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INTRACRANIAL MOBILITY IN MOSASAURS

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INTRODUCTION

Mosasaurs are an extinct family of large marine lizards which have been found abundantly in, and are apparently restricted to, sediments deposited in shallow epicontinental seaways during late Cretaceous time. Among the diverse living groups included in the Lacertilia, mosasaurs resemble the varanids or monitor lizards most closely, a fact that has been generally recognized since the beginning of the nineteenth century. In the course of their adaptation to an aquatic existence, however, the heads and bodies of mosasaurs became more streamlined and their limbs were modified into paddles. As in most lacertilians, the mosasaur cranium was constructed of several rigid associations of bones which were separated by regions of flexibility making it possible for them to be moved with respect to one another. The present discussion is concerned with how these associations may have functioned in life.

Although the nature of intracranial movement in mosasaurs appears to have been simple, its explanation is burdened by the use of a complex anatomical terminology. So far as can be determined the muscles of the mosasaur head (see figs. 2-4) were arranged essentially as in *Varanus*. The works of Lakjer (1926)

and Frazzetta (1962) are recommended for descriptions and figures of the cranial musculature of this genus.

The term *Kinesis* is applied 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 axis of rotation in a kinetic skull (*metakinetic axis*) is located in the extreme posterior region of the head and is fixed on either side by the contact of the paroccipital processes or bones sutured thereto (occipital segment) with the overlying dermal roof bones of the maxillary segment. As the maxillary segment rotates on the paroccipital processes, displacement occurs at the sliding contact (*metakinetic joint*) between the parietal (maxillary segment) and the supraoccipital (occipital segment) above, and on the sliding *basal articulation* formed by the contact of the basiptyergoid processes of the basisphenoid (occipital segment) with the pterygoids (maxillary segment) on each side of the ventral midline of the skull. Further, the maxillary segment may be divided into subordinate units by secondary, transversely oriented axes of rotation. Two such axes are the *mesokinetic axis*, situated between the frontals and parietals on the dorsal surface of the skull, and the *hypokinetic axis* (new term), situated in the region of the overlapping pterygo-palatine contacts on its ventral surface.

The term *streptostyly* is here used to describe the particular condition in which the quadrate has lost its contact anteriorly with the lower temporal arcade, and is only loosely bound medially to the pterygoid and dorsally to the quadratic suspensorium of the braincase. The quadrate is then firmly sutured to neither the maxillary nor occipital segment, and activation of any muscle attaching to it may alter its position relative to both of these segments. Thus the cranium of a given reptile may be kinetic without being streptostylic (*Sphenodon*, see Ostrom 1962), streptostylic without being kinetic (some advanced mosasaurs, see below), or both kinetic and streptostylic (many lacertilians, see Frazzetta 1962).

I am very grateful to Charles M. Bogert of the American Museum of Natural History for generously providing me with a head of *Varanus niloticus* for dissection. I have profited greatly from many instructive conversations with Georg Zappler, my

former classmate at Columbia University, and Herbert Barghusen of Smith College. The manuscript has been vastly improved by the detailed constructive criticism of John H. Ostrom and James A. Hopson of the Peabody Museum of Yale University, to whom I extend my sincerest thanks.

CRANIAL KINESIS IN *Varanus*

Frazzetta (1962) has recently published an excellent analysis of intracranial mobility in *Varanus*, the modern monitor lizard. A condensation of his work is given here to facilitate understanding of the somewhat more complicated situation postulated for generalized mosasaurs.

The skull of *Varanus* is separated by Frazzetta into the two above-mentioned structural segments. The occipital segment is composed of the prootics, opisthotics, supraoccipital, parasphenoid, basisphenoid and basioccipital, which are all firmly sutured together into an inflexible block. The maxillary segment nearly surrounds the occipital segment and meets it at three points, the metakinetic joint above, the metakinetic axis posteriorly and the basal articulation below. Except for the stapes, which is functionally unimportant in the kinetic mechanism of *Varanus*, the rest of the bones of the skull are included in the maxillary segment. This segment is in turn divisible into five structural subunits:

1. The *parietal unit*, composed of the parietal, supratemporals, postorbitofrontals and squamosals. This unit articulates with the muzzle unit anteriorly through the mesokinetic axis, and with the occipital segment ventrally through the metakinetic joint and metakinetic axis.

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.

3. The *basal units*, composed of the pterygoid, ectopterygoid and jugal on each side of the posterior roof of the oral cavity. They are connected posteriorly by muscles and ligaments to the

occipital segment and quadrate units respectively, and anteriorly through the hypokinetic axis to the muzzle unit.

4. The *muzzle unit*, including the premaxilla, nasals, septomaxillae, vomers, maxillae, prefrontals, lacrymals, palatines and superciliares. This unit meets the basal units posteroventrally through the hypokinetic axis and the parietal unit posterodorsally through the mesokinetic axis.

