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## ON THE MORPHOLOGY OF THE SKULL IN THE MOSASAURIDÆ.

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A NEARLY complete specimen of *Platecarpus coryphæus*, Cope, found this summer by the writer in the cretaceous of Kansas, about fourteen miles southwest from Russell Springs, Logan County, makes it possible to clear up different doubtful points in the morphology of the Mosasauridæ. The specimen, now in the possession of the Paleontological Museum at Munich, Bavaria, will be fully described there. I shall restrict myself to the skull, studying some of its characters which have been in doubt from a morphological standpoint. It is impossible to discuss here the difficult synonymy of the Mosasauridæ. I leave it to one who has ample material to work himself through the labyrinth of names, and to find out which can be adopted. Only one word about this point. The specimen on which these researches are based agrees with *Platecarpus coryphæus*, Cope; and I hope that the final description will contain definite characters, at least of this genus.

### HISTORY OF OUR KNOWLEDGE OF THE MOSASAUROID SKULL.

I shall only discuss the principal papers. Every notice, however, of a morphological character, will be included.

*Cuvier*,<sup>1</sup> 1808–1836.

Cuvier considers the skull of the historical *Mosasaurus* from Maestricht, which is known to everybody, as intermediate in osteological characters between the monitors and iguanas. The figure published shows both the halves of the lower jaw, the left maxillary complete, the anterior portion of the right maxillary, and both the pterygoids. What is considered by Cuvier as the right pterygoid is really the left one, and *vice versa*. The four processes of the pterygoid are correctly identified with the corresponding processes seen in this element in Iguana and Monitor. The lower jaw is also compared with that of Monitor, and it is stated that “la composition de cette mâchoire annonce de plus grands rapports avec le monitor qu’avec aucun autre saurien.” Besides these bones others have been worked out afterwards from the matrix of the same piece. A cast which I have seen lately in the Museum at Cambridge, Massachusetts, exhibits a complete quadrate and jugal.

*Goldfuss*,<sup>2</sup> 1834.

In 1834 Goldfuss gave a very exact description, with splendid figures, of a skull of a *Mosasaurus* found in the vicinity of Big Bend, on the Upper Missouri, and presented by Maximilian Prince of Wied, then travelling in America, to the Academy of Bonn. This is by far the best account given of the morphology of the Mosasauroid skull; and if this important paper had been studied more carefully by subsequent writers, much confusion could have been spared.

The skull is in splendid condition. “Es fehlen ihm nur die Schnauzenspitze und die zochbogen (jugal), sowie das Schläfenbein (quadratojugale), und der Pauken- (quadratum), und Zitzenknochen (squamosum) der einen Seite.”

The following bones are described: the single premaxillary, which is co-ossified with the single nasals, forming one element; the maxillaries; the single frontal, showing traces of original

<sup>1</sup> Cuvier, Baron G., *Sur le grand animal fossile des carrières de Maestricht*, Paris, Ann. Mus. Hist. Nat., XII, 1808, pp. 145–176, pl., reprinted in different editions of the *Ossements fossiles*.

<sup>2</sup> Goldfuss, Dr. August, *Der Schädelbaues Mosasaurus, durch Beschreibung einer neuen Art dieser Gattung erläutert*, Aiad. Leon, Vol. XXI, Pl. vi–ix.

division in front; the prefrontals; lachrymals; the single parietal, with the descending processes; the postfrontals; a posterior portion of the jugal; the quadratojugals (Schlaefenbeine, ossa temporalia); the squamosals (Zitzenbeine, ossa mastoidea); the quadrate, the petrosal, basi occipital, exoccipital, supra-occipital, and the sclerotic plates. All these elements are in position. *Pl. VIII* gives a splendid figure of the lower side of the skull. The front portion is in natural position, but the pterygoids are crushed together. This view shows the long vomers, separated behind, the palates and pterygoids in connection. No ectopterygoids were preserved.

The description of the single elements is very good, and this paper alone gives a very much better idea of the skull of the Mosasauridæ than all the others taken together. I may only mention that even the presence of the jugal arch is stated: "Das vorhandene Stück des Iochbeins (2) gibt zu erkennen, dass der Iochbogen geschlossen und sehr schmal und schwach war, wie diess auch der abgebrochene Ioch fortsatz, des Oberkiefers nachweist."

In regard to the affinities of the Mosasaurus, Goldfuss says: "Die niedrige, langgestreckte Gestalt des Vorderkopfes, die schmalen langen Nasenlöcher, die Bildung des Unterkiefers und die Gegenwart der Gaumenzähne bestätigen zwar Cuvier's Ausspruch, dass dieser Thiergattung ihre systematische Stelle zwischen den Monitoren und den Leguanen anzuweisen sei. Verfolgen wir aber den Schädelbau bis zu den einzelnen Theilen, so werden wir überrascht, hier einen Mittelpunkt zu finden, in welchem nicht nur Eigenthümlichkeiten der genannten beiden, sondern sogar der meisten übrigen Saurier vereinigt sind, wobei jedoch mehrere derselben übrig bleiben, die ihm allein angehören und ihn vor allen anderen auszeichnen."

*Cope, 1869.*

In 1869 Professor Cope<sup>1</sup> established a special order Pythonomorpha to include the Mosasauroid reptiles, "which possesses

<sup>1</sup> Cope, E. D., *On the reptilian orders, Pythonomorpha and Streptosauria*, Boston, Nat. Hist. Soc. Proc. XII, 1869, pp. 250-266.

