INTRACRANIAL MOBILITY IN KANSAS MOSASAURS

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ABSTRACT

Three genera of mosasaurs *(Clidastes, Platecarpus, Tylosaurus)* are analyzed in terms of cranial kinesis, streptostyly, and intramandibular mobility. Mechanisms of cranial kinesis found in the mosasaurs are similar to those found in *Varanus*. The specialized quadrate of mosasaurs differs much from the generalized varanid quadrate in that the cephalic condyle is long and has an inward-bending articulatory surface. The mechanical regime provided by the enhanced streptostyly permits the intramandibular joint to be operated by action of the pterygoid and cervicomandibular muscles.

INTRODUCTION

PREVIOUS WORK AND TERMINOLOGY

The primary mechanisms involved in food-getting as related to intracranial mobility in three genera of mosasaurs *(Clidastes, Platecarpus, Tylosaurus)* commonly found in the Upper Cretaceous rocks of western Kansas are presented in the following study.

Early workers dealing with intracranial mobility in reptiles are BRADLEY (1903) and VERSLUYS (1910, 1912). CAMP (1942) and RUSSELL (1964) made corresponding studies of mosasaurs. RUSSELL's work was concerned exclusively with intracranial mobility and is patterned after an excellent work by FRAZZETTA (1962) that treats the same problem in modern lizards. As the present study was under way before RUSSELL's work was published, and as my interpretation differs from his on a number of points, it seems advisable to publish my findings.

Mosasaurs were Late Cretaceous marine carnivorous lizards. Within the Squamata the vara-

noid affinities of the Mosasauridae are well established in the literature (CUVIER, 1808; MARSH, 1872; OWEN, 1877; BAUR, 1892; WILLISTON, 1904; CAMP, 1942; McDOWELL & BOGERT, 1954; ROMER, 1956).

Differences between the varanids and mosasaurs include the giant size and the development of short, paddle-shaped limbs in the latter. Less striking, but certainly no less important, are several differences in the skeleton of the head. Most evident among the latter are the presence of a row of teeth on the pterygoid bones of the palate, the specialized quadrate bones, and the presence of a functional intramandibular joint.

Many of the structural adaptations of mosasaurs are related to capturing, holding, manipulating, and swallowing prey in water. As used here, the term **intracranial mobility** means any freedom of movement between individual bones or rigid associations of bones of the skeleton of the head. Included within this definition are the terms **streptostyly** and **monimostyly** (STANNIUS, 1856) which refer to whether the quadrate is

movable on the braincase or not, and the term **kinesis** (VERSLUYS, 1910), which denotes a movable articulation between the braincase and the dermal roofing bones and is equivalent to HOFER's (1945) **neurokinesis**. FRAZZETTA (1962) reviewed the terminology related to kinesis and provided definitions for classifying kinetic skulls according to positions of the cranial joints as follow.

a) *Metakinesis* denotes the presence of a movable joint between the parietal and supraoccipital bones.

b) *Mesokinesis* refers to the presence of a movable joint between the parietal and frontal bones.

c) *Amphikinesis* relates to the presence of both a metakinetic and mesokinetic joint.

d) *Akinesis* refers to the lack of movable joints in the cranium.

e) *Prokinesis* relates to the presence of a movable joint between the frontals and nasals or to a zone of flexibility in the frontonasal region.

f) *Monokinesis* denotes the presence of only one movable joint in the cranium.

BOCK (1964) has pointed out that streptostylic-monimostylic and kinetic-akinetic are not anatomical, but functional designations. He stated also that although a particular morphological structure is required for streptostyly or kinesis, ". . . the mere presence of these anatomical features does not automatically indicate the existence of the associated movement."

MATERIALS AND METHODS

Five specimens of modern varanid lizards were examined. Four of these (*Varanus salvator*; KU nos. 47150, 50702, 60122; and *V. salvadorii*, KU 23048) are osteological preparations and the fifth (*V. salvator*, KU 98517) is an alcoholic. The head of the alcoholic specimen was dissected. All of the mosasaurs in the paleontological collections of the University of Kansas Museum of Natural History represented by head skeletal material were examined. The heads of three uncatalogued alcoholic lizards (*Lacerta agilis, Xantusia vigilis, Chameleo bitaeniatus*) were sectioned and studied with reference to kinesis and streptostyly. A plaster-of-paris model of the postorbitofrontal-frontal-parietal articulation of *Platecarpus* and wooden models of intracranial mechanisms in both varanids and mosasaurs were constructed.

Catalogue numbers are University of Kansas Museum of Natural History numbers unless otherwise indicated.

DESCRIPTION

Good descriptions of the head skeletons of *Clidastes, Platecarpus,* and *Tylosaurus* are available in the literature (WILLISTON, 1898; OSBORN, 1899; CAMP, 1942). Varanid skull osteology, too, is well represented in published papers (BAHL, 1937; CAMP, 1942; MERTENS, 1942; FRAZZETTA, 1962). In spite of osteological differences (Fig. 1, 2) the arrangement of the head muscles in the two groups appears to have been similar. For further descriptions of the head muscles in *Varanus,* the works of ADAMS (1919), LAKJER (1926) and FRAZZETTA (1962) can be consulted.

OSTEOLOGY OF HEAD REGION

Discussion of the mechanisms of intracranial mobility in mosasaurs is simplified by dividing the head skeleton into groups of bones separated by regions of flexibility. The mosasaurian head skeleton (including the anterior vertebrae) is composed of the vertebral, occipital, maxillary, stapes and mandibular components. The maxillary component is further divided into the parietal, muzzle, basal, epipterygoid and quadrate units. A dentigerous and an articular unit make up the mandibular component.

The bony associations set forth in this work combine those proposed by VERSLUYS (1912), ALBRIGHT & NELSON (1959), and FRAZZETTA (1962). Hereinafter, unless otherwise noted, bilaterally paired structures will be spoken of in the singular.

