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# On the Structure of the Skull in the Mammal-Like Reptiles of the Suborder Therocephalia

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# I—On the Structure of the Skull in the Mammal-like Reptiles of the Suborder Therocephalia

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## I—Introduction

The first-known mammal-like reptiles were discovered by Andrew Geddes Bain (1845) in the Karroo Beds of South Africa about a hundred years ago. The large majority of the species he discovered belong to the Anomodont group, of which *Dicynodon* is the best-known genus—characterized by having a tortoise-like beak with or without permanent-growing, large, upper canines. Carnivorous types are very much rarer than the vegetarian Anomodonts, and Bain was successful in getting only comparatively few specimens, and most of these in a very unsatisfactory condition. Most of his collecting was done in what we now regard as the middle zones of the Karroo, and the majority of his specimens belong to the suborders Gorgonopsia and Cynodontia.

Seeley in 1889 described an imperfect skull under the name *Hyorhynchus platyceps*; but as the teeth were lost and the skull much weathered, the affinities of the form were not very manifest. In 1894 SEELEY described the point of the snout of an allied form which was characterized by having six incisors in each premaxilla. He further greatly added to our knowledge by describing some good skulls of the later carnivorous mammal-like reptiles belonging to the suborder Cynodontia, and to the suborder we now call the Bauriamorpha; but until about thirty years ago very little was known of the earlier carnivorous types.

In 1902 I found in the collection of the South African Museum, Capetown, the anterior half of the skull of a "Theriodont" from the Lower Karroo Beds, in which the palate proved on development to be quite unlike that of the higher "Theriodonts" such as *Cynognathus* and *Gomphognathus* described by SEELEY, and to be essentially similar in type to that of the Rhynchocephalians. I therefore proposed to place the primitive "Theriodonts" in an order or suborder by themselves, the Therocephalia.

During the last thirty years a large number of Therocephalian genera and species have been described from the Lower Karroo Beds, which form the *Tapinocephalus* zone. Only very few small Therocephalians are known from the base to the top of the *Endothiodon* zone; but in the upper beds of the *Cistecephalus* zone a considerable number of fairly large Therocephalians has been found. In the *Lystrosaurus* zone numbers of small Therocephalians are found which connect the typical Therocephalians with the Bauriamorphus of the *Cynognathus* zone. Of these small forms, *Scaloposaurus* and *Ericiolacerta* are the best known. In my recent book (1932) on the "Mammal-Like Reptiles of South Africa", I have retained them among the Therocephalians; while WATSON (1931) has, in a recent paper, placed them among the Bauriamorphs. We certainly have a series of types such as *Ictidognathus*, *Icticephalus*, *Choerosaurus*, *Scaloposaurus*, *Ericiolacerta*—all small mammal-like reptiles where the earlier forms have a typical Therocephalian palate, and the later forms have added a secondary palate, and thus approach closely to the Bauriamorphs proper. It matters little at present where we draw the dividing line.

In the present paper I wish to deal mainly with the primitive Therocephalians, as these are amongst the least satisfactorily known of the mammal-like reptiles. It may seem strange to speak of the group as imperfectly known, considering that in my recent book I recognized 25 genera and 30 species, all known by skulls or snouts, and many by nearly perfect skulls. But though many skulls have been described we know little of the anatomy except the relations of the external bones. Something is known of the palate in half a dozen genera, and a little of the structure of the lower jaw, but little of the occiput or of the structure of the brain-case, and very little of the dental succession. Our ignorance of the earlier Therocephalian skull is largely due to the fact that nearly every skull from the *Tapinocephalus* zone is in a matrix so hard that satisfactory development is very difficult, and in many cases the bones are cracked so that the tracing of sutures is hardly possible.

The Therocephalians of the *Tapinocephalus* zone can conveniently be placed in two groups or families—those with two large functional upper canines, and those with only one. In mammals with a full dentition the canine may be defined as the first maxillary tooth; but in many of the Therocephalians this is not so. Very frequently the first maxillary tooth is quite small, and it is the second tooth that is the killing tooth. Occasionally there are two small maxillary teeth in front of the large supposed canine. One might be inclined to support the view that the first maxillary tooth, even if small, is the true canine, and that the supposed canine is a molar or premolar. But it is not improbable that the canine of the Cynodont and the mammal is the homologue of the third maxillary tooth of those early Therocephalians which have apparently three canines, and that the one or two small anterior maxillary teeth of the lower Therocephalians are completely lost in later forms.

There has been a similar difficulty with those Therocephalians in which there appear to be two large canines. When the first skulls were discovered with two large canines the question naturally arose as to whether they might not be skulls at a stage in development corresponding to a half-grown cat or dog where a deciduous and a permanent canine might both for a time be functional. The type-skull of the Cynodont *Trirachodon Kannemeyeri* has two functioning canines, one of the first and one of the second set. But too many skulls of early Therocephalians have been found with two large canines to admit of the possibility of their belonging to different sets.

To get some light on the dental succession, and to get to know fully the structures of the brain-case, I resolved to have a number of skulls or portions of skulls cut in sections. There was, of course, the difficulty that Therocephalian skulls are rare, and the large majority are types which one would hesitate to damage by having sliced. Fortunately, I had collected at various times quite a number of specimens which were not good enough to be regarded as museum specimens—either badly weathered, or having lost the snouts indeterminate, or specimens where the teeth had been lost and where there was a danger of some thoughtless person making a type of a skull without teeth. I have therefore, with the aid of a grant from the Royal Society, had a number of specimens which are of little museum value cut in slices, and have been able to study most details of the internal structure. Unfortunately, the majority of the specimens have had the outer bones much weathered, and in these it is difficult to trace the outer sutures.

Since the present investigation was started, Dr. L. D. Boonstra, of the South African Museum, Cape Town, has published two papers (1934, 1935) on Therocephalians and four on Gorgonopsians. The earlier Therocephalian paper deals mainly with specimens which I had collected, but concerning which, being steadily engaged in medical practice, I had no opportunity of doing more than giving preliminary descriptions, and which specimens I had disposed of to the British Museum. These specimens, and one or two others in the British Museum, Dr. Boonstra has developed much further, and he has revealed a number of details of the inner structure not previously known. The papers are illustrated by a number of good drawings by Mrs. Boonstra ; but the other drawings are apparently by Boonstra himself. Some of the latter are extremely diagrammatic, and others are so carelessly and inaccurately drawn that one is in doubt as to what reliance can be placed on any of them. For example, he gives a side-view of the skull of *Scylacosaurus sclateri* (B.M. R4055) in which he figures 8 molars, but in the palatal view of the same skull, apparently drawn by Mrs. Boonstra, there are only 7 molars, and in the letterpress Boonstra states that he believes there are only 7. In his side-view of the skull *Arctognathoides breviceps* (S.A.M. 9345) he figures 5 large incisors, but in his palatal view of the same skull he figures 4 extremely minute incisors. In the same figure he shows 6 very minute molars while in the letterpress he says "the molars are large".

Watson, in 1921, had published figures of part of the brain-case in the Gorgonopsians *Scymnognathus whaitsi* and *Leptotrachelus eupachygnathus* showing the anterior process from the proötic [the pleurosphenoid]. These figures of Watson's Boonstra has reproduced with little modification. Watson also showed a similar condition in the Therocephalian *Scymnosaurus watsoni*. Boonstra has shown a somewhat similar condition in the Therocephalians *Whaitsia major*, *Notosollasia laticeps*, and *Trochosaurus major*. But his figures are extremely diagrammatic, and appear to be inaccurate in many details. In one of his figures he shows the fifth nerve passing through what he believes to be the prootic.

Boonstra's later paper (1935) is on some Therocephalian skulls in the Broom collection in the American Museum. The paper deals mainly with questions of taxonomy.

## II—Transverse Sections of the Snout of *Trochosaurus dirus*, sp. nov.

The only specimen I have had cut which shows satisfactorily the front of the snout is the anterior part of the skull of a large Therocephalian which, after it was cut, was seen to belong to a new species. In each premaxilla there are 5 large pointed incisors, and there are two large functional canines. In the lower jaw there are 3 incisors, 1 canine, and 3 molars. The form is manifestly a near ally of *Trochosaurus major*, though very much larger. The type species has 4 upper molars, and possibly this new species may prove to have only 2. It is thus possible that it belongs to a new genus; but one hesitates to establish a new genus on a snout which does not show the upper molars, and little harm can be done by provisionally leaving the form in the genus *Trochosaurus*. The 5 upper incisors measure in length 57 mm, as compared with 45 mm in *Trochosaurus major*. The first canine has an antero-posterior length of 25 mm and a width of 10 mm. The 3 lower molars together measure 23 mm. The snout in the anterior canine region has a width of about 85 mm.

The specimen has been cut first horizontally near the bases of the incisor teeth, and then the upper portion has been cut into five pieces by four transverse cuts. The slabs vary in thickness from about 13·5 mm to about 18·5 mm; and each slice has removed about 2 mm of the specimen. We are thus able to study eight transverse sections of the snout, of which 1 and 2, 3 and 4, 5 and 6, 7 and 8 are each about 2 mm apart and each pair about 15 mm from the next pair. In the figures I give of the sections, sections 1, 3, 5, and 7 have been drawn reversed, so that each section is as it would appear if viewed from the front. And in addition to these, there is the basal section, and a second nearly complete basal section 2 mm higher up. This second differs so little from the other that it need not be considered.

*Basal section*—As will be seen from the figure given, fig 1, Plate 1, this section shows all the ten upper incisors cut across, the peculiar arrangement of the upper canines, and the anterior teeth of the lower jaws cut across. On the left side the 1st, 2nd, and 4th incisors are seen to be well-developed teeth with the pulp cavities completely or nearly filled with dentine; but the 5th incisor is evidently a younger tooth, as its pulp cavity is still fairly large, while the 3rd incisor is evidently quite a young tooth apparently just recently through the gum. On the right side the 1st, 2nd, and 3rd incisors are all old teeth, and the 5th has the pulp cavity nearly filled with dentine. The 4th incisor has been shed and a new tooth, of which the top only appears in the section, is taking its place. The canine condition is very remarkable. On the left side a large functional canine is seen cut across, with a fairly large pulp cavity. This is clearly the principal canine. On its inner side there is seen cut across part of a very young replacing canine. Behind these two canines are two others unfortunately badly preserved, and of these it is the inner one which is functional, the outer one being replaced. On the right side the specimen is very imperfect. There is a large functional anterior canine, and on its inner side is seen the tip of the replacing anterior canine. Nothing is seen of the posterior canines in the section, but the upper part of the specimen reveals much of a large young, but apparently functioning, canine which clearly corresponds to the inner of the two posterior canines seen on the left side. The nature of the dental succession will be further considered when the transverse sections have been studied.

Three lower incisors are seen on the left side, the 3rd being only the tip of the quite young tooth. There is only a single canine, which is very much smaller than the anterior upper canine. On the right side the 1st incisor is represented by only the tip of a young tooth, and the 3rd is not seen. Doubtless a 3rd incisor has just been shed, and the replacing one has not yet reached the level of the section. No molars are seen in the section, but three are well preserved on the base of the specimen.

Transverse section 1, fig. 2, Plate 1. This section in the middle line is about 19 mm behind the front of the snout. It is slightly oblique. On the left side the functional $i^2$ is seen cut obliquely across. On its inner side is seen a small part of the cavity in which the successional $i^1$ is developing. On the outer side of $i^2$ is part of the young $i^3$ seen in the horizontal section. On the right side the condition a little farther back is seen. The second incisor is seen cut higher up, and a little concavity on its inner side is due to absorption by the developing succeeding $i^2$. The developing successional $i^1$ is seen on the inner side of $i^2$ and outside $i^2$ is seen $i^3$ cut across. Above the premaxillaries on each side, portions of the anterior ends of the septomaxillaries are seen, though the ascending internasal processes of the premaxillaries are not preserved in the specimen. I have figured where they would be, had they been preserved. The bases are seen on the top of this first slab.

Transverse section 2, fig. 3, Plate 1. This section, which is about 2 mm behind section 1, shows for the most part the same teeth as seen in the other. As it seems probable that there are more than two sets of teeth, we cannot refer to the one as the deciduous set and to the other as the permanent, but it will be convenient to refer to the older set as A, and the other as set B. Near the middle line are seen the developing first incisors of set B. On the right side the root of $Ai^2$ is seen considerably absorbed by the developing $Bi^2$. Above each premaxillary a considerable part of the septomaxillary is seen in section.

Transverse section 3, fig. 4, Plate 1. This section is 13·5 mm behind section 2; and is very different in appearance. Immediately behind the anterior powerful part of the premaxillaries that support the roots of the front incisors the anterior part of the nasal cavity forms a deep depression whose floor is formed by palatal plates of the premaxillaries. Above these plates are seen near the middle line the anterior ends of the prevomers. Above the upper parts of the premaxillaries are seen sections of the septomaxillaries. The teeth seen on the left side are part of $Ai^4$, and a section of the developing $Bi^3$ with a portion of the root of $Ai^3$. On the right side near the upper part of the premaxilla is seen a section of the root of $Ai^3$ and on its inner side the developing $Bi^3$. In the lower and outer part of the premaxilla is a complete section of the developing $Bi^4$ with portions of the root of $Ai^4$.

Transverse section 4, fig. 5, Plate 1. This section is about 2 mm behind section 3. The teeth shown are practically the same as in the previous section. $Ai^3$, on the right side, is here only represented by the tip of the root.

Transverse section 5, fig. 6, Plate 1. This section is about 15 mm behind the previous one. Here we have only the posterior parts of the premaxillaries seen, but have the anterior part of one maxilla, and a section of each nasal and septomaxilla. The bones of the prevomers are considerably fractured, and it is impossible to say whether all these median bony fragments are part of the prevomers or in part premaxillary. From the condition seen in the next snout to be described, most probably the lower portions are parts of the premaxillaries. The outer fragment on the left side probably is. On the left side of the section is seen a section across the 5th upper incisor apparently of the A set. There is no evidence of any succeeding tooth. On the right side the section passes behind the 5th incisor. On each side is seen a section of one of the lower canines, showing the position of these teeth in natural occlusion.

Transverse section 6, fig. 7, Plate 1. This section is about 2 mm behind section 5, and it is essentially similar, but here on both sides the nasal meets the septomaxillary. On the left side the root of the 5th incisor is seen, but, as in the other section, there is no evidence of a succeeding tooth germ.

Transverse section 7, fig. 8, Plate 1. This section is from 17 to 19 mm behind section 6. Here the nasals are seen as large, thick bones. From the fact that the surface of the nasals is grooved somewhat like the surface of the horn core of an ungulate apparently by blood vessels one may infer that over the nasals there was in life a thick, horny plate or plates. In the closely allied *Lycosuchus* the nasals are united, and there was probably a considerable horny boss developed on the snout. The section passes through the posterior ends of the septomaxillaries. Below the outer sutures of the nasals are seen on either side small bony fragments. These are possibly, but not certainly, detached portions of the nasals. There has been a little crushing of the specimen, and parts of the maxillae are seen to be fractured. The prevomers are well developed. On the left side is seen a section of the large anterior canine. On the right side is a section of the canine with, on its inner side, a developing succeeding canine.

Transverse section 8, fig. 9, Plate 1. This section is 2 mm behind section 7. Here, inside of the canine on the left side, is seen part of the very young succeeding canine. On the right side the large outer canine is seen, with the young succeeding tooth alongside of it.

The sections of the snout of *Trochosaurus dirus* show clearly the general structure and relations of the premaxillary, maxillary, septomaxillary, and nasal bones, and in part the relations of the prevomers. We also have considerable light thrown on the dental succession.

There are five incisors, and certainly replacing teeth developing in connexion with the first four. The five incisors are probably not all of one set, for some are clearly older than others. Thus $i^3$ on the left side is a young tooth not fully developed, and it has replaced an earlier $i^3$, of which remains are seen. And on the right side a 4th incisor has recently been shed and a new tooth is developing in its place. It seems probable that there is a continuous succession of incisors.

The canine condition is of great interest. There are two large functional canines which are placed so close together that they probably function as one. This has long been known in a number of genera and species. We now know that each has a replacing tooth. In the specimen studied each anterior canine has a very young replacing tooth; but the posterior canine on the left side is being replaced by an already well-developed successor. On the right side the specimen is imperfect, but the inner canine is of large size and apparently functional. Probably the outer posterior canine is shed or being absorbed.

We have no evidence in the specimen of the upper molars. In the lower jaw there is clear evidence that there is a dental succession in the incisors. There is only a single canine in each mandible, and though there is no evidence of a dental succession, not improbably this canine is replaced from time to time. There are three lower molars, and the specimen shows no evidence of any succession in these.

## III—Transverse Sections of the Snout of a Moderate-Sized Therocephalian—Probably *Pristerognathus vanderbyli*, Broom

This snout has unfortunately the outer bones very badly weathered; but as it belongs to the group of Therocephalians which have only one large functional canine, and as it shows the greater part of the prevomers in perfect condition, it seems well worthy of being described. The slabs into which the specimen has been cut are from 5 to 7 mm in thickness, and the wheel has probably removed about 2 mm with each cut, so that each even-numbered section is about 5 to 7 mm behind the odd numbered in front, and 2 mm in front of the odd numbered behind it. Each even-numbered section has been figured in the reversed position to facilitate comparison with the odd numbered.

Section 1, fig. 10, Plate 1. This section is through the premaxillaries some distance behind the part of the bones which hold the front incisors, and across the anterior part of the nasal cavity. A part of the 4th upper incisor is seen in section. Portions of the septomaxilla are seen above the right premaxilla. In the nasal cavity the anterior end of the right prevomer is seen above the palatal plate of the premaxilla. Parts of the lower jaws are seen, with sections of what are apparently the 2nd and 3rd lower incisors.

Section 2, fig. 11, Plate 1. This section is very similar to the preceding one. Parts of both prevomers are here seen.

Section 3, fig. 12, Plate 1. This section still shows the palatal plates of the premaxillaries. Above them are broad plates of the prevomers. The nasals are somewhat crushed down, and the exact relations of the septomaxillary are not clearly shown. In the lower jaw the right canine is seen in section. There is no evidence of a replacing canine. It is interesting to note that the symphysis is rather loose, and even as far back as the canine region there is no evidence of the splenial.

Section 4, fig. 13, Plate 1. In this section the pair of large prevomers are seen curved for the support of a pair of large organs of Jacobson. Below the prevomers are a pair of rather stout palatine processes of the premaxillae. In the lower jaw we still have a section of the large canine, with no evidence of a replacing tooth.

Section 5, fig. 14, Plate 1. Here the prevomers are still large. The palatine processes of the premaxillae are cut near their posterior ends. Part of the right upper canine is seen in section. In the lower jaw part of the left canine is seen in section, and on the right side a molar tooth apparently molar 1. There is no evidence of a replacing tooth in connexion with either of these functional teeth. The anterior ends of the splenials are seen.

