ON ANEUGOMPHIUS ICTIDOCEPS BROOM AND ROBINSON

By A. S. Brink

Abstract

The type specimen of *Aneugomphius ictidoceps* Broom and Robinson (1948), after additional development with the acetic acid technique, is now described in greater detail. It is declared a valid genus and species and not, as hinted, an immature specimen of one of the existing members of the Whaitsiid family. Suggestions as to its exact relationship are made, but definite conclusions can be reached only after the genera *Lycideops, Hofmeyria, Alopecopsis* and *Notaelurops* are better known.

Introduction

In 1948 Broom and Robinson described a small Whaitsiid Therocephalian, discovered by Mr. J. W. Kitching on the farm Hoeksplaas in the Murraysburg district, as a new genus and species, *Aneugomphius ictidoceps*. This specimen is registered as No. 11 in the collection of the Bernard Price Institute. At the time of description the skull was superficially cleaned and considering the limited amount of information then displayed, the description is surprisingly comprehensive and detailed. Subsequently, in 1954, the present author mentioned *Aneugomphius* in a paper dealing with some semi-prepared Whaitsiids in the collection of the Bernard Price Institute, where an endeavour was made to indicate some grounds for establishing relationships within the family; but *Aneugomphius* was then not yet additionally developed and on the strength of existing information its exact relationship was left undecided, except for a casual suggestion that it might be more closely related to *Alopecopsis* than to any other Whaitsiid genus. In a paper by Watson and Romer (1956) on Therapsid classification, *Aneugomphius* is queried as probably an immature *Whaitsia,* which seems so unlikely that the author decided to make a new investigation into this specimen. At any rate, the specimen is so beautifully preserved, almost perfectly complete and very little distorted, that it seemed regrettable that its relationship and more of its detailed structure should remain obscure.

Technique

The matrix is so hard and solid, and the specimen itself so delicate, that ordinary preparation techniques could not be further employed without risk of serious damage, while the specimen proved to be more vulnerable to acids than the matrix. After some experimenting it was found that 20% acetic acid was less dangerous than any other concentration, or any other acid, but the specimen itself nevertheless remained grossly vulnerable.

For protection of the specimen a diluted solution of one part glyptal* to two parts

* See paper in this volume.

thinner was used and already exposed surfaces were covered with 4-5 coats. The specimen was subjected to the acid for periods of 5-6 hours, at average room temperature (70°-80°), which allowed the acid to corrode the matrix not more than to a depth of about 1 mm at a time. All exposed bone surfaces were therefore coated with an overlap on to the matrix of 1-2 mm. After every subjection to the acid the specimen was briefly washed in water. Then the specimen was manually prepared with dental probes and scrapers under binocular enlargement, the glyptal marginal "frills" also removed and thereafter left to wash overnight. After drying it was briefly subjected to a thinner bath (2-5 minutes) to allow pores and cracks in the glyptal to "heal". Then the whole specimen was given an additional coat of diluted glyptal, while newly exposed surfaces and new overlaps were given 4-5 coats. When the thickness of the matrix covering a bone surface became reduced to less than a millimeter, the surface of the matrix was given 1-2 coats of diluted glyptal, which allowed a certain degree of penetration and resulted in the matrix being attacked to lesser depths than over exposed areas. The acid was rarely allowed to reach the specimen; when the acid reduced the matrix to a thickness of a fraction of a millimeter, it could be made to flake free in small fragments by applying pressure with a dental scraper along sharp edges in a direction parallel to the surface of the bone.

After every fifth subjection to the acid, the specimen was washed with the aid of an artist's oil-paint brush in a thinner bath to remove as much glyptal as possible, so that fresh glyptal could be applied and to allow structure to be studied more clearly from time to time.

The specimen was placed in the acid at about 9 o'clock in the morning and removed at about 2 o'clock the same afternoon and then, after a brief wash in clean water, directly prepared manually while wet, first by brushing sediment off under water with an oil-paint brush, then probing to investigate depths of corrosion, and finally scraping, after the bulk of the sediment was removed and there was little danger of the sediment obscuring detail. The specimen was continually washed in water to prevent it from drying and forming crystals. The reason for preparing the specimen manually while wet is because the difference between matrix and bone showed up better. After complete manual preparation during the afternoon, the specimen was left overnight to wash in water to which a small quantity of ammonia was added. The following morning it was dried and the same afternoon it was treated with glyptal, the specimen then left overnight for the glyptal to dry properly, so that the whole cycle lasted two days. With short interruptions from time to time, preparation was eventually ceased after three months.

Matrix was intentionally left in certain strategic areas, only for strength but where structural detail is not seriously obscured, such as below the postorbital bars, deeply inside the brain case and nasal cavities where structure can at any rate not be studied, and as a pillar between the pterygoids and frontals.

Structure

The skull of *Aneugomphius ictodoceps* gives no indication that it is very juvenile. All sutures are well closed, some so well fused that they are traced with great

difficulty. There is no indication of active tooth replacement in the incisors while in the toothless post-canine region there is no sign of vestigeal teeth having recently been lost, as suggested by Broom and Robinson (op. cit.). There are two canines, a large anterior and a small posterior tooth and the latter is not replacing the former, because the two teeth are distinctly rooted each in its own socket, into which the anterior ones fit fairly tightly. The shorter third right incisor is not sufficient for considering the specimen as very juvenile, because tooth replacement does occur in Theriodont reptiles up to a fairly mature stage. The second smaller canine is younger than its larger anterior partner, because it shows at about the middle of its length a small pulp cavity, while the anterior canine is solid at the same level. Perhaps, with further increase in age, the posterior tooth may grow to be the larger of the two, as appears to be the case in the lowerjaw. Apparently the anterior canine is fully grown, while the posterior tooth had progressed far in replacing its own predecessor. While the anterior canine is firmly rooted in its socket, the posterior one is loosely lodged in a socket even larger than that of the anterior tooth.

The *basioccipital* (bo, figs. 35, 38) forms the central lobe of the distinctly trilobed occipital condyle. The structure of the condyle is not unlike that of *Ictidosuchops* as demonstrated by Crompton (1955), the only difference being that the basioccipital lobe appears to be similar in size to the exocciptial lobes, while in *Ictidosuchops* it is distinctly the largest of the three. Unfortunately, in the mechanical preparation of the skull for the original description, a dental grinding stone was used on the occiput, whereby the condyle as a whole was abraded to such an extent that it is not possible to ascertain whether the basioccipital lobe actually formed the principal area of the articulation surface as in *Notaelurops, Notosollasia* and *Whaitsia,* or whether the exoccipital lobes extended farther back, forming the principal articulation areas, as in *Bauria.*

The suture between the basioccipital and parashenoid is very indistinct. It appears to run straight transversely across a depression between the basisphenoid bulges on the ventral margins of the fenestra ovales (fo). The concavity on the ventral surface of the relatively short basioccipital therefore extends some three millimeters forward of the parasphenoid suture, to where the latter bone starts forming its median keel. On the right side a small section of the basioccipital-parasphenoid suture can be seen, showing very distinctly that the latter bone overlaps the basioccipital as a thin film of bone, thus covering the actual basioccipital-basisphenoid contact ventrally near the midline. Laterally, near the ventral margins of the fenestrae ovales, this latter suture must be exposed and it cannot be unlike the arrangement as figured. The actual "suture" can be seen, but not as a suture — it appears as a free margin against matrix bulges, and this applies for the parasphenoid as well in these regions. These matrix bulges appear to represent cartilaginous portions of the basisphenoid and their presence should not be interpreted as indicative of immaturity, because this arrangement appears to be quite general even in fully mature Therocephalians.