5. The *eipterygoid units*, each composed of a single strut anchored to the basal unit below, and connected ligamentously to the occipital segment and parietal unit above.

According to Frazzetta, depression of the mandibles and protraction of the muzzle unit are brought about by the activation of mechanically unrelated sets of muscles. Both movements, however, occur simultaneously due to coordinated nervous control. The lower jaws are opened by contraction of the *M. depressor mandibulae*, aided by longitudinal throat musculature. Protraction of the muzzle unit is caused by the contraction of muscles of the constrictor dorsalis group, linking the two major kinetic segments of the skull.* The *M. protractor pterygoid* arises on the prootic beneath the trigeminal incisure and extends ventroposteriorly to insert on the quadratic ramus of the pterygoid. It is evident that activation of this muscle elevates and thrusts the basal unit forward. The *M. levator pterygoid* is a vertical muscle attaching dorsally to the parietal and ventrally to the pterygoid. It assists the *M. protractor pterygoid* in elevating the basal unit. As the basal units are displaced anterodorsally the muzzle unit rotates upward relative to them about the hypokinetic axis, while rotating upward relative to the skull as a whole about the mesokinetic axis. The quadrates are passively pulled anteriorly by ligaments binding them to the advancing basal units.

Frazzetta considers elevation of the mandibles and retraction of the muzzle unit to be mechanically interrelated in *Varanus*. Most jaw adductor muscles arise along the ventral edge of the supratemporal arcade, lateral face of the parietal and anterior surface of

* The *M. levator bulbi* is also a part of the constrictor dorsalis group. In snakes it is termed the *M. retractor pterygoid* (Lakjer 1926, p. 22), and serves to draw the basal units posteriorly. There is no evidence that this muscle operated in a similar manner in mosasaurs.

the quadrate. They descend anteriorly to insert on the dorsal regions of the coronoid and surangular. The vertical component of force from the contraction of these muscles closes the jaws, while their horizontal component acting through the mandibles pushes the base of the quadrates posteriorly. The basal units are bound to the quadrates by the quadratomaxillary ligaments and to the lower jaws through the *M. pterygoideus*. Therefore as the lower jaws and quadrate bases are pushed posteriorly the basal units are passively pulled after them. The muzzle unit then rotates downward about the hypokinetic axis relative to the basal units, while rotating downward relative to the skull as a whole about the mesokinetic axis.

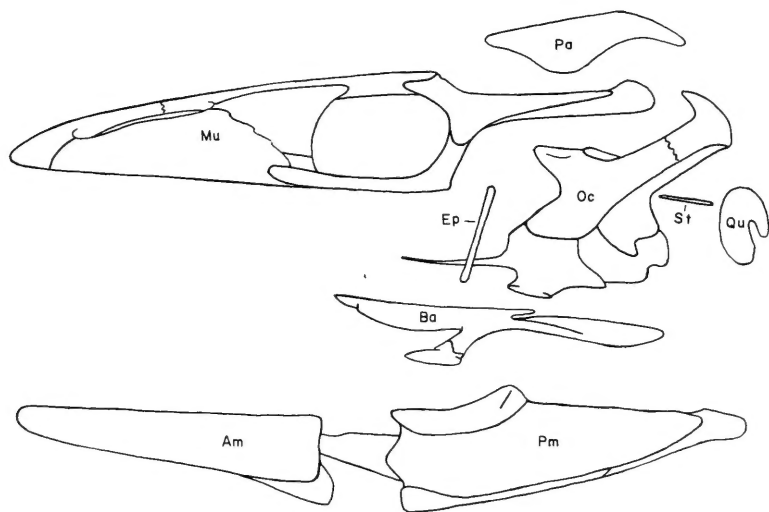


Fig. 1. Diagram of the functional units of a mosasaur skull. Abbreviations: Am, anterior mandibular unit; Ba, basal unit; Ep, epipterygoid unit; Mu, muzzle unit; Oc, occipital segment; Pa, parietal unit; Pm, posterior mandibular unit; Qu, quadrate unit; St, stapes segment.

CRANIAL KINESIS IN MOSASAURS

Although the skull of a generalized mosasaur is basically very similar to that of *Varanus*, there are several differences in the structural subdivision of the maxillary segment (see fig. 1). The upper temporal arcade is firmly attached to the muzzle unit, and

the supratemporal to the quadratic suspensorium of the braincase, leaving only the fused parietals remaining in the parietal unit. The jugal is buttressed against the postorbitofrontal posteriorly and thereby incorporated into the muzzle unit. Because the quadrates could not have been firmly attached to the quadratic rami of the pterygoids (see below) they were probably not as directly involved in the retraction of the basal units as is the case in *Varanus*.

