is overlapped above by a descending wing of the coronoid. In *Clidastes* the internal wing of the angular is very well developed and may contact the coronoid dorsally. The angular of *Plotosaurus* spreads posteriorly over much of the ventromedial surface of the articular. The angular branch of the mandibular nerve emerged through a foramen in *Clidastes, Mosasaurus,* and *Halisaurus platyspondylus,* and through either a foramen or a notch in *Tylosaurus* and *Platecarpus* (?).

SURANGULAR

The surangular is essentially an elongated rectangular piece of bone with a tongue projecting posterodorsally over the lateral surface of the articular to end in a rounded point, usually near the posteroexternal corner of the glenoid fossa. The dorsal surface of the tongue is convex from side to side and forms the lateral boundary of the glenoid fossa. This part of the articulating surface widens anteriorly, finally curving medially behind a transverse ridge of bone that marks the anterior limit of the fossa. The lateral exit for the cutaneous branch of the mandibular nerve lies under the anteroexternal corner of the glenoid fossa. Beneath this foramen a rounded crest of bone descends ventroanteriorly, curving to parallel the horizontal axis of the surangular anteriorly and finally merging with the lateral surface of the bone below the posterior boundary of the coronoid suture. The pars superficialis and medialis of the M. adductor mandibulae externus insert along an identical crest in *Varanus.* Above this crest the surangular becomes laterally compressed and rises to form a vertical posterolateral buttress for the coronoid. The coronoid suture proper is a smoothly rounded, horizontal shoulder lying medial to and partly in front of the coronoid buttress. A branch of the mandibular nerve passes anteroexternally through the shoulder and emerges from a large foramen on the anterior laterally exposed portion of the coronoid suture. The meckelian fossa is located under the posterior half of the coronoid suture and is walled dorsally and laterally by the surangular and medially by the prearticular.



Text-fig. 29. Medial view of mandible of *Platecarpus ictericus* (AMNH 1821, × ⅔).

The posterodorsal tongue of the surangular terminates at the posteroexternal corner of the glenoid fossa in *Clidastes, M. missouriensis, Platecarpus, Ectenosaurus, Prognathodon* and *Tylosaurus.* In *M. maximus* and *Plotosaurus* it extends behind the fossa along the dorsal rim of the articular and covers the dorsolateral surface of the bone. The coronoid buttress is deep and very thin, especially dorsally, in *Clidastes, Mosasaurus* and *Plotosaurus.* It is low and has a bluntly rounded dorsal border in *Platecarpus, Halisaurus onchognathus, Ectenosaurus* and *Tylosaurus.* The condition of the coronoid buttress is intermediate between these two types in *Prognathodon*. In *Platecarpus* and *Tylosaurus* the meckelian fossa has shifted anteriorly relative to *Varanus* and the insertions for the Mm. adductor posterior and pseudotemporalis profundus were probably located on a broad shelf of the surangular lying between the glenoid and meckelian fossae and overhanging the prearticular medially. In *Clidastes* and *Mosasaurus* the meckelian fossa occupies the same position that it does in *Varanus*. The M. adductor posterior probably inserted partly on the posterior floor of the fossa (on the surangular) and partly on the dorsal edge of the prearticular. Further anteriorly the M. pseudotemporalis profundus probably inserted entirely on the dorsal rim of the prearticular.

CORONOID

The coronoid is a saddle-shaped bone straddling the longitudinal "shoulder" on the anterodorsal end of the surangular which it enclosed in a deep ventral sulcus. The anterior end of the coronoid is pointed and cleft along the midline. In lateral profile the upper margin of the bone slopes back to a posteriorly ascending process. Fibers of the Mm. adductor mandibulae externus superficialis and medialis must have inserted on the ventroposterior rim of a large, posteriorly overhanging crest that rises along the lateral surface of the process to its dorsal apex and curves medially to join the vertical posterior wall of the coronoid. The bodenaponeurosis through which parts of the Mm. adductor mandibulae externus medialis and profundus and the M. pseudotemporalis superficialis insert on the mandible probably was attached to the posterodorsal edge of the coronoid, as it is in *Varanus*. The thin posterior wall of the coronoid is sutured ventromedially to the coronoid buttress of the surangular.

The posterior process of the coronoid is small in *Platecarpus*, larger in *Tylosaurus*, and large in *Clidastes*, *Mosasaurus*, *Plotosaurus* and *Prognathodon*. In *Prognathodon* and *Tylosaurus* the anterosuperior margin of the surangular is horizontal on the lateral face of the posterior wall of the coronoid, in *Platecarpus* it rises posterodorsally, in *M. missouriensis* it ascends more steeply, and in *Clidastes*, *M. maximus* and *Plotosaurus* it becomes nearly vertical dorsally. The laterally and medially descending wings of the coronoid are small in *Clidastes*, *Platecarpus* and *Tylosaurus*, are intermediately developed in *M. missouriensis*, and are large in *M. maximus*. In *Prognathodon* the medial wing is very large and broad and covers the anterodorsal edge of the angular, although the lateral wing is only intermediately developed. The lateral wing is small in *Plotosaurus* and the whole lateral aspect of the coronoid is very similar to that of *Clidastes*. There is a "C"-shaped excavation on the medial side of the coronoid process in *M. missouriensis*, *M. maximus* and *Prognathodon* in which the segment of the bodenaponeurosis connecting the M. pseudotemporalis superficialis with the coronoid may have inserted.

A coronoid (USNM 4993) possibly belonging to *Globidens* is very massively constructed and dorsoventrally compressed. The coronoid process is small and the posterior wall of the bone extends in a heavy process back over the anterodorsal rim of the surangular.

ARTICULAR-PREARTICULAR

The portion of the glenoid fossa located on the articular is a triangular, dorsally convex, rounded surface, obliquely cut off anterolaterally by the articular surface of the surangular, and was capped with cartilage in life. The glenoid fossa caps a broad buttress, which elevates it from the dorsomedial-sloping retroarticular process which arises from the posterodorsal and inferior edge of the fossa. The retroarticular process is generally a moderately heavy rectangular bar of bone, although its outline is variable in the different genera, and bears a foramen near the center of its anterodorsal face for the corda tympani. The margin of the process lies at right angles to its dorsomedially and anterolaterally inclined surfaces and is rimmed with a smooth band continuous anteriorly with the glenoid fossa. The M. depressor mandibulae probably inserted over the dorsoposterior surface of this band, and fibers of the pars profundus of the M. pterygoideus inserted on the medial face of the retroarticular process and those of the pars superficialis on its lateral face. The prearticular portion of the fused articular-prearticular is a very long thin ribbon of bone that arises from the ventral margins of the retroarticular process and the glenoid fossa. It extends anteriorly, first forming the ventral margin of the posterior segment of the lower jaw, then rises medially from between the surangular above and the angular below into the mandibular foramen of the anterior segment of the jaw between the splenial and dentary. In *Tylosaurus* (Huene, 1910, figs. 8-10) the prearticular ends in a sharp point beneath the fifth dentary tooth. As the prearticular passes along the surangular, its medial border becomes slightly sulcate to form the lateral wall of the meckelian fossa, but anteriorly it becomes a vertical sheet of very thin bone.

The retroarticular process is triangular in outline in *Clidastes* and has a very massive dorsal rim, probably indicating a strong M. depressor mandibulae. In an articular questionably referred to *Globidens* (USNM 4993) the retroarticular process is very powerfully built, circular in outline, and has a large tuberosity on its ventral margin beneath the posterior end of the glenoid fossa. In *Mosasaurus* the process is rectangular and a scarred surface indicates that the insertion for the M. depressor mandibulae had spread onto its dorsomedial face. The process may be similar in *Plotosaurus*. In *Platecarpus* the retroarticular process is circular in outline, while in *Tylosaurus* it is dorsally rounded and ventrally flat. In *Prognathodon* the process is rectangular. The retroarticular process of *Halisaurus onchognathus* (see Merriam, 1894, pl. 4 fig. 10) is very peculiar. It rises vertically immediately behind the mandibular cotylus, then descends abruptly posteriorly, forming an anteroposteriorly compressed fan in lateral profile. There is a large tuberosity similar to the one in *Globidens* at its ventroposterior border.

Marginal Dentition

In mosasaurs teeth in various stages of replacement entirely fill the alveolar margins of the upper and lower jaws. They are arranged in a single row in each mandibular ramus, with the posterior edge of the bony base of one tooth contacting or nearly contacting the anterior edge of the succeeding tooth base. The marginal dentition of *Mosasaurus* is first described in detail and then the tooth crowns are described for the different genera, since these are often generically characteristic.

The crowns of the marginal teeth in *Mosasaurus* are large and divided into a lingual and buccal surface by a longitudinal carina. The lingual surface of the tooth is "U"-shaped in cross-section; the buccal surface is more nearly flat, both being divided by vertical ridges into prisms. The tips of the teeth are more posterointernally inclined than the main axis of the crown. The thin external enamel layer is underlain by a much thicker layer of dentine which is hollow and forms a pulp cavity in the center of the crown. It fits into an excavation in the form of an inverted cone in the bony base of the tooth (see Leidy, 1865a, pl. 20). The depth of the tooth base exceeds the height of the

Text-fig. 30. Marginal tooth of *Mosasaurus maximus* (NJSM 11052, × 1/4). Lateral and dorsal views.

crown by about one and one-half times and is also posteriorly inclined, its central axis meeting that of the crown in an acute angle. The grain of the bone in the tooth base is finer than that of the surrounding mandible and parallels the longitudinal axis of the tooth base instead of that of the mandible. A tunnel in the center of the base communicates with the pulp chamber inside the tooth crown.

In *Mosasaurus maximus* the teeth are small on the premaxilla and the anterior tips of the dentaries and increase in size posteriorly to a point near the center of the jaws. They then gradually decrease in size posteriorly. The flat buccal surface is located across the anterolateral corner of the anterior teeth. Here the lingual surface of the tooth is strongly "U"-shaped. Further posteriorly the buccal surface is rotated to face directly laterally and the teeth become more compressed from side to side and longitudinally symmetrical. Teeth with only two prisms on the buccal surface may be restricted to the dentaries and those with three external prisms to the upper jaws. There are two teeth on each side of the premaxilla, 13-14 on each maxilla, and 14-15 on each dentary in *Mosasaurus*.

The first stage in the process of tooth replacement occurs when a shallow pit is excavated between the posteromedial side of the tooth base and the surrounding bone of the mandible to house the growing successional tooth. This cavity soon breaks through to the alveolar surface and continues to enlarge at the expense of the bony base of the old tooth. The enamel outline of the successional tooth is formed in this cavity and eventually only the periphery of the old crown rests on its former base. It is then easily broken off and the new tooth rises into the cavity to replace it, at which time dentine is probably deposited into its enamel cap and the new base is formed.

Edmund (1960, pp. 87-91) has described the pattern of tooth replacement in mosasaurs. Replacement waves proceed from the front of the jaws posteriorly, alternatingly affecting even and odd numbered teeth. The method of replacement of an individual tooth is as outlined in the preceding paragraph. Edmund (1960, p. 89) however noted that the newly-formed bony base of a successional tooth is not immediately fused to the bone of the surrounding jaw, and teeth in this stage of development are frequently lost before fossilization occurs. This accounts for the large number of well-formed isolated teeth of *Mosasaurus maximus* that have been collected from the Cretaceous greensands of New Jersey. Third generation replacement teeth have been observed by Edmund in a single alveolus.

In the center of the jaws of *Clidastes* the teeth are bicarinate, laterally compressed, and covered with a smooth coat of enamel. The lingual and buccal surfaces of the crown are subequal and separated from one another by a well-developed anterior and posterior carina. The teeth are broad based and triangular in lateral aspect with slightly posteriorly recurved tips. Anteriorly the teeth are slender and more strongly recurved. The posterior carina is absent and the teeth are triangular in cross-section, with the rounded base of the triangle facing towards the rear. The teeth diminish in size towards the posterior end of the tooth row and become more circular in cross-section and strongly recurved. The teeth are alike in corresponding regions of the upper and lower jaws. There are two teeth on each side of the premaxilla, 14-15 on each maxilla, and 16 on each dentary of *Clidastes liodontus;* in *C. propython* there are 18 teeth on each maxilla and 17-18 on each dentary.

The maxillary teeth of *Globidens alabamaensis* (Gilmore, 1921a, pls. 39-40) are circular in cross-section and nearly so in lateral profile. They are attached to relatively constricted bony bases, lack anteroposterior carinae, and come to an indistinct point distally. Anteriorly the teeth are small in diameter with anteroventrally inclined bases. The teeth increase in size and the bases become upright passing back to the tenth tooth, the last one preserved in the type maxilla. The posteriormost tooth in the dentary referred to *Globidens* (SDSM 4612) is in the form of a small nubbin with a well-defined apical point.

In *Plotosaurus,* "There are twenty teeth in the upper row on each side and seventeen visible teeth and alveoli in each dentary. There are two small premaxillary teeth. Then follow a series of increasingly longer teeth of which the tenth and eleventh are the largest. The anterior teeth are compressed and have delicate anterior and posterior carina, while in the eight smaller hind teeth, both above and below, the cross-section is more circular, the crowns are shorter, blunter and more abruptly recurved, and the delicate buccal and lingual vertical striae are more distinct. There are faint traces of striae on some of the back teeth. The crowns are set higher . . . than in other known mosasaurs." (Camp, 1942, p. 4)

In *Platecarpus* the crowns of the teeth are long and slender. They are nearly circular in cross-section at the base, the anterior and posterior carinae becoming more distinct as the tip of the tooth is approached. The buccal surface of the crown is strongly faceted and the lingual surface is lined with small vertical ridges. The teeth are poorly differentiated along the jaw margins, although the anteriormost teeth tend to be smaller and somewhat procumbent and those from the back of the jaws are relatively shorter and stouter. The teeth in the upper jaws are slightly larger than those in the dentaries. In both jaws the teeth are posteromedially recurved. There are two teeth on each side of the premaxilla, 12 on each maxilla, and 12 (rarely 11) on each dentary in *Platecarpus.* Isolated teeth of *Plioplatecarpus* and *Ectenosaurus* are very similar to those of *Platecarpus.*

The bony tooth bases in *"Platecarpus" intermedius* are peculiarly swollen to a degree surpassing that of other known mosasaurs. The only teeth preserved in entirety are those of the posterior portion of the dentary fragments of the type specimen (see Leidy, 1873, pl. 34 fig. 2). These teeth resemble those of *Clidastes* in lateral outline, but have a much more inflated appearance, with smooth, gently rounded sides. Replacement teeth in the anterior part of the dentary are more compressed and possess sharply pointed tips (see Leidy, 1873, pl. 34 fig. 5).

In *Prognathodon overtoni* the tooth crowns in the center and posterior regions of the jaws are large and triangular in lateral outline (see Williston, 1898b, pl. 30 fig. 1). They are bicarinate, the lingual and buccal surfaces being subequal in size and covered with smooth enamel. The tips of the teeth are only slightly recurved posteromedially. In cross-section the teeth are oval, with the long axis in the anteroposterior direction, and somewhat inflated, instead of compressed. The teeth in the anterior portions of the mandibles are more nearly circular in cross-section, where they are smaller, more slender, and more recurved. The teeth are similar in the upper and lower jaws. There are two teeth on each side of the premaxilla, 12 on each maxilla, and 14 on each dentary.

In *Plesiotylosaurus,* the teeth are, ". . . exceptionally large [and] closely spaced," (Camp, 1942, p. 18). The mandibular teeth appear to be quite similar to those of *Prognathodon,* except that the crowns are higher than in the latter genus. There are two teeth on each side of the premaxilla, 13 on each maxilla, and 16-17 on each dentary.

The teeth of *Tylosaurus* are unusually brittle and are very infrequently preserved in entirety in specimens collected from the Niobrara chalk. In lateral profile they are triangular with slightly posteromedially recurved tips. The teeth resemble those of *Mosasaurus* in cross-section, with a "U"-shaped lingual and a flattened buccal surface. The carinae separating these surfaces are less well-developed than in *Mosasaurus,* however, and the surfaces themselves are not faceted, although there is some vertical ridging on both and the teeth have a somewhat inflated appearance. They are largest in the center of the jaws, becoming smaller anteriorly and posteriorly. The buccal surface is rotated forward to a position on the anterolateral edge of the anteriormost teeth. The teeth are similar in corresponding regions of the upper and lower jaws. There are two teeth on each side of the premaxilla, 12-13 on each maxilla (12 occur more frequently in *T. nepaeolicus,* 13 more frequently in *T. proriger),* and 13 on each dentary.

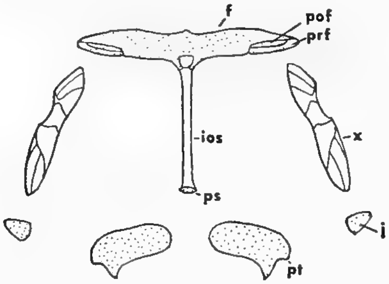
FUNCTIONAL ANATOMY OF CRANIAL SKELETON

The osteology of the mosasaur skull is described in the preceding section. Part of the soft anatomy of the cranium is reconstructed therein on the basis of evidence preserved with the hard tissues. It now remains for the adaptive meaning of various cranial structures to be commented upon.

Sensory Functions

As Camp (1942, p. 40) has noted, the excavation in the undersurface of the frontal for the olfactory bulbs is relatively smaller in mosasaurs than in *Varanus*. This is to be expected, for the sense of olfaction is usually diminished in aquatic animals (see Howell, 1930, p. 74).

The orbits are large in all known mosasaurs. Interlocking sclerotic ossifications are present in *Clidastes, Platecarpus, Tylosaurus,* and also in *Mosasaurus, Plioplatecarpus* and *Prognathodon* (Dollo, 1889b, pl. 9). The function of sclerotic plates (Walls, 1942, pp. 275-279) is to maintain the shape of the cornea and to support the sclera in the region of the origin of Brücke's muscle which affects accommodation in the lacertilian eye. It is likely that about 14 such plates are present in mosasaurs. The curvature of this ring of bone in *Clidastes* and *Platecarpus* shows that the eyeball nearly filled the orbits. The eyeball must have been quite dorsoventrally flattened in *Clidastes,* as is usual in large lizards (Walls, 1942, p. 623), and less so in other genera. The visual axis of the mosasaur eye was directed laterally and a little dorsoanteriorly.



Text-fig. 31. Reconstructed cross section of skull of *Platecarpus* between orbits (× ⅓). X, sclerotic ring.

Vaughn and Dawson (1956) observed the presence of a calcified tympanic membrane in *Platecarpus* and noted that a similar condition of the membrane had been reported earlier in *Plioplatecarpus* and *Tylosaurus.* The membrane is also calcified in *Clidastes* and *Ectenosaurus,* as it may have been in all mosasaurs. A calcified membrane therefore occurs in each of the three subfamilies of mosasaurs and does not in itself indicate that any one of them was better adapted to diving, as has been thought (e.g., Dollo, 1913, p. 621; 1924, p. 188; Williston, 1925, p. 272). The disc of calcified tissue appears to have a diameter always smaller than that of the circular crest of bone that extends from the suprastapedial process around the tympanic ala to the infrastapedial process below on the external surface of the quadrate. The disc must have been suspended from this crest by an outer membranous ring of the tympanum. According to Pumphrey (1950, pp. 11-13) a fish has about the same density as the surrounding water and is therefore virtually transparent to water-borne sound. The displacement of the sound organ relative to the body of the fish is increased if it is anchored to a mass of greater density which would not be so greatly affected by sound vibrations in the surrounding medium, such as the attachment of the saccular macula to an otolith. Since the body of mosasaurs must have been of approximately the same density and homogeneity as that of fish, perhaps the membranous suspension of a dense, calcified portion of the tympanum served a function analogous to that of an otolith by "picking" vibrations out of the water and transmitting them to the sensory apparatus of the inner ear.

In mosasaurines and tylosaurines the tympanic ala of the quadrate is not unusually enlarged over the aigialosaur condition, and the space between the tympanum and body of the quadrate must have been relatively small. In plioplatecarpines *(Ectenosaurus, Platecarpus, Plioplatecarpus, Prognathodon),* however, the tympanic ala is highly developed and projects further anterolaterally to enclose a chamber between the tympanum and quadrate shaft. This chamber is strongly reminiscent of the cavity formed in the quadrate and adjoining squamosal of turtles. According to Wever and Vernon (1956, p. 295) the opening of the tympanic cavity in turtles during hearing experiments had no significant affect on sound transmission through the middle ear. The purpose of the chamber in the quadrate of plioplatecarpines is also unknown; it is perhaps significant that in *Plotosaurus,* a mosasaurine, the stapes is a robust column of bone (Camp, 1942, fig. 23) yet in *Platecarpus,* a plioplatecarpine, the stapes is slender as in turtles and *Varanus.* The otic labyrinth of mosasaurs is practically identical to that of *Varanus.*

Except for the calcification in the tympanum, the hearing apparatus of mosasaurs is not greatly modified over conditions seen in terrestrial reptiles. There is no indication of such elaborate adaptations as in the cetacean ear, where the filling of the external auditory meatus with a wax plug having the same sound conducting properties as water and the complicated pterygoid sinus system regulating air pressure within the middle ear cavity enable whales to hear well over a great range of external pressures (Fraser and Purves, 1960). A partially calcified tympanum may have aided in preventing the tympanum from being ruptured by rapid changes in external pressure as the animal plunged its head into the water when submerging.

Cranial Circulation

The course of some of the major blood vessels in the mosasaur head has been outlined above with the descriptions of the basioccipital and basisphenoid bones. Regarding the cranial circulation in *Plioplatecarpus,* Devillers (1943, pp. 14-15) aptly concludes: ". . . s'il existait deux vaisseaux importants [internal carotid artery, basilar artery] protégés par des canaux, cela ne me parait pas suffisant pour enférer une adaptation à la plongée. Ce fait existe chez d'autre Reptiles non plongeurs (Crocodiliens et Chéloniens) et, d'autre part, il existait aussi d'importants vaisseaux latéraux nullement protégés [internal jugular veins]. Il n'y a rien là de comparable à ce qu'on rencontre chez les Cétacés . . . . la circulation céphalique était certainement moins bien protégée que chez les Chéloniens et les Crocodiliens et surtout que chez les Cétacés."

This statement could be applied equally well to the cranial circulation in *Platecarpus* and *Ectenosaurus.* In other known mosasaurs not even the basilar artery lies in a bony channel.

CRANIAL KINESIS

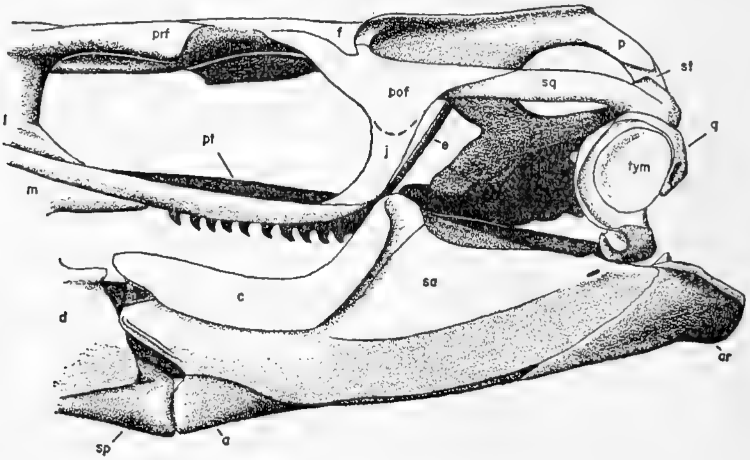
In the preceding section the elements of the mosasaur skull are grouped according to the particular functional unit to which they belong. My paper (1964) has presented some suggestions as to how these units may have operated in life, and these are restated below in a somewhat condensed form. It may be useful to compare cranial movement in mosasaurs with that of *Varanus,* which has been described in detail by Frazzetta (1962). Mosasaurs did not all possess especially kinetic skulls, indeed in some genera *(Mosasaurus, Plotosaurus, Prognathodon* and *Plesiotytosaurus)* kineticism was entirely suppressed. However to the extent that kinetic movement was possible in the skull of a given mosasaur, it is believed to have operated in the following manner.

The term *kinesis* applies to the general condition in which elements of the dermal skull roof and palatoquadrate (maxillary segment) move more or less as a unit with respect to the braincase (occipital segment). The principal or metakinetic axis of rotation between these two fundamental structural divisions is fixed on either side of the posterodorsal corner of the skull by the loose contact of the squamosal (maxillary segment) with the supratemporal (occipital segment). Other sliding planes of contact between the maxillary and occipital segments are situated between the parietal and supraoccipital above (metakinetic joint) and the pterygoids and basipterygoid processes of the basisphenoid below (basal articulation).

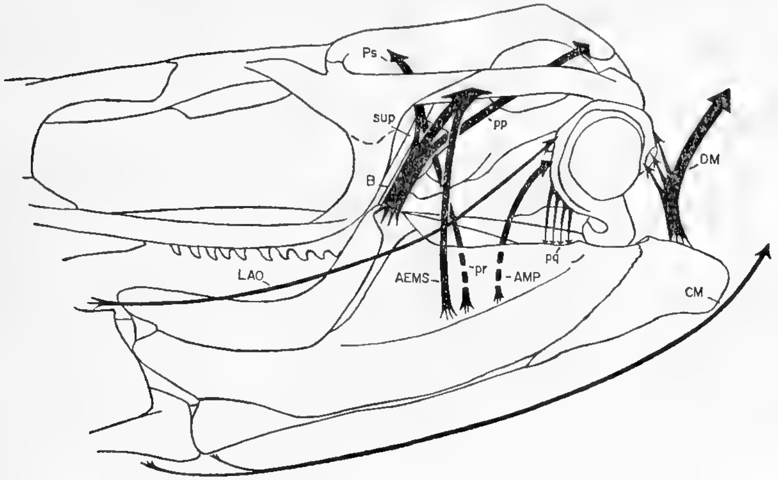
The occipital segment is composed of ten elements (prootics, opisthotics, supratemporals, supraoccipital, parasphenoid, basisphenoid and basioccipital) all solidly sutured together into a rigid block. The maxillary segment in mosasaurs is, however, divided into a number of subunits (see text-fig. 1).

1. The parietal unit, consisting only of the fused parietals. This unit articulates through a transversely oriented hinge (mesokinetic axis) with the muzzle unit anteriorly, and with the occipital segment ventrally through the metakinetic joint and an overlapping suture with the supratemporal.

2. The quadrate units, articulating dorsally with the suspensorial processes of the occipital segment, medially through ligaments with the quadratic rami of the pterygoids, and ventrally with the glenoid fossae of the mandibles. The ventral ends of the quadrates are free to swing in an anteroposterior plane.



Text-fig. 32. Reconstructed temporal region of *Clidastes liodontus* (after YPM 1335, × ½).



Text-fig. 33. Restored superficial musculature of temporal region of *Clidastes liodontus.*

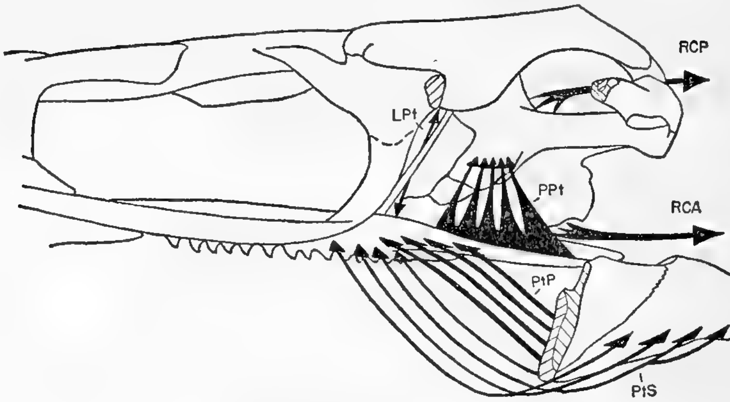
3. The basal units, composed of the pterygoid and ectopterygoid on each side of the posterior roof of the oral cavity. Each unit is bound posteriorly by muscles to the occipital segment and mandible, and by ligaments to the quadrate units. It forms a sliding contact with the posteromedial corner of the jugal, and is attached through an overlapping suture to the palatine (muzzle unit) to form a flat, flexible sheet of bone through which the hypokinetic axis passes in a transverse direction.

4. The epipterygoid units, forming a single strut on each side of the anterior portion of the occipital segment. They are anchored to the basal units below, and connected ligamentously to the occipital segment and parietal unit above.

5. The muzzle unit is the largest rigid structure in the mosasaur skull and includes the premaxillae, nasals, septomaxillae, vomers, maxillae, prefrontals, lacrymals, jugals, postorbitofrontals, squamosals, supraciliares and palatines. The unit meets the basal units posteroventrally through the hypokinetic axis and the parietal unit posterodorsally through the mesokinetic axis.

An understanding of the operation of these numerous structural units will perhaps be facilitated by a consideration of the movement of the muzzle unit about the mesokinetic axis. In *Platecarpus* and *Tylosaurus* the postorbitofrontals are solidly sutured to the ventral surface of the frontal, and this seems to be the case in other genera of mosasaurs as well, although the conditions may not be so unequivocal as in these two genera. This in effect makes the upper temporal arcades extensions of the muzzle unit that project behind the mesokinetic axis, since the postorbitofrontals and squamosals overlap each other in an immovable tongue-in-groove junction. As the muzzle unit was rotated upward about the mesokinetic axis, the upper temporal arcades were depressed, and vice versa.

The elevation and depression of the posterior ends of the supratemporal arcades caused the paroccipital processes, and thereby the occipital segment, to rock up and down about the atlas-occipital joint (see text-fig. 35; and Russell, 1964, pp. 6-8). The squamosals of necessity must have pivoted on the lateral face of the supratemporals. Adjustment in the vertical relations between the paroccipital process and the suspensorial ramus of the parietal took place through slippage on the loosely overlapping parietal-supratemporal contact.

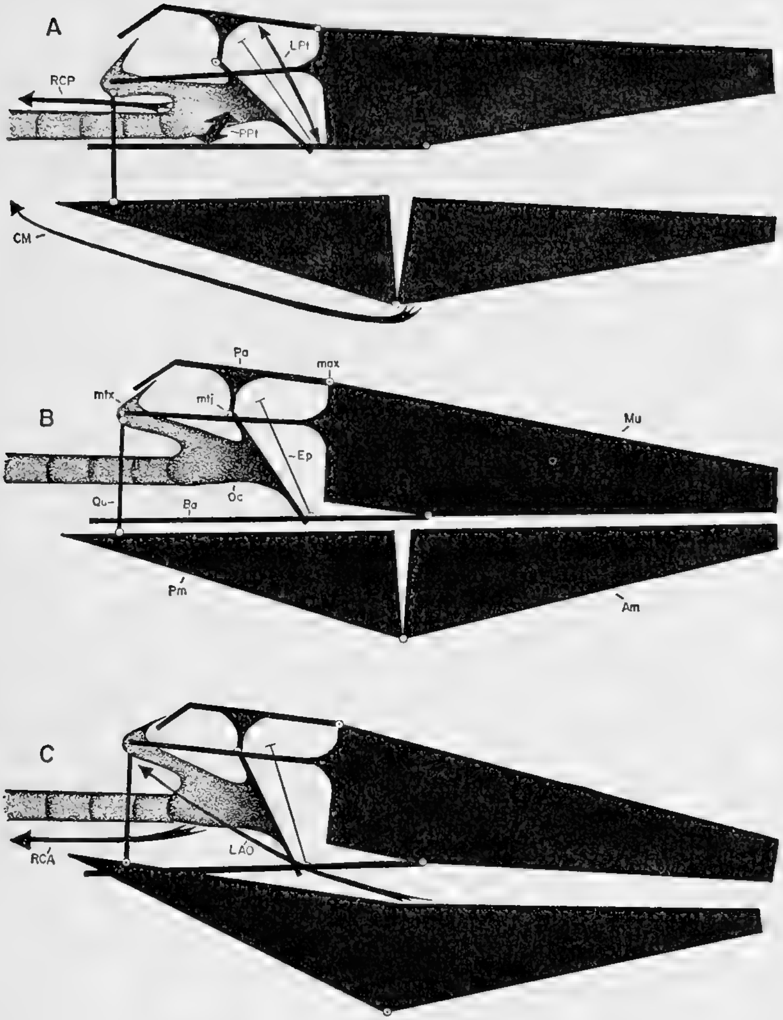


Text-fig. 34. Restored deep musculature of temporal region of *Clidastes liodontus.*

When the muzzle unit was protracted, or lifted in front of the mesokinetic axis, the paroccipital processes were rotated ventrally about the atlas-occipital joint by the descending supratemporal arcades, and the basipterygoidal processes of the basisphenoid were correspondingly brought forward and upward. Thus the basal units were elevated and displaced anteriorly by a push from the basipterygoid processes and a pull from the anteroventral corners of the muzzle unit (palatines). The reverse movement, or retraction of the muzzle unit about the mesokinetic axis, caused a similar reversal in the rotation of the occipital segment and in the movement of the components of the maxillary segment (see text-fig. 35).

The movements of the kinetic units of a mosasaur skull have been described by considering the consequences of rotation of the muzzle unit about the mesokinetic axis. However the most important effectors of kinetic movement in life are postulated to have been the Mm. rectus capitis posterior and anterior, inserting respectively above and below the occipital condyle. If superficial muscles, like the M. spinalis capitis above and the Mm. sternohyoideus and geniohyoideus below, held the maxillary segment and lower jaw fixed relative to the atlas-occipital articulation, then alternative contraction of the two rectus capitis muscles would rotate the occipital segment up and down about the atlas vertebra. The rotation of the occipital segment would then be transmitted through the links of the maxillary segment to protract and retract the muzzle unit (see text-fig. 35).

When the head of a mosasaur was at rest a line drawn from the metakinetic joint to the basal articulation would descend anteroventrally at an angle of about 45° with respect to the horizontal axis of the skull. The line would descend less steeply during protraction, when the occipital segment was rotated upward, and more steeply when it was rotated downward. Thus the metakinetic joint and basal articulation were brought more closely together vertically in the protracted state of the muzzle unit than in the retracted state. The same geometric relations also obtain for a line drawn from the mesokinetic to the hypokinetic axis. Assuming little or no vertical slipping on the metakinetic joint and basal articulation, it will be seen from text-fig. 35 that the vertical separation between them would directly control the vertical separation between the mesokinetic and hypokinetic axes, and thereby directly control the degree of protraction of the muzzle unit. Activation of the constrictor dorsalis muscles would



Text-fig. 35. Kinesis in mosasaurs. A. Muzzle unit elevated, anterior mandibular unit depressed. B. Cranium at rest. C. Muzzle unit depressed, anterior mandibular unit elevated.

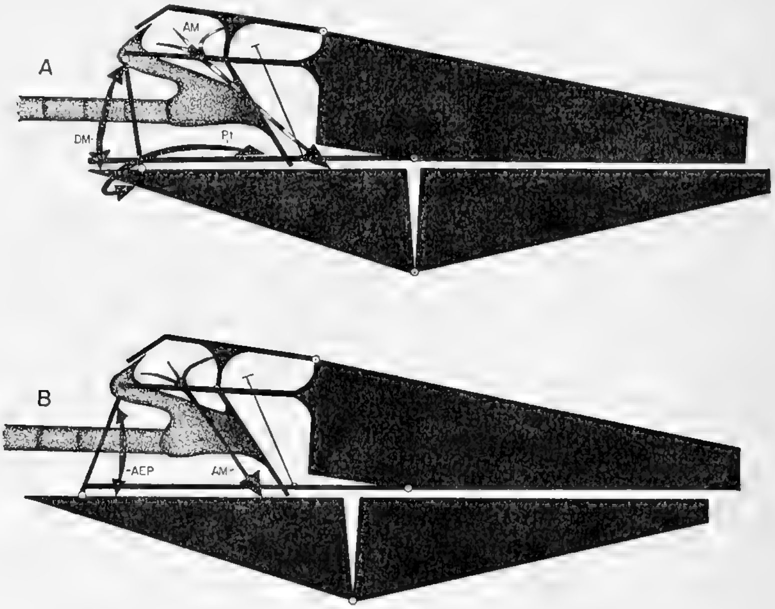
merely accentuate the elevation of the muzzle unit in the protracted state by displacing the hypokinetic axis still further anterodorsally. Note that the quadrates need not have been incorporated into the kinetic mechanism of the mosasaur skull.

STREPTOSTYLY

The term *streptostyly* is here used to describe the condition in which the quadrate has lost its contact anteriorly with the lower temporal arcade, and is only loosely bound medially to the pterygoid. The bone is then flexibly suspended from the paroccipital process dorsally, and the activation of any muscle attached to it will pivot the element about the quadratic cotylus of the paroccipital process. Movement of the quadrate will not necessarily alter the positions of the occipital or remainder of the maxillary segments relative to each other.

Kauffman and Kesling (1960) have studied a large ammonite conch which was repeatedly bitten by a mosasaur. The dentary tooth impressions from one mandible always maintain the same anteroposterior relations to those of the other mandible, indicating there was no anteroposterior movement between the lower jaws in the symphyseal region. However, tooth impressions from the upper and lower jaws did not always align with each other when occluded. This could only occur if the quadrates were independently moveable. Since both basal units are fixed to a single rigid muzzle unit, it follows that in order for the quadrates to have been independently moveable they must have been only loosely attached to the quadratic ramus of the pterygoids. The single solid point remaining upon which the quadrate could have pivoted is the cotylus on the side of the suspensorial process of the occipital segment, which was therefore probably not a sliding articulation.

Muscles that acted to protract the lower jaw (see text-fig. 36) were the M. pterygoideus (the horizontal component of force transmitted through the mandible would pull the base of the quadrate anteriorly) and the M. depressor mandibulae (rotating the mandible ventrally to counteract the dorsal component of the M. pterygoideus). The mandible was retracted by the horizontal component of force from the contracting jaw adductor muscles. Either the presence of prey between the jaws or a stabilizing pull from the M. depressor mandibulae would prevent the upper and lower jaws from entirely closing. Grooves, paralleling the longitudinal cranial axis of the attacking mosasaur, cut into the conch of the above-mentioned ammonite bear witness to the force with which the jaws could be retracted (Kauffman and Kesling, 1960, p. 213).



Text-fig. 36. Streptostyly in mosasaurs. A. Mandible protracted. B. Mandible retracted.

Mandibular Movements

The mosasaur jaw is divided into two halves by a joint near the center of the ventral margin of each mandible. The articular, angular, surangular and coronoid are incorporated into a posterior structural unit, and the splenial and dentary into an anterior one. Dorsally a thin blade-like process of the prearticular spans the gap separating the two units to penetrate deeply between the splenial and dentary into the mandibular foramen of the anterior unit. Ventrally the presence of vertical keels and grooves on the articular surfaces of the ginglymoid splenio-angular joint further restricted movement of the anterior unit to a vertical plane.

Most probably the anterodorsal areas of the coronoid and surangular were bound to the posterodorsal corner of the dentary by elastic ligaments. As the lower jaws hit the body of a victim the anterior units of the mandibles would absorb the shock of impact by rotating down about the splenio-angular joint, putting the ligaments binding the units to the posterior mandibular units under tension. These tensed ligaments, possibly aided by slips of the M. adductor mandibulae externus superficialis, would then act to restore the anterior unit to its former position.

The ratio between the distances from the center of the glenoid fossa to the anterior limit of the insertional area for the adductor mandibulae externus muscles, and the center of the fossa to the anterior tip of the dentary may be taken as an indication of the speed and power with which the jaws were brought together. In *Platecarpus ictericus, P. coryphaeus* and *Prognathodon overtoni* the ratio is about 1:4; in *Mosasaurus missouriensis, Tylosaurus proriger* and *T. nepaeolicus* it is about 1:4.5; and in *Clidastes propython, C. liodontus* and *Plotosaurus bennisoni* (Camp, 1942, fig. 1) it is usually about 1:5.2. *Platecarpus* and *Prognathodon* presumably had the most powerful bite, and *Clidastes* and *Plotosaurus* had the most rapid.

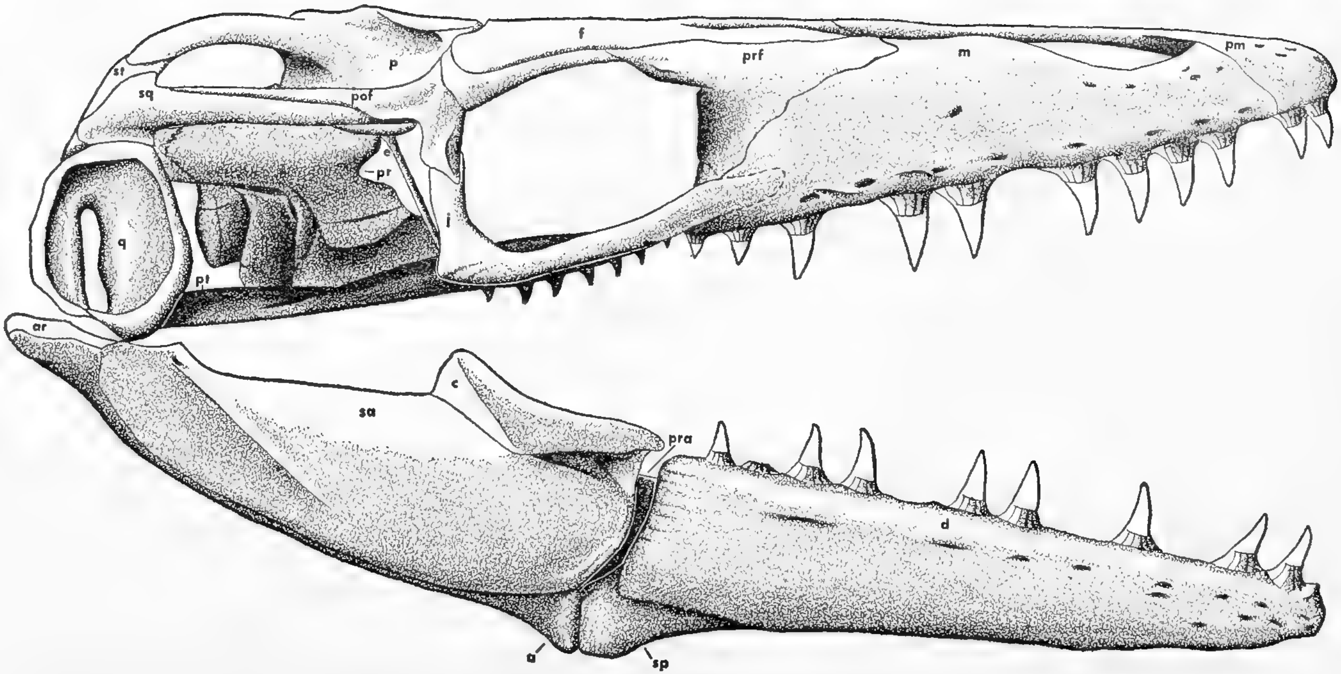
Conclusions

So far as is known all mosasaurs possessed a good sense of sight and balance, good subaqueous and probably impaired subaerial hearing, and a poor sense of smell. The presence of a calcified tympanum in all three subfamilies is no indication that any one of them had an unusual capacity for deep diving. The cranial blood vessels were no more protected than in ordinary terrestrial reptiles. In fact, the large eyes and lack of any special pressure-protective devices suggest a surface-swimming mode of life, although some mosasaurs *(Globidens, Compressidens)* may have subsisted on shallow water benthonic invertebrates.

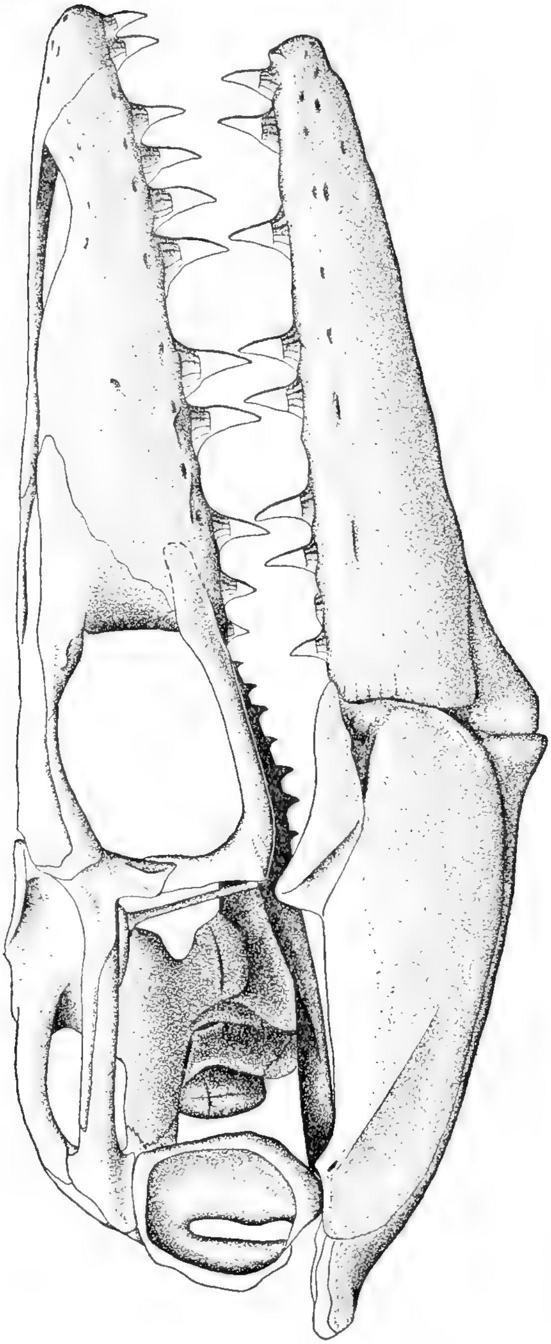
Generalized mosasaurs possessed a kinetic skull primarily activated by the operation of anterior axial muscles rotating the braincase in a vertical plane. Cranial kinesis was evidently lost in many later forms. The quadrates were streptostylic and independently moveable in all mosasaurs and acted to protract and retract the lower jaws. The intramandibular joint moved in a vertical plane and probably served as a shock absorbing device.

Frazzetta (1962) concluded that kinesis permitted the upper jaws to move downward and engage the prey simultaneously with the lower jaws. This lessened the chances of the prey being deflected from the mouth by the lower jaws. Kinesis was evidently not an essential element in the feeding mechanism of all mosasaurs, as is shown by its loss in some later forms. Perhaps the inertia of the bodies of larger prey or the viscosity of the aqueous medium in which mosasaurs lived impaired the usefulness of the kinetic mechanism inherited from their smaller, more terrestrial ancestors.

Streptostylic quadrates are, however, found in all mosasaurs and must have been useful adaptations in aquatic feeding. They permitted the mandibles to



Text-fig. 37. Restored skull of *Platecarpus ictericus* (× ¼) showing the jaws opened, the muzzle and anterior mandibular units abducted, and the jaws protracted.



Text-fig. 38. Restored skull of *Platecarpus ictericus* (× ¼) showing the jaws nearly closed, the muzzle and anterior mandibular units adducted, the jaws retracted.

be retracted and consequently greatly assisted the mosasaur in forcing prey into its throat without the aid of gravity, claws or some solid point of leverage. It is doubtful that the inertial feeding method of lizards described by Gans (1961, pp. 218-219), could have been very effective in underwater swallowing. If a mosasaur lifted its head above the surface, however, the inertial method together with the aid of gravity, would also greatly facilitate the engorgement of large bodies.

The long slender jaws of *Clidastes* were probably adapted to rapid biting. The marginal dentition is trenchant, and alternative protraction and retraction of the mandibles in this genus (and in *Liodon)* might have been effective in sawing a large object into pieces of swallowable size. Dollo (1913, p. 614-620; see below) discussed in some detail the possible food habits of three genera of mosasaurs. Because of the similarity of its large, firmly rooted marginal teeth to those of the killer whale *(Orcinus), Mosasaurus* itself may have preyed upon the larger contemporaneous marine reptiles. Its skull was akinetic. In *Plotosaurus* the skull was akinetic, but the long slender jaws suggest a rapid bite. Remains of small fish were discovered in the visceral region of a specimen of *Plotosaurus tuckeri* (Camp, 1942, pp. 11, 20).

In *Globidens* the jaws are powerfully constructed and the teeth are spherical, indicating a diet of heavily shelled mollusks (Gilmore, 1912, p. 481). Kineticism may have been useful in orienting the prey in the mouth. Because oysters thrive in shallow brackish water (see Priddy, 1954), one might expect to find *Globidens* remains associated with a similar sort of paleoenvironment. The long jaws and laterally flattened teeth of *Compressidens fraasi* (and *"Platecarpus" intermedius?)* were best adapted for crushing the thin shells of the abundant Maestrichtian echinoids. A broken test of *Hemipneustes* was once found between the teeth of one individual of the former genus (see Dollo, 1913).

The jaws are short in *Platecarpus* and the skull is relatively highly kinetic, kineticism here probably serving to minimize the chance of deflecting small prey away from the jaws. The teeth are long, slender, and circular in cross-section. Williston (1899, pp. 40-41) reported that, "Quantities of [food] remains were discovered in the abdominal region [of a *Platecarpus*], matted together and more or less comminuted. A close examination of these remains discloses nothing but fish bones, and usually only those of a small size. The largest observed is a vertebra of an *Empo* [= *Cimolichthys*], or some allied fish, of about four feet in length." As belemnites are very rarely found in the Niobrara Chalk (personal communication, Jeletzky, 1965), they could not have formed an important food source for *Platecarpus* throughout the distribution of the chalk facies. However Dollo (1913) thought that *Plioplatecarpus* may have subsisted on naked cephalopods, as the teeth are weakly implanted and restricted to the anterior portion of the jaws in Maestrichtian species of the genus, as in the delphinid *Globicephala* ("blackfish") which eats squid and cuttlefish. Two belemnite endoskeletons have been found between the mandibles and cervical vertebrae of one specimen of *Plioplatecarpus* (Dollo, 1913).

In *Prognathodon* the skull is akinetic. The jaws are relatively shorter and heavier, and the teeth appear to be better adapted for crushing than in any mosasaur except *Globidens.* It is perhaps significant that in the ammonite described by Kauffman and Kesling the tooth marks of the marginal dentition of the mosasaur have cross-sections similar to those of the marginal teeth of *Prognathodon overtoni.* The jaws of *Tylosaurus* are strongly built, moderately elongated, and filled with heavy teeth similar to those of *Mosasaurus.* The skull is kinetic. The elongate premaxillary rostrum could have been used to stun prey or defend the mosasaur against enemies (sharks). Turtle bones have been found in the body cavity of *Hainosaurus,* a Belgian tylosaurine (Dollo, 1887, p. 520).

There is an instance of possible cannibalism reported from Canada (Anonymous, 1962, p. 5) where fragments of a small mosasaur were found mixed with the skeleton of a larger one.

GENERAL DESCRIPTION OF POSTCRANIAL SKELETON

In life mosasaurs must have resembled what they indeed were, very large marine lizards. They were considerably larger than most extant reptiles, averaging 20-30 feet in length. The chest was more concentrated in the anterior portion of the body than is usual in lizards, and the flanks were probably slender (Williston, 1899, p. 40), merging imperceptibly into the fleshy base of the tail posteriorly. The tail was relatively shorter than in *Varanus,* but was very flat and deep, forming a more efficient sculling organ. The legs were much shortened and the feet were transformed into flippers, the fore and hind flipper being of approximately equal size. The integument has been preserved in specimens of *Platecarpus* (Williston, 1899, p. 41), *Tylosaurus* (Snow, 1878; Williston, 1898b, p. 215, pls. 69-70), and *Ectenosaurus* (FHM 7937), all from the Niobrara Chalk of western Kansas. The body was probably completely covered with small, rhomboid scales.

For additional descriptions of the postcranial morphology of American mosasaurs the reader is referred to the works of Williston (1898b), Merriam (1894), Martin (1953), Osborn (1899a), Camp (1942), Huene (1911), Wiman (1920), and Marsh (1880), listed in order of decreasing importance. As with the cranial skeleton, information relating to Californian material has been taken from Camp's (1942) monograph.

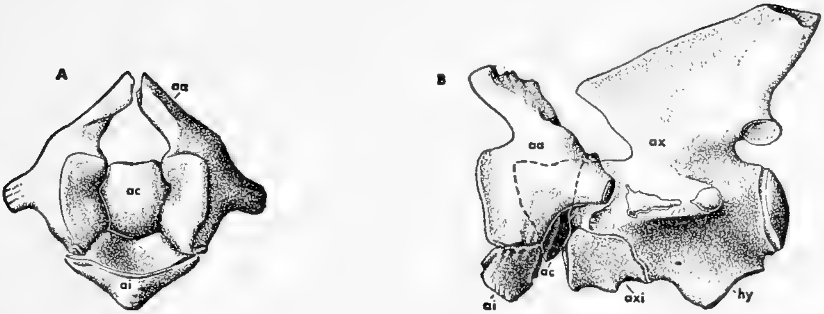
Cervical Vertebrae

ATLAS

The atlas complex in mosasaurs includes the four discrete ossifications typical of all lizards, centrum (odontoid), intercentrum, and two neural arches. There is no proatlas. The neural arches are linked ventrally to the intercentrum to form a ring-like structure between the axis and occipital condyle; the atlas centrum is functionally distinct, being solidly attached to the axis.

Internally the body of the neural arch is subdivided into several surfaces. There is an anterior concavity, elliptical in outline and vertical in position, for articulation with the dorsolateral portion of the occipital condyle. Behind this a triangular facet with a ventrally directed apex faces medially to contact the atlas centrum. The posterior border of this facet is in turn bounded by an oblique surface, inclined both posterolaterally and posterodorsally, for articulation with the axis centrum. These three surfaces are truncated as they converge ventrally by the articulation for the atlas intercentrum. All of these surfaces were covered with cartilage in life. The external side of the atlantal body narrows behind the dilated portion supporting the condylar articulation and terminates posteroventrally in a pointed synapophyseal process. The process is well developed in *Plotosaurus, Platecarpus* and *Ectenosaurus,* varies from large to nearly absent in *Tylosaurus,* and is especially large in *Clidastes* and *Mosasaurus.* Its large size relative to the condition in *Varanus* is suggestive of a high degree of development of the M. iliocostalis cervicis in mosasaurs, which probably inserted in part on its cartilage-capped tip.

The dorsal border of the atlas synapophysis extends anterodorsally to form the posterior margin of a stout, anteriorly inclined spinous process that arched over the spinal cord. Its anterior border rises directly above the condylar articulation (*Plotosaurus, Platecarpus, Tylosaurus*) or is separated from it by a notch



Text-fig. 39. Atlas-axis vertebrae in *Clidastes propython* (YPM 1100, × ½). A. Anterior view of atlas. B. Lateral view of atlas-axis. Abbreviations: aa, atlas neural arch; ai, atlas intercentrum; ac, atlas centrum (odontoid); ax, axis; axi, axis intercentrum; hy, facet for hypapophysis (intercentrum) of third cervical vertebra.

(*Clidastes, Ectenosaurus, Mosasaurus*). Spinal nerves I and II exited in front of and behind the base of the spinous portion of the atlantal arch, respectively. The spinous process expands somewhat distally and has a slightly ventromedially incurved dorsoposterior corner. The tips of these processes are usually longitudinally ribbed and contact each other in *Clidastes* and *Plotosaurus,* are separate in *Platecarpus,* and widely separate in *Tylosaurus* and *Mosasaurus* where the spinous processes are relatively short. Thus a true atlas neural spine is absent in mosasaurs.

Midway between the tips of the spinous and synapophyseal processes on the dorsal margin of the atlas there is a longitudinally grooved region in the center of which is a slight excavation. This pit probably marks the tendonous insertion of the M. longissimus cervicis and anterior attachment of a tendonous sheet that extends dorsoposteriorly through the muscle masses of the Mm. transversalis capitis and articuloparietalis in *Varanus* (Nishi, 1916, p. 233). The site of insertion of the M. obliquus capitis inferior is probably located immediately anterior to the above-mentioned pit. According to Nishi (1916, p. 243) a small group of fibers from the M. obliquus capitis magnus (M. obliquus capitis superior) arises on the surface of the atlas just lateral to the longissimus tendons. In some mosasaurs *(Plotosaurs, Platecarpus, Ectenosaurus, Tylosaurus)* a prominent posterodorsally directed tuberosity is developed at this point, in others *(Clidastes, Mosasaurus)* only a small ridge is present.

Each neural arch meets the atlas intercentrum ventromedially. In the vicinity of their mutual contact the external surface of both elements is strongly ribbed in a vertical direction, indicating the attachment of strong ligaments binding them together *(Clidastes, M. conodon, Plotosaurus, Platecarpus, Ectenosaurus, Tylosaurus)*. In *M. maximus* these ribbings interdigitate lateral to the cartilaginous contact and form a suture solidly uniting the two ossicles.

The atlas intercentrum is in the shape of a prism bowed slightly upwards at the ends so that its flat base is transversely convex ventrally. Because the anterior facet is slightly cupped to receive the condyle from the basioccipital and the posterior contact with the axis intercentrum is flat, these surfaces intersect dorsally to form a rounded, shallowly concave edge. The triangular ends of the bowed prism rise to meet the base of the neural arches. These facets were all covered with cartilage in life. A small tubercle is present on the posterior midline of the rectangular ventral surface. In *Iguana* (Evans, 1939, p. 56, fig. 15) a portion of the M. longus colli inserts on each side of this tubercle.

The atlas centrum is quite constant in shape in mosasaurs. In lateral aspect it resembles a very squat, horizontal cone, the dorsal portion of which has been flattened to floor the spinal cord in its course between the foramen magnum and neural canal of the axis. The whole anteroventral and anterolateral area of the cone was covered in cartilage. Posteriorly the cone abuts against the axis centrum which it meets in two vertical, posteriorly converging flat surfaces, one on either side of the midline. The ventral contact with the axis intercentrum slopes posterodorsally in a transverse direction so that the ridges formed by the intersection of the three surfaces form an inverted "Y". The surfaces themselves are minutely ridged and pitted, suggesting that the atlas centrum must have been rigidly fastened onto the anterior face of the axis complex.

AXIS

The axis vertebra is a very powerfully built structure lying at the functional anterior terminus of the vertebral column and linking it to the cranium. The dual nature of its function is clearly shown in the form of the axis, which posteriorly is not greatly different from that of a succeeding cervical vertebra. Anteriorly it is highly modified to provide origins for muscles acting directly on the skull and to support the skull indirectly through the atlas vertebra.

The neural spine is shaped like a flat-edged hatchet blade, expanding anteriorly and posteriorly above the relatively constricted neural arch to a length about equal to that of the centrum below. The posterior border is very heavy, giving the spine a "T"-shaped outline in horizontal section and providing a large area of insertion for powerful semi-spinalis cervicis and interspinalis muscles. It was capped dorsally by a cartilage-covered surface in life which marked the anteriormost origin of the M. spinalis capitis. The dorsal edge of the spine becomes compressed and descends to a small elliptical expansion at its anterior tip. The superficial portion of the M. rectus capitis posterior may have arisen in front of the spinalis capitis origin and the deeper portion probably from the anteriormost tip of the spine. They arise from comparable areas in *Varanus.* There is a shallow depression, centrally located on each side of the neural spine anterior to the broad posterior buttress and above the neural arches, from which the M. obliquus capitis magnus must have arisen.

The neural arches are fused to the axis centrum and to the centra of all succeeding vertebrae without a trace of a suture in even the most immature specimens. Except for the complete or nearly complete absence of an anterior zygopophysis there is little to distinguish the axis neural arch from that of other cervical vertebrae. The M. obliquus capitis inferior probably arose from its dorsolateral face as it does in *Varanus.* The posterior zygopophyses are normally developed and face ventrolaterally at an angle of about 45°. The first traces of a zygantral articulation may occur on the internal side of the posterior zygopophysis, between the zygopophyseal articulation and a median dorsoventral ridge on the posterior surface of the neural spine. Zygantra may be well developed in *Clidastes,* incipiently developed in *Mosasaurus, Plotosaurus* and *Platecarpus,* and are evidently absent in *Plioplatecarpus* (Dollo, 1894, p. 235) and *Tylosaurus.*

Short epaxial muscles link the posterior edge of the neural spine and neural arch of the axis to the anterior edge of the neural spine and arch of the succeeding vertebra. In *Varanus* these include the Mm. interarticulares, interarcuales, and interspinales. The first muscle originates from the cranial edge of the anterior zygopophysis of the fourth cervical and the anterior surface of the posterior zygopophysis of the third cervical and passes forward to insert on the posterior surface of the posterior zygopophysis of the axis. The other two muscles pass between opposite edges of the neural spine and arch of the axis and third cervical. These three muscles are all more or less intergrown in *Varanus* and bear the same relations to the vertebrae along the entire presacral portion of the vertebral column. There is no reason to think they were any differently arranged throughout the zygopophysis-bearing portion of the vertebral column of mosasaurs.

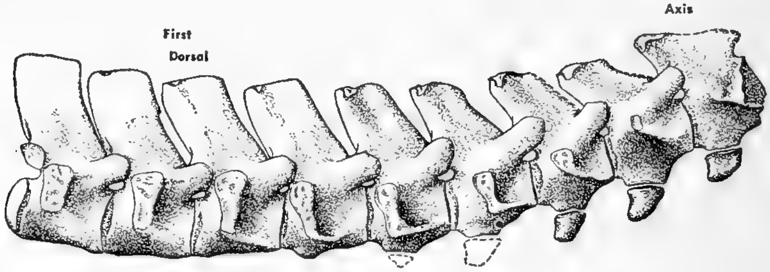
The cranial face of the axis centrum is expanded to a width about equaling the anteroposterior length of the centrum. In anterior aspect it has an approximately reniform outline, with the long convex surface facing downwards. In horizontal cross section the dorsal portion of the cranial face of the centrum resembles a "W," the lateral prongs of the "W" pointing posteriorly. The paired anteromedially inclined planes are square shaped and roughtened to provide an immovable contact for the atlas centrum; the two posterolateral-sloping semicircular surfaces are smooth and articulated with the atlas neural arches. Ventromedially the cranial face is hollowed to form an anteroventral-directed, roughened excavation receiving the posterodorsal side of the axis intercentrum.

The main body of the axis centrum is sharply constricted behind its anterior face, but re-expands slightly to terminate in a convex, elliptical articulation for the centrum of the third cervical vertebra. In posterior aspect this articulation is nearly circular in outline in *Clidastes, Mosasaurus* and *Tylosaurus,* but in *Platecarpus* its width exceeds the depth by about one-half. The axis synapophysis is located on the center of the lateral surface of the centrum and is connected anteriorly by a horizontal ridge of bone to the facet for articulation with the atlas neural arch. The lateral edge of this ridge is roughened in *Platecarpus* and was rimmed in cartilage in *Clidastes, Plotosaurus*? and *Tylosaurus.* The atlas synapophysis overhangs the anterior portion of the ridge in *Clidastes* and *M. conodon,* and it seems likely that this ridge was also an area of insertion of the M. iliocostalis cervicis. In an excellently preserved specimen of *Platecarpus* in the Tübingen Museum, Huene (1911, pl. 3) shows a rudimentary cervical rib articulating with the synapophysis of the axis vertebra. Williston and Case (1892, pp. 20, 24) also report a cervical rib present on the axis of *Clidastes.* Dollo (1894, p. 232) reports its presence on the axis vertebra of *M. conodon* and *Plioplatecarpus.* A large peduncle with a distal facet for articulation with a hypapophysis is located on the ventral surface of the axis centrum. In *Clidastes, Mosasaurus* and *Plotosaurus* it is almost circular in outline and faces ventroposteriorly. In *Platecarpus* it tends to be more triangular, with an apex pointed directly anteriorly. It is similar in *Tylosaurus* but more laterally compressed and usually bears a transverse sulcus across its center. In the last two genera the facet is only slightly posteriorly inclined.

The axis intercentrum is a short, hemicylindrical ossification firmly attached to the anteroventral margin of the axis centrum. The facets for articulation with the axis centrum behind and the atlas centrum above meet at a high angle and are similarly roughened. In contrast, the facet for the atlas intercentrum on the anterior face of the bone is smooth. The ventral surface of the bone is transversely convex and much wider than long. A large posteroventrally directed, tongue-shaped tuberosity is present on the ventromedian surface, which probably represents a major site of insertion of the M. longus colli.

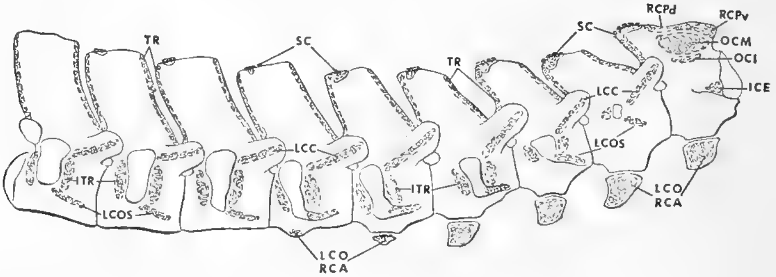
CERVICALS THREE TO SEVEN

The form of vertebrae in the posterior cervical region changes gradually posteriorly into that typical of thoracic vertebrae, making it difficult to define the morphological posterior end of the cervical series. The last cervical vertebra is usually taken to be the one that precedes the first vertebra with ribs reaching the sternum (Romer, 1956, pp. 227, 241). In *Varanus* there are, by this definition, nine cervical vertebra. However, Williston and Case (1892, p. 20) state that in *Clidastes* the first long rib with a possible sternal connection occurs on the eighth postcranial vertebra (see also Williston, 1898b, p. 139). Osborn (1899a, p. 172), and Williston (1910, p. 538) and Huene (1911, p. 49), on the basis of excellent skeletons of *Tylosaurus* and *Platecarpus* respectively, unequivocally give the number of cervical vertebrae as seven. It is highly probable that mosasaurs have two less anterior vertebrae lacking a sternal contact than does *Varanus.*



Text-fig. 40. Anterior portion of vertebral column of *Platecarpus* (YPM 24900, × ⅕).

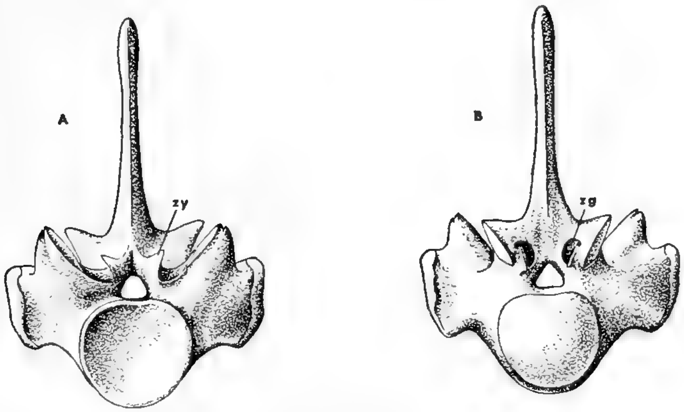
The neural spine of the third cervical vertebra is slender in lateral aspect, with slightly converging anterior and posterior margins. The posterior buttress of the spine is still greatly enlarged and is almost as wide as that of the axis, though the anterior edge is very thin. A transversely oriented elliptical surface, which was capped by cartilage in life, occupies the dorsal tip of the spine. The neural spine changes its shape posteriorly so that by the time the last cervical is reached the spine is parallelogram-shaped in lateral aspect and both longer and higher. Laterally the spine also becomes very compressed, causing the posterior buttress to vanish almost completely and the dorsal edge of the spine to lose nearly all trace of a transverse elliptical expansion on the last cervical. It is thus apparent that few, if any, fibers of the M. spinalis capitis, which arises on the dorsal tip of the neural spines, can have extended behind the last cervical, and that the Mm. interspinalis, spinalis and semispinalis cervicis diminished to normal proportions in the posterior cervical region. It is interesting that these last



Text-fig. 41. Areas of muscle attachment on anterior portion of vertebral column of *Platecarpus.* Abbreviations: ICE, M. iliocostalis cervicis; ITR, Mm. intertransversari; LCC, M. longissimus cervicocapitis; LCO, M. longus colli; LCOS, M. levator costae; OCI, M. obliquus capitis inferior; TR, transversospinalis system. For other abbreviations see text-figure 1.

muscles show no unusual development in the anterior cervical region of *Varanus*.

Zygopophyses are present on the neural arches throughout the cervical series in all mosasaurs. The anterior zygopophyses arise from a position on either side of the neural canal and project anteriorly, dorsally and laterally, the articular facets facing dorsomedially with their centers just in advance of the anterior rim of the centrum. A strong rounded crest curves anterodorsally from the synapophysis to support the anterior zygopophysis laterally in *Clidastes, Mosasaurus, Globidens* (Gilmore, 1912, fig. 3), *Plotosaurus, Platecarpus, Plioplatecarpus primaevus, Ectenosaurus, Prognathodon* and *Halisaurus.* It is straight in *Tylosaurus* and absent in *Plioplatecarpus depressus.* This ridge probably served as an area of origin for the M. longissimus cervicocapitis. The posterior zygopophyses arise from the posterolateral corner of the neural spine and project posteriorly, ventrally and laterally. A small process of bone commonly arises immediately above the neural canal on either side of the vertebral midline in mosasurs. It may bear a laterally facing facet for articulation with the lateral wall of an elliptical excavation close to the vertebral midline and above the neural canal of the preceding vertebra. These accessory articulations lie median to the zygopophyses and are called respectively, a zygosphene and a zygantrum. They are relatively highly developed in *Clidastes, "Platecarpus" intermedius* (Leidy, 1873, p. 282) and *Ectenosaurus* where they may attain a size as great as one-sixth that of the zygopophyses. Functional zygosphenes exist on the cervical vertebra in the type of *Globidens alabamaensis* (Gilmore, 1912, p. 484). In *M. conodon* the zygosphenes are rudimentary on the third and fourth cervical vertebrae, but are functional, though small, on cervicals five through seven. Rudimentary zygosphenes also occur on the vertebrae of the anterior portion of the column in *M. missouriensis* (Williston, 1895, p. 167). Zygosphenes are present but seldom functional in the cervical vertebrae of *Platecarpus* and are evidently very small or absent in the corresponding region of *Plotosaurus, Plioplatecarpus, Prognathodon, Halisaurus* and *Tylosaurus.* The articulating surfaces of both zygopophyses and zygosphenes-zygantra are inclined at an angle of about 45° to the horizontal and, in well-preserved specimens, show traces of growth rings.



