

THE SKULL, JAW MUSCLES AND CRANIAL KINESIS OF DIBAMUS
NOVAE-GUINEAE WITH SPECIAL REFERENCE TO THE SYSTEMATIC
POSITION ON THE DIBAMIDAE

by

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(with text-figures)

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Abstract



Descriptions of the skull, the jaw muscles, the nasal sacs and the middle ear are given. The cranial kinesis and a possible mode of jaw action are discussed. The palate is shown to be of the scincid type. Although the stapes pierced by the stapedia artery suggests geckonid affinity (Underwood, 1957 and Guibé, 1970) the non-geckonid relations of the chorda tympani and the scincid type of palate argue strongly in favour of a close relationship with the Scincidae. There would, indeed, seem to be no valid reason for retaining the family Dibamidae and it is suggested that the genus Dibamus be included in the Scincidae.

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INTRODUCTION

Dibamus novae-guineae is one of the four species of the family Dibamidae. It was first described by Dumèril and Bibron in 1839 and the family Dibamidae was created by Boulenger in 1884. In 1887 he said the following about Dibamus: "A single genus, which appears to stand in the same relation to the Scincidae as Anniella to the Anguidae." Since then other authors (e.g. Schmidt and Inger, 1957; Baird, 1970) have attributed scincid affinities to the genus while tentatively retaining the separate family Dibamidae. Romer (1952, 1966) includes it under the Leptoglossa (Scincomorpha) as a family of dubious validity. Recently Guibé (1970) following a suggestion by Underwood (1957) placed the family under the Gekkota.

This purplish brown, wormlike fossorial lizard is widespread, ranging from southern Indochina to New Guinea, the Phillipines and the Nicobar Islands (Pope, 1956). It is frequently caught in rotten logs (Schmidt and Inger, 1957) and in the Malay peninsula an egg with a fully developed embryo was found (Smith, 1935). The female is completely limbless but the male has a pair of vestigial clasping hind limbs.

The anatomy is poorly known (Romer, 1952). Apart from an intensive study of the eye of D. novae-guineae by Underwood (1970) and of the cochlear duct of D. novae-guineae and D. argenteus by Miller (1966 (a), 1966(b)) knowledge of the cranial anatomy of Dibamus is limited to notes on the exterior features of the skull (Boulenger 1887; Camp, 1923; Smith, 1935; Romer, 1952 and McDowell and Bogert, 1954). The present study attempts to supplement this and was done with the additional purpose of attempting to clarify the systematic position the genus.

MATERIAL AND TECHNIQUE

The specimen was obtained from the Ryksmuseum of Natural History^{at} Leiden, Netherlands and its locality and date given as Sinabang, Simaloer (1913). Simaloer is also known as Simeulue, an island of Indonesia. The specimen^(a) (female) was decalcified in a mixture of 7,5% nitric acid and 70% alcohol for two weeks. It was bulk stained in borax carmine and counter stained in aniline blue orange G mixture and embedded in paraffin wax. It was sectioned at 12 μ . Graphic reconstructions were made by the method developed by Pusey (1939).

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DESCRIPTIONTHE DERMAL BONES

The following dermal bones are absent: lacrimal, jugal, postfrontal, postorbital, squamosal and supratemporal.

Premaxilla: Contrary to Romer's (1952) statement the premaxilla is unpaired, at least in *D. novae-guineae* (Fig. 12). It consists of a horizontal palatal plate and a vertical median plate. The bone bears seven pleurodont teeth, one of which lies in a median position. The palatal^{portion} is joined laterally to the maxillas at an oblique angle. In the posterior part of this suture there is a considerable ventral overlap of the premaxilla on a posterolateral process of the maxilla. In front of this overlap, the premaxilla also makes contact with the septomaxilla

over the entire width of both bones (Fig. 17). The posterior edge of the palatal plate is semicircular in outline. Medianly from near this edge arises a ventrorostrad incisive process (Fig. 8). Arising from the base of the latter is a small posterior protrusion loosely attached to the anterior tips of the vomers.

The median vertical plate slopes down sharply in front to form a short, blunt rostrum (Fig. 4 & 3). Behind this, the dorsal edge of the vertical plate is horizontal and is clamped between the downturned median edges of the nasals. The posterior edge of the vertical plate is concave (Fig. 8). Its lower part meets the free anterior edge of the nasal septum and, more dorsally, it lies between the anterior cupolae of the nasal capsules. The medial nasal ramus of the profundus nerve of each side passes through a channel in the bone near the ventral midline (dotted line in Fig 8).

Maxilla: The palate of Dibamus is unique in that behind the fenestra vomeron^asalis externa the anterior section of the fenestra exochoanalis is obliterated by a suture between the lateral edge of the vomer and the median edge of the maxilla; and the posterior section is hidden from view by a suture between the lateral edge of the vomer and the scincid-type palatal flange of the palatine-pterygoid (Fig. 2 & 7).

The maxilla consists of a lateral oblique vertical flange and a palatal flange united by a thickened base (Fig. 9). The ventral face of this basal portion carries the jaw ridge with nine pleurodont teeth. The whole length of the basal portion is penetrated by a channel for the superior alveolar ramus of the trigeminus nerve and for the maxillary artery. Anteriorly this channel opens through an alveolar foramen (Celrich, 1956) (Fig. 3). Laterally, low down on the outside of the bone, approximately seven

Large labial foramina open from this channel. These are arranged roughly in a horizontal row. The upper part of the lateral vertical flange is also pierced by a number of scattered foramina for the cutaneous branches of the lateral nasal ramus of the profundus nerve (Fig. 4).

The lateral vertical flange forms the greater part of the side wall of the snout. The anterior edge of this flange is more or less vertical and forms the posterior edge of the **fenestra** exonarina. The dorsal edge slopes up slightly towards the back. The anterior two thirds of this edge is connected to the lateral edge of the nasal, and the rest of it slightly overlaps the lateral anterior process of the frontal. The posterior edge of the lateral vertical flange is concave and is for the greater part connected to the prefrontal, except low down where the nasolacrimal duct passes between the two bones. The maxilla is not notched for the lacrimal duct. The upper part of the maxilla overlaps a fairly extensive dorsal anterior process of the prefrontal. Below the lacrimal foramen the maxilla is attached to a small anterior process of the prefrontal.

The median edge of the palatal flange is slightly curved repeating the contour of the skull (Figs. 2 & 7). Anteriorly this edge terminates in a process which is grooved ventrally for the posterior process of the premaxilla (Fig. 2). Lateral to this process the oblique anterior edge of the maxilla is connected to the premaxilla in an edge to edge suture. Dorsally the entire premaxilla - maxilla connection is covered by the anterior part of the septomaxilla (Fig. 7). Behind this, the lateral edge of the septomaxilla is connected to the maxilla just above the slightly downcurved median edge of the palatal flange (Figs. 7 & 9). Posterior to the septomaxilla the median edge of the maxilla is free for a short distance, leaving a small gap between maxilla,

septomaxilla and vomer, through which the nasolacrimal duct passes (Fig. 2 & 7). From this point backwards the palatal flange of the maxilla is dorsally grooved for the nasolacrimal duct. This groove runs obliquely backward to end near the lateral side of the skull where the lacrimal foramen passes between maxilla and prefrontal (Fig. 7). Behind the palatal gap for the nasolacrimal duct, the median edge of the palatal flange of the maxilla is sutured to the vomer thus closing the fenestra exochoanalis in this region (Figs. 7 & 9). Posteriorly the palatal flange forms the median posterior maxillary process. This is dovetailed between the median and the lateral anterior processes of the fused palatine pterygoid (Figs. 2 & 7). Between the median posterior process of the maxilla and a short, thick, lateral posterior process (the latter being an extension of the maxillary base) the posterior edge of the bone is hollowed. In this hollow the maxilla adjoins the ectopterygoid laterally and the lateral anterior process of the palatine-~~p~~terygoid more medially.

The lamina transversalis anterior crosses the palatal flange just posteriorly to the process of the septomaxilla, to unite laterally with the cartilaginous wall of the nasal capsule (Fig. 9). The ectochoanal cartilage lies under the ventral border between the palatal flange of the maxilla and the footplate of the septomaxilla for the length of the suture. The paries nasi is laterally supported by a dorsomedian crest on the lateral flange of the maxilla.

The paired septomaxilla is strongly developed. In response to a burrowing life the bone acts as a buttress between all the other bones of the snout region. It forms a roof for the organ of Jacobson and a floor for the vestibulum and the anterior chamber of the nasal sac.

The bone consists of three portions: an extensive medial vertical flange (Figs. 7 & 9) an anterolateral horizontal process and posterior to the latter a ventrolateral footplate (Fig. 7, right side). The median surface of the extensive vertical flange is applied to the upper two-thirds of the nasal septum and dorsally it meets the nasal (Fig. 8). The upper edge of the flange curves laterally thus increasing the sutural surface between septomaxilla and nasal. The septomaxilla thus serves as a buttress between the nasal on the one hand and the vomer and premaxilla on the other. Anteriorly the base of the vertical flange is pierced by a channel for the ramus medialis nasi of the profundus nerve (Fig. 8). More posteriorly this channel becomes an open groove in the bone, bordered medially by the nasal septum.

The anterolateral process of the Septomaxilla is attached to the dorsal surface where^{re} the palatal flanges of the premaxilla and the maxilla meet making this a strong compound suture (Fig. 7). Laterally the process is also buttressed against the base of the lateral vertical flange of the maxilla (Fig. 7, right side).

The ventrolateral footplate of the septomaxilla is domed to form a bony roof for the organ of Jacobson. It is connected anterolaterally, in front of the passage of the nasolacrimal duct, to the dorsal side of the palatal flange of the maxilla. Median to the foramen for the nasolacrimal duct, the lateral edge of the footplate is connected at an acute angle to the lateral edge of the vomer to form a side wall to the chamber of the organ of Jacobson. The back wall of the organ is formed by a ridge on the dorsal surface of the vomer to which the posterior edge of the septomaxillary footplate is applied. Anteriorly the footplate lies on the cartilage roof of the organ of Jacobson. The ectochoanal cartilage underlies the suture between septomaxilla

and maxilla.

Nasals: This paired median bone forms a slightly arched roof over each nasal capsule. Its anterior edge forms the dorsal rim of the fenestra exomarina (Fig. 4) and overlaps the back edge of the cupular cartilage. Anteromedially the nasals are connected to the upper end of the vertical median plate of the premaxilla (Fig. 1). Behind this suture the two median downcurved edges of the nasals form a deep, strong suture. Ventrally these downcurved edges are connected to the median vertical plates of the septomaxillas (Figs. 8 & 9).

The extensive posterior process of the nasal overlaps the frontal at its tip but medially and laterally it is joined in edge to edge sutures with the two anterior frontal processes (Fig. 1). Laterally the nasal is sutured to the vertical flange of the maxilla. Close to this suture the lower surface of the ^{nasal} ~~basal~~ has a low ridge to which the median edge of the paries nasi adheres.

Vomer: As has been said earlier, the palate of Dibamus is unique in that the lateral edge of the vomer is sutured to both the maxilla and the scineid type of palatal flange of the palatine, there thus being no fenestra exochoanalis visible in ventral view (Fig. 2). The vomer is a median paired palatal bone, best described as consisting of three portions, lying at inclined planes relative to each other: an anterior mainly horizontal floor for the organ of Jacobson and behind this a lateral horizontal flange and a median oblique flange forming with its fellow of the other side a deep medioventral groove housing the posterior vomeral glands (Figs. 2 & 10).

The anterior portion of each bone is dorsally concave to form a floor for Jacobson's organ (Figs. 8 & 7). The median edges are turned up to form adjoining vertical lamellae lying ventromedially to the paraseptal cartilages and below the nasal septum

(Fig. 9). The vertical lamellae^e are extended anteriorly and are connected in front to the posterior elongation of the incisive process of the premaxilla (Fig. 2). The lateral edge of the vomer is free in front of the passage of the nasolacrimal duct.

Behind Jacobson's organ the vomer is expanded dorsally, forming a vertical transverse wall triangular in cross-section (Fig. 9, left & Fig. 7 left). The median sides of the triangles are sutured to one another. This wall is of considerable thickness and is pierced by the vomeronasal nerve innervating Jacobson's organ and also by a small branch of the medial ramus of the palatine nerve. The former leaves the bone by a dorsal foramen to join the olfactory nerve. The palatine branchlet passes through a ventral foramen to join the medial palatine ramus lying ventral to the vomer in a shallow groove (Fig. 2). This groove is short because the nerve soon pierces the vomer to lie on its dorsal surface in a shallow groove that disappears posteriorly where the nerve takes a medio-dorsal course, free of the vomer (Fig. 7).

Behind the foramen for the palatine nerve the median oblique and lateral horizontal flanges differentiate distinctly, the oblique ^{flange} ~~flange~~ being a continuation of the dorsal part of the thickened triangular portion of the vomer and forming the median ~~through~~ housing the posterior vomeral glands (Figs. 2 & 10). This trough deepens posteriorly to ^e ~~reach~~ considerable proportions at the back. Dorsally the two median edges of the vomers curve laterally to form a shallow furrow for the low nasal septum (Figs. 7 & 10). Posteriorly the oblique flanges decrease~~s~~ in height and the median edges diverge from each other (Fig. 2).

← The curved lateral edge of the horizontal flange is connected to the palatal flange of the maxilla, and more posteriorly to the palatal flange of the palatine (Figs. 2 & 7).

The most posterior tip of the bone lies medioventrally alongside the partial median suture of the ring-shaped portion of the fused palatine-pterygoid (see later).

The palatine-pterygoid complex: The palatine and pterygoid bones are so extensively fused that it is extremely difficult to distinguish them. A possible boundary between them is shown on Figure 7 on the left side and the details of this reconstruction are given at the end of the section on the palatine-pterygoid. In ventral view the anterior half of the combined bone is a roughly triangular palatal plate (Fig. 2). Its posterior angle is extended back into a long, slender quadrate process of the pterygoid. The anterior angle of the triangle is forked to form a median and a lateral process. The third angle is directed mesiad towards its fellow, but is separated from it by the small interpterygoid vacuity. This middle portion of the bone is highly complicated: as can be seen in dorsal view it forms a complete ring around a nasopharyngeal duct (Fig. 7 and Fig. 11). Between the two processes, forming the anterior fork, the median posterior process of the maxilla is clamped (Fig. 2). The anteromedian process adjoins the oblique lateral edge of the posterior half of the vomer medially. This suture is continued to where the posterior tip of the vomer overlaps the bony ring medially. Laterally the anterolateral process adjoins the anteromedian edge of the ectopterygoid. Posterior to this connection the two bones diverge to form the small infraorbital foramen, the latter being bordered by the ectopterygoid and apparently by both elements of the fused palatine-pterygoid (Fig. 7). The anterolateral process widens posteriorly to meet the palatal plate at an angle and continues backwards as a latero-dorsal flange (Fig. 7). Anteriorly the ramus maxillaris^S overlies the dorsal edge of the anterolateral process. Posterior to this



the nerve takes a more lateral course and a suture is formed between the dorsal edge of the dorsolateral flange and the posterior portion of the ventral edge of the prefrontal (Fig. 3). Behind the prefrontal a short suture is also formed with the ventrolateral edge of the frontal up to where the dorsal edge of the dorsolateral flange curves medially to form the anterior edge of the dorsal arch of the bony ring (fig. 7). Figure 11 illustrates in cross-section the complicated structure of the palatine-pterygoid in the region of the bony ring. It is clear that we have here a scincoid type of palatine(pterygoid), where a palatal flange of the bone(s) transforms the nasopharyngeal palatal groove of other lizards into a duct of varying degrees of completeness (Fuchs, 1908; Parsons 1971) In Dibamus a ^{culmination} ~~culmination~~ in the process of closure is achieved in that medially the palatal flange is actually fused to the dorsal arch to form for a short distance a complete bony ring around the nasopharyngeal duct (Figs. 8 & 11 right side). The anterior portion of the ring appears like a closed C in cross-section, having a ventromedian suture between the median edges (Fig. 7). This suture is medially covered by the posterior tip of the vomer. It is behind the vomer that the two edges fuse to form the complete ring. The bony ring lies posterior to the planum ant-orbitale, and the solum suprasedale lies dorsally to it (see orbitotemporal region). More posteriorly, at a level behind Figure 11, the median vertical wall of the ring disappears and the bone forms a dorsal and ventral flange that diverge mesiad. These two flanges decrease in width lateroposteriorly, thus tapering towards the posterior quadrate process (Fig. 7).

The dorsal arch is, of course, the original main part (in this region) of the palatine (pterygoid), the palatal flange being a new development in scincoids. In Dibamus the dorsal arch

is insignificant compared to the very large palatal flange and is hidden by it. The anterior edge of the dorsal arch represents the posterior border of the fenestra exchoan^halis and it is here that the nasal sac passes over into the nasopharyngeal duct lying in the bony ring. Externally the fenestra has been closed over by sutural connections between vomer, maxilla and the palatal flange of the palatine (+ pterygoid). In this way a complete bony secondary palate has been formed. Behind the bony palate there is also a soft palate (Fig. 12(b)) which serves to extend the nasopharyngeal duct further back to the point where they open as a single duct, between the two basispterygoid processes and close to the glottal opening.

The lateral wall of the ring is continued laterally as a horizontal edge, the outer edge of which is produced into a dorsal and a ventral ridge, the two ridges forming a roughly vertical flange (Fig. 11). The ventral ridge terminates anteriorly as a lateral process, the ectopterygoid process, which overlies the posterior tip of the ectopterygoid. This connection completes the infraorbital fenestra posterolaterally (Fig. 2). The dorsal ridge and the ring forms a trough between them (Fig. 7). The retractor pterygoideus muscle fills the trough and attaches to its surface anteriorly.

Behind the ring the lateral portion of the bone (presumably pterygoid in this area) is triradiate in cross-section, consisting of a dorsal ridge, a ventral ridge and a median ridge. The ventral surface of the median ridge is padded with a cartilage cushion, the meniscus pterygoideus, for articulation with the basispterygoid process. There is a well-developed synovial cavity. The median ridge tapers backwards to end a little way behind the articular cartilage. The ventral and dorsal ridges continue posteriorly to form the long, slender quadrate process

of the pterygoid. The quadrate process is crescent-shaped in cross-section, its edges curving medially. The lateral edge of the third quarter of the process is connected to the ventro-median edge of the quadrate by means of a thick ligamentous pad of tissue. The posterior portion of the quadrate process projects beyond the quadrate and is almost enclosed by the protractor pterygoideus muscle attached to it, with the bulk of the muscle lying ventral to it (Fig. 2⁴). A wide ligament also attaches the footplate of the stapes to the dorsal edge of the posterior part of this portion of the quadrate process. || The line of fusion between palatine and pterygoid is indicated by a few small irregular strips of connective tissue in the dorsal arch of the bony ring (Fig. 7 right side). An extension of a line through these remnants results in an oblique line ending at the posterior corner of the infraorbital fenestra, making the ectopterygoid process of the fused palatine-pterygoid part of the pterygoid. This would seem to be correct since in most lizards the pterygoid ^{forms} ~~forms~~ the sole or the major connection with the posterior tip of the ectopterygoid. From these facts a tentative reconstruction of the line of fusion is indicated by a dotted line in Figure 7 on the left. The line of fusion on the palatal flange is less easy to determine, unless a notch on the posterior edge of the palatal flange, more or less in line with the dorsal line of fusion, is an indication of its position (Fig. 7).

The ectopterygoid borders the infra-orbital fenestra to the palatine-pterygoid (but see Figure 7 and the previous section). The bone is shaped like a two-bladed propellor with a horizontal anterior blade and a vertical posterior blade (Figs. 2 & 3). The anterior edge of the horizontal blade adjoins the posterior edge of the palatal flange of the maxilla. The median edge of

this blade is connected to the lateral edge of the anterolateral process of the palatine-pterygoid. The dorsal ^fsurface of the anterior blade has a small longitudinal ridge in the middle to which the anteroventral edge of the prefrontal is connected.

|| The median wall of the posterior blade forms the lateral border of the infra-orbital fenestra. The posterior tip of this blade overlaps the ectopterygoid process of the palatine-pterygoid ventrally.

The infra-orbital fenestra is funnel-shaped ventrally (Fig. 2) and houses the lateral portion of the sphenopterygoid mucous glands. The deepened fenestra is continued back as a ventral trough in the palatine-pterygoid, formed between the ventral ridge and the ring, and contains the posterior portion of these mucous glands.

The prefrontal is unusual in that it is a flat bone on the lateral side of the skull, the orbit being virtually absent as a result of the greatly degenerated eye (Figs. 1, 3 & 11). Seen from the side, the bone is roughly square with the four corners facing anteriorly, posteriorly, ventrally and dorsally (Fig. 3). The anterior corner is elongated to form a slender anterior process that lies medially on and ventral to the suture between the lateral flange of the maxilla and the lateral edge of the frontal. The process covers the posterior half of this suture medially (Fig. 8). Posterior to the anterior process the two thirds of the visible anterodorsal edge, seen from the outside, is connected to the dorsal portion of the posterior edge of the maxilla. In this area therefore, three bones, the prefrontal, the frontal and the maxilla meet in edge to edge sutures, except for a posterior overlapping process of the maxilla and an anterior underlying process of the prefrontal. More posteriorly the apex of the prefrontal overlaps the frontal

and this overlap continues down to the posterior corner of the prefrontal.

The anteroventral edge bears a notch, anteriorly closed by the posterior edge of the maxilla to form a lacrimal foramen. Below the notch the prefrontal is sutured again to the maxilla and behind this for a short distance to the dorsal ridge on the anterior blade of the ectopterygoid. The anterior half of the posteroventral edge of the prefrontal is not connected to the ectopterygoid as the maxillary ramus V lies between the two bones. The posterior half of this edge is connected to the dorsal edge of the lateral oblique flange of the ^ap~~l~~altine-pterygoid. Behind the prefrontal this flange is connected to the lateroventral edge of the frontal (Fig. 8). The medioventral wall of the prefrontal adjoins the anterior maxillary process of the cartilaginous nasal capsule (Fig. 11). Laterally the bone is covered by the Harderian gland, the latter enfolding the rudimentary eye (Fig. 10).

The frontal (Fig. 1) is a thick median paired bone covering the olfactory bulb. The median edge is downcurved, forming a deep sutural surface for intimate connection with its fellow (Figs. 10 & 11). Anteriorly it has two large processes, one lateral and one median. These clasp the posterior pointed process of the nasal. The tip of the latter process overlaps the frontal. Anteriorly the lateral edge of the frontal is sutured to the upper edge of the maxilla. Medially to this suture the lateral edge of the frontal is also connected to the anterior process of the prefrontal. Behind the maxilla the frontal is slightly overlapped by the prefrontal. The anterior portion of the frontal is flat and more or less horizontal (Fig. 10).

Behind the prefrontal the frontal bears a lateroventral

flange which helps to form a side wall for the brain (Fig. 3). The anterior edge of this lateral flange is overlapped by the obliquely downsloping back edge of the prefrontal. The extreme ventral tip of the flange is sutured to the dorsal edge of the laterodorsal flange of the palatine-pterygoid. From the lower end of the lateroventral flange a long, slender process, the subolfactory process, projects inwards to lie immediately beneath the olfactory bulb (Fig. 11). This process does not reach the midline and is not attached to the bony ring of the palatine-pterygoid. The base of this process is grooved for the ramus ethmoidalis of the profundus nerve.

Dorsally the posterior portion of the frontal is thickened and forms a rounded transverse edge with a lateral knob (Fig. 3). This edge is joined to the parietal by means of an articulatory hinge suture (the mesokinetic joint). The posterior edge of the lateroventral flange of the frontal is laterally connected by means of a thick pad of connective tissue to an overlapping anterior portion of the side wall of the parietal. This portion is anteriorly rounded and would function as a stop to prevent a sideways dislocation of the mesokinetic joint. The whole fronto-parietal articulatory suture is strengthened to be able to resist a large amount of stress (Figs. 1, 3 & 8).

The median unpaired parietal is the largest bone of the skull (Fig. 1). The anterior two thirds, that lie in front of the otic capsules is arched and forms extensive side walls for the cranial cavity (Fig. 3). In the region of the otic capsules it is a roofing bone only, with three posteriorly directed prongs that are connected to the otic capsules and the supraoccipital (Fig. 1). Both the pineal eye and the pineal foramen are absent.

Anteriorly the bone is considerably thickened and has a

shallow laterodorsal depression on each side of the face of the anterior edge. Into this depression the rounded knob of the frontal fits, forming a "ball and socket" joint. The lateral flanges of the parietal are extended anteriorly to overlap the frontals. The structure of the frontoparietal suture indicates that the mesokinetic joint is well developed (see kinesis).

The posterior edges of the side walls are connected to anterior portion ^{and} consists mainly of the three blunt prongs, the lateral two are remnants of the parietal processes that no longer reach the quadrates. These two prongs lie in shallow grooves in the otic capsules and are connected to them with thick connective tissue. The median prong is much longer and its lateral edges are connected to dorsal median ledges on the otic capsules and its tip overlaps the arch formed by the supraoccipital (Fig. 8). The thick pads of connective tissue might allow some slight metakinetic movement. The processus ascendens tecti synotici is absent.

THE LOWER JAW: [D. novae-guineae has a short lower jaw, a condition correlated with the anterior inclination of the quadrate condyle and the subterminal mouth (Figs. 4 & 6). The sturdy lower jaw has a massive coronoid process at least half of which is contributed by the dentary the other half being formed by the separate coronoid. All the other dermal bones of the lower jaw are fused to the articular forming a complex posterior element. Anteriorly the two halves of the lower jaw are joined by means of a very strong compound symphysis (Figs. 9 & 6). The two Meckelian cartilages are fused anteriorly in the symphysis. The anterior half of this fused portion is ossified, forming a mentomandibular. The posterior half of the fused portion remains as a cartilaginous thickening between the two halves of the mandible (Fig. 6). From the symphysis the Meckelian cartilage

passes directly into the Meckelian canal in the dentary, that lies medially to the inferior alveolar canal. These two canals merge in the vicinity of a large median slit in the dentary into which fits the splenial process of the compound bone. The Meckelian cartilage lies lateroventrally in this part of the Meckelian canal up to where it ossifies posteriorly as the articular.

