On Pareiasaurus bombidens (Owen), and the significance of its affinities to amphibians, reptiles, and mammals / by H.G. Seeley.

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Seeley, H. G. 1839-1909. Royal College of Surgeons of England

#### **Publication/Creation**

London: Published for the Royal Society by Trübner, 1888.

#### **Persistent URL**

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## PHILOSOPHICAL TRANSACTIONS

OF THE

# ROYAL SOCIETY OF LONDON.



VOL. 179 (1888), B, pp. 59-109.

[Plates 12-21.]

### RESEARCHES

ON THE

STRUCTURE, ORGANIZATION, AND CLASSIFICATION

OF THE

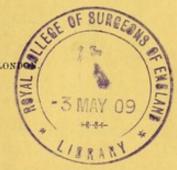
# FOSSIL REPTILIA.

II.—ON PAREIASAURUS BOMBIDENS (OWEN), AND THE SIGNIFICANCE OF ITS AFFINITIES TO AMPHIBIANS, REPTILES, AND MAMMALS.

BY

H. G. SEELEY, F.R.S.,

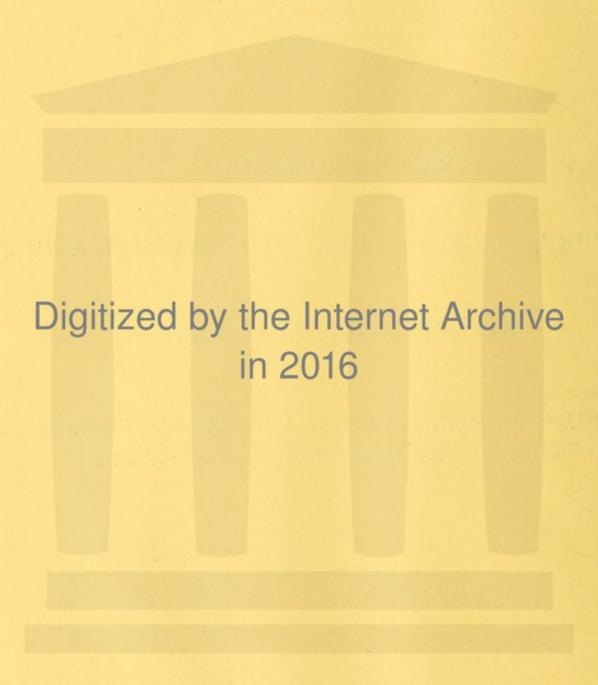
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#### LONDON:

PUBLISHED FOR THE ROYAL SOCIETY BY TRÜBNER AND CO., LUDGATE HILL, E.C. 1888.

B. 22.



[ 59 ]

III. CROONIAN LECTURE.—Researches on the Structure, Organization, and Classification of the Fossil Reptilia.—II. On Pareiasaurus bombidens (OWEN), and the Significance of its Affinities to Amphibians, Reptiles, and Mammals.

By H. G. Seeley, F.R.S., Professor of Geography in King's College, London

Received April 21,-Read May 12, 1887.

[PLATES 12-21.]

The genus Pareiasaurus was instituted by Sir Richard Owen in 1876\* for a large number of Reptilian remains from the Karroo Series of strata of South Africa. It was classed with the Dinosauria in a new family named Serratidentia, and regarded as represented by two species, which were named P. serridens and P. bombidens. Its place among the Dinosauria was held to be established by the teeth, which were compared to those of Iguanodon in their mode of implantation, and to those of Scelidosaurus in their close arrangement and nearly uniform wear, while the margins of the crown are similarly notched or serrate. The cranial characters are stated to concur with the dental characters in supporting the formation of a family in the Dinosaurian order for these fossils. Unfortunately the type-skull of Pareiasaurus serridens is now only known from a plaster cast, and by some small fragments cut from the lower jaw. The immense development of the so-called malar processes, which overlap the lower jaw and suggested the generic name, was regarded as showing a resemblance to the genus Anthodon from South Africa, and in a less degree to Scelidosaurus from the Lias of Charmouth. Regarding the fossil as a vegetable feeder, Sir R. Owen remarked that the homologous descending malar process among Mammals is found only in those types which come nearest to Reptiles in brain structure, such as Kangaroos, Sloths, and Megatheroids.

In the cervical vertebræ sub-vertebral wedge-bones are found, which are likened to those which are said to occur in the fore part of the neck of Ichthyosaurs and Plesiosaurs. A notochordal canal penetrates to the centre of the centrum without piercing it, sometimes in a way almost Ichthyosaurian, but sometimes as a slender conical tube extending from the flattened articular face of the centrum. Sir R. Owen

<sup>\* &#</sup>x27;Descriptive and Illustrated Catalogue of the Fossil Reptilia of South Africa,' 1876.

<sup>†</sup> In the 'Quarterly Journal of the Geological Society,' vol. 32, 1876, p. 45, the family is also named Tretospondylia, and made to include Tapinocephalus and Pareiasaurus.

remarks,\* it is a trace of a lower grade of vertebral structure, and 'recalls the more widely perforated, still less ossified, centrums of the vertebræ of Ganocephalous Reptiles of the Carboniferous Series represented by Parabatrachus, Hylonomus, Dendrerpeton, &c.' The ribs are double-headed, with a parapophysial articulation on the centrum, a diapophysial facet on the neural arch.† The scapula and coracoid are said to be anchylosed together. The humerus is described as relatively broader than in Omosaurus, rather suggesting the breadth of the bone in the Mole. The bone is solid. Other parts of the skeleton are identified; but no further suggestions are made as to the organic relations of the type.

About nine years ago the 'masons' in the British Museum, under the skilful direction of Mr. William Davies, F.G.S., removed the matrix from the skull and axial skeleton of an animal of this genus from Palinut Fontein, South Africa, sent to the Museum by Mr. Thomas Bain in May, 1878. The specimen (Plate 12) gives more ample and exact evidence of the nature of *Pareiasaurus* than was previously available, and renders a re-examination of its affinities convenient. I have undertaken this description in the belief that the structures of *Pareiasaurus* throw more light upon the evolution of the Reptilia than any fossil that has been described. And I would express my thanks to Dr. Henry Woodward, F.R.S., Keeper of the Geological Department, for the facilities afforded me in making this examination.

### The Head.

# (Plates 13-16.)

The skull has the general contours of the head of a Frog, being broadly rounded in front, with the alveolar and jugal margins diverging posteriorly so as to form about two-thirds of an ellipse. The occipital border is transverse, and not evenly truncated. The upper surface of the head is flat, and the moderately deep post-orbital regions are obliquely inclined, so as to look outward and upward. The post-malar bones descend over the lower jaw in broader stronger processes than are seen in *Rhynchosaurus*, but differently shaped from those seen in Edentates. The head is widest over the inferior extremities of these processes, where the width is about equal to the length, which measures 45 centims.

The superficial bones, especially of the cheeks and upper part of the head, are sculptured with a pattern which combines radiating grooves of a Labyrinthodont type with Crocodilian pitting. In structure the skull, examined from above, is essentially Labyrinthodont; but, seen from the palatal aspect, it is altogether Dicynodont. The dentition is distinctive, but on the whole makes a close approximation to that of Dinosaurs. The right side of the head is in less perfect preservation than the left side, especially along the roof-bones, but the specimen has suffered no distortion.

<sup>\* &#</sup>x27;Geol. Soc. Quart. Journ.,' vol. 32, 1876, p. 45.

<sup>† &#</sup>x27;Descriptive and Illustrated Catalogue of the Fossil Reptilia of South Africa,' &c., 1876, p. 10.

I propose first to describe the nasal and orbital vacuities, then the structure of the external bones of the skull, and finally the palate and lower jaw.

#### The Nares and Orbits.

### (Plates 13 and 14.)

The nares are transversely and ovately elongated, but it is uncertain whether they were completely divided. The transverse measurement over them is 15 centims., and the width of the premaxillary process which rises between them is 2 centims, where fractured. It is probable that the nasal apertures were conditioned much as in Gorgonops, in which the nasal bones approach the premaxillaries without forming a bony union with them. But in this fossil the nares are much larger than in Gorgonops, approach more closely together, and are less covered superiorly by the nasal bones, so that the vacuities look upward and forward. Each is about 4 centims. deep in oblique measurement from the concave posterior border on the nasal bone to the convex anterior border on the maxillary. But the vertical depth of the aperture is about 2.5 centims. Their contours approach that of a figure 8 placed transversely. The outer half of the inferior nasal border in the maxillary bone is channelled on its horizontal aspect with a broad concave groove 1.5 centim. wide, which ascends the ascending process of the maxillary bone and is limited externally by a sharp marginal ridge. Towards the median ascending process of the premaxillary bone the ridge dies away, and the bone is obliquely compressed so as to form a flattened area which looks upward and forward, and extends backward almost as far as the ascending premaxillary process, which rises almost vertically from it. There appears to be a bony floor to the nasal passage, but the bones are not in a condition to be determined; and, though a part of the passage is exposed, it only shows, behind the premaxillaries, a small perforation, and a slight median ridge which appears to be vomerine. The nasal bone above the nares is compressed, and impressed on its external half by a broad canal which is fully 3 centims. wide. This canal narrows as it ascends the convex nasal bone, and forms a deep groove with an elevated inner border, which is first directed backward, and then outward and backward, so as to terminate above the anterior angle of the eye, where it descends towards the orbital margin in a wide smooth expansion. I regard this canal as being the lachrymal mucus-canal, comparable to those of Labyrinthodonts, which are similarly placed.

The orbits for the eyes are placed laterally in the middle of the sides of the head. They look obliquely upward and outward, and very slightly forward. They are transversely elongated, 9.5 centims. long, are concavely rounded posteriorly, 5.5 centims. deep in the middle, and pointed anteriorly, so that the outline is somewhat transversely pear-shaped. The anterior corner, which is inclined slightly downward, is 8 centims. behind the outer border of the narine; the space about it, and especially above it, is smoothed and somewhat impressed, indicating, I believe,

the posterior origin of the supra-narial canal, which appears to expand towards the orbit, just as it expands towards the narine. There is no recognisable lachrymal perforation, and the lachrymal bone is either absent, or represented by a scale in the mucus-canal which appears to be perforated. The bones which form the superior border of the orbit are very thick, but the maxillary bone below is comparatively thin. The measurement from the upper border of the orbit to the median line of the skull is 10 centims., and the transverse measurement over the skull at the lower orbital border would be about 28 centims. These are apparently the only vacuities in the skull, though minute temporal fossæ, like those seen in *Capitosaurus*, may exist in the posterior region in the area of the squamosal bone, which is badly preserved; but the evidence on this point is very unsatisfactory.

## The Premaxillary and Sub-narial Bones.

(Plate 14, fig. 1, pm. in.)

The premaxillary bones are separated from each other by a median suture. They are narrow, and rise above the lower nasal border in an inter-narial process, which is There is no evidence which is quite conclusive as to the form and size of the bone. In the type-specimen of P. bombidens (British Museum Register, 43,525) I am clear that each bone only contains two teeth. But besides the suture, which extends obliquely outward, upward, and backward, giving an apparent superior width of 7.5 centims, to the bone, there is also a suture which ascends over the second tooth inward to the lateral margin of the ascending premaxillary process. These two sutures define a triangular plate, the apex of which descends between the second and third teeth, and the base of which extends along the narine. I regard this bone as a dermal plate, which hides the suture between the premaxillary and maxillary bones. It may be termed sub-narial, and is regarded as belonging to the same series as the supra-orbital, infra-orbital, and lachrymal bones of other animals. Professor W. K. Parker, F.R.S., has described skeletal elements above the maxillary and below the nasal, forming a floor to the nostril, as characterising Urodeles and Anurous Batrachia, Varanian and other Lizards, and Snakes,\* with which this ossification may, I think, be compared. In the specimen of Pareiasaurus now described, the structure of this region of the jaw is less clear, because the sub-nasal scale is so perfectly blended with the bones beneath, that its sutural limits are not very distinct. Hence the premaxillaries are narrow bones, formed on the Amphibian rather than a Mammalian type, which become narrower as they extend superiorly towards the nares. Their external surface is flattened, and retreats a little as it ascends, in harmony with the convex rounding of the snout. The fractured superior surface of the premaxillaries is oblong, having an antero-posterior extension

of 4 centims, and a width of 2 centims. The teeth in its alveolar border differ in no respect from those in the maxillary bones. The palatal border of the premaxillary bones, like that of the maxillaries, projects downward below the palate so as to form an arch of bone within which the lower jaw is received.

The Maxillary Bones.

(Plates 13 and 14, m.)

The maxillary bones are moderately elongated, gently convex in length, and appear to contain 18 teeth on each side. Below the anterior corner of the eye the maxillary unites with the malar bone, which extends wedge-like into the middle of the maxillary, so that its anterior extremity has about five teeth below it in the posterior extremity of the maxillary, and there is a much shorter superior overlap of the maxillary upon the malar on the anterior border of the orbit. Measured round the curve, from the median premaxillary suture to the extremity of the sutural union between the maxillary and malar bones, the distance is 26 centims., and along the whole of this distance teeth are developed which are directed downward and inward. The maxillary bone is moderately deep, and has a strong ascending nasal process which is behind its middle portion and inclined a little posteriorly. It separates the orbit from the narine. The depth of the bone at the narine is 5 centims.; the depth at its posterior end is less than 6 centims. The least width of the ascending process between the anterior corner of the orbit and the external limit of the narine is 8.5 centims. The process is in a different plane to the rest of the bone, bulging anteriorly towards the narine, and retreating inward posteriorly towards the orbit. It extends upwards to the canal between the narine and orbit, along which the suture runs which divides it from the nasal and prefrontal bones. The vertical height from the alveolar border to the almost horizontal area external to the lachrymal canal is 10 centims. Round the middle of the external part of the body or dentary part of the bone is a row of large, distant, supra-dental, vascular foramina, which commence about 2.5 centims, above the alveolar border anteriorly, and descend to a height of 1 centim, posteriorly. At least six are seen which penetrate the bone as conical pits and vary irregularly in diameter from 5 to 15 mm. This main mass of the bone is very gently convex from the alveolar margin upward, and shows no trace of the inflated longitudinal ridge which runs along the middle of the bone in the type specimen of Pareiasaurus bombidens,

The Malar Bone.

(Plates 13 and 14, fig. 2, mr.)

The malar or jugal bone is about 17 centims. long, convex from above downward, roughened with small tubercles in front, and rugose behind with a coarser ornament,

which is in harmony with that seen on the whole of the cheek into which it enters. The bone is elongated, concave superiorly, and obliquely truncated posteriorly in the manner of the prow of a barge; hence, while the superior border is about 15 centims. long, the inferior border is relatively short, and does not exceed a length of about 11 centims. Inferiorly it does not quite reach the post-alveolar border of the jaw, being excluded by the attenuated posterior process of the maxillary bone, which underlaps it anteriorly; and posteriorly it is underlapped by the quadrato-jugal, which is similarly attenuated as it extends forward, and it just meets the maxillary bone. The oblique posterior suture which limits the malar bone is about 8 centims. long. Posteriorly the bone has the quadrato-jugal below it, and the supra-quadrate bone behind; its rounded superior hinder extremity penetrates slightly between the front of the squamosal bone and the base of the post-frontal, which forms the upper hinder border of the orbit. On the posterior superior border, wedged between it and the post-frontal there appears to be a small bone, imperfectly preserved, which enters the orbital border, which I regard as the post-orbital bone. The depth of the malar below the middle of the orbit is about 5 centims., and it terminates anteriorly in a broad wedge suture which extends into the maxillary as far as the anterior angle of the orbit.