Text-fig. 42. Vertebra of *Clidastes* showing zygosphene (zy) and zygantrum (zg) (restored after YPM 24916, × ½). A. Anterior view. B. Posterior view.

The centra of the cervical and all succeeding vertebrae are procoelous. The interarticular surfaces are very smoothly finished, indicating a high degree of mobility, and are vertical, instead of anterodorsally inclined as in *Varanus*. These surfaces are dorsoventrally compressed in *Halisaurus*; horizontally oval in *Globidens* (Gilmore, 1912, fig. 3), *Platecarpus, Ectenosaurus* and *Plioplatecarpus*; and more nearly circular in *Clidastes, Mosasaurus, Tylosaurus* and perhaps also *Prognathodon*. The length of the centra increases slightly from the third to seventh cervical in *Platecarpus* and *Plotosaurus*, remains approximately constant in *Clidastes* and *Tylosaurus*, and decreases slightly in *M. conodon* and *Plioplatecarpus* (Dollo, 1894, p. 234). The synapophysis increases uniformly and greatly in depth from a circular tuber on the axis to a narrow vertically rectangular surface on the last cervical. Here it is about equal to the body of the centrum in height and is dorsolaterally inclined in *Clidastes, Globidens* (Gilmore, 1912, fig. 3), *Platecarpus, Ectenosaurus* and *Halisaurus*, or of a slightly lesser height and laterally directed in *Mosasaurus, Plioplatecarpus* and *Tylosaurus* or ventrolaterally directed in *Plotosaurus*. A ridge of bone extends from the ventral edge of the synapophysis directly forward to the rim of the anterior central articulation. This ridge lies well above the ventral margin of the posterior cervicals in *Mosasaurus, Plotosaurus, Ectenosaurus* and *Tylosaurus*, approaches the ventral margin in *Clidastes, Globidens* (Gilmore, 1912, fig. 3), *Platecarpus* and *Plioplatecarpus*, and extends well below the ventral margin in *Halisaurus*. The ridge together with the posterior edge of the synapophysis very likely served as the area of origin for the Mm. levator costae which extended posteriorly to insert on the anterior surfaces of the heads of the cervical ribs (see Olson, 1936, p. 298). The anterior and posterior surfaces of adjacent synapophyses were probably linked by the Mm. intertransversarii (Olson, 1936, p. 297). All of the cervical vertebrae except the atlas bear ribs.

As on the axis, a stout peduncle is situated on the posteroventral surface of anterior cervical vertebrae in all mosasaurs. The flattened distal end, similar to that of the axis in the various genera, articulates with a squat posteroventrally recurved hypapophysis. The axis hypapophysis, morphologically equivalent to the intercentrum of the vertebra behind (Osborn, 1899a, p. 175), is the broadest and most powerful of the series. Succeeding hypapophyses diminish in size, the smallest and last one usually occurring on the sixth cervical in *Clidastes, Platecarpus* and *Tylosaurus*, on the sixth or seventh cervical in *M. conodon*, on the seventh cervical of *Ectenosaurus* and *Plioplatecarpus* (Dollo, 1894, p. 235), on the second or third dorsal of *Plotosaurus* and on the fourth dorsal of *M. missouriensis* (Goldfuss, 1845, p. 191). There are frequently two or three vertebrae with rudimentary peduncles following the last hypapophysis-bearing vertebra. The Mm. longus colli and rectus capitis anterior must have been attached to these processes, as has been pointed out by Camp (1942, p. 5).

Dorsal Vertebrae

The number of vertebrae between the last cervical, here considered as the seventh one postcranially, and the "sacrum" is quite variable in mosasaurs. In *Platecarpus* and perhaps also *Ectenosaurus* only 22, and in *Tylosaurus* 22 to 23 dorsal vertebrae are present, thus about equaling the number (21-22) found in *Varanus*. *Clidastes sternbergi* has 24 dorsals, other Niobrara species of the genus have 35. Thirty-eight dorsal vertebrae are known in *M. conodon* and Camp (1942, pl. 5) restores the number of dorsal vertebrae in *Plotosaurus* at 44. Dollo (1894, p. 237) states there are only 13 vertebrae, which could here be termed dorsals, in *Plioplatecarpus*, an unusually low number. The dorsal column may be divided into an anterior thoracic series bearing long ribs and a posterior lumbar series with short ribs. In *C. liodontus* there are between eleven and twelve dorsal vertebrae with relatively long ribs that may be called thoracic, although several of the more posterior ones probably lack sternal connections (Williston and Case, 1892, p. 25; YPM 1333). *Clidastes sternbergi* has about 14 such vertebrae (Wiman, 1920, pl. 3), and there are between 17 and 18 present in *M. conodon* (Dollo, 1894, p. 233; Martin, 1953). *Platecarpus* has between 12 and 13 dorsal vertebrae with long ribs (Williston, 1910, p. 538; Huene, 1911, pl. 3; Lambe, 1914, pl. 1; Wiman, 1920, pl. 3), *Ectenosaurus* may have about 11 (FHM 7937), and *Tylosaurus* does have 11 (Osborn, 1899a, pl. 23; USNM 8898).

The neural spines of the dorsal vertebrae resemble those of the last cervical very closely, being narrow, parallelogram-shaped and posteriorly inclined, and nearly as long as the vertebral centra. In the thoracic series the anterior and posterior edges of the spine converge distally, but in the lumbars this convergence is almost absent. The neural spines are generally rather uniform in height and inclination, although in *Clidastes, Platecarpus* and *Tylosaurus* the spines in the lumbar region are taller and more vertically oriented than in the anterior regions. In *M. conodon* the spines are nearly vertical in the thoracic series; those of the lumbar region slope more strongly posteriorly (Martin, 1953). Camp (1942, pl. 5) restores the vertebral column of *Plotosaurus* as having the tallest spines of the presacral series in the anterior thoracic region.

In *Varanus* well developed zygopophyses of equal strength extend the full length of the dorsal series. This is never the case in mosasaurs. Zygopophyses are fully developed in the cervical region of *Clidastes, M. conodon, M. missouriensis, Platecarpus, Ectenosaurus* and *Tylosaurus* but are reduced steadily in size posteriorly, so that vertebrae in the posterior lumbar region have zygopophyses of about two-thirds the dimensions of those in the neck. This reduction is accelerated in *Plotosaurus,* where the last functional zygopophyses occur on the seventh dorsal, and in *Plioplatecarpus* where they occur on the third (Dollo, 1894, p. 230). Not only do the zygopophyses diminish in size posteriorly but they also approach the midline more closely. Since the zygopophyses mark the plane of division between the transversospinalis and longissimus systems (Vallois, 1922, p. 511), it follows that the former group must be correspondingly reduced in cross sectional area, and therefore in strength, in the posterior portion of the trunk vertebrae in mosasaurs. The zygosphene-zygantrum articulation is well developed on dorsal vertebrae of *Clidastes* and *Ectenosaurus* and shows little reduction in the posterior region of this portion of the column. In *M. conodon,* however, this articulation becomes non-functional in the region between the third and seventh dorsal vertebra. Zygosphenes are absent in *Plotosaurus, Plioplatecarpus, Prognathodon* and *Tylosaurus.*

The centra of the dorsal vertebrae increase slightly in length up to the middle of the series in *Clidastes,* then decrease gradually in length so that the last dorsal vertebra is about equal to the first in this dimension. A similar tendency to reduce the length of the dorsal centra begins in the anterior thoracic region of *M. conodon.* In *Plotosaurus* the vertebral centra increase in length at least as far back as the eighth dorsal. The longest vertebrae are found near the middle of the lumbar region of *Platecarpus* and *Tylosaurus* where the centra exceed that of the first dorsal by about 1.3 times in length. Further posteriorly they rapidly decrease in length although the centrum of the last dorsal is still appreciably longer than that of the first. The radius of curvature of the central articulations becomes greater posteriorly in all mosasaurs. These articulations increase in area posteriorly in *Clidastes, Platecarpus* and *Tylosaurus,* where they are about twice as large as the first dorsal in the posterior lumbar region. This increase in size is not so great in *Mosasaurus* and *Ectenosaurus.* The articular facets of the anterior dorsal series are circular in *Clidastes, M. maximus* and *Tylosaurus,* transversely oval in *M. conodon, Plotosaurus, Platecarpus, Plioplatecarpus, Ectenosaurus* and *Prognathodon,* and dorsoventrally compressed in *Halisaurus.* In the posteriormost dorsal region they take on the outline of an isosceles triangle with rounded apices and one side facing directly ventrally.

The synapophyses originate on the anterodorsal portion of the lateral surface of the thoracic centra in *Clidastes, Mosasaurus, Plotosaurus, Prognathodon* and *Tylosaurus,* and from high in the center of the lateral surface in *Platecarpus* and *Plioplatecarpus.* They are extraordinarily heavy in an anterior thoracic of *Halisaurus* where their distal ends extend posterolaterally to almost the same vertical plane as that occupied by the posterior central articulation. In the lumbar region they move to a more central position on the anterolateral surface of the centrum, and in *Mosasaurus* and *Plotosaurus* at least, they become progressively more ventrodistally inclined on the last few vertebrae preceding the "sacrum." Because of the usual crushed condition of mosasaur material from the Niobrara Chalk it is difficult to tell how the synapophyses vary in a transverse direction in the vertebral column of Niobrara specimens. In two specimens of *Clidastes* (YPM 1333, 1335) the synapophyses appear to increase slightly in length from the anterior to the posterior end of the dorsal series. In one specimen of *Platecarpus* (YPM 24905) they seem to be longest near the middle of the dorsal series, and Osborn (1899a, p. 176) states they are of uniform length in the lumbar series of *Tylosaurus.* Martin (1953) notes that the synapophyses of *M. conodon* are nearly twice as long in the posterior thoracic region as they are at either end of the dorsal series. In *Clidastes, M. conodon* (Martin 1953), *Plotosaurus* and *Platecarpus* the articular facet for the rib on the distal end of the synapophyses attains its greatest depth in the region of the first thoracic vertebra, diminishes to about two-thirds this size before the end of the thoracic series, and then remains constant in depth to the end of the lumbar series.

In *Varanus* a tendon (Ligamentum tuberculi costae) arises from the lateral surface of the anterior zygopophysis and passes ventrolaterally to insert on the proximodorsal surface of the adjacent rib. In mosasaurs there is a roughened area just medial to the anterodorsal corner of the synapophyseal facet that may have marked the origin of this tendon. It would then have followed a more posterolateral course to insert on the anterodorsal edge of the proximal portion of the rib. The ridge extending from the ventral border of the synapophysis to the anterior rim of the centrum in the cervical vertebrae is gradually reduced in size posteriorly in *Clidastes,* to disappear finally near the beginning of the lumbar series between the thirteenth and fifteenth vertebra. In *M. conodon* it is already absent on the third thoracic, and in *Plotosaurus* it disappears before the fifth thoracic vertebra. It is rudimentary on the first two thoracics of *Platecarpus,* but in *Tylosaurus* the ridge is present at least as far back as on the twelfth dorsal.

Caudal Vertebrae

SACRUM

The ilium has lost all contact with the vertebral column in mosasaurs, making the identification of the homologue of the first sacral vertebra a matter of some dispute. The pelvis has been found associated with vertebrae in the anterior region of the pygal series (Williston and Case, 1892, p. 21; Huene, 1910, pl. 1), with vertebrae near its center (Williston, 1904, p. 51; Capps, 1907, p. 350; J. T. Gregory, 1964, personal communication), and with vertebrae near the posterior end (Marsh, 1872b, p. 453; Osborn, 1899a, fig. 1). Largely or entirely on the basis of vertebral associations several authors (Marsh, 1872b, p. 453; Cope, 1875, pl. 55; Owen, 1879, p. 56) concluded that the pelvis lay in life beneath the center or posterior end of the pygal series. Dollo (1894, p. 224) also held that the pelvis occupied this position, in the conviction that the pygals were true ribless lumbar vertebrae. Other workers (Williston and Case, 1892, p. 21; Williston, 1897c, p. 109; 1898b, p. 135; Merriam, 1894, p. 12; Osborn, 1899a, p. 177; Huene, 1911, p. 50; Camp, 1942, p. 8) have believed that the ilia were connected ligamentously to the transverse processes of the first pygal vertebra and that this vertebra was indeed the true "sacral." The latter opinion finds its strongest support in the fact that the transverse process of the first pygal vertebra is more than twice as long as the synapophysis of the last dorsal. This is a very sharp distinction, nearly as clear cut as the sudden interruption of the dorsal series by the expanded transverse process of the first sacral vertebra in *Varanus* (see also Osborn, 1899a, p. 177). It should be noted that a well defined lumbar region is never present in reptiles (Romer, 1956, p. 228).

CAUDAL VERTEBRAE

The caudal vertebral column of mosasaurs may be divided into three regions, a basal region where vertebrae lack haemal arches, an intermediate region where they possess haemal arches and transverse processes, and a terminal region where transverse processes are absent. Vertebrae of the first type have been called "pygial" by Williston and Case (1892, p. 22) or "pygal" by Williston (1898b, p. 141). Since the sacral vertebra is almost indistinguishable from the anteriormost caudal in mosasaurs, it is here considered as the first pygal vertebra. The following list shows known caudal vertebral counts in mosasaurs.

Counts of caudal vertebra: (See systematic section for sources of information)

	pygals	chvs. and tv. proc.*	terminal**	total
Clidastes liodontus	7	26	approx. 46	approx. 79
Clidastes sternbergi	4	——approx. 72——		approx. 76
Mosasaurus conodon	8	21	approx. 54	approx. 83
Plotosaurus	30	5	approx. 64	approx. 99
Platecarpus	5	26–31	approx. 65	96–101
Tylosaurus	6–7	33–34	56–78	95–119

* caudals with chevrons and transverse processes
** caudals with chevrons only

The neural spines at the base of the caudal series are identical to those of the posterior dorsals. They decrease in height posteriorly, but at a proportionally lesser rate than the centra shorten, with the result that the spines assume a progressively slenderer outline in lateral view. Near the beginning of the posterior half of the tail the neural spines become vertical and slightly elongated in *Platecarpus* (on postsacrals 44-52) and *Tylosaurus* (postsacrals 38-40). They are nearly vertical and more greatly elongated in this region of the tail in *C. sternbergi* (Wiman, 1920, fig. 7, pl. 3). In *C. liodontus* (Williston, 1898b, pl. 62 fig 3), *M. conodon* (Dollo, 1894, pp. 230-231; Martin, 1953) and *Plotosaurus tuckeri* (Camp, 1942, pl. 3) the neural spines become vertical slightly behind the center of the tail. They then slope anteriorly and increase in length until, on postsacrals

41-42 in *Clidastes,* 42-44 in *Mosasaurus* and 42-44 in *Plotosaurus,* they again become vertical and reach a maximum in height amounting to a 50% increase over that of the spines on preceding caudals. The neural spines then resume a posterior inclination and steadily decrease in height to the posterior extremity of the caudal series. In this region of the tail the spines are strongly posteriorly inclined near the base, and become more vertically oriented and slightly expanded distally. In *Tylosaurus* and *M. conodon* (Martin, 1953) the change in slope distally is more abrupt than in *Clidastes, Plotosaurus* and *Platecarpus.*

Functional zygopophyses are never present except on the anteriormost caudal vertebrae in mosasaurs. In *Clidastes, M. missouriensis* (Goldfuss, 1845, p. 192), *M. conodon* (Dollo, 1894, p. 230; Martin, 1953), *Platecarpus, Ectenosaurus* and *Tylosaurus* zygopophyseal contacts between successive vertebrae are lost anterior to the first chevron bearing caudal. Anterior zygopophyses in a very rudimentary form occur throughout the caudal series. In the posterior portion of the tail of *Clidastes* and *Platecarpus,* and to a lesser degree of *Tylosaurus,* the lateral surface of each neural arch projects in a flat plane to buttress the sides of the blade of the neural spine. Such transversospinalis mucles as were present were probably interrupted laterally by these surfaces and thereby concentrated in an interspinal position between them and above the remnants of the anterior zygopophyses.

The central articulations are subtriangular in outline at the base of the tail in *Clidastes, Plotosaurus, Platecarpus* and *Tylosaurus* and tend to become subhexagonal as the transverse processes rise on the centrum in vertebrae behind the pygal series. The central facets in the anterior portion of the tail are relatively high in *Clidastes,* less so in *Tylosaurus,* and lower still in *Platecarpus.* Anteriorly, the height of the facet does not exceed its width in these three genera, although behind the dilated portion of the tail the facets become more compressed and take on a vertically oval shape. According to Martin (1953) the central articulations of an undistorted vertebral column of *M. conodon* are subtriangular at the base of the tail, changing gradually to a vertically oval outline on the thirteenth postsacral, to a circular outline on the twenty-seventh, and to a horizontally oval outline from thence to the end of the tail. The posteriormost caudal centra of *M. maximus* are unknown, but facets of those from more anterior caudal regions are similar to those of corresponding vertebrae in *M. conodon* (see YPM 430, 470). Except for a somewhat less depressed outline, central articulations in the tail of *Ectenosaurus* appear to be similar to those of *Platecarpus.* The central facet of a caudal of *Prognathodon* (Cope, 1875, p. 154), with transverse processes and facets for haemal arches, is subhexagonal in shape and equal in vertical and transverse dimensions. The radius of curvature of central facets decreases as the vertebrae diminish in size posteriorly but never becomes proportionally equal to that found in the presacral portion of the vertebral column.

The caudal centra decrease posteriorly in length but not at a uniform rate. In complete tails of *C. liodontus* (Williston and Case, 1892, pp. 23-24), *M. conodon* (Martin, 1953) and *Platecarpus* (YPM 1429) the centra in the pygal region decrease in length at a rate of about 3% per vertebra; further posteriorly the rate is reduced to about 1% per vertebra. It may fluctuate in the center of the tail but generally increases, and towards the terminal end the rate steadily increases to a maximum of about 5% per vertebra. In *Tylosaurus* (AMNH 221, Osborn's specimen; USNM 8898) the pattern is similar, although the rate of reduction of vertebrae in the preserved portion of the posterior half of the tail of the former specimen is rather low (about 1.5%). The pygal vertebrae of *Plotosaurus* diminish at a lower rate (less than 1% per vertebra) than do those of other mosasaurs, but further posteriorly rates are similar. It must be noted, however, that in no observed case were the rates of reduction regular enough to permit an estimation of the number of vertebrae missing in an incomplete tail.

The transverse processes of the pygal vertebrae are dorsoventrally compressed, narrow alae of bone. They are slightly more than twice as long as the synapophyses of the preceding dorsals in *Mosasaurus, Platecarpus* and *Tylosaurus* and are even more greatly elongated in *Clidastes, Amphekepubis* and *Ectenosaurus.* The transverse processes arise from the anterior portion of the ventrolateral edge of the pygal vertebrae and project ventrolaterally at an angle of about 40° from the horizontal in *Clidastes* and *M. maximus,* about 30° in *M. conodon, Platecarpus* and *Ectenosaurus,* and about 20° in *Tylosaurus.* In *Amphekepubis* they arise from the anteromedial portion of the lateral surface of the centrum and project laterally at an angle of about 10° to the horizontal. It is thus evident that the epaxial muscles were more powerfully developed at the base of the tail in mosasaurs than in *Varanus,* where the transverse processes project at right angles from the anterior caudal centra. In view of the fact that remnants of anterior zygopophyses are very small in the caudal region, it seems likely that the M. longissimus caudae was very much reduced in mosasaurs, as it is to some extent in *Varanus* (Ali, 1949, p. 165), and that the transversospinalis and especially the iliocostalis caudae systems made up the bulk of the epaxial musculature.

In the anterior three or four pygals of *M. conodon* (Martin, 1953), *Platecarpus* and *Tylosaurus,* the transverse processes have a distinct posterior inclination which is lost posteriorly where the processes meet the centra more or less consistently at right angles. On the lateral surface of the posterior pygal centra in *Platecarpus* and *Tylosaurus,* the transverse processes begin a gradual rise which culminates in a rudimentary process occupying an anteromedian position on the lateral surface of the last transverse process-bearing vertebra. In *M. conodon,* however, the transverse processes begin to rise on the 20th postsacral vertebra, thirteen vertebrae behind the end of the pygal series (Martin, 1953), and in *Plotosaurus tuckeri* they begin to rise on the 29th postsacral (last pygal). In *Varanus* the transverse processes are present to the end of the tail; in mosasaurs they are absent throughout the posterior half of the caudal series. The epaxial M. iliocostalis caudae and hypaxial equivalent of the thoracic obliquus system, the M. iliocaudalis (Nishi, 1938, p. 403), must have been powerfully developed only in the more anterior regions of the tail. The ventral surface of the transverse processes also served as part of the area of origin of the Mm. caudifemorales.

Chevrons are present along the entire post-pygal region of the tail in mosasaurs and rudimentary articulations or arches may be present on the last pygals. In the Plioplatecarpinae (except *Prognathodon overtoni* and *Dollosaurus)* and Tylosaurinae the haemal arches articulate with centrally pitted, slightly posterior-inclined peduncles which lie on either side of the ventral midline nearer to the posterior margin of the centrum than to the anterior. In the Mosasaurinae and in *Prognathodon overtoni* (Williston, 1898b, p. 192) and *Dollosaurus* (Iakovlev, 1901, pl. 5 fig. 5) the haemal arches are fused to the same region of the caudal centra. The chevrons are relatively longer in the Mosasaurinae than in other mosasaurs.

In *Clidastes* and *Mosasaurus* the haemal arch is subcircular in cross section and slopes ventromedially to meet its fellow from the opposite side. The lateral surface of the arch continues straight onto the lateral surface of the spine with little or no curving, giving the spine a transversely elliptical cross section at the base, a circular one near the middle, and a saggitally elliptical cross section at the apex. The anterior and posterior surface of the spines are longitudinally ribbed and grooved, and the distal end is truncated at right angles to the long axis of the spine and was covered by cartilage in life. The chevrons are more strongly posteriorly directed at the base than near the apex in both of these genera and in *Plotosaurus.* In *M. conodon* (Martin, 1953) the spines are vertical in the anterior region of the tail, slope more and more strongly posteriorly to meet the centrum, at an angle of 30° to the horizontal vertebral axis on postsacrals 27 to 57, and then resume a progressively more vertical position backwards to the end of the tail. In *Clidastes* the spines generally slope back at an angle of about 40° to the horizontal vertebral axis and show less regional variation in inclination. The spines increase in length from the anterior region of the tail to reach a maximum on postsacrals 36-41 in *C. liodontus* (Williston and Case, 1892, pp. 23-24) and on postsacrals 46-48 in *M. conodon* (Martin, 1953). In *C. sternbergi* (Wiman, 1920, pl. 3) they show no pronounced tendency to lengthen near the middle of the tail, but in all three species they diminish steadily in length from this point to the end of the tail. In *Plotosaurus* the haemal spines are well developed on the first chevron-bearing caudal, where they slope posteriorly at an angle of about 35° to the horizontal vertebral axis. They increase in length, becoming longest in the region of the 42-44th postsacral. Behind this region they diminish in length to the tip of tail and assume an inclination of 45°.

The base of each haemal arch is somewhat expanded in *Platecarpus, Ectenosaurus* and *Tylosaurus* and has a smooth proximal surface with a cone in its center to articulate with the pitted peduncle on the centrum. The haemal arches are more strongly medially inclined in *Platecarpus* and especially in *Tylosaurus,* so that the spines are relatively shorter and heavier than in the Mosasaurinae. The chevrons are straight in a transverse plane and point posteriorly at a rather uniform angle of about 40° throughout the caudal column of these two genera. In *Platecarpus* (Huene, 1911, pl. 3; YPM 1429) the chevrons show little variation in length back to the 50th postsacral, behind which they steadily diminish in length to the end of the tail. In *Tylosaurus* (AMNH 221, USNM 8898) they show a tendency to diminish in length back to the 36th postsacral, then increase slightly over a span of approximately seven vertebrae, and diminish again to the end of the tail. The caudal extension of the rectus system, the M. ischiocaudalis (Nishi, 1938, p. 403; Ali, 1949, p. 165), must have linked the entire chevron series together, while part of the Mm. caudifemorales originated on the more anterior haemal arches.

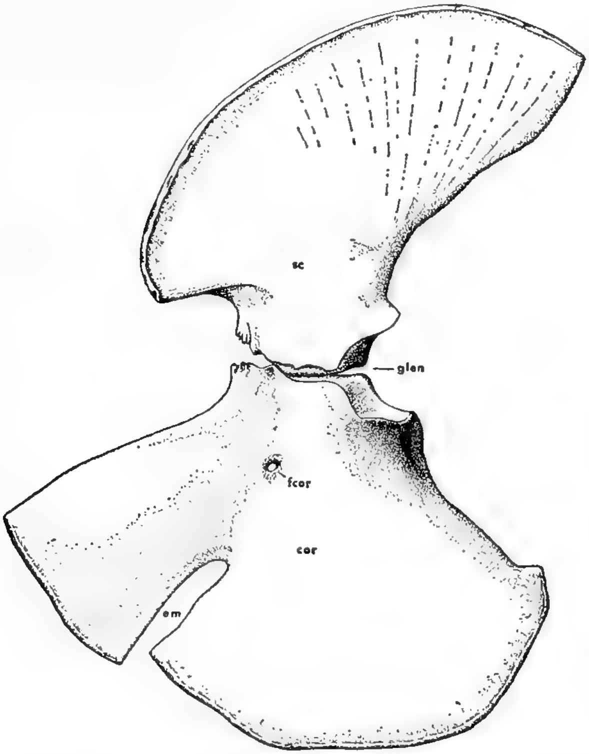
Pectoral Appendage

SCAPULA

The base of the mosasaur scapula is longitudinally elliptical in ventral aspect and is separated into a smaller anterointernal facet articulating with the coracoid and a larger posterolateral one forming the dorsal half of the glenoid fossa. The coracoid facet faces directly ventrally and has an unevenly pitted and grooved surface that was covered with cartilage in life. Inside and in front of it the scapula and coracoid are firmly united in an interdigitating suture in *Clidastes* and *M. conodon,* but not in *Platecarpus, Plioplatecarpus* and *Tylosaurus.* The smoothly concave glenoid fossa is indistinctly subdivided into lateroventrally and posteroventrally facing surfaces in *Clidastes, M. conodon* and

Ectenosaurus. In *Platecarpus* and *Plioplatecarpus* the glenoid articulation is a convex, ventroposteriorly facing condyle; in *Tylosaurus* it faces the same direction but is gently concave.

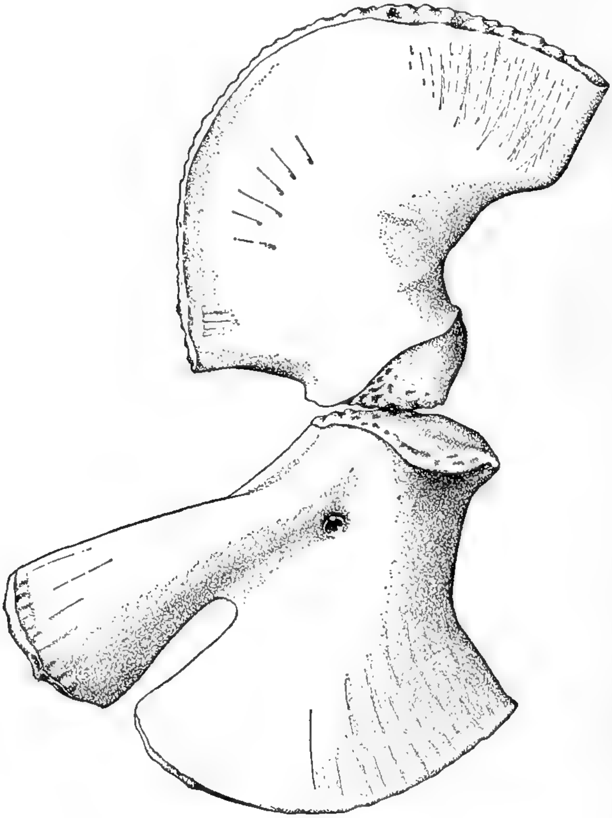
Immediately dorsal to its base the scapula is slightly constricted in all directions and in transverse section tapers to an abruptly truncated, moderately thick dorsal edge. In lateral aspect the scapula is expanded in both directions above this neck into an anterior-inclined, fan-like blade. The superior border of the scapula is gently convex in *Clidastes, M. conodon, Plotosaurus, Plioplatecarpus* and *Ectenosaurus* and is strongly convex in *Platecarpus, Plesiotylosaurus* and *Tylosaurus.* In *Clidastes, M. conodon, Platecarpus* and *Ectenosaurus* the anterior edge of the fan is short, straight and probably nearly horizontal; in *Plotosaurus* and *Plesiotylosaurus* it is relatively longer; and in *Plioplatecarpus* (Dollo, 1882, pl. 6 fig. 1) its length nearly equals that of the posterior border. The anterior edge is very short and ventrally recurved in *Tylosaurus.* In *Plioplatecarpus* (Dollo, 1882) the long posterior border of the scapular blade projects posterodorsally in a direct line. In *Platecarpus, Plioplatecarpus primaevus* and *Ectenosaurus,* and to a lesser extent in *Clidastes, M. conodon, Plotosaurus* and *Tylosaurus,* the anterior half or more of the posterior border is shallowly emarginated. External fibers of the M. serratus anterior superficialis may have inserted on the straight edge of the distal portion of the border. In *C. sternbergi* (Wiman, 1920, fig. 8) and *Plesiotylosaurus* the entire posterior border of the scapula is sulcate, and the M. serratus anterior superficialis may have shifted its insertion dorsally onto the



Text-fig. 43. Scapula-coracoid of *Clidastes liodontus* (YPM 1335, × 1). Abbreviations: cor, coracoid; em, coracoid emargination; fcor, coracoid foramen; glen, glenoid fossa; sc, scapula.

suprascapula. The M. scapulohumeralis posterior probably originated in part on the rounded edge of this emargination and in part above it on the posterodorsal edge of the lateral surface of the scapula and adjacent suprascapula.

Assuming the coracoid was approximately horizontal in life, the scapula lay in a dorsolaterally and anteromedially sloping plane. The blade of the scapula is flat in longitudinal and vertical directions in *Clidastes;* slightly concave externally and convex internally in a longitudinal direction and flat in a vertical direction in *Platecarpus;* convex externally and concave internally in a vertical direction and flat in a longitudinal direction in *Tylosaurus.* In a well preserved scapula of *Platecarpus* (YPM 24904) two short horizontal crests may be seen on the lateral surface of the scapula. The stronger one, representing the origin of the scapular head of the triceps, occurs near the base of the emargination on the posterior border of the scapula. The other one is situated near the center of the emargination and marks the attachment of the proximal end of the scapulohumeral ligament. The M. scapulohumeralis anterior probably arose on the anterior edge of the scapular neck and blade. Although its outline is unknown, a cartilaginous suprascapula was certainly present in mosasaurs. Because the dorsal rim of the scapula is widest posteriorly along its most elevated position, it may be assumed that the suprascapula was most extensively developed in this region. Important muscles supporting the pectoral arch (Mm. omohyoideus, levator scapulae superficialis, anteriorly; M. serratus anterior, internally; M.



Text-fig. 44. Scapula-coracoid of *Platecarpus* (YPM 24904, × 3/8).

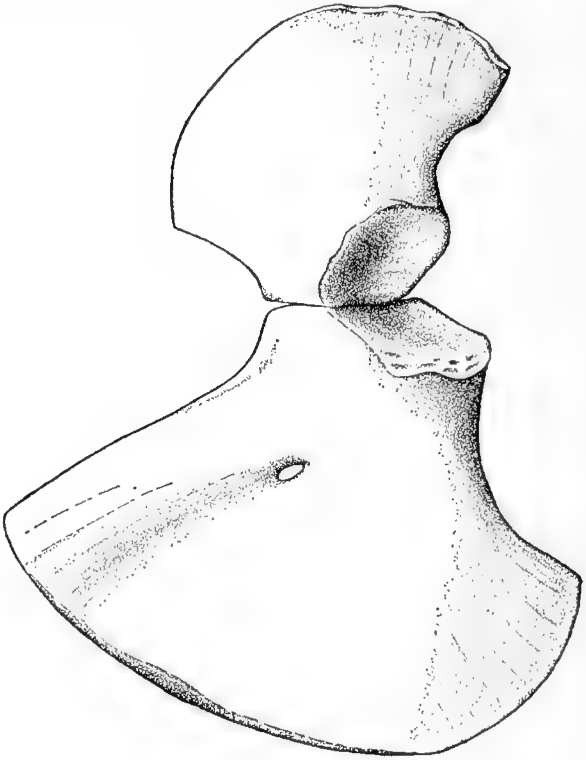
serratus anterior superficialis, posteriorly) insert on the suprascapula of *Varanus*. The scapular portion of the M. deltoides also arises on the lateral surface of the suprascapula in this genus.

The greatest vertical dimension of the scapula is generally slightly more than half the length of the humerus in *C. sternbergi* and *Tylosaurus,* nearly equal to it in *Clidastes, Platecarpus* and *Ectenosaurus,* and is almost twice the length of the humerus in *M. conodon, Plotosaurus,* and *Plioplatecarpus.* The scapula is much smaller than the coracoid in *C. sternbergi* and *Tylosaurus,* slightly smaller in *Clidastes* and *Ectenosaurus,* about equal to it in size in *M. conodon* and *Platecarpus,* and larger than the coracoid in *Plotosaurus* and *Plioplatecarpus.*

CORACOID

The scapular facet on the coracoid is essentially the mirror image of the coracoid facet on the scapula. The glenoid fossa is smoothly surfaced and slightly concave in *Clidastes, M. conodon* and *Tylosaurus;* pitted, grooved and convex in *Platecarpus;* and reduced and convex in *Plotosaurus* and *Plioplatecarpus* (Dollo, 1882, pl. 6 fig. 1). Just medial to the head of the coracoid is an anteriorly inclined neck region which is relatively short and broad in *Clidastes;* longer in *M. conodon* (Martin, 1953), *Platecarpus, Ectenosaurus* and *Tylosaurus;* and long and narrow in *Plotosaurus* and *Plioplatecarpus.* The coracoid thins in a transverse direction and expands anteroposteriorly into a fan-shaped structure as it approaches the ventral midline of the body. This fan is anteriorly elongated so that its anterior border exceeds the posterior border greatly in length in *Clidastes, Platecarpus* and *Plioplatecarpus,* and to a lesser extent in *M. conodon, Plotosaurus, Ectenosaurus* and *Tylosaurus.* Some fibers of the M. scapulohumeralis anterior probably extended along the anterior border of the coracoid, as they do in *Varanus.* The medial border of the coracoid fan encompasses about one-third of the circumference of a circle in *Platecarpus* and *Tylosaurus;* more than one-third in *Clidastes, M. conodon* (Martin, 1953), *Plotosaurus, Plioplatecarpus* and *Ectenosaurus;* and nearly one-half of the circumference in *C. sternbergi* (Wiman, 1920, fig. 8). The posterior tip of the coracoid fan expands broadly behind the glenoid articulation in *Clidastes* and *Plotosaurus;* expands only slightly behind it in *M. conodon, Plioplatecarpus* and *Ectenosaurus;* and does not reach its level in a transverse direction in *Platecarpus* and *Tylosaurus.* The M. coracobrachialis longus probably arose from the ventral surface of this fan.

As in *Varanus,* the ventral surfaces of the coracoid and of the extensive cartilaginous epicoracoid attached to its convex medial edge (see Osborn, 1899a, fig. 9), supplied a large area of origin for the pectoral limb adductor musculature. The M. coracobrachialis brevis probably arose from the broad posterior portion of the coracoid fan; the M. biceps brachii arose medial to it on the epicoracoid. The M. supracoracoideus must have been attached to the anteromedial region of the fan and broad anterior portion of the epicoracoid. Its nerve pierces the anterior region of the neck of the coracoid. Above the center of origin of the M. supracoracoideus the coracoid may be either thin or emarginate. In *C. sternbergi* (Wiman, 1920, fig. 8) and *C. liodontus* the coracoid is emarginate; in *C. propython* it appears to be entire. The coracoid is entire in two specimens of *M. conodon* (SDSM 452; Dollo, 1894, pl. 3) but not in the type (AMNH 1380). It is entire in *M. ivoensis* (Williston, 1902, p. 249). Goldfuss (1845, p. 195) states that the type of *M. missouriensis* may have an emarginate coracoid, though that of Williston's (1895, p. 167) specimen is "apparently not emarginate." The



Text-fig. 45. Scapula-coracoid of *Tylosaurus* (after Williston, 1898b, pl. 46, × 1/3).

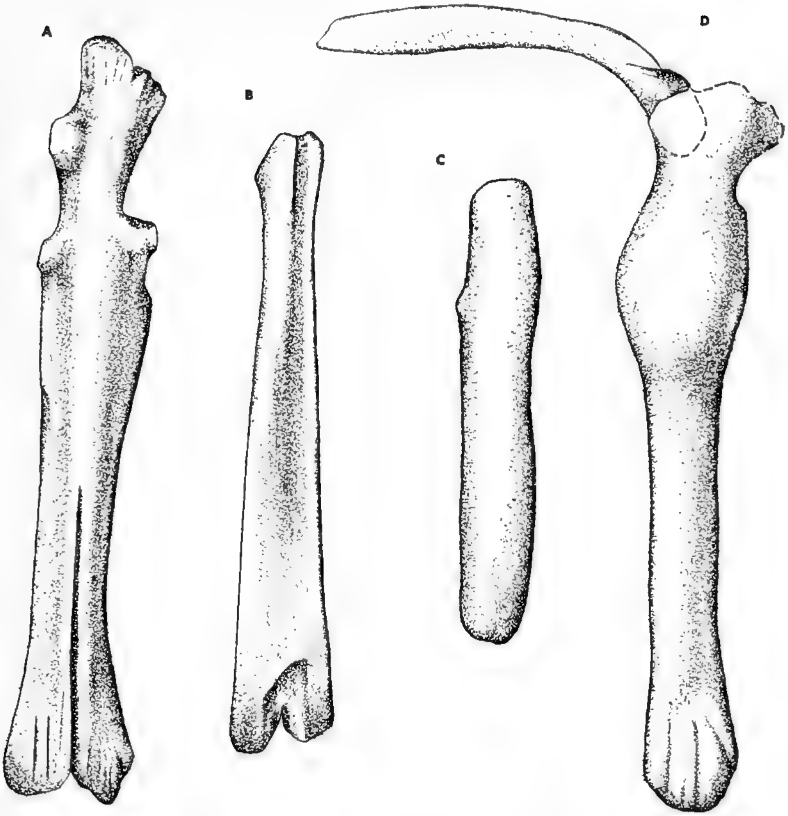
coracoid of *Plotosaurus tuckeri* is entire. In the two Niobrara species of *Platecarpus* the coracoid varies from deeply emarginate to lacking an emargination altogether. The coracoid of *Plioplatecarpus* (Dollo, 1882, pl. 6 fig. 1) is widely emarginate, that of *Ectenosaurus* (FHM 7937) is slightly notched, and that of *Prognathodon overtoni* is deeply emarginate (Williston, 1897a, p. 97). It is usually entire in *Tylosaurus,* but may be slightly notched. In any case the M. supracoracoideus must have been powerfully developed in mosasaurs. The M. subcoracoscapularis arises over nearly the entire medial surface of the scapulocoracoid in *Varanus,* although the M. sternocoracoideus does insert on the anterior rim of the epicoracoid. There is little reason to think these muscles were differently arranged in mosasaurs.

CLAVICLE

The clavicle is known only in *Plotosaurus* but articulations on the interclavicle show that it was present in several other forms as well. In *Plotosaurus* the bone is reminiscent of a jugal but is less sharply recurved. The M. deltoides clavicularis probably took its origin from the posteroventral surface.

INTERCLAVICLE

An interclavicle has been described in *C. propython* (Holland, 1908, fig. 5), *M. conodon* (ibid., figs. 1-4; Martin, 1953), *Plotosaurus bennisoni* (Camp, 1942, fig. 3), *Plotosaurus tuckeri* (ibid., fig. 9), *Platecarpus* (Williston, 1899; Capps, 1907, fig. 1) and in *Plioplatecarpus* (Dollo, 1885b, fig. 1).



Text-fig. 46. Ventral view of interclavicles of mosasaurs. A. *Mosasaurus conodon* (after Holland, 1908, fig. 2, × ⅓). B. *Clidastes propython* (after Holland, 1908, fig. 5, × ⅔). C. *Platecarpus* (after Capps, 1907, fig. 1, × 2⁄7). D. *Plotosaurus tuckeri* (after Camp, 1942, fig. 9, × ¼) with right clavicle.

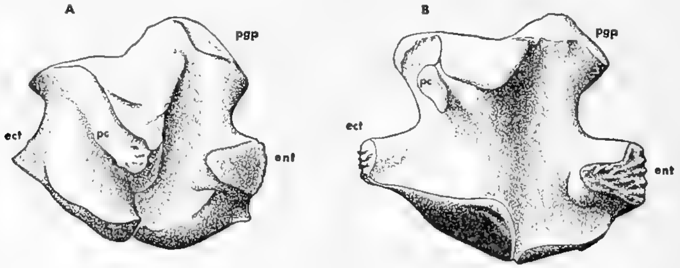
The interclavicle of *Clidastes* is a thin, flat element that tapers anteriorly to a slightly expanded termination. The posterior end is deeply notched medially and rather heavily longitudinally striated.

In *Mosasaurus conodon* the dorsal surface of the interclavicle is concave laterally and anteroposteriorly. The thin posterior end is expanded and medially notched. The bone continues anteriorly in a long blade which is interrupted near its anterior termination by a short lateral process from either side. The shaft then constricts and gives off two asymmetrically diverging processes for articulation with the clavicles. In *Plotosaurus* the interclavicle is oval in cross section and a swelling of the shaft occurs in the region of the lateral processes of *M. conodon,* but the bone is in other respects very similar to that of *M. conodon.* In *Platecarpus* the interclavicle is a simple flattened rod with a suggestion of a swelling near its anterior termination. Williston (in Holland, 1908, p. 163) states that facets for articulation with vestigial clavicles may be present. The interclavicle of *Plioplatecarpus* is probably similar to that of *Platecarpus,* but the swelling in the anterior portion of the shaft appears to be more distinct. The bone served as a line of origin for the M. pectoralis.

CARTILAGINOUS STRUCTURES IN PECTORAL REGION

Marsh (1880, p. 83, pl. 1 fig. 1) described an excellently preserved sternum of

Clidastes liodontus (YPM 1335, see also YPM 1333) as follows: "The sternum in this genus is narrow, and elongate in form, and nearly or quite symmetrical. . . It is thin, slightly concave above, and convex below. Its anterolateral margins are short and rounded and have distinct grooves for the coracoids. The costal margins are much longer and converge posteriorly. Each has facets for five sternal ribs. . ." Much less well preserved, but probably similar sterna also occur in *M. conodon* (Martin, 1953), *Plotosaurus tuckeri* (Camp, 1942, p. 14), *Platecarpus* (Williston, 1899, p. 40), *Ectenosaurus clidastoides* (FHM 7937) and *Tylosaurus proriger* (Osborn, 1899a, fig. 9).



Text-fig. 47. A. Flexor aspect of humerus of *Plotosaurus tuckeri* (after Camp, 1942, fig. 10, × 1/4). B. Same of humerus of *Mosasaurus conodon* (reconstructed after USNM 11904 and 18255, × 3/10). Abbreviations for text-figs. 47-49: ect, ectepicondyle; eg. ectepicondylar groove; ent, entepicondyle; ld, scar for M. latissimus dorsi; pc, pectoral crest; pgp, postglenoid process.

The sternal ribs are flattened, strap-like structures linking the anterior thoracic ribs to the sternum. As noted above, five such bands of cartilage are present on each side of the sternum of *Clidastes*. At least five pairs occur in *Platecarpus* (see Huene, 1911, pl. 3) and *Ectenosaurus* (FHM 7937), and according to Osborn (1899a, p. 180) there are ten in *Tylosaurus*. Only three pair of sternal ribs occur in *Varanus*.

The tracheal rings have been reported in two excellent skeletons taken from the Niobrara Chalk. Osborn (1899a, p. 181, fig. 8) noted that in *Tylosaurus* ". . . the trachea extends from below the axis, is unfortunately destroyed as far back as the fifth rib, and diverges into two bronchi just behind the coracoids." Similar tracheal structures were seen by Williston (1899, p. 39, pl. 12) in a specimen of *Platecarpus*.

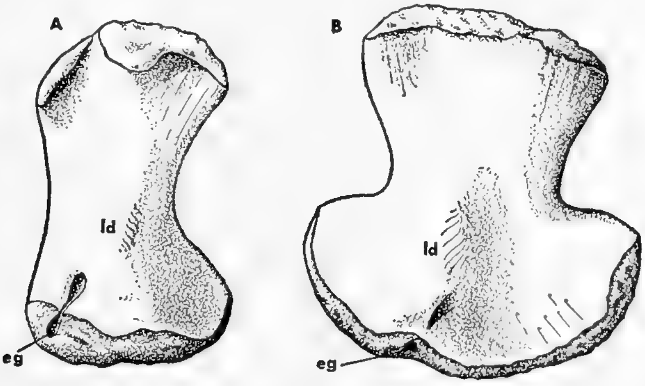
HUMERUS

The humerus of *Clidastes liodontus* and *C. propython* is a rectangular bone, longer than wide, and expanded at both ends. The glenoid articulating surface has its longest dimension and is convex in a dorsoventral direction. A tuberosity for the M. deltoideus lies in front of the glenoid condyle and is separated from it anteroventrally by a deep groove. The crest upon which the M. pectoralis inserted arises on the deltoid tuberosity and is directed posterolaterally across the ventral (flexor) surface of the humerus. As in *Varanus*, the M. supracoracoideus probably inserted along the posterior face of this crest; the M. coracobrachialis brevis was probably attached to the flat triangular area between the crest and the glenoid condyle; and the Mm. humeroradialis and brachialis inferior arose from the anterodistal face of the crest. Behind the glenoid condyle a large process projects medially to form the posterointernal corner of the humerus. The M. subcoracoscapularis inserted on its triangular apex and the M. scapulohumeralis posterior on its dorsal surface.

A distinct, posterolateral-oriented scar is present on the dorsal (extensor) surface of the humerus slightly distal to the constricted midregion of the bone. The M. latissimus dorsi must have inserted on this scar, which separated the origin of the medial and lateral head of the M. triceps humeralis, as in *Varanus.* The M. scapulohumeralis anterior probably inserted on the triangular surface of bone between the latissimus scar and the anterior and posterior corners of the glenoid condyle. The distal end of the humerus is divided into two flat vertical facets. The oval radial facet faces anterolaterally and meets the more compressed ulnar facet behind it at an angle of about 135°. A prominent, anterior-directed, radial tuberosity (ectepicondyle) probably provided the point of origin for highly tendonous, posterolateral-directed extensor musculature and for ligaments extending along the leading edge of the paddle. The ulnar tuberosity (entepicondyle) is very well developed and projects posteroventrally from the posterolateral corner of the humerus. It is capped by a triangular, ridged and grooved surface that probably anchored connective tissue which bound together the M. coracobrachialis longus, inserted on its medial surface, and the distal flexor muscles fanned out anterolaterally from its lateral surface.

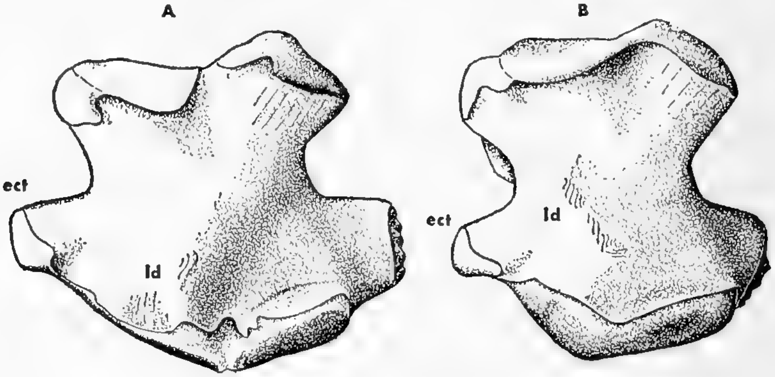
In *Mosasaurus ivoensis* (Williston, 1902, pl. 12), *M. conodon* and *M. missouriensis* (Williston, 1898b, p. 147) the pectoral crest occupies a more central position next to the anteroventral corner of the glenoid condyle. The M. supracoracoideus must have found a new insertion on the anterior surface of the humerus between the deltoid and pectoral crests. In *M. ivoensis* the humerus has the same proportions as that of *Clidastes liodontus* and *C. propython* but the postglenoid process is shorter and the radial process appears to be absent. The humerus is relatively shorter and wider in *M. missouriensis* (Williston, 1898b, pl. 32) and especially in *M. conodon.* All the tuberosities are well developed in these two species. In *Plotosaurus* the humerus is very short and broad. The pectoral ridge appears to be an extension of the ventral portion of the glenoid condyle onto the middle of the humerus. The radial tuberosity is very small. A peculiar prominence is developed on the dorsolateral surface of the humerus, possibly for the origin of the M. triceps humeralis.

In *Platecarpus* the crests and tuberosities on the humerus are not so distinctly developed as those in the members of the Mosasaurinae. At the proximal end of



Text-fig. 48. Extensor aspect of humerus of *Tylosaurus proriger* (YPM 4002, × 4/15). B. Same of humerus of *Platecarpus* (YPM 24904, × 1/3).

the bone, which was covered with a thick layer of cartilage in life, the postglenoid and deltoid processes are hardly differentiated from the glenoid condyle. The pectoral crest is situated in the middle of the proximoventral surface of the humerus, at the ventral termination of the glenoid condyle, and is widely separated from the deltoid tuberosity. The distal end of the humerus is much more expanded than the proximal end. The lateral surfaces of the radial tuberosity, the radial and ulnar facets, and the ulnar process are smoothly united in a half-circle and were also finished in cartilage. In this genus and in *Tylosaurus,* above the anterior portion of the radial facet is a small but deep groove on the dorsolateral edge of the humerus that may have contained the radial nerve. The humerus of *Ectenosaurus* is similar to that of *Platecarpus* but is less well expanded distally; in *Plioplatecarpus* (Dollo, 1882, pl. 6 fig. 1) it is shorter with a proximal end that is convex, instead of straight, in lateral profile. The humerus of *Plesiotylosaurus, Platecarpus* and *Ectenosaurus* has a broad, squarely truncated head. Although it is longer, with the the head more convex in lateral profile and the distal end less expanded, the humerus of *Prognathodon crassartus* (Cope, 1875, pl. 26 figs. 9a-d) shows a striking resemblance to that of *Platecarpus.* In *Prognathodon overtoni* (Williston, 1898b, pl. 30 fig. 6, pl. 62 fig. 1) the head of the humerus is more convex and the pectoral crest is evidently smaller and more anteriorly situated than in the former species.



Text-fig. 49. A. Extensor aspect of humerus of *Mosasaurus conodon* (USNM 11904, × ⅖). B. Same of humerus of *Clidastes* (YPM 24938, × ⅔).

The humerus of *Tylosaurus* is very long and slender and, compared to most other forms, only slightly expanded at the ends. The postglenoid process is small and indistinguishable from the glenoid condyle. All of these surfaces were finished in cartilage in life. On the distal end of the humerus the radial tuberosity is absent, the radial and ulnar facets are indistinct and were also finished in cartilage, and the ulnar tuberosity is very small. The humerus of *Clidastes sternbergi* (Wiman, 1920, fig. 8) appears to be quite similar to that of *Tylosaurus,* except for the presence of a well developed spherical glenoid condyle.

In *Clidastes liodontus* and *Mosasaurus conodon* the humerus exceeds an average anterior dorsal vertebra in length by about 1.25 times. In *Platecarpus, Ectenosaurus, Prognathodon* and *Tylosaurus* the ratio is approximately 1:1.80; in *Varanus* the humerus is about 4.5 times longer than an average anterior dorsal vertebra.

RADIUS

In *Clidastes liodontus* and *C. propython* the proximal end of the radius is thickened to fit onto the oval radial facet of the humerus. A prominence is developed on its dorsoanterior surface upon which the M. humeroradialis and part of the M. biceps brachii inserted. Distally, the radial shaft narrows and then spreads out into a wide fan. A slightly concave, teardrop-shaped facet for the radiale occupies its posterodistal edge. The thinner anterior border of the fan probably supported ligaments arising on the radial tuberosity of the humerus and passing laterally along the leading edge of the paddle. This portion of the fan is not so well developed in *C. sternbergi.*

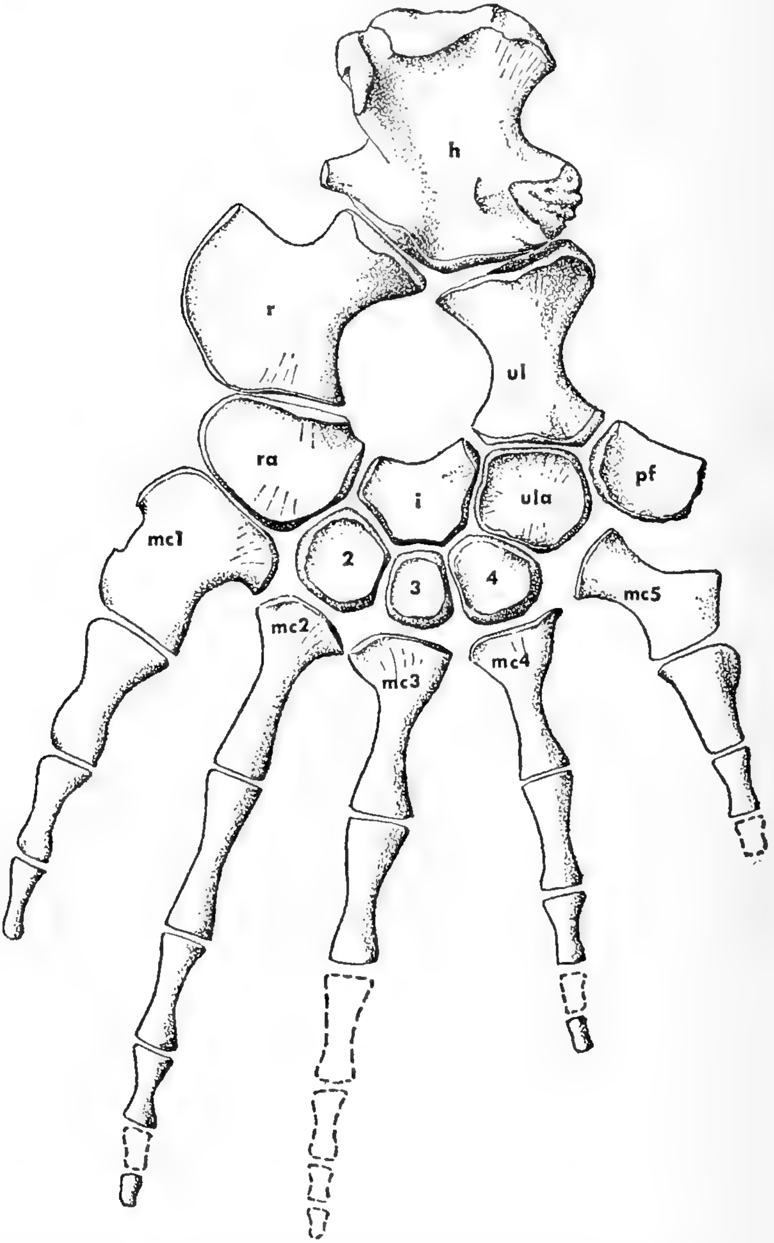
In *Mosasaurus ivoensis* (Williston, 1902, pl. 12 lower figure) the radius resembles that of *Clidastes* but is broader and the distal end is less dilated. The radius is heavy in *M. missouriensis* (Williston, 1898b, pl. 32) and in *M. conodon.* Compared to *Clidastes* the articulations for the humerus and radiale are proportionally much broader and more nearly parallel each other; the anterior flange is thin but large, extends further proximally over the radial shaft, and gives the element a more rectangular outline. The radius of *Plotosaurus* is similar to that of *M. conodon* but the anterior flange is much smaller.

In *Platecarpus* the shaft of the radius is wide and the element is expanded at both ends, distally more so than proximally. The articular surfaces are roughened and were doubtless completed in cartilage. The radius of *Plioplatecarpus* (Dollo, 1882, pl. 6 fig. 1) is identical to that of *Platecarpus* in general form, but is much more heavily proportioned. The proximal end of the radius of *Ectenosaurus* is not expanded, but the bone is otherwise also like that of *Platecarpus.* In *Prognathodon* (Cope, 1875, pl. 26, fig. 11) the radius is very short and broad, having an almost square outline. A similar radius figured by Cope (1869-1870, fig. 49, p. 205) that may belong to *Prognathodon rapax* has a well developed facet on the posterodistal edge of the bone. Perhaps this was for articulation with the ulna. The radius of *Tylosaurus* is long and slender and has a very small anterior flange.

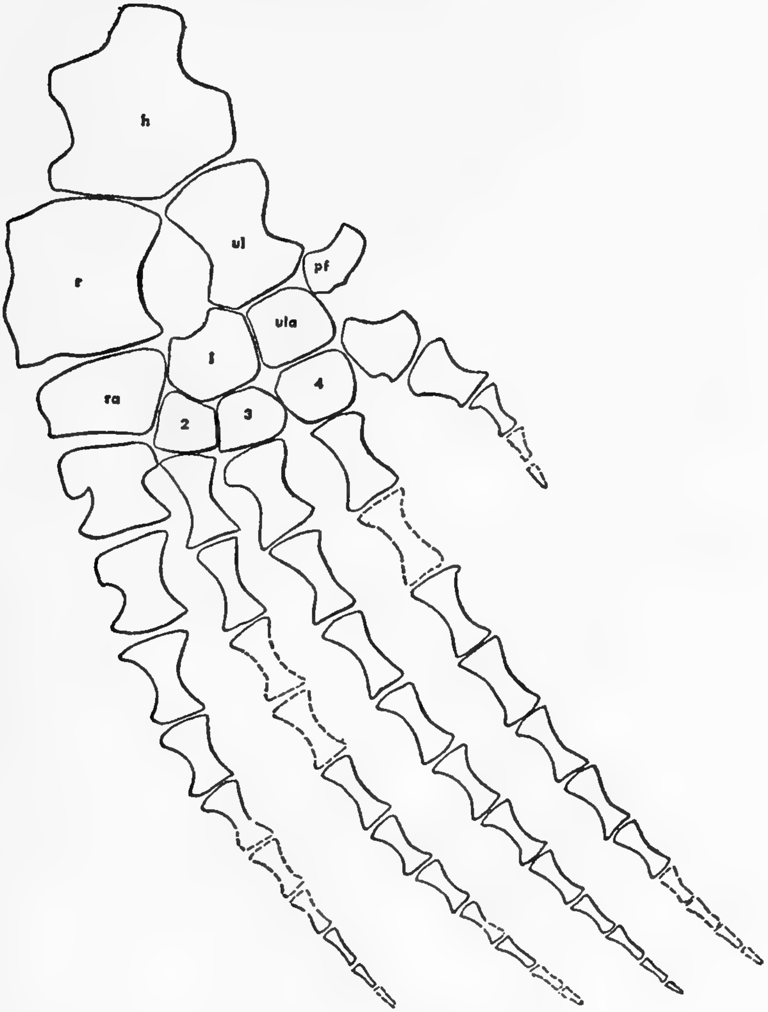
ULNA

The ulna is approximately hour-glass shaped in *Clidastes liodontus* and *C. propython* although the symmetry of the proximal end is broken by an anterolateral-inclined humeral articulation and the presence of a relatively well-formed olecranon process. The M. triceps probably inserted in large part upon this process, but a scarred area lying in front of it suggests that a portion of the muscle inserted further anteriorly. The M. brachialis inferior and part of the M. biceps brachii were probably attached to the ventral surface of the ulnar head. A large median facet for the ulnare, bordered by a small one anteriorly for the intermedium and by another posteriorly for the pisiform, occupied the distal end of the ulna. The M. pronator profundus and part of the M. flexor palmaris profundus probably arose from the anterior border of the ulna. The radius and ulna enclose a circular antebrachial foramen in *Clidastes,* through which the median nerve passed to the flexor muscles of the forearm. The ulna is essentially similar in *Mosasaurus conodon* and *M. missouriensis* (Williston, 1898b, pl. 32), but its distal end is more expanded in *Plotosaurus.* In all three of the latter forms the antebrachial foramen is more elliptical than in *Clidastes.*

The ulna of *Platecarpus* has a wider shaft than that of *Clidastes* and lacks a facet anterodistally for the intermedium. In *Ectenosaurus* the distal end is more greatly expanded than the proximal, in contrast to all of the foregoing genera. In this form and in *Platecarpus* the antebrachial foramen is nearly circular. The ulna of *Plioplatecarpus* (Dollo, 1882, pl. 6 fig. 1) is evidently rather



Text-fig. 50. Flexor aspect of forelimb of *Clidastes* (YPM 24938, × 8/15, phalanges and metacarpal five after Marsh, 1880, pl. 1 fig. 1). Abbreviations for text-figs. 50-51, 53-55: h, humerus; i, intermedium; mc 1-5, metacarpals 1-5; pf, pisiform; r, radius; ra, radiale; ul, ulna; ula, ulnare; 1-4, distal carpals 1-4.

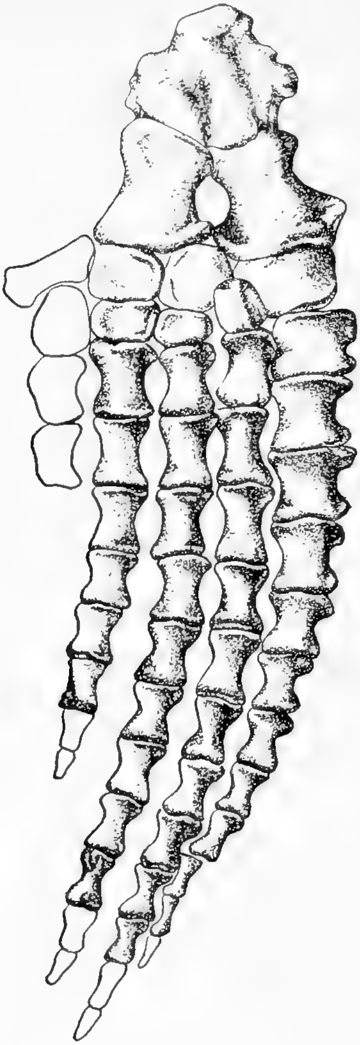


Text-fig. 51. Forelimb of *Mosasaurus conodon* (after Martin, 1953, × ½).

peculiar because both the olecranon process and posterodistal portion of the bone are reduced, giving it a bowed appearance. The antebrachial foramen is circular and very small. In *Tylosaurus* and *Clidastes sternbergi* the long slender ulna is hardly expanded distally, although the olecranon process is well developed. The antebrachial foramen in both forms is lenticular.

CARPUS

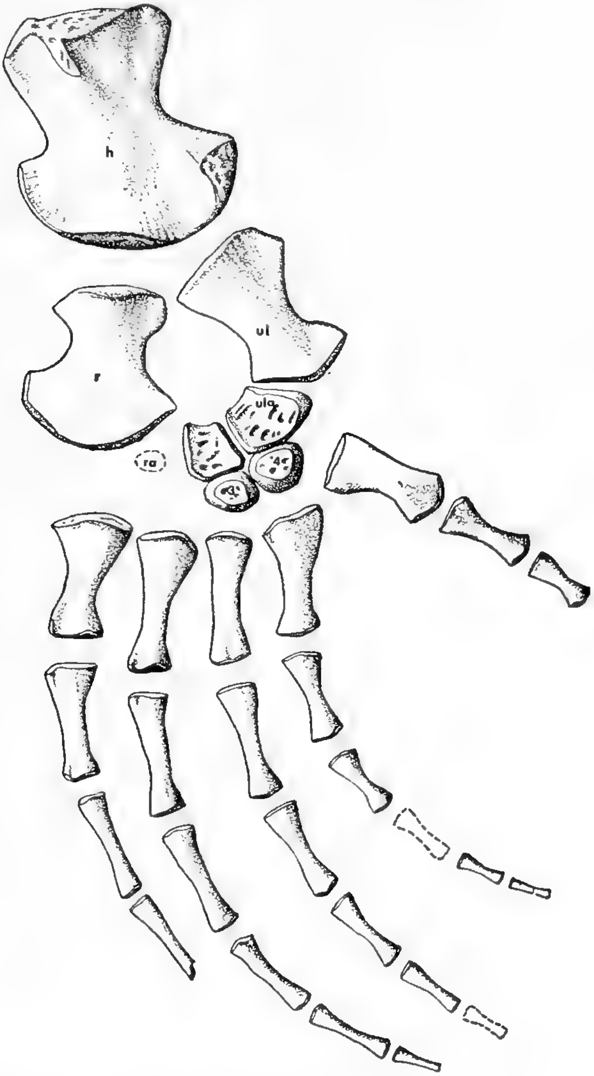
The carpal elements are very similar in *Clidastes liodontus, C. propython, Mosasaurus conodon* and *M. missouriensis,* and their general shape may be easily seen from the figures. The radiale is especially wide and a well-ossified intermedium and ulnare, as well as a second, third and fourth distal carpal, are present. In both genera the intermedium enters broadly into the antebrachial foramen and in *Clidastes* the radiale may also border on it. The carpal elements are quite heavy where they meet the radius-ulna, but decrease to half this thickness at their metacarpal articulations. A thin, kidney-shaped pisiform contacts



Text-fig. 52. Extensor aspect of forelimb of *Plotosaurus tuckeri* (after Camp, 1942, fig. 10, × ⅙).

the ulna and ulnare. All articulations are abruptly squared off, and the flexor and extensor surfaces of the elements are nearly identical. The carpus of *Plotosaurus* is similar, but the intermedium is excluded from the antebrachial foramen by the radius and ulna. The carpal elements of the type skeleton of *C. sternbergi* are somewhat scattered and cannot be surely identified.

In *Platecarpus*, by comparison to the above, the carpus is much less well ossified. Usually only the ulnare, intermedium, and third and fourth distal carpal are present, although occasionally small osslets may be preserved in the positions of the radiale and second distal carpal. Unlike the condition in the Mosasaurinae both the intermedium and ulnare enter equally into the distal border of the antebrachial foramen. The individual carpals are of about uniform thickness. The edges are irregularly surfaced and were continued in cartilage; the flexor and extensor surfaces are more heavily pitted than in the Mosasaurinae. The carpus of *Ectenosaurus* is generally very similar to that of *Platecarpus* but is

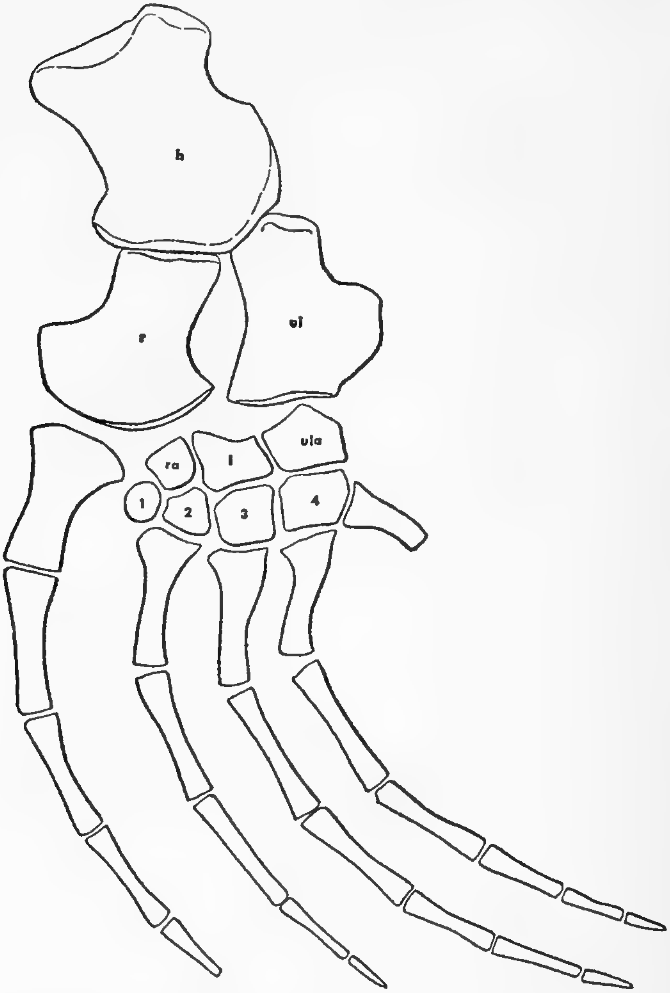


Text-fig. 53. Flexor aspect of forelimb of *Platecarpus* (YPM 1426, × ¼).

more completely ossified, for a small radiale and a first and second distal carpal are also present. The four larger elements, the ulnare, intermedium, third and fourth distal carpal are subequal and broader than those of *Platecarpus*. Only an ulnare (?) and osslet in the position of the fourth distal carpal are present in *Tylosaurus*.

