ON THE FUNCTIONAL MORPHOLOGY OF THE GORGONOPSID SKULL

By T. S. KEMP
Museum of Zoology, Cambridge University

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[Plate 1]

CONTENTS

Cranial material of some gorgonopsids has been prepared by the acetic acid technique. A new species, *Leontocephalus intactus*, has been made for one of the skulls, and generic and specific diagnoses are presented. On the basis of composite information from all the skulls, some aspects of the functional morphology are discussed.

From the form of the dentition and the pattern of tooth-wear, it is deduced that besides a direct closure of the jaws, the lower incisors must have been capable of interdigitating between the upper incisors to produce a shearing type of occlusion. This must necessarily have involved a propalinal shift of the lower jaw forwards, relative to the skull. However, there was no possibility of an anterior movement of the articular relative to the quadrate and the quadrate must therefore have been streptostylic. It is shown that the quadrate and squamosal together formed a basically ball-and-socket joint and that the quadrate rotated about a transverse axis, upon the epipterygoid. The epipterygoid itself was probably capable of a limited degree of movement relative to the pterygoid.

A restoration of the jaw musculature is suggested, on the basis of new information about the lower jaw. A simple mathematical model is constructed to show the feasibility of the muscle restoration. The functional evolution of the gorgonopsid jaw mechanism and musculature is discussed.

The organization of the nasal cavity is described and it is shown that the nasal capsule probably consisted of three parts—an anterior chamber restricted to the dorsal part of the skull, a large, purely olfactory posterior chamber, and a ventro-lateral diverticulum of the posterior chamber, the maxillary sinus. The probable presence of olfactory turbinal cartilages in the latter two parts is indicated. The respiratory air probably passed down a choanal tube, supported by extensive processes of the palatine.

Evidence of the course of the naso-lachrymal duct is given. The position of Jacobson's organ, and a possible function for the septomaxillary foramen, are discussed.

On both functional and anatomical grounds, it is argued that the gorgonopsids had no trace of a secondary palate.

The origin of the organization of the gorgonopsid snout is discussed.

New details of the structure of the braincase are described and the homology of the elements are considered. It is shown that the braincase can be compared to the neurocranium of the mammals in several, but not all respects.

On the basis of the internal form of the braincase, a reconstruction of the brain is given, suggesting that the telencephalon was relatively well developed.

The phylogenetic position of the gorgonopsids as a whole is considered. They are compared with the Therocephalia and it is concluded that their functional organization, as indicated by an extensive suite of characters, differs radically from that group. The cynodonts are shown to be based on the therocephalian-type of organization and therefore to be relatively unrelated to the gorgonopsids. It is apparent that a common ancestor of the gorgonopsids and the therocephalians could have been but barely advanced over the pelycosaurian-grade of structure. Primitive therapsids from the Russian Kazanian deposits are briefly discussed and it is shown that there is some slight evidence for a dichotomy between them into 'pregorgonopsid' and 'pretherocephalian' stocks.

It is formally proposed that the carnivorous therapsids should be classified into two equal ranks, the Gorgonopsia and the Theriodonta and that they were probably derived separately from the sphenacodont pelycosaurs.

Introduction

The gorgonopsids form one of the principal groups of the carnivorous therapsid reptiles, and are restricted to Upper Permian deposits as far as is known at present. The earliest finds of mammal-like reptiles were from the Beaufort series of the Karroo System of South Africa, which Owen described in a series of papers, culminating in his British Museum Catalogue (Owen 1876). Among this material were three skulls now known to be gorgonopsids. However, neither Owen, nor Seeley (1895) who re-examined this material, separated them from other carnivorous forms with the exception of one, *Gorgonops torvus*, which they both believed to have had a complete roofing to the temporal region. For this specimen Seeley established a suborder Gorgonopsia, as distinct from the suborder Theriodonta which contained all the other carnivorous therapsids then known. It was not until 1913 that Broom demonstrated the existence of a synapsid temporal fenestra in *G. torvus* and showed the similarity of this species to several other known therapsids. Among the carnivorous therapsids which lacked a secondary palate, he showed the existence of two distinct groups, the Gorgonopsia and the Therocephalia.

Meanwhile in North America Cope had described a series of Lower Permian forms, the pelycosaurs, noting certain mammal-like characteristics. Broom (1910) showed quite conclusively that these and the South African therapsids are related groups.

The first rigorous attempt to work out the phylogenetic relationships between the various synapsid groups was made by Watson (1921), who concluded that the gorgonopsids lay between the advanced pelycosaurs and the cynodonts, and that the therocephalians had diverged from this line at an early stage, later giving rise to the bauriamorphs. He believed that these four groups were distinct from the rest of the therapsids, forming the Theriodonta.

Doubt has since been cast on Watson's conclusions, notably by Boonstra (1934*b*), who showed that certain features of the gorgonopsid skull were different from both the therocephalian and cynodont conditions, and Broom (1938) who described the first-known procynodonts, showing them to have had a therocephalian rather than a gorgonopsian skull organization. Later work on procynodonts by Brink (1960*a*, 1963) has supported Broom's view. On the other hand, Olson (1944) reached a conclusion similar to that of Watson on the basis of serial sections of therapsid braincases.

Over sixty genera of gorgonopsids have now been described, the majority by Broom and Haughton, in South Africa. They are also known now from Russian (Pravovslalev 1927) and East African (e.g. Huene 1950; Parrington 1955) deposits.

A series of very interesting therapsids from the Russian Kazanian deposits were described by Evremov (1940) and Chudinov (1960) which appear to be intermediate in structure between the advanced pelycosaurs and the gorgonopsids. Olson (1962) has discussed this material and has produced fragmentary evidence of similar forms from North America.

The present paper concerns a study of gorgonopsid cranial material in the collection of Dr F. R. Parrington, made in the Karroo deposits of the Ruhuhu Valley, Tanzania, in 1933. The first detailed geological survey of this region was conducted by Stockley (1932) who found vertebrate fossils including gorgonopsids, which Haughton (1932) described. The next work in the area was that of Parrington, and a series of papers have been produced on material in his collection, including one on gorgonopsids (Parrington 1955). Between 1934 and 1936 Nowack made a further collection in the area and the gorgonopsids which he found have been described by Bröili & Schröder (1936) and Huene (1950).

The geology and homotaxy of the Ruhuhu Valley deposits have been discussed by Stockley (1932), Nowack (1937), Huene (1950), Cox (1959) and Charig (1963). All the known gorgonopsid material has been found in the lower of the two principal bone-bearing strata (Kawinga Formation of Charig (1963)), which is widely agreed to be homotaxial with parts of both the *Endothiodon* and *Cistecephalus* zones of South Africa. A detailed discussion of this point is included in Cox's (1959) paper.

MATERIAL AND METHODS

All the material discussed is from the Kawinga Formation of the Karroo deposits of the Ruhuhu Valley, Tanzania. Certain specimens were found in unconsolidated matrix and had been simply washed clean by Dr F. R. Parrington. In general these have perfectly preserved surfaces, but tend to be fragmentary. For the rest, the matrix is a hard grey limestone. The acetic acid method of preparation (Toombs 1948; Rixon 1949) was found to work exceedingly well. 15% acid was used and 'Vinalak' (polybutyl methacrylate) was used to strengthen the exposed bone. After completion, much of the bone surface was obscured by a thin, red, acid-insoluble layer, along with traces of matrix and thick 'Vinalak'. This could be removed in many cases by the careful use of an industrial abrasive apparatus (Stucker, Galusha & McKenna 1965), leaving a perfect bone surface.

During his collecting, Dr F. R. Parrington made use of the field numbers allotted to bone-bearing sites by Stockley (1932) and these are quoted below. All the specimens belong to Dr F. R. Parrington's private collection which is housed in the University Museum of Zoology, Cambridge. The abbreviation F.R.P. is used to indicate this collection.

The following is a list of the material referred to in the text.

F.R.P. 91. Arctognathus *sp.*

A large skull lacking both post-orbital bars, the right zygomatic arch and the lateral parts of the temporal region of the roof of both sides. The posterior part of the right mandible is also missing. The left squamosal was represented only by an impression on the matrix, but was restored using fibre glass and polyester resin before preparation, in order to record its position. The degree of distortion is very slight indeed. All the matrix was removed by the acetic acid technique.

A remarkable feature of this skull is the presence of an acid insoluble calcite-like material Although clearly occupying cracks in some regions, in others it forms bilaterally symmetrical structures not corresponding to cracks. Thus at the posterior end of the nasal cavity there is a structure which in form and position corresponds to what the posterior wall of the cartilaginous nasal cavity may be expected to have been like. And there is a structure which is exactly continuous with the orbitosphenoid ossification and the pilae antoticae, forming part of the floor and sides of the braincase in front of the pituitary fossa. On one side this material forms a vertical wall at the posterior limit of the maxillary sinus, rising from a transverse ridge across the dorsal surface of the palate. Finally, parts of the median septum are composed of it, in continuation with ossified parts of the septum. In all these cases, the material is occupying regions which must be expected on other grounds to have consisted of cartilage in the living animal. It seems as if during the process of fossilization cartilage has been replaced by calcite. However, there are no signs of certain foramina in the calcite which, as discussed later, must have been present in the original cartilage. This implies that the calcite was deposited in spaces left by the disintegration of the cartilage itself, rather than being a direct fossilization process, which also explains the presence of apparently the same form of calcite in cracks. The whole process must have occurred subsequently to the fossilization of the skull itself.

Locality. Stockley's site B19, between Matamondo and Linyana.

F.R.P. 41. Leontocephalus intactus *new species*

A large skull lacking most of the lower jaw and both quadrates and quadrate rami of the pterygoids. Several fragments of post-cranial material. This specimen was found in unconsolidated mudstone which Dr Parrington washed away, leaving both internal and external surfaces remarkably well preserved. The degree of distortion is slight. Indeed, among Karroo fossils, this specimen appears to be quite unique. The only subsequent preparation necessary was to clean parts of the surface with the abrasive apparatus in order to expose some of the sutures which were obscured by the thin red deposit. In general, this was only done on one side of the skull because of the danger of damage to the surfaces. In the reconstructions, information so gained has been transferred freely to the opposite side of the skull. The reconstructions themselves have been based primarily on the palatal view since the palate is undistorted. The main distortion has been some degree of dorso-ventral crushing, and a slight shearing of the snout region towards the left. Thus there is less confidence to be placed on the vertical measurements of the reconstructed figures than on the horizontal measurements.

Locality. Stockley's site B4, Katumbi vawili.

F.R.P. 37

The posterior half of a large unidentifiable skull, lacking both zygomatic arches and postorbital bars. This specimen had been largely worked out in acetic acid, and the preparation was completed. There is practically no distortion or weathering and the braincase is exceedingly well preserved.

Locality. Stockley's site B4, Katumbi vawili.

F.R.P. 102. Dixeya *cf.* quadrata.

A small severely weathered skull. In no way can this specimen be distinguished from the specimen of *D. quadrata* described by Parrington (1955). Because of its very poor external appearance, it was felt that it had no taxonomic value and therefore it was heavily coated with 'Vinalak', bisected in the vertical plane just to the left of the midline, and each half prepared in acetic acid in order to demonstrate the internal structures.

LOCALITY. Stockley's site B19, between Matamondo and Linyana.

F.R.P. 142

A medium-sized skull more or less complete and undistorted. Also some fragments of post-cranial material. It has been prepared completely in acetic acid. It is hoped to publish a full description and diagnosis of this specimen later, but for present purposes only certain regions illustrating morphological points are referred to.

LOCALITY. Stockley's site B35, Ruanda.

F.R.P. 38

A large, badly distorted and incomplete skull, along with fragments of the post-cranial skeleton. Despite its incompleteness the bone surfaces of this skull, found in unconsolidated matrix, are perfectly preserved. The quadrate complex and quadrate recess of the squamosal were described by Parrington (1946, 1955) and are refigured and discussed further, below.

LOCALITY. Stockley's site B4, Katumbi vawili.

F.R.P. 44

Fragments of a large skull and post-cranial skeleton, found in unconsolidated matrix and perfectly preserved. The occiput and braincase had been bisected previously, just to one side of the midline. This, and the corresponding nasal, frontal and parietal of the right side which have separated from their fellows at the midline sutures, are used in the reconstruction of the brain. Also a slightly incomplete right maxilla showing details of the internal surface is figured.

LOCALITY. Stockley's site B4 Katumbi vawili.

F.R.P. 36

A fairly large gorgonopsid skull, lacking the posterior-most region. It had been partially prepared in acid. Certain details of the basipterygoid articulation are shown well and are figured.

LOCALITY. Stockley's site B4, Katumbi vawili.

Only the first two skulls among this material warrant a formal consideration for taxonomic purposes. These occupy the first part of this paper. Considerable reliance is placed on the figures, which have been made as accurately as possible, instead of extended formal descriptions, since the basic external appearance of the gorgonopsids is now very well known. Subsequently, certain regions of the gorgonopsid skull are described and discussed in functional terms, drawing upon information available from all the material simultaneously. Although it may transpire later that this approach is unjustified because of the degree of functional variation among different gorgonopsid species, at our present limited state of knowledge of the detailed morphology of fossil forms, it appears to be the most reasonable approach.

ARCTOGNATHUS SP.

The material consists of a large gorgonopsid skull. Both post-orbital bars, the right zygomatic arch, and the lateral parts of the temporal region of the roof of both sides are missing. The whole of the right postero-lateral corner of the skull has been lost. The left ramus of the lower jaw is intact but the posterior part of the right ramus is missing. No post-cranial material is present.

The matrix has been removed completely by means of the acetic acid technique.

F. R. Parrington's private collection, Museum of Zoology, Cambridge. No. F.R.P. 91.

Locality

The Karroo deposits of the Ruhuhu Valley, Tanzania. Between Matamondo and Linyana, Stockley's (1932) site B19 of the Kawinga Formation (Charig 1963).

Identification

The specimen falls within Watson & Romer's (1956) family Arctognathidae. The muzzle is relatively short and rounded in section and the maxillary tooth rows are widely separated. The ventral edge of the maxilla forms a segment of a circle. The occipital surface slopes forwards. The ventral edge of the parasphenoid-pterygoid keel is sharp and the basisphenoid does not produce massive tubera.

However, in the present specimen, the intertemporal width cannot be ascertained and the presence or absence of a preparietal bone is not discernible.

Despite the remarkably fine preservation of parts of this skull, several regions critical for diagnosis are missing, particularly the pattern of dermal bones of the roof, and the intertemporal-post-orbital area, and it is not therefore considered justifiable to create a new species for it. Of the three members assigned to the family Arctognathidae, *Lycaenodontoides bathyrhinus* Haughton (Haughton 1929) is known only from the anterior three-quarters of a skull. *Arctognathus whaitsi* Haughton (Haughton 1924) is severely weathered dorsally, lacks the zygomatic arches, post-orbital bars and the posterior part of the skull, and has been figured in palatal view only. The only well-known member is *A. curvimola* Owen (Watson 1921; Boonstra 1934*b*). It is badly weathered and distorted.

The present specimen is considerably larger than these three species and may be a new species but as far as comparison is possible, it is in general agreement with *A. curvimola*.

General description of the skull

A detailed and comprehensive description of this skull (Kemp 1967 MS.) is available in the University Library of Cambridge University, and a copy is also lodged in the Museum of Zoology Library, of Cambridge University, along with the material.

Detailed description of various aspects of the skull are included below as follows: dentition (p. 19); palatoquadrate (p. 27); lower jaw (p. 37); nasal cavity (p. 54); palate (p. 61); braincase (p. 63).

The dorsal surface of the snout of the skull had completely weathered away and the intertemporal region of the roof is largely incomplete. The left squamosal remained as little more than an impression on the matrix and before acid preparation it was restored in fibre glass and polyester resin, both to record the position of the bone and to strengthen the specimen. The palatal surface and lower jaws are unweathered.

The skull is large and more or less triangular in outline. The snout is almost as high as it is wide and is rounded dorsally, except for immediately in front of the orbits where it is somewhat square-cut.

In dorsal view (figure 1) the zygomatic arches are seen to arise gradually from the preorbital region, and are straight. The original posterior extent of the squamosals is not known. None of the suture pattern of the skull roof is discernible and no attempt has been made to restore it in the diagram.

The palatal surface of the skull (figure 2) is exceedingly well preserved and the dentition, as

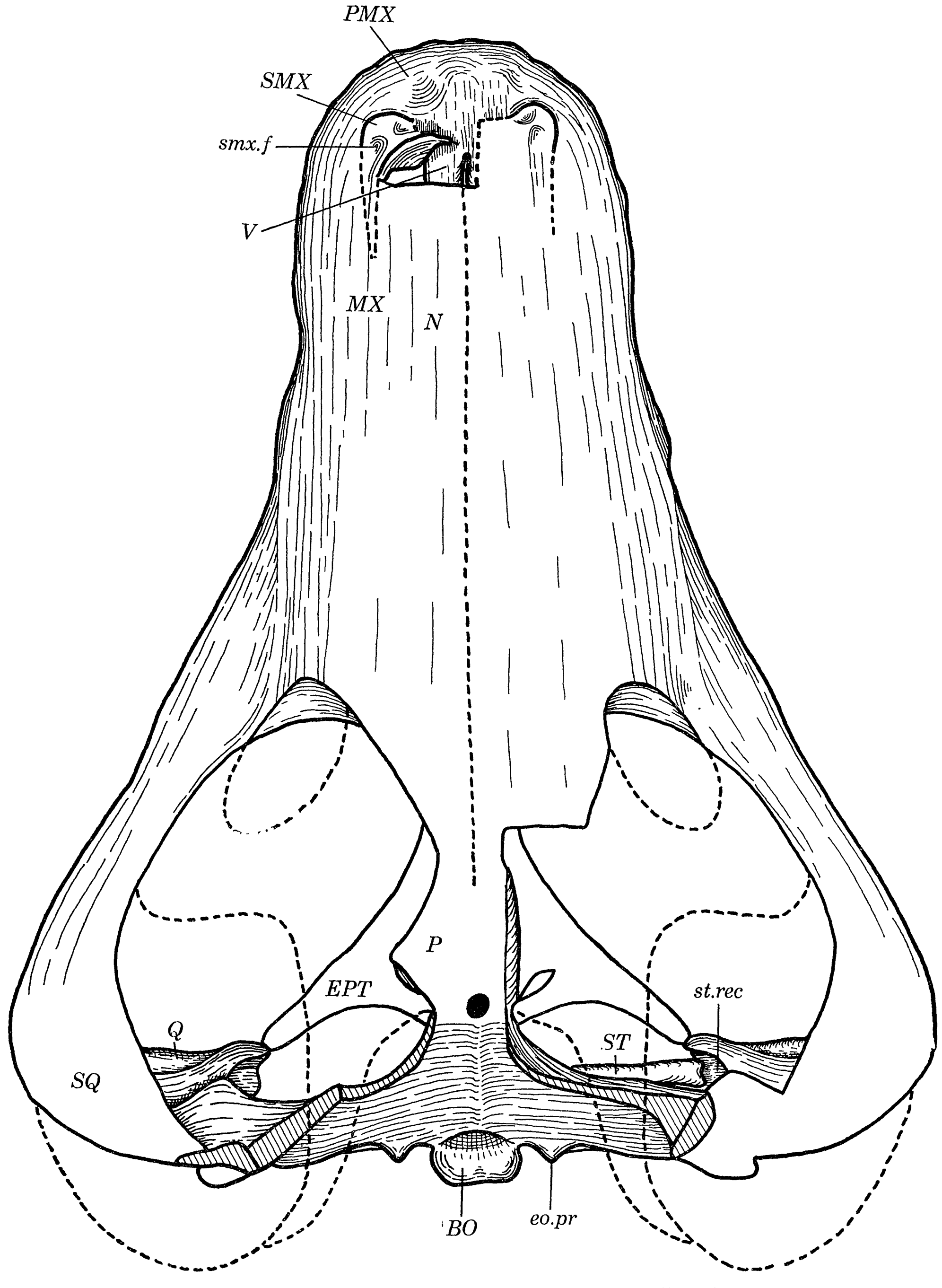


Figure 1. *Arctognathus* sp. Dorsal view of skull, × ½.

described later, is practically complete. The ventral surface of the premaxilla is about 0.5 cm higher than the lateral margin of that bone and the palatal processes of the premaxillae lie slightly higher again. The latter are long in ventral view but almost non-existent in dorsal view. The paired lateral, and the medial ridges of the vomer, are relatively powerful crests.

The median palatal vault is well-developed. Anteriorly, it is continued by the paired choanal processes of the palatines which rise dorsally on either side of the narrow, posterior end of the vomer and vomerine septum. The vault widens but then narrows progressively to its posterior termination.

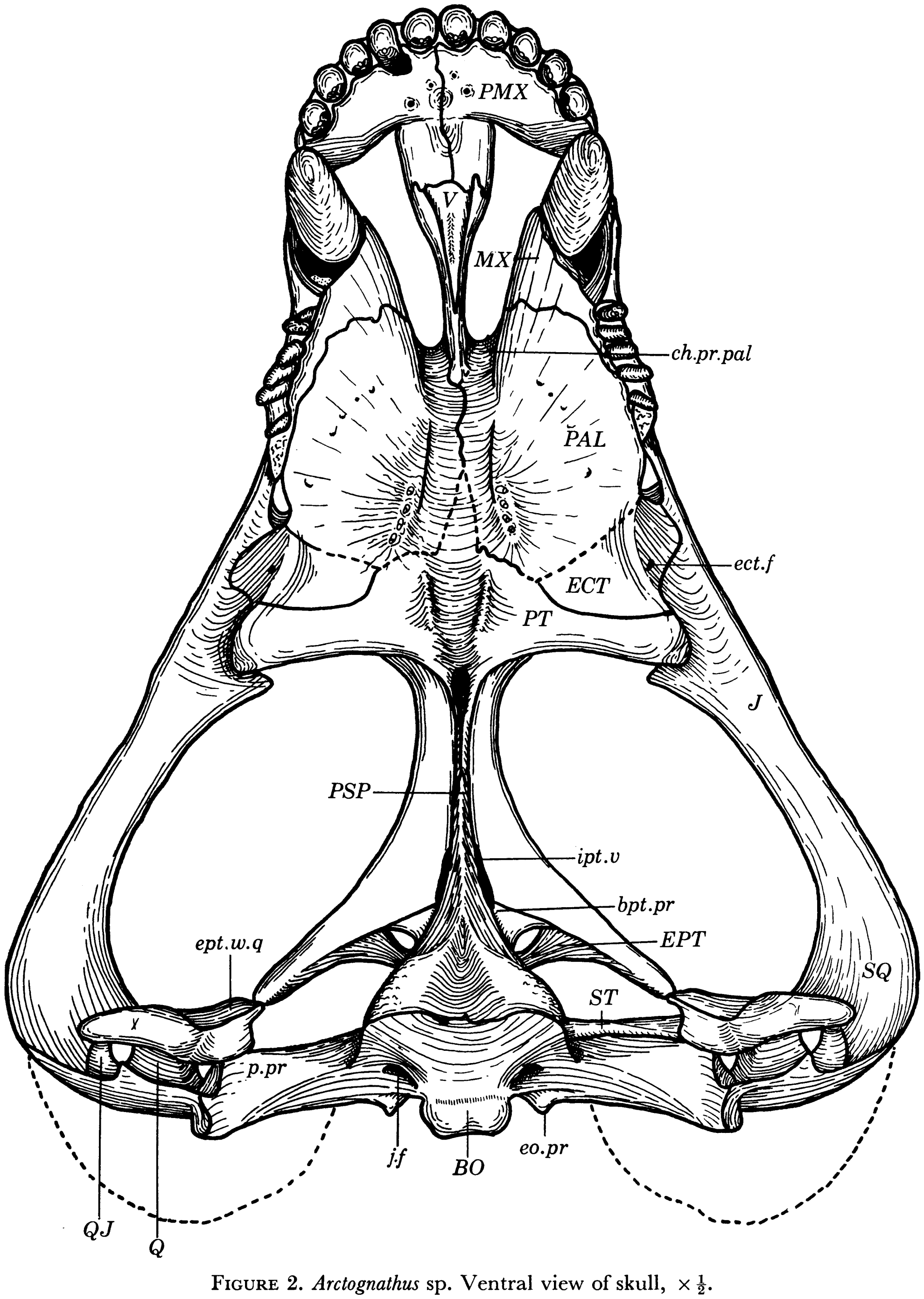


FIGURE 2. *Arctognathus* sp. Ventral view of skull, × ½.

At the extreme end of the vault, a large median aperture opens from the roof of the vault into a space between the paired pterygoids where they form the base of the median septum. The sides of the aperture are smooth and steep, and it does not appear to be the result of damage.

The post-canine bearing part of the maxilla is a raised strip of bone, posterior to which is a deep groove. The medial wall of the groove is formed by the base of the lateral flange of the pterygoid and its overlying ectopterygoid, while the lateral wall is the inner face of the zygomatic arch. Anteriorly the groove runs laterally to the maxilla margin and emerges on to the lateral face of the maxilla (figure 3*a*).

The arrangement of the bones in the region where the zygomatic arch meets the palate is complex, and the ectopterygoid apparently plays an important part in maintaining the junction. The ectopterygoid covers much of the anterior and lateral faces of the lateral pterygoid flange. Internally, the pterygoid, palatine and jugal bones overlap the ectopterygoid extensively (figure 18*B*), but do not quite meet. The free margins of the former three palatal bones are very thin compared to the considerable thickness of the ectopterygoid where it is exposed dorsally. The zygomatic part of the jugal is inclined dorso-medially and rests on the dorsal surface of the jugular process of the maxilla. Medially a flange of the maxilla runs up to overlap the jugal. From the medial surface of the jugal a second sheet of bone arises, inclined ventro-medially, and inserts between the lateral pterygoid flange and the ectopterygoid. This second process of the jugal runs forwards and overlaps the internal face of the maxilla, within the nasal cavity. A third process of the jugal arises near the second process but runs dorso-medially from the zygomatic arch, as the lower part of the preorbital plate. It contacts the lachrymal along a horizontal suture across the preorbital plate.

Several foramina open on to the palate (figure 2). Two pairs emerge on the ventral surface of the premaxilla and between them the bone surface bears a slight depression. A series of antero-laterally directed foramina open from the palatine along a line parallel to the palatine-maxilla suture. A single large foramen pierces each ectopterygoid.

At the posterior end of the post-canine tooth row there is a large space between the maxilla, palatine and ectopterygoid. Although the edges are damaged, this aperture is represented on both sides of the skull.

Behind the palate, the pterygo-quadrate and braincase are almost perfectly preserved, and will be described later.

In lateral view (figure 3*A*) the roof of the skull has a slightly convex outline, reaching its maximum height at about the level of the orbits. The ventral tooth-bearing margin does not bear a sudden step between the incisors and the canine, and behind the canine the margin of the maxilla is a gentle convexity. Alongside the post-canine teeth, the ventral margin of the maxilla begins to flare outwards, and behind the teeth, the margin has turned horizontally. This marks the ventral surface of the horizontal groove that passes backwards as a lateral palatal groove described above. The dorsal wall of the groove is a horizontal thickening of the maxilla continuous with the jugular process.

The suture between the maxilla and the premaxilla appears superficially between the last two incisors but this is a result of the maxilla overlapping the premaxilla externally. The last incisor is in fact held by the premaxilla.

The septomaxilla is not well preserved on either side but appears to have the typical gorgonopsid form. Between the base of the septomaxilla and the base of the (missing) internarial process of the premaxilla the lateral surface of the premaxilla bears a marked depression.

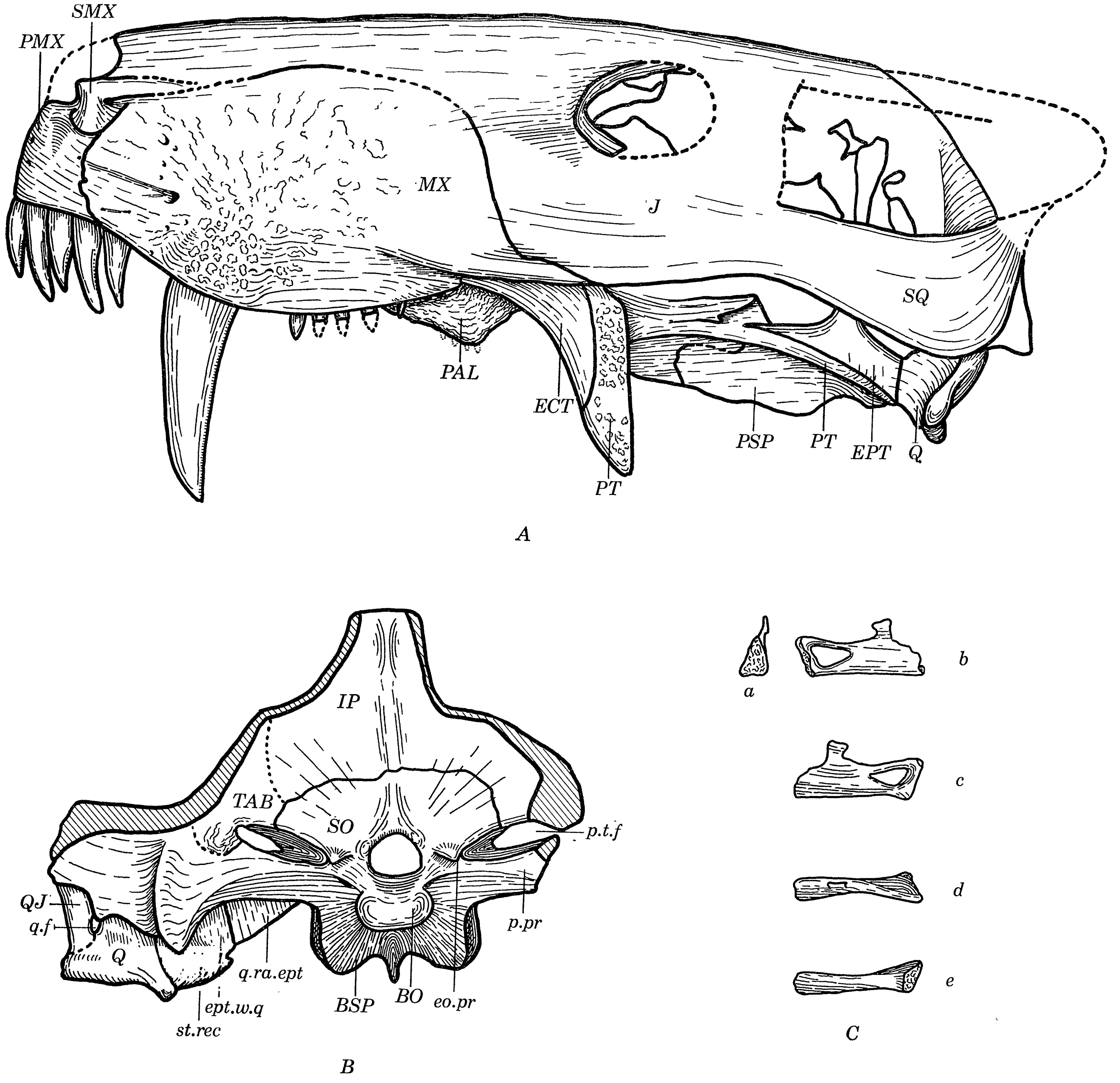


FIGURE 3. *Arctognathus* sp.. *A*, Lateral view of skull, × ½. *B*, Occipital view of skull, × ½. *C*, Left stapes, × ½; *a*, proximal view; *b*, anterior view; *c*, posterior view; *d*, dorsal view; *e*, ventral view.

Several foramina open on to the surface of the snout. Two pairs open forwards and downwards near the suture between the premaxillae. The upper pair are quite large (2 to 3 mm diam.), the lower pair small (1 mm diam.), and on the right side, a sulcus leads from the lower foramen up towards the base of the septomaxilla. There are several anteriorly directed foramina emerging at the premaxilla-maxilla suture. On the left, weathering of the bone surface has exposed canals running forwards to open as these foramina and apparently radiating from a single large canal, represented by its termination in the middle of the lateral surface of the maxilla. The swollen area of the maxilla overyling the root of the canine is marked by pitting, but it cannot be determined for certain whether any foramina open in this region.

The dorsal parts of the occiput (figure 3*B*) have been lost on both sides, and the whole of the right side lateral to the post-temporal fossa is absent. Of the suture pattern, only the outline of the supraoccipital can be determined. The remaining part of the occiput is fairly flat and the median ridge, characteristic of gorgonopsid skulls, is developed in two parts. The lower part swells ventrally to form a low triangular boss immediately above the foramen magnum, Lateral to the foramen magnum is the small pyramidal exoccipital process. The lateral face of the process is a continuation of the medial wall of the post-temporal fossa.

The posterior rim of the post-temporal fossa is a large oval with a thickened dorsal rim. Anteriorly, the exit of the fossa is much smaller because the medial half of the fossa is actually a deep recess, walled anteriorly and facing posteriorly. Apart from this, however, the fossa is a simple direct passage through the occiput.

The left stapes (figure 3*C*) is well preserved except for the distal end which is damaged. However, the bone is spongy here, and may have been completed by cartilage.

LEONTOCEPHALUS INTACTUS NEW SPECIES

The type material of this new species is a large skull, slightly crushed dorso-ventrally and lacking the epipterygoids, the quadrate rami of the pterygoids and the quadrates. Only a few isolated fragments of the lower jaw are present.

Found in association with the skull, and probably belonging to it, were a humerus, a radius, a partial ilium and several fragments of vertebrae and ribs.

The matrix was a soft mudstone which Dr F. R. Parrington had washed away, revealing the skull almost completely clear, inside and out. Subsequently much of the surface was cleaned with the abrasive apparatus in order to reveal the sutures.

Catalogue no. F.R.P. 41.

Locality

The Karroo deposits of the Ruhuhu Valley, Tanzania. Stockley's (1932) site B4 of the Kawinga Formation (Charig 1963).

Identification

Of Watson & Romer's (1956) families of the Gorgonopsia, this specimen can be attributed to the Arctognathidae. It has in common with the other members a large, broad skull and a broad snout which is rounded dorsally and is about half the skull length. The jugal is deep below the orbit, and the occiput stretches forwards between the temporal fenestrae.

Two of the present four members of this family, *Arctognathoides breviceps* Boonstra (1934*a*) and *Aelurognathus haughtoni* Huene (1950), are readily distinguishable from the present specimen by their possession of a preparietal bone and the entry of the frontal into the orbital margin.

Of the other two members of the Arctognathidae; *Leontocephalus cadlei* Broom (1940) is based upon the anterior three-quarters of a skull which is figured only in dorsal and ventral views; *Leontosaurus vanderhorsti* Broom & George (1950) is a complete skull, and is figured in dorsal and lateral views. Broom & George, however, state that these two forms are very similar and, indeed, separate them only on the absence of pterygoid teeth in *Leontocephalus*, and on the presence of four post-canine teeth close behind the canine in this genus, compared to three, placed some distance away from the canine in *Leontosaurus*. As Signogneau (1963*a*) has pointed out, neither of these characters appears to be taxonomically sound and it seems probable that *L. vanderhorsti* should be at least congeneric, and perhaps conspecific with *Leontocephalus cadlei*.