#### The Cheeks.

## (Plates 13 and 14.)

Behind the orbits, the cheeks form a coarsely sculptured mass of bones which extend continuously from the squamosal to the quadrato-jugal, and from the post-frontal to the hinder border of the head. These cheeks have a length of at least 18 centims. and a depth of 18 centims. The left side has not been developed to show sutures distinctly, but on the right side they are strongly marked by the weathering of the specimen. The bones completely hide the quadrate bone from lateral view, more absolutely than in Ichthyosaurians and Labyrinthodonts. The bony elements forming the cheeks are the same as form the cheeks in those orders of animals, and they are similarly arranged. There is a post-orbital bone at the back of the orbit between the jugal and post-frontal; the post-frontal bone, which is large, is placed at the upper hinder angle of the orbit, and meets the squamosal behind. Below the squamosal and behind the malar is the supra-quadrate, and below the supra-quadrate and posterior part of the jugal, is the quadrato-jugal bone.

The Quadrato-jugal.

(Plates 13 and 14, qj.)

The quadrato-jugal is a long wedge-shaped bone, 20 centims. in length, which tapers anteriorly to a point. Its superior border is in contact with the malar bone in

front and the supra-quadrate bone behind by a suture which is nearly horizontal and approximately straight, but undulating. It is this bone which causes the oblique downward descent of the cheeks over the posterior part of the lower jaw, and not the malar bone, as in Rhynchosaurus and Scelidosaurus, so that the analogy with Dinosaurs, which was based upon the supposed resemblance of that development to the downward growth of the malar in Scelidosaurus, cannot be sustained. The quadrato-jugal is fully 6 centims. deep posteriorly, but is slightly abraded; its posterior border is vertically truncated, about 6 centims. long, convexly rounded from within outward, and forms inferiorly a large convex knob. In the middle of the posterior part of the external surface of the bone there is a strong vertical ridge; the whole surface is pitted, but the rugosities are not very marked. The inferior border of the bone is nearly straight, and convex from within outward. The internal aspect of the bone is smooth, concave in length, and, so far as the development of the fossil from the matrix permits determination, apparently free from any connection with the quadrate bone, below which its entire depth extends. The transverse thickness of the bone posteriorly is about 4 centims., but anteriorly the thickness is reduced to little more than half as much.

The Supra-quadrate or Supra-temporal Bone.

(Plates 13 and 14, st.)

The supra-quadrate is a slightly irregular, obliquely oblong bone, with its principal extension in the antero-posterior direction, and the two pairs of sides sub-parallel, and the short pair inclined backward. It is 10 centims, long by 6 centims, deep. The free oblique posterior margin is thickened, and terminates in two large rounded knobs, which form the upper and lower limits, and are separated from each other by a transverse depression. A straight longitudinal suture divides it from the squamosal bone above, and a longitudinal suture which is less straight separates it from the quadratojugal bone below; anteriorly it abuts against the inclined posterior end of the malar bone. The external surface is flattened rather than flat, being undulated with a rugose thickening on the anterior third. It is ornamented with strong radiating ridges, which diverge from its inferior border; they are large rounded ribs, which subdivide, and are sometimes broken into pits: about seven ridges and their interspaces occur in a width of 6 centims. I have no evidence whether the bone is in osseous connection with the quadrate bone.

The Squamosal Bone.

(Plates 13 and 14, sq.)

The squamosal bone is bent at an angle so as to appear upon the roof of the skull as well as upon the upper posterior part of the cheek. The lateral portion of the MDCCCLXXXVIII.—B.

bone is rather smaller than the supra-quadrate, upon which it rests inferiorly. It is 10 centims, long and 5 centims, deep. The free posterior border is thickened, and rounded into a convex boss with an elevated border like those seen on the supra-quadrate and in a less degree in the quadrato-jugal. These three bones have their inclined posterior borders extending further and further back, the higher their position on the side of the cheek, making its posterior outline oblique; but the line is regular because the upper knob on the quadrato-jugal extends rather further back than the two similar rugosities below and the one above, which cause the margin of the cheek to terminate in a row of four mammillate knobs which are nearly equidistant. The external surface of the squamosal bone is marked with very strong ridges and pits, which descend obliquely forward. Its superior border is badly preserved, and the superior horizontal part of the bone is much broken away.

## The Post-frontal Bones.

(Plate 13, pt.f.)

The post-frontal bones lie in front of the squamosals, and are angularly bent in the same way, so as to continue the anterior prolongation of the superior horizontal ridge which divides the roof of the skull from the cheeks. They form the superior hinder border to the middle of the orbit (Plate 14, fig. 2, pt), where the bone is exceptionally thick, and roughened with large mammillate bosses superiorly. Posteriorly the bone is pitted and sculptured like the other bones of the cheek. It is about 7 centims. long and upwards of 4 centims, deep laterally, measuring from the superior angle to the malar bone. The superior horizontal portion of the bone is larger, and overlaps the parietal, but from the condition of the specimen its sutures are less perfectly defined (Plate 13). It is about 6 centims, wide, but is shorter, meeting posteriorly a forward extension of the squamosal, and being in contact anteriorly with the ill-defined supra-orbital bone.

The post-orbital bone is an ill-defined wedge between the post-frontal and malar. It is 3 centims, deep on the orbital border, and appears to be 4 centims, long, extending backward to a point.

# The Roof-bones of the Head.

(Plate 13.)

The bones which cover the upper part of the head and lie between the nares, orbits, and the angles of the squamosal and post-frontal form a shield which is flattened but for a wide, shallow, longitudinal concavity which lies between the lateral bulgings, above the orbital border, and an anterior prominence on the nasal bones. It consists of the nasal, frontal, prefrontal, supra-orbital, post-frontal, squamosal, parietal, supra-occipital, and epiotic bones. Owing to the right side of these roof-bones being more

or less broken away, the extremely weathered condition of the posterior part of the shield, and the presence of some planes of vertical fracture through the bones, the accurate tracing of the sutures is a matter of great difficulty. Moreover the surface of these cranial bones is strongly sculptured with grooves and pits, which have a tendency to longitudinal arrangement in the middle region, and laterally have a tendency to diverge outward more or less at right angles to the lateral border. The distribution of this ornament, as well as of the bosses and tubercles into which the intervening ridges sometimes rise, occasionally helps to define the sutures, which mostly run over comparatively smooth tracts of surface.

## The Nasal Bones.

## (Plate 13; Plate 14, fig. 2, n.)

The nasal bone is only preserved on the left side, and is not quite perfect on the internal border, while it has lost the anterior process which extended towards the premaxillary. Above the compressed anterior narial border of the bone, which is concave in length and extends outward and backward, the bone thickens on its inner two-thirds of width, and rises into a super-nasal nodular transverse crest; and there are some indications that a transverse shallow mucus-canal extended over the anterior extremity of the bone. The nasal bones meet the frontal bones (f) behind; the prefrontals (pf.) and the posterior lateral angle of the maxillary bones (m) join them externally. There is no satisfactory evidence of a median suture between the bones. The posterior border has a general transverse direction, but the frontal elements extend slightly forward between the nasals in a very wide angle, and their hinder extremities extend back so as to form nearly a right angle between the frontal and prefrontal bones, and thus the form of the suture is a drawn-out and inverted W. measurement from the posterior narial border to the posterior angle of the bone is little more than 7 centims. The median posterior extremity is 14 centims. behind the anterior extremity of the skull. The transverse measurement over the nasal bone from the maxillary to the median line of the skull is 6.5 centims.; but externally the nasal appears to extend under the ascending process of the maxillary bone.

# The Prefrontal Bone.

# (Plates 13 and 14, fig. 2, pf.)

The prefrontal bone has a well-defined contour, being broadly sub-pentagonal, with the base inward. It meets the maxillary bone below and externally, and the nasal and frontal bones internally, having its greatest inward extension at the angle between those bones. Its inner border diverges outward, and meets the supra-orbital bone above the middle of the orbit. It enters into the anterior portion of the upper part of the orbital border. Its antero-posterior length is about 9 centims. Its extreme width is 5 centims. Its antero-lateral border is rounded, and extends along the lachrymal canal; its postero-lateral border, which extends along the orbit, is not quite perfect, but appears to have been thick, and most elevated posteriorly, with the external lateral surface vertical.

The lachrymal bone appears to have no separate existence, unless it is present as a perferated scale in the mucus canal.

The Supra-orbital Bone.

(Plate 14, fig. 2, so.)

Owing to the broken condition of the superior margin of the orbit, the supra-orbital bone is very imperfectly defined, and its limits are not satisfactorily determined. It is apparently a narrow crescentic bone above the hinder part of the orbit, with its external and internal borders sub-parallel. Internally it meets the frontal and squamosal; anteriorly it abuts against the prefrontal; and posteriorly, above the hinder angle of the orbit, it meets the post-frontal bone. Its length is about 7 centims., and its width, imperfectly preserved, does not exceed 3.5 centims. It combines with the prefrontal to form an arched ridge above the orbit, and the shallow concavity of the frontal region is limited laterally by these supra-orbital ridges. I believe this bone to be correctly determined, but it may be a dismembered part of the post-frontal.

The Frontal Bones.

(Plate 13, f.)

The anterior contour of the frontal bones is broadly rounded. Each meets the nasal bone in front, and the prefrontal on the antero-lateral border. The transverse width of the bones anteriorly was 11 centims., as may be inferred from the lateral measurement to the median line being 5.5 centims. The sides of the bone are a little constricted and sub-parallel. Posteriorly the frontal terminates in a transverse suture, which penetrates in a shallow V-shape into the parietals. The post-frontal bone probably touches its posterior angle. In the middle line the antero-posterior measurement is 10.5 centims. There is no conclusive evidence of a median suture, owing perhaps to the longitudinal sculpture of the bone; but I incline to believe that it was divided.

The Parietal Bones and Supra-occipital.

(Plate 13, p, so.)

Behind the frontal bones the preservation of the skull is such that, although the bones are made out with some difficulty, their exact limits are not easily traced.

The parietal bones were each sub-ovate, about 7 centims. wide and 9 centims. long. The anterior contours are convex, and the width of the bone is diminished by overlap of the squamosal.

Behind the parietals is a strip of bone 4 centims. long, and which may have been 16 centims. wide; its posterior border is broken. A small median ossification extends between the hinder limits of the parietal bones in a wedge-shaped suture, so that in the median line its length was 5 centims., and it is as wide as long, but probably extended laterally to the epiotic bones. It may be the interparietal.

## ? Epiotic Bones.

## (Plate 13, e.)

Internal in position to the posterior angles of the squamosals and behind those bones is a pair of transversely oblong ossifications, 3 centims, thick, which have the external surface horizontal. Each extends the outer upper corners of the skull further backward than do the bones of the occipital region, and is conditioned like the so-named epiotic bone of Labyrinthodonts. As preserved it is 6 centims, wide by less than 5 centims, long. Its posterior border is rounded from above downward, and its inner surface is vertical.

### The Quadrate Bone.

The quadrate bone is not seen. It would appear to have been a very short flattened bone, with a ball-like articular surface on the palatal aspect of the head, though its width may have had no necessary relation to the great width of the articular element of the lower jaw.

#### The Palate.

# (Plates 15 and 16.)

The palate of the type-specimen of *Pareiasaurus serridens* was worked out, so far as the chisel could do it, with consummate skill, as far back as when Mr. Henry Warburton was President of the Geological Society, but has never been figured or described. Sir R. Owen's cast is in itself a work of great skill, and is now the only evidence of its character. In general structure it is suggestively Anomodont, but it differs generically from any type of the order hitherto described. (See Plate 16, fig. 1.)

First, there is a large oblong basi-sphenoid (bs) in the middle of the hinder region. Its sides, which are rather constricted, I shall show to have been formed by the pterygoids, and its base is channelled in the median line, with the depression deepening as the pterygoids converge inward. From the anterior margins of this pterygosphenoidal mass the pterygoids diverge outward, and soon subdivide into two

processes, one of which extends obliquely backward (presumably to meet the quadrate bone), and the other process is prolonged outward and forward at right angles, so as to meet the malar region just opposite the termination of the maxillary. Hence it is in the position of the transverse bone, but there is no evidence that it is a distinct ossification. The median union of the pterygoids terminates anteriorly in a concave excavation, from the anterior corners of which slender bones extend forward parallel to each other, diverging outward a little anteriorly. They occupy the middle third of the palate, and from their middle send a narrow process upward and inward, which probably formed a median symphysis. Anteriorly the bones unite in the median line, and from this union a bony bar diverges outward and backward so as almost to meet the anterior termination of the forwardly directed process of the pterygoid, with which it is directly connected by a ridge parallel to the jaw, but separated from it by a depression. Anterior to the lateral connection with the palatines the vomer is prolonged forward. I infer that there were two vomerine ridges parallel to each other, as in the anterior part of the skull of Dicynodon pardiceps (OWEN), but the bones are somewhat distorted, and the ridge is only preserved on one side.

In the figured specimen of  $Pareiasaurus\ bombidens$  (No. 43,525), the palate is only known from a transverse section through the median union of the pterygoid bones, which shows the width of the bones and their stout character, with numerous sharp asperities on the palatal surface, which there is some reason for believing to indicate parallel or sub-parallel rugose ridges  $(pt.\ r.)$ ; but, although at first sight they resemble teeth, there is no trace of dentinal structure, and I am aware of no evidence that would indicate a toothed condition of the pterygoid bone. (See Plate 15, fig. 2.)

In the specimen now described (Plate 15, fig. 1) the palate is much less perfectly chiselled out than was the case in *Pareiasaurus serridens*, and only shows certain characters of its hinder region; but these are exceptionally important because some sutures are seen.

The basi-occipital bone (bo) is fractured so as to display the ex-occipital bones anterior to it, and to prove that it was posterior in position to them. Enough remains of its form to indicate that it constituted a large ovate articulation well rounded and defined inferiorly, which was about 6 centims, wide and 4.5 centims, deep. So singular is its relation to the bones behind that it is more like a post-cranial ossification than a constituent element of the base of the skull, abutting against the concave surface of the bones behind by a well-marked suture, which is posterior in position to the hinder limit of the skull, while it overlaps those bones laterally and inferiorly, where it is limited by a deep and characteristic infra-condylar depression. There is a doubtful indication of a vertical suture or groove dividing the bones against which the basi-occipital abuts. The fact that the superior margins of these bones appear to rise and form the lateral boundaries of the foramen magnum leads me to identify them as the ex-occipital bones. There is nothing unusual in the inferior median union of the

ex-occipital bones in South African Reptiles. The tripartite condition of the occipital condyle is seen in many Dicynodont skulls in the British Museum; as well as in the skulls of Chelonians.\* But in the Dicynodonts the basi-occipital has already been received between the ex-occipital bones, so that they take part in forming the condyle, though their extension downward to the base of the skull is not less marked than in Pareiasaurus. The interest of this specimen consists in the evidence it affords that the basi-occipital bone is essentially an intercentral ossification at the back of the skull, which has become enlarged and blended with the skull under mechanical conditions. If it had not been developed, or had not been in bony union with the skull, then the head would have terminated posteriorly in two occipital condyles formed by the ex-occipital bones, between which there would be an inferior notch. Such a hypothetical condition is so suggestive of the Labyrinthodont mode of union of the skull with the vertebral column, as to indicate a possible method of transition from the Amphibian form of occipital condyle to such a type as is seen in Chelonian Reptiles by the blending of a notochordal ossification with the head. If we consider the structure of an Amphibian skull, there can be no à priori difficulty from the fact that it would bring the ex-occipital bones to some extent into bony union with the basi-sphenoid; but the posterior pre-condylar surface of these bones, which is in front of the basi-occipital, appears to project posteriorly for 15 millims. beyond the basisphenoid.

The basi-sphenoid (bs) is partially blended with the pterygoid bone (pt), and the prominent oblong bony mass at the back of the palate is about 9 centims. long. Its external or lateral surfaces are concave in length, so as to constrict the transverse measurement to 5 centims, towards the anterior end, but posteriorly the bone widens, attaining a transverse measurement of about 8 centims, and terminating in two parallel convex bosses which are below and in front of the occipital condyle. In Dicynodon and Ptychognathus the corresponding processes have a much greater development vertically downward, and are seen in many skulls to be formed partly by the ex-occipital bones, for tripartite sutures cross the processes and separate the ex-occipitals from the basi-occipital bone between them. There are some indications in this specimen, especially on the left side, that the ex-occipital bones descend to the base of the skull.