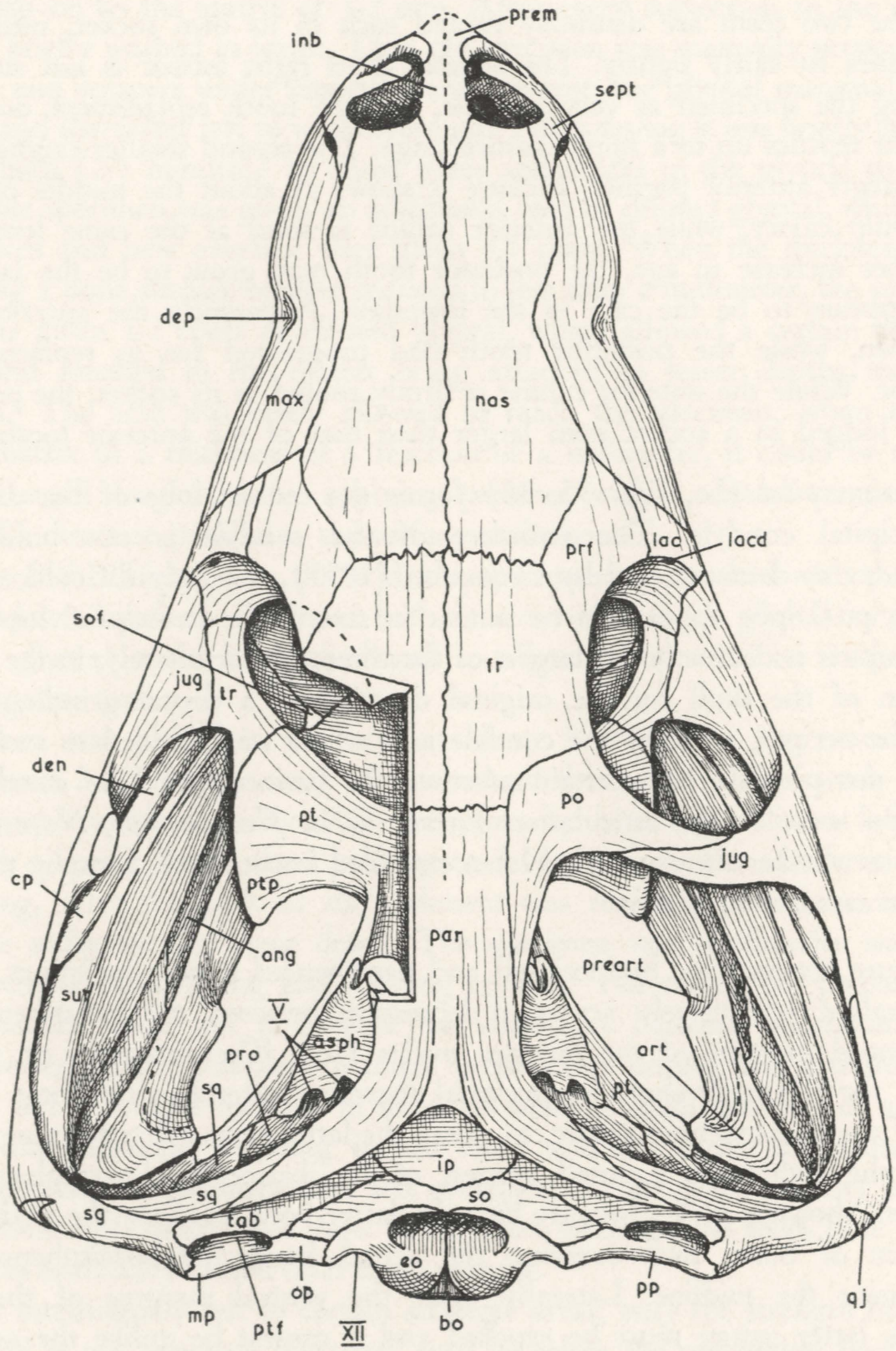

Fig. 34—Dorsal view of the skull of Aneugomphius ictidoceps, left postorbital arch and part of skull roof removed to illustrate the suborbital region more clearly. Twice natural size. For abbreviations see page 114.

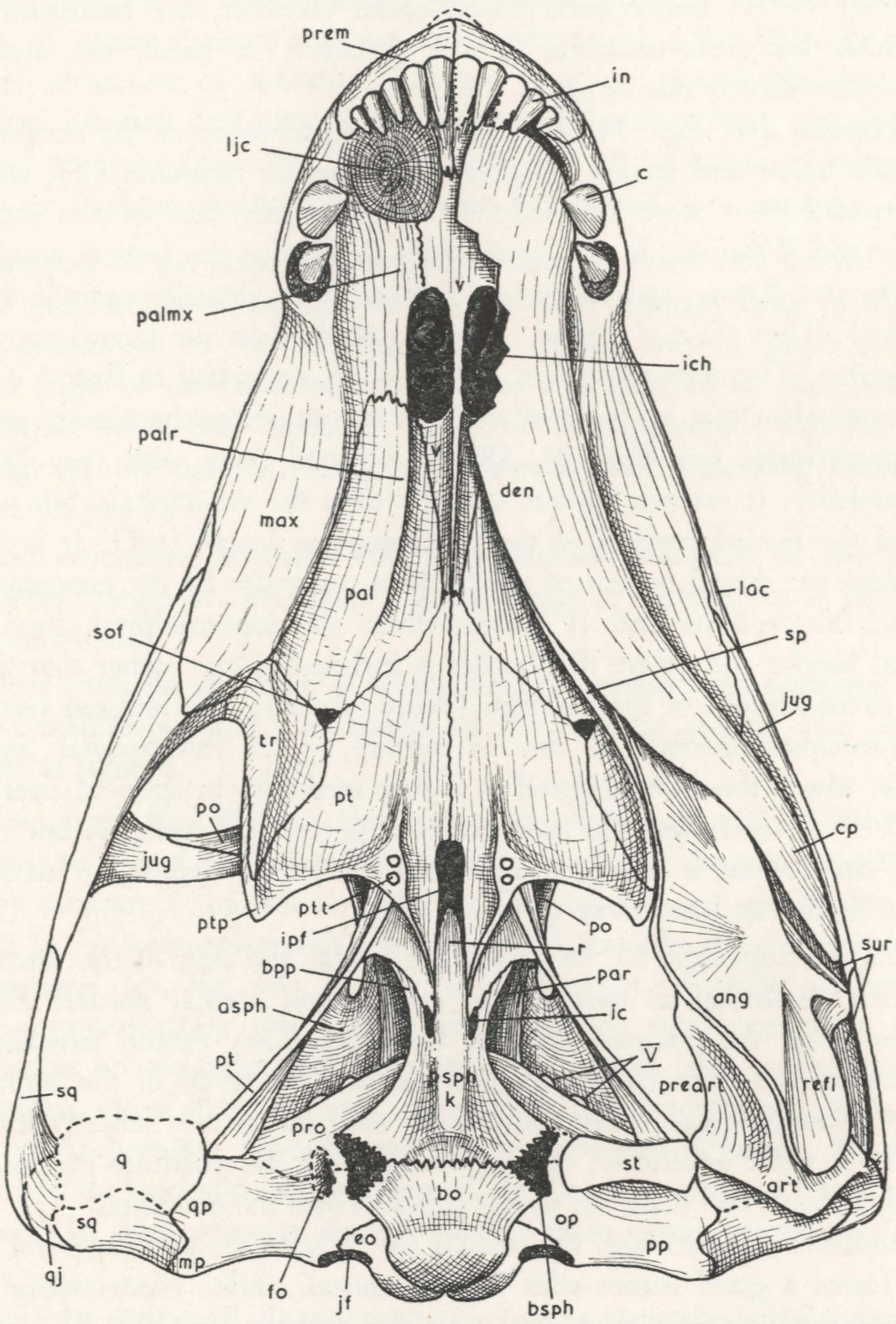

Fig. 35—Ventral view of the skull of Aneugomphius ictidoceps, right ramus of lower jaw removed to show palatal detail. The anterior palatal region, in front of the internal choanae, is illustrated after Notosollasia. Twice natural size. For abbreviations see end of article.

