ON *MILLEROSAURUS* AND THE EARLY HISTORY OF THE SAUROPSID REPTILES

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CONTENTS

In 1938 Broom described a reptile from the Upper Permian of South Africa as *Millerina*, concluding that it was a very primitive cotylosaur 'ancestral' to the mammal-like reptiles. To it he added several other genera, including one, *Millerosaurus*, with a pelycosaur-like temporal opening. Very well-preserved specimens of this last genus make possible a nearly complete description of the whole skeleton of these animals. They are shown by the occurrence of a typical lizard-like columella auris and tympanic cavity to be sauropsids, and are evidently far more primitive in general structure than any other members of that group. The group founded for them is shown to include, with great probability, *Mesenosaurus* from near the beginning of the Russian Permian reptile-containing deposits. The real resemblance of the millerosaurs to primitive captorhinids and pelycosaurs is evidence of a common ultimate derivation from anthracosaurs. The Millerosauria provide a starting point for the development of all sauropsids except perhaps the Chelonia. Thus the first appearance of 'diapsid' reptiles in the Upper Permian *Cistecephalus* Zone, and the immensely rapid development they show in the Lower Trias, is related to the effective disappearance of *Dicynodon*, and of the carnivorous gorgonopsids and Therocephalia which preyed on it, at the end of Permian time. The break is as great as that which separates the beginning of Tertiary from the end of Cretaceous times amongst land-living vertebrates.

INTRODUCTION

In 1916 E. S. Goodrich, discussing the classification of reptiles, divided the members of that class into three groups. One (including some Amphibia) called Protosauria was basal to two groups, Theropsida including the mammals and Sauropsida including the birds. This division into the two latter groups, supported as it is not only by the nature of the hearts and great vessels of the members of the two groups, but also by many other features (of the forebrain for example), is evidently fundamental. It is now possible to split up Goodrich's primitive group of Protosauria, allotting the true reptilian cotylosaurs to the groups of which they are early members, and relegating the rest to the Amphibia. Thus it is possible to divide all reasonably well-known reptiles between the Theropsida and Sauropsida, distinguishing them in those very rare circumstances in which confusion could arise as Reptilia Theropsida and Reptilia Sauropsida.

The theropsids make their first appearance in the Coal Measures, and the nature of their evolutionary history is known in very great detail from then to the disappearance of the group in Middle Jurassic times. The sauropsids, arising at the same time, are known from the highly specialized diadectids in the Lower Permian, and (if it be a sauropsid) from *Bolosaurus* of that age. But these animals can have given rise to no other group. No certain sauropsid is known in later rocks until the appearance of *Youngina* in the Upper Permian of South Africa heralds an active development. The 'cotylosaurs', pareiasaurs and procolophons have a continuous history from the base of the South African series to the *Cistecephalus* Zone, and higher, and indeed go further back in Russia, but like *Diadectes* they appear most unlikely ancestors of any other group; none the less they are sauropsids. No form ancestral to *Youngina* has been recognized with certainty, and the point of its origin is unknown.

Thus I was delighted to find that *Milleretta* from the *Cistecephalus* Zone, described by Robert Broom in 1938, is a sauropsid, and a structural ancestor of all sauropsids except the procolophons and pareiasaurs. We owe to the enthusiasm of Mr S. H. Rubidge, of Wellwood, Graaf Reinet, the collection of most of the scanty material of this group, and I owe my first sight of it to his hospitality. Subsequently I saw in the collection of the Bernard Price Institute the nodule described below, and a small skull belonging to the group which they were good enough to give me. Both were collected by Mr J. H. Kitching.

MILLEROSAURUS PRICEI, N.SP.

History

The Bernard Price Institution possesses a small nodule from the *Cistecephalus* Zone of Swalekranz, Murraysburg, Cape Province, South Africa, which is numbered 720 in the catalogue and recorded as showing signs of five small skulls. The nodule, measuring

11·4 × 5·7 × 4·1 cm, obviously composed of very hard smaller nodules connected together quite irregularly by strips of a somewhat softer material which appears to have been a waterlaid mud, was weathered, sometimes to a very considerable extent, over the whole of its surface, and showed exposures of small skulls of a singularly unattractive kind. Rows of teeth were usually easily recognized, though the teeth themselves had mostly fallen away, in some cases the orbits were visible, but generally the bone had sheared off leaving a sometimes very excellent mould on the rock. But in many cases skull bone was seen only in section. Trial showed that preparation with acid would be extremely difficult and perhaps unproductive. I therefore began with a dental mallet and sharp-pointed needles, and very occasionally used a hammer and needle-pointed chisels. In the process the original block broke up into six major pieces and a number of fragments, some of which proved valuable. The preparation was extremely slow, and it was, I think, impossible to work long periods on it, and eventually I had to stop, having exposed enough to give a nearly complete knowledge of the animal involved.

Recognition of individuals

It finally proved useful to mark each skull, and some other important structures, with a spot of colour or ink symbol placed on the matrix near it. These are as follows:

I. *Red*—a nearly complete skull and lower jaw, well exposed from above and behind. The size, shape and position of the orbit is evident. The snout with the lower jaw in position is seen in section, probably just behind the nostril; the mutual relations of the prefrontal, nasal, lachrymal and maxilla are very well shown. The occiput is extremely important because it shows not only the general structure but also the presence of a tabular and a supratemporal, separated from one another by so large a piece of matrix that their independent existence is obvious. This skull lies just disarticulated from a series of four vertebrae, the last of which is in position between the two scapulae of a complete, well-preserved shoulder girdle, with which a right humerus is in articulation.

II. *White*—the most complete skull, shows the hinder part of the nostril but lacks the extreme anterior parts of the nasals and premaxillae. The lower jaw is in natural articulation, upper teeth are well shown on each side, but the dorsal surface of the skull has mostly been removed by weathering and is represented merely by an impression of the under-surface of the bones. The occiput is good on the left side, the paroccipital and proötic—with the stapes nearly in position—lie in place with respect to the quadrate, squamosal and quadratojugal. The supraoccipital is well shown, and the basioccipital condyle is in position on the atlas, itself articulated with the axis, which in turn is in articulation with the third cervical vertebra.

III. *Light blue*—this skull has its lower jaw nearly in position but its outer surface is largely weathered away. It is important because it shows in natural articulation the anterior part of a quadrate, the quadrate ramus of the pterygoid, an epipterygoid, something of the roof of the skull in this neighbourhood, and a proötic. It also makes certain the existence of osteoderms.

IV. *Dark blue*—a very badly weathered skull, essentially complete, which has not been prepared.

V. *Green*—a skull shown from the occiput to the front of the orbit, but then passing into unremoved matrix. It is important because the hinder part shows not only the upper surface but also a good deal of the occiput and the base of the skull, together with the exoccipitals and basioccipital. The proötic and paroccipital are also well—though incompletely—shown. In addition, the relation of the quadrate to the pterygoid, and of the latter bone to the basipterygoid process is exhibited, and the shape of the supratemporal well displayed.

VI. *Pink*—a skull with its lower jaw in position showing a weathered outer surface but broken in such a way as to give sections across the palate and lower jaw. These are less informative than might be expected.

VII. *Brown*—a skull remarkable because it had to a considerable extent come to pieces before burial. The two frontals are in contact with one another, but whilst that of the left side is continued by a face which retains its original shape, that on the right is turned downwards out of position. The left parietal is present complete, very well preserved, its lateral border being seen directly from the lower surface; its mould lies on the counterpart slab. The relationship between the parietal and the squamosal can be seen quite clearly. In addition, the supratemporal, seen partly as bone and partly as impression, can be studied in its relation to the squamosal and to the end of the paroccipital process, which is in natural position. The palate is seen in section on a fracture. Finally, the complete quadrate lies in position with respect to the squamosal. This skull is therefore of great value.

An eighth skull, with lower jaw, is represented by a weathered impression of the outer surface with attached fragments of bone.

VIII. '*Square*'—an independent shoulder girdle which shows an interclavicle, clavicle and scapulo-coracoid, but has not been completely prepared.

IX. '*φ*' (*phi*)—another independent shoulder girdle which lies near the pink skull and retains both scapulo-coracoids and probably fragments of an interclavicle. It has certainly associated with it a right forelimb in articulation, the carpus having a decayed appearance—though it is still perfectly intelligible—but the distal part of the hand having been lost.

X. ' × ' (*cross*)—a series of ribs and vertebrae in articulation to the number of some nine lying alongside the red skull.

XI. '*Spot*'—a rather irregular chain of eleven vertebrae which crosses obliquely above the piece of column associated with the red skull.

XII. '*? Green*'—a series of seven vertebrae which seem to connect with the green skull.

XIII. ' ○ ' (*circle*)—an excellent caudal vertebra.

XIV. '*Arrow*'—an ilium and ischium with a sacral vertebra and femur and tibia attached.

XV. '*θ*' (*theta*)—a pair of pubes and an ischium with the upper end of a femur in articulation.

XVI. '*γ*' (*gamma*)—the lower end of another femur.

XVII. '*Triangle*'—a very imperfect hindfoot, with a tibia and fibula.

XVIII. '*S*' (*sigma*)—another foot with the distal row of the tarsus and a series of metatarsals. On the other side of the fragment a third set of metatarsals with two phalanges attached to each.

A few abdominal ribs lie in no obvious relation to anything.

Conditions of fossilization

It is not easy to discover in what circumstances eight skulls each about 3 cm in length (three of which are articulated with short lengths of vertebral column), three shoulder girdles (one in correct anatomical relationship to its skull), several other short lengths of vertebral column (which together are evidently much too little for anything like eight individuals), two imperfect pelves, three hindlegs and feet, together with two articulated caudal vertebrae only of a probably quite long tail, and a few scattered bones, could have been so very closely packed to form the core of a nodule.

Remains of reptiles as small as these are very seldom found in the Karroo, but as Karroo fossils are usually discovered as isolated skulls, often filling detached nodules, the extreme rarity of tiny specimens may conceal their abundance during life. The rocks in the *Cistecephalus* Zone appear to have been to a large extent wind-blown deposits like those on a prairie, but some were evidently laid down in river courses or even in shallow pools. Some part of it seems water-laid, the nodules themselves may conceal such origin.

It seems to me difficult to believe that so many individuals, of extremely similar size and structure, should be brought together, without admixture of other animals, unless they had been associated at the time they died. I made a series of measurements (such as interorbital width, back of head to front of eye, back of supratemporal to back of prefrontal, etc.) which showed that the largest individual was no more than one-quarter larger than the smallest in linear measurement. The proportions were also exceedingly similar. But it appeared that skull I, although of very much the same size as II, does really differ from it in ways which can be seen by comparing the drawings of the two occiputs. It is none the less very difficult to believe that the differences are specific, they might be sexual: skull I might be male and II female, or vice versa. *Lacerta jacksoni* Blgr., described by Degen (1911), shows in palatal and occipital views skull differences between male and female of similar kind and scale.

Description

A general account can only be given as a result of a comparison of all these materials which ignores the differences between skulls I and II. The skull is low, nearly twice as wide in the temporal region as it is high at the occiput, and the orbit appears large, longer from back to front than the temporal region behind it, though it is exceeded in length by the preorbital face. This becomes very narrow anteriorly and probably ends in a very short rounded region. The lower jaw is slender anteriorly, deepens at the coronoid region about at the middle of the orbit, and is still fairly deep at its articulation with the quadrate, behind which it is continued as a short, pointed retroarticular process.

Braincase. The braincase articulates with the atlas by a single condyle of which there is no direct exposure. It seems evident from the conditions seen in skull VII that this structure was relatively small, about as deep as it is wide, and that the basioccipital takes only a comparatively small part in its formation, the exoccipitals passing right down to the ventral surface and making a large part, at any rate, of the articular surface.

Basioccipital. The basioccipital extends forward for some distance in advance of the exoccipital but appears to have been separated from the basisphenoid by a considerable distance.*

Exoccipital. Each exoccipital consists of a part lying alongside the basioccipital, and extending down to the parasphenoid with a considerable antero-posterior extension, articulating in front directly with the ventral part of the paroccipital, these two bones

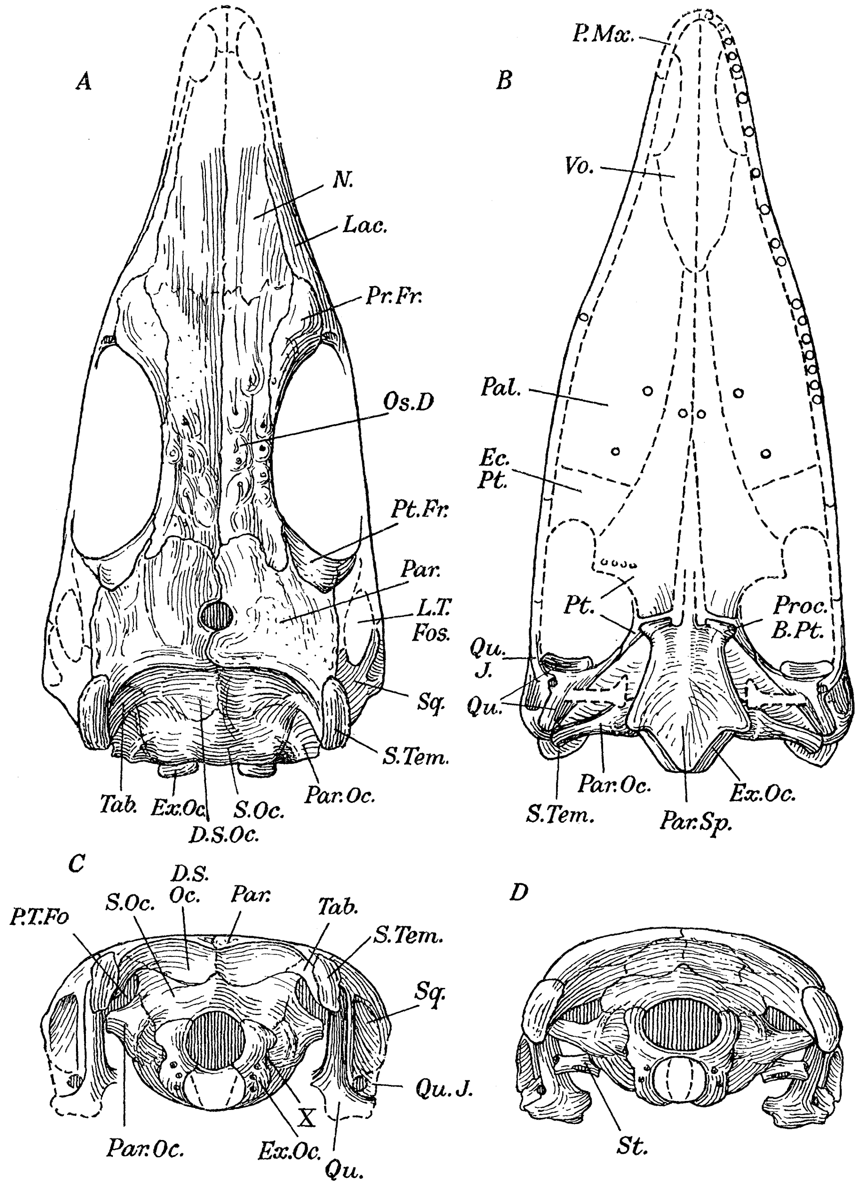

FIGURE 1. *Millerosaurus pricei* n.sp. (no. 720, Bernard Price Collection) (magn. × 3). *A*, dorsal aspect (skull I); *B*, palatal aspect (skulls II, V and VII), the isolated right maxillary tooth is shown in a section (skull VII), also showing palatine and pterygoid teeth; *C*, occiput (skull I); *D*, occiput (skull II, the holotype). For list of abbreviations see p. 400.

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* In millerosaurs the basisphenoid is completely fused with the parasphenoid and is visible from below apparently only at the basipterygoid process. Its extension backward above the parasphenoid varies with the individual's age and is very seldom seen. Thus I have used basisphenoid to mean the joint bone, except where the sense implies a strict interpretation.

being separated by a vagal foramen about at the level of the floor of the foramen magnum. From this level the exoccipital continues upward in contact with the paroccipital until it reaches the supraoccipital, and may then extend inwards for some considerable distance (I and II skulls), ending in a narrow dorsal extremity. This process of the exoccipital, which thus forms the side wall of the foramen magnum, is in skull II perforated by two foramina, no doubt for the XIIth nerve. But in skull I these foramina may be three in number and lie much farther ventrally.

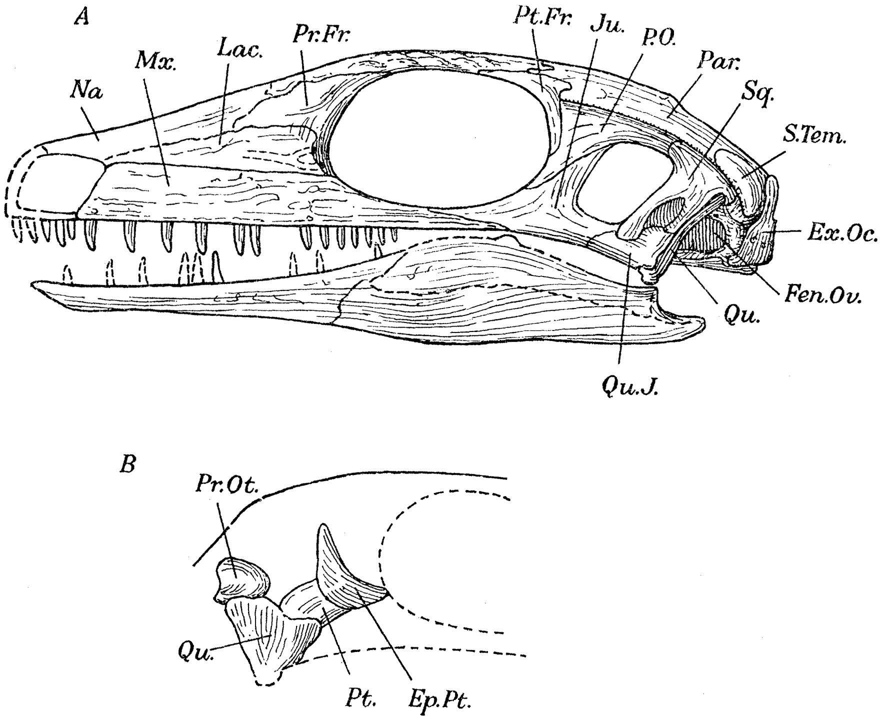

FIGURE 2. *Millerosaurus pricei* n.sp. (magn. × 3). *A*, left lateral aspect (skull II, the holotype, with detail from skulls III, V, VI and VII); *B*, right side of skull III, from which the superficial bones of the temporal region are missing. The quadrate is imperfect behind, but shows the whole pterygoid wing. *Pr.Ot.* a somewhat misplaced proötic; *Pt.* the quadrate flange of the pterygoid.

Basisphenoid. The basisphenoid, seen only in skull V, is evidently widely separated from the basioccipital, but it no doubt forms the core (or the whole) of the basipterygoid process, which is rather far from the middle line, and has a wide articular face directed forward and a very little outward.

Supraoccipital. The supraoccipital is a wide and relatively very large bone overlapped anteriorly by the dermosupraoccipitals, and to a small extent by the tabulars, and it is not impossible that the parietals also have a contact with it. Its outer face bears a low median ridge, narrow and comparatively high where it notches the hinder border of the dermosupraoccipitals but dying out below. The foramen magnum is relatively wide, the supraoccipital forming a somewhat flattened summit. The lateral border of the supraoccipital falls rather indefinitely into two parts, of which the hinder, inclining forwards and outwards, is attached directly to the inner side of the paroccipital.

Paroccipital. The paroccipital is well shown in skulls I, II and V. It is a bone of relatively large size and very elaborate shape. Its dorsal surface (skull V) continues that of the supraoccipital outwards, the two bones meeting in a perfectly straight abutment. At a point not far in front of the contact between the exoccipital and the supraoccipital the upper surface of the latter is raised as a swelling over the middle of the posterior vertical semicircular canal. This swelling passes on to the paroccipital extending outward, backward and very much downward until (best seen in skull II) it expands to house the ampulla which, coated with an obviously very thin layer of bone, forms a marked lateral swelling; below this the paroccipital continues downward as a broad sheet almost to the parasphenoid. It is separated from the exoccipital by a small vagal foramen, but is otherwise in contact with the ventral part of that bone for a very long distance. The paroccipital extends forward in contact with the supraoccipital for some distance, but is usually a little depressed below it, and ultimately ends in a small paroccipital process whose extremity, no doubt still cartilaginous, lies quite far out and high up somewhere on the level of the summit of the foramen magnum.

Proötic. The proötic is a remarkable bone best seen in skulls III and V. The anterior border of its dorsal surface is bounded by a ridge which forms a definite 'corner' over which the bone is turned, being in fact moulded over the anterior vertical semicircular canal and its ampulla. The bone extends very little in front of this, dropping almost vertically to the upper surface of the parasphenoid, so that the whole otic capsule stands out as a block behind the much narrower anterior part of the braincase. The proötic appears not to contribute at all to the paroccipital process, or if it does so, merely as a short blunt anterior continuation. The exact nature of its contact with the basis cranii is unknown because that structure is, in the region under consideration, entirely unossified. The under-surface of the paroccipital process is excavated so that it meets a corresponding though much shorter excavation of the proötic, and the groove so formed is the roof of the tympanic chamber; at its inner end lies the fenestra ovalis, whose summit is evidently a little above the lowest point of the ampulla of the posterior vertical semicircular canal. This is best shown in skull II. In skull I it can be seen that there is an extension of bone ventral to the fenestra ovalis, continuous no doubt with that lower part of the paroccipital which passes far ventrally lateral to and in contact with the exoccipital. The extent to which this is developed probably varies with the age of the animal.

Parasphenoid. The parasphenoid is shown only in skull V where it is exposed by fracture. Its ventral surface is shown quite clearly on the right side of the loose fragment, but the posterior part of the bone is only well seen from above on the main block. The bone is evidently very wide near its hinder end, but terminates at its suture with the exoccipitals and basioccipital in a posteriorly directed point. The basisphenoid is indistinguishably fused with it, but it appears that the parasphenoid ends anteriorly at the root of a short basipterygoid process, extending forward, and with a transversely placed articular surface. The bone is slightly ridged along the mid-line of its ventral surface by a shallow concavity on each side in the region where the exoccipitals must have met it.

The braincase just described is attached to the dermal skull in part through the articulation of the basipterygoid process with the pterygoid, but chiefly by the bones of the upper surface through the supraoccipital.

Dermosupraoccipital. The dermosupraoccipitals are paired bones meeting in a median suture and coating the posterior surface of the supraoccipital below, and the down-turned hinder border of the parietal above. In skull I it is evident that the overlap on the parietal is large, and the whole skull suggests a very considerable overlap of the dermosupraoccipitals on the supraoccipital. Indeed the supraoccipital may even underlie the parietal directly.

Parietal. The occipital surface of the parietal ends at the rounded margin of a nearly semicircular excavation in front of which the bone forms an almost flat upper surface. The total width of the parietals is very great, and each bone has a free lateral margin which is not an interdigited suture but, though thin, is rounded. This free margin passes backward to form a short posterior projection whose inner edge borders the occiput, whilst the outer side has a notch in its upper surface into which the front end of the supratemporal is received. The under-surface of this lateral border of the parietal is shown in the counterpart of skull VII, where is it very evident that the edge is indeed free, in the sense that it is not directly attached to any other bone between the supratemporal and the postfrontal. The parietals are separated by a rather large pineal foramen, and are bounded anteriorly by a sutural attachment to the hinder end of the frontal of such a character that a special narrow spike separates a great deal of the inner border of the postfrontal from the frontal itself.

Frontals and nasals. The frontals are long and form the summit of the orbit for a considerable way between the post- and prefrontals. In front of them lie nasals, incompletely known, which in skull I extend forward for some distance between the anterior nostrils as a comparatively wide structure.

Osteoderms. Skull I shows an ornament of the dorsal surface consisting of two series of very low rounded bosses disposed along the length of the frontal. Similar but less marked bosses pass on to the prefrontal, and there are obscure indications of them on the left parietal. The individual bosses are separated from one another by wide grooves, and each has one, or sometimes two, foramina coming out on to the dorsal surface, these often forming the beginning of a narrow but well-defined groove. Skull III shows similar structures on what remains of the left frontal and parietal, and at the mid-point of the left orbital margin this skull shows the existence of a very thin layer of grey matrix separating the boss from the upper surface of the underlying frontal. This ornamentation must therefore be formed by a series of osteoderms, which are eventually fused with the underlying dermal bones of the skull, and were themselves covered by dermal scutes, whose formative structures received their blood supply through the foramen which pierces the osteoderm.

Maxilla. The face, comparatively high at the orbit, is partly composed of a maxilla which occupied about half its total height at the hinder end of the very large nostril. The maxilla is still quite deep where it enters the border of the large orbit, and gradually shallows towards the middle of that opening, where it is overlapped by the jugal. It bears a series of simple teeth with rather abrupt, slightly back-turned blunt points which are ankylozed to it in a pleurodont manner. The nature of the material makes it very difficult to determine whether or not the maxilla comes into contact with the nasals.

Lachrymal. It is evident that the lachrymal is long; it is, I think, most likely that it does actually reach the nostril, to which in any case it makes a close approach. It is penetrated for some distance by a lachrymal duct (best shown in skull III), and this has two openings to the orbit, lying rather hidden from view where the posterior lachrymal border is seen in front of the prefrontal, which passes down mesial to it at any rate to the level of the upper border of the maxilla.

Prefrontal. The prefrontal is swollen out over its suture with the lachrymal so as to make a boss at the front of the orbit above the lachrymal foramina.

Postfrontal. The postfrontal has a short attachment to the outer side of the frontal and then fits into a depression on the upper surface of the parietal. From this part of the bone a slender postorbital process with a nearly straight posterior border passes directly downward and only very little outward behind the orbit, ending rather abruptly.

Postorbital. The postorbital is a large bone whose anterior part lies mainly behind the down-turned wing of the postfrontal, which rests on it, then forms a small part of the border of the orbit, and is attached to a large upstanding process of the jugal (skull II, right side). The triangular part of the postorbital reaches up to the parietal as a massive bone, turns under it, and extends backward below its lateral border until it reaches the anterior end of the squamosal. This is represented by a relatively thin film of bone which, like the hinder end of the postorbital, supports the under-surface of the parietal for quite a considerable area without any sutural attachment at all. This arrangement is seen from within in the counterpart of skull VII, where the postorbital is missing, and is well seen in skull II. There is, therefore, in *Millerosaurus* a free border to the parietal extending between the two notches in which the postfrontal and the supratemporal respectively are inserted. The arrangement is in fact exactly as in the primitive captorhinid and pelycosaur *Protorothyris* and *Varanosaurus.*

Squamosal. The squamosal which forms the hinder part of this attachment of the cheek to the parietal is a remarkable bone. Its thin upper part, lying below and attached to the under-surface of the parietal lappet, extends backwards and somewhat inwards, forming in effect a cup which receives the upper end of the quadrate. The quadrate then passes downward in contact with the admesial border of the squamosal until that bone ceases, its place being taken over by the quadratojugal. The squamosal rests on the upper part of the quadratojugal and is very notable because its outer surface bears a pair of prominent ridges, meeting dorsally and separating below, between which lies a deep pit, closed above, open below until it is cut off by an out-turning of the lower border of the quadratojugal. This depression and the ridge in front of it are very unusual structures, apparently associated with the attachment of a tympanic membrane. The cap which the squamosal makes over the head of the quadrate has only a very short admesial extension, of which very little is really to be seen in any of the skulls at my disposal except skull VII, where it is shown to continue for about a millimetre down the quadrate. Finally, the relation of the jugal to the squamosal below the single temporal fossa is a little uncertain, but it seems likely that it may have met the squamosal, without any assurance.

Quadratojugal. The quadratojugal (skull II) is a little pushed up with respect to the squamosal, but retains its correct articulation with the quadrate. It is firmly attached to the epicondylar region of that bone, separated from it only in one place where a small quadratojugal foramen passes forward. Its ventral border is a little rounded.

