

On the skull of Mochlorhinus platyceps, from Bethulie, Orange Free State, preserved in the Albany Museum, Grahamstown / by H.G. Seeley.

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Seeley, H. G. 1839-1909.
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Publication/Creation

[London] : [Taylor and Francis], 1898.

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On the Skull of Mochlorhinus platyceps, from Bethulie, Orange Free State, preserved in the Albany Museum, Grahamstown. By H. G. SEELEY, F.R.S., Professor of Geology, King's College, London.

SIR R. OWEN, in 1859, discriminated from *Dicynodon* some fossil reptiles, which were named *Ptychognathus*. That genus was defined by the sharp angular transverse ridge, in which the more or less flattened top of the head meets the strongly ridged long straight face. This character was made more manifest in 1870, in the same author's 'Illustrated Catalogue of South African Reptilia,' by references to the plates in which those characters are drawn. The transverse fold or ridge has been shown in every species of the genus which has been figured. The name represents an important generalization and has been generally used.

Count Marschall recorded, in 1873, that the name had been applied to two different genera, and the references were brought under my own notice by the late Mr. G. R. Crotch about 1869. Subsequently, with the aid of Professor F. Jeffrey Bell, I examined the references to *Ptychognathus*, the crustacean, which occur in the writings of Professor A. Milne-Edwards and Mr. Miers, without finding that the genus had become well known. Mr. R. Lydekker, F.R.S., in 1889, urged that since Stimpson published the name in 1858, it was not available for use by Owen in 1859. In some human

affairs long-continued usage justifies and establishes a title ; and since nomenclature is a matter of convenience, it is a nice point whether the unchallenged use of Owen's name for a long time has given the reptile a preference over the crustacean.

Professor Cope, in 1870, without apology, proposed the name *Lystrosaurus* for a South-African fossil from which he drew many of the characters of the skull in defining the Dicynodontia. When this specimen was accurately figured in 1892 it proved to be a typical example of *Ptychognathus*. If that name should be eventually withdrawn from the South-African fossil, *Lystrosaurus* is the only name which could take its place, as Professor Cope has urged ; Zittel and others have continued to use the name *Ptychognathus*.

In 1889 Mr. Lydekker discarded *Ptychognathus* and adopted in place *Ptychosiagum*, a new name applied by him to the Indian fossil from the Panchet rocks in the Lower Gondwana series, which Professor Huxley referred to *Dicynodon*, which may be conveniently retained for that type. The Indian specimens appear to differ in the shoulder-girdle, humerus, vertebræ, and all known parts of the skeleton from the remains of *Ptychognathus*, which are only obtained from the Upper Karroo rocks of South Africa, while *Dicynodon* is only known from the Middle Karroo series. No entire skull of the Indian genus is recorded, and there is no evidence that it has the generic character of a fronto-nasal angle in the skull which distinguishes *Ptychognathus* from *Dicynodon*.

The determination of the generic name is important because there are some allies of *Ptychognathus* which appear to show that it indicates a small family of South-African reptiles distinguished by the way in which the brain is elevated above the floor of the brain-case as it extends forward. This difference from some types of *Dicynodon* is comparable to that seen in modern crocodiles, in which the front of the brain is supported upon a median plate, while in Teleosaurs it rests upon the basicranial bones.

The subgeneric modifications which have come under my notice are two in number—first, a skull having a narrow longitudinally channelled cerebral region, with outwardly inclined sides, unlike the table-headed type of *Lystrosaurus* ; and, although the straight face makes an angular bend with the roof of the head, the surfaces are not parted by an angular ridge, but round into each other. That genus may be named *Rhabdotocephalus*, with the type *R. Maccaigi*. A second subgeneric form named *Mochlorhinus* is distinguished from the type *Lystrosaurus* by the perfect rounding of the face into the flat table-top of the skull, coupled with the development