OCCIPITAL COMPONENT

The occipital component forms a relatively solid block (Fig. 3) made up of the supraoccipital, basioccipital, basisphenoid, parasphenoid, and the paired prootics and exoccipitals (see WILLISTON, 1898; CAMP, 1942). Posteriorally, the occipital component articulates with the atlas-axis complex
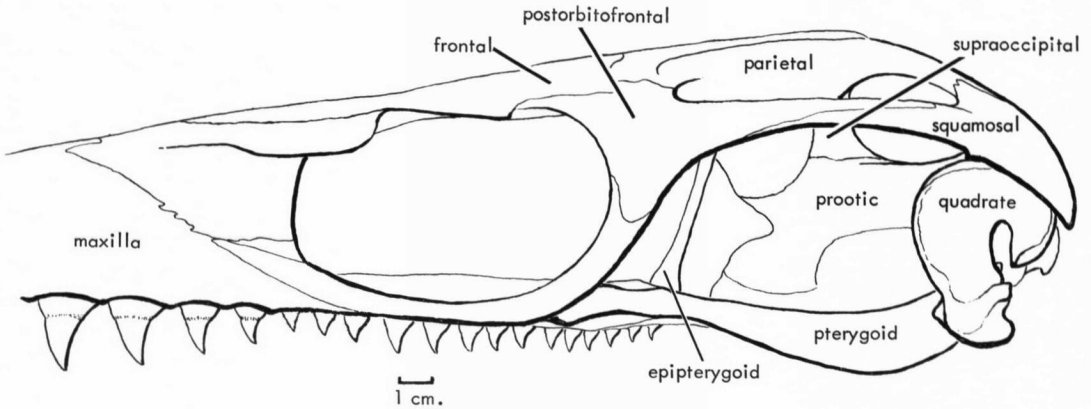
FIG. 1. *Clidastes velox* MARSH, left lateral view of cranium (adapted from Williston, 1898).
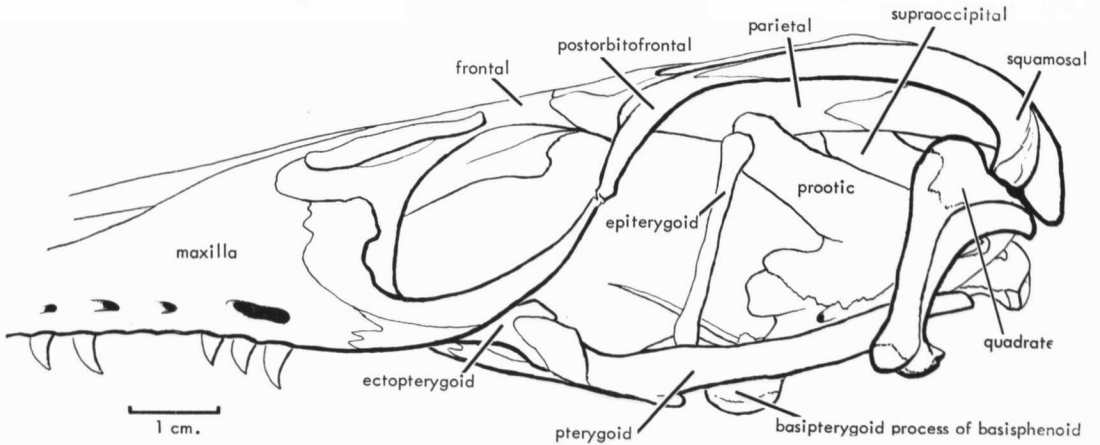

FIG. 2. *Varanus salvator* (LAURENTI), left lateral view of cranium (KU 60122).

(vertebral component). This region has been described by WILLISTON (1898), OSBORNE (1899), and CAMP (1942). Dorsally, the apex of the inverted V-shaped supraoccipital articulates with the middle of the posteroventral surface of the parietal. Anteroposterior grooves on both of these surfaces permit movement of the parietal only in the direction of the grooves.

In *Varanus* (Fig. 4) a small nodule of cartilage (the processus ascendens tecti synotici, DEBEER, 1937) protrudes from the supraoccipital bone into the median groove of the overlying parietal (FRAZZETTA, 1962) and is presumed to have been present in mosasaurs. The junction of the supraoccipital with the alar process of the prootic is anterior and ventral to the apex of the supraoccipital. In *Varanus* this junction is incised, forming
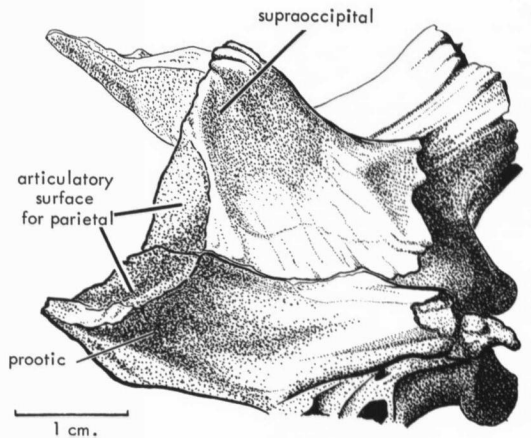

FIG. 3. *Clidastes* (COPE), left dorsolateral view of occipital component (KU 14348).
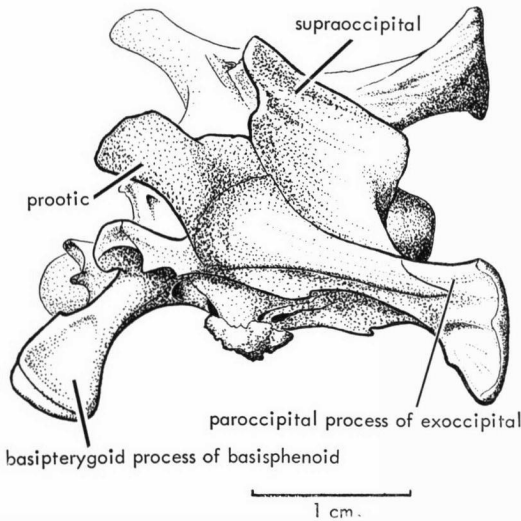
FIG. 4. *Varanus salvadorii* (PETERS & DORIA), left dorso-lateral view of occipital component (KU 23048).

a triangular aperture where the parietal articulates with the braincase (Fig. 2, 4). The anterior border of the supraoccipital-prootic articulation in mosasaurs curves smoothly and shows no triangular embayment (Fig. 1, 3). The anterior border of the supraoccipital abuts on the parietal for a short distance away from the mid-line in *Varanus*.

Mosasaurs differ from varanids in that near the mid-line the supraoccipital abuts on the parietal, but ventrolaterally, the supraoccipital sends a flat process internal to the descending process of the parietal. The alar process of the prootic, which has a flat process internal to the descending wing of the parietal (Fig. 3), is continuous anteriorly with the supraoccipital. The prootic in *Varanus* lies against the lateral edge of the parietal (Fig. 2, 4). Laterally, at the upper corner of the cranium, the occipital component articulates with the parietal and quadrate units of the maxillary component. The paroccipital process of the exoccipital forms a broad, flat joint with the supratemporal bone. The same joint in varanids permits the rotation of the parietal unit about an axis (metakinetic axis) which passes through the paired paroccipital processes (FRAZZETTA, 1962). Presumably, mosasaurs did not differ from the varanid condition at this axis. The metakinetic joint is not the same as the metakinetic axis.

A diarthrosis is formed between the basipterygoid process of the basisphenoid and the pterygoid. The basipterygoid processes are paired projections that extend laterally and anteroventrally from the basisphenoid bone to a posteriorly directed notch in the pterygoid. Varanid basipterygoid processes are relatively longer than their mosasaurian counterparts.

A series of three bones (basioccipital, basisphenoid, parasphenoid) forms the floor of the braincase in the varanids and mosasaurs. In *Varanus* the basioccipital is about half as long as the combined basioccipital and basisphenoid. Mosasaurs have a basioccipital that is about 35 percent of the total basioccipital-basisphenoid length.

A pair of spheno-occipital tubercles is located on the ventrolateral junction of the basisphenoid with the basioccipital bone. The tubercles are better developed in the mosasaurs than in the varanids.

MAXILLARY COMPONENT

FRAZZETTA (1962) divided the maxillary component into five functional units, three of which are bilaterally paired. Four of these units articulate directly with the occipital component. His classification is applicable to the mosasaurian condition and is followed below.

