THE CONSTRUCTION FOR FEEDING IN RATTLESNAKES

by

P. DULLEMEIJER and **G. D. E. POVEL**

Zoölogisch Laboratorium der Rijksuniversiteit, Leiden

With 5 text-figures and one plate

INTRODUCTION

A controversial point in the understanding of the feeding mechanism of viperid snakes is the use of the poison fang in the swallowing mechanism. Some authors believe that the poison fang takes an active part in the swallowing act, although the majority supports the view that the fang is, at least partly, held down (Klauber, 1956). Which kind of construction in the jaws is responsible for the difference between the actions of the fang in striking and swallowing again is a matter of dispute. The pterygoid-ectopterygoid joint, which by most authors (Kathariner, 1900; Willson, 1908; Haas, 1931; Klauber, 1939, 1956) is considered stiff or immovable, may play a crucial role. There is also some disagreement on the strike being either a stab (Van Riper, 1953) or a true bite. This paper reports on new information to solve these problems.

The mechanism itself is interesting from a general functional-anatomical point of view, since it presents a case of formation of a delicate structural balance to meet two contradictory demands in a part of the feeding-construction.

The presence of a large poison fang apparently has far-reaching consequences for the construction of the swallowing mechanism.

MATERIAL AND METHODS

The main observations were made with *Crotalus ruber ruber* Cope. Additional information was obtained from some *Crotalus viridis helleri* Meek.

The movements of the various bony elements were studied with the aid of 16 mm movies, film speed 25 frames/sec. The films were analysed with an analector, Oude Delft.

X-ray cinematography was applied by means of an illumination intensifier of 50 kV., giving a light intensity increase of about 1000 times. Only the noise in the electron beam and on the screen prevented a frame by frame analysis of the very small bones.

To facilitate accurate drawing and measuring of the movements, short shots were taken, a "freezing" of the movements during swallowing and yawning. The shots were made at 100 kV., 400 mA., $^1/_{50}$ sec., with a Siemens Gigantos X-ray tube from a distance of 75 cm. Object-film distance was less than 10 cm. When necessary, the tube was moved electronically without disturbing the animal, the focussing controlled by a light square and by monitoring on a T.V. control panel. The normal movie and the X-ray movie were used as a base to determine the order in the series of randomly taken shots.

The snake was kept in a cage of 50 × 50 × 50 cm. At one corner a 95 cm long, 10 cm wide, thin-walled (0.2 mm) plastic passage of equal height was attached, in which a metal slide could be inserted to separate it from the main cage. The passage gave it enough room to easily swallow relatively big prey. On the other hand, it was narrow enough to keep the snake close to the film. A proper performance was obtained by making use of its normal feeding behaviour (Dullemeijer, 1961). For some days the snake was kept in the main cage with inserted slide. A prey animal, a thin thread tied to its tail end, was brought into the cage through the opened slide.

After the strike, a trail was made by leading the dead prey animal into the passage. After a while the snake started searching for its prey, accurately following the trail to the far end of the passage. The slide was closed and the feeding could easily be filmed and observed. The film was attached to a special holder which could be moved, together with the tube, next to the passage, to keep the distance constant. This combination with a long tube-object-distance provided the conditions for shadows without noticeable geometric unsharpness. Most of the blurring effect on the pictures is caused by the scattering of secondary radiation in soft tissues. It gave a greyish background shadow. For the dorso-ventral shots, a cage with a transparent bottom and lid were used. For the rest the procedure was the same. It took somewhat longer for homing, the snake regularly twisted the head, apparently looking with one eye downward. However, as soon as the prey animal had been inserted, the behaviour pattern became normal.

As control observations a number of radiographs from various angles were made of a snake's head skeleton and of a complete dead head of about the same size. Such control observations provided the necessary information about the differences in shadows of elements projected from various angles. They facilitated a decision on which type of movement took place, e.g., total head movement, sliding or rotating of elements in respect to each other.

MICROTECHNIQUE

Since apparently one or more articulations were involved in the various movements of the swallowing act and the strike, it was appropriate to make a rather detailed study of their structures. Relevant parts of rattlesnakes (1 *Crotalus ruber*, 1 *Crotalus cerastes*, 1 *Crotalus scutellatus*, 2 *Crotalus atrox*, and 2 *Crotalus viridis helleri*) were fixed in formaldehyd 4%. Some parts were cut in paraffin after decalcification and stained with the procedure of Gallego in a modification of Lilie (1954).

Reconstruction and detailed investigations were performed on two heads (*Crotalus viridis* and *Crotalus ruber*) embedded in epon. Polymerisation was done as carefully as possible. The epon, after being placed for some days in an exicator with hygroscopic material, became rather viscous. In order to obtain a good penetration, the skin was removed and the head was immersed as long as possible at room-temperature. The epon hardened in one or two days at 37°C. A completion of the hardening was obtained by placing it a couple of days at 60°C. Epon sections can easily be orientated by milling narrow grooves in the rectangularly sawn block. A fairly large number of reference grooves was used to make corrections possible.

Each head was cut on a rotary microtome (Leitz-Wetzlar Minot, type 1212), the angle of the steel knife was about 55°. Half of each head was cut to parasagittal sections, the other half to transverse sections. The sections were 10 μ thick and stained with Mallory-Cason during 24 hours at room-temperature.

The longitudinal sections of *Crotalus ruber* were of poor quality due to a bad penetration of the epon into the brain, which stayed rather sticky.

Some sections were stained to get a differentiation between collagen and elastic fibres with a modification of the method by Schanz & Schecter (1965).

The following procedure gave relatively good results.

1. Stretching of the sections in water at 85°C.
2. Flooding the sections with 4% Fe $NH_4(SO_4)_2$ in destilled water during 45-50 seconds at 85°C.
3. Cleaning with destilled water and drying at 85°C.
4. Staining during 2 minutes at the same temperature with hematoxylin (10 mg/100 ml alcohol 95% diluted 1 part on 20 parts destilled water), 3 drips of saturated Li_2CO_3 per section added.
5. After rinsing and drying, staining during 1½ hour with 1% safranin O (cert. no. NS-30).
6. Rinsing, drying and covering with neutral epon.

Collagen and reticular fibres stain blue to black, elastic fibres red to orange. The colour intensity depends strongly on the thickness of the sections.

Some paraffin sections were stained with a modification of the orcein-method of Lewis and Jones, modified by Humason & Lushhaugh (1960), by staining during five minutes with Mallory-Cason instead of methyleneblue. A further modification consisted of extending the time of exposure for orcein (1 mg in 70% ethanol and concentrated HCl 0.6 ml) to 15-20 minutes at 37°C.