of teeth upon the palate. There is no evidence of the skeleton associated with either skull; but the skull in the latter type is of some interest from its excellent preservation, which shows the sutures. In a previous paper (Phil. Trans. Roy. Soc. 1889, B, p. 290) I have drawn attention to a certain parallelism between the bones which cover the skull and the elements which roof over the spinal cord in some cartilaginous fishes. This now appears to me not only to explain why the median bones of the skull are sometimes single and sometimes paired, but to elucidate the presence of three bones in the Anomodont now to be described and in some other Vertebrata. Normally every single median bone, such as the intermaxillary (which alone is recognized in the Bidentalia termed Dicynodonts), is flanked by a pair of lateral bones—the premaxillaries. When the one is developed, the other commonly loses its individuality. So that the Theriodonts have a moderate development of premaxillary bones, but in Dicynodonts the intermaxillary is as strongly developed as are the premaxillary bones in *Ichthyosaurus*. The bone which I have termed infra-nasal in *Dicynodon* may be the premaxillary. The second median ossification in the skull—the ethmoid of birds—does not reach the surface in Dicynodonts, but appears to be related to the paired nasal bones in a similar way, though all three are rarely developed together on the surface of the skull. Next succeeds the single frontal of lizards with the pair of frontal bones on its flanks, followed by the single parietal and the pair of parietal bones; the last being the interparietal and the pair of superoccipital bones of Labyrinthodonts. Thus the roof of the skull would include the equivalents of five vertebral arches of fishes if all the elements were simultaneously developed. Without such a recognition of homology the presence of such bones as the interparietal, preparietal*, interfrontal, and intermaxillary cannot be explained. These median superior ossifications of the skull characterize Dicynodonts more than any other group of Anomodonts.

I have seen but one imperfect skull of *Mochlorhinus platyceps*. It was found many years since at Bethulie, a little north of the Orange River, near Aliwal North, by Mr. J. G. Donovan, who presented it to the Albany Museum. There I examined it in 1889. I am indebted to Dr. W. G. Atherstone, F.G.S., and the trustees of that museum for the opportunity of studying the specimen in this country and of

* The bone here named preparietal is named interparietal by Mr. E. T. Newton in Phil. Trans. B. 86, 1893, in explanations of plates xxvi. and xxxii.

removing the matrix. There is no reason to anticipate the recovery immediately of other parts of the skeleton.

This head indicates one of the smaller *Bidentalia* (A. G. Bain), distinguished from many near allies by the singularly smooth texture of the bone, which is almost as well preserved as in specimens from English clays. The sutures are more distinct than usual, and establish relations of some bones which were previously less well shown. The head is a little distorted, in consequence of contortion which has affected the rocks.