PARIETAL UNIT

1) The parietal unit (Fig. 3, 5) is made up of the parietal and the paired squamosal, supratemporal, and (fused) postorbital plus postfrontal (postorbitofrontal) bones. The joints between the parietal unit and other units differ from those in varanids. Bones of the parietal unit articulate with the occipital component along the anterior and dorsolateral surfaces of the prootics and the supraoccipital and with the anterolateral faces of the paroccipital processes. Posterolaterally, the squamosals articulate with the supratemporals internally and with the quadrates ventrally. The squamosal-supratemporal joint is a broad syndesmosis. The squamosal-supratemporal-paroccipital articulation with the quadrate appears to have been a diarthrosis.

Anterolaterally on the postorbitofrontal its beveled, ventral process articulates with the jugal. This articulation could allow some sliding movement.

A broad, flat lamina of the postorbitofrontal underlies the lateral portion of the frontoparietal joint. Much of the length of the frontoparietal

joint (58 percent) is underlain by these laminae (Fig. 5). In *Varanus* only about 12 percent of this joint is underlain by the postorbitofrontal laminae (Fig. 6). In both varanids and mosasaurs there appears to have been a syndesmosis at the postorbitofrontal-frontoparietal joint. The rear edge of the postorbitofrontal abuts solidly on the posterior wall of a depression in the overlying parietal and appears to have been firmly sutured to it. Anteriorly, the postorbitofrontal lamina lies in a shallow depression on the underside of the frontal.

The parietal articulates with the fused frontals anteriorly. This (mesokinetic) joint permits rotation in a sagittal plane. The underlying laminae described above would restrict movement at the mesokinetic joint. The line of contact between the frontals and parietal in *Varanus* is nearly straight (Fig. 6) but in the mosasaurs it is elaborate (Fig. 5). The dorsal configurations of the joints are shown in dashed lines on these figures.
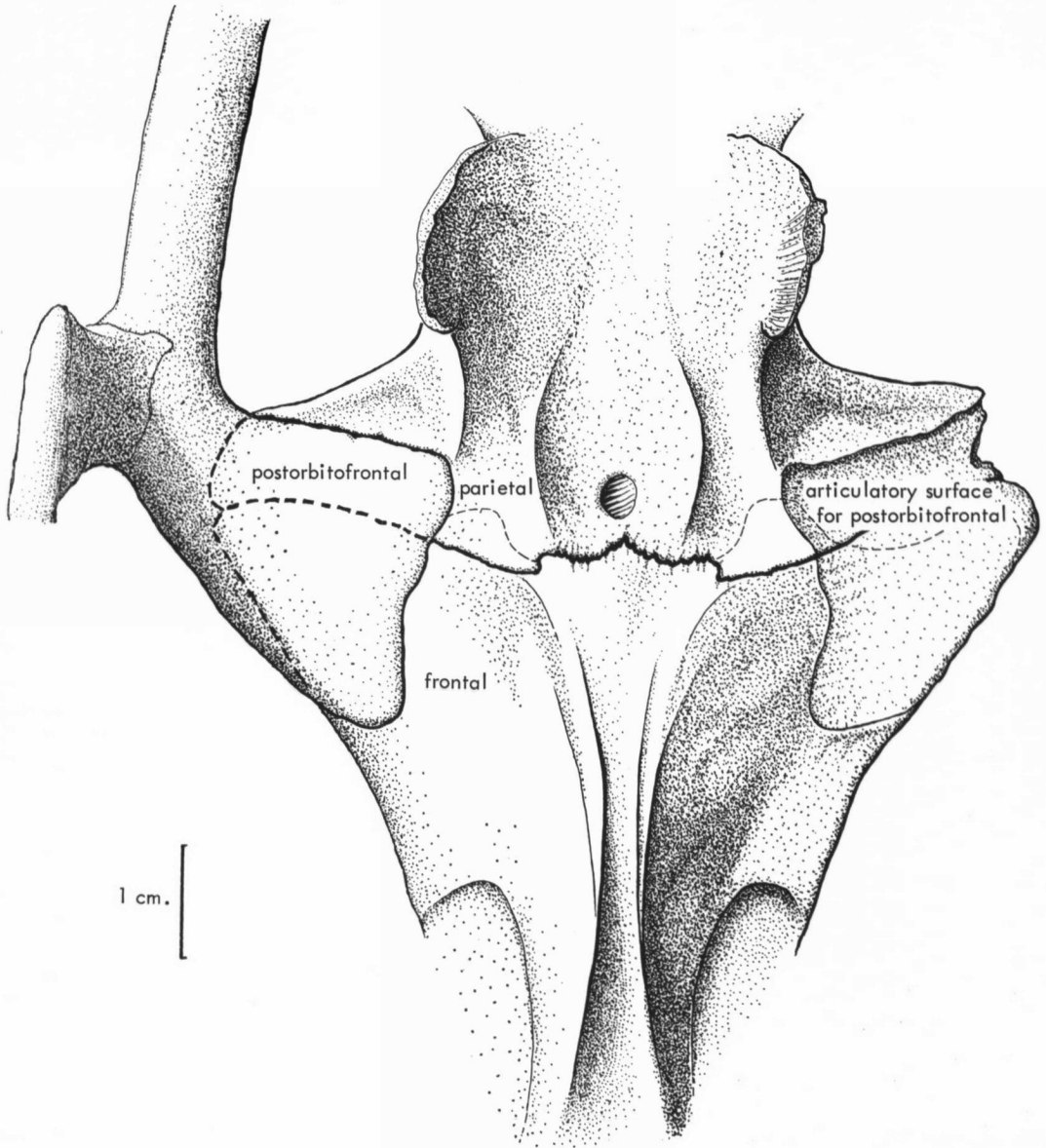

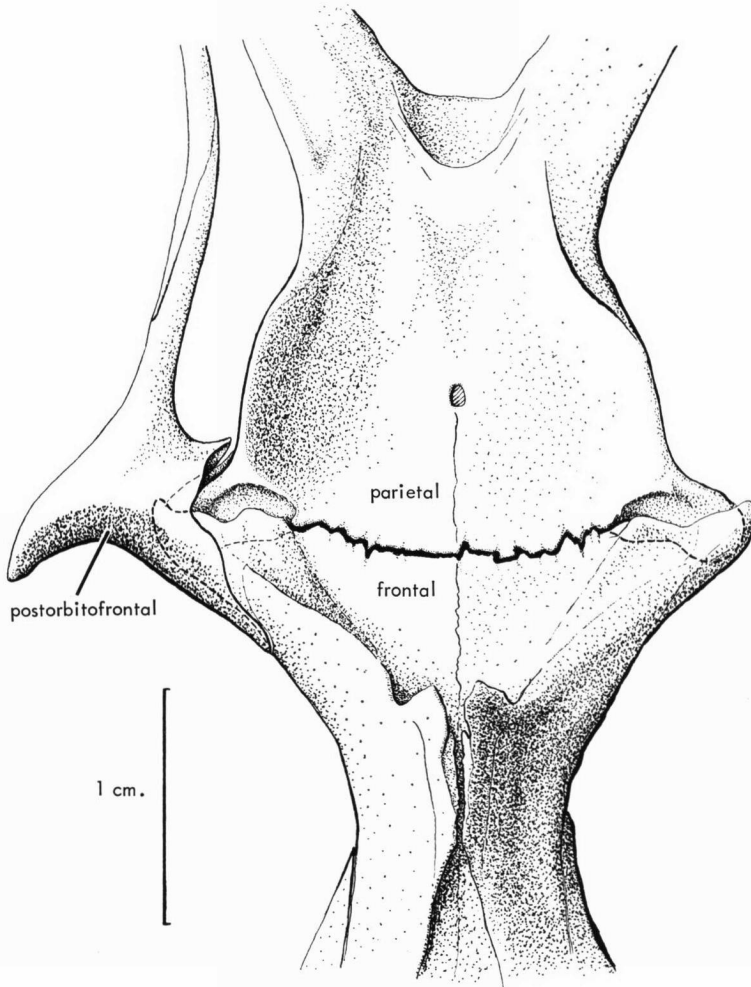FIG. 5. *Clidastes* COPE, ventral view of skull roof (KU 14348).

