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## The Cranial Structure of the Triconodonts

K. A. Kermack

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## THE CRANIAL STRUCTURE OF THE TRICONODONTS

BY K. A. KERMACK

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This paper is a study of the structure of the braincase in two closely related Mesozoic mammals: *Triconodon mordax* and *Trioracodon ferox*. They belong to the order Triconodonta, subfamily Triconodontinae, and are from the English Upper Jurassic (Purbeck).

One specimen of each species was available showing cranial structure, both from the collection in the British Museum. By chemical methods, both petrosals and the sphenoid of the specimen of *Triconodon* and both petrosals of the specimen of *Trioracodon* were prepared.

The material shows that the Triconodonta had a braincase of an essentially reptilian pattern. There was a persistent cavum epiptericum lying outside the ossified lateral wall (formed by the petrosal) of the braincase. The alisphenoid, forming the lateral boundary of the cavum epiptericum, formed no part of the braincase wall in this region. This was also true of the Rhaetic *Morganucodon*, and may have been true of all pre-Cretaceous mammals.

In basic construction the braincase of these mammals differs from that of an advanced therapsid only in the narrower cavum epiptericum in the former. This difference is due to the relatively larger size of the brain in the mammal. To convert a braincase constructed in this way into that of a modern mammal either the alisphenoid would have to be lost—leading to the condition found in the monotremes—or the lateral wall of the neurocranium would have to fail to ossify—thus incorporating the cavum epiptericum in the cranial cavity in the manner typical of marsupials and placentals.

Although on these grounds alone the monotreme stock need not have separated from that which gave rise to the marsupials and placentals until early in the Cretaceous, other considerations suggest that the last common ancestor lived in Triassic times at the reptilian grade of organization. There seems, however, less reason than formerly to consider *Morganucodon* an ancestral monotreme.

Finally, a reconsideration of all the evidence shows that there was no acceleration of evolutionary rates at the time the Mammalia came into existence.

## I. INTRODUCTION

About two hundred years ago the first Mesozoic mammal was discovered in the Stonesfield Slate. Further discoveries of Jurassic mammals were made in the last century at Stonesfield, Durdlestone Bay (both described by Owen 1871) and at Como Bluff, in the U.S.A. Simpson (1928, 1929) monographed the considerable bulk of material so collected and produced a comprehensive study of the Mesozoic mammals.

Unfortunately the specimens upon which his monograph was based consisted almost entirely of jaws and teeth. The latter are known to be reliable for the classification of Tertiary mammals, and were used, in the absence of other criteria, for the classification of the Mesozoic forms. On the other hand, the therapsid reptiles, the immediate ancestors of the Mesozoic mammals, are known by abundant skeletal material, including many thousands of skulls. It is on this that they are classified: very little attention has been paid to their teeth.

This sudden change of emphasis on passing from mammal-like reptiles to mammals has given the impression of an evolutionary spurt at the time the mammals came into being, and has seemed to suggest that the Jurassic mammals were closer in structure to Tertiary mammals than they were to their precursors—the mammal-like reptiles of the Trias.

Recently, however, there has become available a considerable amount of information on the skeletal structure of the earliest mammals of all, those from the topmost Trias. As the work of Kühne (1958) and Kermack & Mussett (1958*a, b*, 1959) has shown, these forms were in advance of contemporary therapsids such as *Oligokyphus* (Kühne 1956) in but two respects: the mammalian jaw joint between the squamosal and dentary had been acquired (although the reptilian quadrate-articular hinge had not been lost), and the post-canine teeth had acquired a form from which the teeth of later mammals could have been derived (Butler 1958).

Between these first mammals in the Upper Trias and the Palaeocene, where are found the first mammals known by adequate skeletal material, is more than one hundred million years; a span of time considerably longer than from the Palaeocene to the present day. It is clearly important to our understanding of mammalian evolution to know whether the salient mammalian characters were all acquired rather rapidly early in the Jurassic, or whether they were acquired by a slow process of evolution covering the greater part of the Jurassic and Cretaceous. To solve this problem, material of an upper Jurassic or Lower Cretaceous mammal was required which would permit of a direct comparison with advanced therapsids. This meant finding cranial material, as mammal-like reptiles are classified largely on their skulls.

It therefore seemed worth while to search the existing museum material for cranial fragments other than isolated jaws. There are only two adequate collections, both of extreme Upper Jurassic age. One comes from the Purbeckian of Durdlestone Bay and the other from the Morrison of Como Bluff. The Morrison collection contains the greater number of individual specimens but these consist almost entirely of teeth and jaws, while the collection from Purbeck contains examples both of other skull bones—albeit badly damaged—and post-cranial elements. In particular Simpson (1928) had already described parts of both petrosals and of the sphenoid of an individual of *Triconodon mordax* (B.M. 47763) along with some parts of the post-cranial skeleton.

By the kindness of Dr E. I. White, F.R.S., these were prepared by Mr A. E. Rixon, using the chemical methods which he has described (Rixon 1949). In the course of this, some further vertebrae came to light, along with what are probably two pieces of the occipital plate. None of this new material has been found useful in the present work. In the course of preparation it became clear, also, that the solitary long bone associated with the specimen which Simpson suggested was a radius was, in fact, an ulna, probably a left.

In addition the rest of the Purbeck collection in the British Museum was examined for any hitherto unrecognized braincase material. On a block bearing part of the skull of a specimen of *Trioracodon ferox* (B.M. 47781), a species closely related to *Triconodon mordax*, a damaged right petrosal was noticed. This was prepared by Mr Rixon. In removing it from the block he discovered and prepared the left petrosal, which is fortunately almost complete.

The two petrosals and the sphenoid of *Triconodon* and the two newly discovered petrosals of *Trioracodon* are described in this paper.

(*Note.* In the descriptions of the petrosals they will be assumed to be oriented as in the figures. 'Top', 'bottom', 'left' and 'right' will be used in referring to them. This will make for accuracy as the petrosal is not oriented in life parallel to any of the main axes of the body. 'Anterior', 'posterior', 'lateral' and 'medial', referring to these natural axes, will be used occasionally in cases when no confusion can arise. There is no difficulty in the case of the sphenoid, and this will be described throughout as in its natural orientation.)

## II. DESCRIPTION OF MATERIAL

### (1) *Left petrosal* (a) *Trioracodon ferox* (B.M. no. 47781)

This is much the best preserved petrosal of the pair associated with this specimen. Except for some damage in the mastoid region it is almost complete. This petrosal (leaving out of consideration the badly damaged pair of petrosals of the closely related *Triconodon mordax*, described below) most closely resembles that of *Morganucodon*, described and figured by Kermack & Mussett (1958*b*). Comparisons between the petrosal of *Trioracodon* and that of *Morganucodon* will be made continually in the ensuing discussion.

The petrosal of *Morganucodon* used for comparison is the almost perfect specimen discovered at Pant Quarry in 1955 (Kermack & Mussett 1958*b*). It is unfortunate in some respects that this, which is from the right side, will have to be compared with a left petrosal of *Trioracodon*, but this is one of the hazards of working with fossil material. The animal from which it came will be referred to as *Morganucodon* in the account which follows. It is probably a member of the same genus as the form from Duchy Quarry originally described under that name by Kühne (1949), although this cannot be certain until we have finished our study of all the material.

The medial side of the petrosal of *Trioracodon* will be described first (figure 1, plate 2). The most striking thing about this bone is the great anterior lamina which can be seen on the bottom right of the specimen in the figure. This lamina is curved in the vertical plane so as to form the considerable depression seen on its left side. In the floor of this depression is a large foramen. In the photograph the bottom border of this foramen seems to be complete. This, however, is due to a film of matrix having been left there for mechanical reasons by Mr Rixon, when he prepared the specimen. It cannot now be determined whether the foramen was closed here by bone in life or not. If the latter alternative were true the 'foramen' would have formed a deep notch, open anteriorly, towards the bottom of figure 1.

In any event, the lamina, with its foramen, compares closely with the similar structure in the petrosal of *Morganucodon* (figure 2, plate 2). In both mammals the lamina helped to enclose the lateral wall of the braincase, as does the equivalent structure in the modern



monotremes. The depression in the lamina lodged the semilunar ganglion of the trigeminal nerve, while the foramen (or perhaps notch in *Trioracodon*) was for the passage of the third, or mandibular, branch of this nerve, and equates with the foramen pseudovale of the monotremes. In the petrosal of *Morganucodon* there is a shallow notch near the bottom of the left side of the lamina which may have formed part of the foramen for the passage of the second, or maxillary, branch of the trigeminal nerve. This notch is apparently absent in *Trioracodon* but owing to the incompleteness of the edge it is difficult to be more definite. This uncertainty is inevitable in this tiny fragile material, which is easily susceptible to damage before and after fossilization.

To the left of the lamina in *Trioracodon* (figure 1) lies that part of the bone which housed the cochlea. The right border of this is straight, with a small flange at the bottom. To the left of this little flange the left edge of the cochlear housing forms a smooth curve. In the upper right portion of this part of the petrosal lies the internal auditory meatus. This forms a distinct depression, and it is divided into two parts by a vertical bar. To the left of this bar is a large foramen passing directly into the cochlea. This undoubtedly served for the passage of the cochlear branch of the eighth (auditory) nerve. On the right of the bar is another, rather smaller, foramen which is directed towards the vestibular part of the petrosal (towards the top of the figure). Through this passed the vestibular branch of the auditory nerve.

Another still smaller foramen can be seen lying just below the foramen for the vestibular branch of the auditory nerve. It forms a vertically elongated slit. The foramen passes directly laterally into the petrosal. It clearly served for the passage of a nerve or a blood vessel into the petrosal, and this is about all that can be said of its function.

Both the large foramina can be exactly matched in the petrosal of *Morganucodon*, and in some specimens of the latter all three foramina are present. In *Morganucodon* these foramina do not lie in a depression on the surface of the petrosal. Thus, unlike *Trioracodon*, *Morganucodon* cannot be said to have an 'internal auditory meatus'. This difference has no significance and the condition in *Morganucodon* is exactly paralleled in the modern shrews where the equivalent foramina lie flush on the surface of the bone. This lack of a definitive internal auditory meatus is almost certainly simply a size effect, *Morganucodon* being a much smaller animal than *Trioracodon*.

Above the internal auditory meatus, in *Trioracodon* (figure 1), and slightly to the right of it, can be seen the deep subarcuate fossa. On the right of the subarcuate fossa the border of the petrosal is much damaged, which is true of the whole posterior mastoid portion of the bone. It is clear though that a thickened rim of bone bordered the subarcuate fossa above and passed down its right side. This rim had its origin in a boss above and to the left of the fossa. Posterior to the subarcuate fossa the mastoid part of the bone is better preserved in the right petrosal, and a further description will be given under the account of that bone.

On the left edge of the petrosal is the jugular notch. There is no sign of an aquaeductus cochleae, and it is quite certain that one did not exist, as the relevant part of the petrosal is quite undamaged and free from cracks.

Finally, there are two foramina which will be discussed in greater detail during the description of the lateral side of this petrosal. There is a fair-sized foramen directly to the

right of the internal auditory meatus, and at the end of the depression which lodged the semilunar ganglion. This will be referred to as foramen 1. It opens from a backwardly directed trough which forms the top of the semilunar depression. The foramen passes completely through the bone to open upon its lateral surface above the fenestra ovalis. Immediately below foramen 1 is another, foramen 2.

In lateral aspect, the anterior lamina lies towards the bottom left of the specimen as oriented in figure 3, plate 2. The right side of the lamina can be seen bulging out towards the observer. This bulge corresponds to the depression on the median aspect of the bone which houses the semilunar ganglion. In the bulge can be seen the large foramen (or notch), the foramen pseudovale, for the passage of the mandibular branch of the trigeminal nerve.

Above the foramen pseudovale, is another considerably smaller foramen, 3, pointing partly to the left. Below this and rather to its right is yet another foramen, 4. This last is situated just to the right of the right edge of the lamina and opens downwards. (The function of these two foramina will be dealt with below during the discussion of the possible path of the seventh (facial) nerve in its passage through the petrosal.) Foramen 4 lies in a deep groove. Lying between this deep groove and foramen 3 is a triangular depression, its apex directed towards the lower edge of the figure. This extends upwards to the paroccipital process passing to the left of the fenestra ovalis. In this depression is a large foramen, 5, which connects with foramen 1 on the medial surface.

Comparison with the petrosal of *Morganucodon* leaves no doubt as to the identity of the passage connecting the two foramina. It is the canalis pro-oticus through which passed the vena capitis lateralis. The only difference in this respect between the two petrosals is that in *Morganucodon* the medial opening of the canal is further towards the mastoid portion of the bone than it is in *Trioracodon*.

Forming the right-hand border of the anterior lamina is the lateral flange of the petrosal. This structure is found in cynodonts (see figure 13, plate 6 of *Diademodon*), bauriomorphs (Crompton 1958), tritylodonts (Kühne 1956) and in *Diarthrognathus* (Crompton 1958). It supports the quadrate ramus of the alisphenoid, bridging the cavum epiptericum. It was called by Kühne the lateral lamina and by Crompton the lateral flange. Crompton's term is to be preferred. The anterior extent of this flange is uncertain due to the damaged state of the bone in this region. However, from the level of the middle of the foramen pseudovale in figure 3, it may be seen passing upwards to terminate just to the left of the opening of the canalis pro-oticus. Above this opening it recommences again and finally ends as the left-hand border of the deep pit (lateral pit) which forms one of the walls of the foramen pterygoparoccipitale.

In *Morganucodon* the lateral flange is known to commence at the anterior end of the petrosal (figure 4, plate 3). It is interrupted, as in *Trioracodon*, at about the level of the fenestra ovalis. The break in the flange, however, is more sharply marked than in the latter genus, and in *Morganucodon* forms a deep notch.

In *Trioracodon* the part of the petrosal which housed the cochlea lies to the right of the anterior lamina and ends in a point. From the shape of this, the cochlea would seem to have been almost straight, as in *Morganucodon*, in the specimen of *Triconodon mordax* described by Simpson (1928), and as in the modern monotremes.

To the right of the lateral opening of the canalis pro-oticus, foramen 5, lies the fenestra ovalis. This is slightly elongate from top to bottom and is rather wider on the side nearest the cochlea. In *Morganucodon* the shape is similar. The fenestra rotunda lies to the right of the fenestra ovalis, and separated from it by a fairly wide ridge of bone. Strictly this fenestra should be called the fenestra cochleae, since it includes the foramen perilymphaticum (Goodrich 1930, p. 254). I have adhered to the more usual term here. It opens downwards directly into the cochlea from the side of a deep recess. Here *Triaracodon* exactly resembles *Ornithorhynchus*, where the fenestra rotunda similarly opens from the side of a depression in the petrosal. The condition in *Morganucodon* is different, as here the fenestra rotunda opens directly onto the surface of the bone.

At the top of the cochlear housing, just below the fenestra ovalis, in figure 3, is a small foramen with a groove running downwards. This can be matched in *Morganucodon*, and in both was probably for minor blood vessels.

To the right of the cochlear housing is a flange, which ends at the jugular notch. In this flange, just below the jugular notch, is a foramen which opens towards the right. There is a foramen or a collection of foramina, in the same place in both *Morganucodon* and *Ornithorhynchus*, again probably for minor blood vessels.

Above and to the left of the fenestra ovalis lies the paroccipital process. This is large and triangular, with the acute angle directed towards the lower edge of the figure. From this angle comes a narrow free-standing process. The edge of this is slightly concave and is directed towards the fenestra ovalis. The paroccipital process of *Ornithorhynchus* (the crista parotica) bears a similar extension and the function in both must have been the same—to support part of the posterior border of the tympanic membrane. The major part of the anterior portion of the main paroccipital process seems also to have been free standing. To the left of this part of the process, in the main body of the petrosal, lies the lateral pit. In *Morganucodon* there is a similar but shallower depression. The depression in both genera lies just ventral to the lateral flange and forms part of the wall of the foramen pterygo-paroccipitale.

In figure 3 the upper (posterior) part of the paroccipital process can be seen to rise to a flat-topped prominence, which probably articulated with the squamosal. Lying to the right of the paroccipital process and above the fenestra rotunda is an elliptical depression in the petrosal, its major axis horizontal. This can be exactly matched in *Morganucodon*. Comparison with *Oligokyphus* is less close, but there is a depressed area in this genus in approximately the same place. Kühne (1956) calls this 'the bed' for the stapedius muscle. Its actual function seems rather obscure, but it may have been for the articulation of the hyoid.