METACARPALS AND PHALANGES

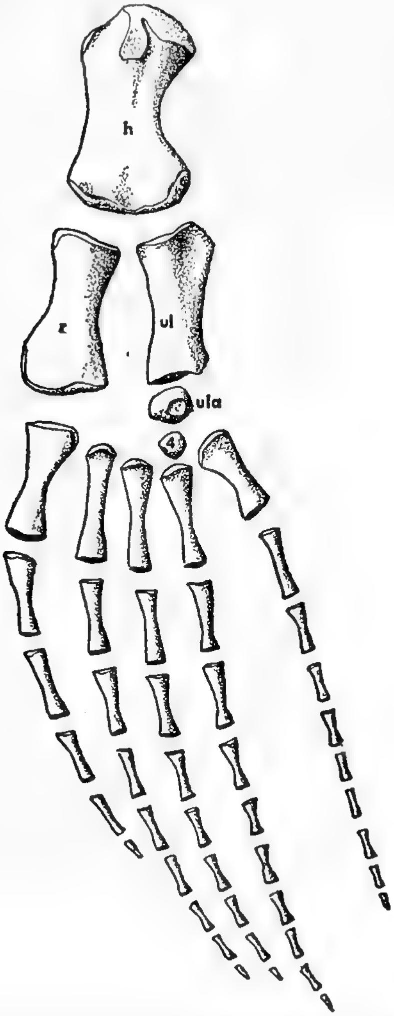
The outlines of the metacarpals and phalanges of the various genera of mosasaurs are well illustrated in the text-figures. Clawed terminal phalanges are uniformly absent. In *Clidastes* the metacarpals and phalanges are flattened and diminish gradually in thickness distally. The articular surfaces are sharply truncated and lie at right angles to the longitudinal axes of the bones. There appears to have been very little cartilage intervening between the successive



Text-fig. 54. Extensor aspect of forelimb of *Ectenosaurus clidastoides* (FHM 7937, × 1/4, from a photograph, courtesy of Myrl Walker).

phalanges. The phalangeal formula of *Clidastes* is not known but may have been approximately 4-5-5-5-3. The fingers are relatively short for a mosasaur and are broadly spaced. The metacarpals and phalanges of *Mosasaurs conodon* are short and wide, but the digits contain a greater number of elements (the phalangeal formula is about 9-10-10-10-4) so that the forepaddle is relatively longer than in *Clidastes*. The digits also appear to be more closely adpressed (see Dollo, 1894, pl. 3). In *Plotosaurus* the multiplication of phalanges is comparable (at least 10-10-10-7-2) to that of *M. conodon* and the digits are likewise adpressed to form a longipinnate paddle.

Because of the more highly divaricate fifth finger the foreflipper of *Platecarpus* appears to be somewhat broader than that of *Clidastes*. The metacarpals and phalanges tend to be more hour-glass shaped in vertical and horizontal aspect, rather than flattened, and the phalanges sweep strongly to the rear. The ends of the phalanges are roughened and were finished in cartilage. The distal portion of the foreflipper of *Ectenosaurus* resembles that of *Platecarpus* more



Text-fig. 55. Flexor aspect of forelimb of *Tylosaurus proriger* (YPM 4002, × 1/6; phalanges after Osborn, 1899a, fig. 9).

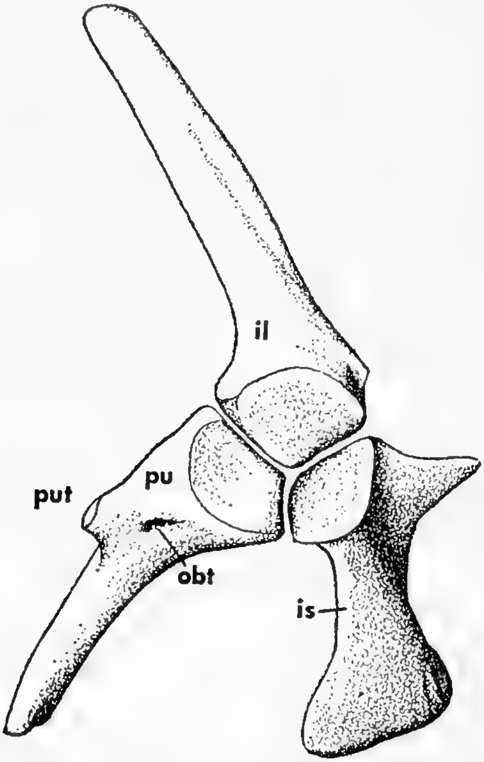
closely than those of the Mosasaurinae. The phalangeal formula of *Platecarpus* is approximately 4-6-7-5-3, that of *Ectenosaurus* is 4-4-5-5-(?).

The digits of the foreflipper of *Tylosaurus* are more compressed than those of *Platecarpus* but less so than in *Mosasaurus conodon* and *Plotosaurus*. The fifth digit is only slightly divaricate (see Williston, 1898b, pl. 48) and the remaining digits sweep only slightly to the rear distally. Proximally the phalanges are longer, slenderer and slightly flatter than those of *Platecarpus* but the ends were similarly terminated in cartilage. The more distal phalanges are relatively quite broad and flat. The phalangeal formula probably varies between 5-7-9-10-11 and 5-8-8-9-9.

Pelvic Appendage

PELVIC GIRDLE

When the elements of a beautifully undistorted inominate girdle of *Mosasaurus conodon* (USNM 11396) are articulated, several interesting features



Text-fig. 56. Lateral view of pelvic girdle of *Mosasaurus conodon* (USNM 11396, × about ⅓) with the elements in natural articulation. Abbreviations: il, ilium; is, ischium; ist, ischiadic tubercle; obt, obturator foramen; pu, pubis; put, pubic tubercle.

are apparent. The beveled edges of their symphyseal shafts indicate that the ischia and pubes of opposite sides met on the ventral midline of the body with a relatively minor amount of intervening cartilage and were oriented in a transverse plane at an angle of about 30° to the horizontal. The pubic shaft is twisted so that its leading edge is rotated ventrally. Because it is longer than the ischiadic shaft, the acetabulum assumes a posterolateral inclination. The symphyseal shaft of the ischium was depressed anteriorly in life, and has a posterodorsally turned ischiadic process. In this specimen the three pelvic elements were closely united by connective tissue to form an imperforate acetabulum. Facets on the pubis and ischium indicate that the shaft of the ilium was vertical in a transverse plane and anteriorly inclined at an angle of about 60° to the horizontal in lateral aspect.

ILIUM

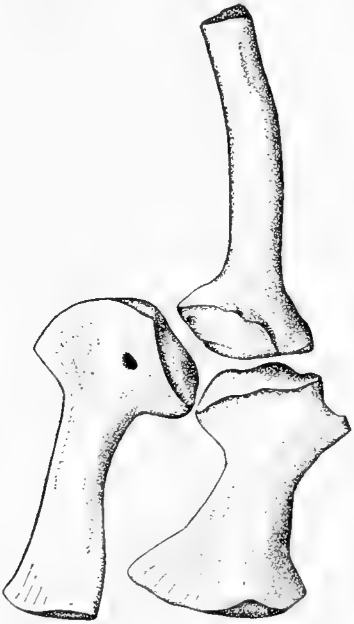
The ilium is a slender, club-shaped bone in mosasaurs. Its ventral end is expanded and, in *Clidastes* and *Mosasaurus conodon,* divided into a ventral facet for the ischium, an anteroventral one for the pubis, and a broad, concave, lateral facet for the acetabulum. These facets are very much less distinct in *Amphekepubis* (Mehl, 1930, pl. 65 figs. 2-3), *Platecarpus* and *Tylosaurus.* In *M. conodon, Amphekepubis* (Mehl, 1930) and *Platecarpus* there is a distinct scar on the posterior surface of the ventral end, possibly for the attachment of a portion of the M. iliocaudalis.

The ilium is constricted into a long, slightly anterior-inclined shaft immediately above the acetabular facet. The shaft is straight in *Tylosaurus,* but the distal end curves more directly upward in *Clidastes, M. conodon, Amphekepubis* (Mehl, 1930), and is short and nearly straight in *Platecarpus.* The shaft is elliptical in anteroposterior cross section and was probably suspended between the vertical sheet of the M. supracostalis anteriorly and that of the M. iliocaudalis posteriorly. The ilioischiadic ligament probably inserted somewhere near the center of the posterior border, as it does in *Varanus.* Origins of the Mm. iliofibularis, iliofemoralis and iliotibialis were probably compressed into the posterior, central and anterior portions, respectively, of the ventrolateral region of the shaft. The iliopubic ligament must have inserted somewhere near the ventral end of the anterior edge. The distal end of the iliac shaft is abruptly truncated in *Clidastes, M. conodon, Platecarpus* and *Tylosaurus* and was probably attached by ligaments to the transverse process of the first pygal (sacral) vertebra. In *Amphekepubis* the ilium seems to have tapered to a point distally.

PUBIS

The pubis is approximately the mirror image of the ischium in shape, although it is longer and more strongly directed anteromedially. In *Clidastes* and *Mosasaurus conodon* the head of the pubis is divided into three subequal facets, a dorsoposterior one for the ilium, a posterior one for the ischium and a concave acetabular facet laterally. As in the other pelvic elements these facets are only indistinctly separated in *Amphekepubis* (Mehl, 1930, pl. 65 fig. 1), *Platecarpus* and *Tylosaurus.* Just medial to the head, the body of the pubis constricts in an anterolateral-posteromedial direction and then curves more directly medially into a long spatulate shaft.

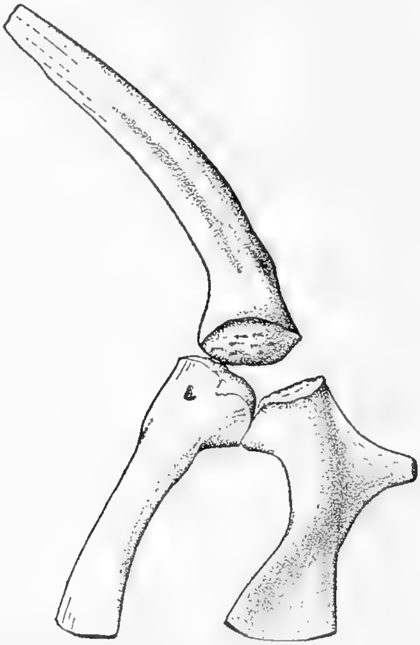
In many mosasaurs a stout process arises from the anterior border of the pubis near the head and projects anterolaterally at right angles to the shaft.



Text-fig. 57. Lateral view of pelvic girdle of *Platecarpus* (after Capps, 1907, fig. 2, × ¼) with the elements lying in a flat plane.

In *Clidastes liodontus* and *C. propython* this process is large and rectangular. In *M. conodon* it is smaller and triangular; in *Amphekepubis* (Mehl, 1930) it is developed into an enormous process that rivals the pubic shaft in length. The pubic process is located relatively closer to the head in *Platecarpus* than in the above forms and is small, triangular and slightly recurved laterally. In *C. sternbergi* (Wiman, 1920, fig. 9) and *Tylosaurus* the process is represented by only a small ala of bone on the head of the pubis just in front of the iliac facet. The puboischiadic and iliopubic ligaments, as well as part of the M. supracostalis, attach to the distal end of the process in *Varanus,* and probably did also in mosasaurs. The M. pubotibialis may have arisen on the dorsal portion of the base of the process, and the M. ambiens probably arose from the dorsal border of the pubis nearer to the acetabulum.

The obturator foramen pierces the pubis between the forks of the pubic process and shaft in the center of the acetabular region of the pubis in *M. conodon* and *Platecarpus;* in *C. liodontus, C. propython* and *Amphekepubis* it lies closer to the acetabular rim. In *C. sternbergi* (Wiman, 1920, fig. 9) and *Tylosaurus,* where the process is rudimentary, the foramen lies closer to the anterior margin of the pubis in this region. The foramen transmits the obturator nerve which passes laterally to enervate much of the ventral musculature of the thigh (Romer, 1942, p. 260). The shaft of the pubis expands medially to about double its width at the base of the pubic process in *Clidastes, M. conodon* and *Platecarpus,* but in *Amphekepubis* (Mehl, 1930, pl. 65 fig. 1) and *Tylosaurus* its medial end is hardly expanded at all. In *M. conodon* the anterior rim of the pubic shaft is twisted ventrally. The M. puboischiofemoralis internus probably arose on the anterodorsal surface of the pubis behind this rim, and the M. puboischiofemoralis externus may have attached to its ventral surface.



Text-fig. 58. Lateral view of pelvic girdle of *Tylosaurus* (after Williston, 1898b, pl. 41 fig. 1, × about 3/10) with the elements lying in a flat plane.

ISCHIUM

The shaft of the ischium is "A"-shaped in ventral aspect, with its base on the ventral midline of the body and its apex in the constricted portion of the shaft, just medial to the expanded, anterolaterally inclined head.

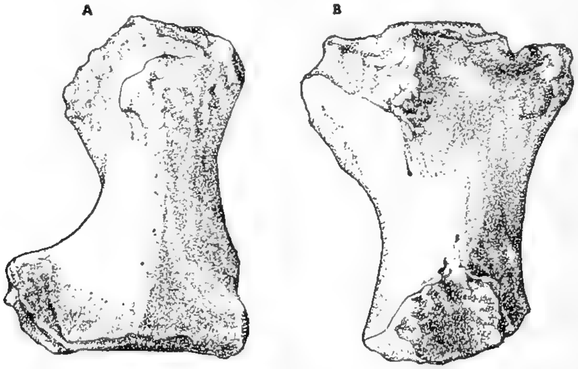
In *Clidastes liodontus, C. propython* and *Mosasaurus conodon* the head of the ischium is divided into three distinct facets, a large dorsolateral one for articulation with the ilium, a small anterior one for the pubis, and a small, lateral-directed segment of the acetabulum. These facets are less distinct in *Amphekepubis* (Mehl, 1930, pl. 65 figs. 4-5) and are absent on the pitted articular surface of the head in *Platecarpus* and *Tylosaurus.*

Medial to the head the shaft of the ischium is vertically elliptical in cross-section and constricted anteroposteriorly in *M. conodon* and *Amphekepubis* (Mehl, 1930). The shaft is narrow in this region in *C. liodontus* and *C. propython,* broader in *C. sternbergi* and *Tylosaurus,* and very broad in *Platecarpus.* The shaft thins vertically and expands anteroposteriorly toward the midline of the body in *Clidastes, M. conodon* and *Amphekepubis* (Mehl, 1930), is more expanded in *Tylosaurus,* and particularly expanded in an anteromedial direction in *Platecarpus.* The ventral surface of the medial portion of the ischium is longitudinally concave in *Clidastes, Platecarpus* and *Tylosaurus,* and flat in *M. conodon* and *Amphekepubis* (Mehl, 1930). The M. puboischiofemoralis externus arose largely from this surface, and the puboischiadic ligament probably arose from the raphe beneath the ischiadic symphasis.

A low, rounded crest runs the length of the medial portion of the dorsal surface of the ischium. At the midline of the body it is beveled off in a vertical plane which meets the long axis of the ischial shaft at an angle of about 60°. The M. puboischiofemoralis internus probably arose along that portion of the dorsal surface anterior to the center of this crest; the M. ischiotrochantericus probably arose behind it. The ischiadic tubercle projects directly posteriorly from the dorsal surface of the shaft. It is separated from the head of the ischium by a short neck in *Clidastes, M. conodon, Amphekepubis* (Mehl, 1930) and *Platecarpus,* and by a much longer neck in *Tylosaurus.* The tubercle is well developed in mosasaurs and served as the point of origin for the tendon of the M. ischiocaudalis and as a point of attachment for the puboischiadic-ilioischiadic ligament.

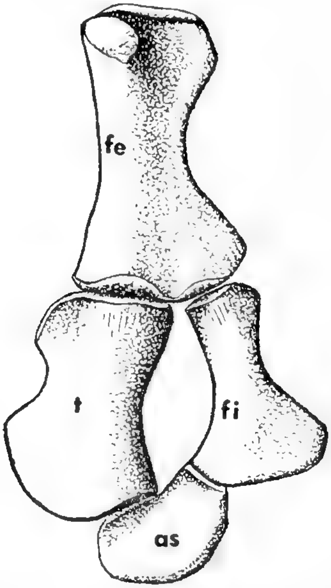
FEMUR

The femur in *Clidastes liodontus* and *C. propython* is a dumbbell-shaped bone, expanded at both ends and constricted along the central portion of the shaft. The head of the femur is probably horizontally oval in uncrushed specimens. A small, internal trochanter lies at the anteroventral corner of the proximal end of the bone, its cartilage-capped apex separated only by a narrow groove from that of the femoral head. As in *Varanus,* the M. puboischiofemoralis externus probably inserted behind the apex of the trochanter, and the M. caudifemoralis was probably attached to the more distal region of the trochanteric crest. The M. puboischiofemoralis internus must have inserted fleshily onto the smooth proximodorsal surface of the femur, with the M. iliofemoralis inserting just lateral to it. The M. adductor femoris probably inserted on the medial portion of the smooth ventral surface of the shaft. The distal end of the femur is abruptly truncated by two smooth vertical facets, anteriorly a larger lateral-facing one for the tibia and posteriorly a smaller posterolateral-facing one for the fibula. A small tuberosity is present above the anterior portion of the tibial facet which may have served as a point of attachment for ligaments extending along the leading edge of the hind paddle. The M. femorotibialis probably originated on the dorsal surface of the distal end of the femur. The femur is slenderer and provided with a well-developed, spherical head in *C. sternbergi* (Wiman, 1920, fig. 9) but is evidently otherwise similar.

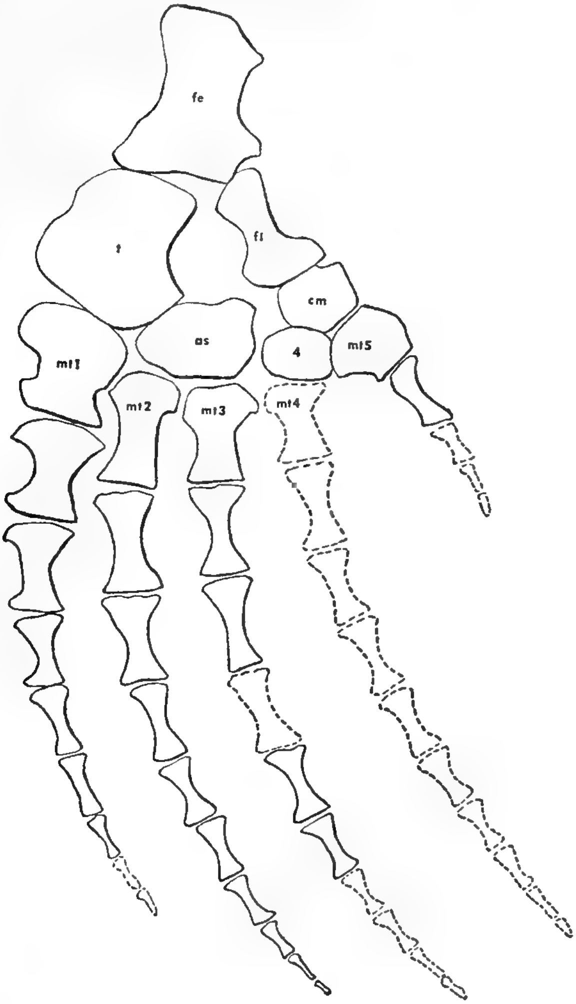


Text-fig. 59. Femur of *Mosasaurus hoffmanni* (after a cast of the type specimen in the Peabody Museum at Yale, × ⅓). A. Ventral view. B. Posterior view.

In *Amphekepubis* (Mehl, 1930, pl. 66 fig. 1, pl. 67 figs. 1-2) the shaft of the femur is very slender. The internal trochanter is rather large and located on the proximoventral surface of the femur medial to the head, with the result that the long axis of the proximal end of the femur lies at right angles to that of the distal end. The femur is more massive in *M. conodon* than in *Clidastes* and *Amphekepubis*. A plaster cast of the type of *M. hoffmanni* (=?*M. maximus*) shows that the femur in this species is more expanded in a vertical direction



Text-fig. 60. Hind limb of *Clidastes liodontus* (after Williston, 1898b, pl. 34, × ⅔), ventral aspect. Abbreviations for figs. 60-63: as, astragulus; cm, calcaneum; fe, femur; fi, fibula; mt 1-5, metatarsals 1-5; t, tibia; 4, fourth distal tarsal.



Text-fig. 61. Hind limb of *Mosasaurus conodon* (after Martin, 1953, × about ⅓).

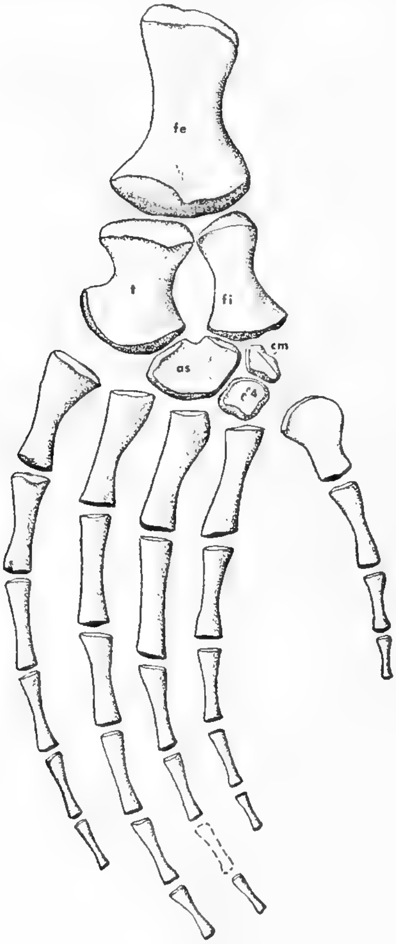
proximally, but less horizontally expanded distally, than that of *M. conodon.* A very large internal trochanter is situated directly beneath the head of the femur. The proximodorsal surface of the femur is developed into a median longitudinal crest in *M. hoffmanni.*

In *Platecarpus, Prognathodon* and *Tylosaurus* the articular ends of the femur are irregularly ridged and grooved, indicating the existence of a thick cartilage cover in life. The tibial and fibular facets are fused into a continuous surface distally, although the region of the tibial articulation is always thicker dorsoventrally. In *Platecarpus,* and especially in *Tylosaurus,* the distal end of the femur is more expanded in a horizontal plane than is the proximal end. The internal trochanter is of average proportions and situated on the anteroventral edge of the proximal portion of the femur in both genera. In *Prognathodon* (Cope, 1875, pl. 26 figs. 10a-d) the proximal and distal ends are about equally expanded in a horizontal plane, and the internal trochanter is moderately large and located in the center of the proximoventral surface of the femur.

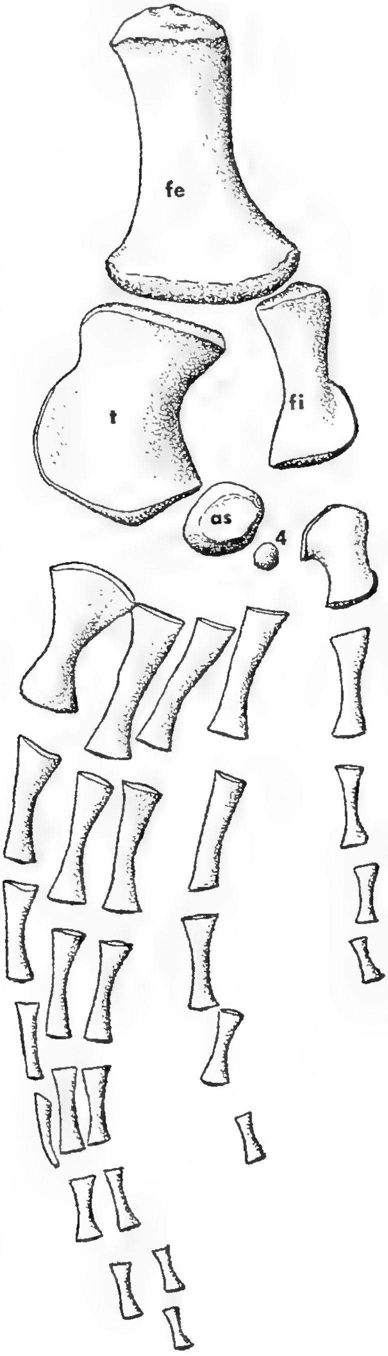
In *Varanus, Clidastes, M. conodon, Platecarpus* and *Tylosaurus* the femur is approximately equal to the humerus in length; in *Prognathodon* (Cope, 1875, pl. 26 figs. 9-10) it is about 25% shorter.

TIBIA

The tibia in *Clidastes* (Williston, 1898b, pls. 34, 36) is a flattened, rectangular element which is somewhat constricted medially. The ventral portion of the bone adjacent to the femur is longitudinally striated for the insertions of the Mm. pubotibialis, puboischiotibialis and flexor tibialis. The opposite surface is similarly roughened for the attachments of the Mm. ambiens, femorotibialis and iliotibialis. An anterior flange is incipiently developed on the anterior rim of the tibia in *Clidastes* (not in *C. sternbergi,* however, see Wiman, 1920, fig. 9) but it is emarginated opposite the central portion of the shaft. This structure probably anchored ligaments supporting the leading edge of the hind paddle. A clearly defined astragular facet is present posteriorly on the distal articular



Text-fig. 62. Hind limb of *Platecarpus* (after Capps, 1907, fig. 3, × ⅕).



Text-fig. 63. Hind limb of *Tylosaurus proriger* (after Osborn, 1899a, fig. 12, × ⅕).

surface. The tibia of *Amphekepubis* (Mehl, 1930, pl. 66 fig. 2) is nearly identical to that of *Clidastes*. The tibia of *Mosasaurus conodon* is also similar, but the anterior flange is larger, only slightly emarginate, and the astragular facet slopes more strongly posteromedially.

In vertical aspect the tibia of *Platecarpus* is rather dumbbell-shaped. The distal and proximal ends are about equally expanded, but may be distinguished in that the distal end is slightly wider and thinner. The articular surfaces are irregular and were finished in cartilage. The anterior flange of the tibia is characteristically expanded to give the bone a more rectangular appearance in *Tylosaurus*, otherwise the tibia is similar to that of *Platecarpus*.

FIBULA

The fibula of *Clidastes* (Williston, 1898b, pls. 34, 36) is a slender, bell-shaped bone. Its thickened and slightly expanded proximal end served as the site of insertion of the M. iliofibularis dorsally. The M. pronator profundus probably arose from the anterior surface of the fan-shaped, distal end. The tibia and fibula enclose a lenticular crural foramen. The fibula is heavier in *Mosasaurus conodon* and its proximal end is more greatly expanded. The crural foramen is proportionally somewhat wider than in *Clidastes*. The proximal end of the fibula in *Platecarpus* is only slightly less expanded than the distal end, giving the bone an hour-glass shaped outline. The posterodistal flange is more heavily developed in *Tylosaurus* and the distal half of the fibula is not so symmetrical as in *Platecarpus*. In both these genera the crural foramen is lenticular.

PES

Only three tarsal elements are known to be present in the pes of mosasaurs. These include a large astragulus, a slightly smaller calcaneum (absent in *Tylosaurus*), and a fourth distal tarsal. The astragulus of *Clidastes, Mosasaurus conodon* and *Amphekepubis* (Mehl, 1930, pl. 67 fig. 5) is broad with the fibular facet located on a short, medial-directed peduncle. The astragulus of *Platecarpus* is nearly circular and has a small emargination proximally for the crural foramen. This emargination is reduced to a slight notch or is altogether absent in *Tylosaurus*.

The metatarsals and phalanges of the known hind limbs are quite similar to corresponding elements of the forelimb, although the fifth matatarsal is broader and more strongly hooked than the fifth metacarpal. The digits sweep rather strongly posterodistally in *Platecarpus* and less so in *M. conodon* and *Tylosaurus*. The fifth digit of both the manus and pes is relatively long in *Tylosaurus*. The approximate phalangeal formula of the pes in *M. conodon* is 8-9-9-9-4, in *Platecarpus* is 4-5-5-5-3, and in *Tylosaurus* is 5-8-8-8-6.

FUNCTIONAL ANATOMY OF POSTCRANIAL SKELETON

Functional Anatomy of the Vertebral Column

The axial musculature of reptiles is generally oriented in an anteroposterior direction and extends from the occipital surface of the skull to the posterior tip of the tail. It is divided by the ribs of the presacral vertebrae and the transverse processes of the caudals into a dorsal, or epaxial, and ventral, or hypaxial series. The epaxial series is in turn divided by two longitudinal tendonous septae, extending dorsolaterally from the region of the zygopophyseal and costal articulations respectively, into proximal transversospinalis, median longissimus and lateral iliocostalis systems (see Vallois, 1922). The hypaxial series may be divided into dorsomedial subvertebralis, lateral obliquus and ventral rectus systems. In general the transversospinalis system acts as a dorsal flexor, opposing the action of the subvertebralis and rectus muscles, and the longissimus (in *Varanus*), iliocostalis and obliquus systems act as lateral flexors. The compressive forces generated are sustained by the vertebral centra.

The epaxial musculature is most typically developed in the dorsal region of lizards (see Nishi, 1916; 1938; Vallois, 1922). The transversospinalis system is composed of three layers. The most superficial layer is that of the M. semispinalis dorsi, which arises on the anterolateral region of the prezygopophyses and medial surface of the dorsal intermuscular septem, and passes anterodorsally to insert tendonously on the posterodorsal edge of the neural spine of a vertebra located several segments anteriorly. The more medial M. spinalis dorsi arises tendonously on the anterodorsal edge of the neural spine and inserts on the dorsal intermuscular septum several segments anteriorly, and on the neural spine and arch of the second vertebra anteriorly. A deep series of short segmental muscles (Mm. interspinales, interarticulares, interarcuales) link the neural arches and spines of successive vertebrae.

In the cervical region of mosasaurs the transversospinalis system was probably as well differentiated as in *Varanus* and was surely more powerfully developed. An M. spinalis capitis originated on the transversely expanded distal ends of the neural spines of cervicals two through seven and, together with the superficial portion of the M. rectus capitis posterior (origin: anterodorsal edge of the axis spine), inserted on the posterior midline of the parietal and served to flex the head dorsally. An M. rectus capitis posterior profundus, originating on the anterodorsal tip of the axis spine and inserting on the supraoccipital and adjacent portions of the paroccipital processes, also served as an accessory dorsal flexor and played an important role in kineticism in the skull. The M. obliquus capitis magnus arose from the posterodorsal edge of the body of the atlas arch, the central portion of the blade of the axis spine, and perhaps also the central portion of the blade of the third cervical, and passed anterolaterally to insert on the dilated distal end of the relatively elongate paroccipital processes. It must have been a powerful lateral flexor.

Behind the atlas vertebra the wide spacing of the zygopophyses and broad posterior buttress on the neural spines indicate a massive development of interspinalis, spinalis and semispinalis muscles. The short anteroposterior length of the neural spines enabled these muscles to flex the cervical vertebrae strongly in a dorsal direction. The neural spines become laterally compressed and abruptly increase in anteroposterior length on the anterior dorsal vertebrae.

From this region back to the middle of the caudal series the zygopophyses gradually approach the vertebral midline. Consequently both the cross sectional area, and thereby strength, of the transversospinalis (dorsal flexor) system and the mobility of the vertebrae in a dorsoventral plane is slowly reduced posteriorly. In the posterior half of the tail the transversospinalis system was probably represented only by short segmental muscles covered with a veneer of connective tissue. It may be worthy of note that in *Varanus* the neural spines of the posterior cervical and anterior dorsal vertebrae are elongated, probably to increase the strength and lever arm of transversospinalis muscles flexing the neck in a dorsal direction and thereby supporting the head. Presumably because the head and neck were usually supported by water, this elongation is not found in mosasaurs (with the possible exception of *Plotosaurus*).

In *Varanus,* according to Nishi (1916, pp. 230-231), fibers of the M. longissimus dorsi originate from the lateral surface of the dorsal intermuscular septum and anterior zygopophyses and extend anterolaterally to insert on the dorsal faschia and posterodorsal edge of the head of the rib four segments anteriorly. In this position it would seem that the muscle would most effectively operate as a lateral flexor and is so considered here. In many reptiles, including lizards (see Vallois, 1922; Nishi, 1938, p. 393), it inserts on both epaxial intermuscular septae and acts to stabalize them against the pull of the transversospinalis and iliocostalis systems (Vallois, 1922, pp. 109, 158). The arrangement of the M. longissimus dorsi in mosasaurs is considered to be similar to that of varanids solely on the basis of the close phylogenetic relationship of the two groups, since most of the attachments of the muscle are by unpreservable connective tissue instead of bone.

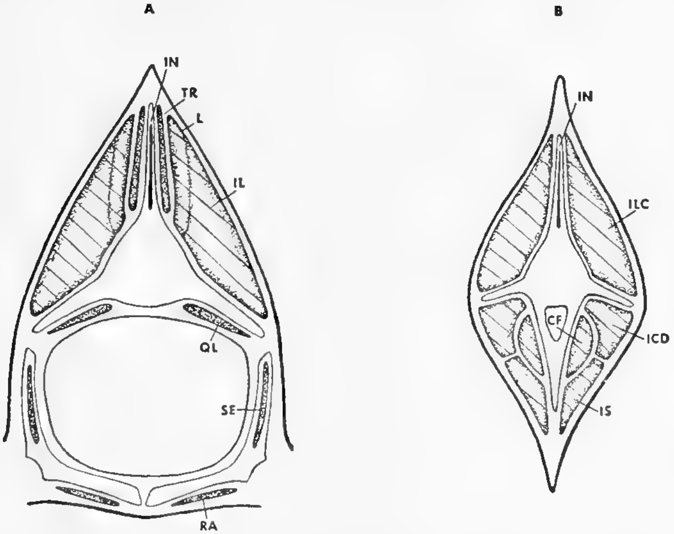
In *Varanus* (Nishi, 1916, pp. 231-233) and presumably also in mosasaurs the M. longissimus cervicocapitis originates on the rounded crest of bone that rises from the synapophysis to the anterior zygopophysis in the anteriormost dorsals and post-axis cervicals. In the region of the third cervical vertebra the longissimus divides into superficial (Mm. articuloparietalis, transversalis capitis) and deep (M. transversalis cervicis) portions. In mosasaurs the former muscles passed forward to insert on the posterior edge of the suspensorial ramus of the parietal and on the supratemporal, respectively. In *Varanus* a tendonous sheet passes anteroventrally through the two muscles to insert on the posterodorsal edge of the atlas arch. A well marked scar for this tendon is also present on the atlas arch of mosasaurs. These superficial longissimus muscles flexed the head in a dorsolateral direction. There is no reason to think they were particularly well developed in mosasaurs. It is possible that dorsolateral-trending fibers similar to those of the M. longissimus dorsi inserted on the heads of the cervical ribs, which are present on all cervical vertebrae except the atlas in mosasaurs.

Zygopophyses are invariably well developed at least as far back as the middle of the thoracic series in mosasaurs. Virchow (1914) has shown that they function to prevent transverse rotation of the vertebrae about their centra, and thus resolve the rotational component of any muscle attaching to the vertebrae into a vertical and/or horizontal direction. However, the axis vertebra represents the anterior limit of the zygopophysis-bearing portion of the vertebral column. The hemispherical surfaces of the odontoid process and occipital condyle hold the washer of the atlantal arch-intercentrum in place, which in turn firmly binds the craniovertebral joint together. Since the atlas arch lacks zygopophyses and a neural spine, there is no hinderance to rotational movement between the skull and axis vertebra. Virchow (1914, pp. 70-71) notes that rotatory movements on the order of 20° are possible between the skull and atlas vertebra in *Varanus*, and that rotation of a somewhat lesser amount can occur between the atlas and axis. In *Varanus* the deep portion of the M. longissimus cervicocapitis (the M. transversalis cervicis) passes anteroventrally from an epaxial position to insert, together with the M. iliocostalis capitis, beneath the craniovertebral joint onto the distal end of the basioccipital tuber. It is evident that the mosasaur skull was also rotated by these muscles, perhaps aided by a small bundle of fibers from the transversospinalis system, the M. obliquus capitis inferior, which may have arisen on the dorsolateral surface of the axis neural arch and inserted ventrolaterally on the posterodorsal tuberosity on the atlas arch.

Zygopophyses are reduced or non-functional in the lumbar region of mosasaurs. Here the interspinalis muscles and ligaments must have aided in preventing transverse rotation of the vertebrae. Because a significant part of the area of origin of longissimus fibers was probably on the anterior zygopophyses, because their trend duplicates that of the iliocostalis system in the dorsal region, and because in the caudal region there are no costal articulations and therefore no necessity for the existence of a distinct longissimus system, it is assumed that the M. longissimus dorsi dwindled in size posteriorly in mosasaurs and its caudal continuation must have been very much reduced.

In *Varanus* (Nishi, 1916, pp. 223-224) fibers of the M. iliocostalis generally originate on the fascia covering the lateral surface of the longissimus and extend anterolaterally to insert on the posterior edge of a rib four or five segments anteriorly. The M. iliocostalis cervicis was more strongly developed in mosasaurs than it is in *Varanus*, as evidenced by the much larger, posterolateral-directed atlas synapophysis and the greater number of cervical ribs.

Posteriorly the M. iliocostalis dorsi increased in width to fill the epaxial space left by the slowly diminishing transversospinalis and longissimus systems. In



Text-fig. 64. A. Cross section of the trunk of a mosasaur in the pelvic region. B. Same of the tail near its base. Abbreviations: CF, Mm. caudifemorales; ICD, M. iliocaudalis; IL, Mm. iliocostalis dorsi et iliocostalis caudae; ILC, M. iliocostalis caudae; IN, interspinalis ligament; IS, M. ischiocaudalis; L, longissimus system; QL, M. quadratus lumborum; RA, M. rectus abdominus; SE, Mm. supracostalis et intercostalis externus; TR, transversospinalis system.

the lumbar region it was limited laterally by the shortened ribs, but gained in depth through the increased ventrolateral inclination of the synapophyses. The iliocostalis system must have been maximally developed at the base of the tail, where the M. iliocostalis caudae filled nearly the entire space between the neural spines and the long ventrolateral-inclined transverse processes. Because the ilium lay distal to the transverse process of the "sacral" vertebra it was largely if not completely bypassed by the iliocostalis muscles. This is in marked contrast to the condition in *Varanus* where the ilium projects into the expaxial region and interrupts a much slenderer iliocostalis system. The M. iliocostalis caudae diminished in strength posteriorly in proportion to the shortening and elevation of the transverse processes and was probably terminated near the middle of the tail. Vallois (1922, p. 105) notes that the M. iliocostalis is "par excellence" a lateral flexor of the body.

The subvertebralis system of the hypaxial series was certainly highly developed beneath the cervical and anterior dorsal vertebrae, but was probably unimportant elsewhere. The muscles arose on either side of the small peduncle on the ventral surface of the anterior dorsal centra and increased greatly in strength anteriorly, passing under and attaching to the large cervical hypapophyses. Many of the deeper fibers (M. longus colli) terminated anteriorly on the axis intercentrum, although a few reached the atlas intercentrum. The more superficial portion of the muscle mass (M. rectus capitis anterior) passed anteriorly beneath the craniovertebral joint and inserted on the posterior face of the large basal tubera of the basioccipital. These muscles were powerful ventral flexors of the head and neck and acted as antagonists of the epaxial transversospinalis system.

Medial derivatives of the obliquus system probably attached to the vertebral column of mosasaurs much in the same manner as they do in *Varanus* (see Nishi, 1916, figs. 9-10; Gadow, 1882, pl. 6 fig. 7). Mm. intertransversarii ran between the synapophyses of the presacral portion of the column and served as lateral flexors. They must have been most powerfully developed where the synapophyses were longest, in the middle and near the posterior end of the dorsal portion of the column. Further posteriorly an M. quadratus lumborum probably originated from the undersurface of the short lumbar ribs and synapophyses and passed back to insert on the ventral surface of the transverse processes of anterior pygal vertebrae. Mm. levator costae were present in the posterior cervical and anterior dorsal region, where they originated on the ridge of bone in front of the ventral margin of the synapophyses and inserted on the head of the succeeding rib. Because of the presence of cervical ribs, more distal portions of the obliquus system probably retained a tripartite division at least as far anteriorly as the base of the neck. Posteriorly, sheets of the supracostals, aided perhaps by the external intercostals, and superficial portions of the M. iliocaudalis suspended the vertical ilium between them on the lateral surface of the body. Behind the pelvis the M. iliocaudalis probably occupied most of the hypaxial space between the transverse processes and haemal spines and acted as a strong accessory to the M. iliocostalis caudae above in flexing the base of the tail laterally.

The rectus system passed from the ventral margin of the mandibles (Mm. sternohyoideus, omohyoideus) to the pectoral girdle and from thence (rectus abdominus mucles) back to insert on the pubic tubercle and puboischiadic ligament of the pelvis. In the lumbar region it served both to support the viscera and hold the anteroventral rim of the pelvis in place. The caudal equivalent of the rectus system (M. ischiocaudalis) originated from the haemal spines and inserted on the ischiadic tubercle, near the acetabulum. Thus a vertical, crescent-shaped space was left free between the pelvis and caudal musculature for cloacal structures. In view of their role in supporting the pelvis it is unlikely that the bulk of the obliquus system and rectus system was of much importance in flexing the body either laterally or ventrally.

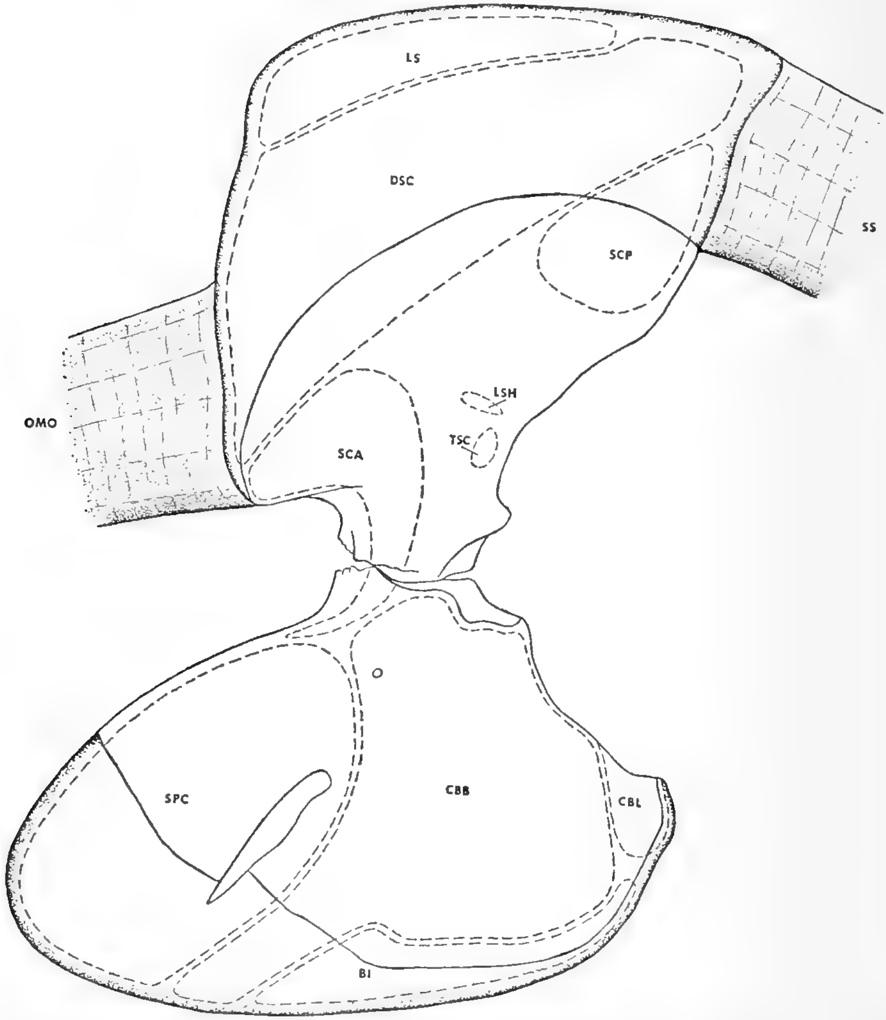
Functional Anatomy of the Forelimb

The pectoral skeleton of mosasaurs lies in the anteriormost portion of the thoracic region and is basically very similar to that of *Varanus*. The clavicles, interclavicle and a well-developed sternum unite both halves of the girdle on the ventral midline. In most cases the scapula seems to have rotated to a more anterodorsal position than in *Varanus*, and the coracoid is more extensive anteromedially. Cartilagenous suprascapulae and epicoracoids were certainly present, and although their outlines are not surely known, they were probably not far different from those in *Varanus*. It seems reasonable to assume that the pectoral girdle was not so flattened ventrally as in *Varanus*, so that the glenoid fossae were elevated somewhat above the ventral level of the body, but below the lateral midline. The glenoid fossa faces more posteriorly in mosasaurs than in varanids and has a sharply defined, hemicylindrically concave- rather than subcircular-articulating surface in the Mosasaurinae, with the axis lying perpendicular to the body surface. The anterolateral rim of the glenoid fossa was probably completed in cartilage to form a similar articulating surface in the other two subfamilies of mosasaurs.

The head of the humerus covers the central portion of the proximal end of the bone and is hemicylindrically convex, fitting perfectly into the glenoid fossa. Thus the long axis of the humerus was held in a plane perpendicular to the body surface and projected posteroventrolaterally at an angle of about 45° from the long axis of the body. This bone is very much shorter than in *Varanus*, and the distal end has been turned so that the medial and lateral proximal processes and the entepi- and ectepicondyles lie in the same plane, perpendicular to the body surface. The shape of the glenoid articulation suggests that the humerus was more free to move dorsoventrally than anteroposteriorly.

The articulating surfaces between the humerus and radius-ulna are flat and at right angles to the long axis of the arm, making the elbow relatively inflexible dorsoventrally. The epipodial elements are very short and broad and support the enlarged pectoral paddle through an also relatively inflexible, often imperfectly ossified, carpal region. It is evident that the only freely moveable joint remaining in the mosasaurian pectoral apparatus was the articulation between the head of the humerus and the scapula-coracoid. Muscles linking the forelimb with the body functioned to displace the forelimb as a unit with respect to the body. A reconstruction (see text-figs. 66-67) of the musculature of the forelimb of *Clidastes* is based on the muscle scars evident on the bones and a dissection of the forelimb of *Varanus niloticus*. The termniology used is that of Romer (1944).

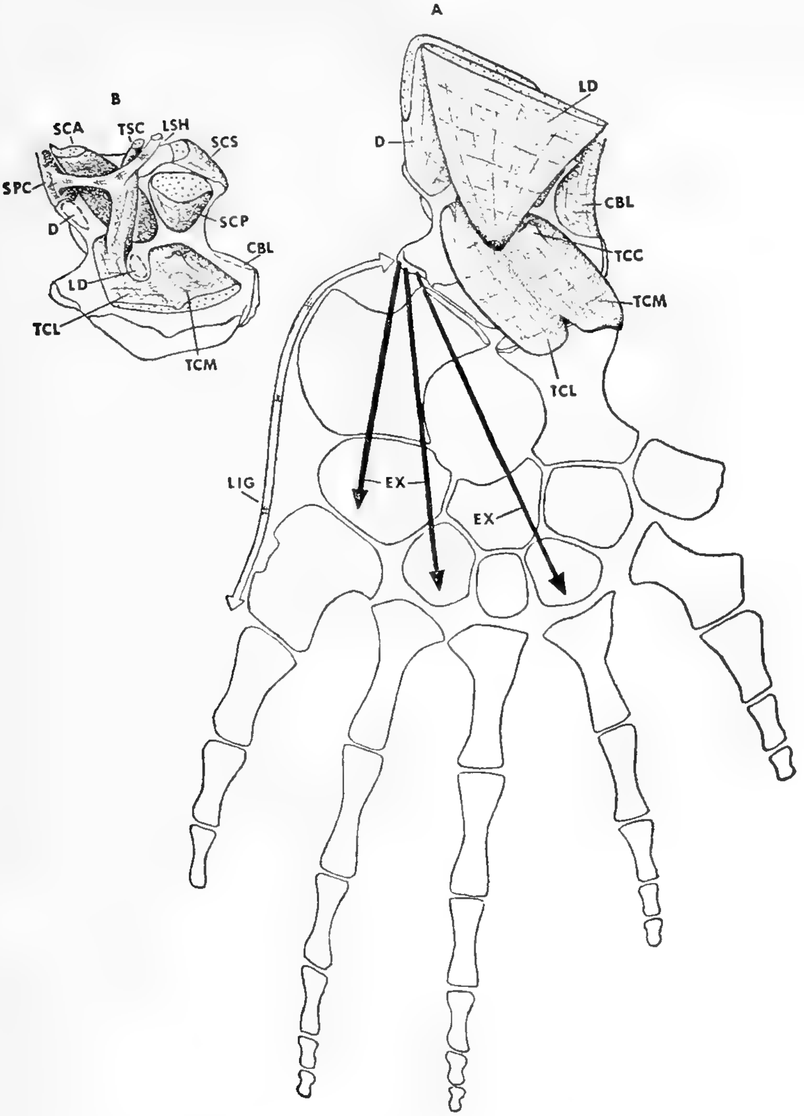
Muscles that abducted the humerus, and therefore the forelimb, were: the M. latissimus dorsi, arising on the fascia over the neural spines of the posterior cervical and anterior thoracic vertebrae and inserting clearly on a scar located on the distomedial dorsal surface of the humerus; the Mm. deltoides clavicularis et scapularis, arising on the clavicle and suprascapula respectively and inserting together on the dorsal surface of the lateral process of the humerus; the M.



Text-fig. 65. Scapula-coracoid of *Clidastes* showing muscle attachments. Abbreviations for text-figs. 65-67: **BI**, M. biceps; **BIN**, M. brachialis inferior; **CBB**, M. coracobrachialis brevis; **CBL**, M. coracobrachialis longus; **D**, M. deltoides, undivided; **DSC**, M. deltoides scapularis; **EX**, extensors (diagrammatic); **FCR**, M. flexor carpi radialis; **FCU**, M. flexor carpi ulnaris; **FPP**, M. flexor palmaris profundus; **FPS**, M. flexor palmaris superficialis; **HR**, M. humeroradialis; **LD**, M. latissimus dorsi; **LIG**, ligament; **LS**, M. levator scapulae superficialis superior; **LSH**, Ligamentum scapulohumerali laterali; **OMO**, M. omohyoideus; **P**, M. pectoralis; **PP**, M. pronator profundus; **SCA**, M. scapulo-humeralis anterior; **SCP**, M. scapulohumeralis posterior; **SCS**, M. subcoracoscapularis; **SPC**, M. supracoracoideus; **SS**, M. serrati superficialis; **TCC**, M. triceps caput coracoideus; **TCL**, M. triceps caput lateralis; **TCM**, M. triceps caput medialis; **TSC**, M. triceps caput scapularis.

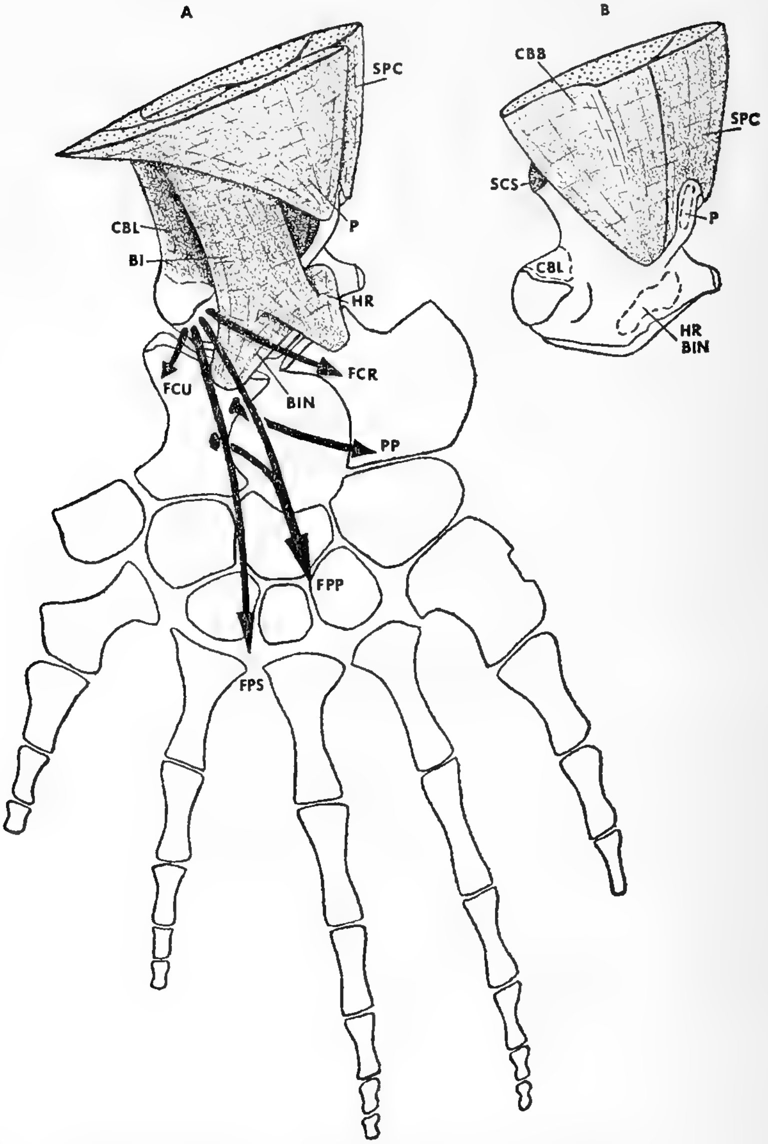
scapulohumeralis posterior, arising on the posterodorsal surface of the scapula and inserting on the dorsal surface of the medial process of the humerus; and the M. scapulohumeralis anterior, arising on the anterolateral surface of the scapula and inserting on the proximomedial portion of the dorsal surface of the humerus.

Muscles that adducted the forelimb were: the M. pectoralis, arising on the interclavicle and inserting on the pectoral crest; the M. biceps, arising on the



Text-fig. 66. Extensor aspect of forelimb of *Clidastes* showing restored musculature. A. Superficial muscles. B. Deeper muscles.

median ventral margin of the coracoid and epicoracoid and inserting on the proximoventral portion of the radius and ulna; the M. supracoracoideus, arising on the anteromedial portion of the coracoid and epicoracoid and inserting on the anteroventral portion of the lateral process and the posterior surface of the pectoral ridge in *Clidastes,* probably inserting on the leading edge of the humerus and the anterior surface of the pectoral ridge in other mosasaurs; and the Mm. coracobrachialis brevis et longus, arising behind the supracoracoideus and beneath the biceps on the ventral surface of the coracoid and epicoracoid and inserting on the proximomedial portion of the ventral surface of the humerus and ventroposterior surface of the entepicondyle respectively.



Text-fig. 67. Flexor aspect of forelimb of *Clidastes* showing restored musculature. A. Superficial muscles. B. Deeper muscles.

Muscles that probably acted to pull the forepaddle anteriorly were: the Mm. scapulohumeralis anterior, deltoides clavicularis, and supracoracoideus, with the M. subcoracoscapularis, arising on the medial surface of the scapulacoracoid and inserting on the inner surface of the medial process, acting as an antagonist. It is apparent, however, that the greatest cross-sectional area of muscle fibers lay above and below the humerus, rather than in front of or behind it. This fact, together with the shape of the glenoid articulation, indicates that the mosasaur forepaddle could be most effectively moved in a dorsoventral, rather than anteroposterior direction, and was much more efficient as an organ of steering than as an organ of propulsion. This contrasts strongly with the condition seen in plesiosaurs (see Watson, 1924).

Because the paddle projected posterolaterally from the side of the body, when it was held in abducted position, the flow of water streaming over it would tend to force that side of the mosasaur's body down. If the leading edge of the paddle were turned down and the trailing edge up, the surface area of the paddle meeting the current would be greater and the downward deflecting force would also be greater. Simultaneous contraction of the "flexor" musculature of the forearm and scapulohumeralis posterior would accomplish this movement. It is significant that the entepicondyle, the site of origin of the flexor musculature, is extremely well-developed in mosasaurs and projects well below the ventral surface of the humerus.

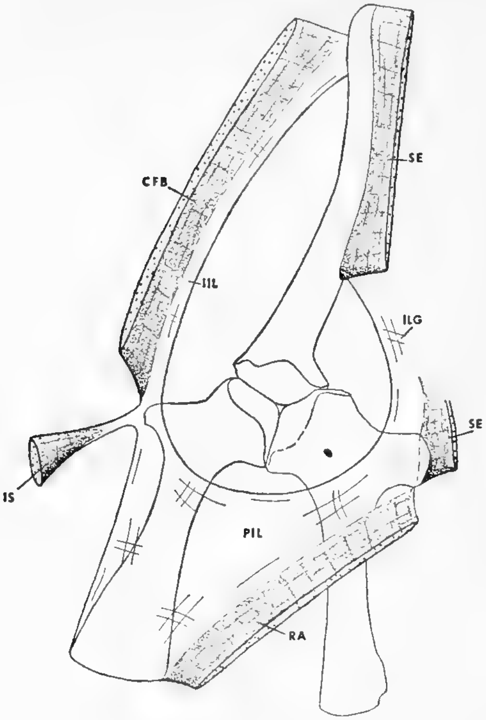
Correspondingly, when the paddle was held in the adducted position, the co-ordinated action of the deltoids and coracobrachialis longus on the humerus would elevate the leading edge and depress the trailing edge, to bring a greater area of the paddle into the water stream beneath it.

Functional Anatomy of the Hindlimb

Although the mosasaur pelvis is clearly derivable from the ordinary lacertilian type, there is much less resemblance between it and that of *Varanus* than between their respective shoulder girdles. In lateral aspect the pelvis of *Varanus* is about as wide as it is high, each of the three elements being broad, powerfully-built bones. The ilium is strongly posterodorsally inclined and solidly united to the anteriormost of the two sacral vertebrae. In mosasaurs the pelvis is much higher than wide and the component elements are slender. The ilium has lost its contact with the sacral vertebra and is vertical or slightly anteriorly inclined in position. Both the pubis and ischium meet on the ventral midline of the body, although the latter contact was much the firmer of the two. The acetabulae were held about midway between the ventral border and the lateral midline of the body, occupying a position similar to that of the glenoid fossae anteriorly.

There is a series of broad, tendonous sheets found in lizards (see Romer, 1922, 1942), which are suspended upon the lateral surface of the three bones of the pelvis and surround the acetabulum. In *Varanus* the puboischiadic ligament arises on the ventral midline along the ischiadic symphysis and spreads anterolaterally to the pubic tubercle and posterolaterally to the ischiadic tubercle. From the ischiadic tubercle the ilioischiadic ligament continues anterodorsally to insert on the posterior border of the ilium. A smaller, tendonous band links the pubic tubercle with the ilium anteriorly. The relations of these ligaments were probably essentially similar in mosasaurs (see text-fig. 68).

Because of the loss of the sacroiliac contact, the mosasaur pelvis was supported entirely by the belly and flank musculature. The epaxial muscles which in *Varanus* are partly interrupted by the pelvic girdle, probably were freely continuous. The pelvis must have been held in place anteriorly by the M. supracostalis, arising on the ribs along the lateral midline of the body and inserting on the iliopubic ligament and pubic tubercle; and the M. rectus abdominus, arising on the sternum and inserting on the anterior edge of the puboischiadic ligament. Posteriorly the pelvis was probably anchored by the M. caudifemoralis brevis, arising on the undersurface of the transverse processes and lateral surface of the haemal arches of the anterior caudal vertebrae and inserting in part on the ilioischiadic ligament, together with the M. ischiocaudalis, arising on the lateral surface of the haemal spines and inserting on the

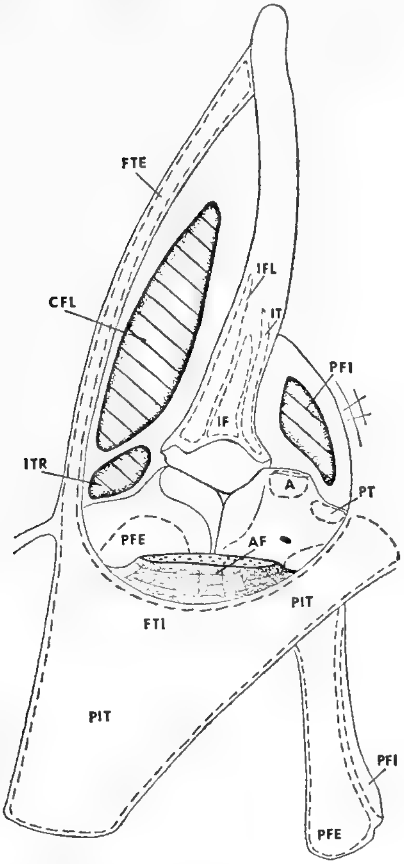


Text-fig. 68. Pelvis of *Clidastes* showing supporting musculature. Abbreviations for text-figs. 68-70: A, M. ambiens; AF, M. adductor femoris; CFB, M. caudifemoralis brevis; CFL, M. caudifemoralis longus; FET, M. femorotibialis; FTE, M. flexor tibialis externus; FTI, M. flexor tibialis internus; IF, M. iliofemoralis; IFL, M. iliofibularis; IIL, ilioischiadic ligament; ILG, iliopubic ligament; IS, M. ischiocaudalis; IT, M. iliotibialis; ITR, M. ischiotrocantericus; PFE, M. puboischiofemoralis externus; PFI, M. puboischiofemoralis internus; PIL, puboischiadic ligament; PIT, M. puboischiotibialis; PP, M. pronator profundus; PT, M. pubotibialis; RA, M. rectus abdominus; SE, Mm. supracostalis et intercostalis externus.

ischiadic tubercle, and M. iliocaudalis, arising on the ventral surface of the transverse processes and inserting on the posterior edge of the ilium deep to the ilioischiadic ligament.

In size and shape the hind limb is very similar to the anterior one. Joints between the propodial (femur), epipodial (tibia-fibula), tarsal and podial elements have similarly lost their mobility. The joint remaining between the limb and the limb girdle is different from that found in the forelimb. The acetabulum is a bowl-shaped structure which opens laterally and a little posteriorly to receive the convexity capping the proximal end of the femur. The hind limb was held in a horizontal plane at more nearly a right angle to the long axis of the body than the forelimb. This probably brought the hind paddle into contact with water undisturbed by the passage of the anterior portion of the body and thereby enabled it to exert greater control over the equilibrium of the body.

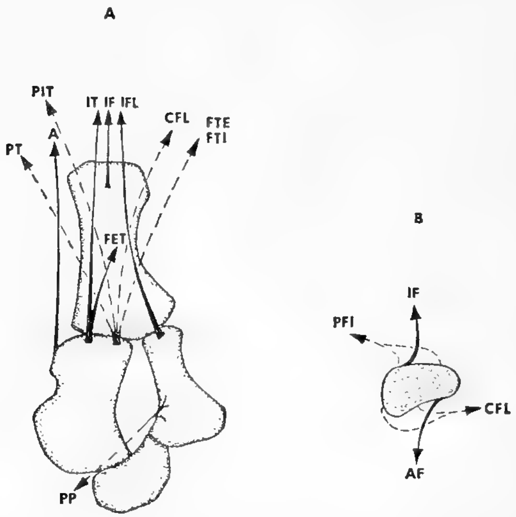
It is quite evident from a dissection of the hind limb that the femur of *Varanus* could be powerfully rotated about its long axis. Muscles linking the femur with the pelvis wrap partially around the proximal half of the femur to insert either fleshily or by tendons at low angles to the surface of the bone. Since the femur is commonly held in a horizontal plane at a high angle to the body



Text-fig. 69. Pelvis of *Clidastes* showing appendicular musculature. Diagonally ruled areas are muscles cut off in the plane of the acetabulum.

surface in lizards, it is at once apparent that, if the crus were held at right angles to the femur and the ground, rotation of the femur would impart a forward motion to the body of the lizard. Speed of progression would depend on the length of the crus and rate in which the femora could be alternately rotated in the power and recovery strokes. Perhaps extension of the crus during the recovery stroke would reduce the rotational inertia of the hind limb and increase the efficiency of rapid progression.

The large size of the internal trochanter, the vertically elliptical cross-section of the proximal femoral shaft, and the circular acetabulum, all suggest that the mosasaur femur could be rotated in a manner similar to that found in *Varanus.* The elliptical cross-section of the femoral shaft together with the large internal trochanter would have increased the lever arm of muscles, M. puboischiofemoralis internus, arising on the medial surface of the pubis and ischium and inserting on the proximodorsal surface of the femur, and M. caudifemorale, arising on the undersurface of the transverse processes of the anterior caudal vertebrae and inserting in part on the anterior and posterior surface of the internal trochanter, depressing the leading edge and elevating the trailing edge of the hind paddle. These are the muscles that provide the power stroke



Text-fig. 70. A. Hind limb of *Clidastes* showing the arrangement of some of the appendicular muscles. Solid lines indicate muscles that are dorsal in position, broken lines indicate those lying more ventrally. B. Cross section of the proximal portion of the femur, showing muscles that rotate the femur about its long axis.

in rotating the femur of *Varanus,* where in each case they insert by a double tendon near the proximal end of the femur.

The complementary movement elevating the leading edge and depressing the trailing edge could have been brought about through the action of the M. ischiotrochantericus, arising on the posteromedial surface of the ischium and inserting on the dorsal surface of the femur, the M. adductor femoris, arising on the lateral edge of the puboischiadic ligament and inserting on the posterior surface of the femur, possibly aided by the M. iliotibialis, arising on the anterolateral surface of the ilium and inserting on the proximodorsal portion of the tibia. In *Varanus* muscles providing the power stroke are more highly developed than those providing the recovery stroke. In mosasaurs, where the functional distinction between the two movements would have been greatly lessened, the two sets of muscles were probably about equally developed.

Because of its relatively lesser anteroposterior dimensions, slenderer proportions and vertical-oriented ilium, the mosasaur pelvis would not have served so well as a site of origin of muscles swinging the hindlimb in an anteroposterior arc as it does in *Varanus.* By far the most effective plane of muscular operation must have lain in a dorsoventral direction. The M. iliotibialis, M. iliofemoralis, arising on the ventromedial portion of the lateral surface of the ilium and inserting on the dorsal surface of the femur, and M. iliofibularis, arising on the posterolateral surface of the ilium and inserting on the proximodorsal portion of the fibula, served as simple abductors, and the M. puboischiofemoralis externus, arising on the lateral surface of the pubis and ischium beneath the puboischiadic ligament and inserting on the proximoventral portion of the femur; and M. puboischiotibialis, arising on the lateral surface of the puboischiadic ligament and inserting on the proximoventral portion of the tibia, also probably acted as simple adductors. The M. ambiens, arising on the dorsolateral extremity of the pubis and inserting on the proximoanterior portion of the tibia, together with the M. pubotibialis, arising near the tip of the pubic tubercle and inserting on the proximoposterior portion of the tibia, would have operated to advance the paddle, with the M. flexor tibialis complex, arising on the ilioischiadic and puboischiadic ligaments and inserting on the proximoposterior portion of the tibia, acting as an antagonist.

In summary, neither the fore nor hind paddles of mosasaurs could have been effectively used as oars, but must have served instead to orient the body in swimming. The forepaddles were held at a low angle to the body surface and abduction and adduction accompanied by minor inversionary or eversionary movements of the flippers would have enabled them to operate like the elevators of an airplane, with the axis of rotation extending along the leading edge. The hind paddles were held at a higher angle to the body surface and rotation of the entire limb about a medial axis possibly played a role as important in equilibrating processes as abduction and adduction. The elbow-knee and wrist-ankle joints had lost their special mobility and the paddles became more uniformly resilient throughout. In some forms (Plioplatecarpinae, Tylosaurinae) the paddles were probably very flexible because of the extensive replacement of bony tissue by fibrocartilage (see Howell, 1930, p. 218, for a description of the same phenomenon in the flippers of cetaceans). In an excellently preserved specimen of *Platecarpus* from the Niobrara Chalk of Kansas, "The edge of the fleshy portion [of the paddle], which is clearly outlined, follows the sweep of the radial side of the fingers about an inch distant. Between the fourth and fifth finger the edge of the membrane is concave to the tip of the fifth finger. Thence the margin extends broadly inward to the side of the body. The paddle evidently [was] not pedunculated, but was broadly connected with the body." (Williston, 1899, p. 40.)