FIG. 6. *Varanus salvadorii* (PETERS & DORIA), ventral view of skull roof (KU 23048).

QUADRATE UNITS

2) The quadrate units (Fig. 1, 7) are made up of the bilaterally paired quadrate bones. In mosasaurs the tympanum and the distal part of the extracolumella are also included in this unit. Quadrates of mosasaurs vary in degree of elongation of the suprastapedial process. A comparison of the ratio, length of cephalic condyle of the quadrate (measured along the curved anteroposterior surface) to height of the quadrate yielded the following indices: *Tylosaurus*, 49 to 73; *Clidastes*, 54 to 83; *Platecarpus*, 88 to 110. A series of *Varanus*, measured from plates in MERTENS (1942), yielded indices of 53 to 73.

Thick, calcified cartilaginous tympanic membranes are found in many genera of mosasaurs

(WILLISTON, 1897, 1914; DOLLO, 1905; CAMP, 1942; VAUGHN & DAWSON, 1956) and have been observed by me in *Platecarpus* (KU 1092, 1113, 1135, 1142, 4862, 14280, 14556; *Clidastes*, KU 1022; and *Tylosaurus*, KU 1194. The extracolumella is also calcified in some mosasaurs (see DOLLO, 1905, fig. 22). In *Platecarpus* (KU 1142), a calcified processus internus is *in situ* as is a portion of the body of the calcified extracolumella extending into the meatus. CAMP's (1942) observation that the extracolumellar characters of the mosasaurs do not differ more widely from *Varanus* than from *Calotes*, *Chamaeleo*, *Phrynosoma* and *Tupinambis* is supported by my findings.

The tympanum has received increased support from the quadrate in mosasaurs by means of en-

largement of the tympanic ala, elongation of the suprastapedial process, and development of the infrastapedial process. These structures are modified in various ways in the three genera of mosasaurs studied.

The suprastapedial process of the quadrate bends inward. The angle (as seen from the rear) that the articular surface on the cephalic condyle makes with the articular surface of the mandibular condyle (Fig. 7) changes from less than 5° (anterior portion) to about 25° (posterior portion). This condition is least developed in *Tylosaurus* and best in *Platecarpus*.

The broad, thin quadrate wing of the pterygoid articulates with the medial face of the mandibular condyle of the quadrate. Shallow ridges on the lateral face of the tip of the pterygoid indicate that movement may have been primarily anteroposterior. This joint was probably a loose syndesmosis.

BASAL UNITS

3) The basal units in the mosasaurs consist of a pair of anteroposteriorly elongated series of bones that roof the lateral parts of the rear of the mouth. Each series is made up of a pterygoid, ectopterygoid, jugal, and possibly the rear half of a palatine. The pterygoid is a slender, tetraradiate, toothed bone sending processes to the palatine anteriorly, the ectopterygoid laterally, and the quadrate posteriorly. Contact is also made with the epipterygoid dorsally and with the basipterygoid process medially. The pterygoid forms syndesmoses with the palatine, ectopterygoid and quadrate. The pterygopalatine joint is formed by extensively intertongued, thin, flat processes. This joint permits some bending in a vertical plane. Vertical bending could also have occurred between the pterygoid and the ectopterygoid as well as between the ectopterygoid and jugal and the jugal and maxillary. The epipterygoid forms a diarthrosis with the dorsal surface of the pterygoid just anterior to the basipterygoid articulation. A well-developed, toothed tuberculum basisphenoideum forms the fourth process of the pterygoid. At the confluence of this process and the quadrate wing, a posteriorly directed notch receives the basipterygoid process. The anterior face of this notch limits the posteriad travel of the pterygoid.
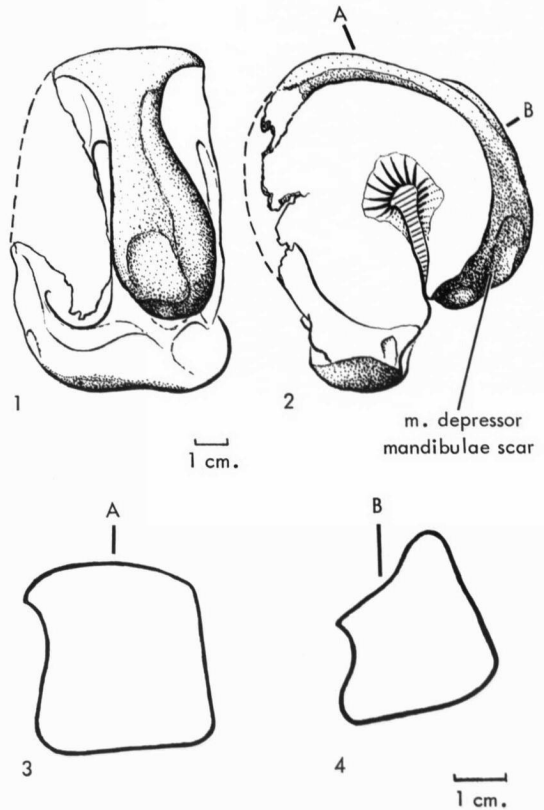

m. depressor
mandibulae scar

FIG. 7. *Platecarpus* COPE, left quadrate (KU 1081).——1, 2. Posterior and lateral views.——3. Cross section of anterior part of cephalic condyle.——4. Cross section of posterior part of cephalic condyle.

MUZZLE UNIT

4) The muzzle unit is composed of the fused frontals, the premaxillae and the paired nasals, septomaxillae, vomers, maxillae, prefrontals, lachrymals and the anterior half of the palatines. These bones are joined syndesmotically into a solid functional unit. Although resembling the muzzle unit in varanids, that of the mosasaurs lacks the palpebrals. The configuration of the contact between the frontals and parietal is more elaborate in mosasaurs (Figs. 5 and 6). The muzzle unit is hinged dorsally to the parietal unit and ventrally to the basal units. A sharp division between this and the basal units is not possible because the pterygopalatine articulation allows bending through a zone. This zone of flexibility would separate the basal units from the muzzle unit when extended to include the jugal and ectopterygoid joint with the maxilla, lachrymal and the anterior half of the palatine.