After rinsing in ethanol and water during 10-15 minutes, 5% phosphomolybdic acid was applied.

Collagen and reticular fibres stain deep blue, elastic fibres brilliant red.

RESULTS

Morphology. — Although most head elements have been described earlier (Dullemeijer, 1956, 1959) and information on related species is available (Bolt & Ewer, 1964; Bourgeois, 1965; Brattstrom, 1964; Liem, Marx & Rabb, 1971) some observations motivate additional and corrective descriptions.

In the scope of this investigation, the loose contact in the articulation between quadrate and pterygoid must be stressed. Two flat surfaces are surrounded by a thin and very wide capsule. A ligament from the pterygoid to the quadrate (Versluys, 1936; Dullemeijer, 1956) gives the pterygoid much freedom of movement (see also Liem, Marx & Rabb, 1971, for *Azemiops* and related species).

The articulation between the ectopterygoid and the pterygoid is generally described as a tight connection between both elements (Klauber, 1939, 1956; Dullemeijer, 1959), or not mentioned at all (Bolt & Ewer, 1964; Liem, Marx & Rabb, 1971), although a fibrous contact exists. The general shape of the articulation surfaces is very similar to that in *Vipera* (Dullemeijer, 1956).

The pterygoid has a convex surface which is slightly more triangular in a caudal cross-section than in a rostral one (fig. 1). Further caudally, the surface becomes flatter. The ventral surface of the ectopterygoid overcaps it over some distance, but deviating laterally. The lateral distance is larger than the medial one. Medially the ectopterygoid extends over a longer distance ventrally. Caudally the articulation surfaces are more incongruent, particularly in the center, where a triangular space filled with fibres is found. There is no articular cartilage. The articular surfaces are covered with a fibrous cushion, a thick direct continuation of the periost. Collagen fibres and a small percentage of elastic fibres fill the entire space. They run in caudodorsal direction from the pterygoid to the ectopterygoid. In rest position

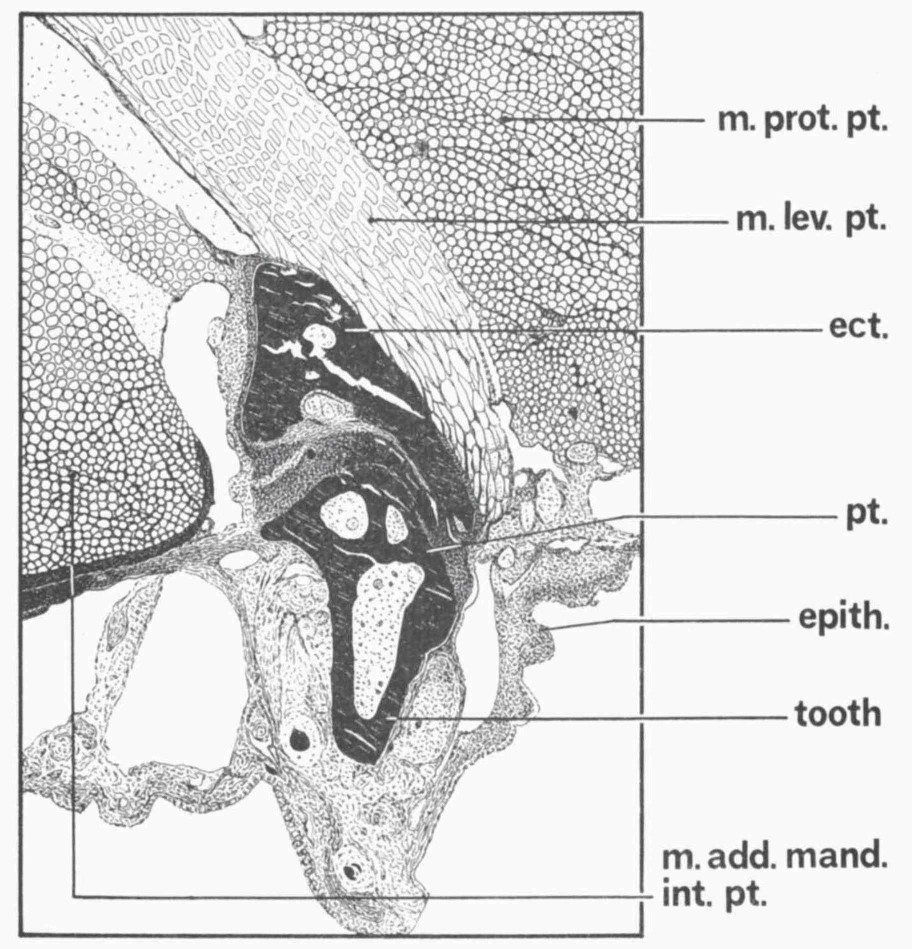


Fig. 1a. Microscopic cross-section through the right ectopterygoid-pterygoid articulation in *Crotalus viridis helleri*. ect., ectopterygoid; epith., epithelium of the mouth; m. add. mand. int. pt., musculus adductor mandibulae internus pterygoideus; m. lev. pt., musculus levator pterygoidei; m. prot. pt., musculus protractor pterygoidei.

the fibres are unstretched, which suggests they allow movement in various directions. The space between the articular surfaces can be increased. Some torsion or change of the angle between the pterygoid and ectopterygoid, as well as a parallel shift of these elements seems possible.

The torsion occurs as a movement of the pterygoid over a conical surface, the tip of the cone being the ectopterygoidal surface. This movement requires only little change in the joint, yet allows the caudal end of the pterygoid to move over a large area. Shift and axial rotation of the pterygoid are limited

