The Evolution of the Labyrinthodonts

D. M. S. Watson

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THE EVOLUTION OF THE LABYRINTHODONTS

By D. M. S. WATSON, F.R.S.
University College London

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CONTENTS

The labyrinthodont Amphibia flourished from Upper Devonian times to the Rhaetic. Amongst them is a series of related forms—covering, perhaps, the longest time span to be found in fossil materials—whose earliest member is *Actinodon* from the French Coal Measures, and latest the cyclotosaurs from the Upper Trias of several countries. The material is good, most of it is South African, but important specimens come from many other parts of the world. The skull shows little change with time in the structure of the dorsal surface, but the palate and braincase change progressively, and the process is described. Some of the skulls have associated lower jaws, which are figured, and may help in the understanding of isolated lower jaws. Postcranial material is too rare to be taken into consideration. The series is important because its long range in time and worldwide geographical distribution make it valuable in the determination of the horizons of the rocks in which its members are found. Two new genera and two new species have been established.

INTRODUCTION

Large labyrinthodonts with a skull in shape like that of *Eryops*, or *Parotosaurus nasutus*, are known from many horizons in South Africa, from the base of the *Tapinocephalus* zone to the summit of the *Cynognathus* zone. There is thus a series of forms, living under climatic conditions not greatly dissimilar throughout the whole period, which serves to bridge the structural gap between these two animals. The story, foreshadowed by *Actinodon* from the French Coal Measures, ends in the later *Cyclotosaurus*, which I have already discussed (Watson 1958). Such a long range is a very rare occurrence amongst fossil tetrapods, and the earlier members of the series in South Africa are not paralleled by materials from any other part of the world, though forms similar to the later ones are found in Germany and Russia, and should thus give valuable evidence for correlating horizons.

Apart from the treatment given to the rhinesuchids and capitosaurs by Romer in his admirable review (1947) the group has been little discussed. Existing accounts, often in obscure journals, are rarely based on effectively prepared material, and very commonly

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only one aspect of the skull is illustrated, indeed it is exceptional to have a complete series of admirable drawings such as those given by Schroeder in his paper of 1913. In general skulls only are available, as very little postcranial material has been discovered, but they are scattered in museums all over the world, none of which contains a series covering a long period of geological time and wide geographical distribution.

I have, therefore, brought together a considerable variety of material, of many ages, and different continents, in the hope of establishing an evolutionary story which would in effect enable one to determine the age at which any particular type of 'capitosaur' flourished. I have also made further preparation and new drawings of the capitosaur skull, B. 122, from the *Cynognathus* zone of Watford, which I figured in 1919 (Watson 1919, figs. 11–16) so that details of its structure would allow of an accurate comparison with other labyrinthodonts.

Actinodon

The story may be said to begin with *Actinodon*, from the 'bituminous shales' of Autun, France. These beds have been variously placed in the Carboniferous and in the Lower Permian, but the most recent authors seem to regard them as being of the top of the Lower Permian in age. At any rate the fauna has the appearance of being a little before that of the Texan Clear Fork. The structure of both skull and postcranial region of *Actinodon* is well known, and serves as an admirable intermediate between the Middle Coal Measure labyrinthodonts such as *Loxomma* and *Anthracosaurus*, and the Lower Permian *Eryops*. The material available has been referred to *A. frossardi*, *A. brevis* and *Euchirosaurus*, which have been shown by Thevenin (1910) to be successive growth stages of a single form, *A. frossardi*, a parallel to which is shown by the abundant materials of *Archegosaurus*. Wadia & Swinton (1928) have described the impression of the upper surface of a small labyrinthodont skull from the basal Gondwana of India as *Actinodon risinensis*; the generic determination seems extremely probable, and represents an important geographical spread of the group. Branson (1935) describes a specimen from Risin Spur, Kashmir, the same locality as *A. risinensis*, which he thinks is closely related to it, and places them both in a new genus *Lysipterygium*.

I have in my collection a plaster cast (B. 139) of a large specimen of *Actinodon frossardi* Gaudry from the Gas-coal of Muse near Autun (figure 1), whose width from the quadrate condyle to the mid-line is 11·0 cm, and also fragments of another skull (B. 139*a*), which I owe to the generosity of the Musée d'Histoire Naturelle in Paris. Though much cracked and damaged by the decay of pyrites, the fragments make possible a clearer understanding of the basis cranii and its attachment to the pterygoid than does the plaster cast. The important fact is that the basis cranii very evidently possesses a considerable basipterygoid process which meets, but does not fuse with, a special internal process of the pterygoid. Behind this articulation the quadrate ramus of the pterygoid extends back to the quadrate, and is widely removed from the side of the braincase. The cast demonstrates this beyond dispute, because before burial the skull had been dorso-ventrally compressed so that the lateral margins spread outwards, and the pterygoid articular processes are pulled away from the undisplaced basis cranii. Branson's figure clearly shows that the basipterygoid articulation was moveable in his specimen, thus the chief lack in the figures of Gaudry (1887) is supplied, and a very interesting comparison with *Eryops* can be made. The comparison suggests that *Eryops* (figure 2) is in essential agreement with *Actinodon* in the basicranial region, but that in it the basipterygoid articulation is a firm attachment by suture, so that the pterygoid and basisphenoid very seldom part, even in young individuals.

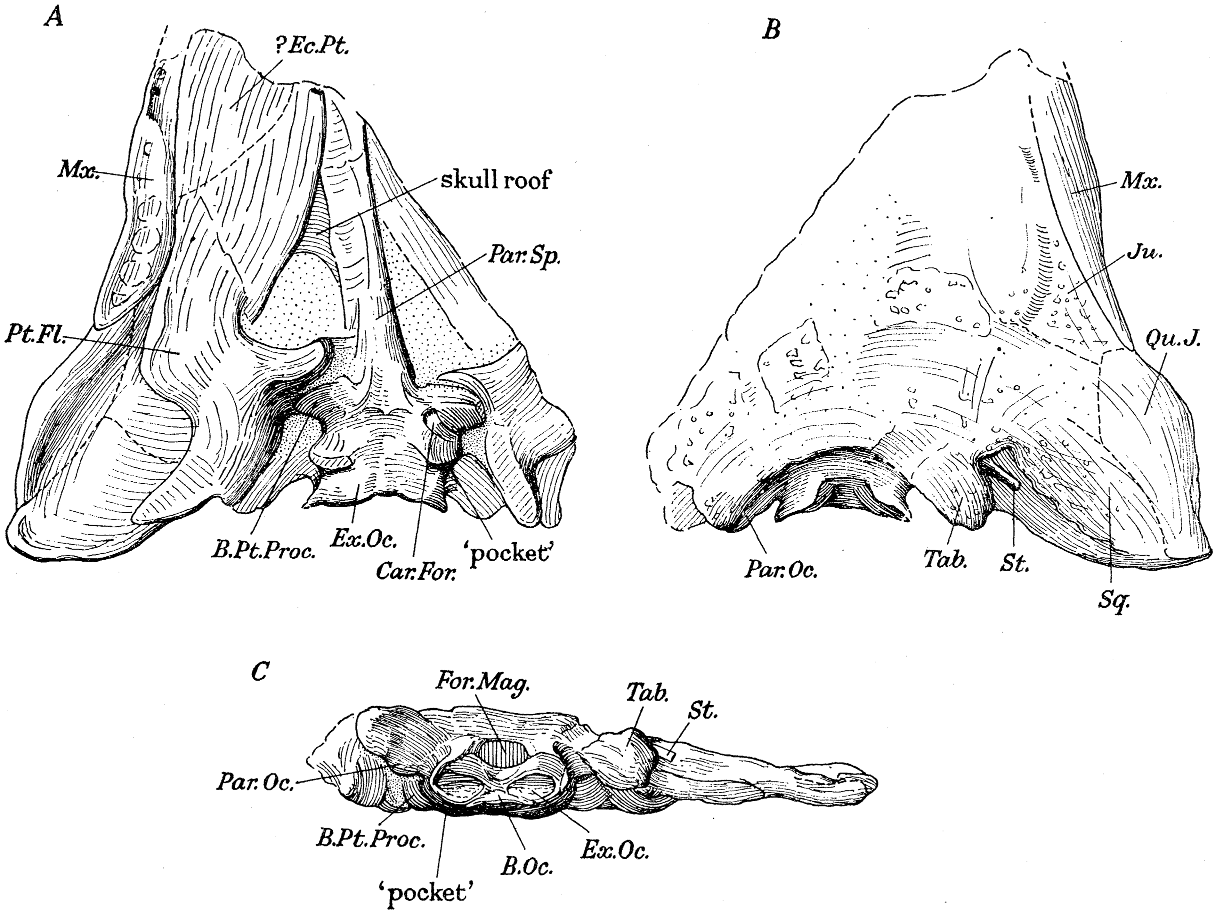

FIGURE 1. *Actinodon frossardi* Gaudry, from the Gas-coal of Muse, near Autun, which is apparently of Lower Permian age (D.M.S.W., B. 139) (× 4/9).

Plaster cast, which has not been coloured and is therefore a reliable reproduction of the specimen as it was, of a large specimen in Paris. The original contained iron pyrites whose decay has effectively destroyed it.

The skull is dorso-ventrally flattened with its lateral border pushed outwards, so that in life the head must have been considerably narrower and deeper. This widening has pulled the articular processes of the pterygoids away from their articulation with the basisphenoid, and thus made evident that they are not rigidly attached by suture. The quadrate rami of the pterygoids are broken short, and much of the dorsal surface of the skull is incapable of interpretation.

A, palatal surface; *B*, dorsal surface; *C*, occiput. For explanation of abbreviations see p. 265.

The basis cranii of *Actinodon* seen from below is wide and short. Just anterior to the condyle the parasphenoid bears a pair of ridges, overhanging depressions, or 'pockets', into which the anterior ends of the recti capitis muscles were inserted. They are quite well marked, widely separated from one another, and extend out a little laterally to the basioccipital more or less as in *Eryops*. The pterygoid is best seen on the right side and its process for attachment to the basisphenoid is quite narrow. The quadrate ramus is a thick sheet of bone and is comparatively short, the quadrate condyle lying little behind the basioccipital condyle. Between the basipterygoid processes the parasphenoid extends forward, its palatal surface being narrow and rounded, though the bone is deep and apparently supported a sphenethmoid. The palatal ramus of the pterygoid bears a very marked square-cut flange, obviously applied during life to the inner side of the lower jaw, which in the cast is flattened down into the general plane of the palate. The bone extends forward and inwards as a wide sheet in which it is impossible to see sutures, and may in fact have reached the parasphenoid so far back that the vacuities form in effect an equilateral triangle. In consequence the palate is completely closed from a point relatively far back, and the interpterygoid vacuities are very much smaller than in *Eryops*. The width of the palatal ramus is about 4·5 cm in a skull whose half-width at the same point is 8·5 cm. No palatal teeth are visible in the cast, but there is evidence of a marginal dentition. The teeth are presumably of circular section, being placed in depressions on the maxillary margin.

The occiput is much flattened by compression, but it seems evident that the general shape of the occipital condyle, and of the tabular horns, is not grossly distorted. The condylar surface is single, slightly notched mid-ventrally, and so much depressed in the mid-line (presumably for the notochord) that the exoccipital contributions are evidently much deeper and more important than that made by the basioccipital. The whole articular surface is concave and shallow, about twice as wide as deep, and is directed backward. The general position of the foramen magnum is seen.

From above it is evident that the occipital border of the skull roof is rather deeply concave, and that the tabulars stand out behind the anterior end of the otic notch as thick rounded masses of bone with a flattened posterior surface, which (shown on the left side) is no doubt in part paroccipital. There is a suggestion that a supraoccipital bone existed. The otic notch is shown on the right side, where its border is well defined by a ridge extending from the squamosal to the tabular. The end of the stapes is visible as a slender bone. The quadrate ramus of the pterygoid does not appear to bear a stapedial groove (to which reference will be made on p. 236).

It may be noted that R. 2999, a specimen from Autun in the British Museum (Natural History), shows traces of a retroarticular process of the lower jaw on the left side.

Eryops

Eryops, from the Lower Permian of Texas, whose skull is of the order of 25 cm in length, is well known from the work of Case (1911), Sawin (1941) and others. The animal, larger than *Actinodon*, of heavier build, and with much more massive legs, was evidently a terrestrial form; indeed the Clear Fork formation, in which it is very common, seems to have been accumulated in an area which was largely arid, although containing rivers and pools. All that seems necessary here is some consideration of how it differs from *Actinodon* in the basicranial region.

Figure 2 was drawn from an admirable specimen of a young individual, no. 1214 in the Museum of Comparative Zoology at Harvard, which shows the structure to be extremely massive. The occipital condyle is dumb-bell shaped and obviously includes a considerable basioccipital contribution, apparently completely fused with the more

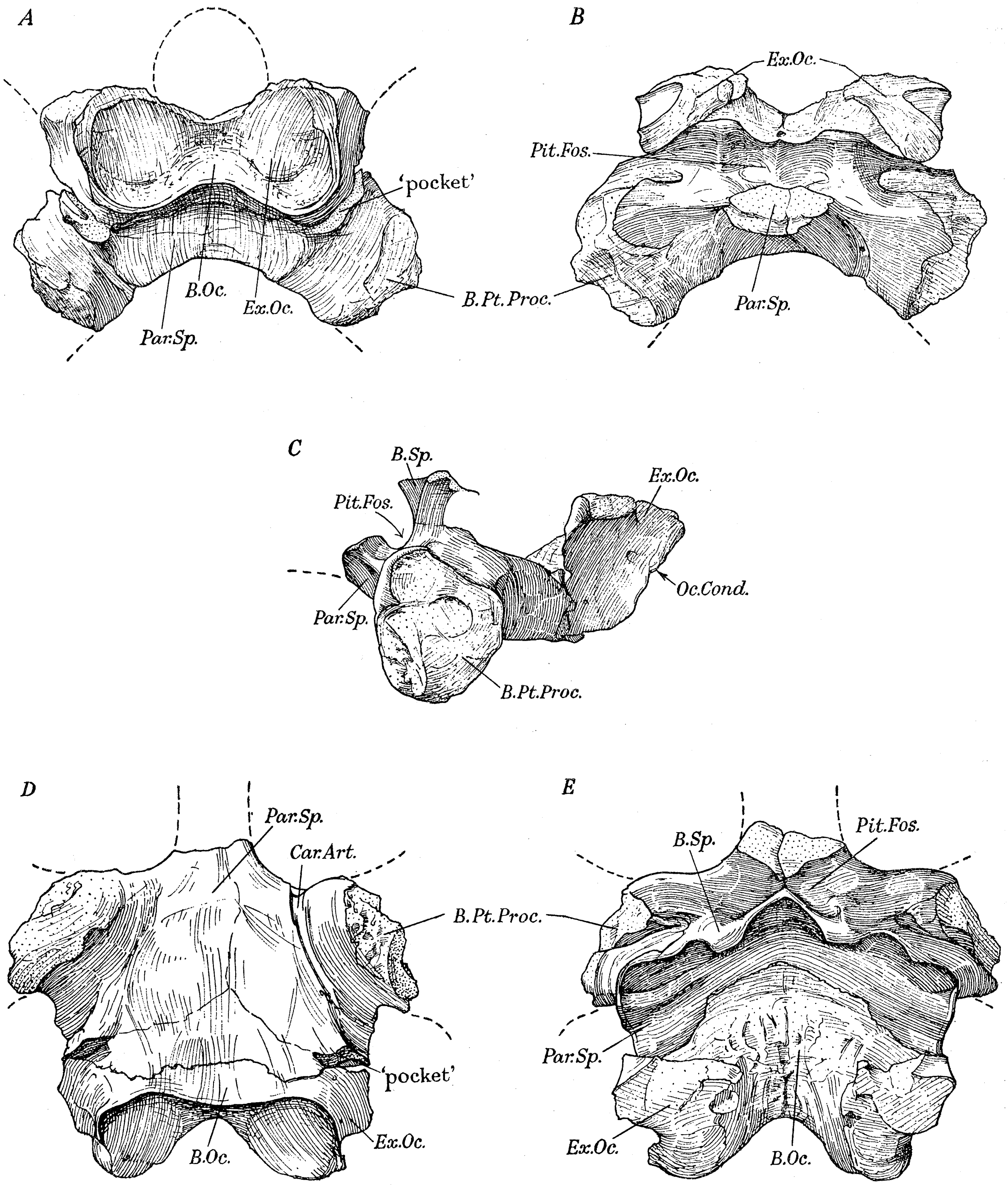

Figure 2. *Eryops* sp. (M.C.Z., 1214), Moran Formation, Lower Wichita (Lowest Permian), Little Bitter Creek, Young County, Texas, natural size.

Basicranial region consisting of the hinder end of a parasphenoid from which the pterygoids have been disarticulated, suggesting that the individual was young. To it the basioccipital, exoccipitals and basisphenoid are fused and remain in natural position. The basisphenoid, which shows the pituitary fossa very well, does not meet the basioccipital, though it is evident that a belt of residual cartilage connected them, resting directly on the upper surface of the parasphenoid. The basipterygoid process is mainly basisphenoid, but has a thin skin of parasphenoid. (Compare with figure 4.)

A, from behind, showing the single condyle whose basioccipital component connects the two exoccipital portions; *B*, from in front; *C*, from the left, showing the relations of the occipital condyle to the basipterygoid process; *D*, from below showing the posterior and extreme lateral position of the ‘pockets’ on the parasphenoid; *E*, from above showing the extent of the basioccipital.

extensive exoccipital components. The joint bone bears what is essentially a single articular surface, the lateral parts of which project backward quite strongly over the mesial basioccipital part. In other words it provides a perfect intermediate between an embolomerous condyle and that of a stereospondyl.

The basioccipital extends forward as bone in contact with the upper surface of the parasphenoid, having in life been continued as a thick floor of cartilage until it met the posterior surface of the basisphenoid. The basipterygoid process is a very powerful projection almost circular in section, composed largely of basisphenoid and ultimately fusing with the pterygoid, which is attached to it by an irregular surface. Mesial of the basipterygoid processes flanges of basisphenoid pass upwards and outwards to meet the proötics (missing in the specimen), and form the hinder wall of an extensive recess, to which were attached the eye muscles. This recess is the pituitary fossa, and through its widely open ends the fifth nerve passed to the Gasserian ganglion. The arrangement seems to differ from that of *Actinodon* essentially in the contrast between the sutural connexion of the pterygoid and basis cranii in *Eryops*, and the moveable articulation in *Actinodon*.

In the M.C.Z. *Eryops* 1214 a very distinct groove runs across the ventral surface at the root of the basipterygoid process. It obviously conveyed a blood vessel (*Car. Art.*) from the otic region to the front of the process, and there are traces of this groove in my cast of *Actinodon*.

The very lateral and posterior position of the 'pockets' in *Eryops*, and the short basioccipital and exoccipitals behind them, are similar to those of *Actinodon*.

Melosaurus uralensis von Meyer

The Lower Permian material of *Eryops* is abundant and admirably preserved, and it is very unfortunate that no tetrapod forms immediately succeeding the Texan Clear Fork in age are known. The earliest of following faunas is that described from the Urals, which has been worked on by a number of authors from the time of H. von Meyer (1860), and contains an important skull, *Melosaurus uralensis* von Meyer, from the Upper Copper Bearing Sandstones of Kazan, West Urals. This is elongated with nearly straight sides, is rounded off in front by a narrow premaxilla, and evidently does not belong to the series including *Eryops* and *Parotosaurus*. However, as the only labyrinthodont of such age, it is valuable in illustrating to some extent the transition between the *Eryops* stage and that of the Upper Permian forms from Africa, such as *Rhinesuchus*.