EPIPTERYGOID UNITS

5) A pair of slender cylindrical epipterygoids form the epipterygoid units. These bones extend dorsally from the pterygoid to the lateral face of the braincase near the anterior border of the prooticoparietal junction. A ligamentous attachment of the dorsal end permits pendulum-like movement of this bone.

STAPES COMPONENT

Previous studies of the kinetics of lacertilians (FRAZZETTA, 1962; RUSSELL, 1964) have treated the role of the stapes in kinesis superficially. The stapes component in mosasaurs consists of the proximal half of the stapes. The slender, cylindrical stapes is expanded proximally for about 12 percent of the total stapedial length. The footplate is much smaller than the oval expanded part (Fig. 8) which fits snugly into the stapedial canal formed by the paroccipital process and the prootic. In *Varanus salvator* (KU 60122), the foot plate is expanded as much as the proximal end (Fig. 8), but in *V. bengalensis* (AMNH-AR 71195) the diameter of the foot plate is less than that of the expanded proximal end. Figure 8 shows the proximal part of this last specimen as figured by COLBERT & OSTROM (1958, fig. 9). The diameter of the body of the stapes has been measured and compared to the estimated length of the stapes. In *Clidastes* (KU 14348) the diameter is about 2 percent of the estimated shaft length; in *Tylosaurus* (KU 1023) it is also about 2 percent, and in *Platecarpus* (KU 14349) it is about 1.5 percent. The left stapes of *Varanus salvator* (KU 60122) was measured and found to have a diameter 3.2 percent of the length of the stapes; *V. bengalensis* (AMNH-AR 71195) (measurements taken from the figure cited above) was 2.7 percent. Distally, the stapes articulates with the extracolumella.

MANDIBULAR COMPONENT

The mandibular component is comprised of two bilaterally paired rami. Each ramus can be divided into two functional units; an anterior, dentigerous unit and a posterior, articular unit.

1) The paired dentaries and splenials comprise the **dentigerous units.** Anteriorly the dentaries unite in a loose syndesmosis that allows some rotation but not independent action of the individual ramus. Posteroventrally the dentary articulates suturally with the splenial and both form a sheath that receives a thin, anteriorly projecting lamina of the prearticular bone (GREGORY, 1951). The posterior face of the splenial forms a modified socket that receives the modified ball-shaped anterior face of the angular bone.

2) The rear half of the lower jaws form the **articular units.** Each of these units is made up of an articular, prearticular, surangular, angular, and coronoid. A well-developed joint, spanned only by the prearticular, is present between the two mandibular units. GREGORY (1951, p. 350) has described this joint in detail. Rotation, but not bending, is inhibited by the conformation of the articulating surfaces of the articular and splenial. The splenial has a radial ridge on the dorsal part of the socket, whereas the angular has a corresponding sulcus in the corresponding ball. A deepening of the articular unit in mosasaurs seems to be correlated with an increase in area for muscle attachment. The relative length of the retroarticular process in mosasaurs has been reduced from the varanid condition (from about 12 percent of the total mandibular length to about 8 percent).

MYOLOGY OF HEAD REGION

a brief résumé of the musculature that is of particular importance to intracranial mobility is presented below and depicted in Figure 9. Most of the ligaments and muscles of the head are bilaterally paired, but are referred to in the singular for the sake of simplicity. The following information concerning musculature is from FRAZZETTA (1962), my dissections of *Varanus salvator*, and my observations on the three genera of mosasaurs in this study. The information pertaining to the innervation of the muscles is from OELRICH (1956) and is given in parentheses next to the names of the muscles.

Musculus levator angularis oris (trigeminal nerve).

Origin.—From fascia covering posterior and external adductors and from anterior surface of quadrate.

Insertion.—On *Mundplatte* (connective tissue mass at angle of mouth).

Ligamentum quadrato-maxillare.

Joins maxillary bone to ventral part of quadrate.

Musculus cervicomandibularis (facial and possibly third cervical nerves).

Origin.—High on muscles of neck.

Insertion.—By aponeurosis on lateral surface of dentary.

Remarks.—This muscle may serve to retract the mandibles, and if so, it was probably better developed in mosasaurs than in varanids.

Musculus intermandibularis posterior (trigeminal nerve).

Origin.—Connects lateral faces of articular units of mandibles.

Musculus depressor mandibulae (facial nerve).

Origin.—From neck musculature, posterior edge of parietal unit and, in mosasaurs, posterior surface of suprastapedial process of quadrate.

Insertion.—On retroarticular process of mandible.

Musculus adductor externus (trigeminal nerve).

Origin.—From temporal arcade of parietal unit and dorsal part of quadrate.

Insertion.—Tendinous on coronoid and certainly in *Varanus* small part on surangular.

Remarks.—In *Varanus* this muscle is complexly pinnate, indicating an increased contractile force over a parallel-fibered muscle mass of equivalent size (Gans and Bock, 1963).

Musculus pseudotemporalis profundus (trigeminal nerve).

Origin.—From anterior surface of quadrate.

Insertion.—On surangular.

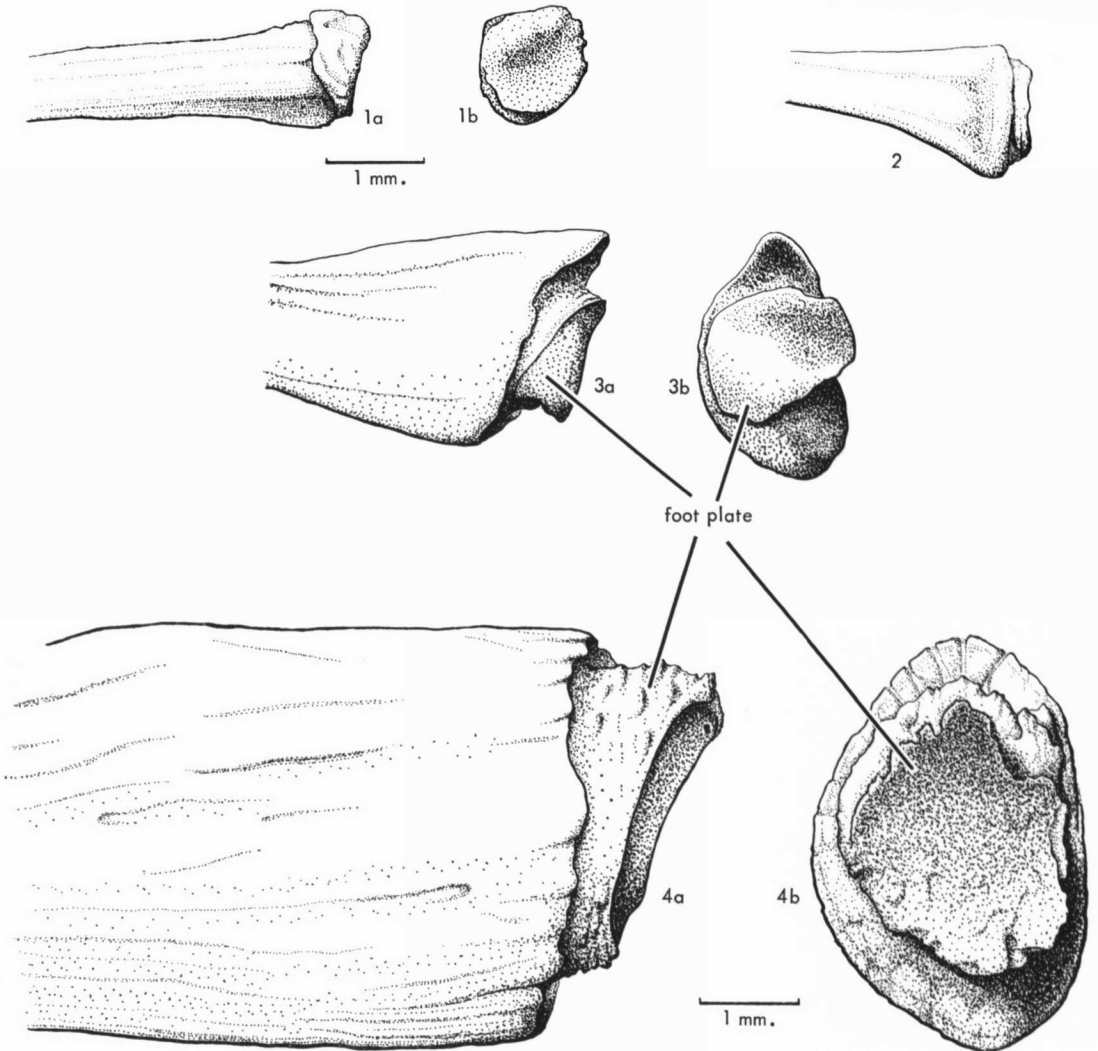*Musculus pseudotemporalis superficialis* (trigeminal nerve).