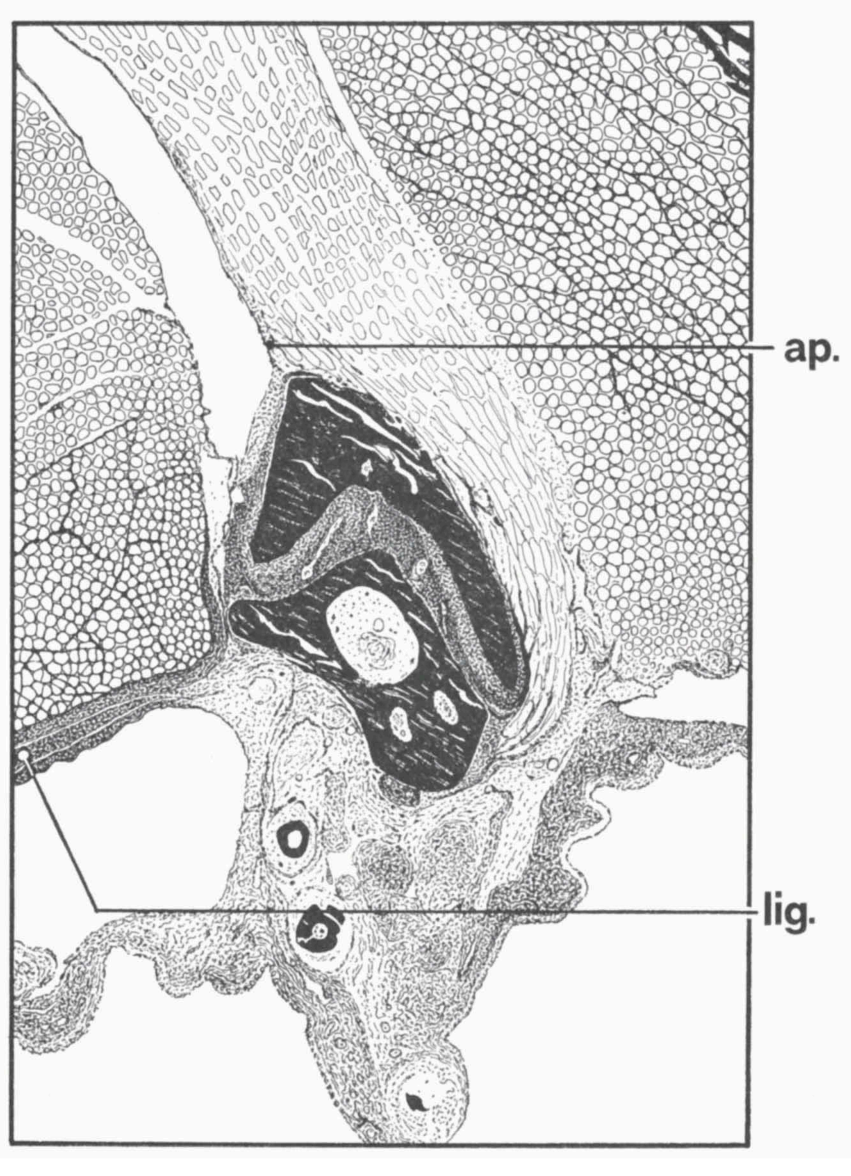


Fig. 1b. Microscopic cross-section through the right ectopterygoid-pterygoid articulation in *Crotalus viridis helleri*. ap., aponeurosis; lig., ligamentum quadrato-maxillare.

by the collagen fibres.

Just in front of the joint is a side branch of the ligamentum quadrato-maxillare attached to the ectopterygoid.

The musculus levator pterygoidei is attached to both the ectopterygoid

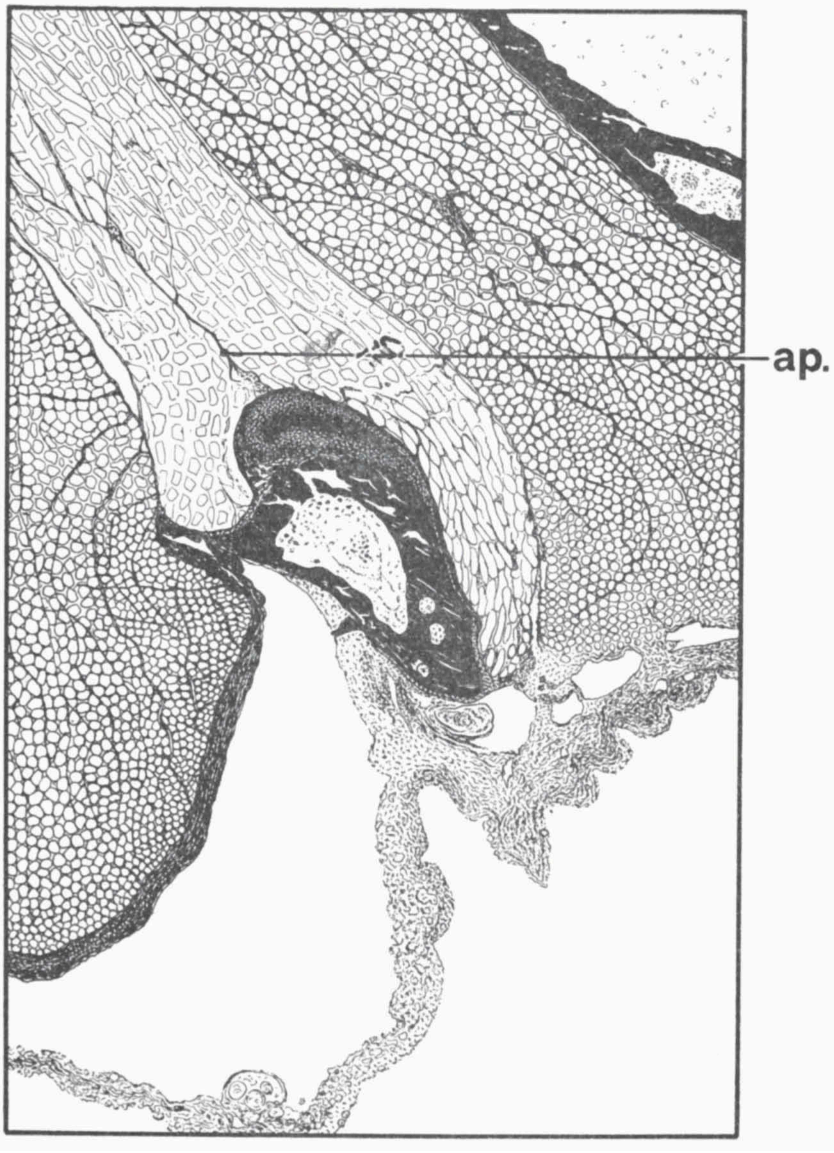


Fig. 1c. Microscopic cross-section through the right ectopterygoid-pterygoid articulation in *Crotalus viridis helleri*. ap., aponeurosis.

and the pterygoid. As can be seen in figure 1b, the area of attachment to the ectopterygoid lies on the medial surface of the bone, which is more or less triangular in cross-section. Laterally the muscle is attached by means of a thin aponeurosis to the top ridge of the ectopterygoid, in cross-section to the top of the triangle. Further caudally, the muscle extends over the articulation and reaches the pterygoid with a small bundle of fibres. Somewhat more caudally the muscle gets a second part laterally, attached to the thin aponeurosis. Caudally this part overcaps the articulation laterally. Here it is musculously attached to a gutter in the pterygoid. The thin aponeurosis is attached to a similar ridge on the pterygoid. Dorsally neither part of the muscle can be distinguished.