The one feature essential to an understanding of cranial kinesis in mosasaurs is the extensive and solid suturing of the postorbitofrontals to the ventral surface of the frontal. 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 squamosal is expanded at its posterior termination and

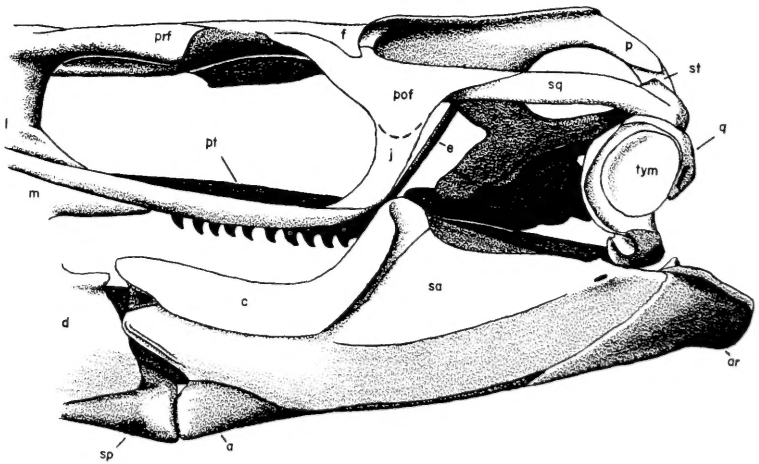


Fig. 2. Temporal region of a generalized mosasaur, *Clidastes liodontus* (reconstructed after YPM 1335, one-half natural size). Abbreviations: a, angular; ar, articular; c, coronoid; d, dentary; e, epipterygoid; f, frontal; j, jugal; l, lacrymal; m, maxilla; p, parietal; pof, postorbitofrontal; prf, prefrontal; pt, pterygoid; q, quadrate; sa, surangular; sp, splenial; sq, squamosal; st, supratemporal; tym, calcified tympanum.

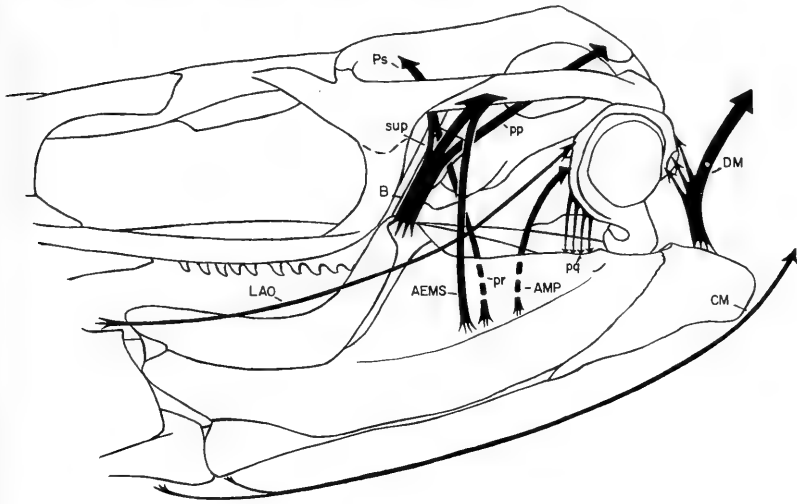


Fig. 3. Restored superficial musculature of the temporal region of *Clidastes liodontus*. Abbreviations: AEMS, Mm. adductor mandibulae externus medialis et superficialis; AEP, M. adductor mandibulae externus profundus, pp, posterior head, pq, quadrate head; AM, M. adductor mandibulae undivided; AMP, M. adductor mandibulae posterior; CM, M. cervicomandibularis; LAO, M. levator angularis oris; DM, M. depressor mandibulae; Ps, M. pseudotemporalis, pr, profundus, sup, superficialis; B. bodenaponeurosis.

caps the supratemporal, which in mosasaurs is firmly sutured to the paroccipital processes of the occipital segment. Assuming the occipital segment to be solidly attached to the overlying parietal unit, one of three things would happen when the muzzle unit was protracted or retracted and the upper temporal arcades were correspondingly depressed or elevated:

- (a) The posterior ends of the squamosals would swing in vertical arcs over the supratemporals.
- (b) The posterior ends of the squamosals would remain fixed on the supratemporals and the upper temporal arcades would bend in vertical planes.
- (c) The posterior ends of the squamosals would remain fixed on the supratemporals, the upper temporal arcades would remain rigid and movement of the muzzle unit about the mesokinetic axis would be suppressed.

Alternative (a) is unlikely for in all mosasaurs the plane of contact between the squamosal and the supratemporal is undulatory to a greater or lesser extent, the axes of undulation lying at right angles to the hypothetical direction of movement. Alternative (b) may be dismissed for the reason that the upper temporal arcade is deeper than wide and particularly resistant to vertical bending. Alternative (c) would negate any reason for having transverse lines of flexure in the maxillary segment, as the skull would be akinetic.