Section 6, fig. 15, Plate 1. This section much resembles the preceding one. The rather oblique right upper canine is partly seen, and there is still no evidence of a replacing canine. In the lower jaw we see on the left side part of the canine, with the root of what is probably the 1st molar. On the right side we see a molar tooth cut in section—probably the second. There is no evidence of any replacing teeth.

Sections 7 and 8, figs. 16 and 17, Plate 1. These sections much resemble section 6. The maxillae, each of which has part of the canine, are peculiarly shaped, approaching each other in the middle line, and having above them a wide expansion of the nasal cavity. In each section of the lower jaw molar teeth are seen in section, but there is not the faintest evidence of any replacing teeth.

Section 9, fig. 18, Plate 1. Here the prevomers are becoming narrower owing to the transverse ledge which supported Jacobson's organ disappearing. Each maxilla is largely occupied by the canine. In each mandible parts of three molars are seen in section. There is no evidence of any succeeding teeth.

Section 10, fig. 19, Plate 2. This section is very similar to section 9.

Section 11, fig. 20, Plate 2. Here are seen in the maxilla of the right side not only a section of the large canine but below it a section of a second tooth smaller than the large canine, but much larger than any of the molars. I regard it as the root of a small second canine once functional, but now represented by the root only which is not yet absorbed. Below this second canine root is part of one of the molars—probably the 1st molar, but possibly the 2nd. The ridge of the maxilla that passes inwards is well developed, and just possibly the inner part is part of the palatine. There is a suture or crack as indicated in the figure, but I incline to regard it as a crack. On the left side there is below the inner part of the maxilla what might readily be regarded as a small upper molar. This is really the tip of one of the lower molars. Small parts of the dentaries and splenials are seen in the sections of the lower jaws.

Section 12, fig. 21, Plate 2. This section is fairly similar to the last, but here we have, on the right side at least, certainly a section of the anterior end of the palatine. On the left side there is above the inner ridge of the maxilla a small bony element which is possibly a part of the left palatine. In the lower part of the left maxilla is to be seen the tip of what is possibly a developing molar. This is the only evidence we have in any of the sections of a developing tooth, and it is not conclusive. Probably the replacing molars if they occur are developed, as in the crocodile, below the functional teeth. On the right side the tip of the root of the 2nd canine is seen below the upper end of the 1st canine. In the lower part of the maxilla a portion of one of the molars is seen. Part of one of the lower molars is seen on the right side.

Section 13, fig. 22, Plate 2. This section is near the posterior end of the free portion of the prevomers. On each side is seen a section of the palatines closely sutured to the lower parts of the maxillae. On the left side are seen sections of the roots of the 1st and 2nd canines ; and on the right side is a section of a root of a molar.

Section 14, fig. 23, Plate 2. This section, which like all the others is a little oblique, is on the right side just behind the internal nares, and on the left side just in front of the posterior end of the nasal opening. On the right side the palatine is seen sutured to the lower part of the maxilla and passing inwards as a thick bone which lies above the prevomer. On the left side part of the palatine is seen above the prevomer, and part sutured to the maxilla. The prevomers are no longer narrow, vertical bones, but broad and thick.

Section 15, fig. 24, Plate 2. This section is only a short distance behind the preceding one. The prevomers are still large and broad, and they are completely roofed over by the palatines, which are developed to form a powerful palate. This is the last satisfactory section cut from the specimen.

## IV—Transverse Sections of the Skull of *Pristerognathus minor* (Haughton)

This skull was badly weathered and had lost the front of the snout, both jugal arches, the whole of the occiput, and the base of the brain case. It seemed likely, however, that sections would show the structure of the anterior two-thirds of the palate ; and this has proved to be the case.

The skull as preserved measured 195 mm in length, and probably measured when complete about 250 mm. By transverse cuts it was divided into 29 slabs. Each slice is about 3·5 mm in thickness, and each cut has removed 3 mm of the specimen. We thus have 57 sections which we can study. Unfortunately, the bones on the outside of the specimen are badly weathered, and very few of the outer sutures can be traced. The centre of the specimen is extremely hard, and the whole of the structure of the palate from near the front of the prevomers to near the posterior end of the pterygoids can be satisfactorily made out. As the base of the brain case is lost the posterior sections need not be considered, as transverse sections of the brain region are much more satisfactorily seen in the next specimens to be studied.

Of the sections of the snout it seems unnecessary to figure and describe more than about half, as many are very similar to the adjoining sections. As the snout is broken off a little in front of the upper canines the first section we have, fig. 25, Plate 2, shows no part of the premaxillaries. The prevomers have broad basal portions and slender, ascending plates. The section is through the lower canines.

Section 3, fig. 26, Plate 2, is a little better preserved than section 1. The basal portion of the prevomers probably here supported a small organ of Jacobson. On the left side the section passes through part of the upper canine. On the inner side of the left maxilla the tip of the palatine is seen. In the lower jaws a molar tooth is seen in section on each side.

The next section figured is section 10, fig. 27, Plate 2. This is probably in the region of the 2nd upper molar, and it is probably this tooth of which a part is seen in section on the left side. The prevomers have very slender ascending plates, partly crushed in the specimen, and rather more strongly developed lower portions. There are here no ledges which could have supported Jacobson's organs. On the left side part of the palatine is seen, but the bones are weathered and the sutures are indistinct. Lower molars are seen in section on each side.

Section 12, fig. 28, Plate 2, is fairly similar to section 10, but more of the palatines are seen. The prevomers are here still more flattened.

Section 13, fig. 29, Plate 2, shows the lower part of each prevomer broadening out as it nears the posterior part of the internal nares. Sections of the palatines are seen on each side, but the bones are somewhat broken. In each maxilla and in each dentary a molar tooth is seen in section, and there is no clear evidence of succeeding teeth in connexion with any of them. On the right side the base of one molar is seen in the dentary, and the upper part of the molar which is in front of it.

Section 14, fig. 30, Plate 2, is just behind the posterior end of the internal nasal opening on the left side, and just in front of it on the right. On the left side the palatine extends from the maxilla to the middle line, the inner part lying above the prevomer. On the right side the outer part of the palatine is seen in connexion with the maxilla, and the inner end above the prevomer. The prevomers have lost the upper thin plates, and the lower parts are relatively broad. The section is essentially similar to section 14 of the last specimen.

Section 15, fig. 31, Plate 2, is a short distance behind the internal nares. On each side sections of tooth bearing portions of the maxillae are seen, each with part of the root of a molar. The palatines and prevomers form a complete palate. The prevomers are here very wide, and they form the greater part of the roof of the mouth.

Section 16, fig. 32, Plate 2, is essentially similar to section 15. Though in both sections the palatines are not quite in contact with the maxillae on the right side this is evidently due to crushing.

Section 17, fig. 33, Plate 3. About the region of this section the palate begins to bend down rather abruptly. The prevomers are still fairly large and wide. The palatines appear more robust, but this is due to their being cut obliquely where they begin to bend down. The section is unfortunately rather badly preserved.

Section 18, fig. 34, Plate 3. Here the palatines are still more bent down. In this and the following three sections it is difficult to determine with certainty whether the slender ascending plates near the middle line belong to the palatines, the prevomers, or the pterygoids. In sections 15, 16, and 17 they seem to arise from the palatines. In the intermediate sections they appear to arise from the prevomers, but as in each section they are fractured it is impossible to be quite certain. Most probably the slender plates in this section, and in those following, are, as I have indicated in the figures, plates passing forward from the pterygoids above the prevomers.

Section 19, fig. 35, Plate 3, is better preserved than either of the two in front of it. We are here near the posterior end of the prevomers, which are seen as little plates on the palatal roof. The ascending median plates are probably pterygoid. One little detached plate on the left side is probably a sclerotic plate cut across. The palatines form most of the roof of the palate, and each has an ascending process which articulates with an inwardly passing process from the wall of the snout. It is, unfortunately, impossible to say with certainty what bone forms this lateral process, as most of the surface bones are completely weathered away, and no sutures can be made out. It seems most probable that it is a development from the anterior end of the jugal. The flat plates at the outer sides of the lower part of the section are the posterior portions of the maxillae.

Section 21, fig. 36, Plate 3, is through the extreme posterior end of the prevomers. Of the slender bones seen near the middle line, only two small parts appear to be prevomers. All the other slender elements are the anterior parts of the pterygoids. The palatines still form most of the palatal roof. The bony ridge seen passing in front of the outer left wall is probably part of the jugal. On the right side it is also probably jugal. Only sections of a more perfect skull will settle the matter.

Section 23, fig. 37, Plate 3. This section is fairly similar to the last one. The palatines here have no longer ascending plates. On the left side the palatine articulates with the maxilla. On the right side there appears to be a little element between the palatine and the maxilla. When the adjoining sections are examined, however, this is seen to be a portion of the palatine. From each outer wall an inwardly directed ridge is seen cut in section. These are probably formed by the jugals.

Section 25, fig. 38, Plate 3. Here, near the middle line, are seen the pterygoids with, on the left side, what is evidently a foramen. On the left side the palatine articulates with the maxilla as in previous sections. On the right side the palatine is in two parts owing to the section passing through the anterior part of the suborbital vacuity. On the outer wall is seen a bony mass which is evidently mainly lacrimal above and in part jugal below.

Section 27, fig. 39, Plate 3. Here we meet for the first time the transpalatines. On the right side are seen just outside the suborbital vacuity three little bony elements. The middle one of the three is the transpalatine. The other two are parts of the palatine. On the left side the transpalatine is a well-developed element. The section is near the posterior end of the palatines. They are here relatively small, and the pterygoids are becoming larger. On the left outer wall are seen the prefrontal, the lacrimal, and the jugal, but the preservation is unsatisfactory.

Section 29, fig. 40, Plate 3. This section is through the front of the orbits. Above we have parts of the prefrontals and the frontals preserved. In the palate we have the pterygoids forming the middle portion, and the transpalatines seen at the outer sides. The lower portions of the orbits are evidently formed by the lacrimals. Above the pterygoid on the right side is seen a triradiating slender element. This can be seen in the following five sections. It is clearly the displaced and inverted and rotated pre-sphenoid, and this is the first time it has been observed in a Therocephalian skull.

Before proceeding further it seems advisable to say something about this little bone. In the Anomodonts (*Dicynodon*, etc.) we have a well-developed cartilage bone which lies below the frontal and lodges the olfactory portion of the brain. It has sometimes been called the ethmoid; sometimes the sphenethmoid. It is clearly homologous with a large bone similarly situated in the Pareiasaurians, which again is undoubtedly homologous with the bone called sphenethmoid in the frog. In the platypus we have a bone similarly situated in front of the brain, and though this has been called the mesethmoid, I have shown that there is no mesethmoid in the lower mammals, and that this bone is undoubtedly the pre-sphenoid. As stated above, it is well developed in the Anomodonts. It is unknown in the Dinocephalians but probably occurs. It is rather feebly developed in the Gorgonopsians. Among the Cynodonts it is unknown except in *Thrinaxodon*, where it is imperfectly ossified. Most probably it will be found well ossified in some of the larger types. That it should occur as a well-ossified though feebly developed element in the Therocephalians is very interesting. In the skull of the *Lycedops scholtzi* described later in this paper, it is seen in position.

Section 31, fig. 41, Plate 3. In this section the pre-sphenoid has the lateral wings more fully developed. The lateral parts of the section have been omitted to avoid overcrowding the plate.

Section 33, fig. 42, Plate 3. This section shows the pterygoids becoming thicker as they near the place where teeth are borne. The pre-sphenoid has here lost the median supporting base. Between the tips is a slender bone which is probably a sclerotic plate. On the right side the transpalatine is seen greatly enlarged, and stretching down to the place where it supports the pterygoid.

Section 34, fig. 43, Plate 3. This section is very similar to the last but shows a tooth in each pterygoid.

Section 35, fig. 44, Plate 3. Here the pterygoids are widening out as they approach the pterygoid process.

Section 36, fig. 45, Plate 3. This is the last section which shows the pre-sphenoid. As these last four sections show only the lateral wings of the pre-sphenoid, we are probably justified in concluding that the little bone is not only displaced and inverted but that the front of the bone is turned to the back. On the left side the pterygoid obscures the transpalatine, but on the right side the transpalatine is still seen.

Sections 37, 38, and 39, figs. 46, 47, 48, Plate 3. These sections are through the pterygoid processes. Between the pterygoids in the middle line there is a hollow space partly filled by bony particles, but as this part is badly weathered it is impossible to say whether these bony fragments are parts of the pterygoids.

The sections behind Section 39 are all rather unsatisfactory in that the base of the skull is almost completely weathered away. Fortunately this region is much better preserved in the next series of sections to be considered. I figure three sections to show how closely the animals agree.

It will be observed that the posterior end of the transpalatine lies entirely in front of the outer process of the pterygoid. And this is the condition in every Therocephalian skull which I have examined where the bones are satisfactorily preserved. It is certainly the condition *Scylacosaurus*, *Trochosaurus*, *Lycedops*, *Hyenosaurus*, *Moschorhinus*, *Enchambersia*, *Ictidosuchoides*, *Hofmeyria*, and *Scaloposaurus*; and the pterygoid forms the back of the process in all known Gorgonopsians, Bauriamorphs, Dinocephalians, and Cynodonts. It is also the condition in lizards, *Sphenodon*, Pelycosaurs, and typical crocodiles. Boonstra (1935), in his recent paper on Therocephalians, while recognizing that it is the condition in *Scylacosaurus*, *Scymnosaurus*, *Trochosaurus*, *Ictidosuchoides*, and *Moschorhinus*, believes that in *Theriognathus*, *Notosollasia*, and *Whaitsia* the transpalatine (*ectopterygoid*) is so largely developed that it completely excludes the pterygoid from coming near to the mandible. If this observation is correct, it will mean that the higher Therocephalians are a little further removed from the early types than is generally believed.

I recently wrote to Dr. Swinton to look into the point, and he replied as follows :—"*Notosollasia* (R. 5699) is quite definitely and clearly as figured by Boonstra; I am of the opinion that *Theriognathus* (47065) is as he has it too. In *Whaitsia* it is a little different because the direction of the Ecpt-Pt suture, is as you have drawn it, but it seems to me to go to the posterior margin all right, and that the postero-lateral direction is due to the crushing the skull has suffered".

When a few years ago I carefully considered the relations of the two bones in both *Notosollasia* and *Whaitsia* I came to the conclusion that in the latter the pterygoid forms the back of the outer part of the process. In *Notosollasia* the evidence was less clear, but as the two forms are closely allied, I saw no reason for doubting that in this respect the two are likely to agree. Whatever be the case with *Notosollasia*, *Theriognathus*, and *Whaitsia*, quite certainly the pterygoid forms the back part of the process in all the other Therocephalians whose palates are satisfactorily known.

Section 41, fig. 49, Plate 3. Here we see the pterygoids united and giving on section an x-like appearance. On the upper part of each pterygoid is a small element which is the anterior end of the base of the epipterygoid. In the upper part of the section we see the frontals, post-frontals, and post-orbitals cut across.

Section 45, fig. 50, Plate 3. The upper part of this section is through the pineal foramen. The lower part shows the base of the epipterygoid a little distance in front of the ascending plate. It rests on the pterygoid and on part of the lateral wing of the vomer (parasphenoid).

Section 47, fig. 51, Plate 3. This section of the pterygoid complex is about 7 mm behind section 45 and immediately in front of the ascending plate. The arrangement of the bones is similar to that in the preceding section. It is not quite clear how far down on the side of the vomerine wing the pterygoid passes.

In sections 48, 49, and 50 we have the ascending plate of the epipterygoid. Owing to much weathering and imperfection these posterior sections are unsatisfactory.

## V—Transverse Sections of the Back Part of Skull of a Therocephalian—Probably *Trochosuchus acutus*, Broom

This specimen, which was cut into a series of slabs, is the imperfect and considerably weathered posterior third of a moderately large Therocephalian. As no part of the anterior two-thirds was preserved, the species cannot be determined with certainty. The specimen was picked up in the same locality and horizon as has yielded a specimen of *Trochosuchus acutus*, and there seems reason to believe that it belongs to this species. Certainly if not identical, it is a closely allied species.

As preserved, the specimen did not seem at all promising. One-half of the base of the skull was weathered away, with the whole of the squamosal region of the left side. Not thinking the specimen was likely to prove of much value, I had it cut into rather thick slabs, each of which is about 8 mm in thickness, and each cut has removed about $5\frac{1}{2}$ mm of the specimen. Fortunately, the sections showed that the interior of the specimen is in excellent preservation, and the sections are thus of great importance.

Section 1, fig. 52, Plate 4. The first section that seems worth figuring is immediately behind the orbit and along much of the post-orbital arch. The frontal bones are here rather narrow, and outside the frontal is seen the very large post-frontal which forms the greater part of the upper third of the post-orbital arch. Outside of the post-frontal and partly below it is seen the relatively small post-orbital. And clasped by the post-orbital on its outer side is the upper end of the jugal. In the lower part of the section, which unfortunately is imperfect, especially on the left side, are seen, in the middle line a section of the anterior part of the vomer (para-sphenoid), and on the right side a little bony complex of which the outer and lower part is pterygoid, and the upper part the anterior end of the basal portion of the epipterygoid, and internal to the epipterygoid is a small portion of the wing of the vomer (para-sphenoid).

Section 2, fig. 53, Plate 4. This section, which is about 8 mm behind section 1, is completely behind the orbit on the right side. Owing to all the sections having been cut a little obliquely, it would cut into the post-orbital arch on the left side were this completely preserved in the specimen. The section cuts through the suture between the frontals and the parietals. Most of the bones near the middle line are parts of the frontals. Outside the lower parts of the frontals are seen portions of each parietal. On the left side is a part of the post-frontal; and on the right side a part of the post-orbital and of the post-frontal. In the lower part of the section are seen two parts of the vomer (para-sphenoid), a large part of the base of the epipterygoid, and a considerable part of the pterygoid.

Section 3, fig. 54, Plate 4. This section, which is about $5\frac{1}{2}$ mm behind the last, is very similar to it. The main bones of the upper cranial wall are the parietals, only a few small parts of the frontals being seen. On the right side are small parts of the post-orbital and of the post-frontal. On the left side are seen a fair-sized part of the frontal, and parts of the post-frontal and post-orbital. In the lower part the vomer is seen as a median grooved portion, and with lateral wings which support the pterygoids and epipterygoids. The basal portion of the epipterygoid is well developed and rests on the pterygoid and vomer. The pterygoid is a slender curved bone which passes down on the outer side of the vomerine wing.

Section 4, fig. 55, Plate 4. This section is about 8 mm behind section 3. The upper part of the section is chiefly made up of the large parietals fused together. On each side are parts of the post-frontals and post-orbitals, and on the left side is a very small part of the left frontal still seen. Below, we have near the middle line two parts of the vomer (para-sphenoid); the part on the left side supporting the epipterygoid, though the suture is not clearly preserved. On the right side both the pterygoid and the epipterygoid are free from the vomer, but they are still articulated to each other. The upper part of the epipterygoid is fractured, but I have drawn it as it is seen in the specimen. Farther out on the right side is a section of the mandible near the articulation. The central element is the large articular. On its inner side is seen a section of the pre-articular, and on its outer side a section of a considerable portion of the sur-angular. Below is a small section of the angular.