A deep median channel extends along the basi-sphenoid, which increases in depth anteriorly so as to separate the pterygoid bones which margin the channel, before they become transversely united anteriorly above it, as well as by converging at its sides; but there is no evidence whether this or any other palatal vacuity is to be regarded as the posterior nares.

From the outer posterior angles of the bony pterygo-sphenoid mass a line of suture extends obliquely forward and inward to the median line on the left side. There is a trace of this suture on the right side, on the external posterior surface, but it is not

<sup>\*</sup> In some Cetaceans the ex-occipital condyles almost unite into one condyle.

defined anteriorly; and I take these characters to show that the palatal surface of the basi-sphenoid is a long triangle, narrowing from a width of 7 centims, posteriorly to a point anteriorly, and defined laterally by nearly straight sutures, separating it from the pterygoid bones which extend along its sides (Plate 15, fig. 1).

Hence the posterior margins of the pterygoid bones are in contact with the basisphenoid in a way more comparable to that seen in a Chelonian than in any existing group of Reptiles, but Chelonians have no such deep notch behind the process which is given off to the quadrate bone.

The present specimen shows that the sides of the pterygo-sphenoid process, seen laterally, are concave in length and gently convex from above downward, with the lateral palatal margin on each side compressed into a sharp rounded ridge. Anterior to the basi-sphenoid the bones unite in the median line at the base of the median sphenoidal depression, but also form by lateral expansion of their palatal surfaces a median union. The anterior lateral pterygoid plates become somewhat expanded, and differ greatly in form from the contours seen on the cast of Parieasaurus serridens, while I am unable to see any indication of the pterygo-quadrate process which is so distinct in that species, and so characteristic of Dicynodonts. It may still exist in the matrix, or it may have been removed by the chisel. The lateral plate of the pterygoid, however, is shown by the vertical section of the skull of Sir R. Owen's type-specimen to be greatly expanded transversely (Plate 15, fig. 2), and there is a similar transverse expansion in this specimen, while sub-parallel lateral ridges of like character are seen upon its palatal surface. There are some indications that a bony process diverges outward and forward towards the orbit; and that the rounded posterior margins of the median pterygoid vacuity are prolonged forward by the parallel pterygoid bones, but no structure of the anterior part of the palate is shown. If the main points of structure of the palate prove, as will be presently shown, to be Dicynodont, the characters in which the bones differ from those of the Anomodont group will prove to be Labyrinthodont.

#### The Lower Jaw.

# (Plate 14, figs. 1 and 2; Plate 15, fig. 1, md.)

The lower jaw is a broad horse-shoe shaped structure with the rami well rounded in front, where they are united by a vertical median suture; posteriorly the rami are not recurved. The position of the jaw is vertical all round the curve. The bone is nearly 7 centims, deep. Each ramus, measured round the curves, has a length of about 34 centims. Its thickness varies from a maximum of about 5.5 centims, below the orbit to 3.5 centims, anteriorly. At the median suture (m.s) there is a slight increase in the thickness of the bone, especially at the infero-posterior angle of the symphysis, which is produced backward in a kind of talon. The inferior surface is rounded from within outward, and rather flattened. But the basal contour of the

anterior end of the mandible is convex from side to side; and there is also on the base, in the antero-posterior direction, a postero-lateral convexity below the orbit, more compressed from side to side than the jaw above, which ends abruptly on each side, at about 12 centims. from the posterior articular extremities of the mandible. Thus the lower jaw is supported on a tripod of three inferior convexities. Behind the superior lateral convexities the jaw becomes compressed, especially on the external aspect, and its depth decreases as it extends backward in a convex curve, by not being produced so far downward; while superiorly, at the posterior end, it expands laterally, both internally and externally, into the diamond-like articulation, which is 9 centims, wide and apparently as long (Plate 15, fig. 1).

The mass of the jaw is formed by the dentary bone. It extends further back upon the alveolar border than upon the inferior border externally, where it is defined by an oblique suture descending downward and forward over the thickest and most convex portion of the jaw. On the inner side of the jaw the dentary bone does not extend so far back, and the suture, which separates it from the splenial bone behind, descends obliquely downward and backward. The angular bone is received between these internal and external lateral flaps of the dentary bone, and it is the downward growth of the angular bone which forms the infero-lateral prominences on the mandible. This bone, however, is exposed for a short distance, being covered posteriorly and externally by the sur-angular. There is no conclusive evidence whether the angular extends backward behind the sur-angular, as seems probable, to support the articular bone. Externally there is an impressed transverse suture between the articular and sur-angular bones, which gives a convex character to the sur-angular and emphasises the external projection of the articular bone. There are no fontanelles in the jaw; and there is no evidence of its internal structure in this specimen. But the example figured by Sir R. Owen shows that a great vacuity like that which is demonstrated in Pareiasaurus serridens by the vertical sections of the jaw (Plate 16, fig. 2) extended forward round the dentary bone, defined superiorly by the thick sub-dental plate which extends obliquely downward and inward from the outer to the inner side of the jaw. In P. serridens this vacuity is higher than wide. It is a typical Labyrinthodont structure.

#### The Teeth.

# (Plate 15, fig. 1; Plate 16, fig. 2.)

The external surfaces and extremities of the teeth are not well preserved. In the upper jaw they are inclined inward so as to have their external surfaces directed almost horizontally. A part of this curvature may be due to distortion, but that it is partly natural may be inferred perhaps from the teeth being directed inward all round the jaw, from their being in no case separated from the alveolar margin, and from the maxillary teeth being directed obliquely inward in the type-specimen of

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P. bombidens.\* None are well enough preserved to show whether the extremities of the crowns of the teeth were similarly serrated. The external enamelled surface is similarly semi-ovate and rounded from front to back, but in several instances it is marked by a few slight vertical ridges. The bases of the crowns are nearly circular; each is about 1 centim. long and rather wider, with a large central pulp cavity which extends above the alveolar margin. The interspaces between the bases of the crowns are about 2 to 3 millims. long, but the summits of the crowns, which become compressed from within outward, are apparently in contact. Some of the crowns are from 2 to 2.5 centimetres long.

In the lower jaw the teeth are directed more or less outward, but this is more obviously an accident of fossilisation than the inward direction of the teeth in the skull. The crowns of the teeth are vertically ribbed. The external alveolar margin rises higher than the internal margin.

No evidence has been adduced as yet concerning the relation of the teeth to the jaw, though Sir R. Owen compares it to the condition seen in *Iguanodon*. In *Iguanodon* the teeth are essentially in an alveolar groove, though on its internal surface there are vertical grooves for the teeth, which terminate at their bases in separate pits. The only material available for settling this question is the small fragment of the lower jaw of *Pareiasaurus serridens* which appears to have been cut from the head of the specimen which Mr. Bain presented to the Geological Society in 1838. Dr. Woodward, F.R.S., has had the kindness to have this specimen cut vertically through the interspace between two teeth, and this section shows the existence of a bony septum between the teeth, thus demonstrating that the teeth are implanted in sockets (Plate 16, fig. 2).

The vertical section figured by Sir R. Owen is remarkable for showing a successional tooth beneath a crown without any fang. The fang is present, however, in the successional tooth, and closed at its base; but the union between the crown and fang appears to have been of the kind seen in *Mosasaurus*. From the position of the successional tooth, interior to the tooth in use, it is probable that it was developed as in *Ichthyosaurus*, *Crocodilus*, &c., so as to be more and more within the fang of the pre-existing tooth as its growth increased; only in this case there is no trace of a fang to the tooth in use, from which it would follow that in the process of fossilisation the fang of the pre-existing tooth disappeared, while the fang of the successional tooth remained; or else, as I think more probable, that the fang of the old tooth was absorbed before the new tooth was fully grown, and that meanwhile the crown was held in its place in the jaw by a deposit of osseous cement, in which case the condition of dentition would make a transition between that of *Protorosaurus* and the Crocodiles.

<sup>\* &#</sup>x27;Catalogue of Fossil Reptilia of South Africa,' Plate 8, fig. 3.

Comparison with the Skulls of the Types of Pareiasaurus serridens (OWEN) and P. bombidens (OWEN).

There do not appear to be any satisfactory dental characters to distinguish the described species of this genus from each other; and it seems to me that their differentiation must rest upon the form, proportions, and structure of the skulls. Although the head is singularly distorted in *P. serridens*, there is, I think, sufficient evidence that it differed from *P. bombidens* in being less depressed; that it was more compressed from side to side anteriorly, as shown both by the contours of the skull and of the mandible; that the post-orbital processes were much deeper vertically, in harmony with the greater height and narrower form of the head. The rami of the lower jaw are straighter, more compressed from side to side, so as to be relatively thinner, though the specimen is larger; and the more pointed form of the lower jaw is manifest. On the palate *P. bombidens* appears to have the pterygoid bones much wider. The specimens appear to show many minor differences; but, as very little is preserved of the skull of *P. bombidens*, and *P. serridens* is only known from the cast of the distorted skull and fragment of lower jaw, no detailed comparison can be profitably pursued.

The skull which I have described agrees with P. bombidens in having the anterior extremity of the mandible well rounded, though in the new specimen it is relatively wider, and the whole skull appears to be relatively broader, and is certainly broader and less pointed than the restoration of the contour of P. bombidens given by Sir R. OWEN.\* The suture between the rami, which is lost in the figured type, is here strongly marked. The maxillary bone of P. bombidens (No. 43,525) is relatively deeper, and carries a strong median longitudinal inflation, which divides the bone into superior and inferior portions, while the specimen described has the bone more rounded from the alveolar margin to the orbital margin, and has only a slight indication of the longitudinal ridge. The number of the teeth is probably the same in both specimens; but no tooth in the specimen described has the extremity sufficiently preserved to show whether it possessed the serrations seen in P. bombidens, and it exhibits, especially on the hinder teeth, a few slight vertical parallel ridges, suggestive of those on the teeth of some Dinosaurs, which presumably indicate serrations, though they are absent from the teeth of the type of P. bombidens, from which, however, the outer film of enamel has in most cases peeled off. The skull appears to have been similarly flattened above, but too little of the bone remains to show whether it resembled the specimen described. And the lower jaw is broken away below the subdental plate, so that no detailed comparison can be made between the two specimens. It is, therefore, quite possible that the differences in form of the snout and teeth may extend to other parts of the skull, but, with the evidence before me, I prefer to regard the skeleton now under description as referable to P. bombidens.

<sup>\* &#</sup>x27;Descriptive Catalogue, Reptilia, South Africa,' Plate 8, fig. 3, a.

Comparison of the Cranial Characters with those of other Animals.

If the teeth had been found without other evidence of the animal, or if the jaws had alone been found, it would have been a fair induction to have classed *Pareiasaurus* with the Dinosauria. There is no other ordinal group in which coarsely serrated compressed crowns to the teeth are found, unless *Echinodon* and *Macellodon* should prove to belong to the Lacertilia, as Sir R. Owen suggests. But placed in sockets, with the crown apparently united to the jaw by bony cement, the fang becomes absorbed by the successional tooth rather in the manner of Ichthyosaurs and Crocodiles, in which the germ is commonly on the middle of the inner side of the fang. The dentition approximates to that of Crocodiles rather than to the other orders of existing Reptiles, the dense packing and lateral compression, as well as the development of distinct alveoli, being Crocodilian characters, though the attachment of the teeth is not Crocodilian.

Turning to the palate, an instructive comparison may be made with the skulls of many species of *Dicynodon* and *Ptychognathus*, from the same geological horizon in South Africa, as well as with the allied animals, which Sir R. Owen has grouped into the ordinal name Theriodontia.

I have made a reduced restoration of the palate of Pareiasaurus serridens (p. 97), and if this is compared with Dicynodon the differences which are most manifest are, first, that the quadrate processes of the pterygoid are directed backward, so that the angle between them and the sphenoidal mass is less opened; while, secondly, the pterygoid processes, which in Pareiasaurus diverge outward and forward, so as to reach the margin of the jaw, are in Dicynodon directed forward, so as (in most cases) to lap along the palatine bones. Otherwise the relation of the pterygoid bones is the same, with apparently the same union with the sphenoid, the same median connection, and the same concavity between the anterior median ends of the pterygoid, which is prolonged forward, so as similarly to separate the palatine bones; and some Dicynodonts have two premaxillary or vomerine ridges. Hence, bearing in mind the variations which the palate exhibits in the Anomodont order, I think it may be affirmed that if no part of Pareiasaurus except the palate had been discovered it would have been a sound induction to have inferred that the animal was an Anomodont. If the teeth had been met with subsequently, they too might have been accepted as Anomodont or Theriodont, for the group presents so many variations of dental condition that the further variation seen in Pareiasaurus would have been no anomaly. Among existing Reptiles the nearest resemblance in the palate, as already indicated, is seen in the Chelonians; but the true Dicynodont palate is more decidedly Chelonian in its structure than this genus, and this condition may eventually have some weight in determining the genetic relations of these organic types.

If we turn to the superior aspect of the skull (Plate 13), it is no more Dicynodont than Dinosaurian. And it has every characteristic of a typical Labyrinthodont skull,

among which may be mentioned its broad flattened form and sculptured surface, the small premaxillaries, the long malar bone, the narrow parietals, and the well-developed supra-temporal, quadrato-jugal, and epiotic bones, not to mention the lachrymal canal, and the probable existence of the post-orbital bone; while all the bones are arranged and conditioned as in Labyrinthodonts. The only other fossil type to which any resemblance can be traced in skull structure is the Ichthyosauria. But, although the form of the skull and positions of the orbits and nares are so dissimilar, the presence of supra-temporal and post-orbital bones is an interesting resemblance to *Pareiasaurus*, because *Ichthyosaurus*, so far as I am aware, is the only other type with a single occipital condyle in which a similarly developed supra-temporal bone is present. To living Urodeles the skull shows no resemblance, except in the unimportant matters of form and the small size of the premaxillary bones.

How these resemblances of the head to different ordinal types which are referred to different classes of Vertebrates can be harmonised, is found, I think, to be materially elucidated by the structure of the remainder of the skeleton.

#### The Vertebral Column.

### (Plates 12, 17, 18.)

The vertebræ are preserved in natural sequence in a straight line. No bone is missing from any part of the column, unless a few terminal vertebræ should be lost from the extremity of the tail. There are only 29 vertebræ, of which 18 are presacral, 2 sacral, and 9 caudal, so that the number of presacral vertebræ is about the same as in the Japanese Salamander, Sibboldia; but the number of caudal vertebræ is only one-third of those in that type. The earlier vertebræ are rather shorter in anteroposterior measurement than the dorsal series, the greatest length and largest size being attained in the lumbar region, beyond which the vertebræ rapidly become small in the tail. Intercentra, or intervertebral wedge-bones of crescentic form, are developed on the ventral aspect of the column, between the dorsal and caudal vertebræ. In the early cervical vertebræ they are anchylosed to the anterior margin and base of the centrum, but in the dorsal and caudal regions these bones are free. The base of the centrum is compressed laterally in the earlier vertebræ into an inferior median ridge, which is moderately prominent, but disappears lower down the column, when the base of the centrum becomes rounded from side to side.

The ribs from the first articulate by double heads, which in the cervical region are upon the centrum made by the extremities of long forks to the cervical rib (Plate 17, fig. 1). The attachments of the dorsal ribs are partly on the neural arch, partly on the centrum; and the attachment to the centrum continues to rise higher, as far as the lumbar region. In the dorsal region the ribs are attached in a peculiar way, which can only be compared among Reptiles to the Crocodilian plan, but is distinct in type, having

articulation with a relatively long parapophysial element from the centrum, and with a diapophysial element from the neural arch.

The neural arch is relatively broad and depressed, and carries an unusually short and massive neural spine (Plate 12, fig. 1).

The entire length of the vertebral column is 197 centims., or about 6 feet  $1\frac{1}{2}$  inches, of which 50 centims. are in the neck, 83 centims. in the back and loins, over 15 centims. in the sacrum, and about 48 centims. in the tail.

#### The Cervical Vertebra.

## (Plates 12 and 17.)

I count all those vertebræ as cervical in which the parapophysial articulation for the rib does not rise appreciably above the level of the side of the centrum, and the vertebræ thus characterised are nine in number.