Melosaurus uralensis is represented by the type skull in Berlin, and by another specimen in Moscow attributed by Konjukova (1955) to this species. The type skull, which is 19·5 cm in length, and shows the whole of the dorsal surface, and a preparation of the palate, was also figured by Hartmann-Weinberg, who gives restorations of the dorsal surface and palate, and a pen-and-ink drawing (1939, fig. 4) interpreting the basicranial region, shown in a photograph (1939, Pl. 2) which is not very easy to relate to it. Konjukova gives drawings of the dorsal surface of her skull, which is some 22 cm long, and the anterior part of the palate.

In Hartmann-Weinberg's drawing (cf. figure 3) the basipterygoid process is a mere knob, laterally placed on the widened floor of the braincase at the point where the palatal vacuities begin. The process must have articulated moveably with a cup on the pterygoid, as she suggests, but nothing in the pterygoid as shown in the photograph or drawing makes the nature of the attachment clear. At the base of the basipterygoid process are shown grooves, reminiscent of those of *Eryops* and *Actinodon*, which run into foramina and presumably housed the carotid arteries.

Further understanding of the basis cranii is exceedingly difficult, because the lower surfaces of the exoccipitals (*Ex.Oc.Art.*), which seem to be visible in the plate, are capable of interpretation in two ways: the exoccipitals may have formed the lateral extremities of a wide condyle whose central part was basioccipital (missing in the specimen), or they may have articulated with the upper surface of a basioccipital which formed the whole single condyle. Hartmann-Weinberg interprets the exoccipitals as forming paired condyles, but it seems to me evident that they cannot provide the whole articular surface of the condyle, and that there must have been a wide basioccipital part connecting them, so that the effective condyle was very extensive.

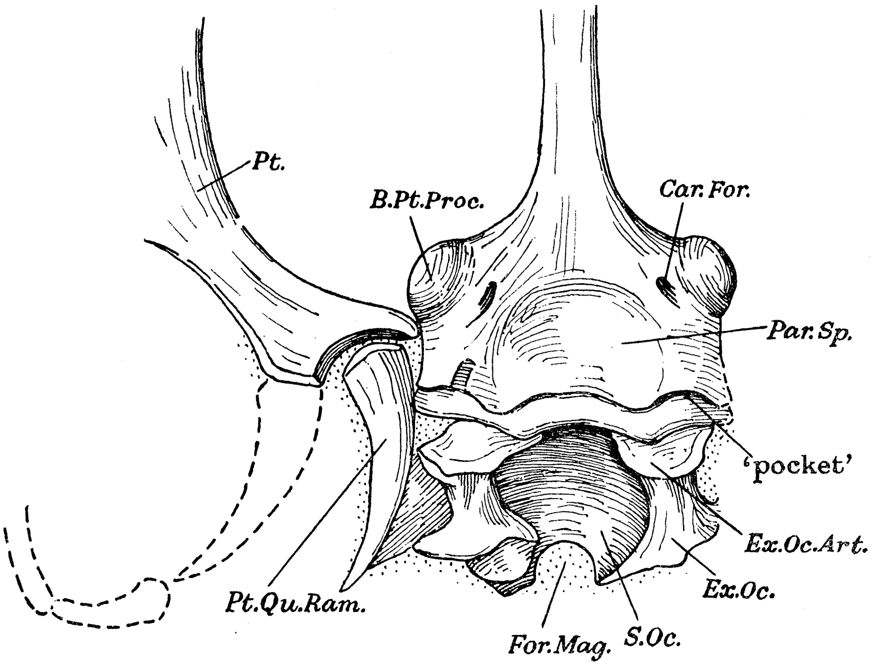

FIGURE 3. *Melosaurus uralensis* von Meyer, Upper Copper Bearing Sandstones of Kazan, West Urals, U.S.S.R., natural size.

Ventral view of the basicranial region of the type specimen in Berlin, redrawn and lettered (but not otherwise altered) from Hartmann-Weinberg (1939, fig. 4).

The pterygoid is disarticulated from the basis cranii, and shows a facet well fitted to articulate with the rounded basipterygoid process of the basisphenoid. The photograph of this region (Hartmann-Weinberg, Pl. 2) suggests that this articulation lay largely on the anterior face of the basisphenoid, and not laterally as her drawing seems to indicate. The quadrate ramus of the pterygoid is broken off and misplaced, but its probable contact with the palatal part of the bone is shown, and the original position suggested in dotted lines. The supraoccipital, seen from its endocranial side, is evidently displaced backwards, and has carried with it the upper ends of the exoccipitals, so that these now lie almost at right angles to their original position surrounding the foramen magnum, whose summit is shown (*For.Mag.*).

In Hartmann-Weinberg's plate and figure the 'pockets' are possibly represented by the lateral parts of the posterior border of the parasphenoid, the line connecting them then being the basioccipital suture; in which case they are far back towards the condyle. The figure shows a notch on one side (not on the other) which suggests that a deep pocket, whose parasphenoidal floor has there been broken away, did exist. If Hartmann-Weinberg's restoration of the palate be correct the palatal vacuities are small, but not so small as in *Eryops*.

Konjukova (1955) gives figures of an admirably complete skull, 28 cm in length, which she attributes to this genus as *M. vetustus*. She shows the occipital condyle as very broad and shallow, the height being about one-third of the width; the continuous surface has a large basioccipital component, a notch for the notochord breaking its dorsal surface. Her specimen does not show the 'pockets', or make the details of the basipterygoid articulation clear, but it does show that the palatal vacuities, although already extensive, still leave a wide exposure of palatal surface lateral to them, confirming the width shown in her specimen of *M. uralensis*, and in Hartmann-Weinberg's restoration. It may also be noted that the quadrate condyles lie far behind the occipital condyle.

Melosaurus, as so described and figured, is remarkable because it is primitive in that the basipterygoid articulation is moveable, as in Coal Measure labyrinthodonts, though differentiated by the spheroidal articular surface of the process, which recalls the cylindroid surface of that process in *Eryops*. On the other hand the palate shows an advanced feature in the relatively large size of the interpterygoid vacuities. The basicranial region vividly recalls that of *Eryops*: the exoccipital condyles are in a similar place, the basioccipital of *Eryops* may perhaps be represented, and the general build of the basipterygoid process, the hinder part of the parasphenoid, and the 'pockets' are remarkably alike. That the carotids pass round the basipterygoid process in grooves in *Eryops*, whilst in *Melosaurus* these grooves are roofed, is a matter of no real morphological importance.

RHINESUCHUS WHAITSI BROOM

The genus *Rhinesuchus* Broom was founded in 1908 for the species *R. whaitsi*, which comes from near Fraserburgh Road Station, Prince Albert in the Gouph, C.P., in the *Tapinocephalus* zone. The type specimen is S.A.M. 1213, the hinder part of a skull with an incomplete but well-preserved palate, whose occiput shows the general character well, though the left side is somewhat damaged.

In 1915 Haughton (Pl. 12, figs. 3, 4) described an almost complete skull and lower jaw, S.A.M. 3009, from the *Endothiodon* zone of Beaufort West, Prince Albert, and later called it the paratype of *R. whaitsi*. In 1919 I reproduced as figure 3 a sketch made by Dr Broom from a skull in the South African Museum, which is probably the one figured by Haughton (1915). In 1925 Haughton published new figures of the type skull. In 1940 Boonstra redescribed (but did not figure) S.A.M. 3009 as a new species, *R. beaufortensis*, a distinction with which I agree. In 1949 I made a series of drawings of the type specimen; and also of the posterior end of a lower jaw (S.A.M. 9135) from Vogelfontein, Prince Albert, *Tapinocephalus* zone, which I refer to *R. whaitsi* on the grounds of its age, and general appropriateness. Finally, I have in my collection a specimen (B. 118) comparison of which with Broom's figure (1908, Pl. 46, fig. 3) shows that it is reasonably determined as a member of that species. It is about the same size, and comes from the *Tapinocephalus* zone of Zeekoegat, Prince Albert.

The life-sized drawings of the type skull which I made by camera lucida and measurement in 1949 show the occiput, the palate from below, the epipterygoid region from in front, and the braincase from right and left sides. They largely confirm, but in some cases modify, Haughton's figures of 1925. The occipital condyles of the specimen are damaged by weathering, but enough remains to make it evident, as Haughton recognized, that the posterior part of the basioccipital did in fact connect the condylar surfaces of the exoccipitals by a strip below the notochord, making a single tripartite condyle 5 cm across, the exoccipital component facing inwards and downwards. The notochord is large, some 14 mm in diameter. Above the condyle the exoccipitals extend upwards to the skull roof, and seem to take part in the border of the post-temporal fenestra. Dorsally they supported a cartilaginous supraoccipital, now represented by a wide but shallow space. The dermosupraoccipital of the left side has a downwards process which meets the exoccipital in a jagged suture.

The parasphenoid, whose anterior extension—broken off at the hinder end of the palatal vacuities—is about 18 mm across, widens below the basis cranii, its lower surface passing out to form a broad area of palate, slightly concave. It bears a pair of shallow grooves, each passing inward and forward from the ear region and dying out before reaching the hinder border of the palatal vacuity, thus showing yet another small variation of detail in this feature when compared with *Eryops* and *Actinodon*. The 'pockets' are shallow depressions, failing to meet in the mid-line by 15 mm, and extending upwards onto the lateral sides of the exoccipitals.

The epipterygoid is attached to the base of the skull at the extreme hinder end of the palatal vacuity. Its lower end is expanded and rests on the pterygoid, though mesially it is just in contact with the parasphenoid. This expanded base only reaches about half way to the skull roof, but from it a slender, rather curved 'columella' rises anteriorly and mesially to reach, or nearly reach, the dermal roof of the skull. The root of this process on the admesial side is notched by a small groove which presumably housed a blood vessel.

B. 118 (figure 4) is a small fragment of basis cranii, with an attached pterygoid and epipterygoid, which was dissolved out of a limestone nodule with acetic acid, leaving both internal and external surfaces free from matrix. It is easy to relate this specimen to *Eryops*, which is about the same size, the main difference between them being due to the fact that the *Eryops* skull—as a whole, and in the details of its basis cranii—is much deeper than that of the later *Rhinesuchus* (compare with figure 2).

In B. 118 much of the basioccipital component of the condyle is preserved, and even the internal structure shown. Its dorsal surface retains a groove in which the notochord lay, only just crossed anteriorly by a small bridge of bone, making it evident that the structure was completed by cartilage, and that the greater part of the ossification lay ventrally. Anteriorly the basioccipital thins out almost to a feather edge, which lies separated by half a millimetre at most from the upper surface of the parasphenoid. The exoccipital lies in position on the left side, in contact with the basioccipital from which it is separated by a suture, and extends forward below an upper lamina of the parasphenoid. Its condylar and dorsal parts are unfortunately missing. In front of the exoccipital the parasphenoid supported the cartilaginous floor of the otic capsule, which had a fenestra ovalis whose position is indicated by a lateral process of the parasphenoid (*St.Fac.*),

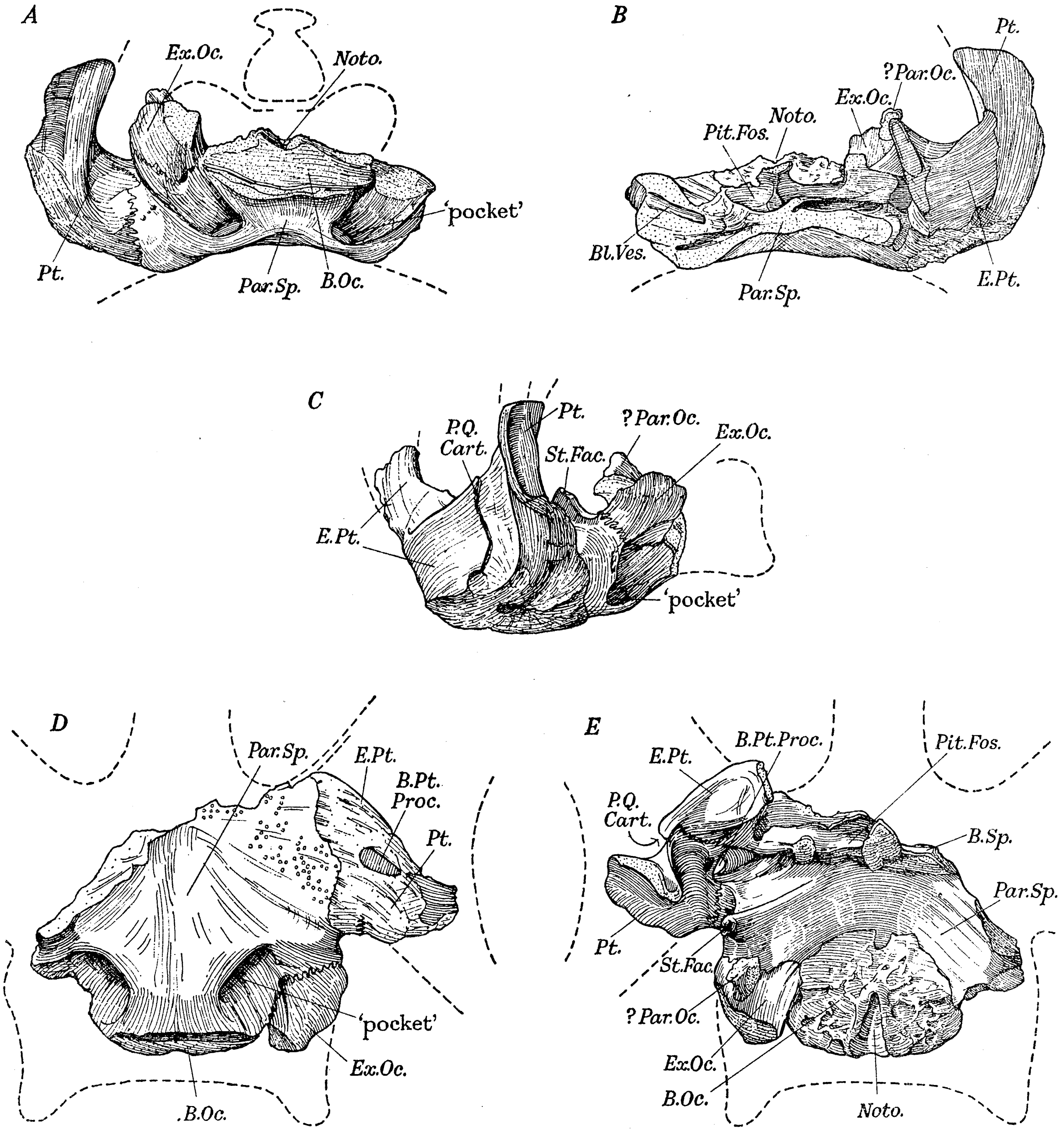

FIGURE 4. *Rhinesuchus whaitsi* Broom (B. 118), *Tapinocephalus* zone of Zeekoegat, Prince Albert in the Gouph, C.P., natural size.

Basicranial region, and root of right pterygoid and epipterygoid, of a skull collected as a rounded nodule with weathered edges. The matrix was rapidly broken down by dilute acetic acid, leaving the bone untouched and showing all detail in perfection. (Compare with figure 2.)

A, from behind; *B*, from in front; *C*, from the left side; *D*, from below; *E*, from above. (In *C*, a loose piece of epipterygoid has been replaced, *B*, and *E*, are shown without it.)

P.Q.Cart., free edge of epipterygoid from which the unossified palatoquadrate cartilage continued to the quadrate in contact with the front face of the pterygoid; ?*Par.Oc.*, small fragment of bone, perhaps of paroccipital; *B.Pt.Proc.*, groove in parasphenoid for the basipterygoid process.

diverted a little upward and backward, which bears at its tip—which is notched—an attachment for a process from the footplate of the stapes. It is evident that the considerable sheet of cartilage which completed the basioccipital stretched forward to the basisphenoid, floored the otic capsule, and extended outward into a long process (now represented only by the cavity left by its decay) which supported the epipterygoid, and was, indeed, the persisting basipterygoid process. Mesially of the epipterygoid the cartilage is ossified as a strip of bone (the basisphenoid), crossing the mid-line of the skull, and projecting forward as a short beak which overhangs the hinder wall of the wide but shallow pituitary fossa. In front of this point the basisphenoid and parasphenoid are broken away, but it is evident that the basisphenoid, as it stands, is essentially complete, the processus cultriformis of the parasphenoid continuing to the prevomers. The basicranial articulation of the pterygoid is essentially a sutural attachment with the parasphenoid, together with the cartilaginous contact with the basipterygoid process, and perhaps a contact—or very near contact—of the lateral end of the basisphenoid with the base of the epipterygoid; and more laterally the epipterygoid is attached to the parasphenoid at the root of its anterior ramus. The suture between the pterygoid and the parasphenoid is well seen; it is short, though relatively longer than in *Eryops*, and in contrast to the rounded lower surface of *Eryops* this region in *Rhinesuchus* is essentially flat.

The ventral surface of the parasphenoid bears the two depressions, or 'pockets', each about twice as long as it is high, originally housing muscles which passed in along a groove on the lateral side of the basioccipital. The inner surface of the 'pocket' is striated—obviously for a ligament or muscle attachment—and carries one or more small foramina for blood vessels supplying the tendon or muscle. These 'pockets' are comparable with the much smaller and less well-developed structures in *Eryops*, but are more strongly marked, and extend nearer to the mid-line. The denticles which are found in the palatal region are all broken off short, but are represented very characteristically by the circular section of their bases, often with an open pulp cavity visible. They cover an area which extends from the mid-line at the extreme anterior end of the specimen, outward and obliquely backward to the hinder end of the pterygo-parasphenoid suture. In fact B. 118, so far as it overlaps Broom's type specimen, agrees with it exactly in this matter.

The lower jaw (S.A.M. 9135) from Vogelfontein, ascribed to *R. whaitsi*, makes a quite satisfactory intermediate between *Eryops* and *Rhineceps* (see p. 251).

Muchocephalus muchos n.gen., n.sp.

The next rhinesuchid to give a satisfactory view of the palatal surface is no. 350, Bernard Price Institute, University of the Witwatersrand, Johannesburg, which comes from the Middle *Cistecephalus* zone of Ringsfontein, Murraysburg, C.P. It is a small complete skull, 24 cm in length, much flattened by fossilization, but showing the basis cranii and the pterygoids connected with it. It differs very considerably from the type specimen of *R. whaitsi*, and I therefore call it *Muchocephalus muchos*, n.gen., n.sp. (μῦχος, a nook, or recess).