It is therefore concluded that the occipital segment could move beneath the parietal unit. In fossil specimens of generalized mosasaurs these structural elements are nearly always disassociated, testifying to their loose interconnections. The occipital segment is here postulated to have pivoted in a vertical plane on the occipital condyle about the atlas vertebra. Any rolling motion would be prevented by the various articulations with the maxillary segment, which limited movement in a fore and aft direction. Thus as the upper temporal arcades were elevated the paroccipital processes were also lifted and the basiptyergoid processes lowered and displaced posteriorly. The reverse motions accompanied depression of the upper temporal arcades (see fig. 5). Adjustment in the vertical relations between the paroccipital process of the occipital segment and the suspensorial ramus of the parietal took place through slippage on the loosely overlapping parietal-supratemporal contact. The squamosal was capable of pivoting on the lateral face of the supratemporal (metakinetic axis).

As will be seen below, the ability of the occipital segment to turn about the atlas-occipital articulation within the maxillary segment could have played an important role in the kinetic mechanism of mosasaurs. It should be noted that the atlas is the fixed structure relative to which all other structures in the skull underwent displacement in kinesis. Frazzetta (1962) considers the occipital segment to be the fixed structure relative to which other structures in the skull undergo displacement during kinetic operations in *Varanus*. Herein lies the fundamental difference between Frazzetta's interpretation of kinesis in *Varanus* and this interpretation of kinesis in generalized mosasaurs.

If the muzzle unit of mosasaurs was protracted and retracted the same way as it is in *Varanus* the occipital segment would be

passively rocked up and down about the atlas with the rising and falling upper temporal arcades. However, important axial muscles must have inserted on the occipital segment ventral and dorsal to the occipital condyle, these being the Mm. rectus capitis anterior and posterior. If superficial muscles, like the M. spinalis capitis above and Mm. sternohyoideus and geniohyoideus below, held the maxillary segment and lower jaws 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. Therefore the occipital segment could at least have aided the kinetic mechanism of mosasaurs by actively pushing the upper temporal arcades up and down with the paroccipital processes.

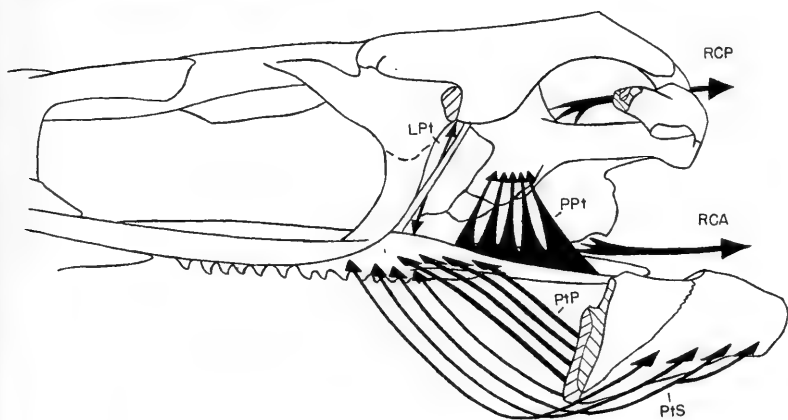


Fig. 4. Restored deep musculature of the temporal region of *Clidastes liodontus*. Abbreviations: LPT, M. levator pterygoideus; PPT, M. protractor pterygoideus; Pt, M. pterygoideus undivided; PtP, M. pterygoideus profundus; PtS, M. pterygoideus superficialis; RCA, M. rectus capitis anterior; RCP, M. rectus capitis posterior.

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 about the atlas, and more steeply when it was rotated downward. Thus the metakinetic joint and basal articulation were brought more