FIG. 8. Stapes.——*1. Varanus salvator* (LAURENTI), left stapes (KU 60122); *1a,* posterior view of proximal end; *1b,* medial view.——*2. Varanus bengalensis* (DAUDIN), right stapes (AMNH—AR 71195), posterior view of proximal end (adapted from COLBERT & OSTROM, 1958).——*3. Clidastes* COPE, right stapes (KU 14348); *3a,* anterior view of proximal end; *3b,* medial view.——*4. Platecarpus* COPE, right stapes (KU 1142); *4a,* anterior view of proximal end; *4b,* medial view.
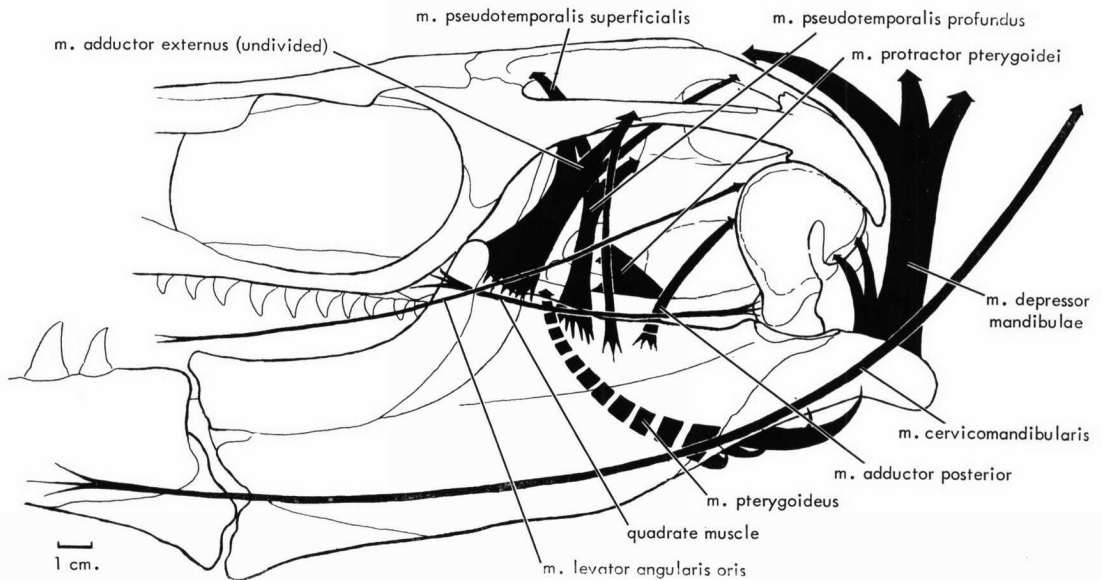
FIG. 9. *Clidastes velox* MARSH, lateral view of temporal region showing restored musculature (adapted from Williston, 1898).

Origin.—From posterior edge of anterior part of parietal unit deep to external adductors.

Insertion.—On coronoid and surangular.

Musculus pseudotemporalis profundus (trigeminal nerve).

Origin.—From anterior part of parietal unit, epipterygoid and prootic internal to superficial pseudotemporal muscles.

Insertion.—On surangular and coronoid.

Musculus pterygoideus (trigeminal nerve).

Origin.—From lateral surface of pterygoid.

Insertion.—On retroarticular process and on posteroventral surface of surangular.

Musculus protractor pterygoidei (motor branch of trigeminal nerve).

Origin.—From lateral surface of anteroventral part of occipital component.

Insertion.—On expanded quadrate wing of pterygoid.

Musculus levator pterygoidei (trigeminal nerve).

Origin.—From ventrolateral border of parietal medial to epipterygoid.

Insertion.—On dorsal surface of pterygoid at pterygoid-epipterygoid joint.

Musculus spinalis capitis (first spinal and hypoglossal nerves).

Origin.—From superficial neck muscles and fascia.

Insertion.—On posterior border of parietal.

Ligamentum nuchae.

A vertical sheet of thick, fibrous membrane that connects the angle of the parietal and the crest of the supraoccipital with the neural spines of the cervical vertebrae.

Musculus rectus capitis posterior (first spinal nerve).

Origin.—Alongside midline from deep neck muscles.

Insertion.—On posterodorsal surface of supraoccipital.

Musculus obliquus capitis magnus (first spinal nerve).

Origin.—Lateral to rectus capitis posterior from deep neck muscles.

Insertion.—On paroccipital process of exoccipital.

Musculus longissimus cervicis (first spinal nerve).

Origin.—Ventrolateral to obliquus capitis magnus from deep neck muscles.

Insertion.—On ventral edge of exoccipital.

Musculus rectus capitis anterior (hypoglossal nerve).

Origin.—From ventral surface of anterior vertebrae.

Insertion.—On posterior and ventral surfaces of exoccipital and basioccipital.

Remarks.—As the basioccipital bone was reduced in the mosasaurs, this flexor must also have been reduced.

Musculus longissimus capitis (first spinal nerve).

Origin.—From transverse processes of anterior vertebrae.

Insertion.—On spheno-occipital tubercle of basioccipital.

Remarks.—The spheno-occipital tubercles of mosasaurs are more prominent than their varanid counterparts. Therefore, this muscle was probably better developed in mosasaurs than in varanids.

CRANIAL KINESIS

The mechanisms of cranial kinesis can perhaps be explained best by following the movements of the links and joints of the cranium during a cycle of opening and closing the mouth. These links

and joints have been diagrammed in Figure 10. The diagram of the cranial linkage systems is patterned from FRAZZETTA (1962, fig. 2) and, following a convention he has established, the occipital component is to be considered as "fixed" with reference to the page, while the maxillary units are moved relative to it. For convenience in comparison of the linkage systems in mosasaurs and varanids I have maintained the lettering system of labelling geometric points employed by FRAZZETTA (1962).