Quadrate. The structure of the quadrate is well shown in skulls II, III, VII and V. Its lower articular end is wide, and the articular surface is saddle-shaped. Immediately above this the posterior surface is nearly flat but rounds off from side to side. The outer part (skull II, left side) forms a distinct step of some width to which the quadratojugal is attached, separated from the quadrate by the quadratojugal foramen. Above this the outer side rises vertically to the extreme summit of the slender bone (skull II, right side). On the outer side, above its connexion with the quadratojugal, it is coated by the posterior part of the squamosal behind the external tympanic groove. Dorsally this part of the quadrate (seen especially well in skull VII) ends in a rounded but not swollen head received in a special notch and pit in the squamosal, which even passes down for a short distance mesial to the quadrate. Immediately above its ventral articular end the quadrate is considerably widened, being drawn out into an apparent special process which is the end of the attachment of the pterygoid. From this the bone passes forward and inward in contact with the quadrate ramus of the pterygoid, the condition being shown from below on the left side of skull V, and from the outer surface in skull III. It finally ends in a face whose cartilaginous continuation passed forward in contact with the whole quadrate ramus of the pterygoid until it joined the base of the epipterygoid. The anterior border of the epipterygoid is quite wide and rounded at its base and rises as a narrow, sharp-pointed process towards the skull roof, standing out quite freely above the upper border of the shallow quadrate ramus of the pterygoid. Above this pterygoidal part the quadrate is very narrow from side to side up to its summit, the cylindrical posterior surface continuing inward on to a flat face to which the pterygoid is attached for the lower part only of its height.

Supratemporal. The supratemporal (seen best in skull I, but also in skulls V, VII and several others) is a bone of somewhat rhomboidal shape whose pointed anterior end is received in a special notch in the postero-lateral corner of the parietal. The bone is not specially thickened, but is powerful and directed ventrally as well as posteriorly. It thus forms the hinder and most lateral part of the occipital excavation, but mesially it is covered by the thin sheet of the tabular. In skull VII the supratemporal is seen in part as an impression of its inner surface and in part as actual bone. Behind its attachment to the parietal the supratemporal has a contact with the top of the squamosal and passes backward from there to reach, and be in some way attached to, the outer end of the paroccipital process, which itself lies behind the upper end of the quadrate, separated from it by a quite considerable space. In side view the supratemporal forms a hook-shaped process hanging over the tympanic region.

Stapes. The stapes is seen very nearly in position on the left side of skull II. The bone is massive, its width midway being more than half its length, and shows a trumpet-shaped widening to the base which lies in the fenestra ovalis. The shaft, about at the middle of its length, is perforated by a large foramen for a stapedial artery. Distally the bone is seen from an unsatisfactory angle, but is shown to be drawn out into a T-shaped widening similar to that much better shown in *M. nuffieldi*, to the account of which one should refer.

Sclerotic plates. Several of the skulls show evidence of the presence of sclerotic plates, which are large, very thin, apparently perfectly smooth sheets of bone adapted to form part of the surface of a large spherical eye, which may have filled the orbit rather completely. As seen they overlap considerably. They are perhaps best shown in skull III.

Palate. The palate behind the basipterygoid articulation is shown by skull V, the most interesting point being that the quadrate ramus of the pterygoid, which is thin from side to side, passes forwards and inwards above the outer part of the basipterygoid process to be attached to the body of the pterygoid. Of this very little is to be seen, but it lies in front of and not lateral to the basisphenoid process. In other words, in a ventral view the attachment of the quadrate ramus of the pterygoid to the rest of that bone is hidden by the basipterygoid process. Except for a broken transverse section across the middle of the palate in skull VII, and a very obscure exposure of part of it in the epipterygoid region and floor of the orbit in skull III, the palate is unknown. It is, however, relatively well shown in the type of *M. nuffieldi*, and there is no reason to believe that the conditions of the present species differ from those there seen.

Lower jaw. The lower jaw (skull II) is comparatively massive. The dentary extends back almost exactly as far as the maxillary teeth, and can be seen in some of the weathered exposures to carry teeth extremely like those of the upper jaw. The jaw contains a large cavity, and its hinder part behind the maxilla is the deepest region of the whole, there being a small coronoid eminence, seen on skull III. The upper part of the lateral surface behind the dentary is made by the surangular, which seems to extend back to the articular, there ending. Below it is a very large boat-shaped angular, extending forward apparently from a point within the retroarticular process to the place, somewhere behind the front of the orbit, where the deep dentary reaches the lower border of the jaw. A splenial shown only as a very slender bone on the lower surface of the jaw anteriorly has a symphysis with its fellow, and presumably passes back to meet the angular. There is a short pointed retroarticular process, which is presumably made of articular partly coated by angular. The jaw lacks vacuities on its outer surface, its inner side is unknown.

Postcranial skeleton

Vertebrae. Three skulls (I, II and V) show the first vertebra of the neck in association. In the case of skull I the head is disarticulated, but the proatlas, the neural arches of the atlas and the dorsal part of the axis are well shown; the third vertebra shows the dorsal and the anterior part of the lateral surface of the neural arch, and the fourth vertebra is seen from above and in section, the section passing through the shoulder girdle. Skull II has a vertebral column in articulation, shows something of the lower part of the atlantal neural arch, the whole of the odontoid, the anterior part of the centrum of the axis, and an oblique rather sectional view of the rest of the bone; the third vertebra is also seen, mainly in section. Skull V is in articulation with its atlas and axis, but shows nothing but a section through these two elements.

The third vertebra, as seen from above in skull I, and in section on an isolated vertebra, is remarkable because the centrum is wedge-shaped, its ventral border being a ridge, the nearly straight sides meeting in somewhat less than a right angle. There is a notochordal canal of comparatively large size, which occurs in every vertebra seen in section. The neural canal is strikingly large, presumably reflecting the small size of the animal as a whole, and the anterior zygapophysis, seen in section with a posterior zygapophysis (presumably of the axis) in place, lies horizontally and its articular face is gently concave.

The axis, which is more completely known, is again a bone whose centrum is wedge-shaped in section, with a sharp ventral ridge; it has a notochordal canal passing into it which appears to die out anteriorly; the neural canal is very large, especially wide. Its anterior face had a nearly straight attachment to the odontoid, the two bones being apparently separated by a very thin layer of unossified material. The neural arch of the axis is very wide and has an elongated neural spine ending posteriorly in a dorsally directed thickening; anteriorly the extremity is forward of the body of the bone and thus slightly overlaps the two neural arches of the atlas. The wide dorsal surface of the neural arch passes over a rounded border on to a pedicel which is drawn out so as to form the summit of a transverse process, not very protuberant, but presumably bearing a rib. The anterior zygapophysis, comparatively large, has its surface looking a little forward and outward as well as upward; it obviously allowed some movement to the atlantal neural arch.

The odontoid is a wedge of bone apparently perforated by the notochord, with a swollen border to the upper part of its lateral surface with which the lower part of the pedicel of the neural arch articulates. There is a well-defined notch and groove on the lateral surface, so that viewed from in front the odontoid must present the customary tripartite face, the paired upper facets supporting the neural arch whilst the median lower facet supports the atlantoid intercentrum, which certainly existed though I have not seen it. The pedicel of the atlantic neural arch supports a rather flat dorsal surface with a definite posterior zygapophysis fitting on to the anterior zygapophysis of the axis. The bone rises towards its fellow at a little upturning which can scarcely be called a neural spine, and anteriorly and laterally where it overhangs the pedicel its lateral surface is rounded, the narrow lozenge-shaped proatlas resting upon it. It is evident from skull II that the neural arch of the atlas does rest in the way I have described on the front face of the summit of the odontoid, and the position that the intercentrum must occupy is also evident. But its shape is not, and it is not immediately obvious how the apparently peculiar occipital condyle of *Millerosaurus* fitted the first vertebra. In the case of skull V (counterpart) the right exoccipital is shown in what is apparently its natural relation to the vertebral column, both bones being seen in section, and it appears to be in some way attached to a convex surface of some part of the atlas lying ventral to the notochord.

There is no evidence to show whether or not there was an atlantal rib. The rather massive transverse process shows that such a structure must have been present in the axis and the third vertebra, whilst one which can only belong to the fourth vertebra is visible in section in specimen I.

It is unfortunately impossible to fix the exact position of any of the other series of vertebrae shown. A series of seven vertebrae (XII) which may be associated with skull V shows rather remarkable conditions. It is exposed from its left side and above so that little can be seen except the neural arch and the attached rib. From behind an oblique section of a vertebra whose neural canal has been excavated gives some further idea of structure.

The first vertebra preserved shows a rather tall, laterally thick neural spine with a posterior zygapophysis projecting little behind it. The next is exactly similar but shows in addition the anterior zygapophysis whose lateral border passes downward and then turns somewhat backward apparently at a transverse process.

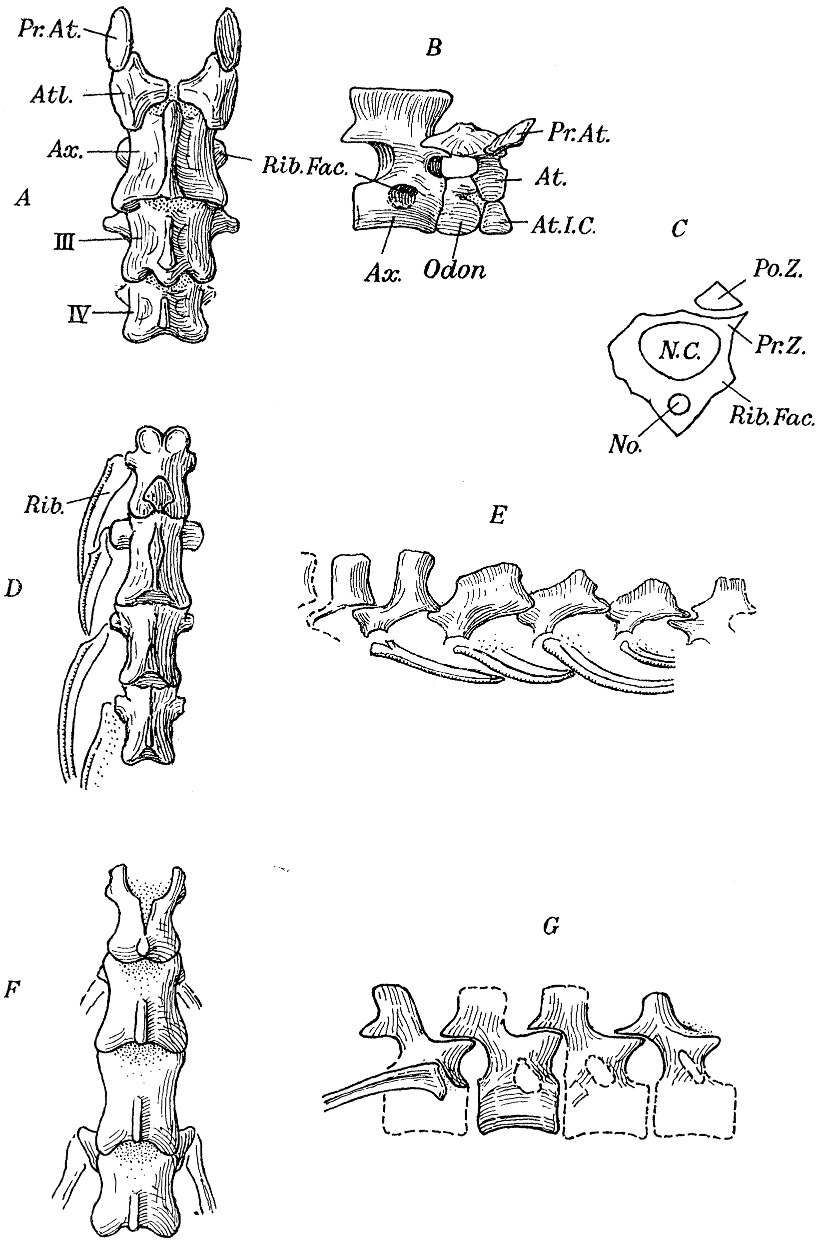

FIGURE 3. *Millerosaurus pricei* n.sp. (magn. × 3). Drawings of parts of the vertebral column. *A*, first four vertebrae, dorsal aspect, belonging to skull I; *B*, atlas and axis, lateral aspect, from skulls I and II; *C*, oblique section across a cervical vertebra; *D*, dorsal aspect of vertebrae nos. ?4 to 7 of complete series from specimen XII; *E*, lateral aspect of *D* with additions (nos. ?2 to 8 of complete series); *F*, nos. ?15 to 18 dorsal aspect (specimen X); *G*, lateral aspect of *F*; III and IV, third and fourth vertebrae.

The third visible vertebra, however, shows a whole side view of the upper part of the neural arch. The massive prezygapophysis has a horizontal outer border and is rather short, and the upper surface of the posterior zygapophysis is a little damaged. It is, however, certain that the neural spine is a short, very massive structure rising to a definite summit, the neural arch spreading laterally below it until the upper end of a short transverse process extends outwards laterally of the zygapophysis. This transverse process carries a short, nearly straight, rather broad rib whose upper and outer surface is deeply grooved.

The next vertebra differs very greatly. The distance from the tip of the anterior to that of the posterior zygapophysis of the third vertebra is $9\frac{1}{2}$ units, whilst in the immediately succeeding vertebra it is 12; in the first case the neural spine has an antero-posterior length of 4, but in the next vertebra the corresponding length is 9. In other words, the neural arch of this vertebra is very greatly elongated and its neural spine, instead of being a somewhat tall column rather angular in section, is an elongated ridge, shallow and not sharply marked off from the rest of the surface of the arch. A well-marked transverse process of quite short antero-posterior length rises from this neural arch only just behind the anterior zygapophysis, and to it is attached a very short rib, whose admedian surface is nearly straight, the outer surface being bowed. The posterior surface of the rib is channelled.

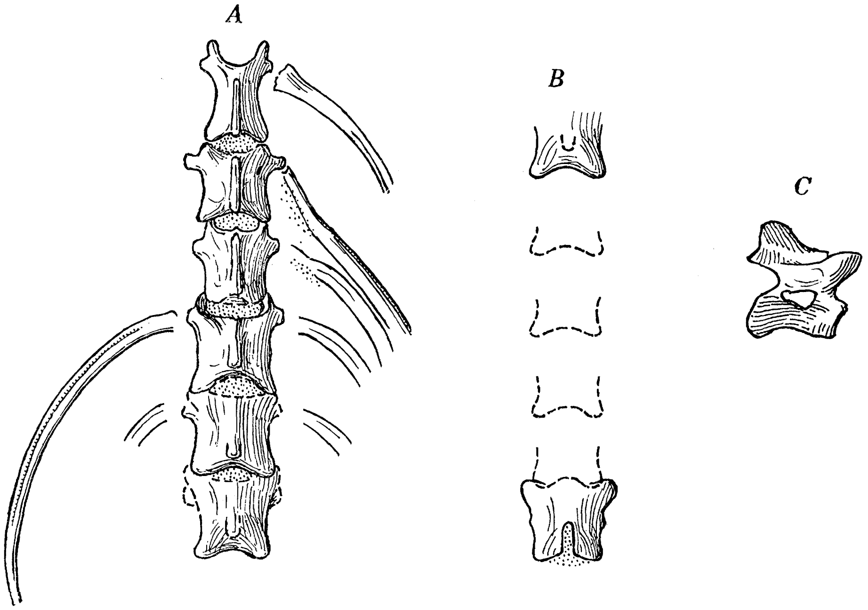

FIGURE 4. *Millerosaurus pricei* n.sp. (magn. × 3). Drawings of parts of the vertebral column. *A*, nos. 21 to 26, vertebrae with ribs (XI); *B*, nos. 26 to 31, vertebrae of same series; *C*, isolated caudal vertebra (XIII).

The next vertebra is shorter than the fourth of the series, which in many ways it resembles, but the neural spine rises to a definite peak posteriorly from which its upper border slopes rapidly downward, there not being the long anterior extension of the preceding vertebra. It has a very marked rather slender transverse process, a little behind the anterior zygapophysis, to which a rib is attached. This rib, though of the same width as that which precedes it, is different because it quite soon bends backward rather abruptly and stretches the length of more than two vertebrae before it is interrupted by a fracture. The two next vertebrae are of practically the same type, and their broken off fragments of ribs are of similar structure.

The abrupt change in character of the vertebrae between the third and fourth, and the fourth and fifth of this series, and of their ribs between that of the fourth, and that of the fifth, is most noticeable and unusual, and I think should allow their position in the column as a whole to be determined. It is natural to suppose that the transition shown is that between the cervical and the pectoral series, that the short ribs of the third and fourth vertebrae here shown belong to vertebrae in the neck, the long ribs lying in the region of the shoulder girdle. This would make (if the shoulder girdle of specimen I be in its natural position, as there is every reason to suppose is the case) the third surviving vertebra of series XII correspond with the fourth or a succeeding vertebra of specimen I; and there is indeed some resemblance, particularly between the fourth vertebra (specimen I) and the second of this series. But the point is doubtful. What is very remarkable and certain is the great difference between the fourth vertebra of the series and those immediately in front of and behind it. It shows no signs of being abnormal in any way, and as the break in the series of ribs lies immediately behind it it may be a normal condition. The next three vertebrae, all much alike, seem to be normal dorsals with long curved ribs.

A partly exposed series of vertebrae (X) is important. The anterior end of the column is wrapped up in a series of seven long bony ribs tightly pressed downward on to it, and begins at a fracture. Thus there were seven rib-bearing vertebrae before the first exposed one. This has a short neural spine and is in general rather short compared with the one behind it. It may well agree with the last of the series XII in general character, but cannot be the equivalent of that vertebra, which is only preceded by two vertebrae bearing long ribs. Thus its position in the total sequence may well be twelve–fifteen. It has a rather pointed neural spine, whose anterior border is cut away towards the front edge of the neural arch. The anterior zygapophyses are rather widely separated and there is a short transverse process for the rib-head, rising from the root of the anterior zygapophysis rather high up and well forward. Behind it is an exposed part of the neural arch passing down to the centrum. The three vertebrae behind differ in having a longer summit to the neural spine, in being individually longer, and apparently in having the facet for the head of the rib slightly more ventrally placed than it is in the preceding one. The column then breaks off, ribs projecting behind it.

The position of this section of column is very difficult to determine. It is evident that most of it, at any rate, lies behind the fragment called XII. It is also evident that the chain of four exposed vertebrae is not at all overlapped by anything in the series called XI.

The series XI is continuous and contains eleven vertebrae, often much damaged, whose individual characters can in most cases be determined with certainty, though incompletely. The first exposed one, seen from above, has a well preserved neural arch of swollen appearance whose spine is a low rounded ridge; the anterior zygapophyses are widely separated and the top of the small transverse process lies at their root. The next vertebra, similar in general character, is much wider in the middle, and the rib facet is larger. Its immediate successor is similar, except that the posterior zygapophysis is less spread and more massive. The fourth, rather well shown, appears longer and is a good deal stouter. Its width across the middle is considerable, and the rib facet is very well shown as a groove starting below the base of the anterior zygapophysis, with a transverse process supporting it. So far as seen it is a cylindroid depression passing almost vertically downwards to the centrum. The next two vertebrae, rather damaged, are similar, the second of them seems to have had a narrow flattened ventral surface, the lateral surface rounding into it but being itself concave so that the ends of the centrum and its contact with the neural arch surround a basin-shaped hollow. This observation can be confirmed on the next posterior vertebra. The next four vertebrae are badly damaged, but do show the existence of a notochordal canal through the centrum, and the great size of the neural canal. Finally, the last preserved vertebra, seen in strict side view, is short and shows little sign of any rib head; indeed, the last three vertebrae show no attached ribs and no evidence of having formerly possessed them. They may have been immediately in front of the sacrum.

No intercentra can be seen between any of the vertebrae here described.

Sacrum. The sacrum (XIV) is represented only by a very battered (presumably second) sacral vertebra and its rib, recognizable because it is still attached to the inner surface of a right ilium in position with respect to an ischium and the head of a femur. The neural arch surrounds a large spinal canal, shows no signs of anything more than a low mid-dorsal ridge, and bears a short, very heavily built sacral rib. This is closely attached by a single articulation, divided by a groove on its posterior surface into two parts, one meeting the side of the neural arch, the other (more massive) attached to a facet carried on a short projection from the centrum. Fragments of one or two anterior caudal vertebrae lie behind, but are not fit for description.

Caudal vertebrae. An isolated caudal vertebra has a relatively slender neural arch, with a posteriorly placed, short, ridge-like neural spine standing immediately above the hinder end of the centrum and the posterior zygapophysis. The anterior zygapophyses are quite narrow and project a little before the centrum. A caudal rib is broken off, but its base is quite large, and is apparently in part of neural arch, and in part of central origin. There is no evidence of the attachment of a chevron, so the vertebra may well be an extreme anterior caudal.

Shoulder girdle. A complete, uncrushed shoulder girdle lies nearly in natural position with respect to the neck vertebrae belonging to the skull I. It is perhaps a little displaced, for whilst on the left side the clavicle is about on the level of the transverse process of the third vertebra, on the right it lies a little behind that process of the fourth vertebra. Otherwise it is naturally articulated and very well preserved. It has a humerus in articulation with the right glenoid cavity. The specimen has been prepared so as to show the greater part of the right side of the girdle from clavicle to extreme posterior end of interclavicle, and the greater part of the primary girdle. On the left side the primary girdle with the glenoid cavity is very well shown.

There are in addition two other shoulder girdles. One (VIII) is incompletely prepared but shows well the anterior half of the interclavicle, the right clavicle, and the right scapula and coracoid in natural relation to it. The third shoulder girdle (IX), very little prepared but showing both scapulo-coracoids, has certainly belonging to it a left humerus and forelimb lacking most of the phalanges.

The two interclavicles (I and VIII) are well preserved and well shown, and they differ. In VIII it seems evident that, from where its admedian border rests in a depression on the ventral surface of the interclavicle, the clavicle extends forward as well as outward, and the point of its attachment to the scapula lies considerably in advance of the front end of the interclavicle. In I, on the other hand, the clavicle from its attachment to the interclavicle extends outwards and backwards, so that the contour of the front end of the shoulder girdle, and the position of the scapula, is different in these two individuals, and these differences necessarily impose changes in the actual shape of the scapula.

The nearly complete interclavicle of the individual I ends anteriorly in a rhomboidal-shaped head which sweeps a little upward from the flat ventral surface of the greater part of its length. The clavicle rests on the lower surface of the anterior face of the bone and, although itself thin, is so placed as to have a wide smooth outer surface passing upwards and backwards, whose outer border is applied to the front edge of the scapula. The bone then narrows to a point some distance below the upper border of the scapula. The rather bowl-shaped anterior part of the interclavicle passes into a straight shaft, with a low median ridge on its ventral face, which narrows at about half its length to little more than a thin rod, with a concave upper surface, ending far behind the most posterior point of the coracoid.

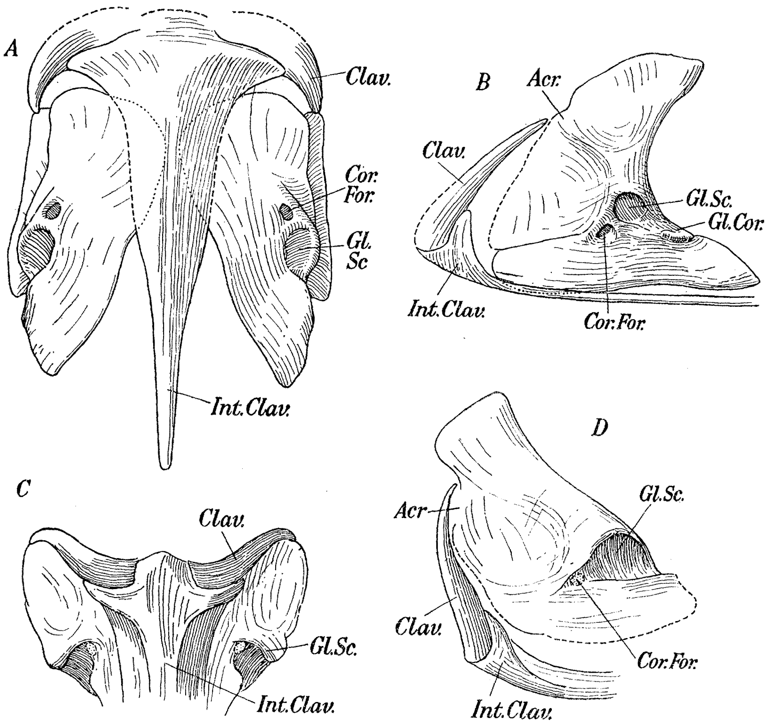

FIGURE 5. *Millerosaurus pricei* n.sp. (magn. × 3). Reconstructions of two shoulder girdles, *A* ventral and *B* lateral belonging to skull I, *C* ventral and *D* lateral marked VIII.

The primary shoulder girdle (well shown in I and VIII) is composed of two pairs of cartilage bones, scapula and coracoid. In each case it is difficult to see the sutures between these bones, only anteriorly (and especially in I) is it possible to determine the plane of junction. The two girdles differ in their extent antero-posteriorly along the suture between the scapula and coracoid, in advance of the 'coracoid' foramen, I being, proportionally to the scapula height, twice as wide as VIII. But in general structure they are very similar.

The scapula is a sheet of bone curved so as to fit round the ribs. Its upper part is thin and, except for the place where a ridge rises from the process overlapping the glenoid cavity and passes forward round a quarter of a circle to meet the anterior border, remains thin until it meets the front of the coracoid in suture. The point of meeting of this ridge with the anterior border is the acromium, and the border of the bone is cut back above it to receive the tip of the clavicle. Below this point the border sweeps forward and downward so as to enclose either a large area of very thin bone (specimen I) or only a small strip (VIII). The coracoid, which seems to be a single bone, joins the scapula in a straight, generally fused suture, and stretches in toward the middle line nearly to touch its fellow for a very short distance, diverging from it widely as it passes back. In front the two bones also separate a little, there being no effective symphysis.

The glenoid region, fortunately well shown in both specimens, is very remarkable. The posterior border of the scapula is a rounded surface which widens greatly until its lateral part is suddenly cut into by the deep glenoid cavity. This is overhung by a thick ridge of scapula, which widens as it rises, its anterior border passing round a quadrant of a circle to the acromium while the posterior border is that of the bone as a whole. This ridge is truncated by the hollowed upper part of the glenoid cavity, which faces downward, but then follows a screw-shaped track as it passes from scapula to coracoid, and ends facing nearly directly upward on the outer border of that bone. Lying a little below and in front of the glenoid cavity is a thick mass of bone perforated vertically by the coracoid foramen, a cylindrical hole whose admesial part presumably lies in the coracoid. This glenoid cavity is unique; nothing like it has ever been described in detail, but its significance is evident. It is an intermediate phase between the screw-shaped glenoid cavity of labyrinthodonts and Lower Permian reptiles in general, and that of modern lizards. The basal Triassic Russian *Microcnemus* (von Huene 1940, fig. 1, p. 5) is a partial intermediate.

The coracoid is widest anteriorly, where it stretches inward above the interclavicle until it closely approaches, but does not meet, its fellow. From here its border diverges from the middle line, the two bones thus enclosing a large triangular space, crossed by the interclavicle, which in life was presumably filled by a cartilaginous sternum reaching backward above the interclavicle.

Humerus. The humerus has a slender shaft, widening greatly to the flattened upper and lower ends. The wide but thin upper end of the bone forms a long slender hemicylinder which fits the glenoid cavity. It suggests that the bone could extend horizontally from the glenoid cavity, at right angles to the body, remaining in articulation when brought in to the side, as in the shoulder girdle (I). The pectoralis muscle is attached to a well-marked process, a good deal turned downward, which subsides gently into the shaft, of circular section. The distal end is greatly widened in a plane at right angles to that of the proximal end; the entepicondyle extends considerably beyond the ulnar articulation, which lies on the end of the bone. There is a hemispherical knob so placed that the radius which articulated with it could move, apparently in a wide cone, round a position at right angles to the broad plane of the humerus. There is a large entepicondylar foramen well up the shaft, and a small ectepicondylar foramen opening about at the level of the proximal border of the radial articulation.