The ligamentum postfrontale-maxillare is probably the rostral part of the ligamentum quadrato-maxillare, which in the common viper runs uninterrupted from the quadrate via the postorbital or postfrontal to the maxilla. In *Crotalus* only the caudal part could be found at the time (Dullemeijer, 1959). Now the junior author succeeded in tracing the rostral part, running from the ventro-lateral ridge of the pit to the distal tip of the postfrontal. It runs between the nerves that innervate the pit. The fibres are loosely packed. More caudally the ligament is tighter and broadens to a flat band.

Movements in the upper jaw. — There are three acts in which the bony elements of the head, particularly those of the upper and lower jaw, take part: the strike, the swallowing and the yawning. Each of them makes specific and not always similar demands upon the construction. Specifically the dissimilarity between striking and swallowing in the demand upon the upper jaw seems to determine the typical crotalid (or viperid?) construction.

It is practically impossible to "freeze" the strike in a röntgenogram, since it is too quick and impredictable as to place and time. High speed photography cannot be applied for X-rays. There is a possibility to obtain some information about the movements during the strike by comparing them with those during the regularly occurring yawn.

After several strikes, particularly after missing the prey, and after many swallowing acts, the snake yawns. A comparison of these yawns with the strikes, filmed with high speed photography, reveals a good resemblance between strike and yawn, as judged from the movements of the outer structures and the position of the teeth, particularly the fang. Although no direct observations on the internal situation could be made, we felt justified in using the yawning movement as a model for the strike.

Before drawings and measurements from the röntgenograms of the yawning snake were made, röntgenograms of a dry skeleton were taken from various angles.

This procedure was necessary because the description of the movements was based mainly on changes in shadow sizes, partly on shadow shapes. Such changes, however, can be caused by a movement of the total head, thus resembling the shadow change of jaw movements. The shadows of the braincase elements served as lines and points of reference to determine the position of the entire head. In this way it could be ascertained whether the changes in shadow of the jaw elements represented movements of these elements only, or which part of the change had to be traced to these movements. Any non-parallel movement of a bony element had to be read off from the change of the shadow form.

Two phenomena were of particular importance: the shape of the shadow of the pterygoid and the size of the shadow of the quadrate.

A comparison of the figures a and b on plate 1 shows an important difference in the shadow of the pterygoid. In lateral projection it is a dark line with a vague, curved area on top. In latero-dorsal projection, the curved area is bordered by a darker shadow, whereas the dark line has become somewhat lighter. Some change also can be observed in the shadow of the ectopterygoid. The shadow of the quadrate has become longer in a latero-dorsal projection. From the pictures it is also apparent that the movement of the entire head and the direction of the projection can best be derived from the shadows of the cerebral skull.

Yawning. — The yawning occurs in two intensities, one in which hardly any movement of the maxilla or erection of the poison fang can be observed, and another in which the fang is completely erected. It is not uncommon that the snake yawns with different intensities for each jaw (pl. 1 fig. f). Figure 2 gives a diagrammatic representation of the movements as observed from the röntgenograms.

In both ways of yawning the medial end of the quadrate moves rostro-dorso-medially. This can be seen clearly in lateral as well as dorsal projection. The supratemporal-quadrate joint leaves much freedom (Dullemeijer, 1959), but nevertheless the supratemporal has to turn medially. In the yawn of the first type, the shadow of the quadrate is enlarged in lateral projection and the caudal end is moved dorsally. The quadrate-lower jaw joint is moved dorso-caudo-medially. The caudal end of the pterygoid hardly changes position with respect to the quadrate. Only the shadow of the pterygoid becomes longer and the angle between the shadow of the ectopterygoid and the pterygoid decreases. The angular point (= the joint between ectopterygoid and pterygoid) stays in the same transverse plane; it moves dorsally along an almost vertical line. An elongation of the shadow together with a change in the angle can only be explained by a rotation of the pterygoid around an axis through the ectopteryoid. This must be due to either a rotation of the entire upper jaw or to a rotation of the pterygoid only in the ectopterygoid-pterygoid joint. As the hinge-joint between the ectopterygoid and the maxilla does not allow such a rotation and the maxilla does not move noticeably, it follows that the joint between the pterygoid and the ectopterygoid must allow it. The change in the angle may be caused by a rotation around a horizontal transverse axis in the joint, but this would not quite explain the enlargement of the pterygoid shadow.

The change in length of the shadow can be explained completely by supposing a rotation around an axis situated in a direct line with the ectopterygoid (fig. 3). The angle of rotation could not exactly be determined, because it was uncertain whether the ultimate position was reached. Supposing it