The articular is a stubby bone with small marrow cavities. Its large, flat, slightly concave articular surface differs from most other lizards in that it faces posteriorly rather than dorsally a change correlated with the change in slope of the quadrate (Figs. 6a & b). The articular surface is separated into two facets by a slight ridge and is covered with articulatory cartilage. The cartilage extends onto the lateral surface of the articular corresponding to the anterior projection of the quadrate condyle. A well-developed synovial joint is present.

From below the lower jaw articulation the rod-shaped retro-articular process projects at a sharp angle, downwards and backwards slightly outwards (Figs. 6, 4 & 26). The process thus lies wholly below the level of the lower margin of the jaw. The posterior tip of the process remains cartilaginous (Fig. 19) and in the bony part no boundary between the articular and pre-articular could be discerned. The only indication of a boundary is the foramen and the groove behind it for the chorda tympani (Fig. 6).

In front of the articular facet lies a small mediodorsal adductor fossa through which the internal mandibular artery and the mandibular ramus (V3) enter the Meckelian canal (Figs. 1 & 6). The fossa is little more than a rather large foramen and no adductor muscle fibres insert in it. Directly laterally to the adductor fossa the auricotemporal branch of the mandibular

nerve leaves the Meckelian canal through a moderately sized foramen in the lateral surangular ⁿportion of the compound bone (Fig. 4). A second lateral foramen lies between the posterior processes of the coronoid and the dentary. The posterior section of the Meckelian canal lies wholly within the compound bone and it is not bordered by the coronoid. Anteriorly the compound bone has a pointed splenial process that is clamped in by the dentary medially to the Meckelian canal (Fig. 6). Anteriorly to the process, the chorda tympani (VII) and the lingual branch of the inferior alveolar ramus (V3) passes from the Meckelian canal through the dentary fork. Anteriorly to this the alveolar canal is separated off from the Meckelian canal. In the dentary there are approximately five lateral foramina for the inferior labial rami of the inferior alveolar ramus of V3 (Fig. 4).

The coronoid forms only the posterior half of the coronoid process and it is a flat triangular bone with its horizontal base sutured to the fused compound bone. Its anterior vertical edge is overlapped laterally by the large dorsal coronoid process of the dentary. The apex of the coronoid is somewhat higher than the wide process of the dentary (Figs. 4 & 6a). Apart from the very large coronoid process the dentary also has a long, pointed posterior process overlapping the compound bone laterally. The anterior tip of the dentary curves inward and slightly up before being connected to its fellow in the jaw symphysis. The dentary bears nine pleurodont teeth.

THE NASAL SAC: [Unless stated otherwise, the nomenclature of Parsons (1959) is followed. It is difficult to distinguish the divisions of the simplified nasal sac, the ^{sac}~~cas~~ being straightened out with the divisions following each other in a more or less straight line (Fig. 12). The anterior section of the choana,

with the exception of the vomeronasal opening, is obliterated by sutures between the vomer medially and the maxilla and the scincidtype palatal flange of the palatine-pterygoid laterally (Figs. 2,9,10 & 13). Only the posterior portion of the inner choana (Bellairs, 1950) remains, where the nasal cavity opens dorsally to the palatal flange into the nasopharyngeal duct (Fig. 12).

The nasal cavity can be divided into two main portions, the anteriorly lying vestibulum and, posterior to the opening of the lateral nasal gland, the nasal cavity proper ("Muschelzone" of Fuchs, 1908) (Fig. 12).

The vestibulum is L-shaped with a laterally directed short anterior leg and a posteriorly directed median leg. The transverse leg opens to the exterior through the laterally facing nostril and is lined with keratinised stratified squamous epithelium that is continuous with and similar in appearance to the epidermal epithelium. Anteriorly the nostril gives direct passage to the outside, but the posterior half of the dorsal rim bears a ventrally directed flap. The base of the flap is supported by the Latero-dorsal edge of the anterior cupola directly anterior to the superior alar process and lies medially to the ventral rim supported by the inferior alar process. Behind the posterior rim of the nostril a nasal muscle inserts on these processes. (See Nasal Capsule & Fig. 23).

The median wall of the median leg of the vestibulum is lined with stratified transitional epithelium composed mainly of large glandular cells. This wall is folded, three persistent longitudinal grooves being recognisable. At the posterior border of the vestibulum these grooves form a small recess medially and dorso-medially to the nasal cavity proper. Except for the median wall mentioned above and for the anterior half of the lateral wall that is lined with keratinised epithelium the rest of the longitudinal

leg of the vestibulum is lined with nonkeratinised stratified squamous epithelium. Posteriorly the tubular vestibulum narrows slightly before opening into the nasal cavity proper. At this point the duct of the lateral nasal gland opens laterodorsally into the nasal sac.

The nasal cavity proper is lined mainly with olfactory epithelium (hence the name olfactory chamber of Bellairs, 1950). There is a ventrolateral strip of ciliated respiratory epithelium indicating the line of closure of the choana as known in other lizards, where the inner choana is bordered by respiratory epithelium (Bellairs, 1950) (Figs. 13a & b). The nasal sac gradually widens posteriorly to obtain its maximum width in approximately the middle of the nasal cavity proper.

In the dibamid nasal cavity proper it is possible to distinguish only an anterior caval zone and a conchal zone, as the posterior portion of the nasal sac is flattened out and no antorbital cavity as such is present (Fig. 12). The only indication of the posterior border of the nasal roof supported by the posterior edge of the cartilaginous planum antorbitale. (See Cartilaginous Nasal Capsule.)

The anterior caval zone takes up the anterior half of the nasal cavity proper. Directly behind the vestibulum it is oval in cross-section, the lateral side of its longest axis tilted ventrad. Because of the dorsolateral indentation of the trough in the paries nasi (Fig. 9), the greater part of the anterior caval zone appears like a flat tube with its edges upcurved, the lateral edge lying on a lower level than the median edge.

In the conchal zone the indentation increases in depth. ~~by~~ The nasal sac here is horseshoe-shaped with the open end laterally directed (Fig. 13). The conchal zone can thus be subdivided into three parts. The portion of the cavity dorsal to the concha

and the conchal flange is the sakter (Fig. 13a). This is continuous with the medial stammteil, while the ventral third corresponds to Fuchs' horizontal portion ("horizontale Schenkel") of the choanengang. The oblique portion ("absteigender Schenkel") of the choanengang is absent since the fenestra exochoanalis is completely closed up. The whole of the ~~chomchal~~ conchal zone is lined with olfactory epithelium except for the lateral strip of respiratory epithelium as described earlier.

Posteriorly the surface lined with respiratory epithelium increases rapidly in extent while that lined with olfactory epithelium decreases (Fig. 12). The last remaining strip of olfactory epithelium ends dorsomedially (at point A in Figure 12^a) and coincides with the dorsal ridge in the roof of the nasal sac and approximately with the anterior edge of the dorsal arch of the bony ring (~~the~~ primary palate, Fig. 12^a) i.e. with the posterior border of the fenestra exochoanalis. This posterior limit of the olfactory epithelium indicates the posterior end of the nasal cavity proper where it goes over into the nasopharyngeal duct (fig. 12^a) ~~border between the~~ the two structures being otherwise indistinguishable. There is ~~no~~ antorbital cavity, the nasal cavity proper passing directly over into the nasopharyngeal duct lying immediately behind it. A definite position for the choana is difficult to pinpoint, but the "inner choana" must in some way be delimited by the border between respiratory epithelium and olfactory epithelium.

Anteriorly the nasopharyngeal ducts of each side lies within the bony ring of the palatine-pterygoid (Fig. 7). A short distance behind the bony ring the ventromedial aspects of these ducts fuse to form an intricate flat median nasopharyngeal duct with a ventrally projecting median ridge on its dorsal roof (Fig. 12 b). The two lateral portions of this flat duct ~~is~~ ^{are} separated by the median ridge and ~~is~~ ^{are} only confluent with each

other by means of a slit ventrally to the ridge. The ridge houses a deep median groove that is Y-shaped in cross-section, the vertical leg of the Y opening ventrally into the nasopharyngeal duct, and the ridge is thus divided into two folds. Anteriorly a continuation of the groove forms a small recess between the paired anterior nasopharyngeal ducts and the recess retains the Y-shaped lumen. This recess is lined with mucous epithelium and is possibly a remnant of the median glandulae sphenopterygoides (Fahreholz, 1937). Posteriorly, behind the secondary choana the groove widens and the folds lateral to it flatten out and disappear opposite the glottis. The secondary choana is a transverse slit that lies between the bases of the basipterygoid processes.

The greater part of the ventral floor of the median nasopharyngeal duct is separated from the buccal cavity only by soft tissues (Fig. 12b). Thus D. novae-guineae has a soft secondary palate in addition to a complete bony secondary palate. This palate forms an interesting analogue with the crocodilian and mammalian secondary palates. (See Discussion.)

THE ORGAN OF JACOBSON

The small poorly developed organ of Jacobson is situated ventromedially to the middle third of the anterior nasal zone and it is separated from it by the septomaxilla. The organ is one and a half times as long as it is wide. Its duct is terminal, opening anteriorly into the buccal cavity (Fig. 12c). A distinct dome of thick olfactory epithelium forms the dorsolateral roof of the small, flat lumen (Fig. 14).

As there is no concha for the organ of Jacobson, there is also no mushroom body. The ventromedian floor of the organ is lined with ciliated epithelium and curves slightly around the paraseptal cartilage and the portion of the vomer immediately ven-

tral to the cartilage (Fig. 14).

The vomeronasal nerve leaves the organ of Jacobson posteriorly and pierces the back wall formed by the vomer (see Dermal Bones). The vomeronasal nerve leaves the channel in the vomer through a dorsal foramen and passes dorsad, lateral to the nasal septum, to join the olfactory nerve dorsally.

The "choonenrinne" (Fuchs 1908) found in some squamates is completely cut off from the buccal cavity and forms the anterior part of the nasolacrimal duct that opens into the ventrolateral aspect of the lumen directly posterior to the terminal duct of the organ of Jacobson (Fig. 12). Fuchs' secondary palate is thus enclosed on both the lower and the upper level. (Fig. 14)

THE CARTILAGINOUS NASAL CAPSULE

The nasal capsule of Dibamus novae-guineae is dorsoventrally flattened and elongated (Fig. 16). It is reduced to thin cartilage strips and thus appears very flimsy in comparison to the "Gaupp-Ziegler" model of Lacerta agilis (Gaupp, 1900) (Figs. ¹⁵ 16 & 17). The fenestra endochoanalis, the fenestra lateralis nasi the fenestra superior nasi and the fenestra olfactoria are greatly expanded. The foramen epiphoniale is confluent with the fenestra olfactoria (Fig. 15).

The dibamid anterior cupola is less dome-shaped than the cupola of Lacerta agilis and lacks a median wall, the latter being replaced by the vertical median plate of the premaxilla that ^{separates} ~~separates~~ the two cupolae. The absence of a cartilaginous median wall allows the ramus medialis nasi of the profundus nerve to pass into the nasal ^{capsule} ~~capsule~~ through a slit between the median edge of the cupola and the vertical median premaxillary plate (Fig. 16). The apical foramen is thus absent. The dorsal portion of the cupola, behind the dome, forms an arched roof for the vestibulum of the nasal sac. The lateral edge of this roof-

ing portion forms a prominent superior alar process and the ventral portion of the cupola extends posteriorly to form a well defined inferior alar process (Fig. 17). The inferior alar process lies in a horizontal plane and its tip reaches the anterior edge of the lateral flange of the maxilla. The superior alar process points downwards and its anterior edge forms the posterior border of the ^{fenestra}~~foramen~~ endonarin. Posteriorly to this process the duct of the lateral nasal gland opens laterally into the posterior part of the vestibulum. (Compare Figs. 12^a & 17)

The inferior alar process seems in lateral view to overlap the ventral tip of the superior alar process laterally (Fig. 17), but is separated from it by the intervention of the anterior portion of the narial muscle that inserts anteriorly on both processes (Fig. 23). This muscle contains a high proportion of fibrous connective tissue and originates posteriorly on the anterior edge of the maxilla, immediately dorsal to the posterior tip of the inferior alar process.

The posterior edges of the dorsal cupolar arches are medially continuous with the nasal septum by means of two cartilaginous strips, these strips being separated by the median vertical plate of the premaxilla. Laterally the posterior edge of the cupola is connected to the paries nasi by means of another thin strip of cartilage (Fig. 15).

The nasal septum is a vertical sheet of cartilage, its vertical anterior edge being free except for the dorsal cupolar connection. The free edge lies immediately posterior to the median vertical premaxillary plate. Anteriorly the ventral edge of the nasal septum is continuous with the two thin laminae transversales anteriores. Except for this, the whole ventral edge of the nasal septum is free to form the median rim of the fenestra endochoanalis (Fig. 16). The anterior portion of the

nasal septum is completely enclosed by the median vertical septomaxillary flanges (Fig. 9). Behind this connection the ventral edge of the nasal septum lies in a groove formed by the two vomers (Fig. 10).

Midway along its length the nasal septum is considerably higher than elsewhere (Fig. 17). At this point of greatest dorsal expansion the dorsal edge is continuous with the much arched transverse tectum nasi (Figs. 10 & 15). Except for this the dorsal edge of the nasal septum is free, the fenestra superior nasi lying anterior to the tectum nasi and the fenestra olfactoria posterior to it (Fig. 15). Behind the tectum nasi the nasal septum decreases in height in correlation ^{to} with the increase in size of the olfactory lobes of the brain, lying above it. The last portion of the nasal septum just anterior to the planum antorbitale is reduced to the rodshaped dimension of a trabecula communis (Fig. 10).

The floor of the nasal capsule is represented by a thin lamina transversalis anterior that crosses the dorsal surface of the palate. Medially it is continuous with the ventral edge of the nasal septum and laterally with the anterolateral tip of the paries nasi. Close to the septum the lamina transversalis anterior gives rise to a posteriorly directed paraseptal cartilage. This is a short, ventrolaterally tilted strip lying ventromedially to the organ of Jacobson and extending over two thirds of its lengthth. It ends posteriorly in two blunt tips. This cartilage represents the anterior part of the paraseptal cartilage and a small anterior tip of the planum antorbitale could represent its posterior vestige (Fig. 16).

Laterally to the paraseptal cartilage, the lamina transversalis anterior is continuous with the posterolaterally directed ectochoanal cartilage. This short cartilage is dorso-ventrally expanded and forms a lateral wall for the organ of

Jacobson (Fig. 17). Dorsally the ectochoanal cartilage has a very shallow lateral groove into which the downcurved median edge of the palatal flange of the maxilla fits. Ventral to this connection the cartilage projects beyond the bony palate to form a perpendicular ridge. The dorsal edge of this portion lies ventral to the suture between the septomaxilla and the maxilla (Fig. 9). The ectochoanal cartilage has a sharp tip that terminates ventromedially to the palatal gap in the bony palate (Fig. 17). The lamina transversalis anterior bears no concha for the organ of Jacobson and forms no floor for it. Thus the whole of the organ lies behind the lamina, its opening being terminal and situated so far forward between ectochoanal and ^aparaseptal cartilages that the duct of the organ is roofed by the lamina.

Laterally to the ectochoanal cartilage the lamina transversalis anterior is a flimsy cartilaginous rod that lies transversely on the palatal flange of the maxilla, behind the anterolateral horizontal process of the septomaxilla (Fig. 9). Laterally this portion of the lamina transversalis anterior curves dorsad, medially to the lateral oblique flange of the maxilla and is continuous with the anterolateral tip of the paries nasi.

The anterior half of the paries nasi is an oblique plate of cartilage, its lateral edge being tilted ventrally. In addition to its ventral connection with the lamina transversalis anterior, the anterior edge of the paries nasi is dorsomedially continuous by means of a thin, lateral rod with the dorsal edge of the anterior cupola. Between these two rods the anterior edge of the paries nasi is notched for the entry of the duct of the lateral nasal gland into the nasal capsule (Fig. 15).

The paries nasi widens posteriorly forming a deepening laterodorsal trough that houses the duct of the lateral nasal gland,

the ramus lateralis nasi of the profundus nerve and several blood vessels (Figs. ¹⁴~~17~~ & ¹⁵~~18~~). The posterior third of the trough houses the anterior part of the lateral ^{nasal}~~nasi~~ gland. The lateral and median edges of the trough in the posterior half of the paries nasi is fused to form a tubular conchal cavity. Immediately in front of this fusion the lateral edge bears a short posteriorly directed process (Fig. 17). The conchal cavity is anteriorly confluent with the trough through the aditus conchae and posteriorly it ends blindly. The dorsal rim of the aditus conchae is notched for the passage of the ramus lateralis nasi (Fig. 15 left side), the notch representing a foramen epiphanicale that is confluent with the ^{fenestra}~~fissura~~ olfactoria. The median edge of the paries nasi is continuous with the narrow tectum nasi immediately anterior to the aditus conchae.

The concha nasalis protrudes into the nasal sac from laterally and the conchal cavity being small, is laterally connected to the dermal side wall of the snout by means of an extensive horizontal flange (Fig. ¹⁰~~13~~). The lateral side of this process adjoins the median wall of the prefrontal. Above the lateral edge of the conchal flange the paries nasi is interrupted by a large fenestra lateralis nasi. Between this fenestra and the very extensive olfactory fenestra the side wall is represented by a slender rod of the cartilage only (Fig. 17). This arises from a small portion of side wall continuous with the anterior edge of the lateral flange. This rod may represent a remnant of De Beer's paranasal cartilage (De Beer, 1937). It is posteriorly continuous with the lateral portion of the planum antorbitale.

The tectum nasi is represented solely by a transverse cartilaginous arch, medially continuous with the ^{nasal}~~nasal~~ septum and laterally with the paries nasi immediately in front of the aditus

conchae, thus separating the fenestra superior nasi and the fenestra olfactoria (Fig. 15).

Although⁹ the planum entorbitale chondrifies as an independent element in the lizard~~s~~ embryo it is impossible to distinguish it from the roof and the side wall in the adult. In Dibamus it is difficult to interpret, because of its form and position. From the course of the ramus ethmoidalis illustrated in Figure 15 it is clear that at least that portion of the posterior cartilage medially to the nerve represents the planum entorbitale. An entorbital cavity, as such, of the nasal sac is absent since the nasal cavity opens straight back into the nasopharyngeal duct. The planum entorbitale, therefore, forms a roofing cartilage to the posterior portion of the nasal sac, (See section on Nasal Sac) rather than a back wall (Fig. 11). Adjacent to the nasal septum this posterior cartilage consists of a horizontal triangular portion with an anteriorly directed apex (Fig. 15). The posterior base of the triangle is slightly downcurved and its edge coincides with the ridge in the nasal epithelium marking the transition between nasal sac and nasopharyngeal duct. Immediately above the downcurved edge and adjacent to the nasal septum there is a short posteriorly directed process. Below the base of this process a second and much larger ventral process is attached by a narrow strip of cartilage (Fig. 17). In lateral view this process appears as a roughly crescent[^]shaped plate. This plate lies on the lateral face of the oblique median flange of the vomer directly in front of its suture with the palatine[^]pterygoid. This process lies wholly ventral to the rod-like nasal septum (Fig. 11). From its position it can only be a posterior remnant of the paraseptal cartilage.

The downcurved posterior edge of the roofing triangle is continuous laterally with a narrow cartilage strip, the posterior

edge of which supports the continuation of the epithelial ridge mentioned above. Laterally the cartilage strip is attached to another roofing ⁰partition that curves laterally and is continuous with the posterolateral edge of the conchal flange (Fig. 15 & 17). A posterolateral cavity is thus formed dorsally to the conchal flange. This posterior attachment of the conchal flange indicates a change in the relations of the posterolateral parts of the nasal capsule caused by the great reduction of the eye. It is likely that the planum antorbitale does not form part of the lateral dome, but without embryological material it is impossible to decide this point.

As a result of the complete loss of the sphenethmoid commissure there is a large fenestra olfactoria advehens only, the fenestra olfactoria evehens and the orbitonasal fissure being absent.

THE ORBITOTEMPORAL REGION OF THE NEUROCRANIUM.

The very degenerate eyes of Dibamus lie on the side of the skull. laterally to the flat prefrontal. Both orbit and interorbital septum are lacking (Fig. 10). Behind the nasal capsule the cartilaginous skull is represented by a median rod and a pair of lateral wings (Figs. 15 & 17). The rod is a continuation of the rodlike posterior portion of the nasal septum. It lies ventrally to the brain and is clearly the undifferentiated orbital part of the trabecula communis. Its posterior tip is unforked and lies in a dorsal groove on the bony basisphenoid and is continuous with it. A fenestra hypophyseos is thus absent.

The anterior portion of the median rod bears dorsally a pair of transverse horizontal wings. Each wing lies a short distance behind the planum antorbitale and immediately behind and in close association with the subolfactory process of the frontal. The lateral tip of the wing is curved anteriorly and overlies the ramus ethmoidalis of the nervus profundus and the nervus opticus.

The wing is thus situated anteriorly to the for^mam opticum (Fig. 15) and is also closely associated with the dura mater, ventral to the anterior portion of the cerebral hemisphere and the posterior portion of the olfactory bulb. For the above mentioned reasons this cartilage is best interpreted as the solum supraseptale.

THE EYE AND HARDERIAN GLAND

The degenerate eyes of D. novae-guinense lie laterally, to the prefrontals, there being no distinct orbits (Fig. 10). Underwood (1970) described the eye of D. novae-guinense. My specimen differs slightly from the drawing by Underwood (1970, Fig. 10 p. 24) as the layers of the retina appear more clearly demarcated and no such large optic nerve could be found. On the contrary to detect the minute nerve at all on the slides (Fig. 21) it was necessary to follow it all the way from the small optic chiasma. The eye muscles are completely absent.

The relations of the eye and the large Harderian gland correspond with that found in Amphisbaena fuliginosa (Bellairs, 1946). The flat Harderian gland enfolds the degenerate eye except laterally where there is a well-developed sub-brillar space. This space is medially lined by the cornea and laterally by the sub-brillar epithelium. Its periphery is formed by the Harderian gland that discharges its secretion into the lumen of the sub-brillar space. Anteriorly this space is drained by the nasolacrimal duct. The layer of sub-brillar epithelium is laterally covered by a thick layer of connective tissue (integumentary thickening - Bellairs 1946). This tissue is more extensive than that in A. fuliginosa, covering the entire surface of the Harderian gland; the latter having more or less the same size and outlines as the prefrontal.

The nasolacrimal duct, after passing through the lacrimal

foramen between maxilla and prefrontal lies in a groove on the dorsal palatal flange of the maxilla. It passes through the palatal gap (Fig. 2 & 17 right side) to the superficial palate where it opens into the organ of Jacobson.

THE OTICO-OCCIPITAL REGION OF THE NEUROCRANIUM

In shape and proportions the otico-occipital region of D. novae-guineae is adapted to a fossorial mode of life. The temporal arches are absent and the braincase is streamlined, having lost most of its processes and impeding projections. The parietal is extensively sutured to the otic capsules and to the supraoccipital to strengthen the braincase. The occipital region is unusual in that the exoccipital is not fused to the opisthotic but to the basi⁺occipital.

Except between the basioccipital and exoccipital, definite boundaries are present between all the elements of the otico-occipital region. These boundaries are indicated either by cartilage strips and/or syndesmoses. The cartilage strips are often enlarged to form extensive structures, sometimes showing signs of perichondral ossification. These cartilage strips obviously represent unossified parts of the bordering bones. That this is so, is proved by the invariable presence of a dividing line of weak chondrification through the cartilaginous areas, corresponding to overlying syndesmotic sutures in the thin, perichondral bony ^Ylayer where this is present. These unchondrified zones would seem to indicate anatomical immaturity. The snout-vent length of the specimen is 126 mm in comparison to the 165 mm recorded by Smith (1935).

The floor of the braincase is formed mainly by the large median sphenoid (parasphenoid & basisphenoid). This more or less flat horizontal bone has a slight transverse ridge that represents the crista sellaris and forms the back wall for the very shallow

pituitary fossa. The reduction of the crista sellaris is due to the absence of the eye muscles that usually originate in the pituitary fossa (Figs. 7 & 8).

The more or less transverse anterior edge of the sphenoid bears a median notch that is continued on the dorsal surface of the bone as a strongly defined groove, the extreme end of which is roofed with a thin arch of bone (Fig. 7). This groove houses the posterior end of the cartilaginous trabecula communis the paired trabecula being probably incorporated in the sphenoid. This median attachment is unusual in lacertilians. There is no cultriform process of the parasphenoid.

Anteriorly, on its ventral surface, the sphenoid bears two anterolaterally directed basipterygoid processes. The cartilaginous epiphysis of each process articulates with the meniscus pterygoideus situated on the medioventral surface of the palatine-ptyerygoid complex (Figs. 2 & 7). There is a synovial cavity between the two cartilaginous portions.

The anterior third of the lateral edge of the sphenoid is not connected to any other bones and is dorsally overlain by the profundus nerve and the maxillary ramus of the trigeminus nerve. In the middle the lateral edge is sutured to the overlying pro-otic bone and behind this to the basal tuber, of which it forms no part. Most of these sutures consists of connective tissue although irregular cartilage lumps are present. Behind the basal tubera the sphenoid has a rounded posterior edge sutured to the basioccipital (Fig. 2).

The lateral suture between sphenoid and pro-otic is complicated by a "parabasal" canal lying in it (Fig. 19). The sutural faces of the bones are grooved, forming the two halves of the canal, the bones being sutured dorsally and ventrally to the canal. In spite of the fact that it carries the internal carotid artery

and the palatine nerve the greater portion of the canal is not a true parabasal canal as it does not lie between the basisphenoid and the parasphenoid. The geniculate ganglion lies within the pro-otic bone and the palatine nerve enters the canal from above (Fig. 19). Posteriorly the internal carotid artery and the communicating ramus between nerve IX and the palatine ramus of VII (Willard, 1915) enter the canal through a foramen in the pro-otic bone anteroventrally to the oval fenestra (Figs. 2 & 20). Laterally to the pituitary fossa the canal opens into the brain-case. Both the palatine ramus and the internal carotid artery leaving the canal through this anterior foramen and a very short section of the canal behind it, could represent the true parabasal canal. The internal carotid artery branches into two, one branch being intimately associated with the pituitary gland on its way to the brain, the other accompanying the palatine ramus anteriad in a groove on the dorsal surface of the sphenoid (Fig. 7). This groove shallows anteriad as the artery and the nerve gradually take a more dorsal course. Anteriorly, while still in the groove, the artery and the nerve each gives off a small branch that pierces the sphenoid (Fig. 7) and leaves the bone through a foramen at the base of the basiptyergoid process (Fig. 2). These serve the buccal lining in the vicinity of the choanal opening.