It seems clear that in life the humerus articulated with the shoulder girdle in such a way that it could be drawn forward until it was at right angles to the body, directed a little downwards, and with its articular head lying below that part of the glenoid cavity which is carried by the scapula. Posteriorly the head of the bone must have rested upon the projecting tip of the coracoid part of the glenoid cavity. How far the distal end of the bone can be brought in toward the body without dislocation seems to be shown on the right side of specimen I, where the humerus is placed in the plane of the ventral surface, and pressed in so that its inner border actually overlies the posterior part of the coracoid, its head being still in position with respect to the scapular facet of the glenoid cavity. From here it can certainly be turned outwards until it lies at right angles to the body.

Radius and ulna. The radius and ulna (IX) are essentially in position, the radius being attached to the appropriate knob on the humerus, and the ulna a little dislocated from that bone. Both are short bones, with expanded ends and comparatively narrow shafts of approximately circular section, which articulate with the bones of the proximal row of the carpus.

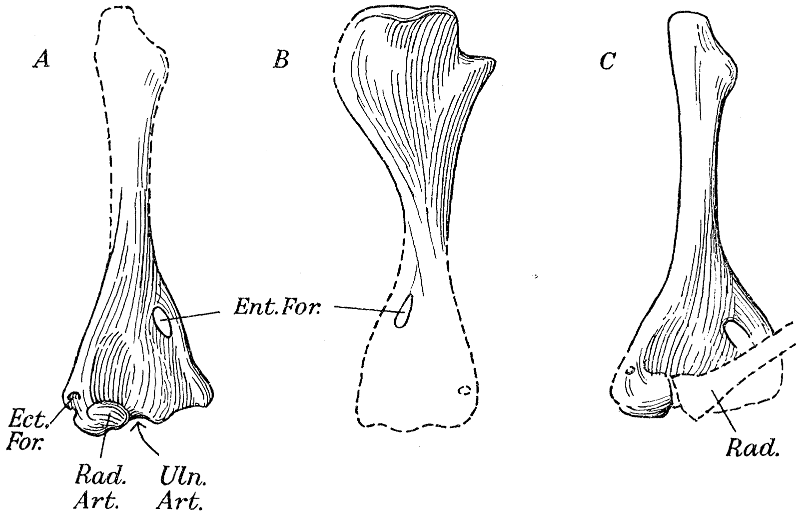

FIGURE 6. *Millerosaurus pricei* n.sp. (magn. × 3). Right humeri, *A*, distal end from in front, *B*, proximal end from above, belonging to skull I; *C*, from in front with radius in articulation (IX).

Carpus. The carpus is not very well preserved, the bone having rotted and being seen chiefly in a rather scraped section, but the general plan is certain. Three bones of the proximal row are visible, ulnare, intermedium and radiale. The large ulnare has a proximal articulation with about two-thirds of the end of the ulna and then joins the intermedium, which occupies the remainder of the distal end of the ulna. The intermedium articulates by a perfectly straight suture with a large bone—the median centrale—which then makes contact with the ulnare, a large open passage lying between the three bones. The radiale is a small incompletely preserved bone which proximally articulates with the radius. It touches the median centrale on its inner border, and has a broad contact with the radial centrale, which is a comparatively large bone to the radial side of the carpus.

There are five distal carpals. The Vth is apparently attached by the whole of its outer border to the base of the Vth metacarpal. The IVth carpal is the largest. The IIIrd, also a large bone, shows what is easy to interpret as a division into a proximal (second central) and the IIIrd distal carpal, but it is uncertain whether such a division be justified. Carpals II and I are well shown.

Nothing but the extreme base of metacarpal I is visible; II, III, IV and V are shown essentially complete, at any rate enough to make clear the length and general nature. The only interesting and remarkable point about them is that metacarpal V (little more than half the length of IV) extends upward to cover almost the whole height of the distal carpal associated with it. The digit is in fact somewhat divaricated in a way whose significance it is not easy to understand. No complete finger is known.

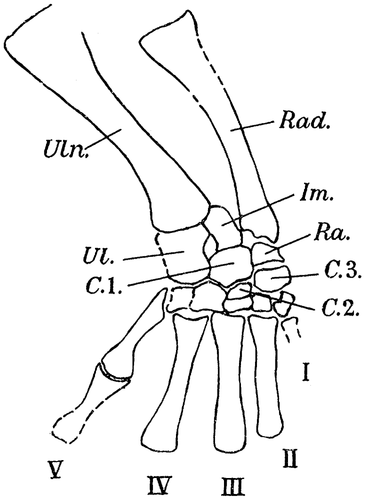

FIGURE 7. *Millerosaurus pricei* n.sp. (magn. × 3). Right forearm and hand, upper aspect (IX). I to V, metacarpals, each articulated with a distal carpal.

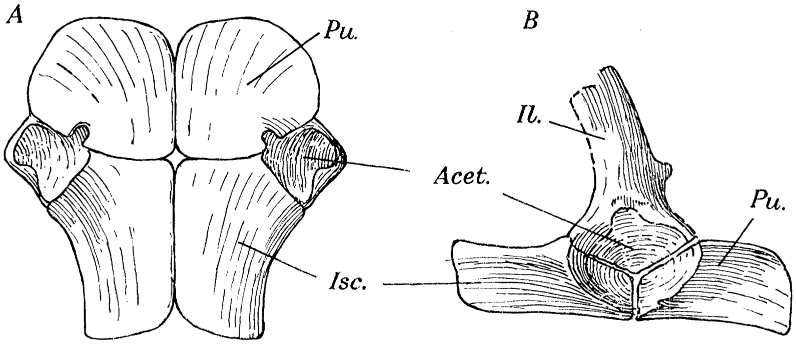

FIGURE 8. *Millerosaurus pricei* n.sp. (magn. × 3). Pelvis, *A*, from below; *B*, right lateral aspect; from XIV and XV.

Pelvis. The pelvis is represented by a sacral vertebra and rib, and an ilium and ischium in articulation (XIV) seen from behind and from the outer surface. In addition, both pubes and an ischium of another individual occur (XV), again nearly in their natural position. It is thus possible to obtain a clear idea as to the nature of this part of the skeleton.

The sacral vertebra and rib, seen obliquely from behind, show a shallow centrum widening to its anterior face and bearing a very powerful transverse process whose rib facet continues that on the neural arch. The rib is short, deep and powerful, and is fastened on to the inner surface of the ilium, so that its own posterior surface and the hinder border of the pelvic bone coincide. It is probable that there is an anterior sacral vertebra, but nothing can be seen of it.

The ilium has a widely expanded lower end with a rather rounded border obscurely divided into two nearly equal faces for attachment of the ischium and the pubis. There is a shallow acetabular cavity extending very far forward, but leaving a rather wide non-articular face exposed laterally in front of the hinder border. There is the customary wedge supporting an outward extension of the dorsal acetabular surface, but this is little protuberant and not very well marked, in contrast to the condition in most theropsid reptiles. The iliac blade is comparatively narrow, directed backward, and soon broken off; its anterior border has a special projection somewhat above the summit of the acetabulum.

The pubis as seen from below is a rounded sheet of bone whose surface has a concavity running across its width, so that the front border of the bone is a little down-turned. Its articular surface has not been cleaned, but it runs in a straight line on the ventral surface and ends at a deep notch, which is the pubic foramen. Mesial of this the border of the bone extends inwards in a slight curve to meet its fellow. The general appearance of the material makes it probable that the two pubes meet in a low ridge along the ventral line, and then rise a little as they are followed laterally, but it is impossible to determine this with certainty.

There are ischia of two individuals visible, one lying nearly in position in contact with the ilium, the other with the paired pubes. The bone had a long straight admesian border which ultimately swings outward to cut the posterior end of the lateral border of the bone at rather less than a right angle. There is no reason to doubt that the front border of the bone had a continuous contact with the hinder margin of the pubis, and its lateral part turns outwards to end where it joins the hinder border of the ilium, a little behind the acetabulum. The heads of both ischia are somewhat damaged, but it is evident that the general arrangement was very much as it is shown in figure 8. The admesian border is shown in both pubis and ischium and makes the general proportions quite certain. The pelvis is thus a plate-like structure of a very primitive character.

Hindleg. Both pelves (XIV and XV) have associated with them the upper part of a femur. There is also the lower end of another femur (XVI) and, belonging to one of the pelves (XIV), the upper part of a tibia. In addition, there are a tibia and fibula (XVII) with an unintelligible tarsus fragment and three metatarsals, the first of which has a phalange and a claw. There is (XVIII) another excellent set of metatarsals with a tarsus which has been etched out, and is represented by an extremely sharp mould of each of its two faces. This lacks a good representation of the bones of the proximal row, one of which has slipped over, or is turned down on to the distal row. Finally, what is apparently a foot and not a hand (opposite side of XVIII) shows a complete series of metatarsals with phalanges (generally two) articulated with them. The structure is a little compressed and is seen on an irregular broken face. It is, however, of some value.

Femur. The femur is a slender nearly straight bone widening a little toward either end. The shaft is nearly circular in section, but where it widens toward the proximal end its ventral surface becomes shallowly concave. Here the bone is abruptly truncated by a gently curved articular face, nearly twice as wide as it is deep and evidently covered by a cartilaginous cap which fitted the shallow acetabulum. The distal end (known only in an isolated bone (XVI) not completely removed from the matrix) is unexpectedly massive, has a slight depression on what is presumably its lower surface, and ends in a rounded knob which is not completely seen. All that can be judged from it is that the distal part of the limb was not turned sharply under at the knee.

Tibia and fibula. Tibia and fibula (XVII) are apparently a good deal shorter than the femur, the foot being comparatively large.

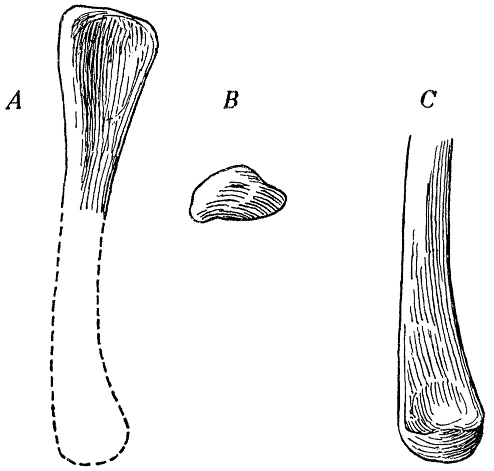

FIGURE 9. *Millerosaurus pricei* n.sp. (magn. × 3). *A*, proximal end of right femur (XIV), ventral surface; *B*, the proximal articular surface of the femur *A*; *C*, ventral surface of distal end of femur (XVI).

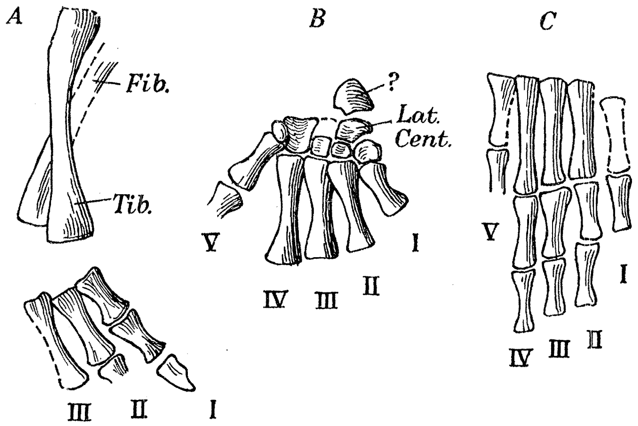

FIGURE 10. *Millerosaurus pricei* n.sp. (magn. × 3). *A*, right tibia, fibula and digits I to III (XVII); *B*, tarsus, metatarsals I to V, a base of one phalanx (as preserved, XVIII); *C*, series of metatarsals and phalanges of one foot straightened out, digits I to V (reverse of XVIII). The distal tarsals in *B* lie at the base of their metatarsals.

Tarsus. The proximal row of the tarsus is represented only by a bone seen in impression in the isolated foot (XVIII). This shows a thin plate-like element, a little curved and lying on the tibial side of the structure, turned down on to what is probably the upper surface. The distal row of the tarsus possesses five elements. The Ist is rather large, the IInd and IIIrd are small bones nearly square on the exposed surface, the IVth is the customary large element, and the Vth is a small rounded nodule with whose lateral surface the Vth metatarsal, somewhat divaricated from the IVth, articulates. There are apparently two centralia, one of which enters the inner margin of the tarsus supporting the Ist and

IInd distal tarsals, the other being a mesial centrale. Nothing is known of the lateral proximal tarsal.

The other foot (reverse of the XVIII fragment), which stands edgeways in the nodule and has its width reduced by the sliding of the bones on one another, appears to show all the toes, none of which, however, is complete. They show little beyond their length and do not extend beyond the second phalanx. The first and second phalanges do not differ greatly in length and are each more than half as long as their supporting metatarsals. The second phalanx of the IInd, IIIrd and IVth digits is of almost exactly the same length, whilst the first phalanx increases in length from the IInd to the IVth. There is evidence that the terminal phalanx was a claw.

Abdominal ribs. A single specimen (XVIII) shows that the animal possessed a series of abdominal ribs, including a mid-ventral element which has an anteriorly projecting point in the mid-line.

General reconstruction

The material already described allows of a general reconstruction of the skeleton which cannot be very seriously in error. It is evident that the pointed skull, widest in the temporal region, was followed by a short neck, the large vertebrae of which are followed immediately by more slender elements extending, with some variation in character, to the sacrum. The fourth and fifth vertebrae bear very short, broad pointed ribs which seem to have lain between the scapulae. The shape of the trunk in this region may have varied a little. In specimen I it seems obvious that the body was rather shallower than it is wide, and that the lower surface was rounded from side to side and rose upwards over the front of the interclavicle towards the head, which was carried above the ground.

The body is shown by direct measurement (individual I) to be at least 8·6 mm deep and 12·9 mm wide at the front of the shoulder girdle, and (from XIV) about 12 mm deep and 11 mm wide at the pelvis. The height at the shoulder in I is no doubt less than in life, for little space remains below the vertebrae and above the coracoids; in fact, the animal may well have been about 12 mm deep from shoulder to pelvis and the same width, the body section being perhaps rather quadrangular. The elaborate glenoid cavity as a whole is directed outwards and little, if at all, downwards. The scapular part of it is directed almost entirely downwards, that on the coracoid mainly upwards, but a little outwards. It follows that the humerus with its widened head projected from the body parallel to the plane of the ground, and that it had some freedom of movement, so that its distal end could move not only up and down, but from back to front parallel to the ground, through a very wide arc.

The size and shape of the ribs suggest that the body in the middle of its length (and even quite posteriorly) was a good deal wider than it is at the shoulder girdle. There is some evidence that the last few presacral vertebrae lacked ribs, and the body evidently narrows at the pelvis. The comparatively narrow pelvis, with the considerable overlay of the ilium over the lower part of the acetabulum, again suggests that the femur may have been a little downwardly directed.

The bones of the forearm, presumably capable of rather extensive movements, must have been carried in the main about at a right angle to the wide distal end of the humerus.

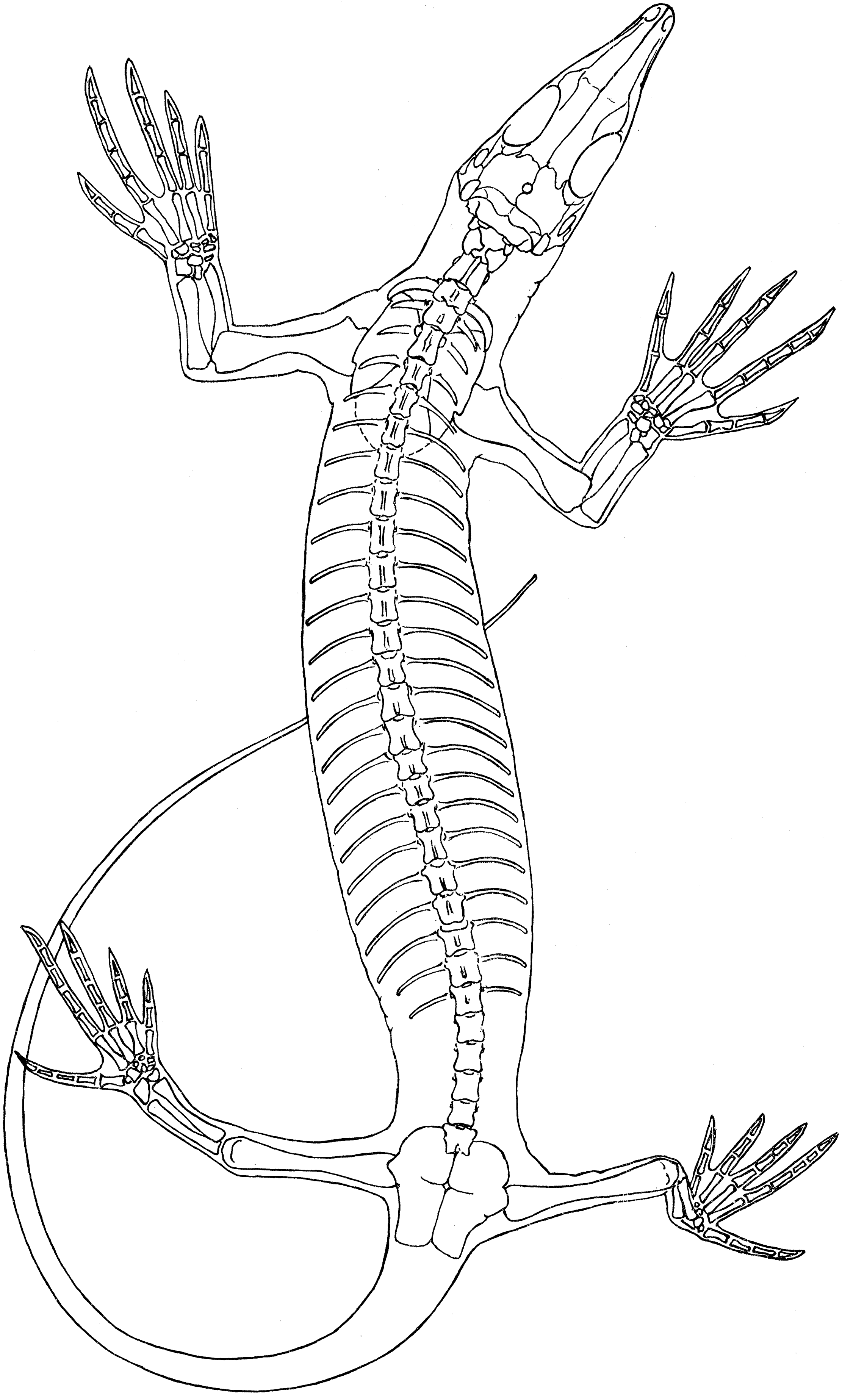

FIGURE 11. *Millerosaurus pricei* n.sp. (magn. $\times 1\frac{1}{2}$). Restoration of skeleton from above.

The hand is spreading, and the position of the Vth metacarpal, which comes up on to the lateral surface of the Vth carpal, suggests that it was a little separated from its fellows. The number of phalanges is not known, but there is no reason to suppose that it was not the normal lizard 2, 3, 4, 5, 3.

The femur is a bone of very much the same length as the humerus and has, of course, considerable range of movement in the acetabulum. Its distal end is so badly known that nothing can be said as to the habitual pose or movements at the knee joint.

The tibia and fibula, much shorter than the femur, correspond in length to the forearm, and the foot agrees in its general character with the hand, but appears to be more slender; there is no reason to suppose that the only hand and any of the three available feet come from the same individual! Unfortunately, nothing can be said as to the level of flexibility in the tarsus. The only known proximal tarsal is a rather delicate shell-like bone which suggests that the effective movements were between the tibia and fibula and the tarsus, and not across the middle of the latter. The Vth digit, which in many ways resembles that of the hand, is stretched outwards through about 45 degrees from the IVth, and is much shorter. It appears in the main to articulate with the lateral side of the Vth distal tarsal, as does the Vth metacarpal with its carpal.

As the tail is represented by only two proximal caudals nothing can be said as to its length, though had it been very long I should have expected to have found strips of caudals to correspond with the lengths of presacral column.

The skeleton as a whole is obviously lizard-like: the general proportions can be matched amongst modern lizards. Nothing can be said as to the food habits, though there is no reason to suppose that the diet differed from that of insect-eating lizards of today. Nothing is known of the nature of the skin, except that it is improbable that it possessed osteoderms other than those of the head.

The present form is directly comparable with *M. ornatus*, described by Broom from a skull lacking the preorbital part. It is evident that the general structure of the two animals is identical. Broom's type is about 30 % larger than the present skulls, its orbits are proportionally smaller, and it is somewhat more depressed, but the skull is said to be considerably crushed and is in any case not very well preserved. There is no reason why the new material should not be referred to his genus *Millerosaurus*, though differences in proportions from the type of *M. ornatus* suggest that they are specifically different. I therefore call the present animal *Millerosaurus pricei*, n.sp., after the late Mr Bernard Price, whose benefaction established the Institute which collected the material, and establish skull II as the holotype.

MILLEROSAURUS NUFFIELDI, N.SP.

History

Further information about the structure of *Millerosaurus* may be gained from an isolated skull (R. 287 in my own collection) from the *Cistecephalus* Zone of Katbos. This specimen is a nodule, a little less than $3\frac{1}{2}$ cm in length by 2 cm wide, which contains a skull with a disarticulated occipital region; the bones behind the left orbit are pushed inwards, and the external surface was somewhat scraped. The actual preservation is good and the skull establishes some structural qualities not easily seen in the material of *M. pricei.* It is a different species, the skull is a little larger, the temporal fossa considerably higher and shorter, and the orbit larger. I therefore call it *M. nuffieldi,* as I obtained it on a visit to South Africa sponsored by the Nuffield Foundation, to whom my thanks are due.

Description

The well-preserved upper surface shows a rather characteristic coarse ornamentation of shallow, meandering wide-bottomed grooves which isolate low smooth bosses and ridges on the parietals and frontals, these being presumably osteoderms. The parietal sends a spike forward between the hinder part of the frontal and postfrontal, as in the type of *M. ornatus* and *M. pricei.* The table is wide, and the lateral border of the parietal on the right side has been broken away, leaving the impression of its lower surface on a very thin film of matrix overlying that subparietal flange of the postorbital which forms almost the whole of the upper border of the temporal fossa. The jugal is very well shown as a slender bone projecting upward so as to form about half the lower and posterior borders of the orbit and to reach the postorbital, which is shown misplaced on the left side of the skull.

The squamosal has a very small anterior projection, meeting the hinder end of the postorbital above the temporal vacuity; the bone passes down behind that opening until it meets the quadratojugal, which it overlaps. It is well shown on the left side of the skull that the upper end of the squamosal underlies the hind corner of the parietal for some distance, and comes into contact with the supratemporal only anteriorly, leaving this bone projecting freely in a way shown on both sides of the skull. The under-surface of this part of the squamosal rests on the rounded upper end of the quadrate, extending inward for a short distance beyond the contact. From this contact the squamosal extends downward along the lateral border of the quadrate until the upper part of the quadratojugal separates the two bones. The quadratojugal is attached to the outer surface of the quadrate, extending down it to rest on an oblique facet some way above the articular surface of that bone. A small quadratojugal foramen is present. The outer surface of the squamosal bears a ridge, which beginning near its upper end, passes forward and downward to the quadratojugal, so as to enclose a deep recess. This recess forms part of a cone-shaped hollow, at the inner end of which still lies the end of the bony stapes. Thus the ridge marks the place of attachment of the tympanic membrane. The quadratojugal stretches forward to meet the hinder end of the jugal in a way shown on the right side.

The maxilla is badly scraped on the right side, and rather better preserved on the left with its teeth only in scraped section. Part of the rest of the face is shown on this side but cannot be interpreted with safety.

The specimen shows extremely well the relations of the supratemporal, tabular and dermosupraoccipital to the parietal. On the right side the parietal (very well shown except for the loss of about a millimetre of its lateral border above the postorbital) has its posterior corner notched, forming a quite deep incision into which the whole of the anterior border and some two-thirds of the admesial side of the supratemporal are wedged. The upper surface of the parietal ends behind at a ridge which marks out a rather gently concave margin directed slightly backward where it joins the supratemporal. From the ridge the parietal descends on to the occiput for some distance, forming a recess which no doubt marked the attachment of muscles. This posterior flange passes outward until it ends in a long attachment to the supratemporal, and is visible to its contact with that bone. It is, however, covered by a pair of dermosupraoccipitals which pass steeply down, meeting one another in a low median rib; the lateral borders of these bones leave freely exposed a small area of the hinder flange of the parietal. On the right side of the specimen this flange bears a depression with a perfectly sharply defined border which clearly represents the attachment of the tabular. The attachment area passes downwards and comes into contact with the lateral margin of the supratemporal in such a way that the tabular (best seen on the left side where the bone is in place) overlaps the parietal, and touches the inner border of the projecting part of the supratemporal for some short distance. The supraoccipital is present, misplaced, lying below and in the main behind the lower border of the dermosupraoccipitals. The remainder of the supratemporal (shown very well on the right side, and almost equally well on the left) passes back behind the squamosal, separated by a space from it, and there is no real doubt that, as in *M. pricei*, it ultimately met the end of the paroccipital process, which is shown misplaced on the right side of the present skull.

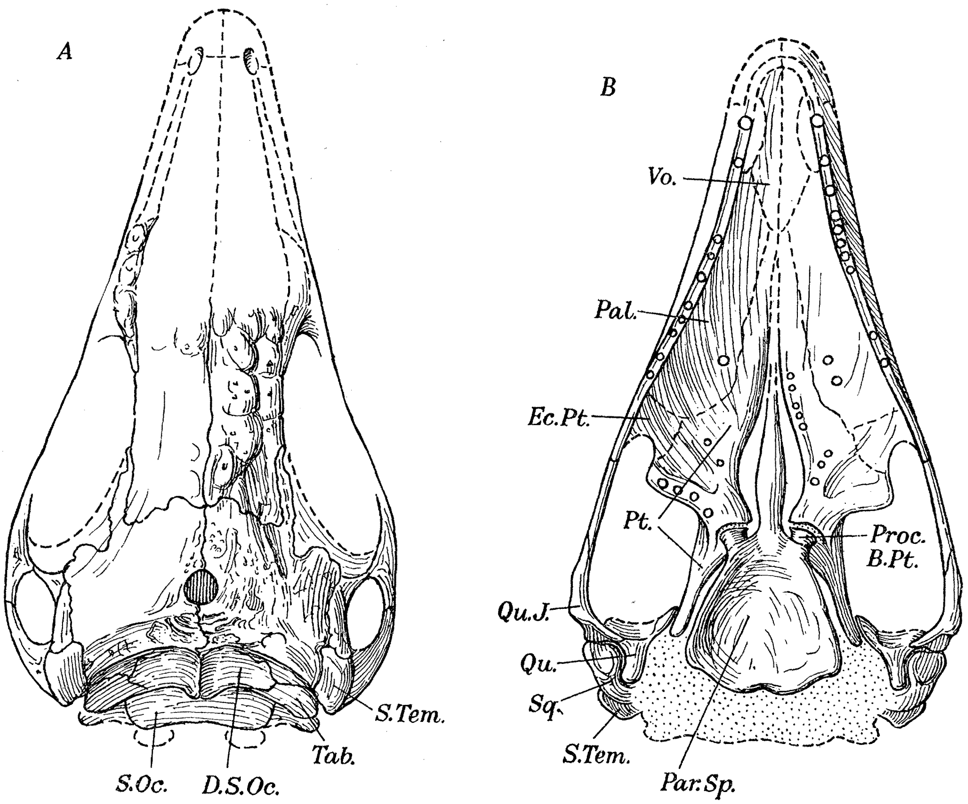

FIGURE 12. *Millerosaurus nuffieldi*, type skull, D.M.S.W. coll. R. 287 (magn. × 3). *A*, dorsal; *B*, palatal surface.