There remains to discuss the function of foramen 2 on the medial side of the bone and foramina 3 and 4 on its lateral aspect. The most obvious suggestion for the function of this group of foramina would seem to be that they serve in some way for the passage of the seventh (facial) cranial nerve. There are obscurities, however, which seem to be typical of attempts to work out the course of this nerve in early mammals and in advanced mammal-like reptiles.

In *Morganucodon* the passage taken by this nerve is known with some certainty and is described by Kermack & Mussett (1958*b*). It seems to have originated from the brain just



anterior to the roots of the auditory nerve. The facial nerve then passed to the left (see figure 2) across the cochlear housing just below the point of entry of the eighth nerve into the petrosal. It then passed under a notch, which sometimes is closed to form a foramen, in the left edge of the cochlear housing. The nerve then passed on upwards and backwards to penetrate the anterior lamina of the petrosal by means of a small foramen just behind the foramen pseudoovale. This is shown in figures 2 and 4.

After passing through the anterior lamina the nerve in *Morganucodon* turns downward again. In its passage across the lateral surface of the bone it passes through the notch in the lateral flange (see figure 4).

The course of the seventh nerve in *Trioracodon* is more obscure than in *Morganucodon*. For one thing there is no notch or foramen in the body of the petrosal dorsal to the internal auditory meatus. The upward passage of the facial nerve within the braincase must have been entirely medial to the petrosal. In this respect *Trioracodon* is even more primitive than is *Morganucodon*.

Foramen 2 in *Trioracodon* corresponds closely in position with the foramen in *Morganucodon* by which the seventh nerve leaves the cranial cavity and probably had the same function. The nerve clearly made a longer passage within the substance of the petrosal in *Trioracodon* than it did in *Morganucodon*, but exactly where it emerged on the lateral surface of the bone is more obscure in the Purbeck genus. Foramen 4 in *Trioracodon* is well situated to be the hiatus fallopi, whence would have emerged the superficial petrosal nerve; but foramen 3 seems to be rather too dorsal in position to serve for the exit of the main trunk of the facial nerve. Unfortunately it is not possible to demonstrate any connexion between any of these three foramina, as is expected in view of the small size and fragile nature of the specimen.

Another possibility would be that the seventh nerve passed through the petrosal by a canal opening on its medial side at foramen 2, and broke into the canalis pro-oticus at its lateral end. Something similar to this occurs in *Ornithorhynchus*, but in *Trioracodon* no opening is visible in the wall of the canalis pro-oticus at this point. The exact course of the facial nerve in *Trioracodon* must be left in some uncertainty.

From the size of the foramina through which it passed, the seventh (facial) nerve must have been of small size in both *Morganucodon* and *Trioracodon*. This suggests that the fleshy mobile muzzle characteristic of the later mammals had not yet been fully developed.

#### (2) *Right petrosal*

This specimen is badly damaged, and it is in a much less complete state than the left petrosal of the same animal described above. Fortunately, however, the mastoid portion of this right petrosal is well preserved while the same part of the left petrosal is badly damaged. Thus the present specimen shows some structures more clearly than its fellow from the other side and these will be mentioned. Figure 5, plate 3, shows a dorsal view of the bone.

In the centre of the bone as figured can be seen a deep pit, called here the medial pit, with a groove running from it towards the top of the figure. Within the medial pit are two foramina, which are not visible in the figure. To the left of the medial pit can be seen the posterior part of the lateral flange, and to the left of this the remains of the paroccipital



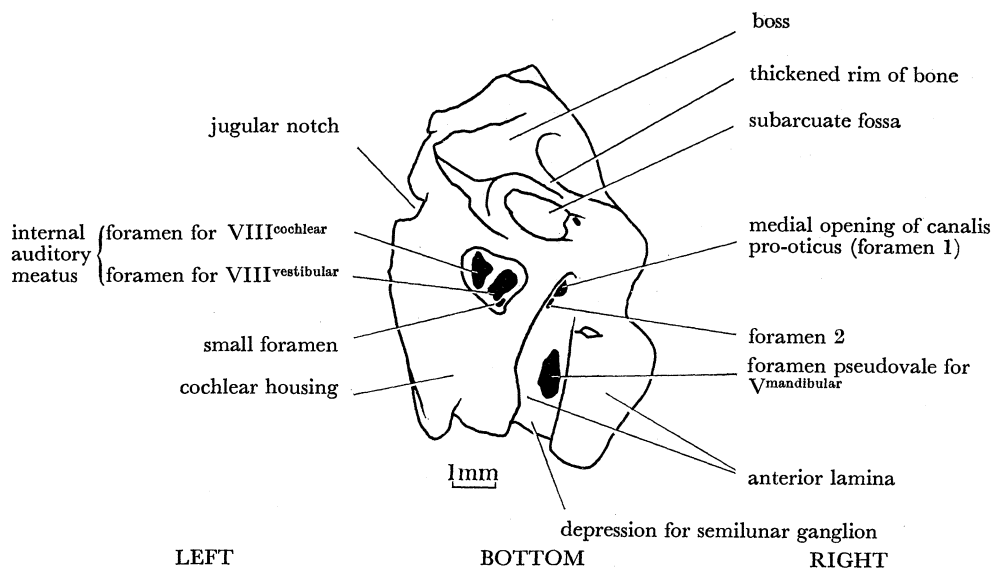


FIGURE 1. Medial view of left petrosal of *Trioracodon ferox*. (B.M. no. 47781.)

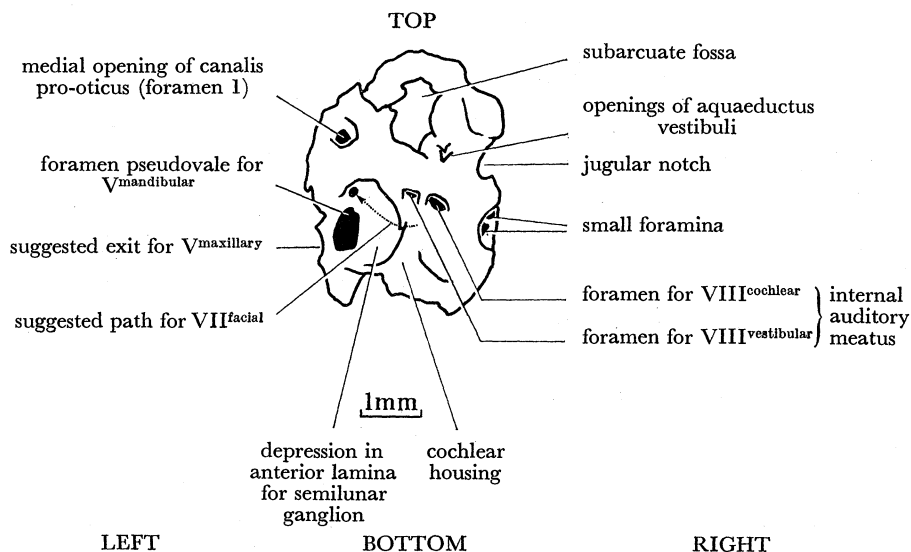


FIGURE 2. Medial view of right petrosal of *Pant morganuodontid*. (B.M. no. M. 21105.)

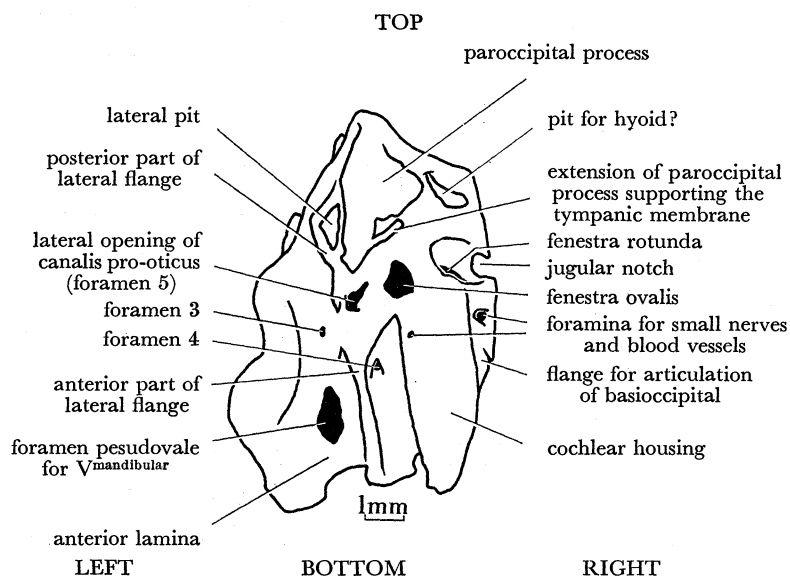


FIGURE 3. Lateral view of left petrosal of *Trioracodon ferox*. (B.M. no. 47781.)



FIGURE 1 ( $\times 6$ )

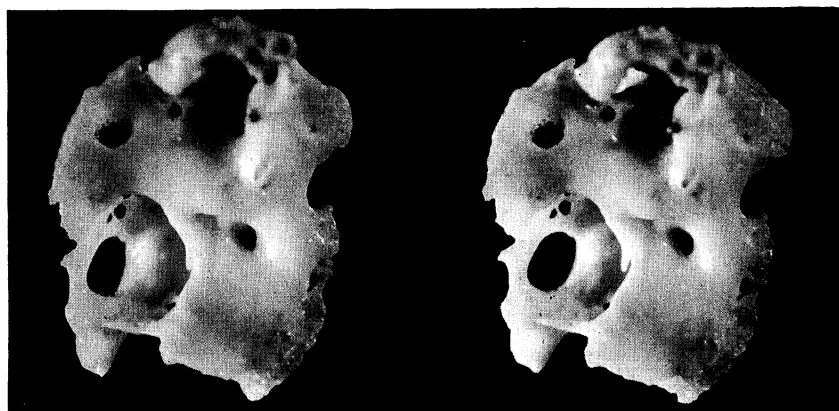


FIGURE 2 ( $\times 11$ )

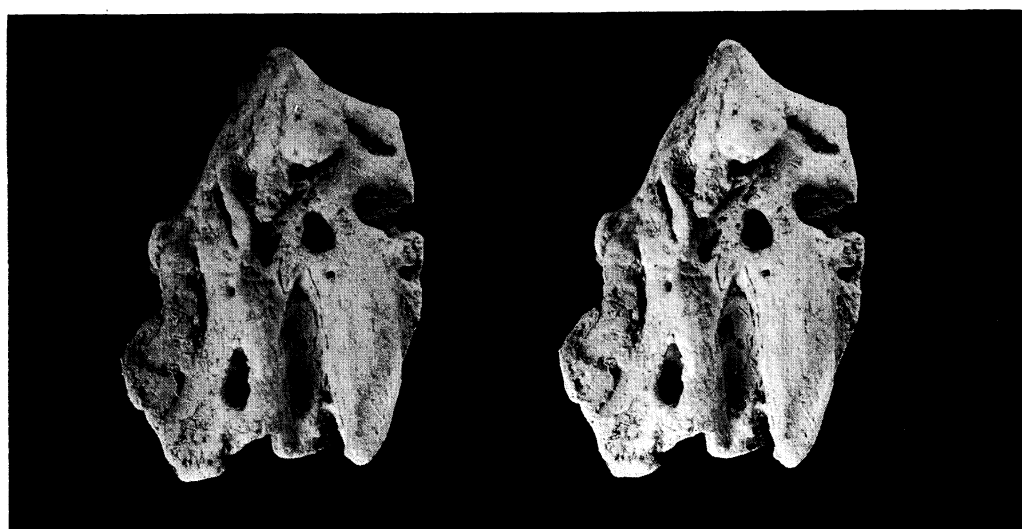


FIGURE 3 ( $\times 6$ )

(Facing p. 90)



FIGURE 4 ( $\times 13$ )



FIGURE 5 ( $\times 6$ )

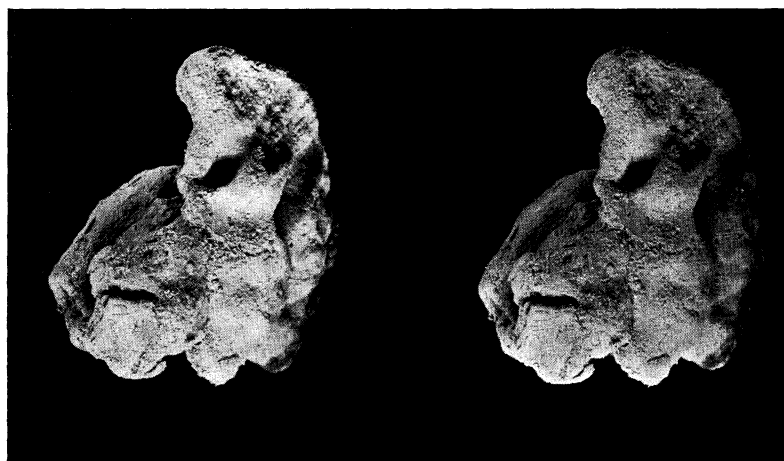


FIGURE 6 ( $\times 6$ )

## THE CRANIAL STRUCTURE OF THE TRICONODONTS

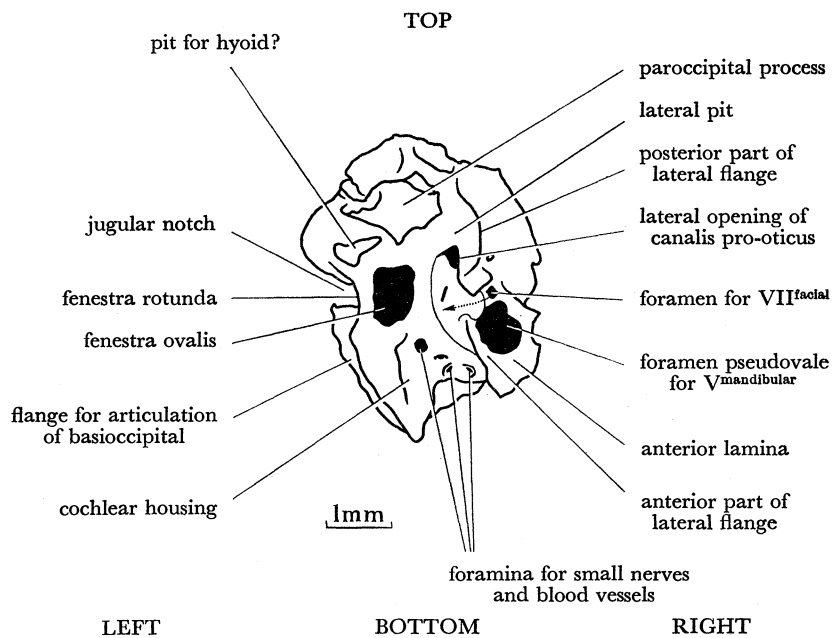


FIGURE 4. Lateral view of right petrosal of *Pant morganucodontid*. (B.M. no. M. 21105.)

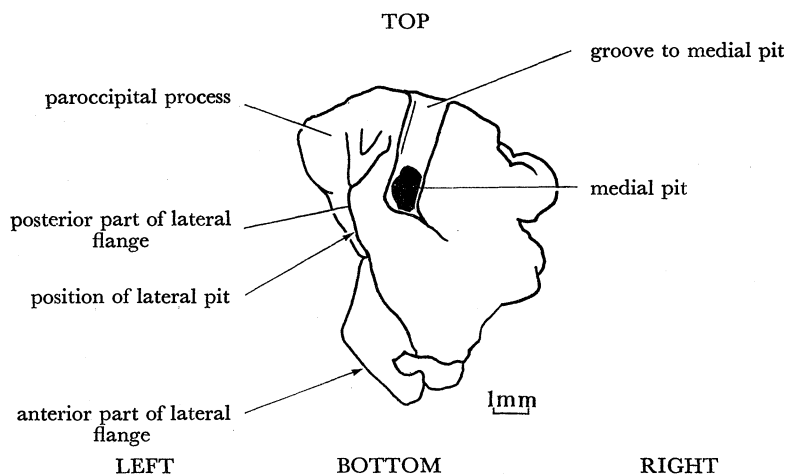


FIGURE 5. Dorsal view of right petrosal of *Trioracodon ferox*. (B.M. no. 47781.)