*Synopsis of the Extinct Batrachia and Reptilia of North America*, Trans. Am. Philos. Soc., Vol. XIV, Part I, 1870, pp. 175-182.

a combination of the characters of serpents with those of Lacertilia, and some others of Sauropterygia."

The characters relating to the skull are the following : —

*a.* "The opisthotic bone projects free from the cranium, and is the suspensorium of the os quadratum."

*b.* "There is no columella."

*c.* "There is no symphysis mandibuli."

*d.* "The parietal is decurved posteriorly, and extends to the sphenoid(?), forming the cranial wall in front of the prootic."

*e.* "The sub-articular and splenial elements of the mandible are connected by articular faces."

*f.* "The pterygoids are elongate and bear numerous teeth, and in one type are free except at the extremities."

*g.* "The brain case is not fully ossified anteriorly."

*h.* "The squamosal bone is present."

*i.* "The angular bone is distinct."

*k.* "The os quadratum is movably articulated to the opisthotic."

*l.* "The os quadratum embraces and encloses the meatus auditorius externus."

*m.* "The opisthotic is supported by a pedestal projecting from the cranial walls, composed of the prolonged prootic in front, and the exoccipital behind, which embraces the suspensorium for much of its length."

Of the above characters, *a-e*, it is said, are those of serpents ; *f-i* are lacertilian ; while *m* is expressed as peculiar and not found in any existing order of reptiles.

How far Professor Cope is correct will be seen from the description of the skull of Platecarpus.

#### *Marsh, 1869-1872.*

In a paper published in November, 1869, Professor Marsh<sup>1</sup> speaks about the suspensorium of the quadrate in *Mosasaurus princeps*, Marsh, "The suspensorium of the quadrate bone is clasped by the pro-otic above and the exoccipital below, and the squamosal forms the greater part of the glenoid cavity." The element called exoccipital is the paroccipital, Owen (opisthotic,

<sup>1</sup> Marsh, O. C., *Notice of Some New Mosasauroid Reptiles from the Green Sand of New Jersey*, Am. Journ. Sci., Vol. XLVIII, November, 1869.

Huxley), = paroccipital process of the exoccipital. The "squamosal" is really the quaratojugal.

In a later paper, published in June, 1871,<sup>1</sup> we find some notes about the quadrate bone. Professor Marsh commits the same error as Professor Cope, describing the inner side of the quadrate as the outer, and *vice versa*. The pterygoid bones are stated to be separated in *Edestosaurus dispar*, Marsh, except, perhaps, at their anterior inner margin. To this I have to state that they are separated completely, as in all Mosasauroids.

The premaxillary of *Edestosaurus velox* is said to be united with the maxillaries, anteriorly, at least, by suture. There are also short notes about the basioccipital in *Clidastes Wymani* and *Cl. pumilus*.

In April, 1872, Professor Marsh published a paper: *Discovery of the Dermal Scutes of Mosasauroid Reptiles*, Am. Journ. Sci., Vol. III, April, 1872.

*The so-called scutes are the bones of the sclerotic ring.* The Mosasauridæ have no ossified dermal scutes, but the scutes are very much like those of the Varanidæ, as I have seen in the original specimen, described by Professor Snow,<sup>2</sup> preserved in the Museum of the Kansas State University, at Lawrence, Kansas.

In June, 1872, Professor Marsh<sup>3</sup> published some notes about the skull.

1. *Position of the Quadrate Bone.*—The quadrate, which had been placed by Cope and Marsh on the wrong side, receives its correct position.

2. *Discovery of the Stapes.*—The stapes is described as a slender rod, nearly round, expanded proximally, and to some extent also at its distal extremity. "The proximal extremity was probably in the fenestra ovale, and its distal end in the meatal pit of the quadrate."

3. *Discovery of the Columella.*—A slender cylindrical bone is considered as the columella (epipterygoid). The bone is some-

<sup>1</sup> Marsh, O. C., *Notice of Some New Fossil Reptiles from the Cretaceous and Tertiary Formations*, Am. Journ. Sci., Vol. I, June, 1871.

<sup>2</sup> Snow, F. H., *On the Dermal Covering of a Mosasauroid Reptile (Liodon dyspe-lor)*, Trans. Kan. Acad. Sci., Vol. VI, 1878, pp. 54-58, Fig.

<sup>3</sup> Marsh, O. C., *On the Structure of the Skull and Limbs in Mosasauroid Reptiles*, Am. Journ. Sci., Vol. III, 1872.

what compressed throughout, slightly sigmoid, and has both ends moderately expanded.

4. *Quadrato-parietal Arch.*—Professor Marsh states that “evidence of the existence of this arch was first observed” by him in the autumn of 1870, but, as we have seen, it was known already to Goldfuss and Cope.

5. *Discovery of the Malar Arch.*—This discovery was also made by Goldfuss long ago; Marsh only found the *complete* jugal. It “is a stout bone, somewhat flattened, and bent at an obtuse angle. It unites by suture with an external process of the post-frontal. Its anterior extremity is united with the maxillary.” It has a pointed tubercle at the posterior external angle. This description agrees with the complete jugals before me.

6. *Pterotic Bone.*—This so-called pterotic bone is nothing but an epiphysis of the paroccipital. It is present in Varanus and other Lacertilia. *The pterygoids, the correct nature of which was established already by Cuvier, are now described as palatines.*

Cope,<sup>1</sup> 1875.