The quadrate is well shown on both sides. It agrees very closely with that of *M. pricei*, especially in having a short pterygoid flange arising from a special internal process above, and mesial to, that lower part which ends in the articular surface.

This specimen is remarkable for the perfect preservation and admirable exposure of the stapes. This bone is only 2 mm long, but shows the whole of its structure. It lies essentially in position attached to the right quadrate, but I think pushed down a little farther ventrally than it normally lay. Part of it is visible behind the quadrate in a direct lateral view. It is a short thickset bone which extends outward from a base inserted in the membrane closing the fenestra ovalis to pass behind the quadrate and divide into three processes. One—that which is outwardly directed and ultimately inserted into the tympanic membrane—was cartilaginous, its existence only shown by the circular hole in the outer end of the stapes left by its decay, whilst the others are represented by short cylinders of bone. The upper, directed vertically, is a dorsal process, no doubt passing up to the neighbourhood of the end of the paroccipital process. The lower passed on to the hyoid arch, extending downwards and forwards, as it does in *Sphenodon*. The shaft which lies mesial of these three processes is very short and massive, ending mesially in a flat surface inserted into the membrane closing the fenestra ovalis. It is perforated from back to front by a foramen for a stapedial artery less than half a millimetre in diameter and leading from a groove on the median side. A processus internus arises from its anterior surface to rest upon the inwardly and backwardly directed posterior surface of the quadrate. It is a remarkable fact that the stapes lies so nearly in position with respect to the quadrate in a skull in which all the bones of the otic capsule are quite grossly misplaced.

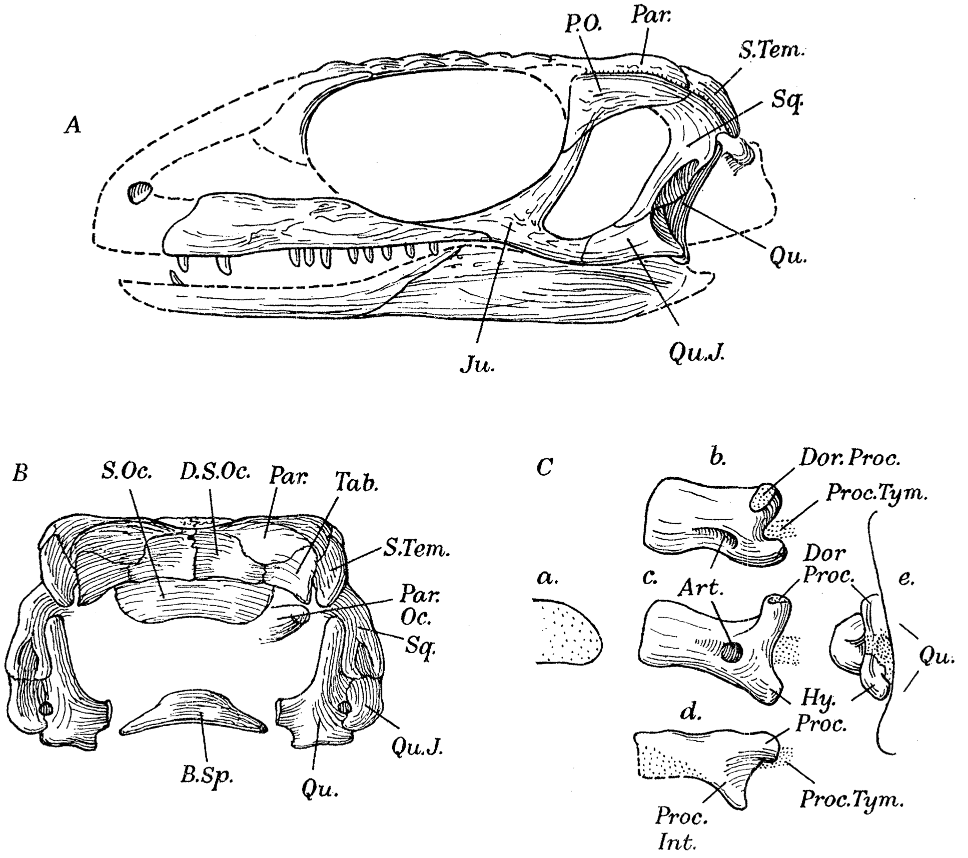

FIGURE 13. *Millerosaurus nuffieldi*, type skull. *A*, left lateral aspect; *B*, occipital aspect (magn. × 3). *C*, right stapes (magn. × 9): *a*, outline of foot; *b*, from above; *c*, directly from behind; *d*, from below; *e*, viewed laterally, the nearly vertical line is the hinder surface of the quadrate.

Palate. The palate has been exposed and is in general well preserved. The basioccipital is misplaced and so is an exoccipital, but the great parasphenoid is shown in place. It is exceedingly wide posteriorly, where its lateral and posterior borders, although damaged by scraping, seem to be complete (left side of the skull) and end in rounded processes. It extends very far back, terminating in the mid-line well behind the articulation of the quadrate with the lower jaw. Its ventral surface is concave, the concavity becoming quite deep anteriorly in the region of the basipterygoid process. This appears to be composed entirely of basisphenoid, projects out laterally beyond the apparent limit of the parasphenoid, and articulates with the pterygoid by an almost transverse face. At the hinder end of the parasphenoid preparation has shown the existence of a mass of bone whose ventral surface is parasphenoid; but it is $1\frac{1}{2}$ mm thick, and evidently includes much more than a membrane bone, and must be the hinder end of the basisphenoid, for the basioccipital lies elsewhere. Anteriorly the parasphenoid is continued for a long distance as a slender processus cultriformis which in front, at any rate, seems to have a ridge along its mid-ventral line; it is possible that still farther forward the ridge bears teeth.

The pterygoid is connected to the braincase by a backwardly directed flat face which articulates with the basisphenoid. This lies on an internal process from the body of the bone from which arises the quadrate ramus, a thick sheet whose cylindrical lower border is continued dorsally by a special thin flange lying behind and lateral to the basipterygoid process. Immediately lateral to the basipterygoid process the pterygoid flange passes outward and a little forward in front of the subtemporal fossa, with down-turned hinder part whose wide lower surface carries a row of teeth. In front of this ridge, which ends against the inner surface of the lower jaw, the palatal surface of the pterygoid is excavated by a deep hollow which must, beyond the point exposed by preparation, be roofed by the ectopterygoid bone. The anterior wall of this hollow is also made by pterygoid which, when it reaches the general level of the palate, forms a low ridge, carrying a row of teeth, directed forward and outward; these extend up to the suture with the palatine. Between this row and the admesial margin the pterygoid forms a very shallow groove, the inner border being a little thickened and down-turned, showing on the left side some evidence of the existence of a single row of teeth. The palatine, so far as shown, has a flat palatal surface bearing a single row of larger teeth just within the lower jaw. The suture separating the pterygoid and palatine is shown on both sides. Difficulties of preparation, and a misplaced bone—possibly a vomer—prevent any further description.

Little can be said about the lower jaw. It seems to agree with that of *M. pricei*, but the retroarticular process is weathered away, and its length cannot be determined.

It is evident that this form is different from *M. pricei* in a number of small ways, but that the two can conveniently, and I think properly, be placed in the same genus. The important new facts from *M. nuffieldi* are the details of the relationship between the tabular and the supratemporal, and the nature of the palate and of the stapes.

That this genus may be called *Millerosaurus* seems evident. Broom's type skull is larger than those above described and much less well preserved. The general structure is clearly the same, the apparent differences being due to a lack of evidence. The large postorbital extending far back to meet the squamosal above the single temporal fossa is similar in the three animals; that it appears lateral to the parietal in Broom's specimen is almost entirely due to crushing, for his creature is only half as deep as it is wide posteriorly, whilst the other two species are relatively much deeper.

MILLEROSAURUS COMPARED WITH OTHER MILLERETTIDS

Milleretta rubidgei

Broom writing on *Millerosaurus* says that the only properly described form from which it can be derived is *Milleretta rubidgei*—the only important difference being the much better developed temporal fossa in the former—and 'that they doubtless belong to the same family'. *Milleretta* from the *Cistecephalus* Zone was described by Broom in 1938 under the preoccupied name of *Millerina*. There are three specimens of this form extant, all in Mr Rubidge's collection, and to him I owe the opportunity in 1949 of examining these skulls, and can in general confirm Broom's account of the structure. There are, however, some differences which are of importance, and I therefore give in figure 14 ink versions of my original pencil drawings made freehand from the skulls with nothing but a pocket lens.

Broom's figures of the side view, dorsal surface and palate seem to me in general accurate. In particular, his account of the very strange ornamented surface—which is unlike that of the Texan cotylosaurs with which he compares it in that it is really composed of rounded projections separated by grooves, whilst that of *Captorhinus* is composed of ridges separated by hollows—is reliable, and the 'incipient' temporal fossa seems to me almost exactly as he has figured it. It now appears that Broom's 'tabular' is in the main supratemporal, no doubt with a tabular contribution on its posterior surface, but when I drew it I was unaware of the existence of this condition in *Millerosaurus*.

A good deal more can be made of the occiput than Broom shows in his figures, which very curiously distort the real shape of the skull. The wide parietal region of the dorsal surface is very nearly flat but dips slightly in the mid-line, and the extensive lateral surfaces of the postorbital and squamosal behind the eye, and lateral to the supraoccipital are slightly concave, and differ very greatly from the rounded form that they are given in Broom's figure. Indeed, the occiput as shown in figure 14*B* is much more nearly that of *Millerosaurus*. Certain points are perfectly evident. The dermosupraoccipitals have very much the shape shown in Broom's fig. 2 (dorsal view), but the supraoccipital meets the paroccipital in a perfectly definite and very nearly straight abutment. The paroccipital extends out laterally, its upper border being in contact with the tabular and presumably also with the supratemporal. The foramen magnum is very large, and its supraoccipital border lies obliquely when seen in side view. The basioccipital lies far back and is shallow, the exoccipital rises as a substantial column (perforated by a foramen for the XIIth nerve) to have a long contact with the paroccipital above the vagal foramen, and finally to reach and just overlap the supraoccipital. The paroccipital passes down below the vagal foramen nearly to the level of the hinder end of the parasphenoid and was, no doubt, in contact with the upper surface of that bone by a cartilaginous continuation. The quadrate is apparently exactly like that of *Millerosaurus*; it has the same widened lower end, of which the middle part is the actual articular surface, extending outwards below the quadratojugal, and inwards as a pterygoid flange. The upper part of the bone is seen only as a narrow vertical column with a cylindroid posterior surface, and is capped by the squamosal, which has a pit for its reception. The outer surface is in continuous contact with the admedial border of the squamosal and quadratojugal, except for a quadratojugal foramen. These bones extend outwards for a considerable distance beyond it and provide a well-marked rather angular border, no doubt for the attachment of a tympanic membrane. The paroccipital has a quite definite rounded end at the level of the head of the quadrate but posterior to it, and in the paratype specimen of *Milleretta rubidgei* the posterior edge of this rather flattened process is overlapped by, and very nearly in contact with, the lower end of what is no doubt the supratemporal.

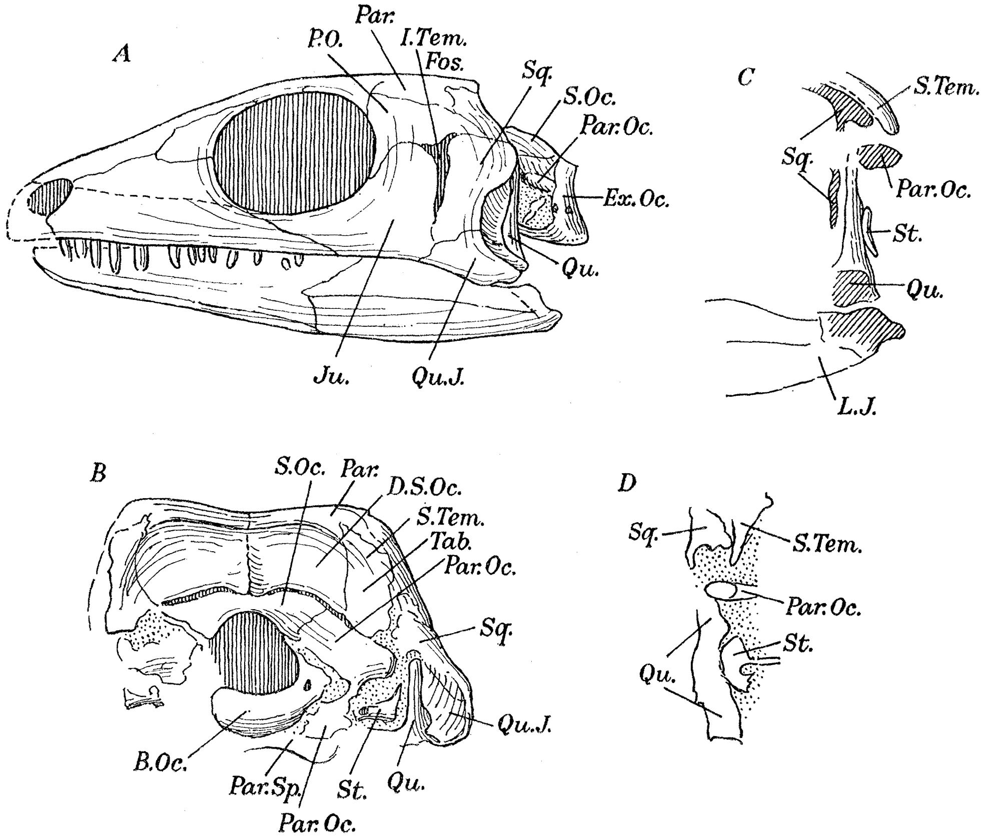

FIGURE 14. *Milleretta rubidgei* Br. Type specimens in Mr Rubidge's collection. Ink versions of unmeasured pencil sketches (magn. × 2¼ approx.). *A* and *B*, the type; *A*, left lateral aspect, *B*, occiput; both are drawn without restoration (except the snout). *C* and *D*, the paratype; *C*, direct lateral, *D*, occipital view as exposed by weathering (which has produced the areas covered by section lines).

In other words, the whole arrangement of the quadrate-otic region of *Milleretta*, so far as it can be seen, is like that of *Millerosaurus*. But it is possible to go further. As Broom recognized, the type skull retains a stapes on each side. On the left little can be seen except a scraped surface below the paroccipital. On the right the preservation is rather better, the bone is narrow proximally where it is perforated by a rather small foramen, and deepens distally where its lateral border lies parallel to, and a little mesial of, the laterally rounded hinder border of the quadrate. But the arrangement is perhaps better shown in the paratype, where a stapes is in position on the left side of the skull. In direct lateral view this skull shows the rounded posterior corner of the supratemporal coming down towards the posterior side of the paroccipital process. The squamosal (figure 14*C*) underlies the supratemporal and its lower surface forms a marked cup whose anterior side (seen in section) breaks off abruptly, its apparent continuation lying immediately in front of the quadrate. The quadrate as preserved shows nothing but its rounded cylindroid posterior surface, and lying attached to it is the widened outer end of a stapes, which, from behind (figure 14*D*), is seen to be cut into by a rather large foramen, dorsal to which a ridge passes inwards to represent the body of the bone. Taking the two specimens together there is little doubt that the condition was essentially as in *Millerosaurus*, the widened outer end of the stapes giving attachment to dorsal, ventral and outer processes not yet separated from one another at the point to which ossification has extended.

There is, therefore, every reason to suppose that *Milleretta* is very closely related to *Millerosaurus*, and that the failure of contact between the squamosal, postorbital and jugal, which leaves an irregular space between these bones in *Milleretta*, is really the equivalent of the very much larger temporal fossa surrounded in *Millerosaurus* by these same three bones. This being so the problem immediately presents itself—is the condition in *Milleretta* the first appearance of a temporal fossa, or is it the last stage of the closure of a formerly more extensive one?

Millerettops

Broom later described a number of animals, all from the South African *Cistecephalus* Zone, represented solely by isolated skulls, which he believed to be related to *Milleretta*. The first of these was described as *Millerettops*. It is well preserved, and rather larger than the original type, *Milleretta*, with which it agrees, except that it is slightly wider, the occiput does not extend so far back, and there is no trace of a temporal fossa. It possesses an ornament of bosses separated by shallow grooves, exactly like that of *Milleretta*, and even such details as the remarkable pointed parietal projection between the hinder ends of the postfrontal and frontal exists in exactly the same form. The relation of the bone which is certainly supratemporal to the parietal is the same. It is probably convenient to retain the generic name *Millerettops*, the most striking difference being really in the extent to which the occiput extends behind the hinder border of the parietal.

Millerettoides

Shortly after the original description of *Milleretta* Broom described as *Millerettoides* a specimen which is little more than the very imperfect palate of a small sharp-pointed skull which he believed to be closely related to *Milleretta*. The specimen seems to be quite indeterminable and can be ignored, though Broom may well be right in his opinion of its relationships.

Nanomilleretta

Finally, in 1948, Broom described another very small skull as *Nanomilleretta*. It is too imperfectly preserved to be identified, but is certainly related to the forms dealt with above. As drawn, however, it does not, as might be expected, show the parietal spike between the postfrontal and frontal, but this may be a failure of recognition. The only other point which seems to be shown is that the snout is extremely short, less in length than the rather large orbit, and that premaxillary teeth are shown.

Temporal vacuity—primitive or secondary?

It is unnecessary to labour the point that *Milleretta*, *Millerettops*, *Millerettoides* and *Millerosaurus* are extremely similar structurally. The resemblance extends to small details of the interlocking of dermal bones, as well as to the general structure of the occiput and otic region. The only point of difference is that *Millerettops*, with a completely closed temporal region, is by definition a cotylosaur; *Millerosaurus*, with a large temporal vacuity, clearly is not; and *Milleretta*, with an irregular space representing its temporal vacuity (which differs on the two sides of the same specimen), forms an intermediate between them. All these animals come from the *Cistecephalus* Zone, and are of very nearly the same date. They admit of two possible interpretations. The completely roofed *Millerettops* may be the primitive form, *Milleretta* may exhibit the first sign of the introduction of a temporal vacuity, which is fully achieved in *Millerosaurus*. Or the history may be the exact opposite, the completely roofed cranium of *Millerettops* may be the result of a secondary closure of a pre-existing vacuity.

The answer is, I think, evident. As Broom (1938, figs. 1 and 2) admirably shows *Milleretta rubidgei* has an ornamentation of the upper surface of the skull extremely similar to that of *Millerosaurus pricei* and *M. nuffieldi*. On this surface the three species agree very closely in the character of the low rounded swellings and the broad grooves separating them, and even in the actual number of such elements. It is therefore extremely probable that the ornament in *Milleretta* is also composed of osteoderms fused with the underlying bones. But in *Milleretta*, in contrast to *Millerosaurus*, osteodermic ornamentation covers the bones of the cheek, postorbital, squamosal, jugal and quadratojugal. As shown in Broom's figures the scales are larger than those of the upper surface, and they are so arranged that the pattern passes from bone to bone with no attention to their borders. Indeed, it continues across the lateral temporal fossa.

In *Millerettops*, where the cheek is completely covered by bone, the same condition of 'scale-like thickenings' covers the whole external surface, even the jugal and maxillae. There can be no real doubt that this ornament is indeed made by confluent osteoderms, below which free margins of genuine membrane bones grow inward to close the temporal fossa, as similar ingrowths roof over the upper temporal fossa of *Lacerta*. In *Lacerta* the upper temporal fossa, which exists in young individuals, becomes covered with a layer of osteoderms, as do the neighbouring parts of the head. As the animal grows larger delicate sheets of bone grow inward (below the osteoderms) from the parietals, supratemporals and postfrontals until they meet, completely closing the fenestra in the adult skull. The osteoderms remain superficial to these ingrowths, which they cover. The existence of this condition in *Lacerta* and other living lizards suggests that a similar ingrowth of membrane bones of the skull (the postorbital, jugal and squamosal) may in *Milleretta* have led to the almost complete closure of the lower temporal vacuity which exists in *Millerosaurus*.

Thus it seems to me very much more probable that *Millerosaurus* retains the ancestral condition of the group than that *Millerettops* does so. Such belief, however, raises the problem whether the wide temporal roof of *Millerosaurus* has retained a primitive condition, or whether it also has been produced by obliterating a supratemporal vacuity by a secondary ingrowth of surrounding bones under a cover of osteoderms.

I think that the existing conditions are primary. Had a supratemporal vacuity once been present—as it is, for example, in a lizard, or in *Youngina*—closure of that opening by ingrowth of its surroundings (parietal, postorbital and squamosal) would have been expected to occur, the three bones meeting in the middle of the area and lying in the same plane. Instead, the parietal extends outward to a free edge, overlying the two other bones without sutural attachment to them, exactly as it does in the primitive theropsid *Protorothyris*, which is as far removed systematically as two reptiles can be.

FORERUNNERS OF *MILLEROSAURUS*

Broomia

Thus we may look for the qualities of *Millerosaurus* in possible ancestors. Broom has already suggested that *Broomia* may be one such, and since my original description in 1914*a* only he has added to our knowledge of this animal. In 1921*a* he referred to the tarsus, and in 1941 justifiably criticized my original description and figure of the skull, and published a new restoration of the palate.

Broom points out that the teeth very obviously visible on the animal's left belong to the lower jaw, as they are set in bone which is evidently continuous with a dentary. This bone, with its attached splenial, comes near to a symphysis with those of the right mandible. Each of the teeth in the middle of this series shows a sudden shelf, the vertical external cylindrical surface stepping outward as it is continued. I interpreted this very peculiar structure as the meeting of blunt-tipped lower teeth with similar, necessarily widened, maxillary teeth, but I was certainly wrong in so doing. It must be remembered that the specimen is a mould retaining scraps of bone in some places, so that preparation is impossible. That the easily visible teeth belong to the dentary has always been obvious, and as the two dentaries now meet at a slightly widened symphysis lying far to the left of the mid-line it is certain they cannot retain a natural occlusion with maxillary teeth. The maxillary tooth row, had it remained in its natural position, should have been clearly seen, the admedian side of its teeth lying some 3 mm lateral to those of the dentary. But there are no teeth in this position. Instead the left mandibular teeth bite on the flat surface of two bones whose lateral margins lie on a continuous line, although they are separated by a wide gap. The posterior of them has an exposed surface which may be traced (with some alteration of plane) into the palatine. The anterior has a well-finished shallow lateral surface turning into a natural pointed hinder end; it is presumably a vomer, and the gap between the two bones a long but narrow internal nostril. The maxillae and premaxillae must have been removed before burial, perhaps when the two dentaries and splenials were pulled away from the hinder part of the jaw.

New casts enable me to add something to earlier accounts of the basicranial region. The narrow rostrum of the parasphenoid seems to have carried a few small teeth, and its base separates two grooves which plunge upward into the skull but seem to lie on the parasphenoid, lateral edges of which pass back so as to lie below the basipterygoid process, which is entirely basisphenoid. The border of the joint bone (para-basisphenoid) passes back and then outward, at the widest point becoming parallel to the middle line, the ventral surface of the bone which it limits being shallowly concave and of considerable thickness. The border soon turns inward, the rather thick bone forming a point, and backward as shown in figure 15, and is lost in a triangular mass. The inner side of this mass is bounded by a suture which can be traced forward and inward, sweeping round to the middle line. This is no doubt the hinder border of the parasphenoid. Behind it the bone is weathered, but is crossed by a cylindrical surface whose axis lies transversely and ends laterally in a smoothly rounded border. The middle of this surface is marked by a narrow, rounded cylinder at right angles to it (the basioccipital condyle), whose shallow surface passes under a deeply V-shaped bone which can only be the atlantal intercentrum.

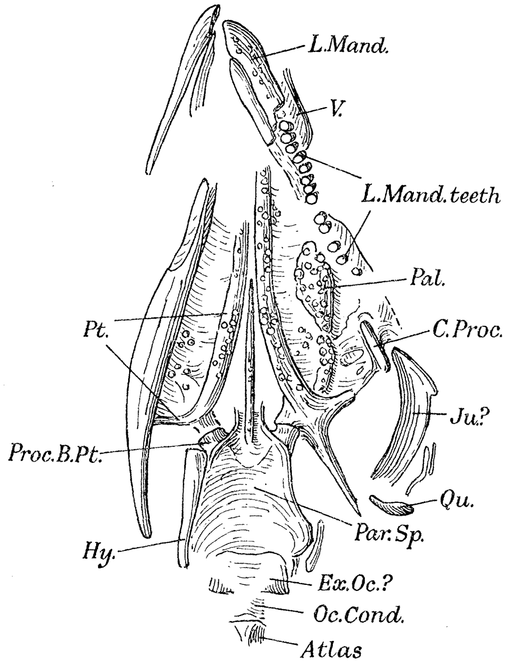

FIGURE 15. *Broomia perplexa* Watson, type, B.M.N.H., R.4065. The palate, as shown in a cast from the impression which represents it (magn. × 2). *Atlas*, presumably atlantal intercentrum; *L.Mand.*, left ramus of mandible; *L.Mand.teeth.*, the left mandibular teeth, the body of the dentary having been stripped off in the counterpart block; *C.Proc.*, coronoid process of left mandible in position with mouth closed, the hinder part of the jaw from which it arose being removed in the counterpart.

The original description of the rest of the skeleton is adequate, but it seems probable that the three vertebrae immediately in front of the sacrum did not carry ribs, and that those in front of this place are a little too long in this restoration.

Broom based his view of the close relationship of *Broomia* to *Milleretta* on the similarity of their palates, to which the new description above adds some evidence. It is clear that the long pointed skull is similar in the extremely anterior position of the quadrate condyle with respect to the basioccipital condyle. The very broad, concave ventral surface of the parasphenoid is a resemblance of a most unusual kind. The independent, forwardly directed basipterygoid process is identical. The wide interpterygoid vacuity and its extension very far forward is an unusual quality common to the two forms. The remainder of the palate, with the distribution of the abundant palatal teeth into three rows, again agrees.

The small occipital condyle is similar, and the sharply wedge-shaped atlantal intercentrum of *Broomia* agrees with the similar structure of the anterior vertebra in both *Millerosaurus pricei* and *M. nuffieldi*. The vertebrae are much alike, and the rib articulation—by a single little deepened head—with an oblique facet on the anterior part of the lateral surface of the pedicel of the neural arch and the centrum—is an unusual quality common to the two. But *Broomia* possesses well-developed intercentra in the presacral part of the column, which seem to have been lacking in *Millerosaurus*. The primary shoulder girdles are much alike, *Broomia* possessing that long downwardly facing groove—bounded laterally by a rounded ridge—which passes forward from the downwardly directed anterior part of the glenoid cavity to be perforated by a large precoracoid foramen. The clavicles and interclavicles have a general resemblance, but the rather bowl-shaped expansion of the interclavicle, seen in *Millerosaurus*, does not occur in *Broomia*.

The limbs of *Broomia* necessarily resemble those of *Millerosaurus* because they belong to a small animal, of very much the same build, and of the same stage of evolutionary development. The hands and feet have a general resemblance, but the *Broomia* wrist differs from that of *Millerosaurus*, as it does from all other known reptiles, in the continuation of the middle row of the carpus from radial to ulnar side. It differs also in the apparent absence of the carpal foramen. The fact that the Vth metacarpal lies parallel to the others in *Broomia*, and does not articulate with the lateral surface of the Vth distal carpal, is a further difference. The hindfoot of *Broomia* differs from that of *Millerosaurus* in that its metatarsals are longer and more slender, but agrees in the presence of two centralia, the mesial coming out to the inner side of the ankle, a remarkably primitive condition.

Thus *Broomia* more resembles *Millerosaurus* than it does any other known reptile. It cannot well be referred to the family which includes *Millerosaurus*, *Milleretta*, etc., but should certainly be included in the same wider group, perhaps an order. The relationship is important because *Broomia* comes from the *Tapinocephalus* Zone, and is hence considerably older than the millerettids.