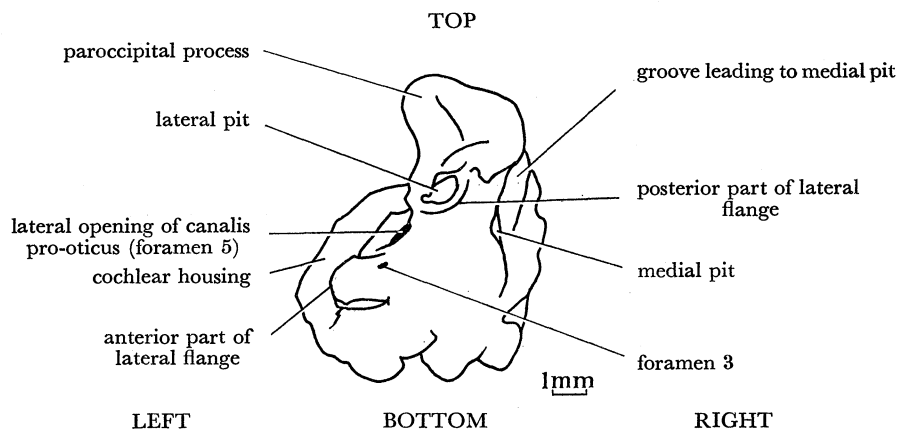


FIGURE 6. Oblique lateral view of right petrosal of *Trioracodon ferox*. (B.M. no. 47781.)



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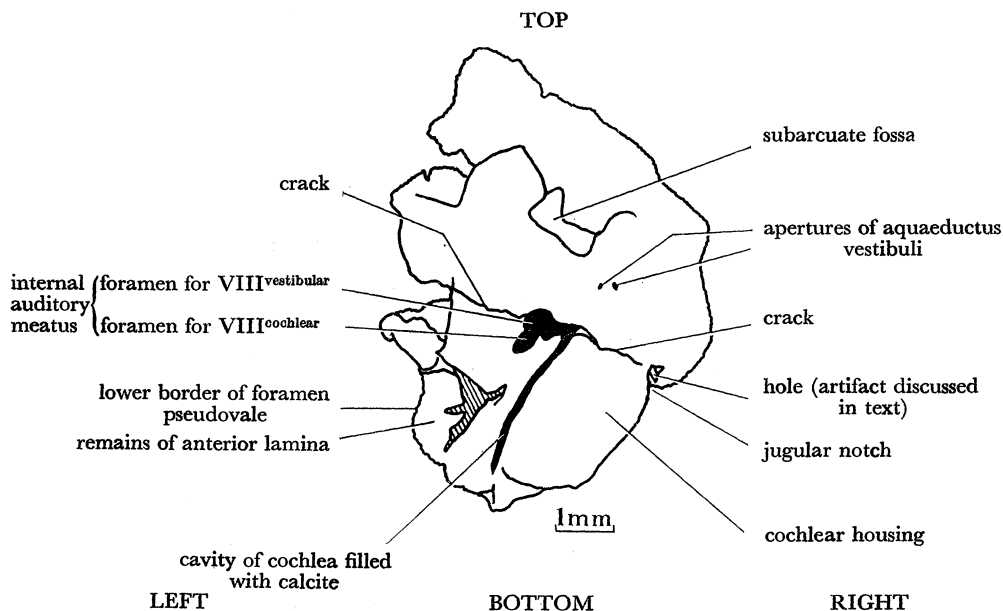


FIGURE 7. Medial view of right petrosal of *Triconodon mordax*. (B.M. no. 47763.)

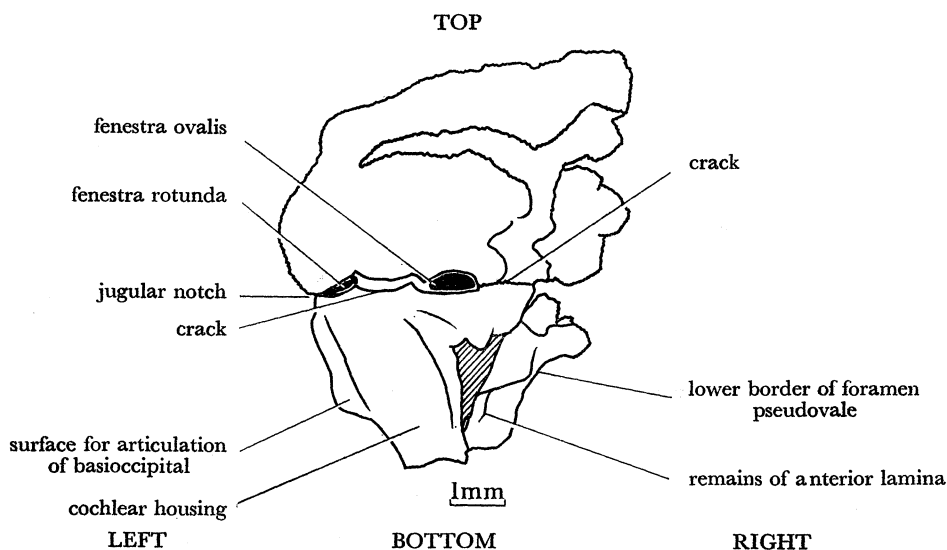


FIGURE 8. Lateral view of right petrosal of *Triconodon mordax*. (B.M. no. 47763.)

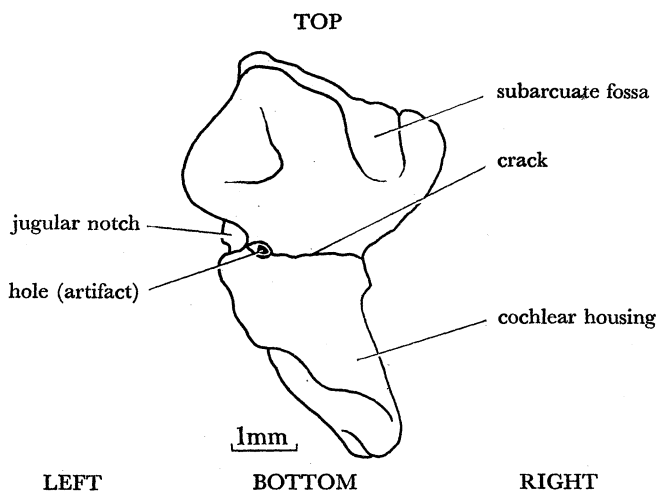


FIGURE 9. Medial view of left petrosal of *Triconodon mordax*. (B.M. no. 47763.)



FIGURE 7 ( $\times 7$ )

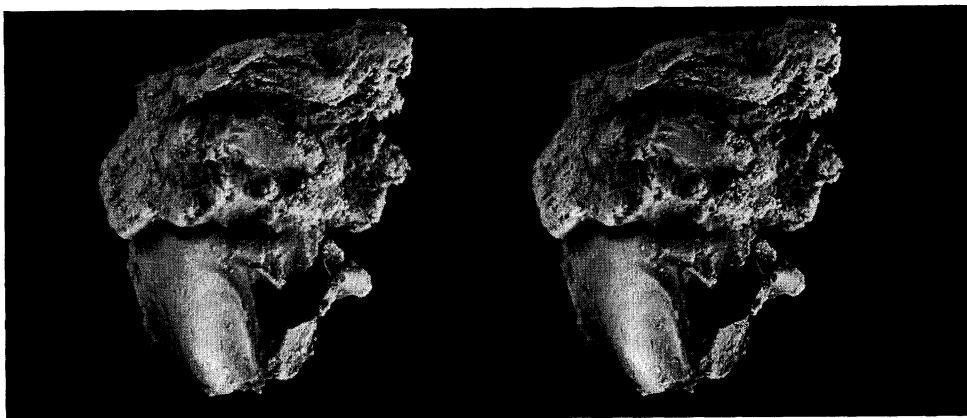


FIGURE 8 ( $\times 7$ )



FIGURE 9 ( $\times 7$ )

*Kermack*

*Phil. Trans. B, volume 246, plate 5*

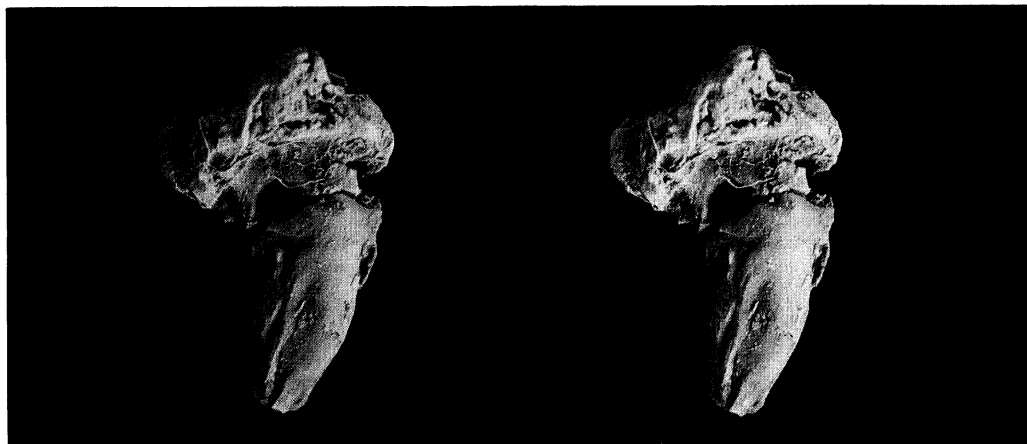


FIGURE 10 ( $\times 7$ )



FIGURE 11 ( $\times 7$ )

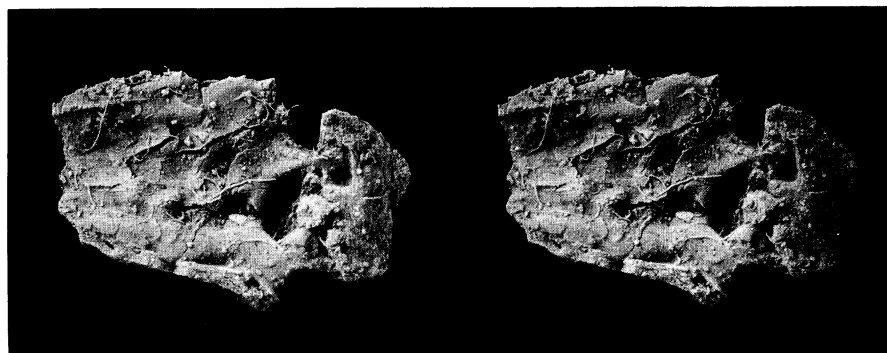


FIGURE 12 ( $\times 7$ )

## THE CRANIAL STRUCTURE OF THE TRICONODONTS

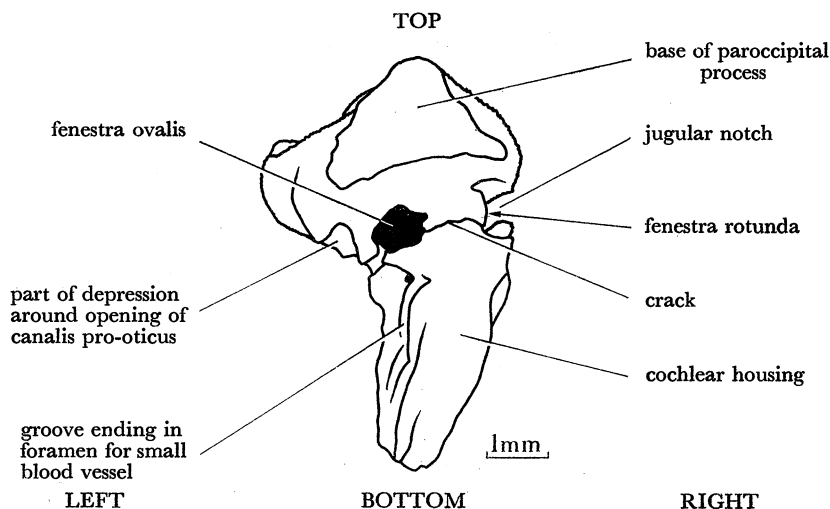


FIGURE 10. Lateral view of left petrosal of *Triconodon mordax*. (B.M. no. 47763.)

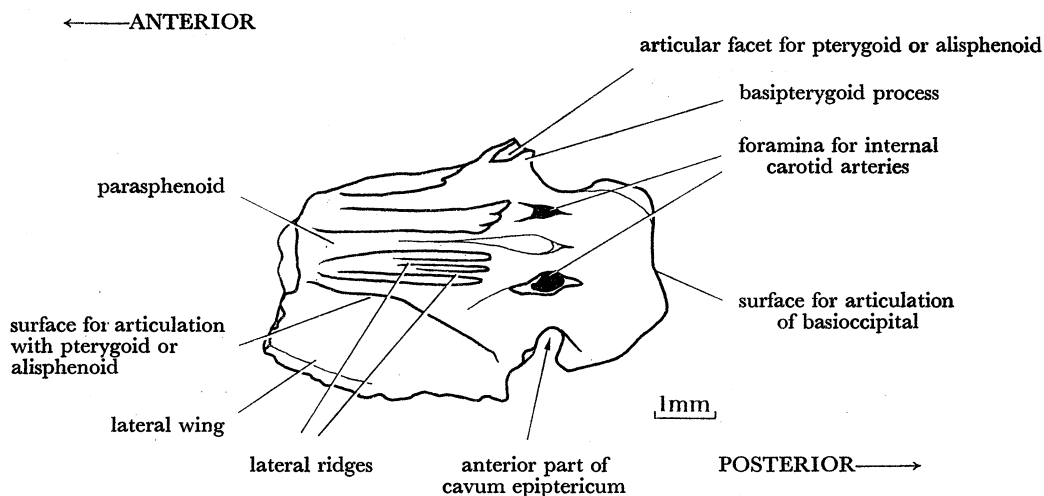


FIGURE 11. Ventral view of sphenoid of *Triconodon mordax*. (B.M. no. 47763.)

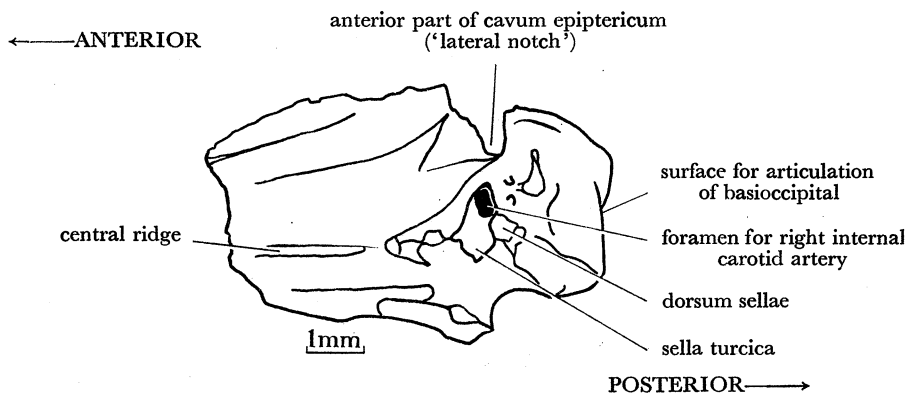


FIGURE 12. Dorsal view of sphenoid of *Triconodon mordax*. (B.M. no. 47763.)



## K. A. KERMACK

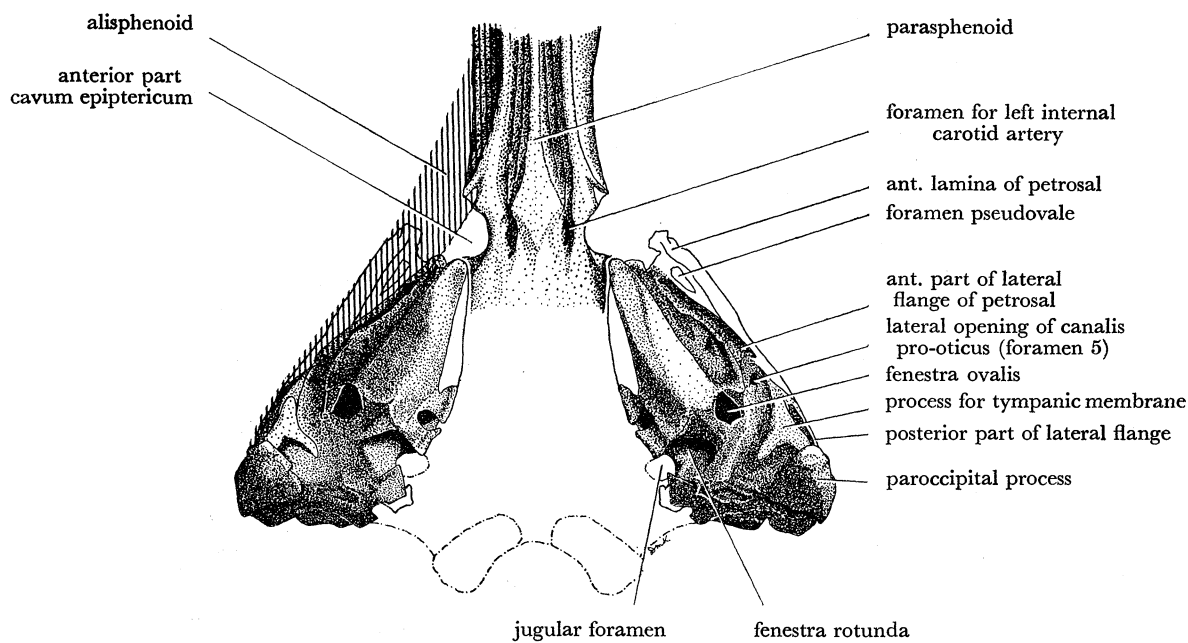


FIGURE 14. An attempted reconstruction of the basicranium of a member of the subfamily Triconodontinae. The sphenoid is drawn from that of *Triconodon mordax* (no. 47763) and the petrosals from the left petrosal of the specimen of *Trioracodon ferox* (no. 47781). No attempt has been made to suggest the position of the foramen or foramina in the alisphenoid through which the maxillary and mandibular branches of the trigeminal nerve passed.