In 1875 Professor Cope published his extensive work on the Vertebrata of the Cretaceous formations of the West. The order Pythonomorpha is retained. The following cranial characters are given, which are said to distinguish the order:—

1. The quadrate bone is attached to the cranium by a ginglymoid articulation admitting of free movement.
2. The opisthotic bone projects free from the cranium as the suspensorium of the quadrate bone, and is supported and embraced by a pedestal projecting from the cranial walls, composed of the pro-otic in front and the exoccipital behind.
3. The stapes lies in a groove on the posterior side of this suspensorium, and is produced to the os quadratum.
4. There is no quadratojugal arch.
5. The parietal bone is decurved posteriorly, forming the cranial wall in front of the pro-otic.
6. The brain chamber is not ossified in front.
7. The squamosal bone is present, merely forming the posterior part of the zygomatic arch.

<sup>1</sup> Cope, E. D., *The Vertebrata of the Cretaceous Formations of the West*, U. St. Geol. Surv. Terr., Vol. II, Washington, 1875.

8. The mandible is composed of all the elements characteristic of reptiles: the articular and surangular distinct; the angular represented by its anterior portion only; and the coronoid present.

After this a full description of the skull is given.

The nasals are said to be co-ossified with the frontals. "The parietal is decurved, and forms a considerable part of the lateral wall of the cranium, though with but moderate antero-posterior extent. The lateral wall extends to the body of the sphenoid, where extensive sutural surface has received it. I can find no suture crossing it; and it is apparently all alisphenoid or all parietal. A part of the parietal is, however, undoubtedly decurved in front of the alisphenoid. The structure is quite as crocodilian as ophidian in this point."—"The anterior ala of the pro-otic overlaps the alisphenoid largely. Its posterior lamina may or may not meet the expansion of the exoccipital on the upper face of the suspensorium. Inferiorly, it is in contact with the outer and posterior face of the sphenoid."—"The *opisthotic* stands obliquely upward and forward, and furnishes a glenoid cavity for the articulation of the quadratum. It has a process, directed upward and forward, which occupies a concavity on the inner face of the squamosal, which has the same direction."—"The presphenoid appears to have been distinct. Its base was small; it is readily lost, and I have not seen it."—"The vomer is divided, and is composed of two slender, compressed bones in contact." The posterior wing of the true pterygoids is considered the pterygoid, the anterior toothed part the palatine. The lower jaw is fully described.

*Owen*,<sup>1</sup> 1877.

The foregoing paper of Professor Cope was strongly criticised by Professor Owen. Professor Cope<sup>2</sup> answered these criticisms in 1878, and it is best to consider the different opinions together.

Professor Owen shows very clearly that the so-called Ophidian characters of the Mosasauridæ do not exist in the skull; that

<sup>1</sup> Owen, Professor, *On the Rank and Affinities in the Reptilian Class of the Mosasauride*, Gervais. Quart. Journ. Geol. Soc., November, 1877, pp. 682-715.

<sup>2</sup> Cope, E. D., *Professor Owen on the Pythonomorpha*, Bull. U. St. Geol. and Geogr. Surv. Terr., Vol. IV, No. 1, Washington, 1878, pp. 299-311.

the whole posterior part is typically Lacertilian. He shows that the nasal region "most nearly resembles that of the *Varanus* and *Monitor* amongst existing Reptilia." But the true nature of the nasal bones is not recognized. The pterygoids, palatines, vomers, are correctly determined. At the end Professor Owen says: "The fossil evidences of the Mosasaurians hitherto made known do not yield a single character peculiar to and characteristic of the Ophidian order." According to Owen, the Mosasauridæ are aquatic Lacertilia, like the Pinnipedia, aquatic carnivora.

Professor Cope in his reply admits his mistake in the determination of the pterygoid and palate. He still considers the squamosal (mastoid Owen) as the paroccipital (opisthotic), and does not admit that this element is confluent with the exoccipital. The order Pythonomorpha is retained, with the following characters of the skull.

1. "The parietal bones are decurved on the sides of the cranium, and are continuous with the alisphenoid and pro-otic elements.

2. "The opisthotic is largely developed, and extends upward and forward to the walls of the brain case.

3. "A distinct element connects the squamosal with the parietal bone above the opisthotic."

We shall see later on how far these characters are correct.

*Marsh, 1880.*

Professor Marsh's<sup>1</sup> latest contribution to the subject was given in 1880.

A peculiar bone is described and figured as a Hyoid; some sclerotic plates are figured. The transverse bone is described: "It is an L-shaped bone, thin and somewhat twisted. One ramus unites by suture with the corresponding process of the pterygoid, and the other extends forward, nearly at a right angle, to join the posterior end of the maxillary." The true nature of the pterygoid, already known since Cuvier and Goldfuss, and again tested by Owen, is expressed again. "Cope has called these dentigerous bones 'palatines,'<sup>2</sup> and stated that they were

<sup>1</sup> Marsh, O. C., *New Characters of Mosasauroid Reptiles*, Am. Journ. Sci., Vol. XIX, January, 1880, pp. 83-87.

<sup>2</sup> The fact is, that Marsh was the one who made this mistake for the first time.



separated from the quadrates by intervening bones; but on both points he was in error." They are "attached posteriorly to the quadrates by ligament, to the basiptyergoid processes in the same way, to the maxillaries by the intervention of a distinct transverse bone, and to the true palatines by squamous suture." — "The true palatines are small edentulous bones, in front and outside the pterygoids. They separate the latter from the slender, distinct vomers." — "In none of the genera were the pterygoids united by suture on the median line, but were more or less widely separated.

