ON THE ANATOMY OF A NEW EAST AFRICAN DICYNODONT

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Christopher Barry Cox, M.A. Oxon., St.John's College

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PREFACE

I hereby declare that, except where specific reference has been made to the publications of other authors, the work embodied in this dissertation is wholly original.

C. B. Cox

FOREWORD

The subject of the work incorporated in this dissertation is a collection of dicynodonts made in Tanganyika in 1933 by Mr. F. R. Parrington, the present Director of the University Museum of Zoology in Cambridge, who was also kind enough to accept responsibility for direct supervision of the research. I should like to express my thanks to Mr. Parrington for the unfailing stimulus of his advice and interest, and also for the loan of his material. In addition, thanks are also due to the Department of Scientific and Industrial Research, whose award made this research possible, and to Professor Sir James Gray, F.R.S., the Supervisor appointed by that Department.

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1. INTRODUCTION

The first remains of dicynodonts, which were described by Owen in 1845, came from Permian deposits in South Africa and, even today, the majority of the known forms come from these deposits. But Permian rocks in other parts of the world (Central and East Africa, Scotland, Russia, India, Indo-China and China) have also yielded dicynodont remains, and Triassic dicynodonts, usually of very large size, have been found in Africa, China, North and South America and may also occur in Europe. In many areas dicynodont remains are the most common vertebrate fossil; this is especially marked in South Africa, where the great abundance of their remains and the presence in the same beds of less common and obviously carnivorous theriodonts would alone lead one to suppose that the dicynodonts were the main herbivorous group at this time, a conclusion supported by their peculiar dental modifications.

The earliest workers on dicynodonts (Owen, Seeley, Lydekker and Huxley) confined their attention mainly to the external surfaces of the skull, since the techniques of development in use during the nineteenth century did not permit an examination of the deeper parts of the skull, and the post-cranial remains of dicynodonts are far less common than their skulls.

The number of named species of dicynodont greatly increased from 1899 onwards, largely due to the work of Broom, who published over fifty papers concerned with the group. Other major contributors to the variety of known forms have been Haughton, von Huene, Broili and Schröder and Boonstra.

Though, scattered through the large number of papers published by the above-mentioned workers, there exists a fair amount of fragmentary information as to the more detailed structure of the skull of dicynodonts, most of our present knowledge of this is due to the work of Broili & Schröder (1935a, b, 1936a, b, 1937) and to the results of sectioning by Sollas & Sollas (1913, 1916) and Olson (1944).

Comprehensive accounts of the skull and post-cranial skeleton have been given by Sushkin (1926a, b) for the Russian form Dicynodon amalitzkii, by Pearson (1924a, b) for the South African Triassic form Kannemeyeria and by Watson (1914, 1917) for the South African form Dicynodon halli. Watson's 1917 paper is one of the few to consider the possible musculature of Dicynodon, while more recently he has surveyed the outlines of the evolution of the Dicynodontia (Watson, 1948). The most recent work on the group has been that of Toerien (1954a, 1955, 1956) who has revised part of the classification, using the structure of the palate as a major taxonomic character.

Thus, though over one hundred and fifty papers concerned with dicynodonts have been published, and a large number of forms of dicynodont have been named, in only a few cases has the detailed structure of any form been investigated. As a result, there is still insufficient information for the comprehensive anatomical comparisons which alone will permit of a satisfactory taxonomic and evolutionary understanding of the group.

The following account is concerned with certain of the dicynodonts collected by Mr. F. R. Parrington from the Karroo rocks of Tanganyika in 1933. The presence of Karroo deposits in the Ruhuhu area of South-west Tanganyika was first suggested by Stromer von Reichenbach (1896) and first definitely established by Bornhardt (1900, summarised by Koert, 1913), who found only plant remains. Further work was done by Dantz (1903) and Gillman

(1927), but the first detailed study of the area and correlation with the South African series was made by Stockley (1932) who found both vertebrate and invertebrate fossils in the course of a five-month survey in 1930. Stockley divided the Karroo beds of the Ruhuhu "into eight distinct groups, based on lithological differences and on palaeontological and economic grounds". He states that all these groups may contain bone, but that bone is most common in two strata to which he refers as "Bone Beds". His use of this term has since been criticised by both Watson (discussion after Haughton, 1932) and Nowack (1937), as it is a term that is normally used to describe a distinct and restricted horizon within which bones are exceedingly abundant. No such horizon is found in the Ruhuhu series; thus Stockley's "Lower Bone Bed" is a stratum 300 ft. thick, bone being found within this at different levels at different localities, though some localities certainly contain horizons at which bone is moderately abundant. It therefore seems better to follow Nowack in referring to these fossiliferous beds as the Lower and Upper Bone-Bearing Strata. The fossils with which this work is concerned come from the Lower Bone-Bearing Stratum.

The vertebrate fossils collected by Stockley were described by Haughton (1932). He concluded that the Upper Bone-Bearing Stratum, containing diapsids and large dicynodonts, was of Upper Triassic age. From the Lower Bone-Bearing Stratum he identified parieasaurs, large and small dicynodonts, including endothiodonts, and gorgonopsids. This fauna led him to conclude that the Lower Bone-Bearing Stratum is homotaxial with the middle part of the Lower Beaufort Beds of South Africa, including parts of both the Endothiodon and Cistecephalus zones, and is thus Upper Permian in age.

The next work in the region was done by Parrington, who in five months in 1933 made an extensive collection of vertebrate remains; work on this collection has resulted in several papers by Parrington (1936, 1946a, b, 1955) and Crompton (1955a). This was followed by Nowack, who in 1934-36 made a collection of reptilian remains, and who was also able to make more detailed observations on the geology of parts of the area.

Work on the fossils collected by Nowack has been done by Broili & Schröder (1936c) and von Huene (1942, 1944, 1950). von Huene agrees with Haughton that both the Endothiodon and Cistecephalus zones of South Africa are represented in the Lower Bone-Bearing Stratum, but considers that it includes only the lower part of the Cistecephalus zone and the uppermost boundary of the Endothiodon zone.

Boonstra (1953) has recently examined a further Ruhuhu area collection sent to him by Stockley, but the remains are very fragmentary and weathered and have not added to the known extent of the fauna.

2. MATERIAL AND METHODS

Mr. F. R. Parrington collected dicynodont material from a large number of localities which he numbered B1 - B35 in accordance with the localities on Stockley's map (1932). The bulk of the present work has been concerned with material from B19, Kingori, but other remains came from B4, Katumvi viwili and B1~~9~~6, Matomondo. All of these are in the Lower Bone-Bearing Stratum.

The bones are preserved in nodules of siliceous mudstone; the matrix is white, tinged with yellow or green, and the bones are a reddish-brown, usually covered by a thin red layer, presumably of an iron oxide. The nodules are often traversed by thin seams, along which calcite crystals have become deposited. These seams do not represent lines of dislocation and the bones are usually undistorted, the only damage being due to weathering of the exposed portions.

As is commonly the case with this group of animals, skulls form the bulk of the material collected; however, with one skull is associated an (incomplete) series of thirty-four vertebrae, with the proximal ends of the ribs and the complete pectoral and pelvic girdles.

It would have been possible to describe the whole of the collection of Permian dicynodonts to the degree of detail found in most of the previous literature but, considering the unsatisfactory taxonomic position that has resulted, it was decided that it would be more valuable to attempt to gain a more complete knowledge of the anatomy of these animals by a detailed investigation of a smaller number of specimens. The recent discovery of the acetic acid technique (Toombs, 1948; Rixon, 1949) has greatly facilitated this more thorough type of investigation. After immersion for about twenty-four hours in fifteen per cent. acetic acid, the specimen is washed in running water for a similar period and is then dried. A solution of perspex in chloroform is applied and allowed to soak into the fossilised bone to strengthen it and a stronger solution of this is used for mending broken bones. In suitable cases, the technique makes possible the complete removal of the matrix, even from within such internal cavities as the braincase, is on the whole less time-consuming than the mechanical methods of preparation and also permits of the preservation of the structure in finer detail.

The response of the matrix to the action of the acid varies greatly. In some cases it was possible to remove the whole of the matrix, leaving everywhere a clean bone-surface, so that the structure could be studied in detail. At the other extreme, in specimen no.82 the matrix is far less responsive; apart from the presence of a hard semi-crystalline acid-resistant matrix over much of the skull and vertebral centra, the bone is everywhere covered by a thin red acid-resistant layer, which makes the detection of sutures very difficult.

3. THE OSTEOLOGY OF KINGORIA

A. Diagnosis of *Kingoria*, gen.nov.

The generic name refers to Kingori, the locality in which the type species was collected.

Type species *Kingoria nowacki* (von Huene).

Small dicynodont, without precanine or post-canine teeth; canines present or absent. Skull oval in dorsal view, greatest width posterior to level of pineal foramen. Breadth of interorbital bar greater than breadth of intertemporal bar. Snout broad, without nasal ridges or bosses. No pineal boss. No postfrontal bone. Long narrow preparietal, surrounding anterior part of pineal foramen. Postorbitals cover lateral portions of intertemporal bar; parietals exposed between them, but this region is not concave from side to side, parietals instead forming median ridge, and there is sharp transition between this region and occiput. Posterior end of zygomatic arch not expanded into lateral wing. Tabular present, extending almost to post-temporal fossa. Distinct tympanic process on distal end of posterior surface of paroccipital process. Stapes without stapedial foramen. Interpterygoid vacuity present, bordered by vomer and pterygoids. Pterygoid separated from maxilla by ectopterygoid. Palatine not forming part of secondary palate, does not meet premaxilla. No pair of stout ridges on anterior surface of palate, but a pair of low sharp ridges on premaxilla just medial to its sutures with maxillae. Ascending portion of epipterygoid very slender, apparently not expanded dorsally to form part of lateral wall of braincase. Marked venous groove on anterior face of prootic. No unossified zone between basioccipital and basisphenoid. Distinct sella turcica, entered by paired internal carotid canals.

Dentaries anteriorly form upwardly-curving, blunt, tapering "beak". Lateral surface of dentary bears strong prominent wing. Articular bears retro-articular process.

Six cervical vertebrae. Atlas neural arch paired, each with neural spine directed postero-dorsally and laterally. Dorsal vertebrae with well developed metapophyses. Five sacral vertebrae. Cervical and anterior dorsal ribs double-headed, other ribs single-headed. No cleithrum. Coracoid foramen between scapula and precoracoid. Well developed scapular spine. No pelvic symphysis. Pubis and ischium posterior to ilium. Ischium contacted by fourth sacral rib.

The genus contains two species, one from the Lower Bone-Bearing Stratum of the Songea Series of the Karroo System, from a level apparently equivalent to the lower part of the Cistecephalus zone of South Africa, in which the other species was found.

<u>The species Kingoria nowacki</u>

The original description of this form, as <u>Dicynodon nowacki</u>, was given by von Huene (1942). His specimens, in the Museum für Geologie und Paläontologie, Tübingen, were examined and found to be conspecific with specimens nos 76 and 98 in the Cambridge collection. All these specimens were extremely like specimens nos 82 and 84 in the Cambridge collection, but differed in that these latter possessed tusks, which are not present in the other specimens. A tusked skull (Cambridge specimen no. 84) and a tuskless skull (Cambridge specimen no. 76) were each prepared by the acetic acid method, and a detailed comparison of the two showed them to be morphologically almost identical except for the difference in dentition. A similar difference is known in several other types of dicynodont, and it appears likely that it was a sex-difference, the males presumably being the tusked sex. In *Kingoria*, eight tuskless skulls are known and two tusked; a similar difference in numbers is found in many modern herbivores, the females being more numerous than the males.

It is therefore considered that the tusked specimens nos 82 and 84 in the Cambridge collection are merely the males of von Huene's species *Dicynodon nowacki*. They have been found to be sufficiently unlike other forms to necessitate the erection of a new genus, *Kingoria*, and the name of the type species is thus *Kingoria nowacki* (von Huene). Though, as will be seen later, one other species of *Dicynodon* also belongs to this new genus, its skull is so badly damaged and distorted that it is not possible to compare the two species in detail, and therefore no comprehensive specific diagnosis of *Kingoria nowacki* can be given. However, it is felt that the species is described and figured in the next section in sufficient detail for it to be distinguished from any other species of *Kingoria* which may subsequently identified.

The following account is based upon the skull of specimen no. 84 in the Cambridge collection, and the post-cranial skeleton of specimen no. 82 in the same collection.

B. The skull and lower jaw of Kingoria nowacki gen.nov.

Material

Specimen 84, from B 19, Kingori, consisted of an undistorted and nearly perfect skull with both stapes and the lower jaw in place. The specimen was preserved as a nodule, its dorsal surface and the outer side of the zygomatic arch and the ventral surface of the symphysial region of the lower jaw being exposed. The median ridge along the intertemporal bar is damaged, and the following parts of the skull are missing: the extreme anterior end of the snout; the left zygomatic arch and post-orbital bar; the posterior dorsal edge of the right zygomatic arch; the medial part of the right post-orbital bar and the lateral edge of the squamosal. The distal parts of the canine tusks are also missing.

The acetic acid technique has proved extremely effective in this specimen; the reddish-brown bone is everywhere completely freed of matrix, including within the brain-case and nasal cavity, and its surface detail is perfectly preserved, except anteriorly on the dorsal surface of the snout where some weathering has taken place. Sutures can in nearly all cases be traced with certainty.

Osteology of the skull

Dorsal view (Fig. 1).

The skull shape is that of an ellipse, tapering anteriorly towards a blunt rounded snout and the squamosals curving inwards posteriorly. The greatest length (taken in the midline from the snout to a line drawn between the posterior margins of the squamosals) is about 15 cms., and the greatest width (which lies posterior to the pineal foramen) is 10.5 cms. The whole of the orbits and post-orbital bars lie in the anterior half of the skull. The interorbital width (3.2 cms.) is considerably greater than the maximum width of the intertemporal bar (2.4 cms.). The orbits face laterally and forwards; they are somewhat triangular in dorsal view, their inner margin being formed by two curves which meet about half-way along the orbit. No trace of sclerotic plates was found. The pineal foramen is of an elongated oval shape.

In the anterior part of the skull the bone surface bears minute wrinkles and pores, but the surface of the bones bounding the temporal vacuity is smooth and polished.

The premaxillae are fused together, there being no sign of a median suture. The interdigitating sutures between the premaxillae and the nasals run backwards and medially from the upper anterior corners of the nares, so that the premaxillae form a median dorsal wedge between the nasals. The premaxilla meets the maxilla on the lower outer corner of the naris, and thus forms the whole of its floor and anterior border.

The septomaxilla is a small bone lying within the posterior part of the external naris; it was somewhat damaged during the preparation. From its expanded base, resting on the premaxilla, arise two laminae, one interior and slightly behind the other. These laminae extend side by side upwards and outwards, their inner surface facing postero-medially. They fuse dorsally after a short distance, and the outer surface of the lateral lamina curves slightly outwards to meet the inner surface of the maxilla. Above the fusion of the two laminae the dorsal end of the septomaxilla curves forwards and outwards and buttresses against the inner surface of the maxilla.

This complex form of the septomaxilla results in the presence of two foramina, each about 1 mm. wide; the outer foramen is between the maxilla and the outer lamina, and is directed forwards; the inner foramen is between the two lamellae and is directed forwards and inwards.

The <u>nasal</u> is large, extending from the external naris, whose upper border it forms, back to the level of the anterior border of the orbit. Anteriorly the nasals mould the greater part of the form of the snout; in the longitudinal plane they curve gently and fairly regularly downwards and forwards, and in the transverse plane they curve strongly downwards at the sides. Anteriorly there is a slight median longitudinal depression, in the bottom of which runs the sinuous median nasal suture. Laterally the nasal slightly overlaps the maxilla, lacrimal and prefrontal, the edge of the nasal being slightly irregularly scalloped. Posteriorly there is an interdigitating suture with the frontal. There are a number of small foramina on the nasals, especially anteriorly on the lateral surface, and the surface immediately behind the naris is finely rugose.

The <u>frontal</u> is large, extending from the anterior border of the orbit back to 3.5 mm. in front of the pineal foramen, and forming about one centimetre of the orbital margin. Anteriorly the frontals have an interdigitating suture with the prefrontals and nasals and bear a slight median swelling, which continues a short distance forwards as a wedge between the nasals. The swelling fades out fairly rapidly posteriorly, but continues as a very slight median ridge on which is the sinuous median frontal suture. On either side of this ridge the frontals are slightly concave, rising laterally to the somewhat elevated orbital edge. The smooth frontal-postorbital suture runs along the crest of a ridge, which anteriorly fades out towards the orbital margin (the actual margin is not preserved here), and posteriorly runs back to join the median parietal ridge at about the level of the front of the pineal foramen. Posteriorly the frontal has a short interdigitating suture with the anterior end of the preparietal but contacts only a small part of its lateral border, as the frontal is constricted into a thin process between two thin anterior processes of the parietal.

The frontal also forms the posterior part of the upper internal orbital wall, meeting the prefrontal anteriorly and the postorbital posteriorly. It continues posteriorly as a narrowing strip of bone which extends to a level 1.0 cm. in front of the pineal foramen; this it is contacted ventrally by the sphenethmoid and is overlapped dorso-laterally by the postorbital.

The <u>preparietal</u> is long and narrow, 18 mm. by 4-5 mm. Anteriorly it has an interdigitating suture with the frontals, and this anterior part is sunk between the paired frontal-postorbital ridges; the straight lateral sutures between the preparietal and the frontal and parietal run along the inner side of these ridges, so that the preparietal is concave in transverse section. Posteriorly it curves upwards in front of the pineal foramen to form the anterior end of the median parietal ridge, and borders the anterior third of the pineal foramen.

The <u>lacrimal</u> forms the antero-ventral border of the orbit and its outer, facial, part is raised above the level of the surrounding bones, so that there is a slight circum-orbital ridge in this region. Dorsally the lacrimal has an interdigitating suture with the prefrontal; this suture is clear on the skull roof, but within the orbit part of the bones is missing. The lacrimal is overlapped by the nasal for a short distance, and then has a gently undulating suture with the maxilla. It has a short facial suture with the maxilla; this suture continues on the floor of the orbit, running medially for 1.5 cms. until it meets the palatine, and then continuing slightly forwards to the edge of the antero-ventral orbital surface.

The elliptical lacrimal foramen, 3.5 mm. high by 1.5 mm. wide, pierces the lacrimal at its extreme anterior end. The foramen is single, but a second foramen opens within the lacrimal foramen and runs ventrally through the roof of the chamber surrounding the root of the canine tusk. The orbital surface of the lacrimal slopes gently downwards posteriorly towards its sinuous suture with the jugal.

The jugal forms most of the ventral border of the orbit and anterior root of the zygomatic arch, and extends along the inner size of the zygomatic arch to half-way along the temporal vacuity. Anteriorly it has a sinuous suture with the orbital surface of the lacrimal, by which it is slightly overlapped; externally on the facial surface this suture continues for a short distance and meets the maxilla. Medially the jugal meets and slightly overlaps the palatine, the sinuous suture running posteriorly to a point slightly in front of the palatal ramus of the pterygoid, the jugal thus forming the whole of the anterior border of the temporal vacuity. At the inner anterior corner of the temporal vacuity the jugal meets the ectopterygoid; the suture between these two bones runs downwards, inwards and forwards on the ventral aspect of the skull, the jugal having a rather narrow projection pointing towards the posterior end of the secondary palate. The anterior border of this projection is slightly overlapped by the maxilla, the sinuous suture running backwards, outwards and upwards until it reaches the ventro-lateral edge of the zygomatic arch and then curving round upwards and forwards to the facial end of the jugal-lacrimal suture.

More posteriorly, the jugal for a short distance forms the whole of the thickness of the zygomatic arch, but the anterior process of the squamosal reaches beyond the level of the post-orbital bar, making a deep groove in the external surface of the jugal. The jugal continues to be visible in lateral view for a distance of over 1.0 cm. behind the level of the post-orbital bar, clasping the ventral border of the squamosal. Part of the dorsal side of the jugal is covered laterally by the foot of the postorbital, whose inner side is covered by the jugal to a level 1.6 cms. vertically above the ventral border of the zygomatic arch in this region. A small corner of the jugal is visible in lateral view immediately behind the post-orbital bar; posterior to this the jugal continues to overlap the inner surface of the squamosal, its border gradually descending to the point where it turns under the ventral margin of the zygomatic arch.

The <u>prefrontal</u> is quadrilateral in dorsal view, having an interdigitating suture anteriorly with the maxilla and posteriorly with the frontal, and a sinuous medial suture with the nasal. It is somewhat concave from side to side, rising medially towards the nasal, by which it is slightly overhung, and laterally towards the elevated orbital margin. The prefrontal forms about 1.0 cm. of the antero-dorsal border of the orbit and projects downwards and inwards to form part of its upper internal wall. Its suture with the frontal runs posteriorly just under the orbital margin for 8 mm. and then turns slightly inwards to reach the edge of the orbital wall.

There is no trace of a postfrontal. The postero-medial edge of the orbit is missing, but the medial base of the post-orbital bar is present and shows no sign of any bone between the frontal and the postorbital, either on its dorsal or ventral surface or in cross-section.

The postorbital is an L-shaped bone which extends from halfway along the orbit to the posterior end of the intertemporal bar. It forms almost all of the post-orbital bar, the lateral end of which is covered internally by the jugal and meets the anterior process of the squamosal. The transverse section of the post-orbital bar has the form of an ellipse, the long axis of which is horizontal at each end but is vertical mid-way along the bar.

As already mentioned, the dorsal suture between the postorbital and the frontal runs along the crest of a ridge which extends backwards and inwards to meet the side of the median parietal ridge. However, from a point 11 mm. in front of the pineal foramen, the inner side of the ridge is formed by an anterior process of the parietal. The postorbital continues to form the lateral part of the ridge to a point 3.5 cm. in front of the pineal foramen; here the upper border of the postorbital curves downwards on the side of the median parietal ridge. The suture continues posteriorly along the side of the parietal to the level of the dorsal apex of the occiput; here it meets the medial process of the squamosal, and it then turns laterally and runs to the edge of the intertemporal bar.

The postorbital thus forms the lateral surface of the intertemporal bar, resting on the parietal. Anteriorly, just behind the post-orbital bar, this surface inclines inwards at an angle of about forty-five degrees to the horizontal, but it gradually becomes more horizontal, being at about twenty-five degrees at the level of the anterior apex of the occiput. Running posteriorly from the lower corner of the post-orbital bar is a low rounded laterally-directed ridge which rapidly becomes more pronounced so that, posteriorly from a level about 11.5 mm. in front of the pineal foramen, the postorbital and the parietal (upon which it is resting) together form a roof-like covering to the medial part of the temporal vacuity. This roof extends outwards to a distance of 6-8 mm. lateral to the vertically descending parietal wall of the braincase. On this roof are two low mounds, the anterior being more marked and situated at the level of the pineal foramen and the other being a short distance behind it. The edges of the roof are turned downwards, so that its ventral surface is concave.

The postorbital-frontal suture anteriorly turns over the edge of the orbit and runs backwards and downwards more or less vertically below its dorsal exposure, eventually reaching the anterior edge of the vertical parietal wall of the braincase. Here the postorbital meets the parietal, the suture at first running slightly forwards and then curving dorsally and posteriorly to run back along the ventral surface of the medial roof of the temporal vacuity. Until a level about halfway along the pineal foramen the suture runs 2-3 mm. medial to the edge of this roof, but behind this level it approaches close to this edge, so that nearly the whole width of the postorbital is supported by the parietal.

The <u>parietals</u> are fused together, there being no sign of a median suture along the broken surface resulting from the loss of the median parietal ridge. The fused bone forms the border of the posterior half of the pineal foramen and extends forwards on each side nearly to the anterior border of the parietal. On each side this anterior process is single as far as a level 3.5 mm. in front of the anterior border of the pineal foramen; here it divides into two thin processes which run on either side of the posterior process of the frontal. The inner parietal process borders the preparietal to near its anterior margin, the lateral process borders the postorbital and forms the inner side of the raised ridge which runs back to the median parietal ridge. Most of the latter is missing, but the width of the broken surface indicates that the ridge must have been fairly high, and the missing part has in the figures been restored as reaching the same level as the undamaged anterior preparietal component of the ridge. Though the sides of the parietal are steeply sloping and, if continued upwards, would meet at about the level of the apex of the ridge as restored it is likely, as shown below, that there was a median groove running down this ridge; such a feature is common in the dicynodonts.

The sides of the parietals are covered by the postorbitals, which extend back to the level of the dorsal apex of the occiput. Here the parietal meets the dorsal part of the medial process of the squamosal, and more posteriorly it progressively disappears underneath this structure. The squamosal at first covers only the more lateral part of the parietal, but the squamosal widens posteriorly until it forms the whole dorsal surface of the dorsal margin of the occiput. The edges of the parietal remain visible on either side of this part of the squamosal, and the parietal extends back to a point 2.5 cm. from the dorsal apex of the occiput. This whole region of the parietal rests anteriorly upon the interparietal, which also forms a median dorsal wedge between the fused parietals; more posteriorly, the tabular interposes itself between the interparietal and the squamosal.

The interparietal is visible in dorsal view as a small wedge of bone between the two diverging posterior wings of the fused parietals. This dorsal exposure is a broken surface, and the interparietal thus probably took part in the formation of the posterior end of the median parietal ridge. The suture between the interparietal and the parietal disappears anteriorly, so that the two bones may be fused in this region. Down the middle of the dorsal surface of the interparietal is a groove, quite similar in appearance to the sutures on either side and, like them, it disappears anteriorly. It is possible that this is an indication of a suture between the two halves of the interparietal bone, but there is no sign of this on the occipital exposure. This median groove disappears at a more dorsal level than do the lateral sutures, and it seems likely that this is in fact the extreme ventral end of a groove running down the middle of the intertemporal bar.

The squamosal is complex in form. Radiating from the posterior apex of the zygomatic arch are three components: an anterior ramus, forming most of the posterior part of the zygomatic arch; a medial process, forming the dorsal surface of the upper margin of the occiput and much of the posterior surface of the temporal vacuity; and a ventral wing, forming the lateral part of the occiput.

The anterior ramus extends to almost mid-way along the orbit, but does not contact the maxilla. It meets the jugal halfway along the temporal vacuity, and is received in a gradually deepening groove in the outer surface of that bone, itself gradually tapering to a point anteriorly. The dorsal side of this point is touched by the lower end of the postorbital. Where it borders the temporal vacuity, the squamosal forms a bar about 3.5 mm. thick which lies at an angle so that its ventral border is slightly medial to its dorsal border, its outer surface facing slightly downwards. The dorsal margin of the posterior part of this bar is missing.

The medial process of the squamosal extends along the posteriorly projecting rim of bone which forms the dorsal border of the occiput; it runs forwards and inwards, covering the posterior end of the parietal, and its anterior end contacts the postorbital. The medial process of the squamosal meets the main body of the bone at its postero-dorsal apex. The margins of this apex are missing, as is the dorsal margin of the posterior part of the zygomatic arch and the outer margin of the lateral squamosal component of the occiput. The probable outlines of these areas have been drawn by restoring the missing parts in plasticine, which is then modelled to produce a structure conformable to the preserved bone.

Ventral to this dorsally-fading surface there is an embayment in the medial process of the squamosal (Fig. 5); this embayment is 5 mm. high and extends laterally to a point above the post-temporal fossa. Below it, the squamosal extends inwards, covering part of the anterior faces of the interparietal and tabular and of the supraoccipital region of the occipital plate. Median to this, the anterior exposure of these latter bones separates the squamosal from the vertical component of the parietal. Ventral to the supraoccipital, the squamosal meets the prootic, the suture running laterally and slightly downwards to reach the dorso-lateral corner of the post-temporal fossa. Below this, the suture between the squamosal and the paroccipital process runs downwards from the outer corner of the post-temporal fossa to meet the loose union of the quadrate with the bones of the occipital plate. The squamosal sends a wedge of bone down for a short distance between the quadrate and the distal surface of the paroccipita process.

The medial process of the squamosal is merely an inward extension of the broad wing of the squamosal which forms the lateral part of the occiput. The anterior face of this wing faces slightly outwards and is slightly concave, the degree of concavity increasing postero-dorsally, below the root of the zygomatic arch. Ventrally it bears the quadratojugal, the upper part of which slots closely into the squamosal and has a sutural union with it.

Occipital view (Fig. 2)

All the cartilage-replacing bones of the occiput are fused together to form a single unit, the occipital plate, but the sutures of the membrane bones are quite clear. The occipital plate is itself fused to the prootic and opisthotic.

As mentioned above, the edges of the lateral squamosal component of the occiput are restored. The occiput is broad, its maximum width being about 9 cms, and it is 5.85 cms. high in the midline. Dorsally the squamosal projects backwards about 8 mm. beyond the level of the occiput, the under surface of the projection being covered by the tabular and interparietal. Above the foramen magnum the occiput is slightly forwardly-sloping and sunken; on either side of this it slopes dorso-laterally and slightly backwards to reach the squamosal overhang. The foramen has a broadly spatulate outline, 13.5 mm. high and 8.5 mm. wide at its ventral, broader, end. The posterior openings of the post-temporal fossae run slightly downwards and medially.

The <u>interparietal</u> is not merely a thin sheet of bone lying on the dorsal surface of the occiput but forms the whole thickness of this region of the occipital plate. In the midline its dorsal part faces posteriorly and bears vertical ridges; below this its surface at first slopes postero-ventrally and then again becomes vertical and overlaps the supraoccipital. This overlap in the midline is leaf-shaped, and on either side of this there is the rather large opening of a cavity which runs forwards for a short distance between the interparietal and supraoccipital. On either side of the midline region, the interparietal extends ventro-laterally, having sutures with the supraoccipital and the tabular. Its postero-ventral extremity is overlapped by the tabular. Its dorsal edge contacts the parietal both in posterior view, along the posterior edge of the dorsal overhanging margin of the occiput, and in anterior view, where it has an exposure medial to the anterior exposure of the tabular and squamosal, being overlapped by the latter bone. However, between the anterior and posterior contacts of the interparietal and parietal the two bones are separated by the dorsal process of the tabular.

The <u>tabular</u> covers the dorso-lateral part of the occiput. Antero-dorsally it overlaps the interparietal and sends two processes dorso-medially. The more ventral of these is quite small, merely forming a slight projection of the tabular dorso-medially between the interparietal and the supraoccipital. The more dorsal process is much stronger and runs forward in the overhanging dorsal margin of the occiput to a point only a few millimetres from the dorsal apex of the occiput. It is only visible in section, being covered anteriorly, ventrally and posteriorly by the interparietal and dorsally by the parietal (the posterior part of which is itself covered dorsally by the squamosal).

The ventral suture of the tabular runs downwards and laterally, overlapped by the supraoccipital region of the occipital plate, to a point above the groove leading into the post-temporal fossa, where it meets the squamosal. At its most posterior lateral point there is the opening of a cavity which runs dorso-medially between the tabular and the squamosal. The tabular does not form any part of the margin of this fossa, the suture turning away upwards and forwards for over 1 cm.; this suture does not run straight to the edge of the squamosal overhang however, but first turns backwards to form a narrow process, 7 mm. long, which runs back along the edge of the squamosal.

Apart from its occipital exposure, the tabular is also visible in anterior view on the posterior face of the temporal vacuity, where it appears in the embayment of the medial process of the squamosal and lateral to the anterior exposure of the interparietal. The exact position of the suture between the tabular and the interparietal cannot be seen due to damage.

The <u>occipital plate</u> is a complex structure formed by the fusion of the supraoccipital, exoccipitals and basioccipital, and is itself also fused to the prootic and opisthotic.

The dorsal, supraoccipital, part of this plate extends upwards to meet and be overlapped by the interparietal. Above the foramen magnum it forms the whole thickness of the brain case, and is thus visible in anterior view, between the anterior exposure of the interparietal, the vertical component of the parietal, the medial process of the squamosal and the periotic region, being fused with the last mentioned. Overlapping the ventral edge of the tabular, it extends far out to the sides and reaches a point dorso-lateral to the post-temporal fossa, where it meets the squamosal. Above the fossa is a marked ridge running upwards and outwards; the interdigitating suture between the upper part of the occipital plate and the squamosal runs down the upper side of this ridge for some distance; it then turns ventrally, crosses the ridge and runs forwards through the post-temporal fossa.

The lower part of the occipital plate meets the squamosal laterally. The suture runs laterally from the inner corner of the post-temporal fossa for 6 mm. in an overlapping but immovable suture, turns ventro-laterally for a short distance, and finally follows a slightly curving course ventrally. This latter part of its course commences as a sunken straight suture, the occipital plate here being at a slightly lower level than the squamosal; further ventrally, the contact rapidly becomes more and more open.

At a level slightly less than halfway up the foramen magnum are small, low, paired facets for the proatlas neural arches; these facets face backwards and slightly upwards. The two exoccipital condyles have a continuous dorsal surface, which is smooth and slightly concave from side to side; the posterior surface of these condyles is convex. The flat basioccipital component is slightly anterior to them. There is a very distinct central notochordal pit. The jugular foramen is directed outwards, backwards and downwards; it is of irregular circular outline, about 4 mm. in diameter. The lower border of each jugular foramen is thickened into a rib running into the condyle; between this pair of ribs there is thus a hollowed area immediately below the basioccipital condyle. The basioccipital tubera in occipital view form a pair of downwardly directed processes, the inner borders of which together form a smooth parabolic curve. On the left side a faint line can be seen running ventro-laterally from the jugular foramen to near the dorso-lateral edge of the tubera; this is probably the vestige of the suture between the basioccipital and the opisthotic, the latter bone thus forming the postero-lateral part of the border of the fenestra ovalis.

The paroccipital process is expanded distally, buttressing against the squamosal and quadrate; dorsally it sutures with the squamosal, but ventrally it meets both the squamosal and the quadrate in a loose contact, as noted above. Distally, its occipital surface is hollowed dorsally, but below this the paroccipital process projects posteriorly to form a tapering blunt rounded process which projects about 7 mm. beyond the general level of the surrounding bones. The nature of this process will be discussed in a later section; in the present section it will provisionally be referred to as the tympanic process.

The squamosal forms most of the border of the occiput. As noted above, it projects dorsally over the occiput, lying over the interparietal; its posterior apex in this region is restored (see above). It forms the whole of the lateral part of the occiput; nearly all of its outer margin here is missing and has been restored. Above the post-temporal fossa, the squamosal has an interdigitating suture with the tabular and interparietal and with the supraoccipital region of the occipital plate; below the fossa, its contact with the paroccipital process becomes progressively more open. Ventrally and ventro-laterally it overlaps the quadrate and quadratojugal, this also being an open contact.

The post-temporal fossa lies at the lower and medial end of a deep groove in the squamosal, which forms the whole of its outer and lower borders and also forms most of the pronounced ridge above the fossa. Near the dorso-lateral end of this ridge is a small tubercle, and there is a similar tubercle ventro-lateral to this, near the lower margin of the groove. At the distal end of the groove on the right side is a small groove running dorsally into a small foramen. More ventrally, the squamosal rises posteriorly to buttress the outer side of the tympanic process.

Palatal view (Fig. 3)

As already mentioned, the anterior border of the premaxilla is missing and has been reconstructed; the posterior border of the secondary palate and its junction with the vomer is also damaged and has been restored. The internal nares are sunk between high walls formed anteriorly by the palatines and posteriorly by the anterior rami of the pterygoids. The deep cavity thus formed is narrowed posteriorly as the pterygoids approach one another, but it does not become appreciably shallower, and has a narrow but steep posterior wall. The relic of the interpterygoid vacuity is long and narrow (20 mm. by 2.5 mm.) and is bordered by the pterygoids and the vomer; through it can be seen the ventral surface of the processus cultriformis of the parasphenoid.

The basioccipital can in palatal view be seen to form the large ventro-laterally directed tubera which form a very marked wall round the anterior, medial and posterior margins of the fenestra ovalis. The apex of this wall is rounded, but there is not a smooth transition into the cavity of the fenestra, as the wall is separated from it by a depressed flattened area for the reception of the head of the stapes. The fenestra ovalis itself is of oval form, 5 mm. by 3.5 mm.; the long axis of the oval is directed antero-laterally. There is also a lower dorso-lateral wall to the fenestra ovalis;

this wall is traversed by a small fissure leading to a small foramen in the ventral surface of the paroccipital process. This fissure and foramen seem to mark the point of fusion of the prootic and opisthotic, and on the left side a faint suture can be seen running from here dorso-laterally up the anterior face of the occipital plate to reach a slight embayment between the distal end of the paroccipital process and the ventro-medial corner of the squamosal (see Fig. 5).

Between the two tubera is a smooth groove, which continues forwards onto the posterior part of the parasphenoid. This latter has a suture with the basioccipital in the midline some way in front of the level of the fenestra ovalis, but more laterally it extends onto the antero-medial part of the wall surrounding the fenestra ovalis, and in this region has a free edge covering the basioccipital.