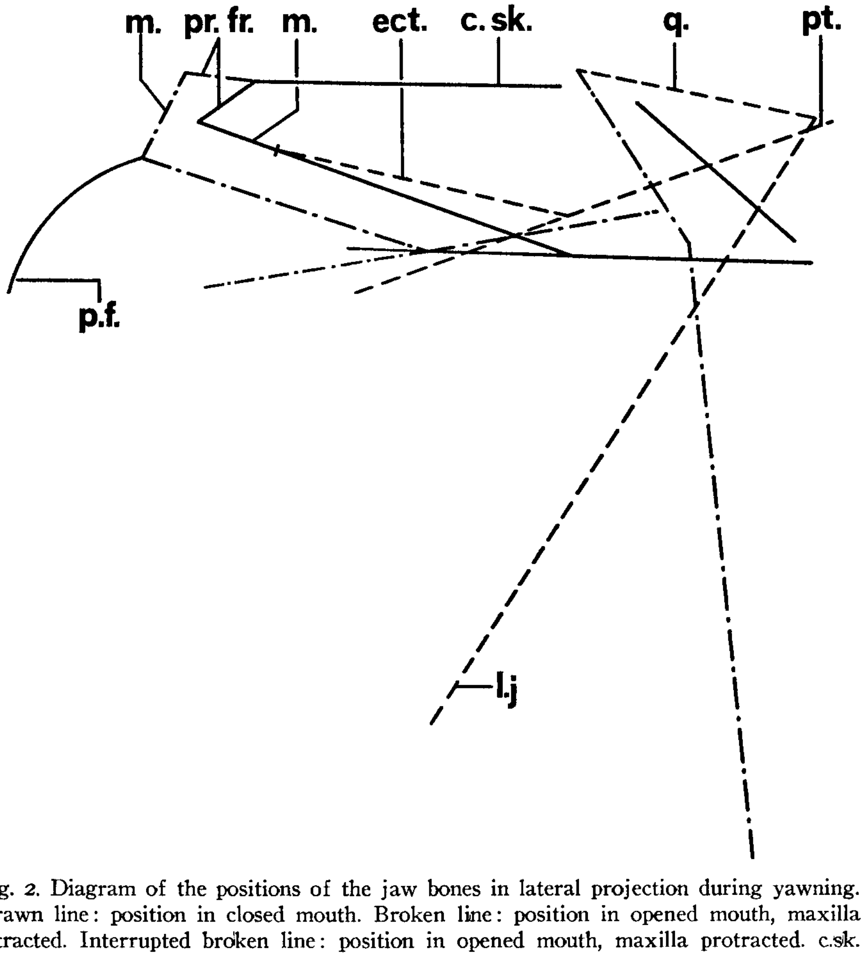


Fig. 2. Diagram of the positions of the jaw bones in lateral projection during yawning. Drawn line: position in closed mouth. Broken line: position in opened mouth, maxilla retracted. Interrupted broken line: position in opened mouth, maxilla protracted. c.sk. cerebral skull; etc., ectopterygoid; m., maxilla; l.j., lower jaw; p.f., poison fang; pr.fr., prefrontal; pt., pterygoid; q., quadrate.

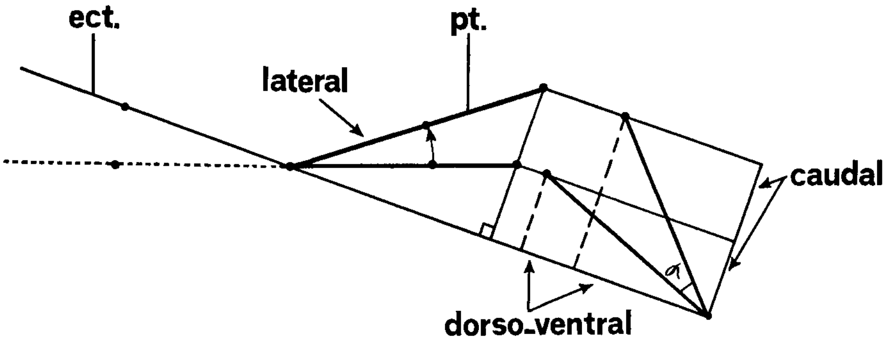


Fig. 3. Diagram of the projection of the pterygoid during rotation around an axis through the ectopterygoid. etc., ectopterygoid; pt., pterygoid; α, angle of rotation. The terms with the arrows indicate the planes of projection.

was, the angle could be estimated at about 45°. The actual rotation is probably far less.

Several muscles can be involved in this type of yawning. The lift of the joint can be carried out by the musculus levator pterygoidei, which may also be responsible for the rotation. It is very unlikely that the musculus protractor pterygoidei should play a part (compare the second type of yawning).

Since the position of the pterygoid in respect of the quadrate stays about the same, there must be other muscles moving the quadrate. Most likely they are the posterior part of the musculus depressor mandibulae, opening the mouth, and the musculus cervico-mandibularis, of which the direction of the working line is dorso-medio-caudal (Kochva, 1962; Liem, Marx & Rabb, 1971). Liem, Marx & Rabb (1971) noticed the difference in size of the two parts of the depressor muscle, which is accounted for by the described activity. The posterior part seems only to pull the joint dorsally both in opened and in closed position of the lower jaw.

In the second type of yawning the poison fang is erected by a turning of the maxilla (pl. 1 fig. f, fig. 2). The maxilla is pushed forward by the ectopterygoid, which in its turn is moved by the pterygoid. The ectopterygoid moves almost parallel to its rest position, the angle between ectopterygoid and pterygoid is slightly decreased, but far less than in the first type of yawning.

The caudal end of the pterygoid moves dorsally with respect to the quadrate. The length of the shadow of the pterygoid does not change. In contrast with the first type of yawning the quadrate now moves forward and somewhat dorsally. Probably the ventral end shifts slightly laterally, judging from the shortening of the shadow in lateral projection. The dorsal end, however, arrives at the same spot as in the first type of yawning.

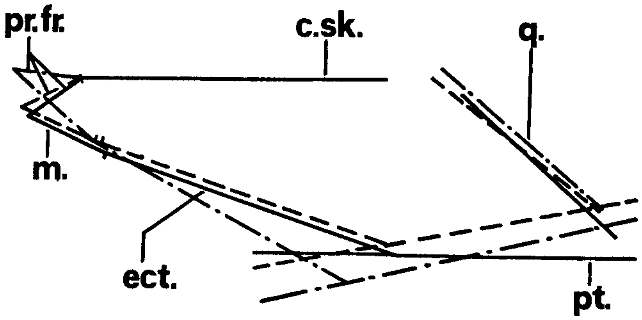


Fig. 4. Diagram of the positions of the jaw bones in lateral projection during swallowing. Drawn line: position in closed mouth. Broken line: position in closed mouth with prey. Interrupted broken line: position with protracted maxilla. c.sk., cerebral skull; ect., ectopterygoid; m., maxilla; pr.fr., prefrontal; pt., pterygoid; q., quadrate.

In dorsal projection a slight lateral turn of the maxilla and the palatine could be observed, which probably implies that the entire jaw is moved somewhat laterally.

The entire movement can easily be explained by the contraction of the musculus protractor pterygoidei. The muscle moves the entire jaw slightly laterally, lifts the pterygoid, but mainly protrudes the ectopterygoid. The angle between ectopterygoid and pterygoid can decrease a little by the flexibility in the joint between both elements. The lowering of the lower jaw is mainly caused by a contraction of the anterior part of the musculus depressor mandibulae, whereas the posterior part can cooperate in the protrusion by moving the quadrate dorsally.

The shape of the shadows of the pterygoid confirm the difference in rotation of the pterygoid in the two types of yawning, as described before.

Swallowing. — In contrast with the yawning and the strike, the swallowing is characterised by a considerable movement of the entire head. To reach a further hold of the prey by the upper and lower jaw on one side, the snake turns its head around an axis somewhere in the caudal region of the two jaws of the other side. No doubt the epaxial as well as the hypaxial muscles in the cervical region play an important role in this act. As was explained earlier (Dullemeijer, 1956), the cervical muscles also act during the swallowing by pushing the cerebral skull forward between the jaws. The total head movement is shown on the pictures in figure 5, drawn from a normal movie.