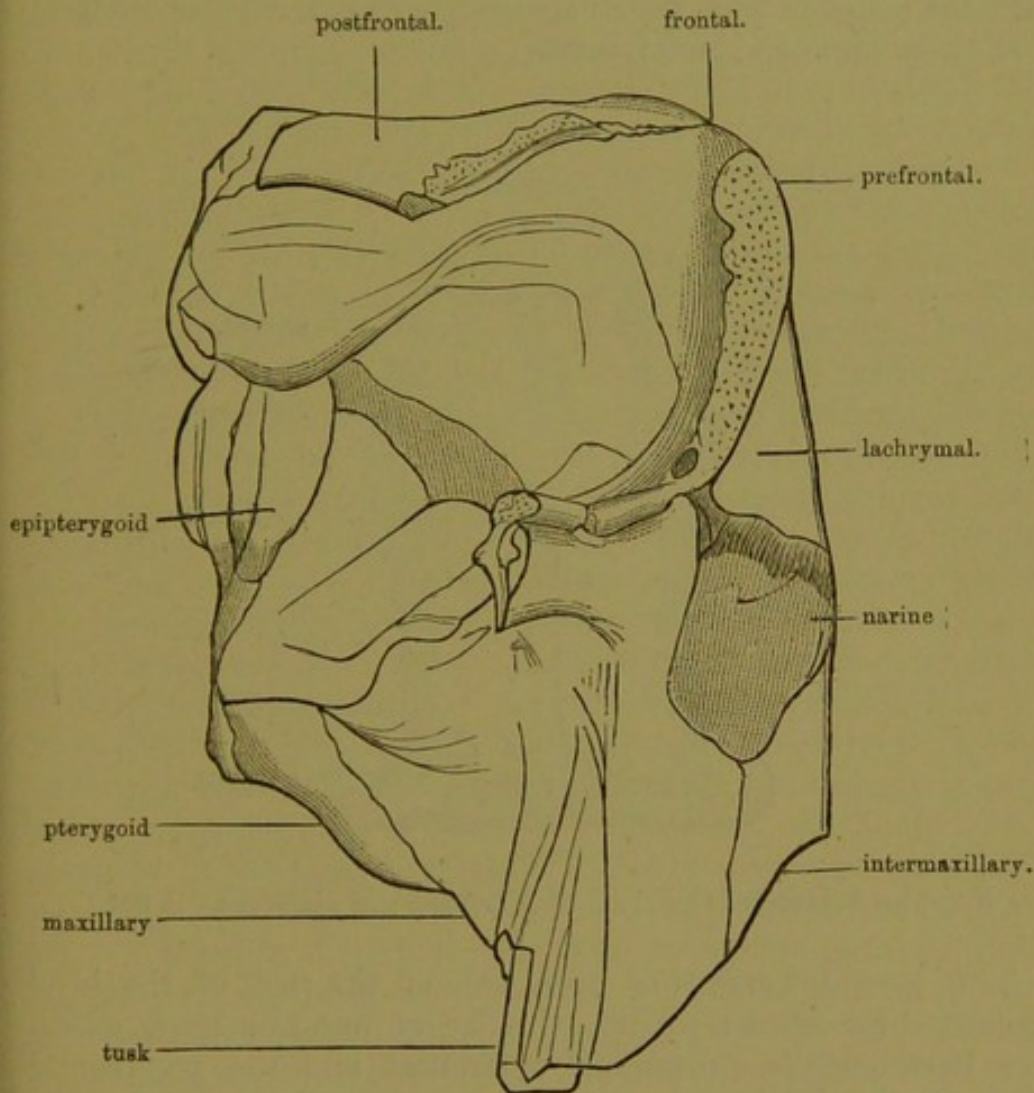
The genus *Mochlorhinus* is distinguished from *Ptychognathus* by three characters. First, the usual angular ridge between the upper surface of the skull and face is wanting, and the two areas, which commonly meet at an angle, graduate into each other in this animal by a smooth rounded transition, convex from above downward, concave from side to side (fig. 2). Secondly, the palate has the vomer elevated in front of the palato-nares, and the palatine bones at their sides so as to form three prominent tubercles. Upon the summits of these tubercles are minute teeth; they are small, flat, and circular on the summit of the vomer, but further back the teeth become much smaller and pointed (fig. 3). Thirdly, the head appears to be much more compressed from side to side than is usual in *Ptychognathus*, in which the skull is relatively wider in front of the orbits, giving the animals a table-headed appearance between the orbits. With this character is associated the position of the face at right angles to the crown of the head, giving an unusual depth from the frontal region to the palate, which exceeds the length from the nasal bones to the interparietal by almost one half that distance (fig. 1).

The genus is placed in the family *Ptychognatharhinidæ*. That group is characterized by the rapid elevation of the brain as it extends forward and abuts against the interorbital septum.

From the occipital plate the head measures 4 inches in length along the flat smooth crown to the rounded fronto-nasal surface. In vertical depth the measurement is about $7\frac{1}{2}$ inches from the frontal bone above the large lateral orbit to the point where the tusks, descending vertically, emerge through the maxillary bones. The roots of the tusks form prominent vertical rounded ridges, $3\frac{1}{2}$ inches long, at the sides of the head; they originate a little below the orbits, at less than 2 inches behind the vertical flattened prominence of the intermaxillary which forms the median part of the face. These lateral ridges give the face a transverse measurement of about 4 inches. The tusks have a diameter of $\frac{6}{10}$ inch at

the base, but both are broken and lost from the positions where they leave the maxillary bones. The transverse width between them on the palate is $1\frac{1}{2}$ inch. The roots of the tusks, as usual, are nearly parallel to each other, but converge slightly as they descend below the vomerine level of the palate. Seen laterally their contour is parallel to the lower part of the anterior outline of the nearly vertical face.

Fig. 1.