The pro-otic, the opisthotic and the supraoccipital all contribute towards forming the otic capsule. In gross anatomy the membranous labyrinth of D. novae-guineae does not differ much from that of other lacertilians described. Although no thorough study was attempted a few small differences were noted. These are mainly differences in proportion, e.g. the ampullae of the anterior semicircular canals are slightly displaced anteriad and posteriad respectively. This condition results from the general streamlining of the skull. Also the posteromedial connection

of the lateral semicircular canal with the crus commune is situated directly ventral to the connection of the crus commune with the anterior and posterior semicircular canals. As is generally the case, the small endolymphatic duct leaves the sacculus medio-dorsally and curves underneath the utriculus. It leaves the otic capsule through the endolymphatic foramen (Fig. 7) and opens into a small endolymphatic sac that lies dorsally to the brain. A detailed study of the dibamid cochlear duct was made by Miller (1966a).

Another difference is that the perilymphatic duct forms a pronounced anterior loop after leaving the large perilymphatic cistern and before making contact with the basilar membrane. This loop lies in a bony channel which is an anterior extension of the cochlear cavity in the pro-otic. This channel thus consists of a dorsal and ventral leg (Fig. 19). The ventral leg opens into the cochlear cavity directly anterior to the oval fenestra and extends anteriorad to turn back above the geniculate ganglion to form the dorsal leg of the channel. The dorsal leg of the channel persists posteriorad past the anterior rim of the oval fenestra to open into the cochlear cavity directly below the posterior foramen for the acoustic nerve, thus forming a bony channel in the median wall opposite the anterior part of the oval fenestra (Figs. 7 & 20). Behind this, the perilymphatic duct adjoins the median aspect of the cochlear duct. The bony channel is continued posteriorad as a shallow groove lying ventrally to the inferior cisternal crest. A similar type of loop, only lying in a horizontal plane, is found in a number of other burrowing lizards such as the amphisbaenids Monopeltis capensis and Rhineura floridana, Anniella pulchra (Toerien, 1963) and the skinks Typhlosaurus caecus and Melanoseps ^t rondoensis to a lesser extent. It is interesting to note that Typhlosaurus lineatus lacks such a long looped channel

because the two species of Typhlosaurus differ also in their palates, T. caecus having a closed palate while that of T. lineatus is normal (Smit, in press).

Behind the papilla basilaris the perilymphatic duct opens into the perilymphatic sac that fills the recessus scala tympani. A fenestra rotunda is absent and only a median perilymphatic fenestra opens into the braincase (Fig. 8). This fenestra is covered by a membrane formed by the perilymphatic sac and possibly the dura mater.

The bony labyrinth consists mainly of the vestibular cavity dorsally and the cochlear cavity^t ventrally. A prominent inferior cisternal crest (Baird, 1970) demarcates the border between the two spaces that are for the rest widely confluent (Fig. 7). The vestibular cavity houses the large sacculus around which the utricle and the semicircular canals are arranged; it thus bears recessi for the ampullae and bony channels for the semicircular canals. Apart from the anterior channel for the perilymphatic duct the lateral wall of the cochlear cavity bears a large ventrolaterally facing oval fenestra that is for its greatest part occupied by the footplate of the stapes. The cochlear cavity also opens posteriorly into the recessus scala tympani.

The pro-otic is the largest bone in the otic capsule enclosing the anterior portions of the vestibular and cochlear cavities. Ventral to the cochlear cavity the pro-otic forms a medioventrally directed flange that is sutured to the sphenoid. This flange decreases in height posteriad corresponding to the increase in size of the otic capsule itself. The suture between the ventral edge of this flange and the sphenoid contains the "parabasal" canal (See sphenoid). The anteroventral end of the flange is extended to form a short anterior process. Between it and the otic capsule above it, there is a notch, the pro-otic incisure, for the

trigeminal nerve (Figs. 8 & 18). Behind the notch the medio-ventral flange is indented laterally for the gasserian ganglion.

Further back the flange encapsulates the geniculate ganglion, the palatine ramus of the facial nerve leaving the ganglion by a ventral opening that enters the "parabasal" canal (Fig. 19). The hyomandibular ramus leaves the ganglion through a laterodorsal foramen directly anterior to the oval fenestra. Medioventrally to the anterior rim of the oval fenestra the flange under the otic capsule is represented by a stubby ridge only and here the posterior foramen of the "parabasal" canal opens laterally for the entry of the communicating ramus of IX and the internal carotid artery (Figs. 2, 18, 20).

Above the pro-otic incisure the pro-otic has an anteriorly directed vertical ridge that is connected to the side wall of the parietal by means of an extensive ligamentous band. The top of this ridge bears a cartilage nodule continuous with a dorsolateral crest on the pro-otic and it can only represent a vestige of the taenia tecti marginalis (Figs. 3 & 18a).

The portion of the roof of the otic capsule formed by the pro-otic bears a shallow excavation for the connection of the parietal process (Fig. 20). Laterally this excavation is bordered by a sharp dorsolateral crest. This crest is posteriorly continuous with the crista parotica, the latter housing the lateral semicircular canal. Above and behind the excavation the pro-otic is connected to the supraoccipital. This line of connection is continued ventrad between the lateral walls of the pro-otic and the opisthotic in the form of a vertical cartilage ridge (Fig. 18a). The very large ventrolaterally facing oval fenestra interrupts this connection ventrally. The dorsal rim of the oval fenestra, including the cartilage ridge, extends ventrad as a pointed process overhanging and obscuring from lateral view part of the

oval fenestra and footplate. This ventral process forms the articular surface for the quadrate and therefore represents the paroccipital process (Fig. 18a). Medioventrally to the oval fenestra the pro-otic adjoins the cartilaginous basal tuber. This cartilage forms part of the ventral rim of the oval fenestra, the rest of the rim being fully ossified.

On the median wall of the otic capsule the pro-otic has a shallow indentation, the acoustic recess (Oelrich, 1956) into which open the small anterior and large posterior acoustic foramina (Fig. 8). Ventrally to the anterior foramen lies the foramen for the facial (Vll) nerve trunk. Dorsally the median section of the pro-otic adjoins the median flange of the supraoccipital and ventrally to this it is connected to the median section of the opisthotic (Fig. 8).

The supraoccipital is a median unpaired bone forming a narrow roofing arch behind the parietal. This arch, the tectum synoticum, is small in comparison to that of most other fossorial lizards (Figs. 1 & 7). It bifurcates laterally to form two flanges on each side that contribute to the formation of the otic capsule meeting the corresponding flanges of the pro-otic and opisthotic. A laterally directed dorsal flange forms a portion of the roof of the otic capsule (Fig. 7), and ^a ventrally directed ^{median flange forms a portion of the} median wall (Fig. 8). This median flange is pierced by the endolymphatic foramen.

Where these two flanges meet anteriorly to the tectum synoticum, a mediodorsal ledge is formed and in this ledge, and where the flanges join the tectum synoticum, the posterior semicircular canals lies in a bony channel (Figs. 7 & 20). This ledge is sutured to the median prong of the parietal (Fig. 1). Behind the long suture with the opisthotic the supraoccipital also meets the upper end of the ~~ex~~occipital over a short extent (Fig. 5).

The posterior portion of the otic capsule is formed by the opisthotic. Ventromedially to the oval fenestra it meets the cartilaginous basal tuber (Fig. 2). The large, flat basal tuber is ~~so~~ similar in structure to the cartilage strips separating most of the bones of the otico-occipital region. It too is partially capped both dorsally and ventrally by perichondral bone and it ^{is} also traversed by a line of weak chondrification corresponding to definite sutures in the perichondral layers. The position of this sutural zone show that the tuber is formed by unossified parts of the opisthotic and basioccipital only, the opisthotic contributing the main portion. This ventral suture is continued dorsad between the posteromedial wall of the opisthotic and a vertical exoccipital pillar that forms the lateral border of the foramen magnum (Fig. 5). This pillar is dorsally connected to the supra-occipital, in a poorly defined boundary (Cp. Figs. 1 & 5). The presence of a suture between exoccipital and opisthotic is most unusual in lizards. That it does not result from the immaturity of the specimen is shown by the fusion between exoccipital and basioccipital. It may perhaps be regarded as a primitive character.

The only indication of boundaries between the basioccipital and the two exoccipitals is the presence of two parallel cartilage strips that lie in the anterior portion of the occipital condyle, dividing the condyle here into three bony strips. This condition is found for only a short distance and is visible only in cross-section (Fig. 2 & 7). The posterior portion of the condyle has no boundaries and is covered by a cartilage epiphysis.

The glossopharyngeal nerve trunk pierces the opisthotic wall of the braincase to pass into the recessus scala tympani, immediately dorsally to the medial perilymphatic foramen (Fig. 8). The nerve lies dorsally to the perilymphatic sac and leaves

the recessus laterally through a foramen in the posterior aspect of the recessus scala tympani. This foramen is not related to a thin zone in the bone of the recessus scala tympani that may represent the closed fenestra rotunda. The vagus nerve passes a little posterodorsally to this, through a diagonal foramen in the cartilage separating the exoccipital portion of the basioccipital-exoccipital from the opisthotic (Figs. 8 & 18a). The hypoglossus nerve has two foramina that open externally immediately postero-ventrally to the foramen for the vagus nerve, but they pass through the bony basioccipital-exoccipital and open medially at a much lower level than the vagus foramen (Fig. 8). Behind the foramina for the hypoglossus nerve a small independent accessory nerve pierces the basioccipital-exoccipital (Figs. 8 & 18) and has its own ganglion encapsulated by the bone. It supplies the longissimus capitis muscles that lies in the direct vicinity of its foramen. The internal jugular veins leave the skull through the foramen magnum, as in other lizards.

THE QUADRATE AND STAPES.

There is no trace of an epipterygoid.

The quadrate is a greatly expanded, flat plate lying in a forward position laterally to the pro-otic part of the otic capsule (Fig. 3). Because of the virtual absence of a paroccipital process the quadrate lies close to the skull, particularly at the back (Fig. 5) and even in front diverges ^{but} a little from the otic wall (Fig. 2). This leaves only a narrow space into which the collumellar apparatus fits. The slope of the bone differs from that of the general lacertilian type, the two articular joints, instead of being dorsally and ventrally situated, lying in almost the same horizontal plane. The quadrate is roughly triangular with the condyle for the lower jaw articulation situated anteriorly on the horizontal base, and the downsloping posterior

edge representing the head (Fig. 3).

Only the lower anterior portion of the bone is thickened and small narrow cavities are ^rrestricted to this condylar part. The condyle for articulation with the lower jaw faces anteriorly and slightly ventrally (Fig. 6). This condyle is rounded and covered by a cartilage epiphysis and an extremely well developed synovial joint is formed with the articular of the lower jaw. The lateral aspect of this joint is formed by an anterior projection of the quadrate condyle that lies laterally to the articular and obviously ^userves to prevent dislocation (Fig. 4). The rest of the condylar surface is smooth and is only slightly grooved in the middle to form two articulation facets.

The quadrate head is extensive and comprises the whole of the mainly cartilaginous posterior edge of the bone (Fig. 3 & 20). It is attached to the side of the otic capsule in a long arc indicated by coarse stippling in Figure 18(a). Anteriorly the arc follows the pro-otic part of the crista parotica, then crosses the pro-otic to end ventroposteriorly on the vestigial paroccipital process overhanging the oval fenestra. Here the quadrate makes a small ~~contact~~ also with the opisthotic. The attachment with the paroccipital process is by means of a synovial joint (the streptostylic joint) the rest of the connection being ligamentous. The area of attachment on the otic capsule is much more extensive than that on the quadrate, especially anteriorly (Compare Figs. 3 & 18a). The anterior ligament fibres are therefore long and are anteroposteriorly orientated. The length of the fibres gradually decreases ventrad up to the well-developed synovial cavity. It is clear that the fulcrum for movement between quadrate and otic capsule lies a little above the synovial joint as the shortest fibres are situated here.

It is clear from the above that the position of the streptostylic joint is not at the base of the quadrate, as is often supposed, but is situated a little above the base of the quadrate, as shown in Figure 18(a). The position of the joint is also shown in Figure 18(b) where the joint is seen in relation to the other structures of the middle ear.

It should be noted that the fulcrum of the streptostylic joint lies very low down, on a level only slightly higher than the articulation between the quadrate and the lower jaw. A similar condition is found in e.g. some *Amphisbaenidae* (Zangler, 1944), the *Leptotyphlopidae* (Haas, 1930), and in *Ophioseps nasatus* (McDowell, 1954), and its significance in a fossorial animal will be discussed under the section on kinesis.

There is a strong and extensive connection between the medio-ventral and more posteriorly the ventral surface of the quadrate and the quadrate process of the pterygoid ventromedian to it (Figs. 2 & 3). This attachment is exceptionally low down. The nature of the connection would restrict individual movement and the two bones will tend to move together. The ventral edge ^{of the quadrate} (the originally posterior concave face) is notched immediately in front of the streptostylic joint (Fig. 3). On the medial surface in front of the notch there is an articular facet for a well-developed synovial joint with the large internal process of the stapes (Figs. 4, 18a & 19).

The stapes consists of a very large oval footplate (Fig. 20) and a much reduced shaft that bears two processes; a large internal process and a small dorsal process (Figs 18a & 18b). An extra-columellare as such and a tympanum are absent. The rim of the foot^tplate is cartilaginous except for a section anteriorly. Except for a large gap anteroventrally to this ossified portion of the rim, the footplate fits neatly into the oval fenestra (Figs. 2 & 7). The gap is filled with thickened connective tissue containing an area with different staining properties. The shaft forms a fairly substantial ridge attached to the horizontal midline in the anterior half of the footplate. The lateral portion of the ridgelike shaft remains cartilaginous for most of its length th (Fig. 20) and it is attached by means of a wide ligamentous

band to that section of the quadrate. The base of the ridge is pierced by the stapedia artery running in a nearly horizontal direction (Figs. 18b & 20). The attachment of the ridge to the footplate is thus limited to two small areas, one anteroventrally to the artery and the other posterodorsally to it. Anteriorly the ridge is continued forwards in front of the footplate as a large internal process (Fig. 18a) and backwards as a minute dorsal process (Fig. 18b). Both these processes are attached to the quadrate.

The internal process forms a synovial joint with the median surface of the quadrate directly in front of the posteroventral notch (Fig. 19). Posteriorly the synovial capsule is continuous with a ligament between the ridge-like shaft of the stapes and the quadrate process of the pterygoid. This ligament appears to be elastic in nature and in section each fibre is folded into a wavy pattern although the ligament itself is not folded in any way. Such a ligament would allow of a considerable amount of movement of the pterygoid-quadrate complex without affecting the stapes. That the minute posterior process is a dorsal process is proved by its relations both to the hyomandibular ramus of Vll (Fig. 18b) and to the streptostylic joint. The nerve lies medial to the process and curves around the stapes behind it and the process is enfolded by an anterior ligamentous continuation of the synovial capsule of the streptostylic joint.

THE SOFT TISSUES OF THE MIDDLE EAR

The tympanum is completely absent, its position being taken up by the flattened quadrate and the m. depressor mandibularis (Fig. 24). The cavity of the middle ear is replaced by extensive lymph sinuses that occupy almost all the limited space available between otic wall, stapes, quadrate and m. depressor mandibularis. There is no sign of an Eust^achian evagination from the pharynx

(Figs. 19 & 20). In D. novae-guineae the ultimate stage of reduction of middle ear cavity has been reached.

The lateral head vein leaves the skull through the dorsal part of the pro-otic incisure and runs posteriad immediately lateral to the otic capsule (Fig. 19). In the region of the stapes the vein branches, forming two large sinuses, one dorsally and one ventrally to the stapedia ridge (Fig. 20). Together with the lymph spaces these sinuses fill the space between stapes and quadrate. Behind the stapedia ridge the two "branches" unite again and further back, behind the footplate, the vein decreases drastically in size and follows a more lateral course.

The internal carotid artery runs ventrally to the lateral head vein and the stapedia artery branches from it dorsolaterally to the basal tuber (Fig. 18b). The internal carotid artery then enters the posterior foramen of the "parabasal" canal. The stapedia artery runs dorsad, medially to the ventral branch of the lateral head vein and passes through the stapedia foramen (Figs. 18b & 20). Here it lies under the dorsal sinus of the lateral head vein, but gradually gains a more lateral position to lie laterally to the single vein in front of the stapes (Fig. 19).

The hyomandibular ramus leaves the cavity in the pro-otic ^{in which} ~~for~~ ^{lies} the geniculate ganglion (Fig. 19) through a dorsal foramen medially to the single lateral head vein (Fig. 18b). Behind the division in the vein, the hyomandibular ramus passes ventrally to the dorsal ^{sinus} ~~stapedia~~ ^{to lie medially to the stapedia artery and dorsally to the} stapedia foramen (Fig. 20). From this point backwards the hyomandibular ramus runs dorsally to the stapes and passes anteroventrad around the minute dorsal process (Fig. 18b). Here the nerve branches into two, a posterior hyoideus ramus and an anterior chorda tympani. The ramus hyoideus innervates the m. depressor mandibularis and the m. cervicomandibularis. The chorda tympani takes an oblique anteroventrad course passing

through the quadrate notch to lie laterally to the base of the quadrate. This nerve enters the retroarticular process, shortly behind the lower jaw articulation through a small, median foramen (Fig. 6).

To get a clear picture of the nerves and the bloodvessels the paragraphs on the "parabasal" canal (Sphenoid) and the section on the Pro-otic should be read (See also Fig. 21).

THE HYOID APPARATUS

The hyoid apparatus is represented by a single triradiate element that is mainly cartilaginous with ossifications in the middle portions of a pair of posterolaterally directed processes (Fig. 22). The anteriorly directed cartilage rod is the lingual process that supports the thick undivided tongue. It ^{is} continuous with the small hyoid body that serves as no more than a base for the three processes.

The posterolateral processes can only be the pair of first ceratobranchials as this element is more often than not the only one to ossify in lizards (Komer, 1950). In a similar triradiate hyoid apparatus of the fossorial Acontias meleagris, Van der Merwe (1944) also names the two ossified posterior processes the first ceratobranchials.

The ossification of the ceratobranchials is complicated as each one forms a bony tube with two to three large oval foramina on its ventral side. Within this tube lies another smaller bony tube also with a number of small ventral foramina. The posterior cartilage tips of the paired element are slightly upcurved to lie in a position laterally to the pharynx and these tips probably represents the first epibranchials. The arytenoid cartilage is an unpaired crescent-shaped structure and the cricoid cartilage is rather poorly developed (Fig. 22).

THE JAW MUSCLES AND KINETIC MUSCLES

Jaw muscles innervated by the trigeminal nerve (Temporal muscles).

The nomenclature used by Oelrich (1956) is followed. The temporal musculature is massive and simplified compared to that of Ctenosaura pectinata. In the adductor mandibulae group there is a clear distinction only between the m. adductor mandibularis internus (m. pseudotemporalis) and the m. adductor mandibularis externus, the m. adductor mandibularis posterior being apparently incorporated in the externus.

It was found impossible to determine the exact divisions of the latter muscle mass from cross-sections, particularly in those areas where the fibres are cut lengthwise. Basically there seems to be three portions anteriorly, one of which is a deep division, the full extent of which is not visible in figure 23. Posteriorly these portions merge into one muscle mass. It is difficult to homologise these partial subdivisions with those described by Oelrich for C. pectinata. This muscle mass will therefore be treated as a whole. Its most posterior origin is an aponeurosis on the neck muscles. In the dorsal midline an extensive aponeurosis is formed with its fellow of the other side. It also originates from the otic capsule above and behind the quadrate; from the anterior and posterior oblique edges of the quadrate; from the median surface of the quadrate; from the m. depressor mandibularis where the latter is interposed between it and the lateral surface of the quadrate; from an extensive dorsal and dorsolateral surface area of the parietal dorsally to the origin of the m. pseudotemporalis; and from the posterior portion of the frontal.

The muscle mass inserts on a short mandibular process lateral to the coronoid process; on the dorsal and posterior rim and on the lateral surface of the coronoid; on the median, dorsal and lateral surface of the compound bone of the lower jaw behind the coronoid and on the posterior process of the dentary (Fig. 23). Only a few fibres insert on the large coronoid process of the dentary.

Contraction of this muscle mass will lift the lower jaw and tend to pull it backwards.

The m. pseudotemporalis (m. adductor mandibularis internus) is an undivided muscle of moderate size and consists of a wide strip of parallel fibres. It originates ventrally to the compound m. adductor mandibularis externus and m. adductor mandibularis posterior on the posterior portion of the frontal and the anterior portion of the parietal. It inserts on the median surface of the coronoid and the compound bone of the lower jaw (Fig. 24). Contraction will lift the lower jaw and tend to pull it in towards the skull.

The m. pterygomandibularis is a large muscle that lies ventrally to the lower jaw and the skull base. It originates from the posterior tip of the ectopterygoid and from the lateral and ventral surface of the fused palatine-pterygoid anterior to the quadrate. It is also connected to the fascia of the anterior portion of the ~~m. pterygomandibularis~~ ^{protractor pterygoideus}. The m. pterygo-mandibularis inserts on the ventral surface of the lower jaw behind the coronoid process up to the posterior tip of the retroarticular process. This insertion is continued posteriad as an aponeurosis with the m. depressor mandibulae (Figs. 24 & 26). Contraction of the m. pterygomandibularis will close the lower jaw and also tend to pull it anteromesiad, being thus antagonistic to the backward pull of the adductor muscle group and serving to stabilise the streptostylic joint.

The constrictor dorsalis group is also innervated by the trigeminal nerve, but is concerned with the kinetic movement of the upper jaw. A well-developed m. levator pterygoideus (Fig. 25) originates from the ventral edge of the lateral wall of the parietal and its fibres lie anteromesiad to insert in the dorsal groove of the fused palatine-pterygoid, laterally to the bony ring (Fig. 7) and this insertion is continued posteriad for some

distance on the dorsal surface of the pterygoid. Some fibres also insert on the lateral edge of the sphenoid and ventrally some fibres insert on the fascia of the m. protractor pterygoideus. This muscle will exert a backward pull on the palatine-ptyerygoid and tend to lift it, thus depressing the maxillary segment of the skull.

The m. protractor pterygoideus is considerably larger than the m. levator pterygoideus and its fibres lie horizontally. It has an extensive fan-shaped origin on the lateral and ventral surface of the sphenoid between the basipterygoid articulation and the basal tuber. From here the fibres run posterolaterally to insert on the posterior portion of the quadrate process of the pterygoid, on the ventral edge of the quadrate anteriorly to its notch and also on the median surface of this bone laterodorsally to the quadrate process of the pterygoid (Figs. 25 & 26). Contraction of this muscle will tend to pull the quadrate and the quadrate process of the pterygoid anteromesiad, thus lifting the maxillary segment of the skull.

The jaw muscle innervated by the facial nerve

The m. depressor mandibularis consists of a distinct anterior portion and a large posterior portion, the m. cervico mandibularis (the latter is not figured). I will use the name m. depressor mandibularis for the anterior portion only. The origin of this is extraordinary in that it lies wholly on the dorsolateral surface of the quadrate. This short stout muscle is very strongly inserted on the whole dorsal surface of the retro^aarticular process as well as on the m. pterygomandibularis behind it (Figs. 24 & 26). Contraction of this muscle will depress the lower jaw by pulling the retroarticular process towards the quadrate.

A separate large m. cervicomandibularis inserts on the

superficial fascia of the lateral surfaces of the m. depressor mandibularis and of the m. pterygomandibularis behind the lower jaw articulation. The origin of the muscle is unfortunately not included in the sections, but none of the fibres have their origin on the skull. The contradiction between its massive size and weak insertion makes it difficult to ascertain its influence^f on the depression of the lower jaw. It would however be safe to assume that it at least resists the tendency of the quadrate to move forwards when the mouth is opened.

JAW FUNCTION AND CRANIAL KINESIS

In 1962 Frazzetta pointed out the inadequacies of the classical account of cranial kinesis of Versluijs (1910, 1912). Versluijs saw in this complicated mechanism of lifting the snout a method of increasing the gape. Frazzetta proved experimentally that in actual fact the gape is lessened with kinesis. He also showed that depression of the snout is as important in kinesis as raising it. The chief deficiency in Versluijs' account seems to be that he made no allowance for the interaction between kinesis and jaw function.

Although Frazzetta (1962) examined some fossorial lizards (Amphisbaena alba, A. fuliginosa, Anniella pulchra) his account is based chiefly on terrestrial forms. The only fossorial form treated by Versluijs (1912) is an amphisbaenid species. Lakjer (1926) in his extensive account of the trigeminal muscles of the sauropsids describes only two fossorial lizards, both amphisbaenids. He gives some consideration to the functional aspects of these muscles, but only as an extension^s of Versluijs' work. More recent work on fossorial forms which include a discussion of kinesis are those of Van der Merwe (1944) on Acontias meleagris, Kritzing (1946) on Monopeltis capensis, Toerien (1950) on Anniella pulchra,

Smit (in press) on Typhlosaurus, Cluver (in press) on Typhlacontias and Boyd (in press) on Melanoseps. All these use Versluijs as a point^{of} departure and lack a full description of the muscles and ligaments involved in lower jaw function.

A full modern account of the kinesis and jaw function of any fossorial lizard is therefore lacking. The following account is based on serial sections of the single specimen available, thus excluding the possibility of experimental proof of the interpretations arrived at.

Dibamus is a pronounced burrower and the obvious change in proportion of the various skull elements (Fig. 25) may be expected to have an influence on the ⁿcranial ^skinesis and jaw function.