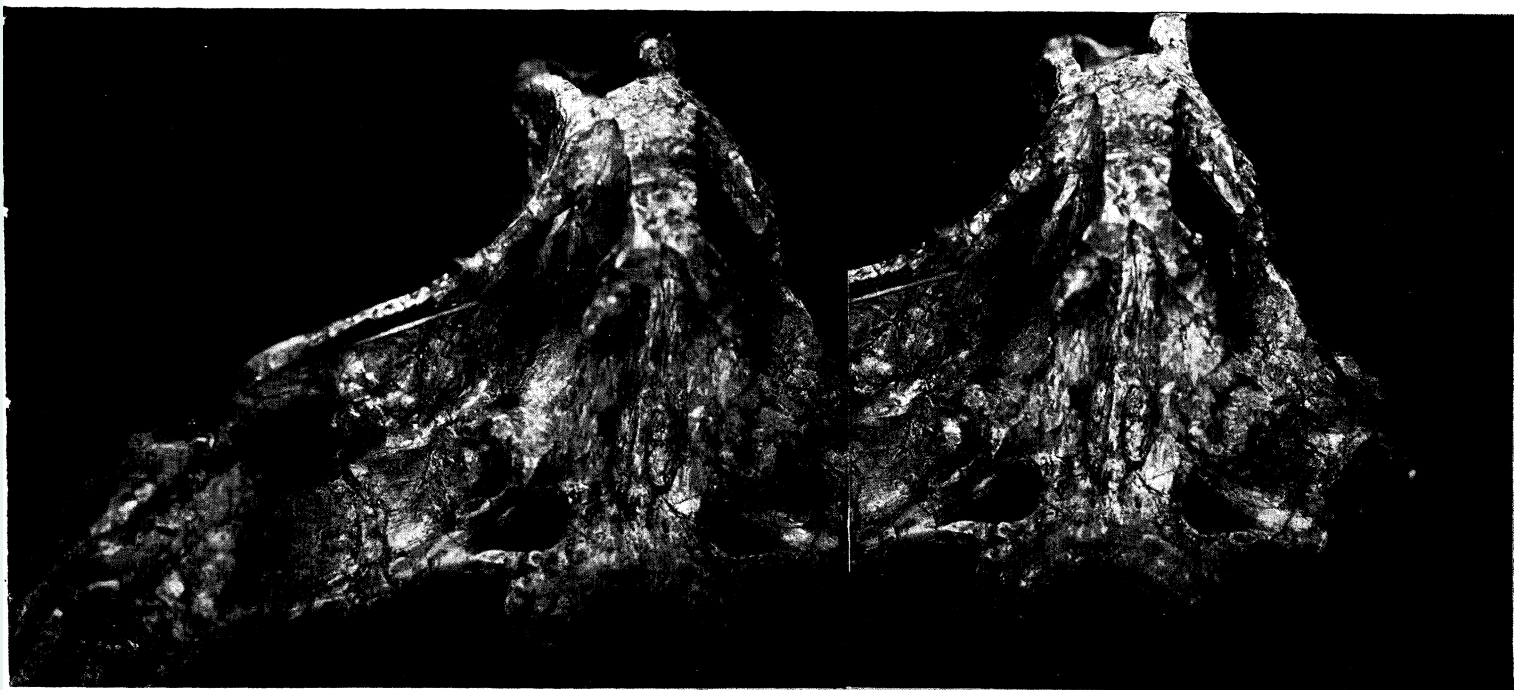


FIGURE 13

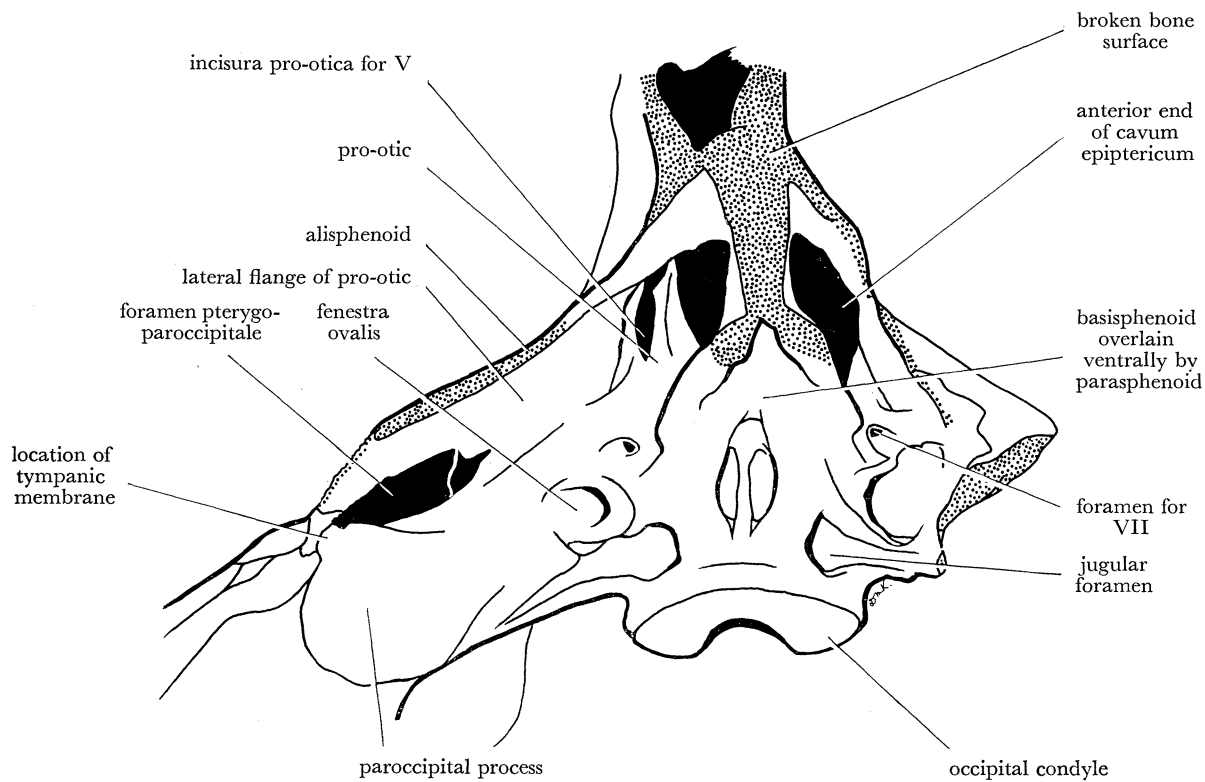


FIGURE 13. Ventral view of the braincase in a specimen of *Diademodon* (D.M.S.W. no. 131.).

process. Towards the lower left of the figure can be seen a fragment of the anterior part of the lateral flange. Although only a small part of it is preserved it is in a better state than is this part of the flange of the other petrosal. Its appearance shows that it articulated laterally with another bone (the alisphenoid).

Figure 6, plate 3, shows the specimen in oblique lateral view. At the top of the figure is the damaged paroccipital process. Below this, and on the left, can be seen a deep pit (the lateral pit). Unlike the medial pit this contains no foramina. Passing around the pit to the right can be seen the posterior part of the lateral flange. The flange hides the pit from view in figure 5. To the right of figure 6 the groove leading to the medial pit is visible, the pit itself being hidden in this aspect. At the bottom left of the specimen can be seen the anterior part of the lateral flange, and, between the two parts of the flange, the lateral opening of the canalis pro-oticus. Just below this opening can be seen another foramen which corresponds to foramen 3 described above.

The system of pits and grooves seen in this specimen can be paralleled in *Didelphis*. Here it is connected with the course of the lateral head vein and its associated vessels.

(1) *Petrosal* (b) *Triconodon mordax* (B.M. 47763)

The two petrosals of *Triconodon mordax* were first described by Simpson in 1928. Only the medial aspect of the specimens was accessible to him, their lateral sides being still embedded in matrix.

The two specimens are badly damaged. This led Simpson into difficulties in interpreting them. These difficulties were not lessened by the absence, at that time, of any closely comparable material. By the kindness of Dr E. I. White, F.R.S., both specimens were removed from the block on which they lay by Mr A. E. Rixon, using chemical methods.

For the sake of completeness the specimens will be figured and briefly redescribed, interpreting them in the light of the much better material of *Trioracodon* and *Morganucodon* now available.

The right petrosal is the more complete. The damage that it has suffered includes the shattering of the anterior lamina. This can be seen in medial view (figure 7, plate 4), with part of the ventral border of the foramen pseudovalve still visible at the left edge of the remains of the lamina. To the right the cochlear housing has split open along its entire length, exposing the almost straight cochlea. This, as Simpson stated, is similar, in this respect, to that of the modern monotremes: it also compares closely with that of *Trioracodon* and *Morganucodon*. Comparison with the last two genera shows that the left of the pair of foramina to be seen at the upper end of the split was for the vestibular branch of the auditory (eighth) nerve and not for the facial (seventh) nerve, as was postulated by Simpson. The close association of the seventh nerve with the eighth in a deep internal auditory meatus is a characteristic of modern mammals which had not yet been evolved in the Upper Jurassic. Comparison with *Trioracodon* and *Morganucodon* shows that the lower of this pair of foramina was for the cochlear branch of the eighth nerve.

Above and to the right of these foramina, close to the edge of the subarcuate fossa, can be detected the paired openings of the aquaeductus vestibuli. They have only become

visible since the specimen was cleaned in acid. The openings are in exactly the same position as in *Oligokyphus* and *Morganucodon*. This evidence for the location of the aperture of the aquaeduct in *Triconodon* is particularly valuable as it is not visible, due to damage, in either petrosal of *Trioracodon*.

Finally, the small hole visible at the apex of the jugular notch was considered by Simpson to be a true foramen and the opening of either the aquaeductus vestibuli or the aquaeductus cochleae. The former was impossible, from its position: the latter is confined to marsupials and placentals and would be remarkable in any Upper Jurassic mammal. However, comparison with *Trioracodon* and *Morganucodon*, neither of which has a foramen in that position, shows that this hole is indeed simply a hole, produced by accident.

The lateral aspect (figure 8, plate 4) was unknown until the recent preparation of the specimen. Unfortunately it is in an even worse state than the other side. Impaction has taken place along the deep crack which can be seen crossing the specimen from left to right, almost obliterating the fenestra ovalis and the fenestra rotunda. The paroccipital process has vanished, leaving no trace of its former presence. Such details as can be identified are labelled in the figure.

The left petrosal is in an even more sorry state. Only that part of the bone which housed the cochlea and a small part of the adjacent area is left. In median view (figure 9, plate 4) there is nothing worthy of special comment. All the important structures present are labelled. In lateral view (figure 10, plate 5) the shape of the fenestra ovalis and fenestra rotunda is reasonably well shown, along with an indication of the base of the paroccipital process, and of the posterior end of the depressed area into which opens the canalis pro-oticus.

## (2) *Sphenoid*

A considerable part of another bone of *Triconodon mordax* was preserved on block 47763. This was identified by Simpson (1928) as a sphenoid—that is the fused up basisphenoid-alisphenoid complex such as is typical of recent mammals. Initially I accepted this identification without reserve.

The bone was originally preserved on the surface of the slab with its ventral surface uppermost and visible. It was taken off the block and prepared by Mr Rixon at the same time as the two petrosals belonging to the same specimen. Its ventral surface will be described first (figure 11, plate 5).

In this view the anterior part of the bone shows a strong central ridge, now much damaged, with two much lower subsidiary ridges running on each side of it. Lateral to the outermost of these lateral ridges the bone rose up to its articulation with the pterygoids. This part of the bone is broken on both sides, and the actual surfaces which articulated with the pterygoids can no longer be seen. Lateral again to this central part of the bone are the remains of its lateral wings. These show no foramina or other structures.

In the posterior third of the bone are a pair of large foramina, each lying at the end of the broad trough between the central ridge of the bone and the remains of the pterygoid articulations. These penetrate the bone to open on its dorsal surface at the base of the sella turcica (figure 12, plate 5). This confirms the suggestion made by Simpson (1928), when only the ventral surface of the bone could be seen, that they were for the passage of the



internal carotid arteries. The central ridge, on the ventral surface of the specimen, extends back and passes between the two carotid foramina. An open groove connects each carotid foramen with the more lateral part of the corresponding trough.

On each side, lateral to the carotid foramen, is a large notch. The projection at the antero-lateral border of each bears a facet for the articulation of another bone. The interpretation of the lateral notches is critical to the interpretation of the whole specimen, and will be discussed after a description of the dorsal side. Posterior to the carotid foramina the bone thickens to form the articulation with the basioccipital. Here it has been much crushed and distorted.

On the dorsal surface of the bone (figure 12) the lateral edges seem to have formed an upturned flange, the dorsal extension of which is broken. This shows most clearly on the left. Running down the centre of the anterior part of the bone seems to have been a much broader and less clearly defined ridge than the central ridge on the ventral surface. The specimen has been much flattened, but it would seem that in life a broad trough ran on either side of the central ridge.

The sella turcica commences about two-thirds of the way from the anterior end of the bone. This again has been flattened by the compression to which the bone has been subjected. In the floor of the pituitary fossa can be seen the pair of openings through which the internal carotids entered the cranial cavity. The one on the right has been completely cleared of matrix by Mr Rixon, and can be followed right through to the ventral surface (see figures 11 and 12). There is no sign of any foramina for the passage of the sixth nerve.

The dorsum sellae has been completely smashed and crushed, and nothing useful can be said about its shape.

The posterior part of the specimen, where it articulated with the basioccipital, has been slightly twisted to the right and considerably flattened. It shows no detail worthy of comment.

The identification of the large lateral notches is the critical point in the interpretation of the specimen and will now be discussed. Simpson (1928) interpreted the specimen on the assumption that it was the ventral part of the sphenoid of what was essentially a modern primitive mammal. On the evidence available then this was a perfectly reasonable thing to do: my own early attempts to interpret the specimen were made on the same basis. With this in mind, Simpson put forward two alternatives for the function of the lateral notch, which he considered to represent a foramen. The first was that it was equivalent to the opening of the transverse canal in marsupials. This is impossible as the transverse canal lies wholly within the sphenoid; while the lateral notch in *Triconodon* penetrates completely through the bone.

The other alternative was that the notch in question was part of the foramen ovale. This is the most plausible suggestion on the hypothesis of a fully mammalian braincase structure in the Triconodonta. It needs further discussion, but first two other possibilities need to be briefly considered. The first of these is that the notch is part of the lacerate foramen. This is situated in mammals between the petrosal and the sphenoid. That the lateral notch in *Triconodon* was part of a lacerate foramen is highly improbable. The latter only reaches a large size in the placental mammals, where it is the means by which the

internal carotid artery gains access to the cranial cavity. In monotremes and marsupials, where the internal carotids penetrate directly through the basisphenoid, the lacerate foramen is vestigial, serving mainly for the passage of the Vidian nerve. In *Triconodon*, as in monotremes and marsupials, the internal carotids penetrated the basisphenoid and there could not have been a large lacerate foramen. The second possibility would make the lateral notches in *Triconodon* correspond to the paired unossified area in the basicrania of *Ornithorhynchus* and the young *Echidna*. Each lies between the basioccipital, the basisphenoid and sometimes extends to reach the petrosal. It was called by van Bemmelen (1901) the foramen lacertum anterius. The name is quite unsuitable: the unossified area is not a foramen—nothing passes through it and it is closed in life by membrane. It has nothing to do with the true anterior lacerate foramen (now usually called the superior orbital fissure) of the Mammalia.