"The new characters above presented are all Lacertilian, rather than Ophidian. The important characters of the Mosasauroids now known indicate that they form a sub-order of the Lacertilia, which should be called *Mosasauria*."

*Dollo, 1882-1890.*

Dollo has published quite a number of papers on the morphology of the Mosasauridæ.

In his first note, printed in 1882,<sup>1</sup> he describes a complete naso-premaxillary of the typical *Mosasaurus*; but he is inclined to consider this element as the premaxillary alone, — a view which is incorrect, since all Mosasauridæ have the nasals co-ossified with the premaxillaries. The true nature of the pterygoids in the type of *Mosasaurus* is recognized, and their complete distinctness from each other admitted.

*Mosasaurus Maximiliani* is made the type of a new genus, *Pterycollasaurus*, on the belief that the pterygoids in this form are united in the middle line. There is not the slightest doubt, however, that these elements are simply crushed together, and that they are really separated from each other as in all Mosasauridæ. The genus *Pterycollasaurus* is therefore not admitted. Another new genus, *Plioplatecarpus*, is established. The principal character of this genus consists in the presence of a "sacrum." In a later paper<sup>2</sup> this genus is elevated on this account to the rank of a special family, *Plioplatecarpidæ*. Other

<sup>1</sup> Dollo, L., *Note sur l'ostéologie des Mosasauridæ*, Bull. Mus. Roy. Hist. Nat. Belg., Vol. I, pp. 55-74, pls. iv-vi.

<sup>2</sup> Dollo, L., *Notes d'ostéologie herpétologique*, Ann. Soc. Scient. Bruxelles, 1885, p. 335.

characters of this family consist in the presence of an interclavice and of a median basioccipital canal and the hypobasilar canals. I do not think that this family can be admitted.

In his first paper on *Hainosaurus*,<sup>1</sup> we find some osteological notes on the Mosasauridæ.

It is shown that the peculiar oval pit on the inside of the quadrate is for the reception of the suprastapedial cartilage, and the name suprastapedial groove is introduced. It is stated that the nasals are co-ossified with the premaxillaries, "comme c'est le cas habituel chez les Mosasauriens." It seems, therefore, that Dollo changed his former view in regard to these elements in *Mosasaurus Maximiliani*. The peculiar arrangement seen in the basioccipital and basisphenoid of *Plioplatecarpus* and the clavicle of this genus are described. These conditions are more fully discussed and figured in his *Notes d'ostéologie erpétologique*. In a paper, *Sur le crâne des Mosasauriens*,<sup>2</sup> the relations of the suprastapedial groove are fully discussed and figured. Figures are also published of parts of the skulls of *Mosasaurus* and *Hainosaurus*. In a still later paper three new genera and a new species are shortly characterized and figured, but no new points of importance are brought out.<sup>3</sup>

In a paper just received, the quadrate of *Mosasaurus* and *Plioplatecarpus* is described and figured, and some ideas on the phylogeny of the Mosasauridæ are expressed.

#### *Description of the Elements of the Skull of Platecarpus*

*Coryphæus*, Cope.

Fortunately the skull was fully macerated before it was covered by the matrix. It was possible, therefore, to work out every bone separately and to compare it with the corresponding element of the Lacertilia. All the bones are preserved with the exception of the lachrymals and perhaps the ectopterygoids.<sup>4</sup>

<sup>1</sup> Dollo, L., *Première note sur le Hainosaure, Mosasaurien nouveau de la craie brune phosphatée de Mesvin-Ciply, près Mons*, Bull. Mus. Roy. Hist. Nat. Belg., Vol. IV, 1885, pp. 25-35.

<sup>2</sup> Bull. Scientif. de la France et de la Belgique, Paris, 1888.

<sup>3</sup> Dollo L., *Première note sur les Mosasauriens de Mesvin*, Bull. Soc. Belg. Geol., Vol. III, 1889, pp. 271-304, pls. ix, x.

<sup>4</sup> The specimen was found by me July 11, 1890, and personally exhumed with the greatest care in the course of two weeks. At first nothing but a caudal vertebra was

The skull as a whole is of the pattern of the Varanidæ, and there is no other group of reptiles to which it shows greater resemblance. Seen from above, we have the same form, the same foramina; the only difference is, that the orbit is completely closed behind by the jugal. Seen from the side, we have the same arrangement as in Varanus, but again the orbit is closed behind. The palatal aspect is also the same; but the pterygoids come nearer together, and the internal process of the pterygoids is more developed. The principal difference consists in the pterygoid, which bears teeth in the Mosasauridæ, but none in Varanus.

*The Basioccipital* (Fig. 11).

The basioccipital is a short element, suturally united in front to the basisphenoid. The occipital condyle projects very little behind, resembling Varanus in this way. It is principally formed by the basioccipital, the exoccipitals forming the outer portion. This element offers only a small base for the brain, the exoccipitals being approached. The canalis basioccipitalis medianus may be present or absent; the ventral portion is absent in one specimen, there being only a fossa basioccipitalis mediana. The basioccipital processes are well developed, and partially covered by the posterior processes of the parasphenoid. The basioccipital is connected with the basisphenoid, the exoccipital, and the posterior base of the petrosal.

*The Basisphenoid* (Fig. 11).