The present specimen is slightly narrower than *L. cadlei*, has slightly larger frontals and smaller prefrontals, and has five post-canine teeth rather than four. Similarly, the present specimen is slightly narrower than *Leontosaurus vanderhorsti* but in this case the shape of the frontals and prefrontals correspond. However, the temporal fenestrae of *L. vanderhorsti* are restored as pear-shaped in dorsal view, with the narrow end anteriorly, and they run postero-laterally. There is no comment on this feature in the description (Broom & George 1950), which is most uncharacteristic of the gorgonopsids, where the temporal fenestrae are normally oval and alined antero-posteriorly. Other differences of *Leontosaurus* from the present specimen are that the squamosals do not extend so far posteriorly and the width of the skull in this region is greater. All these three differences can be explained by dorso-ventral crushing in *Leontosaurus* and, if this were allowed for, then the two skulls would be more or less indistinguishable.

Because neither *Leontocephalus cadlei* nor *Leontosaurus vanderhorsti* are available to the writer, no attempt to revise their taxonomy can be made. The most advisable course is to place the present specimen in the genus *Leontocephalus* in the expectancy that *Leontosaurus* too will be placed ultimately in that genus. The present specimen has been made into a new species, *Leontocephalus intactus*, largely because of the relatively heavy ornamentation of parts of the skull, and on the shape of the frontals.

A new generic and a specific diagnosis are given.

Generic diagnosis Leontocephalus *Broom*

Large gorgonopsids with the preorbital length about half the skull length; the snout slightly broader than high and rounded dorsally, lacking a preparietal bone; the frontal excluded from the orbital margin by a wide contact between the prefrontal and the post-frontal. The palatal process of the premaxilla is long and the mid-ventral contact between the paired palatines is extensive. Type genus: *L. cadlei* Broom.

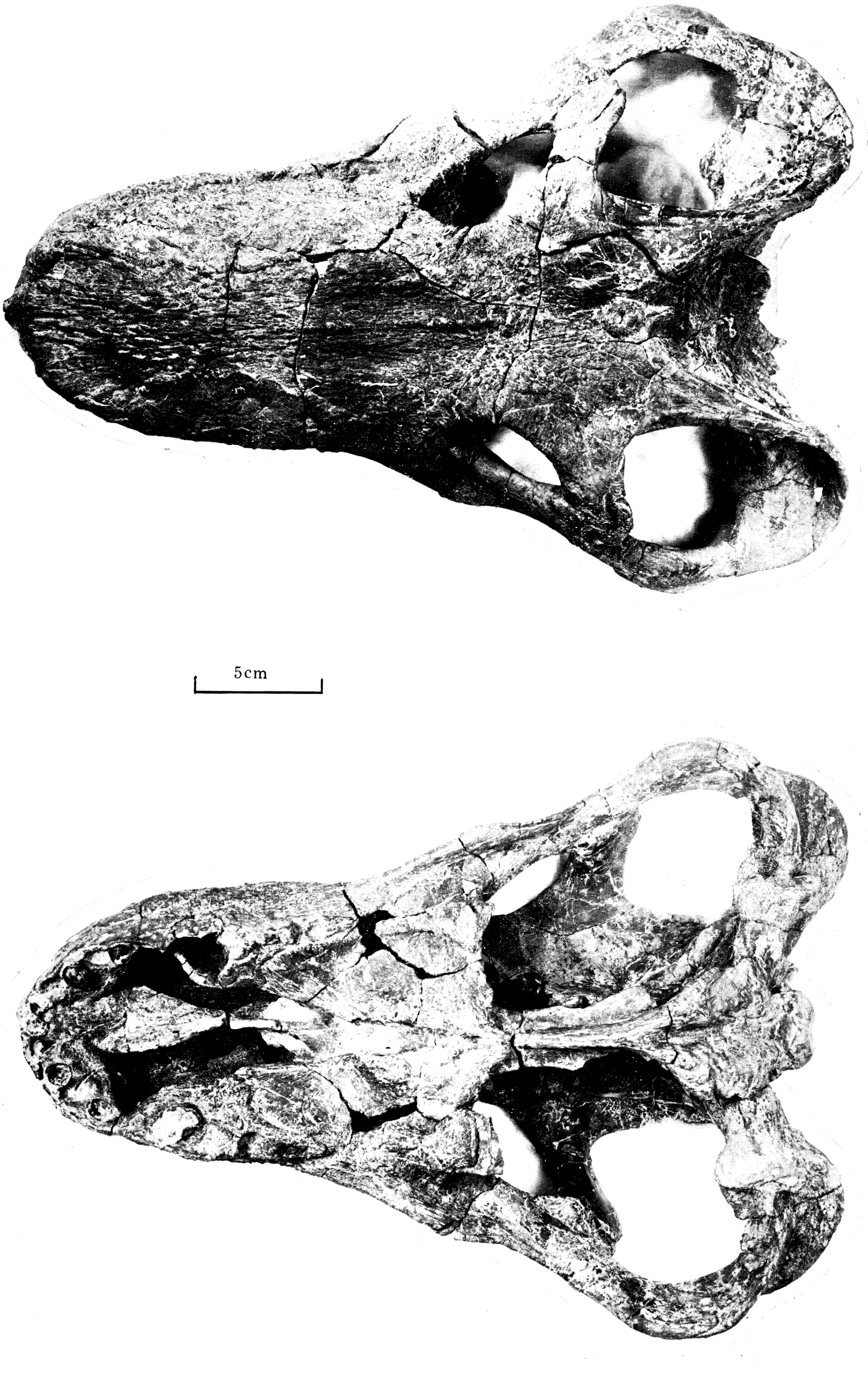
Specific diagnosis: L. intactus *new species*

The skull is only moderately flattened (the height of the snout in the canine region is 7.5 cm, the width is 10.1 cm in the type specimen). In dorsal view the zygomatic arch shows slight swellings both at the level of the orbits and at the level of the temporal fenestrae. The squamosals extend posteriorly for a considerable distance behind the level of the occipital condyle. The intertemporal width is slightly greater than the interorbital width (8.9 and 7.6 cm respectively in the type specimen). The frontals are long and relatively narrow and the prefrontals are very large. The palatal boss of the pterygoid is small and narrow.

Much of the dorsal surface of the skull is heavily rugose, the nasal bones bearing deep elongated pits and the frontals being ornamented with somewhat smaller pits. The dorsal margins of the orbits are heavily rugose. From the pineal boss forwards to the nasals, the mid-dorsal line of the skull carries an irregular but marked ridge.

General description of the skull (plate 1)

A detailed comprehensive description of the skull is available in the University Library of Cambridge University (Kemp 1967 MS), and a copy is also lodged in the Library of the Cambridge University Museum of Zoology, along with the material.



Leontocephalus intactus sp.nov. Skull in dorsal and ventral views.

(*Facing p.* 13)

Detailed description of certain regions of the skull relevant to the following discussion may be found as follows; the dentition (p. 21); the dorsal surface of the palate (p. 44); the internal surface of the roofing bones of the skull (p. 42).

The skull is slightly crushed dorso-ventrally and the snout has been sheared over towards the left a little. The diagrams have been corrected for this distortion and also for photographic parallax. As a result of the crushing, however, slightly less confidence should be placed on the vertical skull measurements than on the horizontal measurements, but the discrepancy is likely to be small.

In general form, the skull is large and rather massively built. It is generally broad and low with a flat dorsal surface. One of the most characteristic features is the relatively heavy ornamentation covering much of the external surface. The central region of the maxilla bears a mass of rounded pits, and irregularly longitudinal pitting tends to radiate towards the dorsal margin of the maxilla, particularly posteriorly. The upper surface of the nasal is heavily ornamented by longitudinal pitting, especially prominent between the maxillae. Farther back, the pitting fades rather. However, it reappears over the frontals, but here takes the form of small irregularly rounded pits, densely arranged. The dorsal margins of the orbits are heavily rugose but the rest of the surface of the prefrontals and post-frontals are fairly smooth. Farther back, the external faces of the parietals and interparietal are almost perfectly smooth. The boss surrounding the pineal is very large, and running forwards from it is a slight, irregular crest, which becomes quite tortuous in the middle of the frontals but then fades out just before reaching the nasals. The more ventral bones behind the maxilla are more or less smooth.

In dorsal view (figure 4) the pattern of the bones is characteristic of the gorgonopsids, with the exception of the absence of a preparietal. Another odd feature is the greater size of the prefrontal on the right side than on the left. A comparison of the pattern of the sutures on the outer and inner surfaces of the roof show several interesting features (figure 5). The nasal is a much more extensive bone than appears superficially, for it underlies the maxilla by up to 3 cm, and a posterior extension runs beneath the antero-dorsal part of the prefrontal. Anteriorly the nasal completely underlies the dorsal part of the septomaxilla, although a slight bulge indicates the position of that bone. Conversely, however, the nasal is slightly restricted internally near to the midline, by an anterior extension of the frontal. In the posterior part of the skull, the internal and external bone patterns more nearly correspond, with the exception of the parietal, which extensively underlies the post-frontal and the postero-lateral part of the frontal.

In lateral view (figure 8*A*), the dorsal edge of the skull is almost straight. The ventral tooth-bearing margin shows a very slight trace of a step between the last incisor and the canine. As in *Arctognathus* sp., described earlier, the suture between the premaxilla and the maxilla appears to commence between the fourth and fifth incisors, but this is the result of a superficial overlap of the premaxilla by the maxilla. All the incisor teeth are in fact within the premaxilla. The ventral margin of the maxilla behind the teeth does not flare laterally, as it does in *Arctognathus* sp., but the thickened jugular process of the maxilla bears the same relationship to the jugal as it does in that specimen. The ventral surface of the jugular process is rounded, and dorsally it forms a groove within which the jugal stands. As it runs posteriorly, the lateral edge of the groove decreases and medial edge increases, until finally there is only a lappet of the maxilla lying on the inner surface of the jugal (figure 6). The free ventral margin of the jugal, behind the maxilla, is a sharp edge. The suture between the jugal and the squamosal is also complex, for there are two processes of the jugal, medially and dorso-laterally, which run backwards, overlapping the squamosal. At the same time, a ventro-lateral process of the squamosal comes forwards over the jugal.

The temporal fenestra is broad and shallow. The narrow lateral-facing surface of the postorbital, which forms the dorsal edge of the fenestra is perfectly smooth. It is marked off from the dorsal surface of the bone by a slight longitudinal ridge, but is continuous with the underside of the roof.

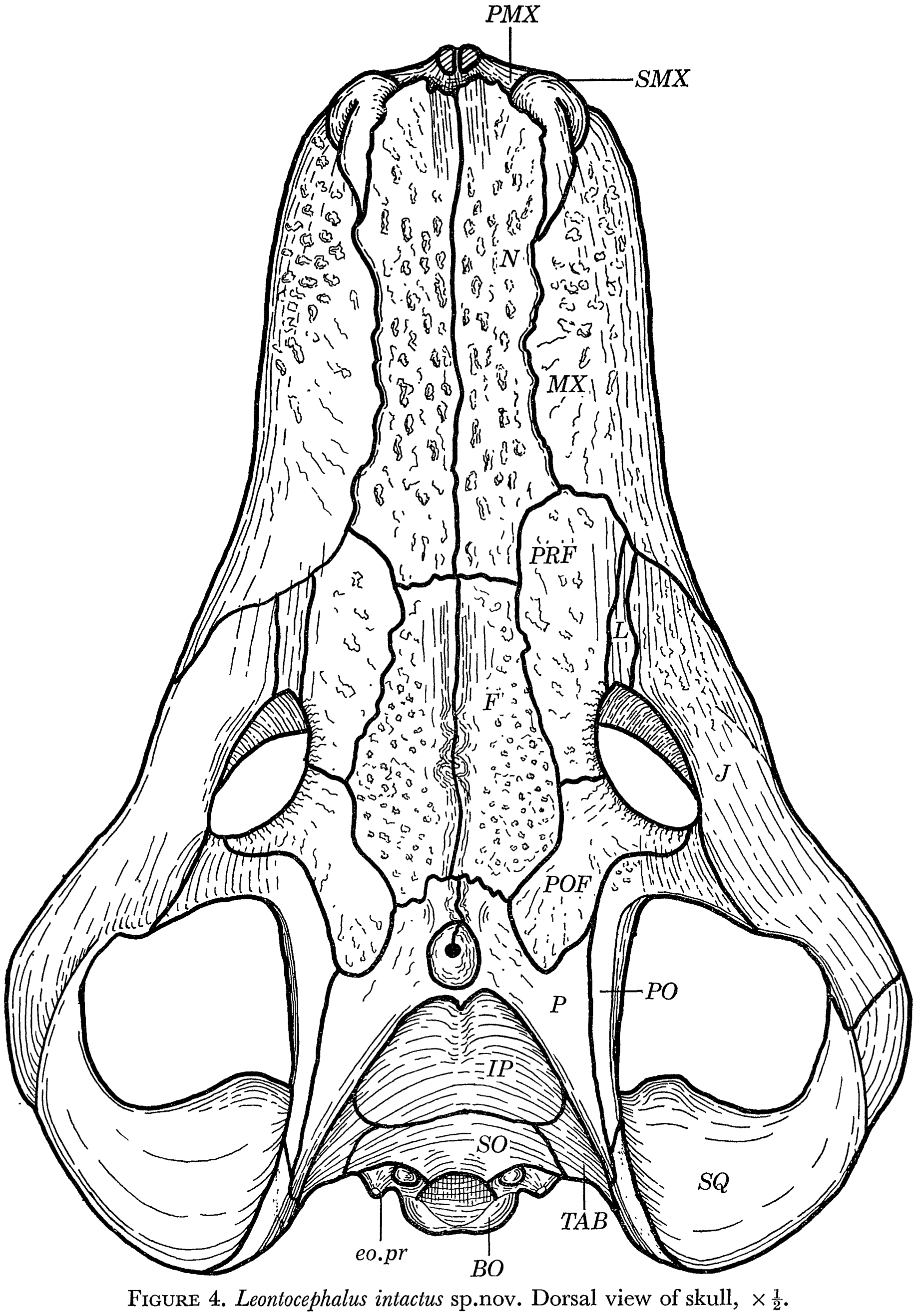


FIGURE 4. *Leontocephalus intactus* sp.nov. Dorsal view of skull, × ½.

In ventral view (figure 6), the palate is similar to that of *Arctognathus* sp. and its mode of attachment to the jugal and maxilla is basically identical. The choanal processes of the palatines, running antero-dorsally at the back of the internal nares are damaged but sufficient remains to show that they were probably extensively developed in life. The paired bosses of the palatines bear the remains of several teeth. As in *Arctognathus* sp. the anterior part of each boss is sharp and overhangs the palatal vault to a small extent. The pterygoid bosses are short, narrow and high, and are set at a marked angle to the palatal vault. There are no teeth within them but both they, and the surrounding parts of the palatal surface, are strongly ornamented by small circular pits.

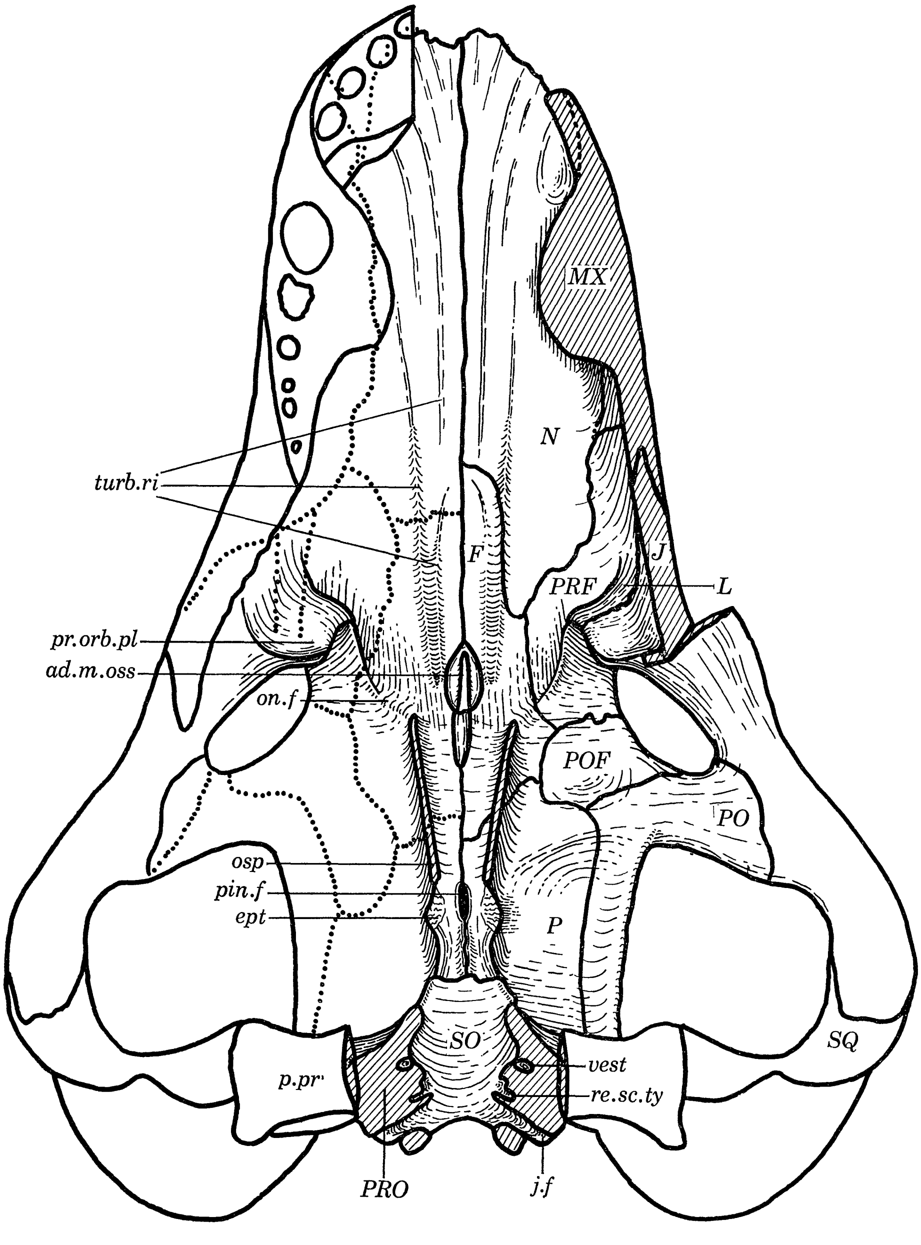


Figure 5. *Leontocephalus intactus* sp.nov. Internal view of skull roof, with the palatal bones removed, × ½. On the left side, the external suture pattern is shown in dotted lines.

The marginal dentition of the palate is described in detail later. As preserved, there were empty sockets at the positions of incisors two and four, on both sides of the skull. This immediately suggests that alternate tooth-replacement (Parrington 1936; Kermack 1956) had been in process when the animal died. Several isolated teeth were collected near to the skull, however, and, as mentioned later, two of the complete ones are upper incisors. These two correspond to the second left and fourth right sockets respectively and thus, whilst they may have been mature teeth about to be shed, or just shed, they prevent any categorical statement being made on the pattern of tooth-replacement in this specimen. In the figure of the ventral view of the skull, the isolated teeth have been restored to their probable positions.

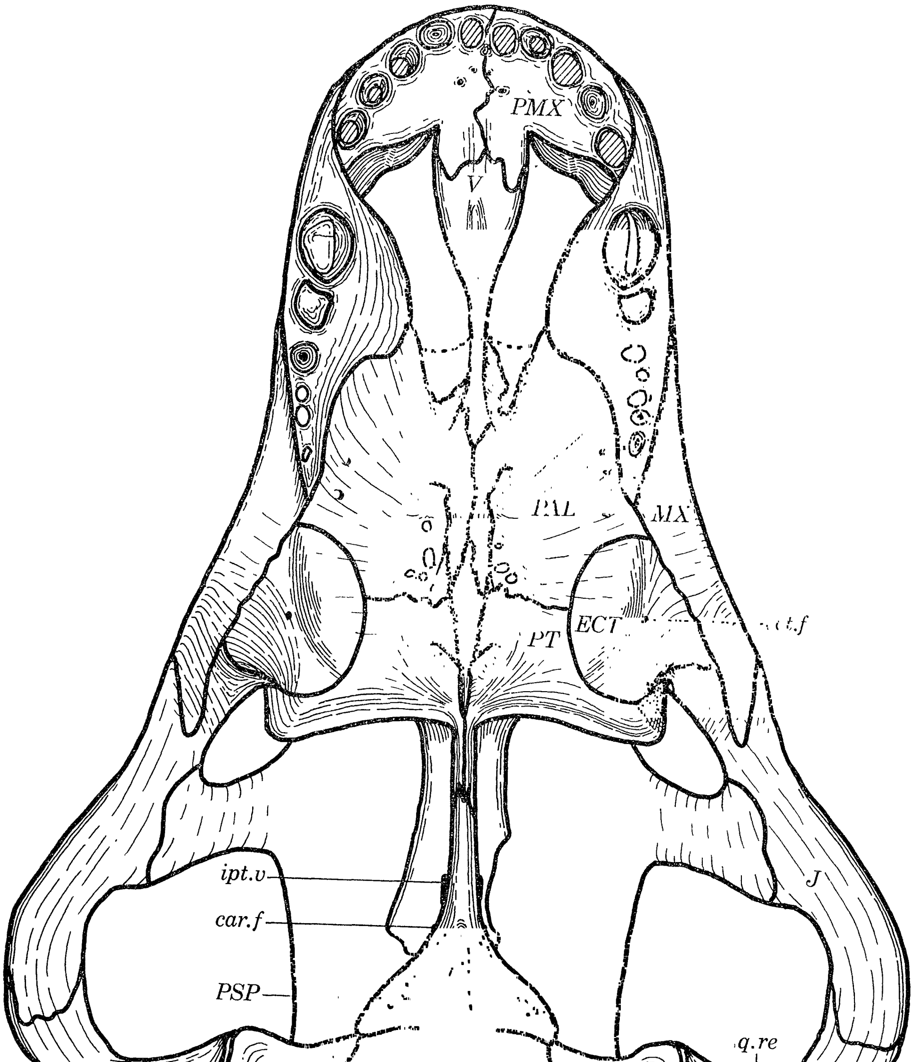


FIGURE 6. *Leontocephalus intactus* sp.nov. Ventral view of skull, × ½.

The palate can be detached from the rest of the skull, when the structure of its dorsal surface is exposed (figure 7). There is a relatively extensive exposure of the ectopterygoid dorsally, surrounded by the very thin margins of the jugal, palatine and pterygoid. An interesting feature of this section of the skull is the exposure of an un-erupted replacement canine, embedded in the left maxilla, behind and slightly medial to the socket of the functional canine.

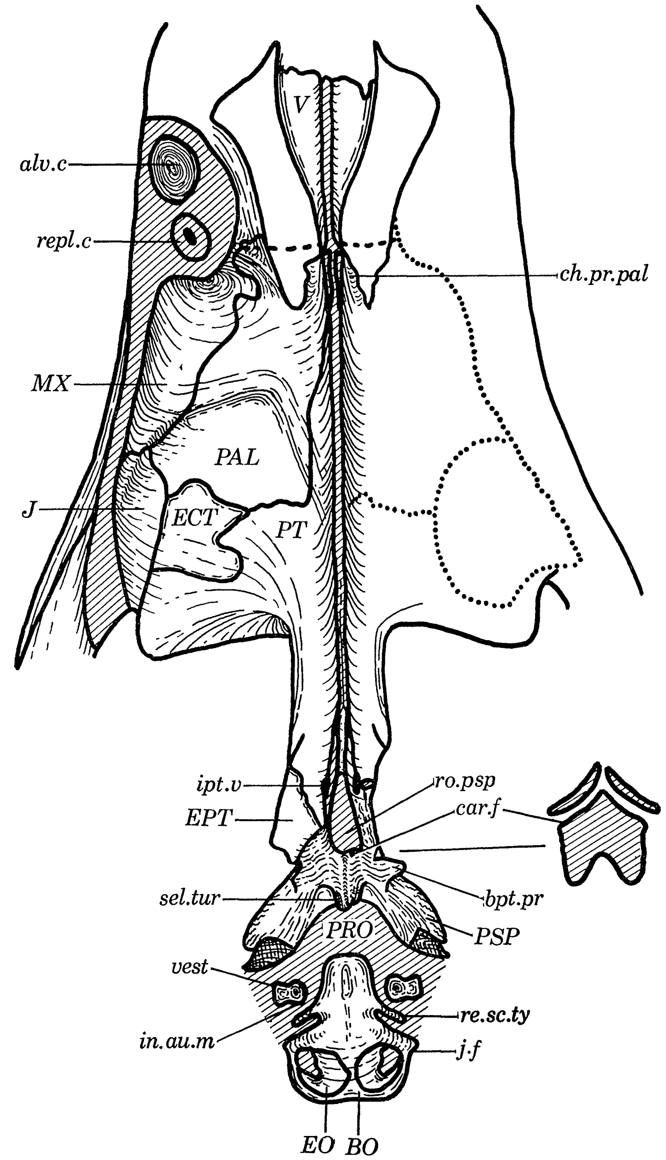


FIGURE 7. *Leontocephalus intactus* sp.nov. Dorsal view of palate and basicranial axis, × $\frac{1}{2}$. On the right side, the external suture pattern of the palate is shown in dotted lines. Inset: transverse section at the plane indicated.

Behind the palate, the ventral keel, compounded of the paired pterygoids anteriorly and the parasphenoid posteriorly, has a thick more or less horizontal ventral edge. The suture between these bones is very deeply interdigitating in ventral view. The ventral edge itself bears two longitudinal grooves for almost the full length of the keel.

The parasphenoidal tubera are massive and rugose, but behind them, the basisphenoidal tubera are rather flat and not well-ossified. The paroccipital processes are particularly flat and wide and their ventral surfaces are slightly concave. The distal end of each paroccipital process is completely capped by dermal bone. Posteriorly it is covered by the tabular and anteriorly by a process of the squamosal. On reaching the antero-lateral corner of the paroccipital process, the squamosal turns medially and forms a small flange flanking the lateral part of the anterior opening of the post-temporal fossa.

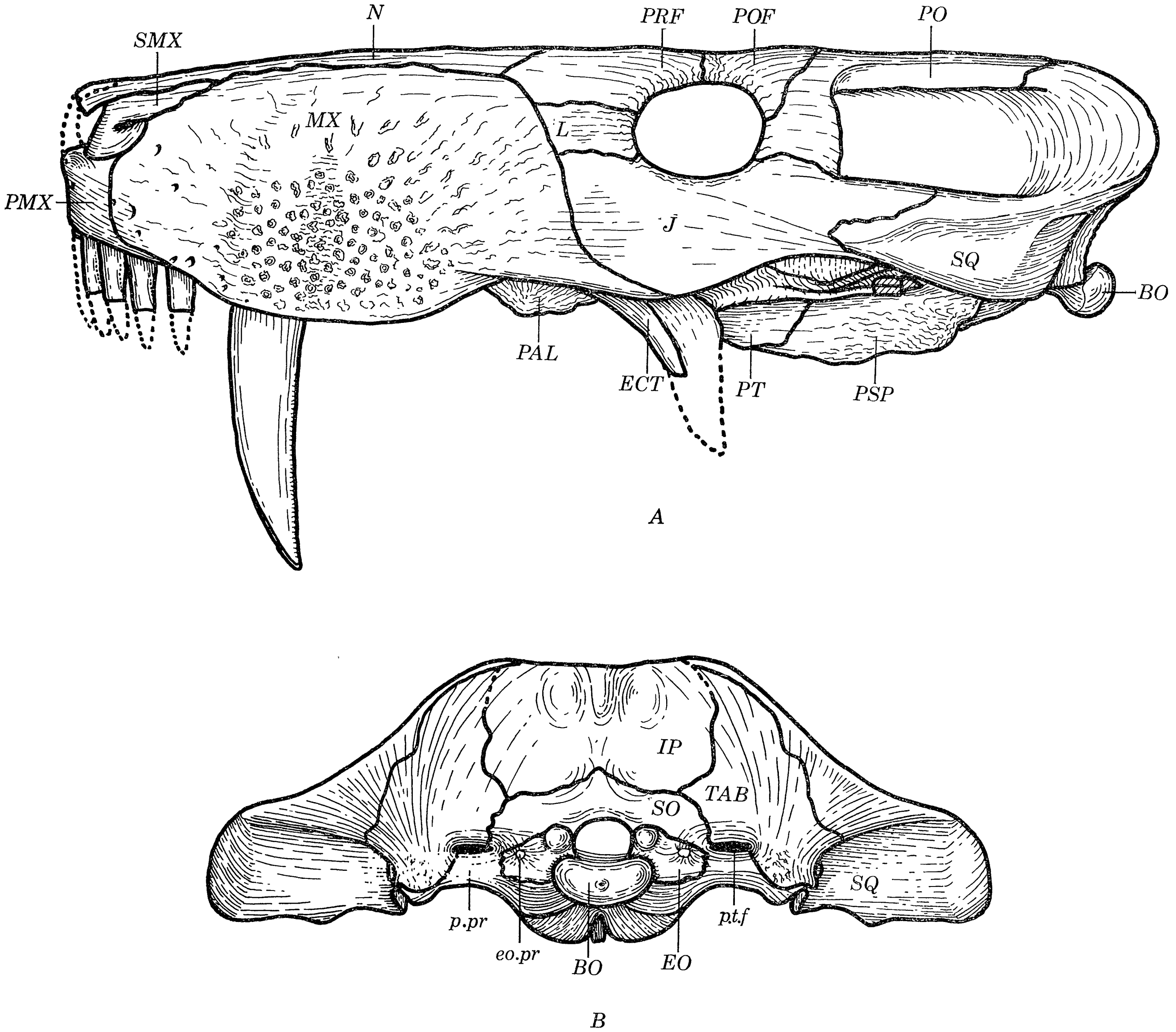


FIGURE 8. *Leontocephalus intactus* sp.nov. *A*, Lateral view of the skull, × $\frac{1}{2}$. *B*, Occipital view of skull, × $\frac{1}{2}$.

The occipital view (figure 8*B*) demonstrates the generally flattened form of the skull. The pattern of sutures shows no uncharacteristic features. The median ridge is particularly well developed in the more dorsal region where it separates a pair of marked oval depressions. More ventrally, the ridge is less marked and separates a pair of wide shallow depressions.

The exoccipital is not fused to the surrounding bones, and is roughly triangular in posterior view. The ventro-medial corner appears to form part of the occipital condyle, and a medially directed process of the exoccipital apparently overlies part of the basioccipital to form much of the floor of the posteriormost part of the cranial cavity (figure 7). The dorso-medial corner of the exoccipital bears a round flat boss immediately lateral to the foramen magnum, whilst the lateral corner forms the small pyramidal exoccipital process, extending posteriorly and bearing a small pit on its posterior extremity.

The tabular bone is large, and its lower part overlies the postero-lateral extremity of the paroccipital process, where it is in the form of a powerful, rugose boss.

A horizontal break through the pro-otic and the exoccipitals has caused the ventral bones of the braincase to be detachable as a unit, thus affording unusual views of both the roof (figure 5) and the floor (figure 7) of the braincase.

Part of the rostrum of the parasphenoid, along with the median cartilage bone and orbitosphenoid, is preserved. However, it is fragmentary and its value lies only in confirming that this part of the skull corresponds closely with the far more complete material described later. Similarly, there are a few fragments of the lower jaw of the skull but of these, only one, part of the right dentary bearing the teeth (figure 10) is of value, and is described in detail below (p. 22).

THE JAW MECHANISM

1. *The dentition*

The specimen of *Arctognathus* sp. has a remarkably complete and well-preserved dentition. In common with the majority of gorgonopsids there are five large upper incisors (figures 2 and 3*A*), four lower incisors (figure 15) and a greatly enlarged upper and lower canine on either side. Some distance behind the canines are five small post-canine teeth in each jaw ramus, upper and lower.

All the incisor teeth, both uppers and lowers, have the same basic structure, consisting of a conical crown that curves lingually to some extent and tapers gradually to a point. Along the distal half of each crown run two finely serrated edges, arranged so that on any two adjacent teeth, two edges are directly opposed. Each serrated edge follows the curving of the tooth right to the tip and the serrations themselves consist of thin rectangular protuberances with the outer edges sharpened and parallel to the tooth axis. There are about 20/cm. The upper incisors differ from the lower incisors in general form by having a larger, more nearly circular base, a taller crown, and a greater lingual curvature. The serrated edges of the lower teeth are raised slightly from the body of the crown so that, when viewed lingually, the top part of the tooth has the appearance of a triangle resting upon a narrower parallel-sided base. In section, the lower teeth are markedly oval.

The canine teeth have the same basic structure as the incisors. The bases are oval in section and the crowns curve posteriorly. Both the anterior and the posterior edges are serrated for the full height of each crown. The lower canines are smaller in all dimensions than the upper canines.

The relative placing of the teeth differs between upper and lower jaws (figure 11*C*). The paired first incisors of the upper jaw are set closely together and curve posteriorly. Their serrated edges lie in a plane at right angles to the long axis of the skull. The following three incisors on either side are rotated to an increasing degree so that a line connecting their tips, or equivalent points along their serrated edges, lies parallel to the outer margin of the premaxilla. The fifth incisor differs from these in having an oval base with its long axis parallel to the premaxilla border, and in being rather shorter. However, it still curves lingually and its two serrated edges continue the series of the serrated edges of the previous teeth. There is a diastema before the upper canine, above and medial to which is the lateral extension of the internal naris, forming the palatal recess for the lower canine. The long axis of the base of the upper canine is set at an angle to the antero-posterior axis of the skull, such that the front edge of the tooth is slightly lateral to the back edge. All these upper teeth lie on a semicircle.

In the lower jaw, the long axis of the oval base of each incisor is set at right angles to the outer dentary margin, and the short axis parallel to that margin. Although the teeth tend to curve lingually, they are slightly procumbent so that their tips in fact lie directly above their bases. The first pair of incisors are relatively widely apart, and again, the rotation of the subsequent teeth is such that both the tips and the serrated edges lie on lines parallel to the jaw margin.