The occipital component is represented by the triradiate structure *XYZ*. The arms of this structure cannot move with respect to each other. The alar process of the prootic at point *Z* is sydesmotically joined to the overlying parietal. This point *(Z)* is considered to be the major point of articulation with the parietal unit *(BX)* at point *F* (metakinetic joint).

The arm indicated by terminal point *Y* represents the basipterygoid process. Its ligamentous attachment with the basal unit is indicated at point *P*.

Point *X* represents the termination of the paroccipital process, the posterolateral corner of the parietal unit and the dorsal end of the quadrate. This point *(X)* indicates the metakinetic axis.

The maxillary component is represented by the remaining framework. The line *BX* symbolizes the parietal unit. Point *B* depicts the axis about which the muzzle unit rotates (mesokinetic axis) and is coincident with the frontoparietal joint.

The quadrate unit is indicated by the line *QX*, point *Q* being the pterygoquadrate articulation.

Line *CQ* delimits the basal unit. Point *C* represents the axis about which the muzzle unit rotates (hypokinetic axis).

The triangle *ABC* denotes the muzzle unit. The line *DE* represents the epipterygoid unit.
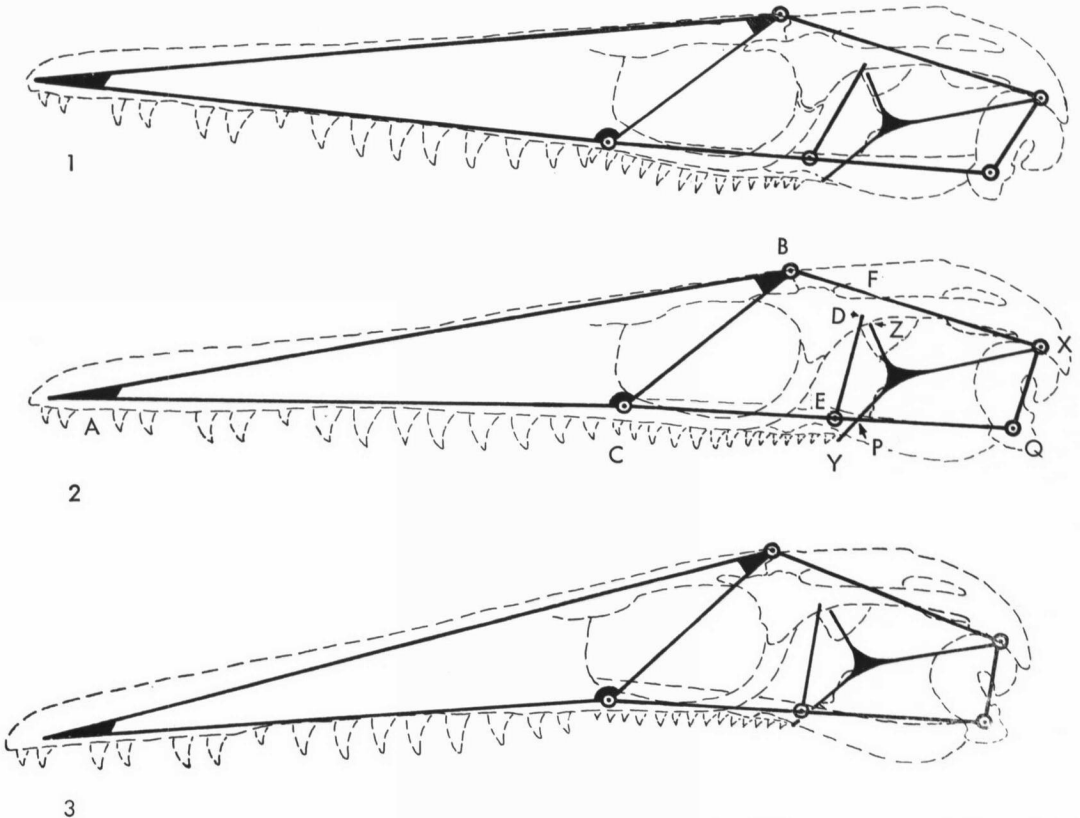

FIG. 10. *Clidastes velox* MARSH, diagrammatic lateral view of cranium showing linkage systems.——*1*. Protraction of basal units.——*2*. At rest.——*3*. Retraction of basal units.

Point *E* indicates the diarthrotic joint between the epipterygoid and the pterygoid whereas point *D* represents its ligamentous articulation with the parietal unit and occipital component.

FUNCTIONAL ROLES OF INTRACRANIAL MECHANISMS

Because of similarities in the structures comprising the head skeletons of *Varanus* and the three mosasaurian genera studied, the following analysis is based, with appropriate modifications, on observations of feeding movements in *Sceloporus*, *Lacerta*, *Gerrhonotus*, and *Varanus* made by FRAZZETTA (1962).

Contraction of the musculus depressor mandibulae (possibly in conjunction with some of the longitudinal ventral throat muscles) brings about the depression of mandible and the concomitant elevation of the muzzle unit. One or more slips of the depressor originate on the suprastapedial process of the quadrate and, upon contraction, draw the retroarticular process and the suprastapedial process toward each other. In effect, mandibular depression causes the rotation of the quadrate about an axis the center of which is determined by the configuration of the articulatory surface of the cephalic head of the quadrate. This rotation, in addition to drawing the head of the quadrate backward, sends the mandibular condyle forward protracting the mandibles.

Varanids have a ligament extending from the lateral face of the pterygoid bone to the retroarticular process that protects the ear from damage by the retroarticular process during excessive depression. In mosasaurs a reduced retroarticular process and a quadrate nearly encircle the tympanum. These modifications of the varanid condition protect the ear in mosasaurs from excessive depression of the jaw. The ligament accompanying the musculus pterygoideus may not have been present in the mosasaurs that had a greatly produced suprastapedial process on the quadrate.

Concomitant elevation of the muzzle unit is also the result of contraction of the protractor pterygoidei and levator pterygoidei muscles. Their contraction activates a series of push-rods represented by the basal units, which then impart both a forward and an upward force through the hypokinetic joint to the base of the muzzle unit.

The musculus depressor mandibulae activates the posterior end of this system. A portion of the depressor originates on the posterior edge of the parietal unit, and thereby pulls the parietal slightly down and back. Anteriorly, coupled with the parietal unit, the posterodorsal portion of the muzzle unit follows passively. Its elevation is facilitated by retraction of the parietal unit. Retraction is limited by the prooticoparietal joint. The downward force acting on the posterior portion of the parietal is opposed by the downward force generated by the musculus levator pterygoidei and the mechanical linkage of the metakinetic joint.