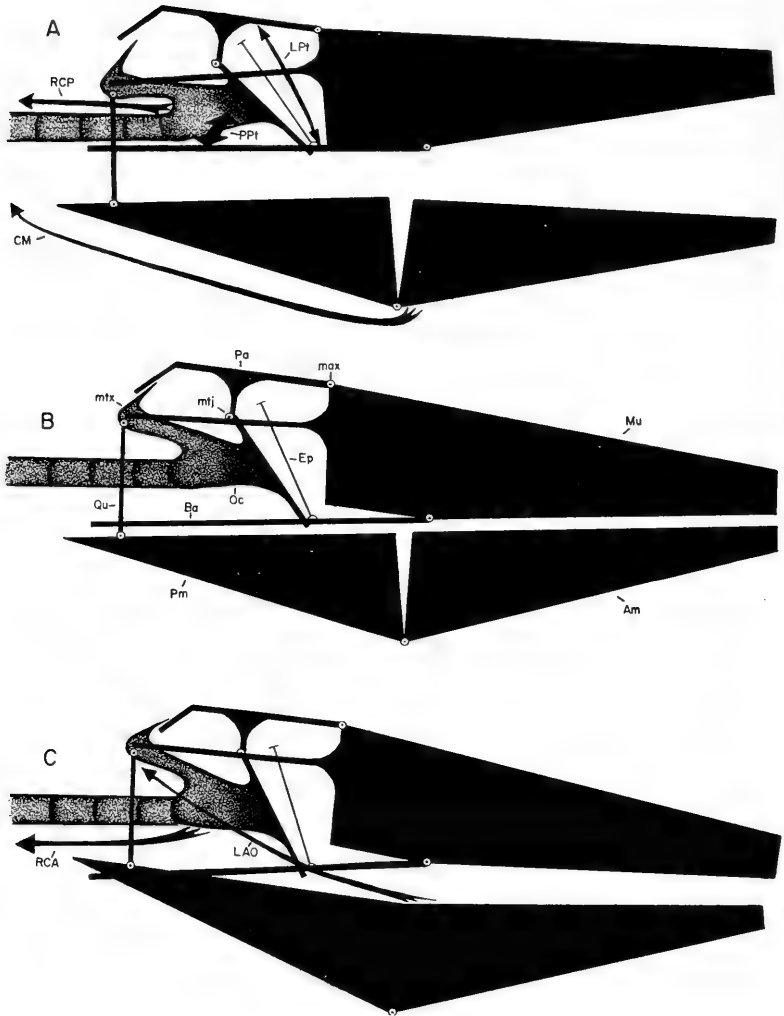


Fig. 5. Kinesis in mosasaurs. Abbreviations: max, mesokinetic axis; mtj, metakinetic joint; mtz, metakinetic axis; other abbreviations as in figs. 1-4. A. Muzzle unit elevated, anterior mandibular unit depressed. B. Cranium at rest. C. Muzzle unit depressed, anterior mandibular unit elevated.

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 figure 5 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 merely accentuate the elevation of the muzzle unit in the protracted state by displacing the hypokinetic axis still further anterodorsally. It is evident then that rotation of the occipital segment could have exerted a profound influence over kinetic movements in the head of mosasaurs.

Ligaments binding the basiptyergoid processes to the pterygoids were probably tensed by the anterodorsal sliding of the basal units during protraction of the muzzle unit. During retraction the basiptyergoid processes would have moved posteroventrally with the turning anteroventral margin of the occipital segment and exerted through these tensed ligaments the force necessary to pull the basal units back. It is possible that the movement of the occipital segment was entirely responsible for the rotation of the muzzle unit downward about the mesokinetic axis, and the quadrates were freed to move the lower jaw independently of kinesis in the skull. This would represent an advancement over the condition in *Varanus* where the quadrates are a necessary element in the retraction of the muzzle unit. It is noteworthy that the quadrates are movable in all known mosasaurs, while kinesis was completely lost in later forms (e. g. in *Mosasaurus*, *Plotosaurus*, *Plesiotylosaurus* and *Prognathodon*). In mosasaurs possessing kinetic skulls it is also possible that the quadrates aided in the retraction of the muzzle unit the same way they do in *Varanus*.

STREPTOSTYLY IN MOSASAURS

Kauffman and Kesling (1960) have published a carefully executed study of an ammonite (*Placenticerus*) conch from the Virgin Creek Member of the Pierre Shale (Upper Cretaceous) which had been bitten repeatedly by a mosasaur. Superimposed rows of tooth impressions on this conch show that the cephalopod was bitten at least sixteen times before the living chamber was crushed and the soft parts were disengaged from the shell, probably to be devoured by the mosasaur. Kauffman and Kesling's study has

yielded much direct evidence of jaw movement in mosasaurs, some of which will be discussed below.

Kauffman and Kesling (*Ibid.*, p. 219) note that the series of impressions from the dentary teeth of each mandible always maintain the same anteroposterior relation to each other, indicating there was no anteroposterior movement between the lower jaws in the symphyseal region. They also observed (*Ibid.*, fig. 4) that the upper and lower jaws did not always align with each other