Section 5, fig. 56, Plate 4. This section, about $5\frac{1}{2}$ mm behind section 4, is fairly similar to it. The upper part of the section is almost entirely composed of the parietals with, on the left side, small parts of the post-frontal and of the post-orbital. In the middle line, below, we have part of the vomer (para-sphenoid), and on the left side part of the base of the epipterygoid. On the right side is seen part of the ascending plate of the epipterygoid fractured near the middle. The lower part is seen articulating with the slender pterygoid. Between the upper part of the epipterygoid and the parietal is seen a small bony element, the greater part of which is seen in the next two sections. This element is, I believe, the pleuro-or latero-sphenoid. Outside the pterygoid is another section of the mandible. The main element is the articular. On its inner side it is clasped by the pre-articular; and on its outer side is seen a portion of the sur-angular.

Section 6, fig. 57, Plate 4. This section is about 8 mm behind section 5. The upper part of the section shows the two parietals with a large space between for the upper part of the pineal organ. Below the parietals there are seen passing out on each side portions of the ascending plates of the epipterygoids. On the left side the lower part of the epipterygoid is fractured, and there is a very distinct oval foramen in the upper part, possibly for a vein. On the right side there is a little part of the lower end of the epipterygoid seen in close association with the pterygoid. Between the epipterygoids are four portions of the pleuro-sphenoids. Inferiorly, in the middle line, we have a part of the basi-sphenoid. On the right side there is an elongated element lying between the basi-sphenoid and the articular. This is probably the slightly displaced stapes. The articular is broad and flat. Above it is a small portion of the quadrate.

Section 7, fig. 58, Plate 4. This section, which is about $5\frac{1}{2}$ mm behind section 6, is of great interest. The parietals are here narrow and anchylozed together. On their upper end is a small hollow, which is part of the pineal foramen. On the right side only a part of the upper end of the ascending plate of the epipterygoid is seen. On the left side there are three parts of the epipterygoid seen. Nearer the middle line are seen the main parts of the pleuro-sphenoids. The bones are very delicate and spongy. On the inner side of each bone is a foramen most probably for the sixth nerve. Each bone rests on the basi-sphenoid. Apparently these bones have formed the supports to a large hypophysis, and apparently they have, to a considerable extent, supported the brain above. On the right side of the basi-sphenoid is a small bony element which is apparently part of the prootic. A little farther out is a fragment of what is evidently the displaced stapes. Still farther out is the large quadrate. In close contact with it below is the flat posterior end of the articular. On the inner side of the quadrate is a section of the posterior end of the pterygoid.

Section 8, fig. 59, Plate 4. This section, which is 8 mm behind the last, is cut through the anterior part of the opisthotic. Below the parietal are two portions of the anterior upper ends of the supra-occipital. In the middle line, below, we have a section of the basi-occipital with, above it, portions of the two prootics. The large bony mass on the right side is probably all opisthotic, and the space between it and the basi-occipital and prootic is the anterior part of the labyrinth cavity; but the details of the outer wall cannot be satisfactorily made out. Above the outer part of the opisthotic is a small portion of the squamosal, and outside the squamosal a large part of the quadrate. Outside the quadrate is a minute bony flake which is apparently part of the quadratojugal.

Section 9, fig. 60, Plate 4. This section, which is only about $5\frac{1}{2}$ mm behind the last, is very similar to it, and most of the bony mass on the right side is apparently the opisthotic. But the upper inner part is probably prootic. Above its outer end is a section of the squamosal, and outside the squamosal a section of the upper end of the quadrate. A small bit of the squamosal is seen below the quadrate. Near the middle line is a part of the basi-occipital, and between it and the opisthotic is another section of the labyrinthine cavity. A portion of the prootic is seen on the left side.

Between this prootic of the left side and the basi-occipital the base of the skull is badly weathered and part lost.

Section 10, fig. 61, Plate 4. This section, about 8 mm behind the last, cuts the brain cavity in the region of the jugular foramen. In the upper part of the section we have the conjoined parietals here broadening out and resting on the well-developed supra-occipital. Farther down we have on the left side a part of the prootic, and on the right side a part of the lateral portion of the supra-occipital. Below the supra-occipital, we have the well-developed par-occipital process of the opisthotic. Articulating both with the supra-occipital and the opisthotic is a section of the squamosal. The space between the squamosal, the supra-occipital, and the opisthotic is the entrance to the lateral occipital foramen. In the lower part of the section is a part of the basi-occipital, and resting on it a very small part of the exoccipital. Between the occipital and the opisthotic is the foramen for the ninth, tenth, and eleventh nerves. The hollow on the inner side of the left is probably for the lodgement of a flocculus.

Section 11, fig. 62, Plate 4. This section is very similar to the last. In the upper part we have the interparietal appearing between the parietal and the supra-occipital. On the left side the supra-occipital still articulates with apparently the prootic. On the right side the supra-occipital meets the squamosal and the opisthotic; while the exoccipital articulates with the opisthotic. In the outer part of the section we see the squamosal supporting the par-occipital process.

Section 12, fig. 63, Plate 4. This section, 8 mm behind the last, is through the foramen magnum. Above we have the parietals still widening out and resting on a large interparietal. The interparietal completely overlaps the upper part of the supra-occipital, and this section shows part of the supra-occipital, in the interparietal. The lower part of the section is mainly formed by the supra-occipital. On the left side is seen a small part of the opisthotic, and on the right side a small part of the exoccipital. On the outer part of the right side is seen a section of the squamosal.

Section 13, fig. 64, Plate 4. This section is through the occiput quite behind the brain cavity. Above, we see the parietals supported by the median interparietal. Below this we see on each side sections of the lateral plates of the supra-occipital. On the right side we still have a section of the squamosal and a small part of the tabular. On the left side below the supra-occipital we have what appears to be a small portion of the exoccipital.

## VI—Horizontal Sections of the Posterior Part of the Skull of a Therocephalian—Probably *Lycedops scholtzi*, Broom

The specimen from which these sections were cut was a skull which had lost the front half of the snout, and with the remaining part of the snout badly weathered. As it seemed hardly worth while having the snout sectioned, I arranged to have the posterior part of the skull cut as this, though embedded in a very hard matrix, appeared to be well preserved. Owing to a misunderstanding, the specimen was cut horizontally instead of transversely, as I had wished. The mistake, however, has proved a very fortunate one, and has resulted in a clearer understanding of the structure of the posterior part of the skull than would have been possible by transverse sections. The horizontal sections are not only in the plane of the frontal and parietal but in the plane of the base of the skull.

Section 1, fig. 65, Plate 5. This section is through the top of the parietal intertemporal crest, and through the top of the post-orbital arch of the left side. It is interesting as showing that the interparietal does not appear on the top of the crest. The pineal foramen is seen to be well developed. The three bones of the post-orbital arch seen are the post-frontal, forming much of the orbital margin; the post-orbital behind it; and a small part of the jugal.

Section 2, fig. 66, Plate 5. The parietal is very similar to that in the previous section, and there is still no evidence of the interparietal. Parts of each frontal are seen in section. On the left side an oval vacuity is seen. This is due to the surface of the bone being concave. Almost the whole extent of the left post-frontal is seen in the section, and behind it is a large part of the post-orbital and a small part of the jugal. On the right side are seen two parts of the post-frontal and the narrow upper edge of the post-orbital.

Section 3, fig. 67, Plate 5. This section shows the upper edge of the interparietal lying behind the parietal except in the middle line. On the outer side of the left parietal at the posterior end is seen the upper and inner end of the squamosal. Much of the post-orbital arch of the left side is seen. The post-orbital is in three parts; the division between the inner two parts is doubtless due to a crack in crushing. A part of the upper end of the jugal is also seen. The post-frontal here still forms much of the orbital wall. Both frontals are well seen, and a vacuity seen in the right one owing to the concavity of its surface. The right post-orbital bar is seen mainly formed by the large post-frontal.

Section 4, fig. 68, Plate 5. In this section the parietal is larger than in the upper sections. In front of the pineal foramen the two parietals are much expended, and there is a marked suture between them, though behind the foramen they are completely fused. On the occipital end of the parietal is seen the large interparietal, and farther out, on the left side the tabular; but in this section the suture between the tabular and interparietal cannot be made out with certainty. On the front of the outer end of the occipital plate of the parietal is seen the inner plate of the squamosal. In front of the parietals are seen parts of the posterior ends of the frontals. Inner and outer portions of the left post-orbital arch are seen. The inner end is only a small part of the post-frontal; and the outer, parts of the post-orbital and jugal. On the right a large part of the post-frontal is seen, and a very small part of the post-orbital.

Section 5, fig. 69, Plate 5. This section is very similar to the previous one, but the pineal foramen is no longer surrounded by bone. On the left side a large part of the tabular is seen, and a smaller part of the squamosal. The interparietal is well shown.

Section 6, fig. 70, Plate 5. Here we are approaching the lower part of the parietal, though it is still of large size. Behind it in the middle line is the well-developed interparietal excavated from below, where it approaches the supra-occipital. On the left side the large tabular is seen connecting the squamosal with the parietal and interparietal. In front no part of the left post-orbital arch is seen; but on the right side we see a large part of the post-orbital and small portions of the post-frontal and jugal.

Section 7, fig. 71, Plate 5. This section is through the base of the parietal, of which considerable portions are still seen. Behind it the interparietal is seen narrower than in the earlier sections. On each side the tabulars are seen as large elements and articulating with the squamosals. In front of the interparietal on the left side is a section through the top of the supra-occipital. Parts of the jugal and post-orbital represent the right post-orbital arch.

Section 8, fig. 72, Plate 5. This section is almost entirely below the parietal, only a tiny portion of the bone being seen on the right side. The top of the supra-occipital is seen as a horseshoe-shaped bone. The small interparietal is closely articulated to it behind. On both sides large parts of the tabulars are seen. In front of the supra-occipital on the left side we have a section of the top of the epipterygoid. A small part of the right post-orbital arch is seen.

Section 9, fig. 73, Plate 5. This is essentially similar to the previous section. Here sections of each epipterygoid are seen.

Section 10, fig. 74, Plate 5. This section is interesting from being mainly through the suture between the interparietal and the supra-occipital. In the middle line a small part of the interparietal is still seen resting on the supra-occipital. On the left side we have the tabular being excavated below by the supra-occipital. On each side the squamosals are seen articulating with the tabulars.

Section 11, fig. 75, Plate 5. In this section the interparietal is no longer seen, and the tabulars are smaller than in earlier sections. On the left side much of the occiput is formed by the supra-occipital. The tabular is partly wedged in between the supra-occipital and the squamosal. In front of the supra-occipital the epipterygoids are seen in section.

Section 12, fig. 76, Plate 5. Here on the left side only the lower end of the tabular is seen resting on the squamosal. On the right side the tabular is fairly large, but has the supra-occipital seen through the middle portion as on the left side of the section 10. In front are the two epipterygoids. Between that of the left side and the supra-occipital is the top of the periotic mass which may be regarded as probably prootic.

Section 13, fig. 77, Plate 5. Here the whole of the middle part of the occiput is formed by the supra-occipital. On the left side the tabular is no longer seen, but on the right we still have a considerable part. In front of the supra-occipital on each side are seen the upper parts of what are probably prootics. A little further in front we have sections of the epipterygoids. Inside each epipterygoid is a little bony element which is continued down into the prootic. It is the rudimentary pleuro- or laterosphenoid.

Section 14, fig. 78, Plate 5. This section is very similar to the preceding one.

Section 15, fig. 79, Plate 5. Here on the occipital face are seen on the right side the squamosal, tabular, and supra-occipital; and on the left side are seen the supra-occipital, periotic mass, and squamosal. It is impossible to trace a suture between the prootic and opisthotic. In front of the prootic are two small elements, the right attached to the prootic. These are the bases of the pleuro-sphenoids. Sections of the epipterygoids also are seen.

Section 16, fig. 80, Plate 5. This section and the next six sections are shown in Plate 5 of larger size, owing to their great importance. I have indicated all the sutures that are manifest, but those between the prootic and opisthotic are not quite clear. In this section the tops of the exoccipitals are seen, with behind them still considerable portions of the supra-occipitals. On the right side the outer limits of the supra-occipital are uncertain. There is a clear suture as indicated between the supra-occipital and what is probably prootic, but articulating with the squamosal farther out is a small portion of what is probably also supra-occipital ; but no suture can be traced between this and the outer part of the prootic.

On both sides we have sections of the top of the cavity for the labyrinth. On the right side the walls of the cavity appear to be formed by the prootic in front and the opisthotic and supra-occipital behind.

In the anterior parts of the prootics are still seen the bases of the pleuro-sphenoids. A little farther back on the left side is seen a fairly large, round opening. This is evidently the cavity in which lay the saccus endolymphaticus. In the following section, fig. 81, the cavity is seen united with the general cavity for the labyrinth. Sections of the epipterygoids are seen near their bases.

Section 17, fig. 81, Plate 5, and fig. 88, Plate 6. This section is about 3 mm below section 16. Posteriorly are seen sections of the exoccipitals on the two sides of the foramen magnum. Behind each is seen what appears to be a portion of the supra-occipital, and behind and outside these lower portions of the supra-occipital are sections across the upper parts of the opisthotics. The outer of the two concavities on the left side about the middle of the prootic is that for the saccus endolymphaticus. Though the labyrinth cavity is widely open into the brain cavity, there are indications of an imperfect wall between the cavities, but the detailed structure could only be made out by having a continuous series of close sections by Sollas's method, which would mean the complete loss of the slabs for any other study. Two large sections of the bases of the epipterygoids are seen. And well in front is a section of the anterior process of the vomer (para-sphenoid).

Section 18, fig. 89, Plate 6. This horizontal section is through the lower part of the brain cavity, and the main part of the labyrinth, and about the middle of the foramen magnum. Posteriorily the two bones bounding the foramen magnum are the exoccipitals. In front of the exoccipital on the right side is the large opisthotic, and in front of this is the prootic. On the left side the opisthotic is apparently very much smaller, but there is some doubt as to the position of the suture between the prootic and the opisthotic. The dotted line on the figure indicates what is probably the division between the bones.

On each side are seen the irregular spaces for the labyrinths, but I am unable to make out much of the structure of the labyrinth from the few bony processes and hollows. Had the sections been more closely cut doubtless we should have been able to make a fair restoration of the inner ear. In front of the exoccipital on the left side and behind a process from the opisthotic is a large oval space. This is part of the jugular foramen for the ninth, tenth, and eleventh nerves.

The prootics approach each other in the middle line, and between them in front is a small part of the basi-sphenoid. In the front part of the section are seen portions of the vomer and of the pterygoids ; and laterally we have sections of the epipterygoids.

Section 19, fig. 90, Plate 6. This section is through the upper part of the floor of the brain-case. In the middle line we have sections of the basi-occipital and basi-sphenoid. On either side of these bones are seen the prootics, with behind the prootics the large opisthotics. The right side of the section agrees fairly closely with the left side of the preceding one. We have the cavity for the labyrinth in front, and the oval foramen for the ninth, tenth, and eleventh nerves. On the right side we have the foramen for the hypoglossal nerve passing through the exoccipital. In front we have a large section of the vomer, with in front of it sections of the pterygoids and outside of these sections of the epipterygoids.

Section 20, fig. 82, Plate 5, and fig. 91, Plate 6. This section is through the middle of the floor of the brain-case. The basi-occipital forms most of the floor. In front of it is seen the basi-sphenoid with the large vomer anchylozed to it. Though there is no suture between the bones, the two bones are very distinct as the vomer is dense bone and the basi-sphenoid spongy bone. Laterally we have the exoccipitals, the opisthotics, and the prootics. In front the vomer articulates with the pterygoids, and on the left side is still seen part of the epipterygoid. The whole section is very mammal-like.

Section 21, fig. 83, Plate 5, and fig. 92, Plate 6. This section is through the lower part of the floor of the brain-case. On the whole, the section agrees with the preceding one. The vomer is large, and is seen articulating laterally with the basi-occipital. A small part of the basi-sphenoid is seen near the hind part of the vomer. The cavity for the vestibule is still seen on each side.

Section 22, fig. 84, Plate 5, and fig. 93, Plate 6. This section is just below the floor of the brain case, and through the large columnar processes at the end of which are the fenestrae ovales. The vomer is seen in four sections. The anterior median one is through the vertical pharyngeal plate ; the two lateral portions are supporting plates against the fronts of the columnar processes ; and the tiny median portion is the posterior end of the vomer which lies against the basi-occipital near the condyle.

The fenestrae ovales are seen nearly surrounded by processes from the basi-occipital and opisthotics.

In fig. 84 we have sections across the back part of the mandible and through the quadrate. The mandibular section shows sections of the articular, pre-articular, and angular. The quadrate is in two portions, but this is doubtless due to a fracture.

Section 23, fig. 85, Plate 5. This section resembles the preceding one so closely that it is unnecessary to comment on it.

Section 24, fig. 86, Plate 5. In this section the only portions of the median elements are a section of the median plate of the vomer, and a tiny section of the pterygoid. The section is through the hinge of the jaw, and shows the articular, pre-articular, quadrate, and probably a portion of the small quadratojugal.

## VII—The Skull of *Lycedops scholtzi*, Broom

In the McGregor Museum, Kimberley, there is a skull of a Therocephalian from the *Tapinocephalus* zone, which I have just made the type of a new genus and species. Though the skull is very considerably weathered, and a portion of the snout in the canine region is missing, it shows satisfactorily a number of details of the Therocephalian structure which were less satisfactorily or not at all shown in the sections that have just been described.

In the transverse sections of the skull of *Pristerognathus minor*, the very feebly developed pre-sphenoid was figured in a considerable number of sections, but displaced from its natural position. In a natural fracture across the skull of *Lycedops* we have the pre-sphenoid in its undisturbed relations with the frontals, fig. 96, Plate 7. It is seen as a ring of bone, or rather as two arcs, which meet below. This section is doubtless through the anterior part of the bone where there is no basal support.

In the lower part of the section, which is slightly oblique, the right-hand side of the figure being very appreciably farther forward than the left, are seen sections through the wide transverse portions of the pterygoids. On the right the pterygoid articulates with the transpalatine, but in the section, the part where the two bones meet has been weathered off. The transpalatine is a deep, rather powerfully developed bone. Above, the transpalatine articulates with three small elements. The larger of these just outside the upper end of the bone is manifestly the jugal, and I think the two small bony structures round the top of the little median element are also parts of the jugal. The small median element is probably a posterior process of the palatine.

A very interesting section of the mandible is seen on the right side. The dentary is cut just a little in front of the angular process, with the upper part, which is the base of the coronoid process, powerfully developed, and the lower part rather feebly. Inside the dentary are seen five elements in section. The two near the lower part of the dentary are the anterior part of the sur-angular above, and a section near the anterior end of the angular below. The three bones lying one above the other more internal, are the coronoid above, the splenial below, and the pre-articular in the middle. On the left side of the section is seen a cut across the mandible considerably farther back. Here the dentary is seen above, with below it the sur-angular and the angular. Internal to the angular are sections of the pre-articular, coronoid, and the splenial.