The complexity of the adductor muscles implies complexity of mandibular elevation. Elevation of the mandible involves the integrated action of the musculus adductor externus group, m. pseudotemporalis superficialis, m. pseudotemporalis profundus, m. adductor posterior and m. pterygoideus. The highly complex, pinnate externus series of adductors indicates that a premium is placed on maximum adduction strength per unit area. The adducting musculature sends fiber bundles anteriorly and downward from their origin in the temporal region. Contraction of these muscles produces tremendous vertical and horizontal vectors. The posterior half of the mosasaurian mandible is relatively deeper than in varanids. The deepening can be explained as an increase of surface area for the attachment of adductor and related musculature. Upon contraction of the adductors and the pterygoideus muscles, the mandibles are elevated, the basal units are drawn back, the muzzle unit is depressed (by an active pulling of the basal struts), the parietal unit is protracted, the quadrate is rotated back into its original position and the mandible is retracted. The musculus cervicomandibularis might also function as a mandibular retractor. In varanids a ligament connects the ventral end of the quadrate with the maxillary bone. This ligament limits the amount of separation between the base of the muzzle unit and the foot of the quadrate.

The pterygoideus exerts a posterolateral force on the pterygoid during contraction. This muscle inserts on the posteroventral part of the mandible. Therefore, it also imparts an anteriorly directed force to the mandible. The latter force is nullified by the posteriorly directed component of the ad-

ductor series. The net result of the vectors produced by the pterygoideus is the retraction of the basal units. Excessive retraction is prevented by the notch formed by the quadrate wing and the tuberculum basisphenoideum coming in contact with the basipterygoid process.

The musculus levator angularis oris and the m. adductor posterior insert on the anterior face of the quadrate and tend to draw the head of the quadrate and the anterior part of the mandible together. The contraction of these muscles, coupled with the retraction of the mandible, also forces the foot of the quadrate backward. The quadrate rotates in a parasagittal plane until the posterior half of the dorsal articulatory surface comes into contact with the articular capsule. The articulatory surface on the suprastapedial process bends inward but cants to the outside. The foot of the quadrate is forced to splay out by the articular structure of the posterior part of the quadrate's articulatory surface. This mechanism has been described by KAUFFMAN & KESLING (1960, p. 222). The mosasaurian quadrate eliminates laterally directed forces on the stapes. Careful measurements show that as the quadrate rotates about an axis (nearly coincidental with the meatus) the foot splays out (because of the articulatory angle) at the same rate the head travels inward (on account of the inward bending of the suprastapedial process). Therefore, the distal end of the stapes is not forced in and out of the fenestra ovalis by this quadrate action. The rotation of the quadrate *per se* produces torques on the sound transmitting apparatus. The tympanum is thick, cartilaginous and in many individuals calcified, as is the remainder of the extracolumellar apparatus. The stapes is long, slender and expanded proximally. The proximal expansion is oval and fits snugly into a stapedial canal. The foot plate is smaller than the expanded part. It is apparent that torques set up in the stapes are not transmitted to the inner ear because of the rotational locking of the proximal end. This mechanism is comparable to the "torsion-bar" suspension in some automobiles. The rotational torques are maintained in the stapes distal to the expanded portion. The stapes is insured against being forced into the inner ear by the mechanical arrangement of the stapedial articulation with the rim of the fenestra ovalis (CAMP, 1942:42).

During protraction of the basal units and ele-

vation of the muzzle unit the postorbitofrontal complex moves with the parietal unit. The lamina extending under the frontoparietal joint hinders, but does not prevent, bending, or muzzle rotation about the mesokinetic axis. The descending process articulating with the jugal shows a smooth surface that overlaps an equally smooth surface on the outer face of the jugal. This joint appears to be movable.

The postorbitofrontals are tightly sutured to the squamosals. Between the squamosal and supratemporal a syndesmosis keeps the two from becoming separated. In conjunction with the firm attachment of the postorbitofrontal with the parietal this articulation insures the inclusion of the postorbitofrontal with the parietal unit.

The irregular configuration of the contact line between the frontals and the parietal gives an indication of the complexity of this joint. Although rotation about a transverse axis is possible, rotation about a logitudinal axis is prevented by the interdigitations of these bones. This property is advantageous to an individual that might strike the prey with only one side of the jaws.

Pterygoid action during the cycle of opening and closing the mouth in interesting to follow. During mandibular depression the pterygoids (toothed) are being thrust forward for a new purchase, while during mandibular elevation they are being drawn backward forcing the food to the rear of the mouth.

Depression of the muzzle unit and elevation of the mandibles bring the tips of the two units together. The mouth is then more open to the rear than to the front. Prey struggling to escape follow the line of least resistance, which, in this case, is toward the throat. Rearward curving teeth and retraction of the toothed pterygoids facilitate the progress of the struggling prey toward the throat. This seems to constitute, in a large part, the adaptive significance of intracranial mobility in the mosasaurs studied.

With extreme retraction of the mandibles the intramandibular joint is brought into play. The splaying out of the mandibular condyles of the quadrates tends to swing the dorsal portion of the articular unit outward. The pterygoideus muscle supplements this mechanism by drawing the ventral part of the articular unit inward. Both of these actions cause a longitudinal rotation of the articular unit of the mandible. This rotation is

transmitted to the intramandibular joint where it is translated into transverse rotation. The torque imparted to the dentigerous unit causes it to rotate upward about an axis extending between the intramandibular joints in opposite rami. Transverse rotation of the dentigerous units may also be aided by contraction of the m. cervicomandibularis. Another possible explanation for the deepening of the articular unit is that the increased lever arm provided by the deepened mandible is advanta-geous in the operation of the intramandibular joint.

The highly developed streptostylic condition seen in some mosasaurs is correlated with drawing prey into the rear of the mouth. This process is also integrated with the retraction of the toothed pterygoids. Both the above and the mechanisms of kinesis provide the mosasaurs with an efficient swallowing mechanism that would be especially advantageous in the sea.

SUMMARY AND CONCLUSIONS

With the aid of models, dissections, examination of fossil material and the literature certain observations and interpretations concerning intracranial mobility in mosasaurs are made.

Mosasaurs considered in this study possess two dorsal, movable joints. According to Frazzetta's (1962) classification, these mosasaurs are amphikinetic. The mechanisms involved in the development of the highly specialized quadrates in mosasaurs seem to result from the maintenance of the hearing apparatus.

In addition to the bony units proposed by Frazzetta (1962) for *Varanus*, mosasaurs possess two units within the mandibular component, the anterior or dentigerous unit, and the posterior or articular unit. A well-developed intramandibular joint separates these two units.

The adaptive significance of cranial kinesis is discussed in terms of providing an "escape route" for the prey toward the throat and the toothed pterygoids. Adaptive significance of streptostyly and intramandibular mobility is also considered as being integrated with cranial kinesis, as all are well adapted to the same end, namely securing prey.

Russell (1964) observed that kinesis is lost in some of the more specialized mosasaurs. The degree of kinesis is variously reduced, depending on the genus, in mosasaurs studied by me as compared with the condition in living varanids. This reduction and loss of kinesis (but maintenance of streptostyly and development of intramandibular mobility) seems to be, as Russell also observed, correlated with a loss in effectiveness of inertial feeding (described by Gans, 1961, p. 218). The maintenance of streptostyly indicates that this method of deglutition is more advantageous in underwater feeding than cranial kinesis. Development and operation of the intramandibular joint are also correlated with the specialization of the quadrate apparatus. This specialization provides a device that permits extreme retraction of the mandibles.

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