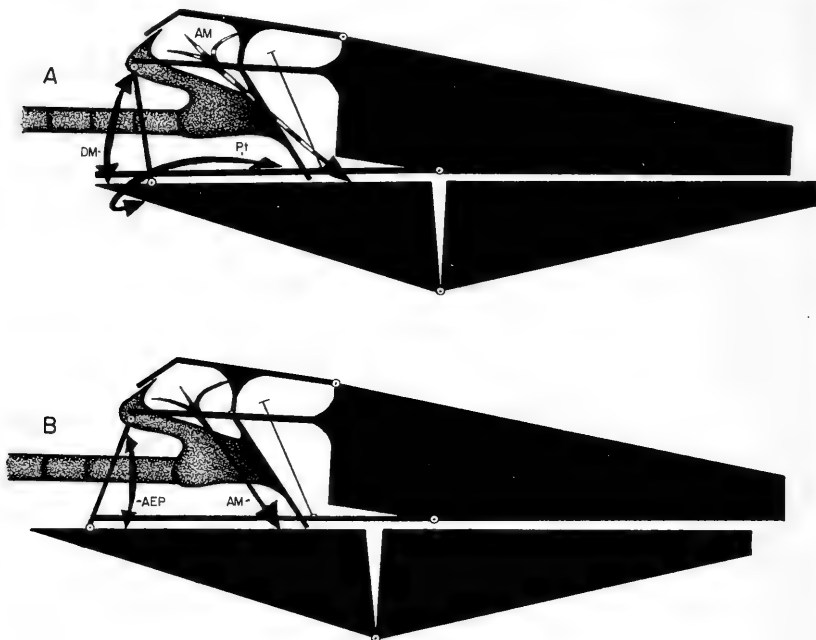


Fig. 6. Streptostyly in mosasaurs. Abbreviations as in figs. 1-4. A. Mandible protracted. B. Mandible retracted.

when occluded. This could only occur if the quadrates were independently movable (the lower jaws bent simultaneously at the splenioangular joint, *Ibid.*, p. 219). Since both basal units are fixed to a single rigid muzzle unit, it follows that in order for the quadrates to have been independently movable 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 evidently was therefore not a sliding articulation.

Muscles that acted to protract the lower jaw (see fig. 6) 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 anterior portion of the mandible ventrally about the quadrato-mandibular articulation so that it would not be swung dorsally into the maxillary segment). Could there have been a separate bundle of the *M. protractor pterygoid* (an *M. protractor quadrati*) that inserted near the base of the quadrate and acted to pull it forward? Such fibers do insert on the quadrate of *Varanus niloticus* (Lakjer 1926, p. 14).

The horizontal component of force from the contracting jaw adductor muscles acting through the mandible would rotate the quadrate and mandible back about the cotylus on the quadratic suspensorium. The presence of prey between the jaws would have kept them apart and allowed the mandible to be pulled posteriorly. Grooves that parallel 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). This mechanism for swinging the base of the mosasaur quadrate back and forth has already been suggested by Camp (1942, p. 35, 37).

MANDIBULAR JOINT IN MOSASAURS

As has long been known, the mosasaur jaw is divided into two halves by a joint in the center 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 there is a ginglymoid splenio-angular articulation which is located beneath the lower edges of the dentary and surangular, and makes a pronounced bump in the center of the lower margin of the mandible. Nearly all previous authors have interpreted this