The <u>parasphenoid</u> and <u>basisphenoid</u> are, as is usual in the Synapsida, fused together to form a "parasphenoid-basisphenoid complex"; it may be presumed that the usual condition obtains here, the complex consisting of a basisphenoid portion sheathed ventrally by the parasphenoid. The parasphenoid thus forms the palatal exposure of the complex and, as described above, meets the basioccipital posteriorly. From this wide posterior exposure it tapers anteriorly due to its progressive ventral overlap by the pterygoids, with which it has smoothly curving sutures. From the tubera a pair of ridges run down the lateral sides of the parasphenoid; anteriorly these ridges approach one another, constricting the groove which separates them, and finally join. The anterior parts of these ridges, together with the median ridge resulting from their fusion, are convexly curved antero-posteriorly. The paired foramina for the internal carotid arteries pierce these ridges on their outer side, close to the parasphenoid-pterygoid suture, and thus open somewhat laterally.

Anteriorly there is a wide, coarsely interdigitating suture running down the posterior apex of the depression associated with the internal nares; it is not possible to be certain whether this suture represents a meeting of the pterygoids in front of the parasphenoid, or whether it is their sutures with a narrow edge of the parasphenoid. Anterior to this, part of the ventral surface of the parasphenoidal rostrum is visible through the interpterygoid vacuity.

The pterygoid is a long, strongly curved bone. As noted above, it is not certain that the two pterygoids have any contact in the midline.

The central part of the pterygoid, from which both the quadrate ramus and the anterior ramus diverge, has a palatal surface which is almost flat laterally but which medially rises up ventrally to flank the median parasphenoid ridge. At about the level of origin of the quadrate ramus there is a small anteriorly directed foramen in the pterygoid, close to its suture with the parasphenoid; a bristle passed through this foramen emerges dorsally through a foramen between the pterygoid and the lateral side of the dorsal part of the parasphenoid-basisphenoid complex. The position of this canal is exactly what might be expected if it lodged the palatine branch of the facial nerve (see Parrington & Westoll, 1940) and it may be presumed that this was in fact the case.

The quadrate ramus of the pterygoid diverges postero-laterally at an angle of about sixty degrees from a position slightly in front of the posterior contact of the bone with the parasphenoid. It is rounded, and slightly compressed dorso-ventrally; distally it is slightly enlarged ventro-posteriorly and approximates to an antero-medially directed recess on the inner surface of the body of the quadrate. Distally it has an unfinished surface, and was in life presumably joined to the quadrate by cartilage.

The anterior ramus of the pterygoid diverges laterally at an angle of about eighteen degrees and forms the wall of the posterior part of the depression associated with the internal nares and the boundary of the posterior half of the interpterygoid vacuity. Posteriorly the flattened surface of the central part of the pterygoid extends forwards for a short distance as a slight ledge on the inner side of the ramus, but anterior to this the ramus has an almost flat internal surface. This surface slopes slightly outwards, so that its smoothly rounded ventral edge is more lateral than its dorsal edge. Halfway along the interpterygoid vacuity the pterygoid has an interdigitating suture with the vomer for a short distance dorso-medially and, ventro-lateral to this, with the palatine, which extends about halfway up the wall of the pterygoid ramus. The ventral edge of the palatine covers the pterygoid, forming a slight ridge which becomes progressively more marked anteriorly. Ventral to the palatine, the pterygoid has a firm anterior suture with the ectopterygoid, which slots very deeply into its anterior end.

The <u>ectopterygoid</u> is a rather small bone, similar morphologically to the anterior ramus of the pterygoid and forming the anterior continuation of that structure. Its inner surface forms part of the wall of the depression associated with the internal nares; the palatine lies more dorsally on its inner side, but the two bones are almost completely separated by a large foramen 5 mm. long, meeting only for a short distance anterior to this. Anteriorly the ectopterygoid has an interdigitating suture with the maxilla, and laterally is covered by the jugal.

The palatine, as described above, lies sunken within the middle part of the depression associated with the internal nares, forming the dorsal part of its wall and the lateral part of its roof. It has an interdigitating suture with the pterygoid posteriorly. Laterally also it meets the pterygoid; at the posterior end of this meeting the ventral edge of the palatine covers the pterygoid, forming a slight ridge, which becomes progressively more marked anteriorly until it enlarges into the large foramen between the ectopterygoid and the palatine. About 6 mm. dorso-medial to the large foramen there is another smaller foramen 1 mm. in diameter, piercing the palatine, which here forms the whole thickness of the roof of the palate. Anterior to the large foramen the palatine meets the ectopterygoid for a short distance; beyond this it has an interdigitating suture with the maxilla. This latter continues antero-dorsally for a short distance and reaches the edge of the opening into the cavity containing the roof of the canine tusk; this part of the suture is out of sight below the premaxilla, which here covers the maxilla ventrally. The palatine does not meet the premaxilla and takes no part in the formation of the secondary palate, forming only the concave side wall of the internal nares, between the maxilla and the vomer; between these two bones it has a free anterior edge, anterior to which the respiratory passage enters the nasal cavity. Medially the palatine covers the lateral part of the vomer, and its antero-medial corner just contacts the sphenethmoid.

The vomer is a single bone, there being no sign of a median suture. Posteriorly it sends back a pair of narrow processes which border the anterior half of the interpterygoid vacuity and whose ends are sutured with the pterygoids. From these processes there are developed anteriorly a pair of ridges, which fuse in the midline, forming the anterior border of the interpterygoid vacuity, and then descend antero-ventrally to form the median septum between the internal nares. From here anteriorly the vomer is roughly T-shaped in cross-section, the cross bar of the T being the roof of the depression associated with the internal nares, and its stem being the median septum. This septum increases in height anteriorly until it joins the premaxilla; its junction with this is not preserved. The roofing part of the vomer is overlain dorsally by the palatine except in the midline. At the level of the anterior border of the palatines the antero-ventral surface of the sphenethmoid contacts the dorsal surface of the vomer, which also sends up slight wings clasping its sides. The vomer here is still a fairly large element, and it seems very probable that it extended for some distance further forwards - i.e. above the dorsal surface of the premaxilla, whose median dorsal ridge it presumably contacted.

The maxilla covers the jugal postero-laterally and has an interdigitating suture with the ectopterygoid and palatine postero-medially; medially it is covered by the premaxilla. The maxilla forms the sides of the oral cavity and its surface here is porous, there being a very large number of small and minute foramina. Postero-medially it bears a smooth groove, which at first runs posteriorly and is overhung by bone on each side, and more posteriorly curves inwards and runs dorsally across the inner surface of the palatine to reach the internal nares. Just medial to this groove the surface of the maxilla is roughened. The root of the canine tusk is sharply delimited by a groove which runs in a curve forwards and outwards from near the antero-medial extremity of the jugal; this groove continues onto the facial surface of the maxilla (see below, p.). In front of the canine the anterior edge of the maxilla runs antero-dorsally; it does not form a cutting edge, the transition from the palatal surface of the maxilla to its facial surface being a rounded edge. Near its anterior end this edge is notched by a groove running from a foramen on the facial surface of the maxilla.

The premaxilla is not complete, its anterior edge and junction with the vomer being missing. Unlike the palatal surface of the maxilla, which it covers laterally, the surface of the premaxilla is not porous. It bears a median posterior ridge which runs forward from the junction of the premaxilla and the vomer, and a pair of low lateral ridges. These latter run just medial to the maxilla-premaxilla suture; they are 1.5 - 2.0 mm. high, with a sharp edge, and gradually subside posteriorly, disappearing just in front of the level of the base of the canine tusk. These ridges do not seem to be equivalent to the more medial, paired, stout anterior palatal ridges found in many dicynodonts, and there is no sign of the latter structures. The only other structural feature of the palatal surface of the premaxilla is a pair of low roughened areas at its postero-lateral corners.

Side view (Fig. 4A, B)

The skull is of rather a long, low shape, the dorsal outline gradually sloping downwards anteriorly. The large canine tusk is slightly curving and projects at a forward angle. The posterior part of the ventral margin of the palate runs more or less parallel to the dorsal surface of the skull, but a short distance behind the pterygoid-ectopterygoid suture it suddenly turns more dorsally. Posteriorly the lateral pterygoid component of the convex ridge on the anterior part of the palatal exposure of the parasphenoid is visible below the quadrate ramus of the pterygoid. Posteriorly the dorsal margin of the zygomatic arch has a progressively greater outward slope, so that there is a hollowing between this part of the squamosal and its ventral wing. This ventral wing is set at a marked angle, thus being more or less at right angles to the force transmitted through the condyles by the action of the muscles attached to the lower jaw.

The maxilla is a very large bone, extending from the nostril to a level halfway along the orbit. It forms the outer border of the naris; from about halfway up the posterior border of the naris the nasal-maxilla suture runs backwards, upwards and slightly inwards, the maxilla being slightly overhung by the scalloped edge of the nasal. When the maxilla meets the anterior edge of the lacrimal the suture curves round outwards and downwards and then runs backwards, more or less following the curve of the lower border of the orbit. The maxilla continues for a short distance behind the lacrimal, contacting the jugal and forming the ventro-lateral portion of the anterior end of the zygomatic arch.

The form of the surface of the maxilla is complex. Ventrally it is markedly convex about the root of the canine, and from this area dorsally the surface is concave, rising to a rounded ridge along the anterior part of the maxilla-nasal suture. There is a low wide ridge running a short distance downwards and forwards from the middle part of the maxilla-lacrimal suture, and the maxilla is very slightly concave on either side of this, rising upwards dorsally to the rounded extension of the maxilla between the nasal and lacrimal, and rising ventrally towards a very marked thickening, which is the continuation onto the maxilla of the root of the zygomatic arch. Finally, there is a groove running round the postero-dorsal edge of the root of the canine and continuing upwards and forwards; within this groove there is a series of four foramina, decreasing in size dorsally. These foramina are directed downwards and postero-laterally; immediately above the most dorsal foramen of the series, and at the anterior end of a horizontal groove, is another foramen directed upwards. The surface of the maxilla anterior and ventral to these foramina is sculptured into fine ridges and grooves, many of the latter running forwards from small foramina or pits. Opening near the anterior end of the maxilla there is another foramen, from which a groove runs onto the palatal surface of the maxilla, causing a notch in the margin of the bone: a bristle passed into this foramen emerges through an internal foramen a short distance in front of the root of the canine tooth.

The distal parts of the large canine tusks are missing, but they were apparently about 2.2 cm. long (measured along the posterior side). They are round in cross-section, and the diameter at the base of the tusk is 8 mm. The tusks project forwards and are slightly curved. Their surface is smooth, with no sign of longitudinal grooves or of wear-facets. There is no evidence of a replacing canine.

The ectopterygoid is in side view separated from the maxilla by the antero-ventral portion of the jugal, by which it is overlapped. Posteriorly it is firmly wedged into the anterior end of the anterior ramus of the pterygoid. Though it forms about one centimetre of the ventral margin of the palate, the pterygoid and jugal almost meet above the ectopterygoid, which is thus roughly triangular in side view. On the dorsal surface of the palate is the upper opening of the large foramen between the ectopterygoid and the palatine.

The <u>palatine</u> forms the inner and anterior borders to this foramen, and meets the ectopterygoid for a short distance at its antero-lateral corner. Immediately above this contact there is a small foramen running antero-laterally into the cavity surrounding the root of the canine tusk; this foramen lies between the palatine and the jugal, the suture between these bones running antero-dorsally onto the floor of the orbit. This antero-lateral part of the palatine has an anterior interdigitating suture with the lacrimal and forms a short length of the internal border of the floor of the orbit. This border and the anterior border of the main part of the palatine both run into the border of a large foramen which runs antero-medially into the nasal cavity; the foramen is incomplete, having no antero-dorsal border. The main part of the palatine is convex transversely; its anterior border is damaged but it was probably contacted by the antero-ventral wing of the sphenethmoid. Medially it overlaps the vomer, laterally and posteriorly it meets the pterygoid.

The <u>sphenethmoid</u> (Fig. 4C) consists of a body which is extended posteriorly to form a trough-like floor for the olfactory nerves; there is no sign of separate orbitosphenoid and presphenoid ossifications, either superficially or in section. The body is thickest in transverse section along a line approximately halfway between its dorsal and its ventral borders, and also becomes thicker anteriorly. The dorsal edge posteriorly contacted the ventral surface of the frontal roof, and was presumably expanded at this point, though its most dorsal part is damaged. Anterior to this, it becomes thin and descends antero-ventrally, finally turning in a more ventral direction and expanding to form an anteriorly-directed triangular surface. The edge now turns sharply postero-ventrally, so that there is a wide antero-ventrally directed surface, which is slightly concave in horizontal section; this surface is smooth and is closely clasped by the dorsal surface of the vomer, which sends up slight wings on either side of the sphenethmoid. In this region the sphenethmoid is also just contacted by the antero-medial corners of the palatines. Posterior to this, the edge of the sphenethmoid turns sharply postero-dorsally; this edge is hollowed in transverse section, so that there are two ridges enclosing a depression which faces postero-ventrally. This depression probably received the anterior end of a cartilage which rested on the grooved processus cultriformis of the parasphenoid and which thus completed the inter-orbital septum. The ridges enclosing the depression converge and meet posteriorly, so that the depression is drop-shaped; the resulting median ridge turns dorsally and runs onto the ventral surface of the posterior trough-like expansion of the sphenethmoid. The dorso-lateral margins of this trough meet the edges of the orbital components of the frontals and extend inside them to rest on the ventral surface of the frontal roof. The posterior edge of this trough is not preserved but was presumably free.

The parasphenoid-basisphenoid complex runs forward nearly to the level of the anterior border of the palatine. Posteriorly its close suture with the braincase runs antero-dorsally onto the periotic region, passing a few millimetres in front of the foramen for the facial nerve. The more dorsal part of the suture is not very distinct, but it appears to reach the edge of the cranial cavity just anterior to the base of the pila antotica, which is thus ossified from the prootic region,and just posterior to the sella turcica.

The dorsal border of the parasphenoid-basisphenoid complex runs antero-dorsally from the periotic until it terminates abruptly, having an anterior poorly ossified face which drops to the level of the parasphenoidal rostrum or processus cultriformis. The thin-walled U-shaped rostrum runs parallel to the dorsal side of the palate, separated from it by a distance of about 2 mm.

In front of the sella turcica the dorsal surface of the parasphenoid-basisphenoid complex is flat and 3-4 mm. wide; the sides at first drop ventrally at right angles to this surface, but then curve ventro-laterally to meet the pterygoid. There is thus a groove running antero-dorsally from the base of the quadrate ramus of the pterygoid; this groove was probably occupied by the anterior part of the vena capitis lateralis. The parasphenoid-basisphenoid complex overlaps the pterygoid, the suture posteriorly running antero-laterally onto the base of the quadrate ramus of the pterygoid, so that there is an extremely short contact between the complex and the epipterygoid, and then running antero-dorsally parallel to the upper border of the complex. There is a foramen in this suture at a level slightly behind the posterior end of the interpterygoid vacuity; as mentioned above (p. 28), this is probably the dorsal opening of the canal for the palatine branch of the facial nerve. The inner side of the foramen is formed by a slight dorsal pterygoid lamella applied to the side of the parasphenoid-basisphenoid complex.

The <u>prootic</u> region of the braincase is the only part of the periotic that is visible in side view, but it is more clearly seen in an anterior view of the occipital plate (Fig. 5). Dorso-laterally it is overlapped by the medial process of the squamosal, dorso-medially it is fused to the supra-occipital region of the occipital plate, and antero-dorsally it is sutured to the posterior edge of the vertical parietal wall of the braincase. The postero-laterally directed foramen for the facial nerve is overhung by a slight dorsal ridge; it opens on the ventro-lateral surface of the prootic, a few millimetres behind its suture with the parasphenoid-basisphenoid complex. Immediately posterior to the dorsal end of this suture, the anterior margin of the prootic is extended into a long antero-dorsally directed process; this is the pila antotica, which is apparently ossified from the prootic. The transverse hypophysial vein presumably ran across the cranial cavity anterior to the pila antotica, whilst the trigeminal nerve and vena cerebralis media left the cranial cavity posterior to it. Behind the notch for these latter structures, the anterior wall of the prootic runs upwards to meet the parietal; at the meeting-place of the two there is a distinct small notch in the anterior wall. This notch lies at the anterior end of a very marked groove, about 4 mm. wide, which runs inwards, upwards and forwards from the anterior opening of the post-temporal fossa; the function of these structures will be discussed in a later section.

The <u>parietal</u> in side view continues vertically downwards below the postorbital to form the anterior part of the wall of the braincase. This wall is a thin lamina, the outer surface of which is not smooth, and sutures are difficult to distinguish. The anterior edge of the lamina runs postero-ventrally for some distance and then turns upwards in a slightly concave arc and meets the anterior part of the prootic region. Between this arc and the anterior edge of the lamina there is thus a downwardly projecting wedge. On the outer side of the lower part of the wedge rests a piece of bone which appears to be the dorsal end of the epipterygoid. However, dorsal to this wedge there is a small opening in the bone lamina, and it is possible that the whole of the wedge is part of the epipterygoid and that the opening represents an unossified gap between the epipterygoid and the parietal. Posterior to the wedge, the posterior suture of the parietal runs dorsally, bordering first the supraoccipital-periotic region and then the interparietal, finally reaching the ventral surface of the postorbital.

The epipterygoid has an expanded lamelliform base 15 mm. long, resting on the quadrate ramus of the pterygoid; medially this base has a very short contact with the lateral edge of the parasphenoid-basisphenoid complex. Rising antero-dorsally from near the anterior end of this base is its ascending process or columella cranii, a slender rod of bone whose dorsal end contacts the parietal; as discussed above, it is probable that it takes no part in the formation of the vertical side wall of the anterior part of the braincase, the whole of this being ossified by the parietal.

The quadratojugal is a laminar bone; its upper portion faces anteriorly and is slotted immoveably into the anterior face of the squamosal (Fig. 5), but its lower portion faces antero-laterally and is fused to the dorsal surface of the outer quadrate condyle. This ventral portion is separated from the body of the quadrate by the quadrato-jugal foramen, and the quadrato-jugal thus has a free anterior border here. The quadrato-jugal foramen is almost completely closed posteriorly by the quadrate approaching the quadratojugal and by the squamosal overlapping the posterior surface of both these bones. The ventral part of the postero-lateral border of the quadratojugal runs in a concave curve laterally and dorsally, forming a distinct embayment in the border of the occiput, the edge of which it here forms. Further dorsally it runs in a convex curve laterally and dorsally, still forming the edge of the occiput, and then runs more medially across the anterior face of the squamosal, to meet the dorsal edge of the quadratojugal.

The quadrate consists of a large dorsal body and two ventral condyles, the outer condyle bearing the quadratojugal dorsally. The rather bulbous body fits into a pocket bordered internally by the squamosal and paraoccipital process and externally by the squamosal and quadratojugal (Fig. 5). In cross-section it can be seen to be composed of spongy bone; its lateral surface has a good superficial ossification, but the medial surface is very rough, and it is apparent that the gap between the quadrate and the paraoccipital process and squamosal was in life filled by cartilage. On its inner side, near to where it merges ventrally with the inner condyle, is a slight antero-medially directed recess for the reception of the cartilaginous end of the quadrate process of the pterygoid.

Both condyles are convex antero-posteriorly, and the tangent to this convexity is directed upwards and forwards. The outer condyle is broad, slightly convex in the transverse plane and faces slightly inwards. It meets the inner condyle about 5 mm. dorsal to the articular surface of the latter and the articular surfaces of the two condyles are thus joined by a surface, facing laterally and somewhat ventrally, which meets the outer condyle at a right-angle and meets the long narrow articular surface of the inner condyle at an acute angle (about seventy-five degrees). The inner condyle projects posteriorly for about 3.5 mm. beyond the occipital surface of the squamosal and is visible through an embayment in the posterior edge of the squamosal and quadratojugal just above the outer condyle. On its medial surface, below the distal end of the paroccipital, there is an antero-posterior ridge which lies slightly dorsal to the articular surface of the condyle; this is the stapedial ridge, against which lies the distal end of the stapes.

Stapes (Fig. 6)

Both stapes were preserved in position and virtually undamaged except for the loss of the postero-lateral corner of the left stapes.

The stapes expands proximally to form the footplate and distally to buttress against the quadrate; both the anterior and posterior borders are thus concave in dorsal and ventral view, but the concavity of the posterior border is more marked. At its narrowest point the shaft of the stapes is 4 mm. in width and 2 mm. thick; there is no stapedial foramen.

The ventral surface is slightly convex in the antero-posterior plane; proximally it drops slightly to form the thick ventral portion of the footplate. In proximal view, the footplate has the outline of a dorsally flattened circle; dorso-medially there is a slight hollow, anterior to which is a very low rounded boss. The footplate has a thick rounded border on all sides except antero-dorsally where the dorsal surface, which here rises upwards, meets the proximal surface at an acute angle. On the dorsal surface can be seen the very marked dorsal process, which rises latero-dorsally from the most distal third of the bone; its anterior margin originates from about the midline of the stapes. The distal end of the dorsal process is flattened, facing dorsally and slightly laterally, and touches the ventral surface of the paroccipital process. In distal view, there is a groove along nearly the whole length of the end of the stapes; posteriorly, the dorsal border of this groove meets the base of the dorsal process. This surface of the stapes contacts the stapedial ridge on the medial surface of the inner quadrate condyle. On the right stapes this groove continues posteriorly onto a short posterior process of the stapes, so that there is a postero-laterally directed facet; this region is damaged in the left stapes. It seems likely that this facet is for the base of the extrastapedial cartilage; this point will be discussed in a later section.

Braincase (Fig. 7)

The sutures within the braincase cannot be traced with certainty. The height of the braincase increases anteriorly; just anterior to the foramen magnum, which is 13.5 mm. high, this increase is quite gradual, but after about 4 mm. the height increases more rapidly to about 30 mm., afterwards increasing slightly until the internal opening of the pineal foramen is reached. The width of the braincase similarly increases anteriorly, being 8.5 mm. wide at the foramen magnum and 13 mm. wide at the level of the prootic incisure.

The dorsal surface of the occipital condyles is concave, and this concavity continues forwards along the posterior floor of the braincase. Just behind the level of the internal openings of the jugular foramina a median ridge develops; at the level of the front edge of the internal auditory meatus this splits into two for a short distance to enclose a small median oval hollow 2 mm. long. Anterior to this a pair of ridges diverge to run antero-dorsally towards the pilae antoticae; the medial surfaces of these ridges are slightly concave. Though they are rather far behind the sella turcica, it seems likely that these ridges represent the dorsum sellae medially and, more laterally, the alae basisphenoidales or clinoid processes, which normally run onto the bases of the pilae antoticae. It is further possible that the concavity in front of these ridges is concerned with the retractor group of eye-muscles, whose origin extends into the pituitary region in some reptiles (Varanus, Sphenodon, Säve-Söderbergh, 1946). In front of these ridges, the floor of the braincase runs forwards and slightly downwards to the posterior edge of the sella turcica.

There is no sign of any unossified zone in the floor of the braincase. The hind border of the sella turcica is slightly in front of the level of the bases of the pilae antoticae, and the sella is about 2 mm. wide. The internal carotid arteries run separately from a postero-ventral direction into the floor of the sella; this floor slopes strongly upwards and forwards and is continuous anteriorly with the dorsal surface of the parasphenoid-basisphenoid complex, so that no anterior limit to the sella can be defined.

The anterior edge of the ossified braincase commences dorsally at the venous notch between the parietal and the prootic (the function of this notch will be discussed in a later section). Below this notch the anterior edge runs ventrally and slightly posteriorly, to form the posterior edge of the prootic incisure; this incisure, posterior to the pila antotica, is a normal feature of the reptile braincase and transmits the trigeminal nerve and the vena cerebralis media. Anterior to this incisure the pila antotica rises antero-dorsally; anterior to this, the anterior edge of the braincase descends slightly to reach the level of the opening of the sella turcica in the floor of the braincase.

There are various foramina and openings in the wall of the braincase. Posteriorly, at the ventro-lateral corner of the foramen magnum, are the two hypoglossal foramina, the posterior foramen being slightly larger than the anterior; these run ventro-laterally into the jugular foramen. The jugular canal runs antero-dorsally and medially to open just anterior to the hypoglossal foramina. Lateral to this canal is a thin sheet of bone which separates it from the vestibule of the inner ear; at its anterior end, the lower edge of this sheet of bone is notched for the fenestra rotunda.

The opening of the vestibule of the inner ear into the braincase is quite large and is at the ventral end of the wall of the braincase; its border shows various features. Postero-ventrally, as just mentioned, there is a notch for the fenestra rotunda, which opened into the jugular foramen. Further forward along its ventral border and separated from the fenestra rotunda by a distinct prominence is another notch, which probably transmitted the posterior branch of the auditory nerve; the anterior branch of this nerve probably ran in a small foramen just anterior to the anterior end of the opening of the vestibule. From the dorsal edge of the opening of the vestibule a marked groove runs up the wall of the braincase; this groove probably lodged the ductus endolymphaticus.

There is no sign of any division of the vestibule into portions for the utriculus, sacculus and cochlea. Ventrally it continues ventro-laterally to the fenestra ovalis as a tube about 3 mm. in diameter. Anteriorly and posteriorly the vestibule extends a short distance beyond its opening into the braincase to join the ampullar recesses. Dorsally the crus communis canalium runs into the vestibule just above the dorsal margin of its opening into the braincase; it is thus just lateral to the groove for the ductus endolymphaticus and medial to most of the vestibule.

Anterior to the opening of the vestibule lies the internal opening of the canal for the facialis nerve; the straight canal runs ventrally and slightly postero-laterally to its external opening. The only other feature on the wall of the braincase is the subarcuate fossa, which lodged the floccular portion of the brain. This runs ventrally and postero-laterally into the side wall of the braincase just antero-dorsal to the vestibule; there is no communication between the fossa and the vestibule. The fossa tapers as it runs into the bone, it being about 5 mm. deep and its opening into the braincase being about 4 mm. in diameter.

Osteology of the lower jaw (Figs 8 and 9)

The lower jaw is almost perfectly preserved. Its antero-posterior length, measured to the mid-line at the level of the posterior end of the articular region, is 20.2 cms. As is usual in the Dicynodontia, there is no coronoid; no sutures are visible between the posterior ends of the articular, the prearticular and the surangular.

The dentary is by far the largest bone. The two dentaries are fused anteriorly and together form the upturned "beak", which in lateral view has a slightly convex antero-ventral surface, rising to a blunt point which extends dorsally above the level of the posterior part of the bone. The dorsal outline is thus concave anteriorly, and in this region the edges of the beak are rounded and rugose. Further posteriorly, where the jaw ramus merges into the beak, there is a flattened dorsal surface which, when the jaw is articulated with the skull, contacts the ventral surface of the ectopterygoid and maxilla behind the root of the canine; the medial part of this flattened surface is slightly rugose. In dorsal view the beak tapers anteriorly to a blunt rounded point which is rendered slightly bifid by a median groove which becomes progressively deeper and wider posteriorly.

From the level of the flattened dorsal area mentioned above, the dorsal margin of the dentary divides into two ridges. The slightly higher medial ridge continues posteriorly as a smooth rounded edge to meet and overlap the surangular, whilst the lower and wider lateral ridge turns slightly outwards, then continuing parallel to the inner ridge for some distance before subsiding. Between the two ridges there is an extremely well defined concavity. In lateral view the lateral ridge can be seen to be the edge of a very marked wing which projects dorso-laterally from the side of the dentary.

The ventral edge of the dentary anteriorly has an interdigitating suture with the splenial; more posteriorly these two bones are separated by the anterior end of the angular. The ventral edge of the dentary thence runs postero-dorsally, having a smooth overlapping meeting with the angular, to a point near the most posterior extremity of the dentary, where it diverges slightly from the angular to leave a very small fenestra which opens internally into the meckelian fossa. Above this fenestra the dentary extends backwards for a short distance and again contacts the angular at the most dorsal point of the latter bone.

In internal view, the fused symphysial region has a vertical posterior face; ventrally this face has a suture with the fused splenials, but postero-laterally the anterior end of the prearticular separates these two bones. More posteriorly, the dentary diverges from the prearticular and has a border running postero-dorsally which overlaps the surangular. The surangular is clasped anteriorly by the dentary, which it thus separates into two parts, the more lateral part being visible below the surangular and forming the outer wall of the meckelian fossa.

The splenials are fused together and form the postero-ventral part of the symphysial region. They thus form the lower part of the posterior wall of this region, meeting the dentary dorsally. Immediately below this suture, but wholly within the splenials, is a small foramen about 1.5 mm. in diameter, leading forwards into the symphysial region and which presumably carried a nutritive blood vessel. Ventral to this foramen the surface of the splenials is concave with a slight median ridge. The ventral surface forms a broad wedge extending forwards between the dentaries, with which there is an interdigitating suture. More posteriorly, the splenial meets the angular, with which it has a smooth suture running slightly dorsally. The posterior border of the splenial is broadly forked, the lower ramus wedging into the angular whilst the upper ramus runs back inside the prearticular, the anterior end of which passes between the two rami and continues forwards between the body of the splenial and the meckelian fossa.

The prearticular is a thin strip of bone which forms the inner wall of the meckelian fossa. Anteriorly it passes between the two posterior rami of the splenial and continues forwards into the inner posterior surface of the dentary. Posterior to the splenial its inner surface rests against a slight shelf on the ventro-medial edge of the angular; more posteriorly the prearticular comes to rest on this shelf, the edge of which becomes deflected upwards and is received in a groove in the ventral edge of the prearticular (see Fig. 9D). Posterior to the meckelian fossa the inner surface of the prearticular meets the articular; there is a suture between the bones in this region, but more posteriorly the two bones are indistinguishably fused.

The angular forms the floor and much of the lateral wall of the meckelian fossa. This fossa extends anteriorly between the dentary and the prearticular, and in this region there is a deep channel in the dorsal surface of the angular. The higher lateral wall of this channel is applied to the medial surface of the dentary, whilst the lower medial wall is applied to the lateral surface of the prearticular. This medial wall subsides posteriorly, but continues as a ledge on the ventro-medial corner of the angular, abutting against the prearticular; further posteriorly this ledge extends below the prearticular and its edge becomes reflected dorsally into a groove in the ventral edge of the prearticular (see Fig. 9D). Anteriorly the angular meets the splenial below the prearticular, its medial surface being grooved to receive the lower ramus of the splenial. In ventral view, this anterior end of the angular has smooth sutures with the splenial and dentary, between which it disappears. In lateral view the angular is overlapped by the dentary, the ventral edge of which rises postero-dorsally until it diverges from the angular to leave the small fenestra between the two bones. The dorsal edge of the angular turns dorsally to form the posterior border of this fenestra, and the angular here comes into contact with the surangular. The posterior part of the bone is a thin lamina applied to the outer side of the surangular and articular, its dorsal and posterior margins being overhung by that sudden lateral expansion of the articular which produces the articular region of the lower jaw; the angular takes no part in the formation of this structure, nor in the formation of the retro-articular process.

The reflected lamina of the angular is very extensive in both lateral and ventral views. Its antero-posterior extent is small dorsally, where it arises just posterior to the meckelian fossa, but its posterior border thence curves sharply backwards and then downwards, so that the lamina becomes progressively longer; its greatest length would appear to have been in its ventro-lateral region. The main stem of the lamina is a stout rounded keel of bone which diverges laterally from the ventral margin of the angular and continues into the ventro-lateral portion of the lamina. This whole lateral portion of the lamina curves outwards and backwards, so that it encloses a considerable cavity, up to 5 mm. wide and 10 mm. long; however, the posterior edge of the lamina is slightly inturned, so that in ventral view it has a slightly curved lateral outline.

Ventro-medial to the continuation of its main stem, the lamina comes to face progressively more and more in a ventral, rather than in a lateral, direction. There are however two distinct regions in this ventral extension of the reflected lamina; laterally, it is smoothly continuous with the lateral part of the lamina, but medially there is a region which has a marked antero-posterior curvature, being convex ventrally. The lateral part of the ventral extension is rather more dorsal than the medial part, and there is therefore a noticeable vertical ridge at their junction; this ridge is most marked posteriorly, but gradually fades out anteriorly and finally ends in a slight hollow. Parallel to the posterior end of this ridge there is a rounded groove in the bone; between the ridge and the groove the bone is convex ventrally, so that there is in effect an antero-posteriorly directed, slightly thickened, keel of bone. The true margin of this ventral component is not preserved; however, it would appear to curve sharply round anteriorly, until its edge is directed forwards, and rejoin the stem of the lamina where it diverges from the main body of the bone.

The surangular forms the dorsal border of the lower jaw immediately posterior to the dentary, by which it is overlapped; this border slopes postero-ventrally to the level of the articular surface of the articular bone. In internal view the surangular-dentary suture runs antero-ventrally, the anterior end of the surangular being wedged into the inner surface of the dentary. The surangular becomes thinner ventrally, and its rounded lower edge forms a smooth dorsal delimitation to the meckelian fossa. Posteriorly this ventral edge turns abruptly antero-ventrally and runs down the inner surface of the angular and forms the posterior part of the lateral wall of the meckelian fossa. Slightly more posteriorly however, this surface of the surangular is covered internally by a thin anterior lamina of the articular, which separates the surangular and the prearticular (see Fig. 9D). The surangular-articular suture runs postero-dorsally, but fades out near the dorsal margin of the lower jaw, and the posterior end of the surangular is thus fused with the articular.

The articular extends anteriorly as a thin lamina of bone between the surangular and the prearticular, its antero-ventral corner bearing a small facet for the reception of the posterior end of Meckel's cartilage (see Fig. 9D). In this region it is not fused with the surangular and prearticular, but more posteriorly the three bones cannot be distinguished from one another. In lateral view the dorsal margin of the articular curves downwards posteriorly to produce the convex articular surface. The main axis of the ramus of the lower jaw continues as the medial part of the lateral condyle, whose more lateral part is formed by an expansion of the articular, which thus overhangs the lateral surface of the angular. The medial condyle is a wing-like projection extending postero-dorsally from the medial wall of the lateral condyle; its articular surface lies more ventrally than the articular surface of the lateral condyle, and the latter thus has a medially directed face. In posterior view (see Fig. 9C) the articular surfaces of both condyles can be seen to be slightly concave in transverse section.

The lateral condyle is produced ventrally to form a well developed retro-articular process. On this structure can be seen three areas of muscle-insertion, distinguishable by the surface texture of the bone. Firstly, in lateral and anterior view there is a large hollow, walled laterally by the lateral surface of the articular and posteriorly and postero-laterally by the ventral continuation of the lateral expansion of the articular; this area of muscle-insertion is defined dorsally by an antero-posterior ridge which continues a short distance forwards onto the angular. Secondly, there is an area of muscle-insertion on the postero-ventral surface of the retro-articular process; this area continues dorso-laterally, gradually becoming narrower, up the side of the lateral expansion of the articular. Finally, in internal view there is a distinct hollowing beneath the posterior end of the medial condyle, this condyle being continued a short distance postero-ventrally as a ridge which forms the posterior delimitation of the area of muscle-insertion.

Hyoid

This bone was not preserved in the specimen (FRP 84) which has been the subject of the rest of the present section, but was present in specimen

FRP 82. The relationships of the two specimens and the post-cranial skeleton of FRP 82 are discussed in the next section, but it seems more convenient to describe the hyoid of specimens FRP 82 here while dealing with cranial osteology.

Only a single bone was preserved on each side and it is therefore impossible to determine which part of the hyoid arch it represents, and it will simply be referred to as the hyoid.

The left hyoid was in good condition, the right hyoid was distinguishable but was badly weathered and could not be preserved. The two hyoids lay at a level slightly below the ventral edge of the lower jaw. They lay at an angle of 40-45° to one another, converging anteriorly but not meeting: their anterior ends lay 0.5 cm. apart.

The hyoid bone is 2.4 cm. long. Seen in ventral view, it is slightly curved antero-posteriorly, the lateral edge being convex. In lateral view, the anterior end of the hyoid turns slightly ventrally. At its posterior end, the hyoid is oval in transverse section, the long axis of the oval being directed dorso-laterally. Seen from behind, this long axis gradually turns in an anti-clockwise direction until at 0.8 cm. from the anterior end it is horizontal. The anterior region of the bone is flattened dorso-ventrally: its posterior end is convex, but anteriorly there would appear to have been a straight edge.