The first centrum is not quite perfect at the anterior end, so that it is impossible to say whether it possessed a regularly concave atlantal cup for the reception of the basi-occipital. As preserved, the centrum is short, being about 4 centims. long. It had prominent rounded margins to the intervertebral articulation. The anterior face as preserved is concave, and appears to have been cupped like the atlas in *Ichthyosaurus*, but the matrix has not been removed from the centre to show whether the notochord was persistent. The width of the superior part of the anterior face was about 10 centims.; its depth was about 8 centims. A double-headed rib was attached to this vertebra.

The neural arch is depressed and greatly produced anteriorly, and diverges outward at its anterior corners, as do the pre-zygapophyses of succeeding vertebræ, and these processes may have served to defend the sides of the basi-occipital bone. The anterior contour between these processes is concave; and the long lateral contours to the post-zygapophyses are constricted. The length of the arch is about 10 centims.; at its posterior extremity, on a level with the posterior articulation, there was probably a very small neural spine, now broken away. There is a small rib-like bone near the anterior process of the neural arch.

The second and third vertebræ both have the centrum about 5 centims. long. The second has a sharp median ventral keel, which is almost lost in the third, where it becomes a rounded ridge. In both the hypapophysial bone in union with the pre-articular basal margin of the centrum is relatively small. In the second it is sub-triangular, about 3 centims. long and as wide anteriorly; in the third it is cordate, retaining its width, but shorter posteriorly and rounded. These bones cover much of the basal ridge of the second vertebra. The sides of the centrum are concave from back to front, but above the middle of the side is a longitudinal ridge, strongest anteriorly, which bounds the impressed facet for the rib. On the right side the inferior process of the rib is still in contact with this facet. This process is 18 mm.

wide, somewhat compressed, and attenuates as it extends backward; its length is 4 centims. The superior process appears also to articulate with the centrum; it is half as long as the inferior process, is compressed from side to side, is as high as long; it is separated from the lower head by a well-marked notch more than 1.5 centim. wide. The length of the rib, which attenuates to its free end, is about 14 centims.

The attachment of the neural arch to the centrum is not seen. The form of the arch viewed from above is remarkable, and has an aspect of leaning forward to terminate in a short, large, truncated neural spine, which is ovate in section and compressed from front to back. Below the flattened slightly convex summit the neural spine is constricted a little from side to side, and then diverges outward and backward in strong, rounded, V-shaped, neurapophysial ridges, which enclose a posterior concavity between the zygapophyses, having a slight median ridge below the neural spine. The width of the neural spine is 5 centims. The width over the posterior extremities of the transverse processes is 10 centims.; the under sides of these processes carry the post-zygapophysial facets, which, however, are not seen in these vertebræ.

The centrum is larger in the fourth cervical, having a length of 6.5 to 7 centims. The intercentral ossification is more flattened, and the base of the centrum is more flattened. The tubercles for the ribs are larger, and elevated a few millimetres above the side of the centrum. The inferior head of the rib, which is still in contact with the centrum, is very massive, and fully 4 centims. deep. The neural arch of this vertebra is not preserved. In the fifth vertebra the centrum is shorter, being only 4.5 centims. long, while in the sixth it measures 6.5 to 7 centims., and in the seventh 7.5 centims. From this point, posteriorly, all down the dorsal series, the base of the centrum is lost, owing to the bone having been removed by a horizontal fracture of the rock in which the specimen was contained. The sides of the centrum, however, now become more constricted in the transverse direction behind the lower tubercle for the rib; the transverse measurement, which was 6.3 centims. in this position on the third centrum, is 5.6 centims. on the fourth and fifth, 5.4 centims. on the sixth, and 4.8 centims. on the seventh, in which the process for the attachment of the rib extends up the whole side of the centrum from a short distance above its base, and gives an aspect of semi-cylindrical excavation to its side. The spines on the neural arches are now all broken away, but appear to have become more vertical; the broken section is triangular. Anteriorly a slight median ridge extends forward, and divides the neural arch, so that the lateral surfaces diverge from it convexly outward and backward. From the anterior corners the pre-zygapophyses extend forward and outward as large sub-circular facets about 3 centims, in diameter. The transverse width over the pre-zygapophyses is about 18 centims., but at the second vertebra the transverse width over the post-zygapophyses is only 9.5, so that the neural arch becomes rapidly wider as it extends backward. There is a broad lateral constriction between the zygapophyses. The eighth vertebra has lost its neural

arch, and is fractured through the centrum, and there is no conclusive evidence whether it should be counted as cervical or dorsal; still, as the skeleton appears to have divided naturally into its several regions, except that the last dorsal is in the same block of rock with the lumbar and sacral vertebræ, it may be that the first eight vertebræ are rightly accounted cervical, though the transition from the neck to the back may have been graduated as among Plesiosaurs. The articular bases of the later cervical ribs are rounded and circular with sharp margins, external to which there is a marked constriction of the shaft. There is no proof that the ribs in any cervical vertebra articulate with the neural arch.

#### The Dorsal Vertebra.

(Plate 12; and Plate 18, figs. 1, 2.)

The dorsal vertebræ are nine in number. The first eight have been chiselled from the hard matrix as a slab which displays the bodies of the vertebræ and dorsal ribs on one aspect, and the neural arches and ribs on the other. In these vertebræ the base of the centrum is in every case lost. Transversely wide intercentral ossifications are seen between the third and fourth dorsal vertebræ, between the fourth and fifth and the seventh and eighth, but probably existed between all, and have been lost in the other intervals with the base of the centrum. Where I begin counting the dorsal vertebræ the transverse process for the lower head of the rib has already risen high upon the side of the anterior margin of the centrum. The head of this horizontal parapophysial process is expanded, and its articular surface flattened; its under side is compressed into an inferior ridge, and its dimensions contract like a neck to its junction with the centrum. It has a slight direction forward as it extends outward. At first the length of the process is about 2 centims., but in posteriorly succeeding vertebræ it elongates, and from the third to the eighth its length is about There is apparently no difference in the relative sizes, lengths, or position of these processes, and all terminate at their articular ends in the same straight line. The process on the ninth vertebra is similar. The interspaces between the bodies of the vertebræ are nearly 2 centims. wide. The sides of the centrum are constricted-4.5 centims, wide in the middle-and form as preserved vertical semi-cylindrical channels; but in the later dorsal vertebræ this hollow halfcylinder is inclined backward as it extends downward, and in the seventh and eighth centrums there is a manifest convergence of these lateral surfaces downward and inward, tending towards a rounding of the base of the centrum, which is perfectly rounded in the ninth and in the lumbar vertebra, and was, therefore, probably The centrum is wider posteriorly than rounded throughout the dorsal series. anteriorly; the sixth is less than 9 centims, wide anteriorly and 9.5 centims. posteriorly, but in the early dorsals there is no difference-both articular margins measuring 8.5 centims. in width.

The intercentra were limited to the ventral surfaces of the vertebræ (i.c.). None appear to have exceeded 3 centims in width or 6 centims in transverse length, but the preservation is so imperfect that no details of their characteristics can be given, beyond saying that in the anterior vertebræ they appear to lie well within the interspaces between the centrums, resting equally upon the basal margins of each adjacent pair; but in the posterior half of the dorsal series the posterior vertebra appears to contribute a larger surface for the support of this ossification, which gives the centrum an aspect of leaning obliquely forward. If this crescentic ossification were to become blended with either the anterior or posterior vertebra adjacent to it, the articulation would in the one case have a tendency to be proceedous, and in the other to be opisthoceelous; but, even though the co-ossification has not taken place, there is a tendency to the opisthoceelous condition in the lumbar vertebra.

Seen from the dorsal aspect, the forms of the neural arches are distinguished by their great transverse width as compared with the antero-posterior extent; by the short, massive, neural spines (n.s), which, though of the same type as in the cervical vertebræ, become wider and wider posteriorly; by the outward and backward divergence of the nearly horizontal post-zygapophysial ridges; and by the way in which the diapophysis for the rib (d) is given off as a process cognate with the post-zygapophysial ridge, separated from the post-zygapophysis by a sub-ovate notch, and bounded anteriorly by a straight transverse line. Since the vertebræ are all in natural contact, the contour of the pre-zygapophysis is not seen. The chief differences in the neural arches as they extend down the back are that the neural spines become successively wider and more circular, and that the post-zygapophysial ridges elongate a little, while the angle between their diverging posterior borders becomes a little wider.

In the first dorsal vertebra the arch is badly preserved. It, however, shows that the diapophysis was rather short, so that the notch between it and the postzygapophysis is wider than in succeeding vertebræ. On the left side the extremity of the post-zygapophysis is broken away, showing the pre-zygapophysial facet below as sub-circular, 4.5 centims. wide, nearly horizontal, but slightly convex from front to back. It is continuous with the anterior border of the transverse process, beyond which it extends as a thin plate. Hence the neural arch extends outward and forward in a wedge, and carries the circular pre-zygapophysis at its anterior corners (pz). This wedge is divided into two unequal and dissimilar regions by a transverse depression of the surface of its anterior half. This separates it from the postzygapophysial ridge, which, somewhat narrower and more elevated, ascends up to the side of the neural spine, but in the later dorsals it is thrown a little further backward towards its posterior aspect and rises higher towards its summit. The neural spine is about 5 centims. long, and at the eighth vertebra is 4.5 centims. wide, though narrower anteriorly. Its superior surface is slightly convex, but flattened. As it descends to merge in the expanded neural arch it experiences a sub-conical

contraction in size; its anterior margin is 3 centims, high, its posterior margin 4 centims, high. There is an anterior ridge on the earliest neural spines, which is lost on the last dorsal vertebra, though the corresponding posterior ridge is continued to the lumbar vertebra, and behind the post-zygapophysial ridges the spine is a little compressed. In no case does the summit of the neural spine rise more than 2 centims, above the post-zygapophysial ridge. The lateral measurement from the centre of the neural spine to the extremity of the post-zygapophysis is 12 centims, in the third dorsal vertebra, giving a length of about 10 centims, to the zygapophysial ridge. The transverse width over the vertebra from one post-zygapophysis to another is fully 22 centims, in the early dorsals and 26 centims, in the late dorsals. The measurement from the anterior margin of one post-zygapophysis to the posterior margin of the next is fully 13 centims, and from the posterior margin of one zygapophysis to the posterior margin of the next is about 9 centims. Hence the neural arch is nearly three times as wide as the centrum is long, and about twice as wide as the neural arch is long.

In no case is the articular extremity of a diapophysis of a dorsal vertebra exposed, so that there is no direct evidence of the nature of the division which separates it from the parapophyses.

#### The Dorsal Ribs.

## (Plate 12.)

The ribs are in their natural relations of contact with the vertebræ, except that in the greater part of the series they are displaced slightly downward. Thus it happens that the diapophysis is seen to be transversely ovate, enlarging as it extends outward to the sharp edge of the articular surface, which is about 3.5 centims. long and 2 centims, deep in the earlier part of the dorsal series, but is deeper in the later dorsal vertebræ. The preservation of the ribs is very imperfect. Seven are seen on the left side, and six on the right side, but there can be no doubt that the ribs were as numerous as the dorsal vertebræ and comprised nine pairs.

The ribs are strong, enlarged at the proximal end, where the bone expands in the vertical direction on the ventral aspect. The anterior surface of a rib is convex from above downward; and the posterior side is incised with a deep median groove, most marked in the earlier ribs, which corresponds to the division between the articular heads, and does not extend far down the rib.

There is a slight antero-posterior compression of the diapophysial tubercle, which accentuates the oblique attachment of the head of the rib which results from the parapophysis being on the anterior margin of the centrum, while the diapophysis is rather more posterior in position. As preserved, the ribs have their dorsal aspect horizontal, and are compressed from above downward at a distance of about 8 centims. from the diapophysis, where the transverse measurement is about

2.5 centims. and the vertical measurement diminishes posteriorly. The ribs are directed outward horizontally, but soon curve backward.

The second dorsal vertebra shows on the anterior face of the proximal end of the rib evidence of a mode of articulation with the centrum which may be termed sub-Crocodilian. The head of the rib, which unites with the parapophysis, is prolonged for about 5 centims, beyond the articular surface for the diapophysis, which is transverse to the direction in which the rib extends. In the later vertebræ, in which the position of the head of the rib is more nearly vertical, the parapophysial process is some centimetres longer than the diapophysial articulation, so that the head of the rib is obviously notched (Plate 18, fig. 1, p) in a way that is only to be compared with the early dorsal ribs of Crocodiles, though the vertebral elements which form the articulation are different. At the sixth dorsal vertebra the transverse measurement over the diapophyses is 21 centims, and over the parapophyses is 16 centims, which gives a mean elongation of the parapophysial head of 2.5 centims.

The ventral aspect of the rib is concave in length from within outward, and convex from front to back; it is somewhat constricted for a few centimetres external to the articulation; and when it widens, the expansion results from the anterior margin forming a sharp ridge, which, as in Crocodiles, is less prominent after extending for a few centimetres.

It is impossible to form any estimate of the original length of the ribs, since the longest fragments preserved measure only 18 centims.

In the last dorsal the rib appears to be almost entirely supported upon the diapophysis, the parapophysis having become very small.

The resemblance in form which these ribs exhibit is quite as striking with types like Anthracosaurus and Ichthyosaurus as with Crocodiles and Teleosaurus; and in some Labyrinthodonts the ribs are probably as long as in Crocodiles, so that the shortness of the ribs in existing Urodeles throws no light on the ribs of Pareiasaurus. No remains of abdominal ribs are preserved.

#### The Lumbar Vertebra.

# (Plates 12 and 19.)

This vertebra has the lateral constriction of the centrum rather more anteriorly placed than in the dorsal series, and these lateral surfaces round on to the base, which is convex from side to side. The posterior end of the centrum is expanded laterally to a width of 11 centims., and terminates in a sharp margin, which overlaps the first vertebra of the sacrum. Anteriorly its width is 10 centims. Its margin is convexly rounded, especially on the base, from which the thin intercentral ossification is lost. The intervertebral foramina between this vertebra and the last dorsal are higher than wide. The transverse process or lumbar rib is compressed from above

downward, and at its base is produced anteriorly along the entire extent of the length of the ninth dorsal centrum, and directed slightly upward. Its antero-posterior extent is about 8 centims. The bone is directed outward and curves slightly backward, with all the characters of a lumbar rib. It is compressed from above downward, is 2 centims. thick, flattened above, rounded on the anterior and posterior margins, and convex from front to back on the ventral aspect. It extends beyond the anterior expansion, which rapidly contracts to a width of 4 centims., with sub-parallel straight sides, its extension being in a line with the interspace between the lumbar and the last dorsal. The neural spine is large and circular.

The Sacrum, Sacral Ribs, and Pelvis.

(Plate 12, sm, sr, i; Plate 19.)

Two vertebræ are anchylosed together in the sacral region, but only the first contributes to the support of the pelvis. The centrum is appreciably smaller than in the last dorsal and the lumbar vertebra; and the neural arch is more depressed, for the post-zygapophysial ridges of the earlier vertebræ have disappeared, and the arches are as completely blended as the bodies of the vertebræ.

The anterior face of the centrum of the first sacral vertebra is expanded, being about 10.5 centims, wide; it is in too close union with the lumbar to permit the form of this surface being seen. On the ventral border it retreats posteriorly just as does the lumbar, but there is no evidence whether this condition was dependent upon the development of a small sub-vertebral wedge-bone. Immediately behind this anterior border the lateral and ventral surfaces of the centrum diminish somewhat in size; and, though the constriction follows the same general plan as in the lumbar vertebra, its posterior limit is not expanded to the same extent on account of the anchylosis, for the greatest transverse measurement between the two centrums is about 8 centims. This less expansion at the anchylosis gives a more cylindrical and relatively longer appearance to the second sacral vertebra. And in form there is much in common between this centrum and the early caudal vertebræ. The height of the lumbar vertebra, from the base of the centrum to the summit of the neural arch, is about 19 centims.; the corresponding height of the first sacral is about 17 centims., and of the second sacral about 13 centims. The transverse width of the postzygapophyses in the lumbar vertebra is about 21 centims.; here it is 9 centims. Thus, with the change to the sacral region, there is a marked decrease in the height of the centrum, the width of the neural arch, and the height of the neural spine.