The basisphenoid is more complex. It is co-ossified with the parasphenoid, which forms the anterior slender process, and which covers the basioccipital processes. The pterygoid processes are short, but broad horizontally. On each side of the basisphenoid is a deep groove. These grooves unite in front into a large transverse foramen below the pituitary body. This foramen may pierce the basisphenoid in the region of the pituitary fossa; a vertical canal may also be present between the

seen, sticking out of a chalk bank. Gradually I developed nearly the complete animal. I take the opportunity here to thank Mr. David Bower, formerly of Russell Springs, Kansas, for much assistance he gave me during my stay at his house.

basioccipital and basisphenoid in connection with the transverse canal (can. hypo-basilaris, Dollo). These hypobasilar canals are also present in *Varanus*. The basisphenoid is well developed in front, and ending in a vertical plane, on the lower face of which the parasphenoid extends in front. The basisphenoid shows the following connections: basioccipital, petrosal, pterygoids.

*The Supraoccipital.*

This is a simple but large element. It is suturally united with the exoccipitals, paroccipitals, and petrosals. It contains on each side portions of the upper semicircular canals. It is not in direct connection with the parietal, but separated from it through cartilage or connective tissue. Above it fits into a groove at the posterior end of the parietals. In shape it is very much like the element in *Varanus*. It takes part in the formation of the foramen magnum.

*The Exo-paroccipital* (Figs. 20, 21).

As in all *Lacertilia*, the paroccipital is co-ossified with the exoccipital. The paroccipital processes are more developed, as in *Varanus*, resembling these elements in *Iguana*. The exo-paroccipital joins the following elements exactly as in *Varanus*: supraoccipital, petrosal (the petrosal forming with the squamosal the anterior portion of the paroccipital process), squamosal. The lower and distal part of the paroccipital process joins the quadrate.

*The Stapes.*

The stapes is a long and slender element, expanding gradually at both ends. Its position was doubtless as in *Varanus*.

*The Petrosal* (pro-otic).

The petrosal resembles the same element in *Varanus*. It shows the same emargination in front for the reception of the trigeminus; but the tendency is to form a regular foramen, a small process projecting from its upper portion to surround the nerve. The connections are the same as in *Varanus*: basisphenoid and anterior portion of basioccipital, supraoccipital,

paroccipital, squamosal. Above, it reaches the descending processes of the parietal.

*The Parietals* (Fig. 8).

The parietals are completely co-ossified. They are more constricted in the middle than in the *Varanidæ*, and the descending processes are not so broad, but extend farther down, to join the petrosal and epipterygoid. The long posterior processes join the squamosal. There is a peculiar upper portion of the parietal; it is triangular behind, and its conditions are better seen in the figure than they can be described. The front portion of the bone is intersected by the pineal foramen. The parietal has the following connections: below, supraoccipital and petrosal; behind, squamosal and quadratojugal (very little); laterally, postfrontal; in front, frontal. The sutures between the two latter elements are very deeply cut, and the elements very strong in this region. The parietals never reach the basisphenoid, *and there is no ossified alisphenoid*, as stated by Professor Cope.

*The Frontals* (Figs. 6, 7).

These bones resemble very much the elements in *Varanus*. They are co-ossified, but a division is visible in front, extending between the long anterior processes. The frontals form a shield-like element, ending in two long separate processes in front; there is an incision behind for the pineal foramen, which in this genus is placed between frontals and parietals. On the sides, they are bent out to meet the prefrontals. Besides the two long median processes in front, there are two other ones, one on each side, which, exactly as in *Varanus*, form the posterior end of the nasal openings. A sharp ridge runs in the middle line of the frontal above, but disappears behind. The olfactory lobe is placed in a deep groove on the lower side of the frontal; this groove is well developed in the middle, but vanishes in front. The shape of the frontal is easily seen in the figures. The frontals have the following connections: behind, parietals; laterally, postfrontal, prefrontal; anteriorly, nasopremaxillaries. The nasopremaxillaries overlap the long anterior processes of the frontals, and extend a little more behind than the nasal openings.

*The Postfronto-orbital* (Fig. 5).

In the specimen before me the postfrontal is suturally united with the postorbital; this suture, however, is obliterated at the ventral side of the bones. The larger portion of the postfrontal articulates with the frontal; the smaller posterior portion with the parietal; behind it is united to the postorbital only. The postorbital is an L-shaped bone; the long posterior branch joins the quadratojugal in its whole length; the short lateral branch is connected with the jugal; both articular faces come together below. The quadratojugal joins, therefore, the jugal at this point. In *Varanus* these two elements are co-ossified, but have the same general position, but the bulk of the sutural part is formed by the parietal; this is probably produced by the reduction of the posterior part of the jugal; in *Varanus* the quadratojugal is very much smaller, never reaching the jugal, which is incomplete behind.

*The Squamosal* (Figs. 20, 21).

This is a relatively small element. It is that bone which has been called opisthotic by Professor Cope; but, of course, it has nothing to do with this element, which is co-ossified with the exoccipital; it is the mastoid of Cuvier, the supratemporal of Parker; the homologue to the squamosal of the *Crocodylia*, *Tes-tudinata*, *Rhynchocephalia*. We can distinguish three portions: first, an upper one, which joins the parietal processes; second, an inner one, which is suturally united to the paroccipital and petrosal, and a lower one, which supports the quadrate. It is connected besides with the quadratojugal, which covers loosely its middle and outer portion. Both the squamosal and quadratojugal support the quadrate. The suture, which unites it with the paroccipital and petrosal, is very strong, and therefore this element generally remains in connection with these bones.