In dorsal aspect the skull is capitosaurine in appearance, wide across the nostrils, with the lateral borders a little convex possibly as a result of the flattening. The orbits lie just behind the mid point of the length, and the interorbital width is similar to that of the jugal.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

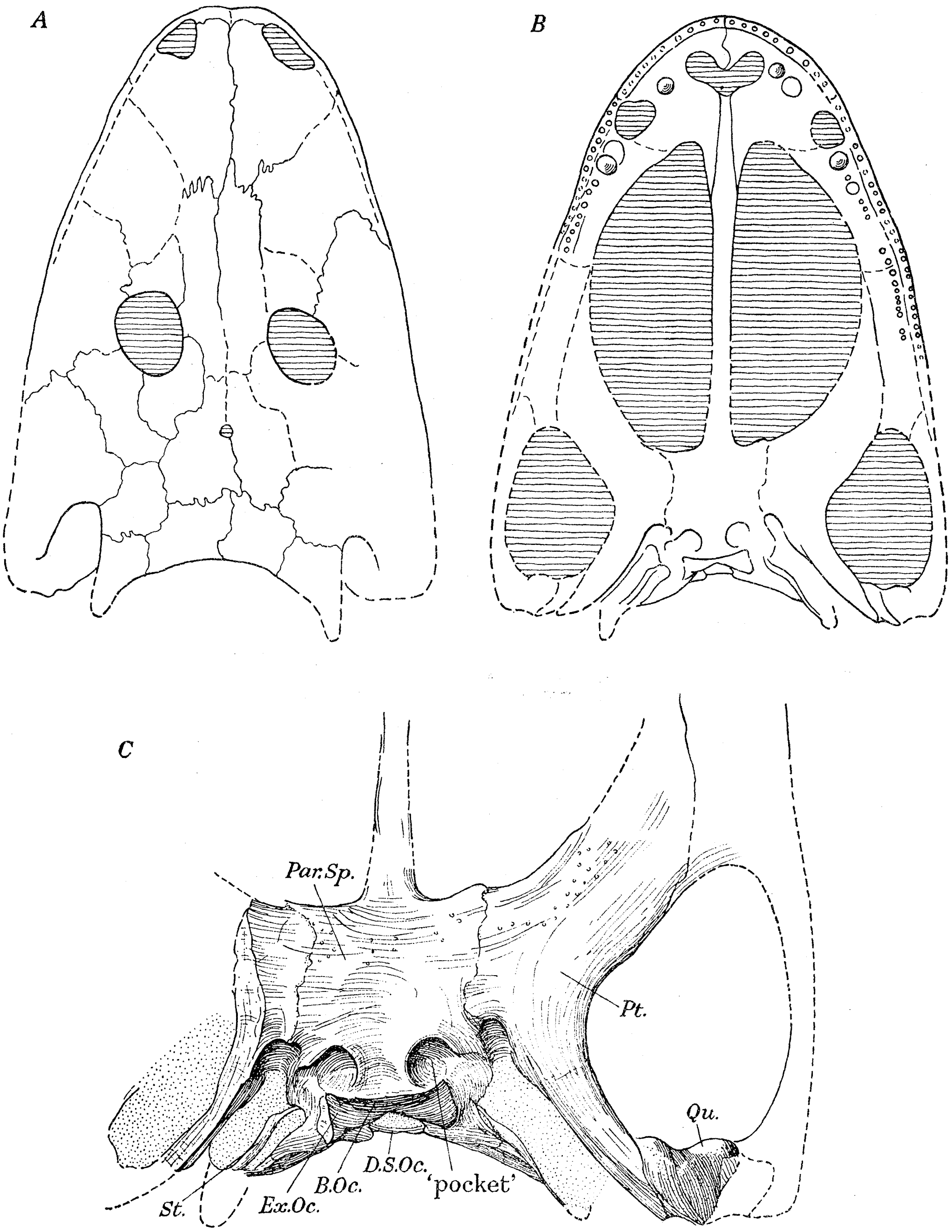

FIGURE 5. *Muchocephalus muchos*, n.gen., n.sp. (B.P.I. 350), Middle *Cistecephalus* zone, Ringsfontein, District Murraysburg, C.P. Collected by J. W. Kitching.

A skull, nearly complete, but so much flattened that it is impossible to reconstruct the occiput. Important because it shows the 'pockets' in a form different from that found in other *Cistecephalus* zone specimens, for instance, *Rhineceps nyasaensis* (figure 7). They are deep, rounded depressions on the lower surface of the parasphenoid, only just in front of the occipital condyle, rather than the shallow insertions of the Chiweta specimen.

A, dorsal surface; *B*, palatal surface (×1/3). *C*, palatal surface to show basicranial region (×2/3).

The otic notch is rather wide, and about as long as the orbit. The table is broad, and its hinder border concave. The palatal vacuity is exceptionally large, the width of bone lateral to it narrowing to the palatine. The prevomers carry the normal vomerine tusks, alternating with one another, the nostril lying behind them. The first palatine tooth is very large, and like all the large teeth has a pit for its replacement tooth; behind this tusk the palatal teeth are small, perhaps fractionally larger in section than those of the maxilla.

The occipital condyle is a unique structure, not readily comparable with that of *Rhinesuchus whaitsi*, for it is essentially a single flat surface instead of a pair of flat surfaces. The articular surface is very much wider than it is high. Its upper surface at the foramen magnum forms a broad V, the lower edge is somewhat concave downwards, and lies entirely on the basioccipital. The lateral extremities, entirely exoccipital, are triangular, their straight-sided lateral borders standing vertical. Thus the whole faces downwards as much as backwards, and its bearing on the atlas must have been almost immoveable.

The 'pockets' are rather deep hemispherical pits, facing directly ventrally, little—if at all—overhung by parasphenoidal flanges. They are rather close to the midline, and anteriorly scarcely reach so far forwards as the hinder end of the basipterygoid suture, whilst posteriorly they end immediately in front of the occipital condyle. These peculiar circumscribed spherical 'pockets' differ from those of most other forms, and the resemblance to those of *R. whaitsi*, in which they are depressions going in obliquely parallel to the surface, is not very striking.

The groove for the blood vessel, which in *R. whaitsi* passes over the hinder part of the parasphenoid just within and behind the parasphenoid-pterygoid suture, does not exist. The pterygoid is attached to the lateral border of the parasphenoid by a suture which appears not to be intricately denticulated and intergrown. The palatoquadrate ramus is rather markedly short, though there remains a trace of the flange against the lower jaw.

Rhineceps nyasaensis (Haughton) n.gen.

The next stage is represented by a magnificent skull collected by Dr F. R. Parrington from the 'Upper Bone Bed' of the Chiweta Beds, Mount Waller area, Nyasaland, which seems to be of latest *Cistecephalus* zone age. The specimen is almost complete, only lacking the posterior part of the left ramus, and the extreme anterior end of the right ramus of the lower jaw. Haughton's specimen of *Rhinesuchus nyasaensis* comes from exactly the same place, and consists of part of the left ramus of a lower jaw, and another fragment, which (in a letter to Parrington, 5 December 1932) he recognizes as the anterior end of the right ramus, and not as a fragment of upper jaw; his figure (1927, figs. 1, 2) agrees very well with the comparable region of Parrington's specimen. Thus it seems to me that they are unquestionably parts of the same individual.

This individual is, then, the type of *R. nyasaensis* Haughton, but it appears to me to be generically distinct from the type specimen of *R. whaitsi* on the following grounds: (i) In occipital view the two skulls are of almost the same width across the tabulars, the Nyasaland skull being 15·0 cm across, and *R. whaitsi* 14·0 cm. The depth, however, from the lowest point of the ventral 'pocket' to the roof of the skull is 5·0 cm in the Nyasaland skull, and 6·0 cm in *R. whaitsi*. (ii) The 'pocket' in *R. whaitsi* is an extensive structure whose posterior opening is 8·0 or 9·0 mm deep, whilst in the Nyasaland skull it lies in a similar position, but its posterior opening is of the order of 3·0 or 4·0 mm deep only, and is thus greatly depressed. (iii) In *R. whaitsi* a groove passes forward from the ear region onto the lower surface of the parasphenoid, extending towards the back of the large palatal fenestra. This groove is absent in the Nyasaland skull. (iv) The pterygo-parasphenoid suture is definitely longer in the Nyasaland skull than in *R. whaitsi*. (v) The denticles in the Nyasaland skull differ somewhat in their distribution in comparison with the type of *R. whaitsi*. (vi) The epipterygoid in the Nyasaland skull, which on the right side has been cleared of matrix, is similar to that of *R. whaitsi*, except that the notch at the base of the ascending ramus is rounded and much bigger, about a centimetre high. It seems, therefore, desirable to put the Nyasaland skull into a different genus from *Rhinesuchus*, and to it I apply the name *Rhineceps nyasaensis*, so that it becomes the type species of the genus *Rhineceps*.

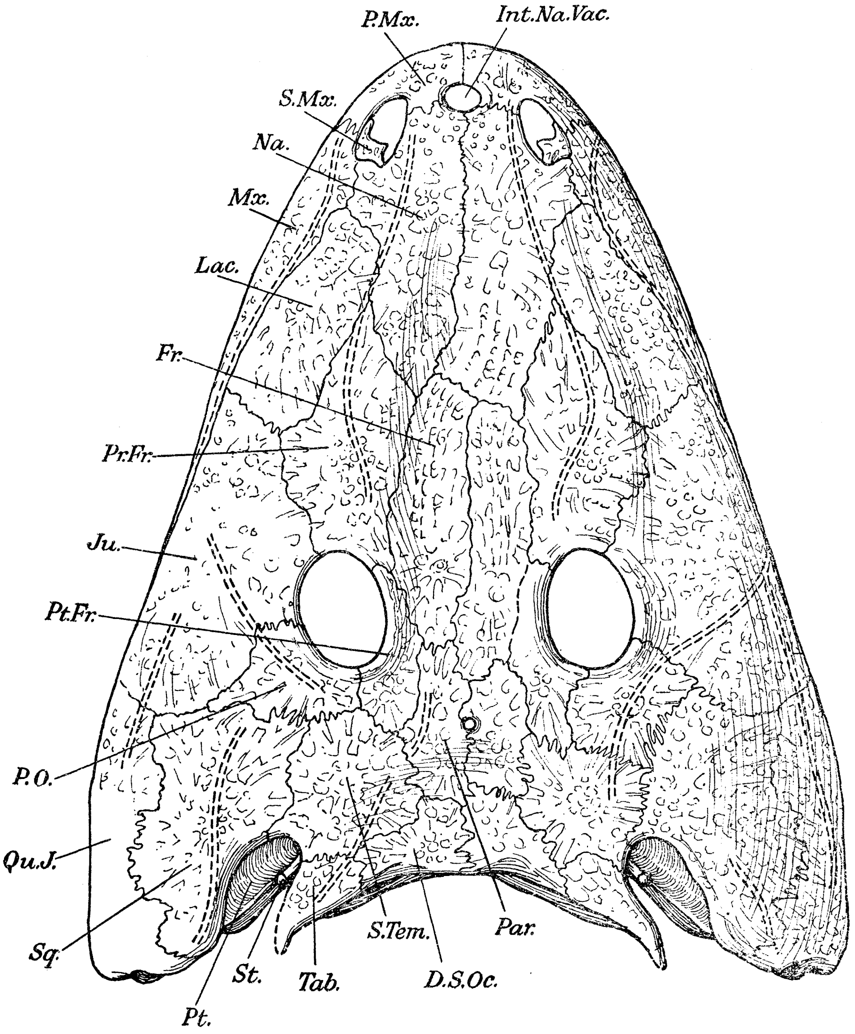

Figure 6. *Rhineceps nyasaensis* (Haughton), n.gen., Parrington Collection. 'Upper Bone Bed', Chiweta Beds (Upper Permian), Mount Waller Area, Nyasaland, dorsal surface (× 1/3).

This specimen, perfectly preserved, lacks only a small fragment in the left postero-lateral corner. It is deformed in such a way that when a grid is imposed on it the transverse lines linking equivalent points are not at right angles to the principal axis. This has been corrected in the figure.

The skull is in very good preservation, and is excellently prepared. It has suffered a small shear, and figure 6 was corrected for this in the following way. A grid with its central axis superimposed on the mid-line of a drawing of the skull was made, and transverse lines placed at an angle to the axis connected originally symmetrical points on the skull. The published drawing was copied freehand on another grid in which the two axes were at right angles to one another, the original shape of the skull being thus restored.

The occipital condyle is effectively single, the whole condylar surface being 57·0 mm wide and effectively 15·0 mm deep on the exoccipital part. The exoccipitals have essentially flat articular surfaces, which slope inwards to meet one another. At this point the articular surface is continued over the mid line by a bone—the basioccipital—which is grooved dorsally, presumably for the notochord, and (as seen in broken section) seems to thin anteriorly, where it was no doubt continued by cartilage to the basisphenoid.

The ventral surface of the parasphenoid bears the customary 'pockets'. They are shallow, considerably separated, and still filled with red haematite which obviously extended for a millimetre or two into the bone in front of their hinder margins. They extend onto the lateral surface of the exoccipital in front of a depressed area bounded posteriorly by the occipital condyle. Between its sutures the surface of the parasphenoid is essentially flat, but is—compared for example with *Parotosaurus*— very short from back to front. The two sutures approach one another as they pass forward and over the hinder margin of the large interpterygoid vacuities. The ventral surface does not show any trace of a pitted area similar to that of *Wetlugasaurus magnus* (p. 244), nor is a similar ornamented area shown on the palatal ramus of the pterygoid as in that animal.

The anterior ramus of the pterygoid extends so far forward that it bears effectively the whole outer border of the interpterygoid vacuity, and overlaps the hinder end of the prevomer anteriorly. It is covered with denticles over most of its ventral surface. They fall into three groups of different sizes: a belt of comparatively large ones—each denticle measuring almost 2 mm across—on the outer side, a belt of somewhat smaller ones along the inner side, and an area of very small ones—some half millimetre or less across—towards the suture with the parasphenoid, just spreading onto that bone, whose median surface is completely free from them. The anterior part of the palate has the expected large interpterygoid vacuities, separated by the parasphenoidal rostrum. The part of the palate lateral to the vacuity is comparatively wide. There is a narrow ectopterygoid bearing posteriorly a ridge which supports a row of small teeth; on the right side this leads up to two enlarged teeth with provision for replacement. The suture between it and the palatine is uncertain. The palatine bears a continuation of the ridge with a row of small teeth leading, on the right side, to two large ones, alternatives of one another. The palatal nostril, whose inner border is carried by the prevomer, lies immediately in front of them.

The specimen has prevomers which do not agree with one another in the character of the teeth which they bear. Anteriorly the right prevomer carries three rather large teeth placed transversely on a pronounced bony ridge a centimetre or so deep. On the left side there is a corresponding ridge, but it shows no large teeth, nor provision for their reception, and the surface carries at most one small tooth and a row of denticles. Behind this region

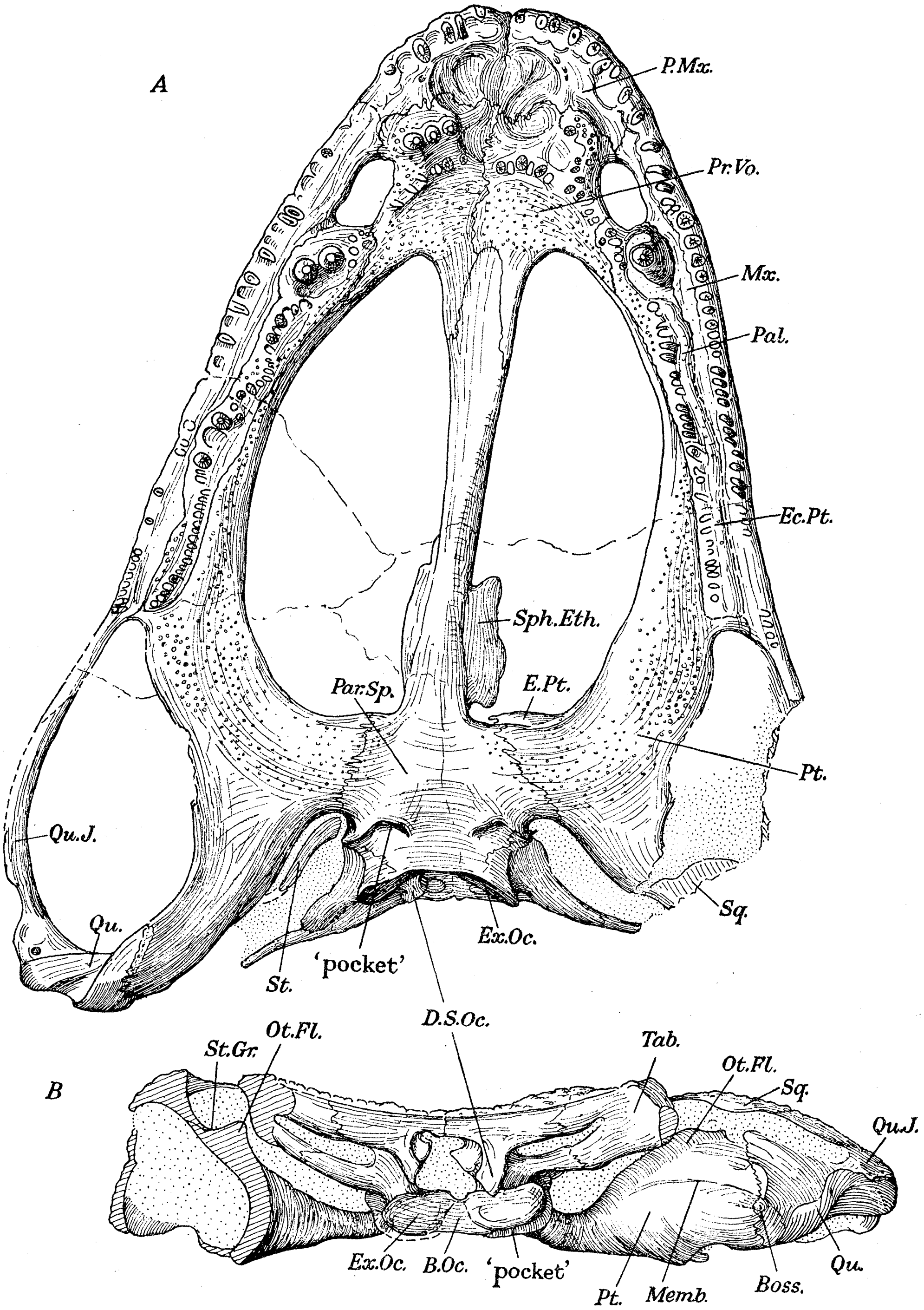

FIGURE 7. *Rhineceps nyasaensis* (Haughton), n.gen., Parrington Collection. 'Upper Bone Bed', Chiweta Beds (Upper Permian), Mount Waller Area, Nyasaland (× rather more than 1/3). Direct drawings with the distortion not corrected.

A, the palate; note the asymmetry of the palatal teeth. *B*, the occiput; note the otic flange seen from behind on the right side, and the flange and stapedial groove seen in section on the left.

Memb., basal attachment of membrane from otic flange to tabular.

on each side there is another tooth row composed of smaller teeth and replacement pits, planted in a more mesially placed bony ridge whose outer surface forms part of the inner wall of the posterior nostril. Posterior to this there is a belt of denticles covering the rest of the bone, except for the two processes which are separated from one another by the anterior end of the parasphenoid. The whole tooth-bearing area shows traces of denticles, in fact on the anterior ridge of the left prevomer it is difficult to distinguish between denticles and teeth.