C. The post-cranial skeleton of *Kingoria nowacki*

Specimen FRP 82 consists of the skull and much of the post-cranial skeleton of a dicynodont. Unfortunately, the dorsal surface of the skull is covered with a hard acid-resistant layer, so that it has not been possible to display the sutural pattern of this region. It was found in the same locality as specimen FRP 84 and in close proximity to it, it is of similar size and outline, and the unusual features already described in specimen 84 are found again in specimen 82. Thus specimen 82 has the peculiarly-shaped lower jaw, and lacks the normal type of anterior palatal ridges but possesses the lower, sharper, more laterally placed palatal ridges; it possesses a reflected lamina on the angular bone similar in detail to that of specimen 84; and it shows evidence of a tympanic process on the occiput. Where the sutures can be detected, they are more or less identical with those of specimen 84 except that specimen 82 does not show the embayed area on the anterior face of the occipital ramus of the squamosal, which in specimen 84 affords an anterior view of part of the tabular. The skulls also differ in that the interorbital breadth is 41 mm. in specimen 82, compared with 32 mm. in specimen 84. It may be that specimen 82 had reached a more advanced stage of ossification than specimen 84, the squamosal extending further over the anterior face of the occiput and the interorbital bar widening. Though it is no larger than specimen 84, it is in the process of replacing the canine tusks, again suggesting that it may have reached a more mature state than specimen 84.

Though there are thus some differences between the two skulls, their common place of origin and their close agreement in major anatomical features indicate that they are closely related. Since the sutural pattern of the dorsal surface of the skull cannot be displayed in specimen 82, and since the limits of infra-specific variation in the Dicynodontia (as in most vertebrate fossils) are unknown, it is impossible to be certain that specimens 82 and 84 are conspecific. However, it is considered that the differences are not qualitatively or quantitatively sufficient to permit the adequate characterisation of specimen 82 as a different species, and it is considered best to refer it to Kingoria nowacki.

The post-cranial skeleton was preserved in three blocks. The most anterior, block A, had originally been attached to the back of the skull, but had become separated from it along a calcite seam. It contained the eleven most anterior vertebrae with their ribs, the pectoral girdle, complete except for the dorsal part of the right scapula, and the proximal parts of the humeri. The second block, B, contained fifteen dorsal vertebrae, with the dorsal parts of their ribs. The third block, C, contained the sacrum and the most anterior caudal vertebrae and a portion of the head of the femur. The relations of the different skeletal elements to one another were preserved within each block.

The three blocks were collected as a single specimen; though they do not key together, the complementary character of the contents of the different blocks, and the morphological similarity of the contents, together with the fact that they were all collected close together, make it beyond reasonable doubt that they all contain remains of the same individual.

VERTEBRAL COLUMN

Block A contained the six cervical vertebrae and the five most anterior dorsal vertebrae, block B contained fifteen dorsal vertebrae, and block C contained the last dorsal vertebra, the four sacral vertebrae and the three most anterior caudal vertebrae. The three blocks thus contained the remains of thirty-four vertebrae, twenty-seven of them presacral, with two regions where the blocks were not continuous and vertebrae may be missing.

It is not easy to estimate the number of vertebrae which are missing. In the more anterior region of discontinuity, the last vertebra of block A (dorsal vertebra 5) is badly damaged and distorted, and only a small piece of the most anterior vertebra of block B is present, so that there is thus a gap of two vertebrae between those which are comparable in detail. In the more posterior region of discontinuity, only the posterior half of the most anterior vertebra of block C is preserved, and the posterior face of the centrum of this vertebra is enlarged to match the large anterior face of the first sacral vertebra, so that this last dorsal vertebra is not readily comparable with the last vertebra of block B.

It is thus not possible to estimate the number of missing vertebrae from the morphology of those preserved. The only other indication of the probable original number of presacral vertebrae is given by statements in the literature as to the presacral number in other dicynodonts, and there appear to be few specimens in which this is known with certainty. von Huene (1931) states that there were twenty-six in <u>Dicynodon kolbei</u> ?, but gives no indication of the state of preservation. Broom (1915b) states that there were twenty-eight presacral vertebrae in an unidentified species of <u>Dicynodon</u>. Sushkin (1926b) states that there were thirty presacrals in <u>Dicynodon amalitzkii</u>; however, the three most anterior vertebrae are not completely visible, and he appears to have taken the atlas neural arch and intercentrum to be parts of two distinct vertebrae, so that the true presacral number may be twenty-nine. Other statements which appear to rest on a fairly firm basis are the following. In Chelyposaurus williamsi, Broom (1905a, p.277) states "Probably only the atlas is missing among the presacral vertebrae, and if this be so then the full number would be twenty-six". In Aulacephalodon peavoti, Olson & Byrne (1938, p.181) state "The twenty-six presacral vertebrae present in the specimen appear to form a complete series". In Prolystrosaurus natalensis, Haughton (1917, p.169) states "Of the vertebral column there are 34 vertebrae preserved - 25 cervical and dorsal, 6 sacral, and 3 caudal". Finally, in Lystrosaurus latirostris, Watson (1912b, p.288) states "The whole vertebral column is beautifully shewn in this specimen, its formula being c + d. 25, s.6, c.10".

It thus appears that twenty-five to twenty-six presacral vertebrae are most commonly reported in the Dicynodontia. Since twenty-seven presacrals are represented in Kingoria, it seems best to regard this as the actual number of presacral vertebrae in that genus, there thus being six cervicals and twenty-one dorsals. The vertebrae from block B are numbered on this assumption.

The vertebrae have amphicoelous spool-shaped centra. The upper corners of the anterior articular faces of the centra bear small facets which face slightly downwards and forwards, contacting corresponding facets on the upper corners of the posterior articular face of the preceding vertebra. These minor facets may be called centrosphenes and centrantra, respectively, following Case (1907). There is a small pit halfway along the ventral floor of the neural canal in each centrum; in some cases this pit is paired, due to the presence of a median septum, and in the second sacral vertebra the pit is entered by a pair of small canals leading to a pair of foramina on the sides of the centrum. The sutures between the centra and the neural arches are not visible.

Cervical Vertebrae

There are 6 cervical vertebrae; this number is indicated by several features. Between vertebrae 2 and 7 the movements possible at the vertebral articulations are both dorso-ventral and rotatory; between vertebrae 7 and 8 and between vertebrae 8 and 9 rotatory movements cannot take place. The size of the parapophysis and diapophysis greatly increases between vertebrae 6 and 7 (Fig. 11); this is correlated with the size of the rib-heads and thus with the size of the ribs. Though their ventral ends are missing, there is a sharp increase in size of the ribs between those belonging to vertebrae 6 and 7 (Fig. 15) and this may indicate that the rib belonging to vertebra 7 was the first rib to curve right round to meet the sternum, thus making vertebra 7 the first dorsal vertebra. Finally, there is a noticeable difference in the angle of the neural spines between vertebrae 6 and 7, that of vertebra 7 being more posteriorly directed (Fig. 11A).

The measurements of the cervical vertebrae and anterior dorsal vertebrae are given in Table 1. Approximate figures are given for the distance across the transverse processes of some vertebrae; this is because the ends of some transverse processes are damaged, but in no case are both transverse processes of a single vertebra damaged.

The right and left proatlas elements (Fig. 10A-F) are not identical, the right being 15 mm. long and the left 13 mm. long; this is due to the

Table 1. Distances in millimetres

Vertebra		Height	Height of neural spine above top of neural canal	Ventral length of centrum	Posterior width of centrum	Posterior height of centrum in mid-line	Width across dia-pophyses	Width across postzyga-pophyses	Width across para-pophyses	Approx. angle of postzyga-pophyses to one another
Cervical	2	28	10	20	13	11	15	13	33	110°
	3	-	-	9	14	12	15.5	12	33	88°
	4	30	12	9	14	12	15	11	33	82°
	5	32	12.5	10	14	12	15	10	32	73°
	6	33	15	10.5	14	12	14.5	8	c. 31	60°
Dorsal	1	33	15	10.5	14.5	12	13	7	29	46°
	2	-	-	11.5	14.5	12	13	6.5	c. 25	52°
	3	32	14	11.5	13.5	11	12.5	5.5	c. 23	46°
	4	-	-	12	12.5	10.5	12	6.5	c. 21	150°

more dorsal part of the element, dorsal to the facet for articulation with the occiput, being slightly longer in the right proatlas. Apart from this, the two proatlas elements are alike. There is a flat posterior surface nearly 4 mm. wide, from which a small protuberance arises at the dorso-medial corner. The bone is 2-3 mm. thick, with a marked facet, 2 mm. high, for articulation with the occiput. The lower end of the bone is abruptly truncated, but this does not appear to be the facet for articulation with the atlas, either from its form or from the positions of the bones in place against the skull, neither is there an obvious facet for the proatlas on the atlas arch.

The atlas (Fig. 10G-L) appears to have consisted of three separate elements: two neural arch elements and the intercentrum. Nothing that can definitely be identified as the intercentrum was found, though one fragment may represent part of it. Both neural arch elements are somewhat damaged; the left is the better preserved, and the figures and description are based on this. The neural arch elements did not meet above the neural canal.

The left atlas neural arch consists of a stout, roughly cubical body, from which run various processes. The body itself bears two very marked facets, one directed postero-medially and contacting the axis centrum, the other, slightly smaller, directed antero-medially and contacting the exoccipital condyle of the skull. There is a smooth rounded transition between the two facets, which are at an angle of 100-105° to one another, and which are both slightly concave.

From the postero-lateral corner of the atlas neural arch runs the transverse process, postero-laterally directed and curving slightly backwards.

Its ventral margin is somewhat damaged, but the extent of the broken surface does not suggest that much bone has been lost. However, the damage does include the area where the atlas intercentrum might have been expected to be attached, and no evidence of this is to be found.

From the dorsal surface of the atlas neural arch rises a fairly stout lamina of bone which forms the lateral wall of the neural canal in this region. It is of rather irregular form, but is mainly directed dorso-medially. The postero-lateral corner of this lamina is continuous with the base and substance of a stout, prominent, postero-dorsally directed process (Fig. 10, n.sp). This process is about 6 mm. long, with a rounded slightly laterally-compressed end along which runs a slight groove.

No distinct facets can be seen on the atlas arch for articulation with either the proatlas or the axis prezygapophysis.

The axis (Fig. 10 M-R) is a massive bone, 20 mm. long and 28 mm. high. In side view a clear groove can be seen on the left side indicating the point of fusion between the axis proper and the atlas pleurocentrum. The axis thus does bear what may be called an odontoid process, though the shape of the process is far from tooth-like. In anterior view, the face of this odontoid process is trifoliate. In the mid-line, just below the level of the floor of the neural canal, is a subcircular area with a slight central pit, perhaps corresponding with the notochordal pit in the occipital condyle of the skull. Postero-laterally from this area extends a pair of facets for the atlas arches; these facets become slightly larger as they run postero-laterally, are directed anteriorly and slightly dorsally, and are somewhat convex. The third element in the trifoliate pattern extends postero-ventrally in the mid-line. After an initial constriction just below the more dorsal subcircular area, it expands slightly before narrowing to a point situated at the level of the ventral surface of the centrum. Its convex surface is directed antero-ventrally, and it probably contacted the posterior surface of the atlas intercentrum.

Behind this atlantal addition to the axis can be seen the true axis centrum; this shows no sign of division into intercentrum and pleurocentrum. The parapophysis is a short, stout, ventro-laterally directed process set low on the centrum. The ventral surface of the centrum posterior to the level of the parapophyses bears a slight median ridge.

The posterior surface of the centrum is subcircular in outline, the dorsal edge of the circle being somewhat flattened by the floor of the neural canal. It is deeply concave, the central cavity being nearly 5 mm. deep and being surrounded by a fairly wide flat surface which articulates with the next vertebra.

No suture can be seen between the axis neural arch and the other elements of the axis vertebra. The diapophysis or transverse process is directed slightly posteriorly and slightly ventrally; it is about 8 mm.long, with an expanded distal end which faces ventro-laterally. The prezygapophyses are fairly well-developed, but are simple horizontal laminae without any well-marked facet for the atlas arch. The postzygapophyses are stout, with large ventro-laterally directed facets. The neural spine is quite stout and thick, with a slightly thickened dorsal and posterior edge, but it is not very large. Its anterior edge is but little in advance of the level of the anterior edge of the prezygapophysis; from here its dorsal edge runs in a convex curve upwards and backwards, but its greatest height is only 10 mm. above the level of the neural canal.

Cervical vertebrae 3-6 (Figs 11, 12A, B, E, F, I, J). As will be seen from the table of measurements given earlier and from the figures, various progressive changes occur in the cervical vertebrae. The centrum itself increases slightly in length and breadth, and the extent of the constriction of the centrum decreases posteriorly. This last feature results in a change in the character of the diapophysis, which anteriorly is a marked laterally directed prominence from the ventro-lateral part of the anterior region of the side of the centrum. Though the distance between the diapophyses remains almost unchanged, the reduction in the constriction of the centrum has the effect of decreasing the extent to which the diapophysis protrudes from the surface of the centrum. This change is also partly the result of the facts that the diapophysis progressively moves up the side of the centrum and that it becomes progressively larger.

The pit in the middle of the ventral floor of the neural canal is divided into two by a thin longitudinal septum in cervical vertebra 6.

Like the diapophysis, the parapophysis or transverse process of the neural arch also progressively moves upwards. In all the cervical vertebrae the transverse process is an elongate structure, roundly pointed in dorsal view, and directed postero-laterally from the side of the neural arch. Its level of origin is slightly below the level of the floor of the neural canal in cervical vertebra 3, but it progressively moves up until in cervical vertebra 6 it originates from a level halfway up the neural canal. It also becomes slightly shorter posteriorly. The articular facet for the tuberculum of the rib is on the distal end of the transverse process, facing postero-laterally and somewhat ventrally. This facet is fairly small in all the cervical vertebrae, since the cervical ribs are small.

As can be seen from Table 1, the postzygapophyses are set at a fairly shallow angle to one another and are set fairly wide apart, though both figures become reduced posteriorly. Anteriorly the ventro-medial part of their surfaces are transversely convex, the dorso-lateral part being transversely concave, but by cervical vertebra 6 the whole surface has become almost flat. Both rotatory and dorso-ventral movements can take place between the cervical vertebrae and also between the last cervical vertebra and the first dorsal vertebra. Very little transverse movement can take place between the cervical vertebrae.

As can be seen from Table 1 and Fig. 11, the neural spines become higher and shorter posteriorly, and that of cervical vertebra 6 has a slight posterior inclination. Their dorsal ends are slightly expanded.

Dorsal Vertebrae

As discussed earlier, the exact number of dorsal vertebrae is uncertain; the remains of twenty - one are preserved, and it has been decided to assume that these represent the complete series.

Anterior dorsal vertebrae (Figs 11, 12C, G, K). Most of the progressive changes which were noted in the cervical vertebrae continue posteriorly into the dorsal vertebrae. The centrum continues to increase in length and its constriction becomes further reduced, but its height and width now become reduced. The centra of dorsal vertebrae 3 and 4 also have a small lateral foramen on each side.

The most important change which these vertebrae show is a progressive fusion of the diapophysis and parapophysis. The diapophysis increases in size and also extends higher up the side of the centrum. On the left side of dorsal vertebra 3 and on both sides of dorsal vertebra 4 it is continuous with the facet for the tuberculum, which has moved down the under side of the transverse process. This fusion can be seen to have gone a stage further in dorsal vertebra 5, which is badly preserved and shows few other features; the rib facet is elongated, sloping slightly upwards and backwards, and reaches to a level halfway up the side of the neural canal. This fusion of diapophysis and parapophysis is reflected in the rib-heads, the left rib belonging to dorsal vertebra 3 and both 4th dorsal ribs being single-headed, like the more posterior ribs.

Though the parapophysis has thus moved ventrally, fused with the diapophysis and become merely a part of a single facet on the centrum, the neural arches of dorsal vertebrae 3 and 4 (and, as will be seen shortly, of the more posterior dorsal vertebrae also) still bear a process arising from the level of the top of the neural canal and directed dorso-laterally and slightly posteriorly. This process has thus no connection with the bony attachment of the rib and, following Owen's (1866) nomenclature, it may from its position be called a metapophysis.

The postzygapophyses of dorsal vertebrae 1 and 2 are set at an acute angle to one another. Their faces are flat, and only dorso-ventral movement can occur between them. The postzygapophyses of dorsal vertebra 3 are at an acute angle to one another but are rounded, so that dorso-ventral or rotatory movements can take place at this point. The postzygapophyses of dorsal vertebra 4 are at a very shallow angle to one another but they are almost flat, and it seems likely that dorso-ventral or transverse movements could occur between this vertebra and dorsal vertebra 5, whose prezygapophyses are not preserved. The different characters of the postzygapophyses in this region, and thus of the movements which they permit, are rather unexpected. The fact that dorsal vertebrae 1-3 cannot rotate with respect to one another though they can do so, as a block, with respect to either cervical vertebra 6 or dorsal vertebra 4, may be connected with the fact that they have double-headed ribs, unlike the more posterior dorsal vertebrae. This in turn may be connected with the very short sternum, and it is possible that the ribs of dorsal vertebrae 1-3 were the only ones attached to the ossified sternum. This possibility is supported by the presence, in Professor Watson's collections, of several dicynodont sterna in which there is a separate facet for the attachment of each rib; in each case there are three pairs of such facets.

The neural spines of the anterior dorsal vertebrae slope posteriorly. That of the first is slightly thickened dorsally like those of the cervical vertebrae, but this is not the case in dorsal vertebra 3, which in lateral view is also more pointed than that of dorsal vertebra 1. The dorsal parts of the neural spines of dorsal vertebrae 2 and 4 are missing.

<u>Remainder of the Dorsal Vertebrae</u> (Figs 12D, H, L; 13B)

The dorsal vertebrae from block B were covered ventrally by a layer of matrix which was resistant to the action of acetic acid. As a result, the details of the centra of most of the vertebrae cannot be seen, and in many cases the head of the rib remains attached to the side of the centrum. Though the thickness of this layer of matrix is not very great, the exact outlines of the centra cannot be distinguished, and they have been indicated by dotted lines in Fig. 13B. On most of these vertebrae it has also been impossible to display the facets for the rib-head; it is clearest on the most posterior vertebrae, indications of its upper border can be seen in several others, and in the remainder its probable position is indicated by the rib-head, which is apposed to the side of the centrum.

The structure of the neural arches can be seen clearly. The metapophyses rise dorso-laterally from a position halfway along the neural arch; their ends and sides are smooth and rounded. The surfaces of the zygapophyses are flat in most of the series; anteriorly the postzygapophyses are set close together, as in the fourth dorsal vertebra from block A, and the prezygapophyses are quite flat and featureless, but in the last few vertebrae the postzygapophyses become more separate and face slightly laterally, and the prezygapophyses become wider and very slightly concave from side to side. The neural spines slope slightly backwards, and their dorsal ends are expanded. The only possible exception to this is the most anterior vertebra of block B; the dorsal end of its neural spine is missing, but the anterior and posterior margins of the spine converge, so that it is possible that it has a rather pointed end without an expansion, like that of dorsal vertebrae 2-4 from block A.

Sacral Vertebrae and Ribs (Figs 13C, 14, 20)

Four vertebrae have ribs with extensive bracing contacts with the pelvis. A fifth, more posterior, vertebra has ribs which, though slender, are directed antero-laterally, and the zygapophyses of this vertebra indicate that movement at this articulation was restricted to dorso-ventral; it is therefore considered that this vertebra and its ribs are sufficiently modified to be regarded as sacral, and the number of sacral vertebrae is thus five.

The ribs of all the sacral vertebrae are fused to the centra, the point of fusion being marked by a slight dilation and rugosity; their size decreases posteriorly. That of the first sacral vertebra is much larger than the others. It has an elongate cross-section, the long axis sloping upwards and forwards; its distal end is 2.5 cms. long. The postero-ventral end of this distal surface is convex and abuts against a projection on the inner side of the ilium, but the remainder of the distal end of the rib is concave, only the ventral and antero-dorsal edges of this region contacting the ilium. This concavity is continuous with the posterior surface of the rib midway along the dorsal edge of its distal end. Both the second and third sacral ribs have distal ends which are concave centrally; like the first, they contact the ilium. The distal end of the fourth sacral rib, however, is convex, and only its anterior half contacts the ilium. The posterior half of the distal end of the rib projects behind the ilium and its lower part contacts the antero-dorsal corner of the ischium, which bears a marked facet for its reception. The rib of the fifth sacral vertebra is much more slender than any of the preceding; it is directed antero-laterally, just contacting the posterior corner of the distal end of the fourth sacral rib, but apparently not contacting the ischium.

The measurements of the sacral vertebrae and ribs are given in Table 2.

The prezygapophyses of the first sacral vertebra are very wide (25 mm. across), and their surfaces are almost horizontal; the postzygapophyses of the last dorsal vertebra are similar, and both dorso-ventral and rotatory movements can take place at this articulation. The postzygapophyses of the first sacral vertebra, and the zygapophyses of the other sacral vertebrae,

Table 2 (Distances in millimetres)

Vertebra	Height	Height of neural spine above top of neural canal	Ventral length of centrum	Posterior width of centrum	Posterior height of centrum	Circumference of rib at narrowest point
Sacral 1	35.5	18	12.5	13	12	31
2	32	17	10	11	10.5	20
3	27	13	10.5	11.5	8.5	18
4	26	11	10	11	9	13
5	23	11	9.5	10.5	8	9
Caudal 1	c.21	10	8.5	10	8	8.5
2	c.20.5	9	8.5	10	8	-

are set close together with their surfaces at acute angles to the vertical, so that only dorso-ventral movements could take place at these articulations; the close appositions of the distal ends of the sacral ribs to one another, and their contacts with the pelvic girdle, make it unlikely that any considerable movement took place.

The neural spines of the sacral vertebrae are quite large and slope backwards; the anterior edge of the neural spine of the second sacral vertebra is missing. The distal ends of the neural spines are slightly expanded.

On the ventral side of the centrum of the second sacral vertebra is a pair of foramina which open into the ventral pit in the neural canal. The neural canal in transverse section has a dorso-ventrally flattened oval shape.

Caudal Vertebrae and Ribs (Figs 14, 20)

Only the first two caudal vertebrae are preserved. The neural spines of both are damaged, as are the ribs of the second. The zygapophyses are set at a shallow angle to one another, so that both dorso-ventral and rotatory movements can take place. The ribs of the first caudal vertebra are fused to the centrum; they are round and slender and extend postero-laterally. The measurements of these vertebrae and ribs are given in Table 2.

RIBS (Figs 15, 20)

The cervical ribs are present almost undamaged. Fairly long proximal portions of the anterior dorsal ribs were also preserved in block A, and shorter proximal portions of the more posterior dorsal ribs in block B. The sacral and anterior caudal ribs are preserved in block C.

Cervical ribs

No trace was found of an atlantal rib, though both may have disappeared with the atlas intercentrum. The remaining five cervical ribs are perfect except for the distal end of that belonging to the last, sixth, cervical vertebra. All are double-headed, the tuberculum in each case being the larger head. In no case is it possible to fit the vertebra and rib together so that both the rib-heads fit smoothly onto their facets on the vertebra, but a good fit can usually be obtained between the tuberculum and the transverse process. Together with the fact that the parapophysis is consistently larger than the capitulum, this suggests that there was a fair amount of cartilage between capitulum and parapophysis. Thus articulated, the ribs are orientated outwards, backwards and downwards.

None of the cervical ribs are large, the length and the circumference just distal to the junction of the two heads increasing steadily from that belonging to the axis, 1.6 cm. long and 7.5 cm. in circumference, to that belonging to cervical vertebra 6, which was probably about 4 cm. long and whose circumference is 14 mm.

The axis rib is quite straight and is flat in both dorso-ventral and lateral planes, but posteriorly the ribs gradually become more curved. A dorso-ventral curvature can be seen in the ribs belonging to cervical vertebrae 5 and 6. The ribs also progressively become more and more curved backwards, their posterior faces thus being somewhat concave, though this is not especially marked. The posterior surface of the ribs belonging to cervical vertebrae 5 and 6 also bear a longitudinal groove.

Dorsal Ribs

As can be seen (Fig. 15), there is a great increase in size between the last cervical and first dorsal ribs. The sizes of the capitulum and tuberculum similarly increase. On the first two dorsal ribs the two heads are still separate and, like those of the cervical ribs, they cannot be simultaneously fitted smoothly onto the transverse process and the parapophysis. The right and left ribs of dorsal vertebra 3 are not identical, the two heads having merged to form a single long head on the left side but still being separated by a small notch on the right side. Both ribs belonging to dorsal vertebra 4 are single-headed. The rib shafts are inclined slightly posteriorly relative to the proximal, rib-head, region.

The second, third and fourth dorsal ribs bear a longitudinal groove down their anterior faces. The dorso-ventral curvature of the third dorsal rib is less than that of the first two and the fourth. In view of the fact that, as mentioned when discussing the dorsal vertebrae, there is some evidence that only the first three dorsal ribs were attached to the sternum, this is surprising.

Only the proximal ends of the more posterior dorsal ribs are preserved. In all of them the rib tapers proximally to a single rounded head, which in most cases was apposed to the side of the centrum of the vertebra.

PECTORAL GIRDLE

The pectoral girdle was extremely well preserved, the left scapula (apart from its antero-dorsal corner) and coracoid plate being undamaged, as are the clavicles and interclavicle. The posterior edge of the sternum is missing and its ventral surface is eroded. The girdle was preserved in position around the anterior vertebrae and ribs and the original relationships of the different elements were only slightly disturbed.

Cleithrum

The above facts, together with the facts that the left scapula was originally completely covered with matrix, that the scapula bears no facet for the cleithrum, and that no cleithrum was found preserved, make it extremely probable that Kingoria did not possess a cleithrum rather than that this absence is a post-mortem condition.

Clavicle (Figs 16E, F, 17A, B, C)

The two clavicles were preserved in attachment to the scapulae and interclavicle. It has not been possible to detach them from the latter and, in view of a slight asymmetry of the two clavicles, these three bones have been figured in articulation as preserved.

The clavicle is of rather complex shape. Its dorsal part, which contacts the acromion process of the scapula, runs backwards and slightly outwards relative to the rest of the clavicle, in side view there being an angle of almost 90° between the two parts of the bone. The dorsal part tapers to a bluntly rounded point and overlaps the inner side of the acromion process of the scapula. The outer surface of this region bears a longitudinal groove, which enlarges anteriorly to form a large hollow area on the posterior surface of the region of junction of the two parts of the clavicle. Beyond this region of junction the clavicle runs medially and slightly postero-ventrally. Initially it is rather slender and of almost round cross-section, but it soon commences to flatten dorso-ventrally and to expand antero-posteriorly. Its medial end is thus of dorso-ventrally flattened spatulate shape, underlying the anterior border of the interclavicle. The medial ends of the two clavicles also curve slightly ventrally, so that they diverge from the median anterior border of the interclavicle and contact one another, their ends being smoothly curved in ventral view.

Interclavicle (Figs 16E, F, 17A, B, C)

The interclavicle is of roughly triangular shape. Its surface is difficult to clean and was probably cartilaginous, and it is therefore difficult to distinguish its antero-lateral corners from the postero-dorsal surfaces of the clavicles, to which it applied. Its posterior corner is bluntly rounded. The maximum thickness of the interclavicle is about 2.5 mm., this being in the midline; it becomes slightly thinner on either side of this, its ventral surface therefore being slightly convex from side to side. The whole bone is also slightly curved backwards and upwards in the plane of the midline, its dorsal and ventral surfaces therefore being respectively slightly concave and slightly convex in this plane.

Sternum (Fig. 17D, E)

The more or less hexagonal sternum was preserved just posterior to the posterior end of the interclavicle and at a slightly more dorsal level. Its posterior border is damaged; the preserved borders are rounded. Unfortunately most of its ventral surface is eroded away; the surface as preserved is slightly convex from side to side, and the remnants of the original surface give the impression that this was also true of this surface. The dorsal surface is slightly concave from side to side; near the lateral corner of the sternum it is raised into a pair of bosses, which probably represent the anterior limit of the area of attachment of ribs to the bony sternum.

Scapula (Fig. 18)

The scapula consists of a rather narrow dorsal blade springing from one corner of a roughly quadrilateral stout ventral region. In anterior or posterior view the whole scapula is curved, its outer surface being convex and its inner surface concave to follow the curvature of the rib-cage.

The scapular blade in lateral view progressively expands dorsally from a rather narrow origin from the ventral part of the scapula. Its posterior edge is almost straight and is slightly flattened. At the postero-dorsal corner is a slightly rugose low thickening. The dorsal border is rounded; the antero-dorsal corner of the blade is damaged. From the region of junction of the blade with the ventral body of the bone originates the acromion process, a stout process curving outwards and forwards to a blunt end. From the dorsal surface of the acromion process arises a very marked scapular spine. Near this ventral origin the spine is a stout lamina of bone, about 6 mm. high, tapering to a fairly sharp edge. It curves round antero-dorsally to parallel the anterior edge of the scapular blade and follows this edge dorsally, gradually decreasing in height, its anterior surface being continuous with the anterior edge of the scapular blade. Just posterior to this spine the outer surface of the scapular blade is slightly concave; ventrally this concavity reaches to the posterior edge of the blade, but more dorsally it first merges into a slightly convex area. The inner surface of the scapular blade is convex ventrally, near its narrow origin from the ventral body of the bone. More dorsally, a low convex ridge runs up parallel to, but a short distance from, the anterior edge of the blade; posterior to this ridge the inner surface of the blade is slightly concave.

The ventral body of the scapula is roughly quadrilateral in shape. Its anterior ventral edge is interrupted by a notch, the coracoid foramen being bordered partly by the scapula and partly by the precoracoid. On either side of the coracoid foramen the antero-ventral edge of the body of the scapula therefore bears facets for the precoracoid, the more anterior facet being the smaller. The ventral corner of the body of the scapula bears a convex area for the attachment of the coracoid bone. Its postero-ventral edge forms the scapular contribution to the glenoid facet. Its postero-dorsal edge is a short rounded area above the slightly overhanging dorsal lip of the glenoid. The scapular blade rises from the dorsal corner of the body of the scapula. The antero-dorsal edge of the latter is a rather thin rounded edge. The outer surface of the body of the scapula bears a slight hollow just below the acromion process; the inner surface is irregular in contour, but has a fairly deep depression just by the inner end of the coracoid foramen.

Coracoid Plate (Fig. 16A-D)

The coracoid and precoracoid are tightly joined together, though the line of junction can be distinguished. The two bones are joined at a slight angle to one another, so that the inner surface and outer surface of the whole coracoid plate are respectively concave and convex along the antero-posterior plane. The whole coracoid plate also tapers from its outer edge to its inner edge.

The precoracoid is the smaller element and takes no part in the formation of the glenoid. It has roughly the shape of a right-angled triangle, the rounded longest edge being the anterior part of the medial edge of the coracoid plate. The dorsal edge is interrupted by a notch, this being part of the border of the coracoid foramen. On either side of this notch the precoracoid has a facet for the scapula, the more anterior being the smaller. The third edge of the precoracoid is attached to the coracoid.

Immediately lateral to its line of junction with the precoracoid, the coracoid is enlarged to form two articular surfaces at a slight convex angle to one another. The smaller, more anterior, of these articular facets is for the scapula; it is at a slight concave angle to the similar, but smaller, neighbouring facet on the precoracoid. The larger, more posterior, of the articular facets on the coracoid is the coracoid contribution to the glenoid; it is roughly shield-shaped in outline and is slightly convex from side to side. The enlarged articular area of the coracoid projects slightly from the lateral edge of the bone. Ventral to it, the lateral edge is flattened; it meets the rounded, convexly curved, medial edge at a rounded point.

HUMERUS (Fig. 19)

Only the proximal ends of the humeri were preserved, the fragment of the right humerus being rather more extensive than that of the left.

The glenoid head faces proximo-dorsally, and its dorsal edge projects above the general dorsal surface of the bone. From about halfway along this dorsal projection arises a ridge which extends distally and somewhat posteriorly. This ridge is the "dorsal antero-ventral line" of Romer (1922), and its presence causes the dorsal surface of the humerus to be convex from side to side.

The glenoid head merges posteriorly into the strong projecting proximal posterior corner of the humerus, which has a similar rounded proximal face. In ventral view, this corner is continued distally into a strong thickening running down the posterior edge of the humerus. Anterior to this thickening, the bone is concave from side to side, rising anteriorly to the delto-pectoral crest. Near the distal end of this ventral surface is a crescentic ridge, the line of which marks a sudden, though slight, thickening of the bone, the concavity of the crescent thus being at a slightly lower level than the bone distal to the crescent. The posterior end of the crescent extends onto the ridge already mentioned which runs down the posterior part of the humerus.

The delto-pectoral crest rises proximally from the anterior end of the glenoid head and runs in a convex curve anteriorly and distally to form the anterior edge of the bone; it has a fairly thick, rounded, edge.

PELVIC GIRDLE (Figs 20, 21A, B, C, D)

The two halves of the pelvic girdle were preserved in articulation with the sacral vertebrae. The left side of the girdle has been badly weathered, but the right side appears to be almost undamaged. Its posterior border is not covered with perichondral bone, but this may be due to tendons having inserted on this edge; the edge is dotted in the figures.

There is no sign of any symphysis between the two halves of the girdle, and their orientation, almost parallel with the vertebral column, would render a transverse connection between their ventral edges so close to the vertebral column as to be anatomically unlikely. The orientation of the girdle is due to the pubis and ischium being posterior to the ilium, the junction between the pubo-ischiadic plate and the ilium being almost vertical. This junction is not a sutural union, the surfaces of the bones being smooth, and the ilium readily separates from the other two bones. Combined with the fact that the junction is almost straight, this suggests that there may have been movement between the ilium and the pubo-ischiadic plate during life.

The small pubis is joined to the ischium by a tight suture. The large obturator foramen runs between the two bones and is directed posteriorly and slightly ventro-laterally; it is 4 mm. wide and 8 mm. high.

Ilium

In lateral view the ilium is more or less triangular in shape. It has a straight edge which contacts the pubo-ischiadic plate, and from this it tapers anteriorly to a rounded point. The bone can in effect be divided into two regions. The strong postero-ventral region contains, externally, part of the acetabulum and its raised borders and, internally, the facets for the sacral ribs. From this strong region tapers the antero-dorsal region, the blade of the ilium, which has a more or less straight ventral rounded border, a thickened anterior corner, and a rather sharp convex dorsal border; in dorsal view it is also slightly curved forwards and laterally.

The acetabulum is quite deeply sunken in the postero-ventral region; its anterior border has a particularly strong and rounded projection, from which a ridge runs anteriorly along the surface of the iliac blade. The ventral edge of the ilium ventral to the acetabulum is strong and rounded; in ventral view this can be seen to continue anteriorly to a strong internal projection. This projection abuts against the posterior end of the very large first sacral rib, and from it the facets for the other sacral ribs run in a line posteriorly and slightly dorsally, to the postero-dorsal corner of the ilium. Anteriorly from the projection the first sacral rib runs along the whole ventral part of the internal surface of the iliac blade.

Ischium

This forms the largest part of the pubo-ischiadic plate, and forms the postero-dorsal section of the acetabulum and the dorsal border of the obturator foramen. The antero-dorsal corner of the ischium is thick, externally forming the strong rounded border of the acetabulum (a small part of this border is damaged), and internally forming another strong rounded ridge which runs to the postero-dorsal corner of the ilium. This latter ridge ends in a facet, directed anteriorly and internally, against which articulated the posterior half of the fourth sacral rib.

From this thick antero-dorsal corner of the ischium there runs posteriorly a ridge which forms the dorsal border of the bone. This is met, at an obtuse angle, by the posterior border of the bone; the actual corner is slightly damaged. The posterior border is rather wide, flattened, and roughened; it descends ventrally in a convex curve and then turns forwards to meet the posterior border of the pubis at nearly a right-angle. The whole postero-ventral region of the ischium is, dorso-ventrally, slightly convex externally and slightly concave internally, so that its rather thin ventral border is directed somewhat inwards.

Pubis

This is quadrangular in shape, and forms the postero-ventral region of the acetabulum and the ventral border of the obturator foramen. Anteriorly and ventrally it is strong, and its ventral border is thick and rounded. Externally, its postero-ventral surface is damaged.

FEMUR (Fig. 21E, F, G)

Only a small portion of the head of the femur was preserved, in the acetabulum. It is sufficient to show that the femur had a quite well-developed lateral condyle, but no more.

4. THE TAXONOMIC POSITION OF KINGORIA

In the following discussion, Kingoria is compared with all other forms of Permian dicynodont. Since no formal taxonomic diagnosis has hitherto been given for a dicynodont genus, the points available for comparison are inevitably few in number, and characters have been used which, were more known in the genus about the allometric changes during growth, might prove to be unreliable. In several cases, differences in the sizes of the skull have been mentioned; this is subject to change during life, but ten skulls of Kingoria are now known, the lengths of all of them lying between 140 and 200 mm., suggesting that this is the normal order of size of the skull of the adult of this genus.