Table 1

	Right upper jaw
Incisor 1	Damaged
Incisor 2	The tip is very flattened which could be wear or damage. Anterior serrations slightly worn. Posterior serrations very slightly worn
Incisor 3	The distal 1 cm or so has broken away. Apparently unworn serrations are visible on the posterior edge of the remaining basal portion
Incisor 4	The tip is damaged but complete. Anterior serrations lightly worn for 1.7 cm from the tip. Posterior serrations lightly worn for 1.8 cm from the tip
Incisor 5	The tip is slightly damaged, possibly there is wear on the lingual face of the distal end. Anterior serrations worn away to a distinct wear facet. Posterior serrations worn near to the top
Canine	The tip is damaged. Anterior serrations worn to a smooth facet. Posterior serrations damaged. An apparent wear facet runs for some of the length but a length of unworn serrations remains near the tip
	Left upper jaw
Incisor 1	The tip is flattened slightly, especially on the lingual side. Anterior serrations apparently unworn. Posterior serrations worn for 1.2 cm from the tip
Incisor 2	Incomplete
Incisor 3	The labial part of the tip has sheared off. No apparent wear on the remaining part of the tip. Anterior serrations show an apparently heavy wear facet for 0.8 cm. Posterior serrations worn to a facet for about 1 cm
Incisor 4	The tip is only slightly flattened. Anterior serrations damaged but appear very heavily worn to a facet. Posterior serrations only very lightly worn if at all
Incisor 5	The tip is damaged, possibly a wear facet on the top, just coming on to lingual face. Anterior serrations well and distinctly worn. Posterior serrations damaged
Canine	The tip is damaged. Anterior serrations clearly worn for the full height of the crown. Posterior serrations completely unworn
	Right lower jaw
Incisor 1	The tip is smoothly flattened, the wear nearly passing on to the labial face. Anterior serrations worn to a facet for 1.2 cm, the whole length of the serrated edge. Posterior serrations worn to a facet for 0.8 cm
Incisor 2	The tip is rounded but with a distinct facet. Anterior serrations worn to a facet for at least 0.9 cm. Posterior serrations not apparent although no wear facet obvious
Incisor 3	The tip bears a wear facet which extends down the labial face for 0.3 cm. Anterior serrations worn to a facet for about 0.6 cm. Posterior serrations worn to a marked facet for 0.9 cm
Incisor 4	The top 0.5 cm or so of the the tip has broken away. There is no apparent wear on the remaining part which is damaged
Canine	The tip is apparently worn on the top 0.8 cm of the labial surface. Anterior serrations lightly worn for the top 2.6 cm. Posterior serrations damaged. Apparently a marked wear facet for the top 0.9 cm. Following this are a few flattened serrations and then what may be a very heavy wear facet almost to the base of the tooth
	Left lower jaw
Incisor 1	The tip is worn to a facet. Anterior serrations only very slightly worn, if at all. Posterior serrations worn to a facet for 0.9 cm
Incisors 2–4	Incomplete
Canine	The tip on the labial side is apparently worn. Anterior serrations distinctly worn, especially heavily over the top 3.7 cm. Posterior serrations worn to a marked facet for 3.9 cm

TABLE 2

Right upper jaw

Incisor 1	Broken off at the base
Incisor 2	Missing
Incisor 3	Tip is broken off for about 0.5 cm to 1 cm. Anterior serrations show slight wearing from 1.4 cm from the base. Posterior serrations are worn to a facet from 1.1 cm from the base
Incisor 4 (figure 9*G* to *I*)	The tip is broken off for about half a centimetre. Anterior serrations worn to a facet. Posterior serrations unworn
Incisor 5	Broken off at the base
Canine	The top is broken 2.4 cm from the base by a fracture that runs steeply downwards and backwards. This may have occurred during life, however, since the remaining stump is apparently heavily worn on the front face, a feature which corresponds to wear on the lower right canine stump

Left upper jaw

Incisor 1	Broken away at the root
Incisor 2 (figure 9*D*, *E* and *F*)	Top 1 cm or so broken away. Anterior serrations worn to a facet 0.7 cm from the base. Posterior serrations show slight wear beginning 1.2 cm from the base
Incisor 3	Broken off 0.3 cm from the base
Incisor 4	Missing
Incisor 5 (figure 9*J* to *L*)	Broken off about 0.5 cm from the tip. There is a very extensive wear facet down the lingual face of the tooth starting 1.0 cm from the base. Anterior serrations are worn to a facet from about the same level. Posterior serrations are worn to a facet from 1.3 cm from the base
Canine (figure 9*A* to *C*)	The tip has a small facet right at its extremity. Anterior serrations are worn to a facet for the terminal 3.9 cm which runs slightly inwards as well as downwards. Posterior serrations are completely unworn

Right lower jaw (figure 10*P* to *R*)

Incisor 1	Broken off at the base
Incisor 2	The tip is worn to a flat facet facing upwards, backwards and partly outwards. Anterior serrations worn to a facet to 0.6 cm from the tip. Posterior serrations worn to a facet to 0.8 cm from the tip
Incisor 3	Missing
Incisor 4	Broken off at the base
Canine	Broken off 3.6 cm from the base, but the remaining stump has apparently been worn smooth on top, the facet extending just on to the posterior surface and extensively on to the anterior surface

Separate lower jaw teeth (assuming all are left for orientation purposes)

Incisor A (figure 10 *A* to *C*)	The tip is worn by a facet which just extends on to the labial surface of the tooth. Anterior serrations are worn to a facet to 1.1 cm from the tip. Posterior serrations are worn to a facet to 0.6 cm from the tip
Incisor B (figure 10*D* to *F*)	The tip is worn to a facet which extends down the labial side of the tooth for 1.0 cm. Anterior serrations are worn to a facet to 0.9 cm from the tip. Posterior serrations are lightly worn to 0.6 cm from the tip
Incisor C (figure 10*G* to *I*)	The tip is worn to a facet which extends down the labial surface of the crown for 0.9 cm. Anterior serrations show very slight wear for the top 3 mm only. Posterior serrations are also very slightly worn for the top 4 mm
Incisor D (figure 10*J* to *L*)	The tip is very worn to a facet which extends for 0.9 cm down the labial side. Anterior serrations are heavily worn to a facet for 0.8 cm from the tip. Posterior serrations are worn to a wide facet widening towards the tip to occupy most of the posterior width of the tooth. It extends to 1.2 cm from the tip
Canine (figure 10*M* to *O*)	The top 0.5 cm or so has broken off. Anterior serrations are worn to a facet for 1.0 cm above the base. Posterior serrations are worn to a facet practically to the base

Together, the lower incisors lie on a semicircle of smaller radius than that of the upper teeth, There is no diastema before the lower canine and that tooth lies medially to the last incisor, rather than being a direct continuation of the tooth-row. Like the upper canine, its base is set at a small angle to the long axis of the skull so that its front edge is lateral to its back edge.

As a result of acetic acid preparation, there has been some loss of surface detail and wear facets are not always readily distinguishable from damaged areas. However, the condition of each tooth and the nature of the wear where ascertainable are shown in table 1.

The dentition of the specimen of *Leontocephalus intactus* is less complete that that of *Arctognathus*, but several of the teeth were found separately from the skull and in a near perfect state, and show wear facets extremely well (figures 9, 10).

In the upper jaw incisors 2 and 4 on both sides are absent, leaving only sockets. On the left, incisors 1, 3 and 5 have broken off at the base and similarly the crown of the first right incisor is wanting. Right incisors 3 and 5 remain with incomplete crowns. The set of these teeth differs slightly from that of *Arctognathus* sp. in that the tooth bases are rather more oval in section, with their long axes all arranged in a more or less anterior–posterior direction. Since presumably the lines of the serrated edges were still arranged parallel to the rim of the premaxilla, then it is to be expected that on any tooth except the first pair, the two serrated edges will lie in a plane at an angle to this long axis and the tooth will have an asymmetrical appearance. This is the case for two of the complete detached teeth, one a right and one a left, and also for one of the incomplete ones, a right. Judging by the degree of asymmetry, the complete teeth can be placed in the positions left 2 (figure 9*D* to *F*) and right 4 (figure 9*G* to *I*), and this is confirmed by the fact that there are large cracks across these two sockets which presumably caused them to become detached. The separate crown (figure 9*J* to *L*) is probably the fifth left incisor judging by the dimensions of the base. The right upper canine has broken off about 2.5 cm from the base, and the left upper canine is a detached complete tooth (figure 9*A* to *C*).

Of the lower jaw, only fragments remain, although one of these is the right premaxillary tooth margin with part of the symphysial face (figure 10*P* to *R*). On this, the first incisor has broken off at the root while the second is complete. Only a socket remains for the third. The set of these three teeth is exactly like that of the lower incisors of *Arctognathus* sp. The fourth incisor, broken off at the base, is small and nearly circular in diameter, and probably had not completely erupted. The right canine is broken off some 3.5 cm from the base. Among the loose teeth are two complete incisors and two incisiform crowns clearly assignable to the lower jaw. However, the almost identical morphology of these prohibits a definite assertion as to their sequence. A complete canine (figure 10*M* to *O*) belongs to the left lower jaw.

Wear patterns show remarkably well (table 2).

2. *Tooth occlusion*

The general pattern of tooth wear in both these forms was the development of wear facets along each serrated edge of both upper and lower incisors, and the wearing of the tips and upper part of the labial face in the lower incisors. It is possible too that the tips of the upper incisors wore, but the resulting facet did not extend to the sides of tthe crown, either lingually or labially. The lower canines became worn along both the anterior and posterior serrations, while wear was restricted to the anterior serrations of the upper canines. It may be assumed that specific wear facets such as these could only be caused by direct friction between teeth, because if a hard form of food were to have caused tooth wear directly, it would be expected to have caused it all round the tooth. Possibly the sharper edges, the tips and serrated edges might have worn at a greater rate but the failure to wear the posterior edge of the upper canine, and the different degrees of wear between the two edges of some of the teeth show that this was not the case.

Figure 11*C* shows, as accurately as possible, a map of the bases and tips of the upper and lower teeth of *Arctognathus* sp. with the jaws closed. The relative positions of the upper and lower jaws are fixed by the jaw articulation posteriorly and by the need for the lower canine to lie in the palatal recess. It is clear that the lower jaw lies too far posteriorly and is too narrow, for its teeth to meet the upper teeth. In all the gorgonopsid specimens at hand which have the

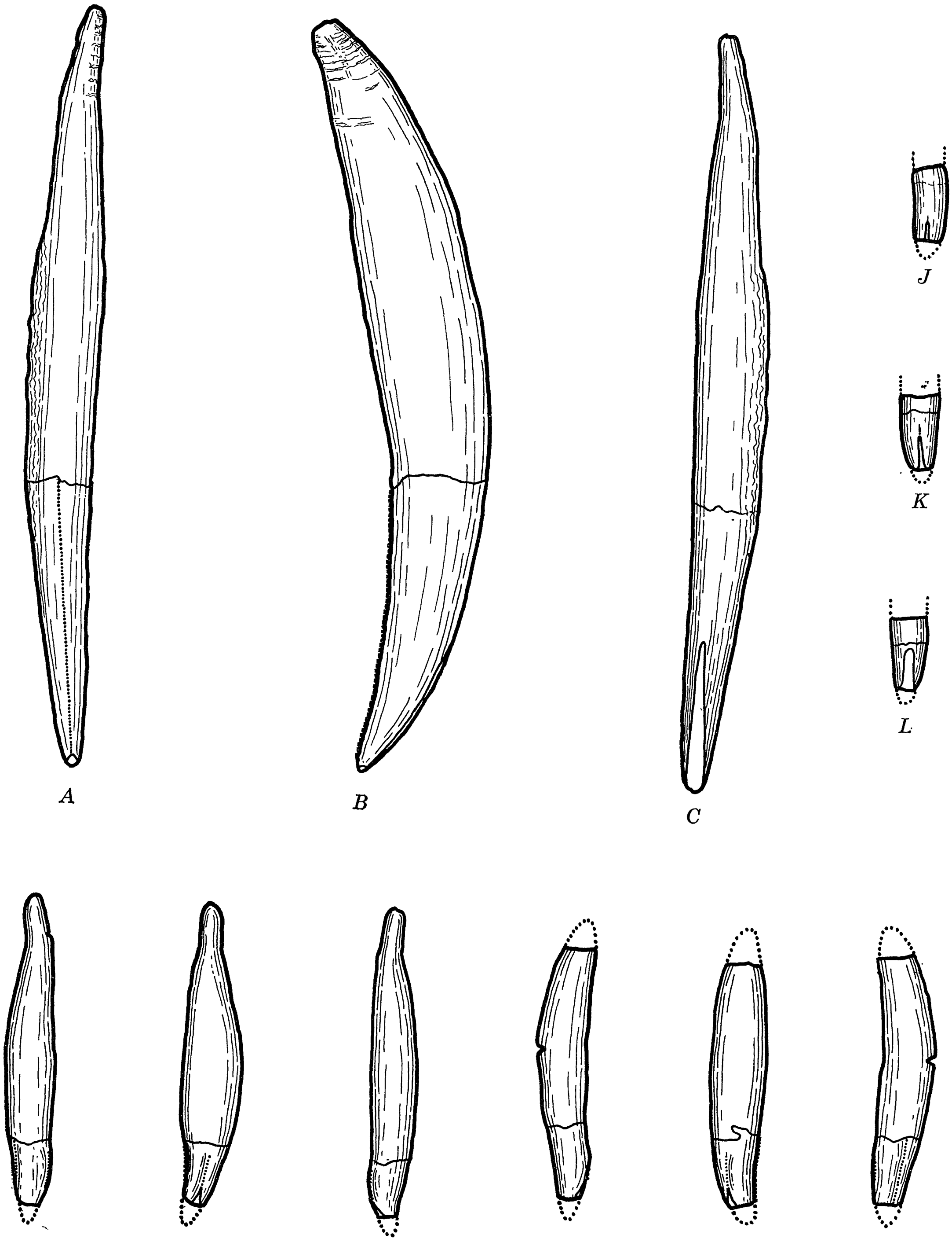


FIGURE 9. *Leontocephalus intactus* sp.nov. Isolated upper teeth, showing wear facets, × $\frac{2}{3}$. *A*, *B*, *C*, Left canine in posterior, lingual and anterior views. *D*, *E* and *F*, second left incisor in lingual, anterior and labial views. *G*, *H* and *I*, fourth right incisor in labial, anterior and lingual views. *J*, *K* and *L*, fifth left incisor in anterior, posterior and lingual views (see table 1).

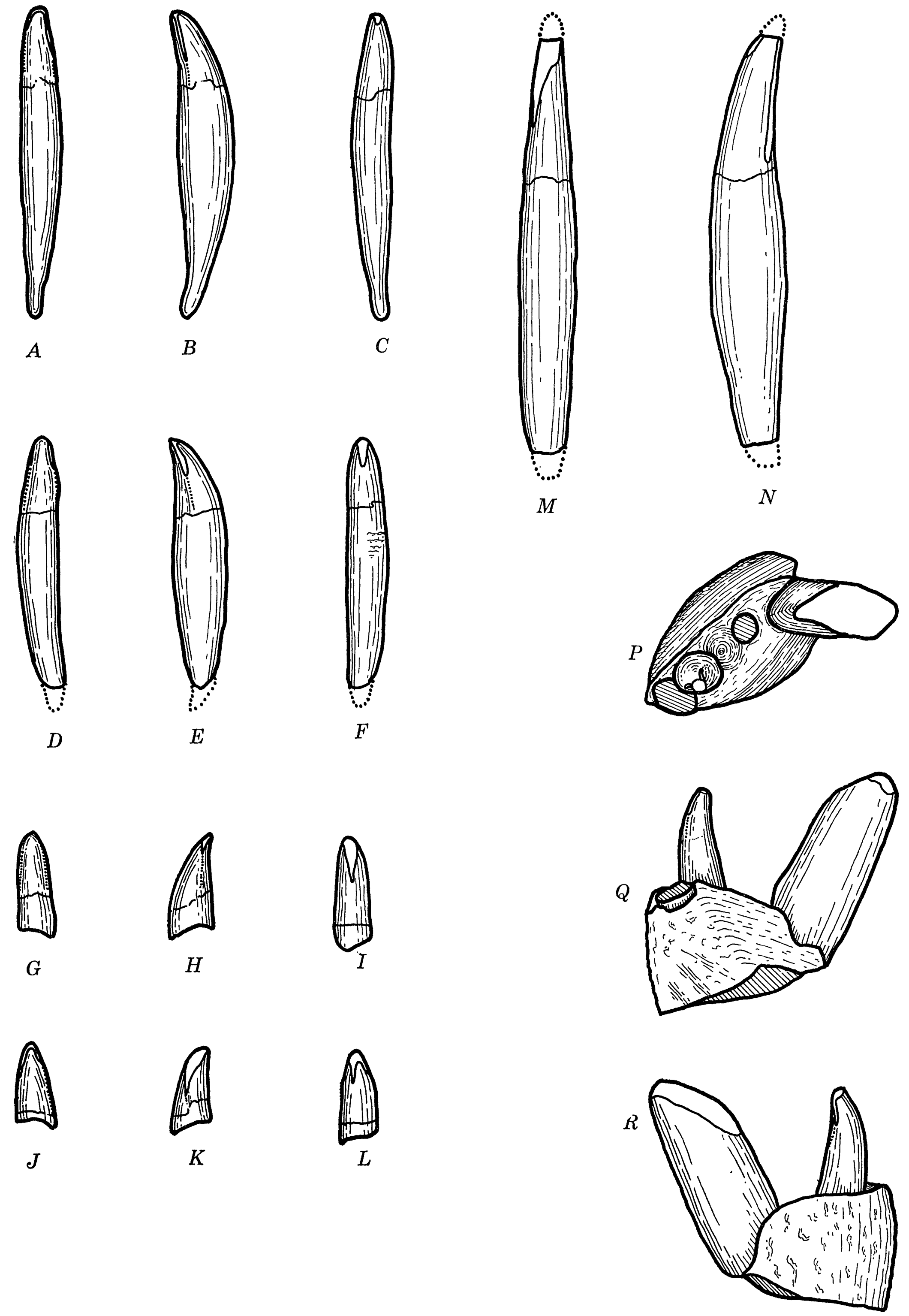


FIGURE 10. *Leontocephalus intactus* sp.nov. Isolated lower teeth showing wear facets, $\times\frac{2}{3}$. *A*, *B* and *C*, incisor '*A*' in lingual, anterior and labial views. *D*, *E* and *F*, incisor '*B*' in lingual, anterior and labial views. *G*, *H* and *I*, incisor '*C*' in lingual, posterior and labial views. *J*, *K* and *L*, incisor '*D*' in lingual, posterior and labial views. *M*, *N* and *O*, left canine in anterior, labial and posterior views. *P*, *Q* and *R*, fragment of right dentary in dorsal, medial and lateral views (see table 2).

lower jaw preserved, and in all adequate figures in the literature, a similar condition exists. It appears to be a characteristic feature of the Gorgonopsidae. Thus there must have been a mechanism allowing a propalinal shift of the mandibles anteriorly during the jaw action, and at the same time a lateral shift of the lower tooth row must have been possible (figure 11*D*).

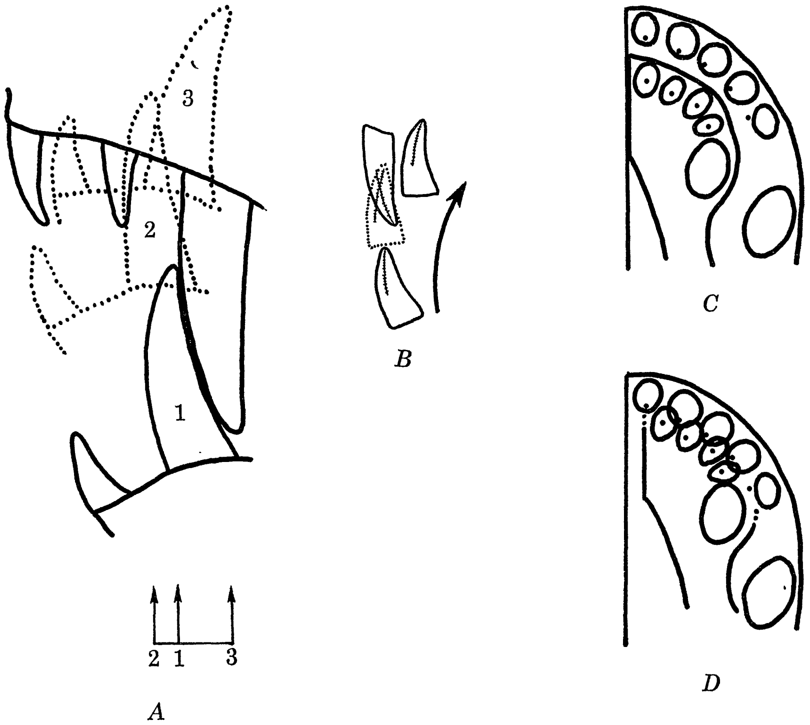


FIGURE 11. Tooth occlusion, diagrammatically. *A*, Definable positions of lower teeth relative to the upper teeth, showing relative anterior shift of the mandible below. *B*, Motion of a lower incisor relative to an upper incisor. *C*, Relative position of the upper and lower teeth, jaws closed. *D*, The same as *C*, but during interdigitation of the incisors.

Consider first the system of the opposing canines and the upper fifth incisor of *Arctognathus* sp. To produce the observed tooth wear the lower canine must have occupied three definable positions during its movement (figure 11*A*): (1) With its posterior edge against the anterior edge of the upper canine; (2) with its front edge against the back of the fifth upper incisor; (3) in the palatal recess, when the jaws were fully closed. Theoretically these three positions could have followed each other in any sequence but in phases 1 and 2 the lower jaw is at its lateral extremity and in phase 3 it has returned medially. Thus part of the cycle involved a shearing motion in the horizontal plane and it seems likely that when the teeth were in food, the energy for shearing was derived from the momentum of the closing jaws. From position 3 the teeth would be pulled directly out of the food along the paths of least resistance. It follows therefore that the normal sequence was probably 1–2–3, or that as the lower jaw closed, it occupied a lateral position to oppose the canines, then shifted forwards and upwards for the lower canine to oppose the upper fifth incisor and finally moved upwards, backwards and inwards to the closed position. By moving one of the mandibles in this manner on the actual specimen of *Arctognathus* sp, the motion of the rest of the incisors becomes apparent. At position 1, the lower incisors are about 6 cm below and slightly lingual to the upper incisors. When the lower canine just makes contact with the upper fifth incisor the gap is 3.5 cm and the lower incisors are almost exactly below the upper incisors. At position 2 the incisor tips are only a few millimetres apart and the lower tooth row lies parallel to and vertically below the upper tooth row. Because of the incurved nature of each upper incisor, their tips actually lie lingual to the tips of the lower incisors. When the mandible moves to position 3, the lower tooth row travels upwards, backwards and inwards. Allowing for some distortion of the teeth on the specimen, each lower incisor moves in a direction perpendicular to the upper tooth row, between two adjacent upper incisors, such that its serrated edges shear against the serrated edges of the upper teeth (figure 11*B*). The first lower incisor passes between the first and second upper incisors and so on around the jaw (figure 11*D*).

Considering both mandibles together, this form of bite must have involved either a separation at the symphysis or else the use of only one jaw ramus at a time. The former possibility is unlikely since the separation would have to have been 1 to 2 cm yet the symphysial face is broad and apparently fairly closely fitting. And because the jaw musculature was posteriorly placed, the accurate control of a single, heavy jaw ramus free at the front would have been difficult, a problem that does not arise when muscles on both the right and the left sides control a functionally single pair of mandibles. Thus only one side at a time must have been used. None the less, the faces of the symphysis (figure 15*B*) are ridged, have a large apparently vascular canal running between them, and in contrast to the equally heavy jawed dicynodonts the jaws readily separate at the symphysis. All these points suggest that there was a cartilaginous layer between the mandibles, a feature presumably necessary to allow a small amount of distortion of one jaw relative to the other when shifting laterally.

This hypothesis accounts for the wear of the serrated edges and is supported by the morphology of the teeth, accounting for the development of the serrated edges along lines parallel to the jaw margins, their restriction to the distal halves of the crowns, the conical rather than spatulate form of the incisors, and the greater incurving of the upper incisors compared to the lowers. Further, the number and arrangement of the teeth, the presence of an upper diastema only and the close set of the front pair of upper incisors are all explicable. But the presence of wear facets on the labial sides of the lower incisors and the tips of the upper incisors are not explained. There must have been an alternative form of bite such that the labial sides of the lowers wore against the tips of the uppers. A straightforward closure of the lower jaw with no lateral shift, but in a slightly anterior position, would account for such wear, especially if it were a powerful stroke with not much regard for accurate placement of the teeth.

Specific examples of occluding teeth in *Leontocephalus intactus* support these conclusions about interdigitation. On the left the anterior facet of the upper canine runs slightly lingually as it is followed towards the base (figure 9*C*), corresponding to the posterior facet of the lower canine which runs slightly lingually towards the tip (figure 10*N* and *O*). The upper fifth incisor on this side bears a marked, wide facet on its postero-lingual face (figure 9*L*) which corresponds very well to the upper part of the anterior facet of the lower canine (figure 10*M*) which is of a similar width. The lower part of this canine facet narrows and presumably it wore against the (missing) tip of the fifth upper incisor, as the lower jaw was moving towards its resting position. On the right hand side of *Leontocephalus* the anterior wear of its upper third incisor corresponds to that on the posterior serrations of the second lower incisor, when the lower jaw fragment is held with the symphysis vertical and lateral of the midline. Further, the absence of any wear on the posterior edge of the fourth upper incisor (figure 9*I*) of this side is matched by the very small size of the base of the lost fourth lower incisor, on the assumption that this latter was a young tooth that had not fully erupted.

The condition of the canines of the right side is difficult to evaluate. Both upper and lower are short stumps (figures 6 and 10*P*, *Q* and *R*), but appear to have natural wear facets upon them. It seems as if they fractured in life and were still used to some extent. This may have caused some degree of malfunction of the incisors of the same side but should not have affected the activity of the teeth of the opposite side, although the two upper incisors of the left are both heavily worn. It may be that the left side was used more, subsequently to the the damage to the right canines.

Presumably tooth replacement had an effect on the occlusion system although neither of the present specimens has a dentition both complete and well-preserved enough to illustrate it in detail.

In behavioural terms then, it is likely that the gorgonopsids had at least two forms of mastication. This is not unexpected. Clearly these beasts were carnivores capable of attacking suitable prey, presumably the contemporaneous dicynodonts in the main. The simple non-interdigitating stroke would be suitable for disabling living prey by embedding the teeth, particularly the enormous canines into it. But to actually tear off pieces of a swallowable size some sort of cutting action would be desirable and exactly this is provided by the interdigitating type of bite. The effect of it would be to use the opposing tooth rows to cut jagged slits in the meat rather than a series of holes. At this stage it would not matter that only one side of the jaw could be used at once. Indeed, an analogy with modern carnivore mammals suggests itself, where the canines are used for daggers and the carnassial molars used subsequently for shredding, but the carnassials of only one side at a time can be used.

3. *The pterygo-quadrate and related strutures*

If, as was concluded from the nature of the tooth-wear, the lower jaw was capable of a propalinal shift of 1 to 2 cm in a 30 cm skull, it is of interest to consider the region of the jaw articulation. On the left side of *Arctognathus* sp. the articular and quadrate bones are preserved, as also are the pterygoid and epipterygoid, complete with their compound quadrate ramus. The whole area has been completely cleared of matrix and there has been practically no damage or distortion.

The articular and the quadrate complex (quadrate and quadratojugal) of *Arctognathus* sp. agree closely with those described by Parrington (1955). The articular bone (figure 15) bears two condyles set on a line at about 60° to the dorsal edge of the post-dentary bones, the lateral condyle being the more posterior of the two. The lateral condyle is a transversely alined hemicylindrical trough which faces postero-dorsally. Its posterior edge is developed as a dorsally directed process. Similarly, unlike Parrington's specimen, the anterior edge is also raised as a distinct process, rising dorsally and somewhat backwards, and descending smoothly in front to join the posterior end of the surangular bone. The medial condyle is continuous with the lateral one and is saddle-shaped. Its anterior edge is raised to form a dorsally directed process almost as marked as that of the lateral condyle. From the top of this dorsal process, running along a line parallel to the post-dentary bones, the articulation surface of the medial condyle descends steeply and then flattens out to a horizontal surface. The last 1 mm or so turns very slightly upwards again. Medial to this line, the surface turns down to face dorso-medially and posteriorly. Laterally to this line, the surface is slightly depressed.

The quadrate complex (figures 2, 3 and 12*A*) is complete, although its anterior surface is not well-preserved and its postero-dorsal part has remained in the quadrate recess of the squamosal, along with a little matrix. It bears two condyles ventrally which, as in Parrington's specimens, correspond closely to the articular condyles. The lateral one is perfectly cylindrical with a diameter of 0.8 cm. It is set at a very slight angle to the lateral axis of the skull, as preserved, and extends 0.4 cm laterally to the lateral edge of the body of the complex. There is therefore a notch in the lateral edge of the complex immediately above the condyle to which Parrington drew attention. The medial condyle is saddle shaped with a convex surface along an antero-medially directed line and a concave surface at right angles to this. Laterally, the articular surface of the medial condyle is continuous with that of the lateral condyle but medially it is limited by an oblique ridge. The anterior part of the medial condyle curves antero-dorsally almost on to the front face of the complex. The diameter of the convexity is much larger than that of the lateral condyle.

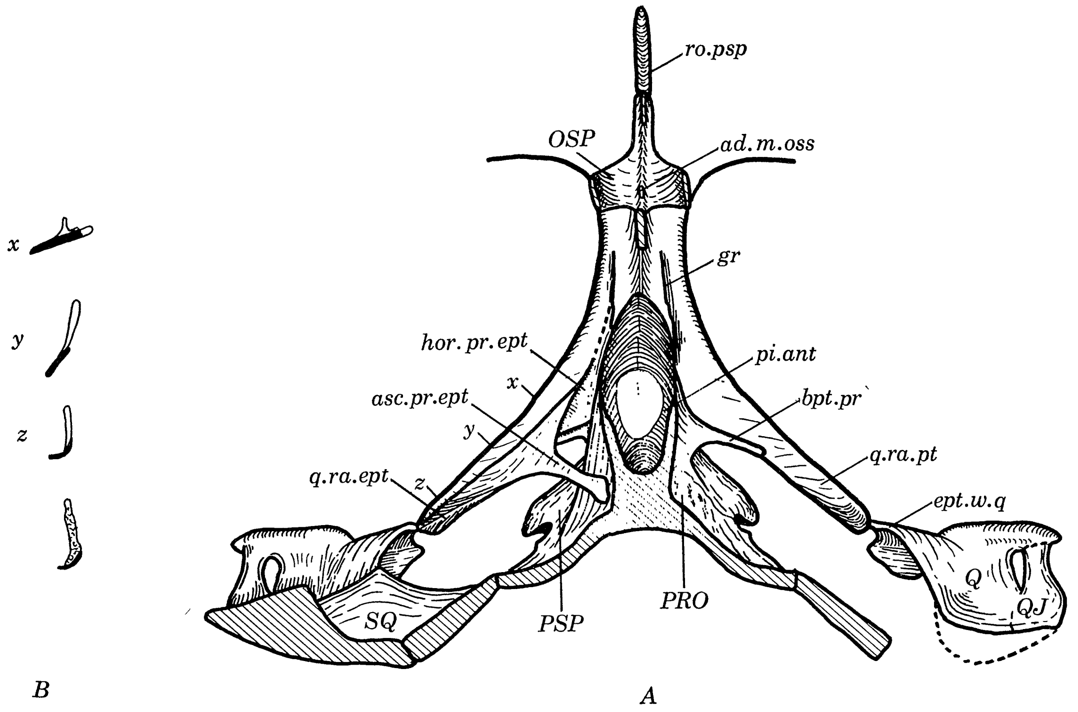


FIGURE 12. *Arctognathus* sp. *A*, Reconstructed dorsal view of braincase and pterygo-quadrate complex, $\times \frac{1}{2}$. Epipterygoid omitted on right side, *B*, Transverse sections through the compound quadrate ramus at positions, *x*, *y* and *z* as shown, and(bottom) distal view of the terminationt of the quadrate ramus. Pterygoid black, epipterygoid and basipterygoid process white.

The complex is constricted immediately above the condyles, both anteriorly and posteriorly. The anterior face is slightly concave and rises more or less vertically, but the antero-dorsal edge is unfortunately damaged. A very large quadratojugal foramen pierces the complex, low down near the lateral edge, and at least dorsally, the foramen is seen to lie on the suture between the quadrate and the quadratojugal. The complex swells postero-dorsally and disappears into the quadrate recess of the squamosal.

The medial part of the quadrate is expanded to form the stapedial recess and the epipterygoid wing* both of which are complete, in contrast to Parrington's specimen. The epipterygoid

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* Parrington (1955) terms this the 'pterygoid wing of the quadrate' but as described, its contact is solely with the epipterygoid bone.

wing is a thin vertical sheet of bone, continuing the front face of the quadrate antero-medially. At its origin from the body of the complex the wing is 3.7 cm high but its dorsal edge slopes downwards so that antero-medially it is only 1.5 cm high. The antero-medial edge itself is straight, vertical, and in the form of a groove or sulcus. The sulcus is continued for a short distance backwards along the ventral edge of the wing. Contrary to all published accounts, the whole height of the medial edge of this wing is in a flush contact with the posterior edge of the broad quadrate ramus of the epipterygoid, and does not quite contact the quadrate ramus of the pterygoid at all (figure 3*A*).

The ventral edge of the epipterygoid wing of the quadrate (apart from the distalmost 3 mm which is grooved) is turned sharply backwards to form a narrow horizontal shelf. Laterally, this shelf is in line with the condyles but is separated from the articular surface by the oblique ridge marking the postero-medial boundary of the medial condyle. The upper surface of the horizontal shelf is the floor of the stapedial recess and anteriorly it curves up gradually to join the posterior face of the epipterygoid wing which thus forms the anterior wall of the stapedial recess. However, there is a low horizontal ridge (figure 3*B*) running mediolaterally and marking the floor of the recess from its anterior wall. The lateral wall of the stapedial recess is formed by that part of the medial facing surface of the swollen body of the quadrate which hangs below the level of the squamosal. The recess is partially roofed by the ventral face of the paroccipital process, but is widely open posteriorly.

Practically no details of the quadrate recess of the squamosal can be seen and its nature is best illustrated by a further specimen of a gorgonopsid, described below (p. 31). The ventral edge of the squamosal bears a ventrally directed triangular process (figure 3*B*) immediately behind the quadrate complex, approximately adjacent to the quadratojugal foramen.

The epipterygoid and pterygoid bones form a complex structure (figures 12 and 18*A*) running along by the midline of the skull and then turning postero-laterally towards the quadrate. Behind the palate, the paired pterygoids form a strut below the braincase which is cross-shaped in section. Ventrally, each pterygoid sends down a thin, deep plate to overlie the thin keel of the parasphenoid while dorsally an extensive median septum is formed by the close apposition of the two pterygoids. Each pterygoid also has a narrow lateral plate with a horizontal ventral surface. A longitudinal groove runs along the anterior part of the dorsal surface, and opens out just in front of the interpterygoid vacuity as a laterally facing recess. For the length of the groove, the dorsal surface of the pterygoid slopes upwards towards the midline, but behind the groove the dorsal surface is horizontal. The width of the pterygoid increases gradually as far back as the basipterygoid process and for this length is closely applied to the median septum (except for the minute interpterygoid vacuity immediately in front of the basipterygoid process).

The basipterygoid process is a flat triangular structure arising almost horizontally from the body of the basisphenoid–parasphenoid complex, and lying in the same plane as the lateral plate of the pterygoid. The posterior edge of the basipterygoid process extends postero-laterally and the anterior edge runs even more sharply backwards. With the latter, the lateral plate of the pterygoid makes a direct, flush suture of considerable length. From here, the quadrate ramus of the pterygoid runs postero-laterally towards the quadrate.

Although the quadrate ramus is a compound of the pterygoid and the epipterygoid, these two bones are clearly distinguishable from one another (figure 12). The pterygoid itself is perfectly flat after it leaves the basipterygoid process, and it has a slight dorso-medial slope.

However, it narrows gradually in ventral view, and the medial edge curves dorsally. Just before the quadrate, the pterygoid is L-shaped in section, with a narrow horizontal part and a relatively high vertical part. At the same time the thickness of the bone progressively decreases and the distal extremity is very thin with no form of articulating facet. It finishes about 1 mm before making contact with the quadrate.