The structure of this region is very similar to that of *Ictidosuchops*. In *Notosollasia* the basioccipital is longer and its suture with the parasphenoid curves forward. This can be interpreted as insufficient overlap by the parasphenoid. In *Bauria* the basioccipital is very long, and the parasphenoid reaches so little backward, that there may be no basioccipital-parasphenoid contract, the basisphenoid suture being exposed, but unfortunately, in the specimen at hand, the suture is not distinguishable, evidently due to age.

The *exoccipitals* (eo, figs. 34, 38) form the lateral lobes of the occipital condyle and the whole upper and medial margins of the jugular foramina (jf), which in this genus is situated even more distinctly on the posterior face of the skull than in *Notosollasia* and *Whaitsia*. It also contributes slightly to the ventral margins, unlike *Ictidosuchops* and *Bauria*, and together the exoccipitals virtually encircle the foramen magnum (fm). They do not extend farther laterally than the lateral margins of the jugular foramina. The arrangement in *Notaelurops*, according to Broom's restoration (1936), is not unlike that of *Notosollasia* and not quite like the present specimen.

The *supraoccipital* (so, figs. 34, 38) is a broad bone with very little height, especially medially. It extends farther laterally than the exoccipitals, but not quite to the levels of the medial borders of the post-temporal fossae (ptf). It is very nearly separated from the dorsal border of the foramen magnum by the exoccipitals, unlike *Notaelurops, Notosollasia* and *Whaitsia*, where the supraoccipital does form part of the dorsal border and where this border is inclined to rise higher than the general line of the circumference of the foramen (*Notosollasia*). The reduced vertical height of the supraoccipital medially is due to overlap by the interparietal, again unlike *Notosollasia*, where the supraoccipital is higher medially, in spite of overlap by the interparietal. In *Notaelurops* the supraoccipital is reduced medially, but the general structure of the occiput is different from that of *Aneugomphius*, on account of the region being higher and narrower (see fig. 38).

The *opisthotics* (op, figs. 35, 38) form the lateral and part of the ventral borders of the jugular foramina, as well as the ventral and medial borders of the post-temporal fossae on the posterior face of the skull. They extend laterally as fairly stout paroccipital processes (pp), not much beyond the levels of the lateral margins of the post-temporal fossae, where posteriorly they bulge very slightly into mastoid processes (mp), while anteriorly, on the ventral side, the quadrate processes are not quite as insignificant, and there are strong contacts with the quadrates.

The opisthotic articulates with the tabular medially to the post-temporal fossa, and laterally it forms a good suture with the squamosal, unlike *Notosollasia* where the contact is more delicate. It does not meet the tabular laterally. The paroccipital process is on the whole more robust in *Notosollasia* and *Whaitsia*.

The post-temporal fossa is small, unlike *Notaelurops, Notosallosia* and *Ictidosuchops*. There appears to be a distinct anterior wall to this fossa, as in *Ictidosuchops*, covered anteriorly by an "otic" flange of the squamosal. The post-temporal fossa opens into the temporal vacuity over this wall and between the "otic" and "parietal" flanges of the squamosal.

The *prootics* (pro, figs. 35, 36) could not be disected in detail with the aid of the acid technique, the structures in the area being too delicate. Alternatively, the matrix is so hard and solid that mechanical preparation could not be used. Judging from what could be exposed, the nature of the prootic is comparable with that of *Ictidosuchops*. Ventrally it communicates with the paroccipital process in the region of the stapes. A suture cannot, however, be distinguished, a circumstance preferably interpreted as indicative of maturity, because, however remarkable the points of comparison are between the present specimen and *Ictidosuchops,* the former is a Whaitsiid and removed from the Scaloposaurid line of evolution to mammals and the structure as a whole should rather not be interpreted as a periotic.

From the region of the stapes the prootic extends forward and inward above the parasphenoid and forms the posterior wall of the large pituitary fossa (pitf). On the dorsal side, posteriorly to the alisphenoid, it appears over a small area in the posteromedial angle of the temporal fossa. Here it is covered by the "otic" flange of the squamosal, while the "parietal" flange of the squamosal, together with the occipital flange of the parietal, forms a horizontal shelf extending forward some distance above the prootic.

The prootic articulates laterally with the quadrate extension of the pterygoid, around the outer margin of the pituitary fossa, where it appears not to be in contact with the quadrate itself.

It is not clear from the specimen to what extent the prootic and opistiotic intervene between the basisphenoid and the margin of the fenestra ovalis. The most likely arrangement is as figured.

The *tabulars* (tab, fig. 38) are flat bones extending outward on either side of the interparietal to a level not beyond the lateral margins of the post-temporal fossae, to which they contribute the dorsal margins. The tabulars are clearly broader and less high than in *Notaelurops* and *Notosollasia,* and very like those of *Ictidosuchops.*

The *interparietal* (ip, fig. 38) is very small, but not relatively smaller than in *Notosollasia.* Unfortunately the dental grinding stone used previously destroyed much information on the exact sutural relationship of this bone to those around it. It is nevertheless clear that the area covered by the interparietal is not deeply depressed as in *Alopecopsis, Notaelurops, Notosollasia* and *Whaitsia.* Neither is the dorsal border of the occipital region, formed by the parietals, as clearly crested as in these genera. In these respects *Aneugomphius* again agrees remarkably well with *Ictidosuchops.*

On the whole the occiput of *Aneugomphius* is convex vertically and flat transversely. In *Ictidosuchops* it is also flat transversely, but slightly concave vertically, while in the other Whaitsiids it is deeply concave both ways as a result of the more strongly developed occipital crests.

The *parietals* (par, figs. 34, 36) do not form a sharp crest. They are indistinguishably fused; no suture can be seen between them in the region posterior to the "parietal foramen".

