A NEW TYPE OF PRIMITIVE CYNODONT

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Abstract

A very interesting ancestral type of Cynodont is described in reasonable detail from serial sections, graphical figures, and a complete wax model, four times natural size. The form is recognised as a new genus and species, for which the name *Scalopocynodon gracilis* is proposed. It is the earliest true Cynodont, from the base of the lower *Cistecephalus*-zone. Although its nearest allies are the somewhat later Silphedestids and Procynosuchids, it has unmistakably very close affinity with the base of the Ictidosuchid-Scloposaurid branch of the Therocephalians. Thus new light is cast on the origin of the Cynodonts and their general relationship with the Therocephalia. The specimen was thought to be a *Scaloposaurus* before it was decided to subject it to serial grinding.

Introduction

When it was decided to subject the present specimen to serial grinding it had been identified, in its unclean state, as a Therocephalian assignable to a species of *Scaloposaurus*. The intention was to incorporate a description of this specimen's detailed structure into the following paper (page 155 of this issue of Palaeontologia Africana) dealing with some Scaloposaurids and related Therocephalians. However, soon after the process of grinding had commenced, on entering the anterior palatal region, it was discovered that the specimen represents a primitive Cynodont on account of its cleft secondary palate. More posteriorly the cheek teeth showed clearly that they are cusped.

At the level of the pterygoid processes sectioning was temporarily stopped, to reconsider the implications of this misinterpretation. It was clear that a description of this specimen would not fit in with the Therocephalians described in the following paper and that it should be dealt with in a separate publication. It was also considered that the specimen might prove to be the type of a new species of Procynosuchid and careful thought was given to the implications of destroying a type. At this stage it was decided to reconstruct in wax the anterior half of the skull, as far as it was then sectioned. The resultant model, although exhibiting some peculiar features, suggested that the specimen very likely represented a juvenile stage of an existing species of *Leavachia, Procynosuchus* or *Galecranium,* and it was decided to proceed with the sectioning.

Immediately on resuming the sectioning certain peculiarities presented themselves as renewed cause for alarm. A distinct Therocephalian-like interpterygoid fossa appeared in the sections. The postorbital bars appeared to have been incomplete. The dentaries terminated at the level where the postorbital bars should have been. Distinct Therocephalian-like reflected laminae of the angulars were encountered. It was then decided to reconstruct in wax, section by section as grinding proceeded, to ensure that wrong impressions would not ensue from misinterpretations of individual sections.

The final result was a rather successful wax model of a specimen which is unmistakably a Cynodont in its anterior half, but still quite Scaloposaurid-like in its posterior half. What the author feared actually happened: this wax model represents the type not of a new species but of a new genus of a Procynosuchid, or more likely a Silphedestid-like Cynodont.

Technique

The technique employed in the preparation of the specimen for this paper is the same as that described for *Akidnognathus parvus* in the following paper (page 155 of this issue). Sectioning was at .5mm. intervals and reconstruction at 4 times natural size. It was discovered, unfortunately too late, that for a specimens of this size, .5mm. intervals were too great. Although results are perfectly satisfactory, it was considered that intervals of .25mm. would have produced better results, especially through the otic regions.

The only difference in the technical procedure followed was that colouring with Alizarine red proved to be unnecessary. Each section was left to dry in the sun for 15 minutes. The bone turned a clear white, while the matrix remained dark grey, giving as distinct a contrast as could be desired. This contrast was further exaggerated when a film of dilute glyptal was applied, to achieve a polish effect.

With this specimen a serious problem was solved. With previous specimens it was discovered that it is virtually impossible to section completely through the specimen up to the last trace of bone, especially when the most posteriorly situated bones (usually the occipital condyle bones) are exposed when the unclean specimen is embedded. Normally, well before the most posterior limit is reached, the specimen disintegrates, or becomes loosened from the embedding material. This difficulty was overcome as follows.

The specimen was made to stand with its long axis vertical, on its occipital condyles, on a pedestal of plasticene, about 1cm. high and of similar diameter, the latter standing centrally on the platform surface of the specimen holder of the grinding machine. A cylinder shaped from paper was placed tightly with an elastic band around the specimen holder and was made deep enough to cover the length of the specimen. Calistone was then poured into the container thus formed until it covered the tip of the snout of the specimen, the latter still standing free from the cylinder sides on the plasticene pedastal. After the calistone had set, the paper cylinder was removed, the calistone "piston" loosened from the platform and the plasticene excavated. It was then left to dry properly.

The pit left by the plasticene was thoroughly cleaned with thinner solution and all traces of plasticene still adhering to the occipital region were removed. The pit was then filled with molten bees' wax at high temperature, allowing the wax to penetrate into the calistone and spread over the surface due to adhere to the specimen holder. After the wax in the pit had solidified the holder was heated and placed over this surface, allowing it to cool in its own time while pressure was applied to ensure that a firm fit was established.

A substantial column of bees' wax was thus extended from the specimen to the specimen holder and held the specimen in position until the last .50mm. of the condyle bone was sectioned.

It should be mentioned that the length of the plasticene pedestal was designed to allow for grinding to proceed to the ultimate limit (while using 1" ball bearings throughout) with still a positive reading on the micrometer screw at the last section. As it happened, the final section was reached with the micrometer reading at zero.

Another problem was, however, encountered where, on reaching the bee's wax in the section surface, the wax absorbed the carborundum paste very successfully and, being the softer medium, it formed effective "emery material" which was inclined to wear away the zinc plate instead of the latter wearing away the specimen. This difficulty was overcome by excavating the wax where exposed, with a dental scraper.

With the great success achieved in the wax model it is felt that the virtues of the particular brand of wax used should be emphasized. As mentioned in the previous paper, Dental Modelling Wax was used, a wax which is characterised by its extreme toughness and stability over wide temperature ranges.

This wax is purchased in plates of standard 1 mm. thickness. The plates are consistently and accurately 1mm. thich throughout, most unlike the "home-made" products achieved with the usual roller apparatus. In addition, it is sufficiently transparent to allow a tracing to be made directly on the wax with the wax plate placed over the section drawing.

The wax does not crumble or crack. It has a phenomenal elasticity. After cutting out the section information in the wax plate, the wax section can suffer considerable distortion and bending, but on superimposing it on the section drawing it can be returned to its proper shape.

Although it was necessary to use supports in the process of reconstruction, the final product is entirely free from such supports. Such supports that were used were lengths or plates cut from the wax. On completion of the model all supports could be removed and the product is so stable that is it virtually like handling a modern mammalian skull. The lower jaw could be made to articulate with the skull.

The procedure in building the wax model was as follows: Each section drawing obtained with the episcope projector was traced directly on the wax, by placing the wax plate over the drawing and recording the information on the surface of the wax with a very sharp pencil. The pencil merely recorded delicate grooves which can clearly be seen, so that any sharp instrument can actually be used. A pencil was found to be more satisfactory, as it is inclined to pass more smoothly over the surface, without sinking into the wax, than a metal instrument is inclined to do.

The bone shapes were then cut out with a very finely pointed scalpel held vertically. The required wax elements representing the bones in the section were then made to adhere, correctly positioned, to the paper containing the section drawing. The wax is sufficiently sticky to adhere effectively to the paper while it is turned upside down and passed over the rods serving as a "base line" guide, until the new section comes to rest on the previous section already in position on the incomplete model. A glass plate was then pressed down over the paper to ensure that the newly introduced section will stick evenly and parallel and more effectively to the previous wax than to the paper, which it invariably did. The paper was then lifted away, the new wax section being in its correct position. To effect a more stable union, a hot probe was pressed through the uppermost two or three layers in as many places as possible, where surfaces were large enough.

With this method it was not necessary to cut whole sections as units. Each bone could be cut individually from small scrap pieces of wax and made to adhere to the paper in the correct positions. Thus a great measure of economy could be exercised with this rather expensive wax. However, expense should be no criterion when considering the time factor, the ease with which this method and material can be used, without continual re-melting and re-rolling of new wax plates.

Another advantage of this method is that it permits the representation of different bones in wax of various colours. The cutting of individual bones brings out sutural relations very clearly, even when using a single colour.

As in the case of *Akidnognathus parvus* no serious zig-zag problems were encountered. Bone surfaces were therefore smoothed over, both for added strength and to bring out sutural patterns more clearly.

At .5mm. intervals and projections at 4 times natural size, the wax thickness should theoretically have been 2mm., but in practice 1mm. plates were found to produce the best results. This is due to the fact that the wax increased in thickness around the margins as the required shapes were cut from it, and as each section was "welded" onto the model with the aid of a hot probe. At regular intervals check measurements were made with calipers to ascertain whether the thickness was increasing in the correct proportion. It was found that throughout the reconstruction every fifth section had to be represented by a double wax plate to ensure that the final total length of the model would also be, in proportion four times the natural length.

The specimen was purposely embedded at a slight angle to ensure that section planes would not be perfectly at right angles to the median plane. Thus information was encountered first on the one side and subsequently, some sections later, the same information was repeated on the opposite side. It often happens that a particular item of interest is missed due to bad preservation, the thickness of the interval, or because it was not expected to be showing at the particular level, and when grinding is continued the particular indistinct information is destroyed. When grinding perfectly at right angles to the median plane, the evidence is destroyed both sides simultaneously, but when grinding at an angle slightly off 90°, one can be on the alert to check on the opposite side for information missed. At the expected level grinding can be interrupted several times within the .5mm. interval to ascertain whether the required information might not present itself more clearly at an intermediate level.

Another useful method employed was to excavate consistently, before grinding each section, all the matrix well removed from the bone, with the aid of a dental emery wheel. The emery wheel was also passed lightly over the general surface to roughen it and to remove the film of glyptal. Grooves were also cut across the calistone surface radiating from the specimen outward to the circumference. These grooves, pits and general rough surfaces allowed for the better absorption and distribution of the carborundum paste. It reduced the actual surface and depth to be ground. It was found that, while the grooving and pitting took hardly a minute per section, a new level could be reached with a quarter the number of revolutions of the machine and consequently a quarter the time otherwise used. It also proved to be very economic as far as the consumption of carborundum powder is concerned. All restoration figures were obtained with the standard graphical method: the model was used only to assist in shading.