The epipterygoid is a complex bone which lies on the dorsal surface of the pterygoid and its quadrate ramus, but there is no evidence that any intimate suture occurs between the two. The ventral part of the epipterygoid consists of a flat plate lying on the dorsal surface of the lateral plate of the pterygoid. In fact, in this specimen the anterior part of the epipterygoid plate has been lost, exposing the perfectly smooth, dorsal surface of the underlying pterygoid. It is apparent, however, that the epipterygoid base originally continued forwards and that the pterygoid folded over it from the medial side as well as underlying it, thus giving the impression that the epipterygoid ran into the longitudinal groove of the pterygoid. The recess marking the posterior end of the groove is therefore the actual point at which the epipterygoid entered the fold of the pterygoid. Farther back, the base of the epipterygoid simply lies on the dorsal surface of the pterygoid, extending to within 0.6 cm of the lateral edge of the pterygoid and making direct contact with the median septum behind the interpterygoid vacuity. Posteriorly, the base of the epipterygoid ends abruptly (but clearly naturally) along the line of contact between the pterygoid and the basipterygoid process, but makes no contact with the latter.

A large triangular plate arises from near the lateral margin of the basal plate and stands almost vertically, but leans slightly dorso-medially. Behind the level of the basipterygoid process this forms the quadrate ramus of the epipterygoid. The ramus is a vertically orientated sheet of bone with its ventral edge turned slightly laterally. It rests on the dorsal surface of the quadrate ramus of the pterygoid and is overlapped medially by the upturned edge of the pterygoid. The quadrate ramus of the epipterygoid maintains its height and thickness for the full distance to the quadrate. The distal extremity is perfectly preserved and was carefully removed in order to inspect its surfaces. Both the lateral and medial faces near the extremity bear a series of irregularly longitudinal rugosities suggestive of sites of ligament attachments. The distal edge itself is in the form of a narrow facet extending for the full height of the ramus (figure 12*B*). It is irregularly grooved in a similar manner to the extremity of the epipterygoid ramus of the quadrate. The adjacent edges of these two respective rami have the same dimensions and are similarly grooved as if for a thin layer of cartilage. As preserved in this specimen the two rami exactly buttress against each other and form a continuous plate of bone, interrupted only by the suture between them (figure 3*A*).

The ascending process of the epipterygoid arises from the apex of the vertical plate just behind the level of the basipterygoid process (figure 18). For most of its height it is oval in section, about 0.5 cm × 0.2 cm. Ventrally the broader face is in the same plane as the vertical plate of the epipterygoid but immediately above, the shaft twists to face postero-laterally and retains this configuration right to the head. A slight median swelling occupies the ventral half of the shaft and an inconspicuous ridge runs up the middle of the postero-lateral face for most of the height of the process. Dorsally, the ascending process ends by a flat broad head resting against the ventro-medial part of the parietal. The anterior edge of the head is a continuation of the line of the shaft but the posterior edge begins to curve postero-dorsally. However, because of a break, the original posterior extension of the head cannot be determined. The lateral facing surface of the head bears a triangular-shaped depression, possibly representing a muscle attachment.

Several important details concerning this region of the gorgonopsid skull may be added from other specimens.

Parrington (1946, 1955) described a perfectly preserved but slightly incomplete quadrate complex and quadrate recess of the squamosal, belonging to a large unidentified gorgonopsid skull (no. F.R.P. 38), found in unconsolidated matrix. These have been refigured in order to draw attention to a number of critical observations of their structure (figure 13*C* to *E*).

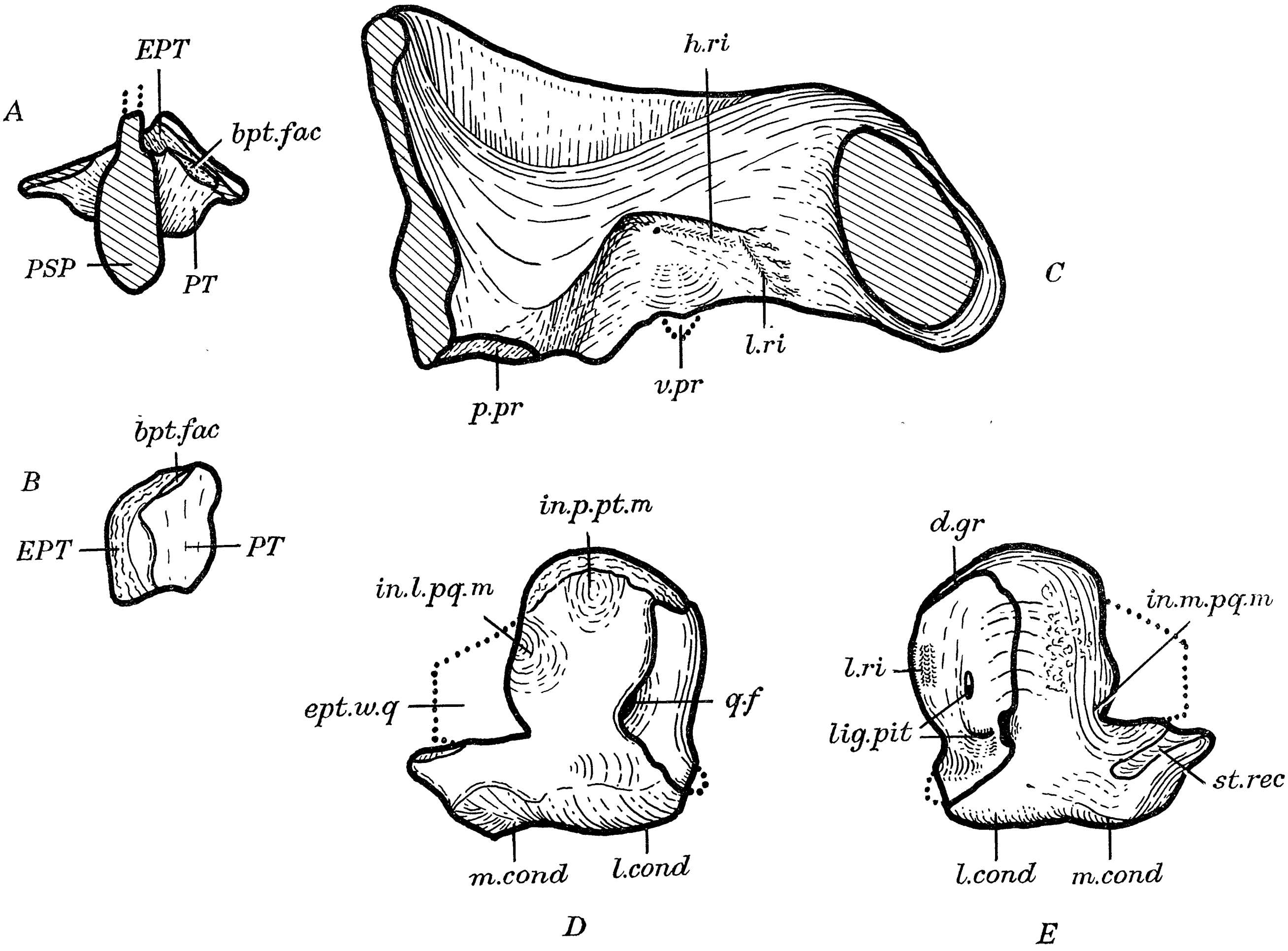

Figure 13. *A*, Unidentified gorgonopsid F.R.P. 36. Posterior view of fragment of pterygoid–epipterygoid complex showing the facet of the pterygoid for articulation with the basipterygoid process × $\frac{3}{4}$. *B*, The same as *A*, in ventral view. *C*, Unidentified gorgonopsid F.R.P. 38. Anterior view of the left squamosal showing the quadrate recess, × $\frac{3}{4}$. *D*, As for *C*, anterior view of left quadrate complex. *E*, As for *C*, posterior view of left quadrate complex.

The quadrate recess of the squamosal faces anteriorly and consists of a pocket in the squamosal roofed over but open ventrally. The medial part is deep and corresponds to the dorsal swelling of the back of the quadrate part of the quadrate complex. The medial wall of the recess slopes steeply downwards and inwards, and comes forwards almost at right angles to the transverse plane of the skull. Moving laterally, the recess gradually becomes shallower and only a low, sharp ridge, which may be called the lateral ridge, marks it from the rest of the inner surface of the zygomatic part of the squamosal.

Between the medial and lateral parts, the lower part of the recess is slightly convex. Although the ventral edge of the recess is a little damaged, it is clear that the ventrally pointing process (noted in *Arctognathus* sp.) arose from the convex region. The surface of the recess is minutely ridged, the ridges tending to radiate from an area high up in the middle. One of these ridges, the horizontal ridge, runs laterally and slightly ventrally from the middle of the recess just below the roof and is more conspicuous than the rest. It ends near the top of the lateral ridge of the recess. Minute foramina cover the upper half of the recess and in addition there are two larger foramina opening from the squamosal.

Immediately lateral to the lateral ridge, the inner surface of the zygomatic part of the squamosal bears a further series of fine ridges, running antero-ventrally.

As Parrington (1946) showed, the posterior face of the quadrate complex (figure 13*E*) consists of the large dorsal swelling of the quadrate medially, and laterally the much less marked swelling of the part of the quadrate that is overlapped by the thin quadratojugal. Between these two areas the bone is concave from side to side and this wide vertical trough corresponds in position to the convex region of the recess of the squamosal. The dorsal half of the swelling of the quadrate is minutely pitted. Ventrally, the condyles, the stapedial recess and the remains of the epipterygoid wing correspond closely to the conditions described for *Arctognathus* sp. The bone surface between the postero-dorsal swelling and the condyles is perfectly smooth. There are two deep pits opening from the lower half of the back of the quadratojugal. The lower one is borne on a small boss and faces very nearly dorsally. About 1 cm above it lies the second pit, which faces postero-dorsally.

On the extreme lateral part of the back of the quadratojugal are three short vertical parallel ridges. They are about 1 mm apart and the lateralmost one, which is in fact the actual edge of the bone, is the best developed. The anterior face of the quadrate (figure 13*D*) is smooth and bears two subcircular depressions. One is placed mid-dorsally and faces antero-ventrally. The second, of about the same size, lies dorso-medially and faces more or less anteriorly.

The antero-dorsal edge of the quadrate consists of a transverse strip of rugose unpitted bone, which stands slightly higher than the postero-dorsal surface of the complex. It extends laterally almost to the edge of the complex but is overlapped both in front and behind by the quadratojugal, which is wrapped around the lateral parts of the quadrate. Between the strip of rugose bone and the posterior flange of the quadratojugal is a slight but definite groove, the dorsal groove. It is horizontal, runs transversely, and occupies the lateral part of the complex.

A fragment of an unidentified gorgonopsid skull partially prepared by acetic acid, no. F.R.P. 36 (figure 13*A* and *B*) confirms the interpretation of the basipterygoid articulation suggested by *Arctognathus* sp. The fragment consists of the basisphenoid–parasphenoid complex with damaged basipterygoid processes. The undamaged facet of the pterygoid which articulated with the basipterygoid process is preserved. It is about the same thickness as the remains of the basipterygoid process and is irregularly grooved. The epipterygoid covers this region dorsally and its undersurface is smooth where it contacted the pterygoid (as shown by a damaged portion of the pterygoid). Medial to the pterygoid, the epipterygoid faces ventro-medially and is irregularly grooved. Although there is a gap between this part and the parasphenoid, the epipterygoid was probably completed in cartilage right up to the parasphenoid, since the latter has a roughened, unfinished appearance.

A few more details concerning the epipterygoid may be added. The nature of the relationship between the pterygoid, epipterygoid and quadrate described for *Arctognathus* sp. contradicts previous accounts of this region of the gorgonopsid skull. No other specimen at hand has a complete quadrate ramus preserved, but one, a medium-sized skull prepared by acetic acid (no. F.R.P. 142), has only lost the distal 1 cm or so of the ramus. As far as it goes, this specimen fully confirms the account for *Arctognathus* sp. The quadrate ramus of the pterygoid has started to narrow and its median edge is turned dorsally. The quadrate ramus of the epipterygoid is a high sheet and has lost none of its height before the break.

The possibility that the head of the epipterygoid of *Arctognathus* sp. bore a posteriorly directed process was mentioned. A small, badly weathered skull (no. F.R.P. 102), attributed to the genus *Dixeya*, was bisected just to one side of the midline, and each of the sections was prepared by acetic acid. The right epipterygoid was exposed intact and its head does indeed have a short wide process, running backwards and overlapping an anteriorly directed process of the supraoccipital (figure 21*A*).

Also in this specimen, the head of the ascending process of the epipterygoid appears, in medial view, to buttress against the underside of the parietal. Yet in *Arctognathus* sp., seen in lateral view, the head appears to overlap the lateral face of the ventral ridge of the parietal. However, this inconsistency is resolved by reference to the specimen of *Leontocephalus intactus*. The ascending processes of both the epipterygoids have been lost and in a ventral view of the roofing bones, the facet on the parietal for articulation with the right epipterygoid is preserved (figure 5). It lies alongside the pineal foramen, at the edge of the broad, deep medial ridge of the parietals which forms the roof of the braincase. The facet itself is an irregularly ridged oval boss, half of which faces ventrally and half of which is turned on to the side of the parietal ridge to face laterally.

Although this specimen lacks both quadrate rami and both quadrates, it confirms a number of the points described. The quadrate recesses of the squamosals are well preserved and show the same form, ridging and pitting as in specimen F.R.P. 38. In the basipterygoid articulation region, the base of the epipterygoid runs anteriorly into a groove on the dorsal surface of the pterygoid (figure 7) as was assumed to have been the case in *Arctognathus*.

4. *Jaw articulation*

Parrington (1955) demonstrated a complex form of jaw articulation in the gorgonopsids, whereby the lateral condyle of the quadrate fits closely into the deep lateral condyle of the articular. As the jaws open, the medial articular condyle screws around the corresponding quadrate condyle in such a fashion as to force the articular bone laterally. The dorsal process behind the lateral articular condyle turns into the notch above the lateral quadrate condyle. Thus a very wide gape is possible and yet the danger of disarticulation at this joint is greatly reduced.

The morphology of this region in *Arctognathus* sp. supports Parrington's conclusions in detail. Indeed the greater height of the anterior edge of the lateral quadrate condyle gives an even more marked impression of the close fit between the lateral condyles. There is no possibility, therefore, of propalinal movement occurring by relative movement in a horizontal plane between the quadrate and the articular bones. Since there is no evidence of either intramandibular kinetism or of cranial kinetism between two parts of the skull itself, it follows that the necessary propaliny must be due to a streptostylic quadrate, capable of moving its condyles anteriorly relative to the squamosal. Circumstantial support for this view is lent by the loose nature of the quadrate-squamosal attachment. In both of Parrington's specimens the quadrate complex had simply fallen out of its recess, and in *Arctognathus* sp. it is by no means closely applied to the back of the recess. In the majority of gorgonopsid skulls preserved without their mandibles, the quadrate complex has been lost but the recess has not been unduly damaged.

Several factors limit the possible movements of the quadrate:

(*a*) The axis of the lateral condyle of the quadrate must have remained perpendicular to the vertical longitudinal plane of the skull, because its fit with the articular condyle is so close. (The only possible exception would be if one quadrate dropped to a lower level than the other, when a tilting in the transverse plane would have been necessary.) However, there must have been provision for a slight rotation in the horizontal plane in order to allow the lateral shift of one mandible or the other, for interdigitation of the incisors of one side, but for a 30 cm jaw to have had a lateral shift of 1 cm from the centre position would require a rotation of under 2° by the quadrate.

(*b*) The quadrate complex must presumably have retained a dorsal contact with its recess Since the teeth are considerably farther forwards than the jaw muscles, there must always have been a strong vertical reaction downwards on to the articular when the animal bit, which must have been transmitted to the rest of the skull, via the roof of the recess.

(*c*) The quadrate complex could probably not have had a ventral component of its motion, relative to the skull, because there is no provision for the attachment of suitable muscles ventral to the complex.

(*d*) It is probable that the quadrate complex had to retain some form of contact with the quadrate ramus of the epipterygoid. As described in *Arctognathus* sp. there is evidence of a direct contact maintained by ligaments on the lateral and medial faces of the quadrate ramus of the epipterygoid and the pterygoid wing of the quadrate respectively.

(*e*) The movement must have been subject to fairly fine control since its object is to allow accurate relative placement of the upper and lower teeth. Partly this may have been achieved by means of the jaw closing muscles, but evidence of an intrinsic controlling musculature is to be expected too.

(*f*) The morphological features of the back of the quadrate complex and of the quadrate recess of the squamosal, described in detail for specimen F.R.P. 38, are presumably related to the form of the streptostyly and must therefore be explained.

Of the theoretically possible ways in which the quadrate complex could move relative to the recess, only one appears to satisfy the above conditions. This is with a ball-and-socket type of joint (figure 14*A* and *B*). In specimen F.R.P. 38 the quadrate complex appears to have rested more or less vertically, with the antero-dorsal strip of rugose bone adjacent, but anterior, to the front edge of the roof of the recess. In this position the complex fits medially against the inner wall of the recess, and laterally the short lateralmost ridge of the quadratojugal exactly overlaps the lateral ridge of the recess. Postero-ventrally, the ventral process of the squamosal, if present, would have fitted exactly into the concave region at the back of the complex, above the quadratojugal foramen. The lower, dorsally facing quadratojugal pit lies about 1 cm below the squamosal edge and the upper postero-dorsally facing quadratojugal pit is about 2 mm below the squamosal. Thus both face in a direction consistent with the view that they were the sites of ligamentous attachments for muscles running dorsally on to the back of the squamosal. From this position the complex can be rotated in the socket to a new position whereby the condyles have moved anteriorly through about 1.5 cm. The dorsal groove of the complex, between the strip of rugose bone and the top of the quadratojugal, fits over the horizontal ridge of the recess. And in doing so, the rugose strip of the bone still does not come into direct contact with the back of the recess, thus explaining why it was not covered by cartilage.

The lateral edge of the quadratojugal fits just inside the lateral ridge of the recess. There is still a good medial fit between the quadrate and the recess and significantly, the ventral process of the squamosal would still fit snugly into the concave region at the back of the complex, but at a higher level. However, the lower quadratojugal pit is now about 2 cm directly below the squamosal edge, and the upper pit is about 1 cm below.

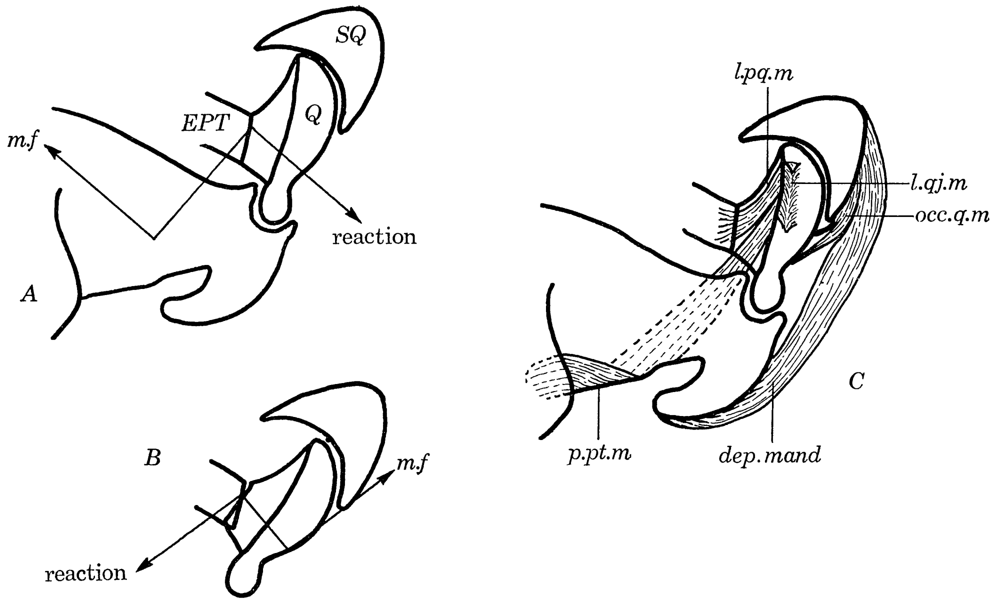

Figure 14. *A*, The basic couple producing displacement of the quadrate complex. *B*, The basic couple producing return of the quadrate complex. *C*, Diagrammatic restoration of the principal intrinsic muscles of the quadrate complex in lateral view.

Because the cartilage layers are absent, it is impossible to know the precise form of motion that would be involved on going from one position to the other, but in general terms it is a rotation of the complex through a horizontal axis about half-way up the bone and 1 to 2 cm in front of it (figure 14*A* and *B*). This more or less corresponds to a point along the attachment of the quadrate ramus of the epipterygoid in *Arctognathus* sp. Thus although this junction must become disarticulated it can retain a point of contact which could act as a fulcrum for the quadrate rotation.

There is evidence that the epipterygoid was capable of a small degree of movement relative to the rest of the skull. The part of the pterygoid underlying the foot of the epipterygoid and the underside of the foot itself are perfectly smooth and similarly, in the construction of the compound quadrate ramus, there does not appear to be fusion, or suture formation between the pterygoid and the epipterygoid parts. Anteriorly, the epipterygoid foot is sandwiched by the pterygoid from the medial side but possibly it could have slid antero-posteriorly within the pterygoid groove to some extent. The basipterygoid process does not contact the epipterygoid, and although the foot of the epipterygoid lies adjacent to the parasphenoid anterior to the basipterygoid articulation, there appears to have been cartilage separating the two (as shown in specimen F.R.P. 36, figure 13*A* and *B*). Dorsally the head of the ascending process of the epipterygoid, forms a suture with a boss on the underside of the parietal. In *Leontocephalus intactus* the surface of the boss is rugose and this may indicate a ligamentous attachment to the head of the epipterygoid, allowing a slight degree of disarticulation between the two. Finally, evidence has been given of a posteriorly directed process of the head of the epipterygoid overlapping the anteriorly directed supraoccipital process, suggesting a device for the control of an anterior movement of the epipterygoid.

An antero-medial movement of the epipterygoid such that its quadrate ramus slid along the quadrate ramus of the pterygoid would be limited by contact between the epipterygoid and the parasphenoid, and prevented in any case by the meeting of the head of the epipterygoid with both the parietal and the supraoccipital. Any rotation of the epipterygoid about its point of contact with the parietal would be limited by the essentially flat ventral surface of the epipterygoid foot overlying the pterygoid. Finally, an anterior shift of the epipterygoid would be limited by the distance to which the anterior part of the epipterygoid foot could slide into the recess in the pterygoid and by the degree to which disarticulation could occur between the ascending process and the parietal. It would have the apparent disadvantage that there would tend to be a complete disarticulation between the quadrate ramus of the epipterygoid and that of the pterygoid.

It does not seem possible, therefore, that any movement of the epipterygoid could be of sufficient magnitude to carry the quadrate passively forwards for a sufficient distance to give the required amount of anterior shift of the lower jaw. However, in view of the relatively loose attachment of the epipterygoid to the skull, it is probable that it was capable of slight adjustment movements, especially in an antero-posterior direction. If the motion of the quadrate complex were not a precise rotation about a point along the epipterygoid-quadrate contact, but also had a small component in the horizontal plane, then it would be necessary for the epipterygoid to move in this plane in order to retain its contact with the quadrate. Otherwise, the design of the epipterygoid can be explained in terms of its function of transmitting the forces, imparted to the quadrate, to the rest of the skull, via ligaments attaching the quadrate ramus to the epipterygoid wing of the quadrate.

The couples producing rotation of the quadrate must have consisted basically of the jaw closing muscles along with reaction forces at the quadrate-epipterygoid fulcrum. Evidence for a powerfully developed anterior pterygoideus muscle with a large forward component is discussed later (p. 44) and this muscle must have been responsible for the forward displacement of the quadrate condyles (figure 14*A*). The return movement of the quadrate would result from the action of postero-dorsally directed jaw muscles. This latter phase, however, would need to be powerful since it would be responsible for the shearing activity of the teeth. The two pits on the back of the quadratojugal do not lead into foramina, and probably they are the sites of insertion of two ligaments from a muscle. The orientation of the pits indicates that the muscle originated on the back of the squamosal. Such a muscle (presumably derived from the depressor mandibuli) would be ideally situated to assist in the return phase of the quadrate complex because its force would be more or less tangential to the arc of movement of the pit-bearing region of the complex (figure 14*B*).

Because the supposed fulcrum of the rotation of the quadrate lies medial to, as well as antero-dorsal to the condyle region, there would be a tendency for the rotation to have a horizontal component but this would be resisted by the bilateral action of the jaw muscles. However, by a slight differential action of the muscles of each side, the small horizontal rotation necessary for a lateral shift of the mandible would be possible.

On top of this basic system, there appears to have been a complex series of intrinsic muscles controlling the movements of the quadrate (figure 14*C*). Evidence for muscles on either side of the quadrate ramus of the epipterygoid has been cited. The stapedial recess of the quadrate is marked off from the back of the epipterygoid wing by a ridge in both *Arctognathus* sp. and specimen F.R.P. 38. Above the ridge the bone is smooth and partially hollowed out as a recess which probably represents the main origin of muscles inserting on the inner face of the quadrate ramus of the epipterygoid. The dorso-medial muscle scar on the front face of the quadrate may be the origin of a muscle inserting on the outer face of the epipterygoid. The relative movement between the quadrate and the epipterygoid would have been that of two thin sheets coming to lie obliquely to one another, leaving only a point contact. Since this is an unstable situation, control by well-developed muscles, and possibly ligaments too, across the junction itself would be essential.

A posterior pterygoideus jaw muscle, discussed later, probably arose near the posterior end of the lower jaw and ran dorso-posteriorly. Its natural termination would be on the dorsal muscle scar of the front face of the quadrate and such a muscle would have the prime effect of preventing disarticulation between the quadrate and the lower jaw. It would also assist in the return phase of the quadrate's action. Although there is no osteological evidence, it would be expected that there should be a corresponding posterior muscle from the smooth region of the quadrate above the condyles down to the retroarticular process of the lower jaw. Again this would retain the relative positions of the quadrate and the articular bones, and would assist in the displacement phase of the quadrate's movement. Finally, it was noted that the fine ridging of the recess continued laterally to the lateral ridge of the recess. It is possible that a short muscle from the smooth antero-lateral surface of the quadratojugal inserted here. It would have been suitably placed to prevent an excessive quadrate motion.

The ascending process of the epipterygoid too shows indications that it bore muscle attachments both on the head and along the length of the shaft. If the epipterygoid were indeed capable of movements, then the muscles would have been for controlling such movements. It is not however possible to deduce their origins.

Thus all the observed features of the system may be explained and the only disadvantage of the hypothesis appears to be the apparent instability of a point contact between the epipterygoid and quadrate, coupled with the lack of a specialized region for rotation somewhere along their line of contact. However, as will be shown presently, the jaw muscle system appears to be adapted so that the horizontal reaction forces at the hinge are reduced to a controllable minimum, yet it would be these forces mainly that tended to disrupt the balance of the quadrate at this point

5. *The lower jaw*

The left lower jaw of *Arctognathus* sp. is almost complete and very well preserved. The anterior three-quarters of the right lower jaw are present.

Gorgonopsid lower jaws have been figured in both lateral and medial aspects by several authors (e.g. Broom 1930; Boonstra 1935; Olson 1937) and thus the basic pattern of bones is well known. However, a great deal of detailed information bearing especially on the jaw musculature is available from the present specimen (figure 15).

From immediately behind the post-canine teeth, the dorsal margin of the dentary starts to rise and continues smoothly up, right to the postero-dorsal tip of the coronoid process. For most of this distance the margin is smoothly rounded. The coronoid process is completely preserved.

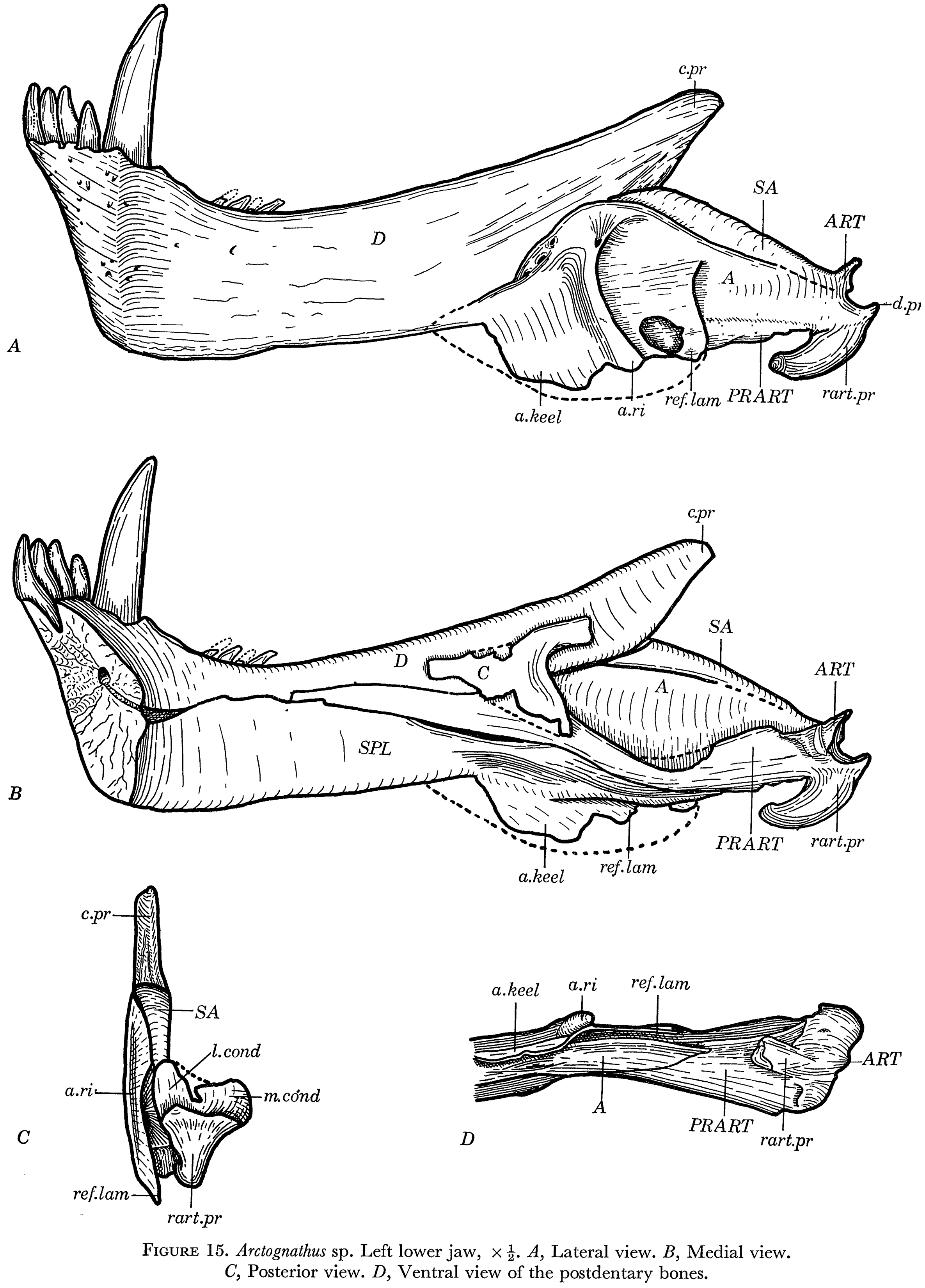

FIGURE 15. *Arctognathus* sp. Left lower jaw, × ½. *A*, Lateral view. *B*, Medial view. *C*, Posterior view. *D*, Ventral view of the postdentary bones.

Its dorsal edge is rounded but becomes progressively sharper towards the tip, while the ventral edge is sharp. The medial face is concave at right angles to its long axis, except towards the tip where it becomes progressively flattened, and the surface bears fine longitudinal ridges. The lateral face slopes medially towards both the upper and lower edges, so that in section the process is obtusely triangular. Near the tip the upper part of the lateral surface is finely rugose, and the lower part bears a series of coarse longitudinal ridges. The tip of the process is bluntly pointed and rugose.

Anteriorly to the coronoid process, the attachment of the dentary to the surangular and angular appears to have been loose. The antero-dorsal edge of the surangular is in the form of a wide groove, which is continued anteriorly by the dorsal edge of the angular, as far forwards as the level of the coronoid bone. The lateral edge of this groove is slightly higher than the medial edge. The opposing face of the dentary is flat. Direct contact between the bones only occurs at one lateral and one medial point of the surangular, and one lateral point of the angular. Elsewhere, there is a clear gap of up to 2 mm between the dentary and the more ventral bones. Farther anteriorly, the dentary and the angular are much thinner and form the lateral wall of the meckelian fossa. The contact between them becomes an intimate abuttment although part of the length of this suture is damaged. At this level the dentary also forms the roof of the fossa and the upper part of the medial wall. It is overlapped medially to a slight extent by the prearticular, which forms most of the medial wall.

The coronoid is a thin triradiate bone plastered on to the medial surface of the dentary and the prearticular. Its posterior margin is concave, thickened and rounded, and forms the posterior limit of the medial wall of the meckelian fossa. Since its posterior margin lies behind the point where the dentary and the prearticular make contact, the body of the coronoid contributes to the medial wall. The thickening of the posterior margin continues on to the postero-dorsal limb of the bone as a curious oblique ridge.

The articular is a large, complex bone which agrees quite closely with the isolated one described by Parrington (1955), but is more complete. The very large ridge on the lateral surface forms an arc of a circle with the concavity facing backwards and slightly upwards. It rises about 1 cm away from the surface of the angular and is about 0·8 cm wide in the middle of its length. Dorsally the ridge widens and passes insensibly into the upper part of the body of the bone, where it meets the dentary. In front of the ridge and just below the dorsal edge, the bone is deeply concave, and ventral to this region a relatively thin but deep keel is developed. Immediately behind the dorsal half of the ridge there is a second deep concavity, bounded above by the dorsal part of the articular, and anteriorly it is actually overhung for nearly 1 cm by the ridge. The reflected lamina of the angular arises behind the lower half of the ridge. The root of the lamina is the horizontal line marking the deepest part of the concavity. In lateral aspect, the upper part of the lamina is dorso-ventrally convex and therefore the vertical lower part is in the same plane as the angular keel, noted above. Although damaged ventrally, it is clear that the keel and the lower part of the lamina form a continuous structure. The anteriormost point of the origin of the lamina is just in front of the level of the ridge. Because the lamina is of constant thickness (about 0.7 mm as preserved), its medial facing surface is concave dorso-ventrally. The corresponding lateral face of the body of the angular is also slightly concave, so that between the two is a relatively wide angular recess (up to 0.6 cm wide) emerging posteriorly to the reflected lamina.

The lateral face of the angular posterior to the lamina is very slightly concave dorso-ventrally. About 1 cm above the ventral jaw margin this part of the angular takes a sudden 0.1 cm step along a horizontal line, so that the lower part is medial to the upper. The step continues anteriorly to a level half-way along the angular recess and then, within the angular recess, it stops quite suddenly. Below the step, the bone is smooth and vertical and ends ventrally as part of the jaw margin, which is sharp, particularly alongside the reflected lamina. The ventral part of the angular expands medially to clasp the prearticular above, forming a smoothly continuous medial surface with this bone. In front of the reflected lamina this part of the angular supports the keel, and bears a curious horizontal depression just above the keel. It is very similar to the one described by Parrington (1955), being narrow anteriorly and posteriorly and fairly wide in the middle.

The medial face of the angular is a high wall below the surangular and the dentary. Its dorsal part is very slightly concave and its ventral part very slightly convex, along a dorso-ventral line. The lower part forms the lateral wall of the meckelian fossa, which is widely open dorsally in the posterior part of the jaw.