Three reasons may be given against the lateral notch in *Triconodon* being such an unossified area:

(a) It is in the wrong place, lateral to the external opening of the carotid foramen and not well posterior to it, as is the unossified area in the modern monotremes.

(b) The edges of the notches in *Triconodon* are sharp and well defined. They lack the slightly irregular outline to be expected in a vacuity which arose simply from a failure of ossification. This can be seen clearly in the skull of *Ornithorhynchus*.

(c) The fenestration in the skull of the modern monotremes are simply due to the extreme thinness of their skull bones. *Triconodon* had a rather thick, solid skull which would not be expected to fenestrate in this way.

On the hypothesis that the triconodont braincase was similar to that of recent primitive mammals this left only the suggestion that the lateral notch was part of the foramen ovale. This seemed very plausible. As Simpson (1928) pointed out, primitive mammals nowadays do have the foramen ovale very ventral in position, and, in fact, at first sight the resemblance between the sphenoid of *Triconodon* and that of *Didelphis* seems remarkably close. The notch in the former seems to encroach into the basisphenoidal part of the bone more than the foramen ovale does in the latter, but despite this I was at first prepared to accept Simpson's identification.

However, a much more telling objection was made by Dr A. W. Crompton when he saw the specimen in September 1960. He pointed out to me that the pituitary develops in ontogeny well in front of the point at which the mandibular nerve passes through the wall of the chondrocranium, and that consequently to find the foramen ovale directly lateral to the sella turcica would be unexpected and remarkable. He went on to suggest that the difficulties could be resolved by interpreting the bone in question not as if it were the sphenoid of a modern mammal but as if it resembled the sphenoid complex of an advanced mammal-like reptile.

In an advanced mammal-like reptile, such as the specimen of *Diademodon* (D.M.S.W. no. R 131) shown in figure 13, the floor of the braincase is formed by the basisphenoid and the basioccipital. The parasphenoid is applied to the ventral surface of the basisphenoid, and covers a large part of it. The two bones have fused together, and, in this specimen, most of the other basicranial sutures have become obliterated. Lateral to the basisphenoid-parasphenoid complex, and separated from it by a deep trough, is a thin vertical sheet of

bone. The ventral edge of the vertical lamina is formed by the quadrate ramus of the pterygoid, the remainder of the sheet being formed by the alisphenoid (epipterygoid).

Dorsal to the basisphenoid and basioccipital the lateral wall of the braincase is formed by the optic capsule. This has ossified in a typically reptilian fashion as two bones: the pro-otic and the opisthotic. From the pro-otic runs the powerful lateral flange which supports the lamina formed by the pterygoid and the alisphenoid. The space formed between this lamina and the lateral wall of the braincase is the cavum epiptericum. In this lay the semilunar ganglion of the fifth (trigeminal) cranial nerve (Goodrich 1930, p. 267). The fifth nerve itself passed out of the braincase through a deep notch in the anterior part of the pro-otic—the incisura pro-otica. Of the three main trunks of this nerve which came from the semilunar ganglion the most anterior (the ophthalmic nerve) passed out through the anterior end of the cavum epiptericum while the maxillary and mandibular nerves passed out through two foramina formed in the posterior edge of the alisphenoid. Finally, it should be noted that this bone plays no part in the formation of the lateral braincase wall, except perhaps at the extreme anterior end.

Interpreting the sphenoid of *Triconodon* in this way, the lateral notch is not a foramen at all, but forms the anterior border of the cavum epiptericum.\* That part of the bone which forms the anterior and lateral border of the notch would be the pterygoid process, the facet at its apex being for the articulation of the quadrate ramus of either the pterygoid or the alisphenoid.

It was clearly vital to determine between these two conflicting hypotheses: whether the basicranium of a triconodont was substantially that of a modern mammal or whether it had a general resemblance to that of an advanced mammal-like reptile, such as *Diademodon*. Fortunately the discovery in November 1960, of the almost perfect left petrosal of *Trioracodon ferox* (47781) enabled the problem to be solved with certainty.

This petrosal, as described above, has a lateral flange for the articulation of the quadrate ramus of the alisphenoid (figure 3). This proves the existence of a cavum epiptericum in this genus and confirms that the braincase in the triconodonts was similar to that of the later therapsids. That the lateral notch in the sphenoid could not have been part of the foramen ovale, as it must have been if the triconodont braincase resembled that of a marsupial or placental, is confirmed by the presence, in this petrosal, of a foramen pseudovale for the mandibular nerve. Thus this nerve could not have left the braincase by a true foramen ovale in the alisphenoid, as it does in the Eutheria.

Thus, interpreting the sphenoid correctly it becomes part of a basisphenoid-parasphenoid complex comparable with that of the more advanced mammal-like reptiles. The whole braincase is shown reconstructed in figure 14. It most closely resembles that of the so-called 'ictosaurs', such as *Bienotherium* (Watson 1942), *Oligokyphus* (Kühne 1956) and *Diarthrognathus* (Crompton 1958). In the only other Mesozoic mammal where there is

\* There is a difficulty about calling this space in *Triconodon* the cavum epiptericum which should be mentioned. In typical reptiles the semilunar ganglion lies outside the wall of the braincase in the cavum epiptericum (Goodrich 1930). In monotremes, however, Watson (1916) showed that the semilunar ganglion lay *inside* the ossified braincase wall. The deep depression surrounding the foramen pseudovale on the medial surface of the anterior lamina of the petrosal shows the same to be true in *Trioracodon*, *Morganucodon* and *Oligokyphus* (Kühne 1956). Thus some time in therapsid evolution part of the cavum epiptericum, along with the semilunar ganglion, was incorporated within the expanding braincase.



evidence of the structure of the braincase, *Morganucodon*, the petrosal has a lateral flange for articulation with the alisphenoid (figure 4). Here too the braincase must have been of the same general pattern, which was probably common to all pre-Cretaceous mammals.

Finally, the central ridge running longitudinally forward along the ventral surface of the more anterior part of the bone would represent the parasphenoid—solidly fused to the basisphenoid as is usual in therapsids. The sphenoid complex in the triconodonts seems to have shown little advance over that of *Bienotherium* or *Oligokyphus*.

### III. DISCUSSION

The lateral flange of the otic capsule is found in mammal-like reptiles down to the level of the Cynodontia. It butted against the alisphenoid and the quadrate ramus of the pterygoid which it helped to support. The space between the alisphenoid and the main body of the otic capsule forms the cavum epiptericum, which lies outside the wall of the braincase.

The continued existence of a lateral flange in *Morganucodon* demonstrates the persistence of the cavum epiptericum, although the latter would have been relatively much narrower than in the cynodonts or *Oligokyphus*. In *Morganucodon*, where the semilunar ganglion lies inside the primary wall of the braincase, the mandibular branch of the trigeminal nerve passes through the foramen pseudovale in the anterior lamina of the petrosal. This last extends much farther forward in *Morganucodon* than it does in the cynodonts. The maxillary branch of the fifth nerve presumably left the braincase passing through the notch at the front end of the anterior lamina. After crossing the cavum epiptericum both branches would have left it by passing behind or through the alisphenoid in some way reminiscent of cynodonts. The exact course of the nerve here obviously cannot be known.

The width of the lateral flange is relatively much less in *Morganucodon* than in any therapsid, so that the cavum epiptericum is relatively much narrower. This is due to the relatively much greater size of the brain in the mammal. I do not think that this is due to *Morganucodon* being absolutely much smaller in size than, say, *Oligokyphus*. A real measure of increase in brain size had almost certainly taken place as well.

In *Trioracodon* the quadrate ramus of the alisphenoid still existed, as is shown by the continued existence of a very narrow lateral flange on the petrosal. The flange is so narrow in this region, that the cavum epiptericum has become almost obliterated. Figure 14 shows an attempt at a reconstruction of the triconodont basicranium.

Kermack, Kermack & Mussett (1956) were the first to comment on the large anterior lamina of *Morganucodon*. They stated, correctly at the time they wrote, that the presence of a foramen pseudovale in this lamina, for the passage of the mandibular nerve, was a character shared only by *Morganucodon* and the modern monotremes. From this they went on to deduce a relationship between these two groups of mammals. Since we now know that *Trioracodon*, and undoubtedly the other members of the subfamily Triconodontinae as well, also possess a foramen pseudovale, they too would be monotremes on this reasoning.\*

\* To call the triconodontines monotremes would mean no more than stating that both groups would have had a common ancestor which could have been classified as a mammal. The known specializations of the Upper Jurassic triconodontines in the dentition, and in the passage of the posterior molars on to the zygomatic arch and into the coronoid process in a manner only reminiscent of *Hyaenodon* (Patterson 1957), would seem to preclude them from the direct ancestry of any other group of mammals. It is worth noting, however, that they seem to share with monotremes reduction of jugal and lachrymal (Simpson 1928).



But with the better understanding of the braincase structure of these early mammals I do not now consider the above reasoning to be sound. In advanced mammal-like reptiles the alisphenoid plays no part in the formation of the wall of the braincase proper, from which it is separated by the cavum epiptericum. In this condition, should an expansion and an extension forward of the brain occur in evolution, the corresponding ossification of the braincase to give it protection could only have been an ossification within the wall of the neurocranium itself: in other words, a forward extension of the petrosal. In growing forward the bone would have surrounded the mandibular nerve. This would have produced the foramen pseudovale we meet for the first time in *Morganucodon*.

The alisphenoid would have been unaffected by these changes, since it would have been separated from the wall of the braincase by the cavum epiptericum. All the time, however, the brain was becoming progressively larger. As we have seen, in *Morganucodon* of the Upper Trias the cavum epiptericum is already relatively narrower than in any therapsid; and, by the time that the Upper Jurassic *Trioracodon* was reached, its posterior part had been squeezed almost out of existence. A little later the cavum epiptericum would finally vanish as the anterior lamina of the petrosal came into contact with the alisphenoid. Then, and only then, had the choice to be made: either to suppress the alisphenoid and form the braincase wall from the anterior lamina of the petrosal, as do the monotremes; or to suppress the anterior lamina and allow the alisphenoid to form the lateral wall of the braincase as in marsupials and placentals. In the first case the mandibular nerve would leave the braincase through a foramen pseudovale, in the second case by means of a true foramen ovale.

In *Trioracodon*, the reduced lateral flange was still functional, and the alisphenoid still existed lateral to the anterior lamina. The Upper Jurassic triconodontines had not yet reached the point of no return where one of the two alternative ways of constructing the lateral braincase wall must be adopted. This would seem to have occurred in the Lower Cretaceous.

Thus we do not need to postulate the separation of the Monotremata from the therian stock, *on this character alone*, until after the end of the Jurassic period. But mammals with tritubercular teeth (to use this term to characterize the various types of teeth found among the Theria—symmetrodon, eupantotheres, marsupials and placentals) are now known as early as the Upper Trias (Kermack & Mussett 1958*a*). This means that unless the Monotremata are derived from Theria, as Gregory (1947) supposed, the therian and monotreme stocks must have been separate at least since some way down the Upper Trias. Gregory's hypothesis has won no acceptance, and as these Upper Triassic Theria have still retained the reptilian jaw articulation the common ancestor of monotremes and Theria must certainly have been at a still more primitive level of evolution, i.e. a reptile.

It is worth considering whether the Upper Jurassic pantotheres also had a cavum epiptericum and possessed a lateral wall to the braincase of the same general pattern. From their teeth, the pantotheres seem to have been related in some way to the marsupials and placentals and at first sight it might seem more reasonable to suggest that their braincase was also comparable in structure with that of these modern mammals. This is possible; but I think that there are two strong arguments against it. For the first we know now that the teeth differentiated very early in the evolution of the Mesozoic mammals. An

excellent example of this is the presence in the Rhaetic of animals which, on the structure of their teeth, are quite definite pantotheres (the symmetrodonts mentioned by Kermack & Mussett 1958*a*) and which at the same time almost certainly retained the quadrate-articular jaw hinge. The second argument against the pantotheres being in effect modern mammals existing in the Jurassic, comes from what we know of the correlation of characters in an evolving complex consisting of a number of parallel lines. Matthew (1926) and Kermack (1954) have discussed the problems involved here, and have shown that a line advanced in one character (teeth in the case of the pantotheres under discussion now) would have to lag in others to compensate, and could not be advanced in all. A good example of this from among the Upper Jurassic mammals is supplied by *Docodon*. The molariform teeth of this animal are the most advanced of any Jurassic mammal. A cusp which functioned as a protocone had been evolved (Butler 1939), although the Theria did not acquire their protocone until the Albian (Patterson 1956) at least 30 million years later. But along with its very precocious teeth *Docodon*, alone among Upper Jurassic mammals, retains the quadrate-articular jaw hinge—a character typical of the Upper Trias rather than of the Upper Jurassic. This juxtaposition of advanced and primitive characters in *Docodon* should induce caution in assuming that pantotheres, with their advanced teeth, have a correspondingly advanced braincase structure.

The synapsid-mammalian phylum first appears in the Upper Carboniferous. From that time until the end of the Trias we have an excellent record of the evolution of the various lines. This covers a period of some 80 million years. With the commencement of the Jurassic, with the solitary exception of *Oligokyphus* early in that period, there is nothing but scraps until the end of the Cretaceous. This is some 100 million years. Then for the 70 million years of the Cenozoic there is again an excellent fossil record. Thus the gap in our knowledge of the evolution of the synapsid-mammalian phylum is 40% of its known duration and comprises about 60% of the history of the Mammalia.

Until recently virtually all that has been available for study in this gap has been teeth. The existence of tribosphenic lower molars in the Middle Jurassic (*Amphitherium*), and the more recent discovery of tritubercular teeth (symmetrodont) in the Rhaetic (Kühne 1950) has given rise, very reasonably, to the concept that when the Mammalia differentiated from the Reptilia they did so rapidly, with the consequence that the mammals of the Jurassic were demonstrably mammalian in the bulk of their attributes (Romer 1945; Simpson 1960).

Now, however, we do know something of the braincase structure of one group of Upper Jurassic mammals—the Triconodonta. The knowledge is admittedly scanty and inadequate, but even so it makes the concept of a rapid burst of mammalian evolution early in the Jurassic no longer tenable. The triconodonts retained a typically therapsid braincase at the very top of the Jurassic, and there is no evidence for postulating that they were in any way archaic in so doing, as I have already said.

By the end of the Trias the evolving therapsid-mammalian stock had acquired the following attributes characteristic of present-day mammals (owing to the imperfections of the material it is impossible to know if they all occurred in any one genus):

- (1) phalangeal formula 2.3.3.3.3 (known in cynodonts, etc.);
- (2) precoracoid excluded from glenoid (known in *Oligokyphus* and *Morganucodon*);

## THE CRANIAL STRUCTURE OF THE TRICONODONTS

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- (3) fused cervical ribs (known in *Oligokyphus*);
- (4) fully formed odontoid (known in *Oligokyphus* and *Morganucodon*);
- (5) articulation between squamosal and dentary (known in *Morganucodon* and almost certainly present in the Upper Triassic symmetrodonts);
- (6) paired occipital condyles (known in cynodonts, in tritylodonts and in *Morganucodon*);
- (7) single bone (petrosal) surrounding inner ear (known in *Oligokyphus* and *Morganucodon*);
- (8) post-orbital bone lost and orbit consequently confluent with temporal fossa (known in bauriomorphs, tritylodonts, and *Diarthrognathus*);
- (9) fully developed secondary palate (known in tritylodonts);
- (10) cheek teeth with fully divided roots (known in tritylodonts, *Microlestes*, *Morganucodon* and the Triassic symmetrodonts).

They had still to lose the following reptilian characters:

- (a) a jaw joint formed by the quadrate (incus) and the articular (malleus) (known in tritylodonts, *Diarthrognathus*, *Morganucodon* and in the contemporaneous symmetrodonts);
- (b) a compound lower jaw;
- (c) parasphenoid (known in tritylodonts and *Diarthrognathus*);
- (d) the cavum epiptericum (known in tritylodonts, *Diarthrognathus* and *Morganucodon*).