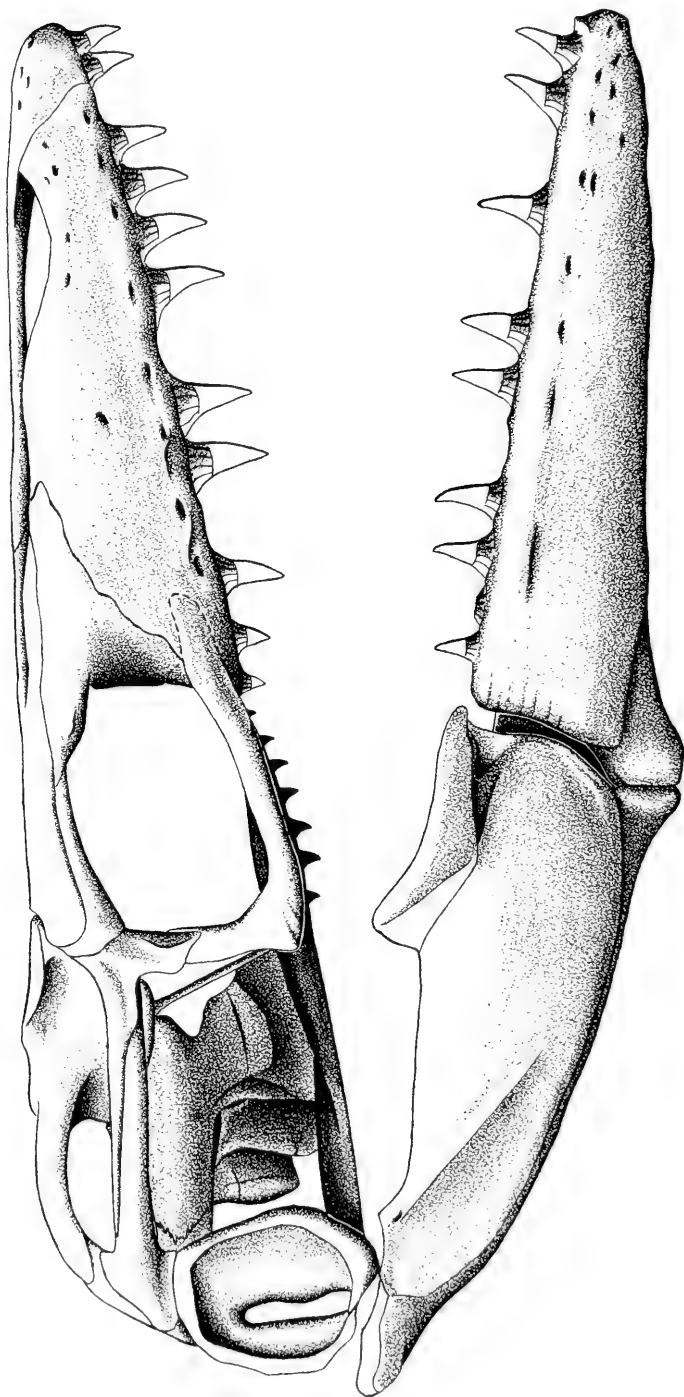


Fig. 7. Restored skull of *Platecarpus ictericus* (slightly larger than one-fourth natural size) showing the jaws opened, the muzzle and anterior mandibular units abducted, and the jaws protracted.

region as a site of lateral flexion in the lower jaw, permitting the ingestment of large objects. Kauffman and Kesling (1960, p. 218), however, from a study of the tooth marks on their ammonite conch, infer that the anterior unit of the lower jaw must have rotated upward about the splenio-angular joint. A vertical keel on the concave articular face of the splenial fits into a groove on the convex articular face of the angular. The joint would be disarticulated by only a slight amount of lateral flexion, although vertical movement would not be inhibited.

As understood here, the twisting mechanism postulated by Kauffman and Kesling (*Ibid.*, p. 222) for the elevation of the anterior mandibular units would operate as follows. Rotation of the posterior units of the mandibles about their long axes would tend to move their upper edges apart. This movement would be transmitted to the upper edges of the anterior units, but the contact of the lower edges of the latter units in the symphyseal region would have prevented the ventral margins of the lower jaws from moving medially. The dorsal margins of the lower jaws would, however, move apart, bending between the rigid surangulars and dentaries. Thus, in a vertical plane drawn through the mandibular cotylus to the anterior tip of the dentary, the longitudinal distance between these two points would remain constant along the ventral margin, and be shortened dorsally, the anterior units of necessity being rotated up and back about the splenio-angular joint.

A large suprastapedial process curves posteromedially from the dorsal portion of the main body of the quadrate in mosasaurs. The base of the quadrate would be swung laterally as the suspensorial cotylus slipped down and back along this suprastapedial process. The lateral movement of the quadrate base then supplied the force to turn the dorsal edge of the posterior mandibular unit laterally and thereby elevate the anterior unit, according to Kauffman and Kesling.

This is an ingeniously devised system and does credit to the creative imagination of its authors. However, it is unlikely that it could have functioned in life for the following reasons:

- a) The articulation of the quadrate with the suspensorium was not a sliding one. Because the pterygoids were but loosely attached to the quadrate there was no point about which the top of the quadrate could have pivoted. The head of the quadrate