The prearticular bone runs forwards from the region of the medial condyle of the articular, although no suture can be distinguished between these two bones. It forms a low vertical wall limiting the meckelian fossa medially and at the level of the condyles, the fossa is 2.2 cm wide. As it runs forwards, the medial wall travels gradually laterally so that the width of the fossa decreases, and at the same time the wall first becomes lower and then rises until it meets and overlaps the dentary, beneath the coronoid. It is here that the fossa, now high and narrow, becomes completely enclosed by bone. The medial face of the prearticular curves smoothly downwards and it has been noted that this bone is clasped by the angular. However, it is exposed ventrally in the posterior part of the jaw, where it forms the ventral margin behind the angular margin, and in contrast to the latter, forms a smooth, wide, rounded edge. The prearticular has a small, lateral exposure in this region, before it becomes overlapped by the angular.

The suture between the lateral surfaces of the articular and angular cannot be distinguished, but in this region, the bone curves quite sharply postero-laterally backwards from the angular part, to join the rim of the lateral condyle, which partly accommodates the increased width of the articulation region as compared to the region of the post-dentary bones. The retroarticular process curves downwards and forwards in a plane almost exactly between the two condyles. It is somewhat compressed laterally with a fairly sharp postero-ventral margin, but the distal end becomes slightly flattened dorso-ventrally. The termination itself is irregularly flattened and rugose. Laterally the process curves smoothly up to the outer side of the lateral condyle. Medially it joins a distinct smooth area of bone just below the medial edge of the inner condyle. This facet is small and saddle-shaped, being relatively long and convex antero-dorsally to postero-ventrally and narrow and concave at right angles to this. It is quite distinct from the rest of the bone except above, where it is continuous with the smoothly rounded posterior end of the inner wall of the meckelian fossa.

A number of foramina open from the mandible. The large one in the middle of the symphysial area has been noted earlier (p. 26). In the region of the incisors, a large number of foramina open from the anterior surface of the dentary and each is associated with a very short sulcus, giving the anterior surface of the bone a roughened appearance. They are most dense (about 25 in each ramus) over the dorsal half and most of them face upwards, or in the lower part of this region anteriorly. Lower down a few foramina emerge near the symphysis and open downwards. Very close to the ventral margin of this front part of the jaw, two noticeably larger foramina are apparent on the left ramus, and on the margin itself, below the canine a very large one opens from the splenial. A second set of foramina are found in the part of the dentary recesses for the upper canine. They number about half a dozen and are restricted to the region of the middle of the jaw. About 2 cm behind the symphysis, two foramina are found on the medial jaw surface, one just above the meckelian fossa and the other in the splenial about 1 cm lower. On the dorsal surface of the dentary, a large number of minute foramina open immediately behind the incisor teeth, and medially to and just below the post-canine series.

On the angular, a large foramen opens upwards from the dorsal end of the articular ridge. Anterior to the ridge, just below the suture of the angular with the dentary, the angular bears a narrow groove facing upwards and running forwards. From the base of the groove three foramina open, all close together.

6. *Jaw musculature*

The first attempt to reconstruct the jaw musculature of a therapsid was made by Adams (1919) who considered the cynodont *Cynognathus* in the light of an extensive study of the comparative anatomy of a large series of vertebrate mandibular musculatures, from fishes to mammals. His main conclusions were that the capiti mandibularis muscle had divided into three parts, a superficial slip (masseter of mammals) between the zygomatic arch and the outer side of the dentary; a medial slip (temporalis) between the temporal fossa and both inner and outer sides of the dentary; and a profundus slip (external pterygoid of reptiles) between the inner side of the temporal fossa and the coronoid process of the dentary. In addition, he proposed an anterior pterygoid muscle from the pterygoid bones, inserting in the post-dentary bones in the postero-ventral region of the jaw, as in most modern reptiles.

Romer & Price (1940), on discussing the reflected lamina of *Dimetrodon*, suggested that it was merely a continuation of the ventral keel of the angular, held laterally to the ventrally expanded articular, and like the keel, carried the insertion of pterygoideus musculature. They suggested that the notch so formed may have carried a slip of the depressor musculature. Watson (1948) concluded that even in *Dimetrodon* the capiti mandibularis had started to divide, with an inner temporalis slip in the meckelian fossa and an outer masseteric slip (deep masseter) to the coronoid and incipient coronoid process of the dentary. He showed that the anterior pterygoideus muscle probably inserted on the external surface of the lower jaw behind the reflected lamina and ran forwards in a smooth trough round the ventral margin of the jaw internal to the reflected lamina, and then antero-dorsally to its origin on the dorsal and posterior areas of the lateral pterygoid flanges. Similarly, a smooth surface runs from the posterolateral part of the prearticular below the condyles, forwards and medially below the rounded margin of the prearticular. This presumably was the course of a posterior or external pterygoideus muscle.

Parrington (1955) reconstructed the gorgonopsid musculature, concluding that the anterior pterygoideus musculature was arranged basically as in Watson's interpretation of *Dimetrodon*. He suggested that the posterior pterygoideus musculature originated to a large extent on the ventral keel of the basisphenoid-parasphenoid complex. However, his main disagreement with previous authors concerned the function of the reflected lamina of the angular which he suggested carried a masseter muscle (superficial masseter of mammals) running forwards up to the zygomatic arch below and anterior to the orbit.

Crompton (1963) agreed in general with Parrington's interpretation and suggested that the gorgonopsids could be fitted into a morphological series of jaw musculatures, from the pelycosaurian to the mammalian condition.

Barghusen (1968) has recently discussed the evolution of the cynodont jaw musculature. He reaches the conclusion that the gorgonopsids did not have a muscle corresponding to the mammalian superficial masseter, and that the vertical ridge of the angular and reflected lamina represents the site of insertion of a postero-dorsally directed slip of the capiti mandibularis which originated from the posterior part of the zygomatic arch.

The lower jaw of *Arctognathus* sp., described earlier, adds considerably to our detailed knowledge of the gorgonopsid jaw structure and suggests certain new interpretations concerning the jaw musculature (figure 16).

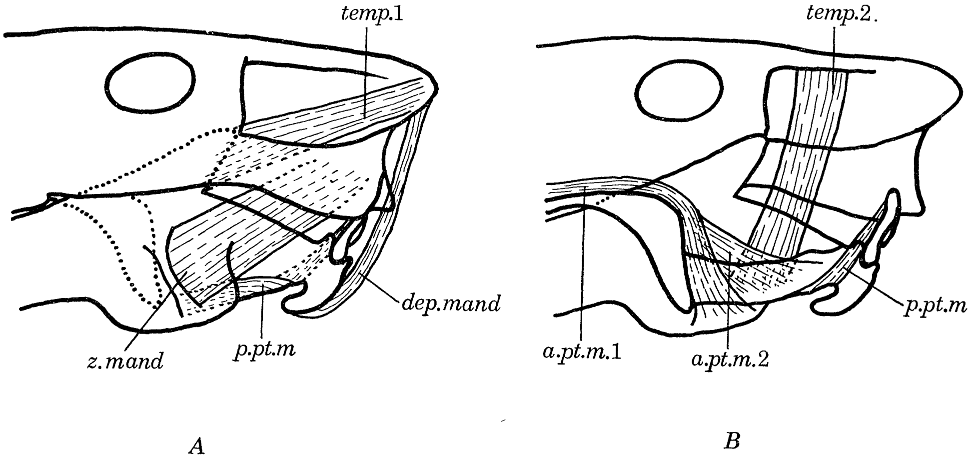

Figure 16. Diagrammatic restoration of the principal jaw muscles, based on *Arctognathus* sp. × ¼. *A*, As seen laterally. *B*, As seen medially.

Parrington (1955) suggested that the insertion of the temporalis branch of the capiti mandibularis lay partly on the outer side of the coronoid process. This is confirmed because the ventrolateral face of the process is coarsely ridged, suggesting a tendinous muscle attachment. The smooth concave medial surface of the process implies a fleshy muscle insertion here. As indicated by previous authors, the origin of this muscle must have been the anterior face of the squamosal, which is carried posteriorly in order to increase the length of the muscle fibres.

The posterior part of the meckelian fossa is very wide and open dorsally. Although the extent of the fossa has not been noted previously there is no sign of distortion and the posterior width is fixed by the width of the articular bone which forms its posterior boundary. Broom's (1930) figures of a sectioned gorgonopsid skull indicate similar conditions in this region. How much the fossa was filled by the cartilage of the primary lower jaw is unknown but certainly its form suggests that it was the site of insertion of a particularly well-developed slip of the capiti mandibularis muscle. The most reasonable origin for the muscle is the underside of the dorsal roofing bones, more or less directly above the fossa. In *Leontocephalus* there is a broad shallow depression on the parietal and post-orbital here (figure 5), suggestive of a large fleshy muscle origin. The muscle itself may be referred to as the temporalis 2.

While Parrington's assertion that the ridge on the lateral surface of the angular and its reflected lamina is concerned with a muscle insertion is undoubtedly correct, it is difficult to accept his view that the muscle was an antero-dorsally directed masseter. He bases his argument on four principal points. First, the arc shape of the main angular ridge is such that at different phases of jaw motion, part of the ridge would always lie along the line of action of the proposed muscle. But as the jaw moved, the angle between each part of the muscle and the ridge would change and therefore parts of the muscle would have to ride over the ridge. Yet the ridge stands almost 1 cm clear of the bone and its posterior edge is sharp. Further, it is incongruous that only a small part of the muscle-bearing surface should be so powerfully strengthened, leaving most of the muscle attached to the relatively thin bone surface. A more likely form of strengthening in this case would be by means of corrugations arranged over the whole surface. A more reasonable interpretation of the ridge therefore is that the muscle from it ran approximately at right angles to it, in a postero-dorsal direction. The muscle could then actually be attached to the hind surface of the ridge and thus the whole area of the muscle insertion supported simultaneously. This agrees with the form of mechanical strengthening seen in mammalian jaw musculature. For example, in the cat skull, a ventral horizontal thickening of the dentary supports the temporalis and masseter muscles, both running at an angle approaching a right angle from the line of thickening.

Parrington's second point concerns the thickening of the jugal region of the zygomatic arch, interpreting it as for the origin of the masseter. But a consideration of the forces acting on the skull when the jaw muscles are contracting shows that when food is bitten, the tendency for the tooth-bearing part of the upper jaw to be forced upwards relative to the muscle-bearing posterior part of the skull will be translated into a tension force along the line connecting the teeth with the muscle origins. A weakness along this line will be the maxilla-jugal suture. To overcome this, the suture is formed by a high area of overlap between these two bones. The jugular process of the maxilla runs posteriorly from the body of the maxilla in the form of a dorsally facing groove in which the jugal stands. The thickening of this region of the skull appears to be due solely to this part of the maxilla, in contrast to the sharper free edge of the jugal behind. The internal surface of this part of the jugal arch opposes the lateral face of the pterygoid flange, the two forming the walls of a deep groove into which the dentary fits when the jaws are closed, and there does not appear to be room for a muscle origin from the internal surface of the jugal as well. Yet the lateral and ventral faces in the region of the thickening are not marked off in any obvious way from the rest of the lateral skull surface as if for a muscle. On the other hand, Parrington's reconstruction does not account for the lateral flaring out of the squamosal and posterior jugal parts of the zygomatic arch, nor the fact that it is inclined, so as to face ventro-medially. The most obvious interpretation is that it supported a powerful slip of the capiti mandibularis muscle, running antero-ventrally. And if this is so, then the muscle could only insert in the region of the reflected lamina of the angular.

Parrington's third point is the presence of corrugations on the outer face of the keel of the angular. These are not preserved in *Arctognathus* sp. but are well shown on his specimen of an isolated gorgonopsid angular (no. F.R.P. 38), and they run antero-dorsally. Undoubtedly they represent strengthening of the keel against the action of an antero-dorsally directed muscle, but could equally be for an internal rather than an external muscle. Since, as is argued below, the anterior pterygoideus muscle probably inserted on the angular keel, there is no need to postulate a masseter muscle to explain the presence of the corrugation.

Parrington's final argument was the analogous position of the masseter-carrying angle of the mammalian dentary with the therapsid reflected lamina. In terms of jaw mechanics, however, a ventral process of the lower jaw simply has the effect of increasing both the moment and the fibre length of an antero-dorsally directed muscle. The reflected lamina of the angular would serve this function equally well for a medial anterior pterygoideus muscle, as for a lateral superficial masseter muscle.

Thus it is concluded that as suggested by Barghusen (1968) a third slip of the capiti mandibularis muscle ran between the posterior part of the zygomatic arch and the reflected lamina and adjacent angular of the lower jaw. The posterior edge of the ridge on the lower jaw which carried this muscle faces posteriorly and only slightly dorsally. However, as the jaws opened, it would face more and more dorsally and at a gape of about 20° would lie more or less at right angles to the line of the muscle. The strengthening effect would be maximal at the moment when the canine teeth were sinking into the food and therefore when the resistance would probably have been maximal. It is proposed to refer to this muscle by the noncommital name of zygomatico-mandibularis.

The anterior pterygoideus musculature was undoubtedly very well developed. In both *Arctognathus* (figure 18*B*) and *Leontocephalus* (figure 7), the dorsal faces of the palatine, ectopterygoid and pterygoid bones form a smooth flat surface bounded anteriorly and medially by ridges, and laterally by the vertical jugal. Posteriorly the bone curves postero-ventrally as the hind face of the lateral pterygoid process of the palate. In view of the continuity of all this surface, it is probable that it represents a wide origin for the anterior pterygoideus muscle. At least one site of insertion of this muscle must have been the medial face of the ventral keel of the angular. It was described in *Arctognathus* how the front part of the keel of the angular is continuous with the part representing the lower portion of the reflected lamina; a ventral extension of the lower jaw such as is represented by the keel was presumably for an antero-dorsally alined muscle, because it would reduce the moment of a postero-dorsally running one through all phases of jaw closing. The fine ridging of the keel noted by Parrington (1955) as running antero-dorsally supports this. If the arguments for rejecting the masseter are accepted, it follows that the keel must be for insertion of the anterior pterygoideus muscle. There could not be a masseter inserting in front of the zygomatico-mandibularis because it would have to elongate to more than double its length when the jaws opened widely, enormously increasing the resistance to the jaw-opening muscles. In contrast, if anterior pterygoideus muscles which inserted on the keel originated well forwards on the dorsal surface of the palate, their length would be adequate. The dorsal limit of the insertion on the part of the keel in front of the reflected lamina is probably indicated by the elongated depression described as running horizontally just above the root of the keel. A second area of insertion was probably along the medial face of the angular and prearticular bones. The bones are smooth and rounded and the area is delimited ventrally by the ridge that forms the ventral margin of the angular. Largely on functional grounds, it is considered that the muscle here inserted originated on the posterior face of the lateral pterygoid process of the palate or from the fascia of the more anterior part of the anterior pterygoid muscle. For with the proposed quadrate mechanism, a muscle with a high anterior component of its force would be required to pull the quadrate forwards. The ventral keel of the pterygoids and parasphenoid was presumably a site for the attachment of muscles which also inserted on the medial faces of the post-dentary bones. The course of these latter cannot be determined with accuracy but since they would act principally in a horizontal plane, they were probably more concerned with the control of the lower jaw than with jaw closing.

Level with the reflected lamina, the ventral edge of the body of the angular is a sharp ridge (figure 15*D*) and it is unlikely that any of the anterior pterygoideus musculature would have wrapped round it to insert in the recess between the reflected lamina and the lateral face of the angular, as supposed by Parrington (1955) and Crompton (1963). A longitudinal step about 1 cm above the ventral jaw margin on the lateral surfaces was noted in *Arctognathus* sp. It commences in the angular recess and runs posteriorly as far as the articular. The area ventral to it is about 1 mm medial to the area above it, is smooth and is limited ventrally by the jaw margin. As noted, the angular part of the jaw margin is sharp but the posterior, prearticular part is rounded and smoothly continuous with the area beneath the step. The morphology thus seems to indicate that a strap of muscle, inserted in the recess, ran posteriorly along the lower lateral part of the jaw as far as the prearticular, and then curved postero-medially around the jaw margin on to the medial face of the prearticular. A natural continuation of the muscle would be postero-dorsally to the quadrate region of the upper jaw and it seems most probable that its origin was from the dorsal muscle scar of the front face of the quadrate, as suggested earlier. However, it could also have attached to the epipterygoid wing of the quadrate. An origin on the lateral face of the quadrate ramus of the epipterygoid seems unlikely since with the jaws closed or with a small gape, the muscle would have to turn fairly abruptly dorsally after leaving the ventral margin of the jaw. The function of this muscle which may be considered as a posterior pterygoideus muscle, has been discussed in the previous section. It was concluded that its importance lay in controlling the relative positions of the quadrate and articular bones rather than in jaw closing.

Parrington (1955) has discussed the jaw-opening musculature. His conclusion that a depressor mandibuli muscle acted between the retroarticular process and the posterior part of the squamosal is fully confirmed. Janensch (1952) considered the possibility that the function of the reflected lamina was for the insertion of a jaw-opening muscle (the colli mandibularis), analogous in action to the digastric of the mammals. The functional consideration of the depressor mandibuli reported below however, indicates that probably no accessary jaw-opening muscle was required, and the function of the reflected lamina, its keel and its recess can be adequately explained as insertions for the zygomatico-mandibularis, anterior pterygoideus and posterior pterygoideus muscles respectively.

The organization of the jaw muscles as deduced from the anatomy must be in accord with two principles. First it must adequately account for the functional requirements of the system and secondly it must be derivable from the ancestral condition. These two aspects are discussed in the following two sections.

7. *Functioning of the lower jaw*

Analysis of the mechanical forces involved in jaw closing is complicated both by the large numbers of factors involved, most of which cannot be assessed in a fossil form, and by the presumably variable nature of the working of the system. However, by making a series of assumptions about the anatomy of the musculature a rather gross mathematical model can be constructed which illustrates the likely function of each muscle, and goes some way towards explaining the manner in which the individual muscles integrate to produce the overall jaw movements. Such a model also assists in an understanding of the morphological changes involved in the evolution of the animal under consideration. Crompton & Hotton (1967) adopted a mechanical approach in their appraisal of the jaw musculature of dicynodonts and Gans (1966) considered the functioning of the depressor mandibuli of gorgonopsids in a similar manner.

The present analysis is based on the reconstruction of the jaw musculature of *Arctognathus* sp. discussed in the previous section (figure 16). The five principal jaw-closing muscles considered are those designated temporalis 1 and 2, anterior pterygoideus 1 and 2 and the zygomatico-mandibularis. The posterior pterygoideus muscle and possible muscles between the parasphenoid keel and the post-dentary bones are not considered because their contribution towards the jaw-closing force was probably very small. The depressor mandibuli is considered to be the only jaw-opening muscle involved. Each individual muscle is assumed to consist of parallel fibres and thus the muscles can be assumed to work about points of contact with the bones. The points are the approximate centres of estimated areas of origin and insertion of each muscle. Lateral components of these muscle forces have been ignored since they would be small in relation to the vertical components.

The significant mechanical features of a muscle action are the force it produces and the geometrical relationship between the moving parts involved, over the range of jaw positions. Of the many possible ways of resolving the factors, it seems most useful to consider the moment producing rotation of the lower jaw about the hinge, and the vertical and horizontal reaction forces acting between the articular and the quadrate. Gans (1965) has pointed out the fallacy of considering the geometrical factors as the only variables when assessing the action of a muscle over a range of movement, because the tension produced by a muscle varies with its length. Parrington (1955) quotes the approximation that a muscle can contract by some 57 % of its fully extended length, which may be true, but it does not follow that the muscle is capable of exerting a significant force at the shorter end of its range. And at the longer end of its range the elastic resistance offered to the antagonistic muscle rapidly increases. Reference to a length–tension diagram (Hill 1953) is necessary in order to show what percentage of its maximum tension the muscle can produce at any given length.

Using the lateral view of the reconstruction of *Arctognathus* sp., and assuming that the maximum gape was 80° (which is in keeping with Parrington's (1955) analysis of the condyle mechanism and gives an adequate clearance of the opposing canine teeth), the two variables, muscle length and angle between the line of action of the muscle and the line between its point of insertion and the hinge was measured for gapes (θ) of 0°, 20°, 40°, 60° and 80°, for each muscle respectively. Using Hill's (1953) length tension diagram for the frog sartorius muscle, a unit value for the length of each muscle was estimated as a compromise between having a reasonably high tension at the lowest length of the muscle and a reasonably low elastic resistance at the highest length. The various lengths of the muscle were converted to fractions of the unit length and the relative tension developed at each length read from the diagram. From this information, along with the two constant values, the length from the point of insertion to the hinge, and the angle between this line and the skull base (taken as the horizontal), the three dependent variables, relative moment, relative horizontal reaction, and relative vertical reaction were measured for each gape, and plotted (figure 17*A*). Also from the length–tension diagram the elastic resistance of each muscle was measured for each length.

For the depressor mandibuli, only the moment produced at different gapes was measured (figure 17*B*).

The implications of these graphs of the individual closing muscles are as follows.

Temporalis 1 (*from the squamosal to the coronoid process*)

A high moment is produced reaching a maximum between about 40° to 0° gape when the canines are opposing and the resistance to jaw closing may be expected to be high. The length of the muscle allows the passive resistance it produces when the gape is wide to remain very low. But the cost is in a high backward force at the hinge.

Temporalis 2 (*from the dorsal roof to the meckelian fossa*)

The turning force produced is more modest but reaches a maximum when the jaws are shut, unlike the other muscles. Its main advantage lies in the low horizontal force produced at the hinge so it was probably important when the intermeshing type of biting was being used and the quadrate lay in its forward position. Its disadvantage seems to be in its shortness producing a high resistance to jaw opening.

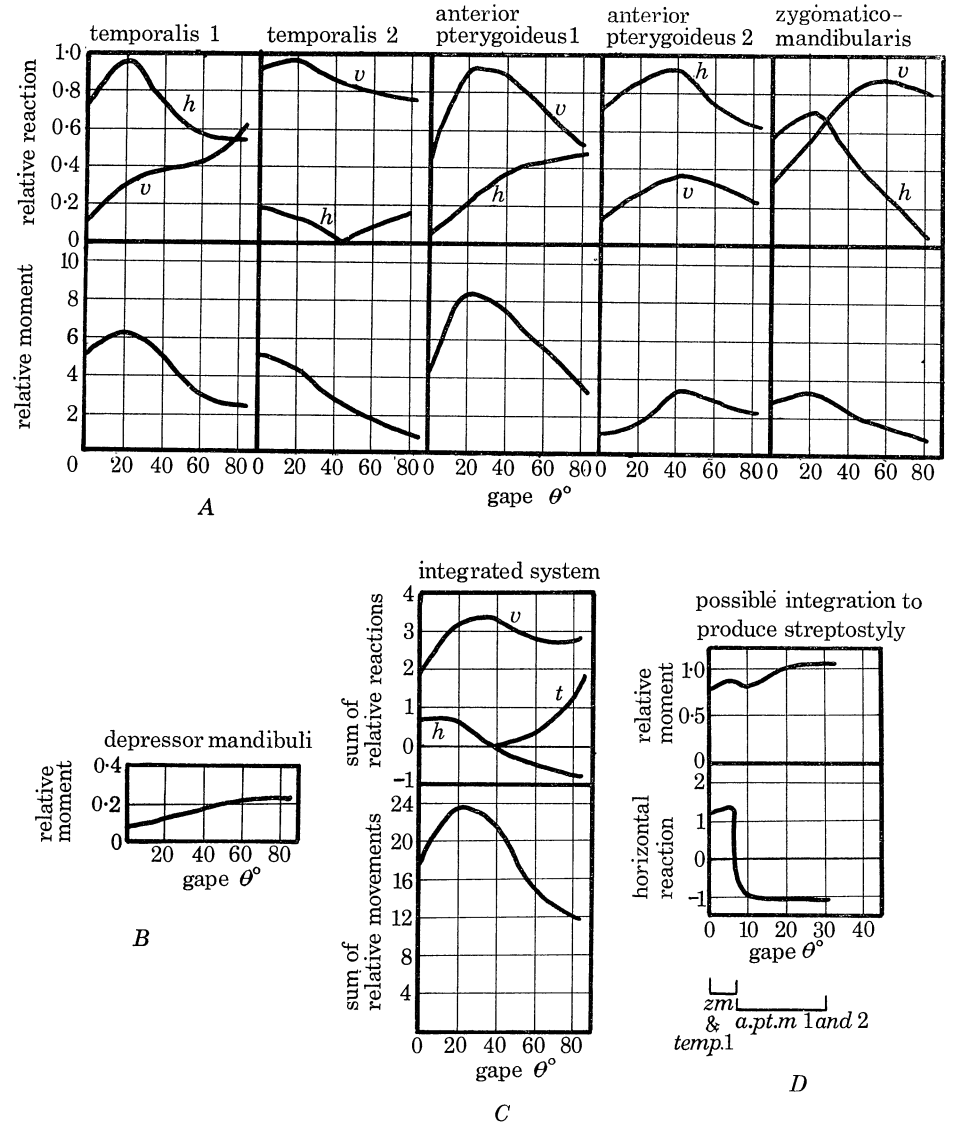

FIGURE 17. Graphical representation of the functioning of the proposed muscle system. See text for explanation. Curves h = horizontal, v = vertical, t = total elastic resistance.

Anterior pterygoideus 1 (*palate bones to angular keel*)

A very high turning force is produced with a maximum at a gape of 20°. The horizontal force is forwards and drops off fairly rapidly as the jaw closes. It was probably of importance in pulling the jaw articulation forwards during the intermeshing type of bite and then allowing it to slide back when the jaws were nearly closed, while retaining a high turning moment. The passive resistance even at a gape of 80° is reasonably small.

Anterior pterygoideus 2 (*pterygoid flange to postero-ventral area of the jaw*)

Only a small turning force is produced but the horizontal reaction is very large and this muscle was undoubtedly the main one for pulling the jaw articulation forwards at the correct time for the intermeshing bite. Even during normal biting it would counteract to a large extent the posteriorly directed forces of the other muscles.

Zygomatico-mandibularis (*zygomatic arch to angular*)

A fairly small turning force is produced, but with its maximum in the phase when the teeth are meeting. The backward force is relatively large at low gapes but the passive resistance remains low.

Depressor mandibuli (*squamosal to the retroarticular process*)

The moment about the hinge produced by this muscle opening the jaws increases steadily to a maximum at a gape of 60° which is about when the elastic resistance of the closing muscles has started. As the maximum moment is about three times the minimum, it is probably adequate to overcome the resistance.

A simple integration of all the closing muscles working as a unit can be made by assuming that they all have the same cross-sectional area and that they all contract maximally throughout the closing of the jaw. A summation of each of the three relative forces is plotted against the gape (figure 17*C*). The turning moment rises rapidly from the fully open position to a maximum at a gape of about 20°, and then falls away somewhat. The opposing canines meet at a gape of about 30° in this animal and therefore the resistance to jaw closing would be increased suddenly at a gape of say, 40° to 50° when the canines met flesh. This high resistance would be maintained until the jaws were fully closed. The muscles appear to be adapted to this, rather than to having a maximum closing force when the jaws are nearly closed.

The total reaction forces at the hinge of this hypothetical integrated system are also shown. While a very high vertical force is unavoidable because the teeth are anteriorly placed, it is interesting to note that the horizontal reaction is reduced to a far lower level by the antagonistic effect of the anterior pterygoideus muscles and the capiti mandibularis branches along the horizontal line, thus allowing the quadrate to be relatively poorly supported in the horizontal plane.

Despite the numerous assumptions, it is suggested that this model approximates to conditions suitable for the use of the teeth in the simple, killing type of bite. To achieve a jaw motion suitable for the interdigitating type of bite, it must be assumed that all the muscles are not contracting maximally all the time. The model can be made to simulate appropriate forces under numerous conditions. Perhaps the simplest is the one shown (figure 17*D*), with both the branches of the anterior pterygoideus contracting maximally over a range of gape from 30° to 7° and then ceasing to act, while the zygomatico-mandibularis and temporalis 1 take over. The turning moment remains roughly constant while the horizontal reaction force at the hinge changes abruptly at 7° from a forwards one to a backwards one.

However it must be stressed that this analysis is probably of very limited quantitative value. Although a quantitative method is adopted, it is for convenience in handling the anatomical observations. At best we can see in qualitative terms the adaptations and general mode of functioning of the system.

8. *The evolution of the gorgonopsid jaw-mechanism*

The gorgonopsid form of jaw mechanism may be interpreted as an adaptation whereby an animal with a very large gape could have propalinal movement of the lower jaw, allowing an interdigitating type of shearing between the upper and lower incisor teeth. The propaliny resulted from a ball-and-socket, streptostylic arrangement between the quadrate and the squamosal, with the quadrate pivoting about the quadrate ramus of the epipterygoid. The musculature was characterized firstly by the division of the capiti mandibularis muscle, into several slips, in order to produce a greater jaw-closing moment without unduly restricting the gape, and secondly by a marked enlargement of the anterior pterygoideus muscle to produce a forwardly directed component of the jaw-closing force with a magnitude comparable to the backwardly directed component of the capiti mandibularis muscles. This whole system appears to have been unique among the synapsid reptiles.

In the advanced sphenacodont pelycosaur *Dimetrodon* (Romer & Price 1940), the quadrate bears two distinct condyles, each with a large radius of curvature, corresponding to the two articular condyles which appear as only slightly concave grooves running antero-posteriorly. As Watson (1948) demonstrated, the probable action of this arrangement was such that propalinal movements of the lower jaw could occur by relative movements between the quadrate and the articular. Above the condyles, the quadrate is a broad plate, alined vertically and almost longitudinally. It is firmly sutured anteriorly to the extensive quadrate ramus of the pterygoid, posteriorly to the squamosal, and laterally to the quadratojugal. In addition, there is a short attachment to the quadrate ramus of the pterygoid and, in well-ossified individuals, to the paroccipital process.

The basipterygoid articulation in the pelycosaurs is a movable joint between the basipterygoid process of the basisphenoid and a facet on the epipterygoid.

A basically similar organization existed in other advanced sphenacodonts, in the edaphosaur pelycosaurs (Romer & Price 1940), and in *Captorhinus* (Fox & Bowman 1966). However, the more primitive ophiacodonts, the primitive sphenacodonts, and the early captorhinomorphs (Watson 1954) all differ in the morphology of the jaw hinge, the condyles being of a relatively small radius of curvature which would presumably not have allowed any propalinal movements.

It is probable that this latter represents the primitive condition and that it became modified in at least two ways. To produce propaliny directly, the radius of the condyles increased, as in the captorhinids and later sphenacodonts. In the pre-gorgonopsids, the condyles became modified to allow a wide gape, principally by retaining a small radius, by gaining a dorsal process behind the lateral condyle and by modifying the medial condyles to produce a lateral shift of the articular as the jaws opened. The development of the streptostyly in the gorgonopsids probably occurred only subsequently to the modification of the condyles, since it is a means of achieving propaliny in a form with a wide gape. Had the gape still been modest then it would be expected that the more normal type of propaliny would have evolved, with movement between the articular and quadrate.

The morphological changes occurring in the development of the streptostylic system can be explained functionally by the following hypothesis. Assuming that the musculature was still in its primitive form with a large postero-dorsally directed capiti mandibularis, an increase in the size of food consumed would need an increase in the muscle forces, and therefore the antero-ventrally directed reaction force between the quadrate and the articular would increase. The squamosal directly behind the quadrate would increase in importance as the route for the transmission of the anteriorly directed component of the reaction to the rest of the skull, and so the area of contact between the quadrate and squamosal would tend to increase, leading to a transversely oriented quadrate. At the same time, it would be advantageous for the quadrate to become roofed directly by the squamosal, rather than to continue relying on its lateral sutures with the pterygoid and the quadratojugal, for transmitting the ventrally directed component of the reaction. Thus there would be selective pressure to form a recess in the squamosal with the quadrate moulded to fit within it. The quadratojugal and the quadrate ramus of the pterygoid would be reduced, in accordance with their decreased mechanical importance.

Meanwhile, the primitive movable basipterygoid articulation had probably become disadvantageous with the increasing muscle forces between the skull and the mandible. It can be imagined that at about this stage, the need for a more sophisticated mode of tooth occlusion coincided with a preadaptation towards streptostyly. On the one hand larger prey was being caught which required tearing up before consumption, and on the other the quadrate was almost free anteriorly and the relations between the basipterygoid process, the epipterygoid and the pterygoid were about to change. Thus a fixed basipterygoid articulation developed between the parasphenoid and the pterygoid. In the specimen of *Arctognathus* sp. the bone forming the anterior wall of the metotic fissure, above the parasphenoidal tubera is spongy in appearance and presumably represents the basisphenoid. Surrounding it laterally and ventrally is smooth compact bone, presumably the parasphenoidal part of the parabasisphenoid complex. The basipterygoid process is formed entirely of this compact bone. It is possible that the core of the process is basisphenoid, but it is also possible, and perhaps likely, that the process is an entirely new development of the parasphenoid alone, and is not therefore strictly homologous to the basipterygoid process of pelycosaurs. This would explain how the process could become attached to the pterygoid, a dermal bone, when in the embryo the basipterygoid articulation must have been between the two cartilages, basisphenoid and epipterygoid. Presumably the latter articulation was lost during development and replaced by the more ventral dermal bone articulation, which partially freed the epipterygoid. The epipterygoid itself enlarged its contact with the quadrate and developed into a supporting fulcrum, allowing the quadrate to rotate about a transverse axis.

Correlated with these modifications of the jaw articulation were changes in the muscle system. The most obvious alteration concerns the division of the capiti mandibularis muscle into discrete slips. Watson (1948), Fox (1964) and Barghusen (1968) have all discussed the organization of the temporal musculature in *Dimetrodon* and although differing in details of their interpretations, they all conclude that the process of dividing the muscle has commenced, and that the increased height of the coronoid region of the lower jaw represents a functionally incipient coronoid process. As discussed in detail by Crompton (1963), it is simple mechanics to explain the development of a discrete coronoid process and the posterior extension of the hind border of the temporal fenestra in the gorgonopsids. That part of the temporal musculature running between these two parts of the skull would have an increased length and produce an increased moment about the jaw hinge. Similarly, the floor of the meckelian fossa in the region of the post-dentary bones is much more ventrally placed in the gorgonopsids than in *Dimetrodon*, which allowed longer muscle fibres between the underside of the roof and the fossa. This in turn allowed this slip of the capiti mandibularis to be relatively farther forwards, increasing the moment produced without excessively restricting gape.

Apparently no muscle corresponding to the gorgonopsid zygomatico-mandibularis was represented in the pelycosaurs (Barghusen 1968). In *Dimetrodon*, there is no evidence of a muscle attachment on the lateral surface of the reflected lamina, and the posterior part of the zygomatic arch is not bayed out as in gorgonopsids, but lies close to the lower jaw. The probable evolution of the zygomatico-mandibularis is indicated by the clear evidence of an attachment of part of the temporalis musculature to the ventro-lateral face of the coronoid process (figure 15). A ventral migration of the insertion of this muscle would lead directly on to the angular in the region of the reflected lamina. Since this slip was presumably the lateralmost part of the temporal musculature, its origin could shift anteriorly along the zygomatic arch at the same time. In this way, the length of the muscle need not have diminished but the moment that it produced about the hinge would have progressively increased, until the muscle reached its present position. Any further anterior shift of the origin along the zygomatic arch would now be prevented by the necessary decrease in the length of the muscle fibres.