Kingoria may be distinguished from a large number of dicynodonts by its lack of post-canine teeth. Of the remaining genera, Kannemeyeria and Lystrosaurus are easily distinguished from Kingoria by the whole structure of these very distinctive forms. The fragmentary form Haughtoniana is much larger than Kingoria, its occiput being 405 mm. across. Dinanomodon (skull length 640 - 760 mm.) is also much larger than Kingoria and has a very narrow intertemporal bar wholly covered by the postorbitals. Eocyclops, Pelorocyclops, Platycyclops, Platypodosaurus and Rhachiocephalus are much larger than Kingoria, their skull lengths ranging from 420 mm. to 730 mm., and these genera possess a pineal boss. Neomegacyclops (skull length 500 - 540 mm.) is also much larger than Kingoria and possesses a pineal boss, and it has a wide concave exposure of the parietals in the intertemporal bar. This last character is also possessed by Aulacephalodon and Pelanomodon; both are larger than Kingoria (skull lengths of Aulacephalodon 320 - 510 mm., of

Pelanomodon 230 - 290 mm.), and *Pelanomodon* also has a laterally expanded squamosal and has bosses on the nasals, prefrontals and post-orbital bars. *Oudenodon* differs from *Kingoria* in having a wide concave exposure of the parietals in the intertemporal bar and in possessing a pair of stout rounded anterior ridges on the premaxillary secondary palate. (These ridges are also found in *Aulacephalodon*, *Pelanomodon*, *Neomegacyclops*, *Lystrosaurus*, *Kannemeyeria* and several species of *Dicynodon*). Its palate also differs in that the palatine forms a large postero-lateral extension of the secondary palate and has a large contact with the premaxilla, whereas in *Kingoria* the palatine does not form part of the secondary palate and has only a short contact with the premaxilla. The genera *Chelyrhynchus*, *Digalodon*, *Diictodon*, *Emydorhinus*, *Emydorhynchus*, *Eosimops*, *Myosaurus*, *Myosauroides* and *Palemydops* may be distinguished from Kingoria by their extremely wide intertemporal bar, which includes a wide concave exposure of the parietals. *Aulacocephalus* is too poorly known for it to be possible to compare it with *Kingoria*.

Dicynodontoides (Broom, 1938) is similar to *Kingoria* in its size (skull length c. 220 mm.), and in having an intertemporal bar narrower than its interorbital bar. In addition, it is similar to it in that the intertemporal bar has a swelling partway along its length, and in that the postorbital covers a large part of the sides of the bar, and also in that the snout is wide. However, it differs in that the postorbitals nearly meet in front of the pineal foramen, so that the exposure of the preparietal is extremely narrow; in that the postfrontals are present and very large; and in that the front of the mandible is broad and much flattened. It remains possible that the genera *Dicynodontoides* and *Kingoria* are related but, without knowledge of the palate, lower jaw, or post-cranial skeleton of Dicynodontoides, it is impossible to be sure.

The only other genus is Dicynodon itself, which has been generally treated as a repository for all "normal" postcanine-less dicynodonts. "Normal" in effect here merely means that the form under consideration has a skull whose intertemporal bar is neither very wide nor very narrow, which does not have a pineal boss, and which has a preparietal bone which borders only the anterior part of the pineal foramen. The skull may be from 50 mm. to 550 mm. in length, tusked or tuskless, and may be from the Tapinocephalus zone, Endothiodon zone, Cistecephalus zone or (rarely) the Lystrosaurus zone. The genus Dicynodon therefore contains within its large assemblage of species such a wide variety of skull sizes, shapes and patterns, that it is impossible to find any characters which will serve to distinguish all of them from Kingoria, except for three characters which thus stand as the only characters which are independently sufficient to diagnose the genus Kingoria. These three characters are the structure of the palate, of the lower jaw and of the sacrum, and they will now be examined in detail.

The palate of Kingoria is unlike that of any other known dicynodont. In most genera the anterior ramus of the pterygoid meets the palatine and ectopterygoid; the palatine is the larger of these two, and in many genera aids in the formation of the secondary palate, having an extensive contact with the premaxilla, while the ectopterygoid is smaller and often displaced laterally. In Kingoria, however, the ectopterygoid forms nearly the whole of the anterior continuation of the anterior ramus of the pterygoid, the palatine forming only the walls and roof of the internal nares; the palatine forms no part of the secondary palate and has only a short contact with the premaxilla.

The anterior end of the lower jaw, which tapers to a blunt point, has a shape quite unlike that commonly found in the dicynodonts, which normally have an extensive sharp transverse cutting edge paralleling the anterior end of the palate. A third type of lower jaw is known, that of the endothiodonts tapering anteriorly to a sharp point which fits into a median notch in the upper jaw, but this is equally distinct from that of Kingoria. The palate of Kingoria is unusual in that it does not possess the stout rounded anterior palatal ridges which are found in many dicynodont genera, and this may reasonably be correlated with the unusual nature of the lower jaw.

The other feature in which Kingoria is unlike any other known dicynodont is the character of the pelvis. In the Dicynodontia, and in primitive synapsids as a whole, the pelvis in side view is usually rather dumb-bell-shaped, having a narrow "neck" in which lies the acetabulum, the ilium extending above this to meet the sacral ribs and the pubis and ischium expanding ventrally. In Kingoria there is no central constriction; the ilium extends antero-dorsally from the acetabulum and the pubis and ischium extend posteriorly from it; and the antero-dorsal corner of the ischium contacts the fourth sacral rib.

The above three characters are thus, as far as is known, all absolutely diagnostic of Kingoria. However, the genus Dicynodon contains a very large number of species, which come from widely separated parts of the world (South and East Africa, Scotland, Russia and China), and in many of these species neither the palate nor the lower jaw nor the sacrum are known. All that is known in these species is a short description of the skull and a figure of the dorsal aspect of the skull, and the distinction between Kingoria and these species therefore rests upon this information. Fortunately, Kingoria is unusual in that the breadth of the interorbital bar is much greater than the breadth of the intertemporal bar, and the great majority of the species of Dicynodon may therefore, on this basis, be excluded from the genus Kingoria. However, a few species remain. Of these, D.whaitsi (Broom, 1913) differs from Kingoria in that it is very much larger (skull length 530 mm.) and has postfrontal bones; D.ingens (Broom, 1907) possesses the stout paired anterior palatal ridges which are absent in Kingoria; D.clarencei (Broom, 1950) and D.dutoiti (Broom & Schepers, 1937) differ in possessing postfrontal bones; and D.howardi (Broom, 1948) differs in its extremely long narrow skull and snout. It cannot be said that the reasons given for excluding these species from Kingoria are definitive; all that can be said is that the small amount of information available does show some points of difference from Kingoria.

The only other species of Dicynodon in which the published information suggests that it might be similar to Kingoria is D.galecephalus from the Cistecephalus zone of South Africa. In their account of this species, Broom & Robinson (1948) both figure and describe a strong lateral wing running along the upper edge of the lateral side of the posterior part of the dentary. The skull is also similar to that of Kingoria nowacki in that the interorbital breadth (23 - 24 mm.) is greater than the breadth of the intertemporal bar (20 mm.), in that there are apparently no postfrontal bones, and in that the parietals extend far back behind the dorsal apex of the occiput. These features were so suggestive of relationship to *Kingoria* that further information on this species was sought from Dr. Brink of the Bernard Price Institute for Palaeontological Research, Johannesburg. Dr. Brink was kind enough to have the type skull sent to England, and examination of it immediately showed that it belongs to the genus *Kingoria*, since it possesses the tapering anterior end to the dentary that is characteristic of that genus. The skull is smaller than those of *K.nowacki*, its probable original length being about 115 mm., the width of the interorbital bar is closer to the width of the intertemporal bar than in *K.nowacki*, and the preparietal is pointed anteriorly, unlike that of *K.nowacki*. Though the skull is too badly damaged and distorted for it to be possible to compare it in detail with that of *Kingoria nowacki*, the above features are sufficient to show that it is probably a different species, and it is therefore transferred to the genus *Kingoria* as *Kingoria galecephalus* (Broom & Robinson).

Little can be said of the relationship of *Kingoria* to the other genera. It is presumably more closely related to the other forms which do not bear post-canine teeth, though parallel evolution and loss of these teeth may well have occurred in the Dicynodontia. Both the lower jaw and the pelvis of *Kingoria* are quite unlike that of any other dicynodont, and no intermediate forms are known. Its palate is also distinct, but can be compared with that of other dicynodonts as Toerien (1954a) has outlined a possible scheme of relationship of the main palatal types. In its large ectopterygoid and lack of a contact between the premaxilla and the palatine, *Kingoria* appears to be primitive, though rather specialised in the great enlargement of the ectopterygoid and the confinement of the palatine to the walls and roof of the internal nares. Of the dicynodonts which do not bear post-canine teeth, Dicynodon is similar in its lack of a contact between the premaxilla and the palatine; in most other genera these bones have an extensive contact and the palatine forms a portion of the secondary palate. Kingoria may be derived from an early form of Dicynodon, in which the stout, paired, anterior palatal ridges of the latter genus had not developed. However, Kingoria is from a level which appears to be equivalent to the Cistecephalus zone of South Africa, while the earliest forms of Dicynodon are from the Lower Tapinocephalus zone; in the absence of any intermediate forms from the Endothiodon zone, suggestions as to the relationship of the very aberrant genus Kingoria must remain tentative.

5. THE ANATOMY OF KINGORIA

In the course of the investigation of the osteology of *Kingoria* various points of interest have appeared, which will now be discussed in detail.

A. Tympanic Process

The most novel and interesting character found in the skull of *Kingoria nowacki* is the well developed process extending posteriorly from the distal end of the paroccipital process, and which has provisionally been referred to earlier as the tympanic process. Its position, in the ventro-lateral portion of the occiput, is such that three possible functions for the process suggest themselves: that it was connected with the occipital musculature, with the jaw-opening musculature, or with the support of the tympanic membrane. These three possibilities will now be considered.

In attempting to reconstruct the muscle systems of *Kingoria*, use has been made of both direct and indirect evidence. The direct evidence results from a study of the skull and the anterior cervical vertebrae, the indirect results from a survey of the muscle complexes reported in modern reptiles and primitive mammals.[1]

Throughout the course of the reconstruction, both the mechanical effectiveness of the individual muscles and the functional competence of the whole system of muscles and articulating vertebrae and condyles have

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[1] FOOTNOTE: Attention has been paid to the following: *Sphenodon* (Osawa, 1898; Nishi, 1916; Vallois, 1922; Byerly, 1926); *Varanus* (Nishi, 1916); *Lacerta* (Vallois, 1922); *Iguana* (Mivart, 1867); *Chamaeleon* (Mivart, 1870); *Platydactylus* (Sanders, 1870); *Liolepis* (Sanders, 1872); *Phrynosoma* (Sanders, 1874); Crocodilia (Vallois, 1922); Monotremata (Mivart, 1866; Coues, 1871; McKay, 1895; Vallois, 1922); *Didelphys* (Coues, 1872); Insectivora (Dobson, 1882-1890); *Felis* (Reighard & Jennings, 1935); *Canis* (Vallois, 1922); Rodentia (Parsons, 1894, 1896).

been considered. Since the dicynodont head is peculiarly specialised, consideration has simultaneously been given to the likely arrangement of the muscles in theriodonts, which are usually considered to be more closely allied to the mammal ancestor than are the dicynodonts.

The Occipital Musculature

Some clues as to the siting of the occipital muscles have been obtained from the depressions and ridges that can be seen on the occiput itself. On some areas of the occiput it is possible to see scarred areas which apparently represent the points of attachment of muscles but, even with this additional evidence, it is impossible to come to any final conclusion, as the character of impression that a muscle leaves on a bone is very variable, mainly according to whether the insertion of the muscle is fleshy or tendinous. Where it is fleshy the bone may bear no indication of attachment; lack of surface marking does thus not indicate that no muscles were inserted in a given area. Where the insertion is tendinous, the bone may be roughened and raised into ridges; the insertion may be wholly tendinous, thus tending to raise a small protuberance on the bone, or it may consist of a tendinous sheath round a fleshy "core", in which case it will tend to produce a ridge delimiting the area of insertion.

It is, therefore, next necessary to turn to the muscle complexes of living reptiles and mammals in order to try to derive some idea as to what might be expected to be the condition in an intermediate form such as <u>Kingoria</u>. As will be seen, little difficulty is experienced with most muscles, complications arising only in the case of those concerned with the actual modifications that mammals have made. Since these changes in the muscle complex have been accompanied by changes in the morphology of the atlas-axis complex, further direct evidence as to the condition in Kingoria was available from a study of these vertebrae.

The Occipital Musculature of Kingoria. (The probable points of insertion of these muscles are shown in Fig. 23).

Certain muscles which are common to nearly all amniotes can be assumed to have been closely similar in position in Kingoria. These are as follows.

The most superficial muscle attached to the amniote skull is the trapezius, which runs from both the occiput and the vertebral column to the pectoral girdle. Its insertion on the skull would be expected to be peripheral, dorsally from the ventral surface of the backwardly-projecting margin of the squamosal, and more ventro-laterally from the posterior surface of the ventral, occipital, wing of the squamosal. The more ventro-lateral part of the trapezius, running to the clavicle, tends to become a discrete muscle, the cleido-occipitalis. There is no direct evidence of the attachments of this muscle on either the skull or the girdle, but it seems quite likely that its origin was from the more lateral, posteriorly-directed, part of the clavicle, and its insertion on the dorsal part of the ventral, occipital, wing of the squamosal.

Normally, the muscle inserted under the trapezius in amniotes is the longissimus capitis, which originates from the transverse processes of the cervical vertebrae. These transverse processes are quite stout in Kingoria, and the muscle probably inserted on the tabular and interparietal, along the dorso-lateral part of the occiput.

Below the longissimus capitis in amniotes is usually inserted the transverso-spinalis capitis (or semispinalis capitis) muscle, which originates from the bases of the spines and prezygapophyses of the cervical vertebrae. There is no direct evidence of this muscle on the cervical vertebrae, but it would be expected to be inserted dorso-laterally on the occiput, just under the longissimus capitis.

Also belonging to the transverso-spinalis system are the suboccipitalis muscles (obliquus capitis, and rectus capitis dorsalis and lateralis), which run between the occiput and the first two vertebrae. The rectus capitis dorsalis major in both reptiles and mammals originates from the dorsal edge of the axis spine and inserts on the dorsal part of the occiput, near the midline. Inserting just ventral to it is the rectus capitis dorsalis minor, whose origin is in <u>Varanus</u> from the anterior edge of the axis spine, in <u>Sphenodon</u> from the dorsal arch of the atlas in addition, and in mammals from the latter alone; it seems likely that in <u>Kingoria</u> it originated from the large dorsal surfaces of the atlas arches.

The remaining rectus capitis lateralis and obliquus capitis muscles are not as readily capable of restoration, because the transition from reptiles to mammals has involved changes in them and the form of the atlas vertebra. In various reptiles (e.g. <u>Sphenodon</u>, <u>Crocodilus</u>, <u>Diadectes</u>, Pelycosauria) the atlas consists of three elements (a pair of neural arches and an intercentrum) and this therefore seems to be the primitive condition. A large obliquus capitis magnus muscle runs to the paroccipital process from the lateral surface of the axis spine and the dorsal surface of the atlas arch and, in addition, there may also be an obliquus capitis inferior (<u>Sphenodon</u> and <u>Varanus</u>, Nishi, 1916) running from the dorsal surface of the axis arch to the atlas postzygapophysis, and an obliquus capitis superior

(Varanus, Nishi, 1916) running from the atlas postzygapophysis to the occiput. In mammals the three elements of the atlas are co-ossified into a ring, within which the odontoid peg of the axis rotates, and the atlas has developed a large transverse process. The obliquus capitis inferior muscle is attached to the axis spine and runs to the dorsal surface of the atlas transverse process, to the ventral surface of which are attached the obliquus capitis superior and a rectus capitis lateralis, both running to the occiput.

The transition between these two conditions has given some trouble to Evans (1939), who was unable to distinguish in Varanus the obliquus capitis inferior and superior reported by Nishi. He states that "apparently they are simply differentiations of the obliquus capitis magnus muscle mass" (1939, p.91), and therefore suggests that the obliquus capitis superior and inferior have come into being because the atlas transverse process has enlarged and interpolated itself into the obliquus capitis magnus, subdividing it into these two muscles, but he gives no clear reason for this intrusion of the atlas transverse process. However, an unusually large specimen of Varanus niloticus in the Museum at Cambridge shows clear traces of the insertion of muscles in the region of the atlas postzygapophysis, whose lateral surface bears a very well marked ridge of bone directed posteriorly and slightly dorsally. (In any case, the atlas of Varanus is unusual in that it is a single ring-like ossification fitting over the anterior end of the axis odontoid, and the musculature of this region is therefore unlikely to be representative of that from which the mammals evolved).

This ridge found in Varanus may be compared with the backwardly-directed spine external to the atlas postzygapophyses which Romer & Price (1940) mention on p.108 and figure in Ophiacodon (Fig. 44) and Dimetrodon (Plate 23).

This region of the atlas shows a similar projection in Kingoria (Fig. 10, n.sp), in which it is stouter and more laterally directed than in the above-mentioned pelycosaurs. It seems likely that this process represents the neural spine, which is also double in Seymouria (White, 1939), and that it was the point of attachment of the obliquus capitis superior and inferior. The identification of this process as the neural spine explains the presence of these muscles, since they would originally have been part of the normal series of interspinalis muscles which connect the neural spines of the more posterior vertebrae.

Though it thus seems likely that Kingoria possessed muscles homologous with the obliquus capitis superior and inferior of mammals, the size of the atlas neural spine does not suggest that these muscles were alone responsible for movement of the skull on the atlas-axis complex. An obliquus capitis magnus muscle was probably also present, as might in any case be expected in a Permian reptile. This would have originated, in the usual manner, from the large axis spine; its insertion was probably in the well marked hollow on the occiput ventral to the post-temporal fossa and dorsal to the tympanic process, and the skull of Kingoria shows marks of muscle-insertion in this area. Such an insertion of this muscle, on the paroccipital process, is found in both Varanus and Sphenodon (Nishi, 1916). The obliquus capitis magnus would thus run close to the atlas neural spine; the obliquus capitis superior would be running from this structure to the occiput and, since the occiput shows no trace of a separate insertion of the latter muscle, it seems quite possible that it inserted close to the obliquus capitis magnus, probably somewhat ventro-medial to it.

Kingoria thus appears to have possessed both the obliquus capitis magnus, which is not found in mammals, and the obliquus capitis superior and inferior, which are today well developed only in the mammals. However, in them the obliquus capitis superior and inferior are attached to the atlas transverse process, whereas reasons have above been adduced for believing that in Kingoria they were attached to the atlas neural spine, a structure not represented in mammals. This has two consequences.

Firstly, if the well developed transverse process in Kingoria did not serve for the attachment of the obliquus capitis superior and inferior, it is necessary to give some other reason for its presence. The fact that Kingoria is mammal-like in apparently possessing well developed obliquus capitis superior and inferior muscles suggests that it may also have been mammal-like in possessing a rectus capitis lateralis, originating from the atlas transverse process (as in mammals); the insertion of this muscle would probably have been near the junction of the paroccipital process and the lateral edge of the basioccipital tubera, since there is a pronounced rugosity at this point.

Secondly, the apparently different attachments of the obliquus capitis superior and inferior, to the atlas neural spine in Kingoria but to the atlas transverse process in the mammals, implies that, in the line leading to the mammals, the neural spine and the transverse process of the atlas have become fused. Such a change is very likely to have occurred if the muscles, and thus the processes themselves, became larger. When the atlas had attained the unitary ring-like structure found in mammals, such an enlargement is likely to have taken place in order to take advantage of the more extensive rotatory movements that this structure permits at the cranio-vertebral joint, and the enlargement of these muscles would presumably have been accompanied by the reduction of the reptilian obliquus capitis magnus muscle, the additional presence of which would no longer be necessary.

The above discussion has covered all the muscles which are likely to have been present inserting on the occiput of Kingoria, and none of them appear to have been concerned with the tympanic process. The rectus capitis lateralis, which originates from the transverse process of the atlas, is the only muscle which could reasonably be suspected of having been inserted on this process, but its insertion in this position appears unlikely in view of the following considerations. Insertion on such a posterior projection from the occiput would significantly reduce the length, and so the range of action, of the muscle; in any case, the tympanic process is directed backwards and not towards the transverse process of the atlas. Conversely, it seems unlikely that the tympanic process represents the point of insertion of a ligament restricting movement between the atlas and the occiput, since there are no signs of tendinous insertion on the tympanic process, and the atlas transverse process is larger than would be expected if it were merely the point of origin of a tendon.

The Occipital Musculature of Theriodonts. During the course of this investigation attention was paid to the conditions of the occiput and atlas-axis complex in the gorgonopsids and cynodonts. In the unidentified gorgonopsid FRP 17, consisting of the braincase, proatlas and atlas arch, the atlas neural arch possesses a well developed neural spine and transverse process, both having similar orientations to those in Kingoria. A well developed atlas neural spine can also be seen in Brink & Kitching's figure of the cervical vertebrae of Prorubidgea robusta (Brink & Kitching, 1954).

In another unidentified gorgonopsid (FRP 142B) the atlas neural spine and the transverse process appear to have been compressed post-mortem, so that they are directed more posteriorly; the axis spine is larger than that of Kingoria, suggesting that a large obliquus capitis magnus may have been present. It is also primitive in that the atlas intercentrum was large and was not sutured to the axis, it thus being unmodified from the pelycosaur condition in this character.

The specimen of the cynodont Galesaurus planiceps described and figured by Parrington (1934) was also available for study. Here the atlas neural spine is poorly developed and not very distinct from the rest of the neural arch, and the obliquus capitis system may therefore have been reptilian, with a large obliquus capitis magnus.

The axis neural spine is unfortunately broken in Parrington's specimen, which he figures (1934, Fig. 3); the anterior margin of the spine is also broken, and Evans' reconstruction (1939), which takes the anterior margin of Parrington's figure to represent the true edge, is in error in this point. Seeley (1895b) has figured the axis of Cynognathus crateronotus; this is damaged, but sufficient of the dorsal edge remains for it to be possible to make a fairly accurate restoration. The spine appears to have been very large, being extended both dorsally and antero-posteriorly, and it is therefore quite consistent with the idea that there was a large obliquus capitis magnus muscle. Evans, however, restores Galesaurus with obliquus capitis superior and inferior muscles attached to the atlas transverse process, but this process is no different from those of the succeeding cervical vertebrae and is not, in either position or orientation, well suited for the attachment of such muscles, for its major faces are directed postero-ventro-medially and antero-laterally. It might, however, have served as attachment for a rectus capitis lateralis muscle. The atlas-axis is more advanced than that of the gorgonopsid in that the atlas centrum is firmly fused to the axis centrum (despite Evans, 1939, p.68), and the atlas intercentrum is reduced.

The size of the axis spine, the lack of development of the atlas neural spine and the condition of the atlas transverse process thus all lead one to suppose that the neck musculature of Galesaurus was of reptilian type. However, Brink has recently (1956) figured the atlas-axis of Diademodon; he shows it with a well developed atlas transverse process and restores a distinct atlas neural spine, so it seems possible that modifications of the atlas-axis complex occurred also in the cynodont line.

Summary. The attachments and courses of the occipital muscles which have above been suggested in Kingoria and shown to be consistent with conditions in theriodonts, are inevitably somewhat tentative, since the bony structures give only slight hints of the soft-part anatomy, and no close relative of the dicynodonts exists today. All that can be stated is that, so far as can be seen, the above reconstruction fits all the facts known to the writer, and also provides a functional intermediate between the reptilian and the mammalian conditions. As thus restored, the occipital musculature does not show any association with the tympanic process or supply any functional explanation for this process. Furthermore, such a bony protuberance, if concerned with muscular insertion, would normally be indicative of a localised attachment, which would be likely to be tendinous, yet the surface of the tympanic process is smooth and devoid of any indication of tendinous attachment.

The Jaw Musculature

The jaw muscles which are generally agreed to be present in the Reptilia are the capiti-mandibularis muscle mass and the pterygoideus muscles. The capiti-mandibularis muscle mass is usually considered to be divided into temporalis and masseter components, though various writers have stated that it is often difficult completely to separate the two components (e.g. Adams, 1919; Becht, 1952).

The deep groove on the prootic, which is discussed in a later section and shown to lodge the vena capitis dorsalis, presumably served to protect that vein from muscular action; this, and the manner in which the parietal and post-orbital parts of the inter-temporal bar overhang the temporal vacuity, both suggest that the temporalis muscle originated from a large part of the posterior and medial walls of the vacuity. It is probable that parts of it also originated from the anterior surface of the quadratojugal and the ventral, occipital, wing of the squamosal, and possibly also from the posterior part of the zygomatic arch. The temporalis was thus a very powerful muscle, and this is also reflected in the size of its insertion on the lower jaw, for it seems very probable that the concavity on the dorsal surface of the dentary, which is strengthened by a strong wing on the lateral surface of the bone, marks the point of insertion of the more superficial portion of the muscle. This superficial portion was probably that which originated lateral to the root of the zygomatic arch, while the portion originating medial to the zygomatic arch presumably inserted on the inner surface of the mandible and into the meckelian fossa.

Parrington (1955) has put forward a strong case for the supposition that the masseter muscle in synapsids ran from the anterior portion of the zygomatic arch to the reflected lamina of the angular. Such a course in the Dicynodontia is supported by the following features. Firstly, in *Kingoria* there is, at the junction of the zygomatic arch and maxilla, a very noticeable flattened area, directed ventrally and somewhat postero-laterally. Secondly, in *Stahleckeria potens* (von Huene, 1944) in the endothiodonts (see Broom, 1921 and 1932 Figs 75C, 77, 78, 79A, B) and in *Aulacephalodon brodiei* and *coatoni* (Broom, 1941), *A.nesemanni* (Broom, 1936a) and *A.whaitsi* (Broom, 1932) there is, under the postero-lateral corner of the orbit, a prominent ventrally or postero-ventrally directed knob similar to that found in the cynodonts *Cynognathus*, *Diademodon* and *Trirachodon*. Thirdly, such a course for the muscle in *Kingoria* would explain the sudden manner in which the anlargement of the dorsal surface of the dentary for the attachment of the temporalis muscle is terminated posteriorly. Finally, if the courses here suggested for the temporal and masseter muscles are correct, the resulting large angle between the two muscles would be well suited to producing the antero-posterior movement of the lower jaw suggested by Watson (1948).

There is some variation in the literature as to the nomenclature of the different parts of the pterygoideus musculature. Adams (1919) states that an anterior pterygoideus is always present in the reptiles, that it arises from the pterygoid and palatine region, and that its insertion typically wraps around onto the outer side of the posterior end of the articular. Though Adams states (1919, p.147) that what is usually called the posterior pterygoideus muscle is really the deepest part of the capiti-mandibularis muscle mass, and that he is naming it the capiti-mandibularis profundus, he does not always follow this procedure, for in both Alligator and Varanus he describes and figures both a capiti-mandibularis profundus and a posterior pterygoideus. In Varanus the capiti-mandibularis profundus inserts on the coronoid region of the mandible while the posterior pterygoideus inserts just behind it. In Alligator the capiti-mandibularis profundus is a small slip attached to the tendon of the capiti-mandibularis medius; the posterior pterygoideus arises on the quadrate and quadrato-jugal and joins with the anterior pterygoideus, the two together wrapping around the postero-ventral end of the mandible.

The distinction between posterior and anterior pterygoideus would thus seem to be that the former, whether a part of the capiti-mandibularis mass or not, inserts on the inner side of the mandible, while the anterior pterygoideus commonly wraps around the postero-ventral end of the mandible onto its outer surface. This distinction is not materially weakened by the fact that in Alligator a muscle formed from a junction of anterior and posterior pterygoideus muscles includes these normal characteristics of the anterior pterygoideus muscle.

Following this, it seems likely that in Kingoria the position of insertion of the posterior pterygoideus is indicated by the marked scar found under the inner articular condyle, the muscle probably running antero-dorsally onto the anterior face of the prootic. Such a course would also explain the way in which the inner articular condyle is undercut ventrally so that it projects as a medial wing from the body of the articular bone.

The anterior pterygoideus in Kingoria probably originated in normal fashion from the dorsal and lateral surfaces of the body of the pterygoid and ran postero-laterally to wrap around the posterior part of the jaw, having insertions on the outer side of the jaw under the reflected lamina, which Parrington (1955) believes to be a structure developed to provide an insertion for the masseter without restricting the anterior pterygoideus muscle. (A very similar structure is to be seen at the posterior end of the lower jaw of the modern rodent Dasyprocta, there being an outer rather thin sheet of bone to which the masseter is attached, and an inner and more ventral solid ridge of bone round which the pterygoideus is inserted). The posterior part of this anterior pterygoideus muscle is probably responsible for the very marked hollow on the anterior face of the retro-articular process; the fibres of this part of the muscle probably ran dorso-medially to an origin on the anterior portion and root of the quadrate ramus of the pterygoid. If this course is correct, those fibres which were attached to the anterior face of the retro-articular process, on the outer side of the mandible, would have at first to run medially. The necessity for providing a clear medial passage for these fibres may explain the manner in which the retro-articular process is sharply delimited anteriorly, instead of merging gradually into the ventral surface of the jaw ramus, for the latter would seem to be a mechanically stronger condition. It may be noted that a similar free medial access to the anterior face of the retro-articular process is still present even when the lower end of the retro-articular process is directed anteriorly. This condition is found in Emydochampsa oweni (Broili & Schröder, 1936a) and in some gorgonopsids, and in such forms the retro-articular process is L-shaped; again, this condition is apparently unsatisfactory from a mechanical point of view, for it would seem that greater strength would have been provided if the angle between the two portions of the retro-articular process had been consolidated. The above interpretation of the anterior pterygoideus muscle would also to some extent reconcile the opinions of Watson and Parrington. Watson, in his 1948 paper, held that the apparent retro-articular process of later synapsids was in reality a process for part of the pterygoideus musculature (though he called this part the posterior pterygoideus), the retro-articular process and depressor mandibuli muscle having been lost; Parrington, in 1955, put forward a strong case for the identity of this process with the retro-articular process of pelycosaurs. Parrington's identification of the ventrally directed process as the retro-articular process would seem to be confirmed by the clear traces of muscle insertion found on its posterior surface in <u>Kingoria</u> but, if the above interpretation is correct, it would seem possible that the same process gave attachment to the depressor mandibuli posteriorly and to the anterior pterygoideus muscle anteriorly.

Several factors make it seem likely that the origin of the depressor mandibuli muscle was from the posterior extension of the dorsal edge of the squamosal. Firstly, the antero-posterior alignment of the condyles on both upper and lower jaws suggests that the origin of the depressor mandibuli lay directly above its insertion so that the action lay in the plane of movement of the lower jaw. Secondly, the origin would be expected to lie some distance from the retro-articular process so that the muscle would have adequate length of contraction. It should be noted here that the extensive antero-posterior movements of the lower jaw which are indicated by its disparity in length compared with the upper jaw, and also by the character of the condyles, and which has been suggested by Watson (1948), means that the depressor mandibuli must be of considerable length if it is to allow these movements to take place. Finally, if the depressor mandibuli did run directly upwards from the retro-articular process, the most lateral part of the posterior extension of the dorsal edge of the squamosal provides a ventrally-directed surface well suited for its attachment. The origin may have extended from there ventrally down the surface of the squamosal, and two small protuberances above and below the groove leading to the post-temporal fossa may indicate the origin of some muscle fibres from this point also. An origin from such a general region, high up on the occiput, is found in most modern reptiles, though this region is in them more usually occupied by the parietal than by the squamosal.

The identification of this ventrally directed process as a retro-articular process is important for the restoration of the muscles opening the jaw. As is well known, the reptiles and mammals differ in the method of opening the jaws. The reptiles possess a depressor mandibuli muscle running from the dorso-lateral corner of the occiput to the posterior portion of the mandible, so that the jaw is opened by a muscle acting on it close to, but posterior to, its articulation. In the mammals the jaws are opened by a muscle acting anterior to the jaw articulation; in the Eutheria, the digastric runs from the mastoid region of the periotic to the inner side of the mandible, in the Monotremata the detrahens mandibulae runs from the mastoid and squamosal region to insert on the side and lower edge of the mandible.

It would seem reasonable to suppose that the change from the reptilian to the mammalian system was correlated with the loss of the post-dentary bones and it therefore would seem to be anachronistic to expect to find the mammalian condition in Kingoria, whose lower jaw is completely reptilian - though muscles equivalent to those of the mammal (but possibly having a different function) may also have been present. One would therefore expect Kingoria to possess a depressor mandibuli muscle, and this expectation is confirmed by the above identification of the retro-articular process, a structure whose function is clearly to provide more advantageous mechanical conditions for a muscle running dorsally. Furthermore, this process bears clear traces of muscle insertion on its posterior surface (Fig. 9A and C).

The above identification of the depressor mandibuli muscle does not in itself preclude the additional presence of muscles equivalent to the mammalian digastric. Furthermore, the process earlier provisionally named the tympanic process is in the region in which there is in mammals a process for the attachment of the digastric, the posterior belly of this muscle originating from a mastoid process of the periotic bone or from a paramastoid process of the occipital bone. In either case, the process is directed ventrally or ventrally and somewhat posteriorly, and the level of the jaw articulation is considerably more dorsal and anterior. The digastric and other muscles attached to the hyoid apparatus are used either to open the jaws or to move the hyoid during swallowing. In Kingoria, however, the tympanic process is directed posteriorly and only slightly ventrally, and is dorsal and just posterior to the jaw condyle. Thus a muscle running from it to the hyoid, and serving to aid in opening the jaw, would have to run antero-ventrally around the middle-ear region. Thus in terms of muscle effectiveness, the attachment of such a muscle on the tympanic process would be no more advantageous than would be a more ventral origin, e.g. on the tubera basioccipitalia. In addition, the character of the tympanic proce does not suggest that it served for muscle attachment; it is too small to form a basis for a fleshy attachment, and its smooth surface makes it unlikely that a tendon originated from it. These factors thus do not support the hypothesis that there was a functional digastric system attache to the tympanic process in *Kingoria*, and this conclusion is strengthened by the apparent presence of a well developed depressor mandibuli muscle.

However, a different explanation of an analogous process was suggested by Watson (1931) in his description of *Scaloposaurus*; he noted the presenc of a postero-laterally directed process of the paroccipital process, suggested that it might be for muscle-attachment, and referred to it as a "mastoid" process. Crompton, in a recent revision of the Scaloposauridae, remarks on this as follows (1955b, p.154):

"The posterior or mastoid process extends postero-laterally and but for a millimeter articulates with the ventral edge of the squamosal. The term mastoid process was first introduced by Watson (1931) who observed it in *Scaloposaurus*. He considered it for muscular attachment, but since his material was poorly preserved and the posterior part of the squamosal badly damaged, the approximation of this process to the squamosal could not be observed. In view of the lack of perichondral ossification on these two processes, it is more than likely that they were both extended laterally by cartilage so as to form definite articulations with the structures towards which they are directed". Crompton considers that the skull of the scaloposaurs is kinetic, one of the points of articulation between the maxillary

Thus, though these more advanced mammal-like reptiles possess a process of the paroccipital process in a region similar to that in which the tympanic process of Kingoria is situated, and though the term "mastoid process" has been used to describe it, there is no reason to believe that it was concerned with the jaw musculature, and its presence therefore in no way invalidates the similar conclusion reached in the case of the tympanic process in Kingoria.

Summary. From the above discussion it appears that the jaw musculature of Kingoria was typically reptilian, possessing a depressor mandibuli muscle but no digastric muscle. Due to the more straightforward nature of the movements which take place, and the correspondingly simpler character of the musculature, and due also to the greater amount of evidence afforded by the marking and relief of the bones, it has been possible to restore the jaw musculature with a greater degree of confidence than was possible in the case of the occipital musculature. Like the latter, the restored jaw musculature does not reveal any feature which is likely to have been responsible for the development of the tympanic process.

The auditory region

The presence or absence of a tympanum in the extinct reptiles is now a subject of major controversy, Watson (1948, 1951, 1953, 1954) being the leading protagonist of the view that the tympanum is absent in the captorhinomorph cotylosaurs and the more primitive synapsids, while Parrington (1955) has disputed this. Watson bases his theory on two main points: the lack of an obvious otic notch and the massive nature of the stapes.

In modern forms the tympanum is lost only in forms whose habit of life is such that the head is usually placed in contact with the substratum, so that conduction of vibrations through the bones of the skull could occur. The skeletons of the synapsids, and especially the therapsids, do not suggest that the head was usually in contact with the ground, and it seems unlikely that any degree of sensitive hearing could have been achieved by transmission of vibrations from the ground to the head via the limbs and general body skeleton. It seems reasonable, therefore, to assume that the loss of the sensitive tympanic method of hearing would place the animal at a disadvantage (especially if it were a herbivore subject to attack by such animals as the gorgonopsids) and, in the absence of definite evidence to the contrary, one might reasonably assume that a tympanum was present. Positive evidence for the presence of such a tympanum might be derived from the contouring of the bone in the regions where a tympanum or external auditory meatus might be expected, or from the structure of the stapes itself. These lines of approach will now be examined in Kingoria.