Anteriorly the prevomer meets the premaxilla, and there is no anterior palatal vacuity, but there is a series of grooves and pits within a depressed area lying between the anterior transverse series of teeth on the prevomers and the premaxillary teeth. This recess is more or less symmetrical, and its continuous bony roof lies about two centimetres above the neighbouring border of the premaxilla. It is reminiscent of a similar structure in *Eryops* (Broom 1913, fig. 12; Sawin, 1941, Pl. 2). It seems clear that this recess, which is comparatively deep with a well-defined margin, has some function other than the reception of the tips of the anterior mandibular teeth. It could well have housed a gland, possibly producing something to lubricate the passage of the animal's prey down the mouth, but it is difficult to believe that it can have had much other function, for the enlarged anterior teeth in the dentary certainly bit into it.

The marginal teeth on the maxilla and premaxilla form a single series, and are not set in sockets, but are fused at their bases to depressions in the bone, the normal arrangement in labyrinthodonts. They were evidently shed and replaced quite readily: for instance, in the right premaxilla the second surviving tooth is presumably number three; it is compressed in the row, so that it is at least twice as broad as it is from 'front' to 'back'. Its neighbour is similar, then there is a gap, and the next tooth is a good deal thicker; but the teeth behind the palatal nostril on the left side are somewhat rounder in section. Posteriorly the teeth become very small, with narrow tips somewhat inturned, exactly agreeing with the corresponding teeth on the palatal and ectopterygoid bones.

In this specimen the distribution of palatal teeth is notably asymmetrical. The three large teeth on the right prevomer are represented (if at all) on the left side by granular denticles. The two tusks on the right palatine may be a matter of tooth replacement, and are matched by one on the left; but a series of larger teeth on the anterior end of the right ectopterygoid is not matched on the other side of the skull. The whole arrangement gives a warning as to the danger in labyrinthodonts of forming species, or—even more—groups of higher order, on variation in the character and distribution of teeth.

Above the anterior depression, on the dorsal side of the skull, there is a circular opening (*Int.Na.Vac.*) more than a centimetre across, which lies between the premaxillae and nasals, effectively in line with the anterior border of the nostrils. It leads into a space floored by the recessed area mentioned above. A similar opening also occurs in *Micropholis*, *Trematops*, *Acanthostoma*, *Dasyceps* and *Zatrachys*. In *Micropholis* it is largely occupied by a small ornamented skull roof bone, not firmly attached, which in 1913 I called the internasal. In *Trematops* no bone in this position has been seen, and in the others—where the vacuity is much larger—it is in all probability absent.

The right quadrate region of the skull is very well displayed, and the whole of the articular surface for its lower jaw has been developed out. The condyle is relatively narrow from side to side. The articulation of the quadrate with the pterygoid is evident; immediately lateral to the pterygoid the quadrate bears a boss projecting backwards, which is distinguished from the inner side of the condyle, and agrees very well with the boss of *Wetlugasaurus magnus* (p. 244). It is slightly smaller proportionately in size, but its summit is broken off, preventing any discussion of the character of its surface, to which a ligament or muscle could have been attached.

Stapedial groove

The specimen shows one feature of interest which has not yet been described: the quadrate ramus of the pterygoid has a flange projecting from its posterior surface in such a way as to form a deep groove passing upwards from the basicranial region to the otic notch, and very evidently forming part of the tympanic cavity. This structure does not occur in *Actinodon*, or *Eryops*, and the region showing it is obscured in the rhinesuchids I have so far described; but it is present in *Rhineceps*, and even better displayed in B. 119, a fragment of an undeterminable rhinesuchid from the *Cistecephalus* zone of Swaalkrantz, Murraysburg, C.P.

This specimen consists of the right posterior corner of a skull, somewhat distorted, and broken into two parts so that extensive preparation has been possible. The posterior part of the pterygoid is very well shown from its articulation with the basis cranii—which is by suture with the parasphenoid—to the quadrate. The stapedial groove begins at the point of articulation of the pterygoid with the parasphenoid, and is effectively semi-circular in section. It opens freely onto the upper surface of the parasphenoid and leads to the fenestra ovalis, within which lies the head of the stapes. The pterygoid stretches back, turning outward through a small arc of a circle as it does so, until it reaches the inner side of the massive quadrate. Immediately above this sutural contact it meets the squamosal, the two together capping the quadrate. Within a centimetre of the highest point of the junction of squamosal and pterygoid lies the outer end of the long stapedial groove, which leads inwards, forwards and downwards to the fenestra ovalis. The anterior wall of this capacious groove—which is somewhat conical in shape—rises to the skull roof, which rests on it at a point a little in front of the anterior border of the otic notch. Its posterior wall is a flange of the pterygoid (see figure 7*B*, *Ot.Fl.*) whose upper border is thin and was obviously connected with the anterior face of a flange of the tabular by a membrane, thus forming the admesial wall of the tympanic cavity. The basal attachment of this membrane to the otic flange is shown by a slight recess in the surface of the pterygoid (*Memb.*). The shape of the cavity is thus well defined. The stapes, a little displaced at its outer end, obviously lay within this groove, attached to the tympanic membrane somewhere about the middle of the otic notch, which was quite long, with well-separated margins. Roepke (1923) gives an account of the skull of *Parotosaurus nasutus* illustrated by a series of transverse sections of the occipital region. One feature quite clearly shown is the stapedial groove in the quadrate ramus of the pterygoid; the author, however, does not comment on it.

The hinder border of the squamosal of *Rhineceps* is produced out into a lappet which partly roofs the space behind the otic notch and above the quadrate, and extends the attachment for the tympanic membrane further backwards and laterally.

Lower jaw

The lower jaw of *Rhineceps* (figure 8) is represented by the greater part of the right ramus, lacking an anterior fragment whose counterpart is preserved on the left side. The jaw thus restored fits the skull perfectly. It reaches its greatest depth approximately a quarter of the total length forward—about the middle of the great fenestra through which the adductor muscle passes into the interior—and from there decreases towards the symphysis, which is unfused. The anterior part of the jaw is wider from side to side than the posterior part of the angular, and approaching the symphysis the width becomes about the same as the height, measured on the internal surface. The structure of the outer surface is made clear less by visible sutures than by the fact that each bone carries its own pattern, so that the junction of one with its neighbour is recognizable. The surangular, just behind its suture with coronoid 3, bears a depression on its thickened upper margin, close up to the outer surface, which is quite clearly a muscle insertion. It is entirely lateral to, and distinct from, the masticatory muscles, and can only be the insertion of a labial muscle, just behind the corner of the mouth. The implication is that even in this large animal the normal amphibian pattern of an extensive mouth exists.

The jaw cavity remains open—nearly up to the extreme anterior end, at any rate, though it is there small—and is entered on the inner side by a number of foramina. A relatively large oval one (*Dent.For.*) lies between the articular and prearticular; from a smooth notch on its hinder border a very shallow, but definite, groove passes backward and upward over the root of the retroarticular process to end in a rounded depression separated by a very narrow partition from the glenoid cavity. Ventral to it are three very much smaller ones, all probably nutritive foramina. A very large foramen lies between the angular, postsplenial and prearticular, and three smaller ones pass in through the postsplenial. The larger of these openings is probably for the provision of space for the thickening of the masticatory muscle during its shortening.

The dentary is well shown; the greater part, at any rate, bears a series of close-set teeth fused onto it, compressed from back to front, sometimes the width of the tooth being three times its antero–posterior spread. The teeth towards the front arise a little mesially of the outer border, whilst posteriorly their outer surface comes down in contact with the slightly raised outer border of the bone. The only variety in the dentition is the presence of a large tusk, close up to the mid-line anteriorly and placed within the continuation of the ordinary row of small teeth, which bit into the depression on the anterior part of the palate in front of the transverse row of vomerine teeth; the rest of the tooth row presumably bit between the inner and outer rows of upper jaw teeth. The coronoids carry a thickening coated with very small granular teeth, with the arrangement shown in figure 8. The isolated tooth at the lower margin of the granular area of coronoid 1 is known only by a cross-section, and there is a pit for its replacing tooth.

The articular end of the jaw is very narrow from side to side, and the condylar region rises above the nearly straight lateral margin of the surangular bordering the opening through which the muscles pass to the interior. The inner wall of this cavity is bounded by a prearticular extending far forward in the jaw, but not entering the symphysis. The articular surface of the lower jaw forms a trough which obviously fits the articular surface of the quadrate with great accuracy, and suggests that the mouth could be widely opened whilst still retaining a considerable bearing on the quadrate. The surface for the inner quadrate condyle extends well forward, and lies on a lower level than that for the outer condyle, and it is evident that the articular face of the inner condyle of both quadrate and articular bones is part of a circle of greater radius than—though coaxial with—the outer condyle. This structure implies that the upper surface of the jaw leans inwards at an angle.

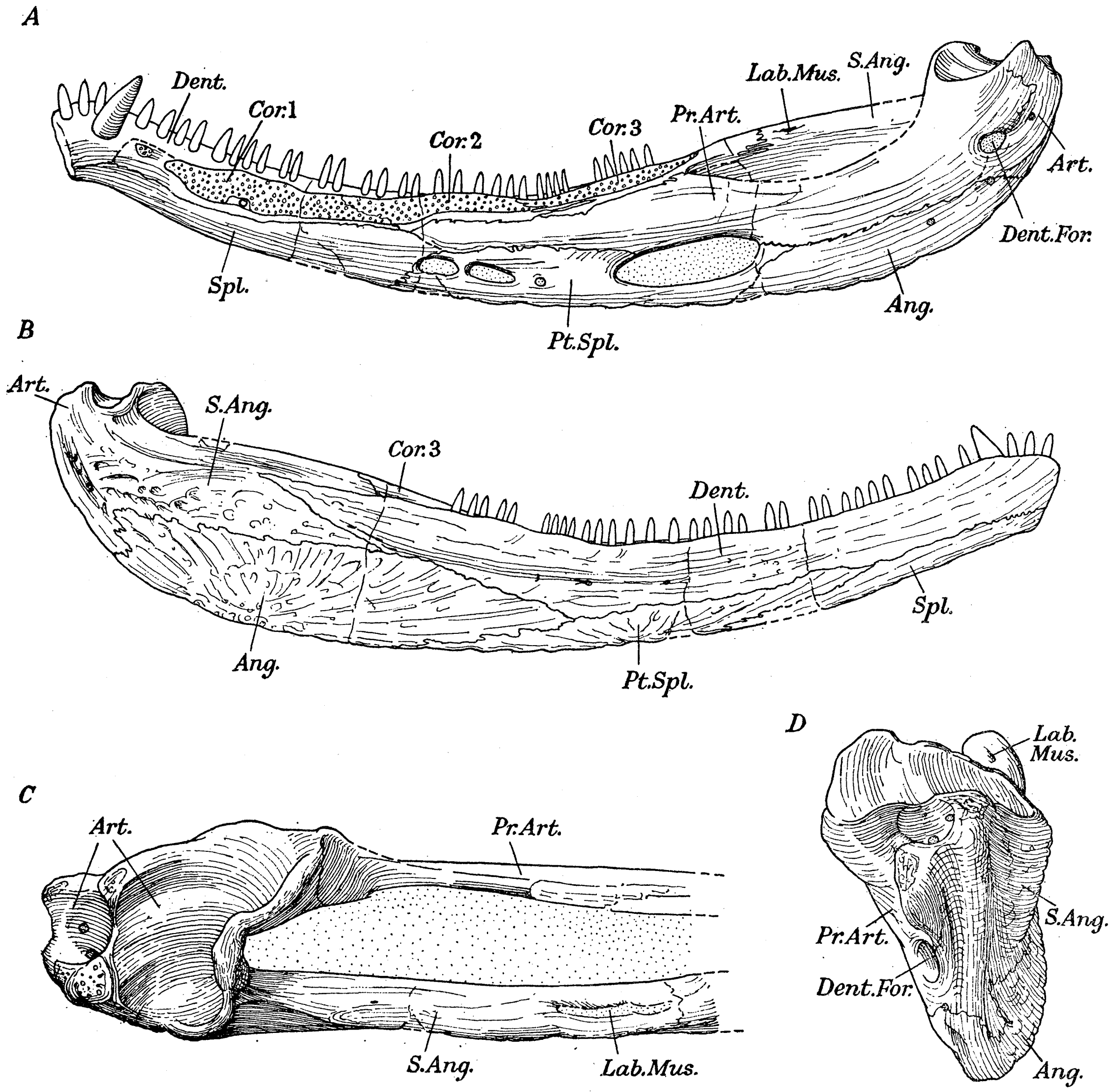

FIGURE 8. *Rhineceps nyasaensis* (Haughton), n.gen., Parrington Collection. 'Upper Bone Bed', Chiweta Beds (Upper Permian), Mount Waller Area, Nyasaland.

Right lower jaw. The three hinder fragments—shown in the drawing by lines of fracture—are in contact, the symphysial fragment belongs to the left ramus and has been drawn reversed to complete the jaw whose length thus determined fits the skull. Representation of the dentition is conventional, but is based on evidence of teeth and tooth emplacements found in the specimen. (Compare with figures 12 and 13.)

A, inner surface, *B*, outer surface (× 1/3). *C*, the hinder end from above, *D*, from behind (× 2/3). *Lab.Mus.*, labial muscle insertion.

The three major openings from the inner surface of the jaw into its cavity possibly imply that the attachment of the temporal muscle lay far forward and was not by a long ligament but by the muscle itself, so that its total length was very great, allowing the mouth to open widely. The articular, indistinguishably fused with the surangular but identifiable by its lack of ornament, has a very short but quite definite retroarticular process springing directly from the ridge which is the hinder margin of the condylar face, on its outer side. The process projects at its maximum for about a centimetre, and is divided into two parts by a deep groove along its hinder surface. The whole anterior border of the glenoid cavity stands up as a powerful flange, apparently largely composed of the articular, buttressed by the surangular and prearticular. The lower border of the hinder part of the jaw sweeps upwards to the retroarticular process in a smooth curve (see pp. 250–252).

URANOCENTRODON SENEKALENSIS VAN HOEPEN

Myriodon senekalensis van Hoepen, 1911, *Ann. Transv. Mus.* **3.**

Rhinesuchus major Broom, 1912, *Trans. Geol. Soc. S. Afr.* **14.**

Rhinesuchus senekalensis Haughton, 1915, *Ann. S. Afr. Mus.* **12.**

Uranocentrodon senekalensis van Hoepen, 1917, *Ann. Transv. Mus.* **5**; Broom, 1930, *Ann. Transv. Mus.* **14.**

The next stage in the series of rhinesuchid labyrinthodonts is shown by magnificent material found in immediate association in a quarry in Senekal, O.F.S., apparently in the *Lystrosaurus* zone. There is a nearly perfect skeleton and skull in the Bloemfontein Museum, and four good skeletons and at least two skulls in the Transvaal Museum, Pretoria. The animal was originally described by van Hoepen (1911) as *Myriodon senekalensis*, but in 1916 he changed the generic name to *Uranocentrodon*, since *Myriodon* was preoccupied. Broom (1930) gives good dorsal and palatal views of the most complete skull (No. 185, Transvaal Museum), disarticulated from its body. In 1949 I made from the same skull measured drawings of the occiput and the posterior part of the palate, showing further detail (figure 9).

The occiput shows most clearly a pair of exoccipital condyles, each some 3·0 cm wide, and 2·0 cm high towards the outer border, separated from one another by a distance of rather more than a centimetre. Their articular surfaces are slightly convex, and the condyles seem too small and feeble to carry and control a skull whose total width is of the order of 37·0 cm, and height 6·5 cm in the mid-line. The basioccipital is present as a considerable bone some 5·0 cm across and 1·5 cm in height, and is seen only from behind; it is separated from the brain cavity by the exoccipitals, which rest on it, and hidden from below by the parasphenoid, and makes no real contribution to the condylar surface. The exoccipitals rise above the condyles by a neck, dorsal to which they expand, the inner surface approaching the mid-line, whilst the lateral surface is carried out into a long process, apparently ultimately reached and embraced by the descending process of the tabular, though it is not evident how much of this area is, in fact, paroccipital—a bone which certainly takes some part in it. The lower surface of the exoccipital has a powerful sutural attachment to the upper surface of the parasphenoid, well seen in figure 9 (*Fac.Par.*) since they have pulled slightly apart. The exoccipital is perforated on its lateral surface by a relatively small foramen for the twelfth nerve. The supraoccipital is unossified, but

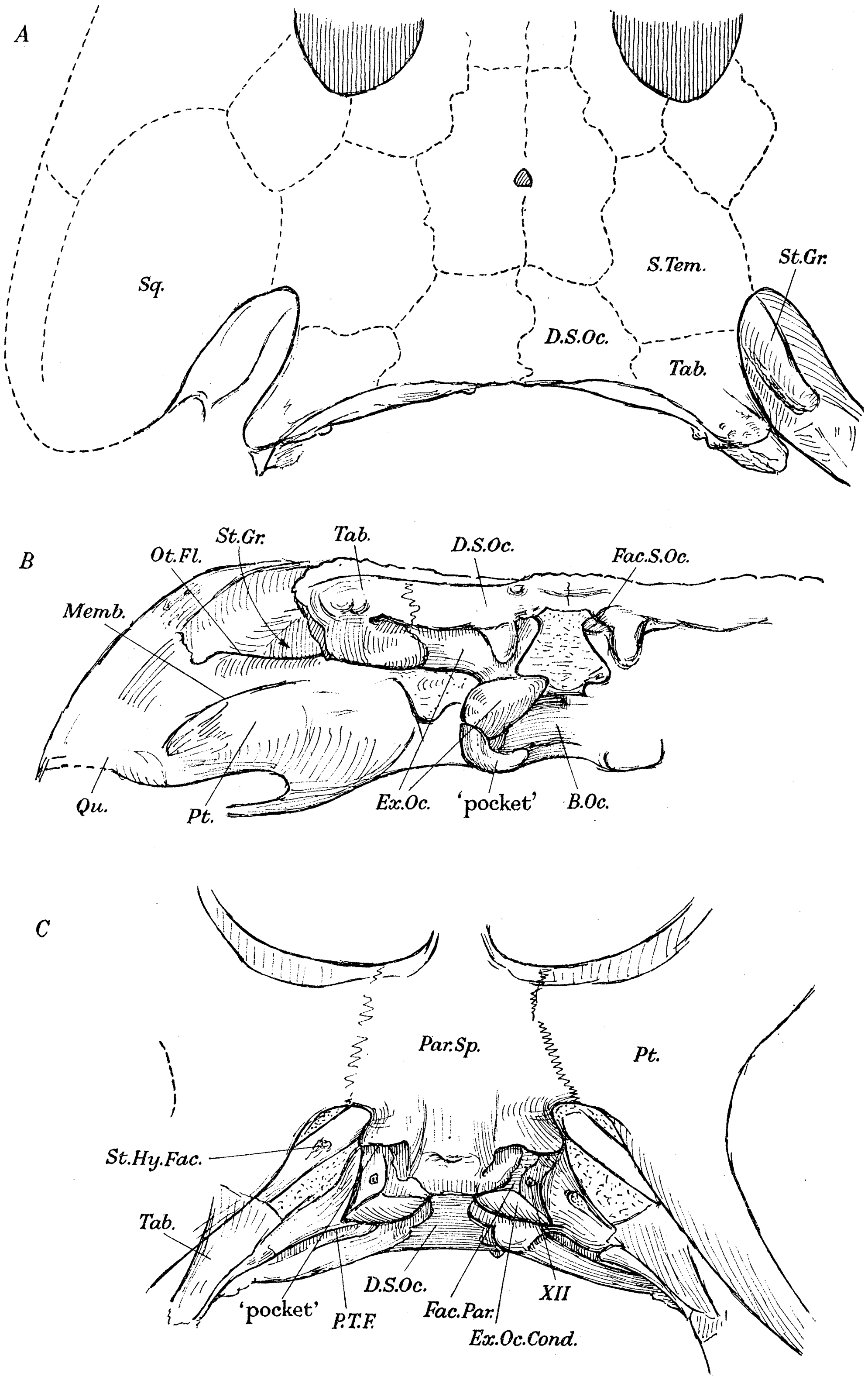

Figure 9. *Uranocentrodon senekalensis* van Hoepen (Trans.Mus.No. 185), Senekal, O.F.S., apparently *Lystrosaurus* zone, from measured drawings made in the Transvaal Museum in 1949 (× 4/9).