They had still to acquire the following fully mammalian characters:

- (i) growth by epiphyses;
- (ii) fused atlantal elements;
- (iii) chain of three bones (stapes, incus and malleus) in middle ear;
- (iv) following on the loss of the cavum epiptericum, either the anterior lamina of the petrosal forms the lateral wall of the braincase and the alisphenoid is greatly reduced or absent (monotremes—Watson 1916), or the alisphenoid forms the lateral wall and the anterior lamina is lost (marsupials and placentals).

By the Middle Jurassic (Stonesfield Slate) the reptilian jaw joint had been lost both in pantotheres (represented by *Amphitherium*), and in triconodonts (represented by *Amphilestes* and *Phascolotherium*). In at least one other group, represented by *Docodon*, the quadrate-articular joint survived until the Upper Jurassic (Kühne 1958; Kermack & Mussett 1958*b*).

The known history of the pantotheres, including the symmetrodonts, extends back to forms in the Rhaetic which retain the quadrate-articular hinge (Kermack & Mussett 1958*a*). Thus, unless the Triconodonta arose from the Pantotheria some time in the Lower Jurassic, the two stocks must have lost independently the reptilian jaw joint. If the latter suggestion is true it accords with the general tendency towards parallelism throughout synapsid evolution. For example, we know now that squamosal-dentary articulation was independently acquired in a number of different lines (Kermack & Mussett 1959), and there is no reason why the quadrate and the articular could not similarly lose their function as part of the jaw hinge independently in more than one line.

When the quadrate and articular ceased to be part of the jaw mechanism they were then free to pass into the middle ear. Kühne (1956) considers that, in view of the complexity of the changes involved, the transformation of the quadrate and articular into the incus and malleus could have happened once only, in one line. From what we know of parallel evolution within the synapsids I can see no reason why this change should not have taken



place, quite independently more than once. For it to have occurred at all it must have had a selective advantage; and a number of lines within the mammals must have been exposed to the same selection pressures. In view of the very fragile nature of the parts involved this is not one of the problems likely to be quickly solved. In any event, whether Kühne is right or I am, one line at least must have evolved the mammalian middle ear by the Middle Jurassic.

The presence of the well marked internal mandibular groove in the Stonesfield Slate mammals would suggest that the splenial had still been retained in the lower jaw (Kühne 1956; Kermack & Mussett 1958*a*). Thus, although the articular had ceased to function as a part of the jaw mechanism, the lower jaw was probably still compound.

We next observe the evolving mammals in the Purbeck and in the Morrison, both these formations being of extreme Upper Jurassic age. Both the eupantotheres and the triconodonts retain the internal mandibular groove, and so, by implication, the splenial. The groove is also to be found in the contemporaneous symmetrodonts. In these symmetrodonts the quadrate and articular had ceased to play any part in the jaw suspension: whether the Symmetrodonta had lost the reptilian jaw suspension independently of the Eupantotheria is unknown but unlikely.

Alongside these three groups which had lost the quadrate-articular hinge but retained the splenial we find two others. In one, the Docodonta, the condition of the lower jaw shows no advance over that found in *Morganucodon*: articular and splenial were certainly retained, and probably the rest of the bones which make up the jaw in a typical reptile as well. In the other group, the Multituberculata, both reptilian hinge and internal mandibular groove are lost. Here for the first time we find a mandible consisting of a single bone, the dentary, as it does in modern mammals. This is the only respect in which the mammals of the Upper Jurassic show any advance over those of the Stonesfield Slate. Also in the Upper Jurassic we now know the structure of the braincase in one order—the Triconodonta. This shows little advance over that of the Rhaetic *Morganucodon*.

The next mammals to throw any light on the evolution of mammalian osteology, as opposed to teeth, come from the Albian (Middle Cretaceous) of Texas. Here jaw fragments show that the internal mandibular groove had disappeared in a symmetrodont and in a mammal which Patterson (1956) considers had reached the Eutherian level of evolution. The term Eutheria was originally coined by Gill (1872) to include both marsupials and placentals. This meaning of the term fulfills a real need, which cannot be said of the alternative use of the term Eutheria, equating it with Placentalia. I shall give Eutheria the meaning suggested by Gill.

In the Albian triconodont *Astroconodon*, the groove, if it exists at all, was vestigial (Patterson 1951). Thus the internal mandibular groove must have been lost independently in at least four mammalian groups: Multituberculata, Triconodonta, Symmetrodonta and Eutheria; and presumably the splenial similarly must have been lost independently at least four times. This is all the information we have about the osteology of Middle Cretaceous mammals.

The next mammalian faunas come from the top of the Cretaceous: from the Belly River, Edmonton, Hell Creek, Lance and Djadochta. Here the triconodonts and pantotheres have vanished and only the multituberculates and eutherians remain.



Thus the picture of mammalian evolution in the Mesozoic, as far as we may glimpse it, is of slow and steady evolution in a number of parallel lines. What we see in the mammals of the Jurassic and Cretaceous seems to be the same as we see in the mammal-like reptiles of the Permian and Triassic, or, for that matter, in the Tertiary mammals: a successive slow and steady evolution of one species from another, without any 'accelerated breakthrough' or speeding up of the evolutionary process at any point. The mammals did *not* evolve suddenly from the therapsid reptiles, and it is certainly not true that 'they (the Jurassic mammals) were already above the monotreme level of evolution', as Romer (1945) and other authors have supposed. In the Jurassic, mammals were nearer to the therapsids than to the recent mammals in their level of evolution. This is not surprising; it is surprising that an exclusive reliance upon dental characters led to the opposite view being held for so long.

The effect of the new information on cranial structure on our knowledge of the relationships of the various groups of Mesozoic mammals is almost entirely destructive. One example of this, which has been discussed already, is the collapse of the attempt made by D. M. Kermack *et al* (1956) to relate *Morganucodon* to the monotremes. Generally it would seem that the gap between the level of mammalian evolution reached at the end of the Jurassic and that reached at the end of the Cretaceous (when the Eutheria were becoming dominant) is too great to be bridged unless a good series of connecting forms are known. These we do not have: our knowledge of the mammals during most of the 70 million years or so which the Cretaceous period lasted is almost nil. Until we know at least as much about the mammals of this period as we do about those of the Jurassic, speculation as to the relationships of the latter with modern forms will remain largely futile.

One group of these early mammals does seem, however, to profit from a reconsideration in the light of what is now known about the braincase structure of Jurassic triconodontines. The multituberculates have the longest known range in time of any of the major mammalian groups, extending as they do from the Kimeridgian (Kühne 1961) to the Lower Eocene—a period of time exceeding the whole length of the Tertiary. Despite the long duration of their existence it is only at the close of their history that anything more than teeth and jaws becomes available for study. What little is known of the structure of the skull is based upon the Palaeocene genera *Ptilodus* and *Taeniolabis* (Simpson 1937).

I have examined this Palaeocene material myself. It is poorly preserved and I do not think it is possible to add to the information extracted from it by Simpson. However, in the light of our new knowledge of the triconodont braincase some differences in interpretation become possible.

Not unnaturally, Simpson interpreted the braincase of these Palaeocene multituberculates in terms of that of a modern mammal. Despite this, his reconstruction of the basicranium of *Ptilodus* (it is unknown in *Taeniolabis*) seems to me to resemble the basicranium of *Bienotherium* (as figured by Watson 1942) as much as it does that of any recent mammal. This would suggest the retention of an essentially therapsid braincase in *Ptilodus*, with a persistent cavum epiptericum. Support for this comes from consideration of the petrosal of this species (specimen preserved in the American Museum, no. 35490). This was described and figured by Simpson (1937). A medial view of this bone is shown in his figure 8(b), and shows some points of resemblance to the petrosal of *Trioracodon* or

*Morganucodon*. The groove, labelled by Simpson as 'sulcus of transverse sinus' could well lead to the opening of a canalis pro-oticus situated as in *Morganucodon* or *Trioracodon*. The internal auditory meatus seems to have been deeper in *Ptilodus* than in either of the other two genera, but the cochlea seems to have been as little curved in the multituberculate (Broom 1914; based on U.S.N.M. no. 6076) as in the other two. The really striking resemblance, however, between the petrosal of *Morganucodon* or *Trioracodon* and that of *Ptilodus* is in the relation of the mandibular nerve to the bone. Above that part of the bone which lodges the cochlea in *Ptilodus* extends a lamina perforated by a large foramen. This is divided into two by a thin bar of bone. Simpson considered that this double foramen was for the passage of the two branches, the masticatory nerve and the main inferior ramus, of the mandibular nerve. If he is correct there is a close resemblance between the lamina and the foramen within it in *Ptilodus* and the anterior lamina and foramen pseudo-vale of *Morganucodon* and *Trioracodon*. The resemblance between *Ptilodus* and *Morganucodon*, in this respect, is heightened by the incipient division of the foramen pseudo-vale into a larger anterior and a smaller posterior part in the latter. Finally, the foramen which Simpson considered doubtfully as the hiatus fallopi may correspond to the foramen for the passage of the seventh nerve noted in *Morganucodon*.

Too much must not be made of these resemblances, but it does seem that the braincase of the Palaeocene multituberculates can be interpreted, on the limited evidence so far published, as well in terms of that of a Jurassic mammal as in terms of a Eutherian. The publication of the better material which exists should solve this problem.

Finally, I should like to thank all who have assisted me in the course of this work. In particular I should like to thank the Trustees and Staff of the British Museum, Dr A. W. Crompton, Dr W. A. Clemens, Mrs Frances Mussett, Miss P. M. Lees and my wife. Professor D. M. S. Watson, F.R.S. kindly permitted me to examine and figure the specimen of *Diademodon* from his own collection.

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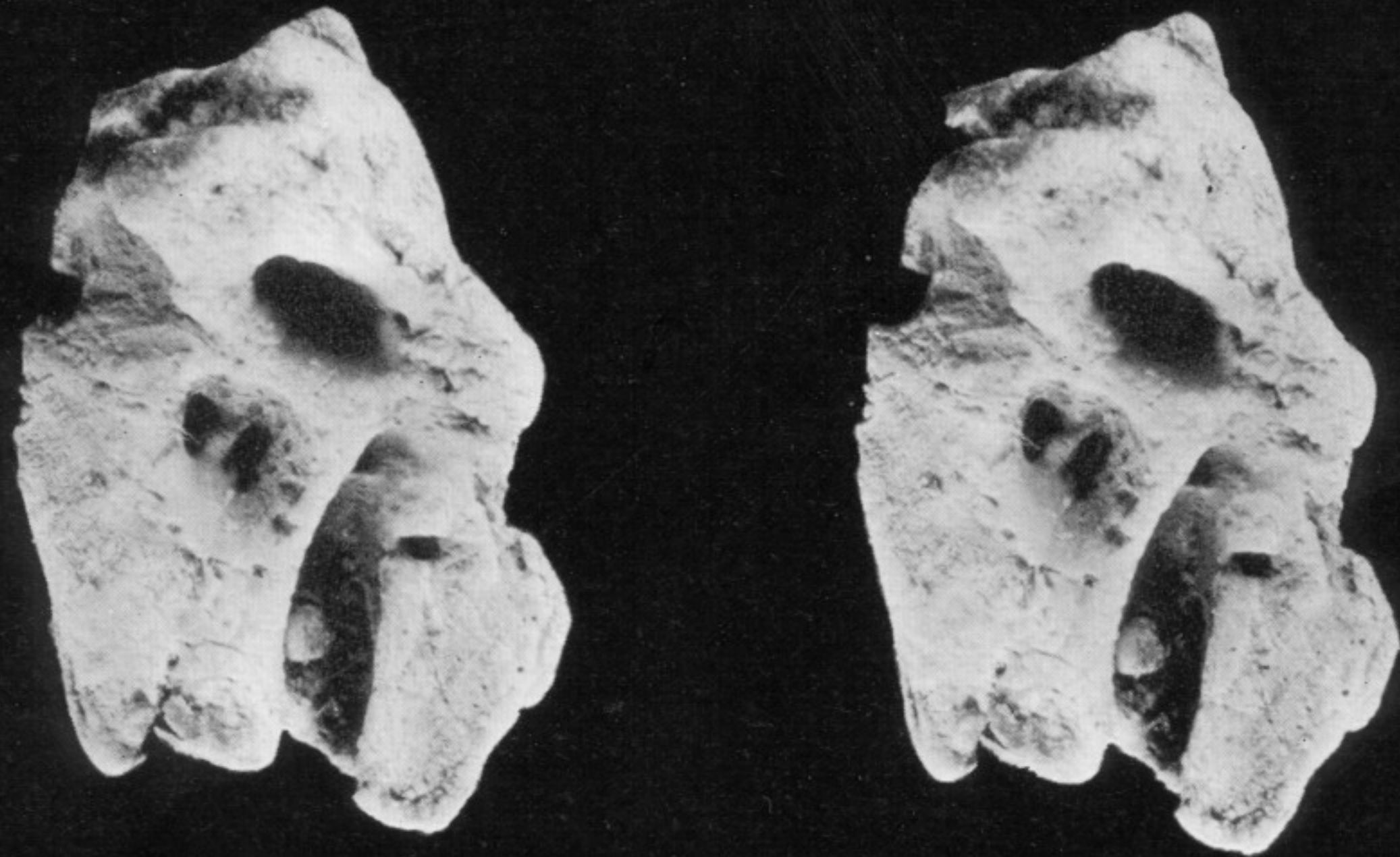


FIGURE 1 ( $\times 6$ )



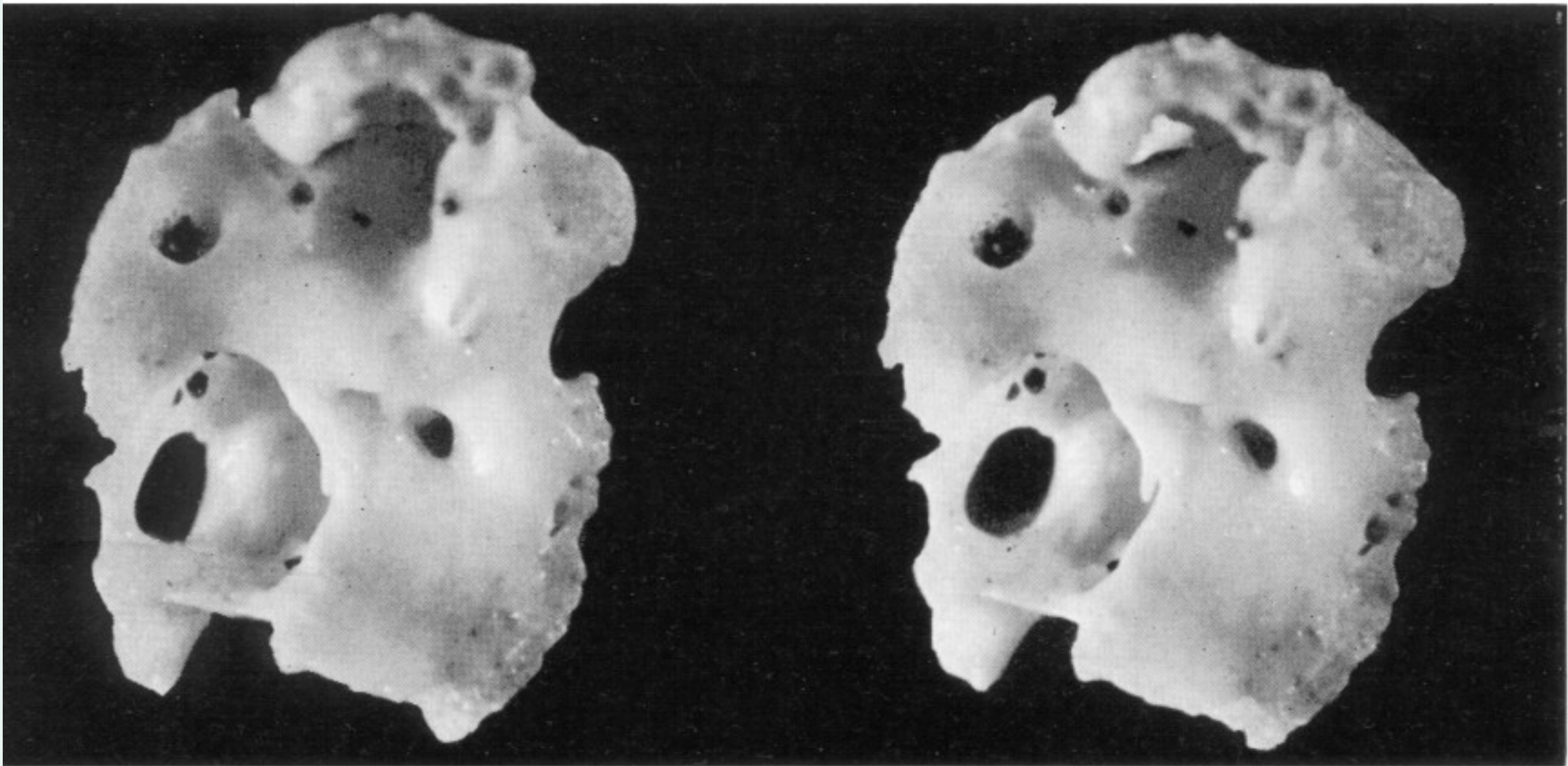


FIGURE 2 ( $\times 11$ )