General Description and Diagnosis

The specimen is a complete skull with lower jaw in situ. In the model the lower jaw was made to articulate with the skull. Preservation on the whole is quite satisfactory. The dorsal surfaces of the nasals (posteriorly), the frontals and the parietals (anteriorly) were weathered, but outlines could be followed. However, in the prefrontal regions sutures could not be seen.

The posterior face of the skull was also badly weathered and damaged on the left side. The right side was complete, but sutural dispositions could not be ascertained clearly, especially between the supraoccipital, interparietal and tabular.

The left quadrate and stapes are lost.

The left alisphenoid is slightly displaced as a result of a force which also caused a fracture across the left pterygoid at the level where the quadrate ramus leaves the main body of the bone.

There are no postorbital arches, but it is difficult to say whether this condition is natural or artificial. There are postorbital bones lying close to the anterior ends of the parietals and some evidence was encountered of these bones having formed at least elementary projections marking the posterior borders of the orbits. On the left side the region of the postorbital bar was badly weathered and the bar could have been destroyed after fossilization, but on the right side the bar should have been encountered if it had not been destroyed prior to fossilization, because the region was well enclosed within the nodule.

Both temporal arches are incomplete from the levels at which the postorbital bars normally join, to the quadrate regions. Again, the left arch could have been damaged through weathering, but the right arch should have presented itself inside the nodule, had it not been damaged prior to fossilization. Enough of these arches is preserved to show that if they were complete they were extremely delicate, unlike the Cynodont condition and in line with the condition encountered in the Scaloposaurids.

The author is, however, thoroughly convinced that both the postorbital bars and the temporal arches were incomplete in the natural condition. The skull as a whole shows very little signs of having experienced rough treatment before fossilization. Both juguls terminate at exactly the same level, slightly forward of where the postorbital bars should join, and in strikingly similar pointed fashion. Furthermore, the squamosals also form very similar shaped projections in the quadrate regions, terminating at exactly the same levels.

The only other damage is distortion, beyond recognition, of the orbitosphenoids and the inevitable missing internasal bridge.

Otherwise every single structural detail revealed itself surprisingly clearly in the wax model. The lower jaw especially is most satisfactory. The only bones among those present whose outlines are somewhat confusing are the pro-otics, supraoccipital, interparietal and tabulars. This is due to weathering, or otherwise to the section intervals having been too great.

The following list of measurements in mm. is useful for comparison with other related forms:

Total length of skull to occipital condyles	60
Length to edge of occipital plate	52
From premaxillaries to pineal foramen	45
From premaxillaries to anterior borders of orbits	25
From anterior borders of orbits to posterior borders of external nares	18
From premaxillaries to basioccipital	58
From premaxillaries to level of fenestra ovales	52
From premaxillaries to internal carotid foramina	43
From premaxillaries to level of pterygoid processes	35
From premaxillaries to anterior end of interpterygoid fossa	33
From premaxillaries to posterior end of vomer	29

From premaxillaries to posterior border of secondary palate	23
From premaxillaries to palatal foramina	20
Length of 7 upper incisors	9
Length of 4 lower incisors	5
Largest diameter of upper canine	3
Largest diameter of lower canine	2.5
Length of 8 upper cheeck teeth	14
Length of 10 lower cheek teeth	18
Breadth of skull across jugals	34
Breadth of skull across squamosals	38
Minimum intertemporal breadth	7
Minimum interorbital breadth	12
Minimum breadth of snout behind canines	15
Breadth of canines	16
Minimum breadth of nasals	7.5
Maximum breadth of nasals	16
Length of dentaries	39
Length of surangulars	22
Breadth of symphysis across lower canines	10
Distance between outer surfaces of pterygoid processes	19
Distance between inner surfaces of upper canines	9
Distance between inner surfaces of lower canines	5
Distance between inner surfaces of last upper cheek teeth	18
Distance between inner surfaces of last lower cheek teeth	13
Total length of lower jaw ramus	53

There are some peculiar features about this skull which will be dealt with in more detail in the following pages; they are mentioned briefly here to indicate the basis on which the present diagnosis is formulated.

The dental formula is i7 cl pc8 for the upper jaw and i4 cl pc10 for the lower jaw. The upper canines are in the act of being replaced, the new teeth, situated anteriorly both sides, having reached about the same length as the predecessors. The two canines on either side are intimately lodged in the same socket and some degree of resorption of the root of the older tooth had taken place to make room for the new tooth. Almost every other tooth, both upper and lower, was accompanied by a successor in its socket, some still in a very elementary tooth-bud stage, others well advanced towards replacing their functioning fellows.

It is quite normal for the lower incisors to be fewer in number than the upper incisors, although in more advanced Cynodonts the difference is usually one tooth. Unfortunately this difference in number between the upper and lower incisors, is not known in the already described Procynosuchids and Silphedestids. The condition as a whole is at any rate different.

The 7 upper teeth are all unmistakably incisors; there are no small anterior canines. The Procynosuchids are all characterised by more than one canine and by only 5 incisors (perhaps 6 in *Galecranium*). The dental formula of the present specimen could in itself be regarded as a substantial criterion for recognising it as belonging to a different family, not unlikely the Silphedestidae.

On the right side there is slight evidence of a very vestigial small tooth in the maxillary in front of the large canine.

The larger number of lower cheek teeth appears also to be normal for such a primitive form. The anterior two lower cheek teeth actually oppose the upper canine.

The premaxillaries are strikingly shallow and highly placed, so that the incisors are generally carried at a level very high above that of the cheek teeth. The premaxillaries cannot accommodate large incisor roots, consequently the incisors are in general much smaller than the cheek teeth, while the anterior three teeth are considerably smaller than the four in front of the canines.

To compensate for a shallow, highly placed premaxillary region, the symphysial region of the lower jaw is very deep indeed. The lower incisors are, however, equally small with the anterior two also much smaller than the posterior two.

The cheek teeth, both upper and lower, increase gradually in size backward, the posterior ones being more distinctly cusped in the typical Cynodont fashion.

The secondary palate is typically Procynosuchid. This type of cleft secondary palate is also found in members of the Galesauridae and it is quite likely also characteristic of the family Silphedestidae. If the Silphedestid palate is substantially different, the present specimen would then be more likely a Procynosuchid. However, on account of the dentition it would still have to be placed in a separate family. Provisionally it is left with a rather vaguely diagnosed Silphedestidae.

Both the absence of the temporal arches and the likely incompleteness of the postorbital bars suggest a close affinity with other Silphedestids, more than with the Procynosuchids. However, as these characteristics are not conclusive, it is inadvisable to be definite on its affinity with the Silphedestidae in this particular respect.

A more definite primitive characteristic is the shortness of the dentaries. The dentaries hardly reach to the level of the back of the orbit. The rest of the lower jaw bones therefore feature prominently through the temporal region. The reflected lamina of the angular is still Therocephalian-like or Procynosuchid-like.

The articular and quadrate bones are delicate and Therocephalian-like. Especially the quadrato-jugal suggests close affinity with a form like *Aneugomphius*. It is attached to the quadrate, but extends deeply as a wedge upward and inward into the squamosal, over the latter's posterior surface where it forms the external auditory meatus groove. The much larger quadrate wedge is loosely located in an excavation on the anterior face of this portion of the squamosal. These conditions are not known well enough in the Silphedestids and Procynosuchids so that it is unsafe to venture opinions on the exact proximity of this specimen to the Scaloposaurid Therocephalians. What can be said in general, and with some measure of confidence, is that this specimen indicates a closer affinity between the Procynosuchids and the Ictidosuchid-Scaloposaurid branch of the Therocephalians than had hitherto been appreciated.

The interpterygoid fossa and the nature of the bones surrounding it are also rather Therocephalian-like. Very odd indeed is the presence of at least one tooth either side on the pterygoid tuberosities. The alisphenoids are, on the contrary, very broad and Cynodont-like.

There are two occipital condyles of typical Cynodont structure. The basioccipital has not been withdrawn properly. The condyles can be described as having jointly a crescent shape, with the basioccipital forming the middle portion, at a level well forward of the lateral exoccipital portions.

Although the posterior face of the skull is not well preserved and somewhat unsuccessfully restored in the model, it is still clearly Therocephalian in form. The paroccipital processes are delicate and short. The post-temporal fossa is, however, rather small.

The interparietal region was not sharply crested. This region rather resembles that of *Ictidosuchops* or *Scaloposaurus*. The pineal foramen is situated far back as in these Therocephalians.

The specimen is undoubtedly pre-mature. Besides dental replacement many sutures are still inadequately closed. However, it does not appear to be very juvenile.

The specimen is introduced here as a new genus and species and is provisionally considered as a likely member of the family Silphedestidae, on condition that this family, when re-evaluated, will actually prove to be, as a whole or in part, ancestral to the Procynosuchids in general. While the present specimen, with at least some Silphedestids, is considered to be more primitive than the Procynosuchids it is acknowledged that in dental characteristics and the loss of the temporal arches and postorbital bars, they had evolved some distance away from the main line leading through the Procynosuchids to the higher Cynodonts.

Scalopocynodon gracilis gen. et sp. nov.

(Figures 33 — 35)

Type: Complete skull with the lower jaw in situ, recorded as No. 346 in the collection of the Bernard Price Institute, from the base of the *Cistecephalus* zone on the farm Uitspanfontein in the Beaufort West district. The original specimen has been destroyed in the process of serial grinding. It is now represented by a complete and detailed wax model, four times natural size, and a full set of section drawings at .5mm. intervals.

Diagnosis: Primitive Cynodont; dental formula i7, cl, pc8 and i4, cl, pc10 for the upper and lower jaws respectively; very shallow premaxillary region; high symphysial region; both upper and lower incisors very small anteriorly; cleft secondary palate; interpterygoid fossa large; pterygoid tuberosities carrying at least one tooth each; pterygoid processes long and slender; postorbital bars apparently incomplete; zygomatic arches evidently absent; quadrates delicate and streptostylic; parietals Scaloposaurid-like with pineal situated far back; paroccipital processes short and slender; post-temporal fossa small; occipital face primitive; two occipital condyles; dentaries short but with well formed coronoid processes; angulars and surangulars large; reflected lamina short, delicate, but still projecting freely behind the dentary.