The initial ~~changes~~^{the loss} in skull proportion follow on the reduction of the eyes and ^{of} the tympanic membrane and the tympanic cavity. The reduction of the orbital region leads to an increase in the size of the parietal relative to the size of the skull and consequently to ^a more forward position of the mesokinetic joint. The origin of the m. pseudotemporalis and of the anterior part of the m. adductor mandibularis externus also lies thfurther forward directly above their insertion on the coronoid process. Apparently the initial reason for the loss of metakinetic movement lies in the need for strengthening the skull for burrowing. The loss of the circumorbital bones, particularly of the jugal allows a forward movement of the lower jaw in that the large coronoid process is unimpeded.

Loss of the tympanic membrane and tympanic cavity, accompanied by the loss of the paroccipital process, allow the quadrate to become platelike with an extensive attachment to the otic wall. The quadrate head thereby becomes large enough to serve as the sole origin of the m. depressor mandibularis. It is interesting

to note the absence of the ligament between lower jaw and palatine-pterygoid complex. As Frazzetta (1962) shows, the ligament normally serves to prevent damage to the tympanum and the middle ear by restricting the depression of the lower jaw. Loss of the tympanum and reduction of the extracolumellare allow the quadrate to become anteriorly inclined, thus bringing the lower jaw articulation to a position from which ~~any~~^{no} forward kinetic movement would raise the lower jaw articulation considerably, instead of merely moving it forwards as in those lizards where the quadrate is vertical. This effect is apparent to a very much smaller degree in Varanus where the quadrate is slightly forwardly inclined (Frazzetta, 1962).

In correlation with the^e angle of the quadrate and to allow an effective length for the m. depressor mandibularis the retro-articular process projects downward at a sharp angle instead of more or less straight back (Fig. 27). A furtherth result of the quadrate angle is the posteriorly facing articular facet of the lower jaw, and a considerable reduction in the length of the jaw at the back (Fig. 6).

The obvious advantage of a subterminal mouth in burrowers also leads to an anterior shortening of the lower jaw (Figs. 4 & 24). This would tend to restrict the size of the gape. ~~In~~^{In} comparison to the size of the skull, and therefore of the mass of the jaw closing muscles, the lower jaw is very small. ^{dentary contribution to the} The coronoid process is mainly a strengthening device because few muscle fibres attach to it.

The coronoid process is forwardly placed on the jaw to allow enough leverage power to compensate for the weakness inherent in a short jaw. Such a position of the coronoid process would tend to restrict the gape even furtherth because it places the angle of the mouth forwards. The presence of a possible mechanism

compensating for this loss in actual gape ~~will be~~ postulated below.

Cranial kinesis in Dibamus does not differ in principle from that of other mesokinetik lizards. The mesokinetik joint ^{is} ~~it~~ placed far forward directly above the equally forwardly placed coronoid process and thus closely behind the angle of the mouth (Figs. 27, 28, 29). There is a well-developed basipterygoid articulation that allows the usual sliding movement of the pterygoid on the basipterygoid process. The quadrate process of the pterygoid is ⁱ ~~l~~igamentously connected to the quadrate medially to the quadrate condyle and below the level of the jaw articulation. The kinetic muscles, especially the m. protractor pterygoideus are better developed than in terrestrial forms and the fibres of the latter are practically horizontal. Contraction of the m. protractor pterygoideus will pull the pterygoid-palatine unit and the quadrate condyle forwards causing the pterygoid to slide over the basipterygoid process. The pterygoid-palatine exerts pressure on the palatal region of the snout which is thus elevated on the mesokinetik joint. The fusion of palatine and pterygoid is an obvious strengthening device. Movement between frontals and parietal is not impeded (as may seem possible from Figure 11) by the subolfactory processes of the frontals as they are separated from the dorsal parts of the palatine ring by a blood sinus. The restricted gape is partially compensated for by the anterior position of the mesokinetik joint relative to the angle of the mouth, thus allowing for the elevation of the snout to a more effective angle.

Contraction of the m. levator pterygoideus will reverse this movement and depress the snout. In this it is aided by the massive adductor mandibulae muscle group that pulls the lower jaw up and backwards as will be shown later (Fig. 27).

The back and forth movement of the pterygoid causes the

quadrate to rotate in the streptostylic joint. As this bone lies at an anteriorly inclined angle an anterior movement of ^{the} pterygoid will not only cause the quadrate condyle to move forward, but will also lift it. When the snout is kinetically raised the lower jaw will thus be raised at the back and the jaw itself will tend to move forward (Fig. 29).

Simultaneously with the kinetic movement the depressor mandibularis contracts, depressing the lower jaw. It is of importance that the m. depressor mandibularis originates on the quadrate only and not on the occipital region of the skull. This allows a forward swing of the quadrate and lower jaw as a unit without the restricting influence of a backward pull on the retroarticular process, particularly in a skull with a forwardly situated jaw articulation. As a muscle can not be stretched for more than half its resting length (Wells, 1955) the vertically directed fibres of the m. pseudotemporalis limit the distance to which the coronoid process can be depressed (Figs. 28 & 29). Furtherthmore contraction of the m. depressor mandibularis will add to the effect of the kinetic movement i.e. to the forward movement of the quadrate condyle and the raising of the lower jaw articulation. This will cause the lower jaw to pivot around the coronoid process insertion of the stretched m. pseudotemporalis and the anterior fibres of the adductor externus group. Movement in the fulcrum at the lower jaw articulation is therefore partially replaced by a pivotal movement directly behind the angle of the mouth. Without kinesis a muscle in this position will restrict the gape drastically (Fig. 28). In combination with kinesis, however, a 30% or more increase over this restricted gape is accomplished (Fig. 29).

In this way a somewhat restricted gape of short jaw length but of large jaw angle is achieved. This effective gape is

accomplished by the forward position of the mouth as well as the pivoting of the lower jaw at the mouth corner. The combination of the two mouth opening mechanisms, apart from increasing the mouth angle, causes the mouth to be slightly protruded~~y~~ and thus to be placed in a more terminal position. A further advantage of this protrusion under burrowing circumstances is that, although the jaws can be opened at a wide angle, the size of the total gape itself does not exceed the largest diameter of the head (Fig. 29).

The neck muscles will aid the *m. depressor mandibularis* and the protractor pterygoideus to overcome the pressure of the soil by lifting the head when the mouth is opened. The subterminal mouth can thus be placed in a completely terminal position. This is an important feature for a fossorial animal that has to catch prey encountered directly in front of it, but would also benefit from a subterminal~~/~~ mouth when burrowing. Kinesis helps to protrude the mouth to a more terminal position but the completely terminal position results from a backward tilting of the head (Fig. 29).

Another adaptive value of the short lower jaw, apart from placing the ^umoth subterminally, lies in the greater leverage power achieved when the massive adductor mandibulae muscle group closes the jaws onto the prey. This muscle group pulls the lower jaw up and backwards. Those fibres that originate from the quadrate and insert on the lower jaw, particularly on the posterior rim of the coronoid process, decreases~~y~~ the angle between the lower jaw and the quadrate behind it when they contract. This causes the quadrate condyle to swing downwards and backwards aiding the *m. levator pterygoideus* in pulling the palatine-pterygoid backwards and consequently in depressing the snout. The depression of the snout is thus synchronised with the adduction of the lower jaw. This simultaneous movement of the upper and lower jaws not only increases the snapping speed, but both jaws

touch the prey at the same moment, a feature of great importance for an insectivore.

Dibamus thus retains cranial kinesis in spite of the weakening effect it would tend to have on the skull, as it increases the angle of the opened short jaws and, together with the other features mentioned above, increases the animal's ability to catch prey. For a fossorial way of life the angle of the jaws in relation to the corner of the mouth is as important as the total gape itself. A gape with larger jaws and a smaller angle is less efficient than the same gape formed by smaller jaws at a larger angle. The former type of mouth would force the animal to work or push its jaws over the prey. Initially the prey would be clamped between the tips of the jaws where much muscle power is lost and where the prey is situated awkwardly for manipulation by the jaws and tongue.

With the same gape and a larger angle the mouth becomes slightly protruded and when the jaws snap on to the prey a larger proportion of the teeth row can sink into it. Also, when caught, the prey is in a more manageable position relative to the jaws and the tongue and ~~to the point where relative to the jaws and the tongue and to the point where the jaw muscle~~ exert their maximum power on the lower jaw.

DISCUSSION

In Romer's "osteology of Reptiles" (1952, p.552) the diagnosis of the family Dibamidae contains several question marks that can now be eliminated. In the species Dibamus novae-guineae, at least, the postorbital, the epipterygoid and the interorbital septum are indeed absent as Boulenger had noted in 1887. Boulenger (1887), Camp (1923), Romer (1952) and Guibè (1970) all say that the premaxilla is paired. In D. novae-guineae there

is a single fused element as Smith (1935) has also shown. Boulenger, Smith and Romer note the absence of an infraorbital foramen (palatine vacuity). This is incorrect, at least for D. novae-guineae, where there is a small but definite fenestra (Fig. ² ~~1~~).

Skull characters that have been correctly noted by earlier authors are the absence of cranial arches, the greatly expanded quadrate (Smith, 1935), the absence of a tympanic cavity and a stapes pierced by the stapedia artery (Underwood, 1957).

The Dibamus skull shows extreme fossorial degeneration approaching in degree that of the Amphisbaenidae, the Pygopodidae and the Leptotyphlopidae. With these (and other) taxonomicallyⁿ widely separated squamate burrowers it shares a large number of adaptive tendencies, summarised by e.g. Romer (1952). In comparison to the extreme forms amongst these the skull is comparatively lightly built, the bones not much thickened and except in the nasal region not particularly closely knit.

THE PALATE

Apart from Dibamus only one other lizard, the burrowing skink Typhlosaurus (Smit, in press) is known to have a completely closed palate with a secondary choanal opening situated far back between the pterygoids, although another skink Feylinia (du Toit, in press) approaches this condition. All skinks, and among lizards skinks only, have an air passage functionally closed off from the mouth cavity proper (Fuchs, 1908). This is accomplished by a lateral flap of skin that, anteriorly, covers the choana and, posteriorly, (where it is supported by a palatal flange of the palatine) converts the post-choanal palatal groove into a functional nasopharyngeal duct. Except at the back where the nasopharyngeal duct opens widely into the mouth cavity through a secondary choana, communication between the mouth cavity on the

one hand and the nasal cavity and the nasopharyngeal duct on the other is reduced to a narrow apparently non-functional slit. The genus Typhlosaurus demonstrates beautifully how a closed type of palate can arise in skinks by a simple elimination of these slits: in T. lineatus the slits are present while in the otherwise closely similar T. caecus they are closed by a fleshy fusion of the lips of the slits anteriorly and further back by a suture between the median edges of the two flanges of each cylinder-shaped palatine (Smith, in press).

In Dibamus there is a complete bony palate, formed anteriorly by a sutural connection between the vomer on the one^e hand and the maxilla and a typically scincid^c palatal flange of the palatine on the other, and, posteriorly, by an actual though only partial fusion between the two flanges of each palatine. In Dibamus the dorsal flange is much reduced (Fig 12) and as in Feylinia (where, however, the palatine and pterygoid are not fused) the palatal flange may contain a pterygoid component. It is extremely unlikely that this type of secondary bony palate could have arisen twice in the lizards and consequently a scincid origin for Dibamus must be accepted. Whereas the genus Typhlosaurus demonstrates the development of a closed scincid palate in one single step, Feylinia illustrates an intermediate stage towards its full development. The anterior two thirds of the vomer is sutured to the maxilla but behind this a typically scincid slit connects the nasal cavity and the nasopharyngeal duct with the mouth cavity (du Toit in press).

Dibamus differs from both Typhlosaurus and Feylinia in that the two palatines are not sutured together in the midline, the interpterygoid vacuity extending ^{them as far as} also between the posterior sections of the vomers. It differs also in having a short soft palate over a posterior common section of the two nasopharyngeal

ducts.

In view of Underwood's (1957) and Guibé's (1970) opinion⁴ that Dibamus belongs in the Gekkota it should be emphasised that in having a bony connection across the ^efenestra exochoanalis behind the organ of Jacobson (secondary palate of Fuchs, 1908) Dibamus has a neocho^{ana}anate type of palate while both the Geckonidae (Lakjer, 1927) and their fossorial derivatives, the Pygopodidae (Stephenson, 1962) are palaeochoanate.

In Dibamus the relations of the ⁿnasolacrimal duct to Fuch's secondary palate is different from that found in a neochoanate such as Varanus. In Varanus the longer of the two nasolacrimal ducts runs ventrally to the short suture between maxilla and vomer (Bellairs, 1950). In Dibamus the duct lies dorsally to the bony palate on the suture between vomer and maxilla as far as the palatal gap between maxilla, vomer and septomaxilla (Fig. 11²). It passes through this gap and then runs ventrally to the septomaxilla to the organ of Jacobson. The palatal gap represents the posterior section of the external vomeronasal fenestra. The Feylinia condition shows how the dibamid condition could have come about. Here the nasolacrimal duct issues from the skull onto the ventral surface of the palate far back through the anterior end of the much restricted choana. It then runs forwards for some distance in a small groove formed by an overlap of the maxilla over the vomer medial to the maxilla-vomer suture, but gradually moves dorsally into the suture where it remains up to the vomeronasal fenestra. In Dibamus where the choana became completely closed off externally the duct eventually came to lie dorsally to the suture.

The organ of Jacobson is more degenerate than in any other known burrower. It also differs from all others in that it lies wholly behind the lamina transversalis anterior and that its duct issues terminally and opens into the mouth cavity some distance in front of the organ. Perhaps as a consequence of this the

anterior rim of the ^eexternal vomeronasal fenestra is formed by the premaxilla and not by the vomer and maxilla.

PARABASAL CANAL

In Dibamus as in e.g. Monopeltis (Kritzing, 1946), Anniella (Toerien, 1950), Feylinia (du Toit, in press) and Typhlosaurus (Smit, in press) the internal carotid artery and the palatine branch of Vll run in a canal in the bony^s side wall of the brain cavity. Toerien (1950) postulates that the posterior part of this canal is[/]not a true parabasal canal but a secondary canal indicating the suture between the fused sphenoid and pro-otic. In Dibamus the suture^e is present and the canal actually lies in it, thus confirming Toerens suggestion. In Dibamus the anteriorⁿ portion of the parabasal canal in front of the rudimentary crista sellaris is open dorsally. This is also the case in many fossorial African skinks e.g. Feylinia and Typhlosaurus.

OTICO-OCCIPITAL REGION

In burrowers, as a ~~result~~ of adaptive changes in the middle ear the proportions and the relations of the components elements of the otic capsule also tend to change. In Dibamus the lengthth of the large fenestra ovalis is greater than its height and it faces ventro-laterally instead of laterally, the whole otic capsule being tilted downwards.

A peculiar^a feature of the inner ear of some burrowers, apparently without adaptive value, is that the perilymphatic duct lies in a bony channel. This character occurs in Anniella, some amphisbaenids and to a lesser extent in some fossorial skinks (Toerien, 1963). It is found also in Dibamus but here the two sections of the loop of bony channel lie in a vertical plane compared to the other burrowers where the loop[/]lies in a more or less horizontal plane.

Dibamus differs from all other ^{known} burrowers in having a very narrow tectum synoticum accompanied by the absence of a processus ascendens tecti synotici. In this region too is a feature which distinguishes Dibamus from all other known lizards: There is a well developed suture between the exoccipital and the opisthotic bones.

QUADRATE AND LOWER JAW.

The greatly expanded, flat plate-like quadrate of Dibamus is in complete contrast to the rod-like quadrates of other extreme squamate burrowers e.g. Ophioseps, Leptotyphlopidae, Typhlo^pidae and many Amphisbaenidae. Anything resembling it is found only in burrowing skinks such as Typhlacontias, Feylinia and Typhlosaurus. In the first two it is a flattened inverted L-shaped bone showing the Dibamus tendency towards enlargement of the head but having a less expanded body. In Dibamus the body is much enlarged for articulation with the enormous internal process of the columella. In Typhlosaurus the bone is also flattened but of a more compact, squarish shape with both head and body enlarged. The shape is influenced by the type of columella, the angle of the basic, inverted L being funnel-shaped to accommodate the much enlarged forwardly inclined extracolumella (Smit, in press). In shape the quadrate of Dibamus thus falls within the range of variation of ^L ~~that of~~ scincid burrowers.

In its approach to a horizontal position the quadrate of Dibamus is surpassed by the rod-like quadrates of the forms mentioned above. In Feylinia the quadrate is also somewhat tilted but whereas here the much reduced paroccipital process lies behind the fenestra ovalis (du Toit, in press), in Dibamus the articulation for the quadrate head lies on an overhang lateral to the fenestra.

Something similar to the peculiar cylindrical, downwardly directed retroarticular process of Dibamus is found also in the amphisbaenid Rhineura floridana but in none of the burrowing skinks. In some of the other amphisbaenids the retroarticular process is absent (Zangerl, 1944).

JAW FUNCTION AND KINESIS

In the descriptive part of the paper it was shown how certain structural adaptations of the dibamid skull and the consequent changes in muscle attachments influence the jaw function and cranial kinesis. These adaptations occur to a ^{re} greater or lesser degree in all burrowers e.g. an anteriorly inclined quadrate, a lower jaw greatly shortened both because of the quadrate angle and because of the subterminally placed mouth, and an anteriorly situated mesokinetic joint (e.g. Zangerl, 1944 on Amphisbaenidae; Mac Dowell et.al, 1954 on Ophioseps nasatus).

The jaw muscles, where they are known e.g. Amphisbaena alba Lepidosteron microcephalon (Lakjer, 1926, figures 82 and 86), Rhineura floridana (own observation) and Leptotyphlopidae (Haas, 1930) show an overall resemblance in general pattern to that of Dibamus. It can be expected therefore that the type of jaw action and cranial kinesis postulated for Dibamus would occur also in these other extreme burrowers. It is interesting to note that although Versluys (1912) does not mention it in his account, his figure on page 633, illustrating the kinesis of Amphisbaina sp., shows a similar tendency for the quadrate-lower jaw articulation to be raised during elevation of the snout.

THE MIDDLE EAR AND SYSTEMATIC POSITION

Since the time of Boulenger (1887) the Dibamidae have been generally regarded as related to the Scincidae. Romer in his "Osteology of reptiles" (1952) places the family as of uncertain

affinity within the Infraorder Leptoglossa (Scincomorpha) and retains this in his latest classification (1966). Guibé (1970), following a tentative suggestion by Underwood (1957), places the Dibamidae in the Infraorder Gekkota close to the fossorial Pygopodidae. This they base chiefly on the fact that in living reptiles the primitive condition where the stapes is pierced by the stapedia artery, is preserved only in Dibamus and in some geckos. The few other points of evidence presented, such as the common lack of osteoderms and the gecko type vertebrae in Dibamus, are at best rather ambiguous and in any case outside the scope of this ~~article~~ paper.

The perforated stapes, although certainly a valid point, loses a great deal of its importance when it is shown that the rest of the middle ear structure of Dibamus is of a definitely non-geckonid type. In neither the geckos (Versluys, 1898; Brock, 1932) nor in the Pygopodidae (Underwood, 1957, p. 218) is there an internal process of the columella. Dibamus has, in addition to a small dorsal process, a prominent internal process in synovial articulation with the quadrate (Fig. 19). A further proof of the non-geckonid origin of Dibamus is the course taken by the chorda tympani through the middle ear. In all non-geckos the nerve is looped around behind the internal process in a proximal-distal direction before running down in front of the columella on its way to the lower jaw. In the fossorial skinks Feylinia (du Toit, in press) and Typhlaconchorda (Cluver, in press) the extracolumella is absent and the chorda tympani passes down behind the stapes to the lower jaw. This is the case also in Dibamus (Fig. 18b). In geckos (Versluys, 1898) and in pygopodids (Underwood, 1957 p. 255) the chorda tympani, in the absence of an internal process, does not pass over the stapes but runs down in front of the columella. We therefore have to explain the presence of a perforated stapes

in an animal with an otherwise non-geckonid type of middle ear and a palate of a definitely scincid type. If on the strength of the palate we regard Dibamus as a scincoid^mmorph, we can interpret the perforated stapes in one of two ways: Firstly, it may be a primitive character retained by an early offshoot of the main skink line in parallel to its retention in the gecko line. It is interesting to note that Camp (1923 p. 333) in a chart illustrating the phylogeny of the lizard^s families regards the Dibamidae as the earliest offshoot (Eocene) of the Scincoid^rea; the Feylinidⁱae (including Typhlosaurus) and the Anelytropidae being later offshoots.

The second possibility namely that the perforated stapesⁱ is a secondary character ~~is incapable of proof~~ ^{cannot be proved} without embryological material. However, the ridgelike nature of the stapes shaft and the nature of the stapedia foramen through it are such that a secondary origin can easily be attributed to the perforation (Fig. 18). The greatly enlarged, forwardly inclined internal process, subjected to the stresses imposed by an articulation with a moveable quadrate would obviously be in need of buttressing to stabilise it against the large footplate. It is possible^t to visualise how a stapedia artery, passing through the narrow space between footplate and internal process, behind the original shaft, could be trapped by an additional skeletal connection between footplate and process (Figs. 5, 18a, & b). In the limbless skink Melanoseps ~~after ^t after~~ there is an anomalous^t condition in which the hyoid branch of the VII th nerve pierces the base of the short stapes (Boyd, in press). This cannot possibly be a primitive condition and is a clear case of trapping by the stapes. Melanoseps thus shows that it is unwise in degenerate lizards to use a perforated stapes as a systematic character. The main argument in favour of a geckonid relationship for Dibamus thus falls away.

Dibamus on the evidence of middle ear structure belongs to the non-geckonid group of lizards and on the evidence of the scincid type of plate is clearly a member of the Scincomorpha.

AFFINITIES WITH OTHER SCINCOMORPHA

The affinities of Dibamus within the Scincomorpha is uncertain, although according to Miller (1966b) the structure of its cochlear duct shows close resemblance to that of Anelytropsis. Among fossorial skinks the skulls of several African forms have been described (Acontias, Typhlosaurus, Melanoseps, Typhlacontias and Feylinia) and the external features of the skull of the Madagascar genus Voeltzkowia are known from the work of Rabanus (Romer, 1952).

The African forms fall into two groups one ~~including~~ Acontias ~~and~~ culminating in Typhlosaurus and the other culminating in Feylinia (de Witte and Laurent, 1943). As far as the skull is concerned the two groups differ chiefly in the structure of the palate and in the form of the stapes and quadrate and the general proportions of the otic region. In palate type Dibamus is closer to Feylinia than to Typhlosaurus. In the structure of the columella curis, and in the proportions of the otic capsule Dibamus differs from both African groups but not more than they differ from each other.

Apart therefore from one or two, perhaps primitive, features (separate exoccipital and opisthotic bones and the perforated stapes) there would seem to be insufficient grounds for separating Dibamus from the Scincidae in a family of its own. If ^f forms such as Typhlosaurus and Feylinia, both equally or very little less degenerate than Dibamus, are to be included in the family Scincidae there is no reason to exclude Dibamus from it.

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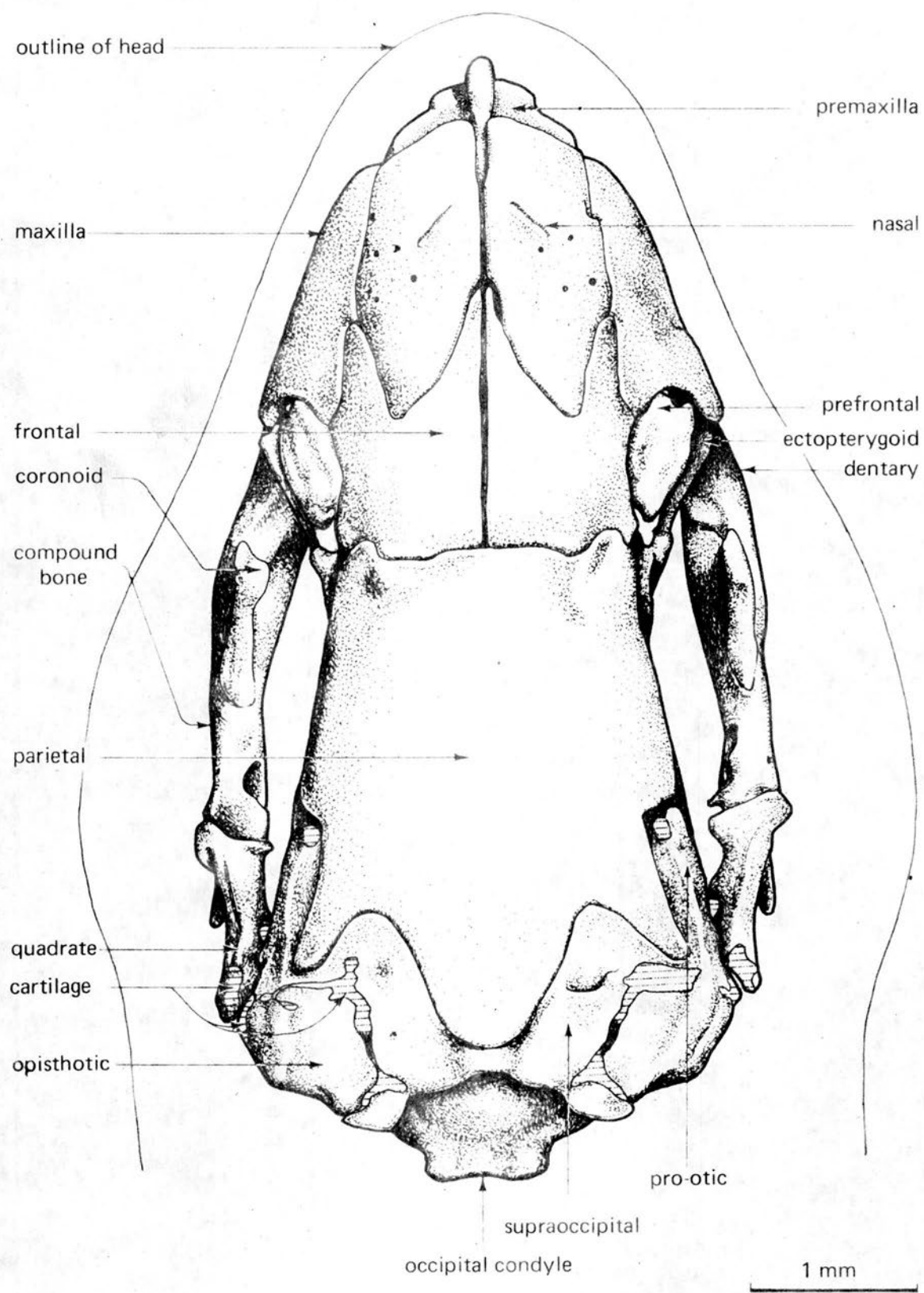


Figure 1. Graphic reconstruction of the skull in dorsal view.