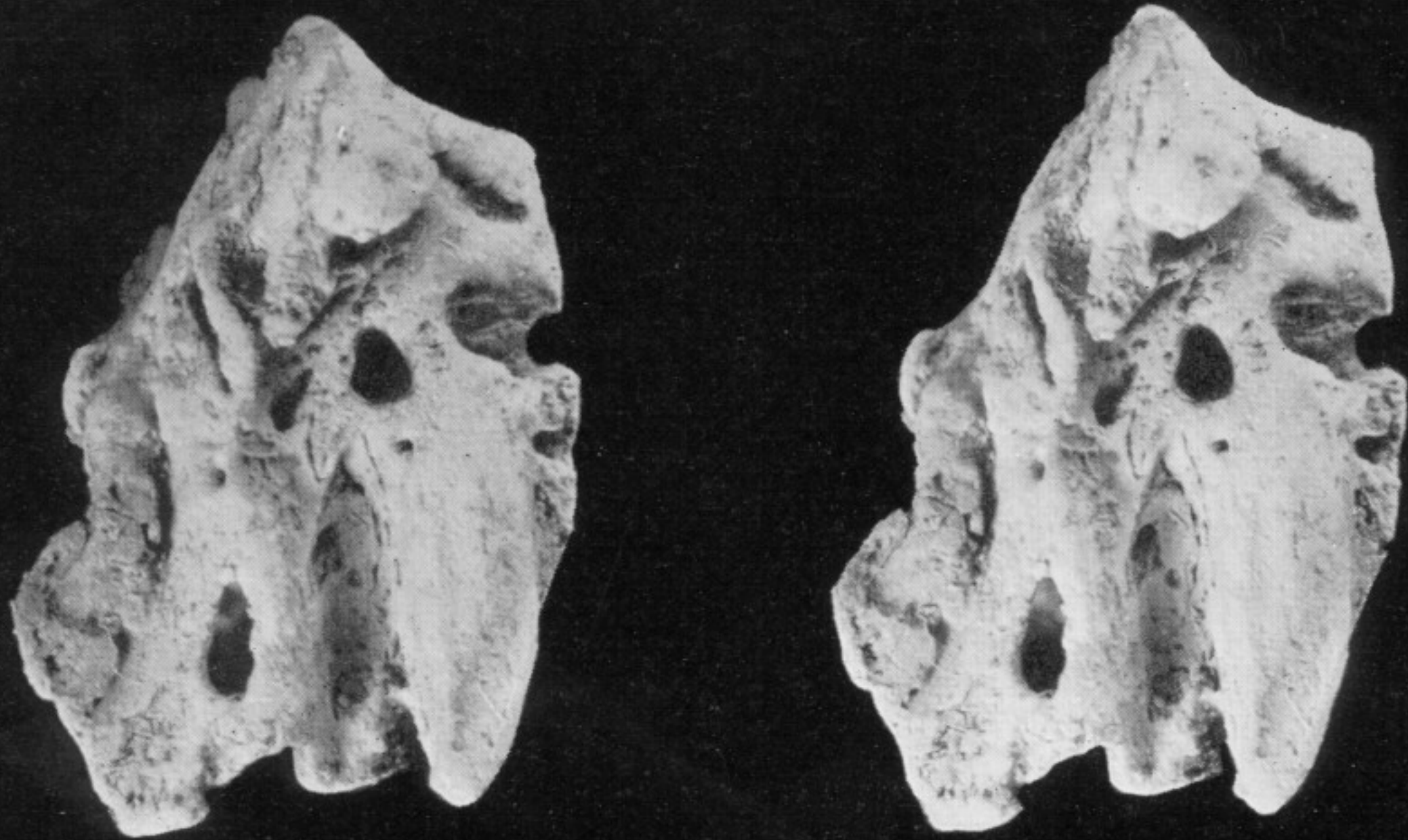


FIGURE 3 ( $\times 6$ )



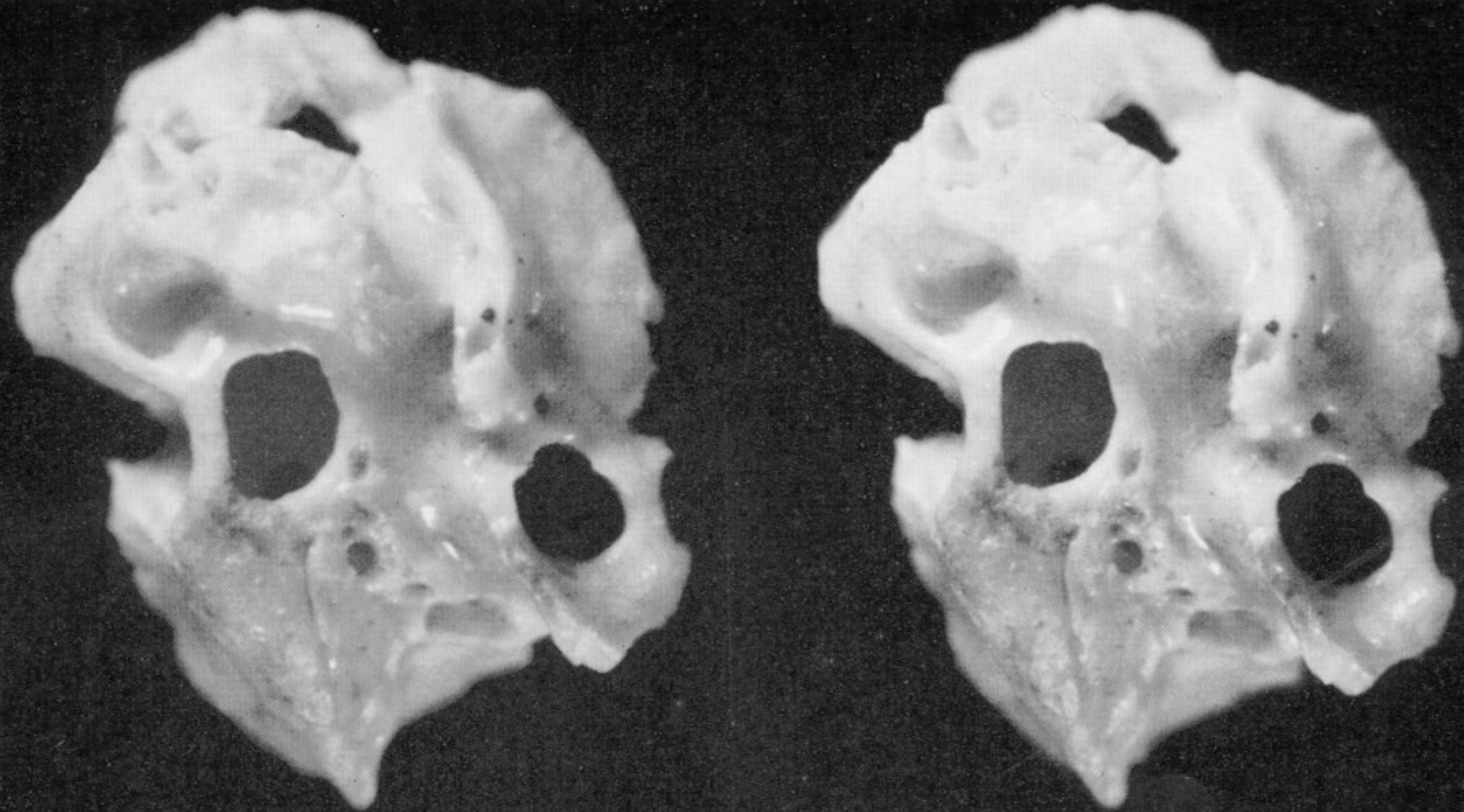


FIGURE 4 ( $\times 13$ )



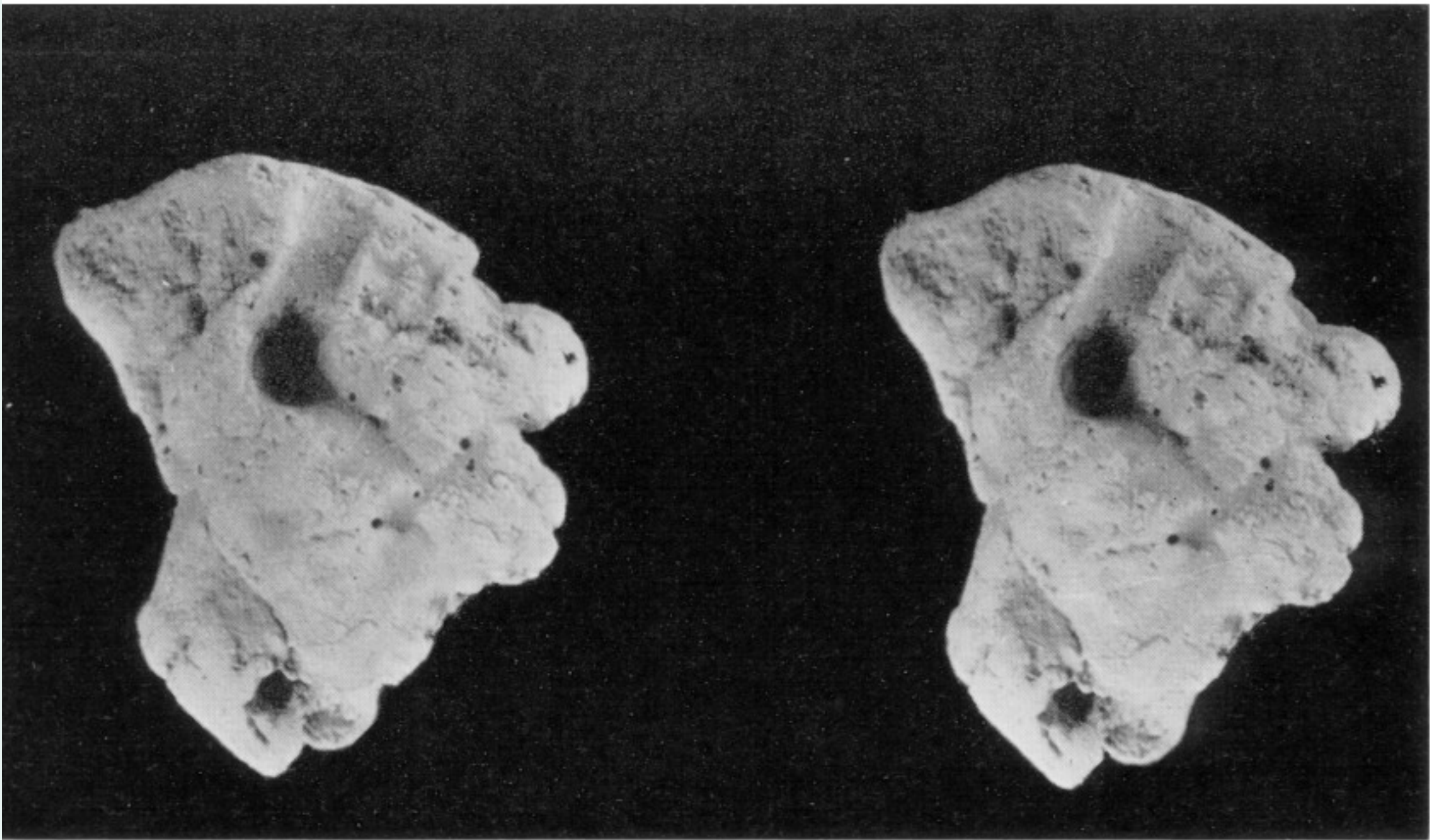


FIGURE 5 ( $\times 6$ )



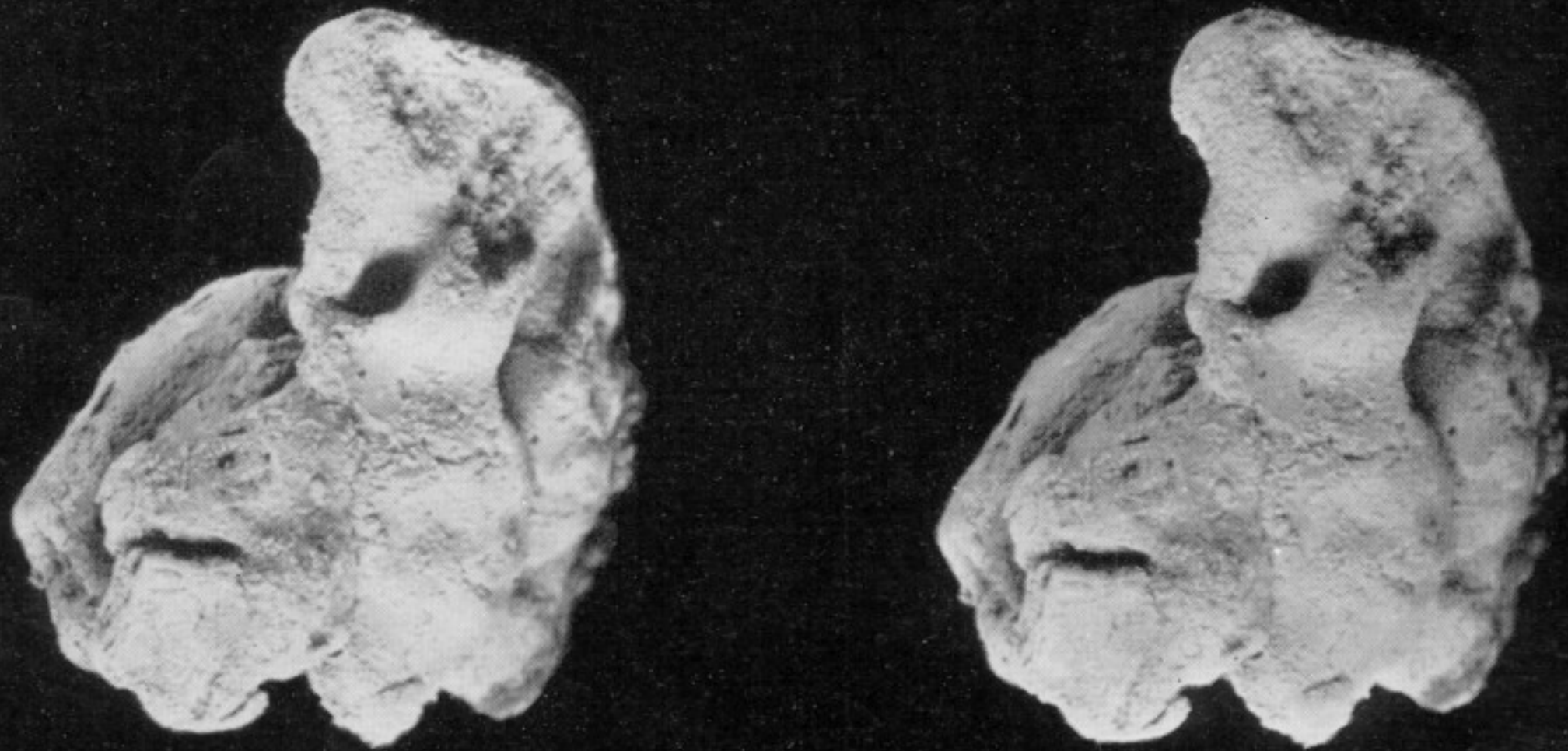


FIGURE 6 ( $\times 6$ )



FIGURE 7 ( $\times 7$ )





FIGURE 8 ( $\times 7$ )