Structure of the Skull

The *basioccipital* is retracted from the occipital condyle to a greater extent than in the Procynosuchids. A similar condition is interpreted by Broom (1938b) for *Procynosuchus delaharpeae,* where the condyle has developed a crescent shape as a result of some degree of reduction on the part of the basioccipital, but the condition in the present specimen is distinctly more advanced. In *Leavachia* the arrangement appears to be more primitive, more like the typical Therocephalian tri-lobed single condyle as found in *Ictidosuchops* (Crompton 1955) or *Aneugomphius* (Brink 1956). The structure of the occipital condyle is not known in the other Procynosuchids or in any form considered at present as belonging to the Silphedestidae.

In other respects the basioccipital is of typical Therapsid build. It does not contribute to the margins of the jugular foramina. It forms, with the basisphenoid, insignificant tubera on the borders of the fenestrae ovales. These tubera are apparent only in the extent to which they reach sideways; they do not drag the lateral margins of the basioccipital downwards. On the ventral surface it has a small median ridge, with a foramen either side. On the side of the brain case it forms a smooth floor, concave in cross section and straight antero-posteriorly, sloping upwards to the front.

Posteriorly to the jugular foramen, on the side of the brain case, the basioccipital is smoothly joined to the exoccipital. In front of the jugular foramen it is, on the contrary, in rather loose contact with the opisthotic. Farther forward it presents a free margin ventrally to the vestibule.

The anterior margin of the basioccipital is fused, quite indistinguishably, with the basisphenoid. Nowhere in the sections could any trace of their suture be seen. This circumstance might indicate that the specimen is not quite as juvenile as other features tend to suggest. The region where this suture should be is covered ventrally by the parasphenoid.

The *exoccipitals* form the two major condyles for articulation with the vertebral column. The arrangement is no doubt typically Cynodont, where these condyles articulate with the separate left and right halves of the atlas, while the loose atlas intercentrum articulates with the basioccipital facet. This arrangement demands a trilobed odontoid process (atlas centrum) on the axis. The structure is, therefore, quite advanced.

The exoccipitals form the lateral borders of the foramen magnum. These margins are sharp and tend to constrict the foramen. They also contribute to the posteromedial margins of the jugular fossae. The sections did not reveal separate foramina for the twelfth nerve, penetrating the exoccipitals.

The portions forming the lateral margins of the foramen magnum have broad dorsolateral surfaces presenting substantial areas which find contact with the supraoccipital. In the specimen the impression is created that these contacts were not very firm.

The exoccipitals are not known properly in nearly related forms. They are comparable with those of *Aneugomphius,* although in the latter form they extend farther around the foramen magnum and jugular foramina.

The *supraoccipital* did not reveal itself satisfactorily in the sections, especially as regards the nature of its lateral margins. It is interpreted as a rather long bone reaching upward and forward from the dorsal margin of the foramen magnum and penetrating deeply between the parietals where the latter diverge to contribute to the occipital flanges.

At its most dorsal extremity it is well ossified, unlike the condition normally encountered in Cynodonts where this portion is often absent on account of it having been cartilaginous. This is added support for the view that this specimen is not very juvenile. At a lower level there are indications that it had been cartilaginous in a restricted section.

The *opisthotics* are not indistinguishably fused with the pro-otics to suggest a single periotic structure as Crompton (1955) found in *Ictidosuchops.* On the contrary, they appear to be in rather loose articulation with the pro-otics, but the exact nature of their relationship is rather confusing in the sections. This cannot be blamed entirely on the thickness of the sections. On the left side there is definitely some damage due to weathering. On the right side a crucial region across the fenestra ovalis, which is better preserved than on the left side, is obscured by a fragment of bone which might be the stapes; it might also be a foreign bone element. If it is the stapes, it lies with its medial end thrust into

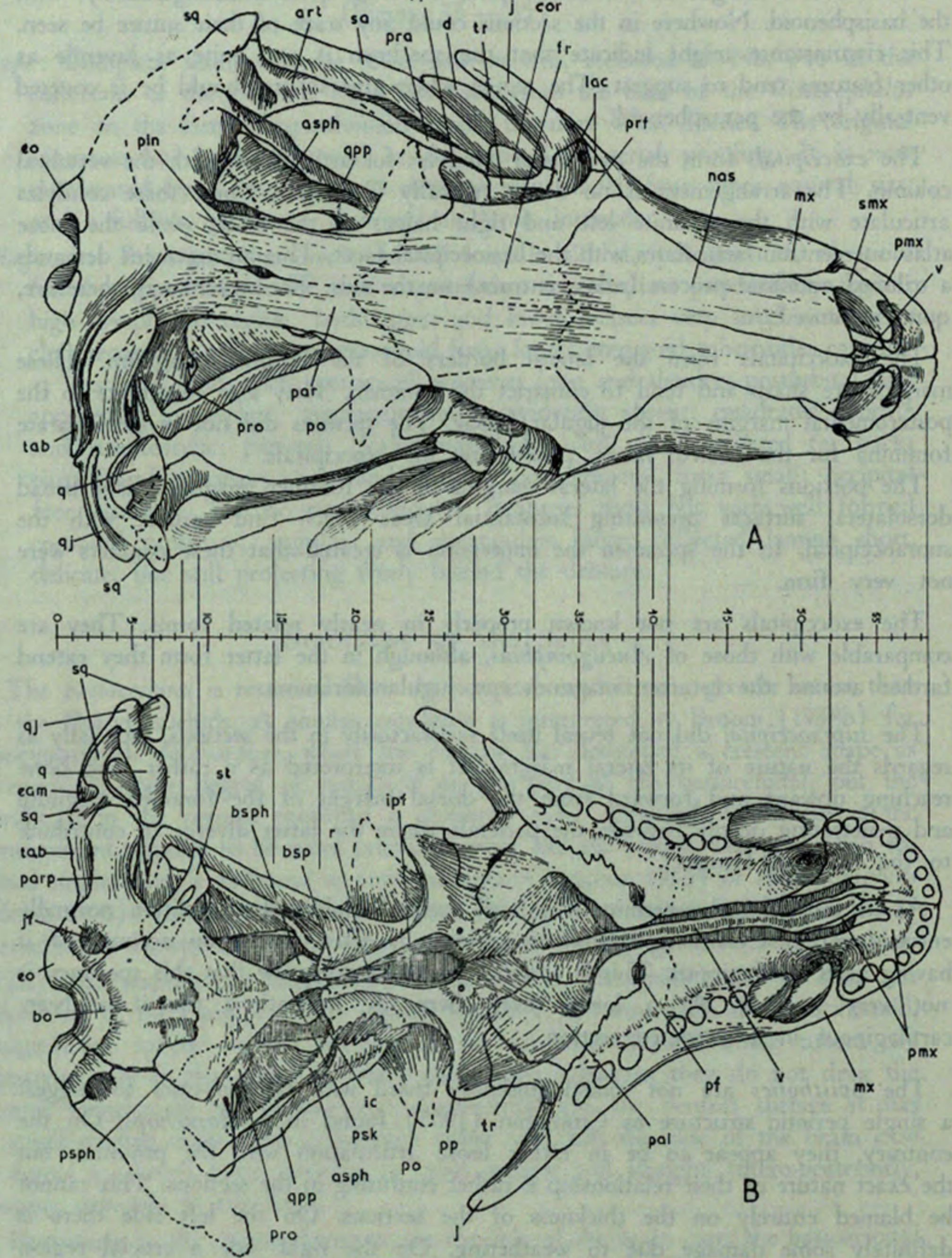


Figure 33

A, Dorsal and B, Ventral view of the skull of *Scalopocynodon gracilis,* graphically reconstructed from serial section. Twice natural size.

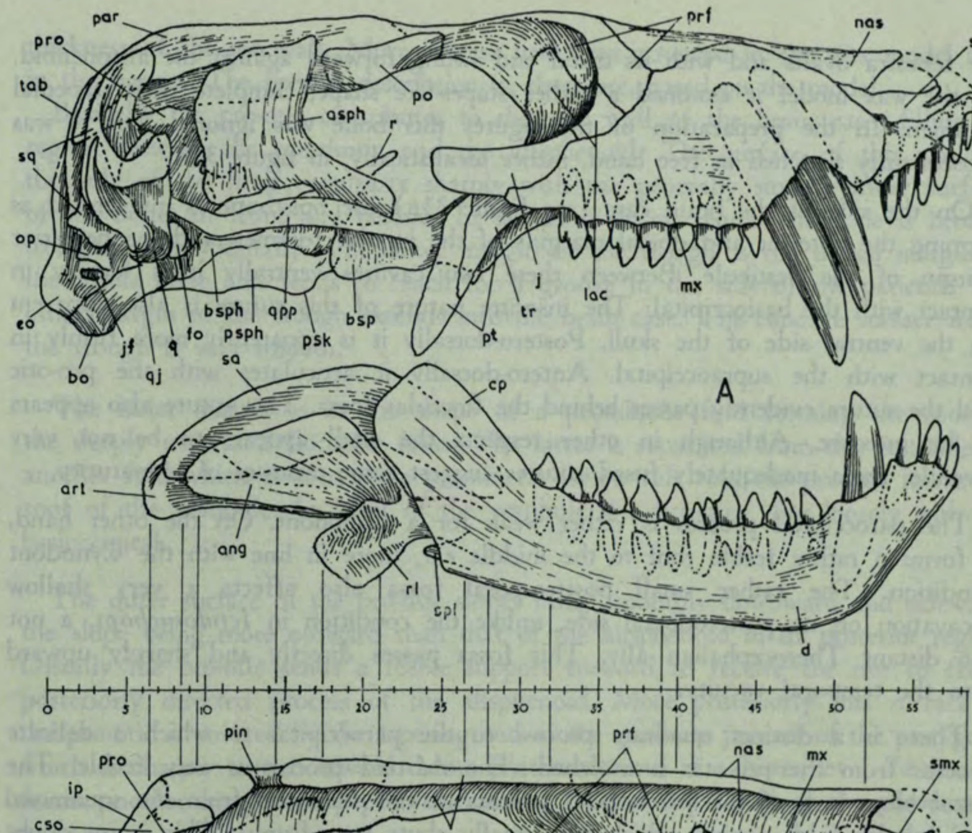


Figure 34

A, Lateral and B, Median view of the skull of *Scalopocynodon gracilis*, graphically reconstructed from serial sections. Twice natural size.