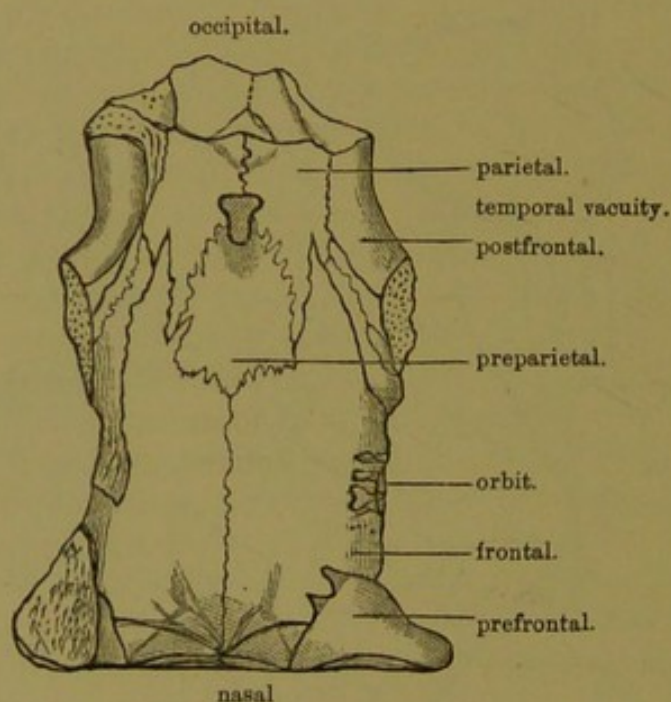
Right side of the skull of *Mochlorhinus platyceps*. $\frac{1}{2}$ nat.

The imperfections of the skull are:—loss of the anterior biting border of the intermaxillary bone between the tusks; the hinder part of the palate is missing, including the basisphenoid, together with all the bones which are about the foramen magnum; the squamosal and quadrate bones are lost with the malar arches which define the temporal vacuities, together with the descending postfrontal arches

which define the hinder border of the orbits. The bones are better preserved on the left than on the right side, but compression has partially closed the left orbit.

The flattened upper surface of the head is smooth, slightly concave from side to side, less than 4 inches long, and limited behind by a transverse ridge. That ridge is made by the interparietal bone, which is not vertical, but somewhat inclined forward. The interparietal makes the upper part of the occipital plate, and it abuts laterally against the pair of parietal bones. The transverse ridge which divides them is a slightly sinuous line of suture.

Fig. 2.



Superior surface of the skull of *Mochlorhinus platyceps*. $\frac{1}{2}$ nat.

The lateral borders of each side of the roof of the head include three areas:—First, the larger anterior part, which lies between the prominent prefrontal and the postfrontal bone, is the thickened, rounded, upper margin of the orbit, which is concave from front to back, formed in the middle by the frontal bone. Secondly, behind the orbits are the broken bases of the external processes of the postfrontal bones, which are thin, and probably descended in the usual way. Thirdly, behind these missing postfrontal processes are the obliquely inclined upper borders of the temporal vacuities. They are concave from front to back, slightly convex from above downwards, over an inch long, and about $\frac{6}{10}$ inch deep, margined superiorly by a sharp ridge, which is a suture separating the

inclined external surfaces, which are formed by the post-frontal bones, from the parietal bones upon which they rest. Underneath these areas the skull is excavated in the usual way.

The parietal bones are three in number. At their junction the parietal foramen is placed; it is oblong, keyhole-shaped, rather wider behind than in front, $\frac{4}{10}$ inch long, $\frac{3}{10}$ inch wide behind, and more than half that width in front; its transverse hinder border is $\frac{4}{10}$ inch from the posterior occipital ridge. The two parietal bones, which meet behind the parietal foramen in a sinuous median suture, form a slight inflation where the hinder end of the suture meets the interparietal bone. The flat parietals extend transversely outward to the margin of the inclined concave temporal vacuity formed by the postfrontal bone. Anteriorly the two parietal bones diverge, and a somewhat heart-shaped median preparietal bone is contained between the long narrow anterior processes of the parietals. External to those processes the frontal bones are prolonged backward upon the parietal bones, so as to divide their anterior border into a longer internal process and a shorter outer process. The single median bone (preparietal) is $1\frac{4}{10}$ inch long, though not measuring more than an inch in the median line, because its narrow hinder margin is notched out by the parietal foramen. It is $\frac{9}{10}$ inch wide in front where widest, and its convex serrated anterior border extends forward somewhat in advance of the narrow inner lateral parallel processes of the parietal bones which flank it. It is usually regarded as a parietal bone; but it is in the linear position of the interparietal, ethmoid, and intermaxillary bones, as occupying a median position in the skull alternately with the paired bones of the brain-case and face, such as the parietal and frontal. In osteology it has been sometimes treated as though it were the principal parietal, when the two posterior bones are often described as its posterior divergent processes among existing reptiles, when the interparietal bone is not separately ossified. Reasons have been urged for comparing these paired and unpaired ossifications with those found arching over the neural canal in the spinal column in *Lamna* and other Elasmobranch fishes, in which there is a similar alternation of paired and unpaired bones, which suggest a certain homology between the cranial and vertebral structures; and since the single median bone now described has much the same relation to the frontal bones that the interparietal has to the parietal bones, it may be known as the preparietal; it appears to be a good distinctive feature of these Anomodont skulls. It probably disappears in many