The most obvious evidence from the contouring on the skull of Kingoria lies in what has above been called the tympanic process. The position of this process, and the posterior extension of the inner quadrate condyle below it, both immediately suggest that these structures supported a tympanic membrane. The only alternative explanation for the tympanic process would be that it served as an attachment for a muscle. However, the musculature of the head has been discussed above, and it appears to be unlikely that the tympanic process had a function of this kind.

If a tympanum was stretched between the tympanic process and the posterior end of the inner quadrate condyle, it is necessary to suggest how an external auditory meatus could have reached the surface. A possible solution is suggested by the contouring of the outer edge of the squamosal. This does not, as one might expect, run in a continuous curve down to the beginning of the articular surface of the quadrate, but instead, as can be seen in anterior view (Fig. 5) it is embayed inwards to cross the lateral edge of the quadrate about 5 mm. above its articular surface. Furthermore, in lateral or postero-lateral views (Figs 4A and B, 24A) this lower part of the lateral edge of the squamosal can be seen also to be deflected forwards. The combination of these two features in effect forms a distinct groove leading outwards and forwards round the squamosal and quadrato-jugal, and it is suggested that the groove marks the position of an external auditory meatus.

As has been mentioned in an earlier section, a clear muscle-scar on the posterior side of the retro-articular process shows that a depressor mandibuli muscle was present. This muscle would be forming the posterior border to the proximal part of the external auditory meatus (and perhaps also of the tympanum itself as in some modern reptiles). It would thus interfere least with the auditory apparatus when the jaw is in its most posterior position, and the associated articular regions of upper and lower jaws in a large unidentified dicynodont (FRP 103) show a marked depression on the dorsal surface of the lower jaw immediately in front of the articular surface. The articular surface of the quadrate fits accurately into this depression, and it seems possible that the lower jaw, when not being used for feeding, was in this form moved back until the quadrate slipped into this depression, the depressor mandibuli muscle thus being then held well clear of the auditory region.

The stapes of Kingoria is certainly a fairly broad bone in dorsal or ventral view, but in anterior or posterior view it is fairly thin. It has also been greatly shortened (and thus lightened) by bringing the fenestra ovalis towards the tympanic region by the development of basisphenoid tubera; this feature itself suggests that the weight and, by inference, the movement of the stapes was important - though the loss of the stapedial foramen in the Dicynodontia is rather surprising. The expanded footplate of the stapes rests quite loosely in the fenestra ovalis, and is composed of spongy bone, thus further lightening the stapes. The stapes lies between the tubera and the quadrate, but is not held tightly in place - indeed, in many specimens of dicynodonts it has dropped out. Additional evidence of the possibility of the stapes having functioned as a sound-transmitting structure lies in the presence of a small facet on its postero-lateral corner; this probably marks the point of attachment of an extrastapedial cartilage which ran to the tympanic membrane. In a larger dicynodont skull (FRP 39, possibly Dicynodon huenei) this part of the stapes bears a large process directed postero-dorsally (Fig. 24B, C).

The above provides a possible theory as to the structures concerned with hearing in Kingoria, and one may next try to determine whether there is any evidence that it represents the typical condition in the dicynodonts as a whole.

Within the genus Dicynodon, one of the earliest and smallest species is D.pseudojouberti from the Tapinocephalus zone of South Africa. Some specimens of this species were kindly provided by the British Museum (Natural

History); the matrix is extremely hard (as noted by Watson, 1948), but the occiput of one specimen was largely freed of matrix and a distinct tympanic process was found, similar to that of Kingoria in both character and position, and the embayment of the squamosal was also present.

Specimens which have been mechanically prepared in the past do not usually show an undamaged tympanic process as, unless its presence is expected, it is very easily destroyed during preparation. Thus breakage facets, showing where the tympanic process has been broken off, are the only traces of its presence in several specimens of Kingoria; such a facet can be seen both in one of von Huene's original specimens (von Huene, 1942, K 12) and in further specimens collected by Parrington. Amongst von Huene's other East African specimens, such breakage facets are also to be found in Dicynodon njalilus, in which the posterior projection of the inner quadrate condyle is also clearly developed, D.bathyrhynchus has a well preserved tympanic process 12 mm. long, and D.locusticeps shows a slight posterior projection of the paroccipital process. Among the South African specimens described by von Huene (1931), D.haughtonianus has traces of the tympanic process. An unidentified specimen of Dicynodon sp. in the British Museum (Natural History) (catalogue no. R 3745), also shows the tympanic process very clearly, and the type specimen of D.tigriceps, described and figured by Owen (1845b) has a broad convex backward process on the paroccipital process. The forward embayment of the squamosal is commonly visible on well preserved dicynodont skulls, or on figures of such skulls.

The tympanic process is not confined to the African species of Dicynodon, as it is both described and figured in the Russian D.amalitzkii by Sushkin (1926b) and is figured in the Chinese D.sinkianensis by Yuan & Young (1934).

To turn next to other genera of dicynodonts, the type specimen of Oudenodon bainii shows a clear breakage facet in the position where the tympanic process might be expected. The forward embayment of the squamosal is very noticeable in figures of Cistecephalus laticeps (Brink, 1950), and C.planiceps (von Huene, 1942). In Kannemeyeria, Haughton (1915b) mentions that "the posterior corner of the paroccipital is prolonged to form a bluntly pointed process"; this can also be seen in Pearson's (1926a) figures of this region in K.erithrea. A breakage facet for the tympanic process can be seen in Tropidostoma microtrema (Seeley, 1889, Plate 11) and the process itself and the forward embayment of the squamosal are visible in another specimen of the same genus (Seeley, 1889, Plate 12).

On the other hand, there are several forms in which no clear trace of the tympanic process itself could be found. In Dicynodon huenei[1] no clear conical process could be seen, but the distal end of the paroccipital process bears a rather thin irregular backwardly directed ridge. Dr. Platt, of the Cambridge University Department of Anatomy, examined the skull and stated that the character of this ridge suggested arthritic changes connected with old age, so that this specimen may not be typical of normal adults of this species. This species also clearly shows the embayment in the lower edge of the squamosal which has above been suggested as indicating the site of the external auditory meatus. Lystrosaurus also shows this embayment but shows no trace of a tympanic process; conditions in this semi-aquatic form with its down-turned snout might well be unusual. Stahleckeria again shows

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[1] The original ascription (Haughton, 1932) of this form to Dicynodon is here retained; von Huene (1942) referred it to Platypodosaurus, but Dicynodon huenei differs from it in its short and deep skull, that of von Huene's Platypodosaurus magnus being very elongate and flattened, in its lack of a pineal boss and of elongate caniniform processes, and in possessing canine tusks.

the embayment, the distal end of the paroccipital process bears a strong low mound, and the stapes has a roughened area at its postero-distal corner which may mark the point of attachment of a cartilaginous extra-stapes.

In Placerias Camp & Welles (1956) state that there is no posterior ridge or process on the paroccipital process. They figure and mention an extra-stapedial facet on the stapes and a groove running laterally along the back of the quadrate. They state, without further discussion, that "it seems unlikely that a tympanum would have been buried in the jaw muscles at any point median to the margin of the squamosal". The stapes also possesses a great proximo-ventral boss adjacent to the footplate, which Camp & Welles interpret as an attachment of one of the sub-cervical muscles, "probably developed powerfully in Placerias to rake the muzzle downward and backward while grubbing in the ground". However, the stapes is not fused to either the tubera or the quadrate.

Finally, in Cistecephalus no trace of the tympanic process can be seen in the very clear figures of Broili & Schröder (1935a) and Brink (1950). However, both the strong box-like skull and the peculiar nature of the manus (Brink, 1953) suggest that Cistecephalus was a burrowing form, and degenerative changes in the auditory apparatus of modern reptiles are most common in forms leading such an existence, presumably because the head is usually in contact with the substrate, so that it is possible for vibrations to be conducted directly through the bones of the skull.

Though an examination has been made of all the available specimens in the British Museum (Natural History), and in the Museums in Cambridge, Oxford and Tubingen, and in the private collections of Mr. F. R. Parrington and

Professor D. M. S. Watson, relatively few specimens show a clear and undamaged occipital surface. The evidence available from the literature in figures or descriptions is similarly scanty and naturally more difficult to assess. It is thus impossible to make any definite statement as to how far the structures found in Kingoria are typical of the dicynodonts as a whole. Enough evidence has been collected to make it appear likely that it was present throughout the rather vague genus Dicynodon, and in Oudenodon and Tropidostoma. The genera which do not show these conditions are thus several large Triassic genera (Kannemeyeria, Stahleckeria and Placerias - though the first two do show a low boss on the paroccipital process), one semi-aquatic genus (Lystrosaurus), and one burrowing genus (Cistecephalus). It would not seem to be unreasonable to suppose that in these cases, either the great increase in size, or the unusual habitat, have rendered unnecessary the retention of a special tympanic process to support the dorsal margin of the tympanum. Dicynodon itself is certainly a more primitive genus, and the presence of the tympanic process in an early (Tapinocephalus zone) species of that genus makes it appear possible that it was a character possessed by the Dicynodontia as a whole. This would support the view of Parrington (1955) that a tympanic membrane was present and functional in the primitive synapsids.

B. Post-Temporal Fossa and Veins of the Head

Though it is lost in most modern Amphibia and Mammalia and some Reptilia, the post-temporal fossa is a fairly constant feature in the structure of the skull of tetrapods, the last vestiges of it being present in the Monotremata. It appears originally to have been merely a gap between the bones of the dorsal roof of the skull and the bones of the dorsal part of the occiput, but its persistence through the tetrapoda implies that it had some functional significance. Though in many fossil amphibia it is large and may have served for the origin of part of the neck musculature (Romer, 1941), its small size in many reptiles, especially in the Synapsida, indicates that its function here is more likely to have been the transmission of a nerve or blood vessel. Its morphological position makes it unlikely that it transmitted a nerve, and its function as a passage for a blood-vessel is supported by the presence in some fossils of well marked grooves running from the anterior opening of the post-temporal fossa. These grooves are known in various archosaurs (Belodon, Erythrosuchus, Mystriosaurus), in the Pelycosauria (Romer & Price, 1940), Dicynodontia and Cynodontia (Watson, 1911, 1920; Parrington, 1946a).

In living reptiles the only blood vessel running through the region morphologically equivalent to the post-temporal fossa is the vena capitis dorsalis, which is described in Lacerta agilis by Bruner (1907). He states that this drains the muscles of the occipital fossa, and that it is formed by the union of two components, a lateral component which rises above the paroccipital process and a medial one which has its origin above the lateral margin of the foramen magnum. These components "unite below the posterior margin of the parietal bone, directly lateral to the crista sagittalis of the supraoccipital" (Bruner, 1907, p.18); the vena capitis dorsalis then continues forwards a short distance and receives from an anterior direction a sinus-like vena parietalis. It then "bends towards the median line and enters the cranium through the caudal end of the great parietal fissure, which lies between the parietal bone and dorsal margin of the prootic" (Bruner, 1907, pp.18-19); the supraoccipital forms the posterior margin of this fissure. Within the cranium the vein joins the vena cerebralis media close to its origin from the vena longitudinalis cerebri. A vena capitis dorsalis with a similar course is described in Sphenodon by Dendy (1909), and by O'Donoghue (1920), who describes an anterior parietalis component like that of Lacerta.

This may be compared with the structure in Kingoria, where a groove runs dorso-medially in a curve from the post-temporal fossa to a slight notch in the anterior end of the prootic just below the postero-ventral end of the parietal. A vessel running in this groove and entering the skull at the notch, in the region of the junction of the parietal, supraoccipital and prootic, would be following exactly the same morphological course as the vena capitis dorsalis of Lacerta and Sphenodon, and it seems likely that the groove in Kingoria was in fact occupied by this vein. No evidence is to be found in Kingoria as to the presence or course of a vena parietalis, but a more extensive system of grooves is found in the cynodonts. In Diademodon (Watson, 1911) there is a groove along or just above the junction of the parietal and epipterygoid. At about one centimetre behind the level of the pineal foramen this groove receives a large oval and backwardly directed foramen, which Watson states must lead into the brain cavity and the internal opening of which he later found (Watson, 1913b); the groove continues beyond the foramen and opens into the post-temporal fossa. The foramen which Watson mentions is also present in Cynognathus sp. (Watson, 1911), Protacmon brachyrhinus (Watson, 1920), Thrinaxodon liorhinus (Parrington, 1946a) and Diademodon mastacus (Brink, 1956). According to the interpretation suggested here, the foramen would be the point of entry of the vena capitis dorsalis into the brain-case, while the groove anterior to the foramen would represent the vena parietalis.

Olsen (1944) found a notch in the anterior border of the periotic, in a position similar to that of the notch which has above been considered to be the point of entry of the vena capitis dorsalis in Kingoria. He states that the notch is present in most of his serially-sectioned specimens, which include dicynodonts, therocephalians, gorgonopsids and cynodonts, and that it is commonly separated from the prootic incisure by an antero-dorsal process of the periotic. However, because the notch does not appear to be present in some forms, and because it is occupied by the epipterygoid in his cynodonts, Olson does not believe that it was traversed by a blood-vessel. Instead he follows Price, who suggested (1935) that a ledge on the anterior margin of the prootic in Captorhinus was the base for a cartilage supporting the orbitosphenoid elements, stating that a comparable shelf with such a function is found in modern iguanas. Olson thus believes that the antero-dorsal process in his therapsids has a similar function, and that the appearance of the dorsal incisure is merely incidental to the development of this structure.

However, though in the iguanas the relatively large size of the orbit and its posterior position have led the supporting elements of the orbitosphenoid to come into relationship with the anterior margin of the prootic, it seems inadvisable to homologise the resulting structural features with those found in these fossil reptiles, in which the orbit is much smaller and is situated very much further forwards relative to the braincase. The lack of an incisure in the cynodonts is not surprising since, as mentioned above, the entrance of the vena capitis dorsalis is through a foramen between the epipterygoid and the parietal, in a position more dorso-anterior than in the other therapsids, so that the vein may well not have passed across the front border of the prootic. The exact course of the vein may well vary in the different therapsids, and this would lead to corresponding variations in the presence or depth of the incisure.

On the above evidence, it seems to the writer more reasonable to explain the incisure as being a result of the presence of a vena capitis dorsalis than to account for it as being merely an incidental in the development of a structure bearing a cartilage supporting the orbitosphenoid elements.

In addition to the grooves mentioned above, Kingoria shows some indications of a groove running downwards from the post-temporal fossa; in the cynodonts a similar groove runs into the pterygo-paroccipital foramen (this latter is wholly within the prootic in Thrinaxodon liorhinus; Parrington, 1946a), and a further groove runs from this latter foramen forwards to the facialis foramen (Watson, 1911; Parrington, 1946a). In Diademodon, at least, the whole system of grooves is covered by thin flanges from the surrounding bones (Watson, 1911).

Watson (1920) has suggested that the vena capitis lateralis passed through the pterygo-paroccipital foramen, then giving rise to one branch which passed through the post-temporal fossa, a second which passed up the dorsal groove along the junction of the parietal and prootic, and a third (presumably the continuation of the vena capitis lateralis) which ran dorsal to the meeting of the prootic and epipterygoid and passed through the trigeminus foramen between those two bones. However, the fact that the post-temporal fossa is occupied by a vein draining forwards makes some modification of this necessary. The post-temporal fossa and dorsal groove were presumably occupied by the vena capitis dorsalis; the vena capitis lateralis presumably ran from the pterygo-paroccipital foramen into the trigeminus foramen. The groove between the post-temporal fossa and the pterygo-paroccipital foramen was probably occupied by a vein joining the vena capitis lateralis and the vena capitis dorsalis, and providing an alternative method of drainage - a common feature in the veins of the head. The groove for this vein is more marked in the cynodonts, where the post-temporal fossa and the pterygo-paroccipital foramen are closer together, and it is possible that in the cynodonts this became the only drainage for the vena capitis dorsalis. This would explain the lack, in <u>Cynognathus crateronotus</u> (Seeley, 1895b) of a foramen at the antero-dorsal end of the groove for the vena capitis dorsalis, the direction of flow in this part of the vein having reversed so that it runs posteriorly, meeting the main inflow through the post-temporal fossa and continuing downwards to meet the vena capitis lateralis near the pterygo-paroccipital foramen.

Watson has suggested that the dorsal canal, here considered to lodge the vena capitis dorsalis, "occupies the same position as the 'sinus canal' described by Parker in <u>Erinaceus</u>" (Watson, 1911, p.320). He is apparently referring to the groove for the lateral sinus which Parker (1885) figures in Plate 20, Fig. 4, and mentions on p.154. However, this groove is on the inner surface of the parietal, within the brain-case. Though it is possible that the vein which ran in the groove in synapsids has been simply enclosed within the cranium by the extension of the meeting between the epipterygoid and the parietal, the extent to which the extracranial venous system of reptiles is replaced by intracranial sinuses in the mammals makes it more likely that the extracranial vein has been replaced by an intracranial vein in this case also.

C. Braincase

The cartilage bones of the braincase are tightly joined or fused together, so that the supraoccipital, exoccipital, basioccipital, basisphenoid, parasphenoid, prootic and opisthotic are all indistinguishable from one another except at one or two points. This is not an unusual condition, but the lack of any unossified zone in Kingoria is a feature worth emphasising. Such a zone, between the basisphenoid and the basioccipital, was found by Olson (1944) in various therapsids; of the six dicynodonts which he figures, three show such a zone and three do not. Olson also states that the sella turcica in his dicynodonts is very shallow or absent, and that the internal carotid canals emerge just anterior to it, whereas in Kingoria the sella is quite deep and the internal carotid canals run into its floor.

The whole braincase region of Kingoria is thus strongly built, and a similar solidity is found in its relations with the surrounding dermal bones. The upper part of the occipital plate is sutured to the tabular and interparietal, and is overlapped anteriorly by the squamosal. Ventrally the occipital plate has a mere apposition against the medial edge of the occipital wing of the squamosal, but more dorsally the two bones have a suture which, above the post-temporal fossa, is of an interdigitating nature. Finally, the prootic is sutured to the parietal.

From the above, it is clear that there could have been no type of kinetic movement in the braincase of Kingoria. Study of the quadrate region shows that this also is immoveable, the lower end of the quadratojugal being fused to the quadrate and its upper end being sutured firmly into the anterior face of the squamosal. It is therefore rather surprising to find that the quadrate fits somewhat loosely into a pocket in the squamosal, the surfaces of the bones suggesting that there was a cartilaginous connection during life; it is possible that this is merely a relic of an ancestral kinetism at this point.

The epipterygoid in Kingoria does not appear to expand dorsally to form part of the wall of the braincase, though Watson (1948) figures such a dorsal expansion in Dicynodon cf. sollasi.

D. Tabular

The tabular is one of the skull bones which is reduced and lost during the history of the Synapsida, and this is reflected in what is known of the bone in the Dicynodontia. In the pelycosaurs the tabular extends far ventro-laterally, forming part of the border of the post-temporal fossa. Olson (1937) has figured it as bordering this fossa in Brachyprosopus broomi, as has von Huene (1922) in Dicynodon sollasi, but in this latter von Huene figures the fossa as being so large that it seems likely that the approaches to the fossa were still filled with matrix, so that the relationship of the tabular to the deeper lying opening of the fossa is uncertain. In Kingoria the tabular approaches the post-temporal fossa fairly closely, but it does not extend so far ventrally in the Tapinocephalus zone forms Synostocephalus vanhoepeni and Eurychororhinus boonstrai (Broili & Schröder, 1935b), or in the Cistecephalus zone form *Oudenodon marlothi* (Broili & Schröder, 1936b).

Two genera of dicynodonts appear to have lost the tabular. Romer & Price (1944) were unable to find one in the large South American Triassic form *Stahleckeria lenzii*, and von Huene (1935), though he believes it to be present in *Stahleckeria potens*, was unable to see any sutures delimiting such a bone. In their very clear account of *Cistecephalus planiceps*, Broili & Schröder (1935a) have found no trace of a tabular, the squamosal forming the whole lateral portion of the occiput, as in other dicynodonts. However, Brink (1950) has described and figured the occiput of *Cistecephalus laticeps*, showing the tabular forming the whole of this lateral region and extending down to the quadrate as a bone covering the posterior surface of the squamosal. It seems likely that Brink is mistaken here; the more anterior bone, which he regards as the squamosal, is probably the quadratojugal, which he neither figures nor mentions, while the more posterior bone is probably the squamosal, as in Broili & Schroder's specimen, the tabular being absent.

As mentioned in an earlier section, the anterior exposure of the tabular found in specimen 84 is not found in other specimens of *Kingoria*, and is probably a juvenile condition. It is interesting to note that a similar condition is found in the adult Pelycosauria, e.g. in *Dimetrodon* (Romer & Price, 1944).

E. Sphenethmoid

The main feature of interest in the sphenethmoid is its lack of division into separate elements. This is contrary to the interpretation of Olson (1944), based on sectioned specimens, who believes that the anomodonts generally show two distinct ossifications. The more postero-ventral ossification, which he interprets as a presphenoid, is medial and lies in the parasphenoidal rostrum. The more antero-dorsal ossification, which he interprets as an orbitosphenoid, is composed of dorsal wings and a ventral keel which, anteriorly, is expanded dorso-ventrally to reach the ventral surface of the frontal; Olson considers that this expansion may represent a mesethmoid. Comparison of this region in Kingoria with Olson's figures suggests several alterations to his interpretations.

In Kingoria the parasphenoid and basisphenoid are difficult to distinguish from one another posteriorly, but anteriorly the parasphenoid continues beyond the basisphenoid as the processus cultriformis, so that the basisphenoid has a distinct anterior face rising from the posterior end of the processus cultriformis. This appears to be the region which Olson interprets as a presphenoid. In Kingoria it definitely appears to be merely the anterior part of the basisphenoid and there is no sign of any other ossification equivalent to Olson's presphenoid.

In Kingoria the element described as a sphenethmoid seems to be equivalent to the element which Olson interprets as an orbitosphenoid. Its anterior part shows no sign of ossifying as a separate mesethmoid.

Kingoria thus shows a single sphenethmoid ossification, not divided into orbitosphenoids and mesethmoid, and shows no ossification equivalent to a presphenoid.

F. Foramina of the Skull

The floor of the braincase shows no sign of any pair of pits similar to those found in Kannemeyeria by Pearson (1924a), which she considered were for the cochleae, and which were also found in Stahleckeria by von Huene (1935).

The canal for the facial nerve runs wholly through the prootic, opening posterior to the prootic-parasphenoid suture, as found in Kannemeyeria by Pearson (1924a) and in Brachyprosopus broomi by Olson (1937). The re-entry of the palatal branch of the facial nerve, to run through the palate and emerge on its dorsal side, is in conformity with the views of Parrington & Westoll (1940) on the course of this nerve and the homologies of the canal which contains it. The ventral end of a similar canal in a cast of the cavities of an unidentified dicynodont skull was figured by Broom (1912b), who thought it to be for the ophthalmic artery.

The foramen between the ectopterygoid and the palatine is found also in Cistecephalus (Brink, 1950) and Kannemeyeria (Case, 1934); it is probably equivalent to the rather larger foramen, found in most reptiles, which Versluys (1936, p.737) calls the lateral palatal fenestra. He states that it probably transmits that branch of the trigeminal nerve which Gaupp, in the frog, calls the ramus communicans cum N.palatini.

There is no sign of the large foramen, ventro-medial to the anterior end of the zygomatic arch, which Sollas & Sollas (1913) found in Dicynodon leoniceps and which they state is presumably for the transmission of a branch of the fifth nerve and accompanying blood vessels. Such a foramen is also found in Kannemeyeria, Aulacephalodon and Lystrosaurus, all of which are forms which invariably bear canines, and in Brachyprosopus broomi (Olson, 1937), Dicynodon grossarthi (Broili & Schröder, 1937) and Placerias (Camp & Welles, 1956).

The lack of a stapedial foramen is normal in the Dicynodontia, the only genera which have been reported to possess it being Cistecephalus

(Broili & Schröder, 1935a) and the Tapinocephalus zone form Eurychororhinus boonstrai (Broili & Schröder, 1935b).

The form of the septomaxilla of Kingoria is very similar to that of Dimetrodon as figured by Romer & Price (1944, Plate 16 A-D). In both forms there are two foramina between the septomaxilla and the inner surface of the maxilla, a larger upper foramen and a smaller lower foramen, and the septomaxilla is pierced by a third foramen. Various explanations of the functions of the foramina are possible; they may have transmitted the duct of the organ of Jacobsen, the anterior portion of the naso-lacrimal duct, the duct of a nasal gland, or minor blood-vessels and nerves. The morphology of living reptiles is of little help, since in none is the septomaxilla pierced by a canal, and since the very extensive unpierced secondary palate of Kingoria makes it unlikely that it could have possessed an organ of Jacobsen of function and relations similar to those found in living reptiles. The internal surface of the nasal cavity gives no indication of the position of the organ of Jacobsen and, though the cavity is so large that the organ might have left no trace on the bony tissues, it seems quite possible that it was either lost or greatly reduced. This is also suggested by the great distance which would have to be traversed by its canal to the buccal cavity; the secondary palate is unpierced, so that the canal would have to run back to the anterior edge of the internal nares. A duct of such a length and with an opening in such a posterior position would greatly reduce the value of the organ of Jacobsen if its function were to sample the contents of the buccal cavity, as in modern Lepidosauria; however, the function of the organ in the mammals is still not fully understood, so that it is not possible to be sure under what conditions its functions would become impossible. It therefore remains possible that the organ of Jacobsen in Kingoria had become modified and opened into the external nares through one of the foramina in the region of the septomaxilla.

It seems very likely that one of these foramina was associated with the anterior end of the naso-lacrimal duct. Posteriorly, the duct pierces the lacrimal bone and emerges in the nasal cavity; from its internal opening a groove runs to the septomaxilla, but it is not possible to be sure whether this groove leads to the upper foramen between the septomaxilla and the maxilla, or whether it leads to the foramen which pierces the septomaxilla itself. A course through the septomaxilla would lead it to a more medial position, which might be advantageous if the lacrimal fluid were used to keep moist the tissues of the external naris. Alternatively, the canal through the septomaxilla might have conveyed the duct of the lateral nasal gland, which in many lizards servesto keep the epithelium of this region covered with a film of mucous (Pratt, 1948).

It is not possible to come to any final conclusion as to the function of the foramina in the region of the septomaxilla, and this is also true of the various foramina which have been found in other parts of the skull, notably in the palatal region and in the maxilla. These foramina are mostly fairly small, so that the nerves and blood vessels which passed through them were minor branches and, in the absence of any thorough account of the relations of the cranial blood vessels and nerves to one another and to the skull in a living reptile, it is impossible to reconstruct these systems in Kingoria.

G. Number of Cervical Vertebrae

No conclusive evidence as to the number of cervical vertebrae has hitherto been found in the Dicynodontia. Suggestions, based upon incomplete or fragmentary remains, have been made by Broom (1905), who thought there were probably seven in Endothiodon bathystoma, and by Seeley (1900), who thought there were probably six in Dicynodon leptoscelus. von Huene (1931) states that there were eight cervical vertebrae in a specimen which he ascribes to Dicynodon kolbei, but he does not give his reasons for this statement. An increase in the size of the transverse processes, similar to that observed in Kingoria between vertebrae 6 and 7, can also be seen in the figure by Olson & Byrne (1938) of the sixth and seventh vertebrae of Aulacephalodon peavoti.

H. Metapophyses

As noted earlier, the large dorsally directed processes on the dorsal vertebrae are not, except in the most anterior members of the series, concerned with the articulation of the ribs, whose only articulation with the vertebrae is on the centrum. These processes may from their position, following Owen (1866), be termed metapophyses.

The presence of these processes in the Dicynodontia has not hitherto been generally recognised, though they can be seen in figures of the vertebrae of Dicynodon tigriceps (Owen, 1845b), Dicynodon pardiceps (Owen, 1876, Plate 53), Oudenodon gracilis (Broom, 1901), and in the vertebrae of the specimen of Oudenodon halli described by Watson (1917). They are first described by Seeley in his account (1900b, p.651) of a cast of natural moulds of the remains of Dicynodon leptoscelus: "Thus there is a marked contrast between the aspect of the early dorsal and lumbar vertebrae, in which the upper part of the neural arch is preserved, due to the circumstance that the transverse processes rapidly become shorter, and disappear by ascending the side of the neural arch and becoming an oblique, sharp, lateral ridge which extends upward and backward, fully 3/4 inch long, terminating in a prominent rounded tubercle (external to the post-zygapophyses) which has no relation to the rib". A similar dorsal extension of the transverse process above the facet for the rib-head is noted by Pearson (1926b) in Kannemeyeria and by von Huene (1935) in Stahleckeria, and appears to have existed in Placerias (Camp & Welles, 1956). An upward migration of the direction of the transverse process is also noted by Olson & Byrne (1938) in Aulacephalodon peavoti and figured by Broom (1905) in his dorsal view of the vertebral column of Endothiodon bathystoma. In both these two last cases the authors believe that the ribs continue to attach to these processes, even in the posterior dorsal region; however, Olson & Byrne state that the presacral ribs are two-headed (though their figure of what they presume to be the seventh rib shows only a slight notch between the two heads), while Broom states that there is little doubt that the ribs of the posterior dorsal vertebrae are single-headed.

Metapophyses thus appear to be common throughout the Dicynodontia, and it seems likely that they must have served as points of attachment for dorsal muscles of the back. The Dicynodontia were probably, in the main, herbivorous forms; animals of this type usually have a bulky body, and reconstructions of dicynodonts by various authors have commonly shown such a body. The support of this bulky structure and its viscera may have been complicated by the fact that the bony sternum is very short, so that few ribs could gain direct attachments to it, and this may well have been the factor which rendered necessary the special modifications of the dorsal musculature which led to the development of the metapophyses.

I. Number of Sacral Vertebrae

Kingoria has five sacral vertebrae, the most posterior of which, though anteriorly directed, is still quite small and is apparently a recent addition to the sacrum; a similar condition is reported in the Russian form Dicynodon trautscholdi by Efremov (1938). Four sacral vertebrae were found in the Endothiodon-zone form Dicynodon sollasi ? by Broom (1925) and in the Russian form Dicynodon amalitzkii by Sushkin (1926b), and Broom (1905) thought that there were probably four in Endothiodon itself. Five sacral vertebrae were reported in the Cistecephalus-zone forms Aulacephalodon (Olson & Byrne, 1938), Platypodosaurus (Owen, 1881) and Oudenodon (Broom, 1901). Six sacral vertebrae are present in Lystrosaurus (Watson, 1912b) and eight in the Russian form Rhadiodromus (Efremov, 1938) and the Triassic Brazilian form Stahleckeria (von Huene, 1935). The number of sacral vertebrae in Kingoria, which is from a level apparently equivalent to the Cistecephalus zone of South Africa, is thus what might be expected if, as seems likely, the Dicynodontia were progressively increasing the number of sacral vertebrae.

J. Rib-Heads and Attachments

The literature provides conflicting evidence as to both the nature and the attachments of the rib-heads in the Dicynodontia. In Kingoria the cervical and anterior dorsal ribs are double-headed, while the more posterior ribs are single-headed. A similar condition was found in Dicynodon kolbei ? by von

Huene (1931), who states that the two heads join in the eighth rib, in *Endothiodon bathystoma* by Broom (1905), in *Stahleckeria* by von Huene (1935) and *Placerias* by Camp & Welles (1956). Efremov (1938) states that all the cervical ribs are double-headed in *Rhadiodromus klimovi*, the dorsal ribs are reported to be single-headed in *Eurycarpus oweni* (Seeley, 1900a) and *Lystrosaurus weidenreichi* (Young, 1939), and Broom (1901) states that there is little distinction between the capitulum and the tuberculum in *Dicynodon gracilis*. On the other hand, Sushkin (1926a) states that in *Dicynodon amalitzkii* the ribs are distinctly double-headed from the fourth vertebra onwards, and Olson & Byrne (1938) state that in *Aulacephalodon peavoti* all the presacral ribs are two-headed, while Watson (1912b) mentions articular facets for both the capitulum and the tuberculum on the vertebrae of *Lystrosaurus*.

The position of the attachment of the rib-heads to the vertebrae is also variously reported. In *Kingoria* the single head of the dorsal ribs appears to attach low down on the anterior part of the side of the centrum, and a similar position is reported in *Eurycarpus oweni* by Seeley (1900a), who states that no tubercular attachment of the rib to the neural arch is to be seen. However, in both *Aulacephalodon peavoti* (Olson & Byrne, 1938) and *Endothiodon bathystoma* (Broom, 1905) the attachment of the rib to the centrum is reported to become intervertebral in the dorsal vertebrae, the anterior and posterior parts of the sides of the centra both bearing part of the articular facet. This difference from the other forms mentioned does not seem to be correlated with the nature of the rib-heads, since in *Aulacephalodon* they are reported to be double-headed, while in *Endothiodon* they are reported to be single-headed.

K. Cleithrum

An examination of the literature shows that, though it is commonly stated that a cleithrum is present in the Dicynodontia, the evidence for this is extremely limited. Broom (1915) mentions the remains of a small unidentified dicynodont, including a portion of the skull and much of the skeleton, with the cleithrum in position on the scapula; he states that, as far as he knows, it is the only specimen of Dicynodon which shows a cleithrum. The only description of this bone in Dicynodon has been by Sushkin (1926b), who describes and figures it in a well preserved pectoral girdle of the Russian form Dicynodon amalitzkii. A cleithrum has also been found in Cistecephalus (von Huene, 1942), a small digging dicynodont which is also primitive in possessing a stapedial foramen. A cleithrum in Kannemeyeria has been figured by Watson (1917) and described by Pearson (1924b). A groove, running down the anterior face of a scapula of Stahleckeria, was thought by von Huene (1935) to be for the cleithrum, but Romer & Price (1944) remark that it is absent in von Huene's two remaining specimens and also in their own additional specimen, and consider that it was due to post-mortem crushing.

In other cases where pectoral girdles have been described, and no cleithrum has been found, it has been generally assumed that the cleithrum had been lost during fossilisation. Though this small bone may well be less commonly collected than the other, larger, bones of the pectoral girdle, the above strong evidence that Kingoria did not possess a cleithrum suggests that it is possible that its absence may be a more widespread phenomenon in the Dicynodontia than has hitherto been thought.

L. Scapular Spine

Apart from *Kingoria*, the only dicynodont in which a scapular spine has been described is *Stahleckeria* (von Huene, 1935). Though it is possible that this structure had been lost from some of the many other dicynodont scapulae which have been described, it seems more likely that its absence is normal in the group, and that *Kingoria* and *Stahleckeria* are advanced in possessing a scapular spine. *Kingoria* is thus surprisingly advanced in this character, since it is from a level apparently equivalent to the Cistecephalus zone of South Africa, and is therefore probably Upper Permian in age, whereas *Stahleckeria* is from the Upper Triassic.

M. Precoracoid

The position of the coracoid foramen is variable in the Dicynodontia; in *Dicynodon kolbei* ? (von Huene, 1931), *Dicynodon amalitzkii* (Sushkin, 1926b), *Kannemeyeria* (Broom, 1937; Pearson, 1924b), *Sinokannemeyeria* (Young, 1937), *Placerias* (Camp & Welles, 1956) and *Stahleckeria* (von Huene, 1935) it pierces the precoracoid. In both *Oudenodon halli* (Watson, 1917) and *Endothiodon bathystoma* (Broom, 1905) it pierces the precoracoid on one side (internally in the former, externally in the latter) and runs between it and the scapula on the other. The advanced condition, in which the foramen runs wholly between the scapula and the precoracoid, is found in *Kingoria*, in *Oudenodon bainii* (Broom, 1901) and in *Lystrosaurus*.

Whether or not the precoracoid takes part in the formation of the glenoid facet appears to be similarly variable. It just enters in *Dicynodon kolbei*? (von Huene, 1931), *Dicynodon amalitzkii* (Sushkin, 1926b), *Oudenodon bainii* (Broom, 1901), *Endothiodon bathystoma* (Broom, 1905), *Prolystrosaurus natalensis*

(Haughton, 1917) and Lystrosaurus latirostris (von Huene, 1931). It does not enter in Kingoria, Oudenodon halli (Watson, 1917), Lystrosaurus hedini (Young, 1935), Kannemeyeria (Pearson, 1924b), Placerias (Camp & Welles, 1956) or Stahleckeria (von Huene, 1935).

N. Sternum

The sternum of Kingoria is of a normal dicynodont type, similar sterna having been described in Lystrosaurus by various authors, in Dicynodon amalitzkii (Sushkin, 1926b), Dicynodon kolbei ? (von Huene, 1931), Opisthoctenodon agilis (Broom, 1905), Platypodosaurus (Owen, 1880), Stahleckeria (von Huene, 1935) and Placerias (Camp & Welles, 1956). The sterna of Platypodosaurus and Placerias are also like that of Kingoria in possessing the pair of bosses at their lateral corners, but that of Stahleckeria, and several dicynodont sterna in the collection of Professor D. M. S. Watson, instead possess two or three facets along their postero-lateral margins, showing the points of attachment of the ventral ends of the ribs.