For abbreviations see page 132.

the fenestra ovalis and with its distal end swung forward against the alisphenoid. In the wax model it assumed a rather stapes-like shape, complete with stapedial foramen. In the preparation of the figures this bone was ignored, but it was subsequently sketched in free hand, rather idealistically, in figure 34B.

On the side of the brain case (see figure 33B) the opisthotic is interpreted as forming the anterior and dorsal margins of the jugular foramen and the posterior margin of the vestibule. Between these two cavities ventrally it is loosely in contact with the basioccipital. The insecure nature of this suture is also apparent on the ventral side of the skull. Postero-dorsally it is apparently more firmly in contact with the supraoccipital. Antero-dorsally it articulates with the pro-otic and the suture evidently passes behind the floccular fossa. This suture also appears to be insecure. Although in other respects the skull appears to be not very juvenile, these inadequately fused sutures suggest some measure of immaturity.

The paroccipital process is rather weak for a Cynodont. On the other hand, it forms a rather feeble roof to the middle ear, more in line with the Cynodont condition. The rather small posttemporal fossa also affects a very shallow excavation on its posterodorsal side, unlike the condition in *Ictidosuchops,* a not too distant Therocephalian ally. This fossa passes directly and sharply upward into the temporal vacuity.

There is a distinct quadrate process to the paroccipital to which a delicate process from the pro-otic is attached. The mastoid process is very feeble. The distal blunt end of the paroccipital process is well separated from the squamosal and tabular folds against which it normally abuts very firmly. This is no doubt artificial.

The opisthotic forms much of the border of the large jugular foramen externally. On the posterior border it forms a distinct bulge before joining the exoccipital and supraoccipital. Here, on the medial side of the posttemporal fossa, the tabular covers the opisthotic with a fold rather similar to its fold over the mastoid process on the lateral side of the fossa.

The *pro-otics* are well preserved on both sides, but it is difficult to interpret their exact shape and disposition from the sections. This is entirely due to the

Abbreviations: ang, angular; appo, anterior process of the pro-otic; art, articular; asph, alisphenoid; bo, basioccipital; bsp, basisphenoid process of the pterygoid; bsph, basisphenoid; cor, coronoid; cp, coronoid process; cso, cartilaginous supraoccipital; d, dentary; eam, external auditory meatus; eo, exoccipital; ff, floccular fossa; fo, fenestra ovalis; fr, frontal; ic, foramen for internal carotid artery; ip, interparietal; ipf, interpterygoid fossa; j, jugal; jf, jugular foramen; lac, lachrymal; lc, lower canine; mx, maxillary; mxp, palatal plate of the maxillary; nas, nasal; op, opisthotic; osph, orbitospennoid; pal, palatine; palp, palatal plate of the palatine; par, parietal; parp, paroccipital process; f, palatine foramen; pin, pineal; pmx, premaxillary; po, postorbital; pp, pterygoid process; pra, prearticular; prf, prefrontal; pro, pro-otic; psk, paraphenoid keel; psph, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; qpp, quadrate process of the pterygoid; r, rostrum; rl, reflected lamina; sa, surangular; smx, septomaxillary; so, supraoccipital; spl, splenial; sq, squamosal; st, stapes; tab, tabular; tr, transverse bone; uc, upper canine; v, vomer; vest, vestibule.

thickness of the intervals. More success had been achieved in the wax model than in the figures. The present description is, therefore, based on the model.

Basically the pro-otic contributes to the side wall of the brain case, filling the region between the opisthotic and the alisphenoid. The surface of this wall, on the side of the brain, contrasts sharply with the generally smooth inner surfaces of the bones in front and behind. In the most dorsal region the bone is broadly troughed longitudinally. The outer margin of the trough is the dorsal margin of the whole bone and tends to reach for a groove in the side of the parietal. The inner margin of the trough extends into the brain case. The concave surface inside the trough is very smooth.

The inner margin is in the shape of a prominent fold forming the roof of the deeply excavated floccular fossa. The latter is separated from the vestibule by another fold which is even more prominent. Below this fold the pro-otic forms the roof of the vestibule. In front of the vestibule it articulates very loosely with the basioccipital.

The outer surface of the pro-otic slopes fairly smoothly downward and sideward, the slope being more outward than that of the alisphenoid in its posterior region. Distally the pro-otic sends a feeble support forward to receive the not so feeble posteriorly directed process of the alisphenoid. More posteriorly this surface of the pro-otic is covered by the tapering end of the quadrate process of the pterygoid, which is sharply turned inward. More posteriorly and at a lower level the prootic forms another long slender process reaching for the distal end of the paroccipital process.

The region of the pro-otic overlapped by the distal end of the quadrate process of the pterygoid is exposed in dorsal view on the right side. On the left side it is covered by an additional fold of the pro-otic.

The dorsal part of the anterior margin of the pro-otic is covered very feebly by the posterior margin of the alisphenoid. This condition is primitive. Higher Cynodonts are characterised by a substantial overlap of the alisphenoid across the whole anterior margin of the pro-otic. Between this overlap dorsally and the junction of these two bones ventrally, there is a wide aperture for the fifth nerve. A separate long and delicate process of the pro-otic projects in a rather peculiar manner through this aperture.

The most conspicuous process of the pro-otic extends as a free projection forward, slightly upward and sharply inward into the brain cavity, from the main body of the bone containing the floccular fossa. This process is the same as the one which Crompton (1955) calls the anterior dorsal process in *Ictidosuchops*. The anterior ventral process which is even larger in *Ictidosuchops* is all but completely absent in the present form.

The *tabular* of the left side is entirely weathered away. It appears to be complete on the right side, but its medial margin is obscure. The portion covering the posterior face of the parietal flange is quite thick. It lies very loosely against this flange. The space between the tabular and the squamosal below the parietal flange is rather considerable. This cavity appears to serve some significant purpose, as it is exaggerated by an excavation in the anterior face of the tabular which renders the bone extremely thin in the area above the posttemporal fossa. The portion of the bone forming the dorsal margin of this fossa is as thick as the portion above the excavation. The excavation is further enlarged by the general concavity of the posterior face of the portion of the squamosal lying in front.

This excavation is continuous with the general passage of the posttemporal fossa immediately below. It also communicates through a wide aperture below the tip of the parietal flange with the general region of the external auditory meatus. This is perhaps due to the fact that the inner margin of the meatus groove, which is usually a prominent fold of the squamosal, is very weakly developed. This fold would otherwise have closed the aperture. The excavation also communicates with the brain cavity directly inward, but this is evidently due, only incidentally, to the poor contact between the pro-otic and the supraoccipital.

Whatever the actual interpretation might be, should the present description be somewhat incorrect on account of the section intervals being too great, or whatever the purpose of the cavity is, the fact remains that the tabulars do not simply cover with firm contact the bones in front of them, as the impression is normally created.

The tabular extends farther downward on either side of the posttemporal fossa where it covers the paroccipital process in the usual manner.

The *interparietal* is evidently completely missing from the specimen. In the wax model an opening presented itself in the central part of the area normally covered by the interparietal. This opening, leading into the brain case, is in the position where the interparietal had contact with the cartilaginous portion of the supraoccipital. The interparietal evidently covered appreciable areas of the tabulars, as the tabular preserved in the specimen extends very close to the opening.

The *parietals* are very different indeed from those of the Procynosuchids. *Leavachia* (Broom 1948, Brink 1953) and *Procynosuchus* (Broom 1938b) are characterised by prominent median crests. In the present specimen the crest is not only absent but the general dorsal surface of the parietals, even behind the pineal opening, does not slope as much as in these otherwise primitive Cynodonts. Admittedly the weathering that affected especially the frontal region could have damaged the crest but the general outlines of the parietals could be traced quite clearly in the posterior region where the crest should have been most prominent. In addition a higher crest would have caused a more pronounced slope of the dorsal surfaces laterally, and it would have given the parietal flange preserved a higher dorsal margin on the border of the occiput. This margin is genuine and undamaged in the sections and from its general nature it can safely be concluded that the crest was absent in the intertemporal region.

The parietal region is shaped more like that of the Silphedestids, where it is broad, moderately sloping outward posteriorly, and without a crest. The region differs, however, in that it does not become constricted behind the pineal. This constriction is also found in the Procynosuchids, as well as in the Scaloposaurids with which favourable comparisons can be made in other respects, such as the shorter and more delicate occipital flanges and the posteriorly situated pineal.