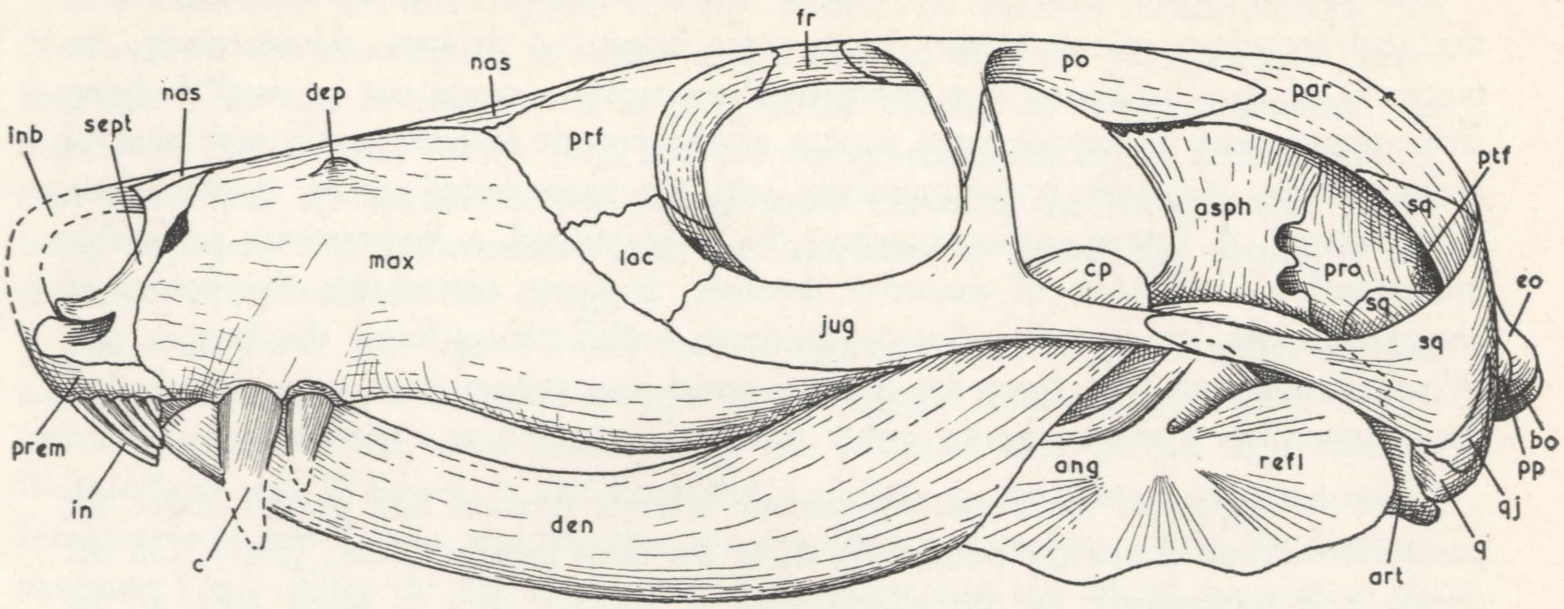

Fig. 36—Side view of the skull of Aneugomphius ictidoceps. Twice natural size.

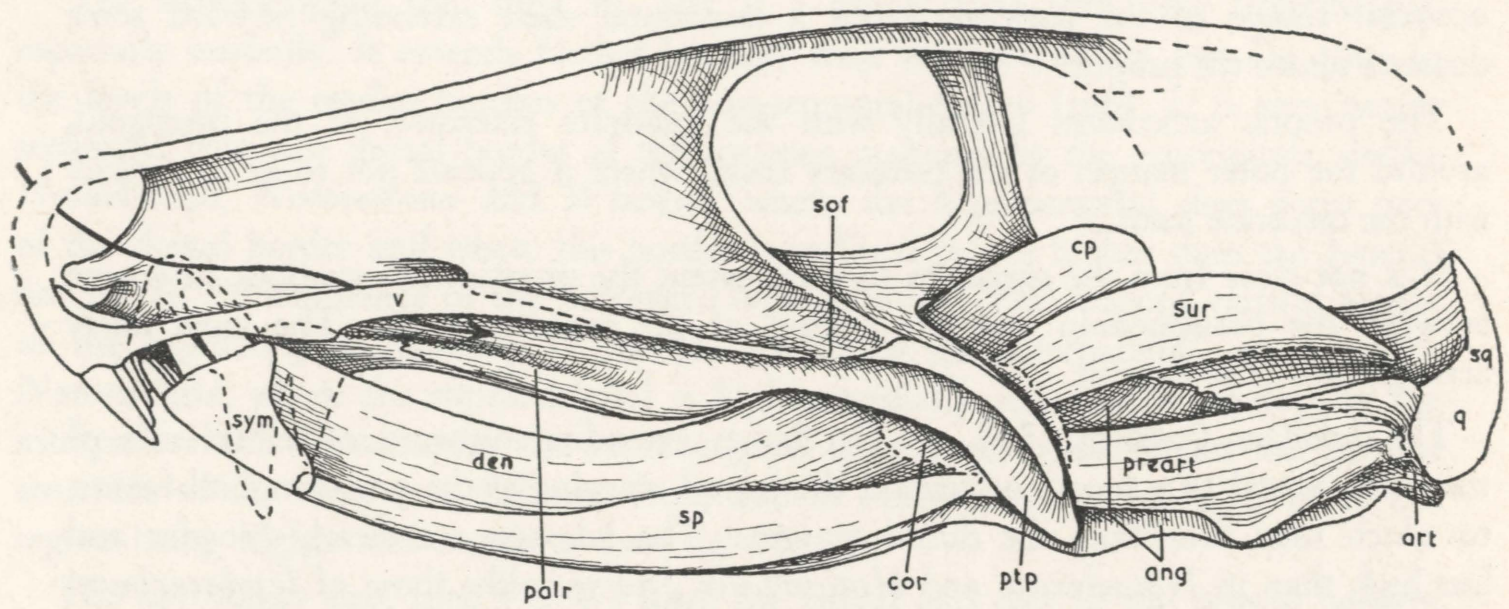

Fig. 37—Complex section through the skull of Aneugomphius ictidoceps to display the medial view of the lower jaw and some related skull structures. The section is median anteriorly. In the region of the pterygoids the section is through the right suborbital foramen. Posteriorly it is through the articulation region, not affecting the lower jaw. Twice natural size. For abreviations see end of article.

In general the parietals are very like those of *Ictidosuchops,* including the extensions to the squamosals, and where they form an insignificant but nevertheless distinct ridge on the border of the occiput. In *Bauria* the parietals form a fairly distinct interparietal crest and quite pronounced crests on the occipital border. These crests are considerably more exaggerated in the other Whaitsiids.

The region where a parietal foramen could be located, is damaged by a vertical transvere fracture, so that neither its actual presence nor its nature could be established.

As stated above, the parietals fold in the shape of a forward extending shelf over the region of the anterior face of the prootic, where they communicate with the "parietal" processes of the squamosals. This arrangement is surprisingly like that of

Ictidosuchops and *Bauria,* but the higher occipital crests create a different impression in *Notosollasia* and the larger *Whaitsia* specimens, although, in *Whaitsia pricei,* where the occipital crests are not as pronounced, the arrangement is again more similar.

The *postorbitals* (po, figs. 34, 36) extend far back on either sides of the parietals, farther than in *Notosollasia* or *Whatsia,* and they form the medial, anterior portions of very delicate but complete postorbital bars. Their sutures with the frontals do not rise into distinct ridges as in *Notosollasia* and they extend very distinctly farther forward and inward over the interorbital region, more as in *Alopecopsis.* The postorbitals are widely separated. In *Whaitsia pricei,* where this region is also broad and apparently not sharply crested (the region is somewhat damaged), the postorbitals nevertheless approach one another closely, thus lying more dorsally to the parietals, than laterally as in *Aneugomphius.*

The *frontals* (fr, fig. 34) form practically the whole of the interorbital region and the area is flat — not depressed as in *Notosollasia* (it is, however, artifically depressed). In spite of the greater extent to which the postorbitals contribute to the dorsal borders of the orbits, the contribution of the frontals to these borders is still greater than in *Notosollasia* and *Whaitsia,* due to the prefrontals not extending as far back. This arrangement is exactly like that of *Alopecopsis.*

Each frontal has a longitudinal ridge on its ventral surface, continuous with the inner margin of the anterior wall of the orbit. Between these two ridges there could have been an orbitosphenoid enclosing the olfactory lobes. There are traces of a very delicate bone in this region, but the exact relationship could not be established.