Mesenosaurus

It is therefore desirable to look to still older faunas and consider if any reptile of uncertain position in them may be related to millerettids and *Broomia*. The only reptile faunas intermediate in age between those of Texas and of the South African *Tapinocephalus* Zone are in Russia, and of these the only one yielding small animals is that from Mesen, so well described by Efremov in 1940*b*. Through the kindness of Professors J. A. Orlov and J. A. Efremov, I had the pleasure in June 1945 of examining all the known materials of *Mesenosaurus* in Moscow. I there made drawings (without camera lucida, or measurements) of the two most important skulls, nos. 158/1 and 162/3. I examined also no. 158/2. In addition, Mr N. A. Yanchenov gave me some magnificent line drawings of the dorsal and right lateral surfaces of the two former. On my return to London I made reconstructions from these drawings, whilst my memory was still fresh—and before I had seen a millerettid.

The material from Mesen varies a good deal in character, some specimens are magnificent, others are difficult to interpret. The matrix is a very fine-grained silt or sand of a 'sandy red' colour, the bones are black and well preserved, but often cracked and crushed so that sutures are very difficult to follow. The preparation, largely by Professor Efremov himself, is excellent.

The most complete skull is the type, no. 158/1. This has been prepared from above and from each lateral surface, but an oblique fracture has removed the left hinder corner. The braincase has fallen out, but the lower jaw is in place. Specimen no. 162/3 lacks the anterior end, but shows the occipital border on the upper surface, and is well preserved postero-laterally. The upper surface of the skull is flat, and wide in the parietal region, the temporal region—though sloping a little outward to the lower border in no. 162/3—was probably very little inclined from the vertical in life. The orbit is large, facing more upward than outward, so that the frontals are narrow. The preorbital region is narrow, the premaxillae making a narrow rounded snout. The external nostril is a large opening notching the premaxilla deeply, embaying the maxilla, and having its border completed by the nasal. The nasal is a large bone separated from its fellow for a long distance by the facial processes of the premaxillae, then having a common medial suture and ending, little in front of the orbit, at a transverse suture with the frontal. (The continuity of the nasal over this region is shown in no. 158/2.) The maxilla deepens behind the nostril, where it has a suture with the nasal, and then parts from that bone to be attached to a lachrymal which forms the front border of the orbit. The hinder part of the maxilla below the orbit tapers until it meets the slender anterior end of the jugal.

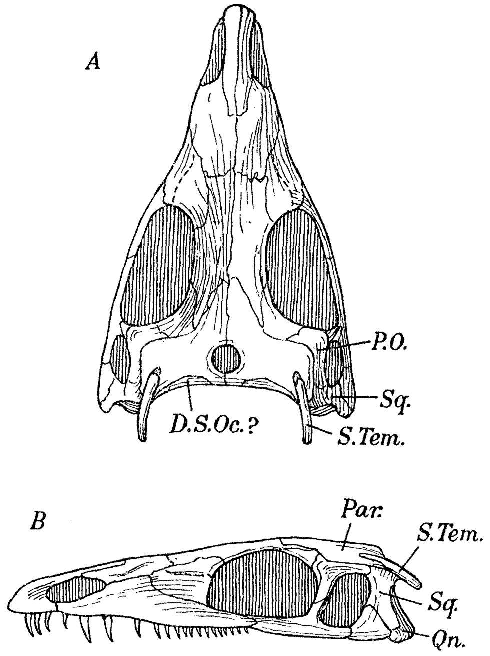

FIGURE 16. *Mesenosaurus romeri* Efr. (magn. × 1). Reconstructions of the skull from the specimens 158/1, 158/2, and 162/3, in Moscow. *A*, dorsal aspect; *B*, lateral aspect.

The frontal forms a large strip of orbital margin which passes from it on to the postfrontal. Behind this point the frontal continues back as a narrow strip held between the anterior part of the parietal and the postfrontal. As is best seen in no. 162/3 the postfrontal ends in a suture with the postorbital, where that bone forms a rounded corner connecting the dorsal border of the orbit and the lateral border of the temporal roof, marking the transition from the horizontal dorsal, to the flat and nearly vertical lateral surface.

The parietal is best seen in no. 162/3, where the bone is complete and little broken on the right side. The large pineal foramen lies quite posteriorly, only just in front of the border where the dorsal meets the occipital surface. This edge of the parietal is very slightly bowed forward on each side of the middle line. In front of the pineal a narrow wing of parietal stretches forward to a suture with the frontal; it has some contact with the postfrontal, where its border swings outwards, rounding off to turn back nearly parallel to the middle line. This lateral border of the parietal has no sutural attachment to any other bone, the full thickness being seen in side view where it rests on the postorbital and squamosal. It ends at a point, separated from the posterior border of the bone by a notch which continues forward of this point. The notch seems to be entirely in the parietal, and is separated by a flange from a thin sheet of bone attached to the slightly embayed hinder parietal border. The posterior surface of this bone is only seen in no. 162/3 as a shallow strip, though an apparent attachment area for it is shown in no. 158/1; it is presumably dermosupraoccipital or tabular, or both. The notch in the postero-lateral corner of the parietal holds a very short broken fragment of bone in no. 162/3, but this bone is well shown in no. 158/1 as a long slender structure, directed back and a very little outward and downward to end far behind any part of the roof or side wall of the skull. It is in fact a supratemporal.

The postorbital of the right side is shown in both skulls. In each it is evident that the whole of its upper surface is a wide, gently rounded but essentially horizontal area lying ventral to the parietal, so that (in no. 162/3) that bone actually rests upon it anteriorly.

The squamosal has a similar slightly rounded and smooth horizontal upper surface, seen in both specimens. In no. 158/1 very little of it shows behind a covering layer of postorbital, in no. 162/3 it is evident that the large expanse of squamosal behind the postorbital depends on a displacement of the squamosal backward, shown also on the cheek. Thus the flat joint upper surface of these two bones really ends (as shown in no. 158/1) at the hinder point of the parietal, which overlay at any rate the greater part of it. The squamosal passes down the cheek nearly at right angles to its upper surface, attached to the quadrate along its hinder border (as shown in no. 162/3) and ending at a suture with the quadratojugal. In no. 162/3 the hinder border of the squamosal is seen to be turned back as a little hook whose upper surface is that which underlies the parietal (this is shown in Efremov 1940*b*, fig. 4).

The quadratojugal coats the lower part of the lateral border of the quadrate and stretches forward to the jugal. The jugal presumably meets the maxilla below the eye, is shown to meet the postorbital behind it, and has a slender process (seen in two skulls) extending back below the temporal vacuity to meet the quadratojugal. The lateral temporal fossa is thus a considerable opening, though much smaller than the orbit. Its borders are provided by the postorbital, jugal, quadratojugal and squamosal.

The quadrate (no. 162/3) is seen from behind as a rather large bone, a narrow exposed strip of whose posterior surface extends from the condyle to the upper part of the squamosal, which must completely cap it. The pterygoid process of the quadrate arises from the inner side of the transverse posterior surface of the bone, some distance above its articular condyle, and is directed inward and forward.

Finally, it must be emphasized that the supratemporal of no. 158/1, though very slender, stretches so far back that it is evident it is likely to have supported the upper border of a tympanic membrane. I have nothing to add to Efremov's account of the palate.

The braincase has fallen out of all the known skulls, evidence that its attachment was unlike that of a theropsid. Indeed, the end of the paroccipital process must have had a contact with the freely projecting end of the supratemporal, the supraoccipital no doubt sloping backward, and the basioccipital condyle lying far behind the quadrate.

That *Mesenosaurus* as so interpreted is related to the millerettids seems to be certain. The whole structure of the temporal region, the free lateral border of the parietal, and the manner in which it rests—without any sutural attachment—on special inturned flanges of the postorbital and squamosal, is that found in *Millerosaurus*. The small notch in the postero-lateral corner of the parietal into which the supratemporal is inserted is exactly as it is in *Millerosaurus*. The quadrate with its special pterygoid ramus arising suddenly some distance above the articular surface is paralleled in millerettids. And the temporal fossa is as in *Millerosaurus*. The face, with its deep maxilla and long, spaced teeth, and with a short lachrymal and prefrontal, is much more advanced than that of a millerettid.

Thus, though evidently it does not belong to the same family, it may well be placed in the same higher group, which is thus traced back to a time before the beginning of the South African series of faunas.

Anningia, Elliotsmithia *and* Heleosaurus

Other reptiles which might belong to the large group, including the millerettids, *Broomia* and *Mesenosaurus*, must now be considered. It should be noted that the presence of a pelycosaur-like temporal fossa makes it desirable to consider animals referred to theropsids, as well as those from more probable fields.

Anningia megalops and *Elliotsmithia longiceps*, described by Broom (1927*a*, 1937), both from the *Tapinocephalus* Zone, are such forms, of which the unique type specimens are now before me. It seems possible that they are really sauropsids, but adequate examination involves much preparation, and it seems undesirable to postpone the description of the millerosaurs.

Another South African animal to be considered is *Heleosaurus scholtzi*, from an unknown horizon at Victoria West. This is contained in a split slab, and might show more with modern preparation. It has a pointed, rather narrow skull presumably with a lower temporal fossa, a jugal-quadratojugal arch being preserved. The palate (Broom 1907, fig. 7) seems to show that there was a basipterygoid process far from the middle line, and a large interpterygoid vacuity. The parasphenoid is evidently very wide, and the occipital condyle far behind the quadrate articulation. The cervical vertebrae are very markedly keeled, notochordal, and have intercentra; the ribs are single headed. The interclavicle is very long and largely expanded anteriorly; the scapulo-coracoid has a large, very thin anterior part, thickening behind, but is not adequately described, or shown. There is a plate-like pelvis, with very large pubes. There are many osteoderms on the dorsal surface, and a considerable series of abdominal ribs. The animal may well be a member of the millerettid group—the Millerosauria.

MILLEROSAURIA COMPARED WITH EARLY THEROPSIDA AND SHOWN TO BE THE MAIN STEM OF THE SAUROPSIDA

It is now desirable to consider the place of the group of reptiles surrounding the millerettids in the evolutionary story of the class. Broom, a fortnight after he had despatched the manuscript of the paper in which he first described *Milleretta*, received the papers by Romer (1937) and Price (1937) in which the very primitive pelycosaur *Eothyris*, and the very primitive captorhinid (cotylosaur) *Protorothyris*, and its successor *Romeria*, are described. He immediately recognized resemblances between these Texan Lower Permian forms and his *Milleretta*. Romer & Price (1940) have further described *Eothyris*, and I (1954, p. 332) have given a short new discussion of *Protorothyris* and *Romeria*. It is the two latter, which are effectively ancestors of *Captorhinus*, which make the best comparison with *Millerosaurus* and *Milleretta*. But they lack a temporal fossa and the primitive pelycosaur *Varanosaurus* is an even better parallel.

In *Protorothyris* and *Romeria* the parietals form a wide, flat surface extending outward to a nearly straight antero-posteriorly directed border, which is free and forms a very shallow vertical face when seen from without. Anteriorly this border begins at the point where the postfrontal extends outward, to pass down behind the orbit and in front of the postorbital. Posteriorly the border ends at a point where the supratemporal begins, that bone generally continuing the direction of the lateral border of the parietal. The piece of parietal which lies between the postfrontal and the supratemporal is the parietal lappet. In *Protorothyris* the lateral border of the supratemporal continues that of the parietal lappet and forms with it a free face. The squamosal coats the upper part of the posterior surface of the quadrate with a flange which is continued until it meets the skull table, below which it turns forward, its lateral border passing downward on the cheek. Its smooth upper surface is attached to the lower surface of the supratemporal and parietal lappet without any sutural connexion.

Essentially the same conditions are found in the primitive pelycosaur *Varanosaurus* fig. 17A, E. I have shown reason (Watson 1954, p. 352, 392 *et seq.*) for believing that this condition in theropsids is directly derived from anthracosaur ancestors. The millerettid skull is exactly similar to *Protorothyris* and *Varanosaurus* in this matter, with one important exception. In all theropsids (cf. Romer & Price 1940, figs. 3–7) the whole lower surface of the supratemporal (when present) is in close contact with the upper part of the squamosal; the contact is indeed so close that the presence of a supratemporal was not generally recognized until 1940. In millerettids the supratemporal is always easily recognizable because it forms a very definite process whose lower surface, leaving a contact with the squamosal, extends backward and downward so as to form an outstanding hook, whose hinder and outer corner is attached to the outer end of the paroccipital process. The millerettid squamosal caps the quadrate, but leaves the whole height of the posterior surface of that bone visible: an extraordinary contrast to the condition in all theropsids. In millerettids the space between the lower surface of the supratemporal and the posterior border of the quadrate is the tympanic cavity, and the tympanic membrane is attached to the supratemporal, squamosal, quadratojugal and probably the retroarticular process of the lower jaw. This space between the supratemporal and the quadrate is absent in theropsids, which lose the tympanic membrane, and whose extremely massive stapes gains a firm attachment to the stapedial recess of the quadrate. In contrast in millerettids the tympanic membrane persists, is perhaps even enlarged, and the stapes remains as a small bone, showing all the processes of both columella and extra-columella of lizards in one single ossification, and there is therefore no stapedial recess.

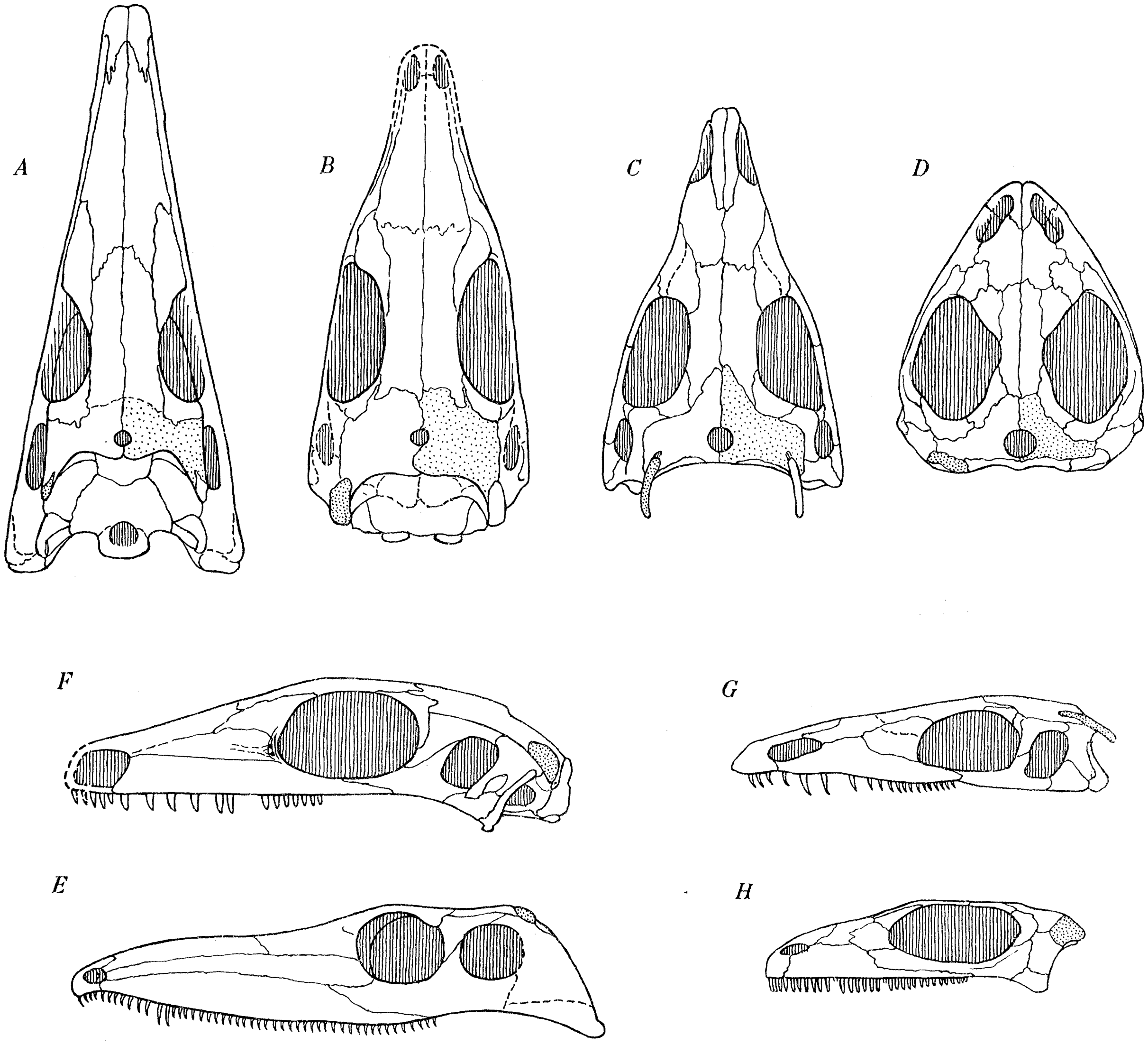

Figure 17. Dorsal aspects of a series of reptilian skulls reduced to the same width across the parietals to allow them to be easily compared. *A*, the pelycosaur *Varanosaurus*; *B*, *Millerosaurus*; *C*, *Mesenosaurus*; *D*, the procolophonid *Nyctiphruretus*. *E*, *F*, *G* and *H* are lateral views of the same series. The left supratemporal is densely stippled, and the right parietal bears more scattered dots.

These are the most generally recognizable diagnostic qualities of the theropsids and sauropsids respectively. Thus the millerettids, and the reptiles associated with them, are sauropsids of more primitive structure than any others. They owe their striking resemblance to early theropsids to common descent from anthracosaurs. It is therefore necessary to consider the Millerosaur's relationship to higher sauropsids.

MILLEROSAURIAN DERIVATIVES

UPPER PERMIAN REPTILES

Eosuchia

The most ancient reptiles possessing upper and lower temporal fossae and arches are *Youngina capensis* and its close allies from the *Cistecephalus* Zone of South Africa. These are referred to five species: *Youngina capensis* Broom, 1914 (the type skull is in New York, a later specimen in the British Museum, Natural History, R. 5481); *Youngoides romeri* Olson & Broom 1937 (University of Chicago Collection in Chicago Museum, no. 1528); *Youngopsis kitchingi* Broom, 1937 (Transvaal Museum); *Youngoides minor* Broom & Robinson, 1948, and *Youngopsis rubidgei* Broom & Robinson, 1948, are in S. H. Rubidge's collection. No other skulls—in recognizable condition—are known. These five species were all founded on complete skulls, usually preserved uncrushed, or little crushed, in nodules; but their real structure is still disputed. I have seen all except *Youngopsis kitchingi*, described by Broom in sufficient detail to make it evident that the type skull can give no useful evidence about the structural features still in dispute.

The five skulls are all much alike in size and general character, though they differ in outline, some being pear-shaped when viewed from above, whilst others are wedge-shaped with the lateral border nearly straight. There are some variations (probably not entirely due to distortion) in the angle which the quadrate makes to the vertical, and minor differences in dentition, but there is no reason to suppose that they differ in fundamental structure. Broom's figures are unquestionably correct in all matters except the structure of the postero-lateral corner of the upper surface, where the squamosal, parietal and postorbital come close together.

Youngopsis rubidgei

Only one skull gives complete certainty as to conditions here—the type of *Youngopsis rubidgei* in Mr Rubidge's collection, where I examined it without the advantage of a binocular microscope. This skull, contained in a nodule, is essentially undistorted and has the surface of its temporal region perfectly exposed. The parietals enclose a small pineal foramen placed about midway along the upper temporal fossa. They extend forward about to the hinder border of the orbit and are there attached to a long pointed posterior end of the frontal. The parietals form the inner border of the upper temporal fossa, and send outward behind it a deep vertical sheet of bone to meet the squamosal and be coated by the dermosupraoccipitals and tabulars on the occiput. The occipital surface of the pair of parietals is bowl-shaped, their upper posterior surface forming a very narrow strip which is the edge of a deep plate whose front face is, for half its length, attached to the hinder surface of the squamosal. The dermosupraoccipitals are rather large bones plastered on to the hinder surface of the parietals (figure 18*C*), extending down and largely back, presumably to rest on the sloping upper surface of a supraoccipital. On the right side a tabular is in position; it is a thin deep sheet of bone touching the dermosupraoccipital, pressed against the hinder surfaces of the parietal and squamosal behind the upper temporal fossa, and extending outward and downward just beyond the point where the squamosal hooks over the head of the quadrate and is attached to the outer end of the paroccipital process. On the left side of the skull the dermosupraoccipital is in place, but the tabular has been stripped away, and the lateral process of the parietal has sprung back so that it is now separated from the upper part of the squamosal by a sheet of matrix less than a millimetre thick.

On the right side the hinder end of the postorbital process—which forms the lateral border of the upper temporal fossa—is seen to pass on to the squamosal, separated from it by a continuous suture. On the left side the tip of the postorbital has been stripped off leaving clearly exposed the groove in which it formerly lay, and the squamosal, perfectly preserved, is obviously continuous round and under it.

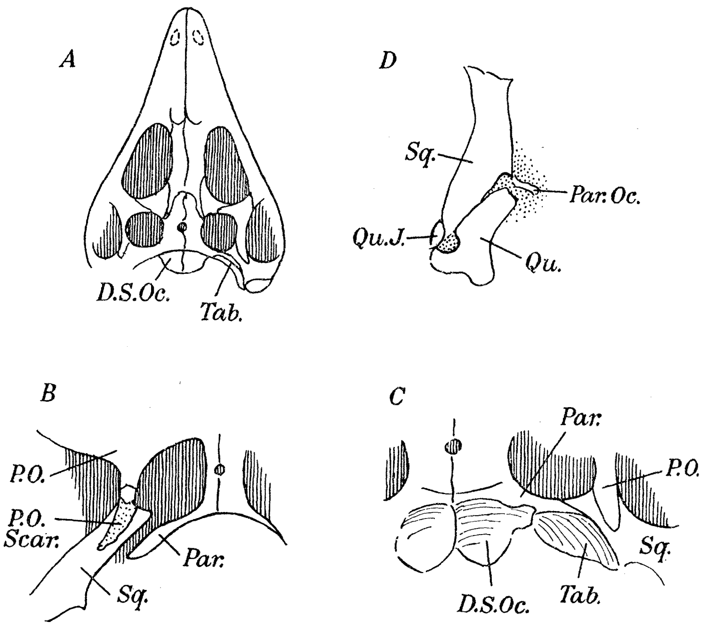

FIGURE 18. *Youngopsis rubidgei* Br. Sketches from the type specimen in Mr Rubidge's collection, not all true to scale, to show the structure of the temporal region. *A*, general dorsal view (magn. $\times \frac{3}{4}$ approx.); *B*, the left temporal region, seen a little obliquely, to show the separation of the upper part of the squamosal from the parietal by matrix, and the absence of the supratemporal; *C*, obliquely from behind to show the dermosupraoccipitals, right tabular, parietal and squamosal and postorbital; *D*, left squamosal obliquely from the side with quadratojugal, quadrate and paroccipital.

There is thus in this specimen no possible doubt that there is no supratemporal, and that a tabular lies on the occiput in the usual place. The specimen shows on the left side the whole height of the quadrate (figure 18*D*), the attachment of its lateral border to the squamosal behind the lower temporal fossa, and the existence of a quadratojugal with a foramen between it and the quadrate. The tip of the hook of the squamosal above the quadrate is in contact with the anterior point of what is apparently the lateral end of the paroccipital.

One interesting feature of this skull which I failed to notice (though it is figured by Broom) is the presence of an anteriorly directed spike from the parietal, which for half its length separates the postfrontal from the frontal.

Youngina capensis

The well-preserved type skull of *Youngina capensis* was in my care for some years, and in 1926 I wrote (but did not publish) the following description:

'Some years ago Dr Broom handed over to me the type material of *Youngina capensis*, with the suggestion that I should examine it and publish an independent account of its structure. Before doing so I removed matrix from the ventral surface, and to a very slight extent from the occiput. The structure will be clear from the figures. In the main I can confirm Dr Broom's account, but differ from him in one or two important respects. The well-preserved occiput shows a small kidney-shaped condyle, above which lies an almost circular foramen magnum, whose side walls are formed by small exoccipitals which probably contribute to the condyle. Each exoccipital is perforated by a minute hypoglossal foramen, and must end at the rather larger vagal opening. The paroccipital, which is not bounded by visible sutures, extends outwards and backwards, its outer end lying in contact with the hinder surface of the tabular bone, where that element forms a hook over the upper end of the quadrate. The proximal end of the paroccipital extends downwards as a flange below the vagal foramen, and the anterior face of the bone is in contact for an uncertain distance with the proötic, the ventral surface of the joint bones forming a groove exactly similar to that which forms the roof of the tympanic cavity in lizards and in *Procolophon*. The fenestra ovalis lies high up on the level of the middle of the foramen magnum. The supraoccipital is a broad bone rising to the parietals and overlapped above by a pair of dermosupraoccipitals. The region where the supraoccipital and paroccipital must meet is swollen, presumably to leave space for the posterior vertical semicircular canal. On the ventral surface the basioccipital is seen to bear a pair of rather prominent tubera,

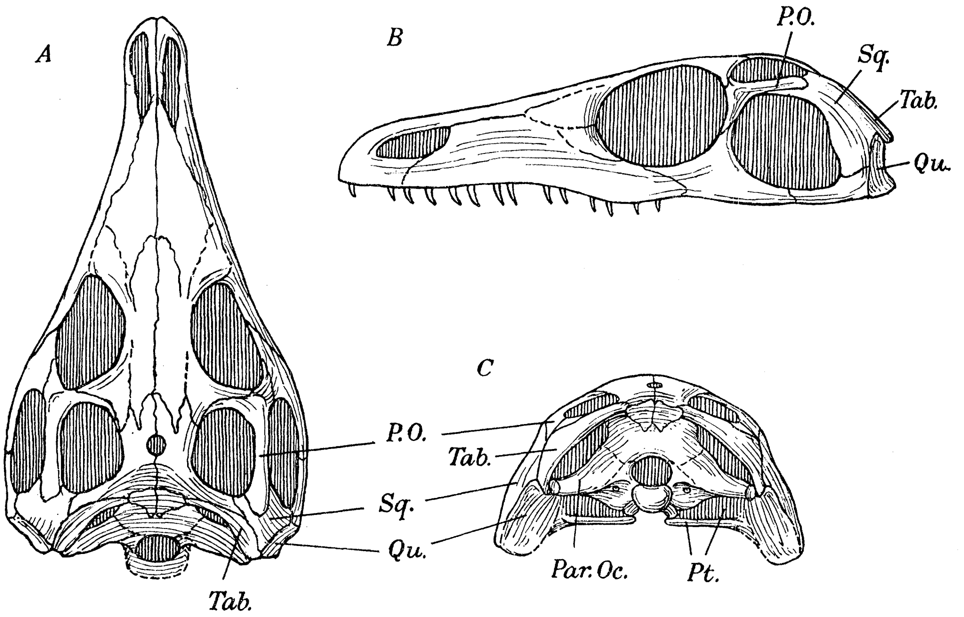

FIGURE 19. *Youngina capensis*. Reconstructions made from the type specimen (A.M.N.H. 5561) in 1926, details being added from the specimen B.M.N.H., R. 5481, given by Dr Broom, who identified it (magn. rather above natural size).

and the suture with the basisphenoid seems to cut these processes. The pterygoid has a well-marked hook-shaped facet for the basipterygoid process, and the quadrate ramus extends back to the quadrate. From the inner side of the lower border of this ramus a horizontal sheet of very thin bone extends inwards to underlie the tubera basisphenoidales. The whole arrangement is not very dissimilar to that of *Captorhinus*. The transverse flange of the pterygoid is powerful, and the only part of its lower border which is preserved bears two relatively powerful backwardly turned teeth. The pterygoid extends forward on the palate, its palatal surface bending upwards mesially until it stands nearly vertically. The two pterygoids are separated in the actual skull by a very wide interpterygoid vacuity, but I fancy that the width of this opening has been exaggerated by a warping of the bones before the skull was buried. There is clear evidence of a transverse bone which descends almost to the tip of the transverse flange and forms the whole of its outer surface. The pterygoid and palatine bear a series of small denticles rather irregularly arranged in rows. The quadrate is a remarkable bone, its summit is turned backwards so as to make a small hook on the outer surface of the skull, and from this point it descends vertically for half its height, the posterior surface facing outwards and backwards. Then suddenly the lower end of the bone turns back and ends in the condylar margin, which is placed very obliquely. The outer edge of the quadrate is in contact with the quadratojugal and squamosal, there being no evidence of a quadratojugal foramen. At the upper end of the quadrate the squamosal is produced backwards as a tiny hook which caps the quadrate, and above this point the upper and posterior surface of the squamosal rises and passes forward so that it comes to underlie the hinder end of the postorbital. The lower portion of this surface of the squamosal is covered by a bone which is clearly tabular.