Two other sections of the mandible are shown. In fig. 97 we have a section fairly similar to that seen on the left side of fig. 96, but cut in a slightly different plane.

Here we have still the same six elements. The coronoid is fairly large and the sur-angular small. In fig. 98 we have a section appreciably farther back. Here the sur-angular is powerfully developed and the angular much the largest bone of the section. The splenial is cut near its posterior end and appears as a very tiny element. The pre-articular is rather better developed than in the other sections shown, and the coronoid is cut near its posterior end.

Fig. 99 shows a somewhat oblique and irregular section through the base of the skull. Above, we have the parietals a short distance behind the pineal foramen. Below it are seen sections of the epipterygoids. In the lower part of the figure we have portions of the basi-occipital, the opisthotics, and the prootics cut across and on each side we have the vestibules in section. There is seen on each side an upward development from the prootic. This is the pleuro- or latero-sphenoid which will be more fully discussed later. There is clearly seen a foramen on one side. This is probably the foramen for the sixth nerve.

Fig. 100, Plate 7, shows a side view of the vomer (para-sphenoid) with its articulations with the pterygoid in front, the epipterygoid above, and the basi-occipital and basi-sphenoid behind. As in the sections figured, the small basi-sphenoid is a porous bone, but completely anchylozed with the denser bone of the vomer. The anterior rostral process of the vomer is not displayed in the section of which only the lower part is median. Most of the pterygoid and the lateral process of the vomer are considerably to the side.

In fig. 102, Plate 7, we have the occiput very satisfactorily shown. Above, in the middle line, we have the fairly large interparietal, and laterally to it we have the tabulars. Below the interparietal we have the large, wide supra-occipital. This forms the upper part of the foramen magnum, and extends laterally to the squamosals. Below the outer part of the tabular the occiput is deeply depressed. In the lower part of the depression and between the supra-occipital and the opisthotic is the moderately large oval opening through the occiput. The opisthotic is rather peculiarly developed. The outer end is very broad and curved. The posterior part has a large articulation with the squamosal. The anterior gives an articulation to the quadrate, and between the two parts of the outer end is a deep depression. The tabular and the squamosal both overlap the outer part of the supra-occipital. It is a little difficult to trace the exact sutures as the squamosal and tabular in this region are reduced to very thin flakes of bone. The exoccipital is moderately developed. It has a long articulation with the supra-occipital and the opisthotic as shown in the figure.

The relations of the squamosal, quadrate and quadratojugal are for the first time in a Therocephalian fully revealed in this skull. The squamosal is a somewhat fan-shaped structure. The sections already described reveal the relations of its inner part to the parietal and tabular. Here we see the structure of the lower part. A ridge runs down from the post-temporal margin of the occiput, and forms the outer wall of the lateral occipital depression. On the outer side of this ridge is a groove in which doubtless lay the external auditory canal, and this becomes more certain as we can see clearly how the tympanic membrane has been attached. Below the squamosal we have the quadrate which is rather curiously shaped. Its articular end is very broad and roller shaped. Its inner side is sharp and curved, and there can, I think, be no doubt that the tympanic membrane was attached to this curved edge of the quadrate. Above, we have the rounded edge of the lower border of the squamosal, and this edge with the curved edge of the quadrate, which is practically continuous with it, forms about three-quarters of a circle. Further, the stapes are preserved in position on both sides of the specimen. The head differs from that of all hitherto known Therapsid stapes in having, in addition to a large articulation with the quadrate, a well-marked process which doubtless gave articulation to a cartilaginous extrastapedial which most probably was attached to the tympanic membrane.

The quadratojugal is perfectly preserved on one side. Fig. 103, Plate 7, shows the posterior aspect of the bone. It has a wide articulation with the lower part of the quadrate, and an upper inner process meets the upper outer process of the quadrate, and between them we have a typical quadratojugal-quadrate foramen. Immediately outside the tympanic region of the squamosal are two descending short processes. Of these the outer one rests on the quadratojugal. A section across this region is shown in fig. 104, Plate 7. Here we see how the upper part of the quadratojugal lies between the quadrate and the squamosal, and how the upper part of the quadrate closely clasps parts of both bones. In this same figure is seen an oblique section of the articular end of the mandible.

Fig. 95 shows the side-view of the skull, with the outer side of the mandible in almost perfect preservation. The dentary forms about two-thirds of the jaw, and is remarkable for the rather thick, abruptly truncated coronoid process. The angular is very large and, as in most Therapsids, the bone consists of an inner main plate and a thin outer fan-like plate. This outer plate is peculiarly folded ; and very manifestly the outer plate has been for the protection of some organ that lay between the two plates. Some years ago I suggested that this may have been a submaxillary gland, and I still think this is the most likely explanation. The underside of the cavity is always freely open, while the top of the cavity is only partly open as if for blood vessels.

Above the angular is seen part of the rather stout, curved sur-angular, and behind it is seen part of the articular. But though the articular appears small from the outside, it is broad and has a large transversely hollow articulation for the quadrate.

Fig. 101, Plate 7, shows the probable appearance of the inner side of the jaw restored from sections of the allied *Pristerognathus minor*, and from the sections of the jaw of *Lycedops*, and from the parts seen in the specimen. The only points that remain in doubt are the exact shape of the coronoid, and how far forward it and the pre-articular extend. The most striking characteristic of the jaw is the great extension backwards of the splenial. In this the early Therocephalian differs markedly from the Gorgonopsian, but in the main agrees with the Cynodont, and to some extent with the Dinocephalian. The coronoid is essentially similar to that of the Cynodonts and Gorgonopsians.

The mandible in having a well-developed coronoid process is less primitive than that of the Dinocephalian, but it is essentially of the same type. The Anomodont is so specialized in the structure of the articular and the absence of canines that it is difficult to determine what characters are primitive and what are secondary specializations. Most likely the ancestral Anomodont had a coronoid process and also a coronoid bone, and if we one day find the jaw of a pro-Anomodont we shall probably find that it resembles the jaw of the Gorgonopsian rather closely. The Therocephalian jaw differs in the greater development of the back of the dentary, and the less development of the anterior parts of the angular.

The resemblances to the jaw of the Cynodont are very interesting, and suggest the possibility of the Cynodont perhaps having been evolved from a Therocephalian rather than from a Gorgonopsian, as we have hitherto suspected. The great posterior development of the splenial and the very short anterior development of the angular are characters common to the Therocephalians and the Cynodonts.

The pro-atlas, atlas, and much of the axis are preserved, though they have not been completely cleared of matrix. The pro-atlas is a small plate. The atlas is very similar to that in the Tapinocephalids, the Anomodonts, and the Gorgonopsians in that the two halves of the arch are quite free from each other, and only loosely attached to the basal portion presumably by ligament. In the Titanosuchids the two sides of the arch are fused, and they are closely attached to the basal portion. In the Cynodonts the halves of the arch are also united, but they are not closely articulated with the basal element.

The axis has the odontoid closely articulating with its centrum, but not at all anchylozed. A small intercentrum lies below the articulation of the odontoid with the centrum. There are probably small ribs on both atlas and axis.



## VIII.—The Skull of *Hofmeyria atavus*, Broom

This little skull, recently discovered by me near Biesjespoort in beds which are either at the top of the *Endothiodon* zone, or the base of the *Cistecephalus* zone, is of very great interest as no very good Therocephalian skulls have hitherto been found at any horizon from the base of the *Endothiodon* zone to about the middle of the *Cistecephalus* zone. A small Therocephalian *Ictidognathus parvidens*, Broom, is known from the base of the *Cistecephalus* zone, but is not sufficiently well preserved to reveal much of the structure, and another skull *Ictidosuchoides longiceps*, Broom, is known from beds that are also probably near the base of the *Cistecephalus* zone, but this lacks the mandible, and the premaxillae and nothing is known of the occiput.

From the base of the *Endothiodon* zone to the very top, only one fairly satisfactory Therocephalian skull is known, *Choerosaurus dejageri*, Haughton, and this is only known by its external characters, and those are not altogether satisfactorily preserved, and though the form is primitive, in a number of characters it is highly specialized. It may be related to the Scaloposaurids.

This newly discovered type resembles the early Therocephalians more than the later forms, but it is possibly a connecting link between the primitive types and the Upper *Cistecephalus* zone forms.

The skull is only about 3 inches in length, and fortunately is beautifully preserved, the only serious defect is that the right side of the occiput with the articular region is somewhat crushed forwards. Owing to the importance of the type, I have given various figures of the skull as preserved and restorations of the side, top, and occiput, with the distortion corrected. In perfect condition the skull probably measured in greatest length 78 mm and in greatest width 50 mm.

The premaxillary bones are small, and there are five incisors which measure 10 mm. The septomaxillary is very short, and the posterior process between the nasal and the maxilla shorter relatively than in any other known Therocephalian. The maxilla is relatively short but strongly built. It carries one small canine and five small, pointed molars. The nasal bones are short and broad, and fairly mammal-like. The pre-frontals are large, and each forms a well-marked tumescence in front of each orbit. The lacrimal is a little smaller than the pre-frontal, and there are, just within the orbit, two lacrimal foramina, as shown in fig. 114, Plate 8. The post-frontal bone is larger than the post-orbital, and each post-frontal forms a large part of the orbital margin, just meeting the pre-frontal and shutting out the frontal from the orbital margin. The post-orbital forms much of the post-orbital arch. The relations and shapes of these bones are shown in the figures.

The frontals are short and broad. Posteriorly they meet the parietals by a transverse serrated suture. The parietals are united and form a short, rather low parietal crest. There is a moderate-sized pineal foramen. Posteriorly, the parietals pass well outwards, forming much of the occipital crest, and in the middle region they form the upper part of the occiput, so that the interparietal does not appear on the upper surface of the skull.

The jugal is long and slender, and it forms much of the lower part of the post-orbital arch. The squamosal is moderately large. Its outer anterior part spreads over the jugal to form the back of the temporal arch. The inner part passes upwards and inwards, meeting and overlapping the parietal and forming a considerable part of the occipital crest. Posteriorly, the squamosal forms a considerable part of the occipital face. It articulates with the opisthotic, and just outside this articulation is the marked descending auditory groove. Above, the squamosal has a large articulation with the tabular, and apparently a small articulation with the outer part of the supra-occipital below the tabular. Inferiorly, the squamosal supports the quadrate and the quadratojugal, though, owing to crushing and the very small size of the bones, the details of structure cannot be so satisfactorily made out as in *Lycedops scholtzi*. But apparently the condition is very similar.

The interparietal is a small bone situated near the top of the occipital face, but entirely confined to this occipital surface. It lies between the parietal, the tabulars and the supra-occipital. It is almost three times as wide as deep. The tabular is a well-developed bone which forms the upper and outer portions of each side of the

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occiput. The supra-occipital is a very broad, shallow bone. Above, it articulates with the tabulars and the interparietal and below with the exoccipitals and the opisthotics. The exact relations of the outer end cannot be determined with certainty. Probably it meets the squamosal underneath the tabular, and forms a small part of the margin of the large occipito-temporal foramen. The opisthotic forms a peculiar paroccipital process. This, at its outer end, is curved upwards to give a long articulation to the squamosal. Above this process is the large foramen, and the opisthotic certainly forms the lower, inner, and greater part of the upper walls of the foramen.

On each side of the foramen magnum is a moderately large exoccipital, which sends out a large process along the posterior side of the opisthotic. Between the inner side of the opisthotic and the exoccipital is a fairly large jugular foramen. Below the opisthotic is seen on each side a slender stapes, which extends from the fenestra ovalis to the inner end of the quadrate. We have seen in *Lycedops scholtzi* that the outer end of the stapes, in addition to articulating with the quadrate, has an upper development of bone which may be the base of some extra-stapedial structure. Here, in *Hofmeyria*, we again see, but much more clearly, what are manifestly the remains of some extra-stapedial structures. On the right side we find passing upwards from the distal plate which articulates with the quadrate, a little bony process which is about half as long as the whole mediostapedial. Another little bony spur passes inwards from the upper process. Of course, as these extra-stapedial structures are not so thick as a horse-hair it is impossible to trace them out fully. On the left side the conditions are a little different. Here the upward process from the outer end of the mediostapedial is directed mainly outwards. It seems, there can be little doubt, that in the Therocephalians there is a rod-like bony mediostapedial passing from the fenestra ovalis to the inner process of the quadrate, while from the upper side of the distal plate a delicate bony structure passes towards the tympanic membrane. Whether the whole of the extra- or supra-stapedial structure is bony is unknown. Very probably it was in part cartilaginous, as in the fowl or lizard. But clearly the tympanic membrane has been attached to the lower inner part of the squamosal, and along much of the inner part of the quadrate; and while the stapes articulates at its outer end with part of the quadrate an extra- or supra-stapedial structure, in part bony but possibly also in part cartilaginous, most probably was attached to the tympanic membrane.

While this important new light on the structure of the middle ear in the Therapsids does not completely solve the problem of the evolution of the mammalian middle ear it does bring us nearer to a definite solution.

In 1912 (Broom, 1912, p. 424), when dealing with the auditory region in *Dicynodon*, I gave a number of diagrams of the possible steps in the evolution of the mammalian auditory ossicles. The new evidence seems to be quite in harmony with the views then expressed. The position in which I placed the tympanic membrane proves to be correct; and the only important modification required in these diagrams is that an extra or supra-stapedial lay between the tympanic membrane and the top of the stapes while the new auditory ossicles were evolving.

The palate of *Hofmeyria atavus* cannot be completely cleared, as the mandibles are in position and make the development of the anterior part impossible, while in the back part we have the hyoid apparatus preserved. It has been possible, however, to clear the middle portion, and the rest can be restored with some probability.

The transverse processes of the pterygoids are well developed, but the anterior processes are rather slender. There is a median vacuity between the two pterygoids, and a little in front of the vacuity is a median boss which has on either side a deep depression. Outside each depression is a short ridge which carries a few teeth.

There is a relatively small suborbital vacuity with, on its outer side, a short, broad transpalatine. The palatines are evidently of large size, but only the posterior halves can be seen.

The lower jaws are well preserved ; that of the left side almost perfectly, but only the outer structure can be seen. The dentary is short and much curved, and though at first sight there appears to be a large coronoid process, the process only rises a very short distance above the sur-angular.

The angular is essentially similar to that of *Whaitsia major*, but differs very considerably from that in *Lycedops* and the other early Therocephalians so far as known. Behind the ascending ramus of the dentary there is an opening between the angular and the sur-angular, and the anterior process of the angular which articulates with the dentary and the splenial is relatively slender. There is a narrow but rather stout process of the angular passing up to articulate with the sur-angular, and behind this is the upper opening into the cavity that lies between the outer and inner plates of the angular, and which I believe lodged a large salivary gland. The inner plate of the angular is continuous with the upper process, and is closely articulated to the sur-angular. The outer part forms a broad, fan-like, thin, corrugated bony plate. It has three depressions and four radiating ridges. Its lower border is very thin, and the greater part of the plate doubtless formed a protection for the gland.

The sur-angular is a well-developed curved bone which forms the upper part of the back third of the jaw. It articulates in front with the dentary, and doubtless also with the coronoid. Behind it passes down inside the angular and articulates with the articular.

The articular is a small, broad bone which forms a wide articulation with the quadrate.

On the back part of the palate is preserved much of the hyoid apparatus. As the hyoid apparatus has usually no articulation with the skull, or only a cartilaginous one, it is hardly to be wondered at that the palaeontologist knows little of fossil hyoids. Where perfect skeletons like those of a Pterodactyls or Ichthyosaurs are preserved, frequently the hyoids or some elements of the apparatus are seen, but in most fossil skeletons it is very exceptional to find any trace of the apparatus. I must have handled between 300 and 400 good Anomodont skulls, but I have never seen a hyoid in any of them, and so far as I know in only two specimens of Therapsids has any hyoid element hitherto been observed. I discovered remains of the apparatus in a British Museum specimen of *Thrinaxodon liorhinus*, and Parrington has discovered the hyoid in a specimen of *Galesaurus planiceps*. In each case it is represented by a pair of slightly curved rods.

In *Hofmeyria* the hyoid apparatus is present as a pair of curved rods with an imperfectly ossified structure connecting their anterior ends and a pair of very small rod-like elements behind the median cross-bar. I have figured the apparatus as it is seen, and given a restoration, figs. 112 and 122, Plate 8.

Opinions may differ as to the interpretation of these elements. When I first described the hyoid of *Thrinaxodon* in my book, " The Origin of the Human Skeleton " (1930), I was inclined to regard the two bony rods as homologous with the mammalian ceratohyal, and a comparison with the condition in the early marsupial *Trichosurus* seemed to render this probable. But I now think it more probable that the bony rods in *Hofmeyria*, *Thrinaxodon*, and *Galesaurus* are, as in the birds and chelonians, really the cerato-branchials or thyrohyals and represent the third visceral arch and not the second. The conclusion to which I came was partly due to the figures of the hyoids of marsupials and *Echidna* given by Flower (1870). In the hyoids of the kangaroo and wombat there figured, the ceratohyal is well developed and looks as if it might have been evolved from a much longer rod which had become reduced, while in *Echidna* the thyrohyal is represented as a short, bony element. Not feeling quite satisfied with my conclusion, I made preparations of the hyobranchial apparatus in both *Echidna* and *Ornithorhynchus*, and found that not only Flower's figure but also Göppert's figure of *Echidna* are by no means satisfactory. The figure given by Wiedersheim (1898) is much better, but not wholly right. The ossified part of the thyrohyal in *Echidna* gives a most misleading idea of the element, as it is continued far back as a cartilaginous rod, and it seems not improbable that this is the homologue of the bony rods in *Hofmeyria*, *Thrinaxodon*, and *Galesaurus*. The uniting bar is doubtless the basihyal, and the two small posterior elements are probably the representatives of the fourth visceral arches.

The hyobranchial apparatus in the typical mammal differs markedly from that in the typical Sauropsid. But if we assume that the early reptiles had an apparatus made up of a cartilaginous hyoid arch, a basihyal possibly ossified, a long rod-like ossified ceratobranchial, and a series of probably three other imperfect arches, we should have an ancestral type from which all the higher types might have arisen. In the higher reptiles and birds where the tongues have little more than backward and forward movements, the hyoid arch became reduced. In the mammals where the tongue became an organ largely for assisting in mastication, the hyoid became highly developed and specialized, and the posterior elements became reduced.

Though not a part of the skull, reference may be made to the upper two cervical vertebrae which are seen in the specimen. The proatlas is well-developed as a broad, short, curved plate. Behind it on the left side is seen the half-arch of the atlas, and on the right side it is even better preserved. This atlantal arch is essentially similar to that of the Anomodonts. On the right side of the specimen there is a delicate bony rod below the transverse process of the atlas. This, I believe, to be the atlantal rib. It passes round, and the lower end approaches close to the posterior end of the ceratobranchial, and it might readily be regarded as an additional bony element of the third visceral arch. But it seems to me more probable that it is the slightly displaced atlantal rib.