The second major adaptation in the jaw musculature, from the pelycosaurian condition, involved the anterior pterygoideus musculature. Romer & Price's (1940) view of the reflected lamina in *Dimetrodon*, following a suggestion by Gregory (1926), was that it was a functional continuation of the ventral keel of the angular. They noted that the lamina is anatomically continuous with the keel and that there is no evidence of a muscle attachment to the lateral surface of the lamina. And they pointed out that even in the ophiacodont and varonopsid pelycosaurs which lack a reflected lamina, a well-developed angular keel is present, suggesting a site of insertion of the anterior pterygoideus muscle. Watson's (1948) interpretation of the course of the anterior pterygoideus muscle in *Dimetrodon* is at first sight at variance with Romer and Price's view. He showed the existence of a broad groove leading from the lateral surface of the post-dentary bones behind the reflected lamina, antero-ventrally to the ventral edge of the jaw alongside the lamina, and then antero-dorsally, leading towards the lateral pterygoid process. The lamina itself, he claimed, was the attachment for an intermandibularis muscle. However, investigation of Watson's specimen suggests that there is no reason why at least part of the anterior pterygoideus muscle should not have inserted on the medial face of the reflected lamina in accordance with the earlier view. It is not inconsistent that some of that muscle should have passed posterior to the lamina as well. Functionally, an insertion on the lamina would have the effect of increasing the moment about the hinge produced by those fibres, at the same time as allowing them to be longer.

The function of the lamina in the gorgonopsids is in accord with this hypothesis and explains its development without having to postulate the development of the zygomatico-mandibularis simultaneously. Presumably this latter muscle merely took advantage of the presence of an already existing reflected lamina. It must be pointed out that the evidence of the jaw hinge discussed above suggests that the gorgonopsids evolved from a pre-*Dimetrodon* stage which may have lacked the reflected lamina, and thus the lamina may have arisen independently in the gorgonopsid line. However, the basic similarity of the lower jaw of both the ophiacodonts and the sphenacodonts, particularly in respect of the angular keel, implies that the lamina probably arose for similar functional reasons.

With the onset of the streptostylic mechanism, the gorgonopsids would have required a muscle with a high anteriorly directed component, sufficient to counteract the posteriorly directed components of the muscles of capiti-mandibularis origin. There is no evidence that any muscle comparable to the mammalian superficial masseter had developed and thus it appears that the anterior pterygoideus muscle was utilized. The final result, as seen in *Arctognathus* sp., is a vast increase in size of this muscle, coupled with an anterior shift in both its origin and insertion as compared to *Dimetrodon.* Both its total force and its unit moment about the hinge must have been magnified. And evidence of its division into two more or less discrete slips has been discussed earlier. Concerning the site of origin of the anterior pterygoideus muscle, the lateral pterygoid flanges have increased in size in the gorgonopsids. A relative increase in the width of the palate and the restriction of the post-palatal section of the pterygoid to a narrow strut have allowed massive muscles inserted on the dorsal surface of the palate to escape postero-ventrally. Indeed, in *Dimetrodon* there is no evidence of an extensive origin of the muscle from the dorsal palatal region at all, for the ridges bounding the muscle attachment are absent, and the area for the escape of the muscle posteriorly is very limited. It is probable that in this form, the principal area of origin of the muscle was restricted to the posterior edge of the palate and the adjacent post-palatal part of the pterygoid. The insertion on the lower jaw for the anterior pterygoideus muscle has been correspondingly increased in the gorgonopsids by the deepening of the angular keel and the much greater extent of the free medial surface of the reflected lamina, continuous with the keel. The relatively anterior position of the lateral pterygoid processes is basically due to the increase in extent of the post-orbital part of the skull. However this has allowed a relative anterior shift of the keel and reflected lamina of the angular, increasing the moment of the muscle but not decreasing the length of the fibres. To accomodate the increased gape however, the fibre length did have to increase, but this was achieved by the anterior invasion of the palate by the area of the muscle's origin.

A final change between the pelycosaurs and gorgonopsids involved the form of the posterior pterygoideus musculature. Watson (1948) demonstrated the probable course of this muscle, in *Dimetrodon*, as running antero-dorsally from the ventral region of the jaw to the quadrate ramus of the pterygoid. In the gorgonopsids it is easy to imagine that with the development of a loose quadrate, there arose a need for a muscle controlling the relative positions of the quadrate and articular directly. Thus at least part of the posterior pterygoideus muscle developed an origin on the quadrate. But with the increased gape, the length of this muscle had to increase. It could not extend along the medial face of the jaw because part of the anterior pterygoideus muscle inserted here. Thus its insertion migrated along the lateral surface, utilizing the angular recess. Further slips of this muscle were probably modified as the intrinsic palato-quadrate musculature between the quadrate and the epipterygoid, although no intermediate stages of this modification are known. The small but important muscle system between the back of the quadrate complex and the posterior face of the squamosal must surely have been derived from the depressor mandibuli muscle.

The functional and morphological changes of the depressor mandibuli muscle itself and the retroarticular process of the articular bone have been discussed by Parrington (1955) and his conclusions are accepted.

Nasal cavity

1. *Introduction*

This is perhaps the least understood region of the therapsid skull, largely because of our lack of knowledge about the cartilaginous structures involved. It is therefore necessary to consider briefly the conditions in living reptiles and mammals.

In modern lizards (Pratt 1948; Bellairs & Boyd 1950) the external naris leads into a small anterior chamber and thence into the main olfactory chamber. Between these two chambers the duct of the mucus-producing gland opens. The olfactory chamber is partly divided by the projection of the concha into its lumen from the lateral wall of the nasal capsule, and is lined dorsally by sensory olfactory epithelium, and ventrally by ciliated epithelium. From the ventral region, the choanal tube runs postero-ventrally to open into the buccal cavity. It is interesting to note that in some forms a lateral recess of the olfactory chamber is developed. Jacobson's organ is well developed, lies below the junction between the anterior and the olfactory chambers, and opens directly into the buccal cavity by a duct passing through the vomeronasal fenestra. Ventrally the organ is supported by the vomer and the palatal process of the premaxilla, and dorsally it is largely covered by the septomaxilla. Medially to the organ lies the paraseptal cartilage and laterally the ectochoanal cartilage, these two elements representing the floor of the nasal capsule. Between the fenestra vomeronasalis and the definitive internal choana a choanal groove is developed on the ventral side of the palate. The lachrymal duct opens on to the palate in the region of the opening of Jacobson's organ and is also in direct contact with the choanal groove along the part of its length.

In *Sphenodon* (Pratt 1948) conditions are similar but generally simpler.

The mammalian nasal cavity is characterized by the development of nasal conchae to form turbinals, typically a ventral maxillo-turbinal, a dorsal naso-turbinal and postero-dorsal ethmoturbinals. As in the lepidosaurs, olfactory epithelium is more or less restricted to the dorsal elements (Parsons 1959) and the function of the maxillo-turbinal is to warm and moisten the inspired air, in relation to the habit of homoiothermy. Jacobson's organ is variously reduced in the living mammals and is closely associated with the paraseptal cartilage, immediately lateral to the palatal process of the premaxilla and the vomer. At least in several primitive mammals it opens directly on to the palate by a vomeronasal duct passing through the incisive canal (Broom 1915 *a*; Clark 1926). The lachrymal duct of mammals opens distally through the zona annulis at the front of the nasal capsule (Roux 1947) and is thus functionally unrelated to Jacobson's organ.

Several authors have considered various aspects of the snout anatomy in synapsids. Watson (1914) suggested that the septomaxillary foramen of the therapsids was for a superficial opening of the lachrymal duct, and later (Watson 1921) he suggested the possibility that it was an exhalent airduct via Jacobson's organ from the front part of the internal nares, the inhalent air passage being from the external nares proper via the olfactory chamber to the posterior part of the internal choana. Simpson (1933) believed that the lachrymal duct of cynodonts emerged from the septomaxillary foramen. In the dicynodont *Kingoria*, Cox (1959) noted two additional foramina between the septomaxilla and the maxilla and suggested that, along with the septomaxillary foramen, they represent the openings of the lachrymal duct, the lateral nasal gland and Jacobson's organ respectively. He noted that between the anterior opening of the bony lachrymal canal and the septomaxillary region was a groove in the lateral wall of the nasal cavity. Furthermore, he failed to find any opening in the secondary palate for a vomeronasal duct. Brink (1960 *b*) studied serial sections through the snout of *Akidnognathus*, a therocephalian, and concluded that the development of a secondary palate terminated the connexion between Jacobson's organ and the buccal cavity, causing the development of a secondary connexion between the organ and the septomaxillary foramen, in relationship with the development of a fluid-secreting gland on the external face of the septomaxillary bone.

Tatarinov (1963) demonstrated the presence of an incisive canal in the palate of *Moschowhaitsia*, a whaitsiid therocephalian, and assumed that it was transversed by a duct from Jacobson's organ, which itself occupied a more or less mammalian position. He later considered (Tatarinov 1965) that the lateral ethmoid nerve emerged from the nasal cavity via the septomaxillary foramen and supported this view by the observation that this nerve follows a similar course in modern reptiles. Further, he considered that the canal within the septomaxillary bone carried a branch of this same nerve.

Another aspect of the snout morphology concerns the presence of turbinals. Watson (1913) noted a series of longitudinal ridges on the underside of the frontals and nasals of cynodonts and concluded that they represented the bases of naso-turbinal cartilages. Subsequently Brink (1960*b*) and Tatarinov (1963) have identified similar structures in Therocephalia, and Kuhne (1956) noted them in the tritylodont, *Oligokyphus*.

2. *The nasal cavity of the gorgonopsids*

The nasal cavity of *Arctognathus* sp. has been cleared completely of matrix (figure 18*B*). Much of this discussion is based on that specimen, but several important details are derived from others.

The nasal cavity is incompletely divided into two parts by a pair of processes of the palatine bones, which run antero-dorsally from the hinder end of the internal nares, and then dorsally to rise high into the skull. These may be termed the choanal processes. Each one meets the high median septum of the vomer medially, and laterally is in contact with the large internal boss of the maxilla which houses the root of the upper canine. In fact, in this specimen of *Arctognathus* sp. the choanal process on each side finishes dorsally rather below the level of the top of the vomerine septum, but a ridge on each side of the septum (figure 18*A*) clearly indicates the original line of contact. Similarly, the lateral parts of each choanal process do not reach the canine bosses of the maxillae, but the postero-medial edge of each boss (figure 18*B*) is sharp and parallels the line of contact between the choanal process and the vomerine septum, suggesting that in life the process connected with the boss, possibly as a partly cartilaginous structure. An isolated maxilla, specimen F.R.P. 44 (figure 19*A*), supports this conclusion for above the sutural surface for the palatal part of the palatine, the postero-medial edge of the canine boss is an almost vertical narrow broken surface running to the dorsal limit of the boss. However, between the palatal and choanal process attachments respectively, there is a smooth notch in the boss suggesting a foramen opening from the posterior part of the nasal cavity to the anterior palatal region. Another specimen, prepared by acetic acid but not figured (F.R.P. 142), has the choanal process complete, demonstrating that it does indeed form a nearly vertical transverse plate between the vomerine septum and the canine boss, up to a considerable height within the skull. The evidence strongly suggests therefore that a large posterior chamber of the nasal cavity is cut off from the anterior part of the snout at all but the dorsalmost part of the skull (figure 20).

The most marked feature of the anterior part of the nasal cavity is the remarkable height of the median septum of the vomer (figure 18*A*). This bears a distinct and completely preserved sulcus along its dorsal edge on which a cartilaginous internasal septum presumably rested. In living amniotes the paraseptal cartilage develops from the base of the internasal septum and represents part of the floor of the cartilaginous nasal capsule. This suggests that in gorgonopsids the nasal capsule was restricted to the dorsal region, above the vomerine septum, in the anterior part of the nasal cavity. Further, if the capsule had extended ventrally alongside the vomerine septum, then the choanal processes of the palatines would have extended into the lumen of the capsule, for no apparent purpose. If, however, the arrangement were as suggested, then a long choanal tube must have passed ventrally from the nasal capsule to the internal choana which would have been supported by the choanal process. A third reason for believing that the anterior chamber was restricted to a high position in the snout is that when the jaws were closed, each lower canine entered its recess in the lateral wall of the nasal cavity (figure 18*B*) and

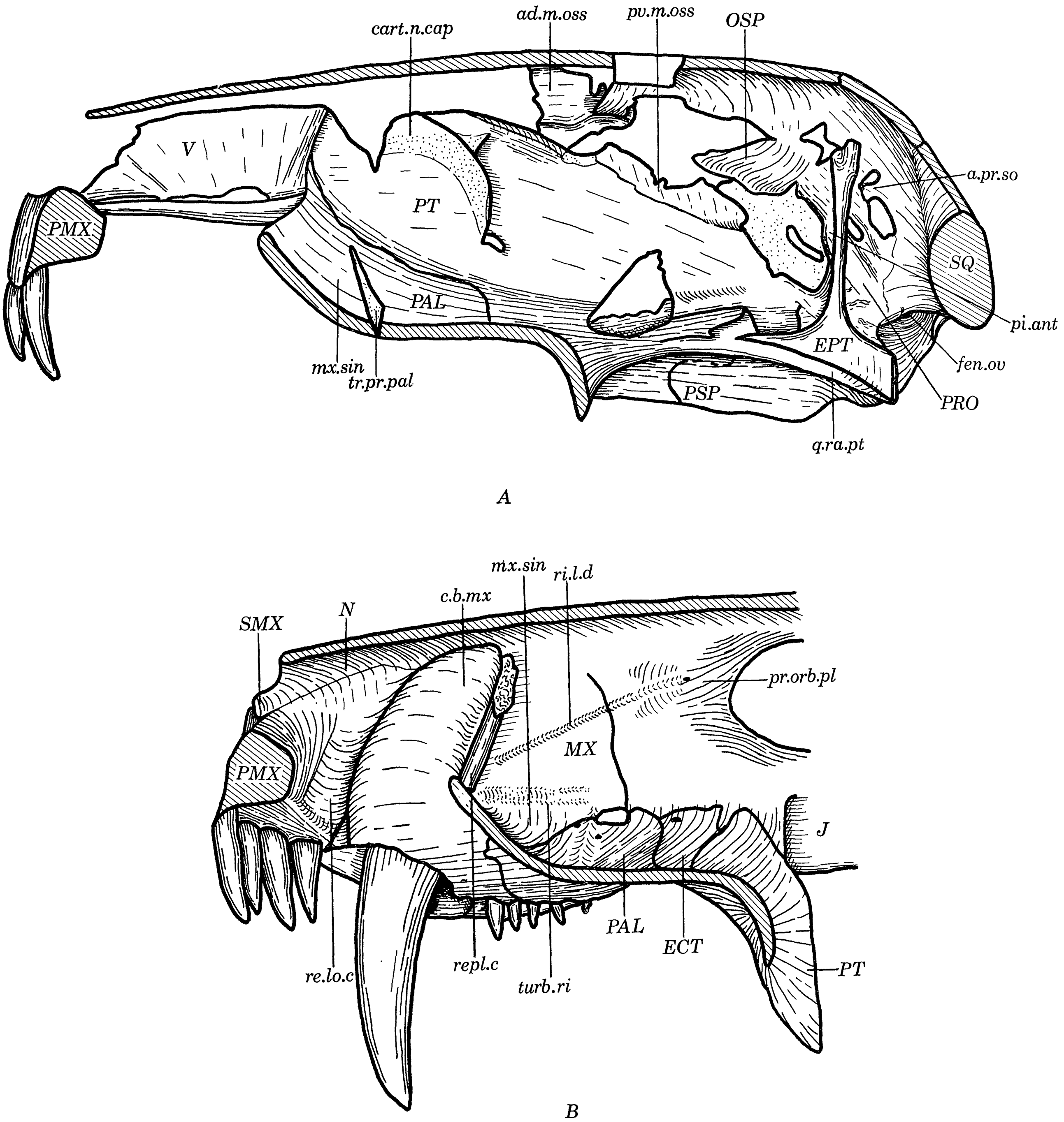

FIGURE 18. *Arctognathus* sp. *A*, Reconstructed lateral view of the skull with the lateral dermal bones removed, × ½. Crystalline material, apparently representing cartilage, is shown stippled. *B*, Internal view of the nasal cavity, with the midline elements removed, × ½.

extended for almost the full height of the vomerine septum. It seems unlikely that the lower canines would enter the actual lumen of the nasal cavity, carrying in scraps of foodstuffs.

There is no direct evidence of the presence or position of Jacobson's organ. Both Broom (1930) and Olson (1938) considered that the organ was lodged on the dorsal surface of the palatal part of the vomer, along with the paraseptal cartilage. On the present interpretation, however, it is more probable that it was held by the paraseptal cartilage at the base of the cartilaginous internasal septum, immediately below the anterior chamber of the nasal capsule. In both living reptiles and primitive mammals, the duct from Jacobson's organ opens on to the palate and, in the absence of evidence to the contrary, there is no reason to suppose that the gorgonopsids had a different arrangement. There is no clear indication of a median incisive canal, but in *Arctognathus* sp. the paired palatal processes of the premaxillae show signs of an incision between them opening at the base of a depression (figure 2), at about the same position as that indicated by Tatarinov (1963) in the whaitsiid *Moschowhaitsia*. Otherwise, it may be assumed that in the gorgonopsids a naso-palatine duct from the organ opened directly into the palate or choanal tube without traversing bone.

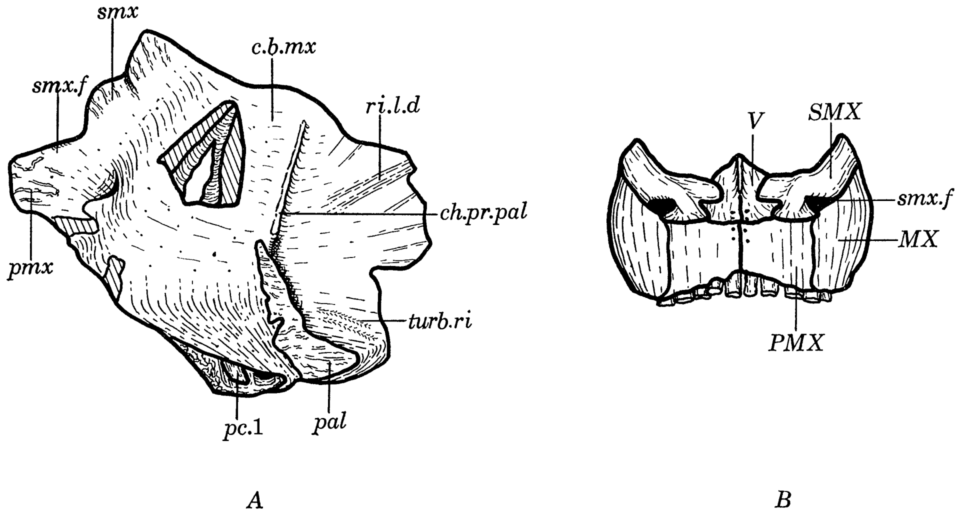

FIGURE 19. *A*, Unidentified gorgonopsid F.R.P. 44. Internal view of isolated right maxilla, × $\frac{3}{4}$. *B*, Unidentified gorgonopsid F.R.P. 142. Antero-dorsal view of snout with the nasal bones removed, × $\frac{3}{4}$.

Posteriorly, the anterior chamber opens widely into the posterior part of the nasal cavity, above the level of the choanal processes. Although not as marked as in the Therocephalia (Brink 1960*b*; Tatarinov 1963), there is a maxillary sinus behind the canine boss of the maxilla (figure 18*B*). Posteriorly its limit is marked by a transverse ridge on the dorsal surface of the palatine in *Leontocephalus intactus* (figure 7) and on the right side of *Arctognathus* sp. (figure 18*B*). On the left side of *Arctognathus* (figure 18*A*), a vertical sheet of the crystalline material (see p. 4) rises from the ridge and probably indicates the presence of a cartilage in life. In the case of the small acid-prepared skull identified as *Dixeya* sp. (figure 21*B*) an actual sheet of bone, a process of the palatine, occupies this position. Thus it seems that in life, a cartilage or bony wall separated the sinus from the area of origin of the anterior pterygoideus muscle, discussed earlier (p. 44). Anteriorly, the maxillary sinus is of course limited by the posterior face of the canine boss, and on both sides of *Arctognathus* sp. there is a partially absorbed root of an old canine tooth immediately behind the boss (figure 18*B*). The sinus is bounded antero-medially by the back of the

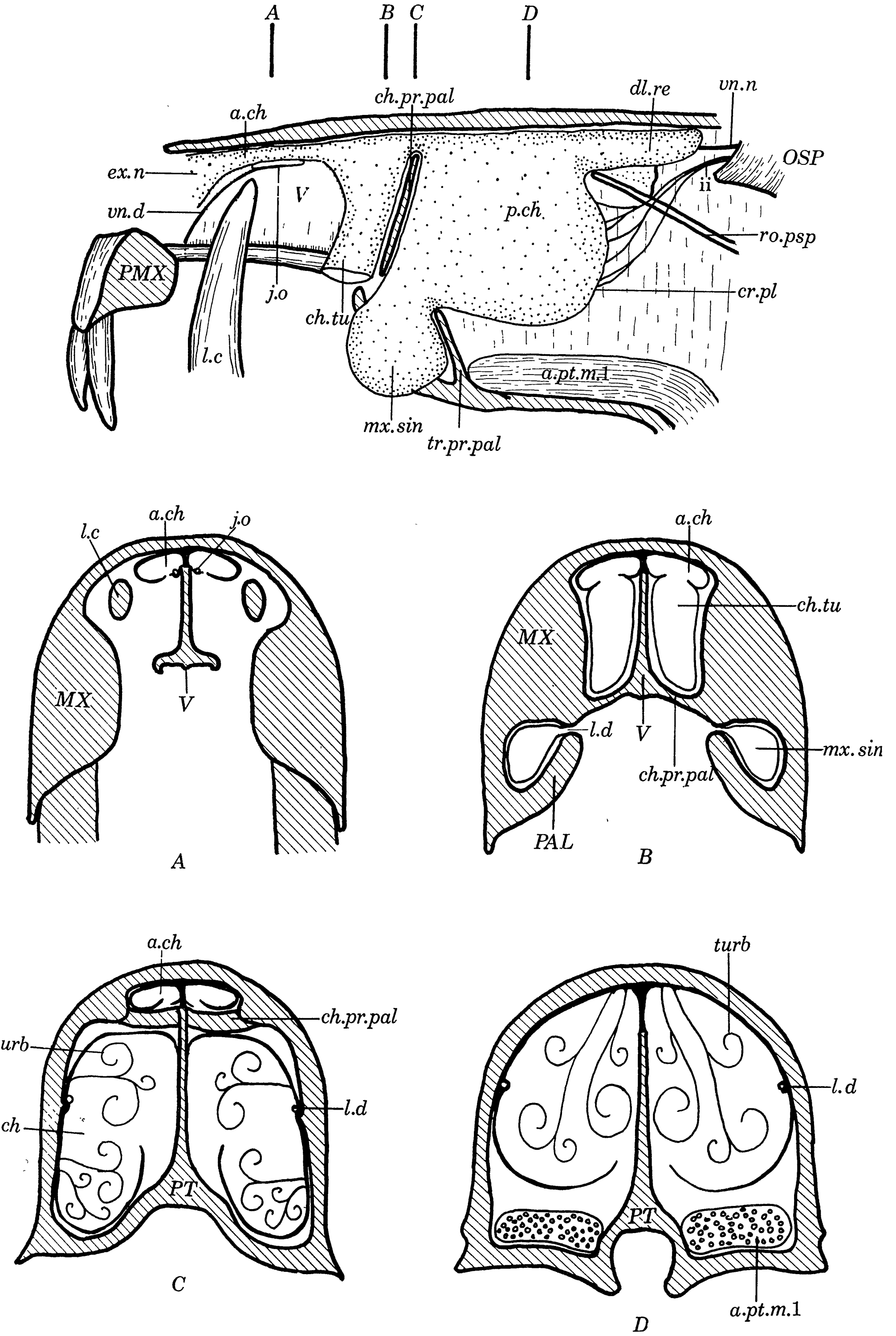

FIGURE 20. Diagrammatic restoration of the structures of the nasal cavity, based on *Arctognathus* sp. × $\frac{1}{2}$. Lateral view with the lateral dermal bones removed, and transverse section at *A*, *B*, *C* and *D* as indicated. Cartilage is shown as dotted shading and, in section, as black.

choanal process, medially by the median septum and laterally by the inner surface of the maxilla. There are indications of the presence, in life, of turbinal cartilages on the lateral wall as discussed below, suggesting that the sinus represents a true diverticulum of the nasal capsule.

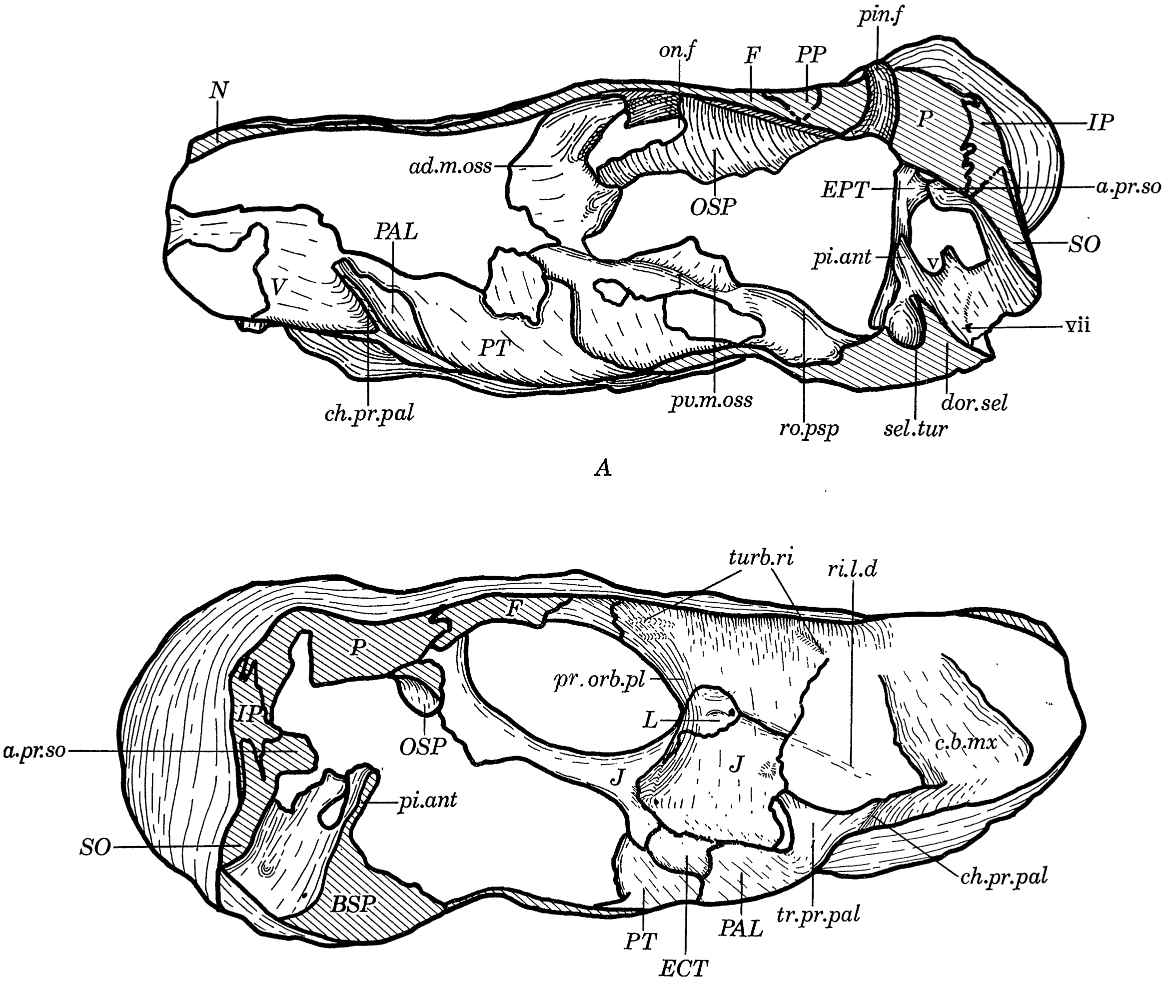

Figure 21. *Dixeya* cf. *quadrata*. Skull sectioned just to the left of the mid-sagittal plane, × ½. *A*, Medial view of the right half of the skull. *B*, Medial view of the left half of the skull.

Dorsally, the maxillary sinus opens widely into the rest of the posterior chamber of the nasal cavity. The median septum of this part is of pterygoid construction. In both *Arctognathus* sp. (figure 18*A*) and *Dixeya* sp. (figure 21*A*), the septum is of a height comparable to that of the vomer, but the dorsal edge is thin, irregular, and lacks all signs of a sulcus. And in *Arctognathus* sp. it is partially composed of the crystalline material. All this suggests that unlike the vomerine septum, this part of the pterygoid septum represents an actual invasion of the cartilaginous internasal septum by the pterygoid ossification and therefore there is no reason why the paired nasal capsules should not have extended ventrally alongside the bony septum. This view is supported by a unique structure consisting of the crystalline material, which apparently represents the original posterior wall of the cartilaginous nasal capsule (figure 18*A*).

Basically it is a paired structure at a level just in front of the orbits, consisting of a segment of a sphere facing antero-laterally and attached medially for its full height to the median pterygoid septum. It ends ventrally within about 3 cm of the floor of the nasal cavity, and rises to within nearly 1 cm of the roof of the nasal cavity. Its lateral extent is about 2 cm. Three extra plates of the cartilaginous material connect the main part to the septum, a dorsal one sloping backwards and upwards, a middle horizontal one, and a ventral one sloping postero-ventrally. A fourth extra plate is present on the right, connecting the front of the main part of the structure to the septum. In view of its position, form and bilateral symmetry, it is difficult to avoid the conclusion that this structure represents the hind end of the cartilaginous nasal capsules and, as such, appears to correspond to the mammalian cribriform plate. Its position, well above the dorsal surface of the palate, supports the conclusion that the palatal surface itself carried an extensive origin of the anterior pterygoideus muscle and was not concerned with the cartilaginous nasal capsule.

The posterior termination of the nasal capsule along the lateral wall of the nasal cavity is probably indicated by the preorbital plate, a medial extension of the anterior half of the orbital margin (figure 18*B*), for there is evidence of the development of turbinal cartilages immediately anterior to the preorbital plate, as discussed below. However, the preorbital plate lies at a level 2 to 3 cm posterior to the medial termination of the nasal capsule, which suggests that the capsule had a postero-lateral extension, ending immediately in front of, and above, the orbit.

Watson (1913) suggested that a pattern of longitudinal ridges running along the underside of the nasal bones in cynodonts, represented the presence of cartilaginous invaginations of the nasal capsule, generally resembling the ossified turbinal bones of mammals. A similar system of ridging occurs in the gorgonopsids, notably well preserved in *Leontocephalus intactus* (figure 5), but clearly present in all the skulls investigated. There are two principal pairs of ridges on the internal surface of the nasal and frontal bones, one pair on either side of the midline. Each pair arises just in front of the anterior termination of the orbitosphenoid, between the preorbital plate and the midline ossification. The two members of each pair are joined posteriorly, and run forwards, parallel, about 2.5 mm apart. Each ridge is raised about 1 mm from the skull roof, is sharp along its free edge, and together they give an impression of a narrow longitudinal trough. The median member of each pair runs almost exactly anteriorly, decreasing in height gradually, and then curves slightly medially to peter out at the level of the nasal-frontal suture. The lateral member runs slightly laterally and increases in height to a maximum of about 2 mm at the level of the nasal-frontal suture. It continues to diverge slightly from the midline, and gradually loses height, but it can be distinguished as far forwards as the canine boss of the maxilla. A third, almost imperceptible, ridge arises near the anterior end of the medial member of the principal pair, but never achieves any prominence. No comparable structures for the support of nerves or blood vessels are known in living amniotes, and the abrupt posterior termination of the paired ridges, their variation in height, their tendency to diverge and the absence of associated foramina certainly do not suggest such an interpretation in gorgonopsids. In view of the great development of the posterior chamber of the nasal capsule, it is not at all suprising to find evidence of nasal conchae or cartilaginous turbinals whose function would be to increase the area of olfactory epithelium, and Watson's conclusion may therefore be accepted for this group.

Other similar ridges are found on parts of the lateral wall of the nasal cavity, which have not been reported in other therapsids. In *Arctognathus* sp. (figure 18*B*) and on the isolated maxilla, F.R.P. 44 (figure 19*A*), a pair of ridges runs horizontally across the lateral wall of the maxillary sinus, again with no evidence that they supported nerves or blood vessels. They must be interpreted as supporting a pair of sinus turbinals, added evidence for the view that the sinus does indeed support a diverticulum of the nasal capsule. In *Dixeya* (figure 21*B*) two short horizontal ridges run across the nasal wall immediately in front of the preorbital plate, a feature repeated in a further unfigured fragment of specimen F.R.P. 44. Finally, there is a single short ridge on the lateral wall of the nasal cavity, high up and half-way between the anterior and posterior limits of the posterior chamber in *Dixeya* sp.

There is another ridge developed on the lateral wall of the nasal cavity which differs from the sharp turbinal ridges in being more or less rectangular in section. It is long, running from the lachrymal bone antero-ventrally into the maxillary sinus. The anterior opening of the naso-lachrymal duct is preserved in *Dixeya* sp. (figure 21*B*) and is at the anterior edge of the lachrymal bone. Although barely preserved in this specimen, the ridge appears to originate at about this point, and in *Arctognathus* sp. (figure 18*B*) it clearly does so. Although rather crushed *Leontocephalus intactus* supports this observation. The ridge is straight and peters out immediately above the maxillary sinus, just before reaching the canine boss of the maxilla. The anterior part is particularly well shown in the isolated maxilla, specimen F.R.P. 44 (figure 19*A*), and it is clearly not associated with a canal in the bone of the maxilla. It is reasonable to interpret the ridge as a support for the nasal part of the nasolachrymal duct because of its origin from the opening of the nasolachrymal canal, its course, and its apparent difference from the turbinal-supporting ridge. Since the ridge ends well below the dorsal edge of the choanal process of the palatine, the canal must have either turned abruptly dorsally to run over the process, or else more probably passed into the maxillary sinus. If it did this, then the only exit would be the notch in the postero-lateral edge of the canine boss (figure 19*A*). The notch is in a direct line with the ridge. Thus it is probable that the nasolachrymal canal emerged from the notch directly into the palate, in the region of the internal choanae. This is essentially a reptilian rather than a mammalian condition.

It may be concluded that the nasal capsule was divided into two parts, an anterior, presumably respiratory section, and a large blind posterior olfactory section (figure 20). In view of this interpretation, the nature of the external nares and the septomaxilla may now be considered. As in all adequately known synapsid reptiles, the septomaxilla of the gorgonopsids separates a postero-ventral septomaxillary foramen from the main external opening of the nostril. Secondly, a medially directed process at least partially divides the naris into dorsal and ventral parts. The structure is particularly well shown in specimen no. 142B (figure 19*B*). A third feature is the canal in the base of the septomaxilla, running anteriorly from the septomaxillary foramen. Immediately in front of the base of the septomaxilla there is a depression near the dorsal edge of the premaxilla, especially marked in *Arctognathus* sp. (figure 3*A*).