The *prefrontals* (prf, fig. 36) form the anterior halves of the dorsal borders, and the upper halves of the anterior borders of the orbits, where they also form distinct walls extending straight inward for a distance of about five millimeters, inclining to separate the orbits from the general nasal cavity. The acid was allowed to penetrate

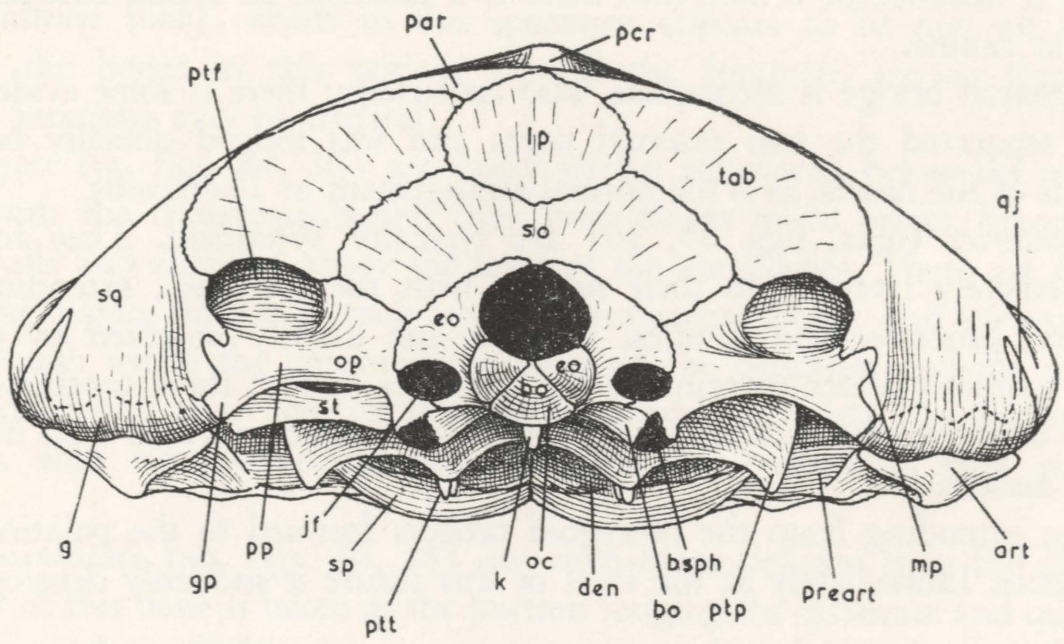

Fig. 38—Posterior view of the skull of Aneugomphius ictidoceps. Twice natural size. For abbreviations see page 114.

some distance forward of these walls into the nasal cavity, but not far enough to establish the relationship, if any, between the prefrontals and palantines, or the nature of the area where the anterior oblique muscles of the eyes were inserted.

The anterior walls inside the orbits, formed by the prefrontals, are formed ventrally by the lachrymals and dorsally they continue as ridges over the ventral surfaces of the frontals.

The *lachrymals* (lac, figs. 34, 36) are very small. They show over small areas on the sides of the snout and they contribute very little to the anterior walls within the orbits. The lachrymal foramen is very insignificant. The lachrymals have little transverse thickness, except where they form the anterior walls of the orbits.

The *nasals* (nas, fig. 34) are broader posteriorly than anteriorly and are constricted exactly at the middle of their lengths. In general they agree in shape with *Alopecopsis*. They are shorter and broader than in *Notosollasia,* and their breadth posteriorly, in the middle and anteriorly, differs more conspicuously than in *Whaitsia platyceps*. In *Whaitsia pricei* the general shape is similar.

The *septomaxillaries* (sept, figs. 34, 36) could not be clearly displayed because of their delicate nature, but their general shape and relationships to the nasals, premaxillaries and maxillaries cannot differ much from the way they are illustrated in the figures. There are large openings between the septomaxillaries and the maxillaries, and horizontal bridges formed by the septomaxillaries do tend to separate infra-narial fossae from the external nares, but these bridges apparently do not meet medially.

The *premaxillaries* (prem, figs. 35, 36) carry five teeth each. The teeth are long, slender and sharply pointed. They decrease in size laterally, from the first to the fourth, with the fifth considerably smaller. This is the typical Whaitsiid arrangement, but in *Alopecopsis* there are six incisors on each side. The teeth incline backward at angles which are certainly artificially exaggerated. Together the incisors of one side occupy a distance of 6 mm, and there is a diasteme of 3 mm between the fifth and the first canine.

The internarial bridge is incomplete, also artificially; there is some evidence that it completely separated the two external nares and was lodged dorsally between the anterior ends of the nasals, as is the normal arrangement in Therapsids.

The *maxillaries* (max, figs. 35, 36) are typically Whaitsiid. They form strong ridges immediately laterally to their sutures with the palatines, extending between the pterygoid processes and canines, along a line usually occupied by post-canine teeth. The toothless upper margins of the dentaries oppose these toothless maxillary ridges, and doubtless, both dentaries and maxillaries were provided with horny plates suitable for mastication.

The ridge extending from the pterygoid process forward to the palatine-maxillary suture is feeble. Immediately at the level of this suture it suddenly develops to great prominence.

Anteriorly there are two canines. The anterior canine is the larger and appears to be fully grown and firmly planted in its socket. The posterior smaller canine has

a separate socket larger than that of the anterior canine, in which it fits loosely. It is a young tooth, judgng from its pulp cavity, and is evidently not yet fully erupted, after replacing its own predecessor. It may grow to a size larger than the anterior canine.

The presence of two canines is peculiar. There are two canines in *Moschorhinus,* but the small anterior canine in this genus functions more like an incisor. A more similar arrangement to that of *Aneugomphius* in a not too distant ally is found in *Lycideops.*

There is a small depression (dep) dorsally on the lateral face of the maxillary, near the nasal suture, reminiscent of similar depressions in the higher Cynodonts. This depression is not present in other Whaitsiids, but it is vaguely present in *Ictidosuchops.* If this depression is to be interpreted as being of similar nature to that of *Diademodon* and *Cynognathus,* we have some evidence that certain advanced mammalian characteristics in the higher Therapsids are not only confined to higher Cynodonts (see Brink on advanced mammalian characteristics in the higher Therapsis, published in the present journal). In *Whaitsia pricei* the outer surfaces of the maxillaries in the region of the canines excellently demonstrate a conspicuous pitted nature, which could be interpreted as due to the supporting of ornamental scales, but in view of the possible condition in advanced Cynodonts, it is perhaps more likely that these pitted areas indicate a richly glandular skin, probably with vibrissae-like hair.

The *transverse* bones (tr, figs. 34, 35) are fairly large and form much of the lateral faces of the pterygoid processes, thus intervening between the latter and the lower jaw. However, posteriorly and dorsally, on the side of the orbits, the pterygoids do extend to the outer surface guiding the lower jaw.