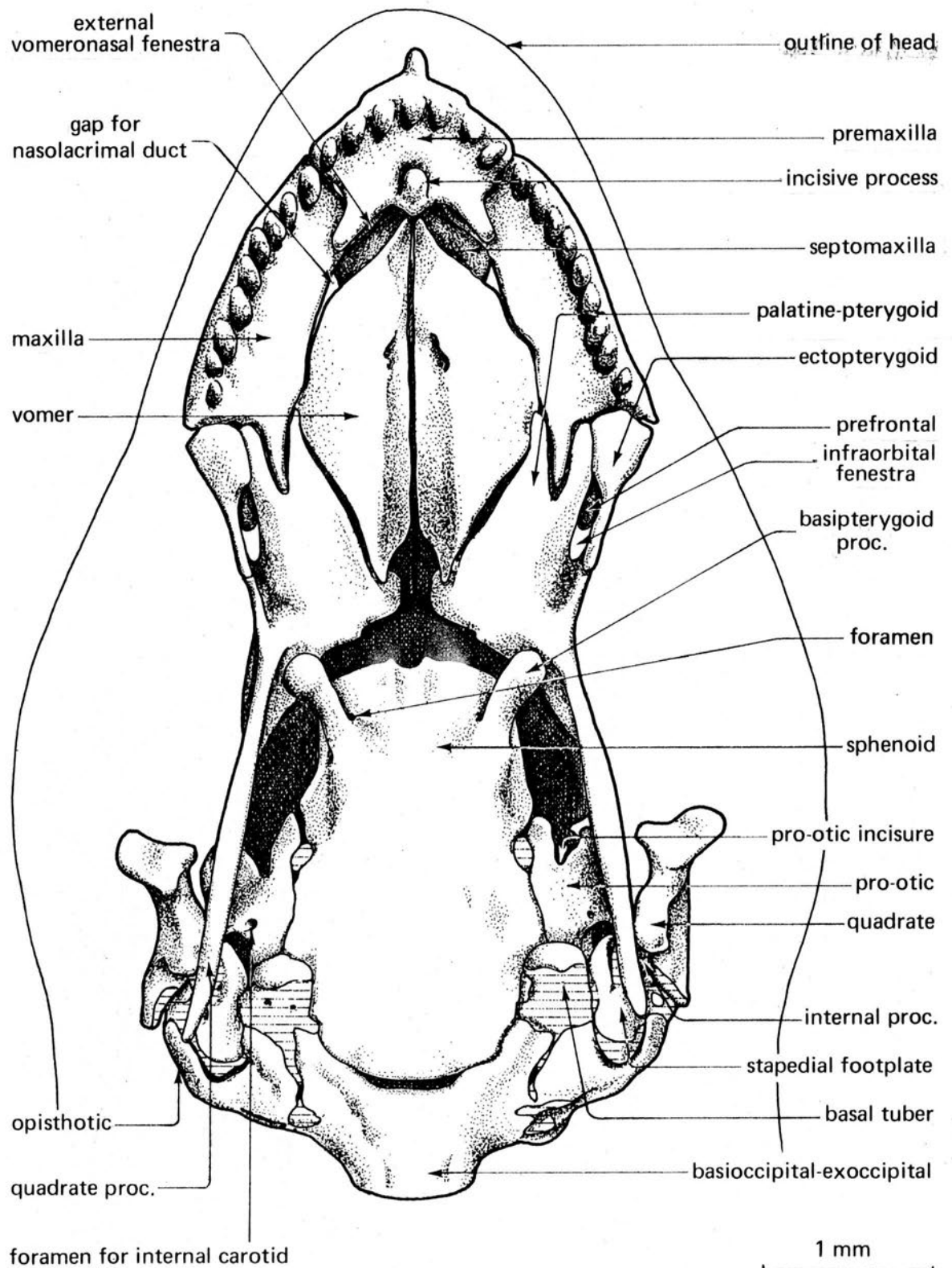


Figure 2. Graphic reconstruction of the skull in ventral view.

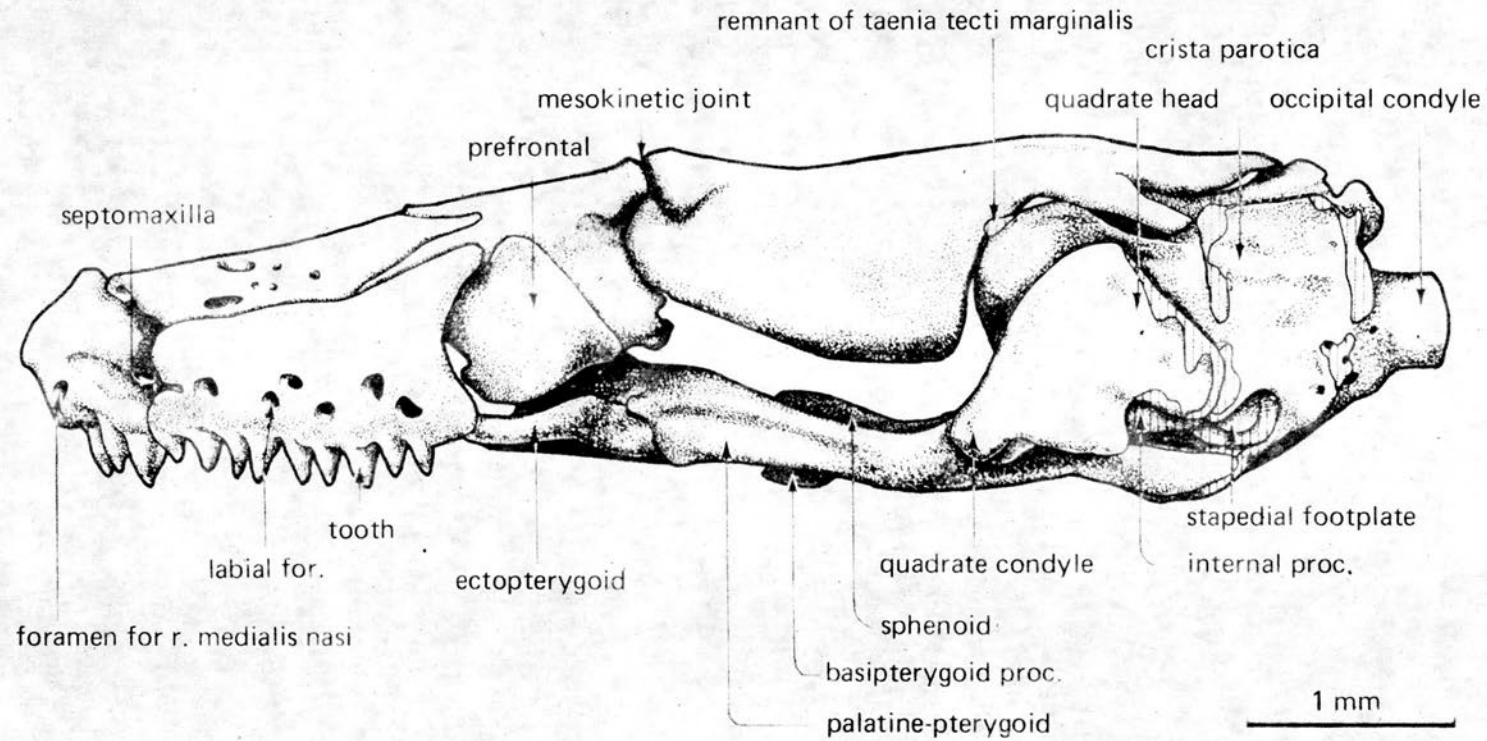


Figure 3. Graphic reconstruction of the skull without lower jaw in lateral view.

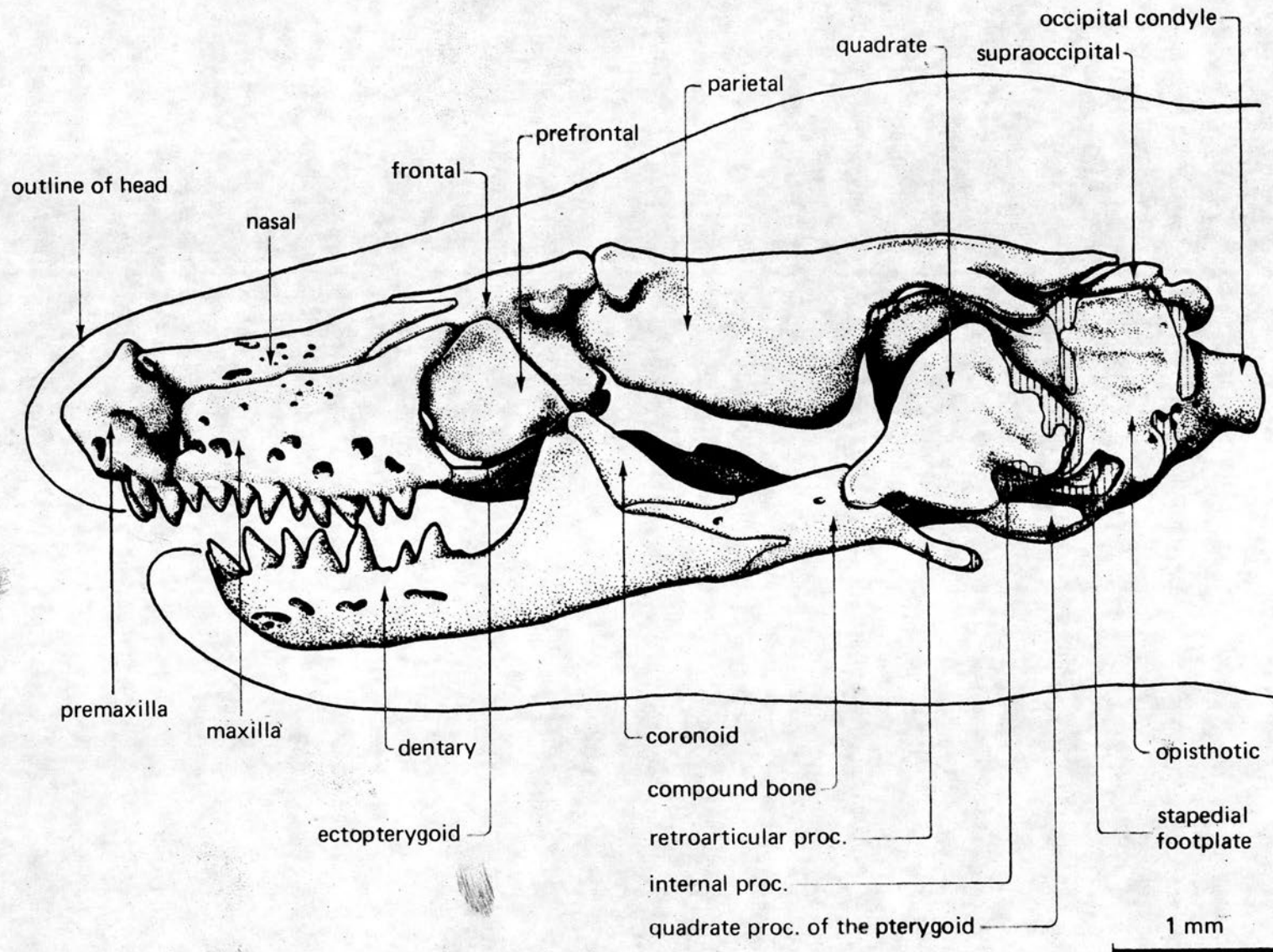


Figure 4. Graphic reconstruction of the skull in lateral view.

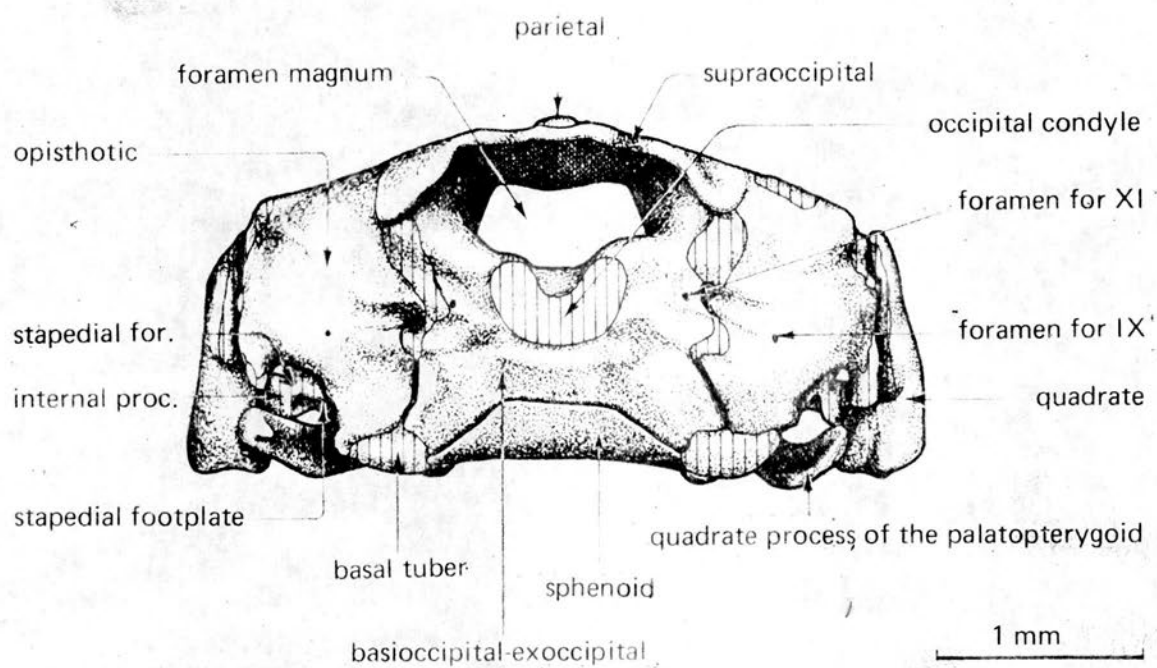


Figure 5. Contour reconstruction of the skull in posterior view.

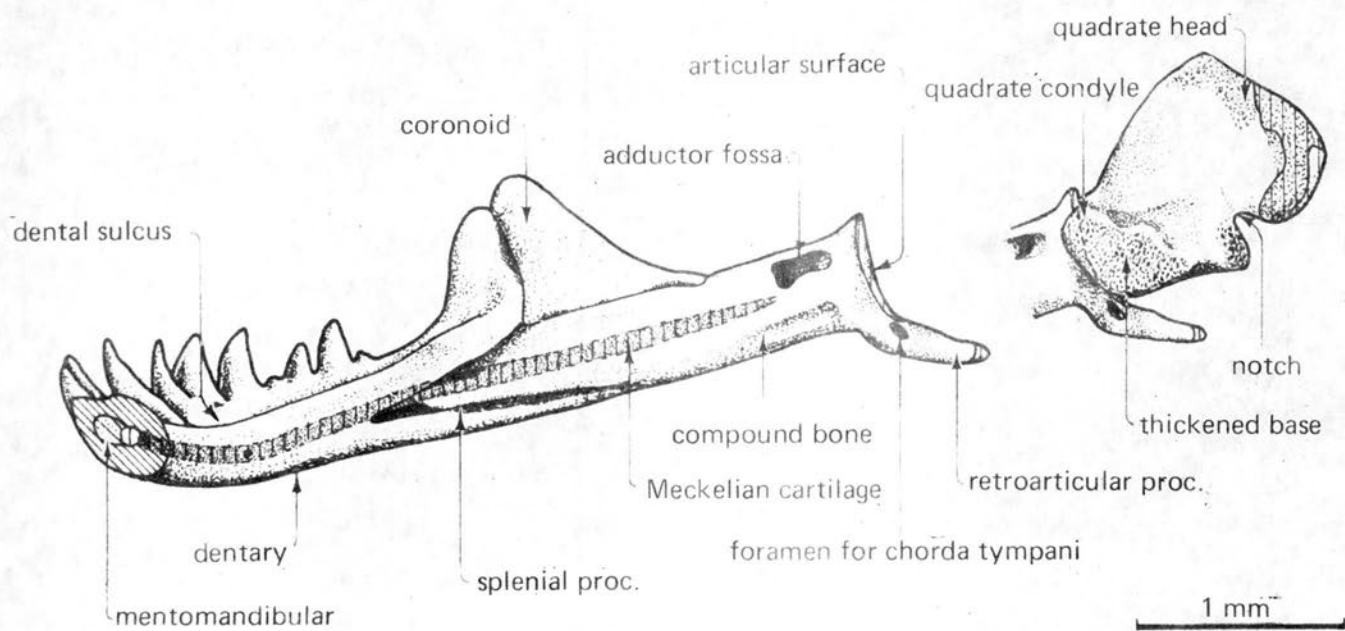


Figure 6. Graphic reconstruction of the lower jaw and the quadrate in medial view.

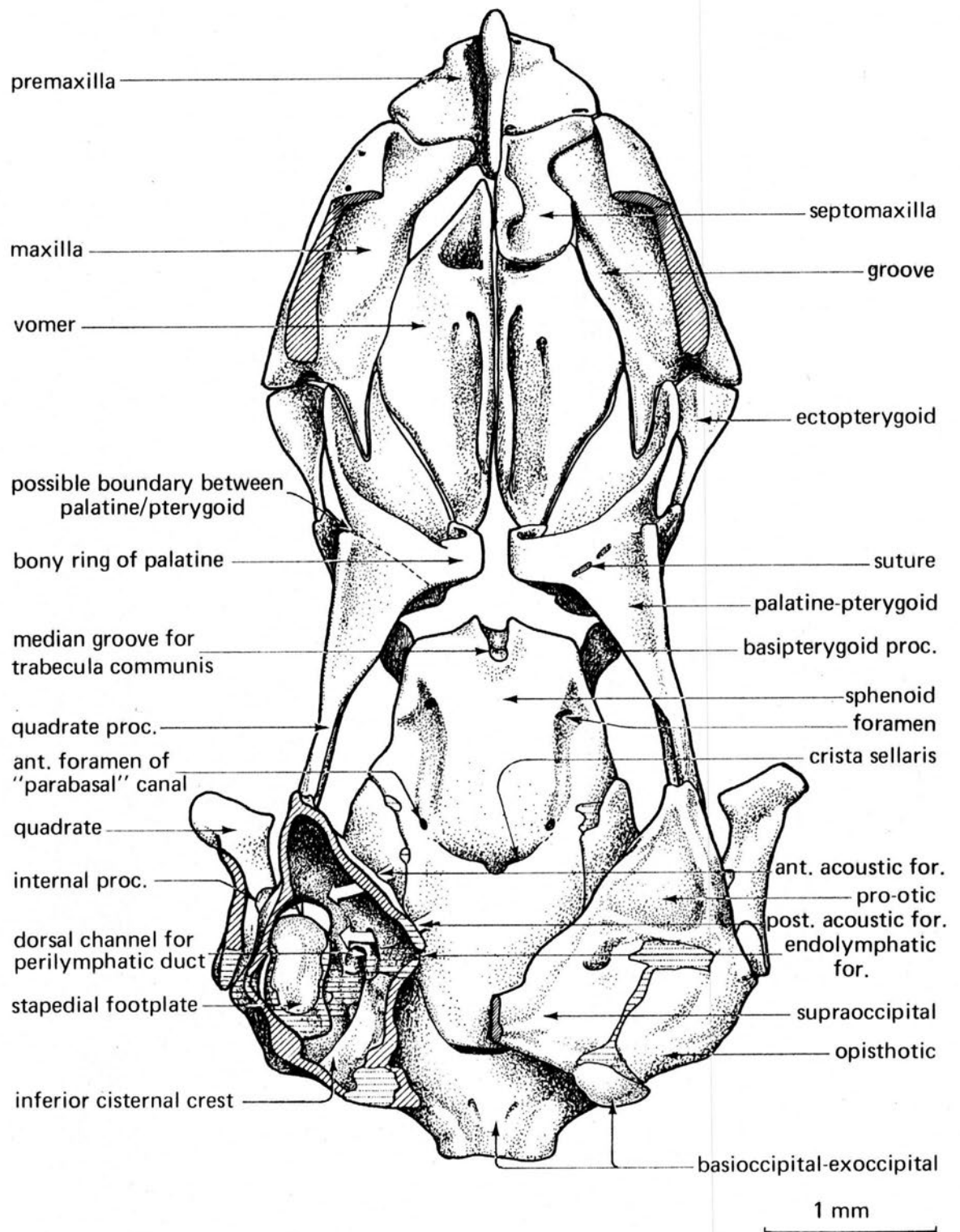


Figure 7. Graphic reconstruction of the skull in dorsal view. The dorsal bones are removed to show the dorsal surface of the palate and a frontal section is made through the left otic capsule.

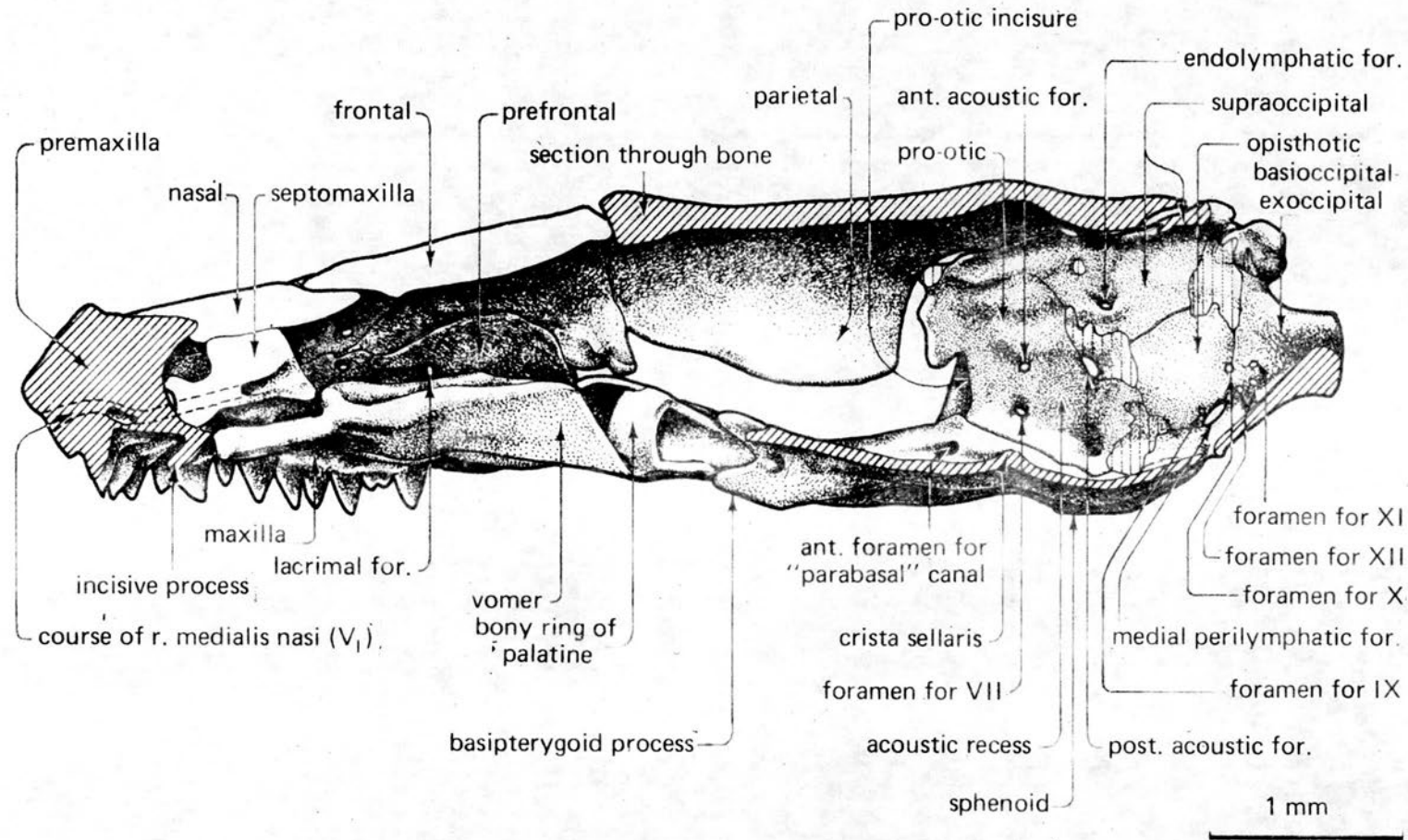
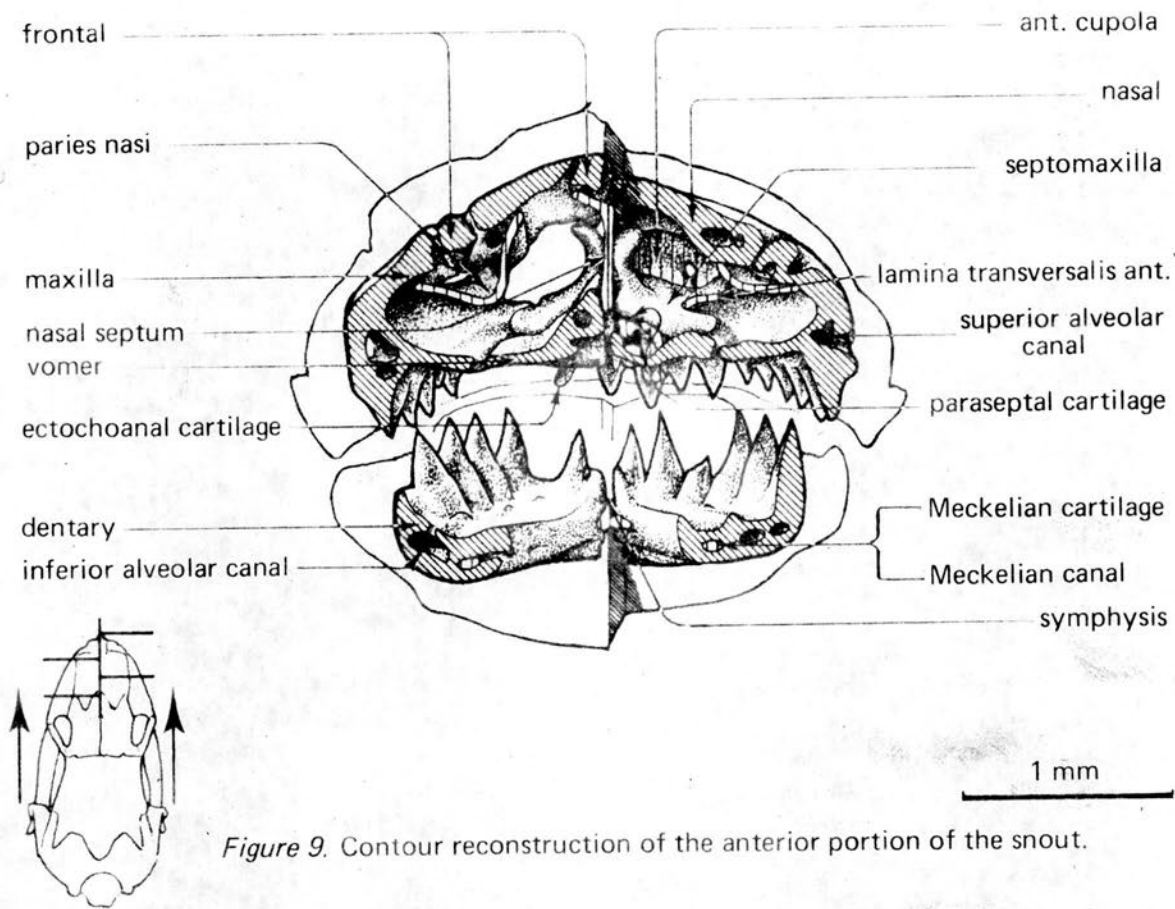


Figure 8. Graphic reconstruction of sagittal section through the skull.
Cartilage indicated by widely spaced stippled lines.