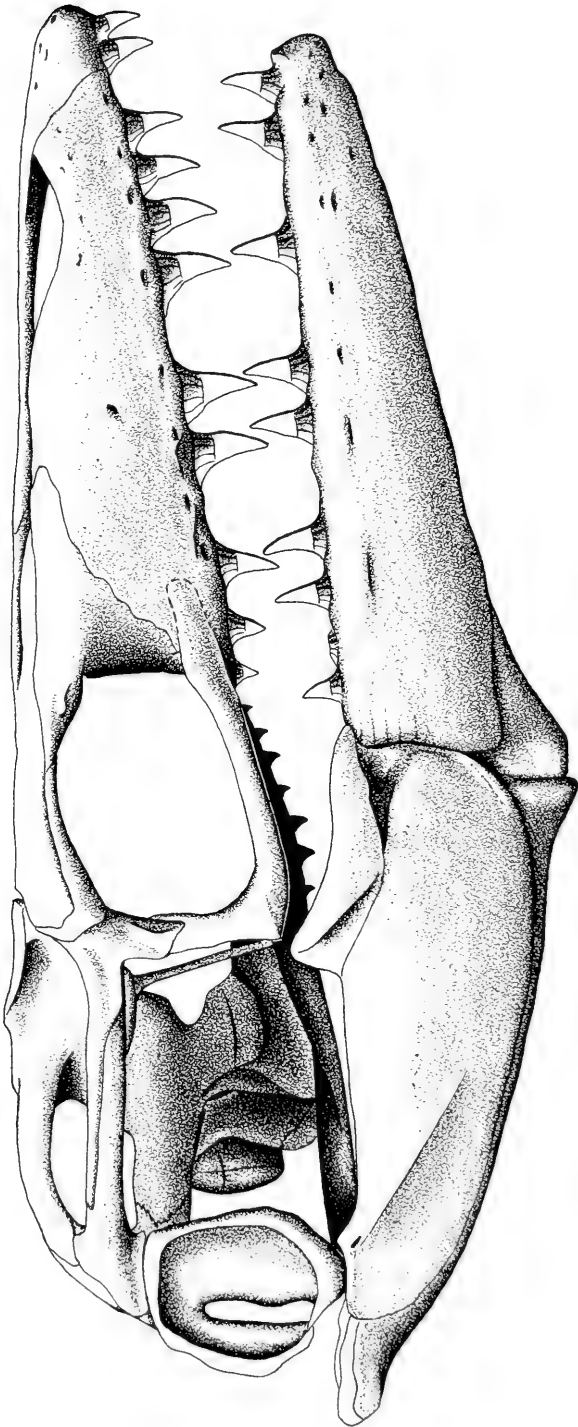


Fig. 8. Restored skull of *Platecarpus ictericus* (slightly larger than one-fourth natural size) showing the jaws nearly closed, the muzzle and anterior mandibular units adducted, and the jaws retracted.

is covered by a smooth surface which is very finely marked with tiny irregularities. This surface, as in *Varanus* and *Python*, probably anchored ligaments binding the quadrate to the suspensorium in a contact that permitted pivoting but prevented any significant amount of anteroposterior slippage. As in these two genera, the mandibular condyle of the mosasaur quadrate is surfaced with a more smoothly polished bone and met the underlying mandibular cotylus in a slipping articulation.

b) The prearticular bridges the gap between the posterior and anterior units of the mandible dorsally. It is approximately "I"-shaped in cross section and would have resisted any tendency of the mandible to bend outward at this point.

c) The alveolar margins of the dentaries would have spread more widely apart from one another posteriorly when the anterior units were elevated, if the above hypothesis were true. Actually the rows of tooth impressions from the dentary teeth were not noticeably more divergent posteriorly when the anterior units were elevated (Kauffman and Kesling 1960, p. 218, fig. 4b, e).

Another mechanism could conceivably have actively operated the splenio-angular joint. A slip of the *M. adductor mandibulae externus superficialis* may have inserted on the posterodorsal corner of the dentary through a tendon passing over the coronoid. The lowered position of the splenio-angular joint would have lengthened the lever arm of the muscle and increased its effectiveness in elevating the anterior mandibular unit. In *Varanus* the *M. cervicomandibularis* arises beneath the *M. constrictor colli* from connective tissue on the neck and passes forward around the quadrate to insert on the ventrolateral margin of the angular and splenial. This muscle may have inserted on a subdued transverse ridge in front of the articular surface of the splenial in mosasaurs, and thus functioned to depress the anterior mandibular unit.

The overhanging of the posterodorsal corner of the dentary by the anterior edge of the coronoid, together with the absence of any unusual groove on the superior surface of the coronoid, make it difficult to visualize any portion of the jaw adductor muscles reaching the dentary. It seems more likely that the anterior edges

of the coronoid and surangular were bound to the posterior edge of the dentary by ligaments, as suggested by Barghusen (oral communication). 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 articulations, putting the ligaments binding it dorsally to the posterior unit under tension. These tensed ligaments would then act to restore the anterior unit to its former position.

CONCLUSIONS

In summary, generalized mosasaurs possessed a kinetic skull with an actively rotating occipital segment, although kinesis was entirely lost in later forms. The quadrates were streptostylic and independently movable in all mosasaurs, and acted to protract and retract the lower jaws. The intramandibular joint operated in a vertical plane and, together with elastic ligaments binding the anterior and posterior halves of the mandible together, probably served as a shock absorbing device.

Frazzetta (1962, p. 317) concludes, ". . . that kinesis is adaptively important in that it makes possible a movement downward of the upper jaws . . . and permits the prey to be engaged by both upper and lower jaws simultaneously . . . thereby diminishing . . . the risk of deflecting the prey away from the gaping mouth by the mandibles before a positive grip can be secured." In larger animals, kinesis may also increase the absolute speed and therefore the momentum with which the upper jaws strike the body of the prey. This might serve to stun the victim and to impale it more securely on the teeth. Kinesis was evidently not an essential element in the feeding mechanism of mosasaurs, as is shown by its loss in later forms. Perhaps the viscosity of the aqueous medium in which mosasaurs lived inhibited rapid movement to such an extent that kinetic movement in the head was no longer useful, as it had been in their terrestrial ancestors. It is interesting that kinesis is developed to a varying degree even among the different genera of earlier, more generalized forms. It would seem that these mosasaurs represent an intermediate adaptive level in the evolution of mosasaurs, a level in which kinesis was being lost.

Streptostylic quadrates are, however, found in all mosasaurs

and must have been useful adaptations in aquatic feeding. As suggested by Camp (1942, p. 37) and Kauffman and Kesling (1960, p. 218) this enabled the mandibles to be retracted, greatly assisting a 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, p. 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. In some mosasaurs (e.g. *Clidastes*) the marginal dentition is trenchant, and alternative protraction and retraction of the mandibles might have been effective in sawing a large object into pieces of swallowable size.

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