The length of the sacrum along the neural canal is nearly 16 centims., but along the base the measurement would scarcely exceed 12 centims. The posterior articular face was slightly oblique. The neural spine of the first sacral vertebra measures 6 centims. from front to back, and is 5.5 centims, wide. The posterior median ridge upon the spine is very slightly developed, and there is no trace of the wide

furrows which occupy the halves of the posterior aspect of the lumbar neural spine. The neural spine in the lumbar vertebra inclines slightly forward; here it is inclined slightly backward. In the second sacral vertebra the neural spine is much smaller, the antero-posterior measurement being 4 centims., while the transverse measurement is 4.6 centims., and the neural arch has diminished in size to the proportions of an ordinary Saurian vertebra. Very little remains of the transverse process and sacral rib in this vertebra, but it was compressed from above downward, expanded on the anterior margin at the proximal end, and formed on the same plan as the caudal ribs and the lumbar rib, though very much smaller than the latter, and but for the anchylosis there would be no character to separate the vertebra from the succeeding caudal series. The transverse processes extend the under side of the first sacral vertebra to a width of 13 centims. They are massive ossifications which extend along three-fourths of the side of the centrum and have a height of 8.5 centims. from the base of the centrum to the neural platform. The process is directed outward and backward, and is only 3 or 4 centims. long, but is continuous with the sacral rib, from which it is divided by suture.

The sacral rib (sr) has a massive and extraordinary development, and is the only support for the pelvis. The bone is compressed from front to back, with its superior and inferior borders concave, so that it is constricted from a depth of 10 centims. at its junction with the transverse process, to 8 centims. at a distance of 5 centims. from that junction. The transverse width of the sacral rib on the ventral aspect is 19 centims. As the bone extends outward from the vertical constriction its plane twists to a more oblique position, which causes the mass of the bone to extend posteriorly, and to reach back to the level of the second caudal vertebra.

The anterior external angle of the rib is broken away. It was relatively thin, and was overlapped superiorly by the ilium (i); and it is not quite clear that it extended as far forward as the ilium. Its external border, which is inclined downward and backward from the level of the neural canal, had an antero-posterior extent of probably about 25 centims., though the posterior part of the bone now left in contact with the ilium along the external border is only half as long. The anterior aspect of this rib is flattened, being gently concave from within outward, and smooth, with slight indications of blunt ridges in its anterior outer angle. The infero-posterior border of the bone is well rounded from front to back, but the anterior edge is compressed, and bordered by a sharp anterior angle. As the bone extends outward it thickens in its posterior half to about 9 centims. on its junction with the ilium, which is received into a groove between the thin inferior expansion of the sacral rib and a strong vertical internal thickening. When seen from above and behind, the posterior 14 centims, of the rib seem to be received into a deeply concave recess in the internal face of the ilium, above which the sacral rib develops a strong tubercle, and anterior to which there is a long foramen, imperfect in front, of which only 6 centims.

are preserved. In front of the foramen the bone thickens, and is extending transversely outward towards the anterior corner of the ilium where it is fractured.

On the posterior side, near the junction of the sacral rib with the centrum, is a longitudinal groove like that already described in dorsal ribs, but relatively less deep, and soon lost as the bone expands outward.

The transverse width over the pelvis at the outer limit of the sacral ribs restored was about 44 centims.

There is no existing Reptile with similarly massive neural spines; and only among the great Salamanders, like Sibboldia, is there anything comparable in shortness, stoutness, and sub-cylindrical character, but in that Amphibian the summit and centre of the spine is a conical cartilage, which remains unossified.

In the large Salamanders the connection between the single sacral vertebra and the ilium is made by an immense sacral rib, which is compressed from front to back, and is similarly wider than deep, so as to have a transversely oblong form.

The only group of Reptiles in which there is a similar development and attachment of the sacral rib for the support of the ilium is the true Dicynodonts, always supposing that the pelvic bones attributed to that type are rightly referred; and I am aware of nothing against the view taken by Sir R. Owen of their association with Dicynodont skulls.

The ilium of Pareiasaurus was inclined to the vertebral column at an angle of 45°; it was chiefly elongated in an antero-posterior direction with its extension forward and upward from the acetabulum. The larger part of the bone lies behind the attachment to the sacral rib. The external surface of the ilium was sub-parallel to the longitudinal axis of the vertebral column. As the bone extends anterior to the acetabulum for the femur (a) it assumes a Mammal-like expansion. Its inferior border extends forward and outward, and the plane of the bone at the same time turns from the vertical, obliquely inward and upward as it extends forward, ending in front in a compressed plate about 2 centims. thick. If the form of the bone is Mammalian, its connection with the one sacral vertebra is a condition as strikingly Mammalian as Amphibian. It is a Mammalian resemblance that the bone lies almost entirely in advance of the acetabulum, while in the Amphibian Sibboldia the ilium is directed downward from the sacral rib and slightly forward. In various Mammals, from the Ratel and Glutton down to the Echidna, there is a vertical compression or depression or notched appearance of the bone above the acetabulum, in front of which its blade expands in a vertical direction as it extends forward.

As preserved, the length of the ilium is 40 centims. The posterior 12 centims, appear to be narrow from side to side, but this appearance may be partly due to state of preservation. The bone is convex from side to side superiorly above the acetabulum. The part of the acetabulum which lies in the ilium, concavely excavates the postero-external part of the bone, and forms a cavity 10 centims, long and 6 centims, wide anteriorly. The pubis and ischium are not preserved, but the marks of their attach-

ment are seen on the inferior face of the ilium, stretching round the acetabulum in a crescent having an attachment which is from 3 to 4 centims. wide. The inferior internal or visceral margin of the ilium is convex from front to back, and there is a corresponding convexity externally in front of the acetabular border, where the bone is 11 centims, wide on the inferior aspect, so that there is a certain approach to symmetry between the external and internal surfaces; for the sacral rib prolongs the curvature inward anteriorly with a contour similar to that which the external surface takes in front, making a triangle, wide anteriorly, with concave sides which converge backward to a width of 9 centims. in front of the acetabulum. Very little of the under-side of the ilium is exposed, since the ischium and pubis covered the whole area behind and around the acetabulum, and the sacral rib underlaps the bone anteriorly except along a narrow external strip less than 3 centims. wide. border, in advance of the acetabulum, a strong narrow groove curves forward for 9 centims., parallel to the rounded angle of the external margin. The greatest depth of the bone as preserved, measuring from the acetabulum to the nearly vertical crest of the bone, is 15 centims., and from the crest to the antero-inferior border is 12 centims. The superior crest is at least 18 centims. long; posteriorly, it thickens on the inner side, and its transverse measurement is nearly 3 centims.; in the middle it is 2 centims. thick, while anteriorly it widens considerably, but its superior border is broken away. The sacral rib extends to within 16 or 17 centims, of the hinder extremity of the bone, and joins the middle of the ilium for about 16 centims., without rising into union with the superior crest of the ilium.

The transverse measurement from the middle of the sacral centrum to the anterior corner of the ilium is about 31 centims.; but the plane of the middle of the acetabulum is about 9 centims. nearer to the middle line of the body. Thus the extreme width of the pelvis is 62 centims., and the width at the femoral articulation was about 44 centims.

#### The Caudal Vertebræ.

(Plate 12; and Plate 18, figs. 3, 4.)

The tail vertebræ diminish rapidly in size, and are noticeable for showing no trace of the notochordal condition attributed to this genus by its founder. In the earlier caudal vertebræ the flat articular surfaces of the centrum are in closer contact than in the later part of the series, as though their movements had been constrained by the extension of the pelvis parallel to them. The thickness of the matrix which separates the early centrums is only about 2 millims.; and this close contact may have caused the early caudal vertebræ in the pelvis, attributed to Dicynodon, to be classed as sacral. But in the pelvis of Pareiasaurus, even the second sacral vertebra might, theoretically, be termed sacro-caudal, since it resembles the caudal series in form, and takes no part in supporting the pelvis.

All the caudal vertebræ have the ventral aspect of the centrum convex from side to

side, but the convexity diminishes in the hinder part of the series, because the transverse processes, which at first are just below the level of the neural canal, gradually descend lower on the side of the centrum in the later vertebræ of the tail. The margins of the articular surfaces of the centrums are sharp and moderately elevated. The antero-posterior measurements of the centrums are, for the first, 6·3 centims.; the second, 5·4 centims.; the third, 5 centims.; the fourth is slightly shorter; the fifth, 4·5 centims.; the sixth, 3·6 centims.; while the seventh and eighth are still shorter, but their bases are so obscured by wedge-bones that the measurement cannot be definitely given. The ninth is only preserved as a fragment, and may not have been the last vertebra, since the neural arch is well developed in the eighth, in which transverse processes are present, though small.

In the earlier caudal vertebræ there is a slight compression of the sides of the centrum below the bases of the transverse processes, which were separate ossifications united by suture to short tubercles from the centrum. These caudal ribs are mostly broken away, and it is only in the sixth, seventh, and eighth vertebræ, in which they are small and rapidly diminishing in size, that the free extremities of the processes are seen. They are horizontal, and are directed outward and backward. The longest fragments have a flattened lath-like form, but are only 6 centims. long. The origin of the process on the centrum is as wide as the centrum is long. Anteriorly its superior angle descends from the front of the pre-zygapophysis, and is marked by a sharp ridge which carries the base of the process forward and helps to define an anterior concave area between this zygapophysial ridge and the tubercle on the centrum to which the base of the costal rib is attached. Hence these ribs have the appearance of being attached to both the neural arch and centrum. After the second caudal, in which the transverse width of the base of the caudal rib measures about 6 centims., its antero-posterior extent diminishes, being 3.5 centims. on the third caudal, and 2 centims. on the sixth caudal. In the fourth to eighth caudals the base of the process is nearly as wide as the centrum, and is sub-quadrate, and the process itself is sub-cylindrical, terminating outward in a rounded hemispherical extremity. In the sixth vertebra the process is about 7 centims. long, in the seventh about 4 centims. long, and in the eighth 3 centims. long. In these vertebræ the size of the rib so rapidly attenuates that its anterior border is convex and the posterior outline concave; while the riblet, when seen from the front, is wedge-shaped.

Between the ventral margins of the earlier caudals there is no trace of a wedgebone; but the intercentrum between the fifth and sixth takes the form of a disc. Between the fifth and sixth it is a small ossification in the median interspace, about 3 centims, in transverse extent. Between the sixth and seventh vertebræ the bone is less than 2 centims, long and about 4 centims, wide, and encroaches on the borders of both adjacent vertebræ. In the succeeding interspace the bone consisted of right and left portions like chevron bones, of which the left, which is alone preserved, is prolonged backward and constricted posteriorly, so as to be, though fractured, 3.3 centims. long. From the last interspace both these ossifications are gone.

The neural arch is characterised by wanting the post-zygapophysial ridges which are so strikingly developed in the dorsal region. The neural spines are broken away from all the vertebræ except the first; but they appear to have been more compressed from front to back than in any other region of the column, and to lean backward. The first caudal neural spine measures 5 centims. from side to side and 3.3 centims. from front to back, so as to be tranversely ovate. The free superior extremity is slightly larger than the shaft of the spine, which is about 4 centims. long. The spine forms much of the mass of the neural arch. Down its anterior median line a slight ridge extends, which is prolonged forward in the median line between the pre-zygapophyses, defining two lateral areas, which are sub-horizontal, and bordered by concave outlines between the zygapophyses, which are prominent laterally. The neural spine is at the hinder angle of the neural arch as in Urodeles, and the postzygapophyses project from below its hinder lateral limits. The transverse width over the zygapophyses of the third vertebra is about 7.3 centims., which is equal to the width of the centrum, so that the abnormal width of the arch in the dorsal region is here lost. The posterior contour between the post-zygapophyses is concave. The arch continues to diminish in width towards the end of the tail, in harmony with the reduced size of the centrum, but it becomes better defined laterally by the constantly lower position of the costal rib, so that after the first three vertebræ there begin to be lateral areas slightly inclined, but almost vertical, between the interzygapophysial ridge and the transverse processes. The superior surface of the caudal neural arch has a flattened aspect of leaning backward. The height of the fourth centrum to the small circular neural canal is about 4 centims.; the transverse width of the neural arch above the transverse process at the end of the caudal series is 4.5 centims. The pre-zygapophyses look upward, inward, and slightly forward.

# The Shoulder Girdle.

# (Plates 12 and 20.)

The massive bones of the shoulder girdle are thrust in between the skull and the atlas. They are imperfectly preserved, and consist of an inter-clavicle and clavicle which unite by suture; and the anchylosed coracoid and scapula, which are more massive than the ilium, but are preserved imperfectly.

The inter-clavicle and clavicles form an anterior or bow-shaped arch which is formed on the general plan of Nothosaurians and certain Lizards. The inter-clavicle is in the median line in front, and is a symmetrical V-shaped bone, with its limbs widely diverging and directed backward. The median anterior extremity was thickened, convex, and inclined slightly downward, but has a truncated aspect, as though broken, or as though forming a boss which helped to support the body when at rest. This

surface is transversely ovate, 5 centims. wide, and nearly 4 centims. long. The antero-posterior extent of the bone is about 11 centims. Its lateral arm extends outward and backward for 21 centims. from the anterior convexity. These arms are external to the clavicles (cl) and beneath them, and thin away posteriorly. On the flattened inferior surface of the bone, which is concave from side to side, a sutural line extends transversely outward, so as to make each half of the border slightly concave, which divides the inter-clavicle from the clavicle. On the internal or superior aspect the entire width of the clavicles is exposed so that they almost meet in the median line as they rest upon the inter-clavicle; and their convex anterior borders fit into corresponding posterior concavities on the posterior side of the bone. Anteriorly the bone is nearly 5 centims. thick, and becomes thinner behind. The anterior border is straight, and rounds somewhat sharply into the external surface; while, as it ascends in a convex curve over the oblique anterior aspect of the anterior border of the clavicle, the median anterior aspect of the inter-clavicle is convex from side to side.

The clavicles are compressed flattened bones, with their external contour convexly curved as it extends backward, and the external and internal borders sub-parallel. Both bones are imperfectly preserved, but the longer one measures 38 centims.; it is about 8 centims, wide in the middle, and becomes narrower towards both extremities, so that the curvature of the convex external margin is greater than that of the concave internal margin. The anterior median extremity of the bone is rounded from within outward. A transverse section (Plate 20, fig. 3) shows that the bone (c) is received as a wedge between superior and inferior flanges of the interclavicle (ic.); the bone is thickest in the middle, and thins towards the posterior margin. The transverse width over the posterior ends of the clavicles was probably about 50 centims.

On the ventral side of the left clavicle are imperfect remains of the scapular arch, formed, it may be presumed, of scapula and coracoid, blended at the humeral articulation, on both sides of which the bone extends. The humeral articulation was probably transversely oval, measuring 14 centims. by 9 centims., and was remarkably shallow in its concavity (g).

At right angles to one extremity of this articular surface is a compressed sheet of bone, less than 2 centims. thick and fully 8 centims, wide, which extends as preserved for 12 centims, beyond the articulation. This may be the precoracoid. At the other end of the articulation, the scapula first contracts in dimensions, and then is prolonged as a massive shaft, sub-ovate in section, which at the fracture is fully 10 centims. from front to back, and about 7 centims, from within outward. What I take to be the internal surface is smooth and unbroken, and similar to the external surface, the only difference apparently being that there is a notch, which appears to extend obliquely through the bone just in advance of the articulation. This structure is approximated to in some Anomodonts from South Africa.