The transverse bone extends forward into the angle between the maxillary and palatine. Laterally it communicates with the jugal and medially it does not quite fill the angle between the palatine and pterygoid, leaving a small aperture — the suborbital foramen (sof), which in this specimen appears to be not yet fully closed. However, the bones in this region, around the foramen, are so thin that these suborbital foramina may be artifical.

The *jugals* (jg, figs. 34, 36) are fairly strong anteriorly, below the orbits, where, together with the transverse bones, they form floors to be orbits, broader than the anterior walls and elevated above the level of the maxillaries. There are deep notches between the jugals on the outside and the transverse bones and pterygoids on the inside, through which the coronoid processes of the dentaries and the anterior ends of the surangulars pass upward into the temporal vacuities. Posteriorly the jugals contribute, with two feeble processes each, to the postorbital bars and temporal arches.

The *squamosals* (sq, figs. 36, 38) are even more delicate than the jugals. If the main body of this bone is taken as the portion lodging the quadrate and quadratojugal, then there are three distinct processes — one extending forward to contribute to the temporal arch (a process not quite as delicate as that of the jugal), one contributing

with the parietal to the occipital crest ("parietal" process) and one extending forward and inward over the anterior faces of the parocciptal and prootic ("otic" process) above the pterygoid extension to the quadrate. On the whole the squamosal appears very like that of *Ictidosuchops,* but the "otic" process could not be dissected in detail. The post-temporal fossa opens forward into the temporal vacuity between the "parietal" and "otic" processes, with the prootic bordering it on the inside.

The *quadrates* (q, figs. 35, 38) are both preserved, but they are not too well exposed by the acid and the regions on both sides are too delicate for risking mechanical preparation.

The *quadratojugals* (qj, figs. 36, 38) are clearly visible as small wedges laterally to the quadrates, penetrating the squamosals.

The *stapes* (st, figs. 35, 38) is a short, stout, solid bone, with no stapedial foramen and not conspicuously constricted in the middle. Only the left stapes is preserved.

The *Vomer* (v, fig. 35) appears to be typically Whaitsiid. Although the anterior portion in the region of the small secondary palate could not be displayed properly, on account of the jaws being in situ, the palate as a whole is so typically Whaitsiid that the arrangement as figured cannot be far from correct. There is, however, the possibility that the region between the canines could be similar to that of *Theriognathus microps* (Boonstra, 1934). The vomer should communicate with the premaxillaries exactly between the pits into which the lower jaw canines close (ljc), judging from the condition in *Notosollasia,* with which the palate of *Aneugomphius* shows the most striking resemblance. The actual communication with the small palatal plates of the maxillaries (palmx), as in *Notosollasia,* could not be seen, but the extent of the palatine relative to this small secondary palate can be seen and is as figured.

Although the secondary palatal portion of the vomer could not be exposed, it is clear, judging from the palatal ridges (palr) extending forward to its posterior border, that this horizontally flattened section is at a level some distance below the posterior horizontally flattened section in the primary palate. The two horizontally flattened sections are linked with a vertically flattened plate, rising medially as a crest on the ventral side of the posterior horizontal section (this can be seen in the specimen) and evidently continuing as a crest on the dorsal side of the anterior horizontal section, as in *Notosollasia.*

The posterior horizontal section tapers backward and communicates very narrowly with the anterior ends of the pterygoids. Laterally it is flanked by the palatines, and anteriorly, in *Notosollasia,* it has free concave crescentic borders on either side of the vertical section. These borders and the posterior borders of the secondary palate circumscribe the structural internal choanae (ich), but the functional choanae were evidently situated behind a soft secondary palate extending between the palatal ridges (palr), at about the level of the vomerine-pterygoid contact.

There is a peculiar similarity in structure and nature of the vomer and palatal ridges between *Aneugomphius* and *Ictidosuchops intermedius.*

The *palatines* (pal, fig. 35) are exatly like those of *Notosollasia*. Their dorsal surfaces on the side of the nasal cavity could not be exposed satisfactorily, except at their very posterior extremities on the floors of the orbits, where they endeavour, with the pterygoids and transverse bones, to close the suborbital foramina. Ventrally, on the side of the palate, they form prominent palatal ridges at the level of the elementary secondary palate (in *Notosollasia*) and there can be little doubt that a soft palate extended from the one ridge to the other. In the region of the functional choanae the primary palate is flat, with no grooves or ridges, and it appears likely that the free posterior margin of this soft palate closed against the primary palate while the animal masticated and swallowed food.

The *pterygoids* (pt, fig. 35) taper forward to very narrow contacts with the vomer. They extend laterally and ventrally into distinct pterygoid processes, but the lateral surfaces of these processes are largely formed by the transverse bones. In front of these processes on the palatal surface, covering areas which include fairly large portions of the transverse bones and the "apparent" sub-orbital foramina, there are slight but nevertheless distinct depressions. Exactly between the pterygoid processes, on the midline, is a distinct longitudinal interpterygoid fossa and on either side of this fossa there is a process carrying two teeth arranged longitudinally. These processes send short ridges forward over the general palatal surfaces on the pterygoids, defining the medial margins of the depressed areas around the sub-orbital foramina. More prominent ridges extend from the tooth-bearing bulges posteriorly and inward to form the ventral margins of distinct flanges which articulate intimately with not very distinct basipterygoid processes of the basisphenoid, with the parasphenoid evidently intervening. The upper margins of these flanges swing outward, losing contact with the parasphenoid and become free anterior margins to the large pituitary fossae (pitf), these margins flattening out against the flat inner surfaces of the pterygoid extensions to the quadrates. The actual ventral margins of these extensions arise immediately dorsally to the tooth-bearing bulges; on the side of the orbits, with distinct excavations between them and the ridges forming the ventral margins of the flanges articulating with the basipterygoid regions. The dorsal margins of the quadrate extensions also arise in the area above the tooth-bearing bulges and remain free for some distance while these extensions themselves grow higher and flatter backward, and are then continued as free anterior margins to the alisphenoids. The rest of the actual pterygoid margins are in sutural contact with the ventral margins of the alisphenoids and more posteriorly they contact the prootics, the "otic" squamosal processes and the quadrates. The ventral margins remain free up to the quadrates. There are no pterygo-parocciptal foramina.

The *alisphenoids* (asph, figs. 34, 35, 36) contribute fully to the side walls of the brain case. They are broad, flat, with free anterior margins. Dorsally they articulate with downward extending ridges on the parietals; and ventrally with the dorsal margins of the pterygoid extensions to the quadrates. Posteriorly their margins appear to overlap the prootics, to some small extent, but on each side two large

foramina are provided for the exit of branches of the Trigeminus nerve. On the whole the alisphenoids are typically Whaitsiid and unlike those of *Ictidosuchops*.

The *parasphenoid-basisphenoid* (psph, bsph, fig. 35) relationship cannot clearly be established, but it appears that only the parasphenoid is visible in ventral view, except at the margins of the fenestrae ovales where the basisphenoid was apparently exposed as bulges, evidently cartilaginous, as these bulges are represented in the specimen by matrix. Medially the parasphenoid extends backward beyond the basisphenoid — basioccipital suture. The parasphenoid forms a distinct keel between the basioccipital suture and the interpterygoid fossa. The keel is not as pronounced as in *Notosollasia* or *Whaitsia,* but similar in nature, and unlike the insignificant little ridge separating the internal carotid foramina in *Ictidosuchops*. Anteriorly, at the level of the basipterygoid articulations, the keel becomes reduced and passes up over the interpterygoid fossa as the rostrum. The internal carotid foramina are enlongated and their anterior margins are bordered by the pterygoid flanges.