## IX—The Skull of *Hyenosaurus platyceps*, Broom

The type and only known specimen of this interesting Therocephalian is in the collection of the Transvaal Museum. The specimen has been in the Museum for many years, but there is no record of whence it came. Dr. v. Hoepen examined the specimen, and had it to a great extent cleared of matrix, but as the specimen consists of only the back half of the skull, much of the palate, with the two jaws, and with the root of only one tooth, he evidently did not care to describe it or give it a name. Fortunately, the specimen, though so imperfect, is really very important, and reveals quite a lot of interesting points in the Therocephalian skull.

The skull is that of one of the later Therocephalians, and probably belongs to the Whaitsidae. Its nearest ally seems to be *Notosollasia*. I think we can safely assume that it came from Middle or Upper *Cistecephalus* beds. When complete, the skull must have measured about 270 mm in length, and the width across the squamosals is 216 mm. The posterior third of the skull is beautifully preserved, except for the upper temporal, and part of the basi-occipital regions, and each jaw is nearly perfect, except for the front of the symphyseal region which is missing in both.

The skull is characterized by the great size and width of the temporal fossae, by a low, very broad occiput, and by the powerful dentaries which are devoid of molars, while the angular part of the jaw is strongly developed but relatively short.

The occiput, as will be seen from the figures given, is exceptionally broad as compared with the height, and it differs in a number of respects from those of *Lycedops* and *Hofmeyria*, and also in many ways from that of *Whaitsia*. The upper part of the middle region is formed by the parietals, which form considerably more than a third of the crest of the occiput proper. The interparietal is relatively small and situated about midway between the crest and the foramen magnum. The tabulars are very large, and together form about half of the whole occipital surface proper. Each articulates on the inner side with the parietal, the interparietal, and the supra-occipital. Externally and inferiorly each articulates with the large squamosal and the supra-occipital, but in no place does it articulate with the opisthotic, or even approach it. Boonstra figures the occiputs of *Whaitsia* and *Notosollasia* with the tabular, giving a large articulation to the opisthotic outside and below the occipito-temporal opening. This is incorrect, the outer part of what he regards as the tabular is really part of the squamosal. The tabular does not appear on the anterior side of the occipital plate.

The supra-occipital is relatively small but fairly wide. It meets the squamosal above the occipital opening. The exoccipital is partly preserved on the right side. It agrees with the exoccipitals in other Therocephalians.

The squamosal is a very large bone, and it is almost perfectly preserved on the left side, and nearly complete on the right side. As in apparently all Therocephalians, it forms part of the true occipital surface, and here as in other higher types it forms a large part. The squamosal might be described as a large bone whose central part is moulded round the front of the paroccipital process of the opisthotic. When viewed from the front the squamosal entirely hides the outer part of the opisthotic. Its anterior inner side forms a long articulation with the parietal, and its inner lower corner articulates with part of the opisthotic, and a process passes inwards and forwards to articulate with the prootic and the pterygoid. Anteriorly, the squamosal forms much of the temporal arch and rests on the posterior process of the jugal. Inferiorly, the squamosal articulates with the quadrate and the quadratojugal ; and a posterior ridge caps the outer end of the opisthotic. On the outer side of this ridge is a marked groove, which leads down towards the inner end of the quadrate, and as in *Lycedops* doubtless ended at a tympanic membrane that was attached to the lower edge of the squamosal and the quadrate.

The quadrate is fairly large. In the specimen it may have been displaced a little inwards. The quadratojugal is a small triangular bone which has been apparently more firmly attached to the squamosal than to the quadrate, as with the apparent lateral displacement of the quadrate the quadratojugal has retained its squamosal articulation. The quadrate has a long, irregularly cylindrical, articular surface, 40 mm in length. There is a well-developed ascending process 13 mm from the inner end of the quadrate. This inner end doubtless gave articulation to the outer end of the stapes as in other Therocephalians, but the stapes has been lost from this specimen. If the quadrate be shifted to the original position about 10 mm farther out, the ascending process which is seen would doubtless be in a pocket in the lower part of the squamosal, and probably the tympanic membrane was attached to the inner border of this ascending process.

The opisthotic forms, as in typical Therapsids, a well-marked paroccipital process, but it differs from that of the lower Therocephalians in having only a single, irregularly oval, outer end. This paroccipital process forms the lower wall of the occipitotemporal opening. The upper part of this process has a large articulation with the squamosal as in *Whaitsia*. The inner end of the opisthotic has similar relations to the supra-occipital and prootic seen in the earlier Therocephalians.

As the posterior part of the basi-occipital is lost with the whole of the left exoccipital and much of the right exoccipital no satisfactory description can be given of the relations to the exoccipital. The occipital condyle must have been relatively small.

There are well-marked processes on the base of the skull formed by the basi-occipital, opisthotic, and prootic, and supported by the vomer, on the base of which are the fenestrae ovales. The processes are shorter than in the early Therocephalians. The prootic is moderately large, and so far as can be seen fairly similar to that of other Therocephalians. In front and partly hidden by the epipterygoid is a small pleuro- or latero-sphenoid, which appears to have a foramen at its base, presumably for the sixth nerve.

The vomer is a relatively short triangular bone. Its posterior end forms supports in front of the processes in which are the fenestrae ovales. In the middle line the vomer passes back some distance under the basi-occipital. In a median section of the base of the brain-case a well-marked suture can be traced between the basi-occipital and the basi-sphenoid; and it is extremely interesting to note that the basi-sphenoid is a well-ossified and distinct cartilage bone that lies exactly as in mammals in front of the basi-occipital. The vomer is quite free from at least most of the base of the basi-sphenoid, a clear suture being quite apparent between the bones. It appears as if the vomer articulates with not only the base of the basi-sphenoid but also with part of the front as shown in the figure; but owing to the condition of the bone it is difficult to be sure whether or not there is an anchylosis in any part between the bones. The vomer has a large, very deep median plate which passes forwards between the pterygoids. Its upper anterior portion is grooved for the lodgement of the inter-orbital cartilage. The full depth of the median plate cannot be determined, but it is certainly large. The shaded patches shown in the drawing, fig. 127, Plate 9, which are drawn from preserved portions of the plate, give a fair idea of its extent. Outer plates of the vomer clasp the posterior pterygoid plates on their outer sides, as shown in the section figured (fig. 126, Plate 9).

The pterygoids are almost perfectly preserved. Quite manifestly the pterygoid forms the back part of the larger outer process, as in all Therocephalians in which the parts are satisfactorily preserved. Boonstra (1934) figures the transpalatine as forming the back of the process in *Notosollasia*, *Theriognathus*, and *Whaitsia*. In the figures I gave of the palates of *Notosollasia* and *Whaitsia* in 1932, I indicated the pterygoids as forming the back of the processes. The fact that the pterygoid certainly forms the back of the process in *Hyenosaurus* seems to render it probable that my interpretation of the condition in *Whaitsia* and *Notosollasia* is correct. There is no suborbital vacuity. Posteriorly, the pterygoid has a long outer process which extends to very near the quadrate—possibly articulating with it.

Above the back part of the pterygoid is seen the large epipterygoid. This has a short, very broad, upper portion, and a long, flat base which extends outwards and backwards on the top of the outer process of the pterygoid; but it ends a considerable distance short of the quadrate.

The transpalatine (ectopterygoid) is relatively large. It forms the front of the outer part of the pterygoid process. It extends well forward on the outer side of the palatine. Internally, it has a long articulation with both the palatine and the pterygoid.

The palatines are very well developed. Along the inner side of the maxillo-palatine suture there is a broad development of thickened bone as if the palatine bone in the absence of molar teeth shared in mastication. On passing forward towards the internal nares the palate is deeply excavated. The prevomers clearly have large palatal plates, but the exact sutures between these plates and the palatines and pterygoids cannot be made out. Between the internal nares the prevomers are in the posterior part narrow. Most probably they broaden out in front.

Much of the parietals is preserved. The two bones are completely fused. There has manifestly been a narrow intertemporal crest, though most of it is missing. So far as preserved, there is no pineal foramen, though one may have been present. Posteriorly the parietals spread out on the back wall of the very large temporal fossae and articulate with the squamosals. Superiorly the parietals form the middle part of the temporal crest.

Each mandible is practically complete, and the detailed structure of nearly every bone can be determined.

The dentaries are large bones which form about three-quarters of the whole jaw. In neither of the dentaries are any molars present, though in each dentary the portion of the bone in which we should look for molars is satisfactorily preserved. In the left dentary we have the root of a fair-sized canine, whose section measures 15 mm by 10 mm. A very small part of the very front of the dentary is missing. So far as preserved there is no trace of incisors. Judging by the curves it seems probable that only 15 mm of the bone are gone, and the incisors must have been small. In the right jaw there is no evidence of either incisors or molars, and there is no trace of a canine. The absence of a canine in the right dentary and the general massiveness of the bone in association with the huge fossae for the temporal muscles is very remarkable. The coronoid process is very short, only rising a short distance above the sur-angular. The symphysis has evidently had only a very loose membranous attachment.

The splenial is a fairly large bone lying on the inner side of the lower portion of the front half of the jaw. It does not quite reach the lower margin of the dentary. Posteriorly, the splenial meets the front of the coronoid, and also articulates with the pre-articular and the angular.

The coronoid is fairly well preserved in the right mandible. When the specimen was developed twenty years ago, the coloured preparator, though he did most excellent work, cleared the dentary a little too far back before he observed the thin coronoid. The coronoid is a crescent-shaped bone whose upper part rests on the dentary and the sur-angular, and whose lower part rests on the pre-articular and the angular, and also articulates with the splenial.

The back part of the jaw is formed, as in other Therapsids, by the articular, the angular, the sur-angular, and the pre-articular.

The articular is a short, wide bone whose articular face is transversely grooved to hinge on the broad quadrate. Much of the outer side is hidden by the sur-angular and angular ; while the greater part of the inner side is hidden by the pre-articular. The short anterior part of the bone is firmly fixed between the pre-articular and the angular.

The sur-angular is a short but exceptionally strong bone. The anterior two-thirds of the bone are closely articulated to the coronoid portion of the dentary, and overlying the anterior end is part of the coronoid bone. The back part of the bone is closely articulated to the articular, and much of the outer side is covered by the angular.

The angular is relatively smaller than in most Therocephalians. The anterior end passes forward between the splenial and the dentary. Part of it is overlain by the coronoid bone, and the greater part of the inner side covered by the pre-articular. The outer side of the bone has a relatively small outer plate, which is unlike that of the earlier Therocephalians, but recalls in some respects the outer plate of the angular in the Titanosuchids. There is an elongated opening above it which is continued round to the narrow opening on the lower margin of the jaw. There seems to be a notch on the lower border of the bone, but how much of this is due to imperfection cannot be determined, probably only a little.

The pre-articular has a well-developed posterior end which clasps the outer side of the articular. The anterior portion of the bone is a comparatively thin plate which lies on the angular and passes forward under the coronoid and splenial.

*Hyenosaurus* is clearly one of the later Therocephalians. It differs from *Whaitsia* and *Notosollasia* in that the occiput recedes very markedly, so that no part of it can be seen from directly above. The structure of the angular also differs very considerably from that of any of the previously known later Therocephalians.

## X—Summary and Conclusions

The Therocephalians first appear in South Africa at the base of the *Tapinocephalus* zone, which may perhaps be regarded as Middle Permian. It is unfortunate that the Ecca beds below the *Tapinocephalus* zone are extremely poor in vertebrate fossils, and the few that are known are too imperfect to throw much light on the origin of the types that appear in the *Tapinocephalus* beds. In the lowest beds of the *Tapinocephalus* zone we find a rich fauna. We have a number of species of Pareiasaurians belonging to the genus *Bradysaurus*, the primitive pro-Therapsid *Anningia*, various Therocephalians, various Gorgonopsians and already Anomodonts and a large number of Dinocephalians, both the herbivorous Tapinocephalids and the carnivorous Titanosuchids. We thus know nothing of the common ancestors of the Dinocephalians, the Therocephalians, the Gorgonopsians, and the Anomodonts.

While we thus know nothing of the direct ancestors of the Therocephalians, the group is of the greatest interest, as there is no reasonable doubt that the Scaloposaurids of the Lower Trias are descended from the earlier Therocephalians, and also little doubt that the Middle or Upper Triassic Bauriamorphs are descended from a Scaloposaurid ancestor. Further, it seems probable that the Rhoetic Ictidosaurians arose from a Bauriamorph, and highly probable that the first mammal arose from an Ictidosaurian. There is thus much probability that the line of mammalian descent passed through some members of the Therocephalia, and thus the group as probably containing our own remote ancestors seems worthy of very considerable study.

The skull, as we have seen, is remarkably mammal-like in general shape and structure. The temporal arch is formed as in the mammal by the jugal and the squamosal. There have manifestly been large temporal muscles which were attached to a coronoid process of the dentaries as in mammals. The teeth already were specialized as incisors, canines, and molars.

On the other hand, there are many striking points of difference. The palate is very unlike that of any mammal. Even if the mammal had no secondary palate the difference between the mammalian and Therocephalian type would be striking. The mammal has a large median vomer situated, in most, well forward and generally extending to near the front of the snout. The Therocephalian has a pair of bones in front of the palate, which I consider are homologous with the dumb-bell-shaped bone of *Ornithorhynchus*, and at the back of the palate is a median bone—the para-sphenoid of most authors—a bone which does not occur in mammals. For many years I have maintained that the reptilian "para-sphenoid" evolved into the mammalian vomer, and the facts now known about the structure in the Therocephalians, the Gorgonopsians, the Anomodonts, and the Ictidosaurians seem to me to confirm this conclusion.

Then we have the lower jaw in the Therocephalians with the posterior third formed mainly by the sur-angular, angular, pre-articular, and articular bones, and the articular hinging on a well-developed quadrate. Further, in the Therocephalian skull we have many bones which are completely lost in the mammal. And yet I think it can be shown how in nearly every feature we have pro-mammalian characters whose evolution into the mammalian condition can be readily understood.

Some of the more important problems raised by the study of the Therocephalian skull may be considered in some little detail.

### *Dental Succession*

In the mammal we have typically a first set of teeth comprising incisors, a canine, and four molars. These are shed and replaced by a second set which consist of incisors, a canine, four replacing molars and three further molars which have no antecedents. In some Cynodonts we have a succession of teeth almost typically mammalian. Certainly a number of anterior molars are replaced. In the Gorgonopsians we have a dental succession in the incisors and the canine, but apparently not in the molars. In the Therocephalians we have certainly a dental succession in the incisors and canines. Whether there are more than two sets is at present unknown. As the succession in the incisors seems to be irregular, it seems probable that there is an indefinite succession of the incisors. But it seems possible that there are only two sets of canines. And so far as the evidence goes there is no satisfactory proof of a dental succession in the molars. The fact that in *Hofmeyria* the molars are not all equally developed suggests that in this later Therocephalian there may be a dental succession. In the Whaitsidae it is probable that there is a set of molar teeth that became lost later on and are not replaced. In the only known skull, *Lycideops longiceps*, which is certainly immature, there is a series of small molars which will probably be shed, and possibly not replaced.

Very probably when more specimens are examined we shall find that in earlier Therocephalians there are three or more sets of incisors, two sets of canines, and only one set of molars.

*Prevomer and Vomer*

When in 1895 (Broom, 1900) I was studying the comparative anatomy of the Organ of Jacobson, I was led to the conclusion that the lacertilian so-called "vomer" is really the homologue of the dumb-bell bone in the platypus, and not of the mammalian vomer, and I proposed for it the name of "Prevomer". This raised the further question of what bone if any in the lizard is the homologue of the mammalian vomer. When one examines a very young lizard's skull one finds a median membrane bone extending forward from the basi-sphenoid region under the interorbital septum in much the same way as the mammalian vomer passes forward under the nasal septum; and it is hard to resist the idea that this median bone in the lizard, which has been called the "para-sphenoid", will ultimately prove to be the real homologue of the mammalian vomer. This view was first suggested by Bland Sutton in 1884.

Owing to the wide difference in structure between the lizard and the mammal, and the complete absence of any living form that in any way helps to bridge the gulf, it has been very difficult to prove that the reptilian so-called "para-sphenoid" is really the mammalian vomer.

For the last 36 years I have been engaged in the study of the fossil mammal-like reptiles of the Permian and Triassic beds of South Africa, and one of the problems that has never been forgotten is whether or not the "para-sphenoid" of the reptile becomes the vomer in the mammal. Of course, the paleontologist has rarely a chance of studying any but adult specimens, and even in good adult specimens it is often very difficult to determine the limit of bones, especially where the specimens are a little crushed and the matrix hard. In fact, it has only been possible to unravel the structure of the base of the skull in the mammal-like reptiles by having sections made.

It is only quite recently that we have known satisfactorily the structure of the base of the skull in the Therocephalians, the Gorgonopsians, the Anomodonts, and the Cynodonts. We also know something of the base of the skull in the Dinocephalians, the Bauriamorphs, and the Ictidosaurians.

In the Dinocephalians, as exemplified by *Dinophoneus*, we find a pair of large prevomers in the front of the palate, and a small median vomer or para-sphenoid in the basi-sphenoid region, and probably extending some distance in front of the basi-sphenoid. The exact condition and size of the basi-sphenoid are unknown, and it is also unknown whether this vomer or para-sphenoid is completely fused with the basi-sphenoid.

In the early Therocephalians, as we have just seen, there are a pair of prevomers in the front of the palate which are always distinct. In the basi-sphenoid region there is a fairly large median vomer or para-sphenoid. It extends well back under much of the basi-occipital, and sends a process forwards, supporting the cartilaginous inter-orbital septum. It would appear from the sections that the basi-sphenoid is quite a small element which is anchylozed to part of the top of the vomer, and articulates with the basi-occipital.

In *Hyenosaurus* the vomer differs considerably from that in *Lycedops*. The basi-sphenoid is here a large, well-ossified element which, as in mammals, is articulated to the front of the basi-occipital by a well-marked suture. Below it is a deep median element, which is clearly separated by a suture from the posterior half of the basi-sphenoid, but is less clearly separated from the anterior half. This large median vomer has a posterior plate which passes back for some distance below the basi-occipital. In front the vomer clasps the inner plates of the pterygoids, the two plates being firmly articulated between the three anterior plates of the vomer. Laterally, the vomer has plates which pass in front of the auditory tubera. And superiorly the vomer has a groove for the interorbital cartilage. In the Gorgonopsians the pre-vomers are always fused into a median bone between the internal nares. The true vomer or para-sphenoid is a median bone which bears some resemblance to that in the early Therocephalians. It differs in having a smaller descending median pharyngeal plate. The relations to the other elements of the basis cranii are only known fully in the immature *Cynarioides*, and here the basi-sphenoid is not yet ossified. Manifestly the vomer is entirely or nearly wholly a membrane bone which passes back for some distance under the basi-occipital.