#### Armour.

From the analogy of Belodon it might have been anticipated that the enlargement of the extremities of the neural spines of the dorsal vertebra would be correlated with the support of a weighty mail of dermal plates. But the form of the spines is more suggestive of Urodeles, in which no such armour exists. No indications of large dermal bones are preserved, and they probably did not exist, since small dermal bones lie in the interspaces between the post-zygapophysial ridges. They are irregular in form, and vary in size and thickness, though they are mostly about 7 millims. thick and are thinner at the margin. The external surface is nearly smooth, though it is slightly keeled in one case. Several plates are 3.5 centims, wide, and were probably sub-quadrate. There is no evidence that they were in close contact with each other. Smaller scutes are found above the sacral vertebræ, and also above the early caudal vertebræ.

## Other Remains referred to Pareiasaurus.

Sir Richard Owen referred to Pareiasaurus bombidens many other bones from the same locality, Vers Fontein, which yielded the type-skull. I am not concerned to discuss the grounds on which this reference may have been made, because no evidences of their relation to the skull are offered. The bones are described as a cervical vertebra, a dorsal vertebra, "the coalesced humeral ends of the right scapula and coracoid," the right and left humeri, the right ulna, the right ilium and portion of the left ilium, and proximal portion of the right femur.\* Another bone, from Jan Willem's Farm, also referred to this species, is the right tibia; and some vertebræ from this locality are referred to Pareiasaurus without the species being determined. These remains, with the possible exception of a vertebra, are proved by the foregoing description to belong to a different genus.

First, the "anchylosed scapula and coracoid" (No. 43,525) are manifestly the anchylosed ischium and pubis. If any difficulty were felt as to this determination, it is removed by fitting the anchylosed bones to the ilium, when the surfaces perfectly correspond and show the bones to complete the pelvic structure of one individual (Plate 21, fig. 1). The type of pelvis, as shown by the ilium, is as different from that of Pareiasaurus as the ilium of a Seal is unlike that of a Bear; and, as it is also attached chiefly to a single sacral vertebra, and unlike in form the ilium referred to Dicynodon, or Platypodosaurus, or any described South African fossil, it probably indicates an undescribed genus. There is a strong enough resemblance to those types to leave no doubt that the animal was an Anomodont. It would be inconvenient to enter now into a detailed discussion of the structure of this type, which may be designated Phocosaurus megischion. The pelvis furnishes the only element of the

<sup>\*</sup> Figured, Owen: "Description of Parts of the Skeleton of an Anomodont, &c.," 'Geol. Soc. Quart. Journ.,' vol. 36, Plate 17, fig. 8.

skeleton, except the vertebræ, which can be compared, and I therefore offer a brief account of this region in justification of the present interpretation which separates it from *Pareiasaurus*.

The pelvis of *Phocosaurus* (Plate 21, fig. 1) is remarkable for the enormous size of the hemispherical acetabular cup for the femur. More than half of the acetabulum is made by the ilium, and its lower portion is made up in nearly equal parts by the pubis and ischium, which are united to each other by a straight suture. The pubic bones were probably united with each other by suture in the median line of the body (Plate 21, fig. 2); but, owing to imperfect preservation, there is no evidence of the relations of the ischiac bones to each other.

The antero-posterior width of the acetabular cup is 25.5 centims.; its vertical height is more than 23.1 centims. The cup is broader below than above, and is so placed that the iliac portion overhangs the part formed by the other bones.

Superiorly within the acetabulum the ilium forms a horizontal, ovate, articular surface, which is rugose as though lined with cartilage; it is 14 centims. long by 9 centims, wide. Its presence greatly thickens the ilium, and I infer the plate to have been developed by supporting the femur in terrestrial movements. And, as this plate is narrower than the acetabulum, I judge the head of the femur to have been smaller than the acetabulum. This superior articular surface is defined anteriorly by a long deep groove, which extends backward from its anterior corner. The iliac surface in the acetabulum below this groove appears to have been a smooth surface, which took no part in supporting the movements of the femur; it is more than 10.2 centims. deep to the sutural union with the pubis, while the corresponding depth posteriorly to the ischium is 3.8 centims. Posterior to the superior articular surface is a corresponding concavity, but the groove is less developed. The transverse width of the inferior border of the ilium is 29.2 centims., divided into two nearly equal parts inclined to each other in a broad V-shape. The contour of this transverse sutural surface for union with the inferior pelvic bones is a crescent, concave from front to back along the acetabulum, convex along the visceral surface. The sutural surface is transverse to the external surfaces; its greatest thickness at the outer limits is 6.3 centims., while its transverse measurement in the middle is only half as much, so that the acetabular cup is part of a smaller circle than the more flattened curve of the visceral surface. Necessarily there is a corresponding difference in breadth of the pubis and ischium.

Superior to the acetabulum, both the anterior and posterior contours of the ilium are constricted to a width of  $16\frac{1}{2}$  centims.; the posterior concavity is the narrower curve from above downward. The external aspect of the bone is convex above the acetabulum, but the convexity diminishes as the bone widens superiorly. Vertically from the superior margin of the acetabulum to the superior crest of the ilium the bone is concave, owing to the crest curving outward. Owing to the increased height of the

crest of the ilium, the depth of this part of the bone is greater in front than posteriorly, but is fully 20.4 centims. in the middle.

Anteriorly the bone is imperfect in both examples. But the curvature of the superior crest in the right ilium as it extends anteriorly leads to the conclusion that the anterior prolongation may not have been greater than the elongation of the posterior angle. So far as I am aware, this is the only example of an Anomodont Reptile in which a distinct posterior process to the ilium is developed. As preserved, the antero-posterior extent of the ilium below the superior crest is about 30½ centims., but I infer the bone, when complete, to have measured 38:1 centims.

The superior crest, which is otherwise thin and sharp, thickens posteriorly, and develops a sharp ridge 7.6 centims. from the posterior extremity of the bone. The whole of the posterior side is thickened from within outward.

The ilium is supported chiefly by one sacral rib, which has a large union with the bone, and a transverse width of 20 to 23 centims. On the right side there appear to be at least two more small ribs in contact with the posterior process of the ilium.

The form of ilium is about intermediate between that of an Ornithosaur (Plate 18, figs. 5 and 6) and the ilium of a Seal (Plate 21, fig. 3).

The pubis and ischium are anchylosed or closely united by a straight vertical suture, so as to form a strong elongated bony plate, which is imperfect posteriorly, owing to fracture of the ischium. As preserved, the antero-posterior measurement in the middle of the united bones is 41 centims., of which the pubis contributes a length of 20 centims., to its junction with the ischium. The measurement downward and inward from the acetabular margin to the median ventral line of the body is 25 centims. The plane of the bones is curved, so that the visceral aspect is concave from within outward, and the bones of the two sides of the body would form a semicylindrical trough: the transverse measurement from the median ventral suture to the suture with the ilium is about 27 centims. External to the comparatively narrow union with the ilium is the oblique contribution which these bones make to the acetabular cup. This surface is concave from front to back, measuring 25 centims. in length; and its width is 11.5 centims, anteriorly and 10 centims, posteriorly. This transverse measurement forms much of the acetabular thickness of the bone, which is 14 centims. at the pubis and nearly 13 centims. at the ischium. Both pubis and ischium are expanded and sub-quadrate in form, though the inner and hinder part of the ischium is not preserved. Below the acetabulum the attenuation in thickness is remarkable, especially in the middle, though the bones thicken laterally to some extent on the anterior margin of the pubis and the posterior margin of the ischium. These margins diverge from each other as they extend downward and inward, so as to lengthen the antero-posterior extent of the bones. The anterior pubic border includes three areas: first, below the acetabulum, is a concave border, smooth, and rounded from within outward; then the bone thickens a little to a rugged surface which forms a rounded angle; and then it extends transversely inward as a long,

straight, rather compressed, cartilaginous surface (p.p.). This surface may have supported a pre-pubic cartilage. The posterior margin of the ischium is preserved for 18 centims.; it is slightly concave below the acetabulum, but is approximately straight as it extends inward and backward. It is smooth, perfectly ossified, and rounded from within outward.

The external surface of the ischium is comparatively flattened, while the surface of the pubis is irregularly concave. The pubic foramen (f) is 10 centims, from the acetabular margin, and an equal distance from the concave anterior border. Below the foramen there is a convexity.

A comparison with the pelvic bones already figured or preserved in the British Museum, and referred by Sir R. Owen to Anomodonts and Theriodonts, demonstrates the generic distinctness of this type, not only from the ilium originally referred to Pareiasaurus, but from every other form. It is, however, necessary to state that the ilium, S. A. 122, described in the 'Descriptive and Illustrated Catalogue,' p. 70, is the specimen originally figured in the 'Transactions of the Geological Society,' vol. 7, Plate 34, figs. 2, 3, sg. It was then regarded as either a scapula or coracoid of Dicynodon; and it is remarked that, if it is regarded as a scapula, the bone which is represented in contact with it in fig. 2 and lettered cp, which is perforated like the ischio-pubic bone, is regarded as probably the coracoid, and likened to that of Iguanodon. In the Catalogue above referred to the former bone is regarded as the left ilium, but it is manifestly the right ilium, since the mass of the bone is always anterior to the acetabulum in these animals; the latter bone is certainly the anchylosed ischium and pubis, and the whole of the pelvic bones are likely to belong to species of Dicynodon.

The characters of the vertebræ referred to *Pareiasaurus* have been fully elucidated by Sir R. Owen in his paper in the 'Quarterly Journal of the Geological Society,' and in the 'Catalogue.' They are proved by the short centrum, small neural arch, different attachment of the ribs, and relatively longer and more slender neural spine, not to belong to *Pareiasaurus*.

On the Nature of the Relation of Pareiasaurus to other reputed Dinosaurs from South Africa.

There are four reputed genera of Dinosauria from the Karroo beds of South Africa. Professor Huxley, in 1866, described Euskelesaurus and Orosaurus; and, although no figures were given, the description leaves no room for doubt that the systematic position of those fossils was well determined. This is not the case with the genera Anthodon and Tapinocephalus, defined by Sir R. Owen. If the affinities of an animal could be inferred from the teeth, there is so close a resemblance between Anthodon and Acanthopholis that there ought to have been certainty as to its place among Dinosaurs, except that the long fangs of the teeth are firmly imbedded in

bone. But although the skull is badly preserved, so that the sutures are made out with difficulty, enough is seen in the post-orbital region to show that the bones are arranged upon the Labyrinthodont plan which characterises Pareiasaurus. The quadrato-jugal bone is similarly formed, and descends below the level of the quadrate articulation. The region above the quadrato-jugal appears to include the malar, supra-temporal, and other bones. The vertebræ attributed to this genus have the neural arch expanded in a way that somewhat approximates to Pareiasaurus, but the centrum is as deeply cupped conically as in any Fish. The resemblances to Pareiasaurus are good evidence that both genera belong to the same group of animals, and better evidence of affinity than the form of the teeth.

Tapinocephalus is too imperfectly known from the extremity of the snout to furnish any certain evidence of its affinities or classificatory position. The head is apparently constructed on a distinctive plan, but the teeth are hollow, as in Labyrinthodonts, and have the fang imbedded in bone, as in Pareiasaurus and Anthodon, while the slight ridges on the crown are not unlike a few seen on some of the hinder teeth of Pareiasaurus bombidens.

I am not aware of any evidence which would justify the association of the skull-fragment with the vertebræ, which have already been described,\* and differ from those of *Pareiasaurus* in not showing any hypocentral ossification.

## The Affinities of Pareiasaurus.

The discussion of the regions of the skeleton described has shown that *Pareiasaurus* combines in one animal characters which are found in Labyrinthodontia, Reptilia, and Mammalia, and it becomes necessary to examine the significance of these resemblances. The investigation is beset with difficulty on account of uncertainty as to the nature of the skeleton in the larger Labyrinthodontia, the absence of knowledge of the limbs and preservation of *Pareiasaurus*, and the necessarily hypothetical interpretation, on such imperfect data, of the relations between classes of animals.

# The Labyrinthodont Characters of Pareiasaurus.

The Labyrinthodontia have been usually grouped with the Amphibia, but there is some reason to believe that many different grades or varieties of organization have been comprised under this name which have no near relation to existing Amphibians. Dr. Fritsch, after carefully describing the varied fauna of Stegocephali from the Permian rocks of Bohemia, concludes that, with our present knowledge, it is impossible to say whether the Stegocephali are Amphibians or Reptiles. The characters by which these organisms are related together are, first, a common structure in the roof of the skull, which is unknown in existing Amphibians and Reptiles; secondly, all the

<sup>\* &#</sup>x27;Geol. Soc. Quart. Journ.,' vol. 32, Plate 4, p. 43.

Labyrinthodont genera have a separate parasphenoid; but Dr. Fritsch does not regard this as an important Amphibian characteristic, since the parasphenoid of Hatteria closely resembles the bone in the genera Hyloplesion and Microbrachis, and there is reason to believe that the bone is not united to the basi-sphenoid in the young of Hatteria; thirdly, Labyrinthodonts agree in the structure of the shoulder-girdle; but Dr. Fritsch states that if the lateral plates of the breast armour are regarded as the coracoid bones, and the middle plate as the inter-clavicle, then the shoulder-girdle has more in common with a true Lizard than with an Amphibian. This is, perhaps, the most obscure and difficult point in Labyrinthodont structure; but it does not appear to me that either the Ichthyosaurian or Nothosaurian shoulder-girdles lend support to Dr. Fritsch's suggested interpretation.

Dr. Fritsch attaches but little importance to the articulation of the skull with the vertebral column by means of two condyles, since two lateral condyles, formed by the ex-occipital bones, are present in the young Hatteria and in Chelonians; but it is stated that the basi-sphenoid\* extends below them, forming a third condyle. This contention may deserve detailed discussion. The genera are grouped into four suborders, which are defined on the ground of vertebral structure, lengths of the ribs, presence or absence of gill-arches, and external resemblance to existing Amphibians and Reptiles. They are named Urodeloideæ, Gymnophioideæ, Saurioideæ, and Crocodilioideæ, but none of these sub-orders are identified as ancestors of existing Amphibians or Reptiles.

The difficulty in determining the systematic position of the Labyrinthodontia has been experienced practically by every student of the group, and, if its classificatory position rests upon the ossification of the gill-arches and the presence of a double occipital condyle, we must admit that the ways in which other parts of the skeleton approximate to structures in extinct and existing groups of Reptiles make the coincidences more suggestive of near affinity with the higher class. They may be technically Amphibians, and yet almost cover the interval between that class and the Reptilia.

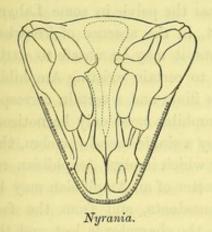
I have long been led to regard the Labyrinthodontia as standing in an ancestral relation to the Reptilia, either of a direct or collateral kind, for many reasons. First, the changes of structure are simple by which characteristic portions of the skeleton in many Reptile orders could be derived from a Labyrinthodont type. Secondly, because the structural resemblances of several extinct orders of Reptiles with Labyrinthodonts are as remarkable as their resemblances with existing orders of Reptilia. Thirdly, because it is manifest that, if the descendants of Carboniferous and Triassic Labyrinthodonts have survived in existing Amphibia, they have undergone changes in their skeletons of as marked a kind as any changes which would be necessary to evolve Reptilian skeletons from the same types. I quite agree with Dr. Fritsch in failing

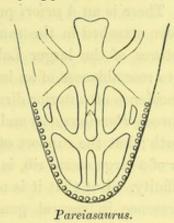
<sup>\*</sup> This statement is repeated in the explanation of the figure, but I am aware of no evidence for questioning the identification of this bone as the basi-occipital.

to recognise any very close relation between the existing Amphibia and the Labyrinthodontia; and, if I urge near affinity between the latter group and the more ancient Reptiles, it does not follow that there is as close an affinity between the more modern Reptiles and existing Amphibians, for the Amphibians have experienced structural changes akin to those which Reptiles have undergone, implying collateral descent.