The dorsal surface of the basisphenoid, on the side of the brain case, could not be exposed.

The *dentaries* (den, figs. 35, 36, 37) are slender, with coronoid processes typically Whaitsiid. There are no postcanine teeth. A cut into the side of the dentary of one side shows the roots of two canines, of which the posterior is the larger. The cut could not be made deep enough to expose incisor roots, for fear of damaging the upper incisors, but the number cannot exceed three, judging from the available space and the size of the upper incisors. Two incisors for the lower jaw seems more likely.

The *splenials* (spl, fig. 37) extend as thin lamina from shortly in front of the pterygoid processes forward to the symphysis. They increase slightly in vertical height in their posterior halves, where they nearly reach half the height of the dentaries. They taper forward and their ventral margins remain along the ventral margins of the dentaries for practically their entire lengths.

The *coronoids* (cor, fig. 37) could not be exposed clearly on account of the pterygoid processes intervening. They are evidently very small and do not cover much larger areas than that covered by the pterygoid prosesses.

The *prearticulars* (preart, figs. 34, 37) extend farther forward than the coronoids and the posterior ends of the splenials. They penetrate in between the splenials and dentaries, with their ventral margins at a higher level than that of the angulars, immediately laterally, which also penetrate in between the dentaries and splenials. Posteriorly the prearticulars reach back very nearly to the level of the quadrates where they are indistinguishably fused with the articulars. Over the best part of their lengths they are straight and vertically flattened. Anteriorly they do not appear to carry much of the strain along the axis of the jaw. Here they lie intimately on the inside of a thickened portion of the angular, the latter carrying the strain, while posteriorly, on the inside of the delicate reflected lamina of the angular, the prearticular is again stronger, with a ridge on the medial face extending forward

and slightly downward to add strength to the feeble ventral margin of the reflected lamina of the angular.

The *angulars* (ang, figs. 35, 36) show large rosette-like surfaces on the outside, behind the coronoid portions of the dentaries, with a distinct reflected lamina. The general antero-posterior axis is relatively thick, especially anteriorly, and appears to carry more of the strain along the direct line between the dentary and articular than the prearticular. The principal strain, however, appears to be taken up by the surangular farther dorsally, and the angular makes a significant endeavour to reinforce the structure of the jaw in this region by sending a process upward and backward on to the lateral face of this bone.

The *surangulars* (sur, figs. 34, 37) contribute principally to the strength of the posterior regions of the lower jaw. They form strong arches ascending backward from the medial faces of the coronoid processes of the dentaries and then downward to the articulars. In *Notosollasia, Whaitsia* and *Ictidosuchops* the ascent anteriorly is negligible compared with the descent posteriorly, while in *Aneugomphius* the acsent is more pronounced. From the ventral margin of the surangular anteriorly, a ridge extends backward over the medial face to the dorsal margin posteriorly. Above this ridge the surangular is thick and strong. Ventrally to the ridge, in the posterior region, the bone extends downward as a thin lamina intimately on the inside of the upward extending process of the angular, so that no fenestra is formed between the surangular, angular and dentary, as is the case in *Notosollasia* and *Ictidosuchops*. Unfortunately the vental margins of the surangulars of both sides were damaged during preparation so that their exact extent and shape cannot be determined.

The *articulars* (art, figs. 34, 35) are relatively small; their exact relationship with the prearticulars could not be ascertained. They have fairly broad surfaces articulating with the quadrates and at the middle of their breadth, postero-ventrally, they protrude backward. From this angle a sharp keel runs forward, but the greater part of this keel appears to belong to the prearticular. This keel joins the ridge on the medical face of the prearticular and assists in supporting the ventral margin of the reflected lamina of the angular. The upper margin of the articular is crested and continuous with the upper margin of the prearticular. Here the articular appears to extend a short distance forward. This crested upper margin extends freely about a millimeter inward of the thin wall formed by the angular and surangular in the region where a fenestra occurs in *Notosollasia*.

Relationship

Aneugomphius ictidoceps is not a juvenile specimen. It is fairly mature and its structural pecularities should not be interpreted as subject to change with further advance in age. It is therefore recognised here as a valid genus and species, and not a juvenile specimen of the genus *Whaitsia* as insinuated by Watson and Romer (1956). It is distinctly different from any other known Whaitsiid, to which it undoubtedly belongs. It is recognised as a distinct genus on the strength of two

significant characteristics: the presence of two canines on each side in both upper and lower jaws, and the two small teeth in the pterygoids. Both these characteristics are foreign to the rest of the Whaitsiid family. In *Moschorhinus* two canines are present, but the anterior tooth functions like an incisor. However, besides this anterior small canine, the presence of post-canine teeth, the broad and extremely un-Whaitsiid-like vomer, the large suborbital vacuities, the absence of palatine ridges, the short pterygoids, the pronounced median keel in front of the long, rather posteriorly situated interpterygoid fossa, and the general aberrant shape of the skull, render *Moschorhinus* a most doubtful member of this family.

Lycideops, or a *Lycideops-like* specimen, has been mentioned as a likely form from which the Whaitsiid family could have descended (Boonstra, 1934, Brink, 1954), which makes *Moschorhinus* even more an unlikely earlier stage to the typical molarless true Whaitsiids. The general structure of the skull in all the other Whaitsiids is so intimately related that a diphyletic origin for this family cannot be considered. If *Moschorhinus* is taken as an advanced representative of a branch from which, much earlier, the true Whaitsiids, diverged, which is fairly likely, it can perhaps still be tolerated within the Whaitsiidae, but is is more likely that with increased information this genus will have to be transferred to a separate family. Recently the Bernard Price Institute acquired a complete Moschorhinid skull from the *Lystrosaurus* zone, which may help to solve the relationship of this genus.

In the above description of the skull of *Aneugomphius,* comparisons are frequently made with the Scaloposaurid *Ictidosuchops intermedius.* The anterior palate of the latter specimen is remarkably reminiscent of the Whaitsiid condition. The vomer is not unlike the Whaitsiid vomer and the palatine ridges are so Whaitsiid-like, that the origin of the Whaitsiidae is considered as not very far removed from the *Ictdosuchops* level in the evolution of the Bauriamorpha. The initial development of a secondary palate is more characteristic of the Whaitsiidae than the toothless post-canine region, and many other similarities in structure between *Aneugomphius* and *Ictidosuchops* suggest that the common ancestry of these two forms is not very far distant. If a *Lycideops-like* ancestor to the Whaitsiidae had a palate not unlike that of *Ictidosuchops,* this ancestor could not have given rise to *Moschorhinus* and the latter genus will then not be a Whaitsiid.

Watson and Romer (op.cit.) considers *Ictidosuchops* as a member of the family Nanictidopsidae. They list the families of the Bauriamorpha in an order suggesting specialization. Thus the families Lycideopsidae, Nanictidopsidae, Scaloposauridae and Bauriidae range in this order more or less along the line of evolution to mammals. If both the infra-orders Bauriamorpha and Therocephalia are to be considered as natural groups, with their families as defined by Watson and Romer, it appears that a branch of the earlier Therocephalia evolved to a Lycideops-like level, where the Bauriamorpha branched off, while the Therocephalian branch continued as the Whaitsiidae. *Moschorhinus* and *Euchambersia* then apparently originated from the same or different stock, earlier than the Lycideops level. The Lycideopsidae may therefore represent a Therocephalian family, or as suggested by Watson and Romer,

the ancestral family to the Bauriamorph branches, one of which continued closely via the Bauriidae to mammals, while another gave rise to the Cynodonts.