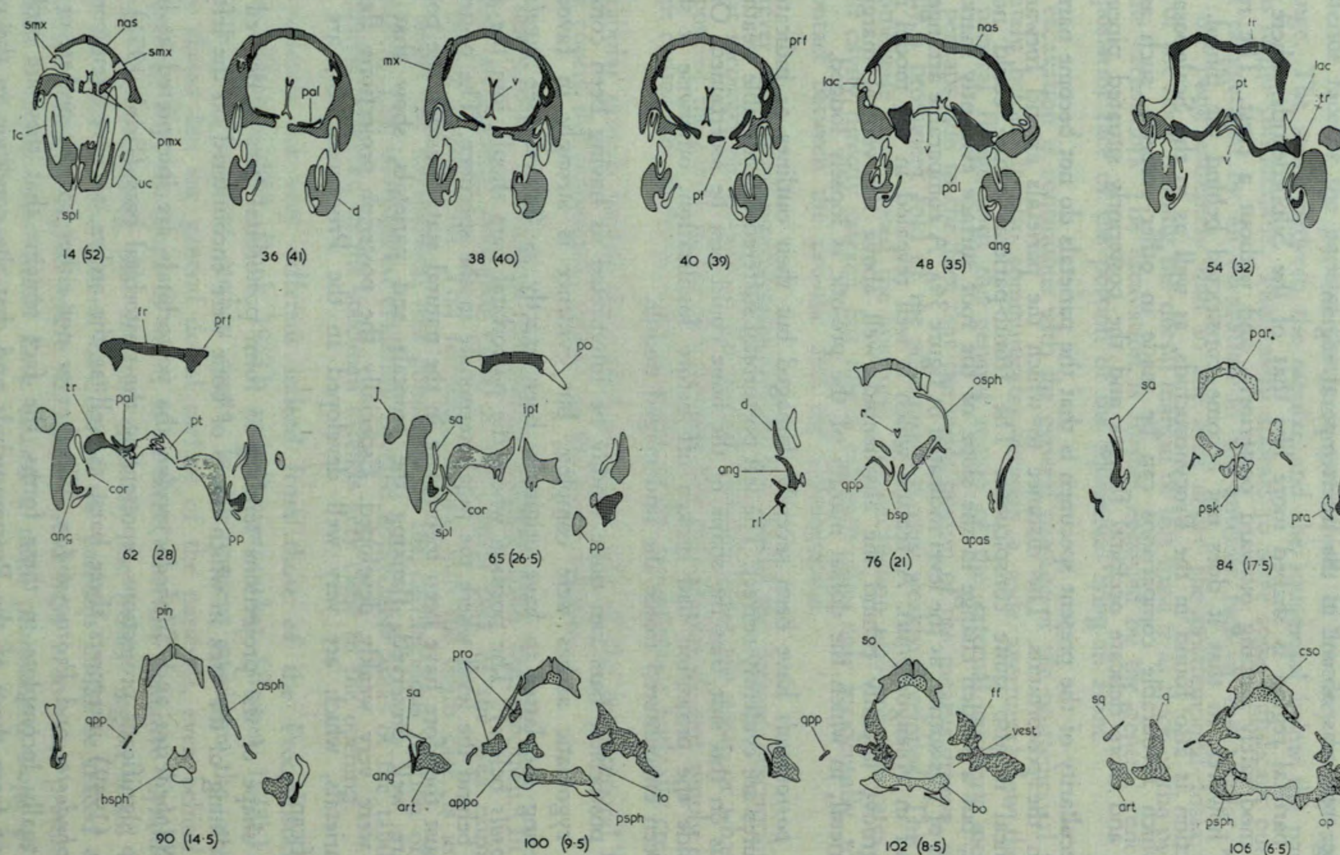
A peculiarity of the present specimen is that the parietals do not become narrower between the postorbitals. The distance to which the parietals extend forward of the pineal is also quite conspicuous. The fronto-parietal suture could not be located, but a sudden change in the slope of the roof surface evidently marks the position of this suture, at the level indicated in figure 34A. A comparable arrangement is found in *Aneugomphius*. A feature which is well revealed in the model is the deep groove laterally behind the alisphenoid, well above the ventral margin of the parietal, in which the dorsal margin of the pro-otic is loosely lodged.

The *postorbitals* have been severely damaged but their outlines as indicated in the figures are evidently correct. The left postorbital suffered considerable weathering but it is on this side that the shape of the bone could best be ascertained. On the right side the projection had broken off before fossilization, otherwise it should have been encountered inside the undamaged nodule.

The postorbital bars can quite readily be interpreted as having been complete, if the zygomatic arches were complete, but evidence is strongly in favour of considering the latter to have originally been exactly as figured (see *jugals* and *squamosals* below). The position where the postorbital bars should join the arches is well behind the level where the jugals terminate in the specimen. The postorbital bars must therefore have been incomplete in the natural state. Besides, the portions that are well preserved, flanking the frontals and parietals, show that these bones were very weakly developed. Especially the posterior projections flanking the parietals, which are very well developed in the Procynosuchids, are quite insignificant.

The shape of the projections tending to form postorbital bars is derived from the outlining of the area in which traces of bone were encountered on the left side.

In *Silphedestes* and *Silphedocynodon* the postorbitals are interpreted as having had no significant projections representing the postorbital bars (Brink 1951) while Broom (1949) interprets these bars, as well as the arches, to have been complete in *Silphedestes* and *Protocynodon*. Whether or not either bars or arches, or both, are actually incomplete in these forms, the fact remains that they are strikingly different from those of the Procynosuchids and that the condition in the present specimen is more comparable with the former than with the latter.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106 (6·5)

Figure 35

The *frontals,* together with the postorbitals, suffered very badly from weathering, although damage was not as severe as in the left occipital region. The frontal region could satisfactorily be restored in the model, but the sutures of the frontal bones could not be traced.

As mentioned above, the fronto-parietal suture is taken as extending at a level where there is a noticeable change in the slope of these bones on the dorsal surface. Anteriorly the fronto-nasal suture is taken as being level with the anterior borders of the orbits, as is the case with all related forms. The fronto-prefrontal sutures are interpreted as extending to the postorbitals, thus excluding the frontals from the dorsal borders of the orbits according to the Cynodont pattern. In view of the several other Therocephalian-like features in this skull it is, however, not unlikely that the frontals could actually have contributed to the dorsal borders of the orbits; the prefrontals are exceptionally long as interpreted in figure 34A, even excluding its considerable projection anteriorly on the side of the nasal cavity, as shown in figure 33B.

The ventral surface of the frontal region is generally flat and smooth, with no indication of fronto-nasal turbinal ridges. Laterally the frontals bend downward quite far to form the inside surfaces of the walls tending to separate the olfactory chamber from the orbits.

If this frontal region is correctly interpreted, it is quite obvious that it differs greatly from that of the Procynosuchids, where the frontals are very narrow. There appears to be a better correspondence in the structure of this region with the Silphedestids, in spite of the poor preservation in these forms.

The *prefrontals,* as mentioned above, apparently exclude the frontals from the dorsal borders of the orbits, but the contrary condition is still a fair possibility. They contribute more extensively to the walls separating the olfactory chamber from the orbits than the frontals. Anteriorly this wall extends low down and is covered laterally by an extensive dorsal fold of the lachrymal. This wall extends straight down only posteriorly where the frontal contributes to its inner surface. Anteriorly, where the lachrymal contributes to its outer surface, it does not extend straight downward, but at first sharply inward from the dorsal border of the orbit and subsequently downward. There is a deeply excavated cavity between this upper orbital wall and the portion above contributing to the roof of the skull in the anterior interorbital region.

The prefrontals separate the nasals from the lachrymals, a feature in which the present specimen differs profoundly from the Procynosuchids and one where

Figure 35
Section through the skull of *Scalopocynodon gracilis.* Figures below every section indicate the numbers of the sections, number 1 being the section where contact was first made at the premaxillaries, and the figures in brackets indicate the levels in millimeters according to the micrometer of the grinding apparatus. For convenience these levels are marked against a scale introduced in figures 33 and 34. All sections are natural size.

there appears to be a comparison with the Silphedestids. This condition is also found in *Aneugomphius* and *Ictidosuchops.*

In the Procynosuchids the prefrontals also fail to broaden in the region across the anterior orbital borders as is the case in the present specimen and the Scaloposaurids.

The *lachrymals* cover very small areas on the lateral face of the snout in front of the orbits, thus allowing the maxillaries to come within close reach of the orbital borders. They do not cover much of the dorsal surfaces of the jugals on the ventral margins of the orbits, unlike the condition in *Ictidosuchops* and somewhat comparable with that of *Aneugomphius.*

In the anterior orbital corner the foramen for the lachrymal duct is large and situated very close to the border. This canal extends forward through the lachrymal bone and is subsequently carried farther forward inside the anterior portion of the prefrontal. Both these bones are more extensive on the side of the nasal cavity than on the outside surface of the snout. The lachrymal canal opens inward at the very anterior extremity of the prefrontal. The arrangement is very similar to that described by the author for *Akidnognathus parvus* in the following paper (page 155 of this issue).

The lachrymal builds the whole anterior inner wall of the orbit, where it broadly overlaps the prefrontal. On the floor of the orbit it contacts the transverse bone.

The *nasals* are Cynodont-like in being very broad posteriorly, but Therocephalian-like in having lost contact with the lachrymals. Anteriorly the septomaxillaries do not penetrate as deeply along their lateral margins as in the Procynosuchids, another feature which is reminiscent of the condition in *Ictidosuchops* and other Scaloposaurids.

Although the anterior tips of the nasals are well preserved in the specimen, no sign of the premaxillaries having penetrated between them could be found.

The lateral margins of the nasals are bent down deeply on the side of the nasal cavity and are in normal fashion broadly overlapped by the maxillaries.

There is no trace of turbinal ridges on the ventral surfaces of the nasals.

The *septomaxillaries* exhibit the same general structure as that described by the author for *Akidnognathus parvus* in the following paper (page 155 of this issue). The only difference in the structure of the whole region which might affect the views expounded by the author in the previous paper on the significance of the septomaxillary structure is to be found in the nature of the floors of the external nares formed by the premaxillaries immediately behind these bones. The opening, situated in the position where the septomaxillary, premaxillary and maxillary meet on the side of the external naris, leads not only directly inwards into the nasal cavity, but also forward to open on the anterior face of the septomaxillary, where it is characteristically roofed by the prominent shelf-like projection of the ventral margin of the naris.

The general shape of this region is, however, rather peculiar on account of the premaxillaries being turned sharply upward. This condition may be slightly exaggerated by distortion, though it is surprising that distortion could influence so profoundly this very local region while the rest of the skull is reasonably unaffected. The height of the symphysial region also suggests that the region as preserved is near to the natural condition. This up-turned nature of the premaxillary region has the effect of making the portions of the septomaxillaries, which normally contribute to the anterior surface of the snout, face almost directly upward, tending to form part of the floor of the external nares.

The portions of the septomaxillaries penetrating the nasals and maxillaries are not exposed on the side of the nasal cavity.

The *premaxillaries* are strikingly like those of *Procynosuchus* (Broom, 1937) in structure rather than shape and, on account of the secondary palate, very unlike those of *Akidnognathus, Ictidosuchops* or *Aneugomphius*. On the midline, immediately behind the anterior incisors, the two maxillaries form a conspicuous small boss, as is typical of even the latest Cynodonts like *Diademodon*. There are, no doubt, two small foramina situated anteriorly on either side of this boss, more directly behind the first incisors, as are found in *Akidnognathus, Moschorhinus,* and apparently all related Therapsids, but these were missed on account of the thickness of the section interval. The cleft in the incomplete secondary palate starts level with the posterior side of the boss. The cleft is very broad anteriorly in the premaxillary region where the ventral margin of the vomer drops to below the general level of the secondary palate. Initially the premaxillaries together form a substantial process supporting the anterior end of the vomer from below, but soon the left and right parts diverge to extend separately as long, slender tapering projections either side of the well-thickened ventral margin of the anterior end of the vomer.