Swimming in Mosasaurs

In previous sections the general morphology of the mosasaur body has been outlined and movements possible for the various skeletel structures, based on the nature of articular surfaces and the presumed strength and disposition of activating musculature, have been evaluated. From this it is clear that mosasaurs swam by lateral undulations of the posterior portion of the body and tail and that the flippers were primarily steering organs, having little capacity for propulsive fore and aft movements. The generally anguilliform body shape of mosasaurs was not so ideally suited for rapid rectilinear locomotion as is the teardrop-shaped body and lunate tail of some bony fishes, sharks and porpoises. One gains the impression from a survey of Breder's (1926, see especially pp. 177, 237, 264-265, 279) study of locomotion in fishes that an anguilliform body shape is most efficient in delivering propulsive energy at low rates and at relatively slower speeds. Conversely a teardrop-shaped body and lunate tail are most effective in utilizing great amounts of propulsive energy at high rates of progression. Bainbridge (1961) has found that in a rather intricate way the maximum speed attainable by a pisciform organism in water is related to its body length. It seems likely that its larger size played an important role in enabling a mosasaur to overtake smaller, more streamlined prey. Like ecologically analogous carnivorous marine mammals, mosasaurs were also probably quite maneuverable. As Howell (1930, p. 207) pointed out, inability to steer (i.e., make sharp turns) in pursuing individual food items would mean a rapid death by starvation for a larger aquatic carnivore.

The paddles of mosasaurs were well suited to stabilize or rotate the body. It is interesting to note that the cervical region is long, not shortened as it is in cetaceans, and was operated by powerful muscles. A simple lateral bending of the neck and anterior portion of the trunk was probably sufficient to make slow turning movements. When making abrupt lateral turns at high speeds, however, it is postulated that the body was first spun on its side by the forepaddles. The neck was then arched in the direction of the turn while the forepaddles were abducted with their flexor surfaces facing into the stream. Simultaneously the hind paddles were rotated like the diving planes of submarines, forcing the posterior part of the body in a direction opposite to that in which the forequarters were moving. As a result the entire body pivoted about its center of inertia and the animal continued at right angles to its former path of motion (for similar turning movements in pinnipeds see Howell, 1930; Ray, 1963). In diving the neck and anterior portion of the trunk were flexed and the forequarters were depressed by the adducted anterior paddles. An abrupt abduction of the hind paddles elevated the posterior region of the body. It is important to remember that in all of the above movements the tail and most of the trunk were nearly inflexible in a dorsoventral direction. The axis-atlas-occipital joint allowed the head to rotate in a transverse plane and must have greatly enhanced the ability of the animal to capture agile prey at close range.

Bodily proportions vary somewhat between different genera of mosasaurs. This variation probably indicates correspondingly different swimming (and thereby predatory) habits. *Clidastes* must have been less agile than some mosasaurs because of its elongate body and small flippers. The development of a caudal fin indicates it was a relatively rapid swimmer. It is suggested that *Clidastes* was better suited to subsist on rapidly swimming fishes which were relatively incapable of sudden evasive movements. The body of *Plotosaurus* is generally similar to that of *Clidastes,* although the narrower flippers and more highly developed caudal fin imply that it was a faster swimmer. In the two above genera and in *Mosasaurus,* a generally much larger animal, it would appear that relative lack of maneuverability might indicate a propensity to feed on faster prey or prey that could not dodge easily.

In comparison to the above-mentioned mosasaurines, the body of *Platecarpus* is shorter, the paddles are larger and the tail is not so appreciably dilated in a vertical direction. *Platecarpus* was probably a slower swimmer than these genera, but must have been able to make more abrupt turns. Like its probable recent analogue, the seals, *Platecarpus* may have fed predominantly on smaller, highly evasive fishes. *Tylosaurus* is a large, moderately slender form with narrow flippers and a tail almost identical to that of *Platecarpus.* It was probably generally similar to *Mosasaurus* in swimming ability, although not so fast. As Williston (1925, p. 272) has observed, the bones of *Tylosaurus* are very cancellous and were probably impregnated with fat (as is also the case in whales, see Howell, 1930, p. 42). Presumably this adiposity increased the buoyancy of the animal.

Bertin (1958, pp. 1889-1891) notes that neritic fish living on the continental shelves are commonly reddish or silver-grey. Since this was evidently the habitat of most mosasaurs, it might be expected that they were similarly colored. Shallow water forms and young inhabiting coastal areas could have been more variably colored.

SYSTEMATICS

A major problem faced in the beginning of this study was the proper application of 86 described species names of American mosasaurs to the hundreds of fragmentary to nearly complete skeletons in the collections of the American Museum and the Peabody Museum at Yale. Because of very poor locality information regarding horizons in the Niobrara Chalk from which specimens were taken and the scattering of usually quite fragmentary specimens from other formations it was felt that a typological approach to the determination of species was the only one possible. The variation in individual elements of the skeleton was studied in detail. When it was found that a certain suite of morphological variations was always associated together in a single specimen and never mixed with variations of another suite, it was assumed that the suites were diagnostic of different taxa. Appropriate suites of diagnostic characters are catalogued under each taxonomic group in the following section.

If possible, all specimens including types were relegated to one or another of the typological groups, which received the name applied to the oldest designated type specimen. In many instances cranial material in types was not adequate to permit assignment to a species group. Names based on such specimens are listed in the last part of the systematic section.

Size was not considered in the delineation of species. A table of measurements of representative specimens may be found in Appendix B. As it turned out most of the specimens referable to a given species fall within a rather limited size range. Only in *Clidastes* and *Tylosaurus* were linear measurements found that varied as much as a factor of two between the smallest and largest known individuals. Juvenile specimens of mosasaurs are rarely found and those that have been collected are usually very incomplete. These specimens cannot be separated from larger individuals by preserved diagnostic characters; this suggests that they are immature and do not belong to a smaller species. For example, the anterior limit of the narial emargination in the dorsal border of the maxilla occupies relatively the same position in large and small specimens of *Platecarpus* and *Tylosaurus*. The surface of the bones is less highly polished and the bones are not so well ossified as in presumed adult individuals of the same species.* It is therefore hoped that errors due to the confusion of species characters with growth allometry have been avoided.

When the characteristics of the various genera were compared, it was found that certain groups of genera appear to resemble each other more closely than other members of the same subfamily. The resemblance is expressed by the introduction of tribal categories within the Mosasaurinae and Plioplatecarpinae. These tribes appear to represent discrete radiations of mosasaurian forms below the subfamilial level of organization.

A summary of mosasaur species recognized in this work is as follows:

SUBFAMILY MOSASAURINAE
TRIBE MOSASAURINI

GENUS *CLIDASTES* (Coniacian-late Campanian, U.S.A.).
Clidastes sternbergi, Santonian(?), central U.S.A.
Clidastes liodontus, Coniacian, central U.S.A.
Clidastes propython, Santonian-middle Campanian, central and southern U.S.A.
Clidastes iguanavus, late Campanian, eastern U.S.A.

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* Gregory (1952) has suggested that the small lower jaws in the type of *Ichthyornis dispar* may belong to a mosasaur hatchling. The arrangement of the elements in the posterior half of these jaws, shape of the retroarticular process of the articular, high number of teeth in the dentary, and excessively small size coupled with the highly polished surfaces of the bones all preclude the possibility of the jaws belonging to an infant mosasaur.

GENUS *MOSASAURUS* (Santonian(?)-Maestrichtian, U.S.A.; Santonian-Maestrichtian, Belgium; Maestrichtian, Holland; Campanian of France and Sweden).

Mosasaurus lonzeensis, Santonian, Belgium.
Mosasaurus ivoensis, Santonian(?), central U.S.A.; early Campanian, Sweden.
Mosasaurus gaudryi, Campanian, France.
Mosasaurus conodon, late Campanian or early Maestrichtian, central, southern and eastern U.S.A.; Maestrichtian, Belgium.
Mosasaurus missouriensis, early Maestrichtian, central U.S.A.
Mosasaurus dekayi, Maestrichtian, eastern U.S.A.
Mosasaurus maximus, Maestrichtian, southern and eastern U.S.A.
Mosasaurus hoffmanni, late Maestrichtian, Belgium and Holland.

GENUS *AMPHEKEPUBIS*

Amphekepubis johnsoni, Santonian(?), northern Mexico.

GENUS *LIODON* (Maestrichtian, U.S.A.; Campanian, England, Belgium, and Sweden; Campanian-Maestrichtian, France).

Liodon anceps, Campanian, England and Sweden; Campanian-late Maestrichtian(?), France.
Liodon compressidens, Campanian, France and Belgium.
Liodon mosasauroides, Maestrichtian, France.
Liodon sectorius, Maestrichtian, eastern U.S.A.

GENUS *COMPRESSIDENS*

Compressidens fraasi, late Maestrichtian, Belgium.
Compressidens belgicus, late Maestrichtian, Belgium.

TRIBE GLOBIDENSINI

Genus *GLOBIDENS* (Campanian, U.S.A.; late Campanian, Belgium; Maestrichtian, Brazil, Jordan, North Africa and Timor).

Globidens alabamaensis, Campanian, central and southern U.S.A.; late Campanian, Belgium.

TRIBE PLOTOSAURINI

Genus *PLOTOSAURUS*

Plotosaurus bennisoni, late Maestrichtian, western U.S.A.
Plotosaurus tuckeri, late Maestrichtian, western U.S.A.

GENUS *TANIWHASAURUS*

Taniwhasaurus oweni, Maestrichtian, New Zealand.

SUBFAMILY PLIOPLATECARPINAE

TRIBE PLIOPLATECARPINI

GENUS *PLATECARPUS* (Coniacian-Campanian, U.S.A.; Campanian, France and Sweden).

Platecarpus tympaniticus, Santonian, southern U.S.A.
Platecarpus coryphaeus, Coniacian, central U.S.A.
Platecarpus ictericus, Santonian-early Campanian, central U.S.A.; early Campanian, France.
Platecarpus somenensis, Campanian, France, Sweden and central U.S.A.
"Platecarpus" intermedius, early(?) Campanian, southern U.S.A.

GENUS *ECTENOSAURUS*

Ectenosaurus clidastoides, Santonian, central U.S.A.

GENUS *PLIOPLATECARPUS* (Campanian-Maestrichtian, U.S.A.; Maestrichtian, Belgium; Campanian, Sweden).

Plioplatecarpus primaevus, Campanian, central U.S.A.
Plioplatecarpus depressus, Maestrichtian, eastern U.S.A.
Plioplatecarpus marshi, late Maestrichtian, Belgium.
Plioplatecarpus houzeaui, late Maestrichtian, Belgium.

Tribe PROGNATHODONTINI

Genus *PROGNATHODON* (Campanian, central U.S.A.; Maestrichtian, central, southern and eastern U.S.A.; late Maestrichtian, Belgium).

Prognathodon crassartus, Campanian, central U.S.A.
Prognathodon overtoni, early Maestrichtian, central U.S.A.
Prognathodon solvayi, late Maestrichtian, Belgium.
Prognathodon giganteus, late Maestrichtian, Belgium.
Prognathodon rapax, Maestrichtian, eastern U.S.A.
Prognathodon(?) *donicus* (see Pravoslavlev 1914).

Genus *PLESIOTYLOSAURUS*

Plesiotylosaurus crassidens, late Maestrichtian, western U.S.A.

Genus *DOLLOSAURUS*

Dollosaurus lutugini, late Campanian, southern European Russia.

?Subfamily PLIOPLATECARPINAE incertae sedis

Genus *HALISAURUS* (Santonian(?)-Maestrichtian, U.S.A.)

Halisaurus onchognathus, Santonian(?), central U.S.A.
Halisaurus platyspondylus, Maestrichtian, eastern U.S.A.

Subfamily TYLOSAURINAE

Genus *TYLOSAURUS* (Coniacian-Campanian, U.S.A.).

Tylosaurus nepaeolicus, Coniacian, central U.S.A.
Tylosaurus proriger, Santonian-Campanian, central U.S.A.; Campanian, southern U.S.A.

Genus *HAINOSAURUS* (Santonian-Maestrichtian, Belgium).

Hainosaurus lonzeensis, Santonian, Belgium.
Hainosaurus bernardi, late Maestrichtian, Belgium.

In the following material, double asterisk (**) preceding a specimen number indicates a complete or nearly complete skull, a single asterisk (*) a fairly complete skull, and no asterisk indicates a fragmentary skull. In the case of specimens with exceptionally complete postcranial material the specimen numbers are italicized.

SUPERORDER SQUAMATA
Order SAURIA
INFRAORDER PLATYNOTA
Family MOSASAURIDAE Gervais 1853
Subfamily MOSASAURINAE (Gervais 1853) Williston 1897

Clidastidae Cope, 1869b, p. 258.
Edestosauridae Marsh, 1876, p. 59, *nomen nudum.*
"mosasauriens mesorhynques" Dollo, 1890, p. 163.
Mosasauridae Williston, 1895, p. 169.
Mosasaurinae Williston, 1897d, p. 177.
Globidensidae Dollo, 1924, p. 188.

Diagnosis. Small rostrum present or absent anterior to premaxillary teeth. Fourteen or more teeth in dentary and maxilla. Cranial nerves X, XI and XII leave lateral wall of opisthotic through two foramina. No canal or groove in floor of basioccipital or basisphenoid for basilar artery. Suprastapedial process of quadrate distally expanded. Dorsal edge of surangular thin lamina of bone rising anteriorly to posterior surface of coronoid.

At least 31, usually 42-45 presacral vertebrae present. Length of presacral series exceeds that of postsacral, neural spines of posterior caudal vertebrae elongated to form distinct fin. Haemal arches fused to caudal centra. Appendicular elements with smoothly finished articular surfaces, tarsus and carpus well ossified.

Discussion. Because the fifth digit of the hind foot was not preserved in any of the known Belgian specimens of *Mosasaurus lemonnieri (M. conodon),* Dollo (1894) assumed that it was tetradactylate in this species. Apparently relying on Dollo's assumption and lacking positive evidence to the contrary, Williston (1895, 1897d, 1898b) diagnosed the Mosasaurinae as all having tetradactylate hind feet. However, Martin (1953) noted the presence of a fifth digit in his Pierre specimen of *M. conodon* and it is in all probability present in earlier members of the subfamily as well.

Tribe **MOSASAURINI** (Gervais 1853) new

Diagnosis. Twelve or less pygal vertebrae present. Radius and ulna widely separated by bridge of carpalia on distal border of antebrachial foramen. The skeletal areas in which these characters occur are as yet unknown in *Amphekepubis, Liodon* and *Compressidens.* The known morphology of these genera, however, is so similar to that found in *Clidastes* and *Mosasaurus* that in the absence of information to the contrary they are included in the *Mosasaurini.*

Genus *CLIDASTES* Cope 1868

(Text-figs. 42, 49B, 50, 65-70)

Clidastes Cope, 1868a, p. 181.
Edestosaurus Marsh, 1871a, p. 447.

Generic Type. *Clidastes iguanavus* Cope.

Additional References. Cope, 1869a, p. 233; 1869b, p. 258; 1869-1870, p. 211; 1871f, p. 412; 1872d, p. 266; 1872f, p. 330; 1874, p. 31; 1875, p. 130, pl. 19 fig. 11, pl. 55; 1878, p. 301. Marsh, 1872a, p. 291; 1872b, p. 463, pl. 11 figs. 1-2, pl. 12 fig. 1; 1872d, p. 496; 1897, fig. 23. Leidy, 1873, p. 281, pl. 34 fig. 11. Owen, 1877, pp. 690, 696, 701. Lydekker, 1888, p. 272. Hoffman, 1890, p. 1321. Williston and Case, 1892, p. 16. Merriam, 1894, pl. 3, figs. 9-10. Williston, 1897d, pp. 179, 181; 1897e, p. 245; 1898b, p. 195, pl. 27 figs. 2-4, pl. 28 fig. 6, pl. 29 fig. 2, pl. 39 lower figs., pl. 42 figs. 5-6, pl. 47 left fig., pl. 54 figs. 4-5, pl. 57 fig. 3; 1914, pp. 165, 166, fig. 68; 1925, p. 273. Hill, 1901, p. 328. Camp, 1923, p. 322; 1942, pp. 35, 37-40, fig. 24E. Gilmore, 1928, p. 87. Nopcsa, 1928, p. 177. Lane, 1947, p. 318. McDowell and Bogert, 1954, pp. 132, 138. Romer, 1956, p. 561, fig. 182F.

Diagnosis. Premaxilla with or without small rostrum anterior to premaxillary teeth. Fourteen to eighteen teeth in maxilla. Prefrontal forms small portion of posterolateral border of external nares, broad triangular ala projects laterally from supraorbital wing. Prefrontal and postorbitofrontal widely separated above orbits. Lateral margins of frontal nearly straight and converge anteriorly, median dorsal ridge weak. Ventral process of postorbitofrontal to jugal confluent with broadly exposed dorsal surface of postorbitofrontal. No ventroposterior process on jugal. Parietal foramen small, located entirely within parietal. Margins of dorsal parietal surface parallel one another and cranial midline to posterior base of diverging suspensorial rami, forming narrow rectangular field medially on parietal. Squamosal sends abbreviated wing medially to contact ramus from parietal. Otosphenoidal crest on prootic covers exit for cranial nerve VII laterally. Fourteen to sixteen teeth in pterygoid. Suprastapedial process of quadrate moderately large; tympanic ala very thick. Stapedial pit elliptical in form. Sixteen-18 teeth in dentary. Small projection of dentary anterior to first dentary tooth. Medial wing from angular contacts or nearly contacts coronoid. Dorsal edge of surangular very thin lamina of bone rising anteriorly to position high on posterior surface of coronoid. Retroarticular process of articular triangular in outline with heavy dorsal crest. Mandibular teeth usually compressed, bicarinate and with smooth enamel surfaces.

Vertebral formula *(Clidastes liodontus):* 42 presacral vertebrae, 7 pygals, 26 caudals with chevrons and transverse processes, about 46 terminal caudals (see Williston, 1898b, p. 143; Merriam, 1894, p. 10; and AMNH 192).

Articulating surfaces of cervical and anterior dorsal centra circular. Synapophysis located high in anterior portion of lateral surface of cervical centra, occupies anterodorsal portion of lateral surface of dorsal centra. Ventral border of anteroventral extension of synapophysis well developed on cervicals and anterior dorsals, reaches level of undersurface of centrum. Anterior zygopophysis of cervicals and dorsals connected by gently rounded, posteriorly descending crest to synapophysis. Zygosphene-zygantrum strongly developed, present at least throughout anterior three-fourths of dorsal series. Anterior base of atlas neural spine arises behind condylar facet; atlas synapophysis long and tubular. Hypapophyseal peduncle located posteriorly on ventral surface of cervical centra, articulation for hypapophysis flat and circular, strongly inclined posteriorly. Five hypapophysis-bearing cervicals, two or three more with rudimentary peduncles. Transverse processes of pygal vertebrae relatively long. Neural spines of caudal vertebrae longest and vertical on postsacrals 41-42 (Williston, 1898b, pl. 72).

Scapula smaller than coracoid. Glenoid articulating surfaces concave on both scapula and coracoid, and smoothly continuous. Superior border of scapula gently convex, posterior border slightly emarginated posteromedially. Coracoid expands broadly behind glenoid articulation. Distal and proximal ends of humerus widely expanded, facets for articulation with other elements and sites of muscle attachment very well differentiated. Proximal end of radius slightly expanded, ends in flat oval facet for articulation with humerus. Shaft of radius narrow. Distal end bears greatly expanded anterodistal flange, is thickened medially to form distinct facet for articulation with radiale.

Radiale very large. Intermedium shallow. Ulnare does not enter posteroventral border of antebrachial foramen. Metacarpal one less than metacarpal two in length, has moderate anterodistal flange resembling that of radius. Proximal ends of metacarpals greatly expanded. Phalangeal formula of manus estimated at 4-5-5-5-3.

Acetabular surfaces of pelvic elements concave, form solid smooth-surfaced bowl. Obturator foramen located near anterior margin of proximal end of pubis, dorsoanterior process large and rectangular. Ischiadic tubercle separated from acetabulum by short neck, ischiadic symphasis very narrow. Distal and proximal end of femur about equally expanded, internal trochanter small and located anteromedially from head. Fibular facet on femur well marked, tuberosity present on lateral surface dorsal to tibial facet. Tibia narrow, cartilage capped area of anterior flange extends from base of tibia nearly one-half way up shaft (Williston, 1898b, pls. 34, 36). Proximal end of fibula very slightly expanded, distal end fan-shaped (Williston, 1898b). Cartilage capped area of posterodistal flange of fibula limited to distal end of bone (Williston, 1898b).

Astragulus reniform, facet for fibula distinctly raised above that for tibia, dorsal notch between facets large (Williston, 1898b, pls. 34, 36). Calcaneum and fourth tarsal equal in size (Williston, 1898b). Metatarsal one expanded proximally, somewhat medially recurved. Metatarsal five hook-shaped, concave medially with wide convex ala laterally (both statements after Williston, 1898b).

DISCUSSION. Vertebrae of the Niobrara species of *Clidastes* closely resemble the type vertebra of *C. iguanavus,* the generotypic species, and certainly appear to be congeneric with it. All of the species from the Niobrara that have been referred to *Edestosaurus* belong to *C. propython* (see p. 128). Except for the cranium, the foregoing diagnosis is based exclusively on *C. propython* and *C. liodontus.* It does not exactly apply to either *C. iguanavus* or *C. sternbergi,* the differences being noted under the respective headings of these species.

Clidastes iguanavus Cope 1868

Clidastes iguanavus Cope, 1868a, p. 181.

Type. YPM 1601, from ". . . a marl pit near Swedesboro', Gloucester Co., N. J." (Cope, 1869a, p. 233). Type specimen consists of a vertebra.

Distribution. Marshalltown Formation, New Jersey.

Additional References. Cope, 1868b, p. 734; 1869b, p. 258; 1869c, p. 86; 1869-1870, p. 220, pl. 5 fig. 3; 1872f, p. 330; 1875, p. 266. Marsh, 1871a, pp. 447-449. Hoffman, 1890, p. 1322. Williston and Case, 1892, p. 16. Merriam, 1894, p. 36. Williston, 1898b, p. 196. Miller, 1955, pp. 904, 909.

Discussion. The type of the species is a single vertebra from the anterior thoracic region showing the general proportions and strong zygosphene-zygantrum articulation characteristic of *Clidastes* material from the Niobrara Chalk. It differs from vertebrae of Niobrara forms in the central articulations which are kidney shaped in outline, with a stronger emargination dorsally for the spinal cord, and in the relatively stouter proportions of the centrum. The vertebra was collected in sediments of late Campanian age and is thus from a horizon comparable to that of the Lower Pierre Formation in the Interior, in which *Clidastes* remains also occur.

Clidastes sternbergi Wiman 1920
(Text-figs. 71, 75C)

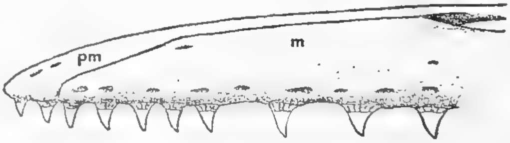
Clidastes sternbergi Wiman, 1920, p. 13, figs. 4-9, pls. 3, 4 figs 5a-b.

Type. In the Paleontological Museum in Upsala, Sweden, from ". . . Beaver Creek, Bilby's Ranch, in Logan Co., Kansas . . ." (Wiman, 1920, p. 13), collected by Levi Sternberg. Type specimen is a nearly complete skull and skeleton.

Distribution. Smoky Hill Member, Niobrara Formation, Kansas.

Additional References. Abel, 1922, fig. 270; 1924, fig. 35. Dollo, 1924, p. 198.

Diagnosis. Premaxilla "U"-shaped in horizontal cross-section, no rostrum present anterior to premaxillary teeth. Premaxillo-maxillary suture rises vertically from ventral jaw margin, turns abruptly and continues posteriorly in nearly straight line to position dorsal to eleventh maxillary tooth. Suture smoothly keeled and parallels longitudinal axis of maxilla. Median dorsal surface of parietal very broad. Parietal foramen moderately large, opens ventrally into lenticular excavation in parietal length of which exceeds that of dorsal opening by about three times. Foramen for cranial nerve VII enters prootic in center of prootic incisure. Infrastapedial process absent on quadrate.



Text-fig. 71. Lateral view of muzzle of *Clidastes sternbergi* (USNM 3777, × ⅔).

Vertebral formula: 31 presacral vertebrae, 4 pygals, 72 chevron bearing caudals (Wiman, 1920, p. 17).

Neural spines of caudal vertebrae longest on postsacrals 30-32, do not become vertical.

Scapula much smaller than coracoid. Superior border of scapula gently convex, posterior border emarginate. Coracoid expands broadly behind glenoid articulation. Distal and proximal ends of slender humerus only slightly expanded, radial and ulnar tuberosities absent, well-developed spherical head present. Radius elongate, proximal end slightly expanded. Shaft of radius narrow. Distal end bears moderately well-developed anterodistal flange.

At least four ossified elements in carpus. Metacarpal one equal to metacarpal two in length, anterodistal flange small or absent. Proximal ends of metacarpals, especially of two and three, not greatly expanded.

Acetabular surfaces of pelvic elements convex, do not form solid, smoothly surfaced bowl. Obturator foramen located near center of proximal end of pubis, dorsoanterior process rudimentary. Ischiadic tubercle separated from acetabulum by short neck. Shaft of femur slender, distal end more expanded than proximal, well-developed spherical head present. Distinct facets for tibia and fibula distally. Tibia and fibula slender, slightly expanded at distal and proximal ends.

DISCUSSION. The following cranial peculiarities are common to the type of *Clidastes sternbergi* and the only specimen (USNM 3777) here referred to this species; a) the parietal is unusually short and broad, and b) the surangular and articular meet at the bottom of a notch on the lateral wall of the lower jaw, below the center of the quadratomandibular articulating surface. These highly distinctive characters are unknown in any other described species of *Clidastes* and necessitate the assignment of the above specimen to Wiman's species. However the type differs from this specimen in that the supra- and infrastapedial processes of the quadrate are broadly fused, and the dorsal margins of the parietal meet posteriorly on the midline of the skull, forming a "V"-shaped parietal surface. The quadrate looks pathologic (Wiman, 1920, fig. 5) and perhaps the converging margins of the parietal are due to faulty restoration, for Wiman (1920, p. 13) mentions that much of the surface of the type skull has been covered with a thin veneer of plaster.

Wiman's type skeleton of *C. sternbergi* presents some very primitive features. The humerus and femur retain a fully-developed spherical head. The pro- and epipodial elements are slenderer than those of any known mosasaurian, approaching their condition in terrestrial lizards, as Wiman (1920, p. 18, pl. 4) has demonstrated. Only four pygal vertebrae are present which, assuming none have been lost, is the least number known for any mosasaur. If the elements identified by Wiman (1920, fig. 4) as nasals are not the vomers which have been crushed upwards into the external narial opening, the nasals then are very large and certainly present a very primitive appearance.

Dollo (1924, p. 198) suggested that Wiman's skeleton was a composite, but in view of the fact that characters separating this specimen from any other described species of mosasaur occur throughout its skeleton this possibility is unlikely. *Clidastes* affinities are shown in the elongation of the caudal spines near the center of the tail, the long fused haemal arches, and the development of a broad anterodistal flange on the radius. If the vertebral column is complete, as would seem to be the case, the small number of thoracic vertebrae together with the small scapula and slender limbs may justify the establishment of a new genus separate from *Clidastes* for this species.

Clidastes liodontus Merriam 1894
(Text-figs. 26, 32-34, 43, 60, 72, 73, 75B, 76B, 98A; Plate I fig. 1)

Clidastes liodontus Merriam, 1894, p. 35.

TYPE. Formerly at Bayerische Staatssammlung für Paläontologie but probably destroyed during the Second World War (personal communication, R. Dehm 1963), from ". . . Niobraraschichten der oberen Kreide von Logan County, Kansas . . ." (Merriam, 1894, p. 3), collected by C. H. Sternberg or G. Baur. Type specimen consists of maxillae, premaxilla and dentaries.

DISTRIBUTION. Smoky Hill Member, Niobrara Formation, Kansas.

Additional References. Marsh, 1880, pl. 1 fig. 1. Owen, 1880, pl. 8 fig. 1. Williston and Case, 1892, pls. 2-3. Williston, 1893a, p. 83, pl. 3; 1895, pl. 17 fig. 1; 1897c, pl. 13 fig. 1; 1898b, p. 204, pls. 10-12, pl. 24 fig. 6, pl. 31 fig. 6, pls. 33-34, pl. 60 figs. 6-7; pl. 62 fig. 3, pl. 71, pl. 72 fig. 1; 1925, fig. 146. Ballou, 1898, figs. 5-6. Osburn, 1906, pl. 8 fig. 26. ?Pompeckj, 1910, p. 136. Wiman, 1920, figs. 8a-b. Gregory, 1951, fig. 6. Romer, 1956, fig. 65. Edmund, 1960, p. 89, figs. 17, 25a-b. Kauffman and Kesling, 1960, fig. 6c. Russell, 1964, figs. 2-4.

Referred Specimens. *AMNH* nos. ***192,* **1548. *YPM* nos. **1333, 1334, ***1335,* 3982, *3996, 4001, 24914, and three unnumbered specimens. *USNM* nos. 6546, **11647, *11719. MCZ* nos. 278, 1618, 1621. *KU* nos. 1039, *1121. FHM* no. **10668. *PU* no. 17249.

Diagnosis. Premaxilla "V"-shaped in horizontal cross-section, small rostrum present anterior to premaxillary teeth. Posteroventral portion of root of second premaxillary tooth not exposed on sutural surface with maxilla. Premaxillo-maxillary suture rises posteriorly to position varying from dorsal to fourth to dorsal to sixth maxillary tooth and parallels longitudinal axis of cranium. Fourteen to fifteen teeth in maxilla. Median dorsal surface of parietal narrow. Parietal foramen small, close to or distinctly separated from frontal suture. Parietal foramen opens ventrally into brain cavity without broadening into wide excavation. Anterior border of prootic descends beneath prootic incisure without forming shelf. Foramen for cranial nerve VII leaves brain cavity through medial wall of prootic. Infrastapedial process absent on quadrate. Sixteen teeth in dentary.

Discussion. In his description of the type of *C. liodontus,* Merriam (1894, p. 35) noted that, "Die maxillen sind vorn bus ungefahr zum 5. Zahn von der Praemaxillare shrag abgeschnitten." The species diagnosed above is the only Niobrara *Clidastes* to which this statement could apply. Incomplete locality information suggests that *C. liodontus* does not occur in the uppermost levels of the Niobrara chalk.

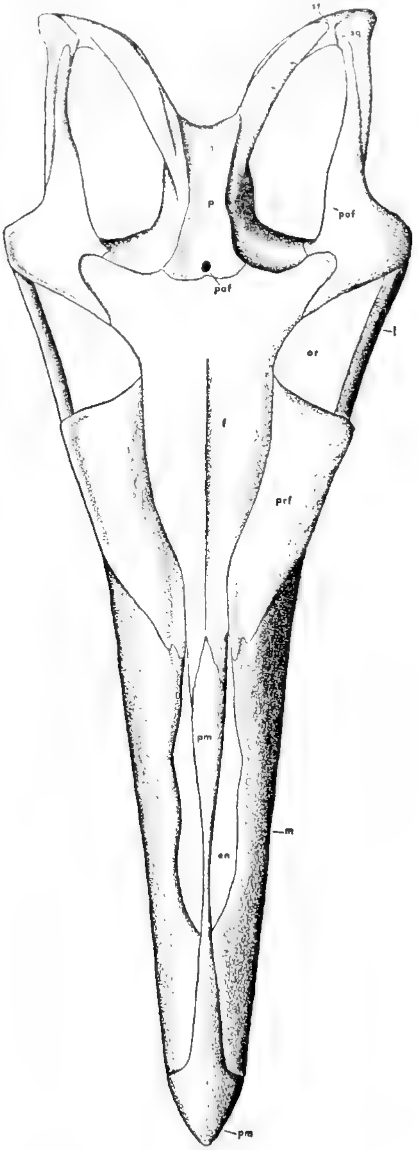
Clidastes propython Cope 1869
(Text-figs. 2B, 4B, 12-14, 22B, 39, 46B, 74, 75A, 76A)

Clidastes propython Cope, 1869b, p. 258.
?*Clidastes cineriarum* Cope, 1871a, p. 572.
Edestosaurus dispar Marsh, 1871a, p. 447.
Edestosaurus velox Marsh, 1871a, p. 450.
Clidastes wymani Marsh, 1871a, p. 451.
Clidastes pumilus Marsh, 1871a, p. 452.
Edestosaurus tortor Cope, 1872a, p. 297.
Clidastes vymanii, Cope, 1872b, p. 170.
Edestosaurus stenops Cope, 1872d, p. 268.
Edestosaurus rex Marsh, 1872b, p. 463.
Clidastes medius Merriam, 1894, p. 34.
Clidastes westi Williston and Case, 1892, p. 29.

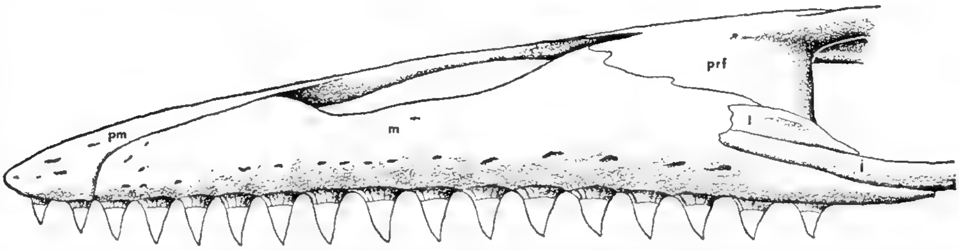
Type. ANSP 10193, from ". . . The Rotten Limestone, near Uniontown in Alabama," (Cope, 1869b, p. 258), collected by Dr. E. R. Showalter. Type specimen consists of a nearly complete skull and skeleton, except pelvic arch.

Distribution. Selma Formation, Alabama; Smoky Hill Member, Niobrara Formation, Kansas and South Dakota; Lower Pierre Formation, Kansas and South Dakota.

Additional References. Cope, 1869f, p. 117; 1869-1870, p. 221, figs. 49(5), 50-51, pl. 12 figs. 1-21; 1871b, p. 583; 1871c, p. 132; 1871e, pp. 217, 220, figs. 15, 19; 1871f, p. 413; 1872b, p. 170; 1872d, pp. 266, 269; 1872e, p. 141; 1872f, p. 330; 1874, pp. 33, 34; 1875, pp. 131, 133, 137, 265-266, pl. 14 figs. 1-2, pl. 16 figs. 1, 6, pl. 17 figs. 1, 7-8, pl. 18 figs. 1-5, pl. 19 figs. 1-6, pl. 21 figs. ?14-17, pl. 36 figs. 3, 4, pl. 37 figs. 1-3, pl. 38 figs. 2-3; 1877, p. 583; 1878, p. 303; 1891, fig. 26; 1898, fig. 27. Marsh, 1871b, p. 104; 1872b, pp. 451, 464, pl. 11 figs. 3-4; 1872d, p. 497; 1897, p. 527. Leidy, 1873, pl. 35 fig. 14. Owen,



Text-fig. 72. Dorsal view of skull of *Clidastes liodontus* (reconstructed after YPM 1335, × 2/5).

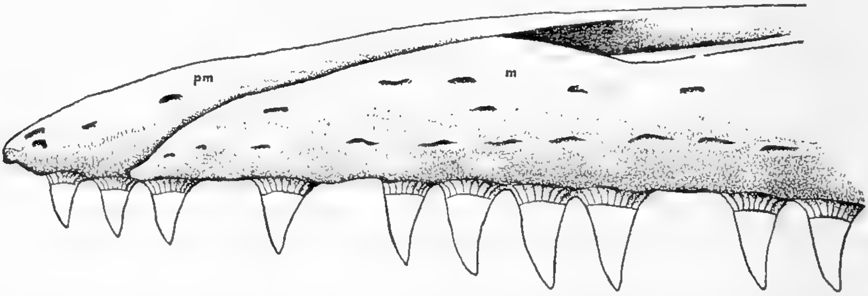


Text-fig. 73. Lateral view of muzzle of *Clidastes liodontus* (reconstructed after YPM 1335, × 1/2).

1877, fig. 23. Hoffmann, 1890, p. 1322. Williston, 1891, p. 345; 1893b, pp. 110, 111; 1897c, p. 110; 1897e, pp. 245-246; 1898a, p. 29; 1898b, pp. 100-234, 197-205, pl. 23, pl. 24 fig. 7, pl. 27 fig. 1, pl. 28 figs. 1-4, pls. 35-38, pl. 39 upper fig., pl. 53, pl. 60 figs. 4-5, pl. 61 fig. 4, pl. 64 fig. 1; 1902, pp. 248-253; 1914, fig. 71; 1925, figs. 58, 158b. Williston and Case, 1892, pp. 17, 28, 30, 31, pls. 4-6. Merriam, 1894, pp. 34-36, pl. 1 fig. 4, pl. 3 figs. 6-7. Iakovlev, 1906, fig. 1. Holland, 1908, p. 162, fig. 5. Sternberg, 1909, p. 135, fig. 6; 1917, p. 21. ?Woodward, 1922, p. 6. Camp, 1923, fig. 22. Chaffee, 1939, fig. 1(2). Lane, 1947, pp. 318, 319, fig. 7. Zangerl, 1948, p. 15. Gregory, 1951, fig. 4b; 1952, fig. 6. McDowell and Bogert, 1954, fig. 32. Romer, 1956, figs. 108c, 145b. Sevon, 1958, p. 145, fig. Edmund, 1960, p. 89, fig. 25f.

REFERRED SPECIMENS. *AMNH* nos. 182, R173, 1507, **1513 *(C. tortor)*, 1525, 1546, 1575 *(C. stenops)*, ?1579 *(C. cineriarum)*, 1593, *ND2, *5812. *YPM* nos. *1100 *(C. dispar)*, 1105 *(C. velox)*, 1120 *(C. wymani)*, 1123 *(C. pumilus)*, 1308, *1310 (C. rex)*, 1314, 1315, *1316, 1317, 1318, 1319, 1321, 1324, 1328, *1368, 1371 and thirteen unnumbered specimens. *USNM* nos. 3765, 3778. *MCZ* no. 1625. *KU* nos. **1000, 1005, 1026 *(C. westi)*, 1058, 1108, 1124, 1134. *CNHM* nos. UR901, **P12856. *CM* no. **1190.

DIAGNOSIS. Premaxilla "V"-shaped in horizontal cross-section, small rostrum present anterior to premaxillary teeth. Posteroventral portion of root of second premaxillary tooth exposed on sutural surface with maxilla. Premaxillo-maxillary suture rises posteriorly in gentle curve to terminate at point above seventh maxillary tooth. Premaxillary suture of maxilla smoothly keeled and parallels longitudinal axis of maxilla. Sixteen-18 teeth in maxilla. Median dorsal surface of parietal moderately broad. Parietal foramen small, lies close to suture with frontal and opens ventrally into elliptical excavation in parietal, length of which exceeds that of dorsal opening by about five times. Anterior border of prootic forms shelf beneath prootic incisure, then descends abruptly to

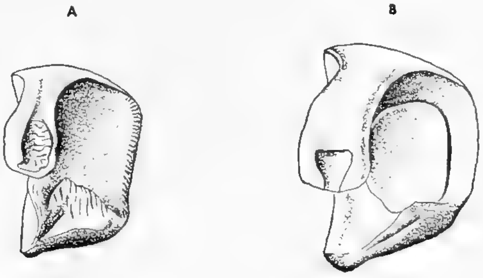


Text-fig. 74. Lateral view of muzzle of *Clidastes propython* (YPM 1319, × ½).

Text-fig. 75. Dorsal view of parietal. A. *Clidastes propython* (AMNH ND2). B. *Clidastes liodontus* (YPM 1335). C. *Clidastes sternbergi* (USNM 3777), all × ½.

basisphenoid. Foramen for cranial nerve VII leaves brain cavity through medial wall of prootic. Infrastapedial process present on quadrate. Seventeen to eighteen teeth in dentary.

Discussion. The type specimens of each species considered above as a synonym of *C. propython* include, with the exception of *C. cineriarum*, good cranial material that would not justify their specific separation from the excellent type of the former species. *C. cineriarum* is provisionally placed here because of the large size of the single pterygoid tooth, the only cranial material preserved with the type. The prefrontal figured with the type of *C. stenops* (Cope, 1875, pl. 14 fig. 2a) has been laterally crushed, and the unusual condition of this element in *C. medius* is probably best considered as due to post-mortem distortion or damage (see also Williston, 1898b, p. 203).



Text-fig. 76. Posterior view of right quadrate. A. *Clidastes propython* (YPM 1368, × ½. B. *Clidastes liodontus* (YPM 3996, × ½).

Genus *MOSASAURUS* Conybeare 1822

(Text-fig. 59)

Mosasaurus Conybeare, 1822, p. 198.
Batrachiosaurus Harlan, 1839a, p. 24.
Batrachotherium Harlan, 1839b, p. 89.
Macrosaurus Owen, 1849, p. 382.
Drepanodon Leidy, 1856, p. 255.
Lesticodus Leidy, 1861, p. 10.
Baseodon Leidy, 1865, p. 69.
Nectoportheus Cope, 1868a, p. 181.
Pterycollosaurus Dollo, 1882, p. 61.

Generic Type. *Mosasaurus hoffmanni* Mantell 1829.

Additional References (North American material). Morton, 1830a, p. 289; 1834, p. 27. Harlan, 1834b, p. 81; 1834e, p. 32; 1835a, p. 285. Bronn, 1838, p. 760. DeKay, 1842, p. 28. Pictet, 1845, p. 621; 1853, p. 504. Holmes, 1849, p. 197. Gibbes, 1851, p. 3. Emmons, 1858, p. 213, fig. 34? Leidy, 1858b, p. 176; 1860, p. 91; 1865a, p. 30, pl. 7 figs. 1, ?15-16, pl. 17 figs. ?12-13; 1865b, p. 69; 1873, p. 279. Cope, 1869b, p. 260; 1869-1870, p. 186, ?fig. 49(2); 1871f, p. 401; 1875, p. 269; 1877, p. 567; 1879b, p. 36. Hayden, 1872, p. 91. Marsh, 1877, p. 346. Lydekker, 1888, p. 261. Merriam, 1894, p. 6. Williston, 1895, p. 166; 1897d, pp. 177, 179, 181; 1898b, pp. 91, 195; 1902, p. 249; 1914, p. 165. Douglass, 1902, p. 212. Pompeckj, 1910, pp. 130, 131. Gilmore, 1912b, p. 2; 1926, pl. 62 fig. 8; 1928, p. 87. Sternberg, 1915, p. 132. Camp, 1923, p. 322. Nopsca, 1928, p. 177. McDowell and Bogert, 1954, pp. 132, 138. Romer, 1956, p. 561.

Diagnosis. Premaxilla with small rostrum anterior to premaxillary teeth. Thirteen to fifteen teeth in maxilla. Prefrontal forms small portion of posterolateral border of external nares, small to large triangular ala projects laterally from supraorbital wing. Frontal not emarginate above orbits, median dorsal ridge present. Parietal foramen moderately large, closely embraced on either side by tongues from frontal. Dorsal parietal field long and narrow. Ventral process of postorbitofrontal to jugal confluent with well exposed dorsal surface of postorbitofrontal. Ventroposterior process on jugal large. Otosphenoidal crest on prootic may cover exit for cranial nerve VII laterally. Seven to ten teeth in pterygoid. Suprastapedial process of quadrate relatively short, tympanic ala moderately thick with groove around external margin. Stapedial pit elliptical in form. Fourteen to seventeen teeth in dentary. Dentary terminates abruptly in front of first dentary tooth. Median descending wing from coronoid incipient or well developed. Dorsal edge of surangular rather thin lamina of bone, rising anteriorly to middle of posterior surface of coronoid. Retroarticular process of articular rectangular in outline. Mandibular teeth usually prismatic with relatively flat external and rounded internal surfaces.

Postcranial skeleton much like *Clidastes* with following exceptions. Zygosphene-zygantrum limited to anterior portion of vertebral column or absent. Transverse processes of pygal vertebrae relatively short. Scapula and coracoid subequal in size. Ischium well expanded at symphysis. Internal trochanter located medially from head of femur. Phalanges more numerous and of stouter proportions than in *Clidastes.*

Discussion. *Batrachiosaurus, Batrachotherium* and *Pterycollosaurus* were based solely on the type skull and skeleton of *Mosasaurus missouriensis,* which is surely congeneric with *Mosasaurus hoffmanni,* the type species of the genus. The names *Macrosaurus, Drepanodon, Lesticodus, Baseodon* and *Nectoportheus* were all based on inadequate material from the Cretaceous of the Atlantic seaboard and are discussed under the genus *Mosasaurus* in the section on names of uncertain taxonomic standing.

Williston (1895, p. 168; 1897d, p. 179; 1898b, p. 195) remarked several times on the close similarity between *Mosasaurus* and *Clidastes.* The only means by which he distinguished them (1902, p. 250) was in the presence of a zygosphene in the latter genus and its absence in the former. *M. conodon* is exactly intermediate in this regard, retaining the zygosphene in the anteriormost portion of the vertebral column only. The species of *Mosasaurus* have almost certainly been derived from *Clidastes.*

M. ivoensis, M. missouriensis and *M. maximus-hoffmanni* all have powerfully constructed skulls with heavy prismatic teeth numbering 13-14 in the maxillae and 14-15 in the dentaries. *M. missouriensis* has 10 hypapophysis-bearing anterior vertebrae and *M. hoffmanni* has 13. These species seem to form a phylogenetic series. *M. conodon,* however, has a slender skull with compressed and, at most, weakly prismatic teeth numbering 15 in the maxilla and 17 in the dentary. There are only seven hypapophysis-bearing anterior vertebrae.

It is quite possible that *M. conodon* descended from *C. propython,* and the *M. ivoensis-M. missouriensis-M. maximus* phylum were derived at an earlier time from a more primitive *Clidastes* stock. A complicating factor exists in the great similarity between the forelimbs of *M. missouriensis* and *M. conodon.* The pectoral crest is, however, medially located on the proximoventral surface of the humerus in *M. ivoensis* just as Williston (1898b, p. 147) states it is in *M. missouriensis;* in *M. conodon* it is nearly as anteriorly placed as in *Clidastes.* The forelimb of *M. missouriensis* might well have been derived from that of *M. ivoensis* and came to resemble in parallel fashion that of *C. propython* and *M. conodon.* Whether this is true or not, the genus *Mosasaurus* may include at least two closely related lines of large mosasaurines evolving in parallel ways, but derived from different ancestral species within the *Clidastes* level of evolution.

Mosasaurus conodon (Cope 1881)
(Text-figs. 46A, 47B, 49A, 51, 56, 61, 77, 78)

Clidastes conodon Cope, 1881, p. 588.
?*Mosasaurus lemonnieri* Dollo, 1889b, p. 278.

Type. AMNH 1380, from ". . . near Freehold, Monmouth County, New Jersey . . ." (Cope, 1881, p. 587), collected by Prof. Samuel Lockwood. Type specimen includes a dentary, splenial, angular, coronoid, articular, squamosal, twelve vertebrae, scapula, coracoid, humerus and pectoral limb elements.

Type of *Mosasaurus lemonnieri* in the Musée Royal d'Histoire Naturelle de Belgique, from ". . . Mesvin, localité située à 4 kil. 5 de Mons," Belgium (Dollo, 1889b, p. 273). Type specimen includes a skull and anterior cervical vertebrae (ibid., p. 274).

Distribution. ?Taylor Marl, Texas; Marlbrook Marl, Arkansas; Verendrye Member, Lower Pierre Formation, Virgin Creek Member, Upper Pierre Formation, South Dakota; Navesink and younger Cretaceous, New Jersey; ?Craie brune phosphatée de Ciply, Belgium.

Additional References. Martin, 1953, pp. 1-62. Miller, 1955, p. 909.

Referred Material, *AMNH* nos. 1387, ?1395, 1397. *YPM* nos. ?379, ?1500, 1510, 1573. *ANSP* nos. 8469, 8480, 8501, 8502, ?8504, ?8509. *USNM* nos. *11396,* 11904, 18255. *SDSM* no. *452.*

Diagnosis. Tuberosity present(?) below stapedial pit on lower medial body of quadrate; suprastapedial and infrastapedial process small in lateral profile. Ventral wing of coronoid well developed on medial surface of lower jaw. Dentary very slender, as in *Clidastes,* dorsal and ventral margins converge gradually anteriorly, element comes to rounded tip anterior to first dentary tooth. Fifteen teeth in maxilla, seventeen teeth in dentary and ten teeth in pterygoid. Marginal teeth slenderer than in *M. missouriensis, M. maximus* and *M. ivoensis,* tips posteriorly recurved. External facets narrow and more numerous than in *M. maximus* (Cranial diagnosis based on Dollo, 1889b, pls. 9-10; 1924, p. 181).

Text-fig. 77. Type dentary of *Mosasaurus conodon* (AMNH 1380, × ⅕).

Vertebral formula: 45 presacral vertebrae, 8 pygals, 21 caudals with chevrons and transverse processes, about 54 terminal caudals.

Articulating surfaces of cervical and anterior dorsal centra wider than deep, smoothly elliptical in outline; posterior dorsals become circular, then vertically oval. Zygosphene-zygantrum present on second through thirteenth postcranial vertebrae. Anterior hypapophyseal facets face ventroposteriorly, facing directly ventrally further posteriorly. Seven hypapophysis-bearing cervicals. Transverse processes of pygal vertebrae relatively short. Neural spines of postsacral vertebrae vertical on postsacrals 42-44, longest on postsacral 36.

Scapula and coracoid subequal in size. Glenoid articulating surfaces concave on both scapula and coracoid, and smoothly continuous. Superior border of scapula gently convex, posterior border slightly emarginated posteromedially. Coracoid expands medially behind glenoid articulation. Distal and proximal ends of humerus widely expanded, facets for articulation with other elements and sites of muscle attachment very well differentiated. Proximal end of radius expanded, shaft bears greatly expanded anterodistal flange. Distal end of radius thickened to form facet for articulation with radiale. Radiale very large. Intermedium of average proportions. Ulnare does not enter posteroventral border of antebrachial foramen. Metacarpal one equal to metacarpal two in length, is greatly expanded anteriorly at both ends. Proximal ends of other metacarpals moderately expanded. Phalangeal formula of manus estimated at 9-10-10-10-4.

Acetabular surfaces of pelvic elements concave, form nearly solid, smoothly surfaced bowl. Obturator foramen located near center of proximal end of pubis, dorsoanterior process large and rectangular. Ischiadic tubercle small, separated from acetabulum by very short neck. Shaft of ischium narrow, well expanded medially at symphysis. Distal end of femur more expanded than proximal, internal trochanter moderately large and located medially from head. Fibular facet on femur well marked, sharply set at acute angle to tibial facet. Tibia with broad anterior flange, cartilage capped area of which extends from base of tibia one-half way up shaft. Distal end of fibula more expanded than proximal, fibular shaft narrow.

Astragulus approximately quadrilateral, sub-reniform; facet for fibula slightly raised above that for tibia, dorsal notch between facets broad and shallow. Metatarsal one strongly expanded at ends, especially proximally. Metatarsal five broad; concave medial border gives it slight hook-shaped appearance. Approximate phalangeal formula of pes 8-9-9-9-4 (postcranial diagnosis based on descriptions and figures of SDSM 452 given by Martin, 1953).

Discussion. The excellent skeleton preserved in the Museum of the South Dakota School of Mines and Technology is assigned to *M. conodon.* It has been described by Harold Martin (1953, unpublished MA thesis) and placed in a new species close to *M. missouriensis.* Unfortunately most of the cranium of this specimen was lost through erosion so that a direct comparison with extant skulls of *M. missouriensis* is impossible.

A comparison of the forepaddle of SDSM 452 with that of *M. missouriensis* (Williston, 1895, pl. 16 fig. 1) shows few significant differences. The intermedium and radius narrowly exclude the radiale from bordering on the antebrachial foramen in Martin's specimen, while they widely exclude the radiale in *M. missouriensis.* The ulnare and fourth carpal are large and subequal in size in the present specimen. Although both elements are small, the fourth carpal is even smaller than the ulnare in *M. missouriensis.* Goldfuss (1845, p. 191) states that there are ten hypapophysis-bearing vertebrae in *M. missouriensis,* but there are only six in the present specimen. These differences suggest that SDSM 452 belongs to a species distinct from *M. missouriensis.*

Postcranial material in the type of *M. conodon* from the Maestrichtian of New Jersey is very similar to Martin's specimen from the Virgin Creek Member of the Pierre Shale. The articulating surfaces of the cervicals and anterior dorsals are similar, and those of the terminal caudals are wider than deep in both specimens. The zygosphene-zygantrum is present on the second through tenth postcranial vertebrae in the New Jersey type; it is present on the second through thirteenth in SDSM 452. There are five hypapophysis-bearing cervicals and an additional vertebra with a large peduncle in the New Jersey type and six hypapophysis-bearing cervicals in SDSM 452. These two specimens are therefore included in the same species. The type of *M. conodon* contains a slender *Clidastes*-like dentary fragment with alveoli for 15 teeth. Probably at least two more teeth were present in the missing anteriormost portion of the element. The atlas synapophysis is compressed as in *M. maximus,* not tubular as in *Clidastes.* The ventral border of the anteroventral extension of the synapophysis does not descend to a level with the undersurface of the centrum in the type specimen.

USNM 18255 from the Verendrye Member of the Pierre Shale is referred to *M. conodon* because of the slender *Clidastes*-like form of the dentary and the similarity of the humerus to that of the type. USNM 11396 from the Marlbrook Marl of Arkansas includes a nearly complete pelvis and 35 vertebrae from the more posterior regions of the column. The pelvis is identical to that of SDSM 452 save that the ischiadic tubercle is more prominent. There are nine pygal vertebrae as compared with eight in the South Dakota specimen, and the articular facets of the terminal caudals are wider than deep. One of the caudals with only a button remaining of the transverse process has an anteriorly sloping neural spine. In SDSM 452 the spine also slopes forward on the last (21st) caudal with transverse processes. USNM 11904, consisting of forearm elements and posterior dorsal vertebrae, was collected by L. W. Stephenson from Cretaceous strata one mile west of Paris, Texas. On a National Museum catalogue card Stephenson indicated that the specimen came from the "upper part of Taylor Marl?" According to the USGS Geological Map of Texas (1937 edition) the Brownstown Marl, not the Taylor Formation, outcrops west of Paris. This unit is of approximately Santonian age (Stephenson et al., 1942). It is surprising that a humerus agreeing exactly in morphology with those of USNM 11396 and 18255, both from the late Campanian, should occur in such an ancient horizon, and it would seem more natural for Taylor strata to produce such a specimen.

There are detailed resemblances between the vertebral column of *M. conodon* and those referred to *M. lemonnieri* from the Maestrichtian of Belgium (see Dollo, 1894). SDSM 452 has a vertebral formula of 7 cervicals, 38 dorsals, 8 pygals and about 75 chevron-bearing caudals, as compared with 7 cervicals, 39 dorsals, 12 pygals and about 76 chevron-bearing caudals for *M. lemonnieri*. In the dorsal series there are 17 thoracics and 21 lumbars as compared with 18 thoracics and 21 lumbars in *M. lemonnieri*. The zygopophyses become functionless on the first chevron-bearing caudal of SDSM 452 and on the fourth pygal of *M. lemonnieri*. In the caudal series the neural spine is vertical on postsacrals 42-44 in SDSM 452, and in *M. lemonnieri* it is vertical on postsacrals 36-37, the longest neural spine occurring on postsacral 36 in both forms. The longest haemal spine occurs on postsacral 47 in SDSM 452 and on postsacral 46 in *M. lemonnieri*, and the transverse processes become rudimentary in the vicinity of the eighteenth caudal in both forms. It should be noted that marginal teeth in SDSM 452 and in the type of *M. conodon* are smoothly surfaced, but the teeth of YPM 1573 and the single tooth preserved in the dentary of USNM 18255 are narrowly faceted, as in *M. lemonnieri*.

Text-fig. 78. Tooth preserved in type dentary of *Mosasaurus conodon* (AMNH 1380, × ¾).

However Dollo (1894, p. 230) did not observe zygosphene-zygantrum articulations in the vertebral column of *M. lemonnieri*, which are functional in the anteriormost presacral series of *M. conodon*. Dollo lists 12 pygal vertebrae in *M. lemonnieri*, in SDSM 452 there are but eight. The posterior caudal centra of *M. lemonnieri* are vertically oval but in *M. conodon* they are horizontally oval.

The zygosphene-zygantrum articulation may be variably developed within a species of *Platecarpus* and it is possible that they were either small and overlooked by Dollo in *M. lemonnieri* or were indeed absent. They are only present in a small portion of the column in *M. conodon*. It is quite possible that Dollo included anterior caudals with rudimentary haemal arches in the pygal region of *M. lemonnieri*, thus accounting for the differing pygal count between the two forms. Except for the more heavily constructed proximal end of the femur, the appendicular girdles and limbs of the American form are identical to those figured by Dollo (1894, pls. 3-4) of *M. lemonnieri*. In summary, there seems to be little justification for separating *M. lemonnieri* from *M. conodon* and for this reason the cranial portion of the diagnosis is based upon the more complete cranial material from Belgium.

Mosasaurus ivoensis Persson 1963
(Text-fig. 79)

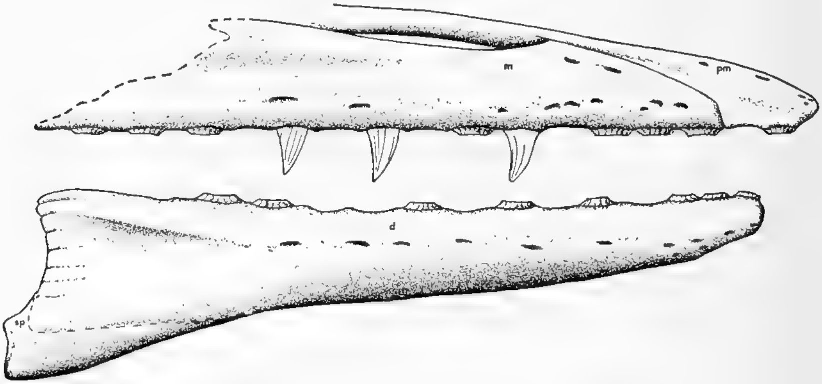
Clidastes stenops Williston, 1902, pp. 248-250, pl. 12 lower fig.
Mosasaurus hoffmanni ivoensis Persson, 1963, p. 5.

TYPE. No. R1292 in Swedish Museum of Natural History, Stockholm. Type specimen is the crown of a tooth (Persson, 1963, p. 5).

Referred Specimen. *KU* no. *1024, from the Niobrara Chalk, collected by Charles H. Sternberg.

Diagnosis. Narial emargination begins dorsal to fourth maxillary tooth. Fourteen teeth in maxilla. Splenial has weak median dorsal keel on articulating surface. Fourteen teeth in dentary. Dentary relatively heavy with parallel dorsal and ventral margins up to point beneath third and fourth dentary tooth, margins then converge rapidly anteriorly to a rounded tip. Marginal teeth short relative to other species of *Mosasaurus* and triangular in lateral outline, prisms numerous (6-7) on external face, as many as eleven distinct prisms on internal face.

Discussion. The referred specimen includes the right side of a muzzle, with the premaxilla, dentary, splenial, jugal and possibly also a pterygoid and ectopterygoid, although the latter two elements may belong to a *Tylosaurus*. The atlas and axis vertebrae, and a large part of the left forepaddle are also present. The maxillary teeth are indistinguishable from those described by Persson (1959, p. 462) from the lower Campanian of southern Sweden, and later named *M. hoffmanni ivoensis* by the same author (Persson, 1963, p. 5). The relationship of the above specimen with *Mosasaurus* is shown by the abbreviated rostrum of the premaxilla and the number (14 each in the dentary and maxilla) and form of the teeth. The articular surface of the splenial is more nearly circular when viewed from the posterior than that of any other mosasaur known to the author. The jugal resembles that of *Mosasaurus* except that the ventroposterior process is very weakly developed.



Text-fig. 79. Muzzle referred to *Mosasaurus ivoensis* (KU 1024, × ⅕).

A zygantrum is apparently absent on the axis vertebra (Williston, 1902, p. 249).

The foreflipper of this specimen was figured by Williston (1902, pl. 12 lower figure). The humerus bears evidence of its *Mosasaurus* affinities by its general proportions, pectoral crest located away from the anterior border of the bone, and the large ulnar tuberosity. The post-glenoid process is, however, very small and the radial tuberosity is apparently absent. The radius resembles that of *Clidastes* more closely than that of *Mosasaurus,* but the shaft is broader and the distal extremity less dilated than in the former genus. The bones of the carpus are evidently in a state of partial disarray. The element in the position of a radiale is very small, which together with the shallow rectangular outline of the intermedium give the carpus a strikingly *Ectenosaurus*-like appearance quite unlike that typical of *Clidastes* and *Mosasaurus.* The first metacarpal is not nearly so short and broad as in *M. hoffmanni, M. maximus, M. missouriensis* and *M. lemonnieri* and has an even less rectangular outline than in *Clidastes.* The element figured by Williston in the position of the ulna is probably a metacarpal.

Mosasaurus missouriensis (Harlan 1834)

Ichthyosaurus missouriensis Harlan, 1834a, p. 440.

Ictiosaurus missuriensis, Harlan, 1834d, p. 124.
Batrachiosaurus missouriensis, Harlan, 1839a, p. 24.
Batrachotherium missouriensis, Harlan, 1839b, p. 89.
Mosasaurus maximiliani Goldfuss, 1845, p. 179, pls. 6-8
Mosasaurus neovidii Meyer, 1845, p. 312.
Mosasaurus missouriensis, Leidy, 1858a, p. 90.
Pterycollosaurus maximiliani, Dollo, 1882, p. 61.
Mosasaurus horridus Williston, 1895, p. 166, pls. 14-16.

TYPE. Geol.-Paläont. Institut der Rhein. Friedrich-Wilhelm-Universität cat. no. GOLDFUSS 1327 (personal communication, H. K. Erben 1964) from ". . . der Gegend des Big-Bend, einer grossen Krummung des Missouri, zwischen Fort Lookout und Fort Pierre . . ." (Goldfuss, 1845, p. 175), collected by Maj. Benjamin O'Fallon. The anterior portion of the rostrum described by Harlan has not been located. Type specimen is a nearly complete skull, most of the vertebral column and fragments of the pectoral girdle (Goldfuss 1845).

DISTRIBUTION. Upper Pierre Formation, South Dakota; Bearpaw Formation, Montana.

ADDITIONAL REFERENCES. Harlan, 1834b, p. 80; 1834c, p. 408, pl. 20 figs. 1-8; 1834e, p. 31; 1835a, p. 284; 1835b, p. 348, pl. figs. 1-6; 1839c, p. 302; 1842, p. 142. Goldfuss, 1847, p. 123. Owen, 1849, p. 382; 1851, p. 32; 1877, pp. 683, 696, 701, figs. 5, 6, 16, 18. Gibbes, 1850, p. 77; 1851, p. 8. Pictet, 1853, p. 505. Hayden, 1857, p. 113; 1872, p. 87. Meek and Hayden, 1857, pp. 117, 119. Emmons, 1858, p. 218. Leidy, 1858c, p. 11; 1860, p. 92; 1865a, pp. 30, 33, 117; 1865b, p. 69. Cope, 1869b, p. 263; 1869c, p. 86; 1869-1870, pp. 189, 195; 1871a, p. 571; 1871f, pp. 386, 401; 1875, p. 269; 1877, p. 567; 1879b, p. 36. Hoffman, 1890, p. 1320. Baur, 1892, p. 9. Merriam, 1894, p. 5. Williston, 1895, p. 165, pl. 16 fig. 1; 1897a, p. 95; 1898b, pp. 103-154, pls. 19-21, 32; 1914, p. 151; 1925, p. 273. Ballou, 1898, fig. 1. Osburn, 1906, pl. 8 fig. 27. Camp, 1942, p. 45. Simpson, 1942, pp. 162, 172. Kauffman and Kesling, 1960, p. 231, figs. 1, 6a, tables 4-6.

REFERRED SPECIMENS. *USNM* nos. 4910, *8086. *KU* no. **1034 (*M. horridus*)

DIAGNOSIS. No median dorsal crest on premaxilla. Fourteen teeth in maxilla. Small triangular ala projects laterally from supraorbital wing of prefrontal. Narial emargination begins dorsal to point between fourth and fifth maxillary tooth. Parietal foramen large, bounded by two short tongues from frontal. Eight to ten teeth in pterygoid. Tuberosity below stapedial pit absent on lower medial body of quadrate, suprastapedial process small in lateral profile, infrastapedial process large. Ventral wings of coronoid poorly developed on medial and lateral surfaces of lower jaw. Splenial has weak median dorsal keel on articulating surface. Fifteen teeth in dentary. Dentary slender, dorsal and ventral margins converge gradually anteriorly, element comes to rounded tip anterior to first dentary tooth. Marginal teeth longer than in *M. ivoensis* with posteriorly recurved tips, prisms fewer in number (4-6) on external face, as many as eight poorly developed prisms on internal face.

DISCUSSION. The type of *M. missouriensis* was one of the first fossil vertebrates to be described from the western part of this continent. It must have come from the Pierre Shale and, according to Goldfuss' (1845, p. 175) description of the matrix, probably from the concretionary zone in the upper part of the Virgin Creek Member (see Crandell, 1950, p. 2338) exposed along the Big Bend of the Missouri River southeast of Pierre, South Dakota. A fragment of the anterior end of the snout was named *Ichthyosaurus missouriensis* by Harlan in 1834, and the remainder of the skull and skeleton was described by Goldfuss in 1845 as *M. maximiliani.* Both Meyer (1845, p. 313) and Camp (1942, p. 45) have pointed out that the rostral fragment figured by Harlan would fit perfectly on the broken anterior end of Goldfuss' skull, thereby making *maximiliani* a junior synonym of *missouriensis.*

In 1895 (pp. 166-167) Williston described a new species of *Mosasaurus, M. horridus,* also from the Pierre Shale of South Dakota. It was distinguished on the basis of the lesser number of pterygoid teeth (8 versus 10 in *M. missouriensis*), the greater depth of the posterior portion of the mandible and the greater size of the skull. It should be noted that the number of pterygoid teeth is variable within the Niobrara species of *Clidastes, Platecarpus* and *Tylosaurus,* and may have been also in *Mosasaurus.* Williston took his measurements of the posterior jaw of *M. missouriensis* directly from Goldfuss' plates, in which the lower jaws may have been figured in a rotated position, not showing their full depth. The type of *M. horridus* is not enough larger (only by about ⅓) than that of *M. missouriensis* to be of taxonomic significance. Therefore the characters given by Williston are not here regarded as sufficient to separate *M. horridus* from *M. missouriensis,* and a comparison of Williston's and Goldfuss' plates will show the striking similarity of the two type skulls. *M. horridus* is here, then, regarded as another junior synonym of *M. missouriensis.*

There are rudimentary zygosphene-zygantra in the anterior portion of the vertebral column (Williston, 1895, p. 167).

Mosasaurus dekayi Bronn 1838.

"saurian . . . resembling famous reptile of Maestricht," Mitchill, 1818, pp. 384, 431, pl. 3 fig. 4.
Ichthyosaurus, de Blainville, 1827, p. 48.
Mosasaurus, DeKay, 1830, p. 135, pl. 3 figs. 1-2.
Mosasaurus dekayi Bronn, 1838, p. 760.
Mosasaurus major DeKay, 1842, p. 28, pl. 22 figs. 57-58.
Mosasaurus maximiliani, Pictet, 1853, p. 505.
Mosasaurus meirsii Marsh, 1869, p. 395.

Type. Specimen not located, originally from ". . . foot of Neversink Hills, Sandy Hook, Monmouth County (New Jersey)," (DeKay, 1830, p. 135). Type specimen is the crown of a tooth.

Distribution. Navesink Formation and younger Cretaceous, New Jersey.

Additional References. Morton, 1830a, p. 289; 1830b, p. 246. Gibbes, 1850, p. 77; 1851, pp. 1, 8, pl. 1 fig. 1. Emmons, 1858, p. 217, fig. 37; 1860, p. 208, fig. 180(1), (5). Leidy, 1860, p. 92; 1865a, p. 32, figs. 7, 13, 14, 26-28, pl. 10 figs. 7, 12-13. Cope, 1869b, p. 263; 1869-1870, pp. 185, 188, 193, 199; 1875, pp. 269, 270. Miller, 1955, pp. 905, 909.

Referred Specimens. *AMNH* no. 1402. *YPM* nos. 443 (*M. meirsi*), 410, 930, 1582. *ANSP* nos. 8468, 8471, 8495, 8511.

Discussion. There is a kind of tooth from the latest Cretaceous of New Jersey that is more or less symmetrically bicarinate, has its external and internal faces strongly divided into prisms, and is bilaterally compressed relative to most of the teeth of *M. maximus.* These teeth apparently correspond to the posterior mandibular dentition of a different species of *Mosasaurus.* The type tooth of *M. dekayi* and *M. major* was of this kind, as is the splinter of a similarly strongly prismate tooth named *M. meirsi* by Marsh.

A short series of anterior caudal vertebrae have been given the same number (YPM 930) as a tooth of *M. dekayi.* They are very similar to corresponding vertebrae of *M. maximus,* although the haemal arches arise at the base of the transverse processes instead of further medially, as is the case in the latter species.

Mosasaurus maximus Cope 1869
(Text-figs. 3, 8, 24A, 30, 80)

Mosasaurus in part, Morton, 1834a, p. 27.
Mosasaurus mitchilli in part, Leidy, 1865a (see below)
Mosasaurus maximus Cope, 1869b, p. 262.
Mosasaurus princeps Marsh, 1869, p. 392.
Mosasaurus fulciatus Cope, 1869-1870, pp. 189, 194.
Mosasaurus oarthrus Cope, 1869-1870, pp. 189-196.