It seems to me beyond question that Pareiasaurus is an animal in which there is transition from the Labyrinthodont to the Reptile exhibited in every part of the skeleton. The head shows five Labyrinthodont characters—(1) the form, (2) the sculpture of the cranial bones, (3) the arrangement of the bones which cover the head, (4) the presence of mucus-canals between the orbits and nares, (5) the absence of the lachrymal bone from the anterior corner of the orbit of the eye. The only difference on the upper surface of the skull from that of a Labyrinthodont is in the large size and close approximation or confluence of the anterior nares, which is a Reptilian character of some importance, as bearing on the mode of respiration.

The palatal surface is at first sight not so obviously Labyrinthodont, and the only genus of that order which I remember as showing any approximation to the palate of





Pareiasaurus serridens is the Permian fossil Nyrania as restored by Professor Fritsch.\* In so far as can be judged from these figures, there appears to be a certain correspondence of plan in the palate; and the condition of the bones in Nyrania is suggestive of the possible limits of the vomera, palatines, and pterygoid bones in Pareiasaurus. The differences from the Labyrinthodont palate are the absence of a distinct parasphenoid bone in Pareiasaurus (which is only conjecturally present in Nyrania), the presence of the basi-sphenoid on the palate, and the existence of a median palatal vacuity, in all of which characters there is rather a resemblance to embryonic stages in the development of the skulls of the existing Amphibia.

At the back of the skull the essential difference from a Labyrinthodont is in the presence of a single occipital condyle. How that condyle comes to be there, formed of one bone, and not contributed to by the ex-occipitals, is a theoretical question to which the specimen suggests only a speculative answer.

<sup>\* &#</sup>x27;Fauna der Gaskohle, &c.,' vol. 2, Heft 2, p. 35.

The vertebral column of the larger Labyrinthodonts is imperfectly known; but the large intervertebral wedge-bones are characteristic of the group, and the biconcave centrum is equally characteristic, while the articulation of the ribs in the dorsal region by double heads to capitular and tubercular facets of transverse processes has been attributed by Professor Huxley to Anthracosaurus.\* Similar vertebræ were figured by von Meyer and Plieninger,† and referred to Mastodonsaurus. Both these types have more in common with Pareiasaurus than has Loxomma, in which the intercentra appear, from the description by Dr. Embleton and Mr. Atthey, to be as well developed as the centra. Whether the cervical, sacral, and caudal vertebræ would present in any Labyrinthodont the characters here described in Pareiasaurus there is not sufficient evidence to demonstrate; but the probabilities all incline towards that conclusion. Still the resemblance of the vertebral column to that of a Crocodile is so marked in the mode of articulation of the cervical and early dorsal ribs, as to leave no doubt that, while it approximates in plan to the Labyrinthodontia, it is equally close to the plan of the Crocodilia. The sacral region, as already observed in the description, is comparable with existing Urodeles in so far as its mode of union with the pelvis is concerned. There is an à priori probability that the pelvis in some Labyrinthodonts may have been attached in the same way; but, in the absence of knowledge of the pelvic structures of the larger Labyrinthodonts, it may be unsafe to attribute much importance to resemblances of an isolated kind to certain existing Amphibia. Therefore the coincidence of anterior direction of the ilium and a certain correspondence in its form between Pareiasaurus and anurous Amphibia need only be noticed for what they are worth; but the support of the ilium by a single sacral vertebra, through the intervention of a large sacral rib, is a character which implies Amphibian rather than Reptilian affinity. But that it is not the character of an Amphibian may be inferred from its presence in several genera of Anomodonts, and from the fact that in Platypodosaurus, which is of Anomodont type, the character is lost, and the pelvis is supported by a sacrum of several vertebræ in the manner seen in Dinosauria and certain Mammalia.

The inter-clavicles and clavicle are less markedly Labyrinthodont than other parts of the skeleton, and yet offer a sufficiently close resemblance in plan to show that the Labyrinthodont type has been modified, but not lost. The divergence which they show is rather towards the corresponding bones of the Nothosauria than to the clavicular arch of the Ichthyopterygia.

Hence I regard the conclusion as evident that, so much of the skeleton of Pareiasaurus as is preserved suggests that the genus arose from a Labyrinthodont

<sup>\*</sup> Professor MIALL remarks that there is no proof that these vertebræ and ribs belong to Anthracosaurus; but there is no reason to question their Labyrinthodont character.

<sup>† &#</sup>x27;Beiträge zur Paläontologie Württembergs,' 1844, Plate 4, fig. 6; 'Geol. Soc. Quart. Journ.,' vol. 19, p. 63, fig. 2.

<sup>‡ &#</sup>x27;Ann. Mag. Nat. Hist.,' July, 1874, p. 57.

ancestry. But, although there is a preponderance of Labyrinthodont characters in the skeleton, they are combined with other characters only found in Reptiles; and therefore the Labyrinthodont characters do not refer *Pareiasaurus* to the Labyrinthodontia. The type, which has lost but few Labyrinthodont characteristics, has yet some of the most striking characters of various orders of Reptilia; and it is upon these facts, which I now go on to state, that the conclusion must rest that *Pareiasaurus* and other Reptilia exhibit evidence that the Reptilia arose from the Amphibia by certain osteological changes which left the fundamental structure of the skeleton substantially the same in most of its parts.

## The Reptilian Characters of Pareiasaurus.

The Reptilian characteristics of *Pareiasaurus* which are not also common to the Labyrinthodontia are few. But they comprise some of the most remarkable characteristics of the Reptilia and of different Reptile orders; and the smallness of their number is evidence that they have been developed upon a basis of Labyrinthodont structure.

First, there is the large single, rounded, occipital condyle, formed of one bone. This has been taken as the test structure in classification, which not only separates the Amphibia from the Reptilia, but unites the orders of Reptiles together, and blends them into one group with Birds. The skull of Pareiasaurus exhibits no trace of ever having had two occipital condyles, and the articulation of the head with the vertebral column is as Reptilian as in any known order of Reptiles. If the two occipital condyles had been present, it would have been difficult to resist the conclusion, notwithstanding other characters of the skeleton, that Pareiasaurus was a Labyrinthodont; and therefore the presence of the single condyle, into which the ex-occipital bones do not enter, is the best osteological evidence that could be produced that the animal is a Reptile. There is necessarily no direct evidence as to the mode of origin of the condyle, but its development in a skull the external characters of which are so conspicuously Labyrinthodont may perhaps justify a consideration of a possible origin which the vertebral column of some Labyrinthodonts suggests. In various well-known genera, such as Loxomma, \* Diplovertebron, † Cricotus, ‡ &c., it is well known that there are large intercentral ossifications developed which may in all respects resemble a centrum of a contiguous vertebra, except that the inter-centrum does not carry a neural arch. In Pareiasaurus such intercentral ossifications are present, but are of smaller size, and limited to the ventral portion of the centrums between which they are placed. If it is conceived that such an intercentral ossification were developed in the part of the notochord between the atlas and the skull, and blended with the skull in the same way that the atlas and axis are often anchylosed

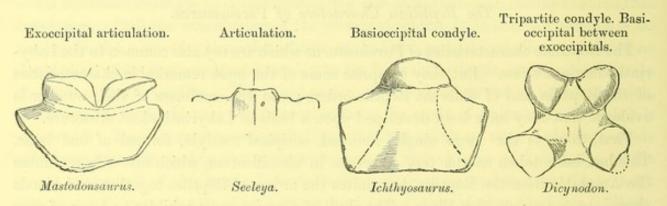
<sup>\*</sup> Embleton: 'Ann. Mag. Nat. Hist.,' July, 1874.

<sup>†</sup> FRITSCH: 'Fauna der Gaskohle,' vol. 2, Heft 1, Plate 52.

<sup>‡</sup> COPE: 'American Naturalist,' January, 1884.

together, then the origin of the single basi-occipital condyle might be accounted for as the modification of a structure which was already foreshadowed in the axial skeleton.

The single condyle would thus lose none of its importance as a mark of affinity between the animals in which it is found, but as the mystery of its existence disappeared it would be realised that the change from the Amphibian to the Reptilian mode of union of the skull with the vertebræ does not necessarily imply a wide difference in organization. It is interesting to remark that the body of the atlas is very short in the great majority of Reptiles, Birds, and Mammals, as it theoretically might be if its anterior half were incorporated with the skull. Some evidence in support of this origin for the single basi-occipital condyle is perhaps furnished by the fact that the bone is



conspicuously large and rounded in the Ichthyopterygia, which preserve a larger number of Labyrinthodont characters than any other order of fossil Reptilia, while in Reptiles which have lost the technical distinctive marks of the Labyrinthodonts it enters further into the skull, and is received between the ex-occipital bones, though at first extending chiefly below them. Among the Anomodontia the basi-occipital bone is embraced laterally by the ex-occipital bones; the same condition, in a less striking degree, characterises the Chelonia; it is seen in the Plesiosauria, Teleosauria, Dinosauria, Rhynchocephalia, and among Birds. If the Reptilian and Avian form of occipital condyle could thus be derived from the Labyrinthodont type, the recurrence of the double ex-occipital condyles in the Mammal may be but the consequence of a still further forward movement of the basi-occipital bone, in consequence of which it has come to occupy a position analogous to that held among Labyrinthodonts by the basi-sphenoid. Such an appearance of forward movement of the basi-occipital would be a consequence of increasing size of the brain, tending to throw the basi-occipital bone into the floor of the brain-case. Hence it is possible that the condylar cranial characters may be related in an evolutionary sequence of gradation, and that the change from one condition to another may be consequences of one plan of Vertebrate organization rather than of entirely independent plans.

The other Reptilian characters of *Pareiasaurus* are shared by Anomodontia, Ichthyopterygia, Nothosauria, Plesiosauria, and Crocodilia; and it may be preferable to consider these resemblances separately, since they appear to me to lead to the

conclusion that the several orders of Reptilia are developed from Labyrinthodont types, and have all preserved more or less of the original skeletal structures. And, if so, it must follow that they are related to each other, not as relatively higher or lower orders, which can be arranged in a vertical sequence, but as parallel groups variously modified upon approximately the same horizon of organization.\* And their evidence will contribute to show that the Labyrinthodont characters of *Pareiasaurus* differ only in degree, and not in kind, from the structures of various Reptiles.

Resemblances to the Anomodontia.—Notwithstanding the many genera which this group includes, no complete skeleton is at present known, and consequently some uncertainty may attach to the association of vertebræ and other remains with the species of skull to which they have been referred, but I see no reason to question the determinations which have referred those pelvic, vertebral, and appendicular remains to the Anomodont order, and to the allied type named Theriodontia.

If the base and palatal aspect of any Anomodont skull, such as Dicynodon leoniceps or Oudenodon megalops, is compared with the palatal aspect of Pareiasaurus (p. 97), the resemblances are more striking than the differences. The basi-sphenoidal mass in both is of similar form, and is similarly concave longitudinally. In both it is blended with the pterygoid bones; in both it sends a slender process backward towards the quadrate, separated from the basi-sphenoid by a deep notch; in both there is a median union of the pterygoids in front of the basi-sphenoid, and a median vacuity in front of the expanded plate; in both there is a parallel pair of palatine bones extending forward: while in some species, like Dicynodon pardiceps \ and D. testudiceps, \ the palate terminates anteriorly in two parallel ridges like those seen in Pareiasaurus. The points in which differences can be detected all concern the anterior lateral part of the skull in the vomerine region, and the mode of union of the palatine bones. But the comparison shows a correspondence of plan which is compatible with both types belonging to the same ordinal group, and the resemblance is more remarkable than that which has been already indicated between Pareiasaurus and the Labyrinthodont Nyrania. And the correspondence seems to me of greater weight as evidence of affinity with Anomodonts than are the external resemblances evidence of affinity with Labyrinthodonts, because the remainder of the Anomodont skeleton shows an equally close correspondence with Pareiasaurus. The dorsal vertebræ referred to Dicynodon pardiceps have a Plesiosaurian length of centrum with biconcave articular ends, such as Plesiosaurs exhibit in many species, but the mode of attachment of the rib is that of a Dinosaur, in the head of the rib being upon the centrum, and the tubercle upon

<sup>\* &</sup>quot;Origin of the Vertebrate Skeleton," 'Ann. Mag. Nat. Hist.,' July, 1872, p. 44.

<sup>†</sup> Owen, 'Descriptive and Illustrated Catalogue,' Plate 26.

<sup>1</sup> Loc. cit., Plate 63.

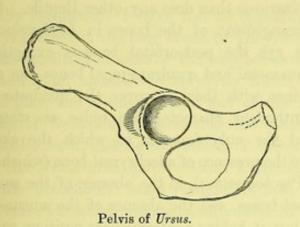
<sup>§</sup> Loc. cit., Plate 38.

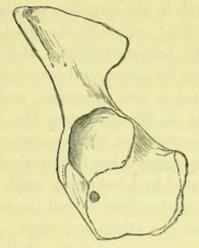
<sup>|</sup> Loc. cit., Plate 44.

<sup>¶ &#</sup>x27;Descriptive and Illustrated Catalogue,' Plate 53.

the transverse process; but this condition is approximated to in the early dorsal vertebræ of Crocodiles and of Pareiasaurus. It is also found in vertebræ of Mastodonsaurus, in which the capitular attachment of the rib becomes elevated above the centrum. as in Parciasaurus,\* but, owing to the shortness of the centrum in that genus, the resemblance to Pareiasaurus is not impressive, especially as the zygapophyses are not conspicuous for transverse expansion. It may be that the difficulty in showing closer correspondence with the vertebral column of the Anomodonts is entirely due to the evidence not having been brought to this country, since the correspondence in the sacral region appears to be absolute. The sacrum referred by Sir R. Owen to Dicynodon tigriceps may include only two vertebræ, though the succeeding vertebræ are in close apposition owing to the influence of the pelvis in limiting movement, and exactly the same condition is seen in the vertebræ of Pareiasaurus, which immediately follow the sacrum. The form of the centrums is essentially the same: in both the sacral rib of the first vertebra is similarly expanded so as to support the pelvis, and is similarly directed outward, backward, and downward so as to give attachment to the ilium along its oblique external margin. Moreover the ilium of Dicynodon tigriceps, in its ordinal characters of form, direction, and relation to the other pelvic bones, is essentially comparable with Pareiasaurus, and every other ilium of Dicynodont type from South Africa is constructed essentially upon the same plan. Hence it must follow either that the whole of these pelvic remains which have been referred to Anomodonts have nothing to do with them, and really belong to near allies of Pareiasaurus, or else Dicynodon and its allies so resemble Pareiasaurus in sacral and pelvic characters that only a generic difference in the form of the ilium can be used to separate them. Now, in view of the correspondences pointed out in the palate, and other resemblances in some characters of the vertebræ, there is no à priori improbability in pelvic and sacral resemblances between these two types, but, on the contrary, some reason for anticipating resemblances. And the weight of evidence seems to me to incline in favour of Sir R. Owen's interpretation of the pelvic characters in the Anomodontia, rather than to support the induction from the extension of the characters of the Pareiasauria which might legitimately follow from my own account of its pelvic structure. This evidence may be appreciated by comparing the bones, or even wood-cut figures, like those which follow, in which representations are given of the forms of pelvic bones in Anomodonts from South Africa which have been described.

<sup>\*</sup> Von Meyer and Plieninger, 'Paläontol. Württembergs,' 1844, Plate 4, fig. 6.





Pelvis of Dicynodon leoniceps (Ow.).

It is evident that the South African Anomodont Reptiles all have the pelvis formed on the same plan, which exhibits as many minor modifications (p. 107) as there are known groups of Reptiles in those rocks; and therefore I see no reason why we should hesitate to accept the other unassociated forms of ilium as rightly referred to the animals which have been grouped as Anomodonts and Theriodonts, and so recognize their near affinity with Pareiasaurus. But if this conclusion be legitimate it gives rise to another inference of some osteological importance, namely, that animals which possess closely similar pelvic structures may differ in cranial structures as much as Dicynodon and Pareiasaurus; but this will not seem improbable when we remember the history of the correlation of pelvic and cranial characters in the Dinosauria, Nothosauria, and Crocodilia, and the diverse crania which go with persistent pelvic structures. But, if the Anomodonts and Pareiasaurus are such near allies, it follows that the Anomodonts are also nearly related to the Labyrinthodonts, and that the covered skull of the parent Amphibian type has undergone processes of change comparable to those which Tortoises show when compared with Turtles, by which the head has lost the bones which are distinctly Labyrinthodont, and has become Reptilian. If there were reason to suppose that this change was exceptional to the Anomodontia, there might be reason to hesitate to admit it as a sufficient explanation of the persistence of Labyrinthodont characters in the upper surface of the skull in Pareiasaurus; but there is probably no order of Reptilia in which marked Labyrinthodont characters may not be traced in the skeleton, though they are more conspicuous in some orders than in others, and the validity of the explanation offered must rest upon the evidence that other orders of Reptiles, in which the skeleton is better known, show proofs of such transition as is inferred to have taken place in Anomodonts.