In some Bauriamorphs, *e.g.*, *Bauria*, the palatal condition is probably very similar to that in the Therocephalians, except that there is a secondary palate formed.

In the Cynodonts there is in the front of the palate a median bone largely hidden by the secondary palate. This is the fused prevomers. In the back part of the palate is a median vomer which passes back a little way below the basi-occipital, and in front passes forward as a long, narrow process which supports the inter-orbital median cartilage. I have been unable to determine how much of the upper part of the bone is basi-sphenoid—probably only a small part.

In the Anomodonts the vomerine condition differs considerably from that in the carnivorous Therapsids. The prevomers are fused to form a deep median plate which lies between the internal nares. Immediately above the fused prevomers is a long trough-like vomerine spur which for a time was believed to be part of the prevomers, but is really quite distinct. This is manifestly a typical " para-sphenoid ". It is also nearly as manifestly a typical vomer. It is completely fused with the large basi-sphenoid behind, as is the vomer in *Ornithorhynchus*. If it was not anchylozed to the basi-sphenoid it would exactly agree with the vomer of higher mammals.

In the Ictidosaurians the palatal condition is imperfectly known. There is, however, undoubtedly a large median vomer which is well forward and separates the pterygoids. So far as is known it is almost typically a mammalian vomer.

Then, as I have elsewhere pointed out, in *Ornithorhynchus* we have a pair of prevomers in the front of the palate to form the dumb-bell-shaped bone, and behind the dumb-bell bone there is a long typical vomer which is remarkable in being very early fused with the basi-sphenoid, and to be thus exactly like the "para-sphenoid" of the reptiles such as *Ichthyosaurus* or the lizards.

There can thus hardly be a doubt that the dumb-bell bone of *Ornithorhynchus* is the homologue of the paired vomers of the reptiles; and the mammalian vomer when traced down proves to be the homologue of the bone which has been called the "para-sphenoid".

### *Pre-sphenoid and Basi-sphenoid*

In the Anomodonts the basi-sphenoid is always a large bone which articulates with the basi-occipital, and it is typically mammalian in its relations. There can thus be no doubt about its homology. Some distance in front of the basi-sphenoid is another median cartilage bone. It articulates with the frontals in front. Lateral canals in this bone appear to have lodged the olfactory lobes of the brain, and in the lower part is a deep sulcus in which probably lay the optic commissure. This bone has given rise to considerable dispute as to its homology. It has been called ethmoid, mesethmoid, sphenethmoid, pre-sphenoid, and even orbito-sphenoid.

A comparison with the condition in the young *Ornithorhynchus* seems to prove that this bone must be not the mesethmoid but the mammalian pre-sphenoid. The bone in the *Ornithorhynchus* supports the two orbito-sphenoids exactly as does the pre-sphenoid in the higher mammals. Assuming it to be the pre-sphenoid, there is then no mesethmoid in any of the lower reptiles, while in most this pre-sphenoid can be traced.

In Gorgonopsians this pre-sphenoid is always present and well ossified. In the Therocephalians it is probably always present, but as it is feebly ossified and loosely attached to the frontals, it has only been found *in situ* in one specimen. In the Cynodonts a fully ossified pre-sphenoid is not yet known. There is little doubt one will be found in the larger forms. In the sections I have made of *Thrinoxodon liorhinus* the pre-sphenoid is not fully ossified, but there are clear indications of the element probably of partly calcified cartilage. In position it agrees with the bone in the Therocephalians. It is present as a well-developed bone in *Bauria*.

The basi-sphenoid is probably present in all Therapsids, but it is difficult in most forms to say how much of the conjoined bone is basi-sphenoid and how much vomer or para-sphenoid. In the Anomodonts most of the bone is manifestly basi-sphenoid. In the Gorgonopsians and Therocephalians most of the bone appears to be vomer. In the Therocephalians and probably in the Cynodonts the basi-sphenoid only forms a small part of the conjoined bone.

### *Pleuro-sphenoids*

When studying the development of the Marsupial skull in 1898 I was surprised to find that the alisphenoid develops from a little cartilage which lies well outside the cranial wall, and has apparently nothing to do with it. Its morphological relations seemed very similar to those of the rudimentary epipterygoid in the lizard *Agama*, and soon I came to the conclusion that the alisphenoid is probably the homologue of the lacertilian epipterygoid.

During the early years of the present century we came to know something of the epipterygoid in the more important groups of Therapsids. In the Anomodonts we found an almost lizard-like epipterygoid or columella, and in the Therocephalians an epipterygoid rather broader. In the Cynodonts what was manifestly the same element was seen to be broadened out into a fan-like bone which one can hardly doubt is an alisphenoid. When more types were studied, and when the relations of the bones to blood vessels and nerves were examined, in living lizards and other reptiles, it became more and more manifest that the alisphenoid of the mammals is the homologue of the epipterygoid of the lizard. And now it is agreed by practically all morphologists that this is so. Goodrich, in his recent book, "Structure and Development of Vertebrates", states that "there is little doubt that Broom's contention that the mammalian alisphenoids are derived from the epipterygoids of lower Tetrapods is correct".

But another question arises. In the crocodile and bird there is a bone usually called "alisphenoid", which is really part of the cranial wall. It thus cannot be the homologue of the mammalian alisphenoid if the alisphenoid is homologous with the lizard epipterygoid. Further, in some reptiles, *e.g.*, the *Phytosaurus*, there is both an epipterygoid and a bone which is clearly the homologue of the so-called "alisphenoid" of the crocodile. When the nerve relations of the bones are examined we seemed forced to the conclusion that this so-called "alisphenoid" is really homologous with the cartilage in the lizard skull called the *pila antotica*. This is a pillar of cartilage which passes up from the front of the prootic cartilage to meet the lateral cartilaginous wall—the *taenia marginalis*. Its base is pierced by a foramen for the sixth nerve, at least in *Lacerta*. It probably represents part of the original cranial wall. When ossified, it seems worthy of a special name, and various names have been suggested—sphenolateral (Gaupp), oto-sphenoid (Broom), latero-sphenoid (Gregory and Noble), and pleuro-sphenoid (van Wijhe). Goodrich prefers the latter form. As a cartilage it can be traced from fishes, through most amphibians and reptiles to the monotremes. It is rarely ossified. Goodrich suggests that the large "sphenethmoid" of some Stegocephalians may include this posterior pleuro-sphenoid, and with this I agree.

In the Phytosaur *Machaeroprosopus gregorii*, as shown by Camp (1935), the pleurosphenoid (latero-sphenoid) is a large bone with a foramen at its base for, it is believed, the sixth nerve and certain branches of the fifth. The upper part of the bone forms a large part of the wall of the brain-case, and it passes forwards to form the interorbital septum and the wall of the olfactory lobes (what I believe to be the presphenoid and most others call the sphenethemoid). Very probably if a young Phytosaur were examined we should find the pleuro-sphenoid and the pre-sphenoid distinct bones. The fact that the two elements are fused in the Phytosaurs, and also in the Embolomerous amphibians seems strongly to support the view that they are ossifications of the same lateral wall cartilage.

In the Therapsids, so far as is known, we only find an ossified pleuro-sphenoid in the Therocephalians, the Bauriamorphs, and some Gorgonopsians. It apparently never occurs in Anomodonts or Cynodonts as a bone. In the Therocephalians, which I have sectioned, it is a somewhat rudimentary structure; but whether in the ancestors of the Therapsids it ever was a large bone is very doubtful. Probably in most early reptiles it was present as a cartilage, while in only a few did it become a well-developed bone. Near the base of the bone in the Therocephalians is a foramen possibly for the sixth nerve. I cannot find any suture between the base of the bone and the prootic.

The presence of the ossified pleuro-sphenoid in the Therocephalians is interesting in view of the same element being present in the monotremes as the pila antotica.

*Auditory Apparatus*

Many have been the attempts that have been made to trace the probable steps by which the middle ear of mammals has been derived from the ear of reptiles. REICHERT's theory that the mammalian incus is the homologue of the reptilian quadrate, and the malleus the articular has in the last 100 years always had the support of many leading morphologists. A number of other theories have from time to time been suggested, but with the steady advance of palaeontology and comparative anatomy the evidence in favour of REICHERT's view has become more and more convincing. GAUPP's advocacy of the view with his wealth of embryological evidence which he published in his book, " Die Reichertsche Theorie " (1913), has completely convinced the scientific world of the main truth of the theory. But we are still in considerable perplexity as to how the change in the hinge of the jaw took place, and how the old hinge bones came into the ear, and where the tympanic membrane was during the changes.

In 1912, in discussing the auditory region in *Dicynodon*, I gave a series of diagrams illustrating what may have been the changes from a condition such as that seen in *Dicynodon* to the mammalian condition. I assumed as probable that, with the dentary articulating with the squamosal, the angular, articular, and quadrate became steadily reduced, and the angular and articular, becoming free from the jaw, shifted a little back and developed into the tympanic and malleus. I assumed that the tympanic membrane always was situated in the earlier stages behind the quadrate and near the outer end of the stapes.

PALMER (1913), from the examination of the jaw in the foetal *Perameles* and the comparison of the back of the jaw with that of the Cynodonts, came to the conclusion that even in the Therapsids the angular had a curved process which probably supported part of the tympanic membrane. This suggestion has been supported by quite a number of morphologists, but has never appeared to me to be at all likely. In the first place, the curved process of the angular in Cynodonts is undoubtedly the homologue of the outer plate of the angular which we can trace up from the Dinocephalians, and we may be perfectly certain that this outer plate did not support the tympanic membrane in Dinocephalians, Therocephalians, Anomodonts, or Gorgonopsians. Then it seems impossible to conceive of the mandible opening widely and closing and with every movement carrying the tympanic membrane into a different position. But if these arguments were not convincing we now have the certainty that in the Therocephalians at least the tympanic membrane was attached to the squamosal and the quadrate, and not in any way to the jaw. In fact, the position of the membrane in the Therocephalian is exactly where I assumed it must be, in my 1912 paper. We thus have a new definite step in the advancement of our knowledge.

The discovery of the extra-stapedial is a second and equally important advance. But it raises a new problem—how the extra-stapedial disappeared and had its place taken by a process of the articular. Unfortunately, the condition of the auditory apparatus is less satisfactorily known in the Anomodonts, the Gorgonopsians, and the Cynodonts than in the Therocephalians. All these groups have a fairly massive stapes as a rule, and so far no evidence of any extra-stapedial has been detected. Possibly a cartilaginous extra-stapedial has been present.

When the jaw had formed its new articulation between the dentary and the squamosal, the quadrate and the articular doubtless rapidly decreased in size, and the articular with its membrane-bone elements, the pre-articular on the one side and the angular on the other, became detached from the jaw, and no longer moved with the jaw. As the new hinge of the jaw was mainly outside of the middle ear the tympanic membrane became more deeply placed in the side of the head, and most probably the old articular came to support part of the membrane, and then with it the angular. The angular as a membrane bone became a more suitable support than either the quadrate (incus) or the articular (malleus), and soon it became the main support of the membrane and developed into the tympanic bone. Very probably the tensor tympani muscle (one of the muscles of the early jaw) played an important part in the transformation of the jaw elements into auditory ossicles.

How the extra-stapedial disappeared and its place was taken by a process of the articular (malleus) is more difficult to imagine. What has probably happened has been that the posterior end of the articular for a time supported the tympanic membrane in front. And then the angular gradually took its place and the articular (malleus) became shifted towards the middle of the membrane and the extra-columella became reduced and lost. If we ever get a good specimen of a skull of *Tritylodon*, or one of the other Upper Triassic mammals, with the ear region perfectly preserved we shall probably have a full solution of the question.

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## XII—Description of Plates

### *Lettering*

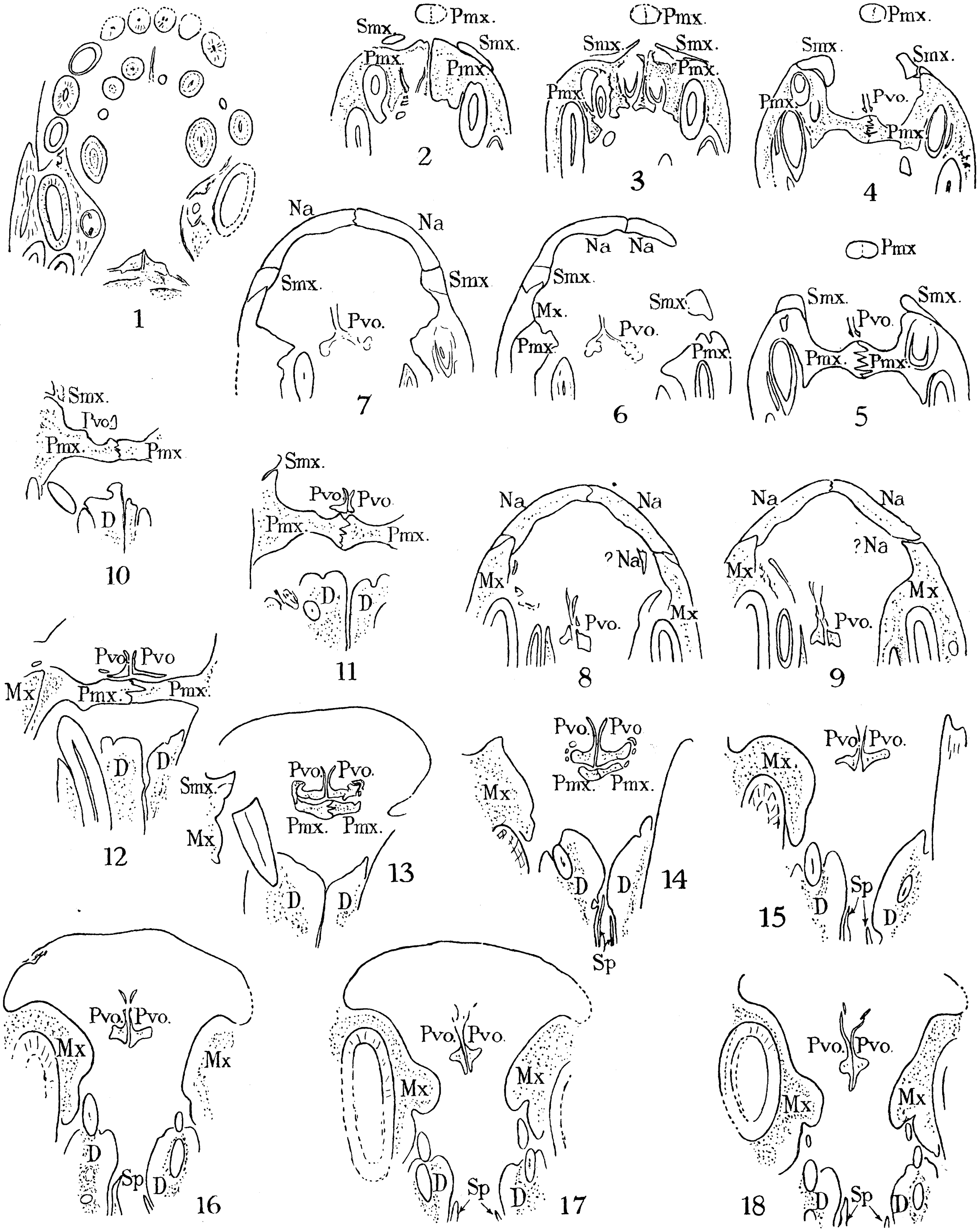
*Ang.*, Angular ; *Art.*, Articular ; *At.*, Atlas ; *Ax.*, Axis ; *Bo.*, Basi-occipital ; *Bs.*, Basi-sphenoid ; *C.Ax.*, Centrum of Axis ; *Co.*, Coronoid ; *D.*, Dentary ; *Eo.*, Exoccipital ; *Ept.*, Epipterygoid ; *Fr.*, Frontal ; *Ip.*, Interparietal ; *Ju.*, Jugal ; *L.*, Lacrimal ; *Mx.*, Maxilla ; *Na.*, Nasal ; *Oo.*, Opisthotic (Paroccipital) ; *O.p.*, Odontoid process of the Axis ; *Pa.*, Parietal ; *Pal.*, Palatine ; *P.art.*, Pre-articular ; *P.at.*, Proatlas ; *Pf.*, Pre-frontal ; *Pls.*, Pleuro-sphenoid (Latero-sphenoid) ; *Pmx.*, Pre-maxilla ; *Po.f.*, Post-frontal ; *Po.o.*, postorbital ; *Pro.*, Prootic ; *Ps.*, Pre-sphenoid (Sphenethmoid) ; *Pt.*, Pterygoid ; *Pvo.*, Prevomer (Vomer) ; *Q.*, Quadrate ; *Q.j.*, Quadratojugal ; *S.ang.*, Sur-angular ; *Smx.*, Septomaxilla ; *So.*, Supra-occipital; *Sp.*, Splenial ; *Sq.*, Squamosal ; *St.*, Stapes ; *Tb.*, Trabecular ; *Trp.*, Transpalatine (Ectopterygoid) ; *Vo.*, Vomer (Para-sphenoid) ; XII., Twelfth nerve.

### Plate 1

Fig. 1—Horizontal section of the snout of *Trochosaurus dirus*, Broom ; cutting through most of the teeth. $\frac{1}{2}$ natural size.

Figs. 2–9—Transverse sections of the snout of *Trochosaurus dirus*, Broom. $\frac{1}{2}$ natural size.

Figs. 10–18—Transverse sections of the snout of a moderately large Therocephalian, probably *Pristerognathus vanderbyli*, Broom. $\frac{4}{5}$ natural size.




*Trochosaurus dirus* and *Pristerognathus vanderbyli*.

Plate 2

Figs. 19–24—Transverse section of the snout of a moderately large Therocephalian, probably *Pristerognathus vanderbyli*, Broom. $\frac{4}{5}$ natural size.

Figs. 25–32—Transverse sections of the skull of *Pristerognathus minor* (Haughton). $\frac{4}{5}$ natural size.