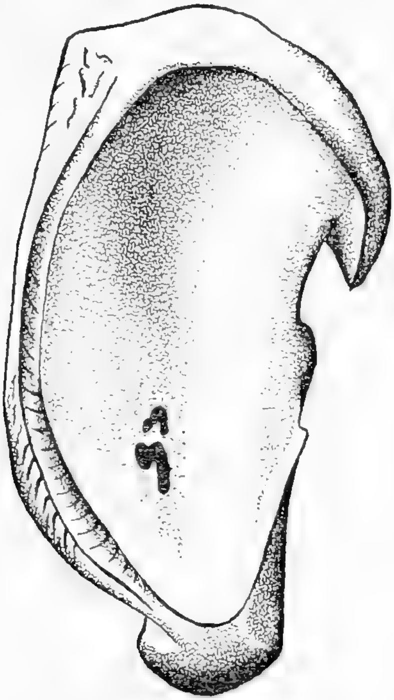
Type. AMNH 1389, from ". . . Monmouth Co., N. J." (Cope, 1869-1870, p. 189). Type specimen includes a quadrate, jaw fragments, and seven vertebrae.

Distribution. Navesink Formation and younger Cretaceous, New Jersey; Ripley Formation, Tennessee; Navarro Formation, Texas.

Additional References. Leidy, 1865a, figs. 1-3, 5-6, 8-9, 12, 15-19, 23, 29-31, 33, pl. 8 fig. 11, pl. 9 figs. 1-3, 5-7, 11, pl. 10 figs. 1-5, 8-10, 16, pl. 11 figs. 6-7, 11-13, pl. 19 fig. 6, pl. 20 figs. 3-6. Cope, 1869c, p. 86; 1869-1870, pp. 188, 189, 192, figs. 48(1), 49(1), pl. 11 figs. 7-8; 1871a, p. 571; 1875, p. 269, pl. 37 figs. 13, 15-17. Lydekker, 1888, p. 264. Baur, 1892, p. 4. Williston, 1897c, p. 110. Whitfield, 1900, p. 25, pl. 4 figs. 1-2, pl. 5 figs. 1-2. Abel, 1922, fig. 269. Gilmore, 1926, p. 191, pl. 71 figs. 6, 8. Chaffee, 1939, fig. 1(5). Miller, 1955, pp. 905, 909. Edmund, 1960. fig. 25d.

Referred Specimens. *AMNH* nos. ?1391, 1392 (*M. oarthrus*), ?1393, ?1397, 1398 (*M. fulciatus*), 1404, 1406, *YPM* nos. 305, 306, 307, 311, ?414, *430 (*M. princeps*), 470, 508, 509, 510 690, ?773, 1504, 1527, 1529, 1530, 1574, 1575. *ANSP* nos. 8462, 8472, ?8473, ?8474, 8476, 8478, 8479, 8481, 8482, 8503, 8505, 8507, 8508, 8513, 8514, 8515, 8516, 8517, 8519, 8520, 8524, 8531, 8540, 8546, 8547, ?9641. *USNM* no. 10540. *CNHM* no. PR491. *NJSM* nos. *11052, **11053. *TMM **specimen.*

Diagnosis. Slight medial dorsal crest on premaxilla. Small triangular ala projects laterally from supraorbital wing of prefrontal. Narial emargination begins dorsal to point between fifth and sixth maxillary tooth. Parietal foramen large, bounded by two long tongues from frontal. Large keel-shaped tuberosity below stapedial pit on lower medial body of quadrate, suprastapedial and infrastapedial process very small in lateral profile. Ventral wings of coronoid well developed on medial and lateral surface of lower jaw. Splenial has strong median dorsal keel on articulating surface. Fourteen teeth in dentary. Dentary deep posteriorly, rapidly narrows coming to nearly pointed tip anteriorly. Marginal teeth long with posteriorly recurved tips, prisms few in number (2-3) on external face, absent or nearly absent on internal face.



Text-fig. 80. Lateral view of left quadrate of *Mosasaurus maximus* (YPM 430, × ⅖).

Articulating surfaces of cervical and anterior dorsal vertebrae circular. Synapophysis located high in anterior two-thirds of lateral surface of cervical and anterior dorsa centra. Ventral border of anteroventral extension of synapophysis weakly developed on cervicals, extending directly anteriorly, absent on anterior thoracics. Anterior zygopophysis of cervicals and thoracics connected by rounded, posterior-descending crest to synapophysis. Zygosphene-zygantrum, if present, not large. Anterior base of atlas neural spine arises behind condylar facet, synapophysis moderately large and compressed. Hypapophyseal peduncle located posteriorly on ventral surface of cervical centra, articulation for hypapophysis flat and triangular, slightly inclined posteriorly. Transverse processes of pygal vertebrae relatively short (postcranial diagnosis based on YPM 430, 690 and 1504).

Discussion. *Mosasaurus maximus* is the earliest name that can be applied with certainty to the commonest species of mosasaur in the New Jersey Cretaceous, *M. princeps, M. oarthrus* and *M. fulciatus* being recognized here as junior synonyms. *M. maximus* must be very nearly related to *M. hoffmanni* from the Maestrichtian of western Europe. The quadrates of the two species are almost identical (see Dollo, 1889b, pl. 10 figs. 12-13; 1909, pl. 9; Cope, 1875, pl. 37 figs. 14-17), and casts of the famous type Maestricht head in the collections of the Academy of Natural Sciences of Philadelphia and the Peabody Museum at Yale show the coronoids, the posterior moiety of the lower jaw and mandibular teeth to be likewise similar. The dentaries of *M. hoffmanni* are slenderer than those of *M. maximus* (see Cuvier, 1834-1836 Atlas vol. 2, pl. 246 fig. 1; Dollo, 1889b, pl. 9 fig. 1) and the premaxilla of *M. hoffmanni* is more acutely pointed (see Dollo, 1882, pl. 4 figs. 1-2).

Because the two species may prove to be identical it may be well to point out certain skeletal features of *M. hoffmanni* which are presently unknown in *M. maximus*. There are 13 maxillary teeth, 14 dentary teeth and eight pterygoid teeth in the European form (Dollo, 1924, p. 181). Cuvier (1834-1836, p. 165) states there are twelve hypapophysis-bearing cervicals in *M. hoffmanni.* Swinton (1930, p. 47) notes that a specimen of this species in the British Museum definitely has zygosphenes, but an anterior dorsal of the same species in the Yale collections (YPM 24933) definitely lacks them. The tail ends in an expanded fin (Dollo, 1917, p. 17).

As Marsh (1872b, p. 455) has pointed out, the bone figured by Cuvier (1834-1836 Atlas vol. 2, pl. 247 fig. 10) is an ischium. The ischiadic tubercle is very widely separated from the acetabulum and points distinctly posteromedially instead of posteriorly, as in other mosasaurs. The shaft of the ischium is broad and evidently well expanded medially at the symphysis. A cast of the femur is present with the above-mentioned plastotypes of *M. hoffmanni.* The shaft of the femur is short, and the distal end is more expanded that the proximal end. The internal trochanter is very large and located medially from the head so that the long axis of the proximal end lies at right angles to the long axis of the distal end of the femur. The fibular facet is well developed and sharply set at an acute angle to the tibial facet.

A very fragmentary skull in the Yale museum (YPM 773) differs in some respects from other large New Jersey mosasaurs. The lateral exit for nerve VII is protected by a short heavy otosphenoidal crest, which is lacking in *M. maximus.* When viewed from the posterior the articulating surface of the splenial in this specimen and in ANSP 9641 is elliptical in general outline, not rectangular as in *M. maximus* or narrowly compressed as in *Prognathodon.* The teeth, coronoid and quadrate are identical to those of *M. maximus.*

In two fragmentary parietals (YPM 1504 and 1582) the margins of the dorsal parietal surface converge slightly at their posterior termination, instead of diverging as in material surely referable to *M. maximus.* Associated elements (quadrates, coronoid, splenial, angular and teeth) with YPM 1504 are like those of *M. maximus,* but although a prootic of YPM 1582 resembles that of *M. maximus,* the associated teeth are those of the *M. dekayi* kind. It is conceivable that *M. maximus* and *M. dekayi* are synonyms and that the teeth of a large species of mosasaur have been unnaturally separated here into two form species. Additional evidence would be very helpful in understanding tooth variation and the meaning of the converging margins of the posterior surfaces of the abovementioned parietals.

The infrastapedial process and a vertical keel beneath the stapedial pit on the medial shaft of the quadrate are independently variable in development in different specimens of New Jersey *Mosasaurus*. These processes are always present, however, and so far as can be told there is no taxonomic significance to their variation.

A coronoid (USNM 10540) from the Coon Creek Formation of McNairy County, Tennessee, described by Gilmore in 1926, is referred to *M. maximus*.

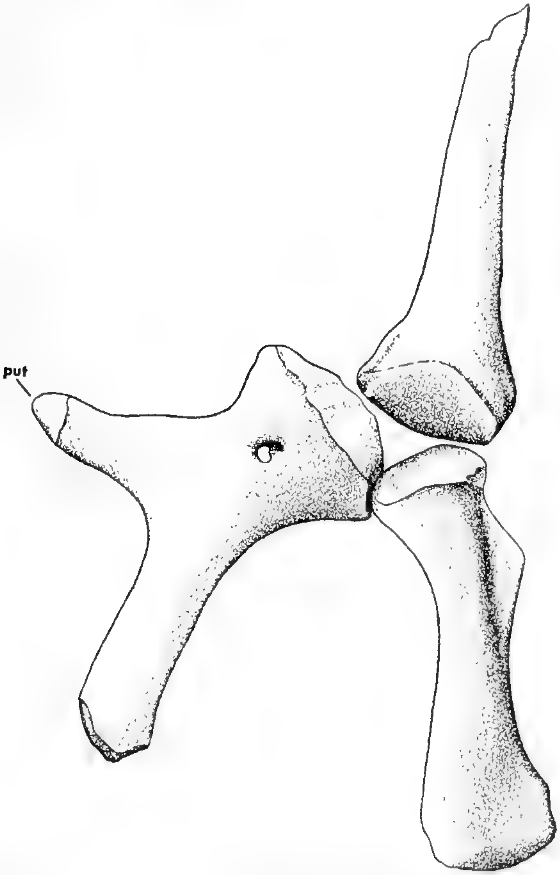
GENUS *AMPHEKEPUBIS* Mehl 1930

Amphekepubis Mehl, 1930, p. 383.

GENERIC TYPE. *Amphekepubis johnsoni* Mehl 1930.

DIAGNOSIS. Transverse processes of pygal vertebrae relatively long.

Acetabular surfaces of pelvic elements concave, form nearly solid, smoothly surfaced bowl. Obturator foramen located near center of proximal end of pubis; dorsoanterior process exceedingly long and slender, distally pointed. Ischiadic tubercle small, distinctly separated from acetabulum by moderately short neck. Shaft of ischium broad, slightly



Text-fig. 81. Lateral view of type pelvic girdle of *Amphekepubis johnsoni* (after Mehl, 1930, pl. 65, × ⅖).

dilated distally. Shaft of femur slender, distal end more expanded than proximal; internal trochanter moderately large and located medially from head so that long axis of proximal end lies at right angles to long axis of distal end of femur. Fibular facet on femur well developed, small tuberosity present on lateral surface dorsal to tibial facet. Tibia narrow, cartilage-capped area of anterior flange extends from base of tibia nearly one-half way up shaft.

Astragulus approximately quadrilateral, sub-reniform; facet for fibula raised slightly above that for tibia, dorsal notch between facets broad and shallow. Metatarsal one expanded proximally, somewhat medially recurved.

DISCUSSION. The known parts of the hind limb are very similar to those of *Clidastes*. The genus is surely separate from *Clidastes* and apparently more primitive in its more slender femur and in the circular instead of trapezoidal outline of the central articulations in the pygal vertebrae. Camp (1942, p. 25) suggested *Amphekepubis* might be synonymous with *Mosasaurus* and figured (ibid., pl. 5) the type pelvic arch in his reconstruction of *Plotosaurus*. In both of these genera however the central articulations of the pygal vertebrae are triangular in outline. The transverse processes of the pygal vertebrae of *Amphekepubis* are much longer than in *Mosasaurus* and arise out of the center of the anterior one-half of the centrum, thus resembling those of *Clidastes* more closely. The very large dorsoanterior process of the pubis at once distinguishes this element from those of *Clidastes, Platecarpus* and *Tylosaurus* (see Mehl, 1930, p. 393).

Amphekepubis johnsoni Mehl 1930
(Text-fig. 81)

Amphekepubis johnsoni Mehl, 1930, p. 383, figs. 2-3, pls. 64-67.

TYPE. Univ. of Missouri no. 509VP, from the ?San Felipe Formation 40 miles east and somewhat north of Monterey, Nuevo Leon, Mexico (Mehl, 1930, p. 383). Type specimen includes pelvic arch and portion of hind limb, and nine postsacral vertebrae.

ADDITIONAL REFERENCES. Camp, 1942, p. 25, pl. 5. McDowell and Bogert, 1954, p. 132. Romer, 1956, p. 561.

GENUS *LIODON* Owen 1841

Liodon Owen, 1840-1845, p. 261, pl. 72 figs. 1-2.

GENERIC TYPE. *Liodon anceps* Owen.

DIAGNOSIS. Premaxilla with small rostrum present anterior to premaxillary teeth. Thirteen to fourteen teeth in maxilla. Fourteen to sixteen teeth in dentary. Small projection of dentary anterior to first dentary tooth. Mandibular teeth become highly compressed and bicarinate posteriorly, enamel surfaces smooth (Gaudry, 1892, pp. 5-9, pls. 1-2).

DISCUSSION. The proper application of the name *Liodon* is still uncertain. The type species of the genus, *L. anceps* Owen, was based on a jaw fragment containing smoothly surfaced, symmetrically bicarinate teeth. Unfortunately no good cranial material has yet been described that can be assigned to this species, but, on the basis of the dentition, Gaudry (1892, p. 4), Depéret and Russo (1925, p. 340) and Persson (1959, p. 465) have suggested that *Hainosaurus* Dollo, a tylosaurine, may prove to be congeneric with *L. anceps*. *Hainosaurus* is surely generically distinct from *L. compressidens* and *L. mosasauroides*, both from the French Cretaceous, upon which the foregoing diagnosis is based. If new material demonstrates that *L. anceps* cannot be included in the same genus as the latter two species, then these two species together with *L. sectorius* Cope will have to be placed in a new genus, within the Mosasaurinae. As it now stands *Liodon* is placed in the Mosasaurini because of the great resemblance of the muzzle of the French species to *Mosasaurus.* No postcranial material of any species of *Liodon* has ever been described.

Liodon sectorius Cope 1871
(Text-fig. 82)

Liodon sectorius Cope, 1871d, p. 41.
Tylosaurus sectorius, Merriam, 1894, p. 25.

Type. AMNH 1401, ". . . from the marl pits of the Pemberton Marl Co., at Birmingham, N.J. . . ." (Cope, 1871d, p. 43), collected by J. C. Gaskill. Type specimen consists of fragments of cranial bones including those of a maxilla, dentary, coronoid and surangular, and one fragmentary vertebra.

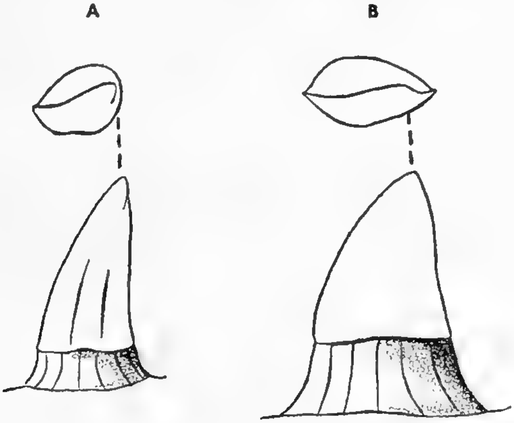
Distribution. Navesink Formation or younger Cretaceous, New Jersey.

Additional References. Cope, 1875, p. 271. Miller, 1955, pp. 905, 909.

Referred Specimens. *ANSP* no. 9669, 9670.

Discussion. The type specimen of this species has been badly damaged and some of its parts have been lost; the original description of its dentition is given here:

"The anterior teeth are less compressed, and have but one, an anterior, cutting edge, the posterior face being regularly convex. The inner face is much more convex than the outer, and the flatness of the latter is marked at the apex of the tooth by a short ridge which bounds it posteriorly. This is a trace of the bounding angle which extends to the basis of the crown in *Mosasaurus.* The anterior cutting edge is in profile convex; the posterior outline concave to near the tip. The cutting edge is acute, and beautifully ribbed on each side, but not properly denticulate. The surface of the tooth is not facetted, but the outer face exhibits the peculiarity of a longitudinal concavity, or shallow groove extending from the base to the middle of the crown. . . This description is taken from the second or third (tooth) from the anterior end of the maxillary bone. The third from the distal end of the dentary is very similar.



Text-fig. 82. A. Anterior marginal tooth. B. Posterior marginal tooth of type of *Liodon sectorius* (AMNH 1401, × ¾).

"The crowns become rapidly more compressed as we pass backwards. From a broad oval section of two crown bases, we reach a flattened oval crown, with the cutting edge sharp behind as well as before, and minutely ribbed. The crown is not facetted, and is more convex interiorly than exteriorly. The exterior convexity is chiefly anterior; the posterior face is slightly concave from the open groove already described as present in the anterior teeth. In two posterior crowns, one still more elongate in section, the external concavity becomes flatter and includes a great part of the outer face. A tooth still more posterior presents the peculiarity of the species in the strongest light. The crown is still more compressed, directed backwards, and only .25 higher than wide anteroposteriorly at the base. . ." (Cope, 1871d, pp. 41-42)

The teeth of *L. sectorius* are approximately intermediate in form between those of *L. compressidens* and *L. mosasauroides,* excellently figured by Gaudry (1892, pls. 1-2), and are more strongly compressed than those of *L. anceps* (see Owen, 1840-1845, pl. 72 figs. 1-2). It will be very interesting to see additional characters of *L. sectorius* brought to light as new material is discovered from the Cretaceous of New Jersey.

Tribe **GLOBIDENSINI** (Dollo 1924) new

Diagnosis. The osteology of *Globidens* remains very incompletely known. It appears to have descended from a *Clidastes*-like ancestor, but because of the highly peculiar nature of its spherical teeth and massive jaws (see below) it is separated from the Mosasaurini into a distinct tribe.

Genus *GLOBIDENS* Gilmore 1912

Globidens Gilmore, 1912a, p. 479.

Generic Type. *Globidens alabamaensis* Gilmore.

Diagnosis. Median dorsal crest on massive frontal present. Frontal not emarginate above orbits. Ventral process of postorbitofrontal to jugal confluent with broadly exposed dorsal surface of postorbitofrontal. Mandibular teeth spherical in form.

Articulating surface of anterior thoracic vertebra wider than deep, subcircular in outline. Synapophysis located in center of lateral surface of anterior thoracic vertebra. Ventral border of anteroventral extension of synapophysis well developed on anterior thoracic, reaches level of undersurface of centrum. Zygosphene-zygantrum present but not large.

Globidens alabamaensis Gilmore 1912

Globidens alabamaensis Gilmore, 1912a, p. 479, figs. 1-3, pls. 39-40.

Type. USNM 6527, from the Selma Chalk of ". . . Bogue Chitto Prairies west of Hamberg . . . Perry and Dallas Co; Ala. . ." (Gilmore, 1912a, p. 479), collected by L. C. Johnson. Type specimen includes a maxilla, frontal, postorbitofrontal, basisphenoid, splenial and one vertebra.

Distribution. Selma Formation, Alabama and Mississippi; Lower Taylor Marl, Taylor Formation, Texas; Lower Pierre Formation, South Dakota.

Additional References. Williston, 1914, p. 167, fig. 80. Gilmore, 1921, p. 273 (fig.), p. 280; 1927, p. 452, Abel, 1922, fig. 266; 1924, fig. 37. Camp, 1923, p. 323. Dollo, 1924, p. 170. Nopcsa, 1928, p. 177. Zangerl, 1948, p. 15. McDowell and Bogert, 1954, pp. 106, 107, 129, 132. Romer, 1956, p. 562. Edmund, 1960, p. 90, fig. 25c. Kauffman and Kesling, 1960, p. 224, table 3.

Referred Specimens. ?*USNM* no. 4993. *SDSM* no. 4612.

Discussion. Gilmore's fragmentary type is the most complete *Globidens* skull yet known. The premaxillary suture of the maxilla is smoothly keeled and parallels the longitudinal axis of the maxilla as in *Mosasaurus* and in some species of *Clidastes,* the emargination for the external nares beginning dorsal to a point between the fifth and sixth maxillary tooth. The prefrontal and postorbitofrontal seem to have been narrowly separated by the ventral surface of the frontal above the orbits. The postorbitofrontal has a widely exposed triangular dorsal surface and a jugular suture similar to those in *Clidastes.* There is no canal through the basisphenoid for the basilar artery. Gilmore (1912a, p. 484) referred *G. alabamaensis* to the Plioplatecarpinae, and Dollo (1924,

p. 188) erected a new family for its inclusion. The characters outlined above indicate that *Globidens* is a derivative of, and closely related to *Clidastes,* although very different in the massive structure of its cranial elements and the spherical form of its teeth.

A very heavy coronoid and articular (USNM 4993) from the ?Marlbrook Marl, Red River Valley of Hempstead County, Arkansas, probably belong to *Globidens.* The coronoid is depressed and extends a long wing posteriorly above the dorsal edge of the surangular. The retroarticular process of the articular is very strongly constructed, nearly perfectly circular in lateral outline, and has a large tuberosity on its ventral margin beneath the posterior end of the quadrato-mandibular joint.

A fragment of the posterior end of a dentary (SDSM 4612) with a single tooth and an alveolus for another, from the Lower Pierre Shale of Fall River County, South Dakota, is probably conspecific with *G. alabamaensis.* There is a deep notch extending anteroventrally from the dorsoposterior edge of the dentary to a point beneath the penultimate dentary tooth, which has not been described in any other species of mosasaur.

Globidens teeth have been discovered in the Selma Chalk in the vicinity of Saltillo, Lee County, Mississippi (Gilmore, 1927, p. 452) and in the Lower Taylor Marl Member, Taylor Formation, near Austin, Texas (Hotton, personal communication 1963). It is very odd that *Globidens* has not been reported from the Niobrara Chalk. *G. alabamaensis* also occurs in the Craie d'Oburg, near Mons, Belgium (Dollo, 1924, p. 170).

Tribe **PLOTOSAURINI** new

Diagnosis. More than twelve pygal vertebrae present. Radius and ulna nearly contact above carpalia on distal border of antebrachial foramen. The structure of the manus in these forms from the Pacific basin suggests they should be placed in a tribe distinct from other members of the Mosasaurinae.

Genus *PLOTOSAURUS* Camp 1951
(Plate II, fig. 2)

Kolposaurus Camp, 1942, p. 2, pls. 5-6 (preoccupied, Skuphos 1893).
Garzasaurus Anderson, 1943, p. 186 *nomen nudum.*
Plotosaurus Camp, 1951, p. 822.

Generic Type. *Plotosaurus bennisoni* (Camp 1942).

Additional References. Hesse and Welles, 1936, p. 157. McDowell and Bogert, 1954, p. 132. Romer, 1956, p. 561.

Diagnosis. Premaxilla with very small rostrum anterior to premaxillary teeth. Eighteen teeth in maxilla. Prefrontal excluded from posterolateral margin of external nares by slender process of maxilla,[1] supraorbital wing with small rectangular ala fused with postorbitofrontal posteriorly over orbits lateral to external edge of frontal. Frontal not emarginate above orbits, median dorsal ridge absent. Pineal foramen large, closely embraced on either side by short tongues from frontal. Median dorsal surface of parietal short, extensively invaded posteriorly by insertional area for cervical epaxial musculature. Ventral process of postorbitofrontal to jugal apparently nearly confluent with well exposed dorsal surface of postorbitofrontal. Ventroposterior process of jugal nearly absent. Twelve-15 teeth in pterygoid. Suprastapedial process of quadrate relatively short, tympanic ala moderately thick with groove around external margin. Stapedial

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[1] Camp (1942, fig. 6) figures the prefrontal of a skull referred to *Plotosaurus tuckeri* as being narrowly separated from the narial margin by a thin lamina of bone from the maxilla, and the postorbitofrontal-parietal contact as occurring in the center of the anterior border of the supratemporal fenestra. Later (ibid., fig. 13) in an illustration of the same skull the prefrontal is shown to enter broadly into the narial margin, and the postorbitofrontal-parietal contact to occur in the anteromedial corner of the supratemporal fenestra.

pit elliptical in form. Seventeen teeth in dentary. Dentary with relatively long projection anterior to first dentary tooth. Dorsal edge of surangular very thin lamina of bone rising anteriorly to position high on posterior surface of coronoid. Mandibular teeth bicarinate, vertically striated, becoming shorter and blunter posteriorly.

Vertebral formula: 51 presacral vertebrae (number restored), 30 pygals, 5 caudals with chevrons and transverse processes, 64 terminal caudals (see Camp, 1942, pl. 5).

Articulating surfaces of anterior dorsal vertebrae wider than deep, subcircular in outline. Synapophysis located in center of lateral surface of cervical vertebrae and anterodorsal portion of lateral surface of thoracic centra. Ventral border of anteroventral extension of synapophysis poorly developed on cervicals and anterior dorsals, does not reach level of undersurface of centrum ventrally. Anterior zygopophysis of cervicals and anterior thoracics connected by gently rounded, posteriorly descending crest to synapophysis. No zygosphene-zygantrum. Anterior base of atlas neural spine arises behind condylar facet. Hypapophyseal peduncle located posteriorly on ventral surface of cervical centra, articulation for hypapophysis flat and circular, initially inclined posteriorly, becoming horizontal posteriorly. Neural spines of caudal vertebrae longest and vertical on postsacrals 42-44. Nine to ten hypapophysis-bearing anterior presacrals.

Scapula larger than coracoid. Glenoid articulating surfaces apparently convex on both scapula and coracoid, do not form a smoothly continuous surface. Superior border of scapula gently convex, posterior border slightly emarginated posteriorly. Coracoid expands broadly behind glenoid articulation. Humerus short and broad. Proximal end of radius expanded. Shaft of radius wide. Distal end bears moderately expanded anterodistal flange. Radius and ulna subequal in size. Radius has distinct facet for articulation with radiale.

Radiale very large. Intermedium of average proportions, has wide articulating facet for ulna. Ulnare does not enter posteroventral border of antebrachial foramen. Metacarpals shorter and stouter than in other genera of mosasaurs. Metacarpal one equal to metacarpal two in length, anterodistal tuberosity present. Proximal ends of metacarpals moderately expanded. Phalangeal formula of manus at least 10-10-10-7-2.

DISCUSSION. The foregoing diagnosis was taken from descriptions and illustrations in Camp (1942). There are at least 38 presacral vertebrae in *Plotosaurus tuckeri* (ibid., p. 21).

Plotosaurus bennisoni (Camp 1942)

Kolposaurus bennisoni Camp, 1942, p. 2, figs. 1-3, 13-15, 17, pl. 1
Plotosaurus bennisoni, Camp, 1951, p. 822.

TYPE. UCMP **32778, 225 feet above base of Garzas Sand, Moreno Formation, Merced County, California (see Camp, 1942, p. 2 for detailed locality information). Type specimen includes a complete skull, 18 vertebrae, an interclavicle and four ribs (Camp, 1942, p. 8.)

DISTRIBUTION. Moreno Formation, California.

ADDITIONAL REFERENCES. Kuhn, 1952, fig. 15(1). Anderson, 1958, p. 71. Kauffman and Kesling, 1960, p. 220, table 3, fig. 5.

DIAGNOSIS. Tongues from frontal embracing parietal opening, long and rectangular. Fifteen teeth in pterygoid. Main body of quadrate broad with moderately large suprastapedial process. Ten hypapophysis-bearing cervicals. Four anterior dorsals bear zygapophyses. Interclavicle relatively small (Camp, 1942, pp. 4, 11, figs. 1-2).

Plotosaurus tuckeri (Camp 1942)
(Text-figs. 46D, 47A, 52)

Kolposaurus tuckeri Camp, 1942, p. 8, figs. 4-10, 13, 23, pls. 2-3.
Plotosaurus tuckeri, Camp, 1951, p. 822.

TYPE. At UCMP, from the Moreno Formation, Fresno County, California (see

Camp, 1942, p. 8, for detailed locality information). Type specimen includes 54 vertebrae and a few limb fragments (Camp, 1942, p. 8).

Distribution. Moreno Formation, California.

Additional References. Stock, 1939, p. 620, pl. 1 fig. b. Welles, 1943, pp. 127, 128, fig. 2. Romer, 1956, fig. 182b. Anderson, 1958, p. 71. Downs, 1959, p. 17.

Referred Specimens. *CIT* nos. ***2750,* 2751, 2755 (fide Camp, 1942, p. 11).

Diagnosis. Tongues from frontal embracing parietal opening short and triangular. Twelve to thirteen teeth in pterygoid. Main body of quadrate narrow with small suprastapedial process. Nine hypapophysis-bearing cervicals. Eight anterior dorsals bear zygapophyses. Interclavicle relatively large (Camp, 1942, pp. 11, 13).

FOREIGN GENERA OF MOSASAURINAE

Genus *COMPRESSIDENS* Dollo 1924

Compressidens Dollo, 1924, p. 176.

Generic Type. *Compressidens fraasi* (Dollo).

Diagnosis. Small projection of dentary anterior to first dentary tooth. Median dentary teeth bilaterally compressed, bicarinate, subrectangular in lateral view and with pointed apices. Anterior teeth circular in cross-section with strongly recurved pointed apices (Dollo, 1913, pl. 23; 1924, pl. 5).

Discussion. The genus *Compressidens* was proposed by Dollo for two species of small Maestrichtian mosasaurs from Belgium, known only from a single dentary and several teeth. The slender anteriorly narrowing form of the dentary is typically clidastoid and the teeth could be easily derived from any of the Niobrara species of *Clidastes.* There are at least thirteen teeth in the dentary (Dollo, 1913, p. 610). The genus may be easily distinguished from *Globidens* by the compressed nature of the teeth and the relatively delicate dentary. The teeth are unicuspid in *C. fraasi* and tricuspid in *C. belgicus. Compressidens* and *Globidens* appear to be separate derivations from older clidastoid stock, but because *Compressidens* is a less divergent form it is still included in the Mosasaurini.

Genus *TANIWHASAURUS* Hector 1874

Taniwhasaurus Hector, 1874, p. 353.

Generic Type. *Taniwhasaurus oweni* Hector.

Diagnosis. Prefrontal lacks broad triangular ala projecting laterally from supraorbital wing. Frontal slightly emarginate above orbits, has prominent median dorsal ridge. Small projection of dentary anterior to first dentary tooth. Mandibular teeth only slightly compressed, lack carinae, and have finely striated surfaces.

Zygosphene rudimentary. Postglenoid process absent on proximoposterior end of humerus. Radius very short and broad. Distal end bears heavy anterodistal flange and distinct facet for articulation with radiale. Radiale very large. Intermedium of average proportions, has articulating facet for ulna. Ulnare does not enter posteroventral border of antebrachial foramen. Distal end of radius and ulna approach each other medially above carpus.

Discussion. The foregoing diagnosis was taken from descriptions and illustrations in Hector (1874).

Taniwhasaurus was described from the Maestrichtian of New Zealand (Wellman, 1959, p. 135). The parietal (Hector, 1874, pl. 31 fig. A) is peculiarly reminiscent of that of *Platecarpus.* The dentaries are unique in that the teeth are directed as much labially as vertically and are separated from the buccal cavity by a median longitudinal parapet (ibid., fig. B′). Could these cranial remains belong to *Plioplatecarpus*?

The forepaddle, however, shows (ibid., pl. 31 fig. C) marked mosasaurine affinities. Unfortunately the humerus was neither well described nor clearly figured. The radius is more than twice the size of the ulna, although in *Plotosaurus* they are subequal, and has a well developed anterior flange which is reduced in the latter genus. Nevertheless *Taniwhasaurus* resembles *Plotosaurus* and differs from *Clidastes* and *Mosasaurus* in that the radius and ulna nearly contact each other distally. It is therefore provisionally assigned to the Plotosaurini.

Subfamily **PLIOPLATECARPINAE** (Dollo 1884) Williston 1897

Plioplatecarpidae Dollo, 1884, p. 653.
"mosasauriens microrhynques" Dollo, 1890, p. 163.
Platecarpinae Williston, 1897d, p. 177.

Diagnosis. Small rostrum present or absent anterior to premaxillary teeth. Twelve or more teeth in dentary and maxilla. Cranial nerves X, XI and XII leave lateral wall of opisthotic through single foramen. Canal or deep groove in floor of basioccipital and basisphenoid for basilar artery. Suprastapedial process of quadrate large, bluntly terminated and with parallel sides. Dorsal edge of surangular rounded and longitudinally horizontal.

Twenty-nine or less presacral vertebrae present. Length of presacral series less than that of postsacral, neural spines of posterior caudal vertebrae at most only slightly elongated, do not form an appreciable fin. Haemal arches usually unfused to caudal centra. Appendicular elements lack smoothly finished articular surfaces.

Discussion. Williston (1897d, p. 181; 1898b, p. 177) characterized the Plioplatecarpinae as having an imperfectly ossified carpus and tarsus. This is true of *Platecarpus* where only the intermedium, ulnare, two distal carpals and occasionally a diminutive ossicle in the position of a radiale occur. But in *Ectenosaurus* the intermedium and ulnare are large; there is a well ossified radiale; and four distal carpals are present. This makes a total of seven elements in contrast to the six in the "fully ossified" carpus of most mosasaurines (excluding the pisiform). Further, only four ossified elements have been found in the carpus of *Clidastes sternbergi*. However the ulnare broadley enters the posteroventral margin of the antebrachial foramen in both *Platecarpus* and *Ectenosaurus* which, with the possible exception of *Mosasaurus ivoensis* (Williston, 1902, pl. 12 lower figure), is unknown to occur in the Mosasaurinae. Perhaps the arrangement, rather than the degree of ossification of the carpals and tarsals, is more important in showing relationships.

Tribe **PLIOPLATECARPINI** (Dollo 1884) new

Diagnosis. Canal through basioccipital and basisphenoid for basilar artery. Delicately proportioned jaws, teeth striated and subcircular in cross-section. Chevrons free. These are generally mosasaurs of moderate size, with relatively short jaws and long, slender teeth.

Genus *PLATECARPUS* Cope 1869

(Text-figs. 7, 9-11, 16, 18-20, 28, 31, 40, 41, 44, 46C, 48B, 53, 57, 62)

Platecarpus Cope, 1869b, p. 264.
Holcodus, Cope, 1872f, p. 331.
Liodon in part, Cope, 1872f, p. 331.
Lestosaurus Marsh, 1872b, p. 454.
Sironectes Cope, 1874, p. 34.
Holosaurus Marsh, 1880, p. 87.

Generic Type. *Platecarpus tympaniticus* Cope.

Additional References. Leidy, 1865a, pl. 8 figs. 18-19; 1873, pl. 36 figs. 4-14. Cope, 1869-1870, p. 199; 1872d, pp. 269, 273; 1872e, p. 141; 1874, p. 35; 1875, pp. 139, 141, pl.

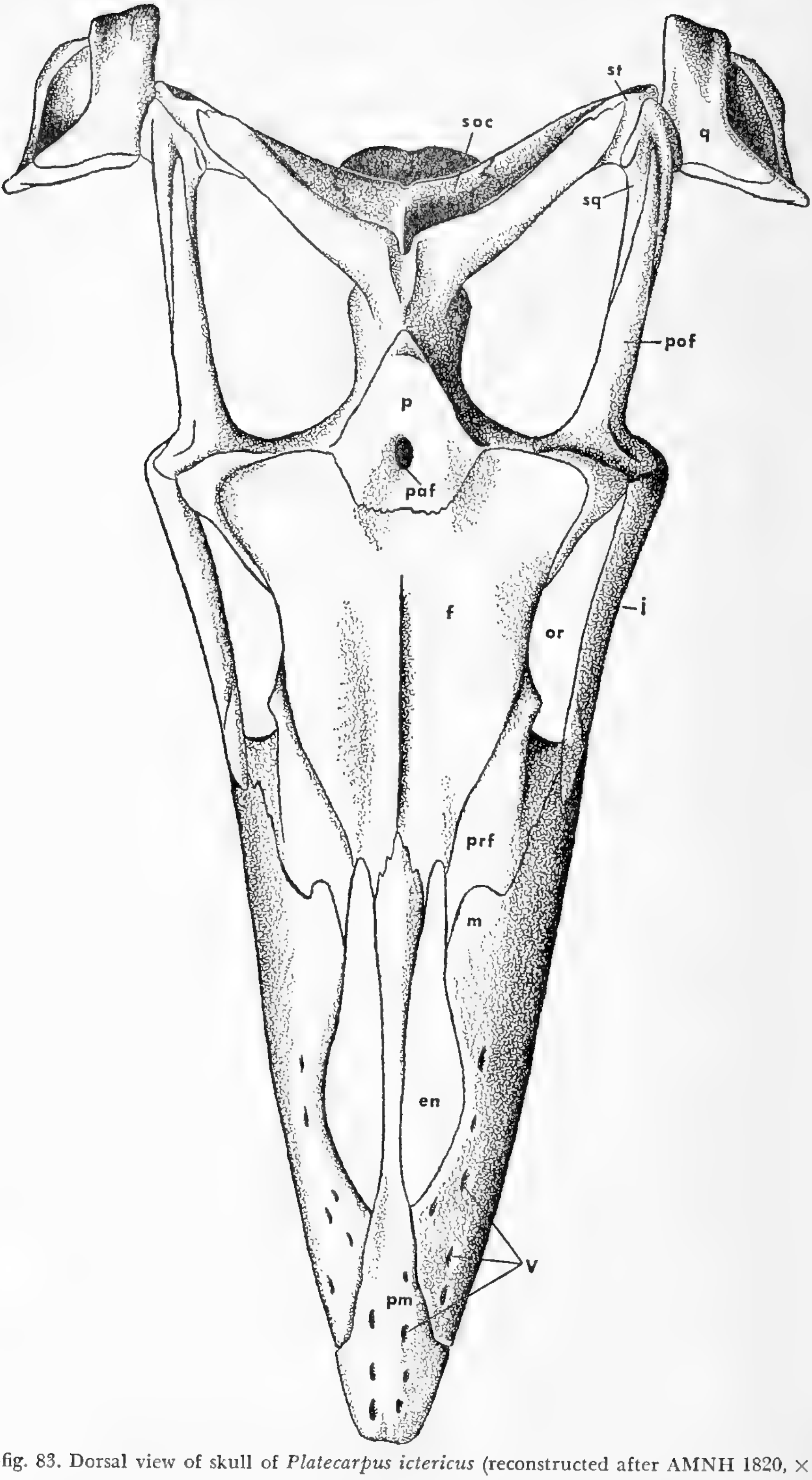
26 figs. 2-3. Marsh, 1872a, p. 291; 1872b, pl. 12 fig. 2, pl. 13 figs. 3-4; 1872d, pp. 496, 497; 1880, pl. 1 figs. 2-3; 1897, fig. 23. Owen, 1877, pp. 690, 696, fig. 15; 1880, pl. 8 figs. 2-3. Lydekker, 1888, p. 269. Hoffmann, 1890, p. 1321. Dollo, 1894, pl. 4 fig. 7. Merriam, 1894, pp. 25, 38-39, pl. 3 figs. 3-5, 11, pl. 4 figs. 2, 8. Williston, 1891, p. 345; 1895, pl. 17 fig. 3; 1897c. pp. 107, 108; 1897d, pp. 178, 181, 183; 1897e, pp. 244, 245, figs. 1(1), 5(2); 1898b, pp. 103-134, 177, 192, pl. 22 fig. 2, pl. 24 figs. 1-5, pl. 25 figs. 3-5, pl. 26 figs. 1-4, pl. 27, pl. 28 figs. 5, 7-8, pl. 29 figs. 3-5, pl. 31 figs. 4-5, pl. 41 fig. 2, pl. 42 figs. 3-4, pl. 43, pl. 45 figs. 1-2, pl. 46 figs. 1-4, pl. 47, pls. 51-52, pl. 54 figs. 2-3, pl. 56 figs. 1-5, pl. 57 figs. 1-2, 5-10, pl. 58 figs. 1-10, pl. 60 fig. 61 fig. 3 pl. 63, pl. 64 figs. 2-3, text fig. 5; 1898c, p .235; 1899, p. 39; 1902, p. 248, pl. 12 upper fig., pl. 13; 1904, p. 48; 1914, p. 166, fig. 73; 1925, p. 273, figs. 57, 80b, 123, 158a. Osborn, 1899a, figs. 2-3, 6a, 7a. Sternberg, 1899, p. 259; 1905, pp. 126, 127; 1907, pp. 122-123; 1908, p. 113; 1909, pp. 50, 204; 1911, p. 17; 1917, p. 162; 1918, p. 205. Loomis, 1904, p. 254. Janensch, 1906, p. 30. Osburn, 1906, pl. 8 fig. 22. Capps, 1907, figs. 1-3. Merril, 1907, p. 73. Pompeckj, 1910, pp. 131, 137. Huene, 1911, p. 49, pl. 3; 1919, p. 183, pl. 8 fig. 2. Broom, 1913, p. 508. Dreverman, 1914, p. 43. Lambe, 1914, pl. 1 lower fig. Wiman, 1920, p. 10, fig. 2, pl. 3 upper fig., pl. 4 fig. 7b. Abel, 1922, figs. 259, 263-264; 1924, fig. 36. Woodward, 1922, p. 6, fig. 2. Camp, 1923, p. 323; 1942, pp. 30-34, figs. 18-20, 24a-b, 25-26. Gilmore, 1928, p. 87; 1943, fig. 13a. Nopcsa, 1928, p. 177. Mehl, 1930, p. 393, figs. 4-5. Lane, 1947, p. 314. Gregory, 1951, figs. 4a, 5; 1952, figs. 4 right, 9. Romer, 1956, p. 562, figs. 120f, 190d. Vaughn and Dawson, 1956, p. 383.

Diagnosis. Premaxilla with no rostrum anterior to premaxillary teeth. Twelve teeth in maxilla. Prefrontal forms large portion of posterolateral border of external nares and has small lateral tuberosity on supraorbital wing, contacts postorbitofrontal over orbits medial to external edge of frontal. Frontal emarginate above orbits, has prominent median dorsal ridge. Parietal foramen large, close to or bordered anteriorly by frontal. Margins of dorsal parietal surface meet in front of diverging suspensorial rami, forming triangular table anteriorly on parietal. Ventral process of postorbitofrontal to jugal distinct from but nearly in same plane as moderately exposed dorsal surface of postorbitofrontal. Ventroposterior process on jugal well developed. Squamosal wing to parietal moderate to large. Otosphenoidal crest on prootic small, may cover exits for cranial nerves VII and IX laterally. Canal for basilar artery through basioccipital and basisphenoid not open ventrally on basioccipital. Ten to twelve teeth in pterygoid. Suprastapedial process not fused to infrastapedial process on quadrate. Tympanic ala very thin. Stapedial pit elliptical in form. Twelve (rarely eleven) teeth in dentary. Dentary terminates abruptly in front of first dentary tooth. Angular widely separated medially from coronoid. Retroarticular process of articular circular in outline.

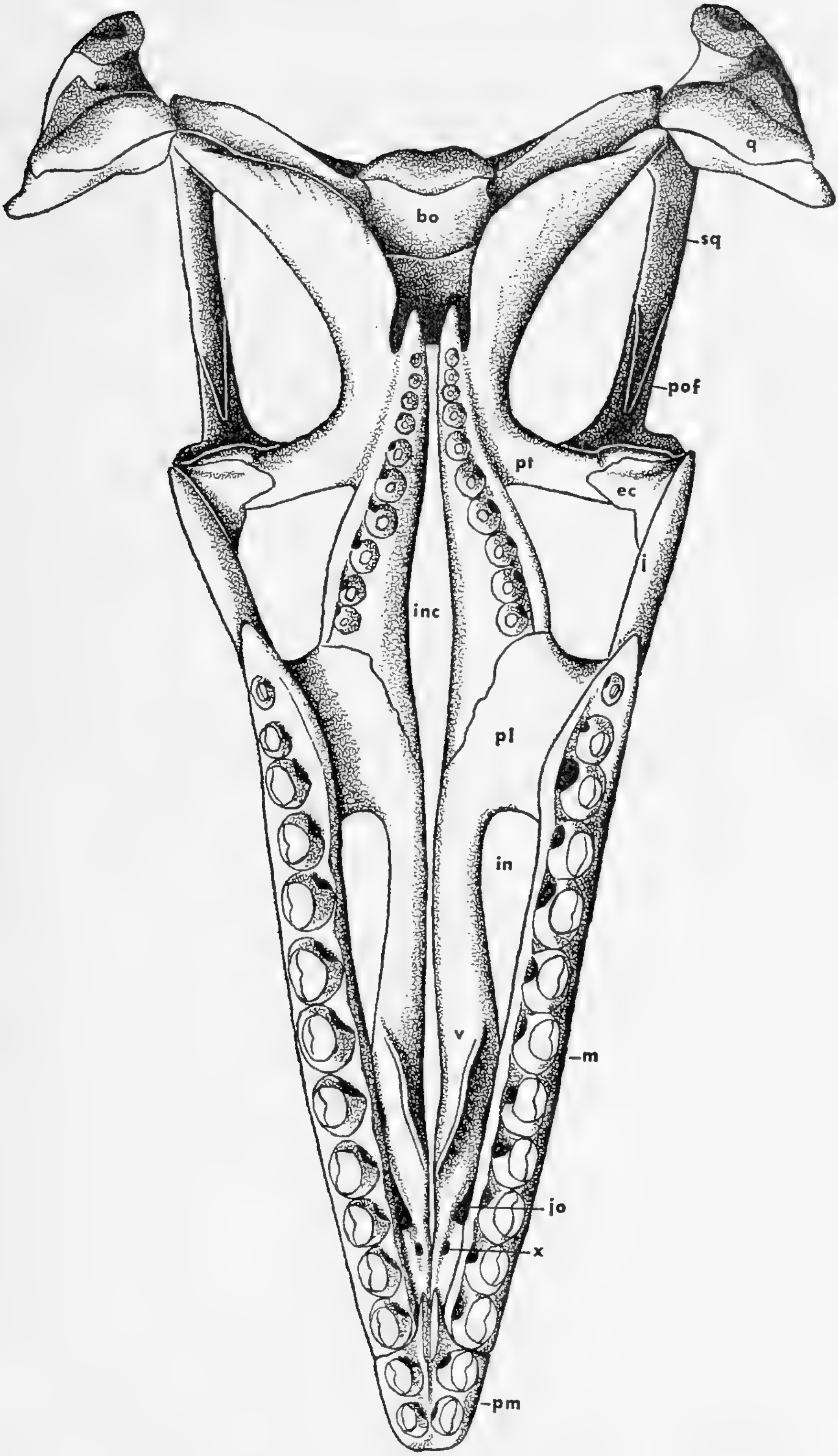
Vertebral formula: 29 presacral vertebrae, 5 pygals, 26-31 caudals with chevrons and transverse processes, about 65 terminal caudals (see Merriam, 1894, p. 11; Williston, 1898b, p. 143; 1910, p. 538; Huene, 1911, p. 50 and YPM 1350, 1429 and 24900).

Articulating surfaces of cervical and anterior dorsal vertebral centra wider than deep, smoothly elliptical in outline. Synapophysis located high in center of lateral surface of cervical centra, occupies anterodorsal portion of lateral surface of anterior dorsal and anterior portion of posterior dorsal centra. Ventral border of anteroventral extension of synapophysis well developed on cervicals and anterior dorsals, reaches level of undersurfaces of centrum. Anterior zygopophysis of cervicals and thoracics connected by gently rounded, posteriorly descending crest to synapophysis. Zygosphene-zygantrum present but not large. Anterior base of atlas neural spine arises directly above condylar facet, atlas synapophysis small and tuberculate. Hypapophyseal peduncle located posteriorly on ventral surface of cervical centra, articulation for hypapophysis horizontal and triangular. Five hypapophysis-bearing cervicals, one or rarely two more with rudimentary peduncles. Transverse processes of pygal vertebrae relatively short. Neural spines of caudal vertebrae vertical on postsacrals 44-52 (Huene, 1911, pl. 3).

Scapula and coracoid subequal in size. Glenoid articulating surfaces convex on both elements, do not form smoothly continuous surface. Superior border of scapula strongly convex, posterior border strongly emarginated posteromedially. Coracoid does not expand medially to point behind glenoid articulation. Distal end of humerus



Text-fig. 83. Dorsal view of skull of *Platecarpus ictericus* (reconstructed after AMNH 1820, × 3/8).



Text-fig. 84. Ventral view of skull of *Platecarpus ictericus* (reconstructed after AMNH 1820, × 3/8).

very widely expanded, much more than proximal end. Facets for articulation with other elements and sites of muscle attachment moderately well differentiated. Proximal end of radius expanded. Shaft of radius wide. Distal end bears greatly expanded anterodistal flange, is thickened medially to form indistinct facet for articulation with intermedium.

Radiale reduced to small ossicle, or absent. Intermedium deep. Ulnare enters posteroventral border of antebrachial foramen. Metacarpal one less than metacarpal two in length, has moderate anterodistal tuberosity. Proximal ends of metacarpals moderately expanded. Phalangeal formula of manus approximately 4-6-7-5-3 plus or minus one phalanyx on each digit.

Acetabular surfaces of pelvic elements convex, do not form solid, smoothly surfaced bowl. Obturator foramen located near center of proximal end of pubis, dorsoanterior process small and triangular. Ischiadic tubercle located close to acetabulum. Shaft of ischium broad, ischiadic symphysis very wide. Distal end of femur more expanded than proximal; internal trochanter of average proportions, located anteromedially from head. No distinct facets on distal end, although femur is thickened in region of tibial articulation. Tibia and fibula difficult to distinguish from radius and ulna respectively. Cartilage capped area of anterior flange extends from base of tibia one-half way up shaft, similar area of posterodistal flange of fibula limited to distal end of bone.

Astragulus elliptical, dorsal notch between subequal facets for tibia and fibula small. Calcaneum slightly smaller than fourth tarsal. Metatarsal one slightly expanded proximally, slightly medially recurved. Metatarsal five not hook shaped, symmetrically expanded proximally. Phalangeal formula of pes approximately 4-5-5-5-3 plus or minus one phalanyx on each digit.

DISCUSSION. The genus *Platecarpus* was named by Cope on fragmentary, though generically diagnostic material from Mississippi. Apparently not realizing that it also occurred in the Niobrara Chalk, he referred Niobrara species of the genus to *Holcodus* and *Liodon* during 1871 and 1872, presumably on dental and vertebral characters respectively. Marsh (1872b, p. 461) recognized the generic distinctiveness of these species relative to other genera in the Niobrara and included them in his new genus *Lestosaurus*. Cope (1872e, p. 141) immediately pointed out that, though agreeing with Marsh that the type tooth of *Holcodus acutidens* was more closely related to *Mosasaurus* (meaning *M. copeanus* = *Plioplatecarpus*), the species under dispute were very probably congeneric with *Platecarpus tympaniticus*. Thereafter Cope used *Platecarpus* for these species and Marsh used *Lestosaurus*.

Platecarpus is indeed a senior synonym of *Lestosaurus* and as such has been generally recognized since 1890. Leidy (1865a, p. 118) and Williston (1898b, p. 177) have suspected that *Platecarpus* might be synonymous with Gibbes' older genus *Holcodus*, here considered a *nomen vanum*. Skeletal material preserved in the types of *Sironectes anguliferus* Cope and *Holosaurus abruptus* Marsh clearly shows that these genera are identical to *Platecarpus*.

Platecarpus tympaniticus Cope 1869

?*Holcodus acutidens*, Leidy, 1865a, pp. 35, 38, 40-41, 118, 131, pl. 7 figs. 4-7, pl. 11 fig. 14.
Platecarpus tympaniticus Cope, 1869b, p. 265.

TYPE. ANSP 8484, 8487, 8488, 8491, 8558-9, 8562, all one specimen from a greenish sandstone (Eutaw Formation) near Columbus, Mississippi (see Leidy, 1865a, p. 38) collected by Dr. William Spillman. Type specimen includes a surangular, quadrate, braincase, pterygoid and three cervical vertebrae.

ADDITIONAL REFERENCES. Leidy, 1865b, p. 70. Cope, 1869-1870, p. 200; 1872e, p. 141; 1874, p. 35; 1875, p. 267, pl. 37 fig. 11. Merriam, 1894, p. 30. Williston, 1897d, p. 185; 1898b, p. 179. Chaffee, 1939, fig. 1(4).

DISCUSSION. The type and only specimen of the species, from the Eutaw Formation of Mississippi, exhibits diagnostic characteristics of the genus *Platecarpus*, such as the large suprastapedial process and delicate tympanic ala of the quadrate, and general form of the basioccipital and anterior vertebrae. The preserved cranial material of this specimen is identical in form to corresponding elements of the Niobrara species *P. ictericus* and *P. coryphaeus,* and when anterior portions of the skull of *P. tympaniticus* are discovered in the Eutaw Formation the species will doubtlessly be shown to be the senior synonym of one of the Niobrara forms. It may be distinguished from *Platecarpus* cf. *P. somenensis* from the Lower Pierre in that the ventroposterior processes of the basisphenoid are separated by a shallow horizontal sulcus only, not by a deep longitudinal cleft.

Platecarpus coryphaeus (Cope 1872)
(Text-fig. 85A)

Holcodus coryphaeus Cope, 1872d, p. 269.
Lestosaurus gracilis Marsh, 1872b, p. 460.
Platecarpus coryphaeus, Cope, 1874, p. 35.
Holosaurus abruptus Marsh, 1880, p. 87.

TYPE. AMNH 1566, from ". . . the side of a bluff in a branch of the Fossil Spring cañon . . . from the yellow chalk," (Cope, 1872d, p. 272) collected by E. D. Cope. Type specimen includes braincase, quadrates, frontal, pterygoid and seventeen vertebrae.

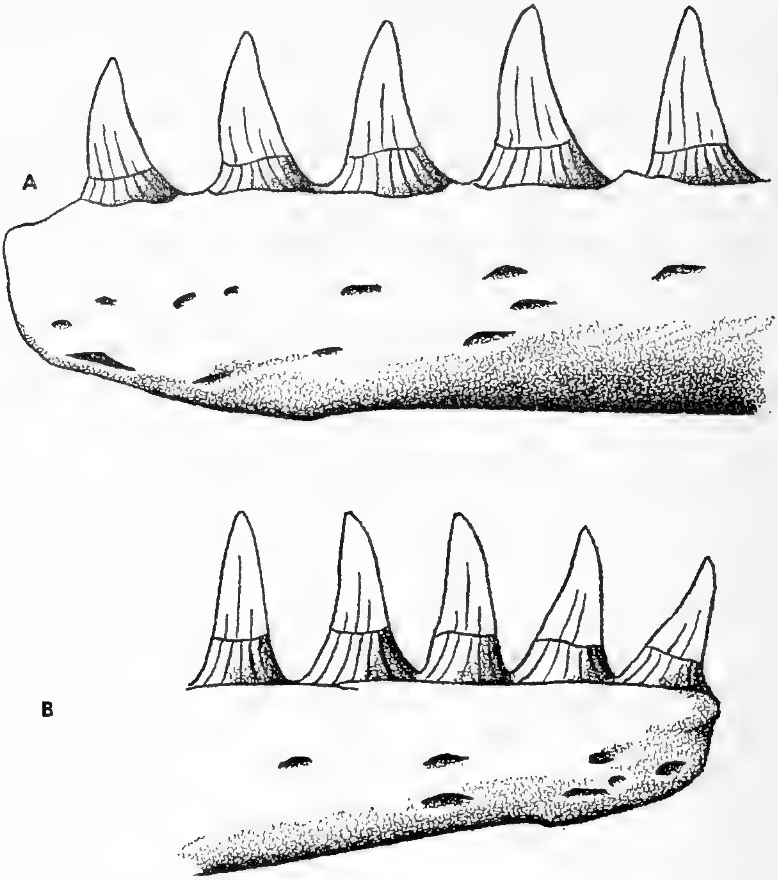
DISTRIBUTION. Smoky Hill Member, Niobrara Formation, Kansas.

ADDITIONAL REFERENCES. Leidy, 1873, pp. 276, 344. Cope, 1875, pp. 142, 267-268, pl. 15 fig. 1, pl. 16 fig. 3, pl. 17 fig. 6, pl. 20 figs. 4-7, pl. 21 figs. 1-2, pl. 36 fig. 6, pl. 37 fig. 9, pl. 55 fig. 3; 1877, p. 584. Owen, 1880, p. 180. Hoffman, 1890, p. 1322. Merriam, 1894, pp. 29, 30, pl. 1 figs. 1-2. Marsh, 1897, p. 527. Williston, 1898b, p. 186. Merril, 1907, p. 73. Sternberg, 1909, fig. 10. Drevermann, 1914, fig. 8. Abel, 1922, fig. 265. Gilmore, 1928, p. 87. Lane, 1947, pp. 316, 317. McDowell and Bogert, 1954, p. 132. Edmund, 1960, p. 89.

REFERRED SPECIMENS. *AMNH* nos. *126, *127, *202, 1510, *1511, **1512, 1645. *YPM* nos. *1264 *(P. gracilis),* ***1350 (P. abruptus),* 1427, *1428, ** 3972, 4004 and twenty-two unnumbered specimens, *USNM* nos. **3774, **3791, 11654, 11655 and one unnumbered specimen. *MCZ* nos. 1606, 1607, *1610, 1614. *KU* nos. **1007, 1092, 1143, 5016 and two unnumbered specimens. *FHM* no. **10902.

DIAGNOSIS. Premaxillo-maxillary suture terminates posteriorly at point above third maxillary tooth. Pineal foramen large, occasionally reaches frontal anteriorly. Squamosal sends very abbreviated wing medially to contact ramus from parietal. Ventroposterior process on jugal moderately large. Otosphenoidal crest on prootic does not cover exits for cranial nerves VII and IX. Articular surfaces of basipterygoid processes large and laterally directed. Ventral posterior processes of basisphenoid separated by shallow emargination. Coronoid descends at steep angle posteriorly to dorsal edge of surangular. Exits for mandibular ramus of fifth nerve separate into two diverging rows anteriorly on dentary and reconverge at ventroanterior margin of bone. Mandibular teeth bicarinate, vertically striated and medially recurved.

DISCUSSION. *Platecarpus coryphaeus* is as far as is known almost inseparable from *P. ictericus.* Only the position of the external nares and exits for the mandibular ramus of the fifth nerve can be used to distinguish them. There is no diagnostic cranial material remaining in the type, although Cope (1875, p. 143) describes a maxilla which has evidently been lost. This element was figured (ibid., pl. 55 fig. 3) in a reconstruction of the type cranium as having the greatest depth of the maxilla anteriorly, which in this species coincides with the posterior termination of the premaxillo-maxillary suture, at a point dorsal to the third maxillary tooth. Therefore the name *P. coryphaeus* is tentatively conserved for this species, even though the type specimen may have come from a level high in the chalk (see discussion on p. 187). *P. gracilis* and *P. (Holosaurus) abruptus* may be recognized as junior synonyms on the basis of the diagnostic cranial characters preserved in their respective types.



Text-fig. 85. Lateral view of anterior tip of dentary. A. *Platecarpus coryphaeus* (AMNH 1511, × 6/7). B. *Platecarpus ictericus* (AMNH 1488, × 6/7).

This species has not been identified from the Pierre and, although locality data is thus far insufficient, future work may show that it is absent in the upper part of the Niobrara as well.

Platecarpus ictericus (Cope 1871)
(Text-figs. 2A, 4A, 5B, 6, 17, 22A, 23, 24B, 25, 29, 37, 38, 83, 84, 85B; Plate II, fig. 2)

Liodon ictericus Cope, 1871a, p. 572.
Holcodus ictericus, Cope, 1872a, p. 298.
Liodon curtirostris Cope, 1872a, p. 298 *nomen nudum.*
Liodon curtirostris Cope, 1872d, p. 10.
Lestosaurus simus Marsh, 1872b, p. 455.
Lestosaurus felix Marsh, 1872b, p. 457.
Lestosaurus latifrons Marsh, 1872b, p. 458.
Platecarpus ictericus, Cope, 1874, p. 35.

Type. AMNH 1559, from ". . . the north bank of the Smoky Hill River, thirty miles east of Fort Wallace, Kansas," (Cope, 1871b, p. 580) collected by B. F. Mudge. Type specimen includes a partial skull, 18 vertebrae and fragments of a pectoral girdle.

Distribution. Smoky Hill Member, Niobrara Formation, Kansas; Lower Pierre Formation, Kansas, Wyoming and South Dakota.

Additional References. Cope, 1871c, p. 132; 1871f, p. 406; 1872b, p. 170; 1872c, p. 176; 1872d, pp. 272, 273; 1872e, p. 141; 1872f, p. 331; 1874, pp. 35, 36; 1875, pp. 144, 150, 267, 268, pl. 14 figs. 3-4, pl. 15 figs. 2-3, pl. 16 figs. 4-5, pl. 17 figs. 2-4, pl. 18 figs. 6-8, pl. 19 figs. 7-10, pl. 20 figs. 1-3, pl. 21 figs. 7-13, pl. 25 figs. 1-24, pl. 36 figs. 5, 7, pl. 37 figs. 8, 10, pl. 38 fig. 1; 1877, p. 584. Marsh, 1872b, p. 461, pl. 10; 1880, figs. 2-4; 1897, p. 527. Owen, 1877, p. 687; 1878, fig. 4; 1879, p. 58. Lydekker, 1888, fig. 59. Baur, 1892, pp. 1-22, pls. 1-2. Merriam, 1894, p. 30. Williston, 1897e, fig. 7; 1898a, p. 29; 1898b, pp. 184, 188, 189, pls. 13-15, pl. 25 figs. 1-2; pl. 44, pl. 72 fig. 2; 1902, p. 253; 1910, p. 537, 1 fig.; 1914, figs. 69, 72b; 1925, fig. 54, 184. Osburn, 1906, pl. 8 fig. 28. Pompeckj, 1910, p. 137. Wiman, 1920 figs. 7a-b. Lane, 1947, p. 315. Kauffman and Kesling, 1960, fig. 6b. Russell, 1964, figs. 7-8.

Referred Specimens. *AMNH* nos. 515, **1488, 1528, 1532, 1550, 1563 *(P. curtirostris),* 1588, 1820, 1821, 2178, **2182, *5811, 6159. *YPM* nos. *1112, 1138, 1153, *1254, 1255, **1256 *(P. latifrons),* *1258 *(P. simus),* 1267, **1269, 1272, 1273, **1277 *(P. felix),* *1284, 1286, *1292, 1306, *3690, 3986, *3994, *3998, **4003, and sixty-five unnumbered specimens. *USNM* no. 18256 and five unnumbered specimens. *MCZ* nos. 1601, 1602, 1603, 1605, 1608, 1609, 1615, 1624. *KU* nos. 1026, **1031, 1046, *1052, 1054, **1081, 1091, 1093, 1094, 1097, 1114, 1118, 1135, 1140, *1142, 1196, 5042. *FHM* nos. **2913, *10760, **10856. *SDSM* no. **30139. *CNHM* nos. ***UC600,* **P12027. *NMC* ?no. **8163. *PU* no. 12999.

Diagnosis. Premaxillo-maxillary suture terminates posteriorly dorsal to midpoint between second and third maxillary tooth, where anterior portion of maxilla has greatest depth. Exits for mandibular ramus of fifth nerve separate into two parallel rows anteriorly on dentary and terminate at ventroanterior margin of bone. Otherwise as for *P. coryphaeus.*

Discussion. The arrangement of exits for the mandibular ramus of the fifth nerve on a type dentary of *P. ictericus,* the earliest name available for a Niobrara *Platecarpus,* shows it to be conspecific with the species diagnosed above. The type specimens of *P. curtirostris, P. simus, P. felix* and *P. latifrons* are also conspecific.

This has been by far the most frequently collected mosasaur from the Niobrara Chalk. Circumstantial evidence supporting its specific distinction from *P. coryphaeus* lies in the fact that crania belonging to *P. ictericus* are usually less completely preserved (see text-fig. 96), and that *P. coryphaeus* has not yet been identified from the Pierre, although *P. ictericus* does seem to occur in the Lower Pierre in some abundance.

Platecarpus cf. *P. somenensis* Thevenin, 1896, p. 907.

Distribution. Sharon Springs Member, Lower Pierre Formation, South Dakota.

Referred Specimens. *CNHM* nos. PR465, *PR466, **PR467. *YPM* one unnumbered specimen.

Diagnosis. Premaxillo-maxillary suture terminates posteriorly above midpoint between second and third maxillary tooth, anterior portion of maxilla has greatest depth dorsal to third maxillary tooth. Parietal foramen very large and broadly bordered anteriorly by frontal. Squamosal sends broad rectangular wing medially to contact ramus from parietal. Ventroposterior process on jugal very heavy. Small otosphenoidal crest on prootic covers exits for cranial nerves VII and IX. Articular surfaces of basipterygoid processes small and anteriorly directed. Ventral posterior processes of basisphenoid separated by deep median longitudinal cleft. Coronoid descends posteriorly at angle of 45° to dorsal edge of surangular. Exits for mandibular division of fifth nerve separate into two parallel rows anteriorly on dentary, both of which terminate at ventroanterior margin of bone. Mandibular teeth heavy, bicarinate, vertically striated and medially recurved.

Discussion. This form is surely distinct from *P. coryphaeus* and *P. ictericus,* although it is sometimes difficult to distinguish from the latter species due to the poor quality of bone preservation in the Pierre. The most obvious resemblances between this form and

P. somenensis, from strata of similar age (middle Campanian) of France, lie in the largeness of the teeth and the heaviness of the posteroventral process on the jugal (see Thevenin, 1896, pl. 30). However the type of *P. somenensis* is not sufficiently well known to make the assignment certain. Thevenin (1896, p. 910) says there is no canal through the basioccipital-basisphenoid, but this statement cannot be relied on for he also states that it is absent in Niobrara specimens of *Platecarpus.*

"Platecarpus" intermedius (Leidy 1870)

Clidastes intermedius Leidy, 1870, p. 4.

TYPE. ANSP 9023-4, 9029, 9092-4, all one specimen, from ". . . Rotten Limestone (Selma) Upper Cretaceous of Pickens Co., Alabama," (Cope, 1869-1870, p. 221) collected by Dr. J. C. Nott. Type specimen includes two dentary fragments and three vertebrae.

ADDITIONAL REFERENCES. Cope, 1871f, p. 412; 1875, p. 267. Leidy, 1873, pp. 281, 344, pl. 34 figs. 1-2, 4-5, 10. Merriam, 1894, p. 36. Williston, 1898b, p. 197. Zangerl, 1948, p. 15.

DIAGNOSIS. Exits for mandibular division of fifth nerve diverge anteriorly on dentary, one row to parallel longitudinal axis of dentary, other to descend to ventroanterior margin of bone. Posterior dentary teeth short and inflated.

DISCUSSION. This species is known only from the type specimen. The general heaviness of the dentary and its abrupt termination directly in front of the first tooth resemble the condition of this element in *Platecarpus* more closely than in *Clidastes.* The axis vertebra likewise is very similar to that of *Platecarpus,* differing only in the more central position of the hypapophyseal facet on its ventral margin (see Leidy, 1873, pl. 34 fig. 10). Leidy (1873, p. 282) notes that the zygosphenes of the two mutilated dorsals are as well developed as in *Clidastes.* The generic reference of this specimen to *Platecarpus* must be regarded as provisional, pending the discovery of new material. If it truly belongs in the Plioplatecarpinae, the inflated tooth bases and swollen teeth are unique among the members of the subfamily and show an interesting parallel to its contemporary *Globidens alabamaensis.*

GENUS ***ECTENOSAURUS*** new genus

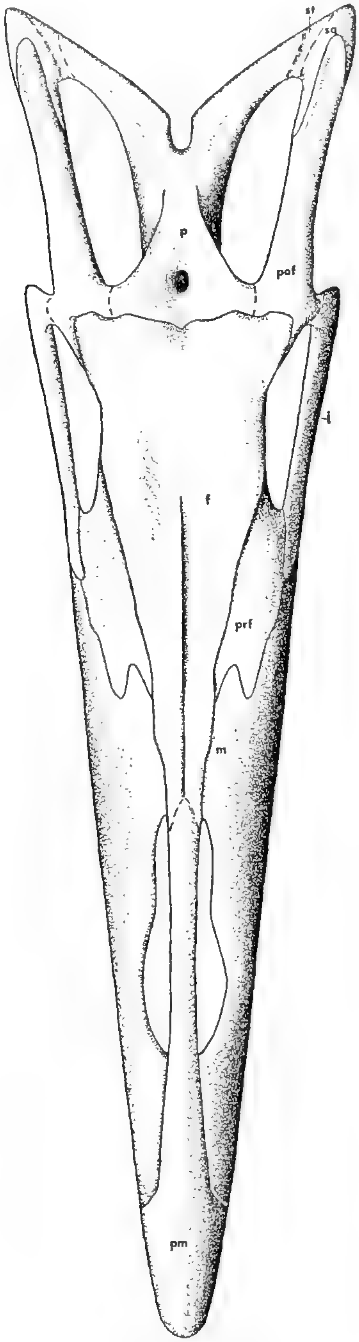
ETYMOLOGY. *Ectenes,* Gr., drawn-out, in reference to the elongated muzzle; *sauros,* Gr., lizard.