'According to the reading of Dr Broom this tabular extends forwards and is wedged in between the squamosal and the parietal, completely separating these two bones and forming part of the border of the upper temporal fossa. On the right side of the specimen it seems clear to me that the tabular stretches inwards unbroken by a suture, although crossed by two cracks, until it is covered by the dermosupraoccipital. On the same side (and even more clearly on the left, where the posttemporal bar is shown on a horizontal fractured surface) it seems clear that the parietal extended out toward the hinder end of the postorbital, and on the left side I believe I can trace a very fine suture separating the parietal in front from the tabular behind. As shown on the fractured surface the parietal is a bone with a very narrow strip of cancellous tissue in the middle of its thickness, enclosed both anteriorly and posteriorly by dense bone, to this posterior lamina of dense bone is applied another of slightly greater thickness which can only be the tabular.

'Only in one other point, and that a very minor one, do I disagree with Dr Broom's figure. He represents the maxilla as not entering into the orbital margin, an appearance clearly derived from the right side of the specimen. On the left side it seems certain that the maxilla overlapped the jugal and formed a very small part of the lower border of the orbit.

'Both rami of the lower jaw are exposed from their outer and ventral faces and are not well shown. It is, however, clear that there was a very small retroarticular part of the articular bone, that the surangular forms about half the height of the lower jaw posteriorly, that the angular is a boat-shaped bone extending forward for about two-thirds of the length of the jaw, and that there is a long splenial mainly on the inner surface but forming the lower border. This bone extends from the symphysis to a point just behind the middle of the jaw. There is no external mandibular vacuity.

'Associated with the type skull is a connected series of vertebrae consisting of eleven presacral, two sacral, and six caudals. All these are very much alike, each possesses a narrow centrum with expanded articular ends, the lateral faces are nearly flat and parallel to one another, the ventral surface is rounded, the neuro-central suture cannot be seen, but the pedicel of the neural arch is long and low. The zygapophyses are powerful and their articulating surfaces appear to be nearly horizontal, the anterior zygapophysis projects a little in front of its centrum, the posterior projects a little backwards and from it the hinder margin of the neural spine rises directly. In the zygapophysial region the neural arch is very wide, much wider than the centrum, and the whole slightly recalls the cotylosaur vertebra. The neural spine throughout the presacral part of the column is long, but very low and narrow. The rib articulation is damaged in every specimen, but by a comparison of all of them it is possible to be quite certain that the articular facet was single, and was carried on the extremity of a very low ridge which descended obliquely from a spot on the middle of the pedicel of the neural arch, just below the level of the zygapophysial articular faces, to a point on the anterior border of the centrum. There are small half-moon shaped intercentra present between all the vertebrae—including the sacrals—in front of the tail. The first sacral differs very little from the vertebra in front of it, but clearly possessed a much larger articular surface for the rib. The second sacral bears a short, very slender process abruptly truncated at the end; this is no doubt the actual sacral rib. In general structure the caudals resemble the presacrals, but their neural arches are less massive, the zygapophysial articular faces are at an angle to one another, and the intercentra are produced into long haemopophyses. The first two postsacrals bear long, flat transverse processes.'

Essence of younginid structure

Thus *Youngina capensis* and *Youngopsis rubidgei* agree in possessing a tabular bone, entirely on the occiput, and in lacking a supratemporal. *Youngoides minor* seems to me too crushed to give any reliable information on this matter. *Y. romeri*, though a well-preserved skull very well prepared, seems to me to leave the nature of the temporal region in doubt. All younginid skulls agree in having no trace of a preorbital fenestra, nor of one in the outer side of the lower jaw. The detail of the face is uncertain but the prefrontal and lachrymal seem always to be small. The palate is only known in the type skull of *Youngina capensis*, in the type of *Y. romeri*, and in the skull B.M.N.H., R. 5481, which agrees with the type in making it very improbable that a subtemporal fossa, of the kind described by Olson in *Y. romeri*, exists.

One important matter is the relation of the quadrate to the squamosal. It is evident from all lateral or posterior views of younginid skulls that the quadrate is short, in association with the rounded occipital surface which all of them show. The quadrate is visible on the occipital surface for the whole of its height, it is broad from side to side, ends just below the small hook by which the squamosal is attached to the end of the paroccipital process, and is shown in specimen B.M.N.H., R. 5481 by a mould of its anterior surface to be firmly attached to the squamosal by suture, there being no visible trace of the *Millerosaurus* condition where the upper end of the narrow quadrate is received in a cup in the squamosal. The pterygoid ramus of the quadrate is a large structure reaching up to the top of the body of the bone and extending forward as a fan, laterally to the deep quadrate ramus of the pterygoid.

The foregoing account of *Youngina* shows that the group Eosuchia is more advanced in the development of an upper temporal vacuity, and in the loss of a supratemporal bone, than the millerosaurs. It is, however, worth considering whether its short quadrate, associated with a rounded occipital surface, and attached to the squamosal by suture, can have been derived from—or can have given origin to—the tall quadrate, articulated by a cartilage-covered head to the squamosal, of the millerosaurs. The millerettids' temporal region, so greatly resembling that of primitive captorhinids such as *Protorothyris*, must I think be primitive, for it is immediately comparable with conditions found characteristically in the amphibian anthracosaurs, from which all reptiles arose. If this be primitive then the inturning of the upper end of the squamosal below the lateral border of the parietal is also the retention of an amphibian condition. In the Amphibia the hinder part of the palatoquadrate cartilage is largely hidden from view by a meeting of the squamosal and pterygoid behind it. The theropsids as a whole retain this condition, which hides the greater part of the hinder surface of the quadrate. But in sauropsids, as part of the enlargement of the tympanic cavity and membrane, those parts of the squamosal which coat the hinder surface of the quadrate withdraw, and that bone is left exposed for its full height, separated from the parietal by a residual cap of squamosal. It is evident that there is no sign in the Eosuchia of the occurrence in their ancestors of the slender exposed hinder rib and upper articular head of the quadrate of millerettids, but they could presumably have come from earlier millerosaurs in which this special, rather lizard-like condition had not been achieved.

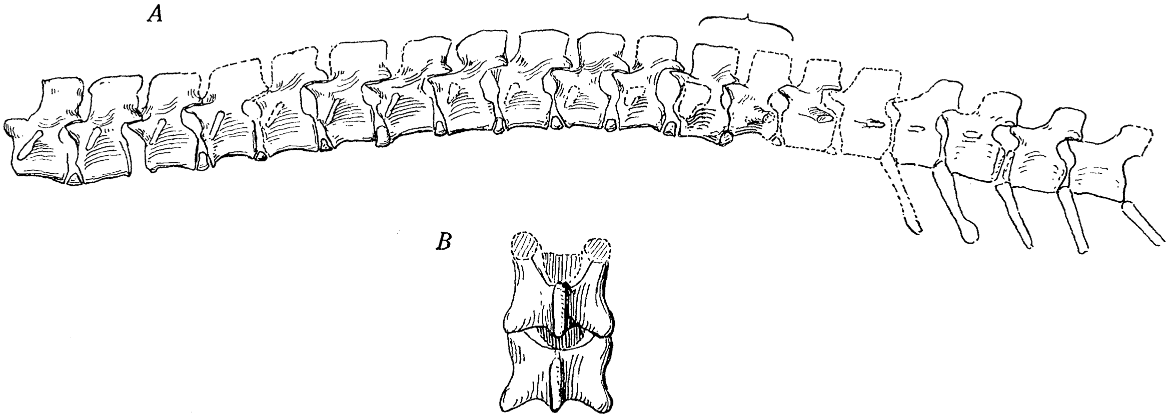

FIGURE 20. *Youngina capensis*, type specimen (A.M.N.H. 5561) (magn. $\times 1\frac{1}{3}$). *A*, articulated series of dorsal, sacral and caudal vertebrae from the side, the bracket marking the sacrum; *B*, two of the vertebrae from above, enlarged and somewhat restored.

Lower Triassic reptiles

Prolacertilia

No skulls of two-arched reptiles other than younginids are known from the *Cistecephalus* Zone, but the succeeding *Lystrosaurus* Zone has yielded *Prolacerta* and *Pricea*, *Elaphrosaurus* and *Chasmatosaurus*. The two latter are evidently closely related to the *Cynognathus* Zone *Erythrosuchus*, and are for these times very advanced in structure, having large antorbital and palatal vacuities, and (in *Chasmatosaurus* at least) possessing a 'laterosphenoid' which agrees generally with that of a crocodile; they are the earliest reptiles to have this structure. They certainly lack a supratemporal, as do all other reptiles which have crocodile-like laterosphenoids.

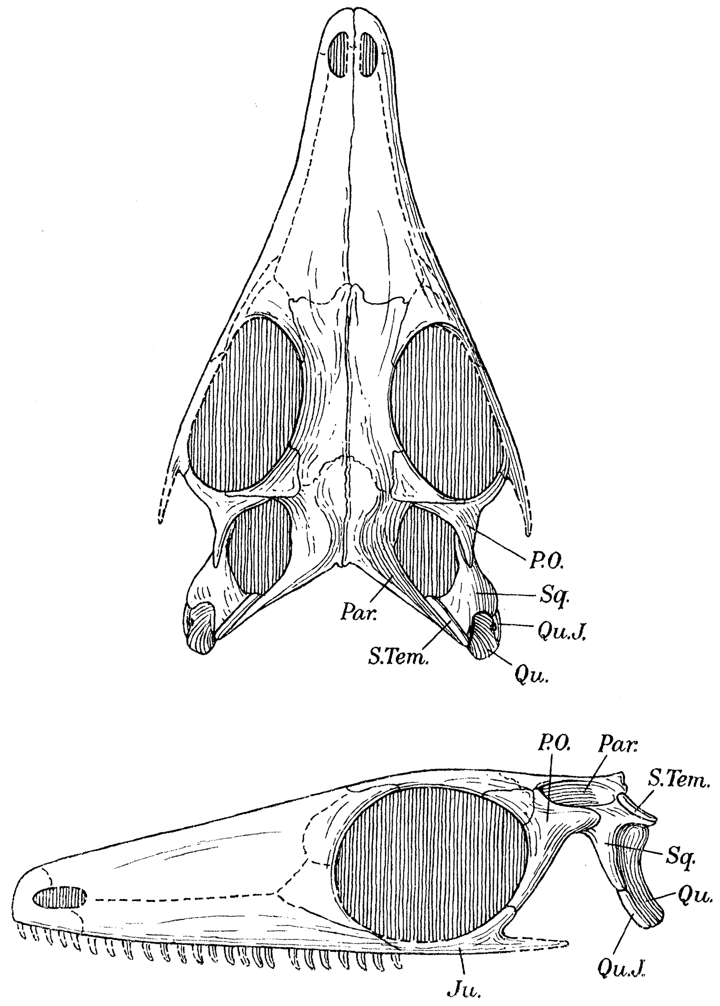

Figure 21. *Prolacerta broomi* Parrington. Reconstructions made from F. R. Parrington's type skull with some additions from C. L. Camp's figures of another specimen (magn. $\times 1\frac{1}{3}$).

Thus *Prolacerta* and *Pricea* are the forms which need comparison with earlier and later animals. The two are evidently close relations, members of the same large group, perhaps to be placed in the same family. They differ in proportions, the skull of *Prolacerta* is twice as wide as high at the occiput, that of *Pricea* only about one and a third times. There are also small differences in detail to be seen in the skull, and the axis of *Pricea* is greatly elongated, much more so than in the long-necked *Prolacerta*.

Prolacerta

Prolacerta broomi has been described from two specimens, both from the *Lystrosaurus* Zone of Harrismith, Orange Free State, by F. R. Parrington (1935) and C. L. Camp (1945 *a*, *b*) respectively; where they differ Mr Parrington's account is to be preferred. The type skull (Parrington field no. 144) shows the structure of the temporal region perfectly on the left side, the parietal, squamosal and quadrate being in natural articulation, though a little spread about, and the supratemporal is in position as Parrington represents it in his text-fig. 1. On the right side, the quadrate stands vertically with the squamosal completely capping it. The anterior process of the squamosal to the postorbital is broken off, but its ventral process (attached behind to the lateral border of the quadrate and broken by a crack) extends so far ventrally that it just reaches the summit of the quadratojugal, which lies in position similarly attached to the quadrate, but separated from it by a quadratojugal foramen. The piece of squamosal capping the quadrate has a nearly flat upper surface bounded posteriorly by the straight border of a groove in which the supratemporal lay. Below this bone the squamosal ends in a shallow face, cylindrically curved, which is attached to the front face of the lateral wing of the parietal. The supratemporal is a slender rod-like bone shown in natural articulation on the left side of the specimen.

It is evident that Professor Camp's specimen is not so preserved as to give any independent evidence on the supratemporal, but otherwise his figures and description make known to us most of the rest of the animal's skull.

Pricea

Pricea longiceps Broom & Robinson is based on an admirable skull from the *Lystrosaurus* Zone of Honing Krans whose description by them (1948) is in general clear and accurate. The original preparation was rough, and sutures have been inaccurately lined in with indian ink by someone unknown! I have, however, done a little further development, making clear some points left uncertain in the original description. But I found that the bones of the braincase had suffered a great deal of post-mortem cracking before burial so that they leave no smooth continuous surfaces to a preparator, and that lateral pressure had separated the quadrate ramus of each pterygoid from its quadrate and displaced it inward. A much cracked axis lies nearly in position, but the elements of the atlas are unrecognizable.

The braincase may be described as follows: the basioccipital has not been exposed (it is hidden by what may be a very greatly cracked atlantal neural arch) but the exoccipital is seen as a relatively slender column rising so as to bound the foramen magnum laterally, and to widen dorsally, where it is pressed against the hinder surface of the paroccipital and touches the supraoccipital. Below their contact the paroccipital and exoccipital separate to leave an exceptionally deep and wide vagal foramen, apparently just touching one another again below this opening. Near the summit of the vagal foramen, but behind it, the exoccipital seems to have a single small foramen for the XIIth nerve. The paroccipital is a massive bone, with small contacts with the exoccipital, and a long abutment on the supraoccipital. The paroccipital and supraoccipital are so large that there is no trace of the swelling over the posterior vertical semicircular canal seen in *Millerosaurus*. Laterally the paroccipital narrows rapidly, ending in a deep rounded bar carried upward by a very slender dorsal process to be attached to the extreme hinder end of the squamosal.

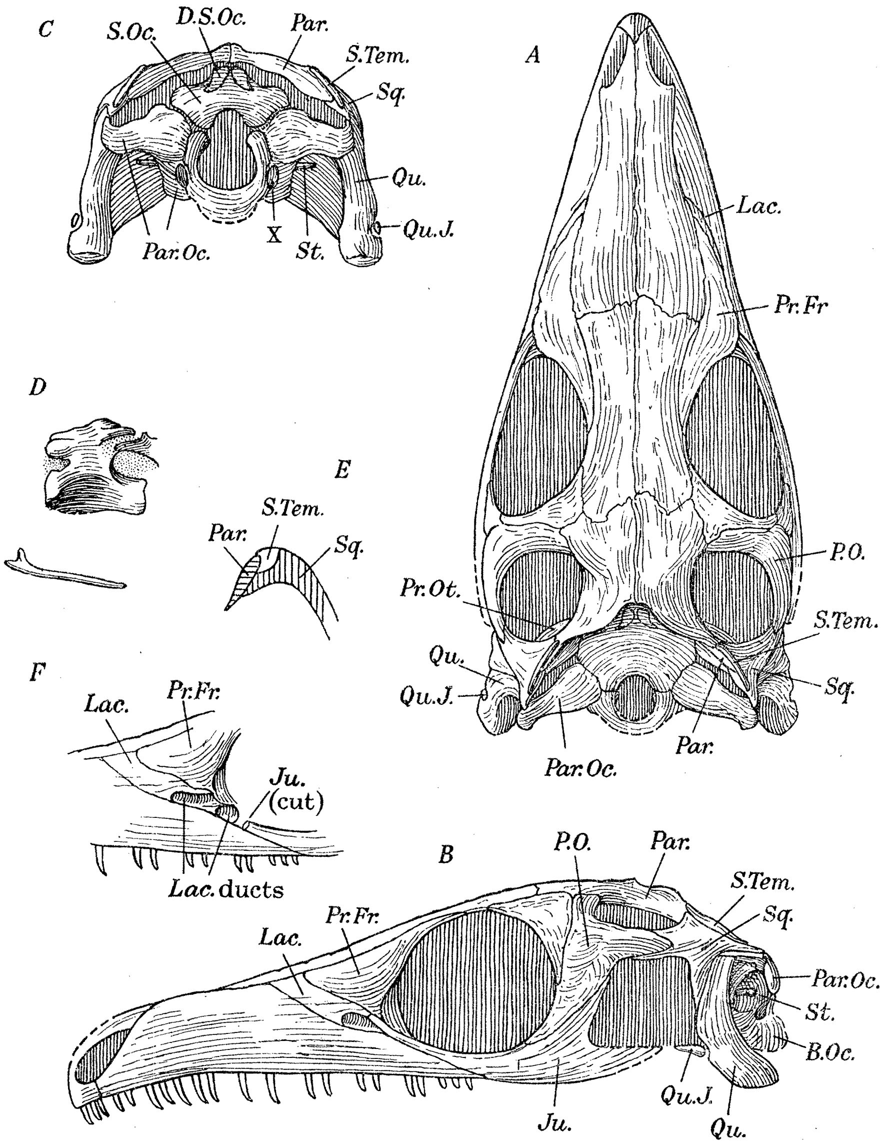

Figure 22. *Pricea longiceps* Broom and Robinson. Type skull, Bernard Price Institute no. 2 (magn. × $1\frac{1}{3}$). Slightly restored drawings of the skull *A*, from above; *B*, left lateral aspect; *C*, occiput; *D*, the axis vertebra and its rib, as preserved; *E*, an imaginary section across the supratemporal, parietal and squamosal about at the point where in *A* the reference line *S.Tem.* meets the bone; *F*, the region in front of the orbit showing canals for the lachrymal ducts, as shown on the left side of the skull, where the front of the jugal is removed; *X*, vagal foramen.

The proötic, cut into by scraping, is misplaced, but can be partially seen in the right and left upper temporal fossae. The flat posterior surface by which it is attached to the paroccipital is shown in section, and it ends where the front face of the bone becomes continuous with that of the paroccipital, a little before the end of that process. The anterior surface of the proötic is sufficiently exposed in the left supratemporal fossa to show that it did not articulate with a laterosphenoid, as it does in a crocodile. On the left side the hinder part of that rounded groove which is the roof of the tympanic cavity is seen with a typical sauropsid character, and the slender stapes is visible as a hollow cylinder of bone about three-quarters of a millimetre in diameter. Behind the fenestra the paroccipital extends far ventrally, presumably resting on the upper surface of the parasphenoid, and stretches forward as a deep process below it, no doubt to meet the proötic.

The original description of the external surface needs modification in a few places, further preparation having made evident matters not originally shown. The most important is in the nature and interpretation of the bone called 'tabular' by Broom. As represented in his drawing this bone lies between the parietal and squamosal and extends freely backward to touch a greatly exaggerated paroccipital. New preparation shows that the lateral wing of the parietal extends outward as a thin but deep sheet of bone, to whose essentially flat anterior face the hinder surface of that part of the squamosal which caps the quadrate, and bounds the upper temporal fossa, is directly attached. The slender supratemporal lies in a groove on the squamosal and overlaps the upper edge of the parietal, thus hiding the contact between those bones (figure 22*E*). It reaches the supratemporal fossa, but ends posteriorly so as to leave the pointed hinder extremity of the squamosal free to meet the paroccipital process.

The remainder of the external surface is correctly shown in the original paper, except immediately in front of the orbit, where I have prepared the lachrymal region on each side. The maxilla has a low posterior region below the jugal, but deepens rapidly on the face, reaching the nasal about at its mid-length. The lachrymal is very well shown on the left side, where at the orbital margin its substance nearly surrounds two relatively large canals for the two canaliculi of the lachrymal duct. The upper is, posteriorly, a large hemicylindrical groove, which passes forward into a canal on the narrow strip of lachrymal above the maxilla. The lower canal, of about the same diameter as the upper, lies a little mesial of it in a gutter posteriorly, soon becoming surrounded by bone as it passes forward to be covered by the maxilla. On the right side the large prefrontal turns down from the top of the head on to the cheek and passes over a rounded surface into the orbit. The suture between the lachrymal and prefrontal lies parallel to that between the lachrymal and maxilla, and like it is abruptly truncated by the nasal. The orbit is completed by a very slender process of the jugal which spans the two ducts—leaving the upper one visible—to end in a suture on the outer surface of the lachrymal just ventral to the prefrontal. The whole arrangement here is reminiscent of lizard structure, though it does not in detail agree with any recent lizard I have seen.

I can confirm the original statement of the existence of a small fragment of an obvious quadratojugal, and (so far as an ink embellishment allows one to judge) of the root of a ramus of the jugal below a lateral fossa. It is evident, if one looks at the left quadrate from behind, that the fragment of quadratojugal lies in a shallow horizontal groove on it, which seems to be the inner side of a quadratojugal foramen. If this be so, then the quadratojugal when complete was much larger than the existing fragments suggest, and may have resembled that of *Prolacerta*. I have cleaned the upper surface of the left quadrate and am satisfied that the bone can have no contact there with any bone except the squamosal. It is evident that the quadrate of *Pricea* (and of *Prolacerta*) resembles that of *Millerosaurus*, because it extends far dorsally and has a cartilage-covered upper end which is capped by the squamosal. It cannot have been derived from the quadrate of *Youngina*, which is short and connected to the squamosal by suture.

That *Pricea* is very closely related to *Prolacerta* is evident; the two agree in all morphologically important qualities, and even in such an unusual matter as the absence of a pineal foramen. But whereas the perfectly preserved quadratojugal of *Prolacerta*, prepared by Mr Parrington, evidently has no connexion with the jugal, it is not unlikely that that of *Pricea* may have reached it.

Relations of Prolacerta *and* Pricea

The wider relations of these two animals should be considered. They are obviously lizard-like, especially in the whole shape of the quadrate, though the depth of the quadrate ramus of the pterygoid in *Pricea* shows that the quadrate must have been less movable than in modern lizards. The face, in the reduced size of the lachrymal, and in the way in which it tends to be hidden by the prefrontal and jugal, is easily capable of conversion to that of a lizard. The braincase provides a satisfactory ancestral structure for that of a lizard, or of *Sphenodon*. And the retention of a small, entirely superficial supratemporal, lying over the contact between the squamosal and the parietal, provides for the carrying on of that bone into *Askeptosaurus* of the Middle Trias, and to the Upper Triassic and later lizards. *Prolacerta* (as Camp has shown) had a long neck, but the axis of *Pricea*, with its long hatchet rib, shows that here the neck must have been both longer and more massive. Indeed, the parts preserved of *Pricea* recall their homologues in *Protorosaurus*, as shown most clearly in Miss G. M. Woodward's splendid and certainly most accurate lithographs (Seeley 1887, pls. 14 and 15). I have had the advantage of comparing the type of *Protorosaurus* (Hunterian Coll., no. 308) and that of *Pricea* side by side. The skulls are nearly the same length, but differ in proportion. The face of *Protorosaurus* is relatively longer and its eye larger than that of *Pricea*, whilst the parietals are of much the same length. Morphologically, however, they seem to agree closely. The parietals form a wide roof, cut out into a rounded edge where the postfrontal met them. The parietals are shown to have low crests passing outward at the upper border of the occiput, and the mould of the lower surface of the parietals in *Protorosaurus* shows a small knob, like that which would fill a pineal foramen, which does not pass through to the upper surface. The frontals of *Protorosaurus* are short, the notch for the prefrontal extending back for nearly half their length, whilst that for the postfrontal is short. The prefrontal and lachrymal have been disarticulated and pressed down a little, so that their full extent is clearly shown. They are short, agreeing very well in outline with those of *Pricea*. In both animals the maxilla has a long attachment to the nasal. The maxillary teeth seem to be pleurodont in both. The axis of *Pricea* and its rib seem to agree well with that of *Protorosaurus*. Thus it is probable that the two animals are very closely related, and presumably contemporary, or nearly so, a condition which would imply that the *Lystrosaurus* Zone is Permian, even Basal Zechstein.

Prolacerta and *Pricea*, slightly younger than *Youngina*, differ by retaining a supratemporal lost by it. They thus cannot have come from the immediate relations of *Youngina*, but they are capable of immediate derivation from the circle of the millerosaurs. All that is necessary is to withdraw the parietal lappet, thus leaving an upper temporal vacuity bounded behind by the occipital part of the parietal and the posterior part of the squamosal in contact with it. The supratemporal remains as a bone resting on the junction of the squamosal and parietal, having no contact with the quadrate. Reshaping of the parietal and squamosal, to provide attachments for the muscles which pass through the fossa, provides the crests which border that opening.

It may be noted that Professor J. Piveteau in 1926 referred the reptile *Tangasaurus menelli*, from the Upper Permian of Madagascar, to the lizards, largely on the evidence afforded by its limbs and limb girdles, and the resemblance of the paired sternal bones found in it to the cartilaginous paired rudiments found by Bogoljubsky (1914) in lizard embryos, the resemblance being confirmed by the fusion later in life of each pair. Examination of a modern 'plastic' cast of the mould of the palate of *Tangasaurus* (Piveteau 1926, pl. IX, fig. 1) shows an astonishing resemblance in all visible characters to Camp's illustration (1945*a*, pl. I) of the ventral surface of his skull of *Prolacerta*. Camp (1945*b*) has already recognized this fact. The resemblance includes the remarkable 'hyoids', whose posterior half turns upward toward the roof of the skull, whilst the anterior part lies horizontally, directed forward and inward.

With *Tangasaurus* in Madagascar is found *Hovasaurus*, agreeing with it in its general character, the nature of the pectoral girdle with its fusion of paired sternal bones to form a median sternum, the pelvic girdle, and the morphology of the limbs; but distinguished by the relative shortness of the limbs, and general appearance of aquatic habit. I have examined a new intelligible cast of the skull of the specimen of *Hovasaurus* figured by Piveteau (1926, pl. ii, fig. 3). The skull is seen from above and has short, very wide parietals surrounding a large pineal foramen, and stretching far forward between the hinder ends of the frontals. The postfrontals are notched into the parietals, and cover the front faces of the postorbitals where they pass inward to the parietal. There is a small supratemporal fossa, bounded laterally by a very long limb of the postorbital. On the left side this rests on a rather badly shown squamosal, which is apparently articulated with a rod-like quadrate; the corresponding bone of the right side, with its quadrate, is misplaced and pressed forward. The whole appearance recalls that of *Prolacerta*, and the animal is no doubt a more aquatic version of *Tangasaurus*. *Tangasaurus* is apparently at least incipiently aquatic; *Pricea* and *Prolacerta* are too incompletely known to give any evidence as to their habits; but the known Middle Triassic lizards, those described by Peyer (1931) and Kuhn (1952) from the Tessin, are all aquatic.

Thus the lizards may have had their origin from the group of which *Prolacerta* and *Pricea* are members, and the retention of the supratemporal in these animals shows that they cannot have come from *Youngina*, in which that bone has vanished. None the less in general skull structure, in the nature of their vertebrae, in the structure of their shoulder girdles with paired sterna—of the pelvis—and of the hindleg including the tarsus, it seems evident that *Prolacerta*, *Tangasaurus* and *Youngina* spring from the same stock. And the only group from which they could have come is that of the millerosaurs, from a stage of *Mesenosaurus* character.