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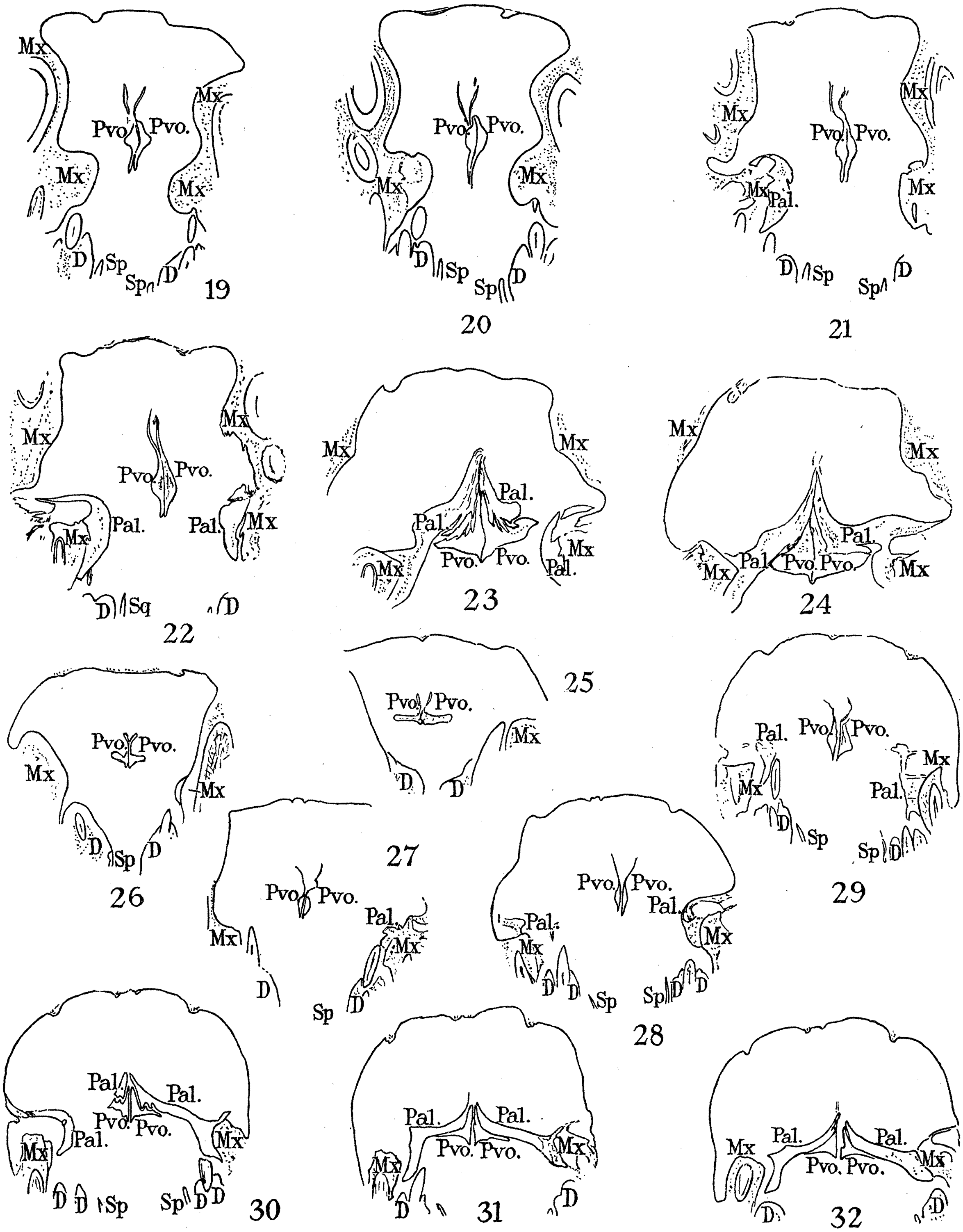


*Pristerognathus vanderbyli* and *Pristerognathus minor*.

PLATE 3

Figs. 33–51—Transverse sections of the skull of *Pristerognathus minor* (Haughton). $\frac{4}{5}$ natural size.

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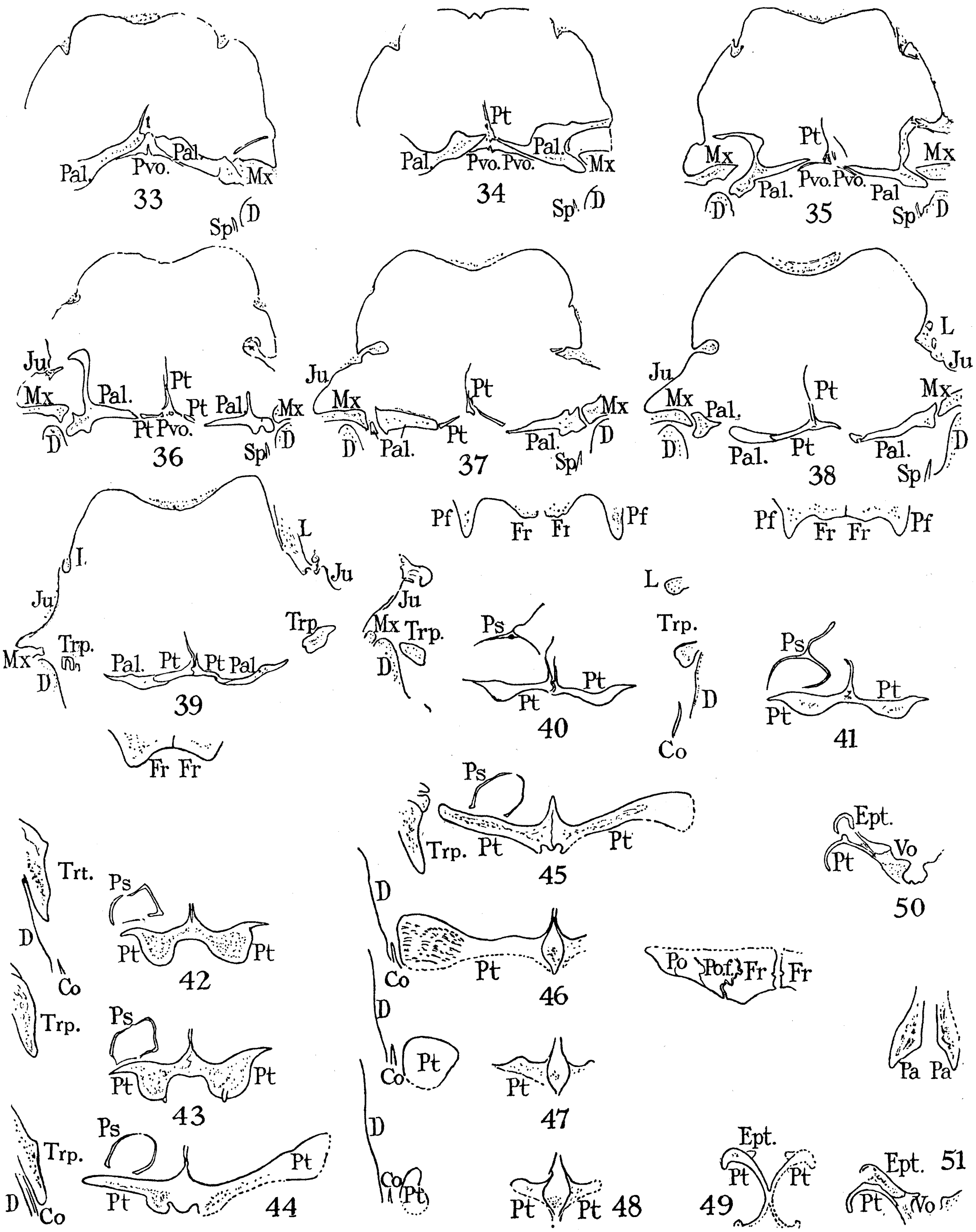


*Pristerognathus minor.*

PLATE 4

Figs. 52–64—Transverse sections of the posterior portion of the skull of probably *Trochosuchus acutus*, Broom. $\frac{3}{5}$ natural size.

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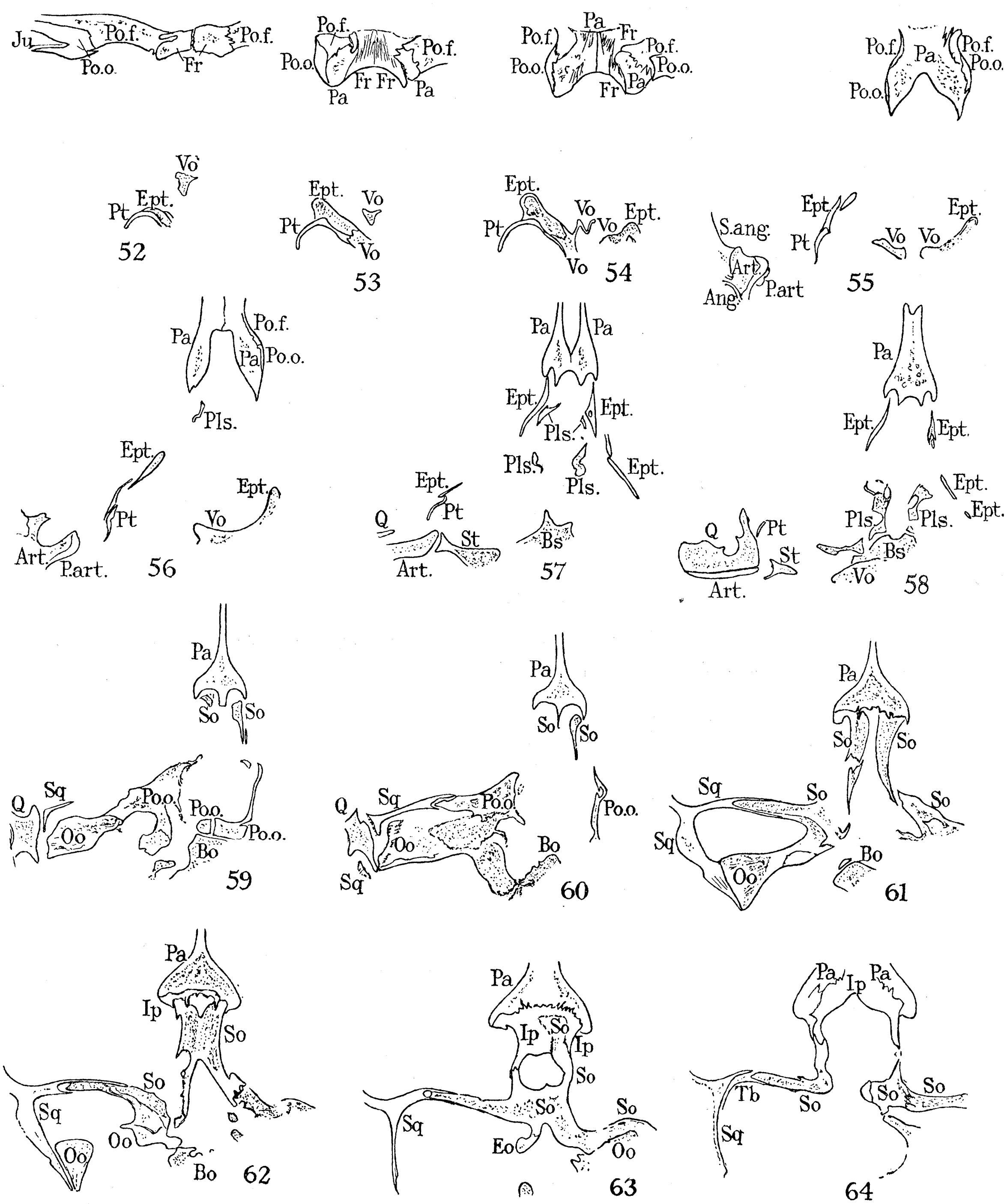


*Trochosuchus acutus.*

PLATE 5

Figs. 65–86—Horizontal sections of the skull of a Therocephalian, most probably *Lycedops scholtzi*, Broom. $\frac{3}{7}$ natural size.

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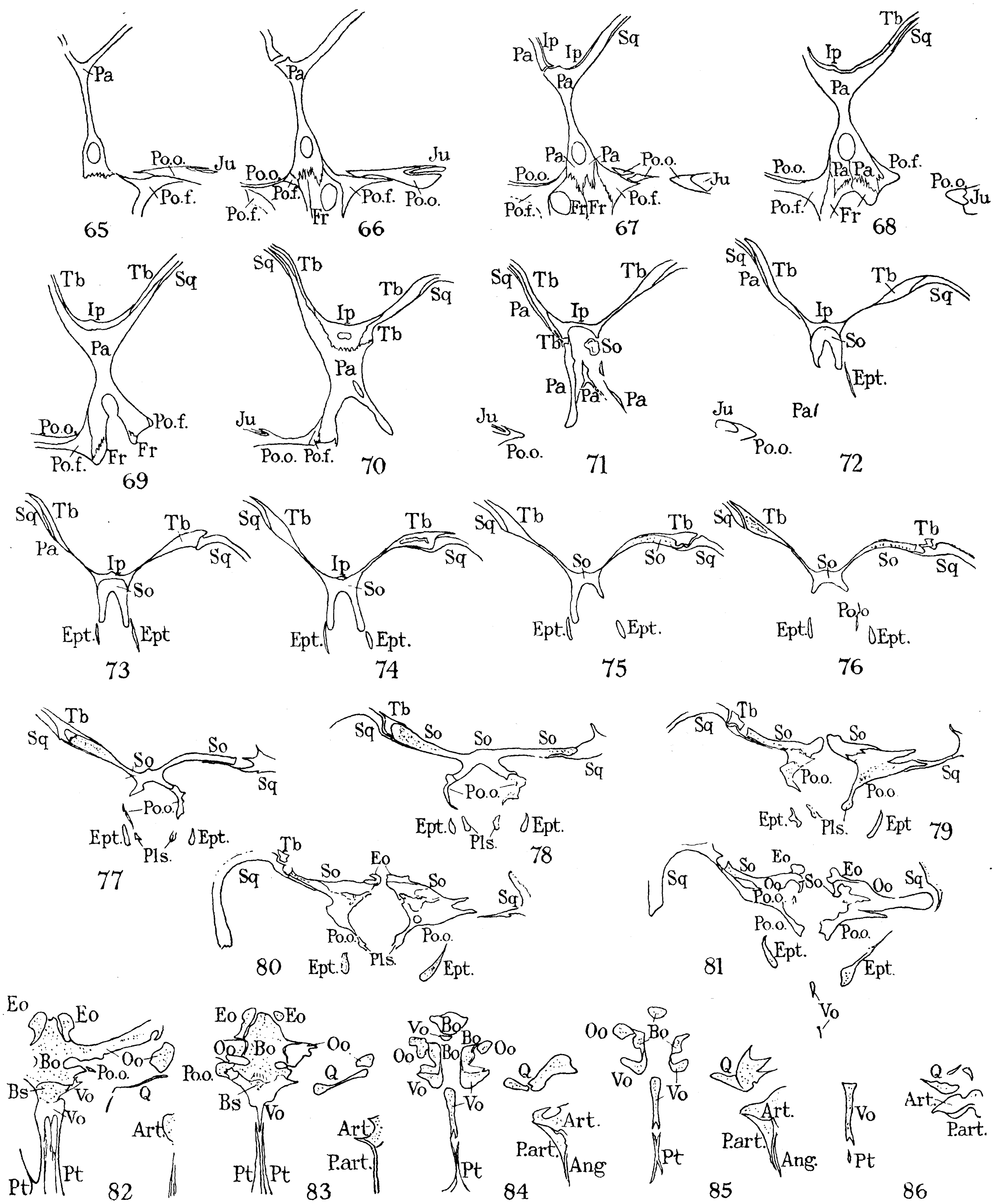


Probably *Lycedops scholtzi*.

PLATE 6

Figs. 87–93—Horizontal sections of the brain-case, and the base of the skull of a Therocephalian, most probably *Lycedops scholtzi*, Broom. $\frac{6}{7}$ natural size.

Fig. 94—Restoration of the vomer of a Therocephalian, most probably *Lycedops scholtzi*, Broom; as seen from below. $\frac{6}{7}$ natural size.



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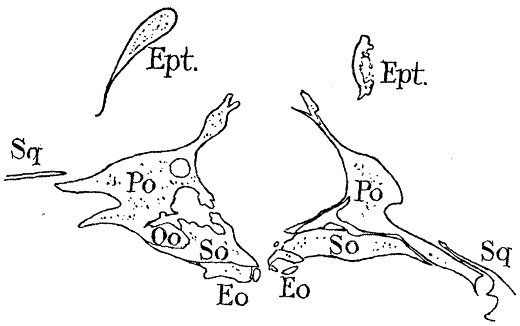


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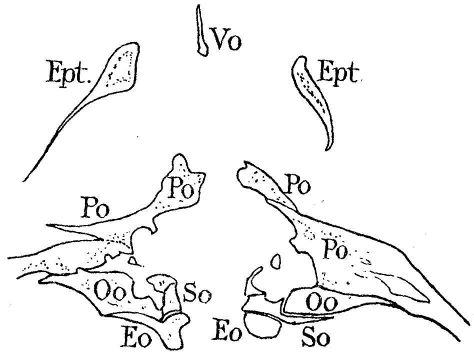


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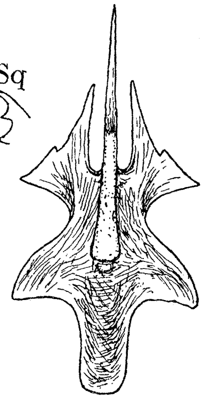

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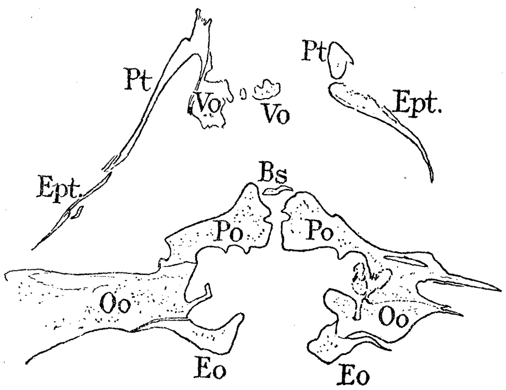


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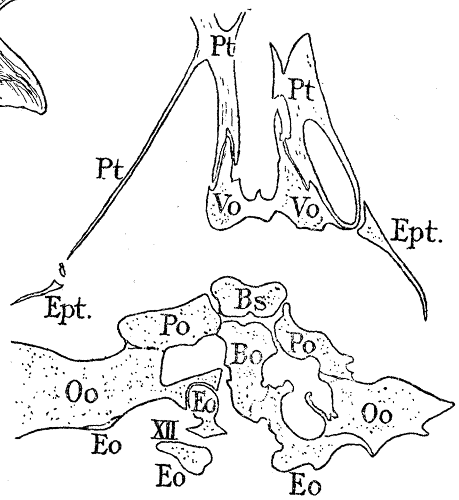


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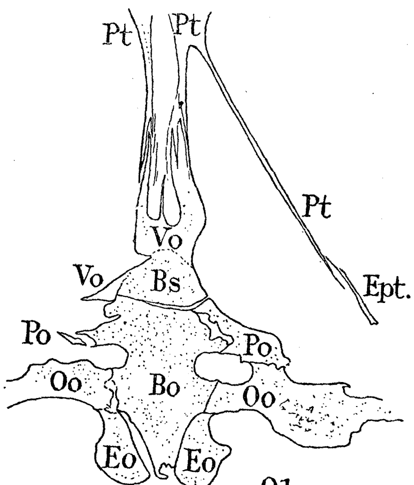


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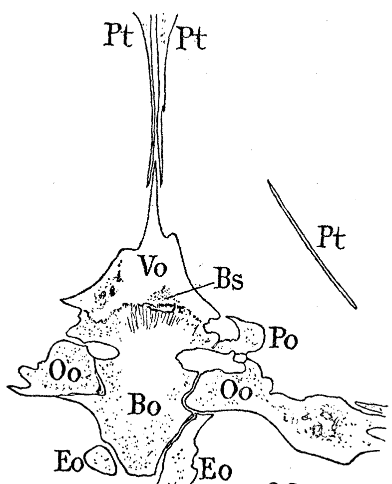


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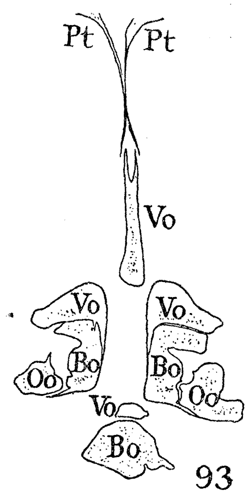


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Probably *Lycedops scholtzi*.