A, dorsal surface, stapes omitted. (Sutures restored from Broom, 1930, fig. 1). *B*, occipital surface showing the braincase and relations of the quadrate and pterygoid to it, and to the stapedial groove. *C*, palatal surface showing the exoccipitals slightly displaced with respect to the hinder edge of the parasphenoid (*Fac.Par.*). The stapes is in position on each side and shows the scar (*St.Hy.Fac.*) to which the hyoid cartilage was attached. (The denticles, shown in Broom's fig. 2, are omitted.)

Fac.S.Oc., facet for supraoccipital; *Memb.* basal attachment on pterygoid of membrane to tabular.

the facets on the exoccipitals on which it lay (*Fac.S.Oc.*) are shown. The foramen magnum is essentially triangular; its wide base, resting on inwardly directed flanges of the exoccipitals, is separated from the upper surface of the basioccipital by a small space, obviously originally filled by a strip of cartilage a few millimetres thick.

The widened hinder part of the parasphenoid is attached to the pterygoid by a long interdigitated suture sloping in somewhat towards the middle line. The 'pockets' are formed by two rounded lappets—deep, well apart, and facing backwards—whose lateral borders continue out beyond the exoccipitals to underlie the root of the stapes.

The deep flange bounding the hinder side of the stapedial groove is seen very well in this specimen. The groove, floored by the pterygoid, passes outwards for some 5 cm beyond the end of the tabular, showing the large size and lateral extension of the tympanic cavity, which seems to project beyond any reasonable attachment of the tympanic membrane, possibly to house the ventral process of the stapes which presumably stretches down to the quadrate. The pterygoid shows, ventral to the otic flange, the basal attachment (*Memb.*) of the membrane closing the posterior side of the otic notch.

The extreme anterior end of the palate I have not seen, but Broom figures it as of normal structure. There is the customary fenestra between the premaxillae and prevomers, and there are only two vomerine teeth, one in front of the other. The proportion that the narrowest part of the lateral border of the interpterygoid vacuity bears to the greatest width of that opening seems to be similar in *Uranocentrodon* and in *Rhineceps*.

Broom (1930) figured a lower jaw from its inner surface, the anterior part and extreme hinder end of which are missing. It differs from *Rhineceps* in being straighter, and in lacking the great posterior curve which carries the articulation up above the lower border of the jaw. The coronoids carry a similar belt of denticles, and there is only one anterior vacuity, corresponding to the three in *Rhineceps*.

There is a very marked resemblance in general proportions between the skull of *Uranocentrodon* and that of *Rhineceps*, but comparison of detail, in particular the basicondylar arrangements, shows that it is convenient to regard them as different genera. In every way where comparison is possible *Rhineceps* is rather more primitive than *Uranocentrodon*.

WETLUGASAURUS MAGNUS N.SP.

This splendid specimen (B. 122) I found in the sandstone capping a small kopje visible from the road on the farm Watford, District Albert, C.P.; the locality is probably low in the *Cynognathus* zone, but is perhaps *Procolophon* zone. The specimen consists of the hinder part of a skull, slightly smaller than *Rhineceps*, in which the detail is beautifully shown, and since it is broken across into several pieces allows a restoration of the braincase to be made. There is also the hinder end, and two fragments, of the right ramus of the lower jaw. I have already given a description of it (1919, pp. 22–29), but have since done further preparation, and made a new series of figures.

The palatal surface of the parasphenoid is of interest because it shows a late stage of the 'pockets', whose history is set out above. They lie very far forward, and are merely grooves, some 5 mm deep, marking the anterior border of a depressed area, and ending laterally at the suture with the pterygoid. They curve in towards the mid-line, where they are nearly confluent, but are separated by a ridge. The suture between the parasphenoid

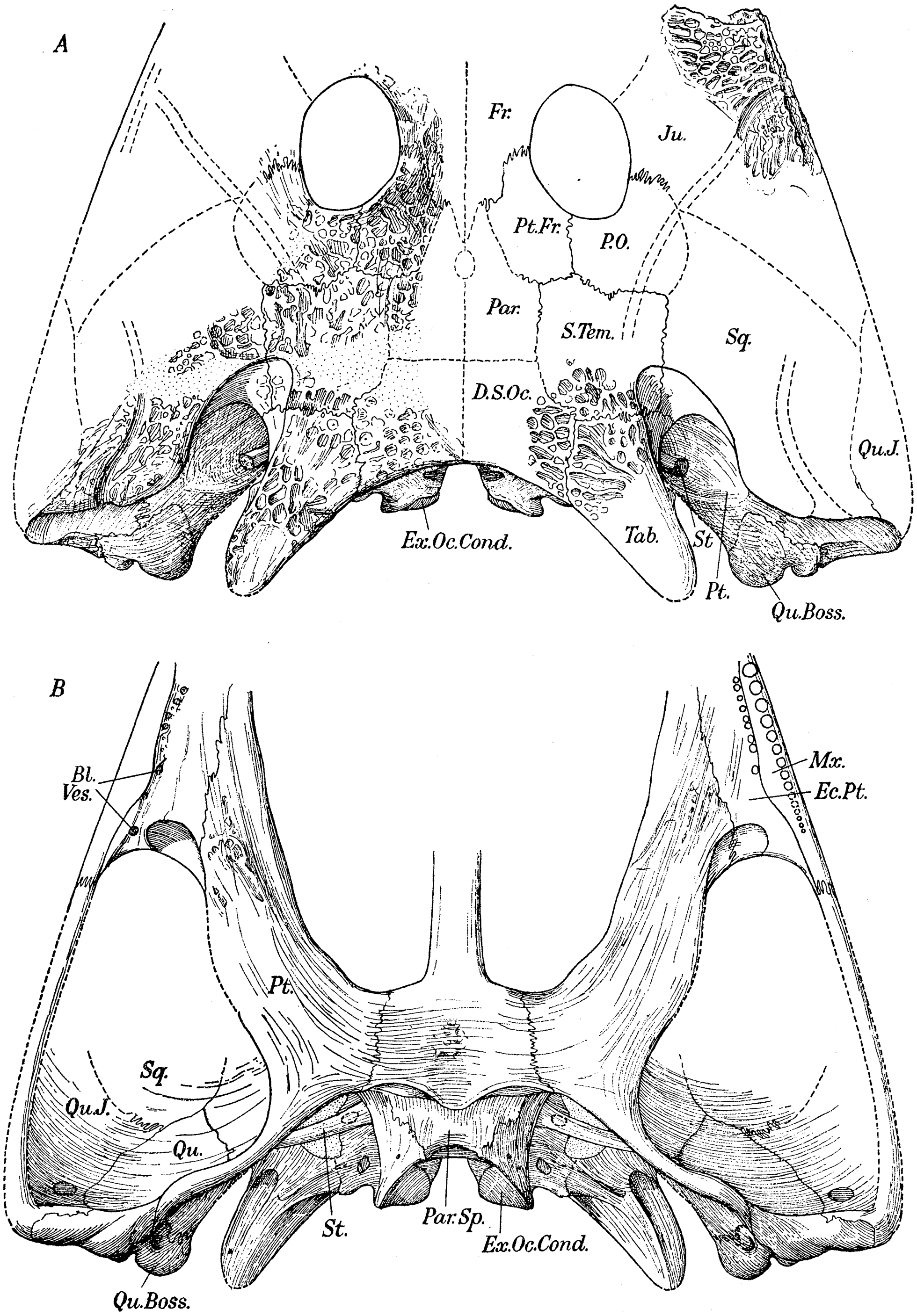

FIGURE 10. *Wetlugasaurus magnus*, n.sp. (B. 122), Watford, District Albert, Cape Province, probably low in the *Cynognathus* zone, perhaps *Procolophon* zone (× 1/2).

The specimen is contained mainly in two large blocks of sandstone—split apart through the quadrate ramus of the left pterygoid, quadrate and quadratojugal—which fit accurately together. Parts of both surfaces of the pterygoid, and the anterior surface of quadrate and quadratojugal, are seen on the two opposing sides of the blocks. The occipital surface of the quadrate, and parts of that surface of the quadratojugal and pterygoid, are seen on the back of the posterior block where further preparation has been carried out. In the drawings the outline of one side has been restored from the other, and the ornament indicates which parts of the original dorsal surface remain. (This specimen has already been figured (Watson 1919, figs. 11 to 16).)

A, dorsal aspect, *B*, palate; the suture between the frontal and prefrontal cannot be found.

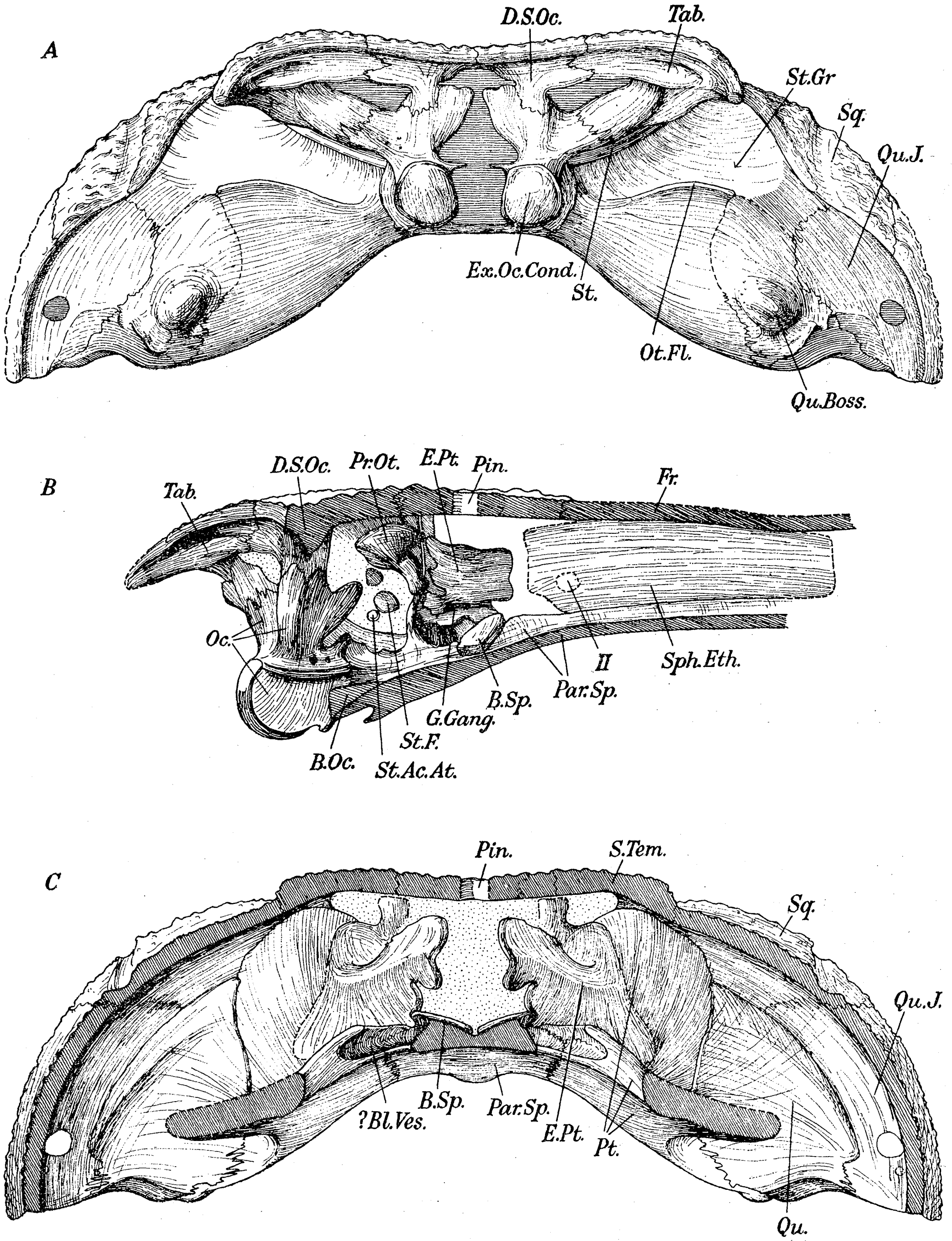

Figure 11. *Wetlugasaurus magnus*, n.sp. (B. 122), Watford, District Albert, Cape Province, probably low in the *Cynognathus* zone, perhaps *Procolophon* zone (× 1/2).

A, the occiput, right side restored from left. The lower border of the tympanic chamber (the otic flange) is exposed only at the point where it meets the quadrate, and is restored from an undeterminable rhinesuchid, B. 119. *B*, the skull drawn as if cut longitudinally through the mid-line, showing the left side with the quadrate region omitted. *C*, the skull drawn as if cut across transversely through the pineal foramen, and viewed from in front. It shows the parasphenoid, the two pterygoids, and the skull roof in section. The hinder part of the pterygoid, where it is attached by suture to the parasphenoid and epipterygoid, bears a deep recess (? *Bl. Ves.*) whose significance is somewhat obscure, but which must be moulded on some structure, perhaps a blood vessel resting upon the parasphenoid. Contributing to the roof of the recess is a pair of thin basisphenoids lying far forward on the upper surface of the parasphenoid. The epipterygoids clasped a cartilaginous or membranous braincase and their anterior ends were continued forward, probably by membrane, to be attached to the hinder end of a sphenethmoid, which is bony, but represented so fragmentarily that little can be made out as to its character. It has, however, towards the hinder end, a foramen in the lateral wall which is presumably for the optic nerve.

G.Gang., groove for Gasserian ganglion; *Oc.*, Exoccipital; *St.Ac.At.*, accessory attachment of stapes; *St.Fo.*, footplate of stapes.

and the pterygoid is well shown, typically interdigitated, but not deeply interlocked. Its length, proportionately greater than in earlier forms such as *Rhineceps*, is small when compared with the condition in extreme forms of capitosaurs. The depressed central area of the posterior part of the parasphenoid bears a delicate ornament of pits, which remain filled with a characteristic red matrix, reproducing on a very small scale something of the ornamentation of external dermal bones. The only other occurrence of this type of ornament on the palate is on the pterygoid, and shows only at its extreme antero-lateral extension, where it meets the ectopterygoid suture; here the bone is quite deeply ridged, grooved, and pitted.

There is no sign of denticles on any part of the palate which is preserved, but a large area of the surface of the pterygoid, where such denticles might well have existed, is damaged and gives no evidence. The upper border of the curious depression in the hinder part of the ectopterygoid (which occurs on both sides) is in part shown with a sufficient coating of matrix to make its existence certain, and the floor which I have indicated is actually shown as a section of cancellous bone; but the nature of the depression seems to be obscure. There is a continuous series of tooth implacements on both ectopterygoids, but the posterior openings on the right side are probably for blood vessels. The series of maxillary teeth is shown in a detached block. The quadrate ramus of the pterygoid is comparatively short, the anterior face of the quadrate condyle lying in a plane which actually cuts the lateral parts of the occipital condyle. Enough of the specimen remains to show quite clearly that the interpterygoid vacuities were very large, proportionately larger than in *Rhineceps*.

'Block 1' (1919, p. 22) has now been prepared so that it shows the quadrate condyle from both external and internal surfaces, and part of the occipital surface of the pterygoid. A remarkable projection occurs above the level of the lowest part of the condylar surface, immediately lateral to the suture with the pterygoid. This forms a distinct boss, a good deal wider than it is deep, which projects backwards so that its admesial border is very nearly parallel to the mid-line (figure 10*A*, *B*; figure 11*A*, *Qu.Boss*). Most of the surface of the boss is less smooth than the rest of the quadrate, and is also characterized by the fact that a large number of small foramina come out onto it, dying out at the shallow depression where they meet the general hinder surface of the quadrate. This boss scarcely has the appearance of an ordinary muscle attachment, but is present in enough examples of capitosaurs to suggest that it had some functional significance. *Rhineceps* is the earliest form at my disposal in which the region is exposed and the boss occurs.

The whole quadrate, except in so far as it is overlapped by the pterygoid and quadratojugal, is now completely free from matrix. The condyle is relatively narrow from side to side, and the articular surface of the lower jaw fits it in a rather remarkable way, ensuring that closure of the mouth is very accurately achieved, and that when the mouth is shut it is held firmly in position by the contact between the anterior part of the inner quadrate condyle and a corresponding very deep groove on the articular. In other words the mouth could certainly be opened widely, and as it was shutting the increasing contact between the inner surfaces of articular and quadrate ensured accurate closure, evidently a matter of great importance in an animal with very tall, sharp pointed, mandibular tusks which fitted into a special opening or depression between the premaxillae and the prevomers.

The base of the right stapes is seen in position in the fenestra ovalis, displayed from below. It is flattened dorso-ventrally, measuring 8·0 mm by some 12·0 mm in section, and bears the root of a small ventral process (*St.Ac.At.*) which passes downward and inward, and—by analogy with other materials—in all probability was attached to the lower border of the fenestra ovalis. The inner surface of the stapes is still embedded in matrix. The distal end of the bone—oval in section, measuring about 4·0 by 5·5 mm—has been exposed by weathering on the left side and is seen in position at a point some 7·0 mm below the level of the skull roof, which must be very near its attachment to the tympanic membrane.

The groove which houses the stapes is not well seen in B. 122, being buried in irremovable matrix, and is displayed better in other forms such as B. 119 (p. 236). Its lateral end, about 14·0 mm below the outer surface, is shown by a centimetre or so of very thin margin of the bony otic flange which arises from the posterior surface of the pterygoid and extends from the lower border of the fenestra ovalis to the otic notch. This arrangement clearly represents an ancestral inheritance, its beginnings being seen, as already shown, in rhinesuchid skulls from earlier horizons, such as *Rhineceps*, and B. 119.

The otic notch is continued forward by a depressed area, some part of which bears the normal surface ornament. This area either provides an extension for the tympanic membrane, or implies that the membrane is sunk below the outer surface of the head, and so made less liable to damage. A lappet on the squamosal, lying on the same level as the present end of the stapes, marks the probable attachment of the outer border of the tympanic membrane.

The occiput as a whole shows how deep are the lateral parts surrounding the quadrates, and how shallow the braincase is. This condition is, in fact, almost perfectly intermediate between that in *Eryops* and in *Cyclotosaurus*.

Lower jaw

The lower jaw is represented only by the hinder end of the right mandibular ramus, exquisitely preserved, a short length very much further forward, probably in the middle of the tooth-bearing region, and a fragment. The articular bone is completely fused with the surangular, though the sutures with the prearticular and angular are still visible. The very small fragment of coronoid preserved shows no sign of denticles on its inner surface. The jaw is directly comparable with that of *Rhineceps* (figure 8) as the two animals are nearly the same size.