The ridge down the posterior part of the ventral surface of the sternum in Kingoria is also found in the other genera. Its presence in Dicynodon amalitzkii led Sushkin (1926b) to restore the shoulder-girdle of that form with the coracoid plate overlapping the ventral surface of the sternum. However, such a relation of these bones would be unusual and also unexpected, since the dorsal surface of the coracoid plate is usually occupied by the costo-coracoideus muscle, running to the rib cage. In addition, such a relation of the bones is not found in Kingoria, which also possesses the median ridge on the sternum, and it therefore seems probable that Sushkin is incorrect in his reconstruction, and that the sternum of Dicynodon amalitzkii occupied a more posterior position than that shown in his figured reconstruction.

O. Pelvic Symphysis

As mentioned earlier, it seems unlikely that there was any bony symphysis between the two halves of the pelvic girdle in Kingoria. An examination of the literature shows that there is very little evidence for such a symphysis in any of the Dicynodontia. The only definite statement of the existence of such a symphysis is in the semi-aquatic form Lystrosaurus; Watson (1912b) states that the two ischia meet anteriorly in a short symphysis, but that posteriorly they diverge widely. Broom (1925) examined two dicynodont sacra: in one, Dicynodon sollasi ?, he thought that there was little doubt that there had been a cartilaginous symphysis; in the other, Dicynodon andrewsi ?, he thought that there had been no symphysis. Statements that there was apparently no pelvic symphysis have been made by von Huene (1931) for Dicynodon kolbei ? and by Pearson (1924b) for Kannemeyeria, and von Huene (1935) states that the two halves of the pelvic girdle were widely separated in Stahleckeria. No other described dicynodont remains give any evidence on this point. It thus appears possible that the absence of any bony symphysis between the two halves of the pelvis is normal in the Dicynodontia; there is no evidence as to whether a cartilaginous or ligamentous connection was commonly present.

P. Musculature of the Girdles

The almost undamaged state of preservation of the girdles, and the excellent state of their bone surface, has revealed considerable evidence as to the positions of attachment of various muscles. This is of additional interest in view of the unusual features of the osteology of the girdles, especially the pelvic girdle. In the following account, the nomenclature and homologies of the different muscles are based upon Romer's (1922) comprehensive study of the muscular systems in reptiles.

Pectoral Girdle

The most noteworthy feature of the pectoral girdle is the presence of a spine on the scapula. The significance of the structure of the scapula is best understood by comparing it with a normal reptile and a normal mammal. In the reptile, the scapular blade bears no spine, its outer surface is occupied by the deltoideus, which runs to the humerus, and the trapezius inserts down its anterior edge (on the cleithrum, where that bone is present); the more ventral muscles (the scapulo-humeralis anterior and supracoracoideus, which run to the humerus) are not attached to the scapular blade. In the mammal, there is a spine down the blade of the scapula; this spine divides the external surface of the blade into anterior (supraspinatus) and posterior (infraspinatus) fossae, from which originate the supraspinatus and infraspinatus muscles, which are derived from a dorsal movement of the supracoracoideus muscle onto the blade; this movement has displaced the deltoideus, which now attaches with the trapezius on the spine of the blade of the scapula.

The scapula of <u>Kingoria</u> occupies a position intermediate between the reptile and the mammal. The scapular blade bears a spine, but this is along its anterior edge, so that there is no supraspinous fossa, while ventrally the scapular blade is so narrow that the spine rises from almost its whole width, blocking any ventral access to the more dorsal part of the blade. It thus seems likely that the main surface of the blade was still occupied by the deltoideus muscle. However, there does appear to have been some dorsal extension of the more ventral muscles. There is a groove running up under the acromion process onto the anterior face of the spine, and part of the supracoracoideus had probably extended up here as a supraspinatus component. However, this was apparently small and restricted to the ventro-medial part of the anterior face of the scapula, since there is a ridge running dorso-medially up this face from the acromion process, and the trapezius thus probably still occupied most of the anterior face of the spine. Though the base of the spine prevented the supracoracoideus from extending up onto the posterior part of the blade to form a large infraspinatus component, a small infraspinatus may have originated from the posterior surface of the ventral end of the spine, where the end of the spine swings round anteriorly onto the base of the acromion process. There is a distinct hollow immediately below the base of the acromion process, and this may have been occupied by another part of the supracoracoideus or, alternatively, the scapulo-humeralis anterior may have extended dorsally onto this area, as in mammals, to form a teres minor muscle.

The possibility that the anterior part of the supracoracoideus had gained a more extensive insertion from the scapular blade than had its posterior part may be correlated with the unusual posture of the scapula. As first suggested by Watson (1917), the scapular blade is not directed simply dorsally from its glenoid region, but has a marked anterior slant; this is also the case in Kingoria. This, in its turn, is probably correlated with the structure of the humerus, which is still a widely expanded bone without a laterally expanded head, suggesting that the humerus was still carried out laterally from the body. Under these circumstances it might well be mechanically advantageous for the anterior part of the supracoracoideus, acting to move the humerus forwards and upwards, to migrate to a more dorsal and anterior position.

Pelvic Girdle

The outer surface of the blade of the ilium is divided into two regions by a ridge which runs anteriorly along it from the raised anterior border of the acetabulum, and it seems likely that this ridge separates two areas of muscle attachment. The region above this ridge was presumably for the ilio-femoralis muscle, which normally originates from this part of the ilium in amniotes. In living reptiles there is no muscle attached to the iliac blade ventral to this muscle, but in mammals this region has been invaded by part of the pubo-ischio-femoralis muscle. In reptiles this muscle runs from the anterior internal surface of the pubis to insert on the femur, but the changes in limb posture which took place during the evolution of mammals have led, as shown by Romer (1922), to a movement of this muscle to a more dorsal position in order to retain its original function of supporting the limb. In the course of this dorsal movement it has split into two components; the component attached to the lumbar vertebrae is known in mammals as the psoas major, and the component attached to the blade of the ilium is known as the iliacus. The condition of the ilium suggests that this iliacus component may have attached to the lower part of the iliac blade in Kingoria, though such a mammalian character is quite unexpected in a Permian therapsid.

The positions of attachment of the ligaments which run between the bones of the sacrum are uncertain in Kingoria. The ilio-pubic ligament presumably attached anteriorly to the anterior tip of the iliac blade; there is no sign of a pubic tubercle on the pubis, but the broken surface on the lower external surface of this bone probably represents the area from which this tubercle has broken off. The ilio-ischiadic ligament presumably attached along the dorsal border of the ilium and ran to the posterior dorsal corner of the ischium, but there is no sign of its attachments on either bone. The ischio-trochantericus muscle normally originates on the internal surface of the ischium and passes under the ilio-ischiadic ligament to insert on the femur; the concave outline of the dorsal border of the ischium is probably to allow the passage of this muscle and also of the coccygeo-femoralis, originating on the caudal vertebrae and inserting on the femur.

The reptilian ambiens muscle (the sartorius of mammals) normally originates from an area on the pubis antero-ventral to the acetabulum and inserts on the tibia. Though the pubis no longer occupies this position in Kingoria, there is an area on the ilium, in the corresponding position and facing antero-ventrally and slightly laterally, which may be the position of origin of the ambiens muscle.

On the internal surface of the iliac blade, the mode of attachment of the sacral ribs leaves only two areas free for muscle insertion; the first lies anterior and dorsal to the sacral ribs, the second lies posterior and ventral to them. There is thus no posterior and dorsal area available on the ilium for muscle attachment, and the extensor caudae lateralis muscle, which usually originates from such a position, probably instead found a more posterior origin from the internal surface of the ischium or from its posterior edge. Similarly, there is also no anterior and ventral area available on the ilium for muscle attachment, and the quadratus lumborum, which normally originates from such a position, probably originated from the ventral surfaces of the sacral ribs themselves.

The lack of a pelvic symphysis has the result that there is no insertion for the posterior end of the rectus system of muscles, and this may instead have inserted on a ligament attached to the postero-ventral corner of the pubis.

6. THE BIOLOGY OF KINGORIA

Due to our almost complete ignorance of the flora of the Permian, and also to the rather unusual characters of the jaw apparatus of Kingoria and lack of evidence of its limb structures, the probable mode of life of Kingoria is a difficult problem. The fact that dicynodont remains are more numerous than the whole of the rest of the South African Permian vertebrate fauna, suggests that the group was herbivorous, occupying a similar ecological position to that filled today by the Artiodactyla. Most dicynodonts have a greatly reduced dentition, and Owen long ago suggested that the jaws of these were probably covered by horn during life. These modifications also suggest an herbivorous mode of life, and this is supported by the whole build of the animal in such better known forms as Kannemeyeria, Placerias and Lystrosaurus, the last-named being semi-aquatic, with a down-turned muzzle and highly placed orbits.

Suggestive as these features are as to the general mode of life of dicynodonts, it does not follow that all the members of the group were herbivorous. Within the modern Chelonia, which also have replaced the teeth by a horny covering, some genera feed on molluscs and others on fish, while birds have adapted their horny beak to an extremely wide range of feeding habits. However, there is one piece of evidence which, though rather indirect and inconclusive, suggests that Kingoria itself was herbivorous: this is the ratio between the numbers of tusked and tuskless forms. It seems likely that the tusked forms are male and the tuskless female, and, since eight tuskless skulls are known but only two tusked skulls, it appears that the males were much less numerous than the females. This in turn suggests that the animals may have lived in herds, each consisting of a number of females and a smaller number of males. Such a social organisation is found today in many herbivores and, though the total number of skulls known of Kingoria is too small for any great reliance to be placed on this, it does suggest that the genus may have been herbivorous.

The bony structures which give the most direct evidence as to the mode of life of an animal are the jaw apparatus and the limbs; unfortunately the latter are missing in Kingoria. Its jaw apparatus contains features which are characteristic of the Dicynodontia as a whole, and also features which appear to be unique to Kingoria.

The nature of the jaw articulation, in which both the quadrate and the articular condylar surfaces are convex in the antero-posterior plane, is found in all members of the Dicynodontia, and Watson (1912a) suggested that it permitted extensive antero-posterior movement of the lower jaw and also, even when the mouth was closed, allowed alterations of the angle which the upper surface of the dentary makes with the palate. Furthermore, the condylar surfaces are double, and there is a considerable difference in level between the inner and the outer condyle; the vertical face which therefore separates the two condyles has the effect of preventing lateral movements of the lower jaw. The canine tusks seem in some dicynodonts to have aided this restriction of jaw movement, since in some specimens the internal surface of the tusks bears a very marked vertical wear facet, apparently caused by the side of the lower jaw. Movement in the antero-posterior plane seems to have been quite extensive, since the lower jaw in dicynodonts is often shorter than the length between the quadrate and the anterior end of the palate, suggesting that the quadrate and articular surfaces may not have remained in contact during all phases of the jaw movement; this feature also is found in Kingoria.

The above normal dicynodont characters of the jaw apparatus appear to be quite comprehensible when combined with sharp cutting edges on the jaws; fragments of the plant food were presumably cut off by means of these cutting edges. The anterior paired ridges found on the palate in many forms may have helped in further mastication of the food, and roughened areas which are present further back on the palate in some forms may also have aided in this. In Kingoria, however, the lower jaw has no sharp cutting edge, instead tapering to a rounded, blunt, slightly bilobed point, and its outline does not conform to that of the upper jaw, so that the jaws cannot have cut off pieces of food by a scissor-like action of sharp edges on the upper and lower jaws. When the articular surfaces of the articular and quadrate are placed in contact and the lower jaw is progressively closed, it is found that, so long as the articular surfaces remain in contact, it is impossible for the anterior end of the lower jaw to contact the palate, since the more posterior part of the dentary meets the ectopterygoid region of the palate before any more anterior contact can take place. It is possible that a contact was achieved by an extensive separation between the quadrate and articular condyles, but the necessity for such a contact in the absence of cutting edges on the jaws is not apparent. Alternatively, it is possible that the outline of the bony jaws is not representative of the outline of the horn which is thought to have covered them in the Dicynodontia, and that sharp horny cutting edges on the horn of the lower jaw may have contacted the edge of the upper jaw. However, a study of the horny beaks of modern

Chelonia and birds shows that, wherever a sharp cutting edge is present, the horn layer is thin and the underlying bone gives an accurate picture of the nature of the beak. It is only when it is forming a crushing surface that the horny layer becomes thick and conforms less closely to the relief of the underlying bone. Thus it seems unlikely that the lower jaw of Kingoria possessed a cutting edge and, furthermore, the curved, tapering shape of the anterior end of the lower jaw does not provide the flattened area which is normally found in those forms (e.g. mollusc-eating animals) in which the jaws are used for crushing.

The shape of the anterior end of the lower jaw could be explained by two possible modes of life. Firstly, it is possible that the blunt point was used for grubbing in the ground for roots. Secondly, it is possible that the narrowing of the anterior end of the lower jaw was to give freedom of action to a very mobile tongue, which gathered bunches of vegetable matter from the surface parts of the flora. The strong jaw musculature, which is indicated by the development of the lateral wing on the dentary, makes the first explanation somewhat more probable, but the problem remains as to how the (presumably vegetable) matter which had been excavated was broken up before swallowing. However, since little is known of the flora of the Permian, and thus of the possible plants upon which Kingoria may have fed, it is impossible to carry useful discussion beyond this point.

7. THE STRATIGRAPHY OF THE LOWER BONE-BEARING STRATUM

As mentioned in the introduction, the first detailed study in the Ruhuhu area and correlation with the South African series was made by Stockley (1932). The vertebrate fossils which he found were described by Haughton (1932); the fauna from the Lower Bone-Bearing Stratum led Haughton to conclude that it was homotaxial with the middle part of the Lower Beaufort Beds of South Africa, including parts of both the Endothiodon and Cistecephalus zones.

More extensive collecting in the area was made by Parrington in 1933. He was soon followed by Nowack, who stayed for a prolonged period (1934-36) in the area and made an extensive collection of reptilian remains. Though he could not make a systematic geological survey of the whole area, he was able to study in some detail the central part of the area between the Lihandje Mountains and the Ruhuhu Valley (Nowack, 1937). He states that the Lower Bone-Bearing Stratum consists of a succession of crumbly marls, with or without septarian-like nodules, and subordinate insertions of mixed coarse sandstones and conglomerates, and he distinguished three different modes of preservation and commented on the probable conditions of deposition.

Firstly, bones are found in stratified accumulations in a coarse clastic stone. This complex occurs in strata 9-12 ft. thick, extending for stretches of up to 300 ft. without, however, forming any continuous horizon. It indicates deposition in the mouth of a fast river, the bones being isolated and often strongly eroded fragments, and the deposits thus seem to be secondary, resulting from the erosion of shoals within which the original deposition had taken place. At one locality bone and fresh-water molluscs were found together in the coarse sandstone.

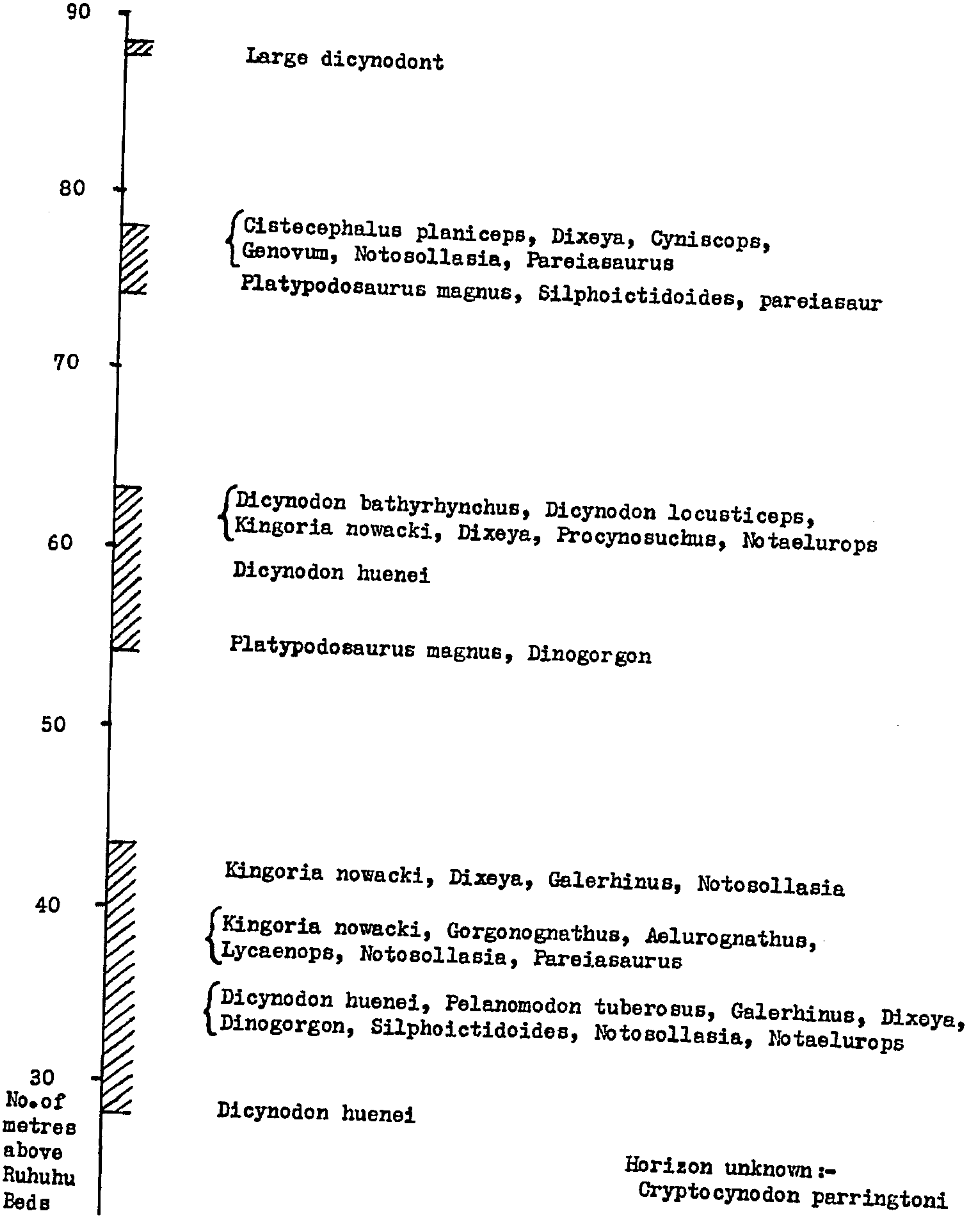
Secondly, bones are found in a yellow-grey marl. The bones are mostly post-cranial, usually dissociated and badly broken. These remains were probably deposited in a lake, and the deposits are again secondary; there are localised accumulations which represent the effect of current-action.

Thirdly, in some localities bone is contained in a proportion of the hard brownish-grey nodules of dolomitic limestone or siliceous mudstone. These nodules occur in bands in the marls or are found weathered-out; they contain most of the skull-fragments and sometimes contain whole skulls. Stockley (1932) states that they represent a slight halt in sedimentation.

Nowack gives a detailed description of profiles through the Lower Bone-Bearing Stratum at three localities, but he states that they show important differences from one another, and it is not possible to make an exact correlation between the various strata at each locality. At Kingori the Lower Bone-Bearing Stratum consists only of a complex of marls, whose profile does not show any sign of stratification, though the finds of fossils show some signs of there being three different bone-bearing levels in the complex (Nowack, 1937, p.403). At both Usili and Mpelisi there is a basal bone-bearing sandstone layer about 9 ft. thick. Though the bone deposits in the higher levels may have been laid down at approximately the same time in the different profiles, the occurrence and thickness of the various beds of sandstone and marl will have been so dependent upon quite local conditions of current that it is not possible to draw up a strict table of stratum-equivalence between the profiles. However, Nowack states that it is probable that the bone-conglomerate layers in the Usili and Mpelisi profiles are identical, and it is also probable that the basal thin bone-bearing sandstone layers found at each are identical.

Though it is thus not possible to subdivide the Lower Bone-Bearing Stratum on the basis of the stratification, it might be hoped that it would be possible to gain some idea of its range in time from a consideration of its fossil fauna. Most of these fossils were collected at Kingori, and Nowack's table (1937, p.403) shows at what level the different finds were made. von Huene, in three publications (1942, 1944, 1950) has described many of these fossils, giving Nowack's field numbers. By comparing these with Nowack's table it is possible to make a chart (Table 3) showing the fauna of each level at Kingori. Nearly all are forms whose affinities are with the Cistecephalus zone of South Africa - *Cistecephalus* itself, large dicynodonts without post-canine teeth, large gorgonopsids, the therocephalians *Notosollasia* and *Notaelurops*, the cynodont *Cynosuchus* and the parieasaurs *Anthodon* and *Parieasaurus*. The only exception is the small dicynodont *Cryptocynodon parringtoni*. This find is not indicated on Nowack's table or map, and its level of origin is therefore uncertain; von Huene (1942) says that, judging by the reddish colour of the matrix, the skull probably came from the lowest zone, slightly more than 30 m. above the Ruhuhu Beds. The genus *Cryptocynodon* was founded by Seeley (1895a) for the badly preserved anterior end of a dicynodont skull, it being characterised by having a row of post-canine teeth placed behind and internal to the canine; its horizon is unknown. Broili & Schröder (1935b) have provisionally placed another specimen in this genus, without assigning it a trivial name; it comes from the uppermost Endothiodon zone. Janensch (1952) has described another form, which he states is probably from the Upper Endothiodon zone and which he provisionally names *Cryptocynodon ? schroederi*, though he does not indicate that the post-canine teeth are internal

Table 3. The Fauna of Kingori



Shading indicates bone-bearing levels. Trivial names given for dicynodonts only.

to the canine; he states that the relationship of this form is uncertain. There is thus some evidence that the genus Cryptocynodon occurs in the Endothiodon zone, but it is quite possible that it might also extend up into the Lower Cistecephalus zone. von Huene (1942, p.184) states that in South Africa the dicynodonts possessing post-canine teeth are characteristic of the Endothiodon zone, but this is incorrect. Of the smaller genera of this group (i.e. those whose skulls are less than 130 mm. long) four come from the Tapinocephalus zone, one from this zone or the Endothiodon zone, six from the Endothiodon zone, two are found in both the Endothiodon and the Cistecephalus zones, and four come from the Cistecephalus zone.

Two additions to the fauna known from Kingori have been made by Boonstra (1953), who describes specimens of Rhachiocephalus ? and Neomegacyclops. The former genus is known from the Cistecephalus zone of South Africa. Three of the four known species of Neomegacyclops are from Tanganyika, but the genus is founded on the South African species N.whaitsi which Haughton & Brink, in their recent bibliography (1954), list as from the Endothiodon zone. However, the type specimen was originally stated to be from the Cistecephalus zone (Haughton, 1917). Furthermore, though the classification of the different genera of large tuskless dicynodonts which bear a pineal boss is rather confused, all definite evidence is that they are from the Cistecephalus zone. Kitchingia is from the Cistecephalus zone; it was originally separated (Broom & George, 1950) from Neomegacyclops because it appeared to lack a preparietal, but this bone was later found (Brink, in addendum to same paper). It is similar to Neomegacyclops in having a wide exposure of the parietal in the intertemporal bar, whereas the postorbitals meet above them in the midline in the other forms which have a pineal boss.

It therefore seems reasonable, the original reason for separating the two genera having proved incorrect, to refer Kitchingia planifrons (the only species of Kitchingia) to the genus Neomegacyclops as Neomegacyclops planifrons (Broom & George). Of the other genera, Rhachiocephalus and Platycyclops are known from the Cistecephalus zone of South Africa; Platypodosaurus magnus (of von Huene, 1942) comes from Kingori from a level which contains Cistecephalus; and the horizons of Pelorocyclops and Eocyclops are not known.

Thus the original ascription of the type specimen of Neomegacyclops, the horizon of another species which was formerly incorrectly placed in a different genus, and the horizons of other related genera, all indicate that Neomegacyclops is a form from the Cistecephalus zone or homotaxial horizons.

Since neither Cryptocynodon nor Neomegacyclops give any firm evidence of the presence at Kingori of a level equivalent to the Endothiodon zone of South Africa, it is apparent that such evidence for this locality is lacking. Furthermore, from the lowest level of the Lower Bone-Bearing Stratum at Kingori was collected a specimen of Dicynodon huenei (Platypodosaurus huenei of von Huene, 1942), a large dicynodont, itself of Cistecephalus zone affinities, which occurs in a slightly higher level with Pelanomodon, a genus which is definitely known from the Cistecephalus zone of South Africa. The lowest level at Kingori thus appears to be equivalent to the Cistecephalus zone of South Africa. However, the presence elsewhere in the Ruhuhu area of an horizon equivalent to the Endothiodon zone of South Africa is shown by the occurrence of endothiodont remains at Usili (Haughton, 1932) and Ruanda (Parrington, in discussion at end of Haughton, 1932). It therefore seems that the Endothiodon zone is represented at Usili but not at Kingori, and it may be relevant to note that the basal bone-bearing sandstone layer found at Usili is not present at Kingori. However, it is not known from what level in the beds the endothiodont remains originated.

8. REMARKS ON THE CLASSIFICATION OF THE AFRICAN PERMIAN DICYNODONTIA

General Introduction

Dicynodonts are known to have existed from the Middle Permian to the Upper Triassic. According to current classification, there are over 50 genera, one genus including over 100 species. The range of size is very great, the smallest skull being about 2 inches long and the largest 2½ feet long and, in addition, there is a considerable range of skull shape.

The present unsatisfactory state of the classification of the Dicynodontia is due partly to the fact that our knowledge of the detailed structure of the group is insufficient, and partly to the confusion of the relationships of different genera resulting from the occurrence of parallel evolution.

In many cases our only knowledge of the structure of a species is an inadequate drawing of the dorsal view of the skull, together with a short description of the sutural pattern in this region, and a statement as to the number of post-canine teeth and as to the presence or absence of canines. As a result, the classification of the Dicynodontia has been based upon the size, shape and structure of the skull in dorsal view and upon the dentition, together with such other occasional features as are available, such as the presence of bosses on the pineal or nasal regions. However, it has been shown in _Dicynodon grimbeeki_ and _D.sollasi_ (Toerien, 1954a) that there may be considerable variation in the detailed sutural pattern of the dorsal aspect of the skull within one species, and the extent of the infraspecific variation is quite unknown in other species. Similarly, the number of post-canine teeth (a feature commonly used as diagnostic in those genera in which they are present) has by Toerien (1954a) been shown to vary within a single genus -

and would in any case be expected to vary due to the reptilian method of alternate tooth-replacement.

The Major Groups of Dicynodonts

As far as those bearing post-canine teeth are concerned, it is clear that a definitive classification of the Dicynodontia will only be reached after a thorough investigation has been made of the exact dentition of each form, since in many cases only a partial lateral exposure of the dentigerous region has been made. The relationships of the smaller genera which do not (as far as is known) bear post-canine teeth must also await fuller investigation; they form a fairly compact group, ranging from the Upper Endothiodon zone into the Cistecephalus zone, and mainly characterised by their extremely broad intertemporal bar, a character developed to its most extreme form in Cistecephalus.

Excluding these forms, one is left with two main assemblages. The first consists of the genera Neomegacyclops, Eocyclops, Platycyclops, Rhachiocephalus, Pelorocyclops and Platycyclops (Kitchingia has been discussed in the preceding section and referred to the genus Neomegacyclops). All are large, tuskless, have a pineal boss and are from the Cistecephalus zone (for the horizon of Neomegacyclops see the discussion in the preceding section). Neomegacyclops is distinct in having a wide exposure of the parietals in the intertemporal bar. In all the other five genera the post-orbitals more or less meet in the midline to cover the parietals. It seems quite likely that these five genera are not really distinct from one another; otherwise very alike, they are distinguished by the composition of the pineal boss, which appears to be formed in varying proportions from however, it would seem reasonable to suppose that the formation of such a bony excrescence might vary considerably within a genus and possibly also within a species, so that the use of this as a generic character is suspect.

The only other dicynodont of comparable size and without post-canine teeth, *Dinanomodon*, is similar in the structure of the intertemporal bar but does not possess a pineal boss, the pineal foramen itself being reduced or lacking; it may be a form related to the above group but which has lost, or never possessed, the pineal boss.

The second assemblage, dicynodonts of moderate to large size, with or without tusks but lacking a pineal boss, includes the majority of all described. It consists of the *Dicynodon*-*Oudenodon* group (containing tusked and tuskless forms and extending from the Tapinocephalus zone to the base of the Lystrosaurus zone), and the Cistecephalus zone forms *Pelanomodon* (tuskless) and *Aulacephalodon* (tusked)[1]. Various relationships between these genera have been suggested, one basis being the belief that tuskless forms were usually only the female of tusked forms. However, no general statement as to the evidence for this supposition has hitherto been made, so one may next examine what evidence there may be on this point in the Dicynodontia as a whole.

The Status of Tusking as a Taxonomic Character

At both generic and specific levels it is often difficult to decide whether the form is tusked in both sexes, tuskless in both sexes, or whether it is sexually dimorphic in this character. This position results from the

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Footnote[1]: The correct spelling of this genus is as given above, Seeley (1898) having originated it as a sub-genus. Broom (1932) advanced it to the rank of a genus, but spelt it "*Aulacocephalodon*", a spelling which has since been almost invariably used.

fact that most species are described on the basis of one specimen only and, furthermore, many genera are themselves monospecific. It is obviously impossible to detect a sex-dimorphism on one specimen and, even if two or three specimens are known, all with tusks or all without tusks, it is still dangerous to come to any final conclusion. (It is, of course, probable that more specimens are known of many of these species, but such information is not available in the literature).

Excluding, for the moment, Dicynodon and Oudenodon, the only genera believed to be tusked in both sexes and in which the presence of tusks has been confirmed in a large number of specimens are Aulacephalodon, Lystrosaurus and Kannemeyeria, and the only genera believed on similar evidence to be tuskless in both sexes are Neomegacyclops, Platycyclops, Emydochampsa, Emydorhynchus, Pelanomodon and Cistecephalus.

The presence of tusks in males only has been described in seven genera, the evidence being as follows:

		No. of tusked specimens	No. of tuskless specimens	
Palemydops	platysoma	1	0	
"	rubidgeae	0	1	
"	minor	-	-	
Pristerodon	buffaloensis	2	1	
"	mckayi	1	1	
"	whaitsii	"some"	"some"	fide Broom 1932
"	agilis	0	1	
"	brachyops	0	1	
"	raniceps	0	1	

	No. of tusked specimens	No. of tuskless specimens	
Emydops longiceps	"some"	"some"	fide Broom 1913
" arctatus	0	1	
" kitchingi	0	1	
" longus	0	c. 10	
" microdon	0	1	
" minimus	0	1	
" minor	0	1	
" trigoniceps	0	1	
" platyceps	0	0	
" murraysburgensis	1	0	
Synostocephalus vanhoepeni	3	1	
Kingoria nowacki	2	8	
Robertia broomiana	Over a dozen skulls known, including both tusked and tuskless specimens		fide Boonstra 1948
Tropidostoma microtrema	Many skulls known, including both tusked and tuskless specimens		

Of these seven genera, the first three appear to be members of a single group, and it is possible that Synostocephalus should also be placed in this group. The description of Robertia makes it not impossible that it is another member of this group, but no dorsal view of the skull has been published. Tropidostoma and Kingoria are not closely related to the other genera.

It is apparent that there is evidence of at least three lines of dicynodonts, in which both tusked and tuskless forms occur, and we may now consider the evidence for the occurrence of such a sex-dimorphism in the

Dicynodon-Oudenodon group. The following is a complete list of the different species in which this has been reported, and the evidence for this in each.

D.trautscholdi Sushkin (1926a) thinks that D.rossica is the tuskless female of this species.

D.pygmaeus The type and another specimen from the same locality (Dunedin, Beaufort West) are tuskless, whilst a skull from Highlands, Beaufort West, is tusked (Haughton, 1917).

D.bolorhinus This species is founded on a very badly preserved specimen; Broom (1912c) states that Watson has obtained two further specimens from the type locality, one being tusked and the other tuskless.

O.huenei Broili & Schröder (1937) described four skulls from the same locality: one tusked (which they named D.huenei; this name being preoccupied, Boonstra (1948) renamed the species D.broilii); one tuskless (D.grossarthi); and two further skulls, one tusked and one tuskless, which they placed in the same species (D.broomi). Toerien (1954a) considers that all four specimens should be placed in the same species, Oudenodon huenei; if this ascription is correct, this species would then be known from both tusked and tuskless specimens.

D.ictidops Known from a number of skulls from Beaufort West Commonage. One tuskless and one in which a "small tusk which perhaps shows through the margin of the bone" (Broom, 1913).

D.vanderhorsti Toerien (1954a) refers 13 skulls to this species, 4 of them being tusked and the rest tuskless.

D.sollasi Over 20 skulls are known, all from the same locality (Toerien, 1954a); both tusked and tuskless forms are found, Toerien's tables showing 10 tusked and 11 tuskless.

D.grimbeeki Over 19 skulls are known, all from the same locality (Toerien, 1954a); 14 are tusked, 3 are tuskless, and in 2 there is a very small tusk in the caniniform process of the left side but no trace of a tusk in the right side. Broom (1936b) states that over 100 specimens are known from one locality, some tusked and some tuskless.

D.pseudojouberti Boonstra (1948) mentions 8 tusked and 12 tuskless specimens. The 150 skulls in the British Museum (Natural History), referred to by Watson (1948), would appear to belong to this species, as far as one can tell from Boonstra's figureless description of the species.

Thus only four species (D.vanderhorsti, sollasi, grimbeeki and pseudojouberti) show definite evidence of tusked and tuskless specimens in the Dicynodon-Oudenodon group. It seems possible that these species are related to the post-canine-bearing forms in which such a sex-dimorphism is established. Dicynodon pseudojouberti and Robertia broomiana were founded by Boonstra (1948) when he examined a large number of skulls which had been ascribed to the Tapinocephalus-zone form Dicynodon jouberti and found that some bore post-canine teeth and that others, though they did not bear such teeth, were still unlike Dicynodon jouberti. Thus Robertia from the Tapinocephalus zone may represent the single point of origin of such a sex-dimorphism, both the Pristerodon-Emydops-Synostocephalus group and the Dicynodon pseudojouberti, sollasi and grimbeeki group being derived from it. However this may be, there is at present insufficient evidence for assuming that such a sex-dimorphism is characteristic of the Dicynodon-Oudenodon group as a whole. Indeed, there is some evidence of species in which both sexes are tusked or both are tuskless. Thus in Dicynodon jouberti, Boonstra (1948) states that there are about 50 skulls, from various localities, all of them being tusked. The large species D.leoniceps is known from 9-10 skulls, from various localities, all of which are tusked. The large species D.huenei is known from 9 skulls, all from the Lower Bone-Bearing Stratum of Kingori, Tanganyika, and all tusked. A number of skulls of D.vanderbyli are known, all the large ones being tuskless - though this may be a sign of old age. Other species are known, which were formerly placed in the genus Oudenodon, and in which all the specimens are tuskless; however, as will be seen shortly, these forms may not really belong in the genus Dicynodon, where they were placed in the belief that they were the tuskless females of tusked Dicynodon species.

It is apparent that there are at present no grounds for any generalisations as to the deductions to be drawn from the presence or absence of tusks in specimens of the genus Dicynodon since, of the total of more than 80 species known, only eight give definite evidence on this matter, four showing a sex-dimorphism, three apparently being tusked in both sexes and one possibly being tuskless in both sexes. With this in mind, we may now return to examine the assemblage consisting of Dicynodon-Oudenodon, Pelanomodon and Aulacephalodon.

The Genera Aulacephalodon, Pelanomodon, Dicynodon and Oudenodon

On the basis of the tusking, it was for a while believed that the tusked Aulacephalodon was the female of the tuskless Pelanomodon; however, Broom & George (1950) dissented from this on the ground that, though Aulacephalodon was quite common, only three Pelanomodon skulls had been found, none of which could be the female of any species of Aulacephalodon. Though rather more Pelanomodon skulls are now known, it is in any case clear that the two genera are not thus related. On examination, the species of Aulacephalodon form compact group and, with two exceptions, are uniformly larger in size than Pelanomodon. Aulacephalodon laticeps (skull length 250 mm.) is within the ormal Pelanomodon size range (skull lengths 230 - 290 mm.), but Broom (1932) otes that this is presumably a young form. Pelanomodon wesselsi (skull ength 510 mm.) is far beyond the normal Pelanomodon size range, and is only just within the adult Aulacephalodon size range (skull lengths 330 - 510 mm.); owever, neither the figure nor the description of this form (Broom, 1948) how any reason for separating it from Dicynodon, and it may be relegated o that genus as Dicynodon wesselsi (Broom). Aulacephalodon and Pelanomodon lso differ in that only the latter possesses a laterally expanded squamosal, nd only the former possesses the large boss on the sub-orbital bar which he writer has suggested earlier as marking the point of origin of the asseter muscle. In possessing this boss Aulacephalodon is similar to the soterodon-Endogomphodon-Emydochampsa group; this group, which possesses ost-canine teeth, comes from the Endothiodon zone and, though they all ossess a pineal boss, it is possible that the group is related to lacephalodon.