## Plate 7

Figs. 95–105—Various views and sections of the skull and upper vertebrae of *Lycedops scholtzi*, Broom.

Fig. 95—Side view type skull of *Lycedops scholtzi*, Broom, partly restored. A portion of the snout in the canine region has been lost so that the exact length of the snout is uncertain. The posterior two-thirds of the skull are satisfactorily preserved. $\frac{8}{15}$ natural size.

Fig. 96—A transverse section through the skull, showing the jaws in natural relations to the pterygoids, and the pre-sphenoid in natural relations to the frontals. $\frac{4}{5}$ natural size.

Figs. 97–98—Section across the mandibles a little posterior to those shown in fig. 96. $\frac{4}{5}$ natural size.

Fig. 99—A somewhat oblique transverse section through the back part of the skull, showing the basi-occipital, prootics, pleuro-sphenoids, and epipterygoids. $\frac{4}{5}$ natural size.

Fig. 100—Side view of the vomer showing its relations to the basi-occipital, the basi-sphenoid, epipterygoid, and pterygoid. The basi-occipital, basi-sphenoid, prootic, and epipterygoid are shown in section. Almost the whole of the vomer and the part of the pterygoid shown are views of outer sides of these bones. $\frac{4}{5}$ natural size.

Fig. 101—Inner view of left mandible—partly restored from sections. $\frac{8}{15}$ natural size.

Fig. 102—Occiput showing most of the elements in undisturbed natural relations. $\frac{4}{5}$ natural size.

Fig. 103—The right quadrate and related bones as seen from behind. 1 and $\frac{3}{5}$ natural size.

Fig. 104—An oblique section through the right quadrate and related bones. 1 and $\frac{3}{5}$ natural size.

Fig. 105—A section through the atlas and axis. $\frac{4}{5}$ natural size.

Fig. 106—A section through the left atlantal arch and the left proatlas. $\frac{4}{5}$ natural size.

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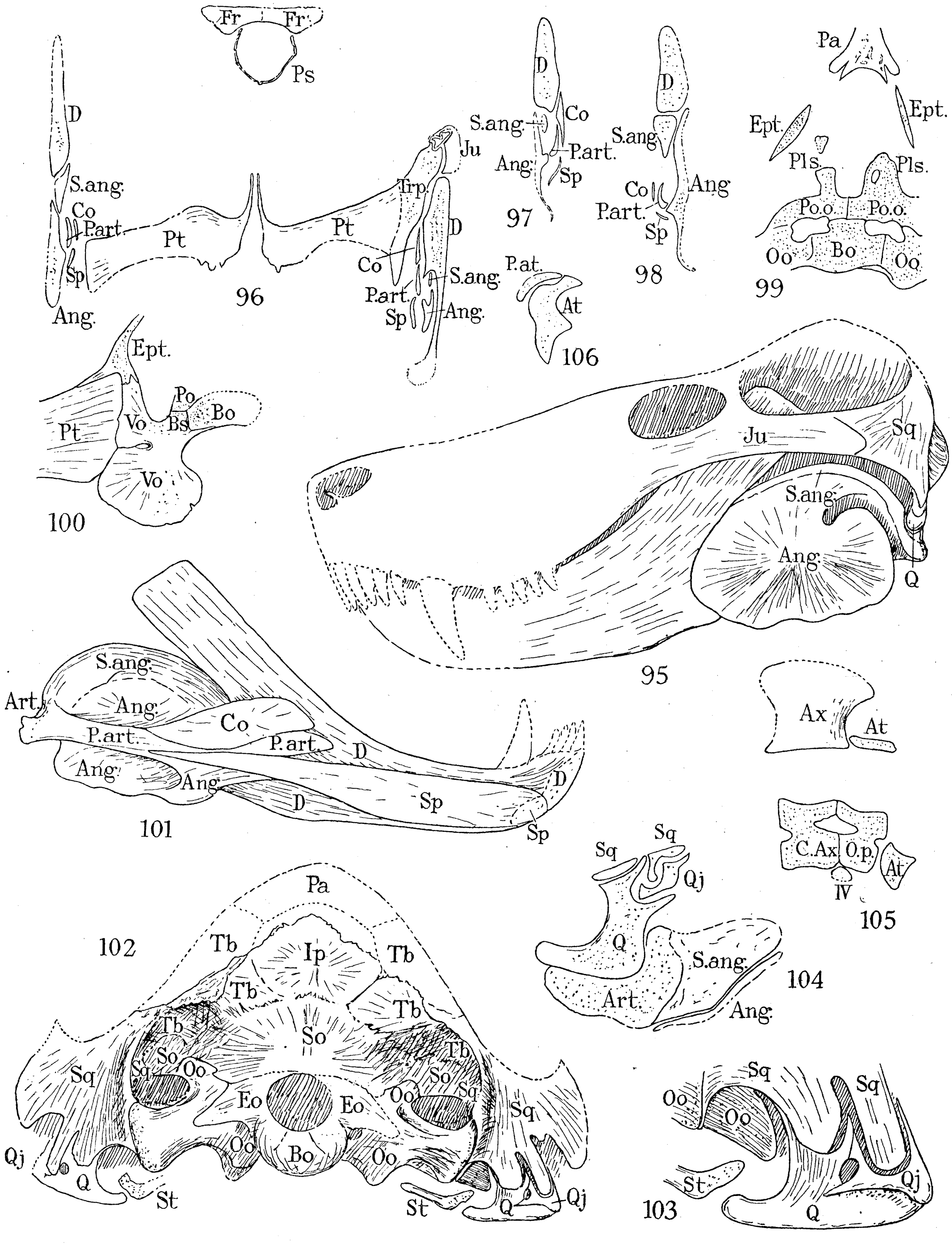


*Lycedops scholtzi.*



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PLATE 8

Fig. 107—Reconstruction of the palate of *Pristerognathus minor* (Haughton) from sections, and with the approximate position indicated of the sections figured in Plates 2 and 3. $\frac{2}{5}$ natural size.

Fig. 108—A median diagrammatic section of the Therocephalian skull. The anterior two-thirds are reconstructed from the sections of *Pristerognathus minor*, and the posterior third reconstructed from the sections of the allied *Lycedops scholtzi*. $\frac{3}{10}$ natural size.

Fig. 109—Right side view of the type skull of *Hofmeyria atavus*, Broom. $\frac{4}{5}$ natural size.

Fig. 110—Left side view of the type skull of *Hofmeyria atavus*, Broom. $\frac{4}{5}$ natural size.

Fig. 111—Top view of the skull of *Hofmeyria atavus*. As preserved. $\frac{4}{5}$ natural size.

Fig. 112—Under view of skull of *Hofmeyria atavus*. As preserved. $\frac{4}{5}$ natural size.

Fig. 113—Occiput with upper cervical vertebrae of *Hofmeyria atavus*, as preserved. $\frac{4}{5}$ natural size.

Fig. 114—Oblique view of right pre-frontal and lacrimal bones of *Hofmeyria atavus*. $\frac{4}{5}$ natural size.

Fig. 115—A section through the pterygoids and anterior part of the vomer of *Hofmeyria atavus*.

Fig. 116—Right stapes and extra-stapedial of *Hofmeyria atavus*. 1 and $\frac{3}{5}$ natural size.

Fig. 117—Part of left stapes and extra-stapedial of *Hofmeyria atavus*. 1 and $\frac{3}{5}$ natural size.

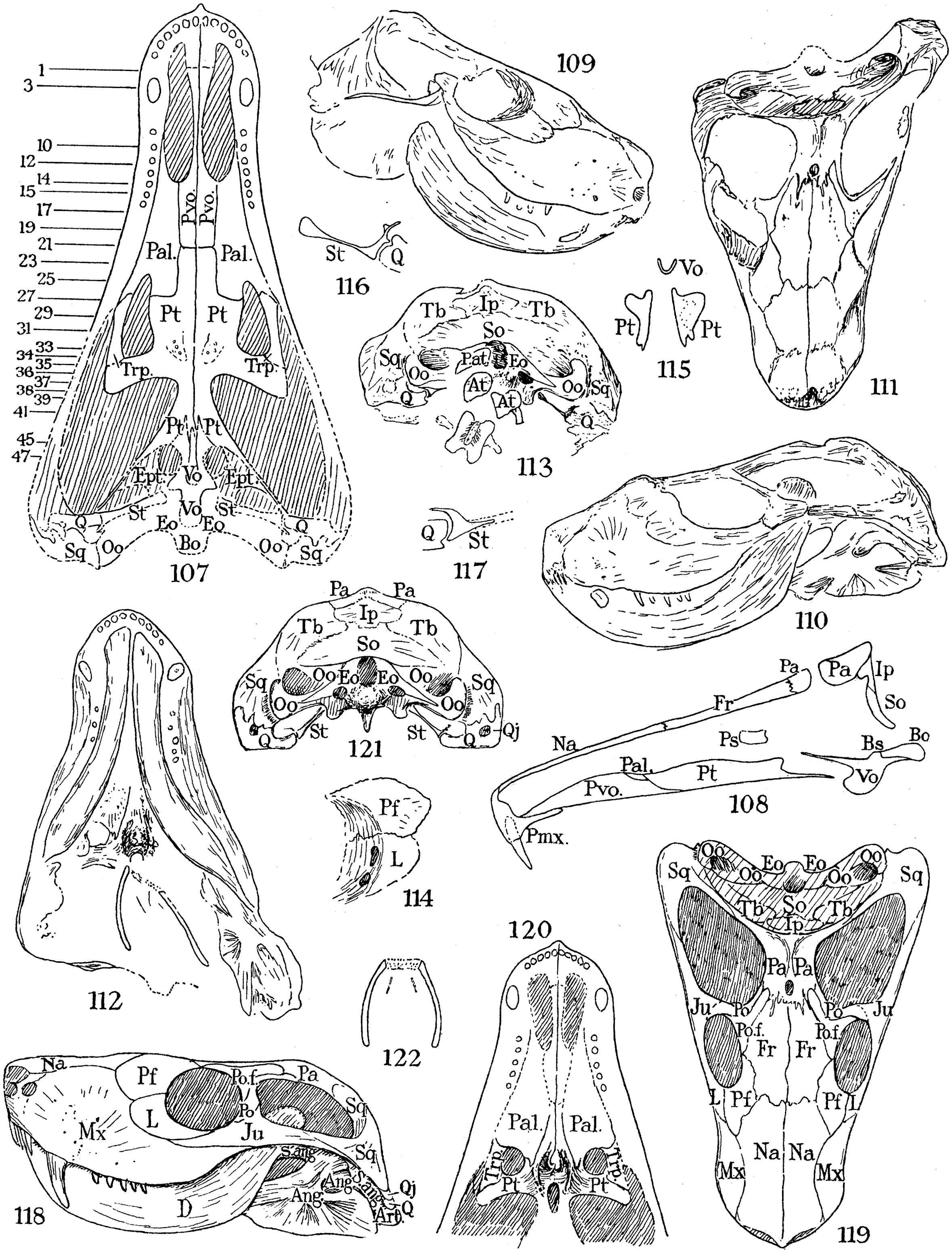
Fig. 118—Side view of skull of *Hofmeyria atavus*, with the slight distortion corrected. $\frac{4}{5}$ natural size.

Fig. 119—Top view of skull of *Hofmeyria atavus*, with the distortion corrected. $\frac{4}{5}$ natural size.

Fig. 120—Restoration of the palate of *Hofmeyria atavus*. $\frac{4}{5}$ natural size.

Fig. 121—Restoration of the occiput of *Hofmeyria atavus*. $\frac{4}{5}$ natural size.

Fig. 122—Restoration of the hyo-branchial apparatus of *Hofmeyria atavus*. $\frac{4}{5}$ natural size.




*Pristerognathus minor* and *Hofmeyria atavus.*

## Plate 9

Figs. 123–132—Various views and sections of the skull, jaws, and parts of the skull of *Hyenosaurus platyceps*, Broom. Figs. 126 and 127 are $\frac{4}{5}$ natural size, all others are $\frac{2}{5}$ natural size.

Fig. 123—Upper view of the posterior third of the skull.

Fig. 124—View of the under side of the skull, partly restored in front.

Fig. 125—View of the occiput as preserved.

Fig. 126—Median section of vomer, showing the relations to the surrounding bones.

Fig. 127—Transverse section through the vomer, showing the vomer and its relations to the surrounding bones. The position of the base of the interorbital cartilage is indicated as a dotted structure.

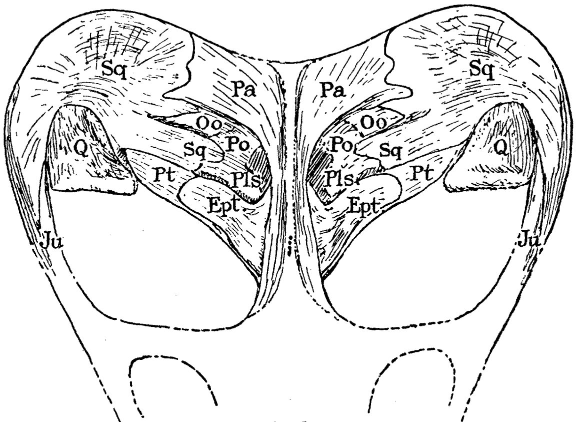
Fig. 128—Outer view of the left mandible, as preserved.

Fig. 129—Inner view of the right mandible, as preserved.

Fig. 130—Restoration of the occiput.

Fig. 131—Outer view of left mandible, restored.

Fig. 132—Inner view of right mandible, restored.

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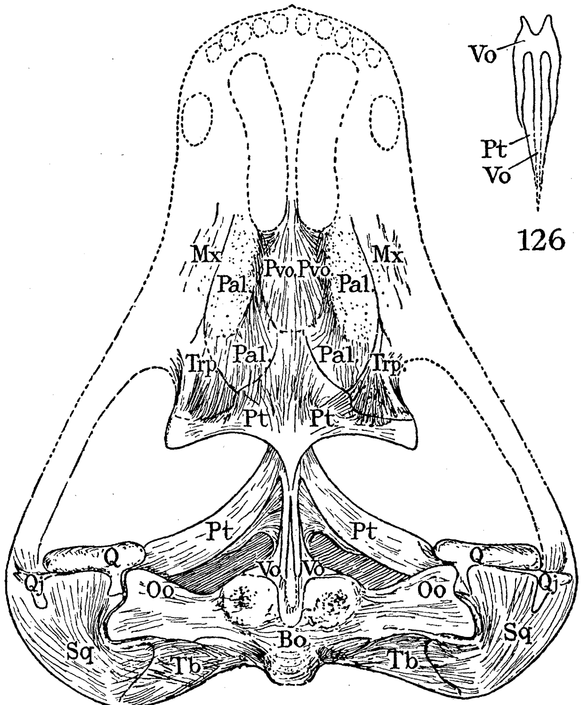


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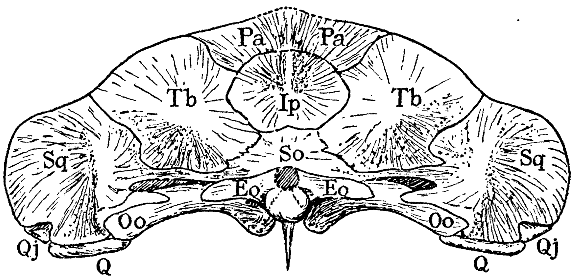


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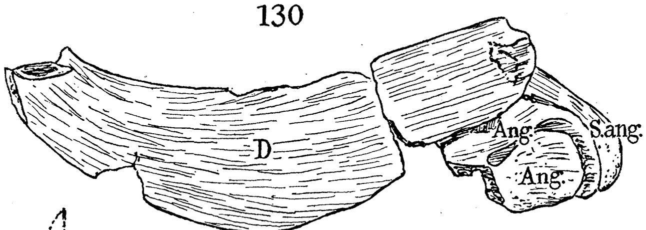


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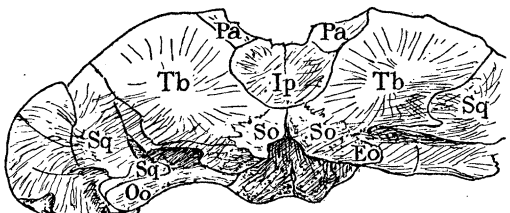


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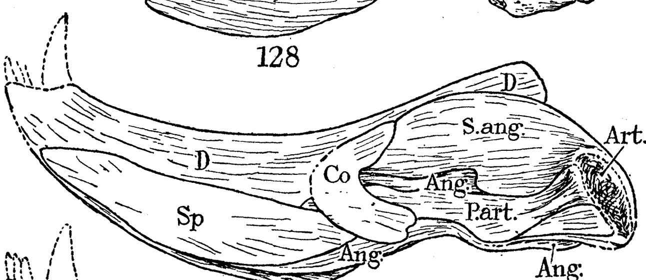


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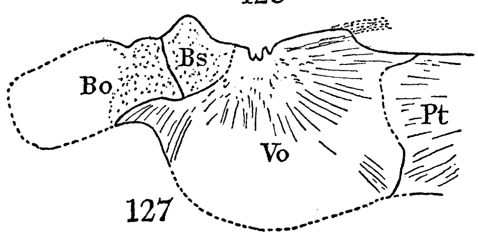


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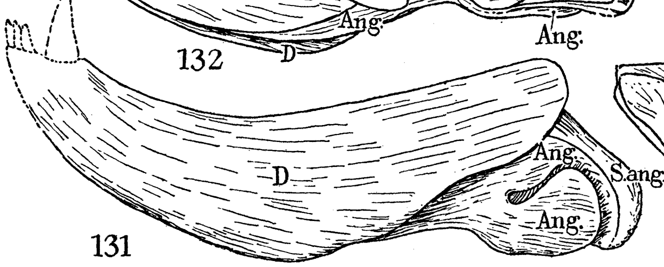


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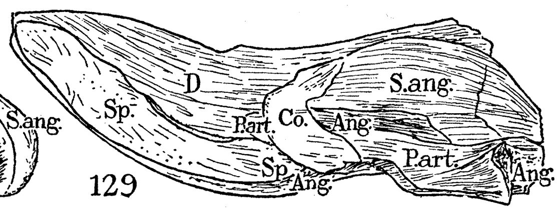


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*Hyenosaurus platyceps.*