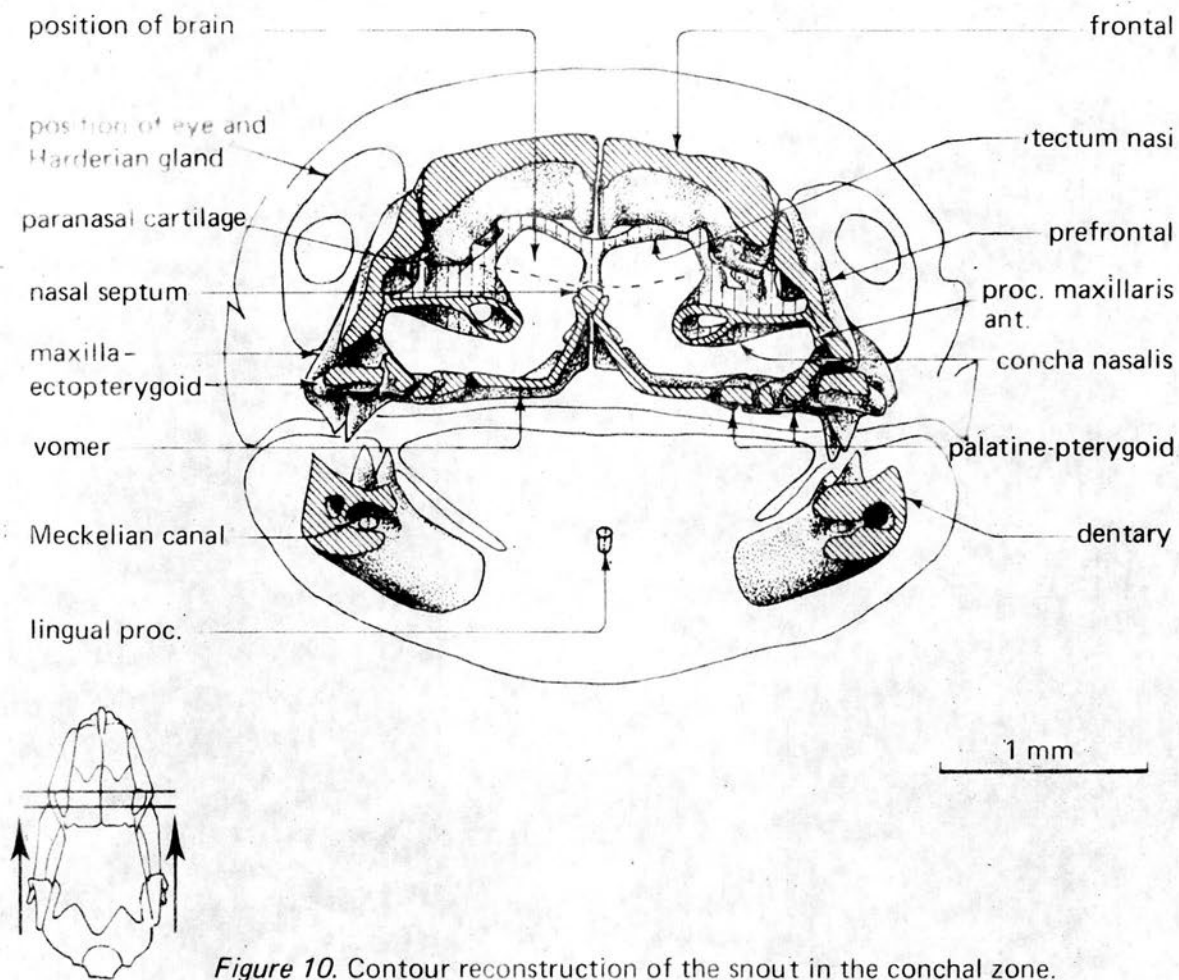


Figure 10. Contour reconstruction of the snout in the conchal zone.

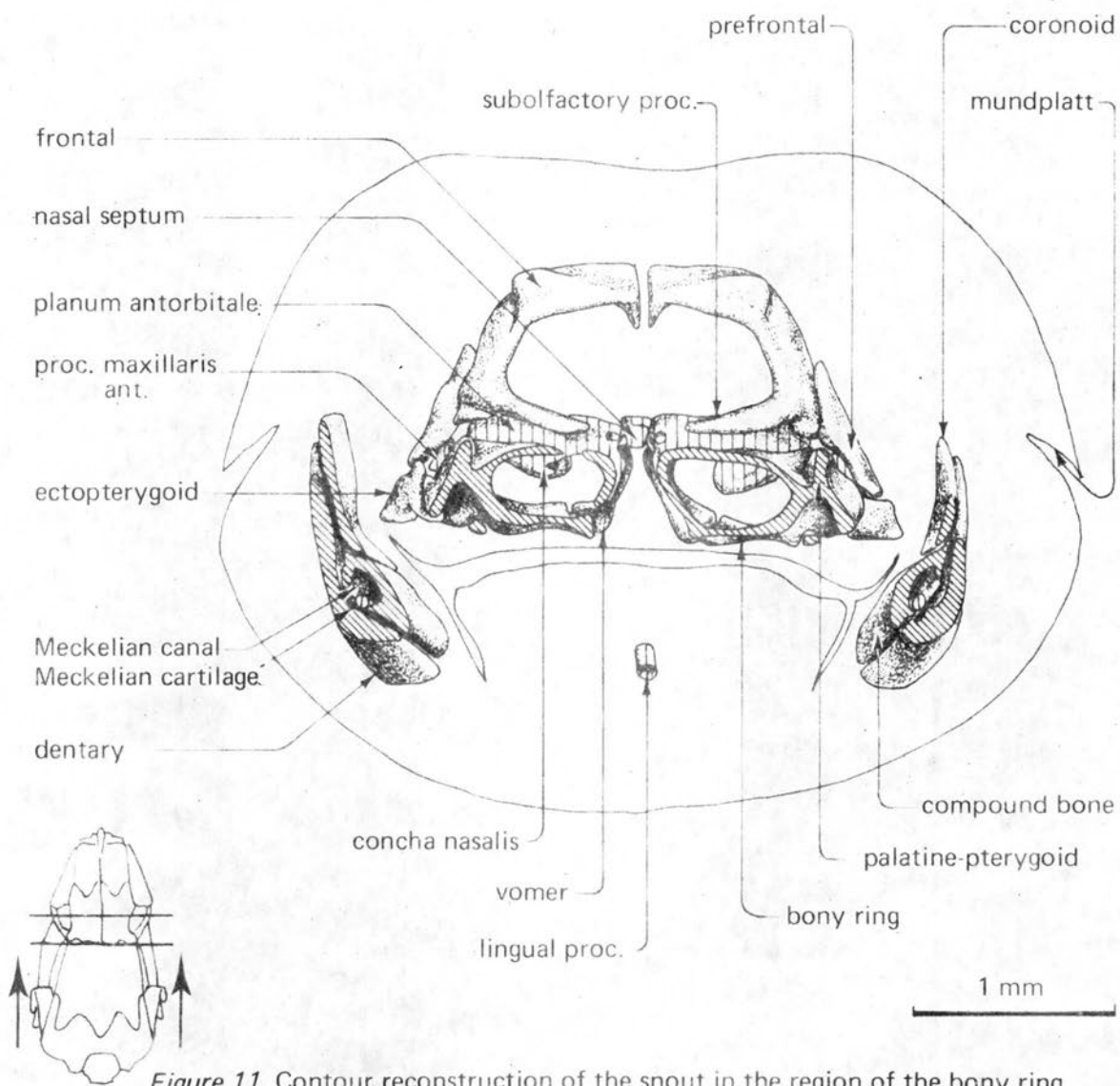


Figure 11. Contour reconstruction of the snout in the region of the bony ring of the palatine.
The parietal is removed to show the subolfactory process clearly.

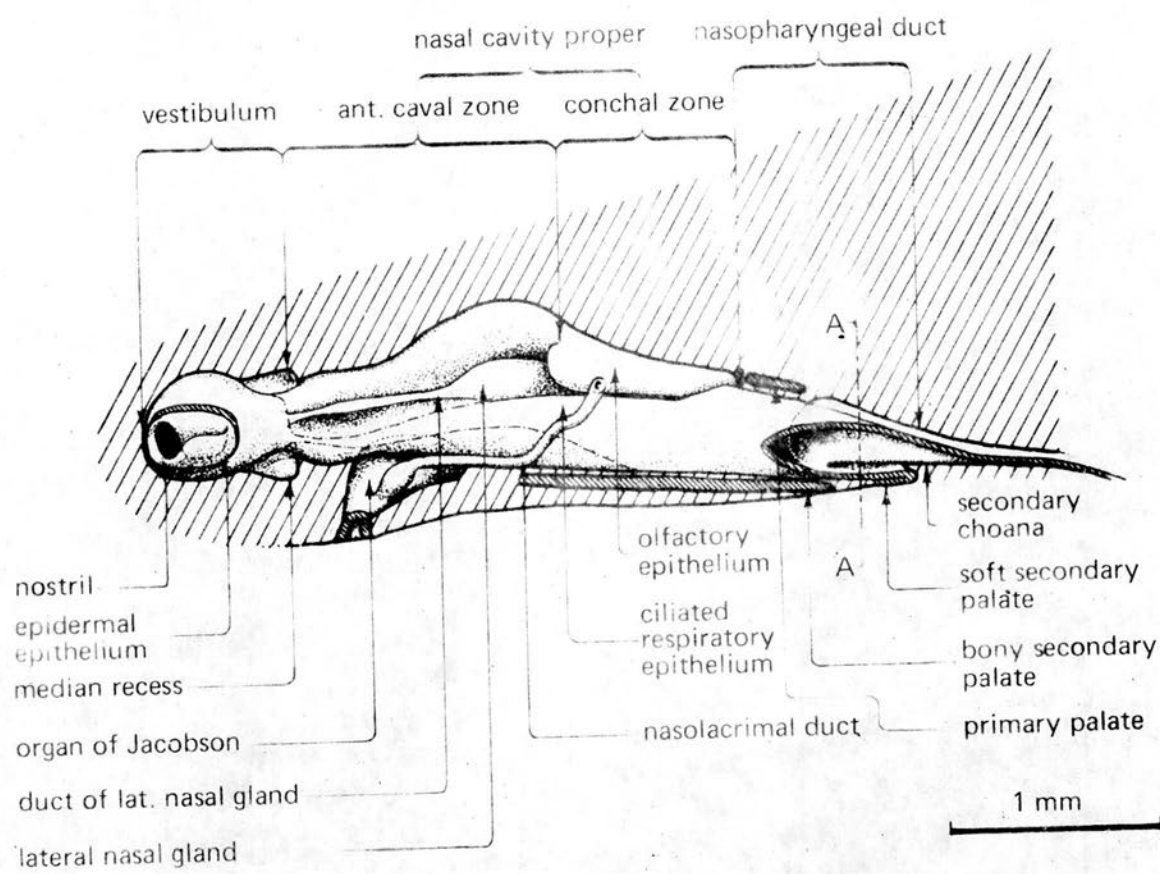


Figure 12(a). Graphic reconstruction of the nasal sac in lateral view.

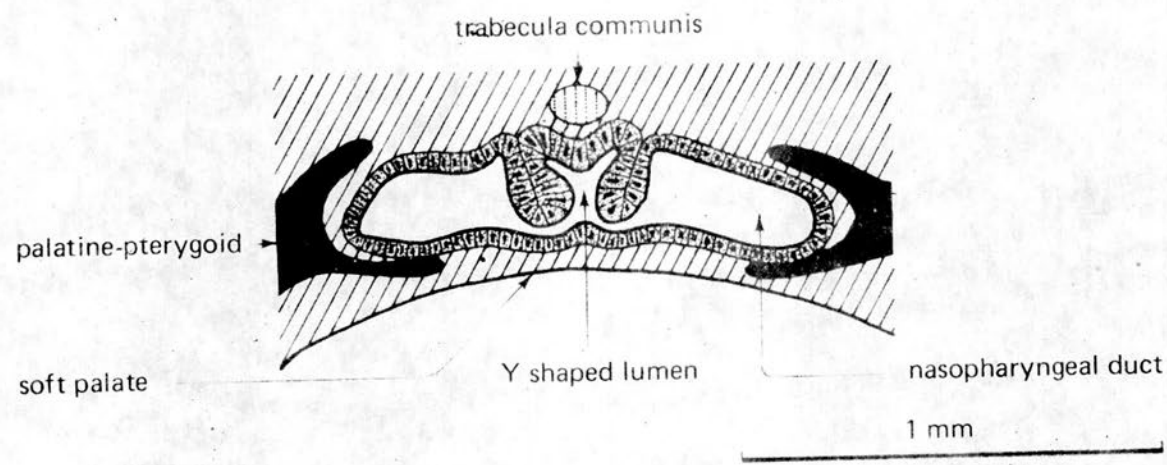


Figure 12(b). Cross-section through the nasopharyngeal duct (section AA)

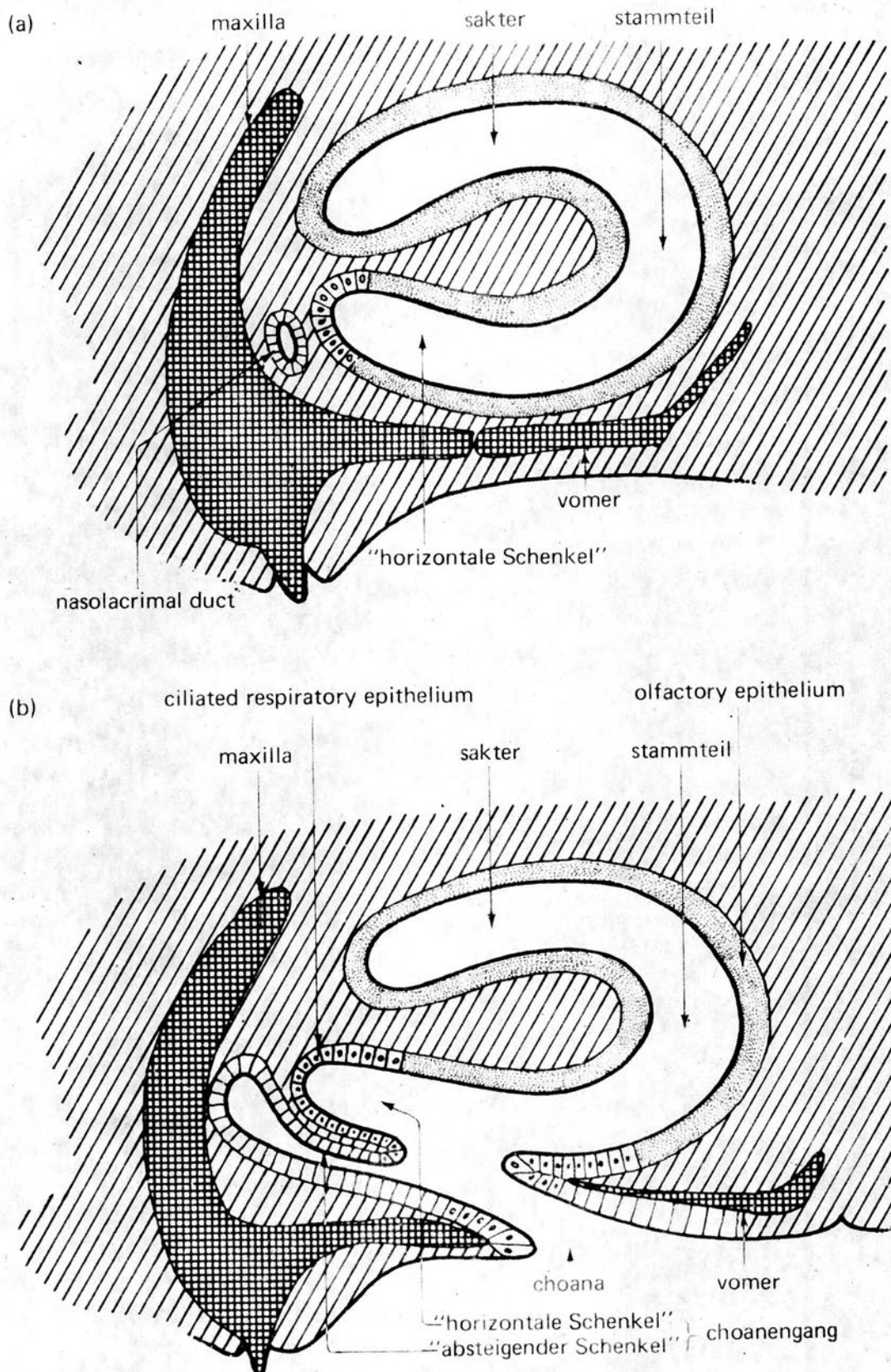
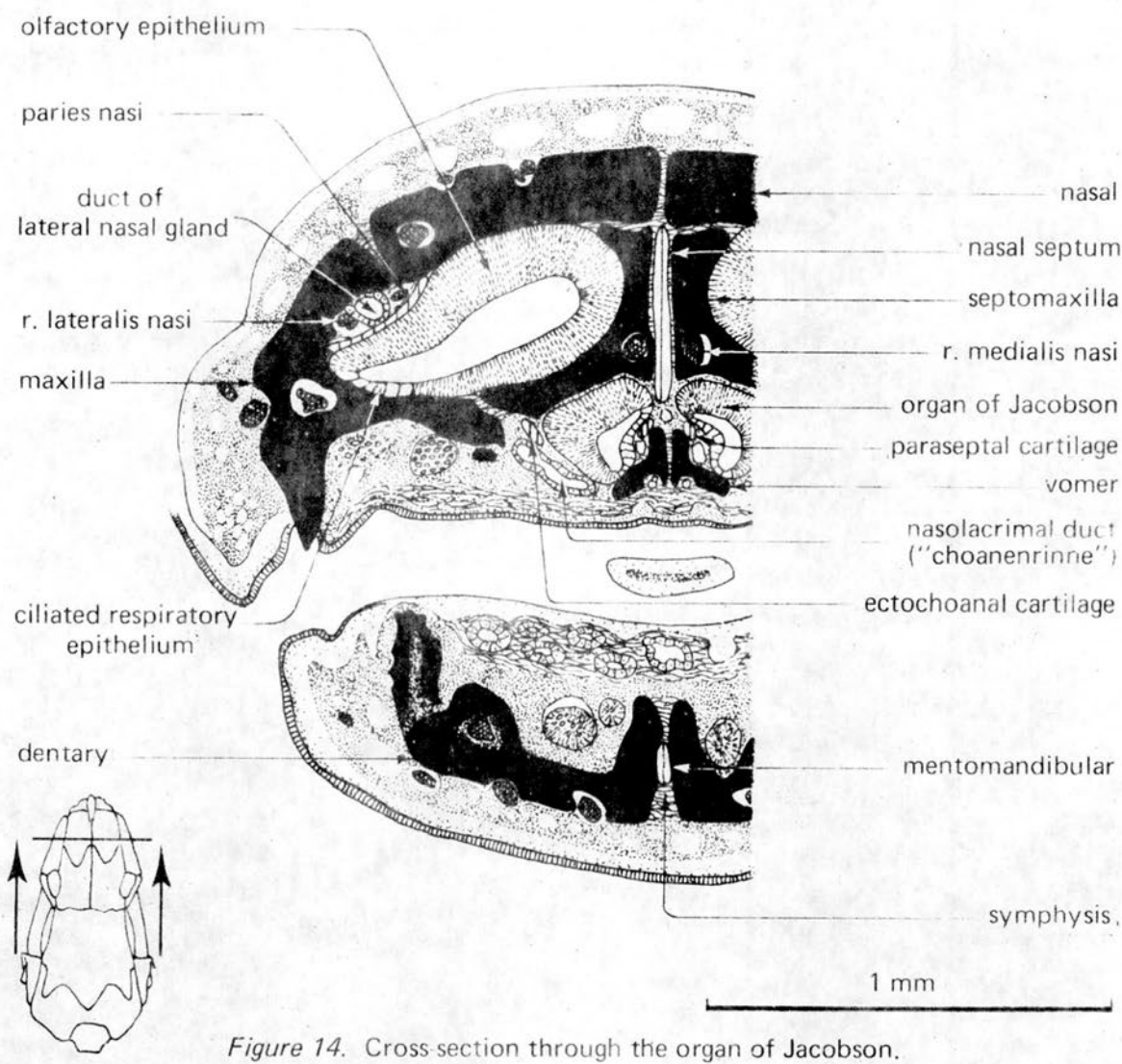


Figure 13. Diagrammatic cross-sections through the nasal sac in the conchal zone of (a) *Dibamus* and (b) in a generalised skink to show the closure of the choana in *Dibamus*.



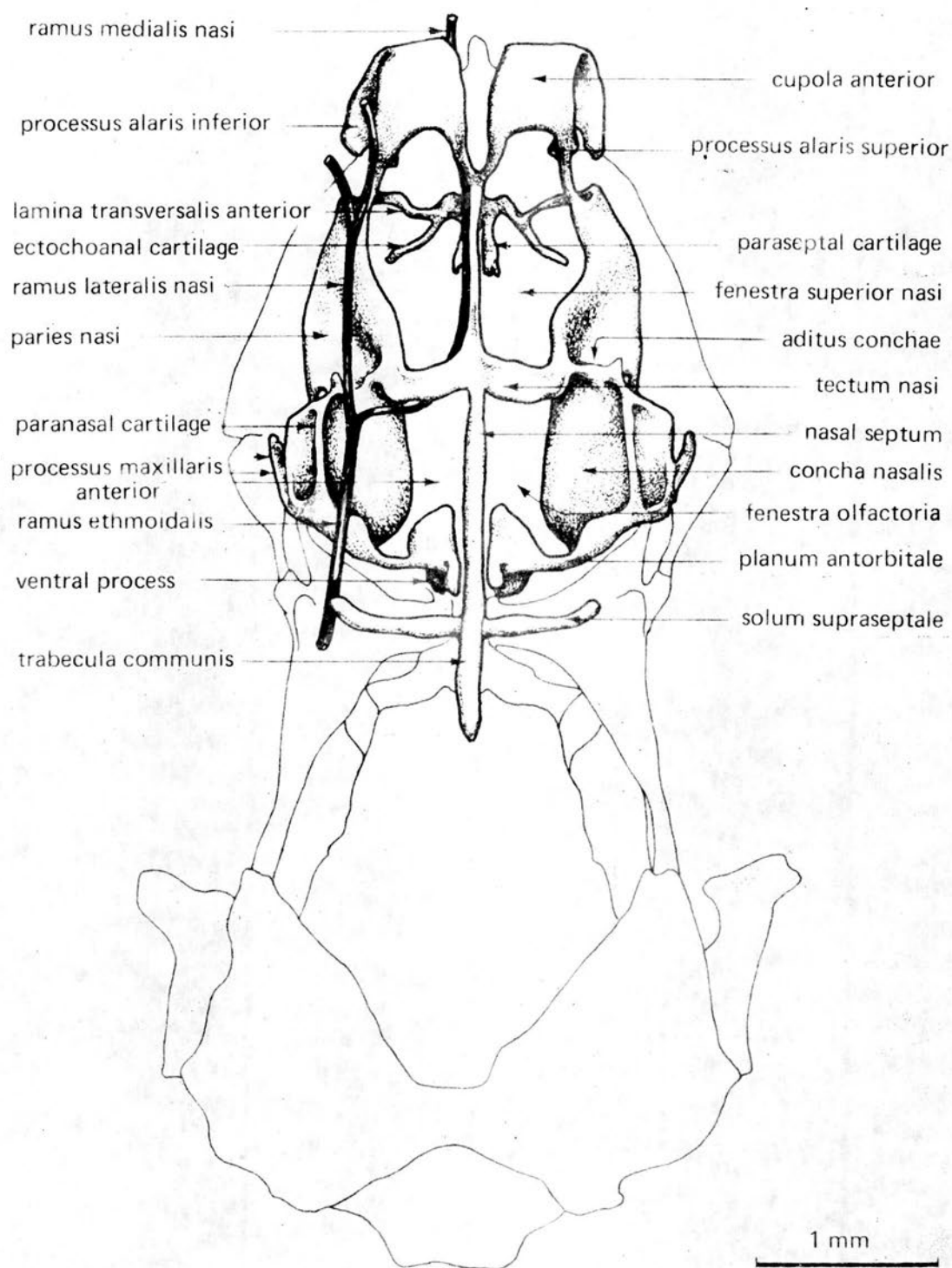


Figure 15. Graphic reconstruction of the nasal capsule in dorsal view.