Quantitative data on the distance of the movements could not be obtained. The movement of the total head considerably hampers cinefluorographic analyses. But we succeeded in obtaining a series of photographs showing fairly well the successive positional changes of the jaws during the swallowing by selecting photographs meeting the above mentioned criteria for comparison. The following general pattern of movement emerges from the various observations (fig. 4). Two phases may be distinguished: a, the closed position of the jaws with the prey and b, the bite.

It is convenient to compare the closed position with the rest position first. In closed position, the quadrate has moved dorsally and the dorsal end has turned somewhat rostrally. There is no turn in the transverse plane, the shadow keeps the same length in both projections. The caudal end of the pterygoid has moved dorsally, considerably caudal to the quadrate. Remember that the ligament and the articulation allow a wide range of movement of these elements in relation to each other. The angle between ectopterygoid and pterygoid has become smaller and the length of the shadow of the pterygoid has slightly increased. This means that the pterygoid has rotated around the axis of the ectopterygoid, which involves a shorter distance from the pterygoid to the skull. There is a very slight upward movement of ectopterygoid and maxilla.

In the bite the shadow of the quadrate is either somewhat shorter or has stayed the same; the entire quadrate has been moved upward. The caudal ends of quadrate and pterygoid have the same relative positions in the two phases.

As in closed position, the angle between the ectopterygoid and the pterygoid has become smaller, only the shadow of the pterygoid has increased considerably in length. It has reached its maximal length, which means that the pterygoid is perpendicular to the X-ray beam. There is a forward movement of the ectopterygoid and the maxilla, but no turn. Only the prefrontal has swung upward. All this means that the upper jaw turns from medial to lateral around a parasagittal horizontal axis on a level with the prefrontal, which is confirmed by the observations from the movies (fig. 5). On these pictures a lateral turn of prefrontal and maxilla can be observed, which movement shortens the distance between jaw and skull at the point of the ectopterygoid-pterygoid joint. In the meantime the pterygoid is rotating around the ectopterygoid axis, its caudal end moving laterally, but staying in the same transverse plane during the entire swallowing act. Such a movement widens the oral cavity substantially. These observations are at variance with those of most authors, who describe a medial movement of the caudal end of the pterygoid. (See for references, Klauber, 1956.) The rotations are allowed by the prefrontal articulations, but not by the maxilla-ectopterygoid articulation.

The muscle that lies in the most favorable position for causing these movements is undoubtedly the musculus levator pterygoidei. Hardly any cooperation may be expected from the musculus protractor pterygoidei, which can be derived from the fact that the caudal end of the pterygoid does not move rostrally. The cooperation, if any, is limited as compared with that in the yawn.

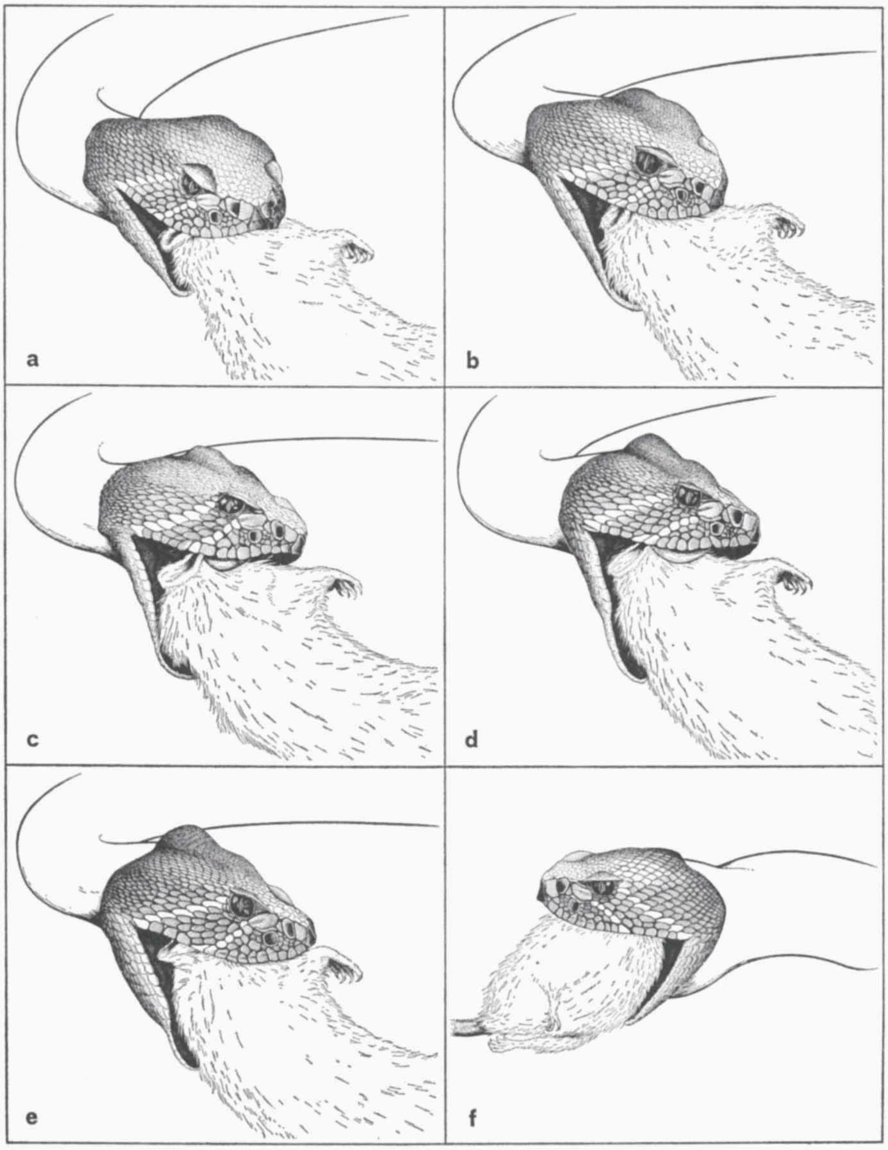


Fig. 5. Drawings of a series of pictures taken from a movie of the swallowing act.

The consequence of the movements is that the rostral parts of the pterygoid and the palatine are moved downward and forward, thus exposing the teeth on these elements beyond the poison fangs, which remain in unerected position. This exposition is amplified by the rotation of the entire head mentioned above. Once the teeth hook into the prey, the lower jaw is elevated, the upper jaw is moved backward and laterally by the adductor muscles, but probably also passively by pushing the prey against the substratum. The teeth are released by a return to the rest position and then the entire sequence is repeated.