The premaxillaries form the anterior halves of the excavations for the lower jaw canines and extend well backward on the margins of the palatine plates. These posteriorly directed processes, and those either side of the vomer, are exactly like those of *Procynosuchus* as illustrated by Broom in 1937 and 1938b.

The premaxillaries carry 7 incisors each, there being no doubt whatsoever that the 7th tooth either side is an incisor and not a canine. In contrast with the cheek teeth there are little signs of tooth replacement. In dental formula the present specimen stands well separated from both the Procynosuchids and the Silphedestids.

Due to the very insignificant depth of the premaxillaries anteriorly, the front incisors are very small. Those in front of the canines are appreciably larger.

There is no trace of an internarial bridge. The region between the septomaxillaries does not indicate the base of such a bridge and there is no sign of this process where it normally penetrates between the anterior ends of the nasals. However, there has no doubt been an internarial bridge which had suffered very effective destruction.

The *maxillaries* are very typically Procynosuchid as far as the secondary palate is concerned. This type of cleft secondary palate is, of course, also found in the Galesaurids, but it is quite evident that the present specimen is not a close ally of this family. It is unfortunate that the palate is not known in the Silphedestidae.

The feeling that the present specimen is closely allied with the Procynosuchids is enhanced by the fact that Broom (1937, 1938b) encountered a very similar degree of tooth replacement activity in *Procynosuchus delaharpeae*. Virtually every tooth, in the lower jaw more than in the upper, has a successor situated lingually. These successors are in various stages of development, from the most elementary tooth bud to almost fully erupted teeth still sharing a socket with the predecessor (in the lower jaw). In some cases it appears as though the new tooth is inclined to erupt from a separate socket well on the inside of the old tooth, these apparently being the most elementary buds.

It is unfortunately not possible to tell from the sections whether a particular tooth bud is very young or far advanced, because a tooth could show large in its full transverse section at a particular level, while at another level a more advanced tooth could be mistaken for a very early stage on account of the level having nearly missed it. For a successful study of the order of tooth replacement, section intervals should have been about .1mm.

From a dental point of view the present specimen is, however, not a typical Procynosuchid. It has only one canine in each maxillary which, on both sides, is in the act of being replaced, the new anterior tooth having reached about the same length as the posterior predecessor. The posterior is obviously the older, as its root had suffered some resorption to make room for the successor. This phenomenon rules out the possibility of considering the two teeth as separate canines.

On the right side there is vague evidence of a very rudimentary anterior canine which might bring the present specimen slightly closer to the Procynosuchids. A similar feeble tooth on the left side was not missed through the thickness of the interval; there is no room for a tooth on this side.

If the anterior canines are taken as a very significant diagnostic feature, which they should really be, the present specimen is even farther removed from the Silphedestids. However, the author feels that these anterior canines have apparently been quite readily discarded by various forms over rather short evolutionary ranges, as is also apparent in the Ictidosuchids and Scaloposaurids. While the number of canines may be taken as a good generic diagnostic feature, it is hardly reliable for a family diagnosis.

The presence of a rudimentary anterior canine obviously indicates that the specimen had very recently evolved from a stage characterised by more than one canine.

There is no maxillary antrum of any description.

The *transverse* bones are large and contribute substantially to the pterygoid processes, in a manner which appears to be rather Therocephalian-like. They also extend deeply inward between the pterygoids and the palatines, quite unlike the condition normally encountered in the Therocephalia. A peculiar feature is the rather loose articulation of the transverse bone with the palatine, leaving a distinct gap halfway along this contact. This opening can rightly be called the suborbital fossa which is as much closed as in *Aneugomphius*. The position of the opening is, however, quite different. The Therocephalian suborbital fossa is always situated between the transverse bone, the palatine and the pterygoid, but in this specimen the pterygoid is well separated from its border. The condition in the present specimen can nevertheless readily be derived from the basic Therocephalian arrangement, with the foramen having nearly closed, apparently as recently as in *Aneugomphius*.

The *jugals* are firmly gripped anteriorly between the maxillaries, lachrymals and transverse bones. They form solid processes extending outward and backward to form in the normal way ventral borders to the orbits. However, in the present specimen, they do not reach back to meet the squamosals: neither do they contribute to postorbital bars. They taper gradually and terminate freely at a level forward of the position where the postorbital bars normally join the zygomatic arches.

The condition as found in the specimen might be interpreted as artificial, the left arch having weathered away if it had been preserved, while the right arch had broken away before fossilization. (The right side of the skull is otherwise undamaged except for the tip of the postorbital process, and was well enclosed in the nodule. The arch should have been encountered if it had not broken away before fossilization.)

The author is, however, thoroughly convinced that the condition as found is quite natural. These processes terminate at exactly the same level and in exactly the same shape. In the last two or three sections either side, in which they are revealed, it is quite clear that they taper to insignificant proportions, contrary to what is expected at this level where postorbital bars should join. The right should also have shown signs of ordinary damage at the tip of the process had the arch been broken before fossilization. Moreover, the squamosal projections which represent the zygomatic processes also terminate feebly at exactly the same level as one another and they are strikingly similar in shape. They appear in the first sections at their levels as minute crescents of bone, hardly what one would expect to find in a damaged zygomatic arch. Finally, a force which could have caused at least one arch to break off completely before fossilization should also have adversely affected the skull as a whole, but such adverse effects are certainly not apparent in the reconstruction. Prefossilization damage is limited to the internarial bridge, one postorbital process, the loss of one very streptostylic quadrate and the loss of apparently only one stapes.

The *squamosals,* as mentioned under *jugals* above, do not contribute towards the building of zygomatic arches, the condition being interpreted as natural and not artificial, for the several reasons given.

The feeble zygomatic projections have a shape which could only develop, as a product of degeneration, from a Therocephalian-like arrangement. This region could at no stage previously have had the characteristic Cynodont structure already elaborately developed in *Procynosuchus* and *Leavachia* where it has appeciable depth, a pronounced angle above the quadrate and where the dorsal margin leans outward to form a well defined external auditory meatus groove. With a great measure of degeneration the present condition could have developed from the arrangement found in *Aneugomphius* or *Ictidosuchops,* where the dorsal margin of the squamosal leans inward.

The zygomatic process extends freely outward and subsequently forward well above the quadratojugal wedge. The quadratojugal wedge rests on a fold of the squamosal which can be interpreted as an elaboration of the outer border of the elementary external auditory meatus groove. The inner border of this groove is apparent only ventrally where the paroccipital process abuts loosely against it. Dorsally this border is resorbed to an extent where it leaves an aperture leading to a conspicuous space between the tabular and the main body of the squamosal (see *tabulars* above). This main portion is concave posteriorly and convex anteriorly in sagittal section, and extends upward and inward to meet the parietal. The ventral half of this process reaches the pro-otic, but it is not comparable with the rather separate process found in the Scalopsaurids and Whaitsiids, extending below the posttemporal fossa to the pro-otic. In the specimen the posttemporal fossa reaches the temporal vacuity from below this process.

The quadrate wedge is loosely received in a cavity in the anterior face of the squamosal. This cavity is so large that the portion of the bone behind has been reduced to only the elementary auditory meatus groove, while the feeble zygomatic process and delicate quadratojugal support are the only porions extending laterally.

The *quadrate* and *quadratojugal* together form the condyle for the articulation of the lower jaw. Although the sections show them to be separable, they should be looked upon as a unit.

The quadrate forms a horizontal and transversely extending slender, cylinder-like condyle, articulating laterally with a small round condyle formed by the quadratojugal. The latter is perfectly in line with the former and is not indistinguishably fused. Above the transverse cylinder-like quadrate condyle the bone is constricted, but soon it expands again upward to form a rather large wedge lodged loosely in a cavity anteriorly in the squamosal. This wedge is nearly in the sagittal plane. It is shaped like a propellor blade, the lower part extending anteromedially-posterolaterally, while the upper tip is fully in the sagittal plane. The anterolateral surface is concave and the posteromedial surface convex. The anterior margin is straight, blunt and vertical; the posterior margin is sharp and broadly curved.

The groove into which this posterior margin of the quadrate wedge fits corresponds on the posterior face of the skull with the ridge forming the outer border of the external auditory meatus groove. The quadrate wedge penetrates so deeply that the outer border of the meatus groove is virtually resorbed, leaving a rudimentary fold medially and a delicate process laterally. The quadrate wedge is visible in between in posterior view. The lateral process supports the quadratojugal wedge from below, while the zygomatic process of the squamosal anterodorsally apparently served as a check to the forward movement of this wedge. Although the slit into which the quadratojugal wedge fits appears to be rather narrow transversely, it still allows for a maximum swing of the quadrate in anteroposterior direction. The quadrate and quadratojugal are therefore jointly streptostylic.

The quadratojugal wedge is in the shape of a cutlass blade, with a moderately and convexly curved posterior blunt edge, while the anterior edge is sharp, convex in the lower half and concave in the upper half. It terminates dorsally in a very fine point. The blade itself is flat both sides and in cross section it lies truly in the sagittal plane, but in its length it extends parallel to the margin of the occipital crest immediately above (or at an angle of 45° to the horizontal plane). It also extends from the condyle somewhat backward so that the tip comes to lie directly behind (and some distance away from) the tip of the quadrate wedge.

The *stapes,* or a bone which can quite readily be mistaken for the stapes, is present on the right side. It is described under *opisthotics* above.

The *vomer* is typically Procynosuchid, and un-Therocephalian-like in that its ventral margin is not horizontally expanded. Anteriorly the ventral margin is thickened conspicuously enough to suggest reasonably close Therocephalian relationship.

On the whole, however, the vomer is a thin vertical plate with both upper and lower margins distinctly grooved. The groove in the upper margin obviously received the ventral margin of the cartilaginous mesethmoid. The grooved nature of the ventral margin evidently suggests that it found support in the soft tissues that linked the left and right palatal plates.

Anteriorly the vomer rests in a groove on the dorsal side of a median process formed by the premaxillaries. This process splits into separate elongated tapering projections which extend either side of the thickened ventral border of the vomer. From this level the median vertical plate extends freely, with no bony support, through the ventral part of the nasal cavity until it reaches the palatines dorsally to the internal nares and at the level of the posterior borders of the palatal plates. Here the palatines form an inverted V-shaped roof to the internal nares and the vomer firmly lodges itself in this groove. In this region the vomer is broadly expanded from its dorsal margin outward and downward, to overlap the palatines and the anterior ends of the pterygoids ventrally. The vertical plate below rapidly loses height and peters out before reaching the posterior horizontal end of the vomer. The ventral margin of the vertical plate is already elevated well above the palatal plates at a level far forward of the palatal foramina. From the level of the posterior borders of the palatal plates backward the median keel is not grooved along the ventral margin.