*The Quadratojugal* (squamosal) (Fig. 3).

This element is of an ancre-like form; the long anterior process receives the postorbital in a very deep sutural groove; in front, it touches the jugal. The broad posterior portion covers the squamosal. It contains an articular groove, which extends

to the squamosal, for the reception of the upper head of the quadrate. There is a small process directed towards the parietal processes, to which it is joined.

*The Prefrontal* (Fig. 4).

The prefrontal is a large bone, in which three portions can be distinguished: first, an inner one, which is attached to the frontal as far as the process extends, which forms the posterior end of the nasal openings. From this point it extends far in front, and is overlapped by the posterior process of the maxillary, which it receives in a deep groove. The outer anterior part is covered by the maxillary, and the lower portion joins the palate. In all these connections it agrees with the Varanidæ.

*The Lachrymal.*

This small element was not preserved, but it is figured by Goldfuss.

*The Superciliare* (Fig. 1).

Two bones which I at first considered the ectopterygoids seem to represent the superciliaria. In form they agree with these elements in Varanus. On the prefrontal, where these bones ought to be connected, there is a distinct roughening.

*The Jugal* (Fig. 2).

The jugal is a slender bone, very thin in front, where it joins the upper and outer portion of the lower maxillary process. Posteriorly it is joined to the postorbital; at this place it is robust and strong, and sends a small process behind, below the junction with the postorbital. Besides the maxillary and postorbital it joined the ectopterygoid and probably the lachrymal.

*The Naso-premaxillary* (Figs. 12, 13, 14).

The nasals and premaxillaries are completely co-ossified into a single element without trace of suture. This element is only comparable to the corresponding bones in Varanus. The shape is better seen from the figures than it can be described. There is a strong median keel below, extending through the whole length and fitting between the anterior processes of the fron-

tals. The nasals are represented by the expanded thin portion which overlaps these processes. The whole arrangement is like that in *Varanus*. The premaxillary contains four strong teeth. From the lower anterior end two processes extend behind to join the inner anterior part of the maxillaries and the vomers. The anterior upper part of the premaxillary contains six vascular foramina. The following connections exist: maxillaries, frontals, vomers.

*The Turbinals.*

I did not find any trace of these bones, but they were doubtless present in the animal.

*The Maxillaries* (Figs. 15, 16).

The maxillaries are strong bones, the general shape of which is best seen in the figures. Posteriorly they show two processes: an upper, slender one (*a*), which fits in the deep groove of the prefrontal; a lower, broader one (*b*), ending in a sharp process, which joins the prefrontal (lachrymal), jugal, and ectopterygoid. In front the maxillary is connected loosely to the premaxillary. The inner face of the bone shows distinct faces for the vomers and the palatines, very much as in *Varanus*. There are twelve teeth in each maxillary. There are ten dental foramina corresponding to the nine or ten front teeth; a number of smaller foramina are found above these, in the region of the nasal opening. The maxillaries are connected with the following elements: naso-premaxillary, prefrontal (lachrymal), jugal, ectopterygoid, palatine, vomer (turbinal).

*The Pterygoid* (Fig. 17).

The pterygoid is a very large bone, resembling in general the same element in *Varanus*. The shape is seen in the figure. The principal portion of the bone is that which contains the teeth (12, 13). It extends from the posterior part of the palate behind the basiptyergoid processes of the basisphenoid, forming a very distinct process. The posterior branch joins the quadrate. It is strong. The distal end shows a very marked, rough face on the outer side, for the ligaments to attach it to the quadrate. The outer branch joins the ectopterygoid. The



anterior branch is a thin plate of bone attached to the lower posterior and inner end of the palate. The pterygoids are completely separated from each other, but are very near together, where they join the basipterygoid processes. The upper face contains in this region a very distinct fossa for the epipterygoid (columella).

*The Epipterygoid.*

This element does not differ from the simple bone in *Varanus*.

*The Palatines* (Fig. 10).

The shape of the palate is best seen in the figure. Its outer end, which is strongest, is connected with the posterior branch of the maxillary, its posterior and inner end to the pterygoid, its posterior upper process to the prefrontal. The long anterior slender process is overlapped by the vomer. The outer wing of the palatine is not perforated by a foramen. The palatines are completely separated from each other.

*The Vomer* (Fig. 9).

The shape of the vomer is given in the figure. The vomers are long slender bones, touching each other in front. They are connected with the premaxillary, maxillary, and palate. They are pierced by a foramen, as in *Varanus*.

*The Ectopterygoids.*

When I wrote my preliminary note (*Science*, Nov. 2, 1890), I considered the elements which I now hold to be the superciliaria as the epipterygoids, their shape agreeing exactly with the description of the "transverse bone" by Marsh, *l. c.*, "It is an L-shaped bone, thin and somewhat twisted." I have now the opinion that the element which I had considered at this time as the interclavicle may be the true ectopterygoid.

*The Quadrates* (Figs. 18, 19).

I have nothing new to add to the descriptions of this element by Dollo. The shape of the bone can be seen in the figures 18 and 19.