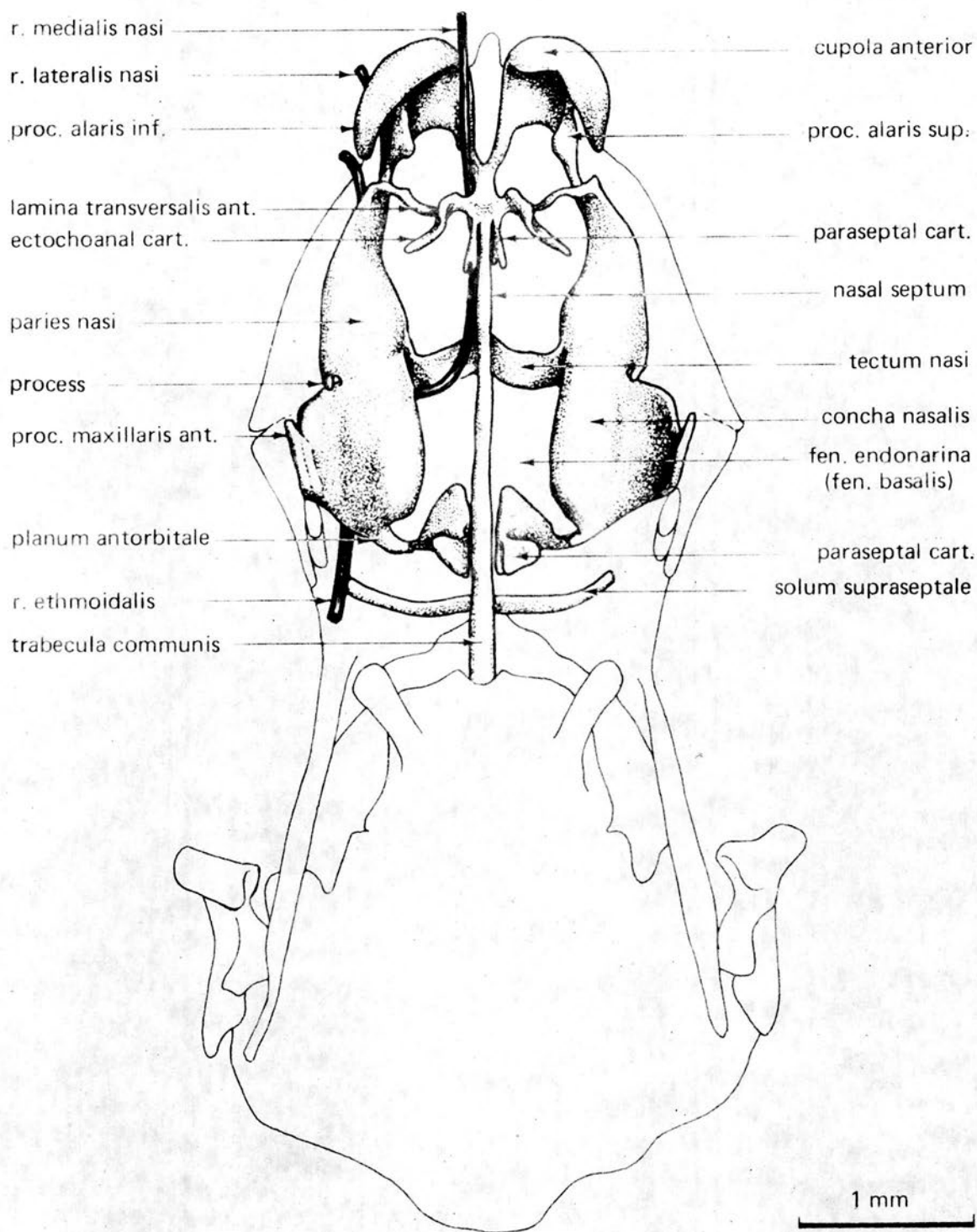


Figure 16. Graphic reconstruction of the nasal capsule in ventral view.

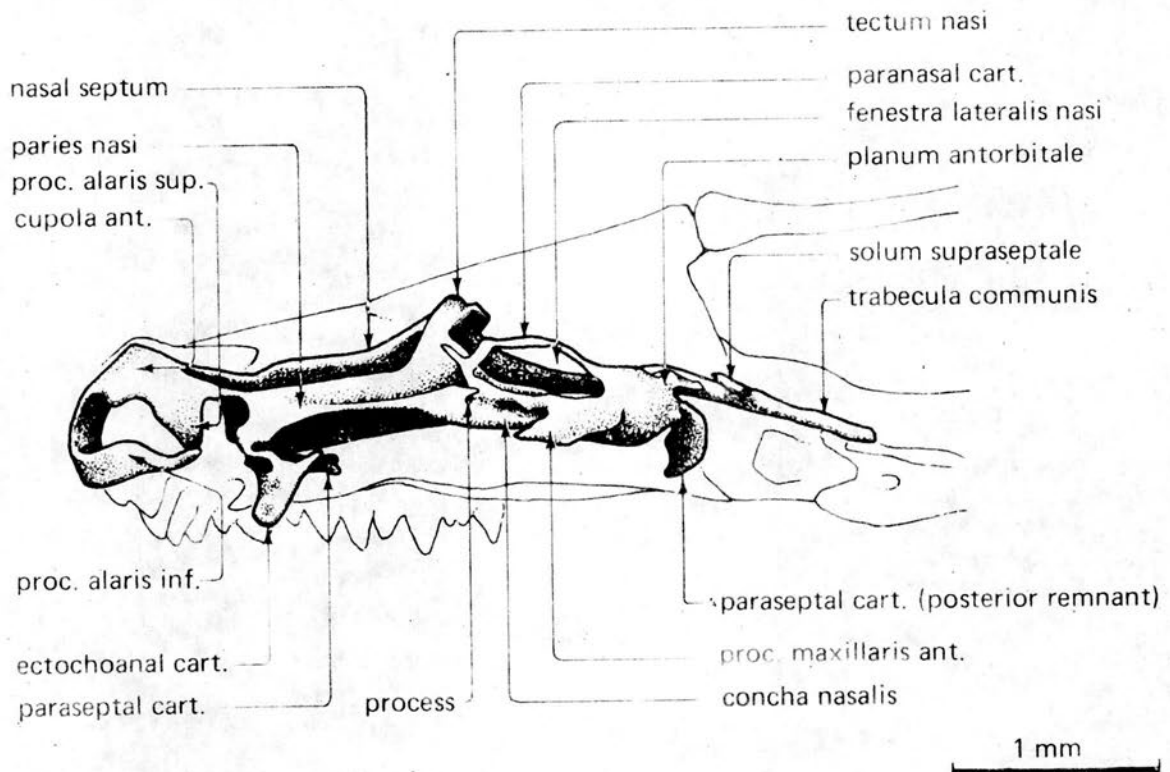


Figure 17. Graphic reconstruction of the nasal capsule in lateral view.

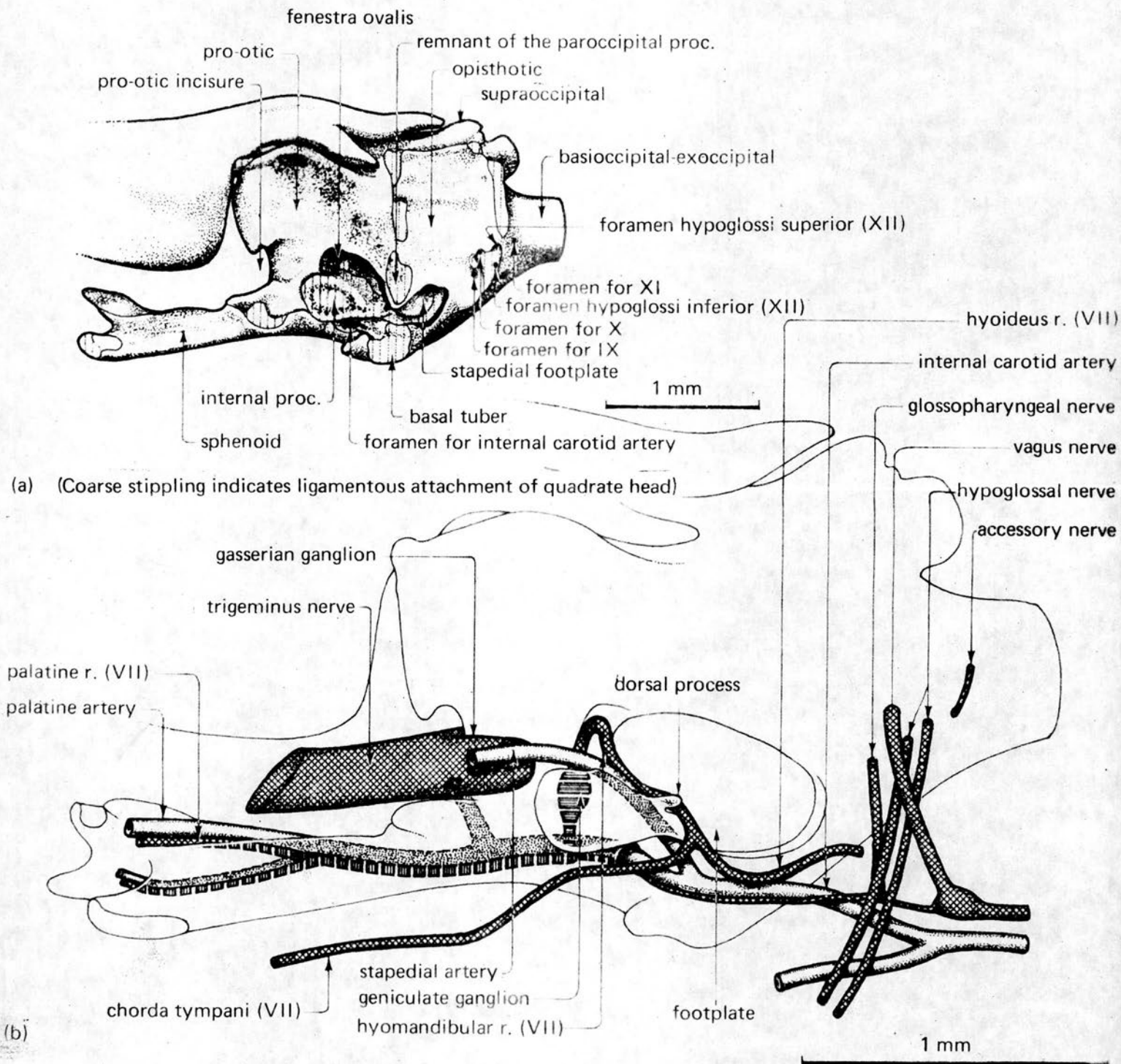


Figure 18(a). Graphic reconstruction of the otico-occipital region in lateral view.

Diagram to show relations of the nerves and arteries of the middle ear. The paroccipital process is removed to show the upper edge of the footplate and the quadrate process of the pterygoid

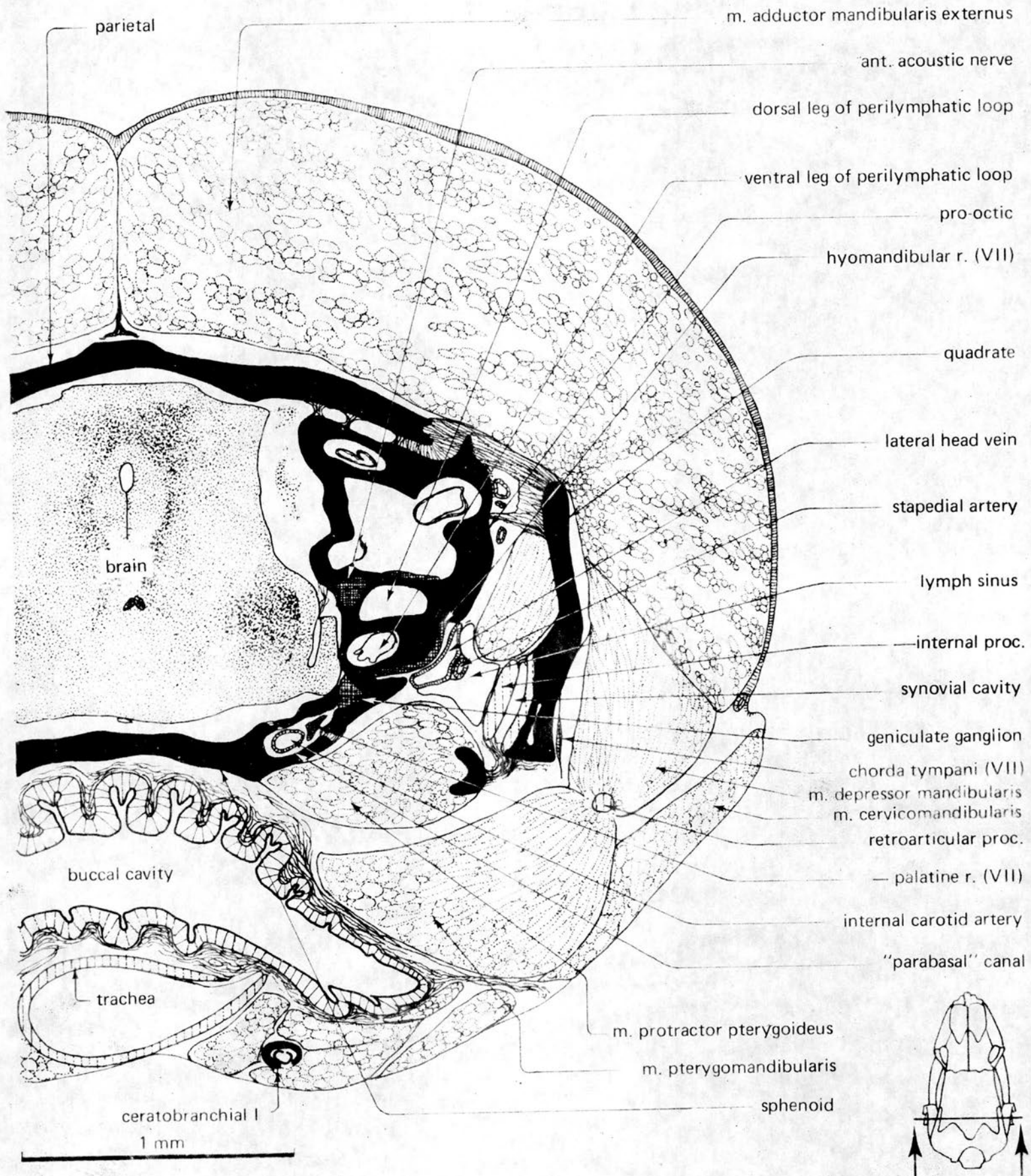
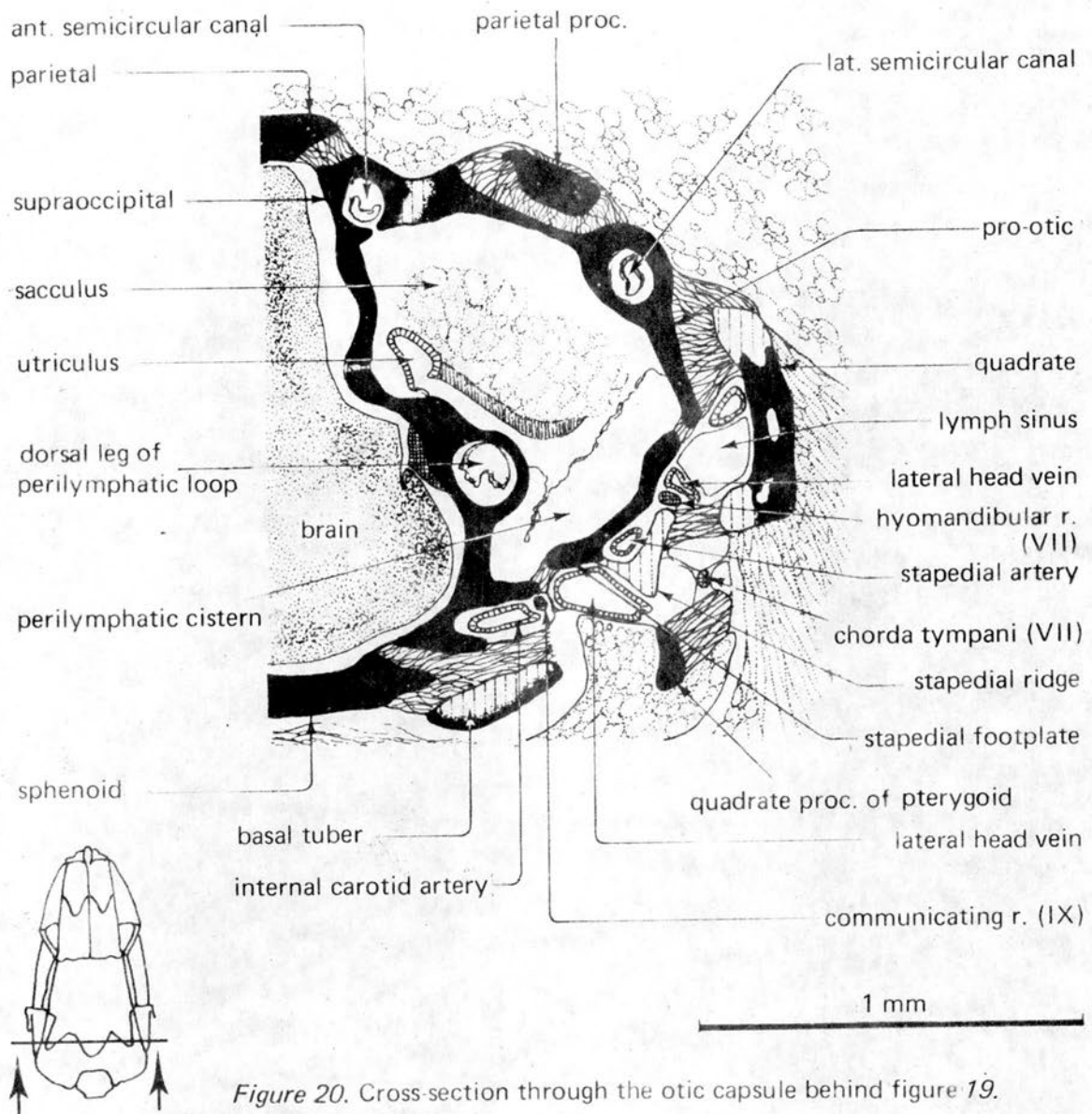


Figure 19. Cross section through the anterior portion of the otic capsule.



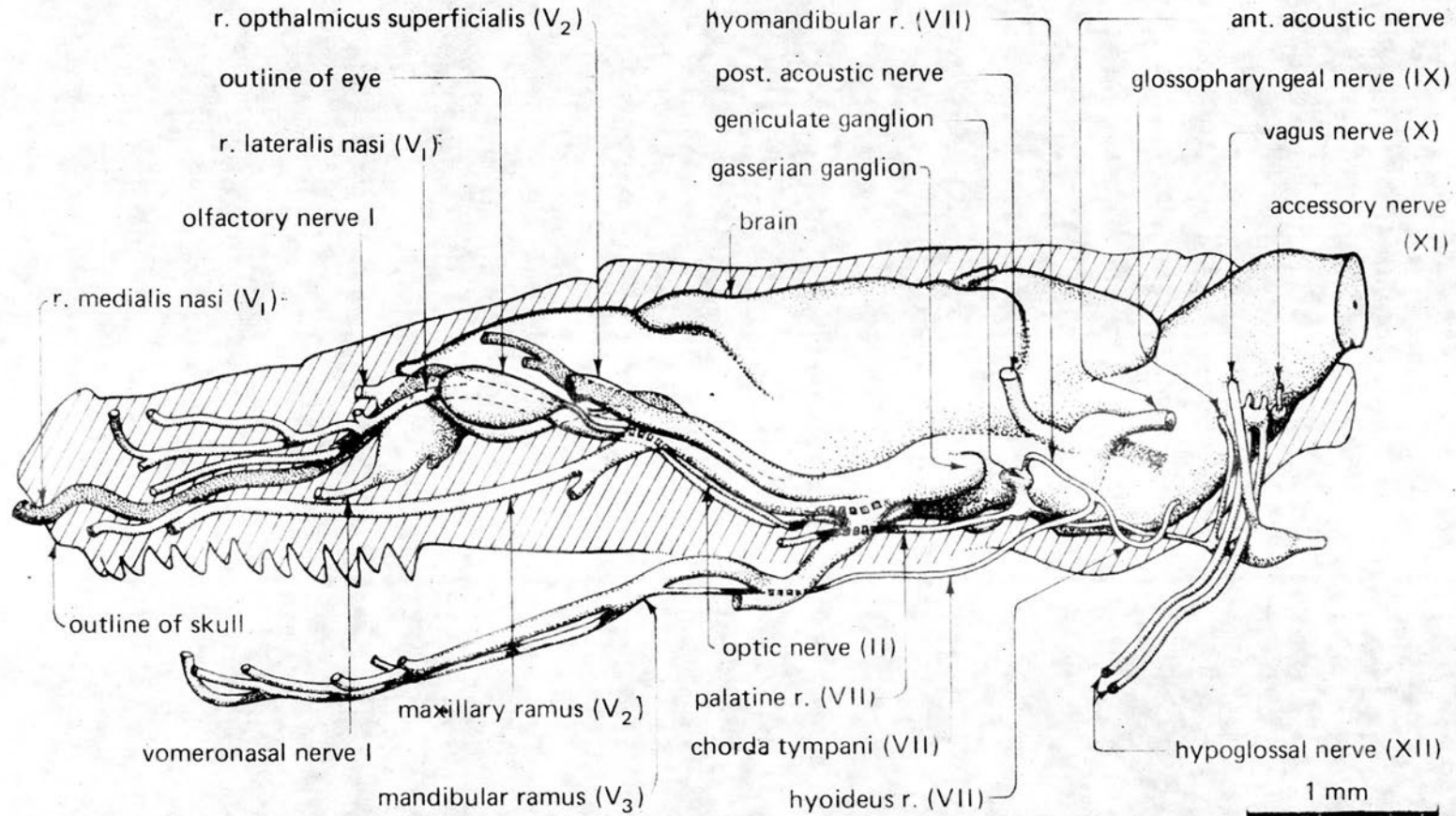


Figure 21. Graphic reconstruction of the cranial nerves and the brain in lateral view.

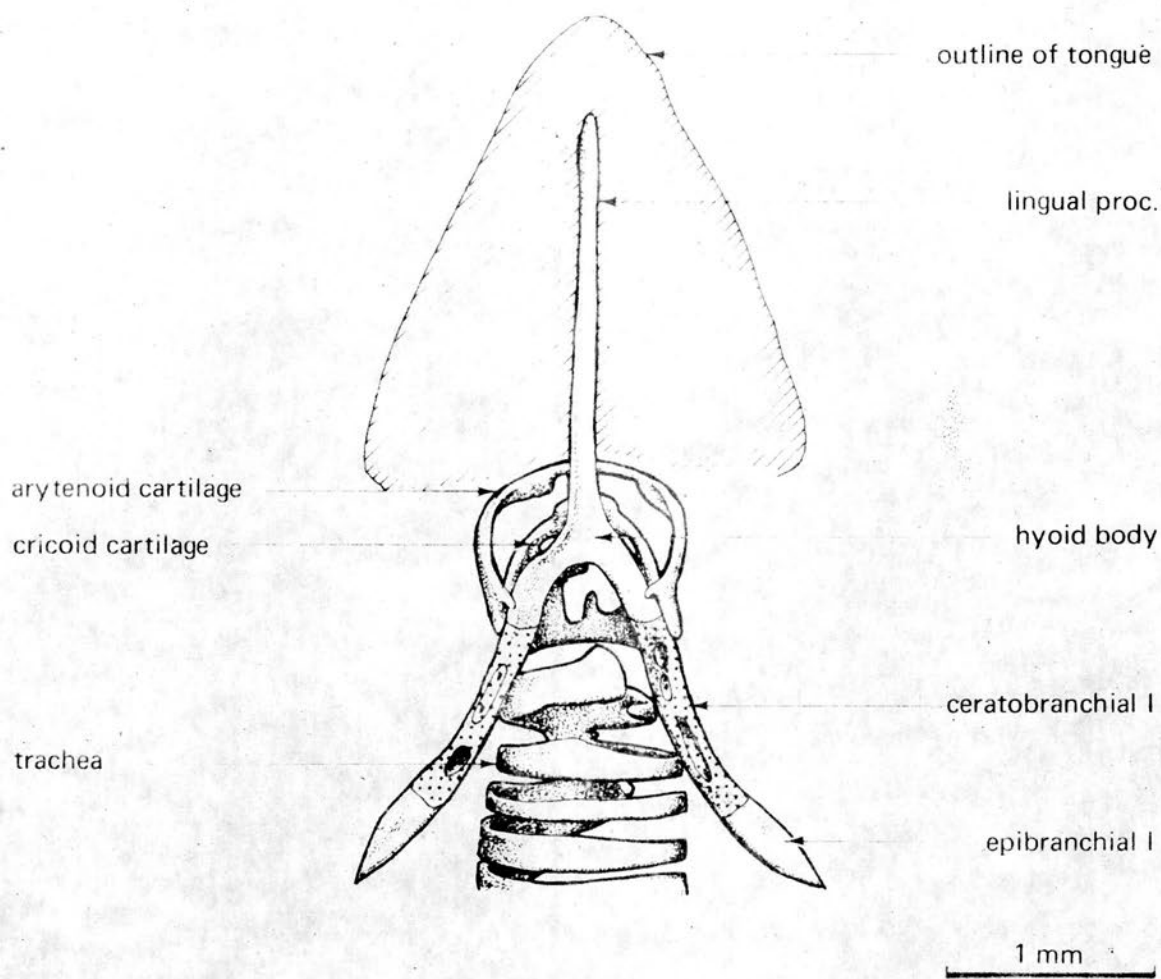


Figure 22. Graphic reconstruction of the hyoid apparatus in ventral view.