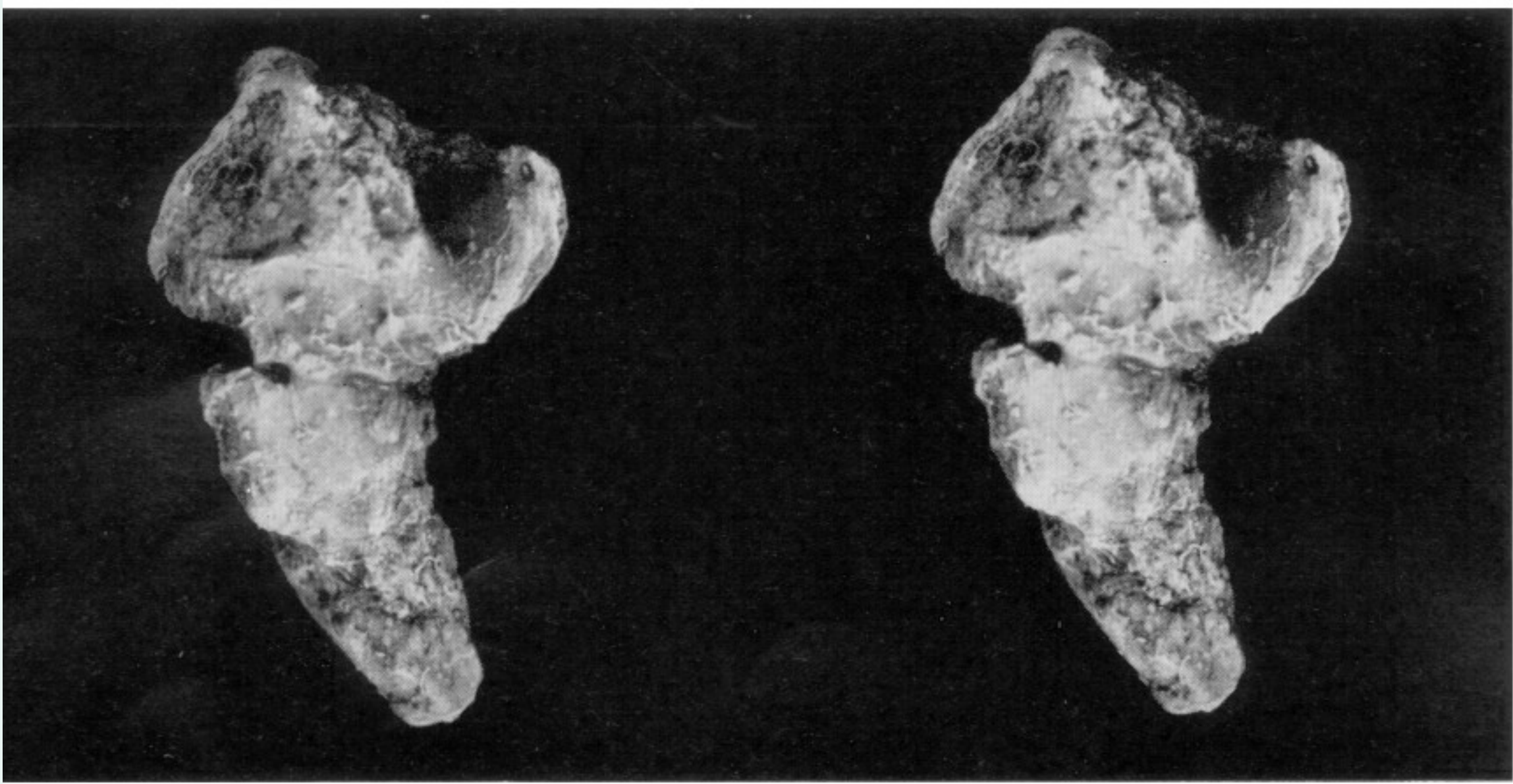


FIGURE 9 ( $\times 7$ )





FIGURE 10 ( $\times 7$ )

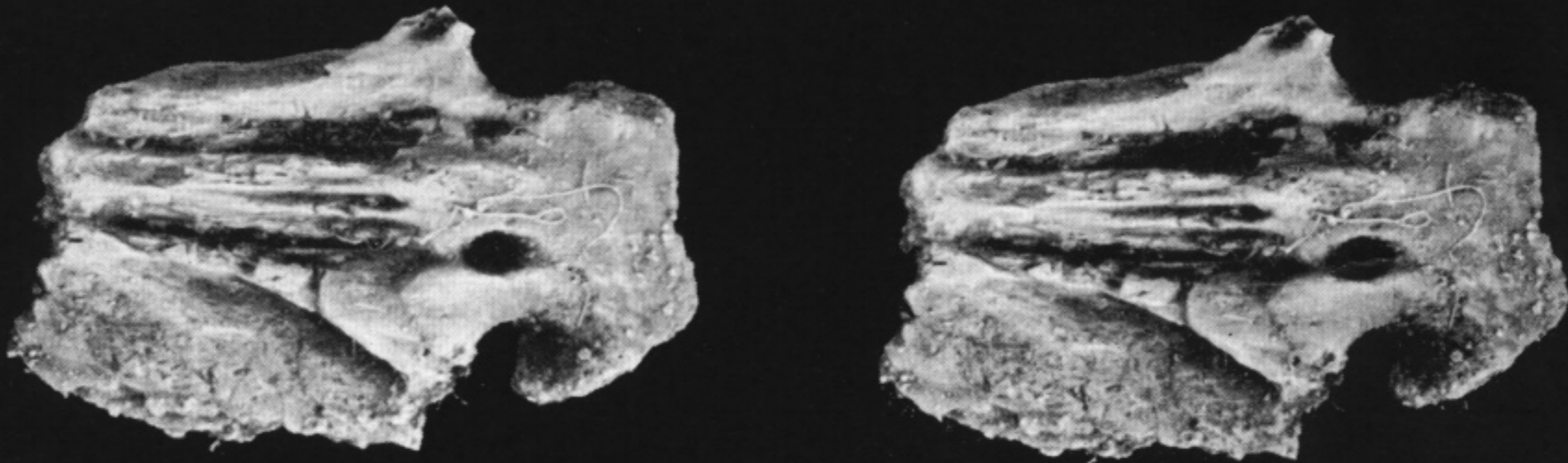


FIGURE 11 ( $\times 7$ )

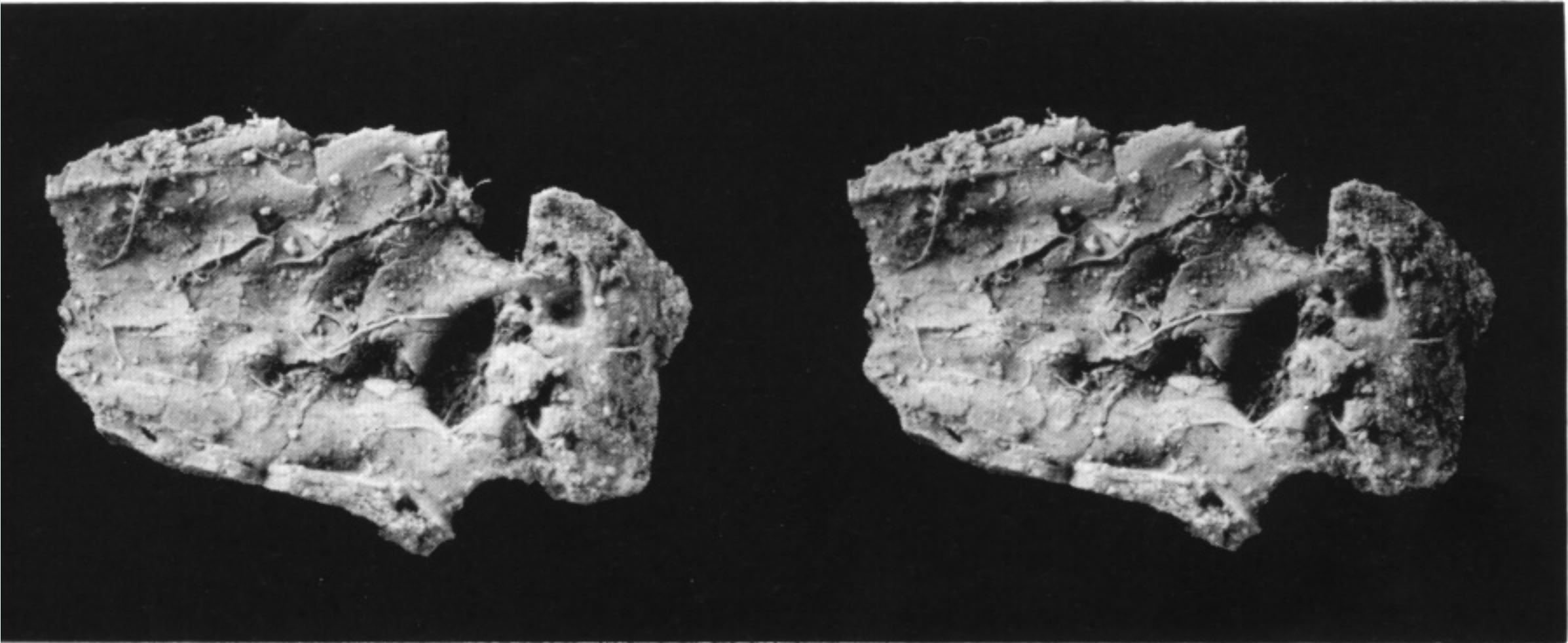


FIGURE 12 ( $\times 7$ )



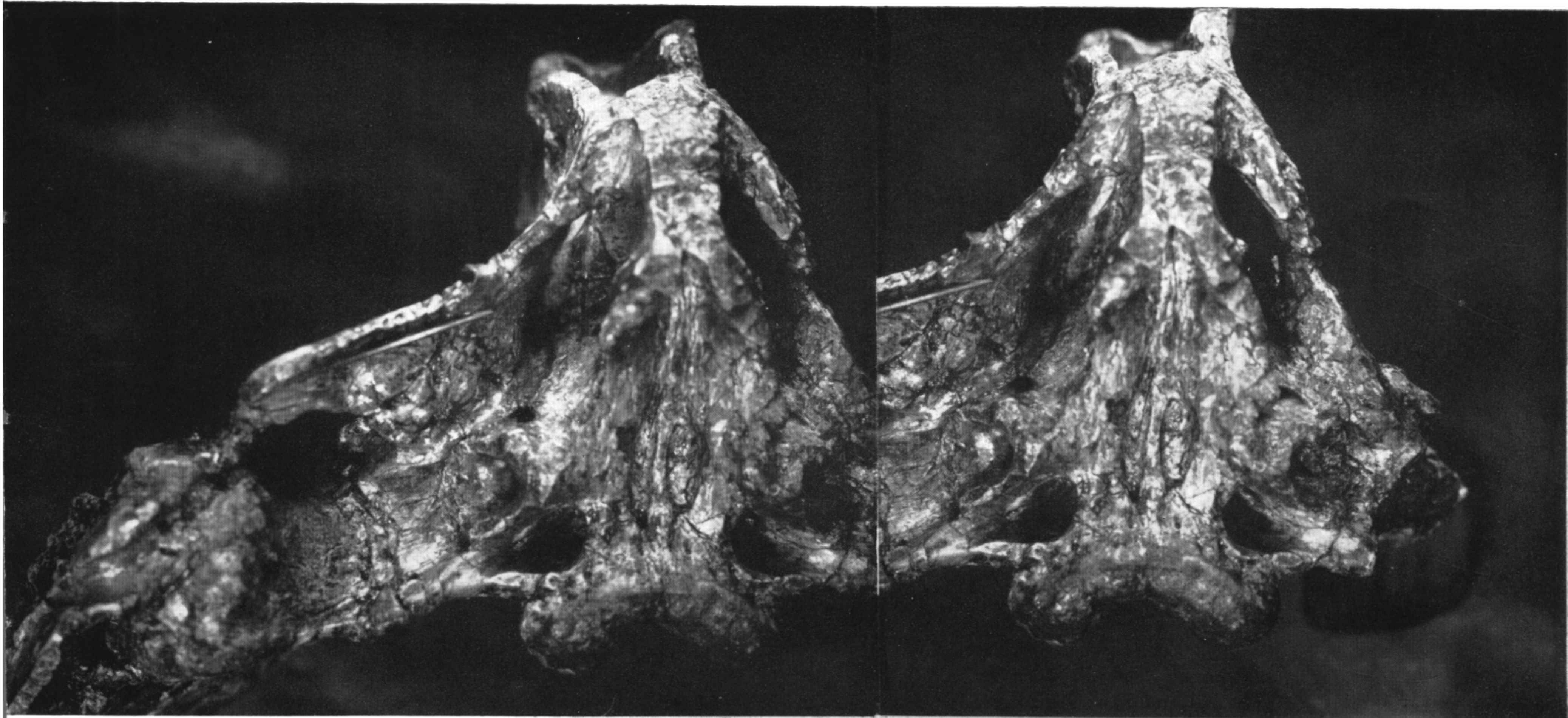


FIGURE 13

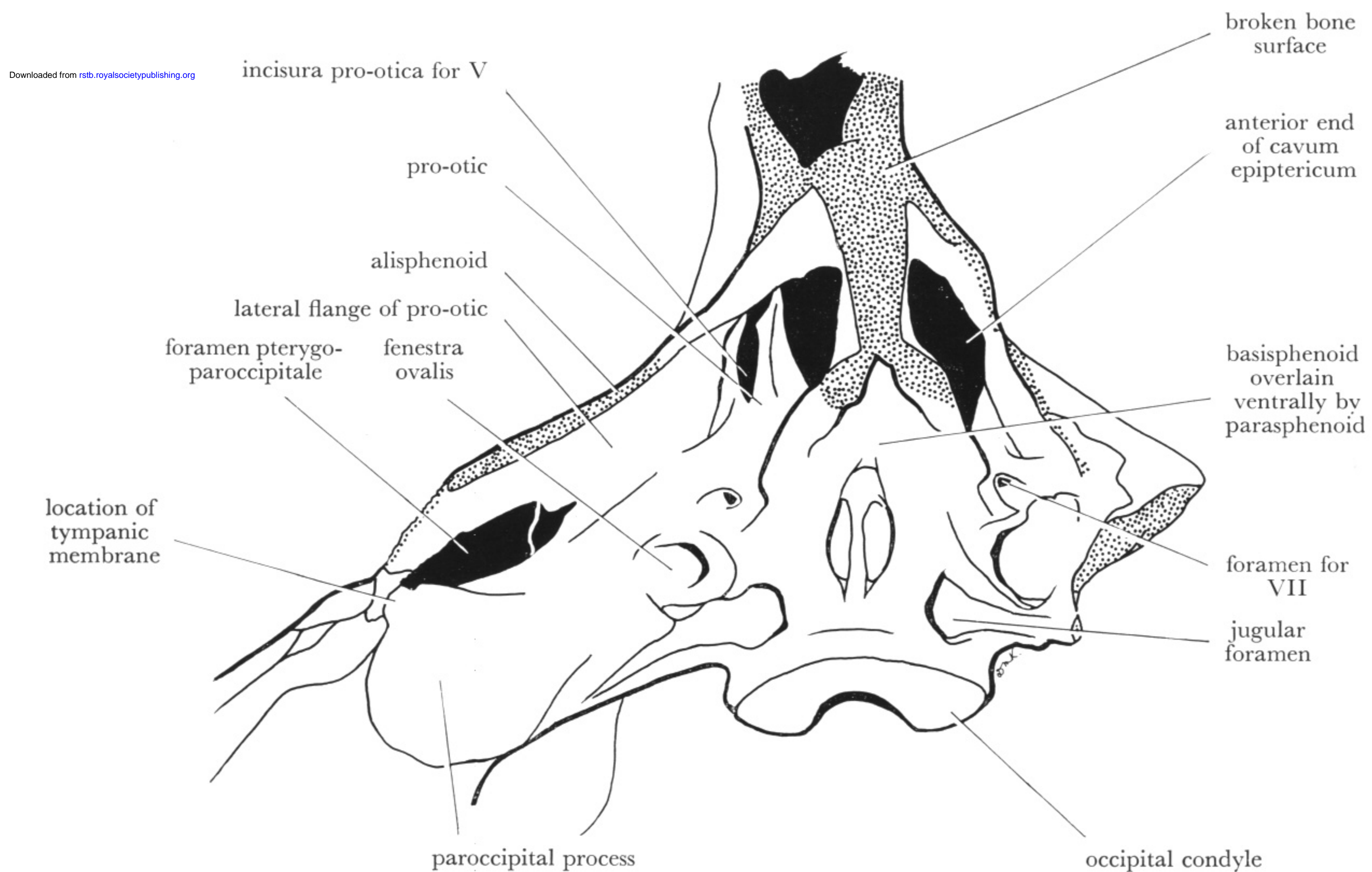


FIGURE 13. Ventral view of the braincase in a specimen of *Diademodon* (D.M.S.W. no. 131.).