*Some Remarks on the Relations of the Mosasauridæ.*

It is evident from the description of the elements of the skull of *Platecarpus* given above, that the Mosasauridæ must be considered as a family of the Lacertilia, without any relations with the Ophidia. The question now is, what rank do the Mosasauridæ have among the Lacertilia? By nearly all authors, the Mosasauroids are considered a sub-order of the Squamata, like the Dolichosauria, Chamæleontia, Ophidia, for instance; but it seems to me that this is not correct. There cannot be any doubt that the Mosasauroids are nearest to the Varanidæ, — nearer than to any other group of Lacertilia. The whole skeleton is Varanoid; and I feel quite confident that Varanidæ and Mosasauridæ developed from a common ancestor, which was already a typical Lacertilian.<sup>1</sup> This ancestral group must have existed during the upper Jurassic or the lower Cretaceous time. The Mosasauroids became true marine animals. The Varanoid limbs were transformed into fin-like limbs similar to those of the sea-tortoises, but still more adapted to the water. At the same time they reached great size, like all higher vertebrates which are transformed from terrestrial to sea-animals.

In *Science* of Nov. 7, 1890, I have expressed the opinion that the Mosasauridæ are very closely related to the Varanidæ. I said: "They simply represent highly specialized aquatic forms. The Helodermatidæ belong to the same group, but the Mosasauridæ are very much nearer to the Varanidæ. For this group I retain the old name Platynota, and divide it into two superfamilies,—(a) *Varanoidea*, 1. *Varanidæ*, 2. *Mosasauridæ*; (b) *Helodermatoidea*, 1. *Helodermatidæ*." Since this was written a paper has appeared by Mr. Boulenger<sup>2</sup> in the Proceedings of the

<sup>1</sup> I may state here that the restoration of the shoulder-girdle given by Professor Marsh, and copied since that time in different handbooks, is not correct. The coracoids did not meet in the middle line as in the Plesiosauria, but were exactly as in the Lacertilia. There were very large cartilaginous portions of the coracoids which overlapped each other, and with these portions the sternum was connected. The sternum was not ossified, but simply calcified, as in the Varanidæ and other Lacertilians. The scapula shows the original simple form which is also seen in the allied Helodermatidæ.

<sup>2</sup> Boulenger, G. A., *Notes on the Osteology of Heloderma horridum and H. suspectum, with Remarks on the Systematic Position of the Helodermatidæ and on the Vertebrae of the Lacertilia*, Proc. Zool. Soc. Lond., 1891, pp. 109–118.

Zoölogical Society of London, in which the view expressed by me is discussed.

Mr. Boulenger considers the Mosasaurs a sub-order of the Squamata, and can see no reason for not regarding the Cretaceous Dolichosauria as the progenitors of the Mosasaurs and at the same time of "the true Lacertilia, of which the Pleistocene and recent *Varanidæ* are a family."

In regard to my opinion that the Mosasaurs represent highly specialized aquatic forms, he asks: "Does this mean that limbs so strongly specialized as those of the Monitors can have been modified into the paddles of the Mosasaurs? A glance at the figures suffices to refute such a theory."

The three sub-orders, Dolichosauria, Pythonomorpha, Lacertilia, are thus characterized:—

"I. *Dolichosauria*, 15–17 cervical vertebræ. Extremities archaic, *i.e.* approaching the Batrachian type.

"II. *Pythonomorpha*, 9 or 10 cervical vertebræ. Extremities paddle-shaped, with hyperphalangy.

"III. *Lacertilia*, 8 or 9 cervical vertebræ. Fibula reduced proximally; fifth metatarsal reduced in length and strongly modified."

We may now first proceed to examine the Dolichosauria. It has to be stated first that Boulenger believes that Kornhuber's<sup>1</sup> *Hydrosaurus lesinensis* belongs to the Dolichosauridæ and possibly to the genus *Dolichosaurus* proper. I do not think it is possible to determine at present whether *Hydrosaurus lesinensis* belongs to the Dolichosauridæ or not; one thing, however, seems certain, that the number of cervicals was not 15–17, but considerably less. But this is of little interest in this question. It only needs to be examined whether these animals represent generalized forms or not. Mr. Boulenger speaks about the archaic extremities approaching the Batrachian type, and gives a copy of Kornhuber's figure of the hind limb, showing 2 3 4 4 3 phalanges.

According to Kornhuber there are four tarsal bones, which he homologizes very properly with the four elements in *Varanus*. In regard to the fifth metatarsal and the phalanges, he says: "Der Metatarsalknochen der fünften Zehe (mt. 5) zeigt deutlich seine obere Fläche, ist entsprechend dem Verhältnisse bei re-

<sup>1</sup> Kornhuber, Dr. A., *Ueber einen neuen fossilen Saurier aus Lesina*, Abhandl. k. k. geol. Reichsanstalt Bd., V, Heft. 4, Wien, 1873.

centen Formen kurz, an seinem proximalen Ende verbreitert und mit der Gelenhfläche allda gegen den grösseren Knochen der zweiten Tarsalreihe, das Cuboid, gerichtet, mit welchem er articulirt.

“Die Phalangenknochen (ph) zeigen die den heutigen Echsen zukommende Zahl, nämlich 2 für die grosse Zehe, drei für die zweite, vier für die dritte, fünf für die vierte und vier für die fünfte Zehe. Auch in ihrer Form entsprechen sie jenen der recenten Verwandten. Die Krallenglieder, nur an der grossen und an der zweiten Zehe noch deutlich, an den übrigen meist nur als Abdruck sichtbar, sind ziemlich gross, unten concav (was am zweiten seitlich liegenden erkennbar ist) und nach vorne etwas zugespitzt.”