The larger the prey, the further the upper jaw is pushed laterally. In such a situation the snake has difficulties in swallowing.

It is understandable that particularly the cervical region plays an important role and that, once the prey has been partly swallowed, the peristaltic movement of the esophagus helps in the act.

Conclusions

The described construction in the rattlesnake's head is a delicate balance between adaptations to striking and to swallowing. In many respects the construction shows compromise situations, particularly in the articulations.

Putting it in terms of demands and design it can be stated that a poisoning apparatus needs a strongly determined movement pattern of the various elements. Actually, the maxilla should only move in one plane and should be held firmly in place during the poisoning. The upper jaw should consist of a stiff bar which should move straight forward, activated by a muscle running in the same direction. Any caudal suspension of the upper jaw to the skull would be superfluous or should be as loose as possible. The lower jaw must be turned away as far as possible. In an earlier paper it is described how this is done and which part the cervical muscles play in this act (Dullemeijer, 1959).

On the other hand, the construction for swallowing needs a highly movable system. The poison fang is more a nuisance than of any help. The upper jaw must be lifted as far as possible, which needs a suspension by a quadrate movable in any direction. The muscles should run almost perpendicular to the jaw, although with some rostral component of their forces. The lower jaw must be able to turn to a certain extent, but not as far as in the strike.

A general survey of the construction shows the following. The prefrontal-frontal and the prefrontal-maxilla articulations show more or less a combination. The joints direct the movement straight forward, but the lateral parts allow a free movement. The dual structure of these joints has also been described for other viperid snakes (Liem, Marx & Rabb, 1971).

By the slight rotation described above, the snake makes use of the second possibility, whereby the poison fang can remain almost unerected notwithstanding the forward movement of the transversum. For the movement, the exact role of each detail in the surfaces of this articulation and the ligament is not yet known. It is clear that the maxilla-ectopteryoid articulation is mainly an adaptation to the strike. It can be used for the swallowing act, but is in fact more of a handicap. (Compare the situation in pythons, Frazetta, 1966.)

The articulation between the pterygoid and the ectopterygoid plays a crucial role in combining the demands. Its stiffness allows the musculus protractor pteryoidei to apply almost its total force in the strike.

From the diagram some inefficiency can be observed, partly by the movability of this joint, partly by the course of the muscle. The movability allows the pterygoid to rotate in two directions during the swallowing act, one around the longitudinal axis of the ectopterygoid and another perpendicular to the medial plane, decreasing the angle between the pterygoid and ectopterygoid. Both rotations allow the exposition of the pterygoid and palatine teeth. It is clear that a looser joint would facilitate these rotations much better.

Apparently we are dealing with a compromise situation of a very delicate nature. A slightly looser connection would interfere considerably with the strike, a slightly more stiff connection would make swallowing impossible. The combined demands explain its structure sufficiently. These demands are:

a. rotation of the pterygoid around an axis parallel to or in the ectopterygoid;
b. rotation around a horizontal axis perpendicular to the midsagittal plane;
c. attachment of the musculus levator pterygoidei;
d. a fairly stiff connection.

The demands a. and b. lead to an elongated cylindrical surface of one of the elements with the other surrounding it like a beak. The distance between the articular surfaces must be smaller in the centre. Demand c. places the cylinder on the pterygoid and demand d. results in a fibrous connection of both surfaces with a specific direction and length of the fibres (fig. 1). The direction of the connecting fibres most likely ranges between very limited values only. Calculations as to this assumption have not yet been made.

The loose connection of the pterygoid with the quadrate is an adaptation to swallowing when the jaw bears a large fang. The pterygoid must be moved far dorsally and medially to expose the pterygoid teeth. It is not quite clear why this is realised in two joints each allowing a certain amount of dorsal movement.

The odds are that on the one hand the supratemporal-quadrate joint is loose because of the adaptation to the strike, given the necessity of a suspension, and on the other the quadrate-pterygoid connection is loose because of the swallowing-demand, given the limited movement of the supratemporal. Here seems to be a kind of compromise too. The supratemporal-quadrate joint is not optimally adapted to swallowing, whereas the quadrate-pterygoid joint seems to be less suitable for the strike.

The curvature in the pterygoid is important in the swallowing act, because a simple rotation widens the mouth cavity considerably. It is hard to see why it must have this very shape.

The course of the muscles corresponds fairly well with the expected one, although some compromise is also present. In each act there are probably different muscles active, which means a separation in activity.

The musculus levator pterygoidei has an almost ideal course, only little of the force is ineffective for the movement. The most plausible inference would be that the position and particularly the curved shape of the upper jaw are adaptations to the position of the muscle.

The musculus protractor pterygoidei has a favorable course too. For this muscle a similar reasoning holds. As said above, some compromise is found because of its slight deviation from the direction of movement.

The musculus depressor mandibulae is divided into two parts (Dullemeijer, 1956, 1959). It is highly probable but not yet proven that the longer part acts in the strike and the smaller on other occasions.

All these observations and deductions make it clear that the combination of striking and swallowing can explain many adaptations in the snake's head. The presence of a poison fang implies a series of adaptive modifications, many of which are compromise situations to a larger or smaller degree.

ACKNOWLEDGEMENTS

We thank Mr. B. van Schie and Mr. J. Simons for their technical assistance in making the röntgenograms and the movies. We are grateful to Mr. J. de Vos for keeping the animals in such excellent condition and Mr. N. Teegelaar for preparing the drawings.

SUMMARY

The position in *Crotalus ruber* of the jaw bones during yawning and swallowing was analysed by means of cinefluorographic technique. The analysis revealed that the joint between ectopterygoid and pterygoid is of crucial importance to produce various positions of the bones during swallowing and yawning.

Microtechnical investigations showed a structure which can be regarded a compromise between the demands of the aforementioned activities.

Literature cited

Bolt, R. E. & R. F. Ewer, 1964. The functional anatomy of the head of the puff adder, Bitis arietans (Merr.). — Journ. Morph., 114: 83-106.

Bourgeois, M., 1965. Contribution à la morphologie comparée du crâne des ophidiens de l'Afrique Centrale. — Publ. Univ. Off. Congo, Lubumbashi, 18: 1-293.

Brattstrom, B. H., 1964. Evolution of the pit vipers. — Trans. San Diego Soc. Nat. Hist., 13: 185-268.

Dullemeijer, P., 1956. The functional morphology of the head of the common viper, Vipera berus (L.). — Arch. néerl. zool., 11: 388-495.