They make an interesting comparison: in *Rhineceps* the lower border curves smoothly up to the retroarticular process and glenoid cavity, in the short length preserved of B. 122 it is straight, and the retroarticular process rests more or less on the ground, so that a considerable distance separates the process and the condylar surface. In both specimens the condylar surface forms a cylindroid hollow, but in B. 122 it is deeper, and the flanges which form the posterior, and inner part of the anterior, borders stand relatively higher, so that at its maximum the condylar surface is almost exactly a semi-circle in section; the outer part of the condyle is not bounded anteriorly by the strong ridge present in *Rhineceps*. The posterior border of the glenoid cavity of B. 122, besides being higher, is narrower, and the long anterior projection of the inner articular surface, though similar in both forms, in B. 122 is also relatively narrower.

The tip of the retroarticular process is unfortunately broken off, and the broken surface weathered. Its ventral thicker portion is extended upwards on the outer surface for a considerable distance, and on the inner surface gives origin to the very marked groove which leads into the dental foramen in the articular, immediately below the condyle.

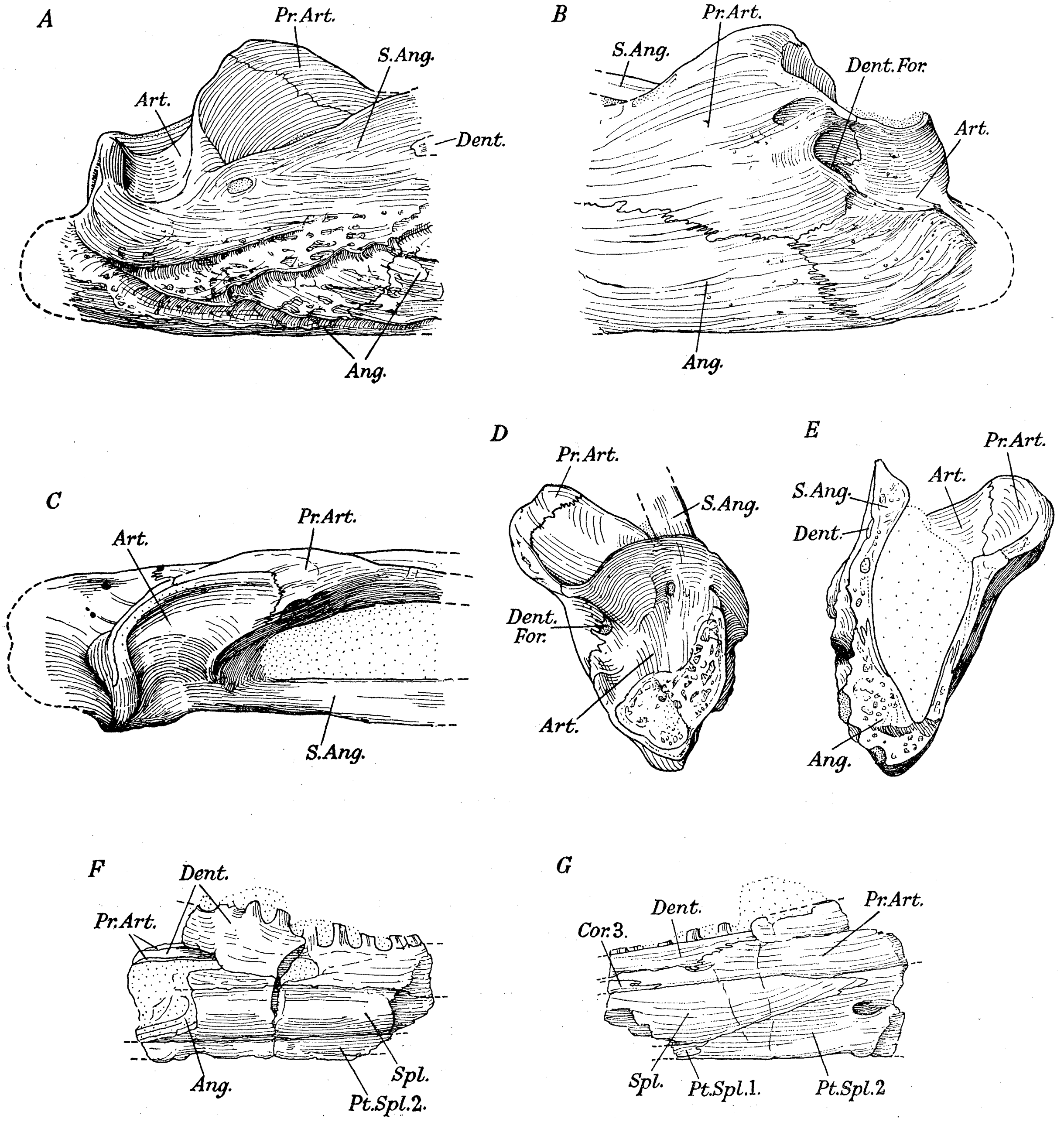

FIGURE 12. *Wetlugasaurus magnus*, n.sp. (B. 122), Watford, District Albert, Cape Province, probably low in the *Cynognathus* zone, perhaps *Procolophon* zone (×2/3).

Fragments of right lower jaw, nearly free from matrix, all sutures being clearly seen. (Compare with figures 8 and 13.)

A to *E*, the posterior end; *A*, outer side, *B*, inner side, *C*, from above, *D*, from behind, *E*, from in front. Note the lateral line grooves: the ventral one is very deep, being overhung by a ridge which projects for a distance of some 5 mm. *F* and *G*, outer and inner aspects respectively of another fragment from about the middle of the tooth-bearing region.

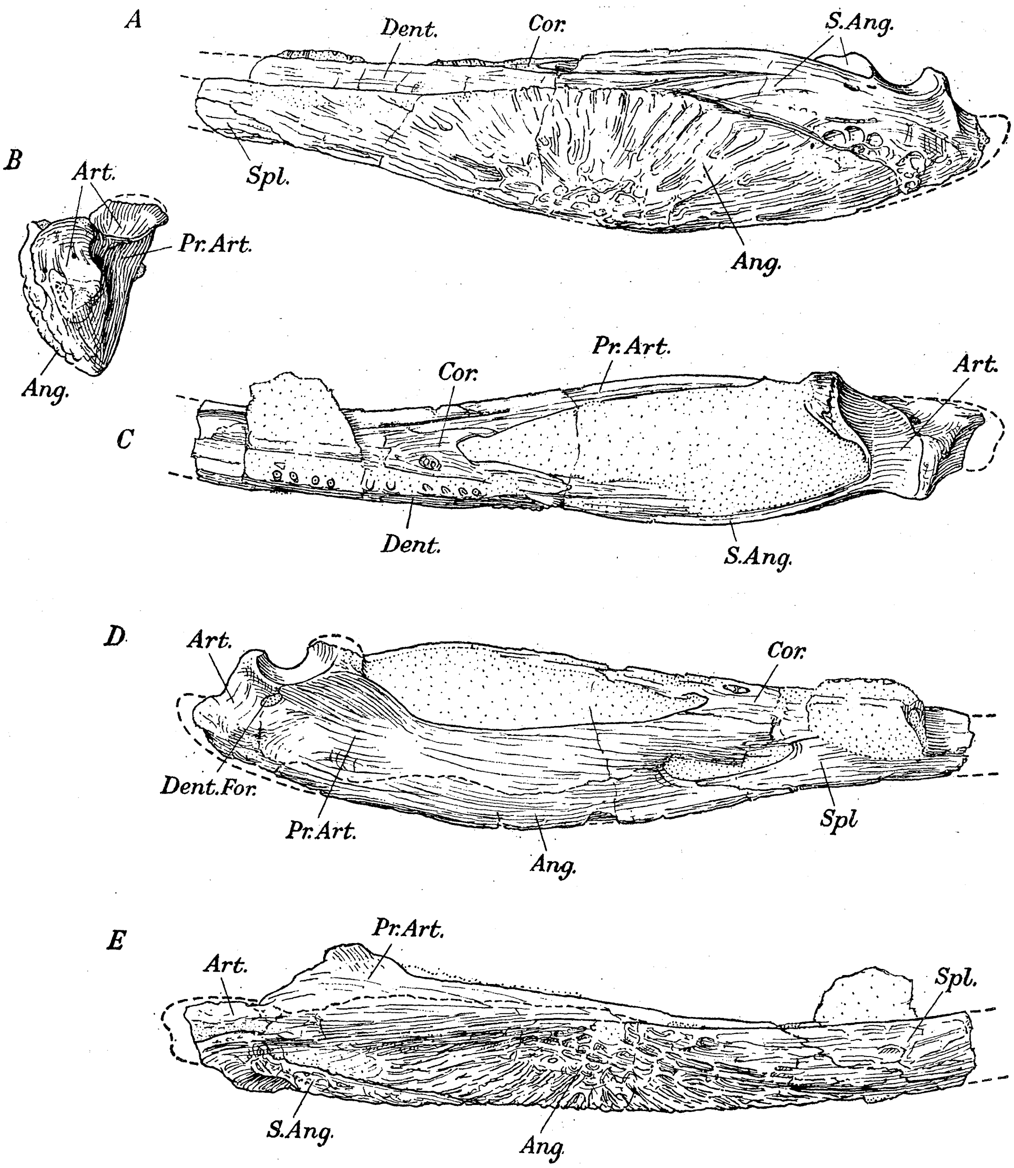

Figure 13. *Parotosaurus* sp. (B. 190), Winaarsbaken, District Albert, C.P., *Cynognathus* zone.

Left lower jaw of a skull to which the right ramus is still attached, given me by the Bernard Price Institute (Field No. B.P.I. 2074a) (× 2/3).

The jaw shows no signs of distortion, but the tip of the retroarticular process is weathered away, and the anterior end is missing. The number of coronoids is unknown, and it is impossible to determine how far forward the posterior coronoid extends. The specimen differs from the jaw of a larger capitosaur (e.g. *Wetlugasaurus magnus*) by being less exaggerated in all its muscle attachments, and other processes; for instance comparison of figures 12 and 13 shows the general agreement in the shape of the glenoid cavity, but the margins of the articulation rise relatively higher in *Wetlugasaurus*. The difference, I imagine, is essentially determined by the very different size of the two animals. Another feature is the straightness of the ventral border of *Wetlugasaurus* in contrast to the convexity in the parotosaur. (Compare also with figure 8).

A, external; *B*, posterior; *C*, dorsal; *D*, internal; *E*, ventral views.

It is obvious that the quadrate condyle fitted into the lower jaw so accurately that with the jaws closed no movement could have been possible. The opening movement, which must have been a strict rotation, could have gone a very considerable distance, but must have been stopped when the ridge bounding the condylar surface of the lower jaw behind came up against the highest part of the quadrate-quadratojugal surface. The arrangement in B. 122 is borne out in B. 190 (figure 13), where the right ramus of the jaw is free from matrix and can be replaced in a nearly natural position against its quadrate condyle.

Comparison of *Wetlugasaurus magnus* with *Parotosaurus nasutus* (von Meyer)

The specimen I have just described, B. 122, is very clearly a capitosaur, and in order to determine it a comparison must be made with *Parotosaurus nasutus*, the type species of that genus. *P. nasutus* from the Middle Bunter of Bernburg, was the first labyrinthodont of such skull shape to be described, and was figured by H. von Meyer (1858, Pls. 24–26). Zittel (1887–90, fig. 396) gave an illustration of the outer side of a lower jaw, showing that the lower border is curved, and the retroarticular process lies well above the ground. A specimen of mine, B. 135, from the Middle Bunter of Bernburg, a natural mould in sandstone showing the impression of the inner and upper surfaces of a lower jaw (which can only be that of *P. nasutus*, very common at this place), largely confirms this; it is remarkable for its depth posteriorly, and its narrowness, but the hinder end is unfortunately indefinite, and gives no information as to its articular surface. Schroeder (1913), from a consideration of a large amount of material, published an admirable restoration of the skull. The British Museum (Natural History) contains many specimens from Bernburg which, taken together, show a good deal of the surface structure.

Thus, a detailed comparison of B. 122 with *P. nasutus*, whose age is firmly determined, can be made, though it must be realized that the comparison can only be, in the literal sense, superficial, for the details of the internal skull structure of *P. nasutus* are unknown, with the exception of one specimen, B.M.N.H. 36255, which shows an impression of the lower part of a right epipterygoid in position on the pterygoid, evidence that there is some parallel to the epipterygoid of B. 122.

The two animals have some features in common: their size is similar, the pattern of the dermal roof sutures agrees very well (though all capitosaurs follow the same general pattern in this respect), and the structure of the occipital surface, the 'pockets', and the occurrence of the lappet on the squamosal are similar. But in the following points the two differ: in B. 122 the eyes are closer together, and further from the lateral borders of the skull, than in *P. nasutus*; the posterior margin of the skull above the occipital surface is a single smooth, deep curve, while in *P. nasutus* the posterior half of the tabular horn is diverted laterally, making a deep bend; the otic notch is longer than in *P. nasutus*; the notch is extended forward by a depressed area of the skull roof which bears a faint ornament similar to that of the general dorsal surface, and is not so extended in *P. nasutus*; the braincase and quadrate region are deeper in proportion to their width—which is equivalent to a statement that the whole skull is less flattened than in *P. nasutus*; the boss on the quadrate of B. 122 exists in *P. nasutus*, but is much less well developed there; the hinder border of the stapedial groove is less high in the skull than it is in Schroeder's drawing of *P. nasutus*; the proportional length of the pterygo-parasphenoid suture is less than in *P. nasutus*; and the delicate ornament in the sunken central area of the parasphenoid is not shown in the figures of *P. nasutus*. Finally, the lower jaw differs very greatly from that figured by Zittel as *C. nasutus*, or from my specimen B. 135.

It is thus evident from the differences pointed out here that B. 122 cannot be referred to *P. nasutus*.

Comparison of *Wetlugasaurus magnus* with *Wetlugasaurus angustifrons* Riabenin

Another form which has a marked likeness to B. 122 is *Wetlugasaurus angustifrons*, from the Lower Triassic of Vetluga-Land in Northern Russia, described by Riabenin (1930). The specimen is beautifully preserved, and though it has lost a small block containing the anterior parts of the orbits, the general proportions of the skull are in no doubt.

B. 122 is two and a half times bigger lineally than *W. angustifrons*, but is exceedingly like it. The pattern of the dermal roof sutures, the position of the eyes, the curve of the posterior margin of the skull, the continuation of the long otic notch forward into a depressed area, the general structure and proportions of the whole occipital surface, and that of the braincase and quadrate wing, the position of the hinder border of the stapedial groove, and of the 'pockets', the length of the parasphenoid-pterygoid suture, and finally, the ornament on the central part of the parasphenoid, are remarkably alike in the two skulls. The squamosal lappet is doubtful in *W. angustifrons*, and the boss on the quadrate—though present in both—is proportionately bigger in B. 122, but this is presumably a size effect, for the eyes and foramen magnum are proportionately smaller. In fact, except for size, and such shape changes as may be related to it, it is barely possible to set down any qualities which distinguish one skull from the other.

The type specimen of *W. angustifrons* has no lower jaw, but another individual from the same locality has part of the left ramus of a mandible associated with it. This is represented in a photograph (Riabenin 1930, Pl. 7, figs. 3 to 5), but is not interpreted in a drawing. In Riabenin's fig. 3 the fragment of lower jaw is possibly placed too far back with respect to its skull; it probably lies in the region between the two surviving fragments of the lower jaw of B. 122, so that no comparison between them can be made. However, it does show that the angular bone extends very far forward on the outer surface, and that on the inner surface there is apparently a well-developed prearticular; also the lower border of the jaw, so far as it is preserved, is essentially straight. Judging from the photograph I see no reason why the jaw should not have resembled that of B. 122.

Riabenin made a new genus for his form on the strength of its rachitomous vertebral column, for at that time a capitosaur skull—which it otherwise resembled—had not been found in connexion with a vertebral column, and *Mastodonsaurus* and the metoposaurs, which were assumed to be close relatives, have 'stereospondylous' columns. But the description of *Paracyclotosaurus* (Watson 1958) shows that some 'stereospondylous' columns are, in fact, effectively rachitomous.

In making the comparison between B. 122 and *Wetlugasaurus angustifrons* it must not be forgotten that there is this difference of size (though it may be due to growth), that the anterior regions of the two cannot be compared, that the braincase and epipterygoid, so well displayed in the one, are not shown in the other, and finally that I have never seen the Russian skull, and have not that familiarity with it which comes from handling, so that the external similarity between the two skulls may hide differences elsewhere. In the light of this it seems undesirable to refer B. 122 to the same species, and I therefore propose to call it *Wetlugasaurus magnus*, n.sp.

Three other species have been attributed to *Wetlugasaurus*: *W. groenlandicus* Säve-Söderbergh (1935), *W. volgensis* (*Capitosaurus volgensis* Hartmann-Weinberg & Kusmin 1936), and *Wetlugasaurus* sp., Efremov (1940), none of which agrees so closely with the type species as does the South African skull here described.

It is unfortunate that the specimen of *Wetlugasaurus angustifrons*, which was found in a river bank, cannot be referred to any strict horizon, though it is certainly of Lower Triassic age. But the general similarity between B. 122 and *Parotosaurus nasutus*, whose age in the standard German succession is firmly established, allows the following comparisons to be made: the occiput, including the quadrate-pterygoid region, is deeper in proportion to its width in B. 122 than in *P. nasutus*; the interpterygoid vacuities are definitely proportionately smaller in B. 122; and finally the pterygo-parasphenoid suture is proportionately shorter in B. 122. Thus, in each of these respects, B. 122 is slightly more primitive than *P. nasutus*, suggesting that the Cynognathus zone of South Africa is slightly older than the Middle Bunter of Bernburg.

Lower jaws

Jaws whose skulls are known

I have before me three lower jaws in association with their skulls, determinable as *Rhineceps nyasaensis*, *Parotosaurus* sp. (B. 190), and *Wetlugasaurus magnus*, (figures 8, 12, 13). The two former are essentially complete, the latter is represented by the beautifully preserved hinder end, and two fragments further forward. The only figures of lower jaws, similar in completeness and certainty of determination, that I can find to compare with them are those of *Rhinesuchoides tenuiceps* Olson & Broom (1937, figs. 6, 7), and *Uranocentrodon senekalensis* van Hoepen (1915), Broom (1930, figure 4). The same general pattern is found throughout, but there is a variation of detail which deserves some consideration.

Among the forerunners of the capitosaurs, the oldest jaw of which there are good figures is that of *Eryops* (Sawin 1941, Pl. 5). Its most characteristic features are that the hinder part of the jaw is very deep, the angulated lower border—a little behind the level of the peak formed by the coronoid on the outer side of the anterior end of the muscle opening—turning up towards the articulation, and that a retroarticular process is absent. The oldest known rhinesuchid jaw, *Rhinesuchoides*, from the *Tapinocephalus* zone, shows that the lower border—except quite anteriorly—is smoothly curved, and rises to a short, rounded retroarticular process, whose detail unfortunately is not clearly shown. This jaw recalls that of *Rhineceps* in general proportions (p. 237), but does, in contrast, exhibit the pronounced peak on the outer border of the muscle entrance, similar to that of *Eryops* though relatively further behind the front of the muscle opening. None of the later forms appear to show this peak, and the jaw in the hinder region is never as deep as in *Eryops*, nor is there any trace of the angulation. The shallow groove passing forwards from the hinder end of the jaw to the large foramen (dental foramen of Sawin), seen in *Rhineceps*, is also present in *Rhinesuchoides*, where the internal mandibular foramen is also very large, and apparently not preceded by others. The groove is foreshadowed in *Eryops* (Sawin, pl. 5, fig. b, *df.*).