animals by blending with the parietal, just as the interparietal appears to blend commonly with the supraoccipital. When it is present, the preparietal has the aspect of being the key-structure of the roof of the brain-case, lying in front of the parietal foramen.

These three bones form the hinder part of the roof of the skull above the brain-case; they meet the frontal bones anteriorly.

Each frontal is an elongated oblong bone, and the pair unite by a slightly undulating median suture which extends forward just over the rounded angle between the face and the upper surface of the skull; their extremities converge in front and diverge as they extend backward.

The length of the median frontal suture is about 2 inches, though their extremities extend back so as to make each bone $3\frac{1}{4}$ inches long. The transverse width over the frontal bones in the middle of the orbits is about $2\frac{3}{10}$ inches, and, owing to the elevation of the margin of the orbit, the superior surface is transversely concave.

The transverse width of the skull increases in front owing to the way in which the prefrontal bones, which make the anterior corners of the orbits, are prolonged outward and downward, giving the orbits a position (fig. 1) which is entirely lateral, where the eyes look outward and very slightly upward. The prefrontal bone is only well preserved on the left side.

The postfrontal bone joins the frontal at the back of the orbit by a suture which is easily traced, and that bone thus enters into the upper surface of the skull, joins the parietal bone behind, and extends backward upon that bone so as to form the inclined concave borders of the temporal vacuities. This backward extension of a flange of the postfrontal upon the parietal is substantially the same condition as is seen in the corresponding region in *Cynognathus* and other Theriodonts, notwithstanding the circumstance that in that group of animals the parietal bones form a median knife-like edge, and in this and many other Dicynodonts those bones form a broad flattened crown between these plates of the postfrontal. The suture is not usually seen, because it runs in the line of the slightly elevated ridge which defines the temporal concavity. Between this suture and the suture which limits the frontal bone there is manifestly another suture on the upper surface of the skull, defining a long narrow oblique bone which enters into the orbit at its upper hinder angle. It is about $1\frac{1}{4}$ inch long and about $\frac{3}{10}$ inch wide on the orbital border. It appears, therefore, to be in the position of the postorbital bones; for

the bone, which is only well preserved on the left side, is essentially an anterior dismemberment of the postfrontal, and it may possibly be prolonged downward to meet the malar bone.

The median upper border of the orbit is vascular and somewhat rugose. The internal surface of the bones of the orbit is smooth and regularly curved, and shows the sutures of the frontal with the other bones. The orbit was probably deeper than wide, the depth being $2\frac{3}{4}$ inches from the frontal bone above to the part of the maxillary which is above the base of the root of the tusk. The eye may have been slightly oblique and possibly looked to a small extent outward and forward as well as upward. The under surface of the postfrontal bones is smoothly excavated.

The external surface of the prefrontal bone differs in texture from the frontal in being less smooth, and agrees in this respect with the nasal bones, from which it extends laterally outward, and is defined by a distinct suture.