The septomaxillary foramen is absent in mammals suggesting that in therapsids it had a function no longer required by the mammalian organization of the snout. This would seem to deny that the foramen was an anterior opening for the naso-lachrymal duct as suggested by Watson (1914) and Simpson (1933), and, in any case, evidence of a quite different route for the duct in gorgonopsids has been discussed above. Similarly, Brink's (1960*b*) and Cox's (1959) interpretation of it as providing an outer opening for the duct of Jacobson's organ is improbable because of the persistence of the reptile-like vomeronasal duct in primitive mammals, opening into the palate. Tatarinov's (1963) demonstration of an incisive canal in *Moschowhaitsia* and the possibility of this structure existing in gorgonopsids, too, suggest that the duct of Jacobson's organ had the standard reptilian route. Watson (1913) believed that the foramen was too large to be interpreted as a nerve foramen. It is not clear upon what this statement is based but certainly the foramen is much larger than comparable mammalian superficial nerve foramina. The large size in the pelycosaurs (Romer & Price 1940), where presumably innervation and vascularization of the external surface of the snout was minimal, implies that nerve transmission, as proposed by Tatarinov (1965), was not the function.

The captorhinomorphs have a septomaxilla in the superficial synapsid position but lack the septomaxillary foramen (Fox & Bowman 1966). The difference between the nasal cavity of *Captorhinus* and of the synapsids is largely related to its increase in size in the latter and presumably therefore its elaboration into a well-developed olfactory organ. Much of this development takes place behind the level of the internal choanae and hence a blind posterior part, not on the main route of the respiratory air stream, appears. There is even the development of an incipient choanal process of the palatine in *Dimetrodon* tending to divide physically the two regions of the nasal cavity, as in the gorgonopsids. It seems likely therefore that the posterior part would require its own specific air current rather than relying on simple diffusion from the respiratory air stream, and thus that the septomaxillary foramen is related to providing this. In the mammals, the definitive internal nares are placed much farther back in the skull than in those therapsids lacking a false palate and thus the posterior part of the nasal capsule becomes incorporated into the route of the respired air, and hence a specific air supply to this region is no longer required. There is no anatomical evidence indicating just how an air stream could be deflected back over the dorsal edge of the choanal processes but a system of cartilaginous sheets acting as deflecting 'baffles' can be imagined, whereby a separate stream of air entered the anterior chamber through the septomaxillary foramen and passed backwards near to the dorsal roof of the cavity. At the same time displaced air would have to be returned to the respiratory air stream, again presumably by a system of 'baffles'. It is quite possible that the median process of the septomaxilla was involved in this process too, but again, because the relevant structures were cartilaginous, there is no indication of their form.

3. *The respiratory air-tract*

From the external nares, the respiratory air has been seen to enter a small anterior chamber of the nasal capsule. It is probable that this chamber was lined principally by ciliated epithelium and acted as a 'dust trap'. From the ventral part of the chamber the air passage to the definitive internal choanae is marked by the paired choanal processes which together form a broad trough running postero-ventrally. It is not known whether the trough alone deflected the air downwards or whether it supported a true choanal tube. At the level of the palate, the choanal processes are continuous with the horizontal palatal vault, a deep groove carrying the respiratory air backwards. It has been suggested that the development of a palatal vault is an indication of the development of a soft secondary palate (Watson 1921). However, there does not appear to be any good evidence that this was the case in the gorgonopsids.

The possible functions of a false palate (Brink 1960*b*) appear to be as follows.

(*a*) *To allow breathing and mastication to be carried out simultaneously*

In the case of the gorgonopsids it is clear from the dentition that the mode of feeding involved tearing off pieces of flesh and swallowing them whole. There could be no mastication by the reduced postcanine teeth. Thus, since the internal nares open well behind the region of the incisor teeth it would only be momentarily, during the swallowing, that respiration would be interrupted. It is interrupted at this point any way in mammals, by the closure of the epiglottis.

(*b*) *To allow moistening and warming of the respiratory air, by first passing it through a length of the nasal cavity*

This cannot apply to the gorgonopsids because of the separation of the posterior chamber of the nasal cavity from the respiratory air tract.

(*c*) *To prevent contamination of the nasal cavity by the contents of the buccal cavity*

This is unnecessary because of the dorsal position of the anterior chamber and the isolation of the posterior chamber. In any case, the major danger of contamination would come from the lower canines, which would have to pass through apertures in a secondary palate.

(*d*) *To act as a rigid or semi-rigid surface against which the tongue could act*

This function was presumably served by the persisting pterygoid and palatine teeth, and by the ridges on the palatal surface of the vomer. Further, if massive palatal tooth-bosses were required, it is not likely that a soft false palate would have the mechanical strength to resist the magnitude of the forces evidently involved.

The absence of functional necessity for a secondary palate supports the anatomical observations. Apart from the antero-medial edges of the palatine bosses (figure 2), there are no flanges along the sides of the vault, which might be expected if a soft palate were present. It is probable that the development of a vault alone is an adequate means of channelling the air between the choanae and the epiglottis.

4. *Comparison with other groups: the origin of the gorgonopsid condition*

The evolution of the internal snout morphology of the gorgonopsids was undoubtedly linked with the development of the specialized dentition. Hypertrophy of the canine and incisor teeth must necessarily have involved a relative increase in the size of the premaxilla and maxilla, in order to accommodate the roots of these teeth. At the same time the enlarged lower canines came to occupy a considerable proportion of the height of the front part of the nasal cavity when the jaws were closed, forcing the anterior part of the nasal cavity to be restricted to a dorsal position. This was achieved by a relative increase in the height of the dermal bone part of the median septum, the vomer. As a result of this process, the distance between the nasal capsule and the internal nares increased, leading to the development of a long choanal passage supported by paired bony processes of the palatines, the choanal processes. On the other hand, there were no such limitations on the posterior part of the nasal capsule which was free to fill the vastly enlarged nasal cavity and form a sophisticated olfactory organ, complete with conchae to increase the sensory area.

Among the pelycosaurs, *Dimetrodon* (Romer & Price 1940) had partially evolved in a similar direction. The vomerine septum is relatively high and incipient choanal ridges are present, running antero-dorsally alongside the septum from the internal nares. In the posterior part of the nasal cavity there is evidence of the appearance of turbinal-supporting ridges both dorsally and in front of the orbit (Romer & Price 1940, plate 9).

The condition of the pristerognathid therocephalians is not well known, although Broom's (1936) figures of sectioned snouts indicate that the vomerine septum was not as high as in the gorgonopsids and that the choanal processes were poorly developed. However, because of the enlarged canine and incisor teeth of these forms, it is quite probable that they had nasal cavities organized in a manner similar to the gorgonopsids. More interesting is the condition in the Therocephalia which did not have hypertrophied anterior teeth. Brink (1960*b*) described a small snout of *Akidnognathus*, reconstructed from serial sections, showing a very low vomerine septum which nevertheless finished dorsally at the same level as the tips of the lower canines, when the jaws were closed. Much the same situation is found in the whaitsiids *Aneugomphius* (Brink 1956) and *Moschowhaitsia* (Tatarinov 1963). Thus it follows that in these latter forms the divison of the nasal cavity into anterior and posterior parts was far less distinct than in the gorgonopsids. The division must have existed functionally because much of the cavity lay behind the level of the internal choanae. However, this type of organization was probably ancestral to that of the cynodonts since, with the development of a secondary palate, the primary internal nares increased in length, bringing almost the whole length of the nasal capsule within the route of the respiratory air. Brink's (1960*a*) reconstruction of the procynodont *Scalapocynodon* shows that even in this group, where the secondary palate was not yet complete medially, the primary internal nares had extended posteriorly, but otherwise the organization of the snout resembles that of the therocephalians.

The appearance of a secondary palate in cynodonts is generally considered to be related to the development of extensive mastication, possible because of the elaboration of the post-canine teeth.

The organization of the nasal cavity and associated respiratory air tract appears therefore to bear a strong relationship to the form of the dentition, which explains most of the differences between the gorgonopsids on the one hand and the cynodonts and mammals on the other. Even the primitive therocephalians (excluding perhaps the pristerognathids) show a pre-adaptation towards the cynodont type.

Presumed turbinal-supporting ridges are now known in the gorgonopsids, the therocephalians (Brink 1960*b*; Tatarinov 1963) and the cynodonts (Watson 1913) among the theriodonts. Although not interpreted as such by the authors, Romer & Price (1940) figure similar ridges in *Dimetrodon* and even in the dicynodont *Kingoria*, there are ridges on the ventral surface of the nasal bones which have an appearance similar to those of the gorgonopsid. Thus they seem to be a widespread feature of the synapsids. It is not at all surprising that the enlargement of the nasal cavity should lead to it being developed as an olfactory organ and that it should have been advantageous to enlarge the surface area of the olfactory epithelium by the development of conchae or turbinals.

It is tempting to try and homologize the gorgonopsid pattern of turbinal cartilages with the turbinal bones of mammals. Generally, the dorsal system would correspond to the nasoturbinals of mammals, and perhaps the postero-lateral pair of ridges are equivalent to the mammalian ethmo-turbinals. The pair of turbinals in the maxillary sinus could be interpreted as the maxillo-turbinals. However, it could equally be true that all these merely represent suitable sites for turbinal development, independently in both groups.

The braincase and brain

1. *The construction of the gorgonopsid braincase*

The braincase of the specimen of *Arctognathus* sp. (figures 18*A* and 23) shows a remarkably extensive degree of ossification and, except for part of the orbitosphenoid, it appears to be complete. Furthermore, part of the side wall consists of the crystalline material discussed earlier

(p. 4) and is interpreted as representing a section of the braincase that remained cartilaginous in the living animal.

The ventral limit of the braincase is the parasphenoid and its rostrum (figure 18*A*). Anterior to the massive parasphenoidal tubera, the parasphenoidal keel runs anteriorly, below the pterygoids, and its ventral edge is very sharp in this specimen, unlike the majority of gorgonopsid species. The rostrum of the parasphenoid arises just above the basipterygoid processes and runs antero-dorsally. Its posteriormost part forms the anterior floor of the sella turcica, which is relatively broad, has rounded edges, and bears a low median ridge. In front of the sella turcica the edges of the rostrum become sharp and the dorsal surface takes the form of a broad, shallow groove. About 3 cm from its origin, the rostrum turns sharply and runs forwards less steeply, but the dorsal surface is still broad, and is now occupied by the widened base of a thin median septum. Further forwards still, however, the rostrum narrows from side to side and is continuous with the pterygoid septum below and a dorsal median ossification above. The sutures between these three bones are difficult to detect, but the anterior 2 to 3 cm of the rostrum are exposed dorsally because the dorsal ossification ceases (figure 12). Here the dorsal surface of the rostrum is a smooth trough, resting on the dorsal edge of the pterygoid septum. The paired pterygoids form a continuous median septum below the rostrum of the parasphenoid for the full length of the latter.

The basal region of the pro-otic is continuous with the lateral surface of the parasphenoidal tubera. The two antero-dorsally directed processes characteristic of therapsid reptiles appear to be better developed than in any other known form. The antero-ventral process is about 1 cm broad at its base but tapers as it rises almost dorsally. The antero-dorsal process is rather narrower. A number of ridges run across the lateral surface of the pro-otic. The anterior edge of the pro-otic and its antero-dorsal process is deflected slightly laterally to form a sharp ridge, and the posterior edge of the antero-dorsal process is also marked by a conspicuous ridge which continues postero-ventrally over the base of the pro-otic. Paralleling the latter ridge is a more rounded ridge along the anterior margin of the antero-dorsal process. The rest of the lateral surface of the pro-otic is rugose. The dorsum sellae is a steeply sloping transverse plate of bone, connecting the paired anterior edges of the pro-otics and the lower parts of their antero-ventral processes.

On either side, the extremities of the two anterior processes of the pro-otic are in ossified continuity with each other and with the orbitosphenoid anteriorly (figure 18*A*), and the two notches embraced by the pro-otic processes are in fact complete foramina. The more anterior one lies between the two processes, and on the left side is partially occluded by crystalline material. It is usually interpreted as the exit for the trigeminal nerve. The more posterior foramen lies above the antero-dorsal process. It is bounded posteriorly by the supraoccipital and an anterior process of the supraoccipital forms its dorsal edge.

This process of the supraoccipital has not been recorded previously. It forms a small part of the side wall of the braincase and is attached anteriorly to the ossified region of the braincase wall that lies above the pro-otic processes. These two elements do appear to be distinct, however, since on the left side there is a very slight gap between them.

The ossified region of the braincase above the pro-otic processes forms a complete side wall to the braincase. Anteriorly it is continuous with the orbitosphenoid. There are, however, grounds for believing that these two elements are distinct because during preparation the orbitosphenoid was detached, exposing a sulcus about 2 mm wide along the right anterior edge of the ossified region. The orbitosphenoid is much thinner and probably rested in the sulcus. To some extent this is confirmed on the left side, for although the orbitosphenoid has broken off farther anteriorly, there is a sudden decrease in thickness on the inner surface of the ossified region at a level corresponding to the grooved edge on the right side. It suggests that on this side, a part of the orbitosphenoid has remained attached to the ossified region.

Between the dorsal edge of the dorsum sellae and the orbitosphenoid there is no bony floor to the braincase. It is in this region that the crystalline material, referred to above, has been deposited (figure 23). A sheet of it arises on either side, from the anterior edge of the antero-ventral process and the ossified region above the pro-otic processes (figure 18*A*). The two paired sheets run antero-medially and meet in the midline along a line parallel to and just above the rostrum of the parasphenoid, and thus form a paired structure, V-shaped in section, that forms the braincase floor. In fact the junction between the two sides of the crystalline structure is displaced slightly to the left but presumably in life they connected to the dorsal surface of the rostrum, probably by a low median septum, Indeed, the median ridge at the base of the dorsal surface of the rostrum probably indicates that such a septum continued as far back as the front of the sella turcica.

The anterior edge of the antero-ventral process of the pro-otic is in the form of a sulcus, into which the side of the crystalline structure fits, showing that the sheet represents a chondrification distinct from the ossified antero-ventral process. On the contrary, the anterior edge of the dorsal ossified zone is exactly continuous with the crystalline sheet.

The posterior part of the crystalline structure stands about 1 cm above the floor of the sella turcica, and contacts the dorsum sellae. There is no foramen preserved to show exactly where the stalk of the pituitary penetrated it.

The antero-dorsal edge of the crystalline structure is exactly continuous with the ventral half of the orbitosphenoid ossification, and the brain space is therefore completely enclosed. The orbitosphenoid itself is preserved in two parts, with a large central part missing. The posterior section is much the larger of the two parts and consists of paired wings running dorso-laterally to contact a pair of longitudinal ventral ridges of the parietals and probably of the frontals farther forward. The upper part of each side of the orbitosphenoid incurves slightly before meeting the roofing bones, so that the widest part of the cranial cavity in this region is about half-way between the dorsal and ventral limits (figure 23*B*). Ventrally, the sides of the orbitosphenoid meet and are continuous with a thin median septum resting upon the dorsal surface of the rostrum of the parasphenoid (figure 18*A*). The dorsal part of this septum consists of the crystalline material, but for the rest it is bone, of a spongy appearance. The base of the septum is expanded so that it matches the width of the dorsal surface of the parasphenoid. Farther posteriorly, this part of the septum is continuous with the crystalline septum that supports the crystalline part of the braincase floor. The septum continues anteriorly between the two preserved portions of the orbitosphenoid.

The internal surface of the orbitosphenoid appears to be smooth and featureless, except that about half-way up, at the posterior end, there is a slight broad depression in the wall.

The more anterior of the two parts of the orbitosphenoid encloses a much narrower portion of the cranial cavity, with its greatest width dorsally, where the paired wings of the orbitosphenoid contact slight ventral flanges of the frontal bone. Between the two sides of the orbitosphenoid is a median septum, resting ventrally on the rostrum of the parasphenoid and contacting the skull roof dorsally. A thickened ridge runs from the front edge of the median septum backwards, and then curves in the form of an arc upwards and backwards to the orbitosphenoid.

It then runs horizontally backwards across the basal region of the latter, some 4 mm from the mid-ventral point. The result is that the base of the orbitosphenoid is stoutly buttressed to the median element.

The acid prepared posterior half of a large gorgonopsid skull, No. F.R.P. 37, has a very well-preserved braincase which confirms much of the description of *Arctognathus* sp. It lacks all trace of the cartilaginous structures, but is more complete in certain respects than *Arctognathus*.

The anterior process of the supraoccipital (figure 22) is much larger than was the case in *Arctognathus* and it makes contact with both the antero-dorsal and antero-ventral processes of the pro-otic, even allowing for the slight degree of crushing of the processes. The ventral edge of the supraoccipital process is sharp and is continuous with the lateral margin of the supraoccipital part of the braincase roof, below. The anterior and dorsal edges of the process are thicker and are in the form of sulci, suggesting that they contacted cartilage in life.

The structure of the pro-otic confirms the presence of ridges supporting the anterior processes, noted in *Arctognathus*. The foramen for the facial nerve cannot be distinguished.

The orbitosphenoid is complete except for the posterior part of the right side. The posterior edge of the left side is thin and irregular and was probably continued by cartilage. Between it and the dermal roof of the braincase is a smooth notch which could be part of a foramen. The roof and the orbitosphenoid together form a cavity which is circular in section (figure 22*C*) but the diameter gradually decreases anteriorly. Farther forwards still, the cranial cavity becomes almost triangular in section with the widest part dorsally. Finally, at the anterior end of the orbitosphenoid the cavity increases in both height and width, before emerging into the nasal cavity. The anterior edge of the orbitosphenoid is slightly in front of the dorsal origin of the preorbital plate. The preorbital plate runs antero-laterally towards the front of the orbit, gradually increasing in height. Between the antero-dorsalmost contact of the orbitosphenoid with the roof, and the preorbital plate, is a rounded notch which is probably the orbitonasal foramen (shown also in *Leontocephalus intactus*, figure 5). Posteriorly, the ventral edge of the orbitosphenoid bears a sharpened keel, not reflected in the form of the brain cavity. Farther forwards, the orbitosphenoid is connected by a thin median septum to the rostrum of the parasphenoid, and, as in *Arctognathus*, the anterior part of the septum rises to the dorsal roof, dividing the cranial cavity into two parts. Just before it reaches the roof, at the level of the anterior termination of the orbitosphenoid, this part of the septum bears a pronounced thickening (figure 22*C*), a feature well shown in *Leontocephalus* (figure 5).

The ridge of the bone developed on either side of the orbitosphenoid, described in *Arctognathus*, is seen. As in the previous specimen, it originates on the median septum and passes backwards over the ventro-lateral part of the front of the orbitosphenoid. However, it then turns postero-ventrally back on to the median septum, and thus has the form of a ventrally facing arch (figure 22*A*).

The skull of *Dixeya* sp. (figure 21) adds little further to the description of the braincase but is of interest in confirming the basic structure in a small species of gorgonopsid. The orbitospenoid is incomplete, but is seen to run forwards some distance in front of the dorsal origin of the preorbital plate. And the anterior median element bears a thickening, not noted in either of the previous specimens. In the region of contact with the orbitosphenoid, the posterior edge of the septum is concave and has a rounded edge. More dorsally, the edge is flattened in the transverse plane so that it consists of an oval area, facing postero-ventrally. The edge reverts to its original thickness just before reaching the skull roof.

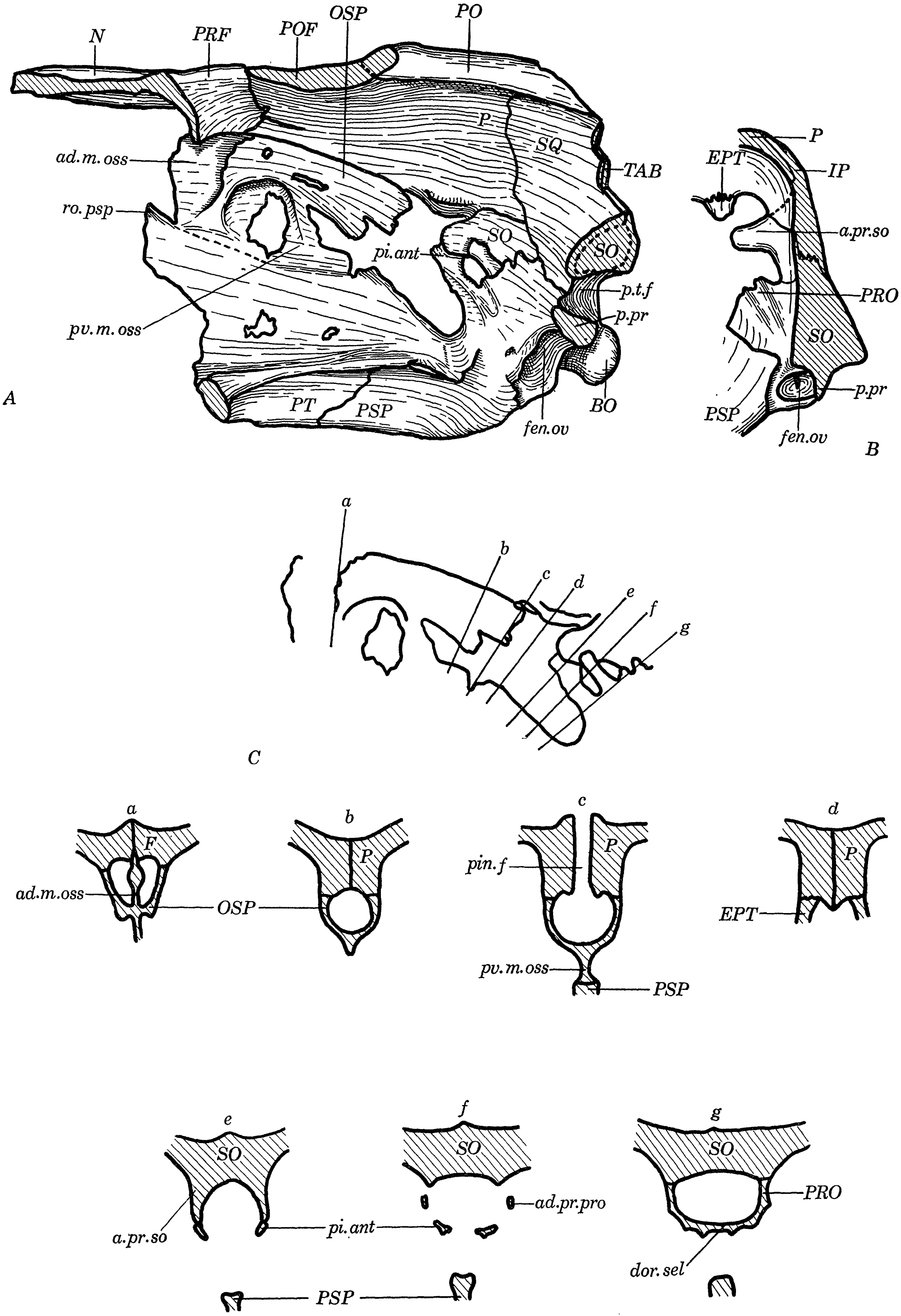

FIGURE 22. Unidentified gorgonopsid F.R.P. 37, × ½. *A*, Left lateral view of posterior half of skull, as preserved. *B*, Lateral view of posteriormost part of the skull, with the occiput sectioned about 2 cm to the side of the midline (right view reversed). *C*, Reconstructed cross-sections of the braincase at positions *a* to *g*, as indicated. Based on internal and external measurements of the acid-prepared braincase.

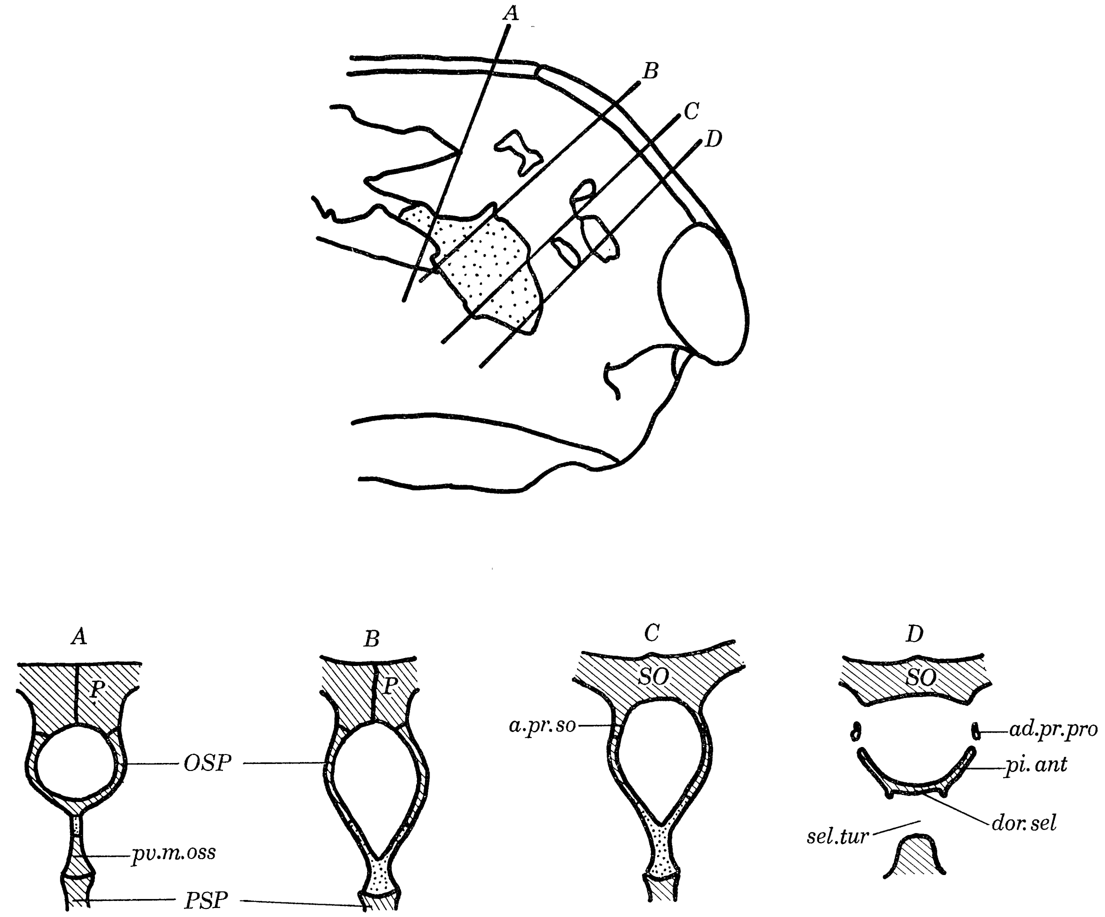

FIGURE 23. *Arctognathus* sp. Reconstructed cross-sections of the braincase at positions *A* to *D* as indicated, × $\frac{1}{2}$. (Compare with figure 18*A*.) Based on internal and external measurements of the acid-prepared braincase.

2. *The elements of the braincase*

Early work by Watson (1914, 1921) and Boonstra (1934*b*) indicated the general organization of the gorgonopsid braincase. They showed the presence of the two anterior processes of the pro-otic, the high degree of ossification of the median septum above the rostrum of the parasphenoid, and the large orbitosphenoid enclosing the anterior part of the brain.

A great deal of detail was added by Olson (1938, 1944) in his studies of serially ground skulls. He discussed earlier interpretations of the cartilage ossifications of the therapsid skull and his conclusions have been generally accepted. These were principally that the antero-ventral process of the pro-otic is an ossification of the embryonic pila antotica and that the antero-dorsal process is part of the pro-otic ossification, developed for the support of the orbitosphenoid. Anterior to the basisphenoid, Olson recognized two ossifications in the median septum, a postero-ventral one which he interpreted as homologous to the mammalian presphenoid (a median ossification of the trabecular cartilage), and an antero-dorsal one which he believed to represent the mammalian mesethmoid (another median, trabecular derivative), along with the orbitosphenoid (a paired ossification of the orbital cartilages).

Roux (1947), however, in his important work on the embryology of insectivore mammals, demonstrated convincingly that earlier interpretations of the ossifications of the central stem of mammals were incorrect, notably by Broom (1926). Only one median element ossifies in the trabecular cartilage, which he terms the mesethmoid. Cases where a second element apppears to be present result from invasion of the basicranial axis by the paired orbitosphenoid ossifications, posterior to the mesethmoid.

There is no reason to doubt earlier interpretations of the antero-ventral process of the pro-otic as an ossification within the pila antotica. It is attached to the antero-lateral corner of the basal plate region, as represented by the basisphenoid (lamina hypophyseosis region of mammals). Between the paired processes lies the hypophyseal foramen, and in *Arctognathus* sp. (figure 18*A*) it is in ossified contact with the orbitosphenoid antero-dorsally, suggesting that in other less well-ossified forms there was at least a cartilaginous connexion. However, since the pila antotica and pro-otic are co-ossified, it is not possible to say whether the pila antotica was merely invaded by ossification from the pro-otic or had its own centre of ossification. In *Arctognathus*, however, evidence was given that it was not co-ossified with the orbitosphenoid, so it could not have resulted from a posterior invasion from the orbital cartilages.

The antero-dorsal process of the pro-otic has also been shown to connect the pro-otic with the orbitosphenoid in *Arctognathus* (figure 18*A*) and therefore Olson's (1944) contention that it is of truly otic capsule origin is rendered suspect. Morphologically it forms part of the side wall of the braincase and bounds the pro-otic fenestra dorsally, and thus it corresponds to the embryonic taenia marginalis or the mammalian equivalent, the parietal plate. Further support for this view is lent by the nature of the anterior supraoccipital process, running forwards above the antero-dorsal process. A very similar condition exists in primitive mammal embryos (Roux 1947), where a large antero-lateral wing of the supraoccipital cartilage develops above the parietal plate (figure 24). Roux claims that the interparietal dermal ossification invades the upper edge of the process (Roux 1947, p. 149), a condition not found in the gorgonopsids, but in them the interparietal does lie immediately postero-lateral to the supraoccipital process. If a homology is accepted between the supraoccipital processes of the gorgonopsid and the mammal embryo, it follows that the gorgonopsid antero-dorsal process must be equivalent to the mammalian parietal plate (figure 24). The foramen bounded by the supraoccipital and the antero-dorsal process is therefore dorsal to the cartilaginous braincase and could not have transmitted the middle cerebral vein to the cranial cavity. The vein must have passed through the pro-otic foramen ventral to the antero-dorsal process.

There is no direct evidence of the position of the optic foramen. Boonstra (1934*b*) clearly mistook the strengthening ridge on the anterior part of the orbitosphenoid as marking the exit of the optic nerve. The completeness of the orbitosphenoid in specimen F.R.P. 37 indicates that the foramen must have lain between that bone and the pila antotica, emerging from the region represented by the crystalline material in *Arctognathus*, in front of the pituitary fossa. Dorsally the pineal foramen opens at about this level indicating that it is the mid-brain region, from which the optic nerves must be expected to arise. If so, then the cartilage presumably represented by crystalline material in *Arctognathus*, must have had both preoptic and post-optic parts and be compounded therefore from the preoptic root and the pila metoptica respectively.

There is no reason to doubt that the paired orbitosphenoid ossifications arise in the embryonic planum supraseptale because they represent the dorsal part of the side wall of the braincase, antero-dorsal to the pilae antoticae. The remarkable length of this bone in gorgonopsids is reminiscient of the condition in *Ornithorhynchus* (De Beer 1937).

The nature of the cartilaginous ossifications of the median septum is more obscure. In the present specimens the basicranial axes are not sufficiently well-preserved to show whether or not

Olson (1944) was correct in his observation that there are two separate areas of ossification, an antero-dorsal one continous with the orbitosphenoid and a postero-ventral one. In *Arctognathus* the latter was seen to be continuous posteriorly with a low septum composed of crystalline material which passed right to the sella turcica (figure 18*A*).

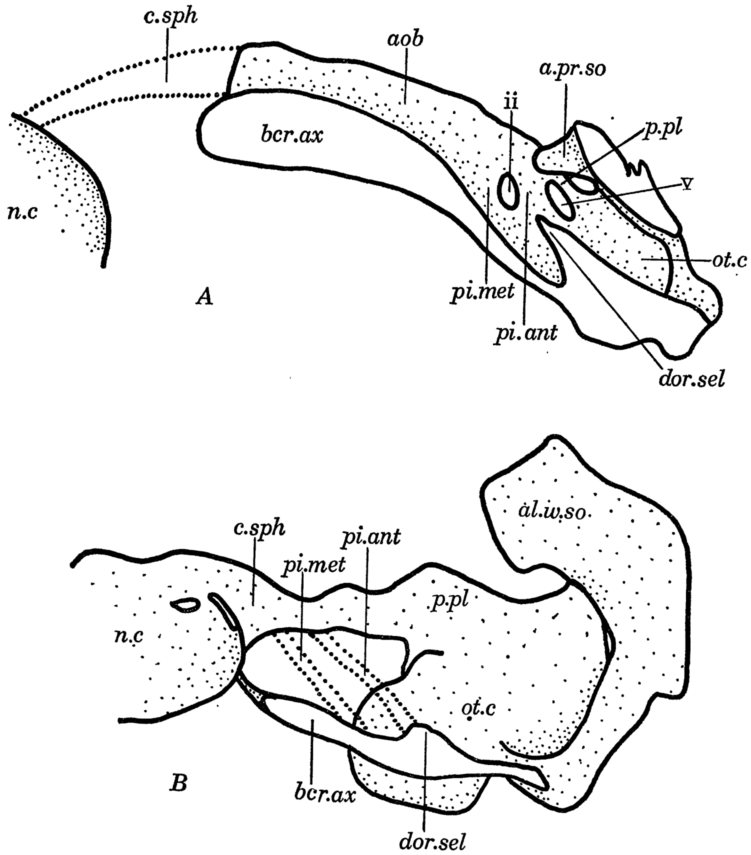

FIGURE 24. Comparison of the gorgonopsid braincase with that of an embryo insectivore. *A*, Reconstruction of adult gorgonopsid chondrocranium in medial view. *B*, Medial reconstruction of the chondrocranium of a 28.5 mm embryo of *Eremitalpa granti* Broom. Hypothetical positions of the pila antotica and pila metoptica shown in dotted lines. (*B* after Roux 1947, figures 39 and 40.)

Both these ossifications are clearly in the basicranial axis. It is of course probable that they include other parts of the neurocranium than the trabecular itself (perhaps adpressed preoptic roots or pilae metopticae), but because both the bones are in contact with the parasphenoid ventrally, they must both be at least partly within the trabecular cartilage. Because the postero-ventral element is not continuous in bone with the basisphenoid, it cannot represent an anterior invasion by the basisphenoid. And if Olson (1944) is correct in stating that the postero-ventral ossification is discontinuous with the orbitosphenoid, then it cannot be a result of invasion of the basicranial axis from the paired centres of ossification of the orbital cartilages (the orbitosphenoids). Yet if Roux (1947) is correct in believing that there is only a single trabecular ossification (and the evidence of Gaupp suggests that the same is true in *Lacerta* (De Beer 1937), then the antero-dorsal median bone must be a secondary invasion of the basicranial axis from the orbital cartilage centres of ossification. However, this is not the mammalian condition, where the secondary ossification, when present, lies posteriorly to the true trabecular ossification.