In *Eryops* the condylar surface on the lower jaw is transversely widened, and antero-posteriorly short. It is also very shallow and cannot really be said to clasp the quadrate condyle; the two surfaces fit quite well, but displacement must be prevented by the capsule of the joint. In *Rhineceps* the condition is quite different, though it could theoretically be derived from that of *Eryops*: the glenoid cavity is much deeper than in *Eryops*, and its hinder border rises into a ridge of very considerable width; its character—considered in conjunction with the quadrate which fitted it—implies a strict rotation, the jaw moving on an axis which is the centre of the articular surfaces. The inner part of the condylar surface is carried far forward, and ends where the prearticular bone rises to its summit. The glenoid cavity thus restricts the movement of the jaw to a rotation on an axis far more completely than the corresponding arrangements in *Eryops*, and the character of the jaw of a true capitosaur is really the result of an evolution which exaggerates the differences in shape between the jaws of *Eryops* and *Rhinesuchus*, carrying them much further. In *Wetlugasaurus* (p. 245) the inner part of the glenoid cavity is proportionately longer still, and carries a larger share of the whole condylar surface. The outer part of the glenoid cavity reduces its anterior ridge, whilst the posterior ridge rises much higher. *Parotosaurus* sp. (B. 190), from the *Cynognathus* zone of Winaarsbaken, District Albert, C.P., though slightly younger in age, conforms to the pattern of *Wetlugasaurus* very well.

The retroarticular process is in *Rhineceps* a small protuberance arising directly from the posterior border of the glenoid cavity: it stands out as a definite projection sharply marked off from the greater part of the hinder surface. In the fragment of lower jaw of *R. whaitsi* there is a small retroarticular process projecting backwards some distance below the hinder margin of the glenoid cavity, well marked off from the outer part of the hinder surface of the jaw by a definite groove, its inner surface being essentially in the plane of the prearticular. The glenoid cavity, obscured by matrix on its inner side, is otherwise well shown; the ridge which bounds it anteriorly sweeps forward to meet a process of the prearticular, laterally the cavity reaches the outer surface, the ridge which bounds it posteriorly there dying out. In *Wetlugasaurus* the retroarticular process (broken off in the specimen) is evidently much bigger, and is separated from the posterior border of the glenoid cavity by a noticeable step. The groove connecting the back of the jaw with the dental foramen is a large channel, but it occupies a place exactly as in *Rhineceps*, and the foramen, now proportionately smaller, still lies between the articular and prearticular.

In *Parotosaurus* sp. (B. 190)—a smaller animal of about the same geological age—the retroarticular process, the groove and the foramen are similar to *Wetlugasaurus*, but relatively smaller, and consequently with less well emphasized peculiarities. In this specimen the lower border of the jaw, from a point well in advance of the muscle opening, follows a smooth shallow curve to the end of the retroarticular process, the anterior end of the jaw being effectively straight; and *Paracyclotosaurus davidi*, of Upper Triassic age, is similar, though the rise to the articular region is steeper, and the retroarticular process lies high above the lower border of the jaw, projecting considerably backward. In *Wetlugasaurus*, however, the lower border of the jaw is horizontal, the retroarticular process forming part of the same straight line, and the glenoid cavity is in a more ventral position. The dorsal border of the surangular is still sloping upwards where it is broken off, and the prearticular on the inner surface of the jaw stands up well above the margin of the outer surface. In *Cyclotosaurus robustus* Quenstedt (1850) from the Keuper—one of the last of the labyrinthodonts—the lower border of the jaw is completely straight from one end to the other, though it is impossible to give its relations with the retroarticular process since this is broken off—as in all late forms. At the posterior end below the articulation the jaw is deep, and from this point becomes progessively shallower. In this form the lower jaw throughout the whole of its length is deeper than the skull which lies above it, an arrangement which is an exaggeration of the conditions found in such earlier forms as *Wetlugasaurus*.

It is tempting to relate the increased length and massiveness of the retroarticular process with the progressive flattening of the animal as a whole, the retroarticular process being important because it gives attachment to muscles whose contraction raises the upper jaw whilst the lower rests on the ground. Indeed, it is precisely the flattening of the lower border of the jaw posteriorly which is the most striking general feature distinguishing *Wetlugasaurus* from *Rhineceps*.

Isolated jaws

There are in the literature good illustrations of various isolated lower jaws which have been referred to capitosaurs, and they make an interesting comparison with those described above.

'*Labyrinthodon*' *lavisi* (Seeley, 1876, pl. 19), a late form from the Upper Keuper of Sidmouth, is somewhat larger than *Wetlugasaurus*, and is figured in admirable detail. The lower margin of the deep posterior part of the jaw is straight, at least as far as the anterior end of the angular, and the glenoid cavity lies nearly on a level with the upper margin of the jaw. The retroarticular process, by definition the extension of the lower jaw behind the glenoid cavity, projects a long way back, and is built up by the surangular and articular. It is wide when seen from above, and its inner side is produced into a knob, which is separated from the glenoid cavity by a very long step. The outer side of the process is produced into a flange which continues the general surface of the jaw and is very deep, ending in a nearly vertical hinder margin and hiding the step. Seen from the outer side the knob, to which the depressor muscles of the jaw must have been attached, is raised slightly above the ventral border of the jaw.

Comparison between '*L.*' *lavisi* and *Wetlugasaurus* shows that the position of the glenoid cavity differs in the two forms, resulting in differences in the proportions of the hinder end of the jaw. In '*L.*' *lavisi* it lies relatively high, nearly on a level with the upper margin of the surangular in front of it: in *Wetlugasaurus* it lies much lower, the border of the surangular in front of it sloping upwards, and leaving exposed a large area of the inner part of the articular–prearticular bone. The cavity itself differs in the reduction in '*L.*' *lavisi* of the long forward projection seen on the inner side of the jaw of *Wetlugasaurus*. In '*L.*' *lavisi* the upper branch of the lateral line groove makes an extremely sharp bend immediately below the glenoid cavity, but in *Wetlugasaurus* the corresponding part of the groove, which is narrow, forms a smooth shallow curve.

?*Parotosaurus* sp. (Edinger 1937, fig. 3, *a*, *b*), from Odenwald, upper Middle Bunter, is an impression in sandstone from which a cast has been made. It thus includes nothing more than the outer surface of the hinder part of the jaw, with a small part of the upper surface of the surangular, the glenoid cavity, and the retroarticular process. The lower border of the jaw is straight, in line with the retroarticular process, and the jaw is much shallower posteriorly than that of '*L.*' *lavisi*, a condition no doubt determined by the fact that it is older. It deepens, however, very gradually towards the anterior part of the length preserved (which extends beyond the posterior tip of the dentary), recalling *Wetlugasaurus*, but the surface of the glenoid cavity is relatively somewhat higher than in this form. The outer surface of the retroarticular process is much more like that of '*L.*' *lavisi*, and it has a similar V in the lateral line below the glenoid cavity. It does, in fact, make a good intermediate between *Wetlugasaurus* and '*L.*' *lavisi*, and is certainly capitosaurine.

The lower jaws of Triassic labyrinthodonts are treated in an admirable paper by Wills (1916). His plate III, *a*, *b*, shows the hinder part of the lower jaw of '*Labyrinthodon*' *jaegeri* Owen, from Cubbington, near Warwick. It is rather larger than *Wetlugasaurus*, and differs from it in several ways. The wide glenoid cavity, bounded posteriorly by a similar deep ridge, occupies a very dorsal position, and the upper margin of the surangular in front of it rises very slightly as it extends forward to its overlap on the dentary. There is no development of the prearticular crest, so prominent in *Wetlugasaurus*. The retroarticular process is unfortunately incomplete, but is wide and suggests that it was very extensive, and was probably carried back at the level of the lower part of the glenoid cavity. The lower border of the jaw is effectively straight but appears to curve upwards to the retroarticular process; the lateral line grooves are inconspicuous.

The specimen figured by Wills as *Diadetognathus*? Miall, Lower Keuper Sandstone, Bromsgrove (Pl. II, A–D), is interesting for it shows a jaw in which the supramecklian fossa is quite wide, and whose upper and lower borders lie nearly parallel to one another. The jaw as a whole is deep. Details of the condylar surface are not clearly shown in the photograph, but it is evident that the glenoid cavity lies on the upper border of the jaw. The retroarticular process, seen from above, is very wide, and clearly has a deep outer flange like that of '*L.*' *lavisi*.

Miall (1874) describes the hinder part of two excellently preserved labyrinthodont lower jaws, though in both cases the inner surface is lacking. They agree with one another quite well in general structure, bear a resemblance to '*L.*' *jaegeri*, and are about the same size. In both specimens the glenoid cavity lies high in the jaw, on a level with the upper border of the surangular, which rises very slightly and is nearly parallel to the lower border. The condylar surface (so far as it remains) is the normal rather deep cylindroid groove. The retroarticular process extends well back, but also lies high up, almost on a level with the glenoid cavity, and consequently the hinder end of the lower border of the jaw curves up to meet it. In '*Mastodonsaurus*' *pachygnathus* Owen (Pl. 26, figs. 3A and B), the retroarticular process has an external flange passing up almost to the border of the glenoid cavity, and ending posteriorly in a sharp point, very reminiscent of Zittel's figure of *P. nasutus*. It is relatively narrower across than that of '*L.*' *lavisi*. The deep V made by the lateral line groove in '*L.*' *lavisi* is here rather more shallow. In *Diadetognathus varvicensis* Miall, the type (Pl. 27, figs. 3A and B), the retroarticular process is relatively much longer than in '*L.*' *lavisi*, although its root is nearly as deep as the rest of the jaw, and its upper surface is almost horizontal.

It is unfortunate that the isolated (and therefore well displayed) lower jaws described above, which—with the exception of ?*Parotosaurus* sp. Edinger—are late Triassic, cannot be compared with the only two known 'capitosaur' jaws of similar age, *Cyclotosaurus robustus* and *Paracyclotosaurus davidi*, whose condylar surfaces are not shown. The published figures of the jaws so far considered show that they may, perhaps, show two trends: '*L.*' *lavisi*, for instance, has an extremely flat ventral margin, continuing into a ventrally placed retroarticular process (? a cyclotosaur quality); *Diadetognathus*, '*L.*' *jaegeri* and '*Mastodonsaurus*' *pachygnathus* have rounded lower borders, and high-set retroarticular processes, like *Paracyclotosaurus*.

Compared with *Wetlugasaurus magnus*—the most advanced capitosaur in which both skull and lower jaw are known, and the posterior end of the jaw is well displayed—the Triassic forms all agree in having the glenoid cavity placed high on the upper surface of the jaw with a relative reduction in the height of the prearticular crest, and in a greater elaboration of the retroarticular process. ?*Parotosaurus* sp. Edinger, of intermediate date, falls neatly between *Wetlugasaurus* and '*L.*' *lavisi* in its structural characters.

Conclusions

In order to extend the series described in the preceding pages, I recorded a number of qualities shown by additional specimens and all the illustrations of capitosaur-like forms that I could find in the literature, arranged in order of time. A tracing was made of each figure, and in this way it became possible to compare one with another without making previous assumptions as to similarity. The species so compared, and the specimen or figures which were used, are listed below.

Ancestral Types

Actinodon frossardi, Lower Permian, Autun, France—from Gaudry (1887, Pls. 1 to 3), and this paper figure 1. *Eryops megacephalus*, Lower Permian, Texas—from Sawin (1941, Pls. 1 to 11), and this paper figure 2. *Melosaurus uralensis* Middle Permian, Urals—from Hartmann-Weinberg (1939, figs. 1 to 4, Pls. 1 and 2); Konjukova (1955, figs. 1 and 2); and this paper figure 3.

South Africa

Tapinocephalus zone (Upper Permian)

Rhinesuchus whaitsi—from Broom (1908, Pl. 46), this paper figure 4, and unpublished drawings 1949. *Rhinesuchoides tenuiceps*—from Olson & Broom (1937, figs. 6 and 7) (= *Rhinesuchus avenanti*, Boonstra (1940)).

Endothiodon zone

Rhinesuchus beaufortensis—from Boonstra (1940, unfigured) (= *R. whaitsi* Haughton (1915, Pl. 12, figs. 3 and 4)). *R. broomianus*—from von Huene (1931, fig. 1). *R. capensis*—from Haughton (1925, figs. 3 and 4).

Cistecephalus zone

Muchocephalus muchos n.gen., n.sp.—from this paper figure 5. Undeterminable rhinesuchid B. 119—unfigured. *Laccosaurus watsoni*—from Haughton (1925, figs. 5 to 7, unpublished drawing 1949). *Rhineceps nyasaensis*—from this paper figures 6 to 8 (= *Rhinesuchus nyasaensis* Haughton (1927, figs. 1 and 2)).

Lystrosaurus zone

Uranocentrodon senekalensis—from Broom (1930, figs. 1 to 4), this paper figure 9, and unpublished drawing, 1949 (= *Myriodon senekalensis* van Hoepen (1911 unfigured), = *Rhinesuchus major* Broom (1912, Pl. 13, figs. 1 and 2) = *R. senekalensis* Haughton (1915, Pl. 12, figs. 1 and 2)). *Laccocephalus insperatus*—from Watson (1919, fig. 10).

Procolophon zone

Kestrosaurus dreyeri—from Haughton (1925, figs. 11 to 14).

Cynognathus zone (Lower Trias)

Wetlugasaurus magnus n.sp.—from this paper figures 10 to 12. *Parotosaurus albertyni* Romer (1947) (= *Cyclotosaurus albertyni*—from Broom (1904, unfigured)). *P. haughtoni*—from Broili & Schroeder (1937, figs. 1 to 9). *P. africanus*—from Broom (1909, unfigured), Haughton (1925, figs. 8 to 10). *Parotosaurus* sp. (B. 190)—from this paper figure 13. *Parotosaurus* sp. (B. 192)—unfigured.

East Africa

Middle Trias

Parotosaurus sp. (Parrington, field no. 48)—unfigured.

Russia

'*Cistecephalus zone*'

Wetlugasaurus volgensis Efremov (1940) (= *Capitosaurus volgensis*—from Hartmann-Weinberg & Kusmin (1936, Pls. 1, 3, 4)).

Lower Trias (Eotrias, Permo Trias)

Parotosaurus bogdoanus—from Sushkin (1927, figs. 3 and 4). *Volgosuchus cornutus*—from Efremov (1940, figs. 8 and 9). *Wetlugasaurus* sp.—from Efremov (1940, Pl. 1).

'*Cynognathus zone*'

Wetlugasaurus angustifrons—from Riabenin (1930, figs. 1 to 3, Pls. 5 to 7).

Greenland

Eotrias

Wetlugasaurus groenlandicus—from Säve-Söderbergh (1935, Pls. 1 and 2).

Germany

Middle Bunter

Parotosaurus nasutus—from von Meyer (1858, Pls. 24 to 26), Schroeder (1913, Pls. 17 to 21), Zittel (1887–90, fig. 396), (= *P. weigelti* Romer (1947)). *P. fronto*—from von Meyer (1858, Pl. 28).

Upper Middle Bunter

Parotosaurus fürstenberganus—from Edinger (1937, fig. 2). ?*Parotosaurus* sp.—from Edinger (1937, fig. 3).

Lower Trias

Parotosaurus helgolandiae—from Schroeder (1913, Pls. 16 to 21). *P. semiclausus*—from Swinton (1927, figs. 1 to 4, Pl. 4) (= *Stenotosaurus semiclausus* Romer (1947)).

Upper Trias, Keuper

Capitosaurus arenaceus—from Broili (1915, figs. 1 and 2) (possibly belonging to the genus *Cyclotosaurus*).

India

Trias

Gondwanasaurus bijorensis—from Lydekker (1885, Pls. 1 to 3).

America

Middle Trias

Stanocephalosaurus birdi—from Barnum Brown (1933, figs. 1 and 2).

Australia

Upper Trias

Subcyclotosaurus brookvalensis—from Watson (1958, fig. 15).

England

Lower Keuper

Capitosaurus stantonensis—from Woodward (1904, Pl. 11) (= *Procyclotosaurus stantonensis*, Watson (1958)). '*Labyrinthodon*' *jaegeri*—from Wills (1916, Pl. 3). ?*Diadetognathus* sp.—from Wills (1916, Pl. 2).

Upper Keuper

'*Labyrinthodon*' *lavisi*—from Seeley (1876, Pl. 19).

Keuper

Diadetognathus varvicensis—from Miall (1874, Pl. 27). '*Mastodonsaurus*' *pachygnathus*—from Miall (1874, pl. 26).

For the end term in the series I chose, because they are well preserved and characteristic, three cyclotosaurs:

Lower Keuper

Cyclotosaurus robustus—from Quenstedt (1850, Pls. 1 to 3).

? *Upper Keuper*

Paracyclotosaurus davidi—from Watson (1958, figs. 1 to 6).

Rhaetic

Cyclotosaurus posthumus—from Fraas (1913, Pls. 18 to 20).

The genus *Rhinesuchus* was founded by Broom for a skull found by Mr Whaits near Fraserburgh Road Station in the *Tapinocephalus* zone. This specimen includes a very good occiput not figured by Broom, of which I made a measured sketch, and gives a sound basis for the interpretation of the meaning of the generic term. To the genus have been ascribed five species, *Rhinesuchus whaitsi* Broom (1908), the type, and *R. avenanti* Boonstra (1940), from the *Tapinocephalus* zone; *R. beaufortensis* Boonstra (1940), *R. capensis* Haughton (1925), and *R. broomianus* von Huene (1931) from the *Endothiodon* zone. Comparison of *R. avenanti* with *Rhinesuchoides tenuiceps* Olson & Broom (1937), also from the *Tapinocephalus* zone, shows great similarity between the two, though neither drawing is very informative.

The narrow elongated skulls are the same size and shape, even to the presence of a turn in the lateral border of the tympanic notch, presumably about at the squamosal-quadratojugal suture; they differ slightly in that the back of the table of *R. avenanti* is represented as a continuous smooth curve, that of *Rhinesuchoides* as having a flattened central strip with more protuberant tabular horns. Boonstra's figure suggests the presence of the stapedeal groove and flange. It is difficult to believe that two labyrinthodonts, so similar, and apparently in the same evolutionary stage, should live in close proximity and be specifically different, so that I propose to call them both *R. tenuiceps* Olson & Broom, regarding them as near relatives of *Rhinesuchus*, distinguished only by the elongated shape.

In the succeeding *Cistecephalus* zone there are three forms which—though obviously closely related to *Rhinesuchus*—seem to me to deserve generic distinction from it, and from one another. *Muchocephalus muchos*, n.gen. n.sp., has been dealt with above (p. 229). *Laccosaurus watsoni* (S.A.M. 4010), from Ferndale, Graaf Reinet, has been accurately described by Haughton, though I think it is possible to interpret his account of the condylar arrangement in another way. (In 1949 I made a sketch of the specimen which shows that the exoccipital extends very far towards the mid-line, and bears a well-developed articular surface, facing backwards and downwards, which has every appearance of forming the lateral end of a single wide and shallow condyle of the type found in *R. whaitsi*, though somewhat more depressed. The 'pocket' is rounded, deep anteriorly, and—as in *R. whaitsi* —may be undercut.) *Rhineceps nyasaensis* from East Africa (p. 231) is the best existing specimen from this zone. These three genera agree with *Rhinesuchus* in having the single confluent condyle, but differ in showing a greater degree of flattening appropriate to their later age. They differ from one another in small structural details.