GENERIC TYPE. *Ectenosaurus clidastoides* (Merriam)

DIAGNOSIS. Premaxilla with small rostrum anterior to premaxillary teeth. Seventeen (?) teeth in maxilla. Prefrontal widely excluded from posterolateral margin of external nares by wing of maxilla and lacks process on supraorbital wing. Frontal emarginate above orbits, median dorsal ridge rounded. Parietal foramen large, situated in center of parietal. Margins of dorsal parietal surface converge, may meet, or before meeting may flow into gently rounded posterior axis of parietal. Ventral process of postorbitofrontal to jugal meets poorly exposed dorsal surface of postorbitofrontal at right angle. Ventroposterior process on jugal well developed. Squamosal wing to parietal moderately developed. Otosphenoidal crest on prootic does not cover exit for cranial nerve VII laterally. Canal for basilar artery through basioccipital and basisphenoid. Nine to 11 teeth in pterygoid. Suprastapedial process of quadrate broadly fused distally with infrastapedial process. Tympanic ala very thin. Stapedial pit rectangular in form. 13 teeth in dentary. Dentary terminates abruptly in front of first dentary tooth. Angular widely separated medially from coronoid. Mandibular teeth bicarinate, vertically striated and medially recurved.

Vertebral formula: at least 29 presacral vertebrae (see FHM no. 7937).

Articulating surfaces of cervical and thoracic vertebral centra wider than deep, smoothly elliptical in outline. Synapophysis located high in anterior portion of lateral



Text-fig. 86. Dorsal view of skull of *Ectenosaurus clidastoides* (reconstructed after FHM 7937, × ¼).

surface of cervical centra, occupies anterodorsal portion of lateral surface of anterior dorsal centra. Ventral border of anteroventral extension of synapophysis well developed on cervicals and anterior dorsals, does not reach level of undersurface of centrum. Anterior zygopophysis of cervicals and thoracics connected by gently rounded, posteriorly descending crest to synapophysis. Zygosphene-zygantrum strongly developed. Anterior base of atlas neural spine arises behind condylar facet, atlas synapophysis small and flat. Hypapophyseal peduncle located posteriorly on ventral surface of cervical centra, articulation for hypapophysis horizontal and triangular. Six hypapophysis-bearing cervicals, one more with rudimentary peduncle. Transverse process of pygal vertebrae relatively long.

Scapula smaller than coracoid. Glenoid articulating surface concave on scapula, probably smoothly continuous with that of coracoid. Superior border of scapula gently convex, posterior border slightly emarginated posteromedially. Coracoid expands medially to point behind glenoid articulation. Distal and proximal ends of humerus moderately expanded, facets for articulation with other elements and sites of muscle attachment moderately well differentiated. Proximal end of radius not expanded. Shaft of radius moderately wide. Distal end bears greatly expanded anterodistal flange.

Radiale present. Intermedium of average proportions. Ulnare enters broadly into posteroventral margin of antebrachial foramen. Metacarpal one equal to metacarpal two in length, has very slight anterodistal flange. Proximal ends of metacarpals moderately expanded. Phalangeal formula of manus approximately 4-4-5-5-?.

Discussion. The form of the teeth, shape of the frontal, large suprastapedial process of the quadrate and presence of a canal for the basilar artery through the basioccipital show that *Ectenosaurus* is closely related to *Platecarpus*. In addition, the narial emargination begins above and a little behind the third maxillary tooth and the exits for the mandibular ramus of the fifth nerve diverge anteriorly on the dentary of *Ectenosaurus*, greatly increasing the probability of confusing it with *Platecarpus coryphaeus* (as the author has done on at least four occasions). However, the elongated snout, exclusion of the prefrontals from the narial borders, fusion of the supra- and infrastapedial processes of the quadrate and peculiarities of the forelimbs necessitate the establishment of a new genus.

Ectenosaurus clidastoides (Merriam 1894)
(Text-figs. 54, 86)

Platecarpus clidastoides Merriam, 1894, p. 30.
Platecarpus oxyrhinus Merriam, 1894, p. 30.

Type. Formerly at Bayerische Staatssammlung für Paläontologie but probably destroyed during the Second World War (personal communication, R. Dehm 1963), from ". . . Niobraraschichten der oberen Kreide von Logan County, Kansas . . ." (Merriam, 1894, p. 3) collected by C. H. Sternberg or G. Baur. Type specimen includes a posterior portion of the skull and several vertebrae.

Distribution. Smoky Hill Member, Niobrara Formation, Kansas.

Additional References. Cope, 1875, pl. 25 figs. 25-26? Williston, 1898b, p. 190. Lane, 1947, p. 317.

Referred Specimens. *YPM* nos. 4671, *4672, **4673, *4674. *FHM* no. ***7937*.

Locality of FHM no. 7937; from the Niobrara Chalk on Garrett Ranch, seven or eight miles northwest of Wakeeney, Trego County, Kansas (personal communication, George Sternberg 1963).

Discussion. The above is the only species presently referable to the genus. The morphologic characteristics of a complete skull in the Fort Hays Kansas State College Museum demonstrate that the posterior portion of the skull of the type of *Platecarpus clidastoides* and the type muzzle of *P. oxyrhinus* actually belong to the same species, if not the same individual.

Genus *PLIOPLATECARPUS* Dollo 1882

Plioplatecarpus Dollo, 1882, p. 62.
Phosphorosaurus Dollo 1889c, p. 68.
Oterognathus Dollo, 1889c, p. 69.

GENERIC TYPE. *Plioplatecarpus marshi* Dollo.

DIAGNOSIS. Premaxilla with no rostrum anterior to premaxillary teeth (Dollo, 1889b, p. 275). Prefrontal forms large portion of posterolateral border of external nares, small lateral tuberosity on supraorbital wing. Prefrontal and postorbitofrontal do not meet above orbits. Frontal rectangular in outline, not emarginate above orbits and has median dorsal ridge. Parietal foramen very large, bordered anteriorly by frontal. Margins of dorsal parietal surface meet in front of diverging suspensorial rami forming triangular table anteriorly on parietal (see Dollo, 1889b, pl. 9 fig. 6). Exit for cranial nerve VII opens directly on lateral surface of prootic, no suggestion of otosphenoidal crest on prootic (DeViller, 1943, pl. 2 fig. 1). Canal for basilar artery through basioccipital and basisphenoid opens ventrally on basioccipital (Dollo, 1885, p. 319). Suprastapedial process not fused to very large infrastapedial process on quadrate. Tympanic ala moderately thick, laterally cup-shaped. Stapedial pit reniform in outline (Dollo, 1904, pl. 6). Dentary teeth reduced in number. Dentary terminates abruptly in front of first dentary tooth (Dollo, 1889b, pl. 10 fig. 14). Mandibular teeth bicarinate (?), vertically striated and medially recurved (Dollo, 1882, p. 64; 1889b, pl. 10 fig. 14).

Vertebral formula: 38 vertebrae anterior to chevron-bearing caudals, 55 caudals with chevrons and transverse processes, 33 terminal caudals (Dollo, 1894, pp. 233-234).

Articulating surfaces of cervical and anterior dorsal centra wider than deep, smoothly elliptical in outline. Synapophysis located in center of lateral surface of cervical and anterior dorsal centra, occupies anterior portion of lateral surface of posterior dorsal centra. Ventral border of anteroventral extension of synapophysis well to weakly developed on cervicals and anterior dorsals, directed horizontally forward from ventral edge of synapophysis on a level with undersurface of centrum. Gently rounded, posteriorly descending crest connecting anterior zygopophysis with synapophysis present or absent on cervical and anterior dorsal vertebrae. No zygosphene or zygantrum. Hypapophyseal peduncle located in center of ventral surface of cervical centra, articulation for hypapophysis horizontal and circular. Six hypapohysis-bearing cervicals (Dollo, 1894, p. 235). Neural spines of caudal centra vertical on postsacrals 54-72, decrease uniformly in length from base to end of tail (Dollo, 1894, pp. 235-236).

Scapula larger than coracoid. Glenoid articulating surfaces convex on both elements, do not form smoothly continuous surface. Superior border of scapula gently convex, posterior border may or may not be emarginated. Coracoid expands medially to point behind glenoid articulation. Distal and proximal ends of humerus moderately expanded, shaft of humerus short and broad. Facets for articulation with other elements and sites of muscle attachment poorly differentiated. Proximal end of radius expanded. Shaft of radius very wide. Distal end bears greatly expanded anterodistal flange (last paragraph based largely on Dollo, 1882, pl. 6).

DISCUSSION. The diagnosis is based on the fragmentarily known North American species *Plioplatecarpus primaevus* and *P. depressus,* supplemented by Dollo's descriptions of the European *P. marshi* (1882, 1885b, 1904a, 1917) and *P. houzeaui* (1889b, 1894, 1904a). Only the last species is known from complete material. The other three forms surely belong to *Plioplatecarpus* and it will probably be necessary to modify the above diagnosis somewhat as their osteology becomes better known. If Dollo's (1894, pp. 233-234) estimate of the vertebral count is correct, *Plioplatecarpus* is the only mosasaur to reduce the number of dorsal vertebrae during the course of its evolution.

Plioplatecarpus primaevus new species
(Text-fig. 87)

Platecarpus cf. *P. brachycephalus,* Dunkle, in Crandell, 1958, p. 14, fig. 8.

TYPE. USNM 18254, from NE corner sec. 35, T112N, R80W, near Pierre, Hughes County, South Dakota (Crandell, 1958, fig. 8) collected by D. R. Crandell. Type specimen includes quadrate, three anterior dorsal vertebrae and both scapulae-coracoids.

Distribution. DeGrey Member, Lower Pierre Shale, South Dakota.

Diagnosis. Large prominence projects posteriorly beneath stapedial pit on quadrate, nearly closes stapedial notch from below. Anterior zygopophysis of cervical and anterior dorsal vertebrae connected to synapophysis by gently rounded, posteriorly descending crest. Functional zygopophyses probably end near posterior end of dorsal series, or in pygal region. Posterior border of scapula strongly emarginated posteromedially. Coracoid foramen small.

Text-fig. 87. Medial view of right quadrate of type of *Plioplatecarpus primaevus* (USNM 18254, × ¾).

Discussion. *Plioplatecarpus primaevus* is confidently referred to *Plioplatecarpus* on the basis of the characteristic shape of its quadrate, the elongate, gently-convex superior border of the scapula, and the greater size of the scapula when compared to the coracoid. It differs widely from *P. marshi* in the larger size of the posterior prominence beneath the stapedial pit on the quadrate, its much smaller coracoid foramen and in the presence of a posteromedial emargination on the posterior border of the scapula (see Dollo, 1904a, pl. 6; 1882, pl. 6). The quadrate of *P. primaevus* is very similar to that of *P. houzeaui,* but the former species differs in that the zygopophyses are well developed in the anterior dorsal region while in the latter they disappear on the third dorsal (Dollo, 1894, p. 235). In *P. primaevus* the anterior zygopophyses of the anterior dorsal vertebrae are linked posteriorly to the synapophyses by a strong crest that is completely lacking in *P. depressus.* It is seen that, except for the absence of zygosphene-zygantra, the anterior vertebrae of *P. primaevus* are nearly identical to those of *Platecarpus.* It is likely therefore, that this species had a presacral count closer to 29 vertebrae, as in *Platecarpus,* than to the reduced number of 20 found in *P. houzeaui. Plioplatecarpus primaevus* must be very closely related to *Platecarpus.*

Plioplatecarpus depressus (Cope 1869)

(Text-fig. 88)

Mosasaurus depressus Cope, 1869b, pp. 262, 263, *nomen nudum.*
Mosasaurus depressus Cope, 1869e, p. 16.
Mosasaurus copeanus Marsh, 1869, p. 393.
Halisaurus fraternus Marsh, 1869, p. 397.
?*Liodon laticaudus* Marsh, 1870, p. 2.

Type. Specimen not located, originally ". . . from Burlington Co., N. J.," (Cope, 1869-1870, p. 196) collected by L. T. Germain. Type specimen includes a quadrate, cranial fragments and dorsal vertebrae (Cope, 1869-1870, p. 196).

Distribution. Navesink Formation or younger Cretaceous, New Jersey.

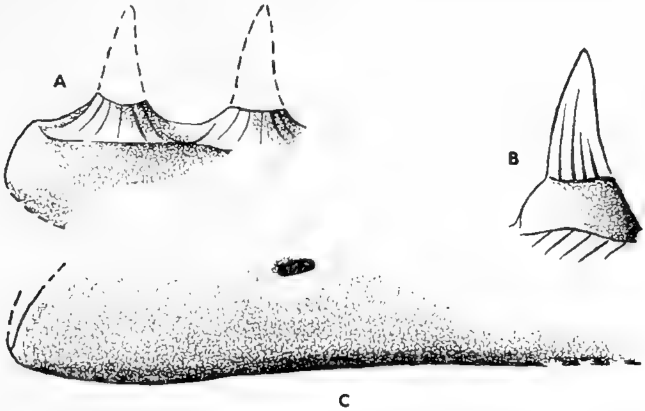
Additional References. Leidy, 1865a, pl. 7 figs. 2-3, ?8, ?9-11. Cope, 1868b, p. 734; 1869-1870, pp. 189, 198, 210, fig. 48(3), ?pl. 5 fig. 4, pl. 11 fig. 6; 1875, pp. 269, 270, 272, pl. 37 fig. 12. Marsh, 1872b, p. 455. Merriam, 1894, p. 37. Williston, 1898b, p. 207. Hay, 1902, p. 472 *(L. laticaudus)*. Gilmore, 1926, p. 191, pl. 62 fig. 5. Miller, 1955, pp. 905, 909.

Referred Specimens. *AMNH* nos. 1382, 1430, 2304. *YPM* nos. 312 *(P. copeanus)*, ?411 *(L. laticaudus)*, 445 *(P. fraternus)*.

Diagnosis. Anterior zygopophyses of cervical and anterior dorsal vertebrae separated from synapophyses by longitudinal sulcus, lateral surface of neural arch smooth. Functional zygopophyses probably end near center of dorsal series.

Discussion. The quadrate belonging to the type of *M. depressus*, figured by Cope (1869-1870, fig. 48(3), pl. 11 fig. 6), has a large suprastapedial process with parallel sides, as is the case in all members of the Plioplatecarpinae. It also has a relatively thick tympanic ala and, in medial aspect, resembles the quadrate of *Plioplatecarpus* more closely than that of any other genus of mosasaur. The New Jersey quadrate cannot be confused with *Platecarpus* because, lying posterior to the ventral margin of the stapedial pit, there is a prominence that nearly closes off the stapedial notch from below, which is lacking in the latter genus.

The blunt termination of the dentary immediately anterior to the first dentary tooth and the bicarinate, medially recurved and vertically striated teeth in the type specimen of *M. copeanus* all strongly support the inclusion of this species in the Plioplatecarpinae. The type is not complete enough to determine conclusively whether it belongs to *Platecarpus*, *Ectenosaurus* or *Plioplatecarpus*, but because it was collected from strata of Maestrichtian age, in which the former two genera are unknown to occur, it is much more probable that it belongs to *Plioplatecarpus*.



Text-fig. 88. A. Lateral view of tip of left dentary. B. Lateral view of mandibular tooth. C. Medial aspect of the left splenial. *Plioplatecarpus depressus* (YPM 312, × ¾).

The type of *Halisaurus fraternus* consists of one cervical and two dorsal vertebrae. They are referred to *Plioplatecarpus* because of the depressed, elliptical shape of the central articulations and lack of zygantra on the cervical vertebrae (see Dollo, 1894, pp. 234-235 for descriptions of the same characters in the vertebral column of *Plioplatecarpus houzeaui*).

The types of *M. copeanus* and *H. fraternus* were collected from Maestrichtian greensands in New Jersey, as probably was the missing type of *M. depressus*. All three of these specimens are referable to *Plioplatecarpus* and in the absence of any evidence to the contrary they are here assumed to belong to a single species, the oldest name available for which being *Plioplatecarpus depressus*. If this is correct, the American Maestrichtian *P. depressus* will resemble the European *P. marshi* most closely, but may be distinct in that the known teeth are less medially recurved (see Dollo, 1913, pl. 25 fig. 2).

The type of *Liodon laticaudus* consists of a single mutilated caudal vertebra with facets for articulation with the haemal arches. It may belong to *P. depressus* or perhaps *Prognathodon rapax*. Additional caudal material of these two forms will be needed to assign this vertebra properly.

TRIBE **PROGNATHODONTINI** new

DIAGNOSIS. Deep groove in floor of basioccipital and basisphenoid for basilar artery. Massively proportioned jaws, teeth faceted or smooth and elliptical in cross-section. Chevrons either free or fused to caudal centra. The following mosasaurs are clearly of plioplatecarpine derivation but have massive jaws and a heavy dentition much more suited to crushing prey than that of members of the Plioplatecarpini.

GENUS *PROGNATHODON* Dollo 1889

Prognathodon Dollo, 1889a, p. 214.
Prognathosaurus Dollo, 1889b, p. 293, pl. 9 figs. 4-5, pl. 10 figs. 8-9.
Brachysaurus Williston, 1897a, p. 96, pl. 8 (preoccupied Hallowell 1856).
Brachysaurana Strand, 1926, p. 54.
Ancylocentrum Schmidt, 1927, p. 59.

GENERIC TYPE. *Prognathodon solvayi* Dollo.

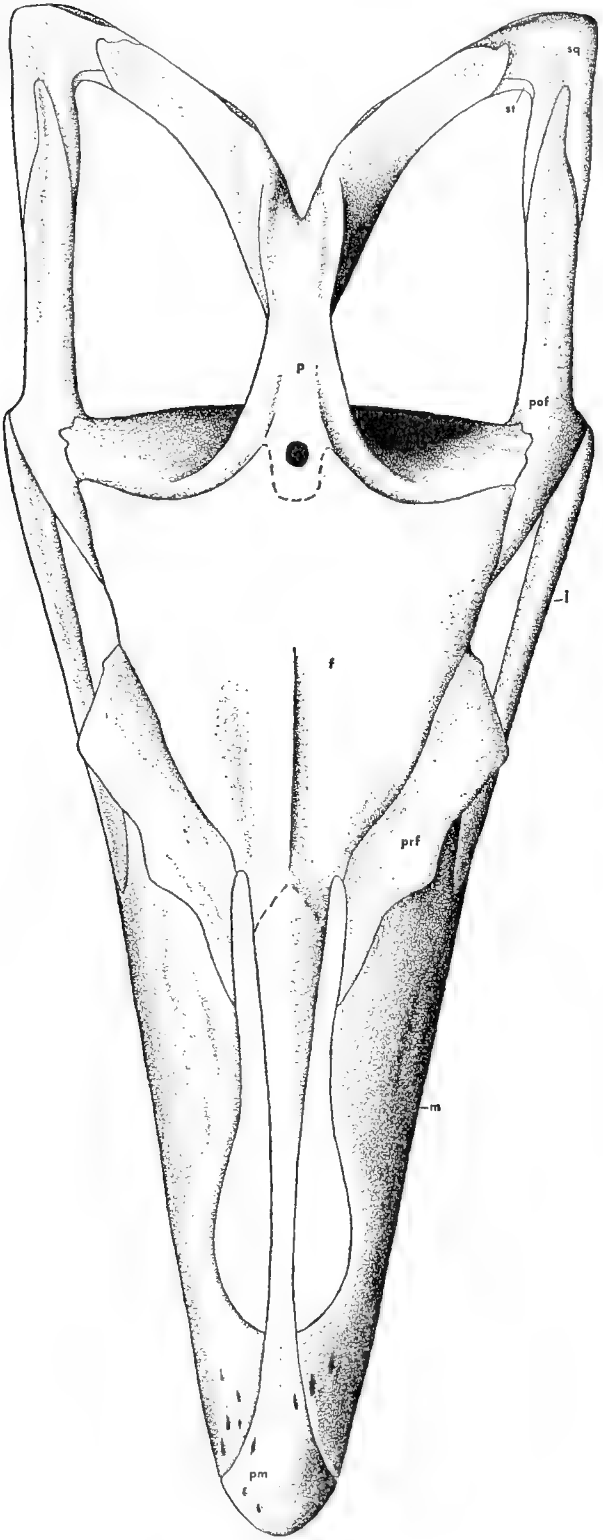
ADDITIONAL REFERENCES. Leidy, 1865a, pl. 3 figs. 1-2. Cope, 1869-1870, fig. 49 (p. 205)?. McDowell and Bogert, 1954, p. 132. Romer, 1956, p. 562.

DIAGNOSIS. Premaxilla with no rostrum anterior to premaxillary teeth. Twelve teeth in maxilla. Prefrontal forms large portion of posterolateral border of external nares; supraorbital wing with heavy triangular ala contacts postorbitofrontal posteriorly over orbit medial to external edge of frontal. Frontal not emarginate above orbits, median dorsal ridge present. Parietal foramen small, located anteromedially on small prominence on parietal, and closely embraced on either side by short tongues from frontal. Margins of dorsal parietal surface parallel one another and cranial midline to posterior base of diverging suspensorial rami, forming rectangular field medially on parietal. Ventral process of postorbitofrontal to jugal indistinctly separated from moderately well exposed dorsal surface of postorbitofrontal. Ventroposterior process on jugal slightly developed. Squamosal wing to parietal large. Deep groove in floor of basioccipital for basilar artery. Seven teeth in pterygoid. Suprastapedial process distally fused to infrastapedial process on quadrate. Tympanic ala thick. Stapedial pit nearly circular in form. Fourteen teeth in dentary. Dentary terminates abruptly in front of first dentary tooth. Medial wing from coronoid contacts angular. Retroarticular process of articular rectangular in outline. Mandibular teeth stout, bicarinate.

Vertebral formula: The type of *Prognathodon solvayi* from the Maestrichtian of Belgium has at least 38 vertebrae anterior to the chevron-bearing caudal series (Dollo, 1889b, p. 294). *Platecarpus* has only 34 such vertebrae. The differing counts may be due to the incorporation of several caudals into the pygal region of *Prognathodon*.

Articulating surfaces of thoracodorsal vertebrae wider than deep, smoothly elliptical in outline. Synapophysis located anterodorsally on lateral surface of centrum. Anterior zygopophysis of thoracodorsals swollen, connected by gently rounded, posteriorly descending crest to synapophysis (see AMNH 1562, type of *P. crassartus*).

Articulating surfaces of lumbodorsal vertebrae wider than deep, gently convex at base, with dorsomedially curving lateral borders. Superior border narrow. Synapophysis located at dorsoventral midpoint of anterior half of lateral surface of lumbodorsal centra.



Text-fig. 89. Dorsal view of skull of *Prognathodon overtoni* (slightly reconstructed, after SDSM 3393, × ¼).

Small, sharply defined crest of bone rises rather steeply from synapophysis to base of anterior zygopophysis (see NJGS 9827, *P. rapax*).

Zygosphene-zygantrum rudimentary or absent (Cope, 1875, p. 153; Dollo, 1889b, p. 297; Williston, 1897a, p. 96). Chevrons articulating in *P. solvayi* (Dollo, 1890, footnote p. 163) and in *P. crassartus;* fused in *P. overtoni* (Williston, 1898b, p. 192). Neural spines of caudal centra decrease uniformly in length from base to end of tail in *P. solvayi* (Dollo, 1917, p. 20).

Scapula of moderate proportions, probably smaller than coracoid (Dollo, 1889b, p. 295). Distal and proximal ends of humerus moderately expanded, facets for articulation with other elements and sites of muscle attachment moderately well differentiated (Cope, 1875, pl. 26 fig. 9; Williston, 1898b, pls. 30 fig. 6, 22 fig. 1). Proximal end of radius greatly expanded, shaft of radius very wide. Distal end bears greatly expanded anterodistal flange, is thickened medially to form indistinct facet for articulation with intermedium (Cope, 1875, pl. 26 fig. 11).

Distal and proximal end of femur about equally expanded, shaft of femur constricted. Internal trochanter moderately large, medial to head. No distinct facets on distal end, although femur is thickened in region of tibial articulation (Cope, 1875, pl. 26 fig. 10).

Discussion. Although excellent postcranial material of *Prognathodon* has been collected from Belgium (see Dollo, 1889b, pp. 293-294; 1890, p. 163; 1917, p. 20) none of it has been described, and of necessity the foregoing diagnosis is based on very incomplete material from this continent. The chevrons are articulating in *P. solvayi* and *P. crassartus* although Williston (1898b, p. 192) explicitly states they are fused to the caudal centra in the type of *P. overtoni*. For this reason he was reluctant to synonymize his *Brachysaurus* with Dollo's *Prognathosaurus* (=*Prognathodon*) in which the chevrons are free. Chaffee (1939, p. 2) asserts that there is no indication that the chevrons are fused to the caudals of *Ancylocentrum hungerfordi* (=*Prognathodon rapax*) on the mistaken assumption that the lumbodorsal vertebrae of his specimen were caudals.

Prognathodon crassartus (Cope 1872)

Liodon near *L. proriger* Cope, 1872b, p. 168.
Liodon crassartus Cope, 1872d, p. 278.
Platecarpus crassartus, Cope, 1874, p. 36.
?*Platecarpus crassartus,* Williston, 1898b, p. 180.

Type. AMNH 1562, from the Pierre Formation near Eagle Tail, Kansas (see Williston, 1898b, p. 180) collected by B. F. Mudge. Type specimen included ". . . a series of dorsal, lumbar, and caudal vertebrae, with some bones of the limbs," (Cope, 1875, p. 153), only five vertebrae of the type have been located.

Distribution. Lower Pierre Formation, Kansas.

Additional References. Cope, 1875, pp. 153, 268, pl. 26 figs. 4-12. Merriam, 1894, p. 31. Williston, 1898b, p. 180, pl. 45 figs. 3-5. Lane, 1947, p. 314.

Diagnosis. Chevrons free. Pectoral crest of humerus large, medially located.

Discussion. Cope's *Platecarpus crassartus* is referred to *Prognathodon,* as was tentatively suggested by Williston (1898b, p. 180), on the basis of the close similarity of its humerus to that of *P. overtoni*. These two humeri resemble each other and differ from those belonging to *Platecarpus* in the rounded profile of the proximal end in lateral profile, which in the latter genus is usually more angular; in the less constricted humeral shaft, and in the lesser degree of expansion of the distal end. The radius of *P. crassartus* differs markedly from that of *Platecarpus* in that it is wider than long and has a much broader shaft. The internal trochanter is medial to the head of the femur in position; in *Platecarpus* it is anteromedial.

Prognathodon overtoni (Williston 1897)
(Text-figs. 89, 90)

(undescribed genus) *overtoni* Williston, 1895a, p. 169.
Brachysaurus overtoni Williston, 1897a, p. 96, pl. 8.
Ancylocentrum overtoni, Schmidt, 1927, p. 59.

Type. KU 950, from ". . . near the top of the Pierre deposits of the Cheyenne River of South Dakota, and probably a hundred feet or more above (the level) of *M. horridus* (synonym of *M. missouriensis*) . . ." (Williston, 1897a, p. 95) collected by T. R. Overton. Type specimen includes a fragmentary skull, 20 vertebrae, humeri and two paddle bones.

Distribution. Upper Pierre Formation, South Dakota.

Additional References. Williston, 1897a, pl. 8; 1897d, pp. 178, 181; 1897e, p. 246; 1898b, pp. 88, 91, 107, 111, 127, 134, 148, 192, pl. 22 fig. 1, pl. 30, pl. 40 figs. 10-11 (undetermined bones), pl. 62 figs. 1-2; 1925, p. 273. Ballou, 1898, p. 217. Osburn, 1906, pl. 8 fig. 24. Gilmore, 1928, p. 87. Nopcsa, 1928, p. 177. Lane, 1947, p. 320. Kauffman and Kesling, 1960, pp. 222, 230, 231, 234, 235, tables 3, 5, 6.

Referred Specimen. *SDSM* no. 3393. Locality of referred specimen; from the Virgin Creek Member, Upper Pierre Formation, six miles southwest of Cuny Table, on Mule Creek, Shannon County, South Dakota (personal communication J. P. Gries, 1963).

Diagnosis. No tuberosity on anteromedian edge of quadrate shaft, suprastapedial process not constricted dorsally. Chevrons fused to caudal centra. Pectoral crest of humerus small, anteriorly located.

Discussion. *Prognathodon overtoni* may be distinguished from its European contemporary, *P. solvayi,* by the smooth enamel surfaces of its teeth (compare Williston, 1898b, pl. 30 fig. 1 with Dollo, 1889b, pl. 9 fig. 4) and the non-procumbant nature of the anterior teeth in a beautifully preserved skull referred to *P. overtoni* in the collections of the South Dakota School of Mines. *P. giganteus,* from the same area and horizon as *P. solvayi,* is defined by Dollo (1904, p. 213) as also possessing smoothly surfaced tooth enamel and, in the absence of other described characters, could be identical to either *P. overtoni* or *P. rapax* (see below).

Prognathodon rapax (Hay 1902)
(Text-fig. 91)

Macrosaurus laevis in part, Leidy, 1865a, p. 75.
Liodon validus, Cope, 1869-1870, pp. 201, 207, fig. 48(5).
Tylosaurus rapax Hay, 1902, p. 473.
Ancylocentrum hungerfordi Chaffee, 1939, p. 1, figs. 1 (1, 3, 6), fig. 2.

Type. AMNH 1490, ". . . from near Barnesboro, Gloucester Co., N. J.," (Cope, 1869-1870, p. 207). Type specimen includes quadrates of two individuals.

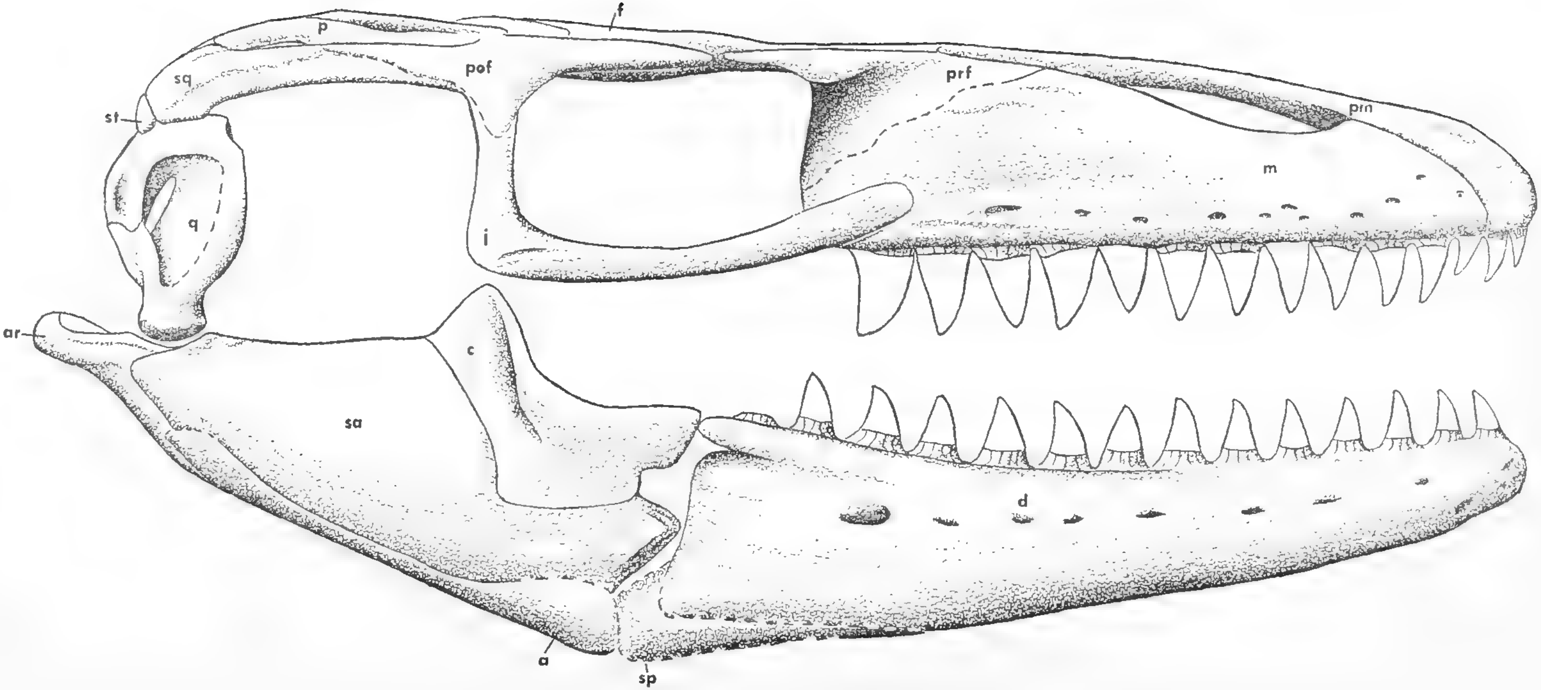
Distribution. Navesink Formation or younger Cretaceous, New Jersey.

Additional References. Leidy, 1865a, ?pl. 9 figs. 8-9. Cope, 1869-1870, fig. 49 p. 205; 1870a, p. 272; 1875, p. 271, pl. 37 fig. 4. Miller, 1955, pp. 905, 909.

Referred Specimens. *AMNH* no. 2205? *YPM* nos. 413, 1597. *ANSP* no. 8550. *NJGS* no. 9827 *(P. hungerfordi).*

Diagnosis. Large tuberosity on anteromedian edge of guadrate shaft, suprastapedial process strongly constricted dorsally.

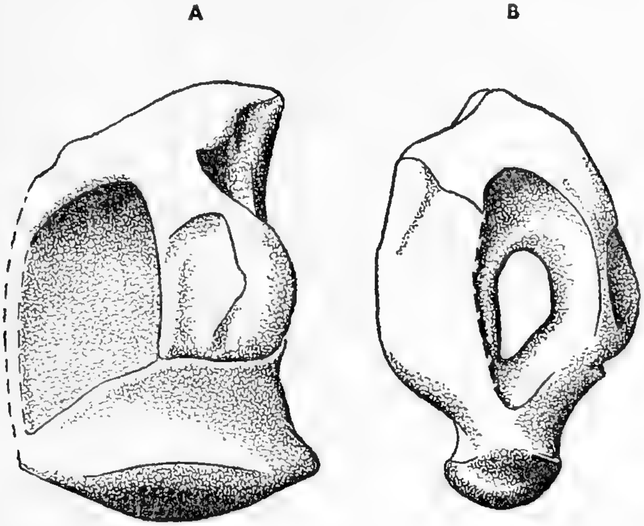
Discussion. Lumbodorsal vertebrae of *Prognathodon rapax* closely resemble those of *Mosasaurus,* but may be distinguished by the depressed form of their centra. Cervical vertebrae of *P. rapax* have not yet been recognized, as the cervical in the type of *Ancylocentrum hungerfordi* (= *P. rapax*) belongs to *Thoracosaurus,* a crocodile. Cope (1869-1870, fig. 49, p. 205) figures a very broad radius from the late Cretaceous green-



Text-fig. 90. Lateral view of skull of *Prognathodon overtoni* (slightly reconstructed, after SDSM 3393, × ca. ⅕).

sands of New Jersey that may belong to *P. rapax.* It has a broad longitudinal facet on its posterodistal margin apparently for articulation with the ulna that is absent in all other known mosasaurs.

Prognathodon rapax is easily separated from *P. overtoni* and *P. solvayi* by the characters of the quadrate, outlined above, in which the latter two species resemble one another. *P. rapax* may be close to *P. giganteus* but both species are much too incompletely known to hazard speculation on interrelationships.



Text-fig. 91. A. Lateral view of left quadrate. B. Posterior view of left quadrate. *Prognathodon rapax* (reconstructed after the quadrates of NJGS 9827, × ⅖).

GENUS *PLESIOTYLOSAURUS* Camp 1942

Plesiotylosaurus Camp, 1942, p. 18.

GENERIC TYPE. *Plesiotylosaurus crassidens* Camp 1942.

DIAGNOSIS. Premaxilla with no rostrum anterior to premaxillary teeth. Thirteen teeth in maxilla. Prefrontal forms large portion of posterolateral border of external nares; supraorbital wing with triangular ala, contacts postorbitofrontal dorsally over orbit lateral to external edge of frontal. Frontal not emarginate above orbits, median dorsal ridge (?)absent. Parietal foramen small, closely embraced on either side by short tongues from frontal. Margins of dorsal parietal field diverge posteriorly. Dorsal surface of postorbitofrontal very well exposed. Squamosal wing to parietal large. At least seven pterygoid teeth. Suprastapedial process distally fused to infrastapedial process on quadrate. Tympanic ala thick, quadrate massive. Sixteen to seventeen teeth in dentary. Small projection of dentary anterior to first dentary tooth. Mandibular teeth large and heavy.

Superior border of scapula strongly convex, posterior border very strongly emarginated. Distal and proximal ends of humerus moderately expanded.

DISCUSSION. The foregoing diagnosis was taken from descriptions and illustrations in Camp (1942). Although the reviewer has not examined the California material, it is his opinion that *Plesiotylosaurus* belongs in the Plioplatecarpinae close to *Prognathodon* because of its bluntly terminated premaxilla and the large maxillary and pterygoid teeth. It is distinguishable from *Prognathodon* in its long and slender snout, the greater number of mandibular teeth and in its peculiar quadrate. The head of the humerus is squarely terminated as in *Platecarpus* and unlike *Prognathodon,* but the radial process is larger than in the former genus.

Plesiotylosaurus crassidens Camp 1942

Plesiotylosaurus crassidens Camp, 1942, p. 18, figs. 11-13, pl. 4.

TYPE. CIT no. *2759, 760 feet above base of Moreno Formation, Fresno County, California (see Camp, 1942, p. 18, for detailed locality information). Type specimen includes a skull and lower jaws (Camp, 1942, p. 18).

DISTRIBUTION. Moreno Formation, California.

ADDITIONAL REFERENCES. Welles, 1943, p. 128, fig. 2. McDowell and Bogert, 1954, p. 132. Romer, 1956, p. 562. Anderson, 1958, p. 71.

REFERRED SPECIMEN. *CIT* no. 2753 (fide Camp, 1942, p. 19).

?SUBFAMILY PLIOPLATECARPINAE *incertae sedis:*

GENUS *HALISAURUS* Marsh 1869

Halisaurus Marsh, 1869, p. 395.
Baptosaurus Marsh, 1870, p. 3.

GENERIC TYPE. *Halisaurus platyspondylus* Marsh.

ADDITIONAL REFERENCES. Cope, 1869-1870, p. 208; 1874, p. 31; 1875, p. 272. Merriam, 1894, pp. 36, 39. Williston, 1897c, p. 107; 1897d, pp. 179, 182; 1898b, p. 207. Gilmore, 1928, p. 87. McDowell and Bogert, 1954, p. 132. Romer, 1956, p. 562.

DIAGNOSIS. Articulating surfaces of cervical and anterior dorsal vertebral centra nearly twice as wide as deep, sub-rectangular in outline. Synapophyses located in center of lateral surface of cervical centra, occupies somewhat more posterior position in anterior thoracics. Ventral border of anteroventral extension of synapophysis weak and horizontal in anterior cervicals, becomes much enlarged in posterior cervicals and anterior thoracics, extending far below flattened undersurface of centrum. Anterior zygopophysis of cervical and anterior thoracics connected by gently rounded, posteriorly descending crest to synapophysis. No zygosphene or zygantrum. Hypapophyseal peduncle located posteriorly on ventral surface of cervical centra, articulation for hypapophysis flat and lenticular, slightly inclined posteriorly.

DISCUSSION. In spite of the great span of time separating the two known species of *Halisaurus,* their vertebrae are so similar and so characteristic that there would be no justification for relegating them to separate genera (see also Merriam, 1894, p. 37). The large, *Platecarpus*-like suprastapedial process of *H. onchognathus* supports the reference of this genus to the Plioplatecarpinae.

It has been stated (Dollo, 1889b, p. 275; Williston, 1898b, p. 207; etc.) that the hypapophyses of *Halisaurus* are fused to the cervical centra. The cervical vertebra of the type of *H. platyspondylus* has a long, laterally compressed peduncle that lacks any articulating facet distally for the hypapophysis. In a larger specimen, surely referable to *H. platyspondylus* because of its greatly depressed centra (YPM 412), the peduncle bears a well-developed facet, as does a cervical in the type of *H. onchognathus.* The cervical vertebra of Marsh's type must have belonged to the posterior cervical or anterior dorsal region, where the peduncles lose the facet for articulation with the hypapophysis.

Halisaurus onchognathus (Merriam 1894)

Baptosaurus onchognathus Merriam, 1894, p. 37, pl. 4 figs. 9-10.

TYPE. Formerly at Bayerische Staatssammlung für Paläontologie but probably destroyed during the Second World War (personal communication, R. Dehm 1963), from ". . . Niobraraschichten der oberen Kreide von Logan County, Kansas . . ." (Merriam, 1894, p. 3) collected by C. H. Sternberg. Type specimen includes a surangular, articular, prefrontal, quadrate and eight vertebrae.

Additional References. Williston, 1897d, p. 179; 1897e, p. 244; 1898b, p. 208, pl. 25 fig. 6, pl. 41 fig. 3. Dollo, 1924, p. 211.

Discussion. No additional specimens of this highly distinctive form have been seen by the author in the collections of American museums. A possible specific distinction between *H. platyspondylus* and *H. onchognathus* may be that in the former the hypapophyseal peduncle is somewhat dilated distally; in the latter it is tapered (Merriam, 1894, pl. 4 fig. 9). *H. onchognathus* is easily distinguished from *Ectenosaurus clidastoides* by the fan-shaped retroarticular process of the articular. Merriam (1894, pp. 36-37) describes the following cranial material with the type of *H. onchognathus:*

"Das einzige Kieferstück . . . stimmt bis auf das abweichende Articulare mit dem von *Platecarpus* oder *Tylosaurus* überein, interscheidet sich jedoch von diesen dadaurch, dass der Oberrand des Articulare unmittelbar hinter der Gelenkpfanne, anstatt sich um etwa 40° nach unten zu biegen, vertical harauf in einem hohen Fortsatz ausgezogen ist. Dadurch erhält das Hinterende des Unterkiefers ein hakenartiges Aussehen. Auch an der unteren hintern Ecke, wo bei *Platecarpus* und *Tylosaurus* eine längliche Verdickung verhanden ist, verdickt sich der Rand plötzlich um mehr als zwei Mal der Dicke hinter dieser Stelle und wird dann plötzlich unter dem Hinterende der Gelenkpfanne dünner . . . Ein stück des Hinterendes des Praefrontale hat viel Aehnlichkeit mit dem von *Tylosaurus,* nur ist auf der Aussenseite desselben keine tiefe Rinne zur Aufnahme des spitzen Vorderendes des Postfrontoorbitale vorhanden. Es liegt auch ein sehr zerquetschtes Quadratum vor, das einem Supracolumellar-Fortsatz, der dem von *Platecarpus* sehr ähnlich sieht, besitzt. Der Flügel des Quadratums ist wie bei *Platecarpus* und *Tylosaurus* in der Mitte sehr dünn und durchbrochen." The intercentral articulations of this specimen become more circular posteriorly (ibid., p. 36).

Halisaurus platyspondylus Marsh 1869

Halisaurus platyspondylus Marsh, 1869, p. 395.
Baptosaurus platyspondylus, Cope, 1869-1870, p. 209.

Type. YPM 444, from ". . . Hornerstown, New Jersey . . ." (Marsh, 1869, p. 396) collected by J. G. Meirs. Type specimen includes an angular and two vertebrae.

Distribution. Navesink Formation or younger Cretaceous, New Jersey.

Additional References. Cope, 1875, p. 272. Merriam, 1894, p. 37. Williston, 1898b, p. 207. Miller, 1955, p. 909.

Referred Specimen. *YPM* no. 412.

Discussion. This species was apparently described verbally as *Macrosaurus platyspondylus* by Marsh during the Salem meetings of the American Association for the Advancement of Science in August, 1869. However a description was not published until November of that year, when it was made the genotype of *Halisaurus* (see also Hay, 1902, p. 468).

There is a fragment of an angular preserved with the type vertebrae. Its articular surface resembles that of the angular of *Platecarpus* but is more symmetrically heart-shaped in anterior aspect. In lateral profile the angular appears somewhat inflated, with a convex anteroventral outline that is gently continuous with the anteroexternal margin of the articular surface, similar to its condition in *Clidastes.*

FOREIGN PLIOPLATECARPINAE

Genus *DOLLOSAURUS* Iakovlev 1901

Dollosaurus Iakovlev, 1901, p. 518.

Generic Type. *Dollosaurus lutugini* Iakovlev 1901.

Diagnosis. Premaxilla with no rostrum anterior to premaxillary teeth. Twelve(?) teeth in maxilla. Seven teeth in pterygoid. Thirteen teeth in dentary. Dentary terminates abruptly in front of first dentary tooth. Mandibular teeth bicarinate, slightly faceted, and slightly posterolingually recurved.

Articulating surfaces of cervical and anterior dorsal vertebral centra wider than deep, smoothly elliptical in outline. Synapophysis occupies anterodorsal portion of lateral surface of anterior dorsal vertebra. Zygosphene-zygantrum strongly developed. Chevrons fused to caudal centra.

Vertebral formula: At least 25 dorsals (see Iakovlev, 1901, pp. 517-518; Dollo, 1924, pp. 193-197; Tsaregradskii, 1935, pp. 53-54).

Discussion. The only known specimen of *Dollosaurus* is a partial skull and skeleton from the upper Campanian of the Donetz Basin, southern European Russia (Iakovlev, 1901, p. 516). The animal is evidently a plioplatecarpine in spite of its co-ossified chevrons and zygosphenes, as Dollo (1924, p. 197) suspected. The dorsally concave alveolar margin of the dentary (Iakovlev, 1901, fig. 2), the "mosasaurine" shape of the coronoid (Tsaregradskii, 1935, p. 53), the extension of the splenial anteriorly into the symphysial region (Dollo, 1924, p. 196; compare with Camp, 1942, p. 19) and the reduction in number and increase in size of the anterior pterygoid teeth (Iakovlev, 1901, pl. 5 fig. 1) all suggest affinities with *Prognathodon* and *Plesiotylosaurus*. However the great enlargement of the first two dentary teeth and large zygosphenes are unique features of the genus (Dollo, 1924, p. 196).

Subfamily TYLOSAURINAE (Williston 1895) Williston 1897

Tylosauridae Marsh, 1876, p. 59, *nomen nudum.*
"mosasaurines megarhynques" Dollo, 1890, p. 163.
Tylosauridae Williston, 1895, p. 169.
Tylosaurinae Williston, 1897d, p. 177.

Diagnosis. Large rostrum present anterior to premaxillary teeth. Twelve or more teeth in dentary and maxilla. Cranial nerves X, XI and XII leave lateral wall of opisthotic through single foramen. No canal in basioccipital or basisphenoid for basilar artery. Suprastapedial process of quadrate moderately large, distally pointed. Dorsal edge of surangular rounded and longitudinally horizontal.

Twenty-nine or more presacral vertebrae present. Length of presacral series less than that of postsacral series in *Tylosaurus*, neural spines of posterior caudal vertebrae at most only slightly elongated, do not form an appreciable fin. Haemal arches unfused to caudal centra. Appendicular elements lack smoothly finished articular surfaces.

Discussion. There is little justification for separating the Plioplatecarpinae and Tylosaurinae on the basis of the postcranial skeleton. The large premaxillary rostrum, widely expanded otosphenoidal crest and lack of basioccipital canals at once distinguish the premaxillae, prootics and basioccipital-basisphenoids from those of members of the Plioplatecarpinae, but otherwise the cranial skeleton is very similar. The two subfamilies must be much more closely related to each other than either is to the Mosasaurinae.

Genus *TYLOSAURUS* Marsh 1872
(Text-figs. 45, 58)

Liodon in part, Cope, 1869-1870, p. 200.
Rhinosaurus Marsh, 1872b, p. 17 (preoccupied, Fischer and Waldheim 1847).
Rhamphosaurus Cope, 1872e, p. 141 (preoccupied, Fitzinger 1843).
Tylosaurus Marsh, 1872c, p. 47.

Generic Type. *Tylosaurus proriger* (Cope).

Additional References. Cope, 1871f, p. 401; 1872d, p. 273; 1872f, p. 331; 1874, p. 36; 1875, p. 160; 1878, p. 301. Marsh, 1872a, p. 291; 1872b, pl. 13; 1872d, pp. 496, 497; 1877, p. 346; 1897, fig. 23. Leidy, 1873, p. 271, pl. 36 figs. 1-3. Owen, 1879, pl. 8 figs. 13-14. Lydekker, 1888, p. 264. Smith-Woodward, 1889, p. 280. Hoffmann, 1890, p. 1321. Williston, 1891, p. 345; 1897b, fig. 1, pls. 9-12; 1897d, pp. 177, 180; 1897e, p. 244; 1898b, p. 171, pl. 40 figs. 1-9, pl. 41 figs. 1, 4-5, pl. 42 figs. 1-2, pl. 46, pls. 48-50, pl. 54 fig. 1, pl. 55, pl. 59 figs. 1-8, pls. 65-70; 1914, p. 166, figs. 70, 79; 1925 fig. 148. Williston and Case, 1892, p. 15. Merriam, 1894, pp. 14, 38, 39, pl. 4 figs. 1, 3-6. Whitfield, 1900, pl. 5 fig. 3. Osburn, 1906, pl. 8 fig. 25. Merril, 1907, p. 80. Huene, 1910, figs. 1-4, pls. 41-42. Camp, 1923, pp. 323, 324; 1942, pp. 28, 32, fig. 23. Gilmore, 1928, p. 87. Nopcsa, 1928, p. 177. McDowell and Bogert, 1954, pp. 106, 132, 138, fig. 10. Romer, 1956, p. 562, fig. 154c.

Diagnosis. 12 to 13 teeth in maxilla. Supraorbital wing of prefrontal covered dorsally by frontal. Prefrontal excluded from posterolateral margin of external nares by wing of maxilla. Frontal not emarginate above orbits, median dorsal ridge prominent to nearly absent. Parietal foramen moderately large, located entirely within parietal. Margins of dorsal parietal surface parallel one another and cranial midline to posterior base of diverging suspensorial rami, forming rectangular field medially on parietal. Ventral process of postorbitofrontal to jugal meets poorly exposed dorsal surface of postorbitofrontal at right angle. Ventroposterior process on jugal present. Squamosal wing to parietal moderately developed. Large otosphenoidal crest on prootic covers exits for VII and IX laterally. Ten to 11 teeth in pterygoid. Tympanic ala of quadrate thin to rather thick, stapedial pit rectangular in form. Thirteen teeth in dentary. Broad projection of dentary anterior to first dentary tooth. Angular widely separated medially from coronoid. Retroarticular process of articular dorsally rounded, ventrally straight in outline.

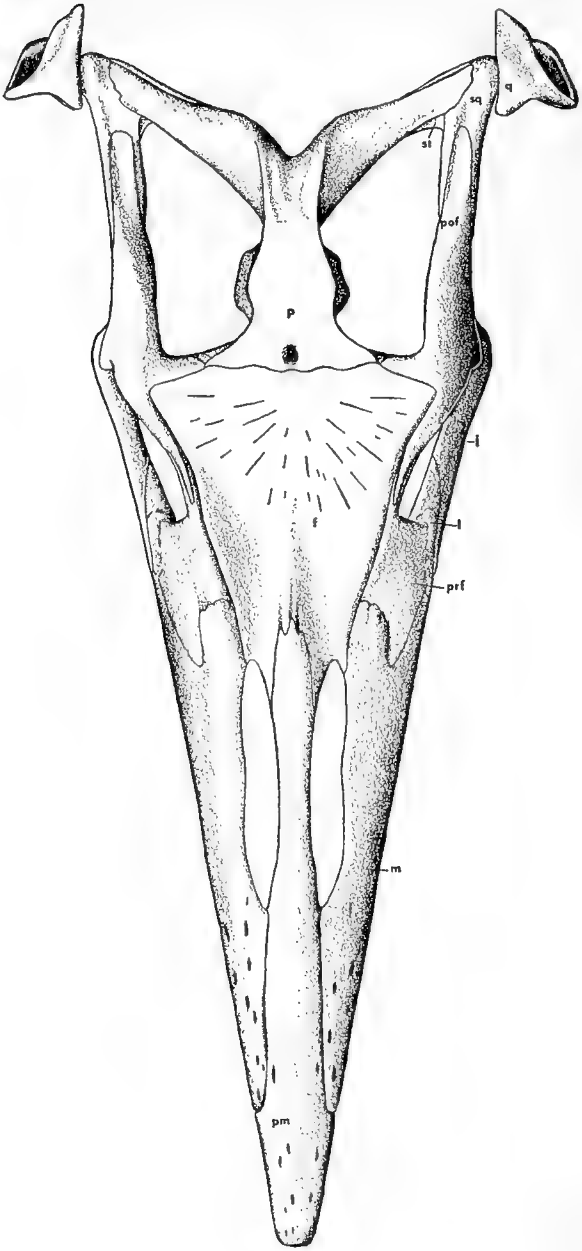
Vertebral formula: 29-30 presacral vertebrae, 6-7 pygals, 33-34 caudals with chevrons and transverse processes, 56-78 terminal caudals (see Williston, 1898b, p. 143; 1910, p. 539; Huene, 1910; Osborn, 1899a; and YPM 1250 and 24908, USNM 8898).

Articulating surfaces of cervical and anterior dorsal vertebrae nearly circular. Synapophysis located in center of lateral surface of cervical centra, occupies anterodorsal portion of lateral surface of dorsal centra. Ventral border of anteroventral extension of synapophysis not strongly developed on cervicals and anterior dorsals, does not reach level of undersurface of centrum. Anterior zygopophysis of cervicals and dorsals connected by sharp, ram-rod straight crest posteroventrally to synapophysis. Zygosphene-zygantrum rudimentary. Anterior base of atlas neural arch arises directly above condylar facet, atlas synapophysis small and flattened or rudimentary. Hypapophyseal peduncle located posteriorly on ventral surface of cervical centra, articulation for hypapophysis teardrop-shaped, slightly inclined posteriorly. Five hypapophysis-bearing cervicals, two or three more with rudimentary peduncles. Transverse process of pygal vertebrae relatively short. Neural spines of caudal vertebrae longest and vertical on postsacrals 38-40.

Scapula much smaller than coracoid. Glenoid articulating surfaces concave on both scapula and coracoid, nearly form a smoothly continuous surface. Superior border of scapula strongly convex, posterior border slightly emarginated posteromedially. Coracoid does not expand medially to point behind glenoid articulation. Distal and proximal ends of slender humerus only slightly expanded, radial process absent. Facets for articulation with other elements and sites of muscle attachment not well differentiated. Radius very elongate, proximal end very slightly expanded. Shaft of radius narrow. Distal end slightly expanded, has only trace of anterodistal flange.

Ulnare and fourth carpal present, lack articulating surfaces. Metacarpal one equal to metacarpal two in length, has very slight anterodistal flange. Proximal ends of metacarpals, especially of two and three, not greatly expanded. Phalangeal formula of manus variable, in one (see Williston, 1898b, pl. 48) it is 5-7-9-10-11; in another (see Osborn, 1899a, p. 183) it is 5-8-8-9-9.

Acetabular surfaces of pelvic elements convex, do not form solid, smoothly surfaced bowl. Obturator foramen located near anterior margin of proximal end of pubis, dorsoanterior process rudimentary. Ischiadic tubercle widely separated from acetabulum.



Text-fig. 92. Dorsal view of skull of *Tylosaurus proriger* (reconstructed after AMNH 4909, × ca. ¼).

Shaft of ischium broad, well expanded medially at symphysis. Distal end of femur much more expanded than proximal; internal trochanter of average proportions and located medially from head. No distinct facets on distal end. Cartilage-capped area of anterior flange of tibia extends two-thirds way up shaft giving bone characteristic broad rectangular outline, similar area of posterodistal flange of fibula extends one-third way up shaft.

Astragulus nearly circular, dorsal notch between facets for tibia and fibula rudimentary or absent. Calcaneum unossified, fourth tarsal small. Metatarsal one expanded proximally. Metatarsal five hook shaped, with strongly concave medial border and shallowly concave or straight lateral border. Phalangeal formula of pes estimated at 5-8-8-8-6 (Osborn, 1899a, p. 183).

Discussion. The first described species subsequently to be included in the genus *Tylosaurus* was *Macrosaurus proriger* Cope. This species was later referred by Cope (1869-1870, p. 201) to *Liodon* Owen, and the latter genus was redefined by him (ibid., p. 200) to include some very incompletely known North American material. Cope (1871b, p. 576) allied his *L. dyspelor* with *Amphorosteus brumbyi* Gibbes, and his *L. proriger* with *Nectoportheus* (see Cope, 1869-1870, p. 208). The single type vertebrae of *Macrosaurus* and *Nectoportheus* belong to the posterior dorsal region of *Mosasaurus,* and the type vertebrae of *Amphorosteus* are indeterminate (see p. 176). These names are thus not available to replace *Tylosaurus.*

Merriam (1894, p. 14) demonstrated that the name *Liodon* should not be applied to the Niobrara species discussed below, because in *Liodon* the enamel surfaces of the teeth are smooth, resembling those of *Clidastes;* in *Tylosaurus* the internal face is striated. It is appropriate to add that the teeth of *Liodon anceps* (Owen, 1840-1845, pl. 72 fig. 1), the type species of the genus, are symmetrically bicarinate although those of *Tylosaurus* are relatively inflated with a flattened labial face and a larger, more rounded lingual face, and lack strong anterior and posterior carinae. These distinctions are of a generic order.

Marsh (1872b, p. 17) recognized for the first time the generic identity of *Tylosaurus,* clearly separated it from *Platecarpus* and proposed for it the name *Rhinosaurus* (preoccupied) supported by an excellant generic diagnosis based for the most part on cranial characters. Cope (1872e, p. 141) adhered to his opinion that "*Rhinosaurus*" was actually synonymous with the English *Liodon,* but proposed the name *Rhamphosaurus* (preoccupied), should the Kansas species prove to belong to a distinct genus. Marsh (1872c, p. 47) replaced *Rhamphosaurus* with *Tylosaurus,* which became accepted by nearly all workers, with the notable exception of Cope.

Williston (1897d, p. 182) suggested that *Lesticodus* might be a senior synonym of *Tylosaurus,* but the type species of this genus is based on a pterygoid tooth of a *Mosasaurus.*

Tylosaurus proriger (Cope 1869)

(Frontispiece; Text-figs. 2C, 5A, 21, 24C, 27, 48A, 55, 63, 92, 93B, 94A;
Plate I, fig. 3; Plate II, fig. 1)

Macrosaurus proriger Cope, 1869d, p. 123.
Macrosaurus pririger Cope, 1869g, p. 122.
Liodon proriger, Cope, 1869-1870, p. 201.
Rhinosaurus proriger, Marsh, 1872b, p. 19.
Rhinosaurus micromus Marsh, 1872b, p. 17.
Tylosaurus (proriger), Marsh, 1872c, p. 47.

Type. Formerly at MCZ, not located, from ". . . vicinity of Monument Rocks, the old overland stage station, (Kansas) . . ." (Williston, 1898b, p. 174) collected by Messrs. Connyngham and Minor and sent to L. Agassiz. Type specimen included the anterior portion of a skull, cranial fragments, and thirteen vertebrae (Cope, 1869-1870, p. 202).

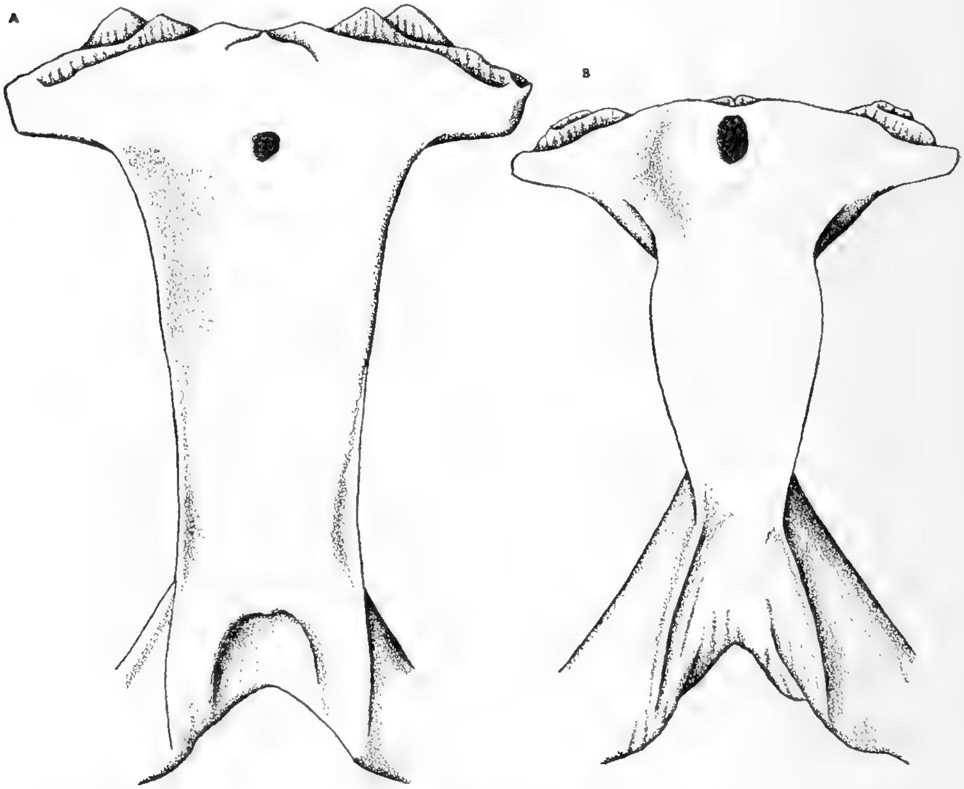
Distribution. Smoky Hill Member, Niobrara Formation, Kansas and Colorado; Lower Pierre Formation, Kansas and South Dakota; Telegraph Creek Formation, Montana.

Additional References. Cope, 1869-1870, p. 201, pl. 12 figs. 22-24; 1871f, p. 401; 1872a, p. 297; 1872c pp. 173-174; 1872d, pp. 279-280; 1872e, p. 141; 1872f, p. 333; 1874, pp. 37-38; 1875, pp. 161, 167, 271, fig. 7, pls. 28-30, pl. 31 figs. 1-4, pls. 32-33, pl. 36 figs. 1-2, pl. 37 figs. 5-6; 1879a, p. 132. Marsh, 1872d, p. 497; 1880, p. 85, fig. 1. Leidy, 1873, pp. 274, 343-344, pl. 35 figs. 12-13, pl. 36 fig. 3. Snow, 1878, pp. 54, 57. Merriam, 1894, pp. 23-24, pl. 1 fig. 3, pl. 2, pl. 3 figs. 1-2, 8, pl. 4 fig. 7. Williston, 1895, pl. 17 fig. 2; 1897b,

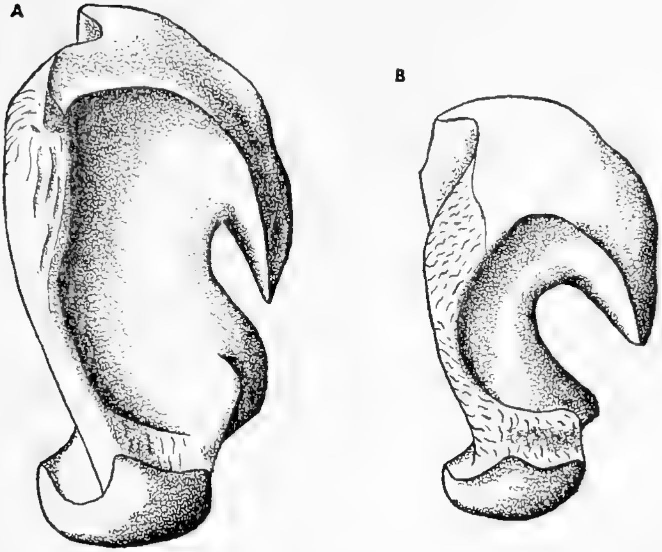
p. 102; 1897c, p. 110, pl. 13 fig. 3; 1897d, pl. 20 fig. 1; 1898a, p. 28; 1898b, pp. 102-134, 173, 175, pls. 16-18, pl. 19 fig. 1, pl. 31 figs. 1-3, pl. 60 figs. 1-2, pl. 61 figs. 1-2, pl. 72 fig. 3; 1902, p. 253; 1914, fig. 72c; 1925, p. 273, fig. 54. Osborn, 1899a, p. 169, figs. 1, 7, 8-9, 11-14, pls. 21-23; 1899b, p. 912. Fürbringer, 1900, p. 616. Merril, 1907, p. 80. Sternberg, 1909, fig. 8; 1917, pp. 13, 162, fig. 5. Pompeckj, 1910, p. 137. Stromer, 1910, pl. 2. Dreverman, 1914, p. 43, fig. 7. Lambe, 1914, p. 402. Fejérváry, 1918, fig. 25. Wiman, 1920, pl. 4 figs. 6a-b. Gilmore, 1921, p. 273. Lane, 1947, pp. 313-314, fig. 5. Romer, 1956, fig. 220. Kauffman and Kesling, 1960, fig. 6d.

Referred Material. *AMNH* nos. ***221,* 1493, 1529, 1535, 1555, 1560, 1585, 1592, 2160, **4909, **7220. *YPM* nos. *1268 *(T. micromus),* 1288, 1302, 1305, *3873, 3977, 3978, 3981, 3984, 3987, 3989, 3990, 3993, *3999, *4002* and about twenty-four unnumbered specimens. *ANSP* no. 5. *USNM* nos. 3776, 3794, 3798, 3897, **6086, **8898,* *17909. *MCZ* no. **1030. *KU* nos. 1020, **1023, **1032, *1033, 1084, 1115, 1135, 1194, *5033. *FHM* no. **4 *CNHM* nos. UR820, **P15144, UR902. *NMC* no. 8162. *PU* no. 12000.

Diagnosis. Anterior tip of premaxilla rectangular in lateral profile, in form of ellipse with vertical long axis in cross-section. Premaxillo-maxillary suture terminates posteriorly at point dorsal to or somewhat behind fourth maxillary tooth. Parietal foramen close to frontal suture. Lateral margin of prefrontal deeply grooved for anterior process of postorbitofrontal. Posterior surface of parietal moderately to extensively invaded medially by insertional area for cervical epaxial musculature. Infrastapedial process on quadrate small. Lateral crest of tympanic ala descends posteriorly nearly to mandibular



Text-fig. 93. Dorsal view of parietal. A. *Tylosaurus nepaeolicus* (restored after AMNH 124 and YPM 3980, × ca. ½). B. *Tylosaurus proriger* (slightly reconstructed, after YPM 3990, × ca. ½).



Text-fig. 94. Lateral view of left quadrate. A. *Tylosaurus proriger* (reconstructed after YPM 3990 and AMNH 4909, × 5/7). B. *Tylosaurus nepaeolicus* (YPM 3992, × 5/7).

articulating surface of quadrate, then ascends to terminate lateral to and slightly below infrastapedial process.

Discussion. The type of *"Macrosaurus" proriger* unfortunately has not been found. Thus far it has been possible to distinguish only two species of *Tylosaurus* from the Niobrara Chalk, one of which may be characterized by a premaxillo-maxillary suture that extends at least as far back as the fourth maxillary tooth. From Cope's (1869-1870, pl. 12 figs. 22-24) figures this would seem to be its condition in the type of *T. proriger,* as it surely is in the specimen from Butte Creek that Cope referred to this species (AMNH 1493; Cope, 1872c, p. 175). One of the points by which Cope (1874, p. 38) separated the type of *T. nepaeolicus* from *T. proriger* was the relatively advanced position of its external nares, thus intimating that in the latter species the external nares were more posteriorly situated and that the premaxillo-maxillary suture was also extended further posteriorly. It seems safe therefore to assume that the correct name has been applied to the species diagnosed above.

Tylosaurus nepaeolicus (Cope 1874)
(Text-figs. 15, 93A, 94B, 95)

Liodon nepaeolicus Cope, 1874, p. 37.
Tylosaurus nepaeolicus, Merriam, 1894, p. 24.

Type. AMNH 1565, from ". . . the gray shale of the Niobrara Cretaceous, a half mile south of the Solomon River, Kansas," (Cope, 1874, p. 38) collected by B. F. Mudge. Type specimen includes a partial skull and one vertebra.

Distribution. Smoky Hill Member, Niobrara Formation, Kansas.

Additional References. Cope, 1875, p. 168, pl. 35 figs. 11-15. Owen, 1879, p. 55. Merriam, 1894, p. 24, pl. 4 fig. 7. Williston, 1898b, p. 176; 1910, p. 539, figs. 5-10. Sternberg, 1908, p. 113, fig. 1. Huene, 1910, p. 297, figs. 5-10, pl. 1, pl. 2 figs. 2-3; 1919, p. 183, pl. 8 fig. 1; 1953, fig. 1. Pompeckj, 1910, pp. 134, 137. Abel, 1922, figs. 260, 267. Renger, 1935, p. 560, fig. 5?

Referred Specimens. *AMNH* nos. **124, 131, **134, 1524, 1561, 2167, 2319. *YPM* nos. 3969, 3970, *3974, 3976, 3979, 3980, 3992, *4000 and about twenty unnumbered specimens. *USNM* no. 3894. *MCZ* nos. 1592, 1604, 1626. *FHM* no. *1654.