The *palatines* contribute much more substantially to the palatal plates than is apparent in ordinary ventral view. Their contributions to the palatal plates extend far forward and sideward above those of the maxillaries. Anteriorly they peter out into very thin films of bone.

It often appears, in a specimen not adequately cleaned, as though the palatal foramina are formed within the suture between the palatines and the maxillaries. In this specimen it is quite clear that these foramina penetrate through the centre of the palatal plates of the palatines, the maxillary plates merely reaching their anterior borders as a result of their broad overlap ventrally. In *Akidnognathus parvus* these openings are almost completely surrounded by the maxillaries, the palatines barely closing them off posteriorly. The whole structure is different, of course, on account of the nature of the elementary "secondary palate" ridges.

Forward of the posterior borders of the palatal plates the palatines contribute subsantially to the side walls of the nasal cavity. Posteriorly these lateral vertical plates turn over inward to form roofs to the choanae. The anterior margins of these roofs are level with the posterior borders of the palatal plates. These margins are not sharp, but considerably thickened to form vertical walls extending transversely and upward, thus presenting with their posterior faces suitable areas for the insertion of the anterior oblique muscles of the eyes.

The posterior borders of the palatal plates are carried backward as two ridges either side, the outer ridge extending to the pterygoid process, while the inner ridge extends to the margin of the interpterygoid fossa. Between the two inner ridges the palatines extend upward and inward over the posterior end of the vomer and the anterior ends of the pterygoids, but they do not quite meet one another on the midline.

The *pterygoids* are strikingly similar to those of *Ictidosuchops*. They are Therocephalian-like, especially as they form between them a large interpterygoid fossa and as they bear at least one tooth each on a rather prominent tuberosity either side between the pterygoid processes. In the Procynosuchids the pterygoids are known to some extent only in *Procynosuchus delaharpeae*. In shape and general disposition there seems to be reasonable similarity, but apparently both the interpterygoid fossa and the tooth-bearing tuberosities are absent. The pterygoids are not known in already described Silphedestid-like forms. In the present specimen the pterygoids are Cynodont-like only in the appreciable length of the pterygoid processes.

The pterygoids meet one another firmly and with broad areas of contact, in front of the interpterygoid fossa, where they contribute to the forming of the dome-like roof to the choanae. Their anterior tips extend forward over the vomer and their joint dorsal margin contains a groove continuous with the groove in the vomer anteriorly. This groove is carried back into the interpterygoid fossa.

At the level of the anterior border of the interpterygoid fossa the pterygoids form large Therocephalian-like tuberosities bearing at least one tooth each, a condition also reminiscent of that found in *Aneugomphius*. More laterally the pterygoids form conspicuously long processes guiding the lower jaw.

Either side of the interpterygoid fossa the pterygoids are continued backward as massive processes with deeply concave ventrolateral surfaces. The ventromedial edges contributing to the borders of the interpterygoid fossa are very thick, in contrast with the dorsolateral edges, bent downward sharply, which are very delicate indeed. At the level of the internal carotid foramina the margins of the former terminate abruptly and the pterygoids are continued backward only by the latter margins, forming the characteristic quadrate processes. These processes maintain their general breadth and thickness throughout; at no point do they lend any significant support to the alisphenoids. In this specimen, however, the quadrate processes do not make contact with the quadrates, but turn abruptly inward level with the latter to cover the pro-otics dorsolaterally. This arrangement has not yet been encountered in other Therapsids, but it may be due to inadequate preparation, preservation or investigation.

The projections tending to close the interpterygoid fossa posteriorly are in loose contact with the basisphenoid and the general articulation is strongly suggestive, as in the Scaloposaurids, of a recent loss of kinetism. This circumstance is supported by the grooves in the parietals into which the dorsal margins of the pro-otics fit very loosely, and the still inadequately ossified dorsal part of the supraoccipital.

The *alisphenoids* are Cynodont-like in being broadly expanded, but Therocephalian-like in their feeble overlap of the pro-otics. Their anteroventrally directed pterygoid processes are long and broad. They swing inward underneath the rostrum, barely touching the basisphenoid, and terminate loosely above the basisphenoid process of the pterygoids. Their terminal margins reach towards crests rising upward from the borders of the interpterygoid fossa, that is, from the medial margins dorsally of the basisphenoid processes of the pterygoids. The rest of the ventral margins of the alisphenoids conform very well with the dorsal margins of the quadrate processes of the pterygoids, but nowhere is there any real contact.

The anteroventral processes of the alisphenoids had evidently lifted away from the basisphenoid processes of the pterygoids. The natural condition must have been the same as that encountered by Broom (1938) in *Procynosuchus delaharpeae*.

The anterior margins of the alisphenoids are very thick. The alisphenoids broadly overlap the parietals dorsally, peculiarly enough, on the outside. How natural this condition is can only be judged in terms of the distortion the skull had suffered, which is exceptionally negligible.

In spite of the difference in the extent of expansion, there is far greater similarity between the alisphenoids of this specimen and those of *Ictidosuchops,* than with those of *Procynosuchus delahapeae.*

The *orbitosphenoids* are very delicate thin plates of bone. They have been pushed out of their normal positions, both lying against the ventral surface of the left frontal and protruding from the brain case in front of the left alisphenoid. They might have suffered some additional damage and it is consequently inadvisable to evaluate them with any degree of confidence. If the two flakes actually do represent the complete bones, the arrangement is different from that encountered in higher Cynodonts like *Diademodon* (Brink, 1955). They could then not have formed a well enclosed chamber with the frontals above, to accommodate the olfactory lobes. Apparently they merely represented platelike ossifications of the sides of the otherwise normal trough-shaped cartilaginous orbitosphenoids, an indication of some degree of immaturity.

The *basisphenoid-parasphenoid* relationship is rather clear. The basisphenoid is a distinct continuation forward of the basioccipital, with which it appears to be already well fused as no suture was encountered. It grows narrower forward but expands again laterally across the internal carotid foramina, actually as two separate left and right swollen projections. These projections have delicate contacts above with the anteroventral processes of the alisphenoids and are very loosely touched ventrally by the basisphenoid processes of the pterygoids. Between them the parasphenoid passes upwards to form the rostrum. The internal carotid foramina are canals passing upward between the anterolateral lobes of the basisphenoid and the parasphenoid keel.

The parasphenoid covers the basisphenoid ventrally and laterally, the anterolateral lobes of the latter being the only parts visible in ventral view. Before passing upwards as the rostrum, the parashpenoid forms a short pointed keel very shortly behind the internal carotid foramina. The rostrum extends upward and forward well above the interpterygoid fossa, no doubt to support the orbitosphenoid structure and the brain behind the olfactory lobes.

The rostrum is V-shaped in cross-section, the V becoming larger and deeper backward. Shortly after the groove reaches the basisphenoid it suddenly becomes much deeper, much wider, more U-shaped, and drops to a lower level. This part is the sella tursica, but the dorsum sellae which is prominent in higher Cynodonts is conspicuously absent. There is a casual rise in the level of the floor, where the lateral border ridges also disappear, in the position of the dorsum sellae. Farther back the floor of the brain case is quite flat, where it widens to the level of the vestibules. The pro-otics have casual contact with the margins of this part of the basisphenoid.

Structure of the Lower Jaw

The *dentaries* are conspicuously short. They barely reach the level where the postorbital arches should be but, peculiarly enough, the coronoid processes are very well developed, better than in the Procynosuchids. They are bent upward more sharply and there is a more distinct angle posteroventrally, features in which this animal contrasts sharply with the Silphedestids. It is difficult to appreciate why these coronoid processes are so well formed, because they are too far forward for the effective attachment of the jaw muscles. This is especially surprising considering the absence of the jugal arches.

Apparently the temporal muscles operate the parietals and the surangulars, while the masseters, extending from the outer surfaces of the coronoid processes to the jugal processes evidently played a very minor role, perhaps largely effecting an antero-posterior movement of the jaw. There could not have been an effective remnant of the levator mandibulae. The degastricus muscles were inserted on the angulars, with the reflected laminae penetrating them in the direction of their pull.

Another conspicuous feature about the dentaries is the very high symphysial region, with a distinctly angled, almost Gorgonopsia-like "chin". This feature suggests that the unusually large lower canines are an established characteristic of the animal.

The four incisors either side are nevertheless very small. They increase in size from the first to the fourth. None of the incisors showed signs of replacement, neither did the large canines except for one very small bud medially to the left tooth. The post-canines, on the contrary, are being replaced in a more prolific manner than the upper cheek teeth. Not only were tooth buds encountered with every tooth; in the case of the fourth tooth on the left side and the second, fifth and ninth teeth on the right side, the successors had erupted quite far, while the predecessors are still functional.

The *splenials* are not rod-like as in higher Cynodonts. They are flat strips of bone with their ventral margins slightly heavier than the dorsal margins. The former margins closely accompany the ventral margins of the dentaries, while the latter margins reach from halfway to the alveolar border anteriorly, to nearly within reach of it at the tenth tooth.

Anteriorly the splenials contribute substantially to the symphysis. From behind the symphysis they cover a well excavated groove on the medial side of each dentary, which run rather close to the ventral borders of these bones in comparison with the condition in higher Cynodonts. These grooves grow larger backward and in the posterior halves of their lengths they accommodate the anterior ends of the angulars. The splenials cover these anterior pointed ends of the angulars and extend backwards below them to just beyond the margin of the dentary. Above the angular tips they cover small corners of the coronoids.

The *coronoids* are small plates of bone lying immediately behind the last post-canine teeth on the inside of the coronoid processes. With the lower jaw closed, they slide against the outer faces of the pterygoid processes. They cover the anterior ends of the surangulars and prearticulars and are themselves covered very briefly over their anteroventral corners by the splenials.