Lower Triassic reptiles, apart from procolophonids, are known only from South Africa and Germany. In the South African *Cynognathus* Zone occur *Erythrosuchus*, *Browniella*, *Euparkeria*, *Mesosuchus*, *Howesia* and *Palacrodon*. *Mesorhinus* comes from the 'Middle' Bunter, Bernberg. This is indeed the first diversified fauna of sauropsids, and should be compared with those from the *Procolophon*, *Lystrosaurus*, and *Cistecephalus* Zones which are of progressively earlier date.

Erythrosuchia

Erythrosuchus *and* Chasmatosaurus

Erythrosuchus is essentially the much-enlarged descendant of the *Lystrosaurus* Zone *Chasmatosaurus*, which is the earliest thecodont, and possesses the characteristic qualities of the group. It has a laterosphenoid which, with its fellow, completely surrounds the anterior part of the brain and is firmly articulated with the roof of the skull, its rounded dorso-lateral process fitting against the skull roof where the frontal and parietal join the postfrontal and postorbital. The paroccipital process tends to be a little antero-posteriorly flattened, and the fenestra ovalis lies at the inner end of a deep groove on its lower surface, the foramen for the VIIth nerve coming out on the lower border of the proötic, whilst the Vth nerve passes out from a foramen between the proötic and the laterosphenoid. The upper temporal fossa is small, the lower enormous, and the squamosal, articulating with the parietal and postorbital, passes backward as a bow (lateral to the quadrate) to end in a suture with the shallow quadratojugal. There is a large preorbital opening, and the premaxillae are decurved so that the anterior teeth point backwards. *Elaphrosaurus* is an allied form from the *Lystrosaurus* Zone, *Proterosuchus* being another ally, perhaps from the *Procolophon* Zone. *Erythrosuchus* is well known, though incompletely described, and is certainly thecodont, its maxillary, premaxillary and dentary teeth being set in deep sockets, within which replacing teeth arise.

Pseudosuchia

The remaining thecodonts of the Lower Trias are of much greater importance, all similar to one another in significant ways and allotted to the group Pseudosuchia (Cope 1898), except *Mesorhinus*.

In this group the existence of definite tooth sockets made possible a dentition with long teeth capable of being driven far into large prey. Such teeth can only be used to advantage if the mouth can be opened sufficiently widely to separate the tips of the upper and lower teeth by at least the exposed length of the teeth. At the same time the musculature must be powerful, of large transverse section, and hence extending far in front of the jaw articulation. Thus provision must be made for large temporal muscles which are also so long that the lower jaw can be much depressed. This lengthening can in part be made—especially for the more anterior fibres of the muscles—by moving their insertion forward in the cavity of the jaw, and making provision for the thickening of this muscle during shortening by a vacuity in the outer surface of the jaw. But the lengthening of the mass of muscle can only be done by increasing the distance from the upper surface of the temporal region where it arises to the jaw; that is, by lengthening the quadrate. This happens in all Pseudosuchia.

The outer border of the quadrate in early sauropsids such as *Youngina*, *Prolacerta* and *Pricea* usually lies on a thin rib external to the main body of the bone, the surface which it limits being recessed for accommodation of the tympanic cavity, immediately mesial of the tympanic membrane which is stretched across the frame of squamosal and quadratojugal. This condition is capable of being derived from that in millerosaurs. The membrane is best circular, the stapes meeting its centre. Thus although in *Youngina* its attachment may have been to the whole border, in *Pricea* it evidently left the lower part of the quadrate free.

Euparkeria

Euparkeria from the South African *Cynognathus* Zone is the best known Lower Triassic form, but still remains without other description than that by Broom in 1913*b*. Its skull is characteristically thecodont, the maxillary and dentary teeth being inserted by long roots into independent sockets. There are fenestrae in the lower jaw and antorbital regions, and the anterior part of the brain is surrounded by laterosphenoids which articulate with the skull roof. It retains dermosupraoccipitals, but has lost the tabulars and supratemporals its ancestors certainly possessed. But it has a quadrate whose small, rounded, cartilage-capped head is received in a pit in the squamosal, the articular condyle for the lower jaw lying far ventrally to the basioccipital condyle. In fact, presumably to provide for the insertion of long flattened piercing teeth into the jaw and to allow the mouth to be opened sufficiently widely to enable them to be used, the quadrate has been greatly lengthened, with concurrent change of the basipterygoid processes, so that their articular faces lie below the basioccipital condyle. As a result the lower temporal fossa is greatly deepened, and the quadratojugal extends very far—in later forms much more than half way—up its posterior border. The fenestra ovalis remains unaffected, and the stapes also passes outward as it always did at right angles to the tympanic membrane which is attached to the outer border of the squamosal and part of the quadratojugal; but this membrane is unlikely to have extended far down the quadratojugal border. Thus it comes about that the hinder border of the lower temporal fossa of all pseudosuchians and their descendants is divided into two unequal parts at the point of junction of the small squamosal and large quadratojugal, which forms a 'knee' lying in its hinder border, a secondary condition designed to secure long temporal muscles and a wide bite, and keep a tympanic membrane into which the distal end of the stapes is inserted about on the level of the lowest point of the squamosal. This arrangement is extraordinarily persistent. It may be used to separate a group of forms of most varying adaptive character. *Euparkeria* is completely typical as, so far as is known, it lacks specializations which would cut it out from the ancestry of the greater part, at least, of the members of the group which show an extraordinarily rapid evolution through Triassic times. *Browniella* is no doubt a close relative of *Euparkeria* known only by postcranial fragments.

Phytosauria

Mesorhinus

Contemporary with *Euparkeria* is *Mesorhinus*, 'Middle' Bunter, Bernburg, known only from the hinder part of a single, somewhat damaged skull in the University of Göttingen. Jaekel's figures (1910) are excellent, and substantiated by a photograph. I have handled the specimen sufficiently to know that it is well enough preserved and prepared to justify restorations of the hinder part as complete as those given by Jaekel, though the nostrils and everything in front of them are hypothetical. It is likely to be an ancestor of the belodonts and retains a primitively flat-topped parietal region with a small supratemporal fossa whose posterior border lies in the plane of the top of the skull. Jaekel presents the lateral temporal fossa without a 'pseudosuchian' inflexion of its restored hinder border, and von Huene (1956, fig. 490) confirms this arrangement. In later belodonts there is an enormous enlargement of the quadratojugal. The belodont squamosal has a cup to receive the smooth, condyle-like upper end of the quadrate, and continues down the upper part of the lateral border of the quadrate until it meets the huge quadratojugal, in a way very well described and figured by Camp (1930, p. 100, fig. 30). The quadratojugal extends so far forward from its contact with the vertically (or even backwardly) directed lower part of the quadrate that the pseudosuchian inflexion of the hinder border of the temporal fossa is completely hidden. But with certainty it formerly existed, for the squamoso-quadrate articulation cannot otherwise be explained.

Mesosuchus *and* Howesia *compared with Rhynchosauria*

Mesosuchus and *Howesia* are the next *Cynognathus* Zone forms to be considered. I originally described *Mesosuchus* (1911) without figures, and in confusion with *Euparkeria*; Haughton (1921) gave a good, well-illustrated account of a good skull; Broom (1925) gives some original figures differing little from Haughton; in 1929 I examined the skull prepared by Haughton, and have some drawings of other fragments made in 1911.

The skull is a good deal wider posteriorly than it is high, and its dorsal mid-line descends rapidly from the high occiput to the single terminal nostril. The lateral surfaces are nearly vertical. The two temporal vacuities are remarkably large so that the masticatory muscles were very powerful, the effective pressure they could produce on food in the mouth being further increased because the quadrate lower jaw articulation lies far behind the occiput. These qualities are presumably associated with the dentition, which includes a pair of thick, short, blunted teeth ankylosed to each premaxilla, and two irregular rows of low rounded teeth in each maxilla, the total number being about ten. The quadrate is shown from its outer and hinder surface in Haughton's specimen (Cape Town 6536), and by a perfect impression of its admesial surface, in contact with the pterygoid, in the type (Brown Collection 'F''). The bone has a head which is rounded from side to side and capped by a corresponding groove on the lower surface of the squamosal. From the head the hinder surface of the bone passes downward and backward through a quarter of a circle to end at the articular face, which is also directed downward and backward. From this posterior margin the pterygoid flange passes forward as a vertical flat sheet with a nearly semicircular anterior edge whose lower half rests on the overlapping ramus of the pterygoid. The lower border of the quadrate passes back horizontally from its pterygoid attachment to the articular condyle. The posterior surface of the quadrate passes over a rounded border into a short lateral surface, of which the dorsal half is sheathed by a descending flange of the squamosal. This just meets the upper end of the quadratojugal, which is attached to the rest of the quadrate except where a rather large quadratojugal foramen separates the two bones. The pterygoid is slender, attached to the quadrate by a delicate and rather shallow ramus, and passes on to the palate as a narrow strip to extend forward to the mid-point of the maxilla, where it reaches a delicate tooth-bearing vomer.

The dermal skull is perfectly shown in the Cape Town specimen, well figured by Haughton and Broom; their figures differ slightly from one another, and from the sketches I made in 1929. The three sets of drawings agree exactly about the supratemporal; it is an unusually large bone apparently completely separating the squamosal from the parietal on the dorsal and posterior surface. Mesially it lies in contact with the parietal in such a way as to make it very unlikely that the parietal can extend outward below it to meet the squamosal. The long suture between the supratemporal and squamosal is abruptly truncated by a suture attaching them to a very small bone of about 2 mm^3 lying behind the groove which rests on the upper end of the quadrate. This might either be an ossification in the dorsal process of the extracolumella, or an epiphysis on the end of the paroccipital process, and is most unlikely to be the latter for the small bone is present in position on both sides, and the braincase has been disarticulated and is misplaced in the specimen.

In my description of the type (1911) I referred to 'an epipterygoid, widened, with a deep notch for the optic nerve', which was so determined by comparison with the laterosphenoid of a crocodile, at that time sometimes regarded as epipterygoid. Judging by my original drawing the 'epipterygoid'—which lies high up to the skull roof above the large parasphenoid—does bear some resemblance to that bone of the crocodile, its narrow ventral stem separating large rounded excisions for the Vth and optic nerves. The lower jaw is really 'crocodilian' with an external vacuity.

That the *Mesosuchus* skull could have come from one of the general nature of *Pricea* seems evident. The shape of the quadrate and the widening of the postorbital part of the skull are evidently associated with the animal's durophagous habits, and can easily be derived from the conditions in *Prolacerta* or *Pricea* by such an exaggeration of the temporal musculature, and backward displacement of the jaw articulation, as are demanded by such a diet. Such a widening might well involve expansion of the supratemporal, and would explain simply the way in which from being a bone resting on the upper surface of the suture between the parietal and squamosal, it came to be interjected into that suture to connect the two bones. The disappearance of the internasal processes of the premaxilla is a quality found in all Rhynchosauria, and, with the crushing dentition, gives *Mesosuchus* a resemblance to the members of that group. Haughton has referred Broom's *Howesia* to the neighbourhood of *Mesosuchus*. The drawings I made in 1911 agree well enough with those published by Broom (1906*b*) and Haughton (1921). The bone regarded by Haughton as a supratemporal—and ignored by Broom—is, I think, most probably a squamosal, the bone so labelled by Haughton being something else. The right quadrate, seen from without, is fundamentally like that of *Mesosuchus*, and seems to me to imply that the two animals had skulls of similar shape. The maxilla figured by Broom confirms this interpretation. Thus I agree with Haughton's conclusion.

The derivation of *Howesia* and *Mesosuchus* from the neighbourhood of *Pricea* and *Prolacerta* presents little difficulty. In principle the temporal regions agree very well, the square-cut shape of the postfrontal and its articulation with the postorbital are very similar, the entry of the postfrontal into the border of the temporal fenestra merely reflecting the very large size of that opening. The quadrate is an exaggeration of *Pricea* conditions, the very short face a concomitant of the animal's durophagous habits. The vacuity in the side of the lower jaw is a most unexpected quality, but it is perhaps a further consequence of habit. It would probably imply a migration of some anterior part of the mouth-closing musculature far forward into the mandible, a device to extend the length of the muscle, very necessary in an animal with a short mouth intended to take in and crush hard food, presumably 'nuts' of considerable size. The long and powerful retro-articular process evidently makes provision for a mouth-opening muscle capable of acting as an antagonist to the powerful temporal muscles. It may be emphasized that the contrast between the narrow and short preorbital part of the skull and the wide but still deep and very voluminous postorbital region is most striking; it even recalls the conditions found in dicynodonts, where the tortoise-like crushing mouth is associated with a greatly widened and lengthened temporal region, at least in all larger skulls. The premaxillae of *Mesosuchus* are powerful; attached to spikes of nasal above, and having a face of contact with the front border of the maxilla, they are well fitted to carry two relatively powerful, blunt teeth fused to the bone, directed vertically downward and certainly overhanging the front of the lower jaw. The whole arrangement fits the animal to pick up and take into the mouth quite large hard objects. The immensely powerful musculature shows that the food must have been not only hard but tough and requiring crushing, indeed the animal appears to have been fitted to deal with a walnut! Such a diet would almost demand a premaxilla with short teeth coming down below the level of the maxillary dentition to prevent the nut being squeezed out of the mouth when pressure was first applied to it.

The shoulder girdle, axis and fragmentary humerus figured by Haughton show nothing unusual, these are normal bones of 'diapsids' of their time. It may be mentioned that the type skull of *Mesosuchus* is about four-fifths as long as the skull figured by Haughton, and that it differs in having the articular part of the premaxilla less erect, and in the much shallower maxilla, which is actually only about half as high as that of the new specimen. The difference might well be one of sex; it cannot readily be attributed to age.

Thus it is easy to explain the many remarkable features of *Mesosuchus* by its rapid adaption to a peculiar diet, and thus to derive it from the Prolacertilia. The retention of the supratemporal supports such derivation, rather than one from *Youngina* without a supratemporal and with a quadrate attached by suture to the squamosal. The single nasal opening, the deepened premaxilla, and the multiple rows of teeth on the maxillae and dentaries (at least in *Howesia*) have naturally led to comparisons with the Rhynchosauria*

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* The age of the rocks which contain Rhynchosauria in East Africa and Brazil cannot be directly determined. It rests on the following considerations. I regard the *Cynognathus* Zone in South Africa as being of Lower Triassic age because it contains typical skulls of *Capitosaurus* and *Trematosaurus*, and there is evidence that the *Cistecephalus* Zone is Permian. The *Cynognathus* Zone is succeeded by the Molteno Beds, which have yielded no vertebrates, but many plants, which Dr Hamshaw Thomas tells me are of Lower Middle Triassic age. They in turn, after a revolution in conditions of deposit from those leading to the formation of peats, which have become coal seams, to the red dust of arid land deposition, pass into the Upper Triassic Red Beds containing deinosaurs, so that they are of the upper half of the Upper Trias, the Cave Sandstones being probably Rhaetic. The East African and Brazilian 'Karroo' deposits, with extremely similar faunas, contain cynodonts allied to, but differing from, those of the *Cynognathus* Zone and lack all deinosaurs. They are therefore Middle Triassic equivalents of the Molteno Beds, perhaps extending somewhat higher.

which in the case of *Rhynchosaurus* itself—which may well be of Lower Triassic age—confirm the association.

Middle and Upper Triassic reptiles

No other Lower Triassic (Bunter) pseudosuchian has been described, but later rocks have yielded many. It is nearly impossible to discuss the material because much of it is very incomplete, or the age of the rocks from which it came is uncertain.

One group (to which the name Pseudosuchia was first attached) is easily recognizable, and will shortly be discussed by Mr A. D. Walker, of Newcastle on Tyne. It contains *Aëtosaurus*, *Stagonolepis*, *Desmatosuchus* and *Typothorax*; they have ventral scales and a heavy armour of paired rows of dorsal scutes. Unfortunately the family Stagonolepidae, which might naturally be founded for them has been extended to include a series of remarkable animals of which *Prestosuchus* and *Rauisuchus* of Middle Triassic age are the significant forms. They are large animals of heavy build, whose skulls are scarcely known; they are no doubt pseudosuchians, though the foot of *Prestosuchus* with the exaggerated fifth digit capable of acting as a prop (as it does in cheirotheroid footprints) suggests that the animal was effectively digitigrade and bipedal. The pelvis and femur are in a pre-'deinosaur' stage, but the family might well be ancestral to some groups of that stage of development.

The lightly built pseudosuchians similar to *Euparkeria* are not known by any valuable remains of certain Middle Triassic age, but *Ornithosuchus* from the Elgin Trias is an early form, still quadripedal, and retaining dorsal scutes, but extremely like the earliest Theropoda, and capable of derivation from *Euparkeria*. A later form is *Saltoposuchus*, actually contemporary with the earliest theropods. From these thecodonts an immense variety of reptiles arose in the upper part of the Upper Trias. Here three independent lines of pseudosuchians—the Coelurosauravia, the Pachypodosauria, and the Prosauropoda—gave origin to Saurischia which even in Upper Triassic times became very abundant in Europe, North America, Asia and South Africa, more than fifty species being known. The Ornithischia begin with *Geranosaurus* from the South African Upper Trias, and *Poposaurus* from that of Wyoming, no doubt also of pseudosuchian origin. *Sphenosuchus* and *Pedeticosaurus*, *Erythrochampsa* and *Notochampsa* of the African Upper Trias lead up to *Protosuchus* of North America, a true crocodile of probable basal Jurassic age. And from some Pseudosuchia the pterodactyls first appeared, certainly by the Lower Lias, perhaps in Rhaetic times. In the Upper Trias a number of fully developed and very varied lizards appear in Upper Triassic fissure infillings in England and Wales. And finally, before the Upper Jurassic, birds appeared—again certainly from a thecodont stock.

The summary account of the Thecodontia which occupies the preceding pages is intended to show that the group is a unit, and that it could well have been derived from a form, antecedent to *Prolacerta* and *Pricea*, which retained a complete lower temporal arcade. It could not have come from *Youngina* because in that animal the short quadrate suturally attached to the squamosal is further removed from the primitive millerosaur condition than is that of thecodonts. *Mesosuchus* is closely related to the thecodonts. The rhynchosaurs and Rhynchocephalia may be related to—and can theoretically be derived from—*Youngina* with which they agree in the character of their quadrate. The lizards and snakes come from the *Prolacerta*/*Pricea* circle.

MILLEROSAURIAN AFFINITIES WITH OTHER SAUROPSID REPTILES

Chelonia

Of present day reptiles only the Chelonia remain without certain ancestry: the earliest certain form, *Proganochelys* (*Triasochelys*) from the Upper Trias, is already an obvious tortoise differing only in detail from some still living. *Eunotosaurus africanus* (Watson 1914*b*; Broom 1941) may, or may not, be a chelonian ancestor but it exists. The skull is known only by a badly preserved palate, in which the wide hinder part of the parasphenoid, and the mainly forwardly directed flat articular surface of the basipterygoid processes, the palatal teeth and the lack of a suborbital vacuity, are not inconsistent with some relationship to the millerosaurids. The quadrate is far in advance of the basioccipital condyle. The shoulder girdle has one point of similarity, the carrying inward of the bone supporting the anterior part of the glenoid cavity as a ridge on the 'coracoid', so as to form a groove into which the precoracoid foramen opens. But there appears to be a precoracoid as well as a coracoid, a condition unknown in Millerosaurs and their immediate allies. The humerus and femur, though incompletely known, have some general resemblance to those of *Millerosaurus* and *Broomia*. The pelvis is uncharacteristic, and the vertebrae and ribs so modified that they cannot be compared with those of any other early reptile. But a better comparison of *Eunotosaurus* may perhaps be made with the procolophons.

Procolophonia

Procolophon itself is well known from an abundant well-preserved material, but it is of presumable Lower Triassic age. Broom on good evidence holds that *Owenetta* from the *Cistecephalus* Zone is ancestral to it. Professor Piveteau has shown me splendid materials from the Permian of Madagascar which are of similar structure to *Owenetta*, though perhaps somewhat aquatic. To such forms *Nyctiphruretus* and *Nycteroleter* from the Mesen Fauna of Russia provide satisfactory ancestral conditions, whilst they have considerable similarities to the contemporary millerosaurid *Mesenosaurus*, if interpreted as in the present paper. In *Nyctiphruretus* and *Nycteroleter* (Efremov 1940*b*, figs. 5, 20 and 24) the parietal has a 'lappet' which separates the postorbital from a bone called tabular (which may, however, be regarded as a supratemporal) in a characteristic manner, found also in millerettids. Indeed the comparison between the figures of *Mesenosaurus* in the present paper and those of *Nyctiphruretus* (figs. 5 and 6 in Efremov's paper) is striking (cf. figure 17).

But the condition in *Nyctiphruretus* differs from that in *Mesenosaurus* because in the procolophonids the lateral edge of the parietal has a sutural attachment to the squamosal, whilst in the millerettid it rests upon that bone, having a free outer border. The difference is exactly that which distinguishes the primitive pelycosaur *Eothyris* from *Varanosaurus*, or the ancestor of *Paracaptorhinus* from *Protorothyris*. It is therefore probable that the enlarged supratemporal of procolophonids—in contrast to the small and vanishing supratemporal of millerosaurids and their descendants—is a parallel to the large supratemporal of paracaptorhinids and *Eothyris*, and the vanishing supratemporal of captorhinids and varanosaurids. In each case the contrast is between animals with a wide smoothly rounded skull, and their relatives with a tall skull which has an abrupt edge where the table rests on the cheek.

The possibility of such a comparison between very early members of the theropsids and primitive sauropsids of much later date, implies a community of origin; whether from seymourids, or directly from anthracosaurs it is difficult to decide. Diadectids, the earliest known sauropsids, are remarkable for the immense expansion of the parasphenoid under the hinder part of the braincase and otic capsules, so that the fenestra ovalis becomes extremely laterally placed, and the stapes short. Their whole structure recalls that in *Seymouria* and leads easily to the view that *Diadectes* is of Seymourian origin. It is, however, difficult to see any specific resemblance to *Seymouria* in millerosaurs and procolophons. In *Nyctiphruretus* only is it shown (Efremov 1940*b*, fig. 7, description p. 422) that the hinder end of the parasphenoid is enlarged to more than one-third of the whole skull width, and that the fenestra ovalis lies at its extreme lateral point. This enlargement, though smaller than in *Diadectes* and *Seymouria*, is none the less considerable, and could be used to support the view that all sauropsids sprang from seymouriamorphs rather than direct from anthracosaurs. But *Nycteroleter*, whose extraordinary skull at once recalls that of *Seymouria*, has a narrow parasphenoid, and the pattern of its temporal region—with a parietal lappet attached by suture to the squamosal—might have come from that of such a seymourid as *Discosauriscus* (cf. Watson 1954, fig. 36) by loss of the intertemporal.

Pareiasauria

The last remaining division of the sauropsids is that containing the pareiasaurs. Only with the description by Broom (1936) of two individuals—to which he gave the name *Nanopareia*—belonging to this group, has the structure of their skull roof become known with certainty. I have examined the type of *N. luckhoffi* Br. in Mr Rubidge's collection and can confirm Broom's figures of the upper aspect of the skull. It is, however, open to a different interpretation. The bone Broom called 'tabular' is probably a supratemporal, whilst 'A', which borders Broom's interparietal (=fused dermosupraoccipitals) is the real tabular. Bone 'B' exists, but is presumably a fused dermal scute. If so interpreted, the skull in many ways resembles that of an early procolophonid, differing in retaining as large bones tabulars and dermosupraoccipitals, of which the former are already lost in *Nyctiphruretus*, and both are lost in *Owenetta*. This possible association agrees with the suggestion which Efremov has made, that the Pareiasaurs were derived from such an animal.

Sauropterygia

The Sauropterygia and placodonts are aquatic reptiles, whose structure from Middle Triassic to Cretaceous times is well known. They have no resemblance to any theropsids and are thus certainly sauropsids. Their skulls are never diapsid and show no trace of such ancestry. But their origin is completely obscure.

Choristodera

The Choristodera, known only from the Upper Cretaceous and Basal Eocene, and with some doubt from the Rhaetic, might here be mentioned. These are two-arched reptiles, highly advanced for an aquatic life, but of rather primitive fundamental structure. They show no thecodont features, but do not retain a supratemporal. What their origin may be remains completely obscure. I refer to them only because they are often forgotten.

CONCLUSIONS

The conclusions from this discussion are that the millerosaurs are sauropsid reptiles with more primitive qualities than any others except the early ancestors of the procolophons and pareiasaurs (the diadectids being ignored).

From the early members of the group *Youngina* could be derived by changing the moveable articulation of the head of the quadrate with the squamosal to a rigid sutural attachment, and withdrawing the parietal lappet to leave an upper temporal vacuity, the supratemporal vanishing in the process.

Prolacerta and *Pricea* could be derived from the millerosaurs, much as *Youngina* was, but in such a way that the quadrate retained its rounded head, articulating with a cup in the squamosal, and leaving intact a supratemporal resting on the junction of squamosal and parietal.

Prolacerta, *Pricea* and their apparent close relative *Protorosaurus* agree in having long cervical vertebrae which in the last become relatively enormous, so that the skull is only about half as long as the neck, the neck is as long as the body, the tail long.

The palate of *Tangasaurus* agrees most closely with that of *Prolacerta*, and the less well known dorsal surface is equally similar. But the neck entirely lacks elongation, its vertebrae are no longer than the dorsals which follow them.

The implication is that *Prolacerta*, *Pricea* and *Protorosaurus* belong to the same close group with elongated neck vertebrae, that *Tangasaurus* and its relative *Hovasaurus*—belonging to the same stock—avoided the specializations requiring a long and thick neck. The group so put together may be called the Prolacertilia.

One remarkable character shown by both *Tangasaurus* and *Hovasaurus* is their possession of a sternum which ossifies as paired lateral elements. The condition—in the modified form that the sternum arises from paired cartilaginous centres—exists in living lizards, whilst the sterna of 'Deinosaurs' of all groups are paired bones which do not fuse. The original paired sternal ossifications of birds always fuse ultimately. Thus the existence of paired sternal ossifications in *Youngina* throws no light on the relations of this animal within the later Sauropsids.

Camp found that some of the cervical ribs of *Prolacerta* are two-headed, the hatchet-shaped articular process being slightly more than 1 mm wide although said to be divided into two separate heads. Otherwise all Prolacertilia have single-headed ribs apparently throughout the column. All known *Youngina* ribs are single-headed, and so are those of millerosaurs.

It is evident that the Prolacertilia are, in the structure of their skulls, completely fitted to give origin to the Lacertilia, and that they have much of the appearance of being members of that group. Their vertebral columns, and the single-headed ribs which they retain, are essentially lizard-like, the presence of a neck is a normal lizard feature, and the hand and foot shown in *Protorosaurus* and in *Tangasaurus* agree sufficiently well with those of lizards, though the hind foot of the latter in spite of having suppressed the Vth distal tarsal and somewhat divaricated that digit has not produced the characteristic 'hook-shaped metatarsal'.

The position of the Rhynchocephalia requires discussion. No one who has ever dissected *Sphenodon* is likely to doubt that—though more primitive in the structure of many organs, the heart, for example, or the brain—it is in general very lizard-like. It is therefore natural to consider whether *Sphenodon* and its allies of extremely similar structure back to the Upper Triassic *Clevosaurus* came from the same stock. There is no doubt that they could have done so, for *Pricea* no doubt possessed a complete lower temporal arcade, though in *Prolacerta* it is incomplete. But until some Triassic Rhynchocephalia are more completely described it is impossible to decide whether '*Prolacerta*' or '*Youngina*' is their more probable source. The firmly fixed quadrate of *Youngina* distinctly recalls that of *Sphenodon*, but the movable quadrate of *Prolacerta* is foreshadowed by that of millerettids, and may have been a condition ancestral to many forms other than the lizards.