*There cannot be any doubt whatever that the hind foot of “Hydrosaurus lesinensis” is typically Lacertilian, has no trace of any archaic structure, not approaching in any way whatsoever the Batrachian type.*

There is no evidence to consider the Dolichosaurs as a more generalized group of the Squamata. The supposition that the ancestral groups of the Squamata had a larger number of cervicals than the more recent ones is not supported by any facts. On the contrary, there is much evidence that all the forms with longer necks have developed from forms with shorter necks, in which the “original” number has been not more than eight. It is only surpassed among living forms by the Varanidæ, in which we have nine cervicals. All forms which show a greater or smaller number of cervicals have with very little doubt developed from forms with eight cervicals.

According to Boulenger the ancestors of the Lacertilia had many cervicals. This number became gradually reduced, until the Rhiptoglossan number five was reached. This is at least an improbability; for we would have to imagine that the Rhynchocephalian ancestors of the Squamata had a great number of cervicals, which doubtless was derived from a smaller number. In other words, we would have at first increase in number, then gradual decrease again; but there is no evidence for such a supposition.

It seems to me very much more probable and more natural to assume the following course of development:—

*The Rhynchocephalian ancestors of the Squamata possessed eight cervicals. All the generalized Squamata originally showed*

*this number. In some forms there was an increase of this number (Dolichosauridæ, Varanidæ, Mosasauridæ), in others a decrease (Chamæleontidæ).*

That the Dolichosauridæ are not ancestral to any of the larger groups of the Squamata is absolutely evident. From all that we know, it seems to me that the Dolichosauridæ are related to the Anguidæ or Varanidæ ; but so far it is impossible to determine the exact position of the family.

After having given reasons why the classification of Mr. Boulenger cannot be accepted, I have to return to the Mosasauridæ. Since Mr. Boulenger's diagrams of the evolution of the limbs of the Squamata are of no use, we have to examine the question whether we can imagine "that limbs so strongly specialized as those of the Monitors can have been modified into the paddles of the Mosasaurs."

I do not see any difficulty here whatever. In the first place, I do not believe that the limbs of the Monitors are more specialized than those of other Squamata, or even the Rhynchocephalia (at least in regard to the phalanges) ; and I have no hesitation to assume that unguiculated limbs can be transformed into paddles with numerous phalanges. If we examine, for instance, the Testudinata, we find many instances that the end-phalanges have been modified, that the nails have disappeared (Pinnata, Trionychia, Carettochelyidæ), and that in some (Trionychia) even the number of phalanges has been increased. That all these more or less paddle-shaped forms of limbs have developed from true unguiculate limbs, there is no doubt. In the Sirenia we find an increase of phalanges and the absence of ungues ; but nobody doubts to-day that the Sirenia developed from unguiculate land-mammals. The same is true for the Cetacea. Therefore I do not see any difficulty in assuming that the Mosasaurs developed from unguiculate Lacertilia, which were very close to the Varanidæ. To express this affinity, I placed the Varanidæ and Mosasauridæ in a superfamily, the Varanoidea. By this I wanted to say that the Mosasauridæ cannot be separated from the true Lacertilia, to which the Varanoidea belong ; in other words, that they cannot be placed as a sub-order of the *Squamata*, but have to be placed among the sub-order *Lacertilia*. In this opinion I have nothing to change.

WORCESTER, MASS., December, 1891.

## EXPLANATION OF PLATES I AND II.

(Figures two-thirds natural size.)

- FIG. 1. Probably the superciliare.
- FIG. 2. Left jugal from side: *m.* connection with maxillary.  
*po.* connection with postorbital.
- FIG. 3. Left quadratojugal: *q.* face for quadrate.  
*p.* face for paroccipital.  
*po. o.* face for postorbital.
- FIG. 4. Left prefrontal: *pal.* face for palatine.  
*f.* face for frontal.  
*m.* face for maxillary.
- FIG. 5. Left postfronto-orbital: *pof.* postfrontal.  
*po.* postorbital.  
*j.* face for jugal.  
*qj.* face for quadratojugal.
- FIGS. 6, 7. Frontal bone: *n.* face for nasal.  
*prf.* face for prefrontal.  
*pof.* face for postfrontal.
- FIG. 8. Parietal bone: *pfo.* pineal foramen.  
*pof.* face for postfrontal.  
*d.* descending process of parietal.  
*a.* posterior process of parietal.
- FIG. 9. Vomer.
- FIG. 10. Left palate from above: *m.* face for maxillary.  
*pl.* face for pterygoid.  
*v.* face for vomer.
- FIG. 11. Basioccipital, *bo.*, and basisphenoid, *bs.*: *bopr.* basioccipital process.  
*ptpr.* basispterygoid process.
- FIGS. 12, 13, 14. Naso-premaxillary: *no.* nasal portions.  
*prm.* premaxillary portion.  
*fr.* face for frontal.
- FIGS. 15, 16. Left maxillary: *a.* face for prefrontal.  
*b.* face for jugal.  
*pal.* face for palate.  
*v.* face for vomer.
- FIG. 17. Left pterygoid from below: *pal.* face for palate.  
*ect. pt.* face for ectopterygoid.  
*pt. pr.* face for pterygoid process of basisphenoid, a posterior process of pterygoid.
- FIGS. 18, 19. Right quadrate: inner and outer view.
- FIG. 20. Portion of right exo-paroccipital, with squamosal in position, from behind: *po.* paroccipital; *sq.* squamosal; *a.* process of squamosal for connection with parietal process.
- FIG. 21. The same from front: *pet.* petrosal.