Having thus recognised Aulacephalodon and Pelanomodon as recognisably eparate genera, one may now turn to the relationship between Oudenodon and icynodon. It has long been recognised that the genus Dicynodon, with ver 100 species, is merely a convenient repository for any specimens which re not sufficiently distinct to allow of being placed in a different genus. contains both tusked and tuskless specimens; some of the latter were at e time placed in a separate genus Oudenodon, until Broom (1912c) stated that these were merely female forms of *Dicynodon*. However, though many specimens have been described, it has not been found generally possible to make pairings of tusked and tuskless skulls, alike in all except this character, to form a single species showing both male and female forms. Though, as mentioned earlier, there is some variation in the sutural pattern of the dorsal surface of the skull, it seems unlikely that this would be so great as to prevent such pairings being made within the very large number of skulls of *Dicynodon* that have now been collected. It therefore seems reasonable to enquire as to whether it may not be possible to recognise some, at least, of the tuskless forms as really forming a distinct group.

The forms which had originally been placed in the old genus *Oudenodon* were first compared, after deleting *O.pithecops* and *O.raniceps* which had been referred to the genus *Pristerodon* (Broom, 1913, 1915a), and *O.strigiceps* which had been referred to the genus *Emydopsis* (Broom, 1921). *O.pusillus* (Jaekel, 1904) was also deleted, since Jaekel himself notes that it bore a canine tooth; it may be referred to the genus *Dicynodon* as *Dicynodon pusillus* (Jaekel). It was soon realised that there was, within the remaining forms, a distinct group consisting of *O.bainii* (Owen, 1860), *O.kolbei* (Broom, 1912a), *O.margaritae* (van Hoepen, 1934) and *O.marlothi* (Broili & Schröder, 1936b). This group can be distinguished as follows: the snout is extremely short, the post-orbital bar therefore being far forward; all have a prefrontal; the interorbital region is narrow; the pineal foramen is usually rather large; the intertemporal bar is wide, consisting of a slightly concave wide expanse of the parietals, bordered on each side by a slightly downwardly-sloping component from the postorbital bone; there is a smooth transition from the intertemporal bar onto the occiput; in side view, the snout is rounded but very blunt; there are no tusks; where the horizon is known, it is Cistecephalus zone; the skull size ranges from a length of 144 mm. with a breadth of c.120 mm., to a length of 325 mm. with a breadth of 280 mm.

With this in mind, the published figures of the tuskless "*Dicynodon*" skulls were next examined, to ascertain whether any of these properly belonged in the apparently valid genus *Oudenodon*. The published figure of *Dicynodon hartzenbergi* (Broom, 1940) is almost identical with that of *Oudenodon margaritae* (van Hoepen, 1934), there being only a slight difference in skull size. The skull of *Dicynodon halli* (Watson, 1914) in the British Museum (Natural History) (catalogue no. R 4067) was examined and found clearly also to belong to the genus *Oudenodon*. From the published figures, *Dicynodon corstorphinei* (Broom & Haughton, 1917), *D.mustonis* (Haughton, 1915a), the Rhodesian form *D.euryceps* (Boonstra, 1938) and the fragmentary forms *D.breviceps* (Haughton, 1915a), *D.andrewsi* (Broom, 1921) and *D.leptoscelus* (Broom, 1932) were considered also to belong in this genus, and possibly also *D.maccabei* (Broom, 1940). *D.platyceps* (Broom, 1913) is also similar in skull structure, but the smaller, presumably younger, skulls of this species are tusked (Broom, 1948); this would seem to indicate that the absence of tusks in some adult dicynodonts is achieved by the non-replacement of the milk-canines, rather than by a complete failure of the canines to develop at any stage.

This identification of species considered to belong to the genus *Oudenodon* was done wholly on the outline of the skull in dorsal and lateral view, and it is of interest to note that Toerien (1954a) has recently also suggested reviving the genus *Oudenodon*, basing this on the structure of the palate, the palatines and premaxillae having a long sutural contact in *Oudenodon* but no contact in *Dicynodon*. On this basis, he believes that the following forms belong in the genus *Oudenodon*: *O.margaritae*, *O.marlothi* and *D.platyceps*; *O.kolbei* also possesses this type of palate (Broom, 1912a), and the writer has also found that the type-specimen of *Oudenodon*, *Oudenodon bainii* (Owen, 1860), has this type of palate. However, Toerien also believes that *Dicynodon grossarthi* (Broili & Schröder, 1937) and *Dicynodon sollasi* of von Huene (1922) belong to this genus. *D.sollasi* is tusked and, though *D.grossarthi* is tuskless, Toerien considers that it is synonymous with the tusked *Dicynodon huenei* (Broili & Schröder, 1937); his genus *Oudenodon* would therefore include a species in which he believes both tusked and tuskless forms to occur. However, all three specimens are much smaller than the other species mentioned, and very different from them in skull proportions, while the figured palates of these species are quite unlike that of any other dicynodont, the palatines of *D.grossarthi* extending very far forwards between the premaxillae and maxillae, while the palatine of *D.sollasi* nearly reaches the border of the alveolus of the canine. It seems to the writer unlikely that these two species belong in the genus *Oudenodon*.

The addition of palatal characters as an aid to understanding the evolution of the Dicynodontia is to be welcomed, but its use as the sole criterion of relationship seems as undesirable as was the former exclusive use of the sutural pattern of the dorsal aspect of the skull. There is much overlapping of the bones of the palate in this group, so that any loss of bone during preparation may radically alter the visible pattern of bone relations. Indeed, though few palates are known in detail, that of

Propelanomodon devilliersi (Toerien, 1956) is markedly asymmetrical. The presence or absence of a contact between the premaxilla and the palatine seems to be unreliable as a distinction between *Dicynodon* and *Oudenodon*; the large tusked species *Dicynodon huenei* has an extensive contact between the two bones, while in the large species *Dicynodon leoniceps* the two bones just touch, and Toerien has therefore placed this form in a separate genus, *Daptocephalus*.

Though some species of *Dicynodon* have above been relegated to *Oudenodon*, the genus *Dicynodon* nevertheless remains unmanageably large, with over 100 species[1]. The present basis for division into species is, in general, only the shape and sutural pattern of the skull in dorsal view. As mentioned earlier, Toerien (1954a) has shown that the sutural pattern may vary considerably within a single species. The shape of the skull is in many cases only imperfectly known, since the edges of the squamosal are commonly damaged; also, in a genus which includes specimens of skull length from 50 mm. to 550 mm., it is to be expected that some of the differences in skull outline might be due to allometric growth. The basis of the taxonomy of the genus is thus questionable, and it is likely that a comprehensible picture will only emerge when more detailed investigations have been made on large numbers of skulls of a single species, to find both the limits of variation and the changes that occur in skull proportions during growth.

Footnote[1]: Toerien (1954b) has renamed *Dicynodon anneae* of Broom (1940), giving it the new name *Dicynodon whitsonae*. His reason for this is that he believes that Broom's trivial name is identical with that given to a species of *Gordonia* by Amalitzky & Karpinsky (1922) and later referred to the genus *Dicynodon* by Sushkin (1926a). However, the trivial name given by Amalitzky & Karpinsky, and followed by Sushkin, was "annae", not "anneae", so that the species named by Broom in 1948 may still correctly be referred to as *Dicynodon anneae* Broom.

9. LIST OF TAXONOMIC CHANGES

A new genus, *Kingoria*, has been established. *Dicynodon nowacki* (von Huene, 1942) is transferred to the new genus as its type species, *Kingoria nowacki* (von Huene), and *Dicynodon galecephalus* (Broom & Robinson, 1948) is also transferred to it as *Kingoria galecephalus* (Broom & Robinson).

The genus *Kitchingia* (Broom & George, 1950) is shown to be invalid, and its single species is transferred to the genus *Neomegacyclops* as *Neomegacyclops planifrons* (Broom & George). It is considered likely that *Neomegacyclops* is from the Cistecephalus zone, not from the Endothiodon zone.

It is considered likely that the original establishment of the genus *Oudenodon*, by Owen (1860), was valid, and that it does not merely represent the tuskless female of the genus *Dicynodon*. The genus is considered to include the species *O.bainii* Owen, *O.kolbei* Broom, *O.margaritae* van Hoepen and *O.marlothi* Broili & Schröder. It is considered likely that *Dicynodon hartzenbergi* Broom is another specimen of *Oudenodon margaritae*, and that *Dicynodon andrewsi* Broom, *D.breviceps* Haughton, *D.corstorphinei* Broom & Haughton, *D.euryceps* Boonstra, *D.halli* Watson, *D.leptoscelus* (Seeley) and *D.mustonis* Haughton, and possibly also *D.maccabei* Broom and *D.platyceps* Broom, belong in the genus *Oudenodon*.

Udenodon pusillus of Jaekel (1904) is referred to the genus *Dicynodon* as *Dicynodon pusillus* (Jaekel).

Pelanomodon wesselsi (Broom, 1948) is transferred to the genus *Dicynodon* as *Dicynodon wesselsi* (Broom).

Platypodosaurus huenei of von Huene (1942) is returned to its original ascription (Haughton, 1932) to the genus *Dicynodon* as *Dicynodon huenei* Haughton.

In the belief that the trivial name of *Dicynodon anneae* (Broom, 1940) was homonymous with the trivial name of *Dicynodon annae* (of Sushkin, 1926a, from *Gordonia annae* of Amalitzky & Karpinsky, 1922), Toerien (1954b) had renamed the former *Dicynodon whitsonae*; since these two names are not homonymous, the specific name *Dicynodon anneae* Broom may be retained, *Dicynodon whitsonae* being synonymous with it.

The spelling of the genus commonly referred to as "*Aulacocephalodon*" is corrected to *Aulacephalodon*, the latter being its original form proposed by Seeley (1898).

10. SUMMARY

1. Certain dicynodont remains collected by Mr. F. R. Parrington in 1933 from the Lower Bone-Bearing Strata of the Ruhuhu area of South-West Tanganyika have been examined, using the acetic acid technique.
2. A new genus, *Kingoria*, is proposed and defined. The genus contains both tusked and tuskless specimens, these presumably being the males and the females, respectively. Some tuskless specimens of the genus were originally described by von Huene as *Dicynodon nowacki*, and the type species of the new genus is therefore *Kingoria nowacki* (von Huene). *Dicynodon galecephalus* Broom & Robinson, from the Cistecephalus zone of South Africa, has been found also to belong to the new genus.
3. A detailed written and illustrated account is given of *Kingoria*.
4. *Kingoria* is most clearly distinguished from the other genera of dicynodonts by the characters of its lower jaw, palate and pelvis.

   (a) The anterior end of the dentary forms an upwardly-curving, blunt, tapering "beak", and the postero-lateral surface of the dentary bears a prominent ridge.

   (b) The palatal surface of the premaxilla does not bear the pair of stout anterior ridges found in many genera of dicynodonts, but has a pair of more lateral low sharp ridges.

   (c) The ischium and pubis are posterior to the ilium, which does not extend behind the level of the acetabulum. The fourth sacral rib contacts the antero-dorsal corner of the ischium.

. On the occiput of *Kingoria*, a well-developed process, named the tympanic process, was found extending posteriorly from the distal end of the paroccipital process. The possibility of this process having had a function concerned with the occipital musculature, the jaw-opening musculature, or the tympanum, are discussed in turn.

6. In the course of the reconstruction of the occipital musculature, a new theory is suggested as to the evolution of the muscles which run between the atlas-axis complex and the occiput in mammals.

7. In the course of the reconstruction of the jaw-opening musculature, the differing interpretations of Watson and Parrington as to the identity of the ventrally directed process of the articular bone are reconciled.

8. The tympanic process does not appear to have been associated with either the occipital or the jaw-opening musculature, and it is suggested that it held the dorsal border of the tympanic membrane. It is thought that a groove in the edge of the squamosal just above the quadrate condyle may represent the position of the external auditory meatus. The stapes of _Kingoria_ bears a facet which may have been for the attachment of an extrastapedial cartilage.

9. The available specimens and the literature of the dicynodonts have been examined to find how far the condition of the auditory region of _Kingoria_ was typical of the group as a whole. The presence of a tympanic process in the small Tapinocephalus zone form _Dicynodon pseudojouberti_ makes it appear possible that it was a character possessed primitively by the Dicynodontia, but no clear trace of it could be found in several large Triassic genera (_Kannemeyeria_, _Stahleckeria_, _Placerias_), nor in the semi-aquatic genus _Lystrosaurus_, nor in the burrowing genus _Cistecephalus_. Conditions in these genera may have been unusual owing to their great size or unusual habitat.

10. The structure passing through the post-temporal fossa in reptiles is identified as the vena capitis dorsalis. Markings on the anterior face of the prootic show that this vein ran into the braincase at a notch in the dorso-anterior margin of the prootic. The functions of the more extensive system of grooves found in the cynodonts is discussed.

11. The braincase of Kingoria is very solidly built; there is no unossified zone, and there could have been no kinetic movement, nor could the quadrate have moved relative to the squamosal.

12. Kingoria has a single sphenethmoid ossification, not divided into orbitosphenoid and mesethmoid, and shows no ossification equivalent to a presphenoid.

13. Kingoria has six cervical vertebrae; this is the first occasion on which conclusive evidence of the number of cervical vertebrae in a dicynodont has been found.

14. In the dorsal vertebrae of Kingoria the upper part of the transverse process becomes free of the attachment of the tubercular head of the rib and forms a blunt, rounded, dorso-laterally directed process, which is called a metapophysis. Comparison with specimens and figures of the vertebrae of other dicynodonts shows that these processes may be normal in the group. They were presumably for muscular attachment.

15. The cervical and anterior dorsal ribs of Kingoria are double-headed, while the more posterior dorsal ribs are single-headed and appear to attach to the side of the centrum. There appears, from the literature, to be some variation in the Dicynodontia as to the structure of the rib-heads and the positions of their attachments.

16. There is no cleithrum in Kingoria, and a survey of the literature shows that this bone is definitely known only in one unidentified dicynodont, in Cistecephalus and in Kannemeyeria. It is possible that its absence is a more general feature in the Dicynodontia than had been thought.

17. The scapula of Kingoria bears a well-developed spine along its antero-external edge.

18. It is unlikely that there could have been any bony connection between the two halves of the pelvis of Kingoria. A survey of the literature shows that the only evidence of a pelvic symphysis in the Dicynodontia is the report of a short contact between the ischia in Lystrosaurus, and it is possible that the absence of a pelvic symphysis is an usual feature in the group.

19. The probable musculature of the girdles is discussed. It seems likely that a small supraspinatus muscle, but no infraspinatus muscle, was present attached to the scapula, and that an iliacus component of the pubo-ischio-femoralis muscle had gained an attachment on the ilium.

20. The probable mode of life of Kingoria is uncertain; it was probably herbivorous, and may have rooted in the ground for its food.

21. Study of the fossil fauna of Kingori shows that the whole of the Lower Bone-Bearing Stratum at this locality is probably equivalent to the Cistecephalus zone of South Africa, though a level equivalent to the Endothiodon zone of South Africa may be present at some other localities in the Ruhuhu area.

22. The classification of the African Permian Dicynodontia is discussed. The reliability of the presence or absence of canine tusks as a taxonomic character is examined; it is found that in some genera tusks were

probably present in both male and female, that in other genera both male and female were probably tuskless, and that in other genera it is probable that the male was tusked and the female was tuskless. In the genus *Dicynodon*, some species were apparently tusked in both sexes, while in other species only the male bore tusks. Though various species in which neither sex bore tusks have in the past been placed in the genus *Dicynodon*, it is considered that these species together form a group recognisably distinct from *Dicynodon* in the osteology of the skull, and Owen's original erection of a separate genus, *Oudenodon*, for them is considered to be justified.

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Notes to Figures

Except where otherwise stated, all figures are natural size.

A thick continuous outline indicates that the edge of the bone is undamaged except for very minor losses of bone. A thin continuous line indicates that the preserved edge of the bone at this point is damaged and does not represent its original outline; this is bordered externally by a broken line, which indicates what appears likely to have been the original outline of the bone. In Figure 13 a dotted line has been used to indicate bone outlines whose exact positions are uncertain due to a thin layer of matrix.

Bilaterally symmetrical specimens have been drawn from the right side. In the case of paired bones, those of the right side have been illustrated; exceptions were made for the atlas neural arch, the coracoid plate and the scapula, as only a portion of those of the right side were preserved.

The shading convention employed has been that the specimen is illuminated from the upper right-hand side.

The abbreviations of the names of bones have been inserted in capital letters; the key to these abbreviations is to be found on the next page. The abbreviations of the names of structures have been inserted in small letters; the key to these abbreviations is to be found on the explanatory pages facing the figures.

Key to Abbreviations of Names of Bones

A	Angular
ART	Articular
BO	Basioccipital
CL	Clavicle
CO	Coracoid
D	Dentary
ECT	Ectopterygoid
EPT	Epipterygoid
F	Frontal
ICL	Interclavicle
IL	Ilium
IP	Interparietal
IS	Ischium
J	Jugal
L	Lacrimal
MX	Maxilla
N	Nasal
OP	Opisthotic
P	Parietal
PAL	Palatine
PCO	Precoracoid
PMX	Premaxilla
PO	Postorbital
PP	Preparietal
PR.ART	Prearticular
PRF	Prefrontal
PRO	Prootic
PSP	Parasphenoid-basisphenoid complex
PT	Pterygoid
PU	Pubis
Q	Quadrate
QJ	Quadratojugal
SA	Surangular
SMX	Septomaxilla
SO	Supraoccipital
SPL	Splenial
SQ	Squamosal
STA	Stapes
T	Tabular
V	Vomer

Figure 1

Kingoria nowacki, specimen no. 84

A. Dorsal view of skull

B. Section through interorbital bar 1 cm. in front of pineal foramen, seen from behind.

Abbreviations:-

p.te.fs	post-temporal fossa
XII	foramen for hypoglossal nerve

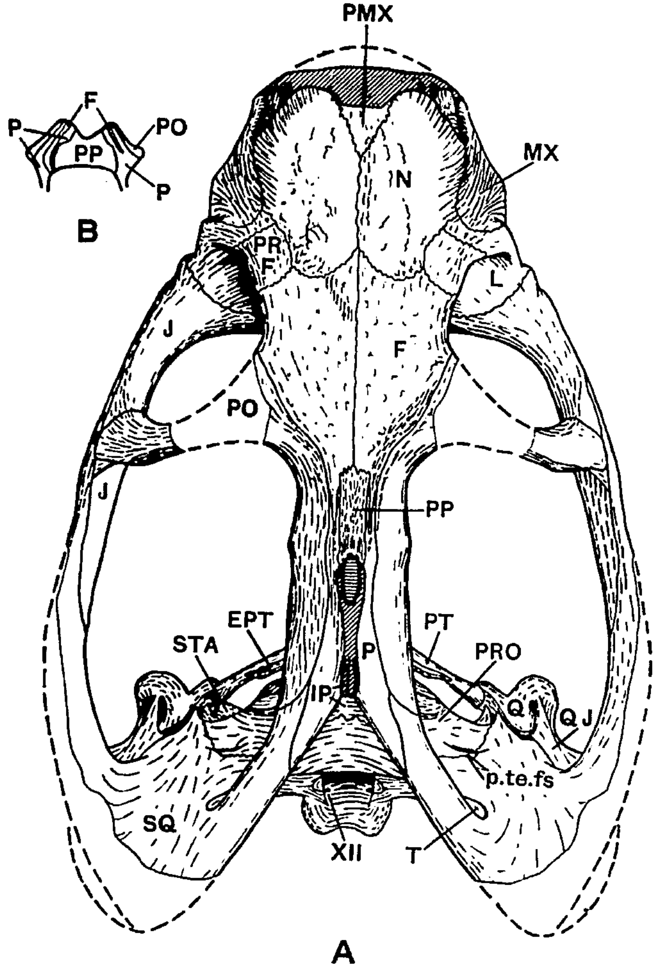
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Figure 1

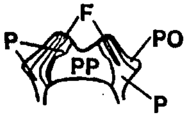
Kingoria nowacki, specimen no. 84

A. Dorsal view of skull

B. Section through interorbital bar 1 cm. in front of pineal foramen, seen from behind.

Abbreviations :-

p.te.fs	post-temporal fossa
XII	foramen for hypoglossal nerve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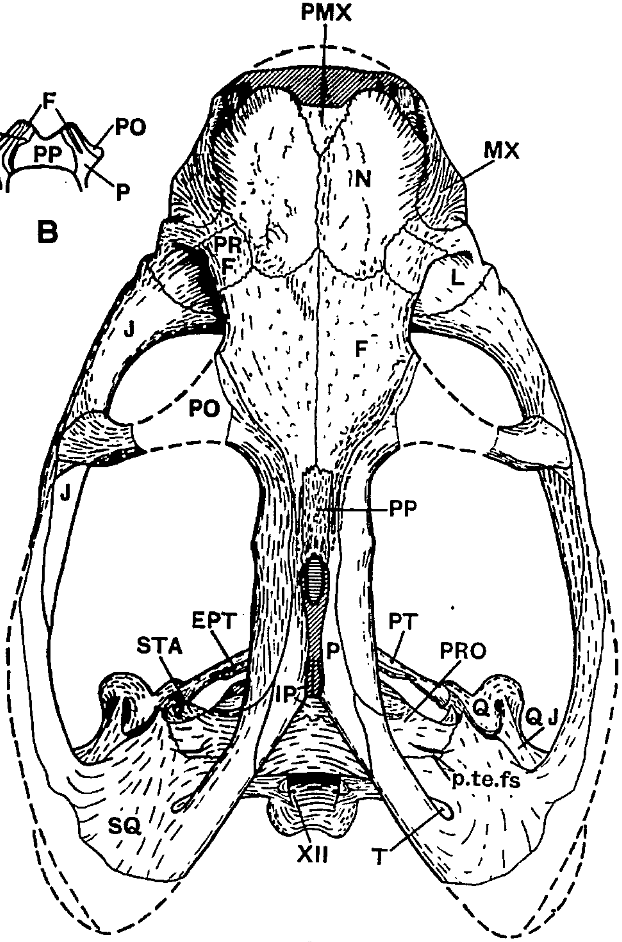
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Figure 2

Kingoria nowacki, specimen no. 84

Occipital view of skull

Abbreviations :-

j.f	jugular foramen
par.pr	paroccipital process of opisthotic
p.te.fs	post-temporal fossa
tymp.proc	tympanic process

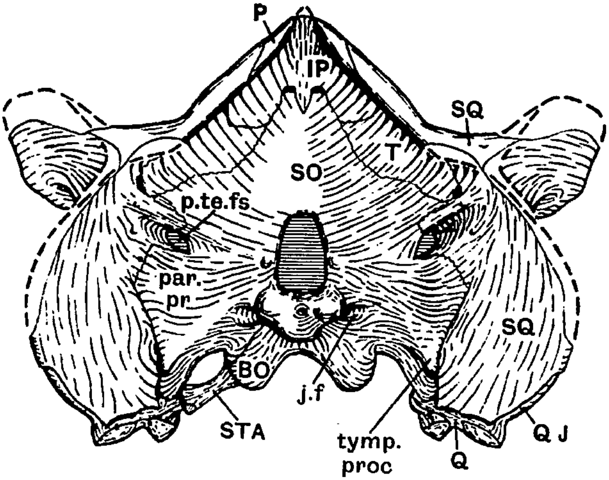
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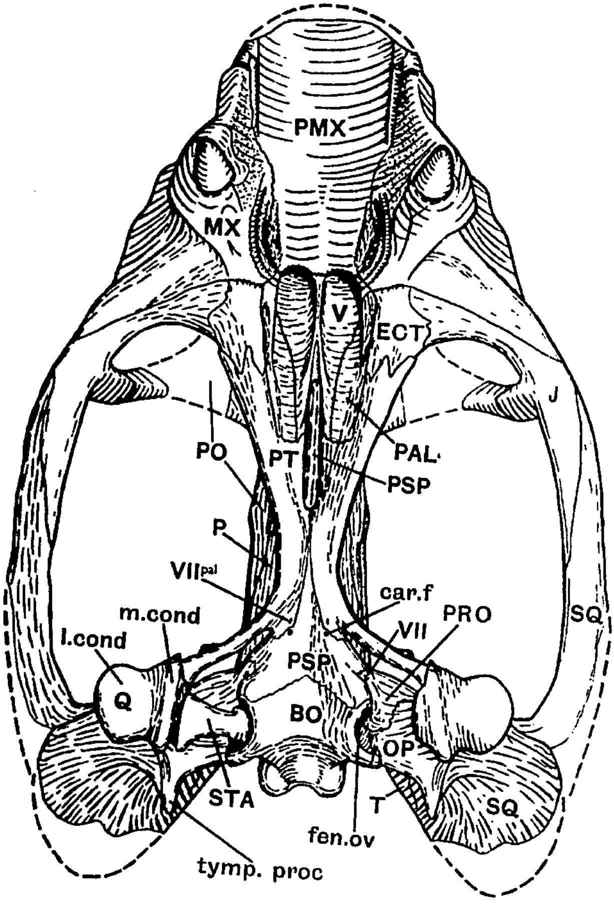
Figure 3

Kingoria nowacki, specimen no. 84

Palatal view of skull

Abbreviations :-

car.f	carotid foramen
fen.ov	fenestra ovalis
l.cond	lateral quadrate condyle
m.cond	medial quadrate condyle
tymp.proc	tympanic process
VII	foramen for facial nerve
VII^{pal}	foramen for palatine branch of facial nerve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tymp. proc

Figure 4

Kingoria nowacki, specimen no. 84

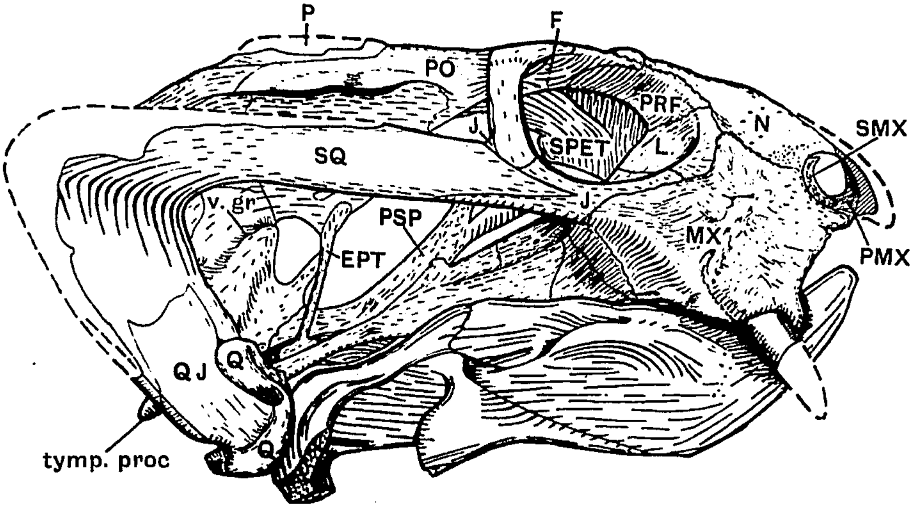
A. Side view of skull

B. Side view of skull after removal of zygomatic and post-orbital arches

C. Side view of sphenethmoid

Abbreviations:-

p.ant	pila antotica
p.cult	processus cultriformis of parasphenoid
tymp.proc	tympanic process
v.gr	venous groove
vom.fac	facet for vomer
VII	foramen for facial nerve
$\mathrm{VII}^{\mathrm{pal}}$	foramen for palatine branch of facial nerve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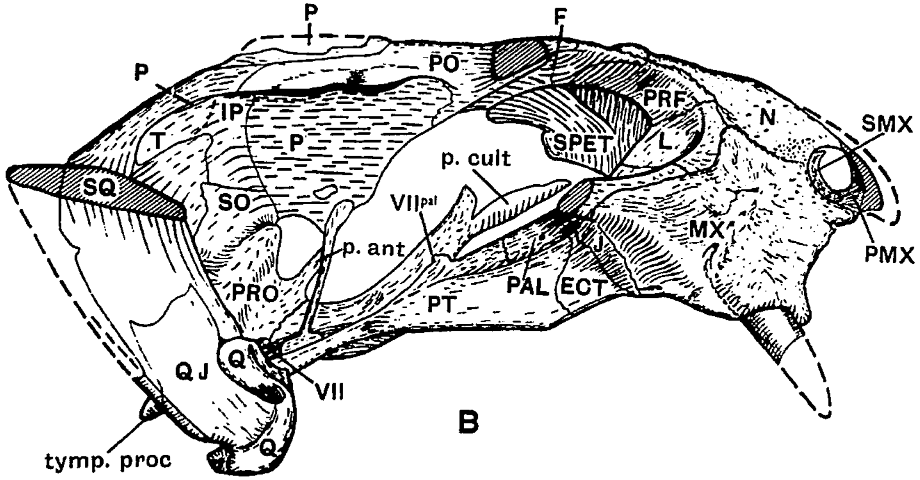
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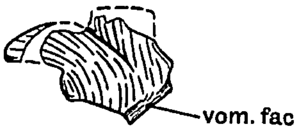
vom. fac

C

Figure 5

Kingoria nowacki, specimen no. 84

Anterior view of hind part of skull

Abbreviations :-

p.te.fs	post-temporal fossa
q.f	quadrato-jugal foramen
VII	foramen for facial nerve

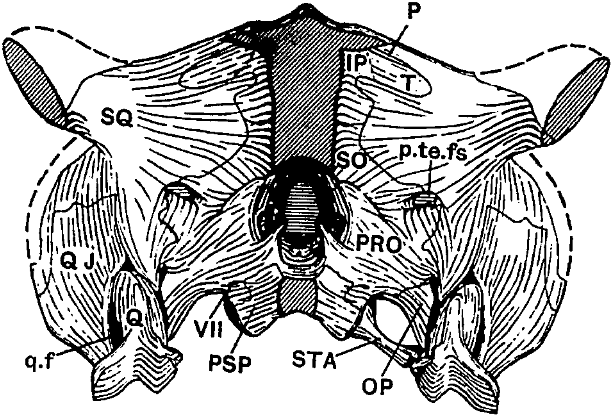
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Figure 6

Kingoria nowacki, specimen no. 84

Stapes, x2½

A-F, left stapes   G-K, right stapes

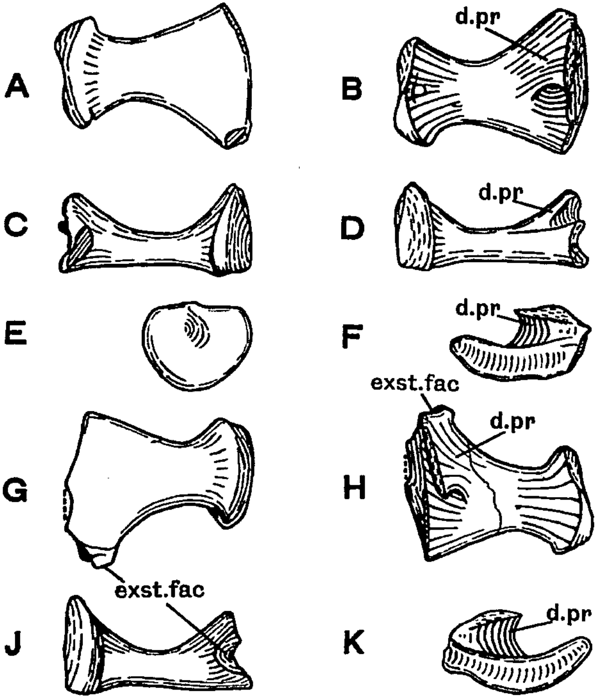
A,G, ventral views   B,H, dorsal views   C,J, posterior views

D, anterior view   E, proximal view   F,K, distal views

Proximal end to left in A and B, to right in G and H. Dorsal side uppermost in remainder.

Abbreviations :-

d.pr	dorsal process
exst.fac	facet for extrastapes


A
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B
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G
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H
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J
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K

Figure 7

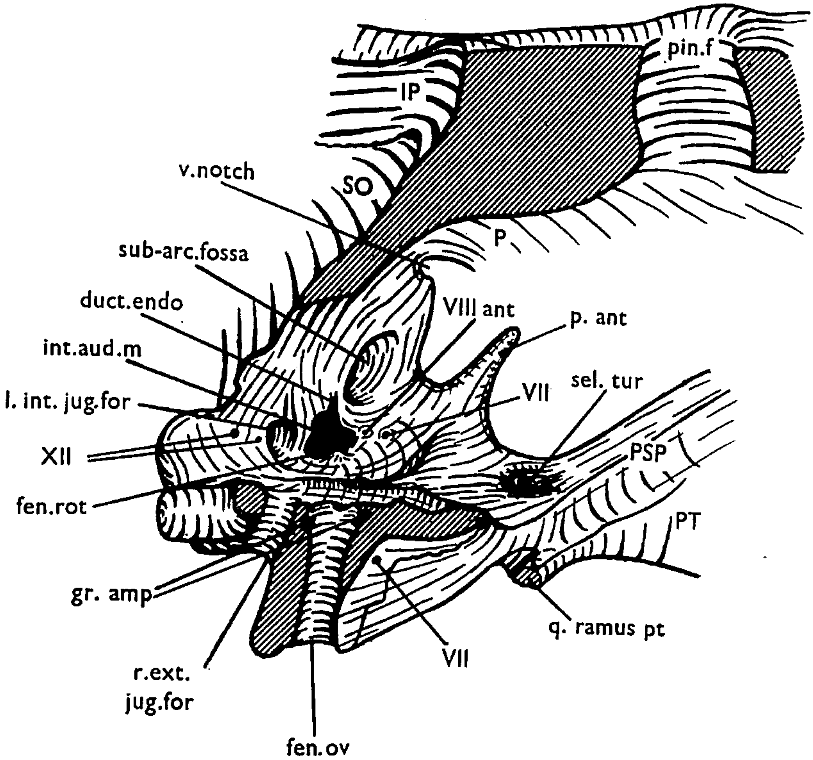
Kingoria nowacki, specimen no. 84

Braincase, x 1½

View from right side Dorsally the section passes along the midline, ventrally it runs through the right jugular canal and the vestibule of the right inner ear.