The *surangulars* are flat plates of bone extending in arch-like fashion from the coronoid processes to the articulars. Each bone is properly boomerang-shaped, not only where the posterior half extends at an angle to the anterior half, but also where the two blades are not in the same plane. The anterior blade is nearly in the vertical plane while the posterior blade leans with its dorsal margin outward. The outer surface of the posterior blade is concave. Far back a ridge arises in the middle of the inner face, tending to cover the articular dorsally.

From behind the margin of the dentary the surangulars have rather strong dorsal margins. The ventral margins are very sharp.

The *angulars* are peculiar in that they fulfil three different functions. Consequently each bone consists of three contrastingly different parts. The most important part forms a stem which carries the dentary. It is projected forward as a long tapering process lodged firmly in the mental canal. Its dorsolateral surface is deeply troughed so that the mental canal is not properly filled by this process. The process is covered posteriorly by the prearticular and anteriorly by the splenial, but the mental foramen is left as a gap between these bones.

The second almost equally important part of the angular bone is a wide fan-like plate extending backward across the outer faces of the articular and the surangular. It serves to strengthen the rather delicate structure of this post-dentary region. It has a thick ventral margin accompanying the articular and a sharp dorsal margin where it broadly overlaps the surangular.

The third portion forms the characteristic reflected lamina with its peculiar Z-shape in cross section. The function of this lamina is obscure. It developed probably as a "reaction" to the substitution of the digastric muscles for the depressor mandibulae.

In this form the reflected lamina is smaller than in the Procynosuchids. They project more outward and downward, leaving substantial spaces between them and the fan-like posterior portions.

The *prearticulars* are elongated plates continuous with the anterior ends of the articulars. Their slightly expanded anterior ends penetrate below the coronoids, where they overlap the tips of the surangulars.

The *articulars* increase substantially in breadth backward, from where they join the prearticulars to where they form broad surfaces for articulation with the quadrates. These surfaces slope downward medially and extend convexly in approximately an anterior-posterior direction. The central parts of the articulation areas are slightly depressed to correspond with a slight swelling in the rod-like quadrate condyles.

There is a short process directed ventrally at the posterior end of each articular bone.

Relationship

For a proper evaluation of the relationship of this interesting form it is best to summarise its characteristics and peculiarities while classifyng them into various relevant categories. Firstly its Therocephalian-like features are balanced against its Cynodont-like features. Thereafter its proximity to the Procynosuchids or the Silphedestids is tested against lists of relevant characteristics. An endeavour is made to list the various items roughly in the order of their significance, but this order is somewhat prejudiced in favour of structural continuity.

A. *Therocephalian-like features.*

1. The interpterygoid fossa is perhaps the most striking Therocephalian feature. It is comparable in almost every detail with that of the Ictidosuchid-Scaloposaurid branch of the Therocephalia. It is absent in the Procynosuchids and all later Cynodonts but unfortunately the condition is not known in the Silphedestids.

2. The posorbital arches are evidently incomplete. This is a striking Scaloposaurid characteristic, but it is also found in the Silphedestids.

3. The zygomatic arches are interpreted as incomplete. If this interpretation is incorrect, the alternative is very delicate Scaloposaurid-like arches, most unlike the Cynodont type. However, incomplete arches are found in the Silphedestids. This condition could only develop from a Scaloposaurid-like arrangement.

4. The tooth-bearing tuberosities of the pterygoids are typically Scaloposaurid. This condition is not found in any Cynodont described so far. The region is, however, unknown in the Silphedestids.

5. Besides the interpterygoid fossa and the tooth-bearing tuberosities the general build of the pterygoids is more Therocephalian-like than Cynodont-like.

6. The transverse bones contribute rather substantially to the pterygoid processes. This is not very apparent, as the portions formed by the pterygoids are very elongated in the Cynodont manner.

7. The parasphenoid keel and rostrum is very similar to those of the Scaloposaurids and quite different from the condition in the Procynosuchids or later Cynodonts. This region is not known in the Silphedestids.
8. The sella tursica is not deeply excavated and the dorsum sellae is consequently weakly developed.
9. The posterior face of the skull is Therocephalian-like in general build, especially in the shallowness of the occiput and external auditory meatus areas. The occipital crests are low and not very sharp.
10. The paroccipital processes are short and slender. The Cynodont paroccipital is rather long and heavily built.
11. The squamosals have a feeble structure in the region of the quadrates.
12. The parietal region is not sharply crested. It is very like the Scaloposaurid condition, but a similar arrangement is found in the Silphedestids.
13. The pineal is situated far back.
14. There is a weak overlap between the alisphenoid and the pro-otics. While the alisphenoids are broad as in the Cynodonts they are in height more comparable with the Therocephalia.
15. There is no naso-lachrymal contact, a rather pronounced Therocephalian feature.
16. The prefrontals tend to broaden the antorbital region as in the Scaloposaurids.
17. It is not clear whether the frontals contribute to the orbital borders. If they do, which is just possible, this would be a significant Therocephalian feature.

B. *Cynodont-like features*

1. The cleft secondary palate is very typical of the type found in the Procynosuchids and Galesaurids. This type of palate is found nowhere in the Therocephalia. In spite of the long list of Therocephalian features given above, this characteristic alone is sufficient for reaching the conclusion that the specimen is a Cynodont. It is most unfortunate that the Silphedestid palate is not known.
2. The postcanine teeth are cusped in the typical Procynosuchid fashion.
3. The occipital condyle is Cynodont. It is more deeply crescent-shaped, presenting two more distinctly separate exoccipital condyles, than in the Procynosuchids.
4. The lower jaw symphysis is very advanced Cynodont-like.

5. In spite of their size the dentaries form good coronoid processes of rather advanced Cynodont shape.
6. The alisphenoids are very broad.
7. The pterygoid processes are very elongated.
8. The posttemporal fossae are small and they cause no serious excavation of the posterodorsal surfaces of the paroccipital processes. These processes also form feeble roofs to the middle ears.
9. The suborbital foramen had closed nearly completely.
10. If the frontals are actually excluded from the orbital borders, this circumstance can be taken as a good Cynodont feature.
11. The bone interpreted as quite likely a stapes has a stapedial foramen.

C. *Procynosuchid and un-Silphedestid-like features*

1. The secondary palate is similar in every respect to the type found in the Procynosuchids.
2. The vomer agrees perfectly with the Procynosuchid arrangement. It is not known in the Silphedestids.
3. The double exoccipital condyles appear to be even more advanced than in *Procynosuchus*.
4. The dentaries are short but with distinct coronoid processes.
5. The manner and extent of tooth replacement is similar to that found in the type of *Procynosuchus delaharpeae*.
6. The pterygoid processes are significantly elongated.
7. There is no significant suborbital fossa.

D. *Silphedestid and un-Procynosuchid-like features*

1. There are no zygomatic arches.
2. The postorbital bars are incomplete. The Silphedestid postorbitals are, however, apparently larger and do not form significant postorbital processes.
3. The interparietal crest is absent and the region is rather broad. The position of the pineal is not known in the Silphedestids.
4. The Silphedestid occiput appears to be comparable with that of the present specimen.
5. There is no naso-lachrymal contact.
6. The squamosals have a delicate build in the region of the quadrates.

E. *Features both un-Procynosuchid and un-Silphedestid*

1. The dental formula is different from both in that there are 7 incisors and one canine.
2. The highly placed and weakly developed premaxillaries are peculiar.
3. The depth of the symphysis is also unique for so early a Cynodont.
4. The anterior incisors are smaller than the posterior ones, an arrangement which is foreign to the Therocephalia and Cynodontia as a whole.
5. The canines are very large.
6. The parietal region is not constricted behind the pineal.
7. The height of the alisphenoid and the extent to which they overlap the parietals laterally is also rather peculiar.

The above analysis makes it unmistakably clear that the present specimen is a Cynodont, but one which has retained a remarkable number of Therocephalian characteristics. In fact, disregarding for a moment its few advanced characteristics like the loss of the anterior canines and the incomplete zygomatic arches and postorbital bars, this specimen can be taken as a form representing the stage where the Cynodont branch actually diverged from the Ictidosuchid-Scaloposaurid branch of the Therocephalia. The divergence must have taken place at the lower Ictidosuchid level, as both structure and age tend to suggest.

When the advanced features are taken into consideration it is clear that the present form had made some progress away from the level of origin, as the Scaloposaurids had progressed beyond the Ictidosuchid stage. It is interesting to note the similar changes occurred along both lines; the loss of anterior canines and the reduction of the postorbital and zygomatic arches.

It is also sufficiently clear from the above analysis that the present specimen is more at home with the inadequately known Silphedestids than with the Procynosuchids. However, the palate suggests that there is close affinity between these families, the Procynosuchids having specialized very early away from the Silphedestid line, as had the Bauriidae diverged from the Scaloposaurid line.

It is rather apparent that the "Silphedestids" actually represent more than one family. *Protocynodon* is a member of this branch, a form which appears to be structurally more primitive, but it is more recent in time than *Scalopocynodon*. *Silphedestes* and *Silphedocynodon* are also later forms and the branch apparently continued into the Cynognathus zone. No doubt, while the already described Silphedestids may represent more than one family, the present *Scalopocynodon* may represent yet another family.

The present investigation has made it eminently clear that the "Silphedestids" are not assignable to the Scaloposaurids as suggested by Watson and Romer (1956). In their classification they put the "Silphedestids" with the Scaloposaurids, thereby suggesting that although they are earlier in time, they are advanced forms, even if this is apparently based only on the extent of their degeneration. In all fairness it should, however, be noted that Watson and Romer did not know of a Silphedestid-like form with a Procynosuchid-like palate. Although the palate is unknown in the already described Silphedestids, their temporal regions are sufficiently comparable with that of *Scalopocynodon* to permit their transfer back to the Cynodontia, to conform with the classification suggested by Haughton and Brink (1954).

Watson and Romer (op. cit.) are also inclined to doubt whether the absence of the postorbital bars and zygomatic arches is natural. They suggest that the condition is due to damage. With these small specimens it is difficult to arrive at a definite conclusion either way; one can merely describe what the specimens tend to convey. However, for the several reasons mentioned above, the author is convinced that the absence of postorbital bars and zygomatic arches is the natural condition in *Scalopocynodon*. If it can be demonstrated that the already described "Silphedestids" actually had close affinity with *Scalopocynodon*, their missing arches might not be quite as artificial as Watson and Romer are inclined to believe.

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