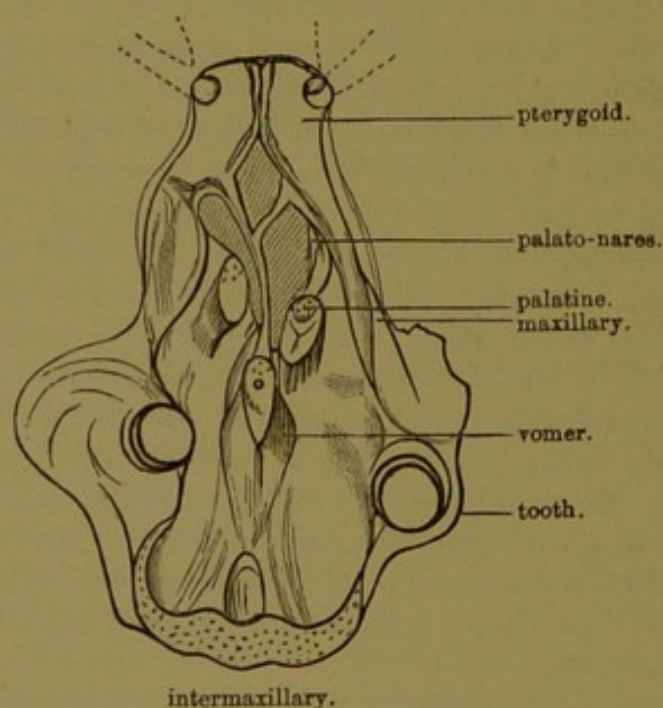
The skull of *Dicynodon tigriceps* has shown that the nasal bones extend transversely across the face, so as to meet the frontal bones behind them, where their transverse width exceeds the width of the prefrontal bones. In this genus the nares are relatively further forward and differently conditioned, so that the nasal bones are elongated from back to front. They constitute the upper border of the nares, are about $3\frac{1}{4}$ inches long and $2\frac{1}{4}$ inches wide. In the median line the nasal bones are overlapped in front by an unpaired bone—the intermaxillary—and that overlap causes them to appear to diverge as they extend forward. The hinder border of the nasal bone meets the lachrymal, which is large and placed between the prefrontal and nasal in front and the maxillary behind. It extends forward into the nasal vacuity, forming its hinder floor. The cavity which lodged the lachrymal gland was behind the nostril and below the eye, about $2\frac{1}{2}$ inches long and $\frac{6}{10}$ inch wide, rather narrower in the middle. The lachrymal duct is circular and has the usual position.

The single unpaired condition of the intermaxillary is not associated with a pair of premaxillary bones in this animal. The face comprises three regions—a narrow median anterior area, $1\frac{1}{2}$ to $1\frac{3}{4}$ inch wide, marked with a slightly elevated median ridge, and parallel to this are the rounded angles which separate this median anterior region from the oblique lateral areas. This long flat nose is very gently convex from above downward. A well-defined suture extends from the lower angle of the large diamond-shaped narine and divides the

anterior intermaxillary from the large maxillary bone behind it (fig. 1). This suture is straight and parallel to the base of the tusk in the maxillary bone, which is about an inch behind it. The face, which is about $2\frac{1}{2}$ inches in lateral depth from the flat nose to the roots of the teeth, has the aspect of being compressed from side to side. In the middle length of this compressed area, below the orbits and slightly in front of them, are the anterior nares. Another compression (parallel, vertical, and further backward) defines the inflation of the maxillary caused by the roots of the teeth (fig. 3).

In front of the tooth the palatal edge of the maxillary bone is compressed to a thin sharp cutting border, which descends below the palate, so that the sides of the lower jaw could work between the teeth. There is no doubt that the intermaxillary formed a continuation of this arch, which had the usual concave upward recession, though the cutting-edge of the middle part is fractured and lost. Behind the narine the jugal process of the maxillary bone is partly preserved, and behind and below this process the maxillary bone is greatly com-

Fig. 3.



The palate of *Mochlorhinus platyceps*. $\frac{1}{2}$ nat.

pressed, for the head is narrower in transverse measurement behind the socket for the tooth than in front of it. The maxillary is prolonged backward above the pterygoid bone behind the palato-nares, as is shown in lateral aspect of the skull, and forms a wedge which narrows to its hinder termination (fig. 1).

In general plan the palate closely resembles that of the short-faced *Dicynodonts*. Its distinctive features consist in the development of a strong descending median ossification, which is a little behind the tusks and in advance of the palato-nares. It corresponds in position with the vomer and forms a compressed prominence, which is nearly 2 inches long and is prolonged backward as the narrow median ridge which divides the palato-nares. This ridge may be paralleled in many *Dicynodonts* and has been figured by Sir Richard Owen in the species of *Dicynodon* named *D. pardiceps*, *D. testudiceps*, and others. Another remarkable feature is the evidence that the bone internal to the maxillary and pterygoid and behind the vomer, which I regard as the palatine, develops a strong tubercle, flanking and defending the outer anterior corners of the palato-nares. The sutures are not shown which define the palatine from the pterygoid, but there is no reason to question the identification of these eminences as palatine tubercles. There appears to be a slight approximation to a similar condition in the palate of *Dicynodon pardiceps*. In view of the fact that the vomerine and palatine bones in *Pareiasaurus* and other allied reptiles bear teeth upon elevated ridges upon those bones, I was led to infer that, since they are on the same level, they might have a similar function. On the highest part of the vomer there are small teeth which are flat and rounded in front, though few are preserved. They are similar to the teeth figured in the South-African *Cynodont* *Ælurosaurus felinus*. On the hinder border of the vomer and palatine there are minute pointed teeth, recognized by their black enamel. I have not observed such strong palatine tubercles in any other fossil, nor are there evidences of teeth on the palate in the present condition of any *Dicynodont* skull in the British Museum.