It may be argued that centres of ossification can fragment as seen, for example, in the presphenoid of *Homo* (De Beer 1937), but it would be expected that fusion of the areas of ossification would occur. In the case of the gorgonopsids, the sutural separation of the two adjacent bones does suggest a real morphological distinction. To bring the gorgonopsid condition into line with the mammals, it would be necessary to show that Olson (1944) was wrong in differentiating between the two elements and that the whole of the ossification of the basis cranii in front of the basisphenoid was a single unit, with perhaps a small component from the orbitosphenoid. This appears to be the condition of *Dimetrodon* (Romer & Price 1940).

However, it must be borne in mind that the argument does not concern the basic structure of the chondrocranium but merely the pattern of ossification within it. The evidence shows that the gorgonopsids probably had a fairly standard type of amniote tropibasic cartilaginous braincase, quite suitable as a representative of the forerunner of the mammalian type. Ossification within this was probably readily modifiable, complying with a topological requirement rather than with a basic morphological plan. Examples of this are seen in living amniotes. Broom's (1926) quite artificial division of the mammals into 'palaeotherida' and 'neotherida' depends on whether the orbital cartilage ossification invades the basicranial axis (Roux 1947). And the orbitosphenoid of *Lacerta* develops in the pila metopica, not the orbital cartilages. It is not too disturbing therefore that the gorgonopsids appear to differ markedly from the mammals in their orbitotemporal region but is probably a reflexion of the increased size of skull in an animal with a relatively primitive brain, and hence a small braincase.

It would be misleading, however, to attempt to homologize the median ossifications of the gorgonopsids with those of mammals and thus it is better to use the non-commital terms antero-dorsal and postero-ventral median ossifications respectively, for the orbitosphenoid invasion of the cranial axis and the trabecular ossification.

Certain features of the ethmoid region of the braincase are evident. The probable position of the orbitonasal foramen, between the orbitosphenoid and the preorbital plate, has been mentioned. The profundus branch of the trigeminal nerve and the orbitonasal artery presumably passed through it into the cavum orbitonasalis. This is an extra cranial space (De Beer 1937) lying between the orbit and the nasal capsule and besides the orbitonasal foramen, the aperture for the exit of the olfactory nerves opens into it on each side. This aperture, the foramen olfactorium evehens, is bounded by the anterior end of the orbitosphenoid laterally and the internasal septum (ossified here in gorgonopsids) medially.

Reasons for believing that the crystalline structure in the nasal cavity of *Arctognathus* (figure 18*A*) represents the cartilaginous hind wall of the nasal cavity have been discussed earlier. If true, then it presumably represents the lamina orbitonasalis which has extended medially to contact the nasal septum and form a more or less transverse plate. Assuming that it was originally perforated for entry of the olfactory nerves, it resembles the mammalian cribriform plate. Further, the anterior edge of the orbitosphenoid is thin and irregular and was therefore probably continued forwards as cartilage. This must have been the sphenethmoid commisure, running from the orbital cartilage to the nasal capsule, and if it were reconstructed in *Arctognathus* it would more or less contact the latero-dorsal corner of the cribriform plate, again very reminiscent of the mammalian condition (figure 24).

However there appears to be two specialized conditions in *Arctognathus*, not met with in the mammals. First, evidence that the nasal capsule extended postero-laterally behind what has been interpreted as the lamina orbitonasalis has been discussed in an earlier section (p. 59).

Thus although the cavum orbitonasale was apparently quite long near the midline, it must have been largely occluded dorso-laterally, giving it a quite different shape from that of the mammals, where it is wedge-shaped with the apex medially (De Beer 1937). Secondly, the presumed lamina orbitonasalis is in contact with the dermal, pterygoid part of the median septum. While undoubtedly it is formed by the pterygoid, parts of the septum are here formed from the crystalline material in *Arctognathus* (figure 18*A*), and in *Dixeya* (figure 21) this part of the septum appears to be more or less complete yet does not bear the marked sulcus on its dorsal edge found in the case of the vomer and parasphenoid. It is probable therefore that the pterygoid ossification has here partially invaded the true internasal septum, including that part in contact with the lamina orbitonasalis.

3. *Reconstruction of the brain*

The gorgonopsid braincase (figure 25*A*) has been restored in internal view from the evidence of several specimens. The section through the roofing bones, the occiput and the view of the hind-brain region is based on part of specimen F.R.P. 44. This is a fragment of a large gorgonopsid skull consisting of the occiput and the left parietal, frontal and nasal. The latter three bones have separated from their fellows along the midline sutures and therefore give an accurate view of a median plane of the skull roof. The specimen is completely free of matrix and the occiput has been bisected previously in a longitudinal vertical plane, just to one side of the midline. Therefore a view of the hind-brain cavity is exposed.

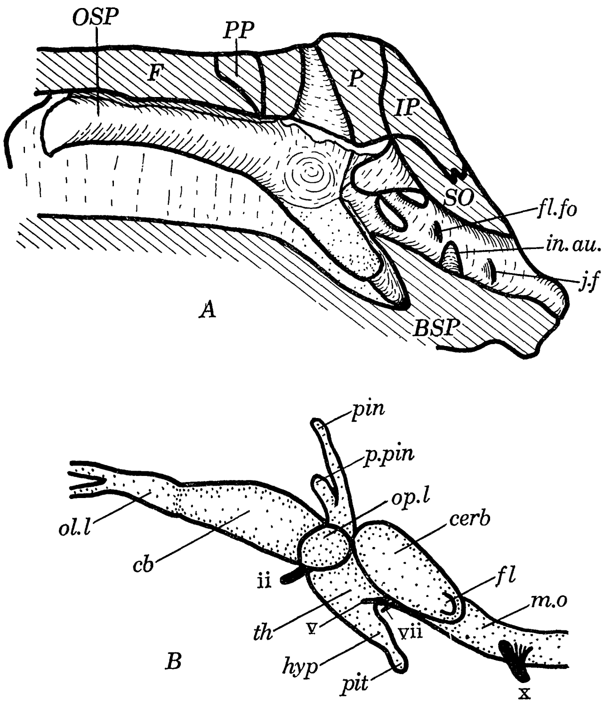

FIGURE 25. *A*, Composite reconstruction of the gorgonopsid braincase in internal view, approximately $\times \frac{1}{2}$. Persistent cartilage shown stippled. *B*, Restoration of the gorgonopsid brain in lateral view $\times \frac{1}{2}$.

The mid-brain region is based on the specimen of *Arctognathus* sp. The orbitosphenoid and supraoccipital process are taken from specimen F.R.P. 37. The reconstruction of the actual dimensions of the cranial cavity has been based on the reconstruction of cross-sections of the braincase of *Arctognathus* (figure 23) and specimen F.R.P. 37 (figure 22*C*).

Although these three specimens are of slightly different sizes, specimen F.R.P. 44 being the smallest and specimen F.R.P. 37 the largest, the discrepancy is considered sufficiently small for a tolerably accurate reconstruction to be made from the three of them. One most obvious point of difference is the varying degree of ossification of the anterior pro-otic processes between specimen F.R.P. 37 and *Arctognathus*, but it is reasonably certain that in the former there was a cartilaginous continuity between the processes and the orbitosphenoid, which had become ossified in *Arctognathus*. A second difference concerns the size of the supraoccipital process, which is much larger in specimen F.R.P. 37 than in *Arctognathus*. But again the gross morphology of this region is similar in the two and the relative contributions of the supraoccipital process and the more anterior elements respectively, to the formation of this part of the side wall was probably a variable feature.

The braincase of the gorgonopsids is very reptilian in that it is principally composed of cartilage ossification. The dorsal dermal bones, frontal and parietal, have a very limited role in the formation of the side walls and the epipterygoid is not involved at all. In contrast to mammals, the brain of the reptiles does not fill the cranial cavity and therefore its form cannot be deduced from the osteology in detail. The same is apparently true of gorgonopsids, and only a fairly general picture of the brain anatomy can be deduced. Nevertheless, several anatomical points are shown or can be deduced by reference to the normal reptilian condition.

Points of reasonably certainty are:

(1) The floccular fossa, marking the lower part of the cerebellum.

(2) The pituitary, marking the posterior limit of the mid-brain.

(3) The position where the trigeminal nerve emerges from the cranial cavity. Assuming that this is fairly close to the point where the nerve leaves the brain, the anterior region of the cerebellum is indicated.

(4) The broad depression in the lateral wall of the posterior part of the orbitosphenoid probably marks the swelling of the optic lobes of the mid-brain.

(5) The pineal foramen, marking the junction between the forebrain and mid-brain.

Inferred points are:

(i) In a large animal the cerebellum was probably well developed.

(ii) The cartilaginous part of the braincase (as shown by crystalline deposition in *Arctognathus*) anterior to the sella turcica probably housed the thalamus-hyptothalamus region of the brain which apparently therefore was well developed.

(iii) The optic nerve must have emerged posteriorly to the ossified orbitosphenoid since there is no foramen in the latter.

(iv) The shape of the pineal cavity which widens rapidly towards its base suggests the presence of a parapineal body anterior to the pineal itself.

(v) The large size of the orbitosphenoid, both in length and in cross-sectional area suggests a strong development of the telencephalon. The olfactory bulb cannot be distinguished from the cerebrum, but in living reptiles and mammals, the cerebrum is invariably the larger.

(vi) The boss on the ossified median septum partially dividing the anterior opening of the orbitosphenoid into paired dorsal and ventral parts may indicate the presence of two olfactory nerves, the olfactory nerve proper and a vomeronasal nerve.

Based on this evidence, a reconstruction of the brain is given (figure 25*B*).

CONCLUSION: THE PHYLOGENETIC STATUS OF THE GORGONOPSIA

Early work by Broom (1903, 1908) established the main groups of therapsid reptiles and in his Croonian Lecture (Broom 1915*b*) he postulated that the Gorgonopsia, Therocephalia and Cynodonta were the principal taxa of the known carnivorous forms. Watson (1921) undertook a detailed analysis of the cranial anatomy of a series of forms. He concluded that the carnivorous therapsids formed a natural group, the Theriodonta, consisting of Broom's three groups, and also the Bauriamorpha, which Broom had tentatively retained within the Cynodonta. Watson assumed that the pelycosaurs, especially *Varanosaurus*, were a close approximation to the primitive synapsid condition, and that the cynodonts, particularly *Diademodon*, represented the advanced condition. By taking a series of gorgonopsid skulls in what he believed to be the correct chronological order, he purported to show that the gorgonopsids had evolved from a near-pelycosaur type to a near cynodont-type. Two important deductions came from this observation. First, he supposed that the gorgonopsids were in fact close to the ancestry of the cynodonts, and secondly he developed the concept of a series of gorgonopsid cranial characters to be regarded as either primitive or advanced. Of the other two theriodont groups, Watson believed that the Therocephalia had been derived as a sideline from an early gorgonopsid stock, and that the Bauriamorpha evolved from the Theracephalia, via the scalaposaurids.

Watson's views can now be criticized on a number of grounds. At the time that he was writing, the Therocephalia were a poorly known group, and the procynodonts of the *Cistecephalus* zone of South Africa were not known at all. Thus much of the information that now demonstrates a similarity between these two groups and the cynodonts themselves was unavailable to him. Similarly, a large number of gorgonopsids have been described from the *Tapinocephalus* to *Cistecephalus* zones. These cast considerable doubt on Watson's ideas concerning evolutionary trends within the group. The taxonomy is chaotic, much of it being based on ill-preserved or ill-described material, often of doubtful horizons. Even so in several cases specimens from quite different horizons belong in the same genus. For example, *Scylacognathus* has one of its species from the *Tapinocephalus* zone and another from the *Cistecephalus* zone, as is also true of *Broomisaurus*. And many of the well-known genera such as *Aelurosaurus*, *Cynarioides* and *Scymnognathus* have members reported from both the *Endothiodon* and *Cistecephalus* zones (Haughton & Brink 1954). Whether this is a result of bad taxonomy or bad stratigraphy, or whether the diagnostic features used for taxonomic purposes are indeed dispersed throughout the time range of the group, is far from clear. Sigogneau (1963*a*) doubts the value of several of the characters traditionally used in gorgonopsid taxonomy, including one stressed by Watson, namely the presence or absence of a step in the alveolar border of the upper jaw. Several other characters used by Watson involve the form of the snout, temporal region and occiput, which are features likely to suffer greatly by distortion and damage to specimens. And finally, Watson did not take the absolute size of his animals into consideration which may well be a factor influencing, for example, the relative massiveness of the braincase elements. However, whatever view one may take of the state of taxonomy of the group, it is manifest that the Gorgonopsia were singularly stable in their cranial morphology and that is it difficult, if not impossible to trace any consistent trends through their history as Watson attempted to do.

That Watson misinterpreted the structure of the gorgonopsid palate was demonstrated by Boonstra (1934*b*) who showed that the paired palatines met mid-ventrally, preventing a contact between the vomer and pterygoids in palatal view. In both the cynodonts and therocephalians, Boonstra pointed out, the vomer does meet the pterygoids posteriorly in this view.

He considered that the failure of the ascending process of the epipterygoid to expand and become incorporated into the side wall of the braincase was a second important difference between the gorgonopsids and the therocephalians. Although not offering any explanation for these facts, Boonstra suggested that they showed that the gorgonopsids could not have given rise to the cynodonts.

The first known of the *Cistecephalus* zone procynodonts were described by Broom (1938) who pointed out their generally therocephalian-like form. He believed that they indicated a direct relationship between the Therocephalia and the Cynodonta.

Olson (1944) studied a series of serially ground therapsid skulls and by a comparison of various features of the braincases reached a conclusion similar to that of Watson (1921). However he based his argument on very limited evidence; the length, and point of origin from the crus communis, of the posterior vertical semicircular canal; the position of the opening of the fenestra ovalis from the sacculo-cochlea recess; the position of the facial canal relative to the labyrinth; and the angle that the anterior margin of the periotic makes with the skull base. Each of these points are of only slight variability between the relevant groups and only one or two members of each group were studied. In many more of the characters Olson studied, in the same region of the skull, he did not find evidence either way concerning the origin of the cynodonts. And his conclusions depended on the assumption that the sphenacodont pelycosaurs (i.e. *Dimetrodon*) represent the completely primitive condition. It is not felt that such characters can be considered so free from adaptive variation that the rest of the cranial anatomy can be safely ignored.

Attridge (1957) compared the superficial aspects of the skulls of gorgonopsids, therocephalians and cynodonts, concluding that 'the Therocephalia constitute a satisfactory ancestral group for both the bauriamorph and cynodont groups', a position that the gorgonopsids could not have held. In addition to the features noted by Boonstra (1934*b*), Attridge cites the width of the inter-temporal region, the contact between the post-orbital and the squamosal, the large postfrontal and the presence of a preparietal as gorgonopsid characters not represented in either the therocephalians or the cynodonts.

The structure of the *Cistecephalus* zone procynodonts is now well known as a result of the work of Brink (1960*a*, 1963). In a detailed discussion of the affinities of the genus *Scalapocynodon* (Brink 1960*a*), he lists both the therocephalian and the cynodont features of the skull. Although this particular form is specialized in having apparently lost the zygomatic arches and postorbital bars, it demonstrates an unmistakeable relationship between the cynodonts and the therocephalians and is probably close to the stage of organization that the cynodonts must have passed through.

Although wide opinion today is in favour of a therocephalian rather than a gorgonopsian derivation of the cynodonts, such influential workers as Romer (1961, 1966), Lehman (1961) and Olson (1962) have recently retained the converse view.

In the present study, an attempt has been made to relate anatomical features of the skull to their functional significance. The conclusion to be drawn, in so far as it is justifiable to generalize from the limited amount of material investigated, is that the gorgonopsids were highly adapted towards the very limited role of large-prey carnivores, which would explain the marked degree of structural conservatism in what was apparently a very successful group of animals. The adaptation was manifested both directly in the structures concerned with the jaw mechanism, and indirectly in the effect of the jaw functioning on the total architecture of the skull.

The contemporaneous therocephalians were a much more diverse group, but as far as known at present they all shared a basic functional organization quite distinct from that of the gorgonopsids. They lacked almost all of the specialization of the latter group, as the following comparison indicates.

Table 3

Gorgonopsid condition	Therocephalian condition
(*a*) Features reflecting the mechanical movements of the jaws	
Characteristic form of the canine and incisor teeth, with conical crowns, two rows of serrations, and developing a pattern of wear facets showing that both interdigitation and direct closure of the jaws occurred	Condition of the teeth is not well known. Certain forms, especially the pristerognathids, have a dentition similar to that of the gorgonopsids, but wear facets have not been described.
Articular quadrate-hinge adapted for a very wide gape, characterized by the small radius of curvature of the lateral condyles, and saddle-shaped medial condyles and the dorsal process behind the lateral articular condyle	Not well known in therocephalians, but the figures of Broom (1936) and Brink (1956) indicate that the lateral articular condyle has a large radius and faces almost posteriorly. No dorsal process apparently present
Quadrate complex-squamosal joint in the form of a ball-and-socket allowing streptostyly	Both the quadrate and the associated quadratojugal have dorsal processes which wedge into longitudinal slits in the ventral edge of the squamosal (e.g. Broom 1936; Boonstra 1953, 1954; Brink 1956, 1958)
Quadrate ramus of the pterygoid fails to meet the quadrate, but an extensive contact between the quadrate ramus of the epipterygoid and the quadrate, acting as a fulcrum for the quadrate movements	Quadrate ramus of the pterygoid meets the quadrate in an overlapping contact, but the quadrate ramus of the epipterygoid does not, in all adequate descriptions of therocephalians
No contact between the epipterygoid and the basipterygoid process, and no expansion of the ascending process of the epipterygoid. Probably an adaptation to allow a small degree of epipterygoid movement	Epipterygoid articulates with basipterygoid process (Broom 1936; Olson 1944; Crompton 1955). Ascending process of the epipterygoid expanded
(*b*) Features reflecting the jaw musculature	
Broad intertemporal region, related to a large postfrontal bone, and postorbital-squamosal contact and possibly the presence of a preparietal in most gorgonopsids	Intertemporal region narrow
Behind the level of the coronoid process, the floor of the meckelian fossa is broad and ventrally positioned	Condition not know in therocephalians.
Reflected lamina of the angular attached along its dorsal margin to the angular, and bearing a single, approximately vertical ridge	Reflected lamina free dorsally, and bears several ridges radiating from the antero-dorsal point of attachment of the lamina (e.g. Broom 1936; Boonstra 1934*c*; Brink 1956, 1958; Crompton 1955, 1963; Sigogneau 1963*b*)
Extensive smooth dorsal surface of the palate, bounded by ridges, continuous behind with the broad posterior surface of the lateral pterygoid flange	In *Aneugomphius* (Brink 1956) a ridge across the dorsal surface of the palate near its posterior edge presumably limited the area of the palate available for the anterior pterygoideus muscle
No suborbital fenestra in the palate	A suborbital fenestra pierces the palate in all groups, except the whaitsiids
Recurving of the retroarticular process of the articular bone.	No form known with a recurved retroarticular process
(*c*) Features indirectly related to jaw functioning	
Anterior part of the nasal cavity restricted to a dorsal position, as shown by the very high vomerine septum	No form with a high vomerine septum described
Very well-developed choanal processes of the palatines	Choanal process absent or only weakly developed
Stapes probably does not abut directly on to medial face of the quadrate.	Stapes abutting directly on to quadrate

Table 3 (*cont.*)

(*d*) Other features

Contact between the paired palatines mid-ventrally (possibly related to the development of the choanal processes), although there is a contact between the vomerine septum and the pterygoid septum internally	The vomer meets the pterygoids posteriorly, in ventral view
Parasphenoid rostrum rises high in the skull and runs forwards almost to nasal cavities	Parasphenoid rostrum reduced
No contact between the pro-otic and the quadrate ramus of the pterygoid	In the whaitsiids at least (personal observation) a process of the pro-otic runs laterally to meet the quadrate ramus of the pterygoid, in front of the paraoccipital process
A narrow deep termination posteriorly of the palatal vault	The palatal vault ends widely and shallowly, probably a preadaptation towards the development of a secondary palate

It may well prove that not all gorgonopsids have all the adaptations listed, and that certain therocephalians have specializations different from the conditions stated for that group, but none the less the list is formidable. There are, of course, many points of similarity between these two therapsid groups, but the majority of them are also found in the sphenacodont pelycosaurs which suggests that they are part of the basic synapsid organization. Indeed, if these characters are discounted, then it is clear that there are very few modifications common to both the gorgonopsids and the therocephalians, and even these will usually bear only superficial comparison. Thus, for example, the quadrate is reduced in size in both groups but as suggested earlier (p. 50) this is a result of the need to gain a more extensive quadrate–squamosal contact with increasing jaw-muscle forces. The actual form of this contact is quite different in the two groups (table 3), suggesting that the quadrate has reduced independently. Other similar instances are the development of the discrete coronoid process (which is obtusely triangular in section in the gorgonopsids but oval in section in those therocephalians which the writer has seen), the enlargement of the reflected lamina with a different pattern of strengthening ridges in the two groups respectively (table 3), and enlargement of the temporal fenestra (largely at the expense of the temporal roof in the therocephalians, but by a posterior and lateral extension of the squamosal in the gorgonopsids). The enlargement of the canine with its inevitable effect on the size of snout has occurred in both groups but even here there is possibly a difference. For in the case of the gorgonopsids the result of this has been the restriction of the anterior part of the nasal cavity to a dorsal position, correlated with the development of a high vomerine septum and choanal process of the palatine. No therocephalian is known to have had a high vomerine septum or choanal process, and in the writer's possession is a large whaitsiid skull, partially prepared in acetic acid, which has a process of the premaxilla surrounding the crown of the lower canine when the jaws are closed. Finally, the dentary has increased in size relative to the postdentary bones in both groups.

All these superficial similarities can be explained in terms of improvement of the jaw musculature, but the detailed differences are a clear indication that the two groups modified their musculature in two quite different ways.

It is not proposed to discuss the therocephalians in detail at present, but it appears that they improved their jaw mechanisms in a manner which did not commit them too rigidly to any particular ecological habitat. The gape of the jaws probably remained fairly modest, while the power of the bite increased. Indeed, several aspects of their cranial morphology suggest that they were approaching the mammalian type of jaw musculature. From this basic organization a variety of different adaptive types probably arose, modified to deal with a variety of different types of food. Among these were the pristerognathids which show a superficial resemblance to the gorgonopsids, notably in their size, and in the hypertrophy of the incisor and canine teeth, along with the reduction of the post-canines. However, if they are viewed against a background of more general therocephalians, it is clear that they lack the majority of the gorgonopsid specializations and merely paralleled that group, presumably as a result of adopting a similar mode of life.

Perhaps more interesting, in retrospect, the basic therocephalian organization seemed to have been capable of responding to the appropriate environmental changes by evolving into the cynodonts. For all the features of the therocephalians listed in table 3 apply equally well to the cynodonts, with the exception of the suborbital fenestra and the detailed form of the reflected lamina of the angular. The principal modifications which occurred were a further elaboration of the jaw musculature toward the mammalian condition (Parrington 1955; Crompton 1963; Barghusen 1968), the development of a secondary palate and the development of multicusped post-canine teeth. None of these changes could have occurred readily in the gorgonopsids with their commitment to a highly specialized jaw-mechanism. On the other hand, the therocephalians were apparently preadapted towards the cynodont organization. The detailed similarity between many of the structures concerned with the jaw mechanism in therocephalians and cynodonts implies a similar organization. The wide, shallow, posterior part of the palatal vault of the therocephalians, unlike that of the gorgonopsids, resembles the posterior end of the primary palate of the cynodonts, and because the therocephalians were not committed to choanal processes of the palatines, it would not be difficult to retract the anterior end of the palatines and bring most of the nasal cavity into the path of the respiratory air when a secondary palate evolved. Finally, as far as is known all gorgonopsids have reduced both the size and the number of their post-canine teeth. This is not the case in the smaller, primitive groups of the therocephalians.

It therefore appears that the therocephalians, cynodonts and bauriamorphs constitute a natural assemblage of forms distinct from the gorgonopsids. The differences are sufficiently marked for it to be certain that the common ancestor was considerably more primitive than either. Assuming that there was no marked reversal of evolution in either lineage, then the ancestral form probably had the following features: canines not greatly enlarged and therefore the snout still relatively small, which would suggest that the skull had a convex dorsal margin; full complement of post-canine teeth; temporal fenestra not greatly expanded; coronoid process not yet fully developed and probably therefore no great enlargement of the dentary; reflected lamina of the angular not greatly expanded; jaw musculature still in a relatively primitive form; quadrate not closely applied to the anterior face of the squamosal; basipterygoid articulation probably still movable. All these points follow inevitably upon the noted differences between the two groups, yet such a diagnosis of the common ancestor represents a creature that undoubtedly could be contained within the sphenacodont pelycosaurs. It appears therefore that the diversification of the gorgonopsid stock from the rest of the theriodonts occurred at a stage in history far earlier than has previously been supposed.

If this is true, then therapsids known to be intermediate in structure between the sphenacodonts and the *Tapinocephalus* zone gorgonopsids and therocephalians might be expected to fall within one or the other of these latter two groups. There are some hints that this is true of the carnivorous therapsids of the Russian Kazanian deposits (Olson 1962). It is not proposed to discuss these specimens in detail since the writer has not studied the original material and published information on the structure of the critical regions is scant. There appear to be three relevant groups, the phthinosuchids (Evremov 1954; Chudinov 1960), the biarmosuchids (Chudinov 1960) and the brithopods (Evremov 1954; Orlov 1958; Chudinov 1960), all of which Olson (1962) places in a group Eotheriodonta. Boonstra (1963) classifies them rather differently, considering that the brithopods are embraced by the anomodont taxon and that the other two are members of a group, the Eotitanosuchidae, which have an equal ranking with the Anomodontia and Theriodonta respectively. However, it is apparent from the published figures that the phthinosuchids have a number of gorgonopsid features of their skulls. Thus in both groups the intertemporal region is wide, and the palatines meet mid-ventrally. In contrast, the intertemporal region of the brithopods is tending to become narrow, with indications that the muscles had gained an origin from its broad, lateral-facing surface. The post-frontal is largely excluded from the dorsal surface of the skull and apparently overlies the post-orbital to some extent. Orlov (1958) figures the reflected lamina of *Titanophoneus* as being free from the angular along its dorsal edge, in the therocephalian fashion. In ventral view the vomer meets the pterygoids.

The biarmosuchids are not yet sufficiently well known for comparison but the possibility is strong that the phthinosuchids lie within the gorgonopsid assemblage and the brithopods within the therocephalian assemblage, which would support the present conclusion about the phylogenetic position of the gorgonopsids.

In conclusion, it is proposed that the gorgonopsids should be removed from the rest of the theriodonts to form a suborder the Gorgonopsia, of equal rank to the Theriodonta.

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LIST OF ABBREVIATIONS

A	angular
a.ch	anterior chamber
ad.m.oss	antero-dorsal median ossification
ad.pr.pro	antero-dorsal process of the pro-otic
a.keel.	angular keel
alv.c	alveolus of the canine
al.w.so.	antero-lateral wing of the surpaoccipital
aob	ala orbitalis
a.pr.so.	anterior process of the supraoccipital
a.pt.m. 1	anterior pterygoideus muscle, first branch
a.pt.m. 2	anterior pterygoideus muscle, second branch
a.ri	angular ridge
ART	articular
asc.pr.ept.	ascending process of the epipterygoid
bcr.ax	basicranial axis
BO	basioccipital
bpt.fac	facet for the basipterygoid process
bpt.pr	basipterygoid process
BSP	basisphenoid
C	coronoid
car.f	carotid foramen
cart.n.cap	cartilage of the nasal capsule
cb	cerebrum
c.b.mx	canine boss of the maxilla
cerb	cerebellum
ch.pr.pal	choanal process of the palatine
ch.tu	choanal tube
c.pr	coronoid process
cr.pl	cribriform plate
c.sph	sphenethmoid commissure
D	dentary
dep.mand	depressor mandibuli muscle
d.gr	dorsal groove
dl.re	dorso-lateral recess
dor.sel	dorsum sellae
d.pr	dorsal process
ECT	ectopterygoid
ect.f	ectopterygoid foramen
EO	exoccipital

eo.pr	exoccipital process
EPT	epipterygoid
ept	sutural surface for epipterygoid
ept.w.q	epipterygoid wing of the quadrate
ex.n.	external naris
F	frontal
fen.ov	fenestra ovalis
fl	flocculus
fl.fo	floccular fossa
gr	groove
hor.pr.ept	horizontal process of the epipterygoid
h.ri	horizontal ridge
hyp	hypothalamus
i	olfactory nerve
ii	optic nerve
in.au.m	internal auditory meatus
in.l.pq.m.	insertion of the lateral pterygoquadrate muscle
in.m.pq.m.	insertion of the medial pterygoquadrate muscle
in.p.pt.m.	insertion of the posterior pterygoideus muscle
IP	interparietal
ipt.v	interpterygoid vacuity
J	jugal
j.f.	jugular foramen
j.o.	Jacobson's organ
L	lachrymal
l.c.	lower canine
l.cond.	lateral condyle
l.d.	lachrymal duct
lig.pit	ligamentous pit
l.pq.m	lateral pterygoquadrate muscle
l.qj.m	lateral quadratojugal muscle
l.ri	lateral ridge
m.cond	median condyle
m.f.	muscle force
m.o.	medulla oblongata
m.pr.pmx	medial process of the premaxilla
MX	maxilla
mx.sin	maxillary sinus
N	nasal
n.c.	nasal capsule
occ.q.m.	occipito-quadrate muscle
ol.l	olfactory lobe
on.f	orbitonasal fissure
OP	opisthotic
op.l	optic lobe
OSP	orbitosphenoid
osp	sutural surface for otbitosphenoid
oss.zo	ossified zone
ot.c	otic capsule
P	parietal
PAL	palatine
pal	sutural surface for palatine
*pc.*1	first post-canine tooth
p.ch	posterior chamber
pi.ant	pila antotica
pi.met	pila metoptica
pin	pineal
pin.f	pineal foramen
pit	pituitary
PMX	premaxilla
pmx	sutural surface for the premaxilla
PO	post-orbital
POF	post-frontal
PP	preparietal
p.pin	parapineal
p.pl	parietal plate
p.pr	paroccipital process
p.pt.m	posterior pterygoideus muscle
PRART	prearticular
PRF	prefrontal
PRO	pro-otic
pr.orb.pl	pre-orbital plate
PSP	parasphenoid
PT	pterygoid
p.t.f.	post-temporal fossa
pv.m.oss	postero-ventral median ossification
Q	quadrate
q.f.	quadrate foramen
QJ	quadratojugal
q.ra.ept	quadrate ramus of the epipterygoid
q.ra.pt	quadrate ramus of the pterygoid
q.re	quadrate recess of squamosal
rart.pr	retroarticular process
ref.lam	reflected lamina of the angular
re.lo.c	recess of the lower canine
repl.c	replaced canine
re.sc.ty	recessus scala tympani
ri.l.d	ridge supporting the lachrymal duct
ro.psp	rostrum of the parasphenoid
SA	surangular
sel.tur	sella turcica
SMX	septomaxilla
smx	sutural surface for the septomaxilla
smx.f	septomaxillary foramen
SO	supraoccipital
SPL	splenial
SQ	squamosal
ST	stapes
st.rec	stapedial recess
TAB	tabular
temp. 1	temporalis muscle, first branch
temp. 2	temporalis muscle, second branch
th	thalamus
tr.pr.pal	transverse process of the palatine
turb	turbinal cartilage
turb.ri	turbinal-supporting ridge
V	vomer
v	trigeminal nerve
vest	vestibule
vii	facial nerve
vn.d	vomeronasal duct
vn.n	vomeronasal nerve
v.pr	ventral process
x	vagus nerve
z.mand.	zygomatico-mandibularis muscle

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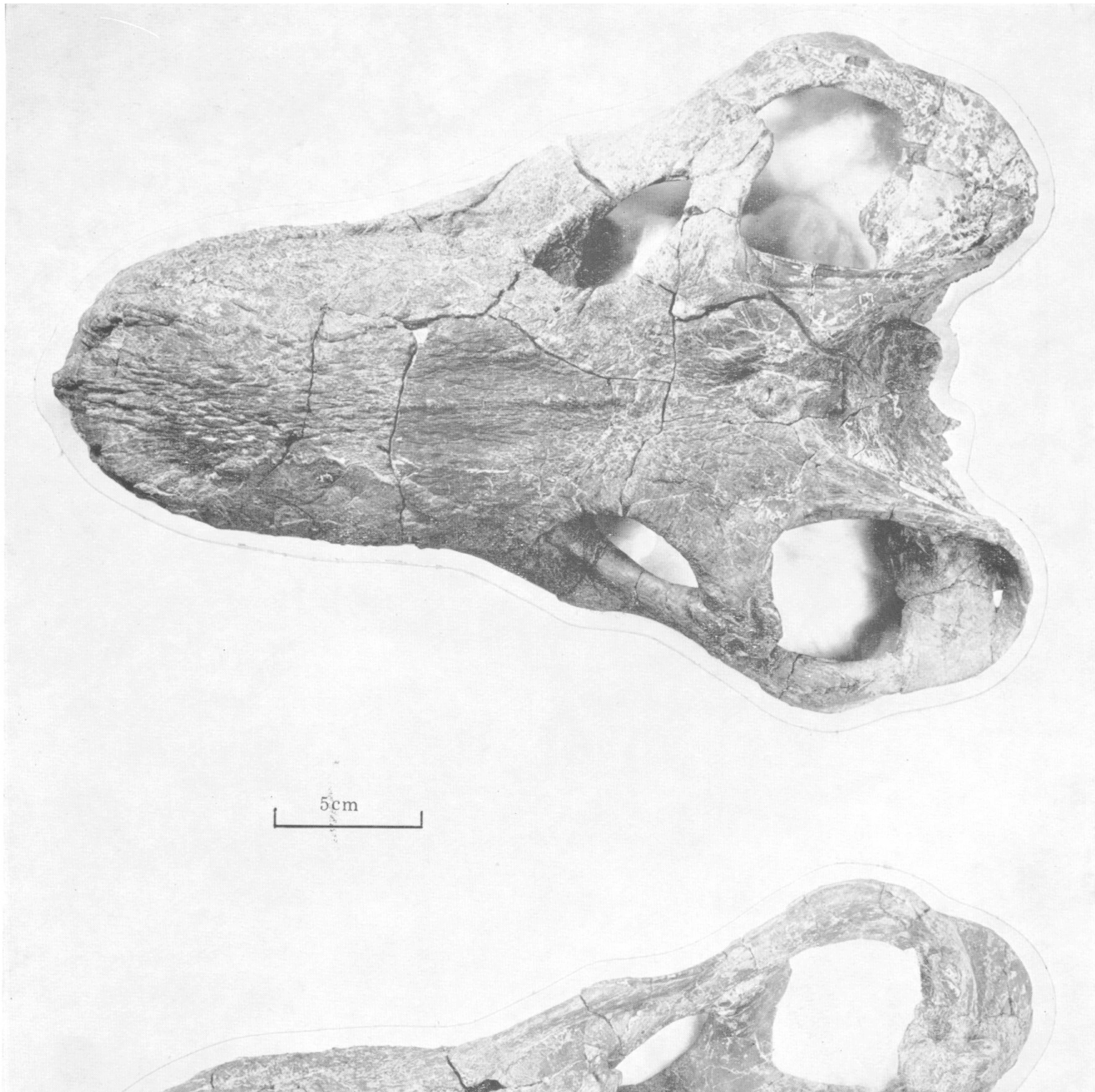

Leontocephalus intactus sp.nov. Skull in dorsal and ventral views.