The Rhynchosauria can only be judged by their most primitive form *Rhynchosaurus*. This much needs a modern description before determining whether or not it can conveniently be derived from *Mesosuchus*. *Mesosuchus*, as shown on p. 381, shares many qualities with 'prolacertids', but is more advanced than they are in seeming to have a thecodont laterosphenoid.

The thecodonts, from which very many Mesozoic reptile groups, and the birds, arose, divide into two or more main branches. They all lack a supratemporal, possess a laterosphenoid sheathing the side of the forebrain, and have a tall quadrate with a rounded cartilage-covered head housed in a hemispherical pit in the lower surface of the squamosal.* They develop fenestrae on the lateral surface of the face, on the palate in front of the transverse bone, and in the outer side of the lower jaw, which allow the expansion of lengthy and thick muscles during their shortening. By the loss of the supratemporal they could have been derived from prolacertid ancestors which retained a lower temporal arcade or—by freeing the quadrate from sutural attachment to the squamosal—from *Youngina*. At present there is no conclusive reason for preferring either alternative; they could have come direct from millerosaurs.

But amongst them were the Pseudosuchia, a group which, beginning in small Lower Triassic forms, gave origin to crocodiles, 'deinosaurs' of all kinds, pterodactyls and birds. It was in fact unique in the shortness of the time in which it produced these greatly varied animals, tied together though they be by community of structure of their hearts and brains, so far as they are known, or can safely be inferred. The earlier millerosaurs are nearly related to the contemporary procolophonids, bearing to them the same kind of relationship as *Varanosaurus* has to *Paracaptorhinus* amongst mammal-like reptiles. The relation which the millerosaurs and procolophonids have to the earliest sauropsid *Diadectes* is entirely obscure. *Diadectes*, arising in Pennsylvanian times, is almost the oldest known reptile. Within its time-span the whole evolution of captorhinomorphs and pelycosaurs takes place. The former group becomes extinct; the latter dies out in most of its branches (one surviving and giving rise to therapsids) before the first appearance of procolophonids and millerosaurs in the Mesen fauna, somewhat above the first appearance of mammal-like reptiles in the Russian succession, but after the end of those Upper Clear Fork Permian deposits in Texas found by Professor Olson (1951–6) to contain the remains of land reptiles. Only *Bolosaurus*—and then with some doubt as to its real affinities—accompanies *Diadectes* in the fossiliferous Texan Permian. This lack is a striking indication of how scanty

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* The only known squamosal of *Erythrosuchus* seems to be damaged on its inner face so that it is impossible to decide how it was attached to the large cartilage-covered upper end of the quadrate.

is our record of early reptiles, and reflects, perhaps, the extent to which such knowledge as we have is concerned with a special, perhaps unusual habitat.

Distribution of reptiles in time

It is interesting to compare the history of the sauropsid reptiles, as it is developed in this paper, with that of the theropsids. This can most easily be done by drawing up for each group a genealogical tree which takes account of all known forms. The possibility of such a chart depends on a world correlation of geological horizons. This has been done by bringing together evidence of various kinds; it is, for example, sometimes possible to use marine transgressions into land deposits, or fossil plants may be used as time markers. The time of greatest difficulty is the Permian, where in western Europe only the short Zechstein (and its equivalents) is marine and the bulk of the formation terrestrial in origin. In North America a very extensive marine series of Middle Permian age is known in West Texas, but cannot be correlated with any beds yielding vertebrates. The great Russian Permian succession, with several horizons yielding reptiles, begins later than the Artinskian, but of no part of it can the age be fixed by the evidence of marine fossils, and the plants and fresh water lamellibranchs from it are uncritical. The Karroo system is even worse dated. The reptiles and Amphibia which it contains can be allotted to successive zones, which can be recognized in Russia and China, but even plants are absent in most of the Beaufort series. Triassic faunas in Europe can be related to the Muschelkalk, and thus by analogy African and South American faunas can be allotted to times fixed on European faunas. None the less the relative ages of most important fossil reptiles are known or inferred with much probability. The lowest beds of the Wichita formation of Texas (the Pueblo) are regarded as the beginning of the Permian time.

It is the basis of ecology that the source of all life is that of plants: they alone can draw all their supplies from the air around them, and the soil in which they are rooted, and take from the light of the sun the energy needed to synthesize their substance. Thus, fundamentally, plants are the basis of all animal life. The nature of the vegetation which covered the Karroo during the time when the 'Karroo fauna' was living on it is very little known. During Permian times it is likely to contain *Glossopteris* as its main element.* At the beginning of Triassic times this plant, and the group of which it is a member, seems to have died out completely for no known reason.

The reptiles of the Lower Karroo zones, from *Tapinocephalus* to *Cistecephalus* (which are Permian) are, to the collector, overwhelmingly dicynodonts. These are present in immense specific and generic variety, ranging in skull length from about an inch to a yard in adults. Their skeleton is little known,† and therefore scarcely described, but the few

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* *Glossopteris*, occuring in immense abundance, is restricted to the Southern hemisphere, and does not occur in Russia where, none the less, dicynodonts of quite normal character occur in several localities, presumably feeding on something else.

† The extreme rarity of dicynodont skeletons is a remarkable fact. To some small extent it is due to the habit of collectors of picking up a skull in a nodule and ignoring the skeleton belonging to it, which often passes into shale, and is difficult to collect. But personal experience shows that this explanation is quite inadequate; there are perhaps a dozen reasonably complete skeletons known, and several thousand skulls. The aquatic *Lystrosaurus* is very commonly found as skeletons; for example, at Orange Farm, 8 miles east of Bethulie, Orange Free State, where I saw the broken up remains of some fifteen skeletons in less than an acre of ground.

Thus it is reasonable to assume that most dicynodonts, with their bulky bodies were eaten, and so scattered.

existing specimens agree in implying a bulky barrel-like body, with short, powerful legs, a short pointed tail, a definite neck, and a head with a horny beak like that of a tortoise set in jaws which could be closed and moved on one another by a most powerful musculature. They were obviously herbivores, the basis of the food supply of all carnivorous reptiles of their time, and may well have depended largely on *Glossopteris*.

The sauropsid reptiles of the *Cistecephalus* Zone are small delicate animals with skulls not known to exceed 8 cm in length. They have rather uniform marginal dentitions of close-set small pointed teeth, and palates roughened by multiple rows of denticles, the most posterior of which on the transverse flanges of the pterygoids may be pointed teeth 1 mm or more high, sometimes backwardly directed. The only possible food for them would be invertebrates.

Up to the summit of the *Cistecephalus* Zone dicynodonts of all sizes are found in great abundance, but suddenly with the beginning of the *Lystrosaurus* Zone they vanish.* With them the food supply of most carnivorous therapsids—gorgonopsids and Therocephalia—went, and these groups have their end.

The common animal in the *Lystrosaurus* Zone is that aquatic dicynodont itself. Very much rarer are the small primitive cynodonts (*Thrinaxodon et al.*), presumably carnivorous or even insect eating, and the rat-sized scaloposaurids which can only have eaten invertebrates. The relatively large, probably aquatic *Chasmatosaurus* (a sauropsid) must have been flesh eating—perhaps *Lystrosaurus* itself, perhaps only fish.

The rocks which succeed the *Cistecephalus* Zone are different in appearance because, whatever their colour, the shales usually break up into little scale-like fragments very different from the cubical blocks resulting from weathering in *Cistecephalus* shales. This difference arises because, whilst the *Cistecephalus* rocks are largely wind-sorted 'loess-like' deposits on land, the *Lystrosaurus* shales were deposits in extensive lakes. This change in conditions may be in part responsible for the faunal change, but can scarcely be expected to have had similar world-wide effects, though the resulting condition is exactly paralleled in Central Asia.

Succeeding the *Lystrosaurus* Zone in South Africa is a *Cynognathus* Zone, not to any extent of lacustrine origin but representing dry land conditions with some slow running rivers and ponds, not greatly unlike—though probably more arid than—the *Cistecephalus* Zone. At this time only the large specialized *Kannemeyeria* (the size of a 'Large White' pig) remains to represent the dicynodonts, and there is the cynodont *Cynognathus*, with a skull some 40 cm in length and flesh-cutting teeth, as a carnivore. In the Middle Trias the even larger *Stahleckeria* occurs alone in Brazil, and a large *Sinokannemeyeria* in China, and an enormous and very odd *Placerias* in the Rocky Mountains, are the last dicynodonts. The absence of any flourishing group of really herbivorous habits led even such members of normally carnivorous groups as diademodons to develop flat surfaced teeth ground down by wear obviously on plant material.

Apart from *Kannemeyeria*, and such cynodonts as *Diademodon*, insects are likely to have been the main herbivorous creatures, and insect eating as a mode of life may have been

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* Two species of 'dicynodon' have been attributed to the *Lystrosaurus* Zone. *Myosaurus* (Haughton) and *Dicynodon leontocephalus* by Broom. The former represented by two associated individual skulls, each about 1 in. long, is certainly from the zone. The latter, a single skull, may well be lower.

widespread in Triassic times, such animals as *Ericiolacerta* amongst theropsids, and most sauropsids, living in this way. Thus, once insect eating became well established, it is natural that groups of small reptiles fitted for it should flourish, and such animals were available more freely amongst the sauropsids than in residual decadent members of the theropsids.

Only when the exploitation of all land habitats by the theropsids was reduced in scale was it possible for sauropsids to get an opportunity of spreading to modes of life more difficult than those suited to small insectivores.

It is remarkable that one of the earliest sauropsid faunas is that found in Madagascar, of presumed Upper Permian age, consisting predominantly of complete skeletons of small reptiles (some allied to *Prolacerta*) preserved in well-bedded nodules no doubt of fresh-water origin, and showing characteristic aquatic adaptation. Only later in the Middle Trias do the sauropsids invade the sea producing the marvellous series of great 'lizards'—*Clarazia*, *Hescheleria*, *Askeptosaurus*, *Macrocnemus* and *Tanystropheus* from Lombardy—described by Peyer and Kuhn, with very many nothosaurs and placodonts of uncertain but probable Sauropsid derivation. Of all these only the plesiosaurs—not in fact represented by true ancestors in the Trias—lived on into the Lias, and indeed until Cretaceous times.

The Millerosauria, with their immediate relatives the Eosuchia and Prolacertilia, can only have been insectivores. None of them show teeth fitted to eat plants, none is large enough to have been predaceous on most other reptiles. But their descendants soon increase in size, *Chasmatosaurus* (head about 46 cm long, and teeth some 1·2 cm high) is fitted to catch and eat large prey, perhaps only fish, but perhaps the abundant *Lystrosaurus* itself. And in the *Cynognathus* Zone *Erythrosuchus* (jaw 80 cm or so long, tooth crown 7 cm high) is fitted to eat really large animals, perhaps even *Kannemeyeria*. The largest therapsid carnivore at this time is *Cynognathus* with a skull some 40 cm long.

Definitions

It seems desirable to provide a formal diagnosis to characterize the Millerosauria, and this is most readily made if the two antithetic groups of reptiles, Sauropsida and Theropsida be first diagnosed.

Reptilia Theropsida

Reptiles in which the middle ear usually remains as a cavity, roofed by the grooved lower surface of the paroccipital process, which ends mesially at a fenestra ovalis lying ventrally, usually entirely below the level of the base of the brain, and often carried still further down by a special downgrowth. There is no tympanic membrane in most theropsids, though their ancestors obviously possessed one. But in some lines of descent a new membrane arises from a new contact of the middle ear cavity with the skin at a point ventral and anterior to that which existed in the ancestors of the group, and is in effect still preserved in Sauropsids. The stapes in all theropsids is a single structure, a bony rod, whose proximal part lies in the fenestra ovalis whilst the distal ends in a contact directly—or through a cartilaginous cap—with a groove (the stapedial recess) on the inner surface of the quadrate, the bone, except in some later forms, not reaching a tympanic membrane. The stapes, none the less, seems to be homologous with the whole stapes of a sauropsid,

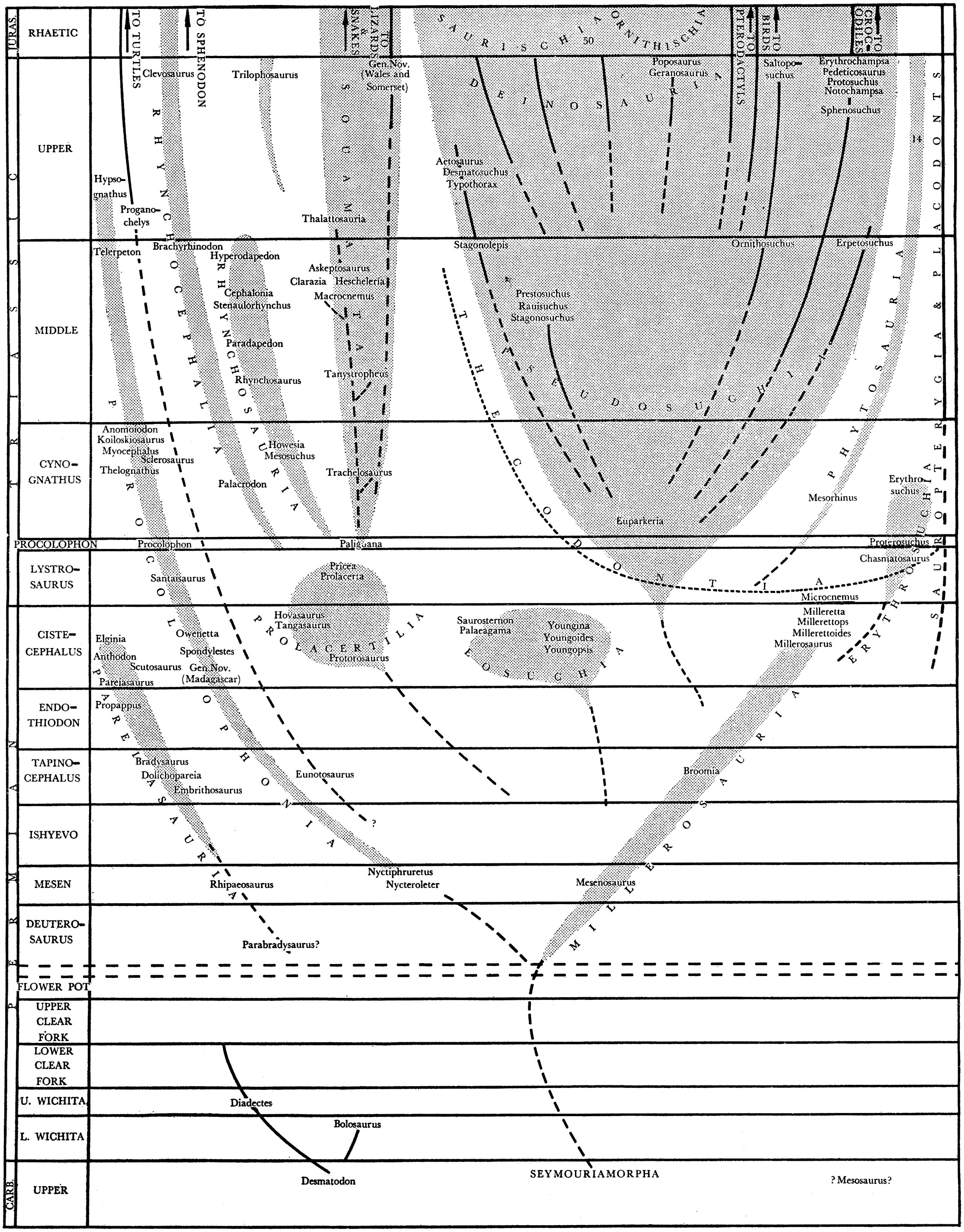
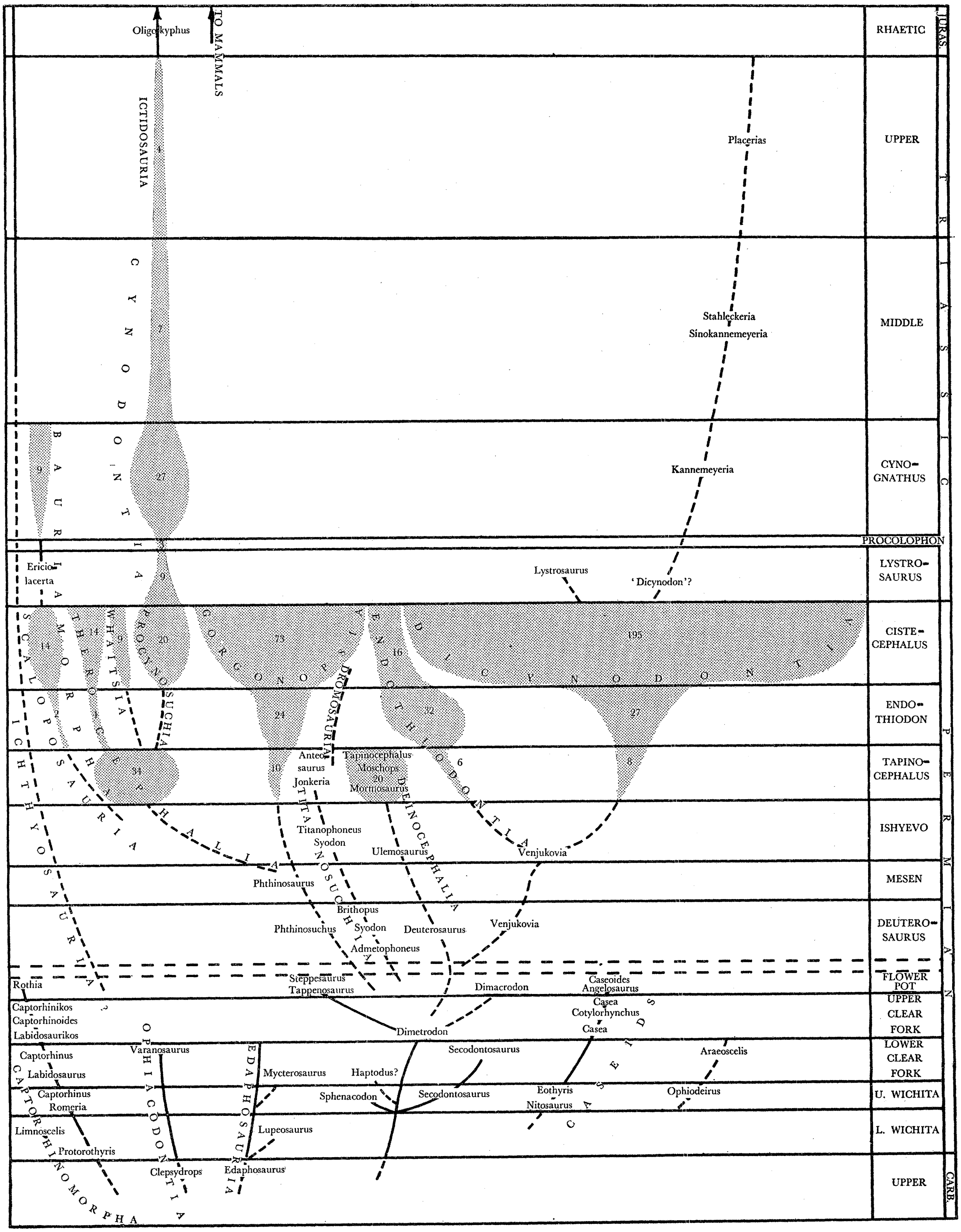


FIGURE 23. Chart setting out the distribution of Pre-Jurassic reptiles in time. The Theropsida are to the right, the Sauropsida to the left. The figure is intended to illustrate the relative abundance of each group at any particular time. It is inevitable that to a very large extent the faunas plotted from the *Tapinocephalus* Zone onward are South African, as those for the Lower Permian are North American. But there is no reason why this geographical bias should gravely distort the world pattern. Indeed such evidence as exists from other places confirms the story. The break



between the Permian and Trias is made at the base of the *Lystrosaurus* Zone, which is known by identical rocks and faunal type in South Africa and Central Asia, and follows a change of sedimentary type in Africa. But *Protorosaurus* from the Basal Zechstein Kupferschiefer of Germany appears to be very closely similar to *Pricea* of the South African *Lystrosaurus* Zone, though somewhat advanced in structure, suggesting that the real beginning of the Trias might well be at the beginning of the *Cynognathus* Zone. The numbers included within shaded areas are the number of species which have actually been recorded in the zone.

possessing a dorsal process articulated with the paroccipital process (usually on the proötic), and having attached to its lower border a ligament perhaps homologous with the upper end of the hyoid. The absence of a tympanic membrane enables the quadrate to lie far back, so that the outer end of the paroccipital process directly abuts the squamosal where it sheaths its inner surface. And generally the otic capsule is hidden in direct side view.

Reptilia Sauropsida

Reptiles in which the middle ear usually remains as a cavity, roofed by the grooved lower surface of a paroccipital process, which ends mesially at a fenestra ovalis lying high in the side wall of the ear capsule above the floor of the brain cavity. The tympanic membrane, almost always preserved as a functional structure, is usually parallel to the animal's principal plane and high on the lateral surface, so that it is largely seen in side view. It is attached in front to the lateral border of the quadrate, or the bones covering it, and above to the squamosal and supratemporal. The stapes passes continuously as a straight rod from the fenestra ovalis to be inserted into the tympanic membrane about at the middle of its height. It may, or may not, be perforated by a foramen for the stapedial artery. But at some stage of development at least the straight rod bears a dorsal process connected in some way with the paroccipital process, and a ventral process at some time attached to the upper end of the hyoid cartilage. To permit the tympanic membrane to be large, and to enable the straight columella to pass to it at right angles, the quadrate is necessarily placed far forward with respect to the occipital condyle, and the squamosal lies essentially at its outer margin. Thus the lateral surface of the otic region and occiput is widely exposed laterally in the complete skull.

In some sauropsids the stapes, passing behind the quadrate to the tympanic membrane, has a special 'processus internus' projecting forward on the inner surface of that bone. In snakes the tympanic membrane and cavity vanish, and the articulation of the columella and quadrate, by either the dorsal process or processus internus, conducts sound waves to the ear.

The reptilian group including *Milleretta*, *Broomia* and *Mesenosaurus* is evidently of high rank, and may well be regarded as an Order, defined as follows:

Order Millerosauria

Sauropsid reptiles in which the skull retains a table composed of parietals each of which passes out laterally as a parietal lappet to rest upon the upper surfaces of the postorbital and squamosal, which meet below it. The 'lappet' is bounded anteriorly by a suture with the postfrontal and has posteriorly a notch into which the anterior end of a supratemporal is inserted. There is a single, laterally placed temporal fossa, surrounded by the postorbital, squamosal and jugal. This may be secondarily closed by ingrowth of the three bones which surround it. The face is of 'normal' structure without a vacuity, the lachrymal being of very variable length, sometimes reaching the nostril. The braincase is remarkable because the paroccipital and proötic meeting one another in a large flat contact combine to form a relatively long and slender paroccipital process which comes into contact with the lower posterior corner of the supratemporal, leaving a space—the tympanic cavity—between the process and the hinder surface of the squamosal and quadrate. The upper end of the quadrate is a cartilage-covered knob received in a pit in the squamosal. Its posterior surface, rounded from side to side, is visible from summit to articular condyle. The lateral border is coated by squamosal and quadratojugal which in some forms, but not all, bear a crescentic ridge mapping out a recess which is part of the tympanic cavity. The stapes, inserted into the membrane closing the fenestra ovalis, passes outward behind the quadrate to divide into three processes—dorsal, tympanic and hyoidean. Much of these processes remains cartilaginous, but their roots are surrounded by cylinders of bone in many cases. The stapes may be attached to the inner surface of the hinder ridge of the quadrate by a typical, lizard-like processus internus. The palate shows a wide lower surface of the braincase, largely parasphenoid. The basipterygoid processes, widely separated, project forward and articulate by transverse faces with the pterygoids. The palate has a wide interpterygoid vacuity, is of normal primitive reptilian character, and bears three belts of small teeth radiating in effect from the basicranial attachment of the pterygoid. The lower jaw lacks an outer vacuity. There is a shoulder girdle in which the glenoid cavity is screw-shaped, though differing from that of pelycosaurs in that the scapular part faces downward. There is no cleithrum, the interclavicle has a wide anterior end to which the lower ends of the clavicles are attached. The pelvis has a continuous lower surface, there being no obturator foramina. The limbs are pentadactyl, the Vth digit of the pes lacking a hooked metatarsal.

Mesenosaurus, *Broomia* and the millerettids would belong to independent families, which it seems unnecessary to diagnose, for their characteristics are obvious from consideration of the detailed descriptions earlier in this paper. The resemblance between the Millerosauria (and especially the millerettids) and the captorhinomorphs—which is genuine—depends, I think, on the fact that the two groups were derived from similar amphibian ancestors. The skulls of *Varanosaurus* and *Protorothyris* on the one hand and *Millerosaurus* on the other agree in almost all details, except for those which concern the braincase, the middle ear, and the tympanic membrane. There the difference is great, and is of a kind shown by comparison of any theropsid with any sauropsid reptile, no matter how close be the resemblance between them in other matters.

But the millerosaurs do not recall the diadectids in general character. In particular there is in no millerosaurid—nor, with the doubtful exception of *Nycteroleter*, in any procolophonid—any trace of the immensely widened posterior part of the parasphenoid, which stretches out to the widely separated fenestrae ovales of *Diadectes*, and suggests a derivation of that animal from seymouriamorphs. Is it perhaps possible that '*Diadectes*', which, in the form of *Desmatodon*, is one of the oldest of known reptiles, is an early sterile offshoot perhaps actually from a seymouriamorph stock, which retained the labyrinthodont tympanic membrane and enlarged it in a typical sauropsid manner, although it left no descendants of different structure, and may not even be directly related to the normal sauropsids, all of which may well have come from a common procolophon—millerosaur stock which did not show seymourian peculiarities?

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EXPLANATION OF ABBREVIATIONS USED IN FIGURES

Acet.	acetabulum
Acr.	acromium process
Art.	foramen for stapedial artery
At.	atlas
At.I.C.	atlantic intercentrum
Ax.	axis
B.Oc.	basioccipital
B.Sp.	basisphenoid
C_1, C_2, C_3,	the centralia
Clav.	clavicle
Cor.For.	coracoid foramen
D.S.Oc.	dermosupraoccipital
Dor.Proc.	processus dorsalis
E.Pt.	epipterygoid
Ec.Pt.	ectopterygoid
Ect.For.	ectepicondylar foramen
Ent.For.	entepicondylar foramen
Ex.Oc.	exoccipital
Fen.Ov.	fenestra ovalis
Fib.	fibula
Gl.Cor.	glenoid cavity coracoidal part
Gl.Sc.	glenoid cavity scapular part
Hy.	hyoid
Hy.Proc.	hyoidean process
I.Tem.Fos.	infratemporal fossa
Il.	ilium
Im.	intermedium
Int.Clav.	interclavicle
Isc.	ischium
Ju.	jugal
L.T.Fos.	lateral temporal fossa
Lac.	lachrymal
Lat.Cen.	lateral centrale
Mx.	maxilla
N.	nasal
N.c.	neural canal
No.	notochord
Oc.Cond.	occipital condyle
Odon.	odontoid process
Os.D.	osteoderms
P.Mx.	premaxilla
P.O.	postorbital
P.T.Fos.	post temporal fossa
Pal.	palatine
Par.	parietal
Par.Oc.	paroccipital
Par.Sp.	parasphenoid
Po.Z.	postzygapophysis
Pr.At.	proatlas
Pr.Fr.	prefrontal
Pr.Ot.	proötic
Pr.Z.	prezygapophysis
Proc.B.Pt.	basipterygoid process
Proc.Int.	processus internus
Proc.Ty.M.	tympanic process
Pt.	pterygoid
Pt.Fr.	postfrontal
Pu.	pubis
Qu.	quadrate
Qu.J.	quadratojugal
Ra.	radiale
Rad.	radius
Rad.Art.	radial articulation
Rib.Fac.	rib facet
S.Oc.	supraoccipital
S.Tem.	supratemporal
Sq.	squamosal
St.	stapes
Tab.	tabular
Tib.	tibia
Ul.	ulnare
Uln.	ulna
Uln.Art.	ulnar articulation
Vo.	vomer