The anterior terminations of the pterygoid bones external to the palatine tubercles are compressed from side to side and well separated from the maxillary bones in front of them by a vertical suture. The middle of their most convex anterior part, which makes the outward limit of the palatal border, is rough with short irregular sinuous wrinkles, as though pterygoid muscles had extended from them to the lower jaw.

The palato-nares are distorted; they were apparently almond-shaped, about $1\frac{1}{4}$ inch long, narrower in front than behind, and parted posteriorly by a median excavation like that seen in *Dicynodon pardiceps*, *D. Copei*, and other forms.

The transverse measurement over the anterior termina-

tions of the pterygoid bones is $1\frac{7}{10}$ inch. The palate begins to contract in transverse width from the moment that the pterygoid replaces the maxillary bone in forming its lateral margin; and behind the median post-narial vacuity, where the convex contour of the anterior process is exchanged for a contour concave from front to back, the transverse width of the united pterygoid bones is $1\frac{1}{10}$ inch. The pterygoid bones meet in the median line in a slight ridge; they are fractured transversely just behind the bases of the slender processes which appear to have been given off to the quadrate region, and all the hinder part of the smooth post-palate, with the adjacent bones, is lost.

The superior surface of the pterygoids supports the remarkable median plate first studied by Huxley in *Ptychognathus Murrayi*. It extends upward as a vertical partition between the orbits, and joins both the brain-case and its frontal prolongation forward. This thin partition consists of several bones; the uppermost and most anterior is identified as the orbito-sphenoid, and is most absolutely between the orbits, below the front of the brain-case, and below the frontal bones. A film of matrix may separate it from the bones below, which may be compared with those of *Dicynodon tigriceps* figured in the Phil. Trans. 1888. On the posterior fracture this median plate is shown as an extremely thin vertical film (fig. 1), but matrix rests upon it supporting a vertical bone external to the plate, which may be the element termed the columella or epi-ptyergoid, since it is between the parietal and pterygoid regions, though neither its upward nor downward terminations are preserved. In front of it, manifestly rising from the pterygoid, are the two films of bone which extend towards the orbito-sphenoid; the hinder of these I have generally termed the median plate of the pterygoid, but it now seems not improbable that this thin ossification should be the alisphenoid, since it is immediately under and apparently continuous with the brain-case and extends downward to the sphenoidal region. An oblique suture which extends upward and forward separates it from the presphenoid. Both those bones appear to be truncated above and to meet the orbito-sphenoid, though the matrix already referred to either intervenes between the bones or hides their junction. In front of the presphenoid there is manifestly another bone immediately above the position of the vomer. It is situate between the nares and extends forward to the position of the nasal bones, so that it is in the position of the ethmoid.

All that remains of the occipital region is the median part

of the interparietal bone, which is about an inch deep, broken on each side, has a vertical median ridge, and at its base shows a fractured fragment of the supraoccipital, which is excavated on its anterior border by a vertical concavity like that seen in figured *Dicynodonts* in the British Museum, which display the cerebral aspect of the occipital plate. The bone is obviously narrow; at its sides are the thin walls of the brain-case; those walls meet inferiorly in the median line, so as to rest upon the interorbital septum which has been described; and it extends backward to the supraoccipital and interparietal bones, but not much in advance of the anterior angle of the bevelled concave temporal region, where the postfrontal rests on the parietal. The parietal bones form the upper covering of this brain-case.

All the allied skulls which I have seen from the Upper Karroo rocks are remarkable for side to side compression, while the *Ptychognathus* type widens superiorly to the flat interorbital table on the top of the head.