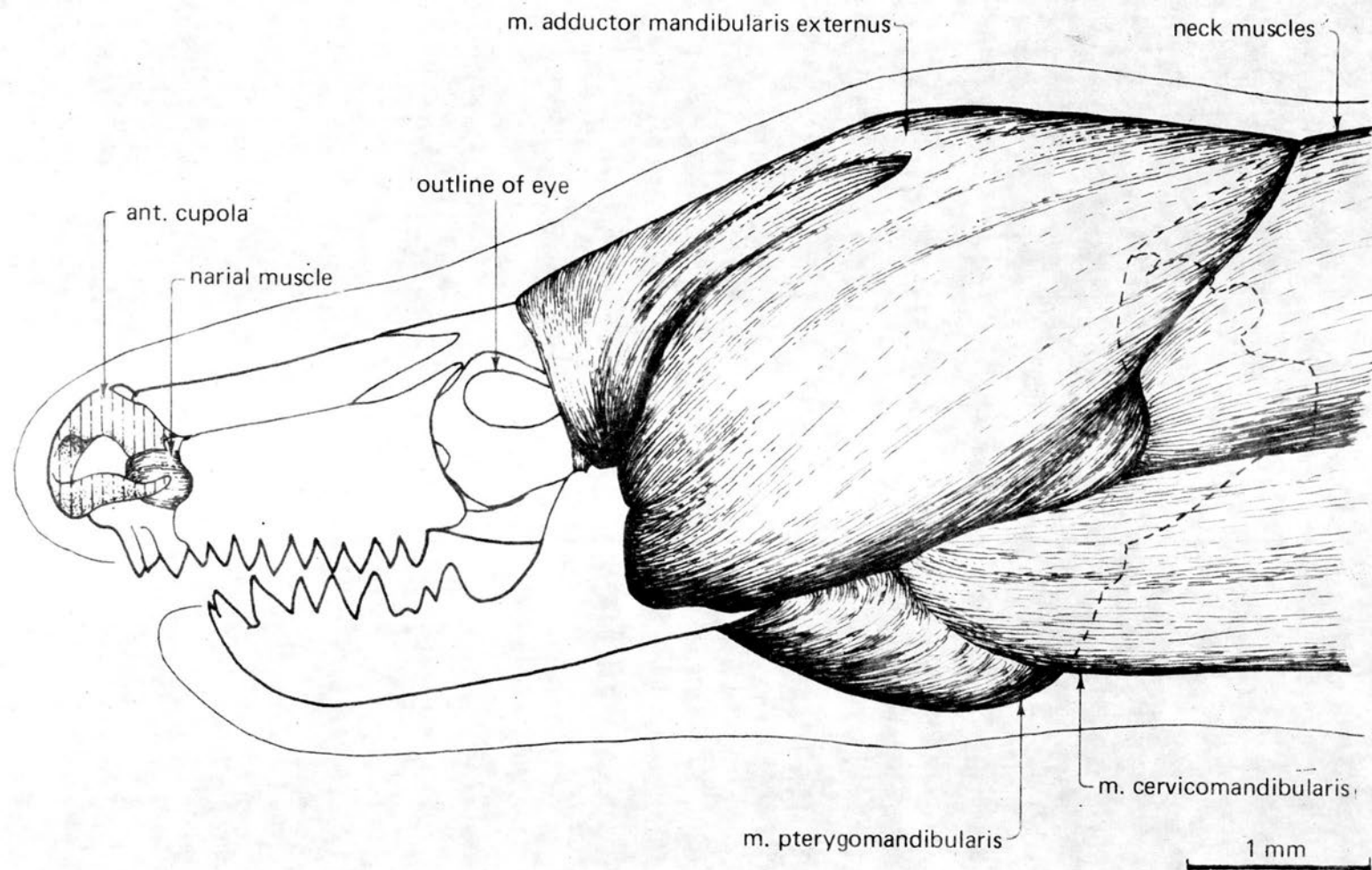


Figure 23. Graphic reconstruction of the jaw muscles in lateral view.

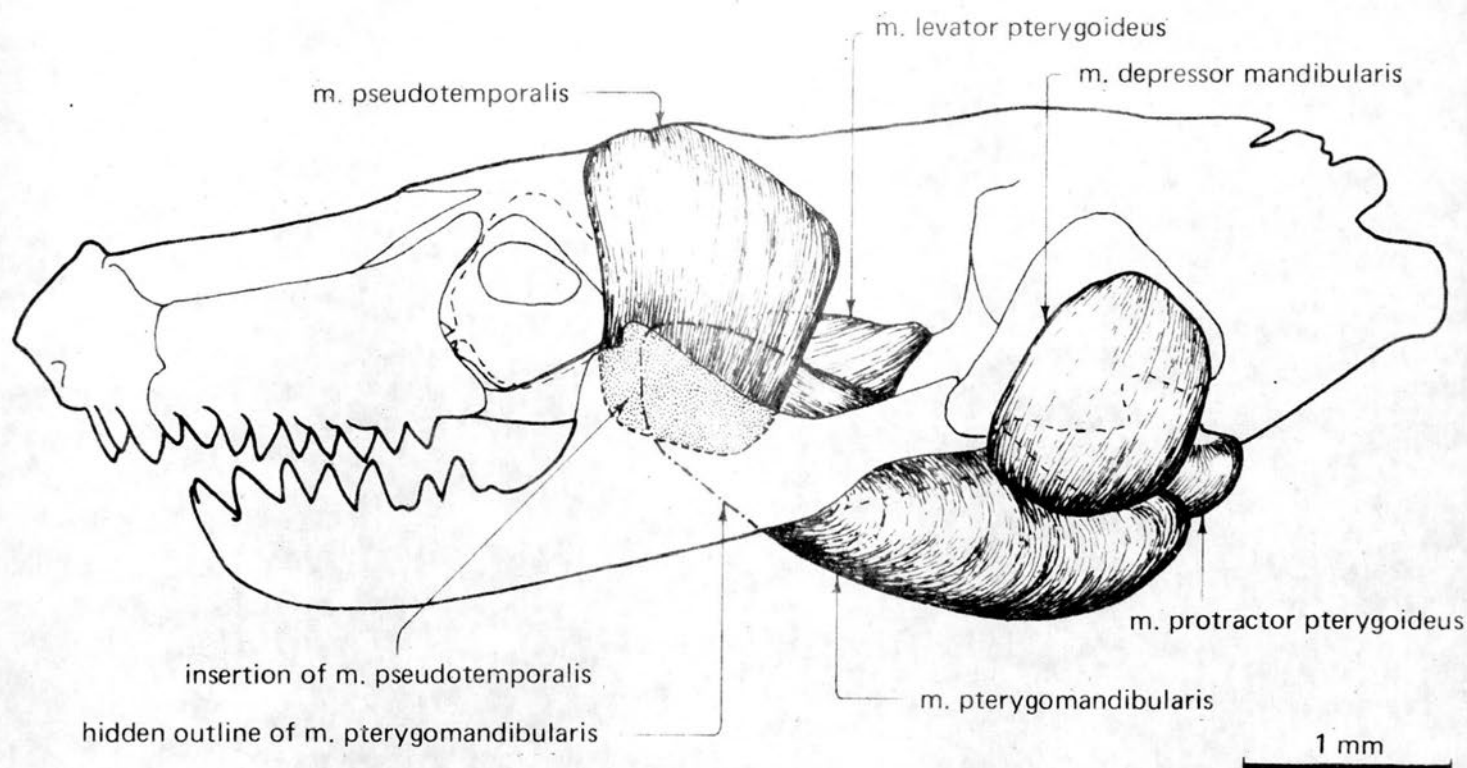


Figure 24. Graphic reconstruction of the jaw muscles in lateral view with the external muscles removed.

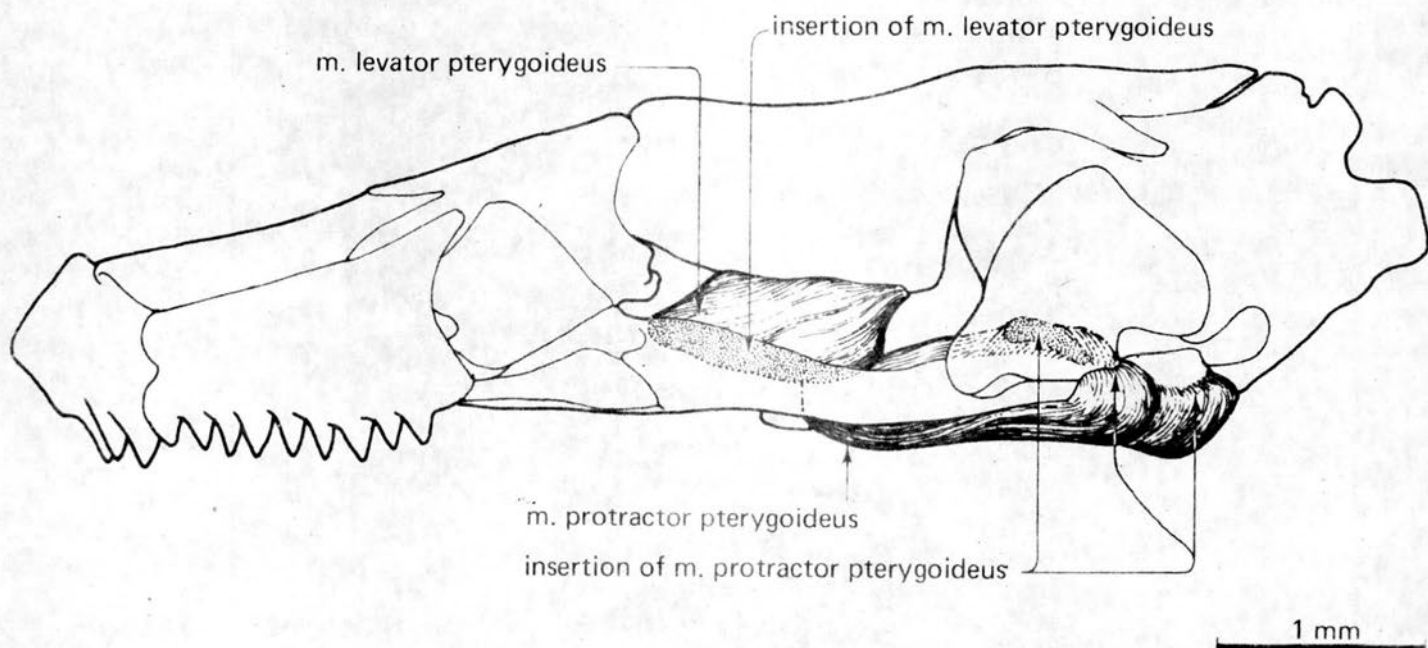


Figure 25. Graphic reconstruction of the constructor dorsalis group (kinesis muscles) in lateral view.

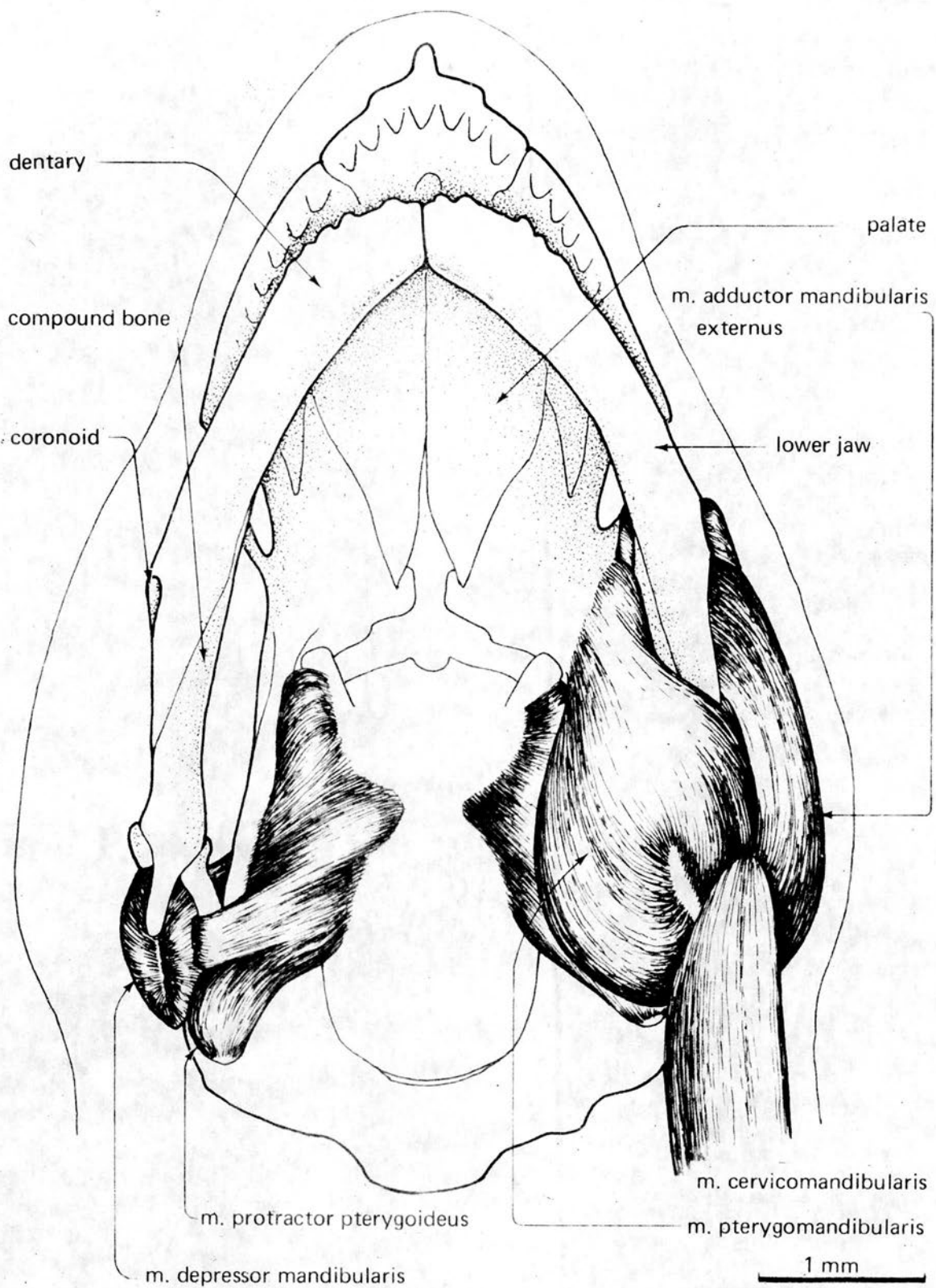


Figure 26. Graphic reconstruction of the jaw muscles in ventral view.

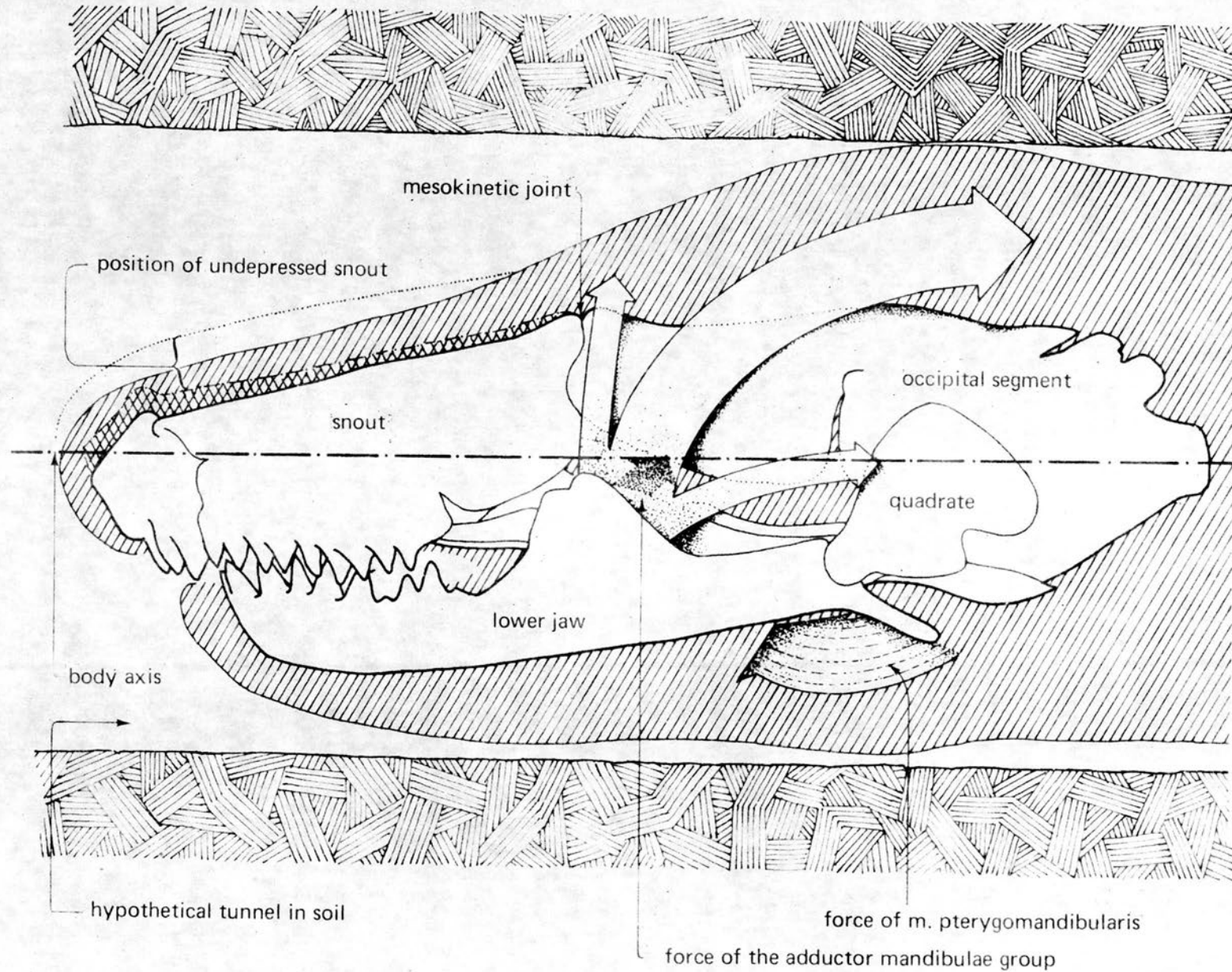


Figure 27. Diagram to illustrate the influence of kinesis on the closure of the mouth. Arrows indicate the forces exerted on the lower jaw and snout by the muscles.

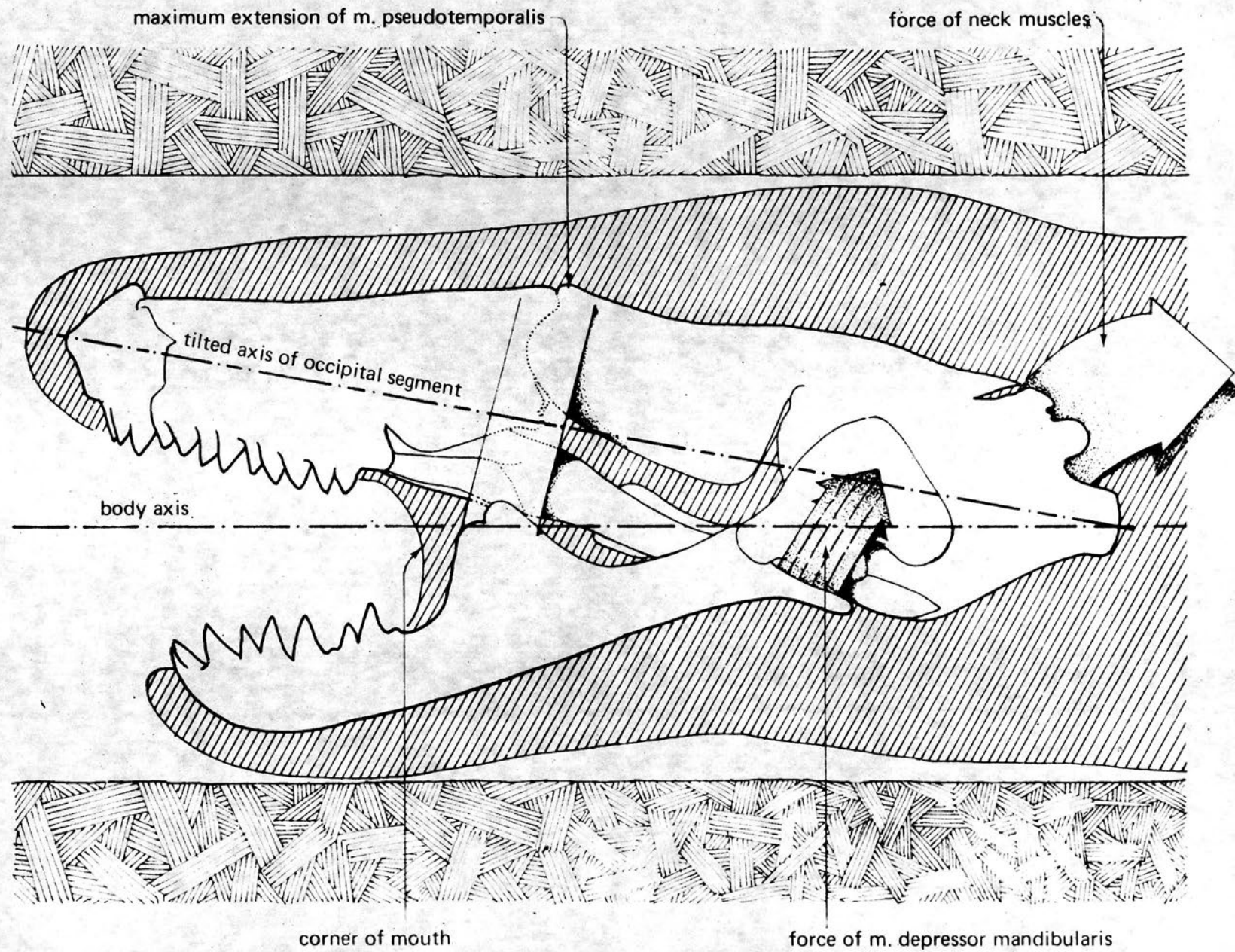


Figure 28. Diagram to illustrate the size of the gape if the mouth should be opened without utilizing kinesis.

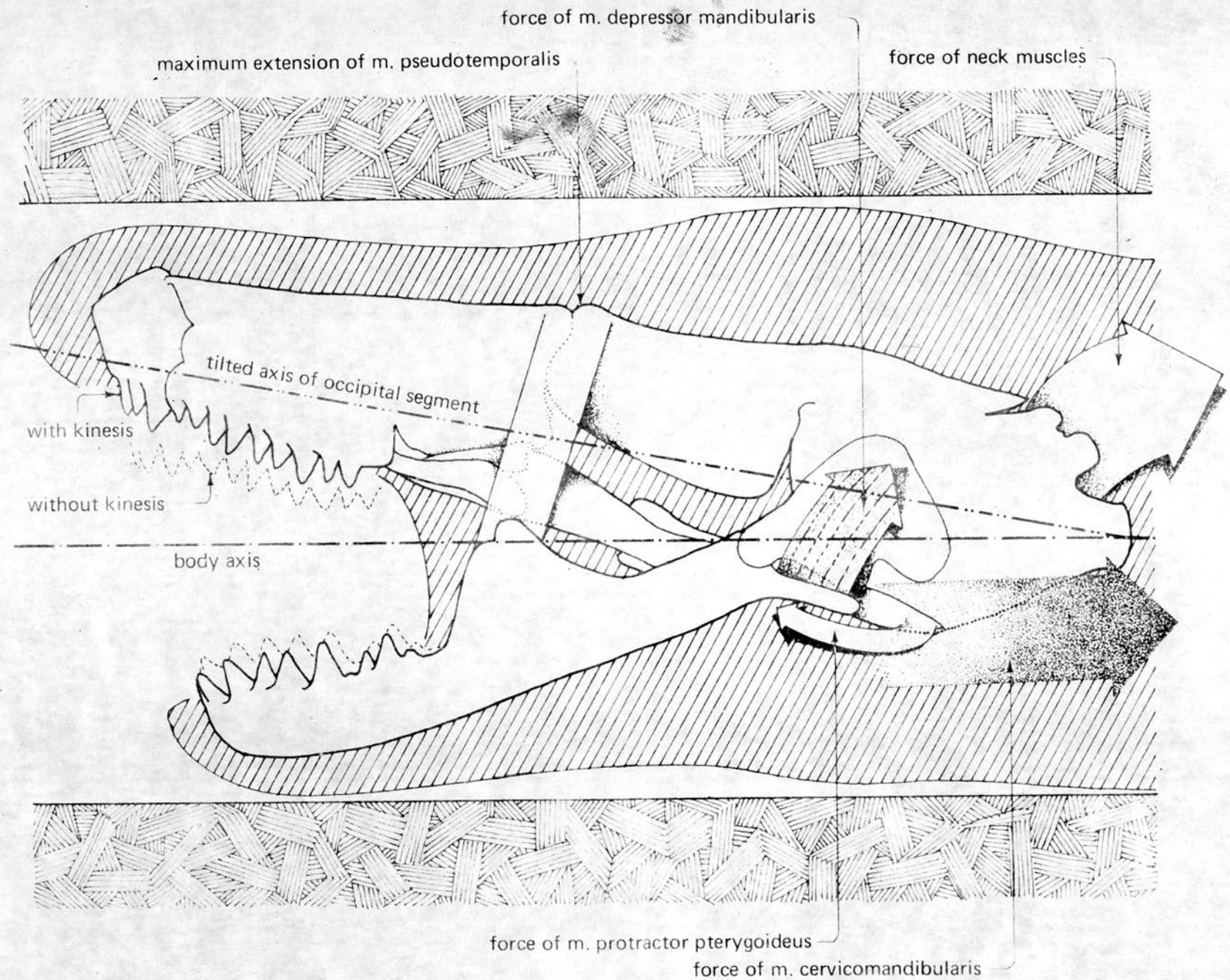


Figure 29. Diagram to illustrate the increase in size of the gape when kinesis is utilised. Note that for the same tilted axis of occipital segment, as in fig. 28, the mouth is placed more terminally.