Diagnosis. Anterior tip of premaxilla rounded in lateral profile, nearly circular in cross-section. Premaxillo-maxillary suture terminates posteriorly above midpoint between third and fourth maxillary tooth. Parietal foramen widely separated from frontal suture. Lateral margin of prefrontal rounded, abuts against postorbitofrontal posteriorly. Posterior dorsal surface of parietal slightly invaded medially by insertional area for cervical epaxial musculature. Infrastapedial process on quadrate small. Lateral crest of tympanic ala ends posteriorly near mandibular articulating surface of quadrate.

Discussion. *Tylosaurus nepaeolicus* seems generally to be a smaller species than *T. proriger.* It does not occur stratigraphically above the Niobrara Chalk, and incomplete locality information suggests that it may not even occur near the top of this formation.

FOREIGN TYLOSAURINAE

Genus *HAINOSAURUS* Dollo 1885

Hainosaurus Dollo, 1885, p. 288.

Generic Type. *Hainosaurus bernardi* Dollo, 1885, p. 288.

Diagnosis. 72 teeth in skull *(Tylosaurus* has 70-74). Ventroposterior process on jugal present. Stapedial pit in form of longitudinally compressed ellipse. Broad projection of dentary anterior to first dentary tooth. Retroarticular process of articular dorsally rounded, ventrally straight in outline.

Vertebral formula: 52 vertebrae in cervical-dorsal-pygal region (35 are present in *Tylosaurus),* at least 33 diapophysis-bearing caudals.

Anterior zygopophysis of cervicals and anterior dorsals not ramrod straight, arise high on neural arch and project horizontally anteriorly. No zygosphene-zygantrum. Neural spines of caudal centra decrease uniformly in length from base to end of tail.

Scapula much smaller than coracoid. Superior border of scapula strongly convex, posterior border strongly emarginated posteromedially. Distal and proximal ends of slender humerus moderately expanded, radial process small. Facets for articulation with other elements and sites of muscle attachment not well differentiated. Radius very elongate, proximal end slightly expanded. Shaft of radius narrow. Distal end somewhat expanded, has small anterodistal flange.

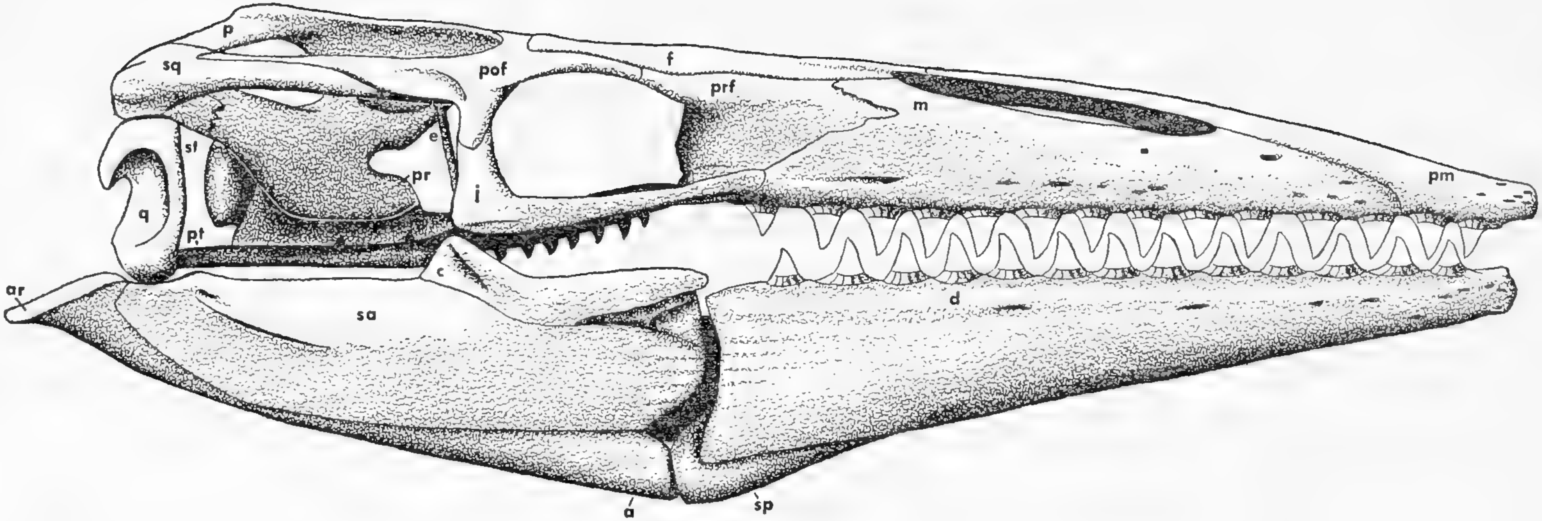
Carpus poorly ossified, as in *Tylosaurus.* Femur longer than humerus (Dollo, 1885; 1889b, pl. 9 fig. 3, pl. 10 figs. 1-3; 1917, p. 19).

Discussion. *Hainosaurus* has been identified only from the late Cretaceous of Belgium. Dollo (1885, p. 288) states that the suprastapedial process of the quadrate is absent. It would seem from his figures (1889b, pls. 9-10) that the type of *H. bernardi,* although nearly complete, is badly preserved, and the quadrate may have originally had a suprastapedial process as large as in *Tylosaurus.* As it now stands the only good character separating *Hainosaurus* from *Tylosaurus* is the greater number of vertebrae between the cranium and the chevron bearing caudals in the former genus. One other species is known, *H. lonzeensis* (Dollo, 1904a, p. 213; 1909, p. 102), based on a premaxilla and vertebra.

MOSASAURS OF UNCERTAIN TAXONOMIC POSITION

Amphorosteus brumbyi Gibbes 1851 *nomen vanum.*

Amphorosteus brambyi Gibbes, 1850, p. 77 *nomen nudum.*



Text-fig. 95. Lateral view of skull of *Tylosaurus nepaeolicus* (reconstructed after AMNH 124, 134, × 8/29).

Amphorosteus brumbyi Gibbes, 1851, p. 11.
Mosasaurus brumbyi, Cope, 1869b, pp. 260, 264.

Type. Specimen not located.

Additional References. Leidy, 1865a, pp. 32, 118. Cope, 1869-1870, pp. 186, 198; 1871b, p. 576; 1871f, p. 411; 1875, p. 270. Lydekker, 1888, p. 267. Zangerl, 1948, p. 15.

Discussion. *Amphorosteus brumbyi* is based on two vertebrae from the Cretaceous of Alabama, figured by Gibbes (1851, pl. 3 figs. 10-16). They are indeterminate.

Clidastes? congrops (Cope 1870) *nomen vanum*

Liodon congrops Cope, 1869-1870, p. 206.
Tylosaurus congrops, Hay, 1902, p. 472.

Type. Specimen not located, originally from the Selma Chalk of Alabama (Cope, 1869-1870, p. 207) collected by Dr. E. R. Showalter.

Additional References. Cope, 1870a, p. 271; 1875, p. 272. Merriam, 1894, p. 25. Zangerl, 1948, p. 15.

Discussion. The type specimen of *Clidastes? congrops* is a single cervical vertebra, which has apparently been lost. It would appear from the original description that the vertebra belongs to *Clidastes,* as Cope (1875, p. 272) later suggested.

Elliptonodon compressus Emmons 1858 *nomen dubium*

Elliptonodon compressus Emmons, 1858, p. 222, figs. 41-42.

Type. In Museum of Williams College, from ". . . the miocene near the Cape Fear River, in Bladen county (North Carolina)," (Emmons, 1858, p. 223).

Additional References. Emmons, 1860, p. 208, fig. 180(2), (5). Cope, 1869b, p. 263; 1869-1870, p. 186. Gilmore, 1928, p. 87. McDowell and Bogert, 1954, p. 132.

Discussion. The type and only specimen is a symmetrically bicarinate, somewhat inflated and gently posteriorly recurved tooth that looks mosasaurian and resembles most closely teeth of *Prognathodon.* It differs from any species of this genus however in that the enamel surface of the tooth is strongly vertically striated. The name *Elliptonodon compressus* must be regarded as a *nomen dubium* due to the incompleteness of the type and the uncertainty regarding the original horizon of the reworked tooth.

Gilmore (1926, p. 192, pl. 72 figs. 1-2) described and figured a large fragment of a mosasaur dentary from the Coon Creek Formation of McNairy County, Tennessee, mentioning that the teeth were similar to that of *Elliptonodon compressus.* The dentary probably belongs to *Prognathodon,* and its dorsally concave alveolar border resembles that of *P. solvayi* more closely than the more nearly straight border of *P. overtoni.*

Holcodus acutidens Gibbes 1851 *nomen vanum*

Holcodus columbiensis Gibbes, 1850, p. 77 *nomen nudum.*
Holcodus acutidens Gibbes, 1851, p. 9, pl. 3 figs. 6-9.
Mosasaurus acutidens, Marsh, 1872b, p. 455.

Lectotype. ANSP 8594, from the "Cretaceous of Alabama," (Gibbes, 1851, p. 9).

Additional References. Leidy, 1865a, pp. 32, 71, 118, 130, fig. 33, pl. 10 fig. 17. Cope, 1869b, p. 265; 1869-1870, p. 210; 1872d, p. 269; 1875, pp. 141, 270. Marsh, 1869, p. 394. Merriam, 1894, p. 30. Williston, 1897d, p. 185; 1898b, p. 179. Gilmore, 1928, p. 87. McDowell and Bogert, 1954, p. 132.

Discussion. *Holcodus acutidens* was originally proposed by Gibbes for three teeth, one from the Cretaceous of Alabama, a second from the Cretaceous of New Jersey, and a third from the Eocene of Orangeburg, South Carolina. The third tooth has not been located but if it was indeed from the Eocene it could not have been mosasaurian. The second tooth was identified as crocodilian by Leidy (1865a, p. 32), leaving the tooth from Alabama which Williston (1897d, p. 184) treated as a lectotype. This tooth is indistinguishable from those of *Platecarpus, Ectenosaurus,* or *Plioplatecarpus* and certainly is plioplatecarpine. Because of the inadequacy of the type material *Holcodus acutidens* must be considered a *nomen vanum.*

Mosasaurus caroliniensis Gibbes 1851 *nomen vanum*

Mosasaurus caroliniensis Gibbes, 1850, p. 77 *nomen nudum.*
Mosasaurus caroliniensis Gibbes, 1851, p. 8, pl. 2 figs. 1-3.

Type. Specimen not located.

Additional References. Leidy, 1860, p. 92; 1865a, p. 32. Cope, 1869b, p. 262; 1869-1870, p. 193; 1875, p. 269.

Discussion. The type is a mandibular fragment probably of a *Mosasaurus.* It is from the Pliocene of Darlington, South Carolina, and was derived from the underlying Cretaceous (Gibbes, 1851, p. 7).

Mosasaurus couperi Gibbes 1851 *nomen vanum*

Mosasaurus couperi Gibbes, 1850, p. 77 *nomen nudum.*
Mosasaurus couperi Gibbes, 1851, p. 7, pl. 2 figs. 4-5.
Mosasaurus cowperi, Cope, 1869b, p. 262.

Type. Specimen not located, originally from ". . . the Cretaceous deposits of the banks of the Chattahoochie, Georgia, discovered by J. Hamilton Couper, Esq. . ." (Gibbes, 1851, p. 7).

Additional References. Leidy, 1860, p. 92; 1865a, p. 32. Cope, 1869-1870, p. 193; 1875, p. 269.

Discussion. The type teeth figured by Gibbes (1851, pl. 2 figs. 4-5) may belong to the pterygoid dentition of *Mosasaurus.*

Mosasaurus? crassidens Marsh 1870 *nomen dubium*

Mosasaurus crassidens Marsh, 1870, p. 2.

Type. At Museum of Williams College, from ". . . the Cretaceous of North Carolina," (Marsh, 1870, p. 2) collected by E. Emmons.

Additional References. Cope, 1869-1870, p. 198; 1875, p. 270.

Discussion. The type specimen is a fragment of a right maxilla with a well-marked dorsal narial emargination and large non-prismate teeth. It could belong to either *Mosasaurus* or, more likely, to *Prognathodon* and new material from the North Carolina Cretaceous may make it possible to recognize this species.

Mosasaurus impar (Leidy 1856) *nomen dubium*

Drepanodon impar Leidy, 1856, p. 255.
Lesticodus impar, Leidy, 1861, p. 10.
Mosasaurus impar, Leidy, 1865a, p. 33.

Type. At Museum of Williams College, from ". . . Elizabethtown, Cape Fear, North Carolina," (Leidy, 1858, p. 224) collected by E. Emmons.

Additional References. Leidy, 1857, p. 271; 1858, p. 224, figs. 45, 46. Cope, 1869b, p. 263; 1869-1870, pp. 185, 205; 1875, p. 270. Merriam, 1894, p. 25.

Discussion. *Mosasaurus impar* is based on a pterygoid tooth, probably of *Mosasaurus.* Pterygoid material of Atlantic Coast mosasaurs is too poorly known to assign this tooth to any described species.

Mosasaurus laevis (Owen 1849) *nomen vanum*

Macrosaurus, de la Beche, 1849, p. xliii.
Macrosaurus laevis Owen, 1849, p. 382.
Tylosaurus laevis, Miller, 1955, p. 909.

Type. Specimen not located.

Additional References. Leidy, 1865a, pp. 74, 118; 1865b, p. 70. Cope, 1868b, p. 734; 1869b, p. 260; 1869-1870, p. 205; 1875, pp. 161, 270. Owen, 1879, p. 24. Merriam, 1894, p. 24. Williston, 1897d, pp. 182, 183; 1925, p. 273. Gilmore, 1928, p. 87. McDowell and Bogert, 1954, p. 132. Romer, 1956, p. 562.

Discussion. *Macrosaurus laevis* is based on two vertebrae from the New Jersey Cretaceous, figured by Owen (1849, pl. 10 figs. 1-6). They belong to the posterior dorsal region of a species of *Mosasaurus.*

Mosasaurus? mitchilli (DeKay 1830) *nomen vanum*

Geosaurus mitchilli DeKay, 1830, p. 140, pl. 3 figs. 3-4.
Geosaurus soemeringi, Bronn, 1838, p. 534.
Mosasaurus mitchilli, Leidy, 1860, p. 92.
Liodon mitchilli, Cope, 1869-1870, p. 205.
Tylosaurus mitchilli, Miller, 1955, p. 909.

Type. Specimen not located, originally from ". . . foot of Neversink hills, Sandy Hook, (New Jersey)," (DeKay, 1830, p. 135).

Additional References. Morton, 1830b, p. 246; 1834, p. 28, pl. 11 fig. 10. DeKay, 1842, p. 28, pl. 22 figs. 55, 56. Pictet, 1853, p. 506. Leidy, 1860d, p. 92; 1865a, pp. 32, 116; 1865b, p. 69. Cope, 1868b, p. 733; 1869b, pp. 262, 263; 1869c, p. 86; 1869-1870, pp. 185, 205; 1875, p. 270. Merriam, 1894, p. 24.

Discussion. The type tooth of *"Geosaurus" mitchilli* is indeterminate. DeKay's (1830, pl. 3 figs. 3-4) figure looks like that of a mandibular tooth of a mosasaurian.

Mosasaurus occidentalis Morton 1844 *nomen nudum*

Mosasaurus occidentalis Morton, 1844, p. 133 *nomen nudum.*

Additional References. Gibbes, 1850, p. 77. Leidy, 1860, p. 921; 1865a, p. 32. Cope, 1869-1870, p. 193.

Mosasaurus reversus (Leidy 1865) *nomen dubium*

Baseodon reversus Leidy, 1865a, pp. 69-70, 118, pl. 10 figs. 14-15.
Mosasaurus dekayi, Cope, 1869-1870, pp. 186, 194.

Type. Specimen not located, originally "... from Freehold, Monmouth County, New Jersey," (Leidy, 1865a, p. 69).

Additional References. Cope, 1868b, p. 734; 1875, p. 269.

Discussion. *Baseodon reversus* is based on two pterygoid teeth of *Mosasaurus,* which are specifically unassignable due to the lack of good pterygoid material from the Cretaceous of the Atlantic Coast.

Mosasaurus validus (Cope 1868) *nomen vanum*

Nectoportheus validus Cope, 1868a, p. 181.
Macrosaurus validus, Cope, 1868b, p. 734.
Liodon laevis in part, Cope, 1869-1870, p. 205.
Liodon validus, Cope, 1869-1870, p. 207.
Clidastes antivalidus Cope, 1869-1870, p. v.
Tylosaurus validus, Merriam, 1894, p. 25.
Clidastes validus, Miller, 1955, p. 909.

Type. AMNH 1415, from the Navesink Formation or younger Cretaceous, "... near Medford, N. J. ..." (Cope, 1869-1870, p. 206), collected by Charles Braddock.

Additional References. Cope, 1869b, p. 260; 1869c, p. 86; 1870a, p. 272; 1871b, p. 584; 1871f, p. 414; 1874, p. 36; 1875, pp. 161, 271. Williston, 1897d, pp. 182, 183; 1898b, p. 173. Hay, 1902, p. 467. Gilmore, 1928, p. 87. McDowell and Bogert, 1954, p. 132. Miller, 1955, p. 905.

Discussion. Cope (1868a, p. 181) proposed the name *Nectoportheus validus* for a single vertebra from the "middle green-sand bed" near Medford, New Jersey. It was distinguished from other known mosasaurs by its "compressed elevated form." Later (1869b, p. 260) Cope referred the species to *Macrosaurus,* again noting that the dorsal vertebrae were compressed and elongate. In his Synopsis (1869-1870, p. 208) however, describing *Liodon validus,* Cope stated, "The posterior dorsals are so much more *depressed* (italics mine) than in *Liodon laevis,* that future discovery may justify the generic separation of the genus *Nectoportheus,* which I originally applied to this animal." It is apparent that these last dorsals do not resemble the original type of *Nectoportheus validus.* On a preceding page (ibid., p. 206) a vertebra "found near Medford, N. J., in the second green sand bed" was assigned to *L. laevis.* This vertebra (AMNH 1415) corresponds both in morphology and in collecting locality to the type of *N. validus.* Cope (1869-1870, pl. 5 fig. 5) figured this specimen under the name of *Macrosaurus validus* and founded the new species *Clidastes antivalidus* on it in the explanation to the plates. Hay (1902, p. 467) correctly referred *C. antivalidus* to *N. validus* in the belief that the type specimen of both species was the same vertebra. Both this species and *Macrosaurus laevis* are founded on vertebrae belonging to the posterior dorsal series of a species of *Mosasaurus.*

The following four nominal species of *Platecarpus* belong either to *P. ictericus* or *P. coryphaeus* but adequate material is not present in the types to assign them to one of these species.

Platecarpus mudgei (Cope 1871) *nomen vanum*

Liodon mudgei Cope, 1871a, p. 572.
Holcodus mudgei, Cope, 1872d, p. 273.
Rhinosaurus mudgei, Marsh, 1872b, p. 463.
Platecarpus mudgei, Cope, 1874, p. 36.

TYPE. AMNH 1501, from ". . . yellow chalk at a point six miles south of Sheridan, Kansas," (Cope, 1871b, p. 581).

ADDITIONAL REFERENCES. Cope, 1871c, p. 132; 1871f, p. 405; 1872f, p. 331; 1875, pp. 157, 268, pl. 16 fig. 2, pl. 17 fig. 5, pl. 37 fig. 7. Merriam, 1894, p. 31. Williston, 1898a, p. 29; 1898b, p. 186. Lane, 1947, p. 317.

Platecarpus affinis (Leidy 1873) *nomen vanum*

Clidastes affinis Leidy, 1873, pp. 283, 344, pl. 34 figs. 6-7.

TYPE. USNM 69, from ". . . Cretaceous formation on the Smoky Hill River, Kansas," (Leidy, 1873, p. 283).

ADDITIONAL REFERENCES. Cope, 1874, p. 33; 1875, p. 266. Williston and Case, 1892, pp. 17, 28. Merriam, 1894, p. 35. Williston, 1898b, p. 198. Merril, 1907, p. 66.

Platecarpus planifrons (Cope 1874) *nomen vanum*

Clidastes planifrons Cope, 1874, p. 31.
Platecarpus planifrons, Williston, 1898b, p. 188.

TYPE. AMNH 1491, from "Niobrara . . . Kansas," (Cope, 1875, p. 265) collected by B. F. Mudge.

ADDITIONAL REFERENCES. Cope, 1875, p. 135, pl. 22 figs. 1-7, pl. 23 figs. 1-15, pl. 35 fig. 16; 1878, p. 299. Williston and Case, 1892, p. 17. Merriam, 1894, p. 35. Lane, 1947, p. 317.

Platecarpus anguliferus (Cope 1874) *nomen vanum*

Sironectes anguliferus Cope, 1874, p. 34.
Platecarpus anguliferus, Williston, 1897c, p. 107.

TYPE. AMNH 1551, from ". . . gray calcareous shale of Trego county, Kansas," (Cope, 1874, p. 34) collected by B. F. Mudge.

ADDITIONAL REFERENCES. Cope, 1875, pp. 139, 267, pl. 23 figs. 16-18, pl. 24 figs. 1-15. Merriam, 1894, p. 39. Williston, 1891, p. 345; 1897d, p. 181; 1897e, p. 244; 1898b, p. 192. Gilmore, 1928, p. 87.

The following three nominal species of *Platecarpus* are based on vertebrae alone.

Platecarpus latispinus (Cope 1872) *nomen dubium*

Liodon latispinus Cope, 1872b, p. 169.
?*Platecarpus latispinus,* Cope, 1875, pp. 155, 268, pl. 27 figs. 1-4.
Platecarpus latispinus, Merriam, 1894, p. 31.

TYPE. AMNH 1536, from ". . . one mile south-west of Sheridan near the 'Gypsum Buttes' " (Cope, 1872d, p. 277) collected by B. F. Mudge from the Pierre Shale.

ADDITIONAL REFERENCES. Cope, 1872f, p. 332; 1874, p. 38. Williston, 1898b, p. 181. Loomis, 1915, p. 557.

Platecarpus tectulus (Cope 1872) *nomen vanum*

Holcodus tectulus Cope, 1872d, p. 271.
Platecarpus tectulus, Cope, 1874, p. 36.

Type. AMNH 1570, from ". . . a low bluff . . . on Butte Creek, fourteen miles south of Fort Wallace," (Cope, 1872d, p. 272) collected by E. D. Cope, from the Niobrara Chalk.

Additional References. Cope, 1875, pp. 159, 269, pl. 21 figs. 3-6, (referred specimen) pl. 27 figs. 5-10. Merriam, 1894, p. 31. Williston, 1898b, p. 183. Loomis, 1915, p. 557.

Platecarpus glandiferus (Cope 1872) *nomen vanum*

Mosasaurus near *M. depressus,* Cope, 1872b, p. 168.
Liodon glandiferus Cope, 1872d, p. 276.
Platecarpus glandiferus, Cope, 1874, p. 36.
?Platecarpus glandiferus, Cope, 1875, p. 268, pl. 26 figs. 13-14.

Type. AMNH 1553 (from Niobrara Chalk), "This species is represented by portions of two individuals (in each case only a cervical vertebra) from localities twenty-five miles apart. (One) . . . was found . . . at the foot of a bluff on the lower part of the Butte Creek; the second . . . from a point one mile southeast of Sheridan near the North Fork of the Smoky River," (Cope, 1872d, p. 276). The first vertebra was collected by E. D. Cope, the second by B. F. Mudge. The second vertebra has not been located; Williston (1898b, p. 182) noted that it must have come from the Pierre.

Additional References. Cope, 1872f, p. 332; 1875, p. 156. Merriam, 1894, p. 31. Williston, 1898b, p. 182.

Platecarpus brachycephalus Loomis 1915 *nomen dubium*

Platecarpus brachycephalus Loomis, 1915, p. 556, figs. 1-9.

Type. AC 389, from ". . . the head of Mule Creek, 20 miles due west of Edgemont (South Dakota) . . ." (Loomis, 1915, p. 555), ". . . from DeGrey, Verendrye, or Virgin Creek (Member of Pierre Formation) . . ." (Kauffman and Kesling, 1960, p. 232).

Additional References. Crandell, 1950, p. 2345.

Discussion. Loomis (1915, pp. 559, 560) stated as a specific character the presence of only 11 teeth in the jaws of the type and cotype, but the preservation of cranial elements is not adequate to maintain this with any degree of certainty, nor for that matter to identify the skulls on a specific level.

The scapula figured by Loomis (1915, fig. 6) has a constricted neck and gently rounded dorsal margin reminiscent of *Plioplatecarpus.* Another scapula identified as a coracoid (ibid., fig. 7) has a small but sharply defined emargination anterodorsally, but is otherwise similar to that of *Platecarpus.* The hind limb (ibid., fig. 9) is very peculiar and was not found associated with other material. The femur is unusually broad for that of a mosasaur, the tibia is hardly expanded at its ends and the element in the position of a fibula resembles the ulna of *Plioplatecarpus* (see Dollo, 1882, pl. 6 fig. 1). It is not at all certain that the material referred by Loomis to *P. brachycephalus* all belongs to the same form as that of the type skull.

Platecarpus? minor (Gibbes 1850) *nomen vanum*

Mosasaurus minor Gibbes, 1850, p. 77.

Type. Specimen not located.

ADDITIONAL REFERENCES. Gibbes, 1851, p. 7, pl. 1 figs. 4-5. Leidy, 1860, p. 92; 1865a, p. 32. Cope, 1869b, p. 264: 1869-1870, pp. 189, 198; 1875, p. 270. Zangerl 1948, p. 15.

DISCUSSION. *Mosasaurus minor* was based on three vertebrae from the Cretaceous of Alabama and two indeterminate teeth from unspecified localities in Georgia and Alabama. A vertebra figured by Gibbes (1851, pl. 1 fig. 3) resembles those of the posterior dorsal region of *Platecarpus.*

Tylosaurus dyspelor (Cope 1871) *nomen vanum*

Liodon dyspelor Cope, 1871a, p. 572.
Rhinosaurus dyspelor, Marsh, 1872b, p. 19.
Tylosaurus dyspelor, Leidy, 1873, p. 271, pl. 35 figs. 1-11, pl. 36 fig. 16.

TYPE. AMNH 1580 and USNM 41 (same individual), ". . . from the yellow beds of the Niobrara epoch of the Jornada del Muerto, near Fort McRae, New Mexico," (Cope, 1875, p. 167), collected by Dr. W. B. Lyon.

ADDITIONAL REFERENCES. Cope, 1869-1870, errata and addenda p. ii; 1871b, p. 574; 1871c, p. 132; 1871f, p. 410; 1872b, p. 169; 1872c, p. 280; 1872f, p. 333; 1874, p. 38; 1875, p. 167, pl. 31 fig. 5. Merril, 1907, pp. 74, 80.

REFERENCES TO NON-TYPICAL MATERIAL. Merriam, 1894, p. 23, pl. 4 figs. 3-4. Williston, 1897c, p. 110; 1898b, p. 175; 1902, p. 253. Sternberg, 1908, p. 111. Huene, 1910, p. 297, fig. 1. Lambe, 1914, p. 402.

DISCUSSION. *Tylosaurus dyspelor* cannot be referred to either of the two species of Niobrara *Tylosaurus* and must be regarded as a *nomen vanum.* Because of the large size of the type it is more likely to be a junior synonym of *T. proriger* than a senior synonym of *T. nepaeolicus.*

Tylosaurus? perlatus (Cope 1870) *nomen vanum*

Mosasaurus brumbyi, Cope, 1869-1870, p. 198.
Liodon perlatus Cope, 1869-1870, errata and addenda, p. ii
Tylosaurus perlatus, Merriam, 1894, p. 25.

TYPE. AMNH 2391, from the Selma Chalk of Alabama (Cope, 1870b, p. 497).

ADDITIONAL REFERENCES. Cope, 1871b, p. 576; 1874, p. 37; 1875, pp. 161, 271. Lydekker, 1888, pp. 267-269. Zangerl, 1948, p. 15.

DISCUSSION. The type specimen of *Tylosaurus? perlatus* is a single vertebra from the posterior thoracic region. It is generically indeterminate.

Mosasaurus FROM NEW JERSEY, species uncertain.

Harlan, 1825, p. 235, pl. 14 figs. 2-4; 1834b, p. 81; 1834e, p. 32; 1835a, p. 285; 1835c, p. 384, pl. figs. 2-4. Morton, 1830a, p. 289; 1834, p. 27, pl. 11 fig. 9. Pictet, 1845, p. 64. De la Beche, 1849, p. xliii. Owen, 1849, p. 382, pl. 10 fig. 5. Holmes, 1849, p. 197. Meek and Hayden, 1857, p. 127. Leidy, 1858b, p. 176; 1860, p. 91; 1865a, figs. 4, 20, 21, 25, 32, pl. 7 figs. 9-14, pl. 9 figs. 8-9, pl. 10 fig. 6, pl. 11 figs. 1, 2, 4, 5, 15. Emmons, 1860, p. 207. Cope, 1869b, p. 260; 1869c, pl. 2; 1869-1870, figs. 47(2), 49(4); 1895, pl. 31 figs. 2-2a. Owen, 1877, p. 683. Hoffmann, 1890, p. 1321.

UNDETERMINED MOSASAURS FROM THE WESTERN UNITED STATES.

Leidy, 1865a, pl. 2 figs. 15-16, pl. 7 figs. 17-20, pl. 8 figs. 6, 8; 1873, pl. 36 fig. 15. Cope, 1875, pl. 26 fig. 1, pl. 27 fig. 11, pl. 34 figs. 1-42, pl. 35 figs. 1-10. Williston, 1898b, pl. 31 fig. 7.

STRATIGRAPHIC
AND PALEOECOLOGIC CONSIDERATIONS

In North America mosasaur remains have been discovered wherever marine rocks of upper Cretaceous age outcrop and there is reason to believe that the animals lived in abundance in coastal waters around the entire continent at that time. The ecology and faunal succession of mosasaurs will now be considered in the light of information contained in the sediments in which they are found. All known occurrences of American mosasaurs are listed (see Charts 1—4).

GULF COAST CRETACEOUS
(Charts 1 & 2)

The earliest known occurrence of mosasaurs in the New World is in the Turonian of Texas, where a continuous sequence of mosasaur-bearing rocks extends up to the top of the Cretaceous section. However most of the material consists of isolated specimens taken from localities widely scattered both in time and space. We have much to learn about the history of mosasaurs in this region. According to Scott (1940, p. 1193) ammonites that inhabited depths of 100 fathoms or more are not found in the outcropping Texas Cretaceous and the seas must have been shallow in this area. Foraminifera from the Taylor Formation in the Brazos River Valley (east central Texas) suggest deposition in normal marine water not more than a few hundred feet deep, but the shoreline may have lain far to the northwest (Smith, 1959, pp. 7-8). The Navarro Formation was deposited under similar conditions, although occasional shallow marine or beach sands indicate that at times the shoreline moved as far gulfward as the present area of outcrop.

The mosasaurs studied by Gilmore (1926, identified in the present paper as *Mosasaurus maximus, Plioplatecarpus* sp. and *Prognathodon*? sp.) probably came from the Coon Creek Formation of McNairy County, Tennessee (see Pryor, 1960, p. 1481). This unit was deposited in marine waters of inner neritic depths (about 300 feet) along the growing edge of a delta front, fed by a river flowing from the Appalachians into the northeast corner of the newly-formed Mississippi embayment (Pryor, 1960, p. 1496, fig. 17). Oxygen isotope ratios in mollusk shells from the Coon Creek Formation indicate water temperatures of 68°-84°F and subtropical climates comparable to that of present-day Bermuda (Lowenstam and Epstein, 1954, p. 229).

During periods of maximum transgression part of the Cretaceous sea over Mississippi and Alabama may have exceeded 100 fathoms (600 feet) in depth, but most of the sedimentation occurred on the continental shelf, and the Cretaceous rocks in northern Mississippi and western Alabama were laid down along the seaward edge of a highly indented coastline (Mellen, 1958, p. 10; Conant, 1964). The Eutaw Formation and shales in the Mooreville Member of the Selma Chalk were apparently deposited in shallow, brackish water (Priddy, 1954, p. 164), though most of the Selma Chalk was probably laid down in deeper offshore waters (Pryor, 1960, p. 1481). *Platecarpus* occurs in the Eutaw Formation and a large undescribed mosasaur fauna has been collected from the Mooreville Member (Zangerl, 1948, p. 15).

New Jersey Cretaceous
(Chart 3)

In most instances locality information is inadequate to determine exactly the mosasaur-producing horizons of the New Jersey Cretaceous, but it seems certain that nearly all of the material has come from the Navesink, Redbank and Tinton Formations, and equivalent portions of the New Egypt. Benthonic-planktonic foraminiferal ratios indicate these units were deposited in 100-300 feet of normally saline water (Olsson, 1963). Parasitic sponges on the oysters further suggest clear, silt-free water and the presence of a nearby river mouth to supply an abundance of nutrients. The occurrence of interlocked aggregates of oyster shells show that the generally quiet bottom conditions were occasionally disturbed by strong currents (Krinsley and Schneck, 1964, p. 278). According to Lowenstam and Epstein (1954) oxygen isotope ratios taken from belemnite rostra indicate water temperatures of 67°F, but as belemnite paleotemperatures usually fall below the mean, the ocean temperatures were probably similar to those found for the Mississippi embayment (Coon Creek Formation) and the general climate must have been subtropical.

Niobrara Formation
(Chart 4)

The Niobrara Formation of western Kansas has yielded more mosasaurs of more different kinds and generally in a better state of preservation than any other formation in the world. Niobrara specimens made up by far the greatest number of those examined in the course of this study.

According to Reeside (1957, pp. 525-528, figs. 15-16) the extent of the Cretaceous sea over the midcontinent was at its greatest during the period of time in which the Niobrara Formation was being deposited. The marine invertebrates found in the chalk suggest shallow depths; well-bedded deposits and articulated vertebrate remains suggest relatively quiet waters. Lithologic evidence indicates a low elevation and slow rate of erosion of the bordering land some 200 miles to the east of western Kansas, with a land of considerable relief about 600 miles to the west, and low coastal swamps to the southwest. LeRoy and Schieltz (1958, p. 2461) note that the foraminiferal fauna of the Smoky Hill Chalk Member along the Front Range in Colorado implies a ". . . normal, well-circulated, open sea, shelf environment." According to Merriam (1963, p. 67), "The Fort Hays Limestone (at the base of the Niobrara Formation) indicates a clear-water marine environment. A moderate change in conditions, seemingly marked by increased turbidity of the shallow sea, resulted in deposition of the Smoky Hill Chalk. Volcanic activity must have been at a maximum at this time in order to produce the many bentonite beds in the Niobrara."

Reeside (1957, p. 528) postulated that subsequent to Niobrara deposition the sea became restricted to a narrow north-south band (Telegraph Creek—Eagle deposits) in the western portion of its former basin, though Niobrara deposits to the east were subjected to erosion. Jeletzky (1955), Gill and Cobban (1961, p. D185) and Scott and Cobban (1964, p. L26) have shown, however, that the Telegraph Creek Formation and Eagle Sandstone are lateral equivalents of the upper portion of the Smoky Hill Chalk. Merriam (1963, p. 42; see also Gill and Cobben, 1961) notes that the Niobrara-Pierre contact in western Kansas appears to be gradational, and that there was no break in the continuity of sedimentation. As seen below, vertebrate evidence is suggestive of a shallowing of the sea and/or approach of the eastern shoreline during latest Niobrara time.

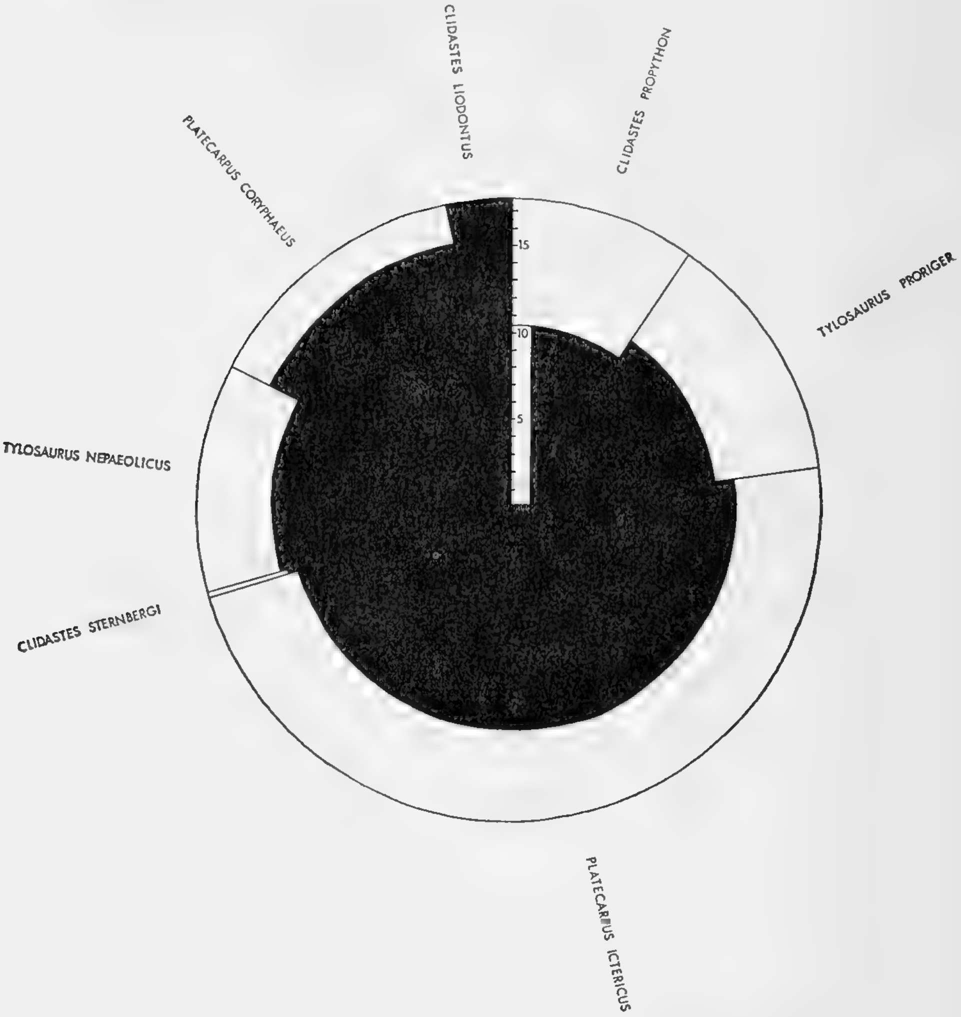
Williston (1897e) separated what is now called the Smoky Hill Member into two units, the yellowish *Hesperornis* beds above and white *Rudistes* beds below. The smaller pterodactyls, toothed birds, turtles and *Clidastes* were restricted to the upper unit, and vertebrates of all kinds except plesiosaurs were relatively far more abundant there. Williston interpreted this as evidence of shallowing water and approaching shore lines near the top of the formation. Zangerl (1953, p. 270) also noted that the species of toxochelyid turtles from the Niobrara are endemic and considered this as evidence of progressive isolation of the Niobrara Sea from the Gulf Coast.

There are indications of a subdivision of mosasaur assemblages within the Smoky Hill Chalk of western Kansas, which may correspond approximately to Williston's original divisions. During the Yale expedition of 1871 Marsh and his crew worked along the banks of the Smoky Hill River east of Fort Wallace, where only the uppermost part of the Niobrara is exposed immediately beneath the Pierre Shale. Marsh's locality data are good and, of the specifically determinable specimens collected, ten were of *Clidastes propython,* nine were of *Platecarpus ictericus,* and four were of *Tylosaurus proriger.* Two skulls of *P. coryphaeus* were discovered near Russell Springs about 24 miles east of Fort Wallace, but except for the first three species no other kind of mosasaur was found in the chalk west of this point. It is postulated that the Smoky Hill Chalk may be divisible into an upper *C. propython-P. ictericus-T. proriger* zone and a lower zone in which *C. liodontus-P. coryphaeus-T. nepaeolicus* occur, perhaps to the exclusion of other forms. Negative evidence supporting this hypothesis lies in the fact that *C. propython, P. ictericus* and *T. proriger* all occur in the lower Pierre, but the other three species do not. The presence of the latter three species in the lower Pierre also supports Jeletsky's (1955, p. 883) contention that there can be little, if any, break in time between the end of Niobrara and beginning of Pierre deposition.

Of the 36 generically identifiable skulls collected by Marsh in 1871 from the upper part of the Niobrara about 21% are of *Tylosaurus,* 30% of *Clidastes* and 49% are of *Platecarpus.* Considering the total number of skulls (398) taken from the Niobrara by Marsh or his collectors, 25% are of *Tylosaurus,* 13% are of *Clidastes* and 62% are of *Platecarpus.* These figures show that *Clidastes* becomes relatively more abundant higher in the formation, and support Williston's (1897e, p. 245) statement of the fact. This may be taken as evidence that *Clidastes* inhabited near-shore waters and that *Platecarpus* and *Tylosaurus* ranged more widely out to sea.

Pierre Formation
(Chart 4)

Following the Eagle regressive phase, the sea expanded to the west over most of the area it had formerly occupied, at the same time dark shales were being deposited in the central and eastern portions of the seaway. The western strand line then moved eastwards, bringing with it littoral sands and continental sediments (Mesaverde group) out into the central region of the seaway. The sea again re-advanced, depositing muds far to the west, ultimately to withdraw to the east where sands (Fox Hills Formation) mark the closing phase of Cretaceous marine deposition on the midcontinent (see Reeside, 1957, pp. 530, 540, modified by Gill and Cobban, 1961). From a study of the foraminifera of the lower



Text-fig. 96. Mosasaur skulls in the Marsh collections at the U. S. National Museum and Peabody Museum at Yale, collected from the Smoky Hill Member, Niobrara Chalk of western Kansas. Total number of generically recognizable skulls = 398. Sixty-two per cent of these skulls belong to the genus *Platecarpus*, 25% to *Tylosaurus* and 13% to *Clidastes*. *Ectenosaurus*, which makes up 1% of the Marsh collection, has been omitted. Of the skulls identifiable to the species level:

In *Platecarpus*	22.6% are *coryphaeus* (26 individuals)
	77.4% are *ictericus* (89 individuals)
In *Tylosaurus*	52.75% are *proriger* (19 individuals)
	47.25% are *nepaeolicus* (17 individuals)
In *Clidastes*	72% are *propython* (33 individuals)
	26% are *liodontus* (12 individuals)
	2% are *sternbergi* (1 individual)

The average number of elements collected of the skulls of specifically recognizable specimens is indicated by the numbers on the vertical radius. Thus in *Clidastes propython* on the average about 10.5 elements were collected of each skull. This is presumably an indication of how many elements were originally preserved.

It may be possible to divide the Smoky Hill Chalk into two zones on the basis of mosasaur species (see text), specimens from which would be mixed in this chart. Note that the three species from the lower zone (*Clidastes liodontus, Platecarpus coryphaeus, Tylosaurus nepaeolicus*) are apparently more completely preserved on the average than the other species.

Pierre (Gregory Member) of South Dakota, Johnson (1959, p. 49) suggested that the waters of the Pierre sea were shallow, warm, slightly alkaline and of marine to brackish salinity. Crandell (1958, p. 18) postulated that during Pierre deposition the eastern shoreline lay 200-300 miles to the east of central South Dakota. He also noted that at least part of the Pierre in central South Dakota accumulated in rather deep water. Fine layers of bentonite indicated deposition in quiet water below the wave base. Mosasaurs known from the lower Pierre include *Clidastes propython, Globidens alabamaensis, Platecarpus ictericus, P. somenensis* and *Tylosaurus proriger. Mosasaurus conodon* and *Plioplatecarpus primaevus* occur in the middle Pierre, and *M. missouriensis* and *Prognathodon overtoni* are known from the upper Pierre (see Appendix B).

The Pierre mosasaurs, although as yet poorly understood, promise to be a very rich and diversified assemblage. In view of the survival of at least three Niobrara species into the lower Pierre it would seem that physical changes in the sea caused by the replacement of chalk by dark shale deposition were of little consequence to mosasaurs. The time during which the Pierre Formation was being deposited spans nearly the entire period between the end of Niobrara sedimentation and the close of the Cretaceous. The Niobrara mosasaur fauna is grossly very well known and scattered collecting has indicated that a good succession of mosasaur faunas is present from the base to the top of the Pierre. Further sampling would doubtless reveal highly interesting changes in the composition and ultimate fate of the mosasaur community.

Additional Occurrences of American Mosasaurs

1. Three vertebrae (Holmes, 1849, p. 197) from the "marl" of Ashley River, South Carolina. See also the section on systematics for miscellaneous nineteenth century occurrences in the southern Atlantic states, (p. 176).
2. The type vertebra of *Clidastes iguanavus* from the Marshalltown Formation of New Jersey (see Cope, 1869a, p. 233).
3. Mosasaur teeth (Leidy, 1873, pp. 279-280, pl. 34 figs. 18-22) from the Pierre (?) Formation near Santee, L'Eau qui Court County, Nebraska.
4. Vertebral fragments (Cope, 1877, p. 569) probably from the Judith River Formation, Judith River region, Montana.
5. A *Clidastes* skeleton from near Flager, Colorado, and mosasaur bones from near Canyon City, Colorado (Lee, 1897, p. 614; Williston, 1898b, p. 196).
6. A *Clidastes* (identified by Lucas in Hill, 1901, p. 328) from the top of the Eagle Ford Formation, southwest of Waco, Texas.
7. Mosasaurs (Douglass, 1902, p. 212) from the Bearpaw Formation of Sweetgrass County, Montana.
8. A *Platecarpus* hind paddle (Williston, 1902, p. 252) probably from the Niobrara Chalk near Milton, North Dakota (see also Laird, 1951, p. 12).
9. *Platecarpus* remains (Loomis, 1904, p. 254) from the Pierre redeposited in the Chadronian of South Dakota.
10. *Mosasaurus* teeth (Gilmore, 1912b, p. 2) from the Fox Hills Formation south of Bismark, North Dakota. K. M. Waage has also recently discovered mosasaur teeth in the Fox Hills Formation of Montana and Wyoming.
11. *Mosasaurus*? caudal vertebrae (Sternberg, 1915, p. 132) from the Bearpaw Formation, Judith River region, Montana.
12. *M. conodon* from the Marlbrook Marl near Columbus, Arkansas.
13. The type of *Amphekepubis johnsoni* from the ?San Felipe Formation, north and east of Monterrey, Nuevo Leon, Mexico (Mehl, 1930).

14. Mosasaur vertebrae from Rayon, Tamaulipas, Mexico (Müllerried, 1931).

15. *Tylosaurus* skeleton (Renger, 1935) from the lower Selma Formation, near West Greene, Greene County, Alabama.

16. *Platecarpus* skeleton (Dowling, 1941) from the lower Selma Formation, five miles southeast of Eutaw, Greene County, Alabama.

17. Skeletal remains of *Plotosaurus bennisoni, P. tuckeri* and *Plesiotylosaurus crassidens* from the Moreno Formation (Maestrichtian) along the west side of the San Joaquin Valley, California (Camp, 1942).

18. *Mosasaurus*? dentary (USNM 3026) from the Tombigbee Sands of Plymouth Bluff on the Tombigbee River, Lowndes County, Mississippi.

19. *Mosasaurus* tooth (USNM 12287) from the upper part of the Selma Chalk, one and one-half miles northeast of Scooba, Kemper County, Mississippi.

20. *Globidens*? posterior half of a mandible (USNM 22965) from the upper part of the Austin Chalk, one and one-half miles northeast of Spofford, Kinney County, Texas.

21. *M. maximus* skull and skeleton (TMM) from the Navarro Formation on an east bluff of Onion Creek, about 300 yards north of the bridge on the Austin-Bastrop highway, Travis County, Texas (personal communication, Langston, 1963).

22. *Tylosaurus proriger* quadrate (TMM 40601) from the Taylor Formation, Texas (personal communication, Langston, 1963).

23. *T. proriger* skull (USNM 17909) from the Telegraph Creek Formation, Bighorn County, Montana (see appendix B).

24. *Tylosaurus* and *Clidastes* skulls (USNM 18496, 22964) from the Taylor Formation, one mile east of Culeoka in the Lavon Reservoir area, Collin County, Texas.

25. Large *Platecarpus* cranial fragments (Museum of Southern Arkansas State College) from the Brownstown Formation, northeast of Columbus, Arkansas, and midway between Prescott and Delight (personal communication, Chapman, 1963).

26. *Platecarpus* skull (YPM 1444) possibly from a marine sandstone tongue of the Mesaverde Formation, along one of the tributaries of Crow Creek, Wyoming.

27. *Platecarpus* cf. *somenensis* (YPM unnumbered) from the Pierre Shale, near Fort Randell, South Dakota.

28. Mosasaurs have been discovered from the Arctic Coast of the Northwest Territories, Canada (Russell, 1967).

Foreign Occurrences of Mosasaurs
(Charts 5, 6, & 7)

Outside of the United States, the best known superposed succession of mosasaur faunas occurs in Belgium. Other countries with a wide vertical range of mosasaur-producing horizons are France, Sweden and England. These faunas are listed in stratigraphic order along with those from the different regions of the United States in the accompanying charts (Charts 1—7).

Fragmentary remains of mosasaurs have been discovered on all of the continents of the world except Antarctica. In Europe they have also been reported from Ireland (Swanston, 1886), Germany (Pompeckj, 1910), Italy (Leonardi, 1946) and southern european Russia (Iakovlev, 1901, 1906; Bogoliubov, 1910; Pravoslavlev, 1914, 1916; Tsaregradskii, 1927, 1935). Mosasaurs are known from Israel (Raab, 1963) and Jordan (Repelin, 1915, Avnimelech, 1949, Signeux, 1959) in western Asia. In Africa mosasaurs are known to occur in the Union of South Africa (Broom, 1912), Nigeria (Swinton, 1930), northwestern Africa (Arambourg, 1952), Libya (Quass, 1902), Egypt (Stromer and Weiler, 1930; Zdansky, 1935, Leonardi and Maloroda, 1946) and Angola (Telles Antunes, 1964). They occur in Venezuela (Pierce and Welles, 1959), Brazil (Price, 1957) and Argentina (Ameghino, 1918) in South America. In the southwestern Pacific mosasaurs are known from Timor (E. Huene, 1935), Australia (Lundelius and Warne, 1960) and New Zealand (Hector, 1874).

In general the material from these localities is too incomplete to be of much use in understanding the paleozoogeography and evolution of mosasaurs. It is interesting to note that spherical teeth of the *Globidens alabamaensis* kind have been found in the Maestrichtian of Brazil (Price, 1957), North Africa (Arambourg, 1952; Zdansky, 1935), Jordan (Signeux, 1955) and probably also Timor (E. Huene, 1935), and from the lowermost Upper Campanian of Belgium (Dollo, 1924). Thus, the distribution of *Globidens* very likely coincides with the tropical "Mediterranean belt" of coral and rudistid reefs (see Berquist and Cobban, 1957, p. 871).

Tylosaurus or a very closely related form occurs in the Santonian or lower Campanian of Russia (See Tsaregradskii, 1927, p. 572, pl. 8 fig. 1), and in the Maestrichtian of New Zealand (Hector, 1874, pl. 30; Wellman, 1959) and Belgium (*Hainosaurus bernardi*). In North America, however, tylosaurines seem to disappear after early Campanian time. The osteology of mosasaur species inhabiting North America east of the Rocky Mountains and western Europe during the Maestrichtian is generally not well known, but it is quite possible that the same forms were common to both regions. An excellent skeleton of *Mosasaurus conodon* from South Dakota agrees in astonishing detail with other complete specimens from Belgium. If Funnell's (1964) observation is correct that the North Atlantic Ocean may have been 1,500 miles narrower at the close of Cretaceous time than it is now, it would not be surprising to find that species of large marine reptiles ranged across it.

It has commonly been assumed that individual genera of mosasaurs did not have a wide geographic distribution, but it is now evident that this was not the case. However, an indication that some faunal provinciality existed lies in the occurrence of apparently endemic mosasaur genera in Californian sediments of Maestrichtian age. An extensive north-south land isthmus perhaps linked to South America, or an ecologic barrier of some other kind must have prevented the dispersal of eastern genera into the California seas. Unfortunately almost nothing is known of the mosasaurs that inhabited other regions of the Pacific basin at that time, although *Taniwhasaurus* from New Zealand does show some similarity to the Californian *Plotosaurus*.

Ecological Conclusions

Stratigraphic evidence demonstrates that in the United States during late Cretaceous time mosasaurs inhabited shallow epicontinental seas, or in some cases, brackish water, near-shore environments. Oxygen isotope ratios derived from mollusk shells indicate water temperatures similar to those found in subtropical regions today. In the Niobrara Chalk *Platecarpus* and *Tylosaurus* may have frequented deeper water located farther from the coast more often than did *Clidastes*. Mosasaurs in the interior of North America have been found at least 400 miles away from the nearest contemporaneous strand line. Assemblages from the upper Niobrara and lower Pierre are similar and show that changes in deposition between the formations had little effect on them. Similarly *Mosasaurus conodon* has been found in shales (South Dakota), greensands (New Jersey) and chalk (Belgium), and *T. proriger* has been found in sandstone (Montana), shales (Kansas), calcareous shales (Colorado) and chalk (Kansas). The change in mosasaur faunas from the base to the top of the Pierre is attributed to a gradual evolution of the Atlantic mosasaur population.

The remains of only one obviously immature mosasaur hatchling (YPM 4818) have been seen by the author and a few juvenile specimens have been collected, all from the Niobrara Chalk. Many excellent adult skeletons are known in which even the stomach contents and cartilagenous parts are preserved, but embryonic young have never been found inside the body cavity. This is rather compelling negative evidence that mosasaurs were not ovoviviparous. Female mosasaurs may have crawled, probably with great difficulty, out onto the banks of large rivers in order to lay their eggs in the vicinity of shallow protected waters offering an abundance of small prey for the newly-hatched animals, as suggested by Williston (1904, pp. 48-50; 1914, pp. 163-165). Another possibility for which there is at present no evidence is that mosasaurs, like the pinnipeds and some marine turtles (see the recent work of A. Carr and associates), may have migrated to island or offshore bar rookeries where the adults were safe from large terrestrial carnivores. In this case, however, it seems that the young would have been at a more serious disadvantage because of their greater exposure to marine predators.

EVOLUTIONARY CONSIDERATIONS

Mosasaurs were the largest lizards that have ever lived. Their sudden appearance early in the fossil record of lizards and truly spectacular though brief success in the oceans of late Cretaceous time underline their uniqueness in the evolutionary history of reptiles. Although their derivation and initial radiation are as yet poorly documented, enough information is at hand to obtain a general notion of the relationships and phylogeny of mosasaurs.

Mosasaurs Compared with Platynotan Lizards

One of the few things that has been nearly universally agreed upon regarding the classification of mosasaurs is that they resemble the varanids more closely than any other group of extant lizards, a fact that Camp (1923, 1942) has demonstrated in detail. It is instructive, however, to point out certain skeletal features in which mosasaurs consistently differ from living varanids:

1. There are alveoli for only four premaxillary teeth instead of eight.
2. The anterior portion of the maxilla is never bent horizontally to floor the nasal capsule.
3. The nasals are vestigial and separated from each other by the internarial bar of the premaxilla instead of being fused along the midline and forming the bridge between the premaxilla and frontals.
4. The frontals are always fused in mosasaurs; they are separate in *Varanus.*
5. The lacrymal is relatively much smaller.
6. The jugal and postorbitofrontal are in contact behind the orbits, and the "quadratomaxillary" ligament was probably attached to the posteroventral corner of the jugal instead of to a tuber located near the juncture of the jugal, maxilla and ectopterygoid.
7. The parietal and postorbitofrontal meet in a vertical suture on the anterior margin of the supratemporal fenestra; in *Varanus* a wide wing from the parietal extends anterolaterally between the frontal and posteromedial process of the postorbitofrontal.
8. The foramina for nerves X-XII open on the lateral instead of occipital face of the skull.
9. In cross-section the long axis of the parietal-suspensorial arcade is horizontal instead of vertical.
10. The pterygoids possess a single row of teeth.
11. The incisura piriformis is relatively quite narrow.
12. The suprastapedial process of the quadrate and the tympanic ala are very much larger.
13. There is a well-developed, transversly-oriented joint between the splenial and angular. In *Varanus* these elements loosely overlap one another without forming articulating facets.
14. The long, posteromedially curving process from the coronoid which bounds the meckelian fossa internally in *Varanus* is lacking in mosasaurs.
15. The intercentral articulations of mosasaur vertebrae face directly anteroposteriorly; in *Varanus* they are inclined in an anteroventral-posterodorsal direction.
16. There are seven cervical vertebrae in mosasaurs as compared to nine.

Cervical ribs occur on every vertebra but the atlas, instead of only on the last 3-4 cervicals.

17. At least five ribs have cartilaginous sternal connections in mosasaurs; only three such ribs exist in *Varanus.*
18. The presence of long ribs indicates that the thoracic cavity was restricted to the anterior portion of the dorsal region. Long ribs occur on all but the last six dorsal vertebrae in *Varanus* and the thoracic cavity is correspondingly more elongate.
19. The vertical dorsal tip of the ilium could have been only ligamentously bound to a single sacral vertebra; in *Varanus* the posterodorsally sloping ilium contacts two sacral vertebrae.
20. There are never less than five pygal vertebrae. In *Varanus* there is but one.
21. Transverse processes do not occur on vertebrae behind the center of the caudal series in mosasaurs; in *Varanus* they occur to the end of the tail.
22. The limbs have been transformed into paddles with a concomitant shortening and broadening of the pro- and epipodials, hyperphalangy and loss of ungual phalanges. The limbs in *Varanus* are of the normal lacertilian type.

On the island of Hvar (Lesina) in the Dalmatian archipelago and near Comeno (Kómen) north of Trieste in Yugoslavia, the remains of small aquatic lizards, called aigialosaurs, have been discovered in rocks of Cenomanian-Turonian age (Langer, 1961*). So far only two aigialosaur skeletons with associated skulls have been described, one by Kramberger (1892) of *Aigialosaurus dalmaticus* and another by Kornhuber (1901) of *Opetiosaurus buccichi.* Another excellent skeleton lacking the skull was named *Carsosaurus marchesetti* by Kornhuber (1893). The descriptions and figures of these animals given by Kramberger and Kornhuber are compared point by point with the list of characters separating modern varanids from mosasaurs given above.

1. Upon comparison of Kornhuber's (1901) plates 2 and 3 showing the course of the premaxillary-maxillary suture over the top of the rostrum with the alveoli in the same region on the undersurface of the skull in *Opetiosaurus,* it seems probable that four premaxillary teeth were present.
2. In *Opetiosaurus* the condition of the anterior portion of the maxilla is as in mosasaurs.
3. The nasals are unknown.
4. The frontals are fused in *Opetiosaurus.*
5. The lacrymal is relatively large in *Opetiosaurus* and *Aigialosaurus.*
6. The jugal and postorbitofrontal are in contact behind the orbit in *Opetiosaurus.*
7. In both *Opetiosaurus* and *Aigialosaurus* the parietal-frontal-postorbitofrontal contact is as in *Varanus.*
8. The braincase is unknown.
9. The parietal-suspensorial arcade is not well-preserved.
10. Nopcsa (1903b, p. 121) in a footnote observes, "It cannot be certainly known whether the pterygoids of the Aigialosaurs bore teeth, but I am inclined to believe they did, since in *Opetiosaurus* the crown of a tooth lying near the hyoid bone seems to differ in size both from the mandibular and (presumably also) maxillary teeth of this animal." Camp (1923, p.

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*I am indebted to Mr. George Callison of the University of Kansas for bringing this reference to my attention.

321) states that the pterygoid teeth of aigialosaurs are large, from a source of information unknown to the present author.

11. The incisura piriformis appears to be relatively as wide in *Opetiosaurus* as in *Varanus.*
12. The suprastapedial process of the quadrate and tympanic ala are as well developed in *Opetiosaurus* and *Aigialosaurus* as in mosasaurs.
13. There is a well-developed, transversly oriented joint between the splenial and angular in *Opetiosaurus.*
14. The medial surface of the lower jaw is unknown.
15. The nature of the intercentral articulations is unknown.
16. There are eight cervical vertebrae in *Opetiosaurus* and all but the first three bear ribs.
17. Five ribs have cartilaginous sternal connections in *Carsosaurus.*
18. The last four dorsal vertebrae in *Opetiosaurus,* at least the last five dorsals in *Aigialosaurus* and the last seven dorsals in *Carsosaurus* bear short ribs (the last dorsal may lack ribs in *Aigialosaurus* and *Carsosaurus*). This is true of the last six dorsals in *Varanus* and at least the last nine dorsals of mosasaurs, by comparison.
19. The posterodorsally sloping ilium contacts two sacral vertebrae in *Aigialosaurus, Carsosaurus* and *Opetiosaurus.*
20. There is only one pygal vertebra in *Carsosaurus.*
21. Transverse processes do not occur on vertebrae behind the center of the caudal series in *Opetiosaurus.*
22. The epipodials are shorter relative to the propodials in *Carsosaurus, Aigialosaurus* and *Opetiosaurus* than in *Varanus,* but are not broadened. The manus and pes in *Opetiosaurus* have the normal reptilian phalangeal formula, and the terminal phalanges are clawed in *Carsosaurus* and *Opetiosaurus.*

It is evident that the two aigialosaur skulls are very similar to those of mosasaurs, although they do possess several *Varanus*-like characteristics. There are some additional noteworthy features of these skulls. The prefrontals and postorbitofrontals fail to contact in *Aigialosaurus* and *Opetiosaurus.* In both genera there appears to be a triangular ala projecting from the lateral margin of the supraorbital wing of the prefrontal. In *Opetiosaurus* the posterodorsal process of the coronoid is very high and may have been buttressed by a thin sheet of bone from the dorsal rim of the surangular, and there is a large number of teeth (at least 17) in the dentary. In *Aigialosaurus* the suprastapedial process is very large and apparently fused to the infrastapedial process, although the bone may have been partially crushed. The appearance of the quadrate in *Opetiosaurus* is very similar to that of *Clidastes,* and in both *Aigialosaurus* and *Opetiosaurus* the tympanic ala is heavy. The latter series of characters is also found in mosasaurs of the subfamily Mosasaurinae and among these is especially reminiscent of *Clidastes.*

The retention of a solid sacrum, clawed digits and a well-developed joint between the pro- and epipodial elements gives a strongly varanoid appearance to the post-cranial skeleton of aigialosaurs. Certain features, however, such as the incipient concentration of thoracic cavity into the anterior portion of the dorsal region and the lack of transverse processes on the vertebrae of the distal half of the tail, are highly suggestive of mosasaurian affinities. Thus, although some portions of the aigialosaur skeleton resemble corresponding elements of the mosasaur skeleton more closely than do others, the known aigialosaurs surely represent a complex of lizards which is admirably suited in morphology to give rise to the mosasaurs.

Kuhn (1958) has recently described a small varanoid from the Solenhofen Limestone near Eichstätt in southern Germany. It is evident from his illustration of the outline of the skull (ibid., fig. 1) that the maxilla was not bent medially to floor the nasal capsule, and that the jugal was sutured to the postorbitofrontals behind the orbits, both characteristics being typical of aigialosaurs and mosasaurs. Kuhn concludes that his *Proaigialosaurus* demonstrates the existence of an aigialosaurian type of semiaquatic lizard as early as late Jurassic time.

The dolichosaurs are another group of small aquatic lizards that occur together with aigialosaurs in the middle Cretaceous strata of Komen and Lesina, with one form (*Dolichosaurus*) known from equivalent rocks in England. Cranial material has been described in three species, *Adriosaurus suessi, Pontosaurus lesinensis* and *Dolichosaurus longicollis.* A head of *Adriosaurus* (Nopcsa, 1908, pp. 51-52, pl. 3 figs. 1-2) is small and poorly preserved. The nasal and frontal are separated by sutures from their opposites along the midline of the skull. The orbits, external nares and parietal foramen are relatively large. Kornhuber (1873, pl. 21) shows a large lacrymal in *Pontosaurus* and a well-developed splenio-angular joint. The tiny mandibles of *Dolichosaurus* figured by Owen (1849-1884, lacertilians pl. 8 fig. 2) appear to lack a splenio-angular joint, although it is difficult to be certain. In general, the relatively short skull, high pre-sacral vertebral count (at least 34, usually more), long neck (11 or more cervical vertebrae) and reduced forelimbs of known dolichosaurian skeletons (see Nopcsa, 1923, pp. 105-107), including those of *Mesoleptos zendrini* (Nopcsa, 1923, p. 107), *Acteosaurus tommasini* (Meyer, 1860, pp. 223-231, pl. 24, which is probably conspecific with the imperfectly preserved type skeleton of *Adriosaurus suessi* Seeley, 1881, see also Romer, 1956, p. 562; Nopcsa, 1908, pl. 3), *Pontosaurus lesinensis* (Kornhuber, 1873, pls. 20-21) and *Dolichosaurus longicollis* (Owen, 1849-1884, lacertilians pl. 8 fig. 1, pl. 9 fig. 4), exclude them from the aigialosaurs and the possible ancestory of the mosasaurs.

The fossil record of terrestrial platynotans is very poor. For the present purposes only the skeleton of *Saniwa* (Eocene of North America) is sufficiently well known to be compared usefully with those of mosasaurs and living varanids. For a review of other Cretaceous and Tertiary platynotans see Féjerváry (1918), McDowell and Bogert (1954, p. 53) and Estes (1964, pp. 128-137). The following information on *Saniwa* was taken from Gilmore (1928, pp. 53-83, figs. 31-42, pls. 3-10).

1. Alveoli for six premaxillary teeth are present in the premaxilla.
2. The anterior portion of the maxilla is bent horizontally to floor the nasal capsule.
3. The nasals are unknown.
4. The frontals are unknown.
5. The lacrymal is relatively almost as large as in *Varanus.*
6. The jugal and postorbitofrontal probably contacted behind the orbits and there is a slight indication of an angulation on the posteroventral corner of the jugal, indicating a possible area of attachment for the "quadratomaxillary" ligament.
7. The parietal-frontal-postfrontal contact is as in *Varanus.*
8. The foramen for nerves X-XII opens on the occipital face of the skull

but the thin crest of bone separating it from the lateral face of the braincase is not half so large as in *Varanus*.

9. The parietal-suspensorial arcade is not known.
10. The pterygoids possess a single row of teeth.
11. The incisura piriformis is relatively narrower than is usual in *Varanus* but not so narrow as in mosasaurs.
12. The suprastapedial process of the quadrate is relatively small as in *Varanus*.
13. The splenio-angular joint is similar to that of *Varanus*.
14. There is a posteromedial process of the coronoid to the prearticular around the meckelian fossa.
15. The intercentral articulations are inclined in an anteroventral-posterodorsal direction.
16. The number of true cervical vertebrae is unknown, but the first ribs occur on the fourth? or fifth vertebra postcranially.
17. The number of dorsal ribs with cartilaginous sternal connections is unknown.
18. The rib cage is inadequately preserved in known specimens of *Saniwa*.
19. The posterodorsally sloping ilium contacts two sacral vertebrae.
20. The number of pygal vertebrae is unknown.
21. The posterior portion of the caudal series is unknown in *Saniwa*.
22. The epipodials and feet are practically unknown, but from the shape of two preserved phalanges it seems likely that *Saniwa* possessed a clawed manus and pes of the normal varanoid type.

Saniwa is clearly more closely related to the varanids than to mosasaurs, although it does possess a few features that are intermediate between the two groups. The postorbital-postfrontal ossifications are separate in this genus and in *Telmasaurus* (Gilmore, 1943, p. 380), a questionable saniwinine from the Cretaceous of Mongolia. Teeth are present on the palatines of *Saniwa* and there is an unusually high number of marginal teeth on the maxilla (24) and dentary (22).

Besides the monitors (varanids) there are only two living genera of rather peculiar terrestrial lizards that have ever been considered as having a special affinity to the mosasaurs. One of these, *Lanthanotus*, is a small obscure creature from the rain forests of northern Borneo. The other, *Heloderma*, is a larger, sluggish venomous lizard from the deserts of the southwestern U.S.A. and northwestern Mexico. In *Lanthanotus* (see McDowell and Bogert, 1954) the twenty-two characters under discussion are as follows:

1. There are eight premaxillary teeth.
2. The anterior portion of the maxilla is bent medially to floor the nasal capsule as in *Varanus*.
3. The nasals are relatively large, fused, and form a bridge between the premaxilla and frontal on the internarial bar.
4. The frontals are separate.
5. The lacrymals are small.
6. The jugal and postorbitofrontal are in contact behind the orbits.
7. The postfrontal-parietal-frontal contact is as in *Varanus*.
8. The foramen for nerves X-XII opens on the occipital face of the skull.
9. The suspensorial arcade from the parietal is nearly vertical in cross-section, as in *Varanus*.
10. The pterygoids have a single row of teeth.