Resemblances to Ichthyopterygia.—The Ichthyosaurians are in some respects the most primitive of the Reptiles, and, both in the skull and vertebral column, show the characters of Labyrinthodonts. It is the single occipital condyle which marks the order as Reptilian, and in its large size and transversely rounded ball it makes a nearer

approach to the condition seen in Pareiasaurus than does any other Reptile. In the post-orbital region of the head the arrangement of the bones in Ichthyosaurus is entirely Labyrinthodont. Behind the eye the post-orbital bone is exceptionally strongly developed, and between the squamosal and quadrato-jugal bones the supratemporal is also preserved, and combines with them to cover the quadrate bone, so that in these respects the Labyrinthodont characters are quite as strong in Ichthyosaurus as in Pareiasaurus, and the only features in which the skull of Ichthyosaurus is less Labyrinthodont are the presence of a lachrymal bone (which is not perforated by a lachrymal canal as in Ptychognathus), in the absence of the so-called epiotic plates from behind the squamosal bones, and the absence of the mucus-canals between the orbits and nares. And thus it holds an intermediate position, so far as the preservation of those osteological conditions is concerned, between Pareiasaurus and ordinary Reptiles. And, since the supra-temporal bone covers the auditory region of the head, it is manifestly a bone which, with advantage to the animal, may be replaced by a membrane in terrestrial and littoral animals.

In the shortness of its vertebræ and absence of the transverse expansion of the neural arch, no less than in the mode of attachment of the ribs, *Ichthyosaurus* is totally unlike *Pareiasaurus*. But its vertebral characters are in many respects Labyrinthodont. The deep biconcave form of the centrum is paralleled in *Eosaurus*, and in other genera the centrum is equally short. The neural arch is not unlike that of *Mastodonsaurus*, and the ribs are similar in *Anthracosaurus* and other genera. The mode of their attachment is distinctive, but may be correlated with oceanic habits, since *Pareiasaurus* has both attachments for cervical ribs on the centrum, and *Ichthyosaurus* preserves the double-headed attachment in all presacral vertebræ.

The Oxford Clay genus *Ophthalmosaurus* has the clavicles more expanded than other Ichthyosaurs, and the clavicles embrace the inter-clavicle by a mode of union which is like that seen in *Pareiasaurus*; but the resemblance of the clavicular arch, like that of the vertebral column, is much less obvious with *Ichthyosaurus* than with Nothosaurs.

Resemblances to the Nothosauria.—The skeletons of the Nothosaurians are imperfectly preserved, but, although the skull is typically Reptilian, as showing no traces of Labyrinthodont structures, the remainder of the bones have preserved evidences of their origin from an Amphibian ancestor, which are well marked in both the vertebral column and the limbs. The large transversely expanded neural arch, the elevation of the ribs to the neural arch in the dorsal region, the structure of the shoulder-girdle and pelvic bones and limbs, are all strongly Labyrinthodont. And, the group is represented in South Africa, in rocks apparently of the same age as those which yield the Parciasaurus, by species of the genus Mesosaurus. All the long bones of the Nothosauria and Plesiosauria ossify in the same way as the long bones of living Frogs, and consist of cylindrical girdles into which long conical epiphyses penetrate, so as to meet, or nearly meet, in the middle of the shaft, from which they are often easily or

naturally separated. I have had no opportunity of determining whether this condition is present in the long bones of Labyrinthodonts, and I only otherwise know it as a rare condition in some of the long bones of Chelonia from the Cambridge Greensand, and in an undescribed epiphysis, which I believe to be Dinosaurian, from the Oxford Clay, and in the proximal end of the tibia of Protorosaurus. A section of a vertebra of Nothosaurus shows that the centrum has ossified in the same way, as a periosteal sheath, and by conversion of the notochordal substance into bone at both ends. In Mesosaurus, and its South American representative named Stereosternum, a tubular notochordal canal remains at each end of the centrum like that figured in the vertebræ which were originally referred to Pareiasaurus. Although the mode of articulation of the ribs in Mesosaurs is different, and the form of the neural arch is not the same, there is enough in common to make the correspondence in the clavicular arch important as a mark of affinity, for in no other group have the bones either similar forms or arrangement. The resemblance is closer with Nothosaurus than with any of the smaller types. Labyrinthodon rütimeyeri\* demonstrates the resemblances of the limbs, and pelvic and shoulder-girdle bones, with these Nothosaurs in a striking way; and the femur and smaller limb-bones of Mastodonsaurus are essentially of the same forms as in Nothosaurus, Neusticosaurus, and Pachypleura. The ilium is essentially like a diminutive ilium of a Teleosaur, which is not altogether incomparable with some forms of the bone in Crocodiles and in Theriodonts. Hence I would urge that, if Nothosaurs, and their marine representatives, the Plesiosaurs, have ceased to be Labyrinthodont in their skulls, the original characters have been retained in a remarkable way in the skeleton, which, in the vertebral column, and especially in the double attachment of the cervical ribs of Plesiosaurian genera, offers instructive collateral evidence of the nature of similar conditions in Pareiasaurus.

Resemblances to Ornithosauria.—Even in this highly modified group of animals instructive resemblances in the pelvis are detected with primitive types like the Protorosauria and Anomodontia, which indicate a common origin. And, if the forms of the pelvic bones in Rhamphorhynchus, Cycnorhamphus, Phocosaurus, and Platypodosaurus are compared, the conclusion follows that the pelvic bones in these widely divergent groups—like the sacrum—are similar in plan; and this similarity is not without its suggestive side as to the relation of the more highly differentiated types of Reptiles and Birds to the groups which are but little modified from the Labyrinthodont condition.

Resemblances to Crocodilia.—The upper surface of the skull of an Alligator or Crocodile is perhaps more like the skull of a Labyrinthodont than is that of any other existing Reptile. The positions of the vacuities in the head, the small size of the premaxillary bones, no less than the external sculpture, make it suggestively comparable But in the post-orbital region there is a vacuity which in the living animals is closed with a stout membrane. That membrane occupies the positions of the post-orbital and

<sup>\*</sup> Wiedersheim: 'Schweizer. Paläont. Gesell.,' vol. 5, 1878.

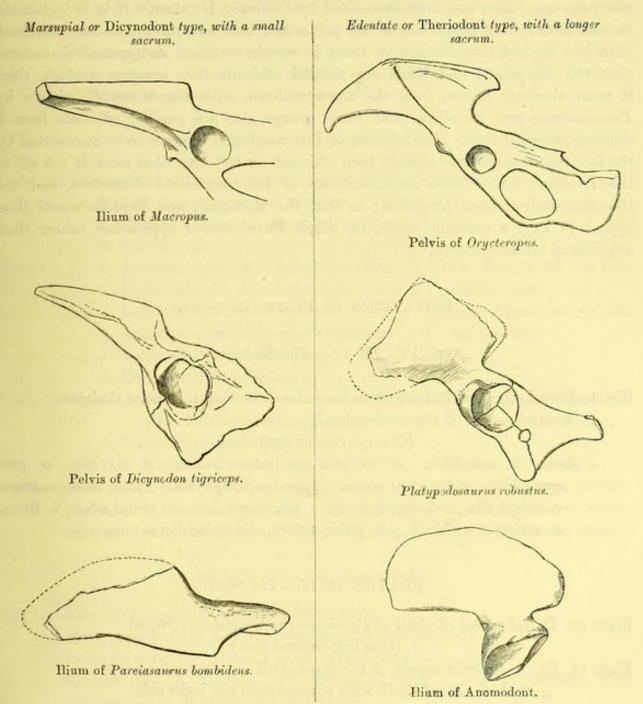
supra-temporal bones, so that if it were ossified a bone would stretch from the squamosal to the quadrate, and completely cover the quadrate, as in Labyrinthodonts and Ichthyosaurs, and a bone would border the back of the orbit and stretch from the post-frontal to the jugal in the position of the Labyrinthodont post-orbital. Hence I suggest that, although these bones have ceased to be ossified, the preservation of a membranous representative in the Crocodilian skull is strong evidence of the mode by which the Labyrinthodont skull lost its external characteristics and became Crocodilian. It therefore furnishes evidence of some importance as to the nature of the relation between the skulls of Pareiasaurus and ordinary Anomodonts. We should search in vain for any condition which so nearly approximates to the mode of attachment of the ribs in Labyrinthodonts and Pareiasaurus as is seen among Crocodiles, especially in their early dorsal vertebræ, in which the head of the Crocodilian rib is inferior in position to the tubercle. There is no doubt that in most vertebral characters the Pareiasaurus is intermediate between Crocodiles and Nothosaurs.

Hence, without examining the Amphibian characters of Dinosaurs and Birds, on which Crocodilian structures throw much light, it may be affirmed that there is conclusive evidence that many orders of true Reptiles preserve Labyrinthodont characters in their skeletons which are comparable to the characters of *Pareiasaurus*, so that, though *Pareiasaurus* is more Labyrinthodont than other Reptiles, it is only in the sense of showing for the first time Labyrinthodont characters in some parts of the skeleton in which they had not previously been observed, just as other Reptiles had previously shown Labyrinthodont characters in different parts of the skeleton; and on that account the characters of *Pareiasaurus* may not imply nearer affinity with Labyrinthodonts than is shown by Ichthyosaurs, Nothosaurs, and Croçodiles. On this evidence I am constrained to recognize the preponderating evidence of affinity with the Anomodontia and Theriodontia, and regard *Pareiasaurus* as the type of a sub-order, the Pareiasauria, which may probably be included in the Anomodontia.

# The Mammalian Characters of Pareiasaurus.

Resemblances to the Mammalia in certain of the South African Reptilia have been pointed out by Sir R. Owen in the general character of the Theriodont skulls, in their dentition, in the sacrum, pelvis, and certain of the limb-bones. Similar conclusions have been urged by Professor Cope on the evidence of many remains of allied animals found in the Permian rocks of the United States, which he refers to a group named Theromorpha. The resemblance to a Mammal in the pelvis referred to Dicynodon is quite as marked as in that which has been named Platypodosaurus; and in this respect Pareiasaurus is strictly comparable with them. Many isolated bones of different generic forms show that these characters are not accidental characteristics, but pervade all the known representatives of the Anomodont group. The significance of these resemblances seems to me to admit of exactly the same kind of

#### DIAGRAM OF MAMMALIAN PELVIC CHARACTERS OF THE ANOMODONTIA.



demonstration as the Labyrinthodont characters of *Pareiasaurus*; and I would urge that, just as we are entitled to infer from the presence in that Reptilian genus of Labyrinthodont structures that the characters have been inherited, so we are led to conclude from the presence of Mammalian characteristics in that and allied genera that the Mammalian structures have been transmitted to Mammals, if not in a direct line, which is improbable, by collateral derivation from a common ancestry. The evidence in this argument is very similar to that which led to the recognition of the

Avian affinities of certain Dinosaurs, and is about as complete as that evidence was when the conclusion was first enunciated by Professor Huxley. If it is legitimate to infer from certain characters of the pelvis and hind-limb of Iguanodon, combined with less marked resemblances to Birds in certain vertebral and cranial characters, that the Dinosauria and Birds are parallel offshoots from a common stock, then it must similarly follow, from the correspondence with the Mammalia shown by Pareiasaurus and its allies, that those groups also are parallel offshoots from a common ancestral type. The interest of this conclusion appears to be augmented by the fact that reasons have already been adduced for believing that most, if not all, of the Reptilian orders have an inheritance of Labyrinthodont characters, and are therefore derived from Amphibia; so that the Mammalia and Reptilia would thus appear to have a common origin, to which Pareiasaurus approaches nearer than any animal hitherto known.

### Explanation of Plates 12 to 21.

### PLATE 12.—The Skeleton.

- Fig. 1. Dorsal aspect of Pareiasaurus bombidens, showing the entire skeleton.
  - ,, 2. Ventral aspect of the same animal.

(One quarter natural size.)

s. skull. m. mandible. sc. scapula. ic. inter-clavicle. cl. clavicle. sr. pre-coracoid. n.s. neural spine. par. parapophysis. in.c. inter-centrum. r. dorsal rib. d. diapophysis. sm. sacrum. sr. sacral rib. i. ilium. a. articular surface. p.a. pubic suture. is.a. ischiac suture.

## PLATES 13-16.—The Skull.

Plate 13. Dorsal aspect of skull of Pareiasaurus bombidens (OWEN).

(One half natural size.)

Plate 14. fig. 1. Anterior aspect of the same skull.

" 2. Left side of skull, with sutures from the right side.

(One half natural size.)

Plate 15. fig. 1. Palatal aspect of the same skull, one half natural size.

" 2. Outline of section of pterygoid bones in the type skull, of the natural size.

Plate 16. fig. 1. Palatal aspect of skull of Pareiasaurus serridens (OWEN), one half natural size.

" 2. Section of tooth in the lower jaw of the same species, natural size. pm. pre-maxillary bones. i.n. infra-narial bone. m. maxillary. mr. malar.

natural size.

natural size.

These figures are of the

qj. quadrato-jugal. sq. squamosal. st. supra-temporal. pt.f. post-frontal. po. post-orbital. pf. pre-frontal. n. nasal. f. frontal. p. parietal. ? so. supra-occipital. e. ? epiotic. bo. basi-occipital. bs. basi-sphenoid. pt. pterygoid. pt.r. pterygoid ridges. m.d. dentary bone. m.s. mandibular suture. d. teeth. x. position of attachment of lower jaw to skull. v. palatal vacuities.

### PLATES 17-19.—Vertebral Column.

- Plate 17. Restorations of the natural size, partly based on measurements.
  - fig. 1. Left side of a cervical vertebra.
  - " 2. Posterior aspect of a cervical vertebra.
  - ,, 3. Cervical rib.
- Plate 18. fig. 1. Anterior aspect of a dorsal vertebra. \(\) These figures are one half
  - ,, 2. Right side of a dorsal vertebra.
  - ,, 3. Left side of a caudal vertebra.
  - ,, 4. Anterior aspect of a caudal vertebra.
  - ,, 5. Pelvis of Rhamphorhynchus.
  - " 6. Pelvis of Dimorphodon.
- Plate 19. fig. 1. Anterior aspect of pelvis, sacral rib, and ilium in natural position.

  (One half natural size.)
  - " 2. External view of ilium.

(One third natural size.)

pz. pre-zygapophysis. ptz. post-zygapophysis. d. diapophysis. p. parapophysis. t. transverse process. i.c. sub-vertebral wedge bone or intercentrum. n.s. neural spine. s.r. sacral rib. i. ilium. n.c. neural canal.

#### PLATE 20.—Shoulder Girdle.

- Fig. 1. Left side of clavicular arch seen from above.
  - " 2. Lateral aspect of left side of clavicular arch, and scapular arch.
  - " 3. Section showing the relations of the clavicle and inter-clavicle.
    - ic. inter-clavicle. c. clavicle. s.c. scapula showing g. articular surface, with pre-coracoid in front, pierced by foramen.

#### PLATE 21.—Pelvis.

- Fig. 1. Pelvis of *Phocosaurus*, five-twelfths natural size.
  - " 2. Diagram showing anterior aspect of the pelvis restored.
  - " 3. Outline of pelvic bones of Phoca vitulina.
    - i. ilium. p. pubis. p.p. pre-pubic process. f. obturator foramen. isc. ischium. su. ischio-pubic suture. a. articulation.

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