——, 1959. A comparative functional anatomical study of the heads of some Viperidae. — Morph. Jb., 99: 881-985.

——, 1961. Some remarks on the feeding behaviour of rattlesnakes. — Proc. Kon. Ned. Akad. Wetensch., Amsterdam, (C) 64: 383-396.

Frazetta, T. H., 1966. Studies on the morphology and function of the skull in the Boidae (Serpentes). Part II, Morphology and function of the jaw apparatus in Python sebae and Python molurus. — Journ. Morph., 118: 217-296.

Haas, G., 1931. Die Kiefermuskulatur und die Schädelmechanik der Schlangen in vergleichender Darstellung. — Zool. Jb., Abt. Anat. Ontog., 53: 127-198.

Humason, G. L. & C. C. Lushhaugh, 1960. Selective demonstration of elastin, reticulum and collagen by silver, orcein and aniline blue. — Stain Technology, 35: 209-214.

Kathariner, L., 1900. Die Mechanik des Bisses der solenoglyphen Giftschlangen. — Biol. Zbl., 20: 45-53.

Klauber, L. M., 1939. A statistical study of rattlesnakes. VI, Fangs. — Occ. Papers San Diego Soc. Nat. Hist., 5: 1-61.

——, 1956. Rattlesnakes, their habits, life histories, and influence on mankind. Univ. California Press, 1476 p.

Kochva, E., 1962. On the lateral jaw musculature of the Solenoglypha with remarks on some other snakes. — Journ. Morph., 110: 227-284.

Liem, K. F., H. Marx & G. B. Rabb, 1971. The viperid snake Azemiops: its comparative cephalic anatomy and phylogenetic position in relation to Viperinae and Crotalinae. — Fieldiana, Zoology, 59: 65-126.

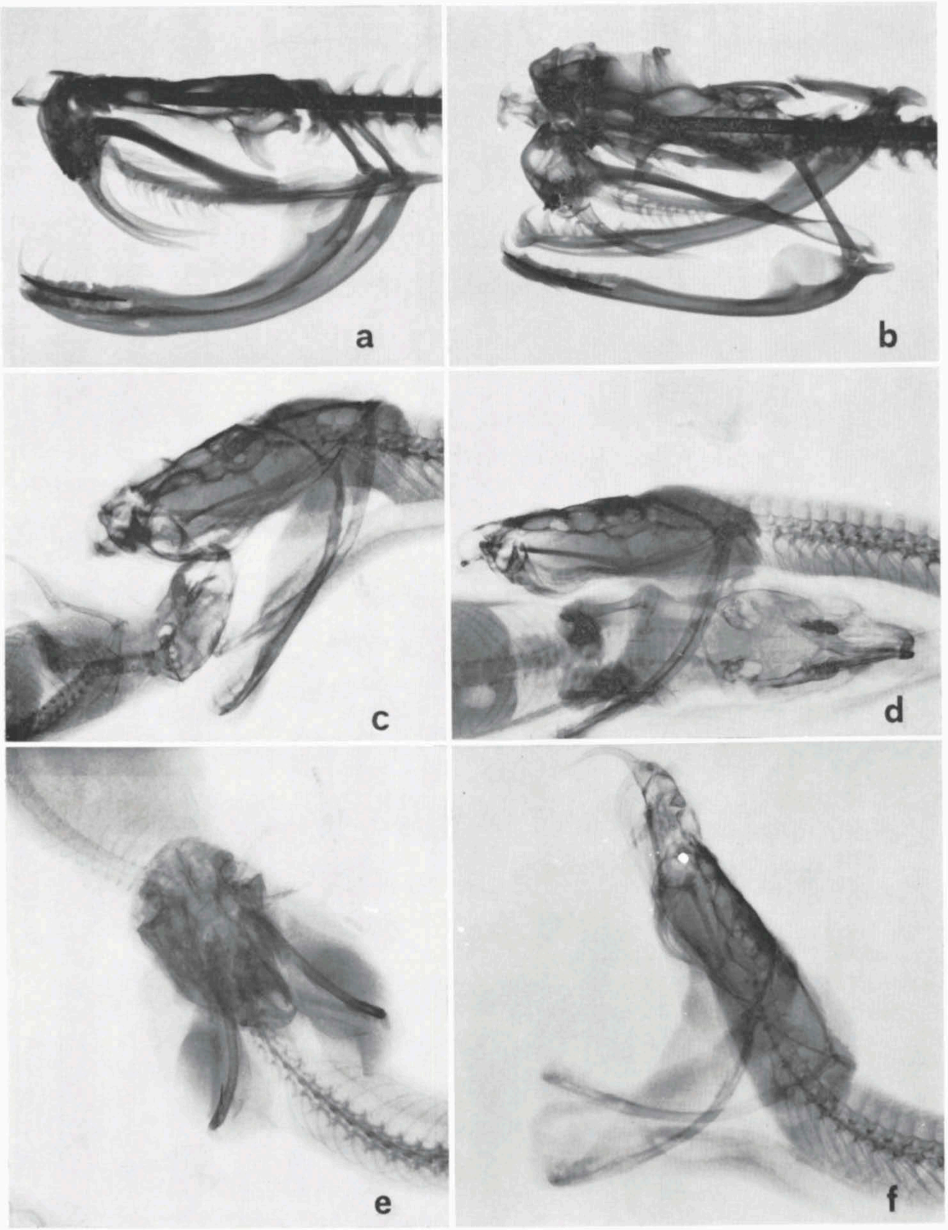
Lilie, R. D., 1954. Histopathologic Technic and Practical Histochemistry. The Blakiston Co., New York.

Schanz, A. & A. Schecter, 1965. Iron hematoxylin and safranin O as a polychrome stain for epon sections. — Stain Technology, 40: 279-282.

Van Riper, W., 1953. How a rattlesnake strikes. — Sci. Amer., 189: 100-102.

Versluys, J., 1936. Kranium und Visceralskelett der Sauropsiden. I. Reptilien. In L. Bolk u.a., Handb. vergl. Anat. Wirbelt, Bd. 4.

Willson, P., 1908. Snake poisoning in the U.S.; a study based on an analysis of 740 cases. — Arch. Int. Med., 1 (5): 516-570.



Röntgenograms. a. Skeleton of a head, lateral view; b. Skeleton of a head, latero-dorsal view; c. Head during swallowing, lateral view; d. Head during swallowing, lateral view; e. Head during swallowing, dorsal view; f. Head during yawning, lateral view.