11. The incisura piriformis is broad as in *Varanus.*
12. The suprastapedial process of the quadrate is small as in *Varanus.*
13. The splenio-angular joint is approximately intermediate in development between varanids and mosasaurs.
14. A long posteromedial process from the coronoid curves around the anterior border of the meckelian fossa to contact the prearticular.
15. The intercentral articulations are inclined in an anteroventral-posterodorsal direction.
16. There are nine cervical vertebrae in *Lanthanotus,* with cervical ribs on all but the first three.
17. Three of the anteriormost dorsal ribs have cartilaginous sternal connections.
18. Only four of the posteriormost dorsal vertebrae lack long ribs, and the thoracic cavity is long and slender.
19. The posterodorsally sloping ilium contacts two sacral vertebrae.
20. The number of pygal vertebrae is unknown.
21. Transverse processes occur to the end of the tail.
22. Propodial-epipodial ratios are not known in *Lanthanotus.* The manus and pes have the phalangeal formula of 2-3-4-4-3 and the terminal phalanges are clawed.

Lanthanotus also possesses teeth on the palatines. In spite of the loss of the supratemporal arcade and parietal foramen, and the lesser number of marginal teeth, *Lanthanotus* has more characters in common with the saniwinine (*Saniwa*) varanids than with any other group of extinct platynotans. It is believed that the evidence supports a varanid ancestry for *Lanthanotus* more strongly than a derivation from the Cretaceous dolichosaur-aigialosaur-mosasaur complex as suggested by McDowell and Bogert (1954, p. 57).

In *Heloderma* the twenty-two characters are:

1. There are usually eight premaxillary teeth.
2. The anterior portion of the maxilla is bent medially to floor the nasal capsule as in *Varanus.*
3. The nasals are moderately large, sutured together along the midline and form a bridge between the premaxilla and frontal on the internarial bar.
4. The frontals are separate.
5. The lacrymals are relatively as large as in *Varanus.*
6. The jugal and postorbitofrontal are firmly sutured together behind the orbits, and there is a prominent angulation on the posteroinferior corner of the jugal indicating a possible area of attachment for the "quadratomaxillary" ligament.
7. The postfrontal-parietal-frontal contact is as in *Varanus.*
8. The composite foramen for nerves X-XII opens on the occipital face of the skull, but the thin crest of bone separating it from the lateral face of the braincase is very small.
9. The dorsal surface of the parietal-suspensorial arcade is flattened, making the arcade triangular in cross-section.
10. The pterygoids have a single row of teeth.
11. The incisure piriformis is relatively as broad as in *Varanus.*
12. The suprastapedial process of the quadrate is as small as in *Varanus,* but the tympanic ala is better developed.

13. The splenio-angular joint is similar to that of *Varanus.*
14. A long posteromedial process from the coronoid curves around the anterior border of the meckelian fossa to contact the prearticular.
15. The intercentral articulations are inclined in an anteroventral-posterodorsal direction.
16. There are eight cervical vertebrae in *Heloderma,* with cervical ribs on all but the first three.
17. Four of the anteriormost dorsal ribs have cartilaginous sternal connections.
18. Six of the posteriormost dorsal vertebrae lack long ribs, and the thoracic cavity is long and slender.
19. The posterodorsally sloping ilium contacts two sacral vertebrae.
20. There is one pygal vertebra.
21. Transverse processes occur to the end of the tail.
22. The epipodials are not reduced in *Heloderma.* The manus and pes have a normal reptilian formula (2-3-4-5-3), and the terminal phalanges are clawed.

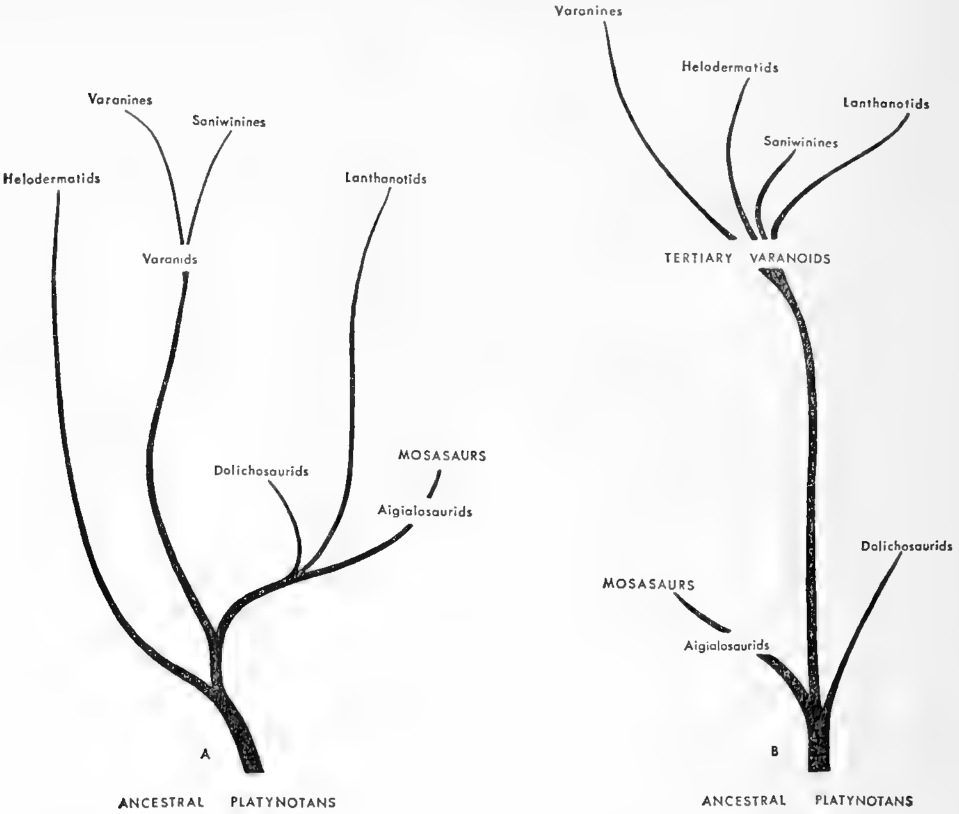
The premaxillae are not fused posteriorly in *Heloderma* and teeth are present on the palatines. The number of teeth in the marginal dentition is comparable to that found in *Varanus* and less than in *Lanthanotus* and *Saniwa.* The parietal foramen and supratemporal arcade are also lost, and *Heloderma* appears in some respects to approach the saniwinine (*Saniwa*) varanids more closely than *Lanthanotus.*

PHYLOGENY OF PLATYNOTANS

Although the fossil record of lizards is very incomplete, it is believed that the following conjectures are consistant with our present knowledge of the skeleton in platynotan lizards. They are partly at variance with the interpretation presented in the detailed and richly illustrated work of McDowell and Bogert (1954).

A diagnosis of the hypothetical ancestral platynotan may prove to be: Four premaxillary teeth. Anterior portion of maxilla curves dorsomedially, not bent horizontally to floor nasal capsule. Nasals separate; contact premaxilla, frontals and maxilla; external nares do not reach prefrontals. Frontals separate. Lacrymal relatively large. Jugal and postorbitofrontal contact behind orbit; process on posteroinferior corner of jugal for "quadratomaxillary" ligament. Wide wing from parietal extends anterolaterally between frontal and posteromedial process of postfrontal; postfrontal and postorbital separate. Foramina for nerves X-XII open on lateral face of braincase. Parietal-suspensorial arcade with horizontal long axis in cross section. Single row of teeth on pterygoids and palatines. Incisura piriformis broad. Suprastapedial process on quadrate small. Splenial and angular overlap in loose joint in lower jaw. Distinct posteromedial process from coronoid extending around meckelian fossa to prearticular. Intercentral vertebral articulations face anteroventrally or posterodorsally. Nine cervical, 20 dorsal, two sacral and one pygal vertebrae. Transverse processes present on all caudal vertebrae. Three to four cartilaginous ribs articulate with sternum, long ribs present on all but last four dorsals. Pelvic girdle and limbs of normal lacertilian type.

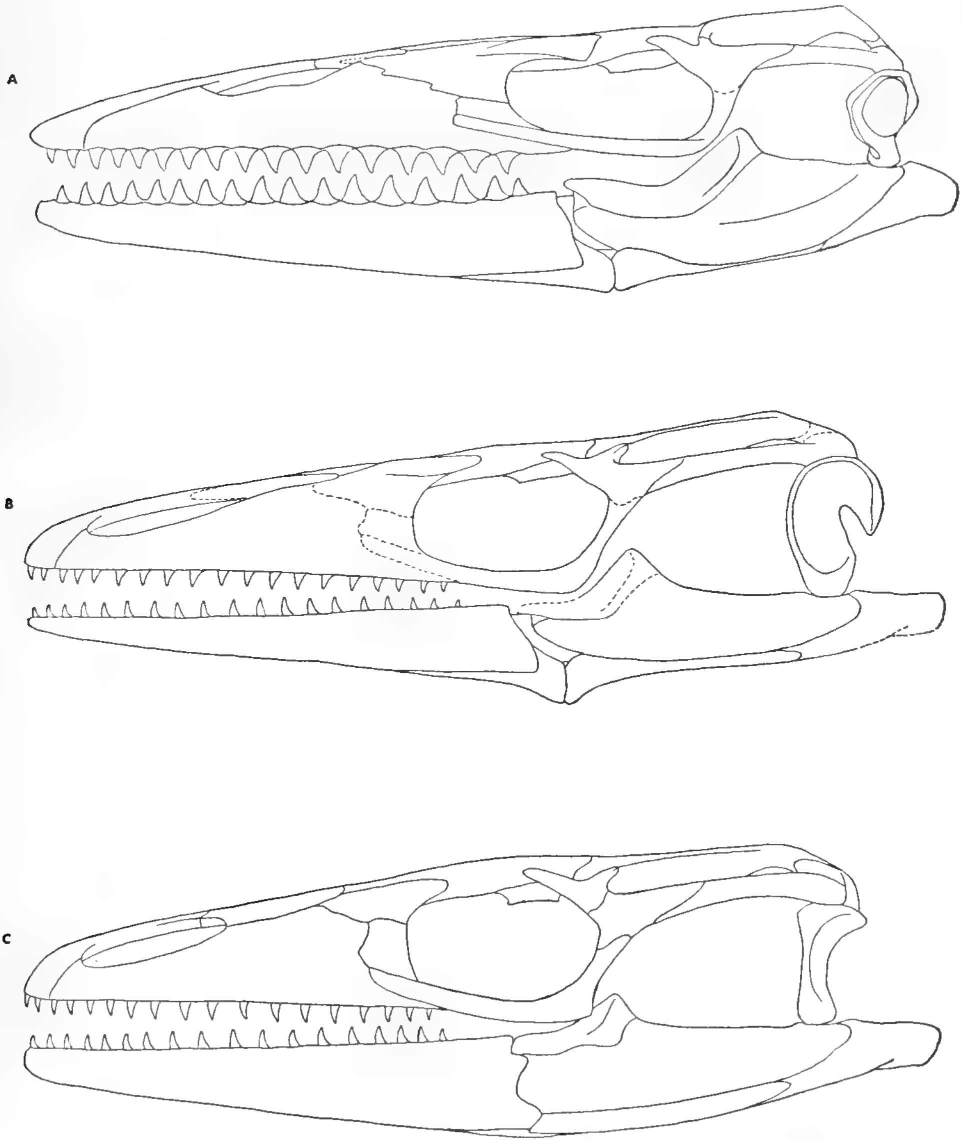
Dolichosaurs were probably derived from primitive platynotans, but their tiny skull, long neck and reduced forelimbs preclude a close relationship with either the aigialosaur-mosasaur or varanoid lineages. Primitive varanoids (ex-



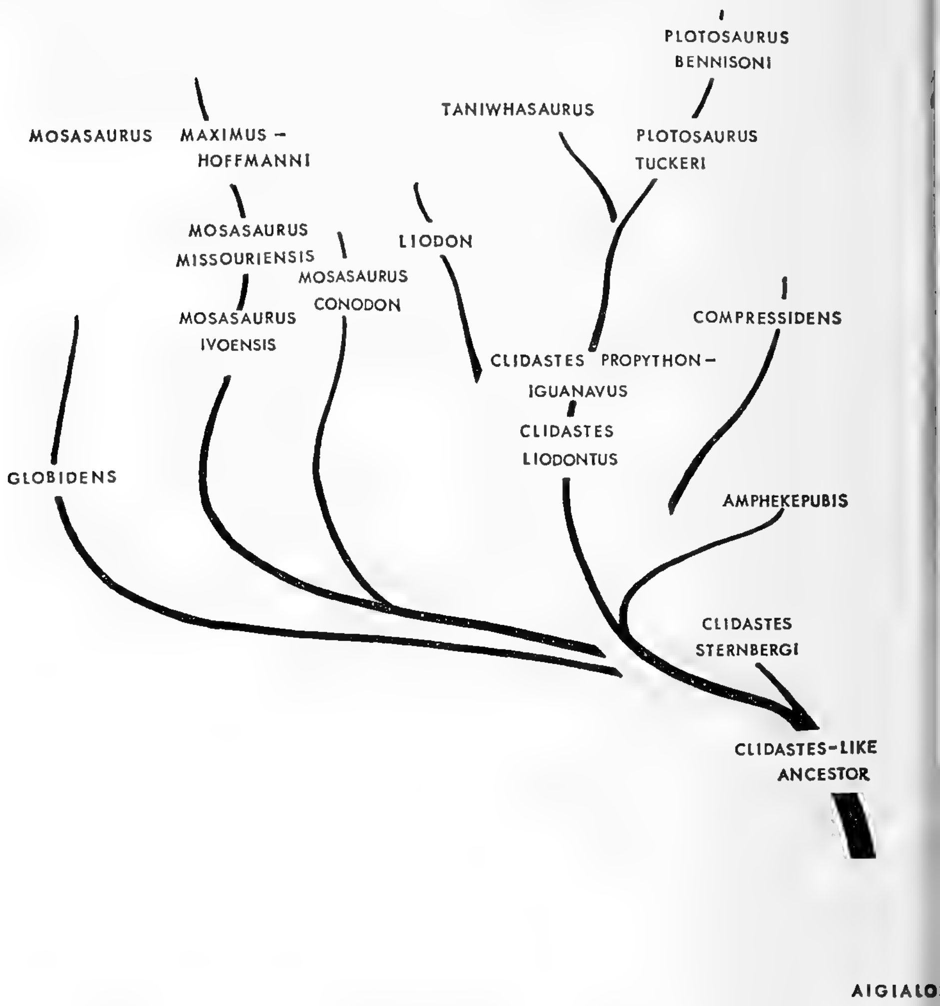
Text-fig. 97. Phylogeny of platynotans. A. After McDowell and Bogert (1954). B. The present interpretation.

cluding aigialosaurs) may have been derived from the foregoing hypothetical ancestral platynotan through several structural modifications: two teeth were added to the premaxilla, and the anterior portion of the maxilla curved medially under the nasal capsule. A ridge of bone grew up beneath the paroccipital process that separated the exit for cranial nerves X-XII from the lateral face of the braincase off onto the occipital faces. In cross-section the long axis of the parietal-suspensorial arcade became vertical. In varanines proper the postorbital arch is broken and the point of attachment of the "quadratomaxillary" ligament shifts onto a tuber located near the juncture of the jugal, maxilla and ectopterygoid. The postorbital and postfrontal are fused as are the two nasals, and the row of teeth on the palatine and pterygoid has been lost. Four teeth have been added to the premaxilla making a total of eight present. The Helodermatidae and Lanthanotidae are derived separately from saniwinine stock through the addition of two more premaxillary teeth to the primitive number and the loss of the supratemporal arcade and parietal foramen. The nasals are fused in *Lanthanotus* and the splenio-angular joint is more highly developed. Teeth are retained on both the palatines and pterygoids. About six more vertebrae have been added to the dorsal region of *Lanthanotus* and *Heloderma* and the limbs have become slightly reduced.

The skull of aigialosaurs would be modified from (hypothetical) ancestral platynotans in the fusion of the frontals, the development of a large suprastapedial process of the quadrate, and the highly developed articulation between the splenial and angular. As the mosasaurian grade was attained the nasals were reduced and separated from each other by the internarial bar of the premaxilla and frontal. The palatine teeth were lost as was the posteromedial process of the coronoid to the prearticular. The lacrymals were reduced, the postorbitals and postfrontals were fused, and the anteromedial portion of the parietal lost its contact posteriorly with the postfrontal. The intercentral artic-



Text-fig. 98. Restored skulls. A. *Clidastes liodontus* (after YPM 1335). B. *Opetiosaurus bucchichi* (after Kornhuber, 1901, pls. 1-2). C. Hypothetical primitive platynotan. All are drawn to approximately the same length, showing the suggested transition from a primitive varanoid to the mosasaurian type of skull.

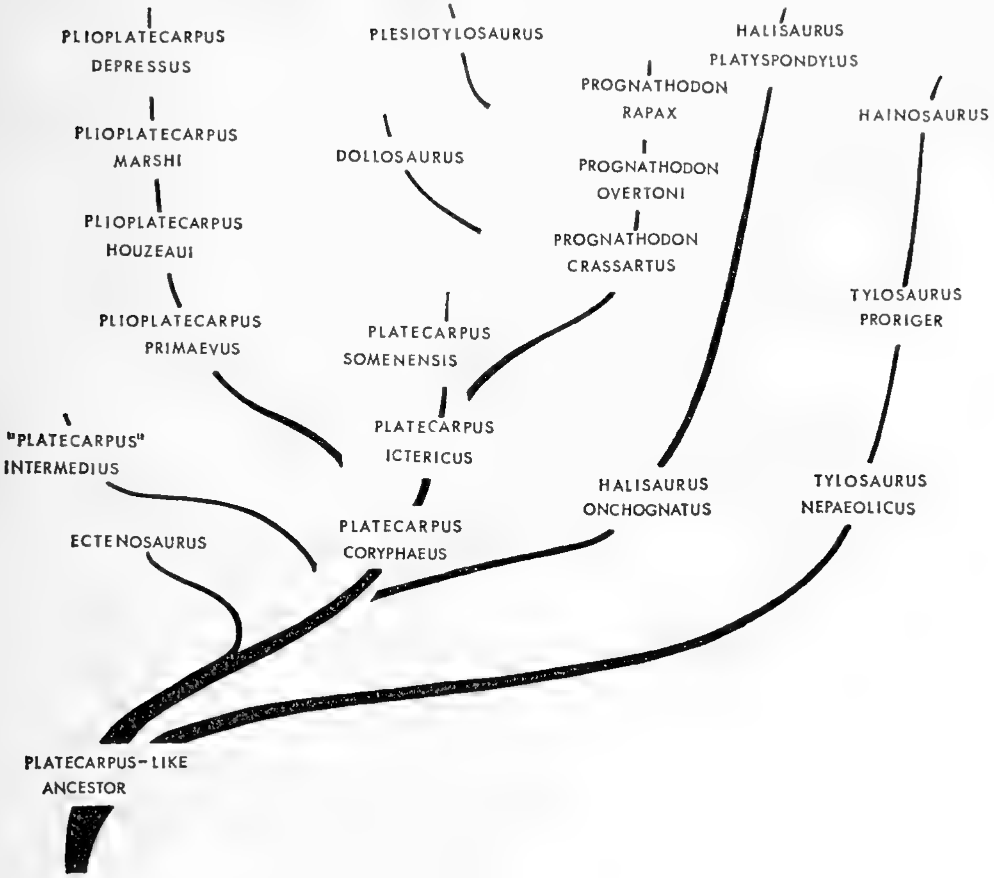


Text-fig. 99. Diagrammatic family tree of the mosasaurs.

ulations became vertical and the tail was changed into a sculling organ, losing the transverse processes on the vertebrae of the distal half of the caudal series. There are indications of an increase in the number of long ribs with cartilaginous sternal connections and of posterodorsal vertebrae lacking long ribs. Mosasaurs may have descended from aigialosaurs through primitive forms similar to *Clidastes sternbergi.*

PHYLOGENY OF MOSASAURS

As has been shown, the mosasaur skeleton could easily have been derived from that of an aigialosaur. Typical aigialosaurs are, however, known only from the Cenomanian-Turonian of the Balkans, and the record of mosasaurs clearly begins with the succeeding Coniacian stage. Although these aigialosaurs may or may not have given rise to true mosasaurs, as here considered, it is well to remember that *Proaigialosaurus* from the late Jurassic indicates that aigialosaurs were surely present during earlier Cretaceous time.



SAURIDS

Probably sometime during the Cenomanian two basic types of mosasaurs separated off from somewhat advanced aigialosaur stock. In one type, represented by the Plioplatecarpinae and Tylosaurinae, the number of marginal teeth is slightly reduced, the dorsal edge of the surangular is rounded and the lateral exits for cranial nerves X-XII fused into a single foramen externally. With the possible exception of *Hainosaurus* there are never more than 29 presacral vertebrae, and this section of the column is less than the caudal series in length. The tail is not especially dilated distally and the articular surfaces of the limbs were finished in thick cartilage. These two subfamilies are obviously closely related but they soon developed divergent characters in the cranium. In one (the Tylosaurinae) the otosphenoid crest became very large and a long conical rostrum appeared in front of the teeth on the premaxilla. In the other (the Plioplatecarpinae) a large channel or groove for the basilar artery developed in the basisphenoid-basioccipital, and the suprastapedial process of the quadrate curved ventrally to reach nearly to the base of the quadrate.

The tylosaurines manifest relatively little specific diversity and may have disappeared on this continent before the beginning of Maestrichtian time, although some forms survive into the late Maestrichtian of Europe *(Hainosaurus)* and New Zealand. Generalized Plioplatecarpines appear in abundance from the Santonian through Campanian in the United States and probably also in Europe. Known genera include *Ectenosaurus, Platecarpus* and *Plioplatecarpus,* the last genus continuing until the late Maestrichtian of North America and Europe. In the late Campanian and Maestrichtian these forms were joined by plioplatecarpines of the *Prognathodon* type *(Dollosaurus, Plesiotylosaurus, Prognathodon).*

The Mosasaurinae represent derivatives of the other basic stock of mosasaurs, and *Clidastes* may be considered as morphologically close to the ancestral type of the subfamily. The number of marginal teeth in the jaws of members of this group is greater than in the Plioplatecarpinae-Tylosaurinae. The dorsal edge of the surangular is a thin ala of bone that rises anterodorsally to buttress the posterior end of the coronoid. Cranial nerves X-XII consistently exit through two foramina on the lateral wall of the braincase. There are never less than 31 presacral vertebrae and usually more than 40 are present, since this portion of the column exceeds the caudal series in length. The neural and haemal spines are elongated near the center of the tail and support a well-formed caudal fin. The individual elements of the limbs articulate with a minimum of intervening cartilage.

Mosasaurus and *Liodon* are large typical mosasaurines, ranging from the Santonian to Maestrichtian of North America and Europe. *Plotosaurus* from western North America and *Taniwhasaurus* from New Zealand may be considered as late, highly advanced *Clidastes* derivatives. Possibly in the latest Cenomanian a type of clidastoid acquired shellfish-eating habits and developed into *Globidens,* the characteristic spherical teeth of which have been found in sediments of later Campanian and/or Maestrichtian age on five continents. Another less divergent shellfish-eating form of more delicate proportions is known from the Maestrichtian of Europe *(Compressidens).*

Evolution of Mosasaurs

In spite of the great numbers of mosasaur specimens collected from the late Cretaceous deposits of the world and the detail in which their osteology has been studied, several difficulties are encountered when an attempt is made to discern evolutionary trends within the group. The early Cretaceous record of reptilian life is as yet rather sparsely documented and this is especially true for platynotan lizards. As a consequence new discoveries may greatly modify any suggestions offered here on the mode of derivation and early radiation of mosasaurs. Even the relatively excellent record of late Cretaceous mosasaurs presents difficulties. Although late Santonian, early Campanian and late Maestrichtian forms are well known, those from rocks of an intermediate age are not, and even good faunas from the former two ages have been described only from the United States and Belgium. As it stands, the well-preserved portion of the mosasaur record covers only about 20 million years, which allows little time for the development of adaptive grades such as have been demonstrated in the teleost fishes. The following remarks must be considered in the light of these limitations.

The reason behind the sudden appearance and rapid proliferation of mosasaurs must have lain in the exploitation of an unoccupied or inefficiently occupied zone. All the evidence indicates that mosasaurs were near-surface carnivores and actively pursued their prey. The remarkable convergence of some of the later mosasaurs (*Plotosaurus,* Camp, 1942, pl. 5) with primitive Triassic ichthyosaurs (*Mixosaurus,* Huene, 1925, fig. 3) shows that they were an ecological replacement of the declining ichthyosaurs. Whatever the habits of plesiosaurs were, there must have been little direct competition with mosasaurs, for mosasaurs were able to enter and thrive in a marine environment and both groups inhabited the same seas until the close of Maestrichtian time. Perhaps plesiosaurs subsisted on fish living closer to the bottom of shallow marine bodies of water.

Aigialosaurs possess no character that would prevent them from being ancestral to the mosasaurs. As in other forms that bridge the morphologic gap between two categories (DeBeer, 1954), aigialosaurs are not simply intermediate between varanoids and mosasaurs but present a "mosaic" of ancestral (varanoid) and descendent (mosasauroid) characters (characters possessed by aigialosaurs are italicized):

VARANOID CHARACTERS	MOSASAUROID CHARACTERS
A. *external nares located far anteriorly on rostrum.*	A. external nares located nearer center of rostrum
B. incipient suprastapedial process on quadrate	B. *large suprastapedial process on quadrate*
C. splenio-angular joint imperfect	C. *splenio-angular joint well-developed*
D. *two sacral vertebrae present*	D. sacrum absent
E. *tail tapers gradually to a sharp point*	E. tail comes more abruptly to a rounded termination in lateral profile
F. *terrestrial limbs*	F. limbs modified into paddles

Aigialosaurs approach mosasaurs more closely in the skull than in the postcranial skeleton. The highly streptostylate quadrates and splenio-angular articulation apparently gave the mandibles sufficient mobility to force objects into the throat without the aid of gravity or some solid point of leverage. This adaptation, which freed aigialosaurs from the need of surfacing or climbing out upon the land to swallow their prey, was probably critical in enabling them to become truly pelagic carnivores. As a consequence the body and limbs were later modified into more effective organs of aquatic locomotion. With this last development the mosasaurian level of evolution was attained.

The radiation of mosasaurs into two distinct lineages by Santonian time suggests the presence of two subzones within the general adaptive zone occupied by the mosasaurs. That the clidastoids were shallow-water forms is strongly suggested by their evolutionary proximity to the aigialosaurs, their abundance in portions of the Niobrara Chalk that were apparently deposited in shallower water, and by the fact that shellfish-eating forms (*Compressidens, Globidens*) were derived from them and not from the remaining groups of mosasaurs. Plioplatecarpines and tylosaurines separated at an early point in their history and may represent an invasion of mosasaurs into the surface regions of deeper waters. In *Platecarpus,* a generalized plioplatecarpine, the body appears to have been very maneuverable and the animal is assumed to have fed on small fish. The large size and heavy marginal dentition of *Tylosaurus* suggest that it preyed upon large fish and marine reptiles.

By the latter half of the Campanian the composition of the mosasaur faunas of North America had changed. The tylosaurines were evidently replaced by ecologically analogous large mosasaurines *(Mosasaurus, Liodon),* and smaller, advanced clidastoids *(Plotosaurus, Taniwhasaurus)* inhabited the Pacific basin. The genus *Platecarpus* had given rise to belemnite-eating *(Plioplatecarpus)* and possibly ammonite-eating forms (prognathodonts).

There are indications that these later Campanian reptiles represented a slightly higher adaptive level in the evolution of mosasaurs. There is an average increase in size over pre-late Campanian forms and suggestions of telescoping in some of the cranial elements (although not nearly approaching the condition seen in cetaceans). For example, tongues of the frontal spread over the anterodorsal portion of the parietal in *Mosasaurus, Plotosaurus, Prognathodon* and *Plesiotylosaurus,* and the surangular extended over the dorsolateral edge of the articular in *Mosasaurus* and *Plotosaurus.* A high degree of streptostyly is preserved in all mosasaurs, as is the splenio-angular articulation, but in most of the genera characteristic of the late Campanian-Maestrichtian *(Mosasaurus, Plotosaurus, Prognathodon, Plesiotylosaurus)* cranial kinesis was limited or lost, in contrast to earlier forms. Interestingly, there is no marked tendancy for the external nares to migrate posteriorly in these late forms. There is a widespread tendency to increase the number of pygal vertebrae *(M. conodon, Plotosaurus, Plioplatecarpus),* and in members of the Mosasaurinae the number of presacral vertebrae is also generally increased with time. The digits of *M. conodon* and *Plotosaurus* tend to be pressed together into a flipper rather than divaricate and supporting a web, as in earlier mosasaurs (see Camp, 1942, p. 17), and the individual phalangeal elements are shorter. The humerus is more massively proportioned and the scapula is relatively larger in *Mosasaurus, Plotosaurus, Plioplatecarpus* and *Plesiotylosaurus.*

The present state of our knowledge of the general natural history of the reptiles which form the subject of this review may be summarized as follows. Between 100 and 63 million years ago, during the concluding phases of the Age of Reptiles, a group of giant marine lizards lived in great abundance in the shallow tropical to subtropical seas then covering vast areas of the North American continent. Adult animals, depending on the particular species, ranged in length from six to over fifty feet. Their heads were conical and their bodies were elongate, attaining a maximum diameter in the chest region. The tail was a laterally compressed sculling organ. The dorsal portions of their bodies were probably dark with a reddish or silverish tint and the underparts were lighter. As in many kinds of vertebrates, the smaller species or fry living close to the shore may have been marked with brighter color patterns tending to obscure the outline of the body.

These reptiles were powerful swimmers, guiding their progression by vertical and rotational movements of the paddles and turning movements of the neck. They were generally voracious carnivores. The severe wounds occasionally inflicted on others of their kind bear witness to a dumb, extremely savage disposition. They roamed surficial waters relying on their keen sense of sight and hearing for locating their prey. Medium-sized fish formed the preponderant element in the diet of many of these reptiles, but various species were especially adapted for feeding on shallow water benthonic echinoderms or pelecypods, small squid-like cephalopods, shelled cephalopods, or larger aquatic vertebrates such as turtles and large fish. An additional articulation between the upper and lower jaws at the back of the head enabled them to dismember and swallow prey more effectively under water. Their breeding habits remain conjectural, although it is probable that the eggs were laid in subaerial nests of some kind.

These reptiles descended from small semi-aquatic lizards of a normal lacertiform appearance. Two ancestral stocks quickly radiated into a profusion of different lineages. Generally members of these lineages improved in aquatic adaptation and increased in size throughout the brief geologic duration of the group. The initial diversity and abundance of these reptiles were maintained until they suddenly vanished along with many other groups at the close of the Age of Reptiles. Their extinction was most likely due to a failure in food supply, as they had no obvious competitors, but how this was related to the contemporaneous causes of extinction of aquatic and terrestrial organisms is unknown.

APPENDIX A MEASUREMENTS

TABLE 1

MEASUREMENTS OF REPRESENTATIVE MOSASAUR SKULLS

The specimens within each species of mosasaur are arranged according to size from the smallest to the largest. The same is true of the species, so that *Clidastes sternbergi* possesses on the average the smallest known skull and *Tylosaurus proriger* the largest. All measurements are in millimeters, a small "a" preceding the number indicates that it is approximate. The distance between the first and sixth tooth in a dentition is measured from the anterior base of the first tooth to the posterior base of the sixth. The length of the dentary is measured from its anterior tip to the posterior apex of the alveolar margin of the bone.

A. Length of skull along midline. B. Length of premaxillary rostrum. C. Width of frontal between orbits. D. Length between first and sixth maxillary tooth. E. Height of quadrate. F. Length of lower jaw. G. Length of dentary. H. Length between first and sixth dentary tooth.

	A	*B*	*C*	*D*	*E*	*F*	*G*	*H*
Clidastes sternbergi								
Type (Wiman 1920)	313	—	32	—	38	356	—	—
USNM 3777	—	—	—	38	44	—	—	—
Clidastes liodontus								
USMN 11719	315	—	52	64	35	372	216	61
USNM 6546	337	—	51	70	39	—	222	66
YPM 1335	340	—	50	62	38	388	223	58
YPM 24914	—	—	60	69	—	—	239	65
YPM 1333	—	6	53	75	42	—	—	—
USNM 11647	—	—	60	72	43	—	255	59
Plotosaurus bennisoni								
Type (Camp 1942)	397	—	69	78	57	485	—	—
Clidastes propython								
YPM 1368	—	7	65	—	45	—	—	—
YPM 1318	—	—	—	—	58	—	338	84
YPM 1319	—	11	—	89	63	—	355	82
KU 1000	658	—	—	110	—	—	428	110
"Platecarpus" intermedius								
ANSP 9023	—	—	—	—	—	—	—	83
Platecarpus coryphaeus								
MCZ 1610	—	—	55	81	49	—	—	—
YPM 4004	—	—	99	129	80	—	—	113
YPM 3972	—	—	110	121	82	—	296	—
Platecarpus ictericus								
YPM 1256	—	—	81	105	77	—	246	104
YPM 1277	—	—	79	108	80	—	—	96
YPM 4003	—	—	—	121	88	—	282	112
YPM 3690	—	—	—	—	90	a560	301	129
AMNH 1820	431	—	97	126	92	—	—	—
AMNH 1821	—	—	—	—	—	559	292	124

	A	*B*	*C*	*D*	*E*	*F*	*G*	*H*
YPM 1258	—	—	a99	130	94	—	284	122
Globidens alabamaensis								
USNM 6527	—	—	135	120	—	—	—	—
Plotosaurus tuckeri								
(Camp 1942)	588	—	148	—	96	791	—	—
Ectenosaurus clidastoides								
FHM 7937	645	—	83	—	86	—	—	—
Plactecarpus cf. *P. somenensis*								
CNHM PR 466	—	—	107	138	—	—	—	132
CNHM PR 467	a680	—	150	191	137	—	452	194
CNHM PR 465	—	—	—	—	—	—	535	237
Prognathodon overtoni								
SDSM 3393	702	—	188	167	119	867	472	167
KU 950	—	—	a188	222	145	—	—	193
Prognathodon rapax								
NJGS 9827	—	—	—	—	135	—	—	—
Mosasaurus ivoensis								
KU 1024	—	—	—	173	—	—	a508	151
Tylosaurus nepaeolicus								
YPM 3979	—	10	—	85	—	—	236	83
FHM 1654	—	—	56	—	a40	—	242	—
YPM 3992	—	—	62	a99	46	—	247	a90
YPM 3974	—	23	—	139	—	—	391	149
YPM 4000	—	28	103	—	68	—	355	135
AMNH 124, 134	717	19	116	176	91	828	444	180
YPM 3980	—	—	142	181	110	—	—	—
YPM 3976	—	33	—	—	109	—	—	—
Mosasaurus missouriensis								
Type (Goldfuss 1845 and Harlan 1834c)	614	—	142	a126	98	667	—	—
KU 1034	832	23	187	182	133	1002	570	176
Plesiotylosaurus crassidens								
(Camp 1942)	880	—	156	—	100+	980	550	—
Mosasaurus maximus								
NJSM 11053	1091	—	262	298	167	1230	—	270
YPM 773	—	—	—	—	200	—	—	—
Tylosaurus proriger								
AMNH 1585	—	—	55	83	—	—	—	—
YPM 1268	—	—	a108	141	78	—	—	130
USNM 6086	a585	—	118	a142	79	650	373	163
AMNH 4909	600	29	113	146	78	686	402	143
YPM 3977	—	33	136	—	82	—	399	144
USNM 8898	a710	—	—	a223	—	a935	565	215
YPM 4002	—	36	—	234	—	—	—	220
FHM 4	1058	—	—	546	a145	1225	667	225
KU 1032	1195	—	—	—	—	—	—	—
YPM 3981	—	57	—	—	158	—	—	—

TABLE 2
BODILY PROPORTIONS OF MOSASAURS

	HEAD	NECK	TRUNK	TAIL	OVERALL LENGTH
Varanus (YPM Osteology 4568)	6.85%	8.65%	24.10%	60.50%	1.94m = 6 1/3 ft.
Clidastes sternbergi (Wiman, 1920, pl. 3)	13.2%	*43.2%		43.5%	2.65m = 8 3/4 ft.
Clidastes liodontus (Williston, 1898b, p. 143)	12.1%	6.5%	39.2%	42.2%	3.465m = 11 1/2 ft.
Platecarpus (Huene, 1911, p. 49)	9.8%	5.7%	31.0%	53.5%	5.60m = 18 1/3 ft.
Platecarpus (Lambe, 1914)	10.4%	*33.5%		56.1%	6.25m = 20 1/2 ft.
Tylosaurus (Williston, 1898b, p. 143)	13%	5.6%	31.5%	49.9%	6.341m = 20 3/4 ft.
Tylosaurus proriger (Osborn, 1899a, p. 170)	13.8%	6.9%	27.6%	51.6%	8.83m = 29 ft.

* includes combined length of neck and trunk

TABLE 3
ADDITIONAL ESTIMATED LENGTHS OF MOSASAURS

Clidastes (YPM 4818) juvenile	1.22m = 4 ft.
Mosasaurus conodon (Dollo, 1894, p. 248)	7m = 23 ft.
Mosasaurus conodon (Dollo, 1917, p. 19)	10m = 32.8 ft.
Mosasaurus hoffmanni (Dollo, 1917, p. 17)	15m = 49 ft.
Mosasaurus hoffmanni (YPM plastotype) given length of jaw equals 10% of body length	12.4m = 40.66 ft.
Mosasaurus maximus (NJSM 11053) given length of jaw equals 10% of body length	12.4m = 40.66 ft.
Plioplatecarpus houzeaui (Dollo, 1894, p. 250)	5m = 16.33 ft.
Plioplatecarpus houzeaui (Dollo, 1917, p. 19)	6m = 19.5 ft.
Prognathodon solvayi (Dollo, 1917, p. 20)	6m = 19.5 ft.
Prognathodon giganteus (Dollo, 1904a, p. 213)	10m = 32.8 ft.
Hainosaurus bernardi (Dollo, 1917, p. 19)	17m = 56 ft.

APPENDIX B
LOCALITIES OF PIERRE MOSASAURS

Because scattered collecting indicates that mosasaurs are probably abundant and diversified in the Pierre Shale, and the formation appears to contain distinctive mosasaur associations at different levels, a list of mosasaur species and their localities is appended to encourage future collecting.

I. Mosasaurs from the lower Pierre (Sharon Springs, Gregory and Crow Creek Members and equivalents):

Clidastes propython

AMNH 5812, from bluff near A. Finney's ranch, Cottonwood Creek, SSW of Edgemont, Fall River County, South Dakota. Collected by B. Brown, 1903.

KU 1026, (type of *C. westi)*, from near McAllister, Wallace County, Kansas.

Globidens alabamaensis

SDSM 4612, from 2 miles S of Buffalo Gap, Fall River County, South Dakota, low in Pierre. Collected by J. D. Bump.

Platecarpus ictericus

AMNH 2182, from N half section 7, T38N, R60W, Niobrara County, Wyoming, near base of Pierre. Collected by Bobb Schaeffer and Walter Sorenson.

AMNH 5811, from in and near pasture of Mr. J. Doo, N and middle Alkali Creek, tributaries of Indian Creek, 18 miles SSW of Edgemont, Fall River County, South Dakota. Collected by B. Brown.

USNM 18256, from Missouri River valley near Yankton, Yankton County, South Dakota, from the Sharon Springs Member. Collected by Simpson, 1948.

KU 1026 (mixed with the type of *Clidastes "westi")*, same locality as given for KU 1026 above.

KU 1081, from Wallace County, Kansas. Collected by G. P. Crazer.

KU 1093, from the Pierre, no locality data.

SDSM 30139, from 26 miles W of Edgemont and 1 mile N of Red Bird, Niobrara County, Wyoming. Collected by J. D. Bump and H. Martin.

Platecarpus cf. *P. somenensis*

CNHM nos. PR 465, 466, 467, from W side NW quarter, SW quarter section 29, T5N, R8E, Custer County, South Dakota, from Sharon Springs Member. Collected by John Clark.

Platecarpus, unidentified species

AMNH 1570, from 14 miles S of Wallace, Wallace County, Kansas (the specimen must have come from SE of Wallace as there is no Pierre exposed 14 miles due S of Wallace).

AC nos. 389, 398 (type and referred specimen of *Platecarpus brachycephalus)*, from the head of Mule Creek, 20 miles due W of Edgemont, Niobrara County, Wyoming.

SDSM 4910, from 2½ miles E of Provo, Fall River County, South Dakota. Collected by J. D. Bump and H. Martin.

CNHM nos. PR 215, PR 216, from 8 miles S of Fairburn, Custer County, South Dakota. Collected by G. Langford, 1946.

Tylosaurus proriger

AMNH 7220, from SW quarter, SE quarter section 36, T29S, R65W near Walsenberg, Colorado. One-third mile NW boundary between Huerfano and Las Animas Counties. From top of Niobrara very near Pierre contact. Collected by E. H. Colbert.

USNM 17909, from NE quarter, SE quarter section 36, T2S, R33E, Bighorn County, Montana, from Telegraph Creek Formation. Collected by C. H. Rogers, 1947.

KU 5033, from 2½ miles S of Wallace on Pinnell Ranch, Wallace County, Kansas. Collected by C. D. Bunker, 1911.

CNHM 820, from Pierre Formation, South Dakota. Matrix looks like Sharon Springs Member.

II. Mosasaurs from the middle Pierre (DeGrey and Verendrye Members and equivalents):

Mosasaurus conodon

USNM 18255, from E center section 28, T6N, R8OW, Hughes County, South

Dakota, from the DeGrey or Verendrye Member. Collected by D. R. Crandell, 1948.

SDSM 452, from NE quarter, NE quarter section 6, T127N, R64W, spillway of Elm Lake 10 miles W of Fredrick, Brown County, South Dakota, possibly from the Virgin Creek Member.

Plioplatecarpus primaevus

USNM 18254, from NE corner section 35, T112N, R80W, near Pierre, Hughes County, South Dakota, from the DeGrey Member. Collected by D. R. Crandell, 1948.

III. Mosasaurs from the upper Pierre (Virgin Creek, Mobridge and Elk Butte Members and equivalents):

Mosasaurus missouriensis

The type specimen was collected near the Big Bend of the Missouri River, between Fort Lookout and Fort Pierre.

USNM 8086, from NW quarter, NW quarter section 33, T19N, R21E, Feigns County, 35 miles N of Lewistown, Montana, from the Bearpaw Shale.

USNM 4910, from the Pierre Shale of South Dakota. Collected by J. B. Hatcher.

KU 1034 (type of *M. horridus*), from the Pierre Shale along the Cheyenne River, Custer County, South Dakota.

Prognathodon overtoni

KU 950, from Pierre Shale along the Cheyenne River, 100 feet above the level of KU 1034, Custer County, South Dakota.

SDSM 3393, from 6 miles SW Cuny Table, on Mule Creek, Shannon County, South Dakota, from the Virgin Creek Member.

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Italicized numbers refer to pages with text-figures. **Boldface** numbers refer to pages where a particular taxon is characterized. A list of all the figures of a species or genus may be found under the heading of the taxon in the Systematics section.

CHART 1

WESTERN GULF MOSASAURS

Correlation after Stephenson et. al. 1942; Young 1963; Jeletzky 1965 personal communication

Time scale after Kulp 1961

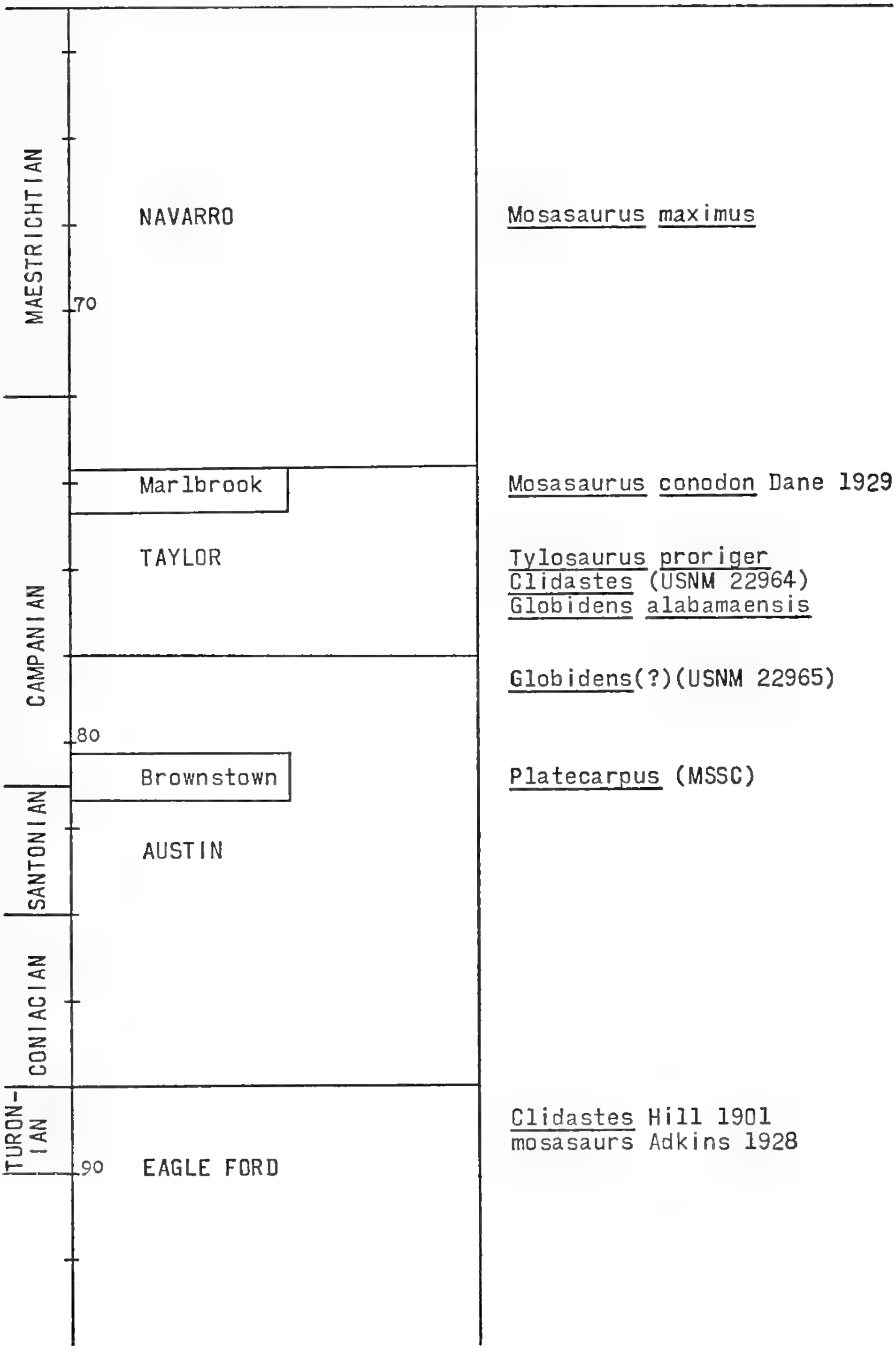


CHART 2

EASTERN GULF MOSASAURS

Correlation after Stephenson et. al. 1942; Young 1963; Jeletzky 1965 personal communication

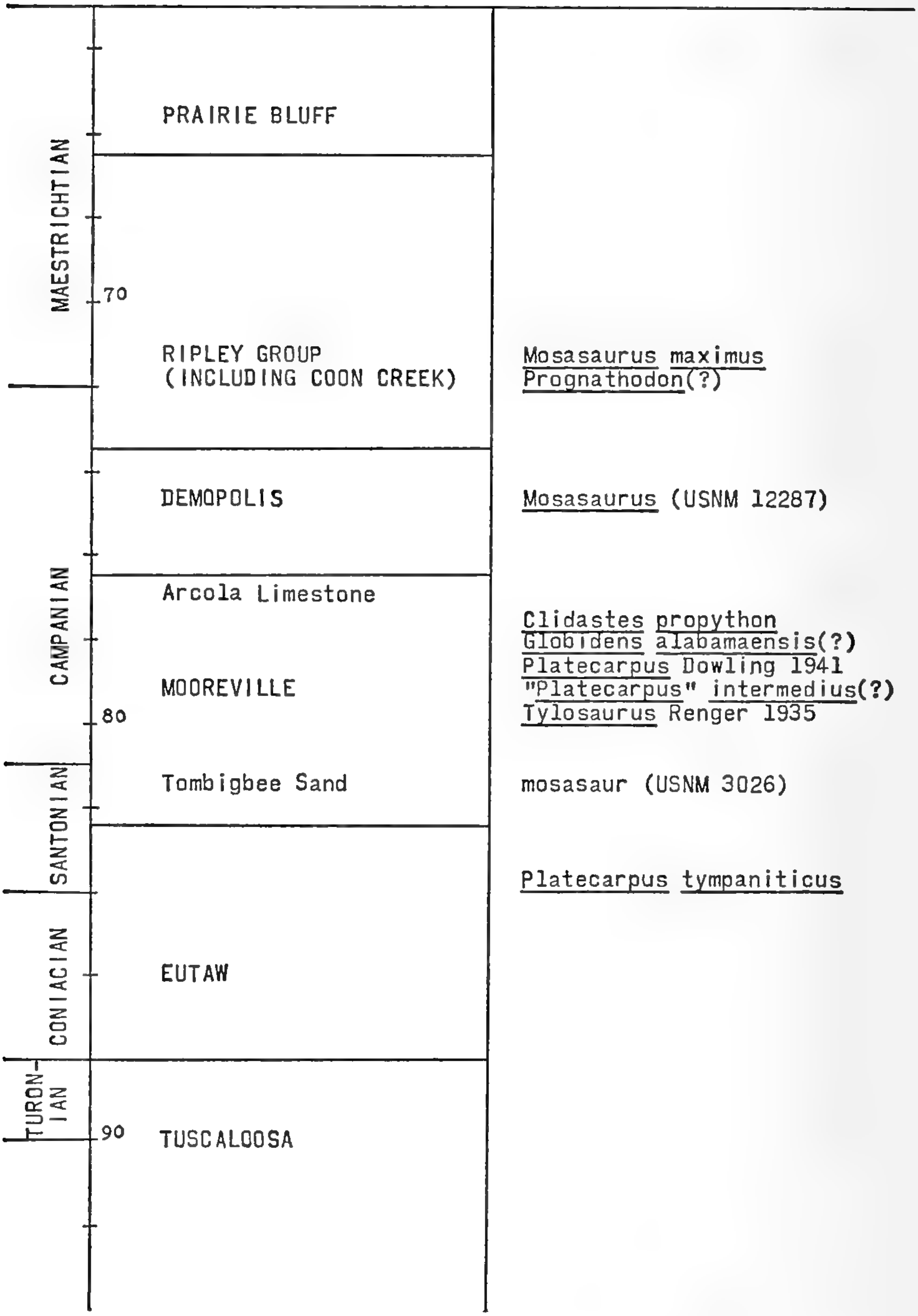


CHART 3

NEW JERSEY MOSASAURS

Correlation after Stephenson et. al. 1942; Olsson 1963; Jeletzky 1965 personal communication

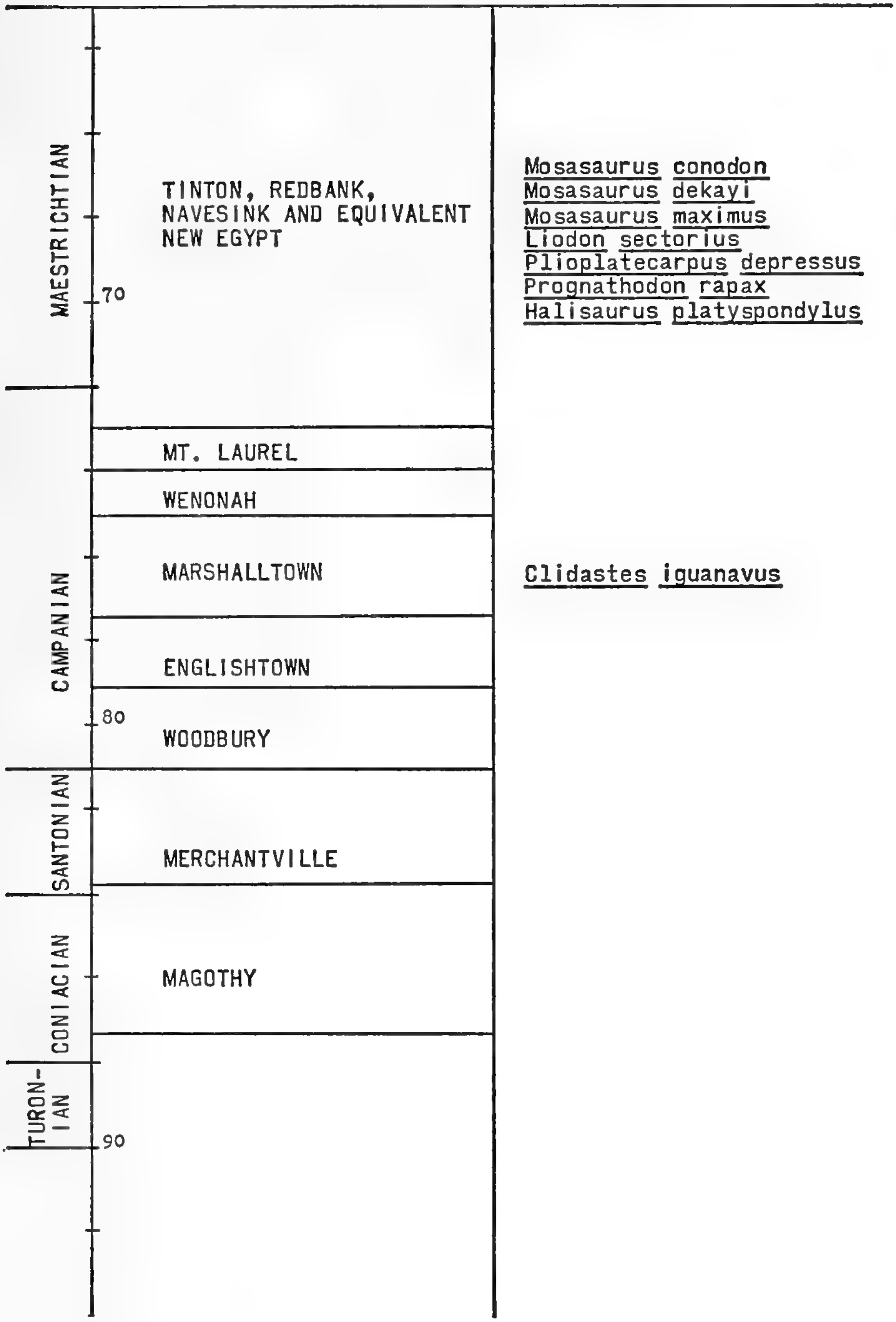


CHART 4

MOSASAURS OF THE INTERIOR

Correlation after Jeletzky 1955, 1962

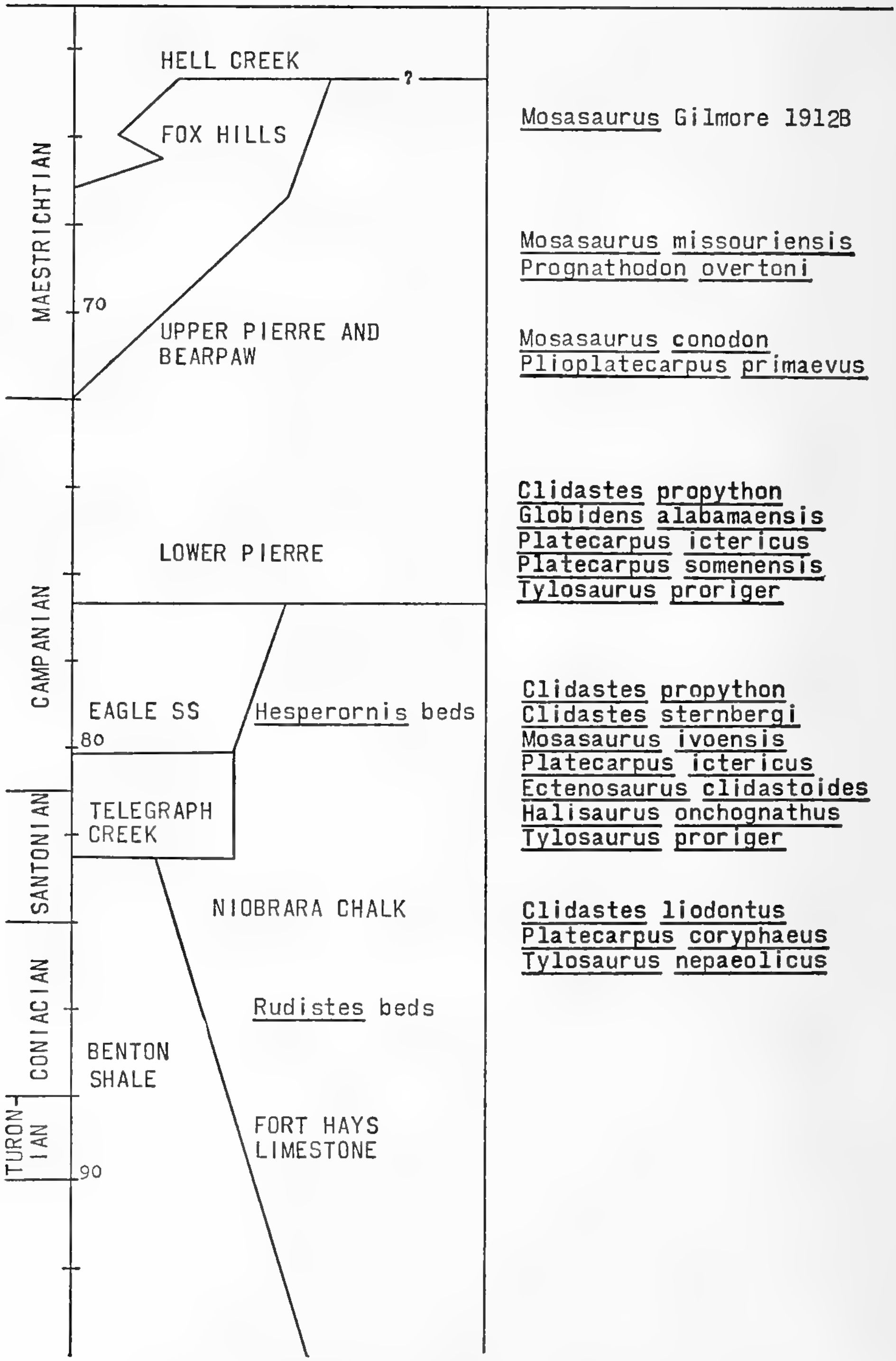


CHART 5

BELGIAN MOSASAURS

Correlation after Leriche 1929, 1934; Marie 1956; Schmid 1959; Hofker 1959. 1960A, 1960B; faunas after Dollo 1924

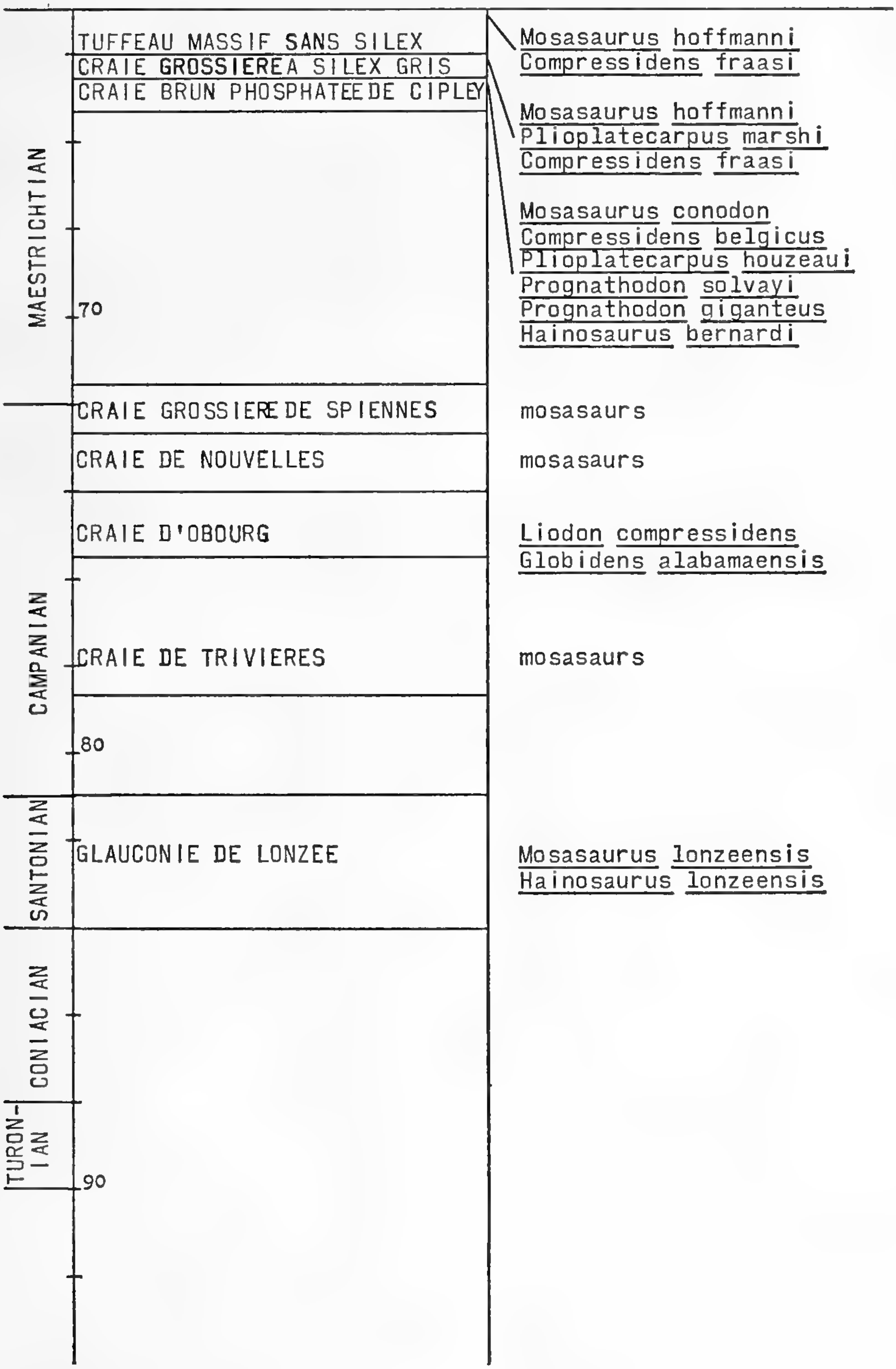


CHART 6

FRENCH MOSASAURS

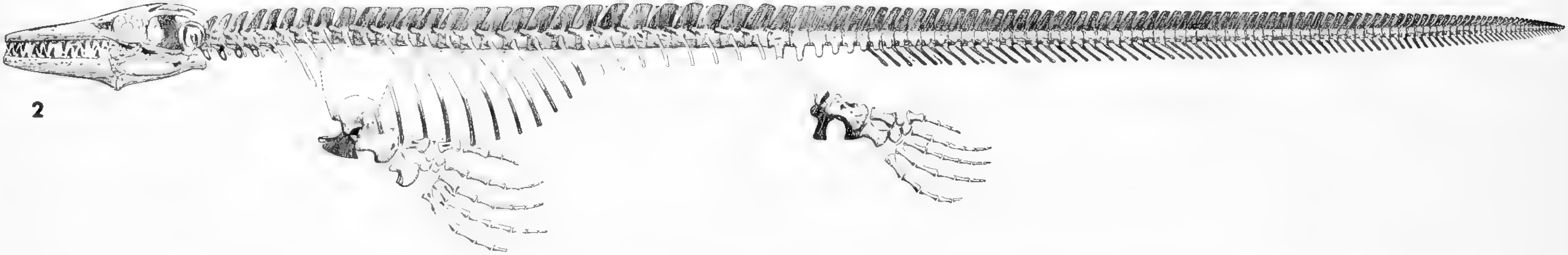
Correlation after author's name

MAESTRICHTIAN		Prov. of Charente Infer.	"*Liodon*" Zurcher & Arnaud
		Prov. of Basses-Pyrenees	*Liodon mosasauroides* Gaudry 1892
	70		
CAMPANIAN		CRAIE DE MEUDON Leriche 1934	*Liodon anceps* Gaudry 1892
		CRAIE PHOSPHATEE DE LA PICARDIE Leriche 1934	*Mosasaurus gaudryi* Thevenin 1896 *Platecarpus somenensis* Thevenin 1896
		CRAIE DE MICHERY Sornay 1957	*Liodon compressidens* Gaudry 1892
	80	Prov. of Aude	*Platecarpus ictericus* Corray 1927
SANTONIAN			
CONIACIAN			
TURONIAN	90		

CHART 7

		ENGLISH MOSASAURS Correlation after Cox 1962	SWEDISH MOSASAURS Faunas and correlation after Persson 1959, 1963
MAESTRICHTIAN	70		
CAMPANIAN		?*Liodon anceps* from the "chalk of Norfolk" fide Owen 1851	*Liodon anceps* *Plioplatecarpus*
		?*Platecarpus* from the "chalk of Sussex" fide Lydekker 1888	*Mosasaurus ivoensis* *Platecarpus somenensis*
	80		
SANTONIAN			
CONIACIAN			
TURONIAN	90		
		mosasaur Smith Woodward 1905	

1



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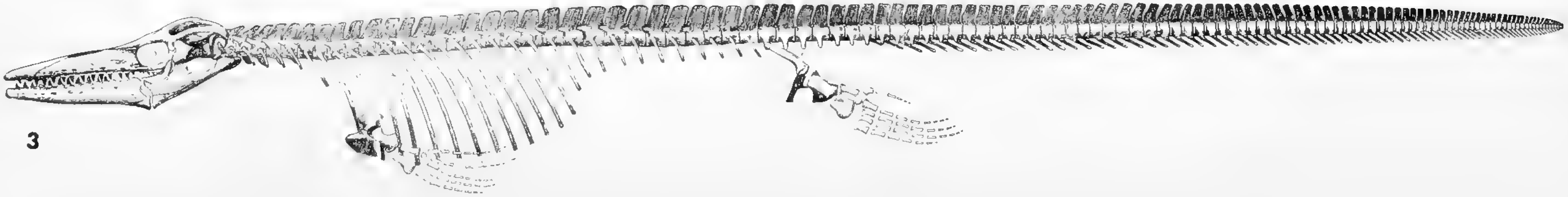


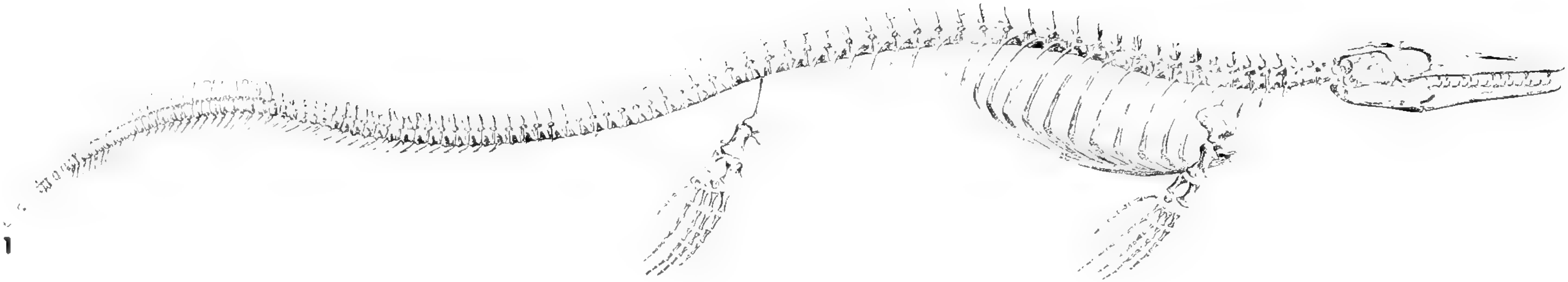
3

PLATE I

Figs. 1-3. Restorations of mosasaurs, after Williston (1898a, pl. 72). 1. *Clidastes liodontus*, × 1/16. 2. *Platecarpus ictericus*, × 1/19. 3. *Tylosaurus proriger*, × 1/32.

PLATE II

Figs. 1, 2. Restorations of mosasaurs. 1. *Tylosaurus proriger,* × 1/34, after Osborn (1899a, pl. 23). 2. *Plotosaurus,* × 1/47, after Camp (1942, pl. 5).



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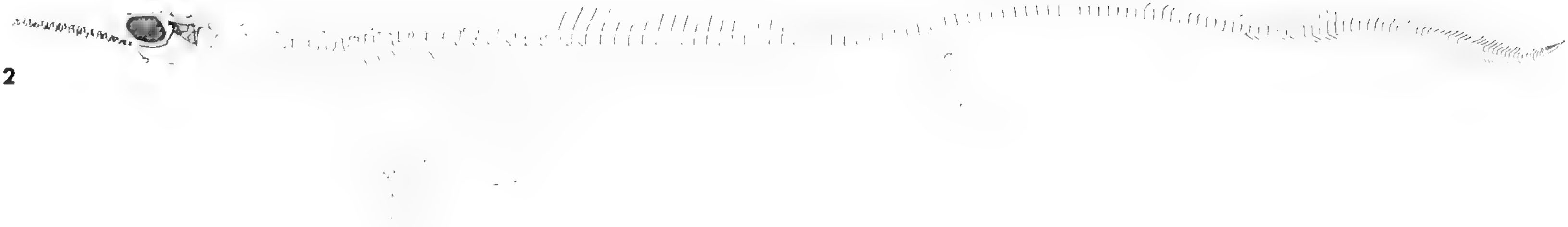

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