Lycideops is an interesting form showing a series of such degenerated post-canine teeth that it is considered that with further degeneration and subsequent total loss of these teeth, the Whaitsiid stage is reached. Unfortunately the palatal structure of *Lycideops* is not known, and total loss of postcanine teeth is not a characteristic confined to Whaitsiidae. It is therefore safer to refer to a *Lycideops*-like ancestor to the Whaitsiidae pending additional information on the palatal structure of this genus. Nevertheless, *Lycideops* has two canines in the upper jaw, which may explain the presence of two canines in *Aneugomphius*. It would be interesting to know whether *Lycideops* or the actual *Lycideops*-like ancestor had pterygoid teeth.

There can be little doubt that *Hofmeyria atavus* represents a fairly recent ancestral form to *Aneugomphius*. *Hofmeyria* has the tooth-bearing pterygoid ridges on either side of the interpterygoid fossa, from which the *Aneugomphius* condition is inherited. If *Hofmeyria* had two canines, it appears that only the loss of the post-canine teeth, loss of the postfrontals, and further reduction in the size of the suborbital foramina would produce the genus *Aneugomphius*. *Hofmeyria* is quite correctly a member of the family Whaitsiidae as suggested by Watson and Romer (op.cit.).

Both the double canines and the pterygoid teeth suggest that *Aneugomphius* is not an advanced Whaitsiid. It is regrettable that the genera *Alopecopsis* and *Notaelurops* are not sufficiently known to allow some detailed comparisons, because these two genera appear to be more primitive than *Whaitsia* and *Notosollasia*. There are two or three specimens in the collection of the Bernard Price Institute which, on closer investigation after preparation, may prove to be near allies of *Alopecopsis* and *Notaelurops,* and may even turn out to be members of the latter genus. These will be studied in the near future and may assist in solving the relationship of *Aneugomphius*.

Besides the presence of two canines and the pterygoid teeth, the palate of *Aneugomphius* appears to be as advanced as that of *Notosollasia*. The palatines do not extend as far forward as in *Whaitsia,* a condition which is interpreted as more primitive than that of *Notosollasia,* on the strength of the information displayed by the palate of *Promoschorhynchus*. In *Whaitsia* the palatines appear to participate in the elementary secondary palate — although this circumstance may still prove to be an incorrect interpretation, in which case there will be few characteristics on which to distinguish *Notosollasia* as a genus distinct from *Whaitsia*. Nevertheless, in *Waitsia pricei* the palatines do extend into the region of the elementary secondary palate. In *Aneugomphius* the palatines are like those of *Notosollasia,* but the region of the elementary secondary palate could not be properly exposed and may be not unlike that of *Theriognathus*. However, the palatines of *Theriognathus* extend much farther forward than those of *Aneugomphius*.

Other more primitive characteristics of *Aneugomphius* which separate it from *Whaitsia* and *Notosollasia* are the absence of a parietal crest, insignificant occipital crests, a not very deep basisphenoid keel, and very delicate postorbital and

temporal arches. Its primitiveness is, however, of a totally different nature of that of *Promoschorhynchus* and the relationship between these two genera, both of which should together throw some light on the origin and phylogeny of the Whaitsiids, is most uncertain. It appears that a *Lycideops*-like ancestor gave rise to a *Promoschorhynchus*-like branch, which lead on to *Moschorhynchus,* and another *Hofmeyria-Aneugomphius-Alopecopsis-Notaelurops*-like branch, which lead on to *Whaitsia* and *Notosollasia,* but the earlier members of this branch persisted along with *Whaitsia* and *Notosollasia* into the *Cistecephalus* zone as the actual *Aneugomphius, Alopecopsis* and *Notaelurops*. There appears, therefore, to have been some marked divergence in the ancestry of the Whaitsiids, with a remarkable convergence subsequently, to the three fairly similar genera *Moschorhynchus, Whaitsia* and *Notosollasia. Hofmeyria* cannot be too far removed from the Bauriamorph origin, while *Moschorhinus* and its aberrant ally *Eucambersia* are evidently less closely related.

Abbreviations

ang	Angular.
art	Articular.
asph	Alisphenoid.
bo	Basioccipital.
bpp	Basipterygoid process.
bsph	Basisphenoid.
c	Canine.
cor	Coronoid.
cp	Coronoid process.
den	Dentary.
dep	Depression, possible lodging a gland.
eo	Exoccipital.
fo	Fenestra ovalis.
fr	Frontal.
ic	Internal carotid foramen.
ich	Internal choanae.
in	Incisors.
inb	Inter-narial bridge.
ip	Interparietal.
ipf	Interpterygoid fossa.
jf	Jugular foramen.
jug	Jugal.
k	Parasphenoid keel.
lac	Lachrymal.
lacd	Lachrymal duct.
ljc	Pit for reception of lower jaw canine.
max	Maxillary.
mp	Mastoid process.
nas	Nasal.
oc	Occipital condyle.
op	Opisthotic.
pal	Palatine.
palmx	Palatal plate of the maxillary.
palr	Palatine ridge.
par	Parietal.
pcr	Parietal crest.
po	Postorbital.
pp	Paroccipital process.
preart	Prearticular.
prem	Premaxillary.
prf	Prefrontal.
pro	Prootic.
psph	Parasphenoid.
pt	Pterygoid.
ptf	Post-temporal fossa.
ptp	Pterygoid process.
ptt	Pterygoid teeth.
q	Quadrate.
qj	Quadratojugal.
qp	Quadrate process.
r	Rostrum.
refl	Reflected lamina of the angular.
sept	Septomaxillary.
so	Supraoccipital.
sof	Suborbital foramen.
sp	Splenial.
sq	Squamosal.
st	Stapes.
sur	Surangular.
sym	Symphysis of lower jaw.
tab	Tabular.
tr	Transverse bone.
v	Vomer.

References

BOONSTRA, L. D., 1934, A contribution to the morphology of the mammal-like reptiles of the suborder Therocephalia. *Ann. S. Afr. Mus.*, xxxi, ii, p.215.

BRINK, A. S., 1954, On the Whaitsiidae, a family of Therocephalian mammal-like reptiles. *Trans. Roy. Soc. S. Afr.*, xxxiv, i, p. 43.

BROOM, R., 1932, The mammal-like reptiles of South Africa and the origin of mammals. H. F. & G. Whiterby, London.

BROOM, R., 1935, On some new genera and species of Karroo fossil reptiles. *Ann. Transv. Mus.*, xviii, i, p. 55.

BROOM, R., 1936, On some new genera and species of Karroo fossil reptiles, with notes on some others. *Ann. Transv. Mus.*, xviii, iv, p. 394.

BROOM, R. & ROBINSON, J. T., 1948, On some new types of small carniverous mammal-like reptiles. *Broom Comm. Volume Roy. Soc. S. Afr.*, p. 29.

CROMPTON, A. W., 1955, A revision of the Scaloposauridae with special reference to kinetism in this family. *Res. Nat. Mus.*, i, 7, p. 149.

WATSON, D. M.S. & ROMER, A. S. 1956, A classification of Therapsid reptiles. *Bull. Mus. Comp. Zool. Harvard*, 114, 2, p. 37.