Uranocentrodon, from Senekal, O.F.S., presumably in the *Lystrosaurus* zone, is represented by magnificent material, including a skeleton. It is generally capitosaur-like in its skull shape, and has paired occipital condyles—though the basioccipital is fairly well developed. But its quadrate condyles are relatively far behind the occipital ones, agreeing in general with the earlier forms, and the 'pockets', still behind the end of the parasphenoid-pterygoid suture, are separated and deep. It shows in fact an intermediate stage between a rhinesuchid and a capitosaur, presenting an assemblage of early features with later ones. *Laccocephalus insperatus*, whose age though uncertain might well be *Lystrosaurus* zone, is similarly of interest. Although its condyles are large, and formed entirely of exoccipital, they nearly meet, and there is a considerable basioccipital bone, lying on the upper surface of the parasphenoid, which may have continued to the condyle, for in the only known specimen it is exposed on a broken face which cuts across the exoccipital condyle without making it clear if the basioccipital did contribute to it. The basipterygoid attachment is obviously short, and made by a deeply interdigitated suture, hence this form also exhibits the retention of a primitive feature in an otherwise advanced structure.

In the South African labyrinthodonts so far discussed a considerable structural change takes place between the first and last, but they are evidently closely related, and are held together by the common possession of a series of primitive structures, so that it is convenient to call them all rhinesuchids, in contrast to their descendants the capitosaurs. It is indeed probable that more than one rhinesuchid passed on to attain a capitosaur structure, and that we are dealing not with a single line evolving, but with a change which was taking place throughout the whole group, whose members were pursuing similar evolutionary courses. This may only mean that the selection which determined which individual would survive was so widely exercised that it covered members of the group widely distributed over the world.

The single capitosaurine specimen from the *Procolophon* zone is *Kestrosaurus dreyeri* (Haughton 1925). Its shape is not that of a normal capitosaur, for the skull is elongated, straight-sided, and trematosaur-like, and the quadrate condyles are nearly on the same level as the exoccipital condyles. But the basioccipital region, as figured by Haughton, generally resembles that of a capitosaur in the following ways: the pterygo-parasphenoid suture crosses a flat ventral surface; it is relatively shorter than in a trematosaur, the two sutures separating from one another posteriorly, so that here the basis cranii is wide; the exoccipitals each bear a single ovoid articular condyle, well separated from its fellow; a basioccipital bone lies in—but does not fully occupy—the space between the parasphenoid and the flanges of the exoccipitals, which meet one another to form the floor of the foramen magnum. This form is perhaps more capitosaur-like than rhinesuchid, its basicranial region agreeing well enough with such a form as *Wetlugasaurus magnus*.

In the *Cynognathus* zone in South Africa the capitosaurs proper begin. They include *Wetlugasaurus magnus*, *Parotosaurus albertyni*, *P. haughtoni*, *P. africanus*, and the two specimens *Parotosaurus* sp. (B. 190) and *Parotosaurus* sp. (B. 192). They are of great importance, because the belief that the *Cynognathus* zone is of Bunter age depends on the structural peculiarities of its forms in comparison with *P. nasutus*, from Bernburg, Germany, which is Middle Bunter. The best preserved individual is *Wetlugasaurus magnus*, which I have already discussed in comparison with *P. nasutus*, coming to the conclusion that it is, if anything, slightly earlier in date, thus relating the *Cynognathus* zone more closely to the Bunter.

The most familiar capitosaurs are those from the German Trias. They include the type species *P. nasutus*, and *P. fronto* from the Middle Bunter of Bernburg, and *P. fürstenberganus* from the upper Middle Bunter, which are well dated; and *P. helgolandiae*, which comes from an island, so that its stratigraphical position cannot be determined by external relationship, and it is conventionally—and no doubt rightly—called 'Lower Trias'. *P. semiclausus* (*Stenotosaurus*) comes from the Bunter Sandstone of the Black Forest of South Baden, of Lower Triassic age. It may be noted that *P. helgolandiae* and *P. semiclausus* show a constriction of the otic notch beyond the stage found in *P. nasutus*, and are in fact intermediate between capitosaurs and cyclotosaurs, *P. semiclausus* making a very near approach to that animal.

The species attributed to the genus *Parotosaurus* present a difficulty. The type, *P. nasutus*, is represented by several essentially complete skulls, but *P. polaris* (Wiman 1915), for instance, and many of those from South Africa are fragmentary, and although often showing admirable detail may be singularly difficult to compare with it; I have not, indeed, attempted to do so in the present paper.

The end term of my rhinesuchid–capitosaur evolutionary series is, of course, a cyclotosaur, and I have taken for consideration three such forms from the Upper Triassic. *Cyclotosaurus robustus* is the type species; *Paracyclotosaurus davidi* differs generically from it; and *Cyclotosaurus posthumus* is probably the most extreme form, and last survivor of the line. All these animals have a closed otic notch.

Two forms come from the Middle Trias. *Stanocephalosaurus birdi*, a large skull from Arizona, the only American capitosaur, is represented by an impression of the anterior part of the palate. The fragment does not give enough information to allow of its position in this family to be determined, nor does it give any useful suggestion as to the age of the rocks in which it was found, except that it is probably in the Trias. *Parotosaurus* sp. (Parrington Field No. 48, cf. Watson (1958, p. 257)) is one of three large skulls from East Africa in which the otic notch is just not closed, and the skull is quite deep, not agreeing with *Cyclotosaurus robustus*, but closely approaching *Paracyclotosaurus*.

Capitosaurus arenaceus, from the Keuper of Bavaria, though so-called, could well be referred to *Cyclotosaurus* on the shape of the palatal ramus of the pterygoid, the width of the palatal vacuities, and shallowness of the whole skull, but it is represented by a single broad, flat individual, so broken that the otic notch cannot be seen. *Procyclotosaurus stantonensis* (*Capitosaurus stantonensis*), Lower Keuper of Staffordshire, is a small animal with a wedge-shaped skull, it has a closed otic notch, the tabular horn, though very narrow, meeting the squamosal. It also has the appearance of being an intermediate between *Parotosaurus* and *Cyclotosaurus* proper. *Subcyclotosaurus brookvalensis* is represented only by an impression in the matrix of a small capitosaur skull in which the tabular horn is a rounded process turned laterally to make a definite approach to a projection of the squamosal behind the position of the tympanic membrane. '*Labyrinthodon*' *jaegeri*, '*L.*' *lavisi*, *Diadetognathus* and '*Mastodonsaurus*' *pachygnathus* are isolated lower jaws, and as such are dealt with on pp. 252 to 254.

Five capitosaurs have been found and described in Russia, the majority apparently of Triassic age. *Wetlugasaurus volgensis* is represented by the hinder corner of a skull, described as *Capitosaurus volgensis* by Hartmann-Weinberg & Kusmin in 1936, with a series of excellent figures. It is clearly 'capitosaurine', but was found with pareiasaurs, and is hence of Upper Permian age. The most interesting features shown are the general rhinesuchid appearance; the comparative shortness of the pterygo-parasphenoid suture, and the effective flatness of this region; the presence of a well-developed stapedial groove on the quadrate ramus of the pterygoid, in which still lies an unusually slender stapes; the constriction of the otic notch by a definite process from the squamosal; and the fact that the quadrate condyles are only a little behind those of the occiput. The figures also show that the exoccipital condyles are paired, apparently the first occurrence of this condition in labyrinthodonts. In general *Wetlugasaurus volgensis* agrees structurally with contemporary South African forms, but differs in three ways: the paired condyles, the shortness of the quadrate ramus of the pterygoid (the distance of the occipital condyle in front of the quadrate condyle, as a ratio of the width across the quadrate condyles, is 1:10, in contrast to about 1:5 in South African forms), and the position of the 'pockets', which are level with the hinder end of the pterygo-parasphenoid suture. These qualities are evidently 'advanced' for the animal's time, but it should not be assumed that other structural features, not shown in the fragment, would necessarily confirm them.

The other Russian forms are *Wetlugasaurus* sp., *Parotosaurus bogdoanus*, *Volgosuchus cornutus* and *Wetlugasaurus angustifrons*, all from the Lower Trias, but the age determinations probably mean very little, their mutual time relationships are unknown, and nothing except the labyrinthodonts themselves throw light on them. Their structure suggests that they are really of essentially the same age, probably not far from the base of the South African *Cynognathus* zone, in which case they would fit excellently into the succession of South African forms, for the occipital condyles are separated from one another, and taken as a whole the distance of the occipital condyle in front of the quadrate condyle is small, contrasting with that in all the Permian rhinesuchids. The apparent identity between *W. angustifrons* and *W. magnus* undoubtedly exists, but it must be remembered that neither of the two specimens is even a complete skull, and it is unsafe to assume that they are of precisely the same age, though evidently they cannot have lived at widely different times.

W. groenlandicus comes from the top beds of the 'Eotriassic' of Cape Stosch, and its age is firmly determined by its position in a sequence which includes a succession of ammonite zones having a worldwide significance. It lies above the *Proptychites* beds, which form the summit of the Lower Triassic, and is thus probably of slightly later date than the other wetlugasaurids. It is represented by rather more than half of the hinder part of a skull, and differs from *W. angustifrons*, the type of the genus, in that the basipterygoid process of the pterygoid is much elongated, and the anterior ramus of the pterygoid is exceedingly narrow (as shown in Säve-Söderbergh's Pl. 1). The differences between them are of a character that could well depend on the somewhat later date of the Greenland form.

According to Lydekker *Gondwanasaurus*, the Bijori labyrinthodont, is of Lower Gondwana age, perhaps just below the Panchets, essentially the same age as *Brachyops laticeps*. *Brachyops* appears from its structure to be an early form of its group, less advanced than *Batrachosuchus* from the South African *Cynognathus* zone. On this evidence *Gondwanasaurus* comes about at the Permo-Triassic junction. I have never seen the specimen, and am hence entirely dependent on Lydekker's description of 1885, which is accompanied by lithographic drawings by Miss G. M. Woodward. Detail of the basicranial and occipital regions is lacking: the only structural evidence as to the systematic position, and hence probable age of the animal, is the general shape, and the outline—though not the details—of the palate. The head is clearly markedly depressed, its width at the hinder end being about five times the height. In association with this the interpterygoid vacuities are exceptionally large, the pterygoid separating the subtemporal fossa from the palatal vacuities being extremely narrow. The junction of the pterygoid with the parasphenoid—although its suture is not shown—is very long. On this evidence it appears to be a late labyrinthodont. The arrangement of the structure called 'epiotic', which at any rate includes the tabular horn, is not capable of interpretation from the drawings, but does not really resemble any capitosaur known to me. Lydekker (1885, p. 5) states definitely that *Gondwanasaurus* 'has no postarticular process' in the lower jaw. This is a primitive condition: even such forms as *Rhinesuchus* and *Rhineceps* from Permian beds already possess a well-developed retroarticular process, and well-marked muscle insertions, and so does *Mastodonsaurus*. On the whole evidence it is singularly difficult to determine the affinities of *Gondwanasaurus*. It does not seem to resemble *Mastodonsaurus* and is in general like the capitosaurs, but the table, known only from the badly marked impression of its lower surface, suggests that the relations for instance of the squamosals (*S.T.*) to the supratemporals (*Sq.* of Lydekker, *sic.*) are not those found in capitosaurs. And finally *Gondwanasaurus* differs from capitosaurs in apparently lacking a retroarticular process. It is thus impossible to use *Gondwanasaurus* in any strict comparison of the beds in which it was found with other successions.

In dealing with figures of specimens, themselves usually inaccessible, only a limited comparison is possible, but I found fifteen structural qualities which were both recognizable and varied. Few specimens were determinable for every quality, but the arrangement of the data in columns in a table allowed a definite comparison to be made between one skull and another, and brought out quite well the differences between them. The general course of evolutionary change in capitosaur-like skulls may be found in my paper of 1919 and the points listed below are additional to them. The series illustrates admirably the proportional decrease in width of the palate lateral to the palatal vacuity. In *Eryops* the ratio is 1:2·3, in *Cyclotosaurus posthumus* it is 1:4·6.

(1) The largest skull known is that of *Parotosaurus albertyni* (probably a cyclotosaur), which is 70 cm in length: the smallest skulls in the series are some 15 cm in length. Out of thirty-one skulls measured, seven were between 50 and 55 cm long. It appears that the bigger forms tend to be later in time.

(2) The early forms tend to have round orbits, in later forms the orbits are oval.

(3) The position of the orbit, with respect to its fellow and to the lateral border of the skull, varies in a random way.

(4) The distinction between 'wedge-shaped' and 'shield-shaped' skulls, even if it may be drawn, seems to have no significance in time distribution.

(5) The distance from orbit to otic notch, divided into total length of skull, gives a figure which tends to increase in the later forms, showing that the nose lengthens disproportionately with time. This is not entirely related to increase in size.

(6) In early forms the otic notch is parallel-sided, or wedge-shaped. Several *Cistecephalus* zone species (e.g. *Laccosaurus* and *Rhineceps*) have begun to close it by small outgrowths from squamosal and tabular. In species from the *Endothiodon* zone, and earlier, the tabular horn tends to be short and blunt; in some *Cistecephalus* zone species it is longer and narrower; in the *Cynognathus* zone species with long, narrow horns predominate, several possessing a tabular which turns markedly outwards towards the squamosal. The trend so established continues until the tympanic membrane is completely enclosed by a meeting of tabular and squamosal, achieved in late Triassic forms.

(7) The braincase (as distinguished from the occiput as a whole) does not show any constant tendency towards flattening with time. For instance, *Parotosaurus* sp. (Parrington no. 48), is nearly a cyclotosaur, and yet the proportions of the braincase are similar to those in *Actinodon* or *Uranocentrodon*. (It may be noted that the posterior surface as a whole is difficult to compare in a complete series of forms because very few figures of it exist; the large flattened skull tends to be crushed, even though the braincase may show little sign of distortion.)

(8) There is a continuous exoccipital-basioccipital condylar surface in *Actinodon*, *Eryops*, *Melosaurus*, and all South African forms up to the end of *Cistecephalus* zone times (see reinterpretation of *Rhinesuchus whaitsi*, p. 227). In tetrapods in general the basioccipital—if present as bone in the cartilaginous skull base—takes part in the condyle: in the Russian labyrinthodonts included in the table a basioccipital bone sometimes occurs, but does not contribute to the condyle. A small basioccipital is similarly present in

Wetlugasaurus magnus, and in *Parotosaurus* sp. (B. 192) it is considerably better developed, surrounding the anterior end of the notochord, and connecting the exoccipitals but still not taking part in the condyle. Information about the bone is lacking in most other capitosaurs, and in cyclotosaurs it is represented by cartilage.

(9) The otic flange forming the hind wall of the stapedial groove is probably absent in *Actinodon* and *Eryops*, but is seen throughout the rest of the series in cases where suitable preparation has been possible.

(10) The anterior palatal vacuity may be single, paired, or even absent.

(11) In early forms the 'pockets' for the recti capitis muscles are widely separated, and lie far back near the occipital condyles. They move steadily forward with time, tending to become less deep, and to approach one another, until in forms later than the end of *Cistecephalus* zone times in South Africa they are on the level of the hinder end of the pterygo-parasphenoid suture. In later Triassic forms such as *Paracyclotosaurus* they become less marked, and ultimately may almost vanish, as in *Cyclotosaurus posthumus*. In all forms up to the end of the South African *Cistecephalus* zone the lip of the 'pocket' passes out onto the lateral surface of the exoccipital well behind the posterior end of the pterygo-parasphenoid suture.

(12) The boss on the quadrate, although very conspicuous in my specimen of *Wetlugasaurus magnus*, does not show well in photographs or drawings, hence it is not possible from figures to be sure whether or not it is there. The boss is, however, absent in both *Actinodon* and *Eryops*. It is present—though small—in *Rhineceps*, *Parotosaurus* sp. (B. 190), *Parotosaurus* sp. (B. 192), and *Parotosaurus* sp. (Parrington, no. 48), and is probably present in *Volgasuchus*, *Wetlugasaurus angustifrons*, *Parotosaurus nasutus* and *P. haughtoni*.

(13) The ventral border of the posterior end of the lower jaw may be flat, with the retroarticular process on the same level, as in *Wetlugasaurus magnus* and '*Labyrinthodon*' *lavisi*, or it may be curved, so that the retroarticular process lies well above the ground, as in *Rhineceps* and *Paracyclotosaurus*. These two types of jaw seem perfectly recognizable, and there are no obvious intermediates between them.

(14) The retroarticular process is not present in *Eryops*; it becomes progressively bigger and more elaborate with time in both the groups mentioned above.

(15) There is a progressive change in the glenoid cavity of the lower jaw shown by a series from *Eryops* to *Wetlugasaurus magnus*. In *Eryops* it is shallow, wide transversely and short antero-posteriorly. In *Wetlugasaurus* it is deep, and the inner part has become elongated spreading forward as a long groove. This suggests that in *Eryops* the jaw was capable of some lateral movement and did not work with the accuracy implied by the structure of that of *Wetlugasaurus*.

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Explanation of abbreviations used in figures

Ang.	angular
Art.	articular
B.Oc.	basioccipital
B.Pt.	basipterygoid
B.Pt.Proc.	basipterygoid process
B.Sp.	basisphenoid
Bl.Ves.	blood vessel
Boss	boss on quadrate
Car.Art.	carotid artery
Car.For.	carotid foramen
Cor.	coronoid
D.S.Oc.	dermosupraoccipital
Dent.	dentary
Dent.For.	dental foramen
E.Pt.	epiterygoid
?*Ec.Pt.*	?ectopterygoid
Ex.Oc.	exoccipital
Ex.Oc.Art.	exoccipital component of condyle
Ex.Oc.Cond.	exoccipital condyle
For.Mag.	foramen magnum
Fr.	frontal
Int.Na.Vac.	internarial vacuity
Ju.	jugal
Lac.	lachrymal
Mx.	maxilla
Na.	nasal
Noto.	notochord
Oc.Cond.	occipital condyle
Ot.Fl.	otic flange
P.Mx.	premaxilla
P.O.	postorbital
P.T.F.	post temporal fossa
Pal.	palatine
Par.	parietal
Par.Oc.	paroccipital
Par.Sp.	parasphenoid
Pin.	pineal
Pit.Fos.	pituitary fossa
‘*Pocket*’,	point of attachment of recti capitis muscles
Pr.Art.	prearticular
Pr.Fr.	prefrontal
Pr.Ot.	prootic
Pr.Vo.	prevomer
Pt.	pterygoid
Pt.Fl.	pterygoid flange
Pt.Fr.	postfrontal
Pt.Qu.Ram.	quadrate ramus of pterygoid
Pt.Spl.	postsplenial
Qu.	quadrate
Qu.Boss	boss on quadrate
Qu.J.	quadratojugal
S.Ang.	surangular
S.Mx.	septomaxilla
S.Oc.	supraoccipital
S.Tem.	supratemporal
Sph.Eth.	sphenethmoid
Spl.	splenial
Sq.	squamosal
St.	stapes
St.Fac.	facet for articulation of stapes
St.Gr.	stapedial groove
Tab.	tabular
II	optic nerve
XII	twelfth nerve