Abbreviations :-

duct.endo	ductus endolymphaticus
fen.ov	fenestra ovalis
fen.rot	fenestra rotunda
gr.amp	grooves leading to ampullar recesses
int.aud.m	internal auditory meatus
l.int.jug.for	internal opening of left jugular foramen
p.ant	pila antotica
pin.f	pineal foramen
q.ramus pt	quadrate ramus of pterygoid (cut)
r.ext.jug.for	external opening of right jugular foramen
sel.tur	sella turcica
sub-arc.fossa	sub-arcuate fossa
v.notch	venous notch
VII	foramen for facial nerve
VIIIant	foramen for anterior ramus of auditory nerve
XII	foramina for hypoglossal nerves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gr. amp
q. ramus pt
VII
r.ext. jug.for
fen.ov

Figure 8

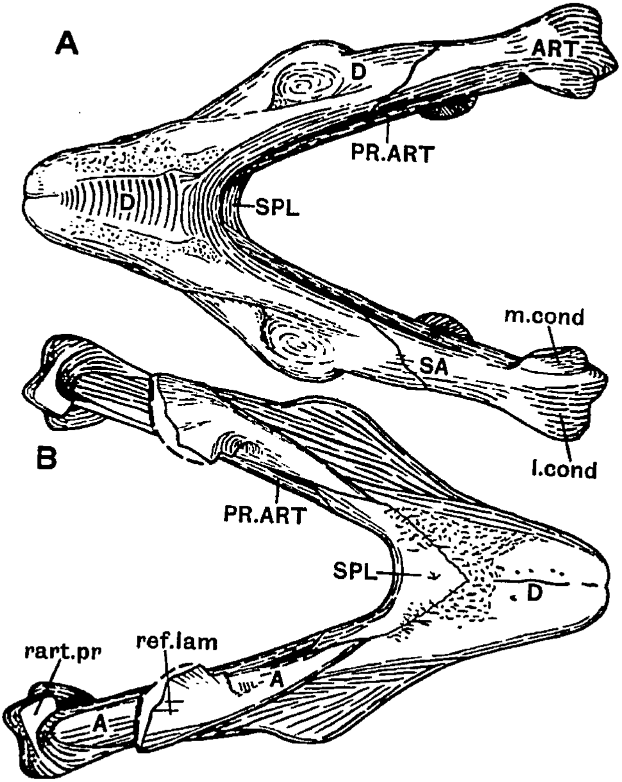
Kingoria nowacki, specimen no. 84

A. Dorsal view of lower jaw

B. Ventral view of lower jaw

Abbreviations :-

l.cond	lateral articular condyle
m.cond	medial articular condyle
rart.pr	retro-articular process
ref.lam	reflected lamina of angular



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A

Figure 9

Kingoria nowacki, specimen no. 84

A. Lateral view of right ramus of lower jaw

B. Medial view of left ramus of lower jaw

C. Posterior view of left articular region

D. Anterior view of section taken through left ramus of lower jaw at level X-X on figure B

Abbreviations :-

l.cond	lateral articular condyle
m.cond	medial articular condyle
meck.fac	facet for posterior end of Meckel's cartilage
rart.pr	retro-articular process
ref.lam	reflected lamina of angular

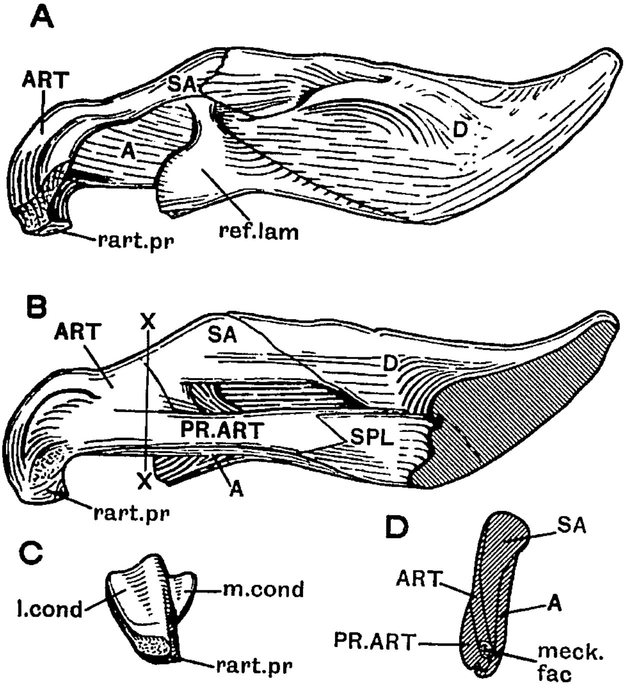
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Figure 10

Kingoria nowacki, specimen no. 82

A-F, right proatlas

G-L, left atlas neural arch

M-R, axis (with right atlas neural arch added in all except N)

A,G,M, anterior view B,H,O, posterior view
C,I,N,Q, lateral view D,J, medial view
E,K,R, dorsal view F,L,P, ventral view

Abbreviations:-

ax.fac	facet for axis
con.fac	facet for occipital condyle
intc.fac	facet for atlas intercentrum
n.sp	neural spine

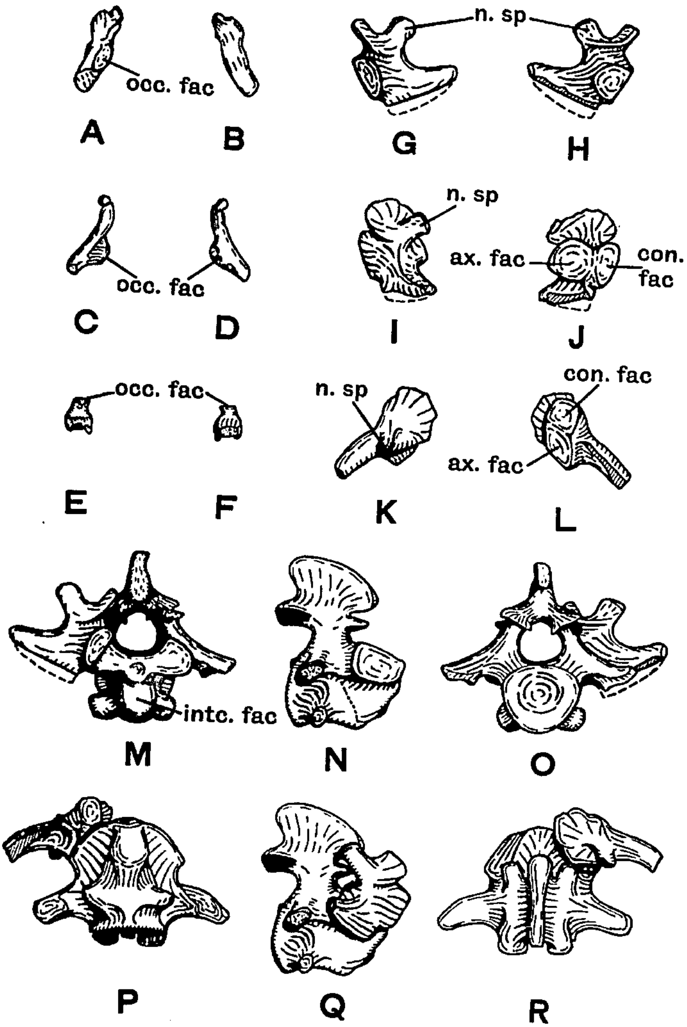

occ. fac
A
B
n. sp
G
H
occ. fac
C
D
n. sp
ax. fac
con. fac
I
J
occ. fac
n. sp
con. fac
ax. fac
E
F
K
L
intc. fac
M
N
O
P
Q
R

Figure 11

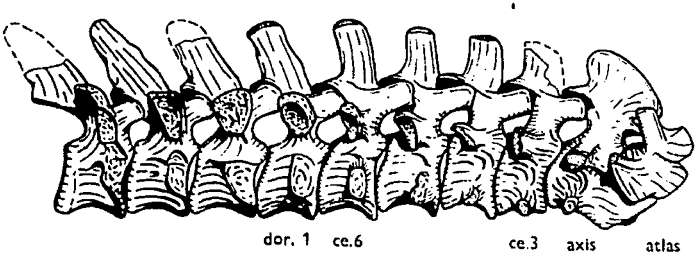
Kingoria nowacki, specimen no. 82

A. Lateral view of cervical and anterior dorsal vertebrae

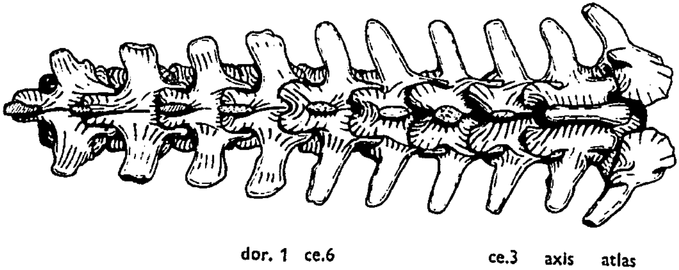
B. Dorsal view of cervical and anterior dorsal vertebrae

Abbreviations :-

ce.	cervical vertebra
dor.	dorsal vertebra



A



B

Figure 12

Kingoria *nowacki*, specimen no. 82

A,E,I, third cervical vertebra

B,F,J, sixth cervical vertebra

C,G,K, second dorsal vertebra

D,H,L, eighteenth dorsal vertebra

A-D, anterior views

D-H, posterior views

I-K, ventral views

L, dorsal view

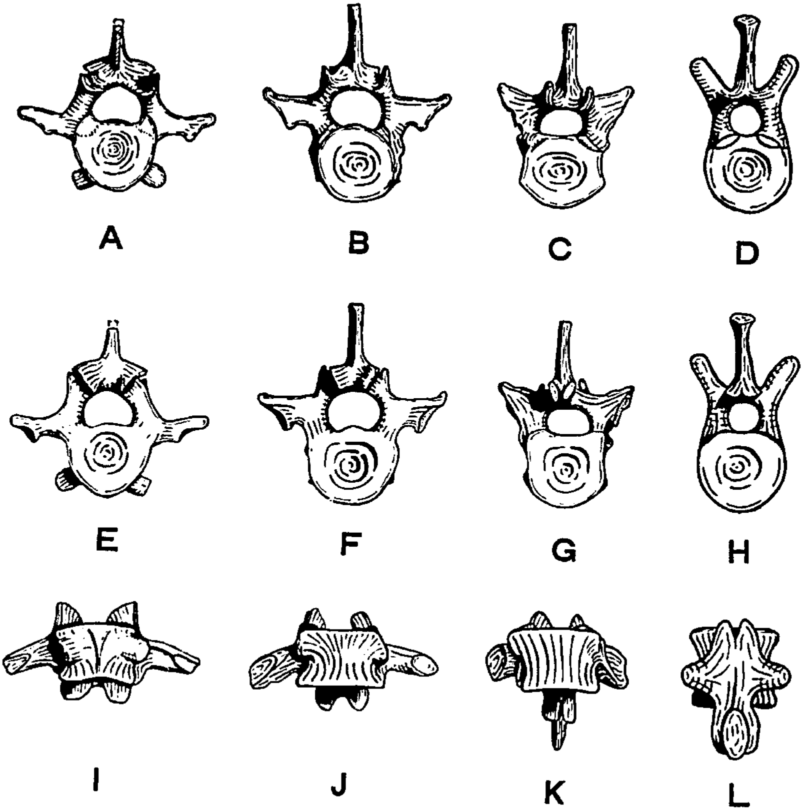

A
B
C
D
E
F
G
H
I
J
K
L

Figure 13

Kingoria nowacki, specimen no. 82

A. Lateral view of vertebrae from block A

B. Lateral view of vertebrae from block B

C. Lateral view of vertebrae from block C

Abbreviations :-

ca.	caudal vertebra
ce.	cervical vertebra
dor.	dorsal vertebra
sa.	sacral vertebra

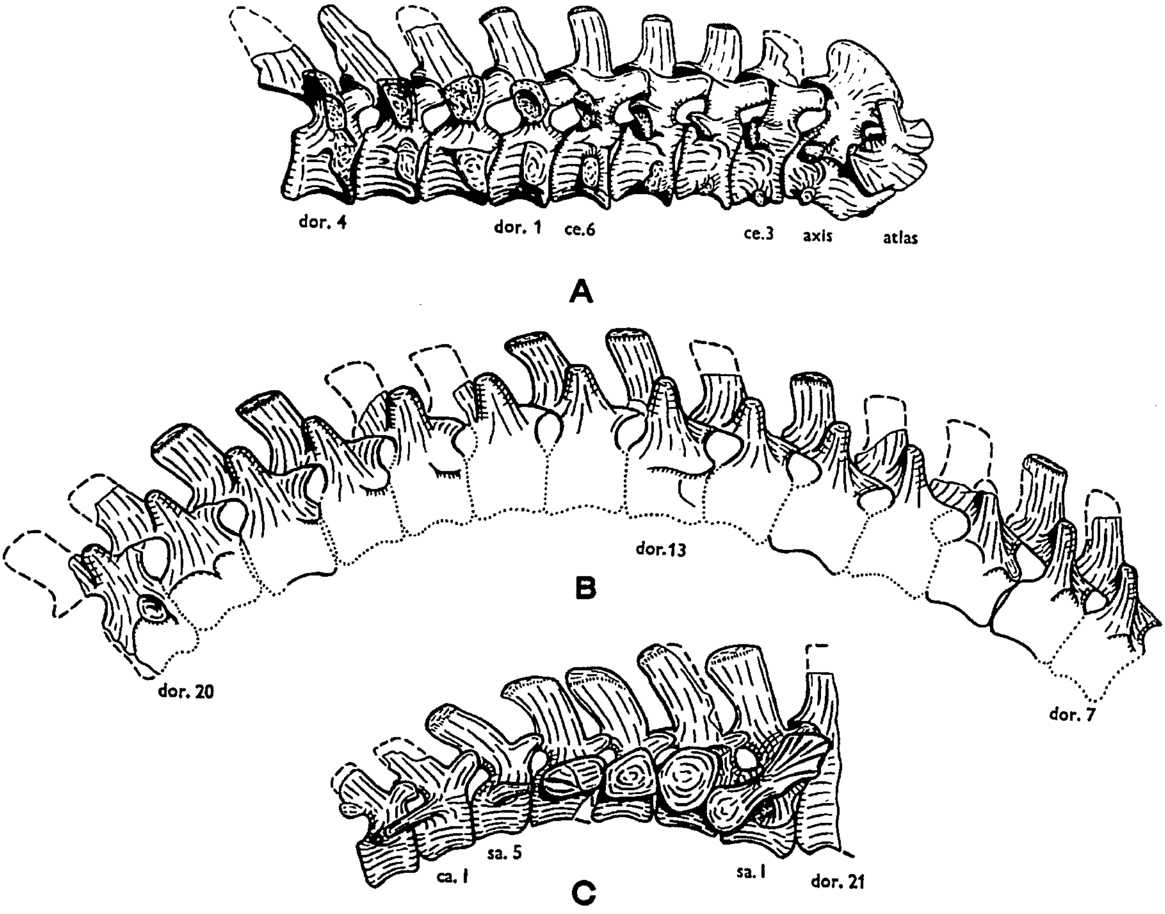

dor. 4
dor. 1
ce.6
ce.3
axis
atlas
A
dor.13
dor. 20
dor. 7
B
sa. 5
ca. I
sa. I
dor. 21
C

Figure 14

Kingoria nowacki, specimen no. 82

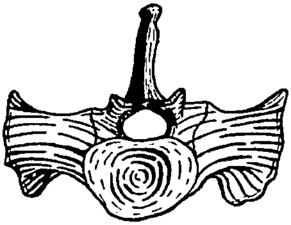
A. Anterior view of first sacral vertebra and ribs

B. Anterior view of fourth sacral vertebra and ribs

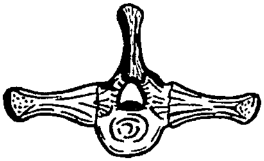
C. Posterior view of fourth sacral vertebra and ribs

D. Anterior view of first caudal vertebra and ribs

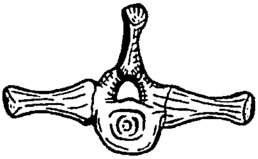
E. Posterior view of first caudal vertebra and ribs



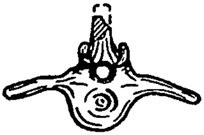
A



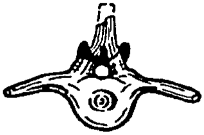
B



C



D



E

Figure 15

Kingoria nowacki, specimen no. 82

Posterior views of ribs

A-E, cervical ribs

F-I, dorsal ribs 1-4

J,K,L, dorsal ribs 7,11,19

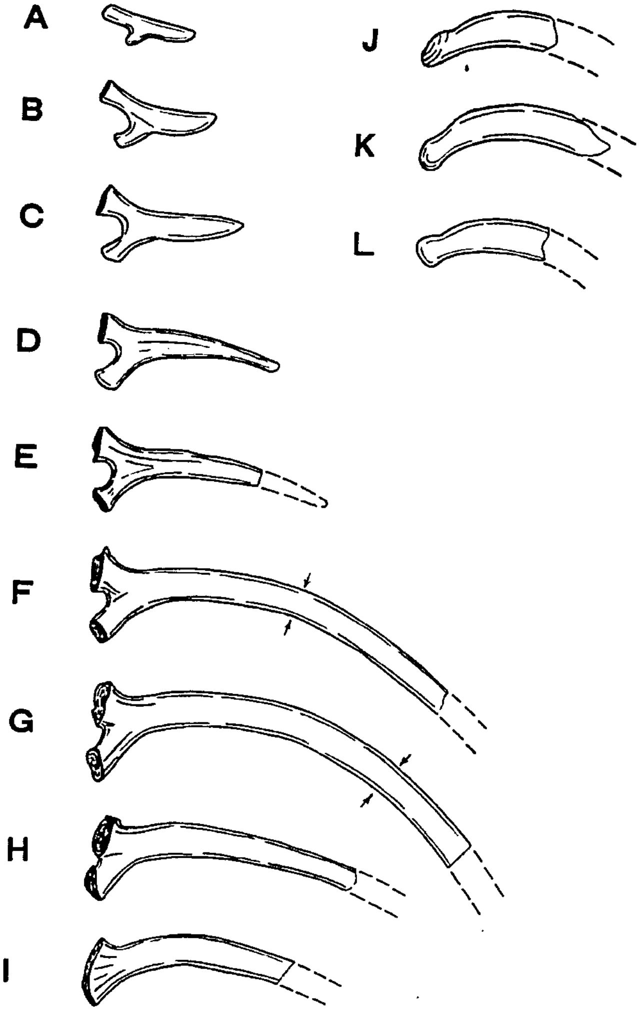

A
B
C
D
E
F
G
H
I
J
K
L

Figure 16

Kingoria nowacki, specimen no. 82

A-D, left coracoid plate

A, external view B, anterior view

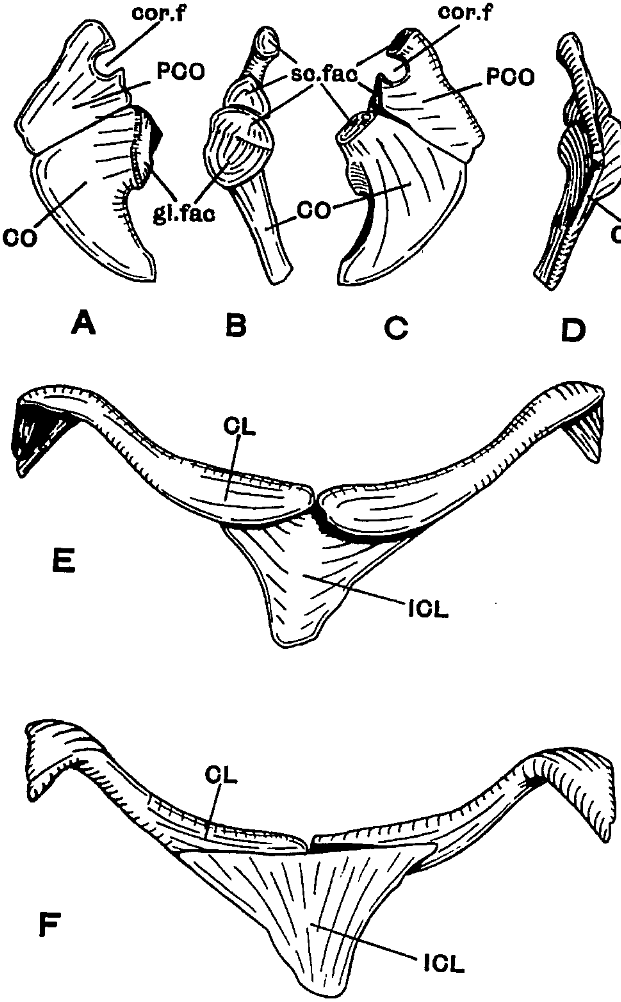
C, internal view D, posterior view

E,F, clavicles and interclavicle

E, ventral view F, dorsal view

Abbreviations :-

cor.f	coracoid foramen
gl.fac	glenoid facet
sc.fac	facet for scapula


cor.f
PCO
CO
gl.fac
sc.fac
CO
cor.f
PCO
CO
CO
A
B
C
D
CL
E
ICL
CL
F
ICL

<u>Figure 17</u>

Kingoria nowacki, specimen no. 82

A-C, clavicles and interclavicle

A, anterior view B, posterior view C, right lateral view

D,E, sternum

D, dorsal view E, anterior view

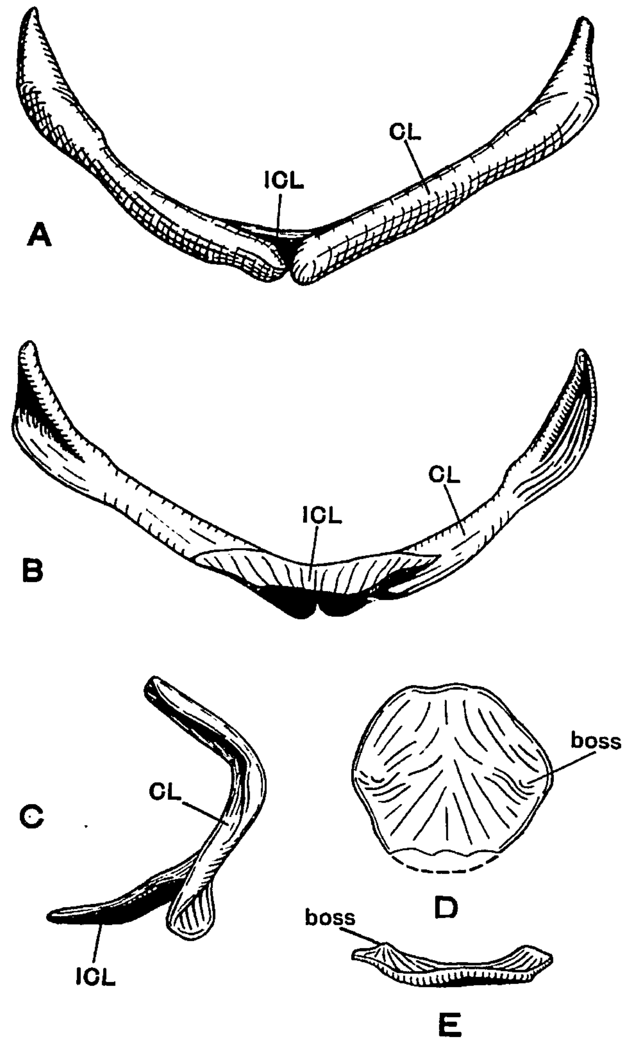

CL
ICL
A
CL
ICL
B
C
CL
ICL
boss
D
boss
E

Figure 18

Kingoria nowacki, specimen no. 82

Left scapula

A, lateral view B, section taken at level X-X in figure A

C, posterior view D, internal view

E, ventral view of ventral end F, anterior view

Abbreviations:-

acr.pr	acromion process
cor.f	coracoid foramen
gl.fac	glenoid facet
pcor.fac	facet for precoracoid

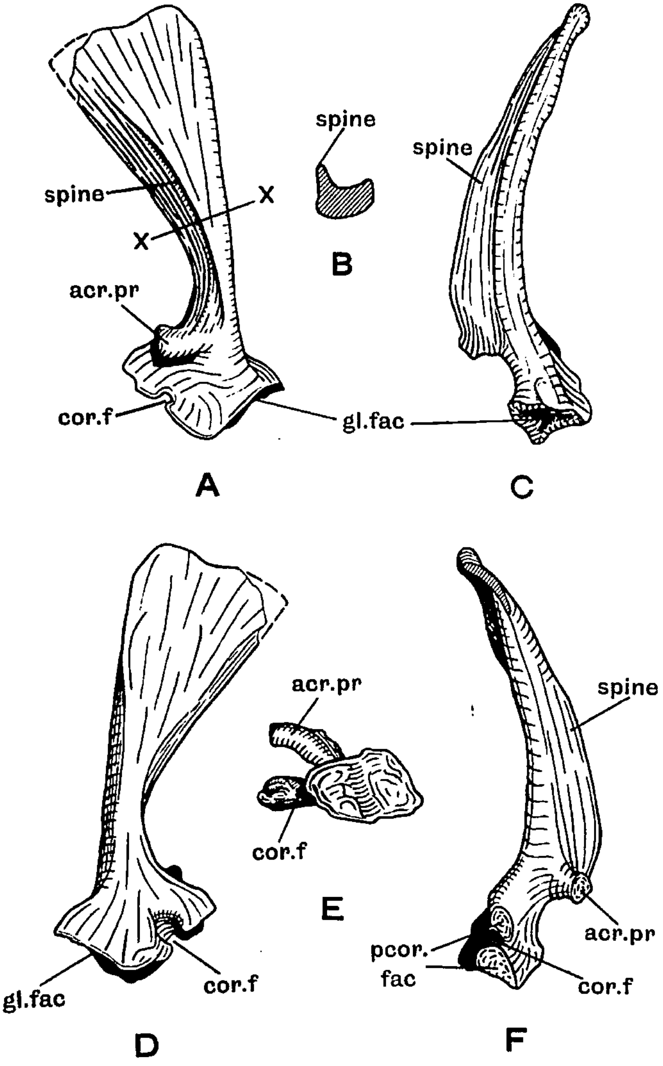

spine
X
X
spine
B
spine
acr.pr
cor.f
gl.fac
A
C
acr.pr
spine
cor.f
E
acr.pr
pcor.
fac
cor.f
gl.fac
cor.f
D
F

Figure 19

Kingoria nowacki, specimen no. 82

Proximal end of right humerus

A, dorsal view B, anterior view

C, ventral view D, posterior view

E, view of proximal end F, view of distal end

Abbreviations-

d-pect.crest	delto-pectoral crest

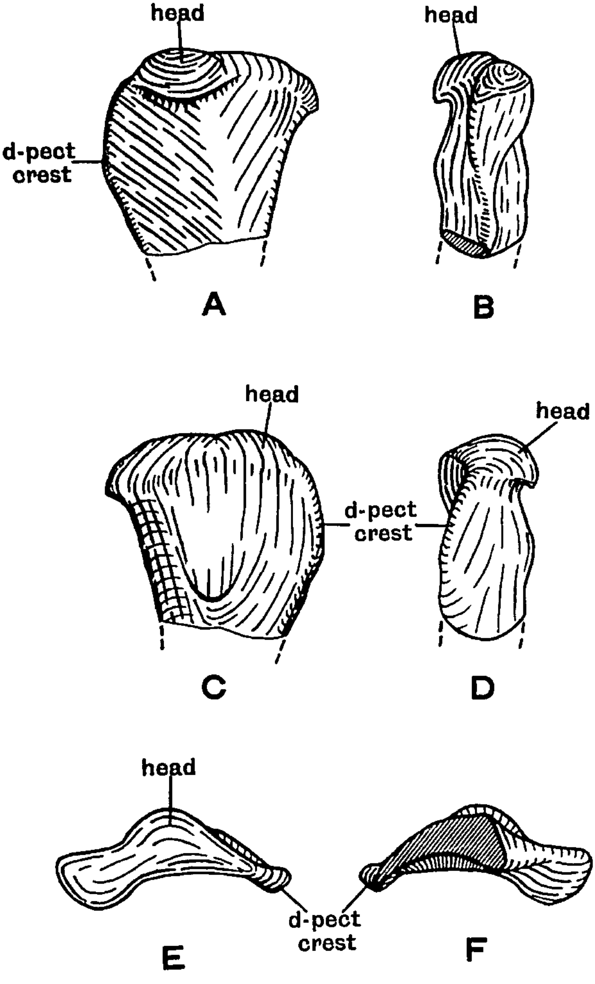

head
d-pect crest
head
A
B
head
head
d-pect crest
C
D
head
d-pect crest
E
F

Figure 20

Kingoria nowacki, specimen no. 82

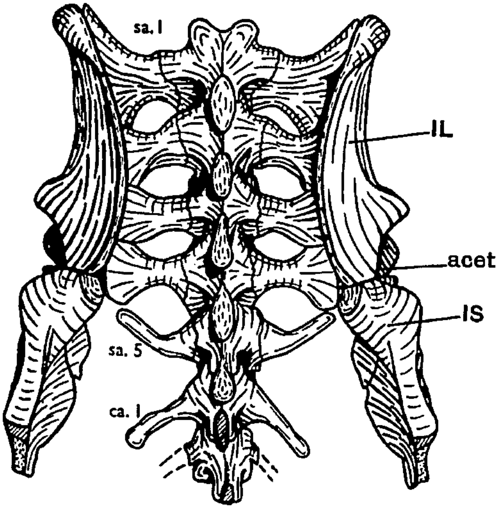
A. Dorsal view of sacrum

B. Ventral view of sacrum

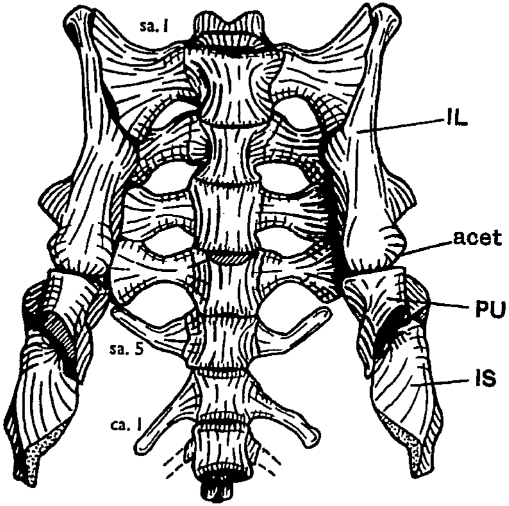
Abbreviations:-

acet	acetabulum
ca.	caudal vertebra
sa.	sacral vertebra

A



B



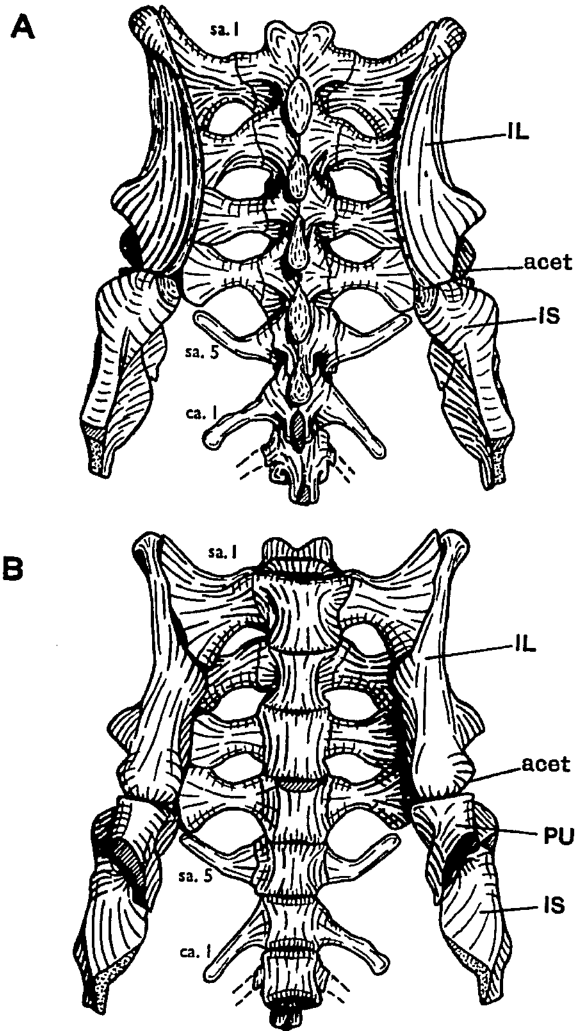

A
sa. 1
IL
acet
IS
sa. 5
ca. 1
B
sa. 1
IL
acet
PU
sa. 5
IS
ca. 1

Figure 21

Kingoria nowacki, specimen no. 82

A. Lateral view of pelvis

B. Medial view of pelvis

C. Posterior view of ilium

D. Anterior view of ischium and pubis

E-G. Portion of proximal end of femur

E, medial view F, anterior view G, proximal view

Abbreviations:-

acet	acetabulum
obt.f	obturator foramen
sacr.fac	facets for sacral vertebrae

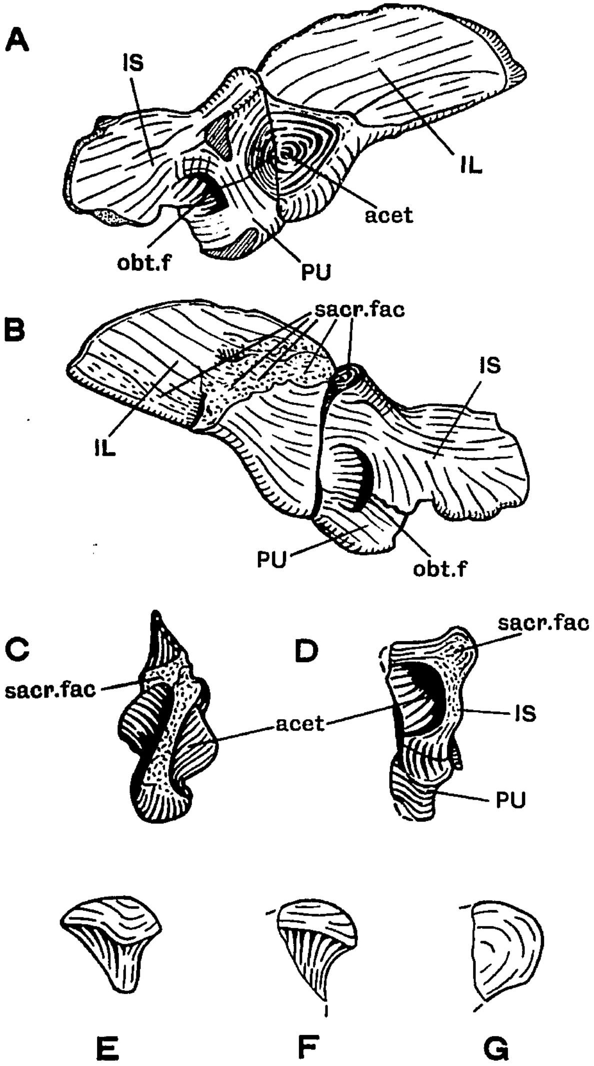

A
IS
IL
acet
obt.f
PU
B
sacr.fac
IS
IL
PU
obt.f
C
sacr.fac
acet
D
sacr.fac
IS
PU
E
F
G

Figure 22

Kingoria nowacki, specimen no. 84

Occipital view of skull. On the right half, the form has been indicated by shading; on the left half, the posterior extension of the dorsal edge of the squamosal has been opened out dorsally, and the inferred positions of the occipital muscles have been indicated.

Abbreviations :-

clei-occ	cleido-occipitalis muscle
dep	depressor mandibuli muscle
lig.nuch	ligamentum nuchae
long.cap	longissimus capitis muscle
obl.cap.mag	obliquus capitis magnus muscle
obl.cap.sup	obliquus capitis superior muscle
rect.cap.lat	rectus capitis lateralis muscle
rect.cap.major	rectus capitis major muscle
rect.cap.minor	rectus capitis minor muscle
trans-spin	transverso-spinalis muscle
trap	trapezius muscle

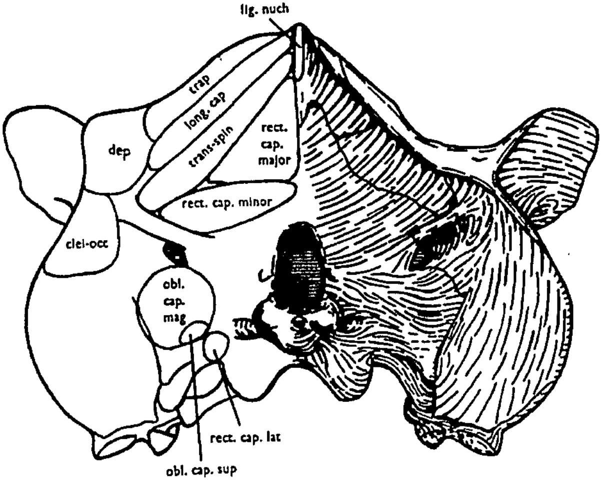

lig. nuch
trap
long. cap
trans-spin
rect. cap. major
dep
rect. cap. minor
clei-occ
obl. cap. mag
rect. cap. lat
obl. cap. sup

Figure 23

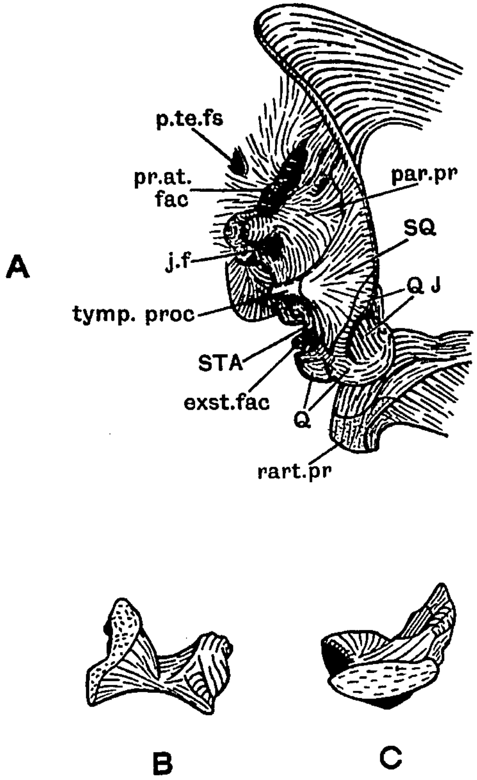
A. *Kingoria nowacki*, specimen no. 84. Postero-lateral view of right posterior quadrant of skull and posterior end of right ramus of lower jaw.

B,C. Left stapes of unidentified dicynodont, specimen no. 107.

B, posterior view C, distal view

Abbreviations :-

exst.fac	facet for extrastapes
j.f	jugular foramen
par.pr	paroccipital process of opisthotic
pr.at.fac	facet for proatlas
p.te.fs	post-temporal fossa
rart.pr	retro-articular process
tymp.proc	tympanic process


A
p.te.fs
pr.at.
fac
par.pr
SQ
j.f
Q J
tymp. proc
STA
exst.fac
Q
rart.pr
B
C