THE PRIMITIVE CYNODONT *PROCYNOSUCHUS*: FUNCTIONAL ANATOMY OF THE SKULL AND RELATIONSHIPS

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[Plates 1–3]

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An acetic acid prepared skull of the Upper Permian Karroo cynodont *Procynosuchus delaharpeae* Broom is described and an attempt is made to interpret its anatomy in functional terms.

The dentition is adapted for an insectivorous habit with an incipient form of tooth occlusion between specific upper and lower postcanines. A specialized form of tooth replacement ensures that the posterior postcanine teeth remain functional for as long a period as possible. The adductor jaw musculature shows a masseter-like muscle between the zygomatic arch and the lateral surface of the angular bone, in addition to the large temporalis muscle which has invaded the lateral face of the coronoid process. The possibility of a monotreme-like detrahens muscle rather than a reptilian depressor mandibuli being present for jaw opening is suggested. The quadrate is moveable.

The anatomy of the internal nares indicates that an arrangement of Jacobson's organ and associated nerves, blood vessels and glands comparable to that of monotremes was present. Interpretations of the various foramina of the snout are presented. Fleshy lips were probably present but the skin over the dorsal surface of the snout was tightly applied.

The venous system of the head involves reduction of the vena capitis lateralis and the development of emissary veins comparable in general to those of mammals. The brain is comparable in size and relative development of its parts to that of living primitive mammals. There was incipient development of a monotreme-like membranous anterior lamina of the prootic.

The stapes had a mechanical rôle associated with the moveable quadrate, in addition to its sound conducting rôle. It may have been capable of transmitting low frequency sound from the lower jaw as well as higher frequency sound from a tympanic membrane.

The more advanced, Triassic cynodonts form a monophyletic group, of which *Procynosuchus* is the sister-group. The archaic but highly specialized *Dvinia* is the sister-group of all other known cynodonts.

INTRODUCTION

As the group of mammal-like reptiles from which the mammals are almost universally believed to have evolved, the cynodonts are of particular interest to evolutionary biologists. The earliest known and most primitive forms are of Upper Permian age and the first to be discovered was the Russian *Dvinia prima*, which, along with the synonymous *Permocynodon sushkini* was reported briefly by Amalitzky in 1922. Subsequently Tatarinov (1968) has redescribed it in detail, demonstrating a number of primitive features but also a highly specialized dentition. Broom (1937, 1938) described a series of forms from the Beaufort Beds of the Karroo of South Africa, which occurred in what is now termed the *Daptocephalus* zone (Kitching 1977). Although originally described as several genera and species, Hopson & Kitching (1972) concluded that they are all members of the single species *Procynosuchus delaharpeae*, including the forms widely known as *Leavachia duvenhagei*. Tatarinov (1968) placed *Dvinia* and *Procynosuchus* in separate families within the superfamily Procynosuchoidea, but Hopson & Kitching have preferred to retain the two genera in a single family Procynosuchidae.

A further related form is *Parathrinaxodon proops*, described by Parrington (1936) from the anterior threequarters of a skull which he collected in the Kawinga Formation of the Ruhuhu Valley, Tanzania. It is usually regarded as a procynosuchid, although van Heerden (1976) has suggested that it may be a member of the more advanced family Galesauridae. The Galesauridae are largely restricted to the basal Triassic *Lystrosaurus* zone of South Africa, but

Cynosaurus suppostus from the *Daptocephalus* zone is evidently a member of this family (Hopson & Kitching 1972).

The external features of *Procynosuchus* have been described in detail by Brink (1963, as *Leavachia*) and a certain amount of the internal structure is known from the serially ground specimen of '*Scalopocynodon*' described also by Brink (1960). Mendrez (1972) has described the dentition of the probably synonymous *Cyrbasiodon* and, in the course of a general survey of the cynodont jaw articulation, Crompton (1972*a*) attempted a reconstruction of this region of *Procynosuchus*. Knowledge of the postcranial skeleton of procynosuchids is restricted to Broom's (1948) rather superficial account of '*Leavachia*', and a very short note by Konjukova (1946) mentioning some postcranial bones of *Dvinia*.

The single specimen of *Procynosuchus delaharpeae* which forms the basis of the present work consists of a virtually complete skull, lacking only the left quadrate complex and the right premaxilla. It is associated with a near complete postcranial skeleton. It was collected in 1974 from the Madumabisa Mudstones of the Middle Luangwa Valley of Zambia, at field locality 2b (Kemp 1976) and has the field number TSK 34. The Madumabisa Mudstones are regarded as equivalent to the *Daptocephalus* zone of the Beaufort Beds of the South African Karroo, and indeed the very presence of *Procynosuchus* supports this interpretation.

The specimen occurred as a much-fragmented calcareous nodule, along with pieces which had weathered out before collection. The material responded well to acetic acid preparation and the individual pieces were prepared separately. Further information about the internal structure of the skull was revealed by cutting some of the pieces with a 'Lastec' wire saw, after preparation. A soft, reddish deposit remained over much of the specimen (and also filled cracks and the spaces of the Haversian system of the bone), but could be cleaned off with fine brushes and acetone. The substance has since been identified as the zeolitic mineral Heulandite, and its deposition is probably a post-fossilization event associated with the extensive hot-spring activity of the Luangwa Valley (K. C. Davies, personal communication).

It was originally intended to deal with the whole skeleton in a single publication. However, so much detail requiring biological interpretation has emerged that it seemed expedient to publish an account of the skull at this stage. Work on the postcranial skeleton is in progress and this, along with a general discussion of the palaeobiology of *Procynosuchus*, will constitute the second part of the study.

The aim of the following account is primarily to explain the anatomy in terms of its immediate functional significance to this particular animal, and the arrangement of the descriptive parts is designed to serve this end. It is hoped that a straight-forward, anatomical description is implicit in the figures and plates. Comparison with other fossil and living groups is largely restricted to where this aids the functional interpretations offered.

General description†

The skull is very well preserved and the only regions missing are the right premaxilla and the left quadrate and quadratojugal, although weathering has affected the extreme right posterolateral region and the occipital condyle. The whole skull has suffered moderate distortion towards the right hand side, enlarging the left and reducing the right temporal fenestrae and orbits, and causing the muzzle to be skewed.

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† See figures 1–3, and figures 19–21, plates 1–3.

The overall length of the skull is 110 mm and it is therefore within the range of sizes known for *Procynosuchus delaharpeae*. The muzzle is relatively long and slender and the dorsal surface rounded, with the large external nares facing more laterally than forwards. The slender internarial process of the premaxillae separating the nares is perfectly preserved.

Between the orbits, the skull roof is flat; the orbits themselves face dorso-laterally. The intertemporal region is in the form of a well developed, sharp sagittal crest formed from the very deep parietals, which are continuous with the epipterygoids ventrally. The dorsal edge of the

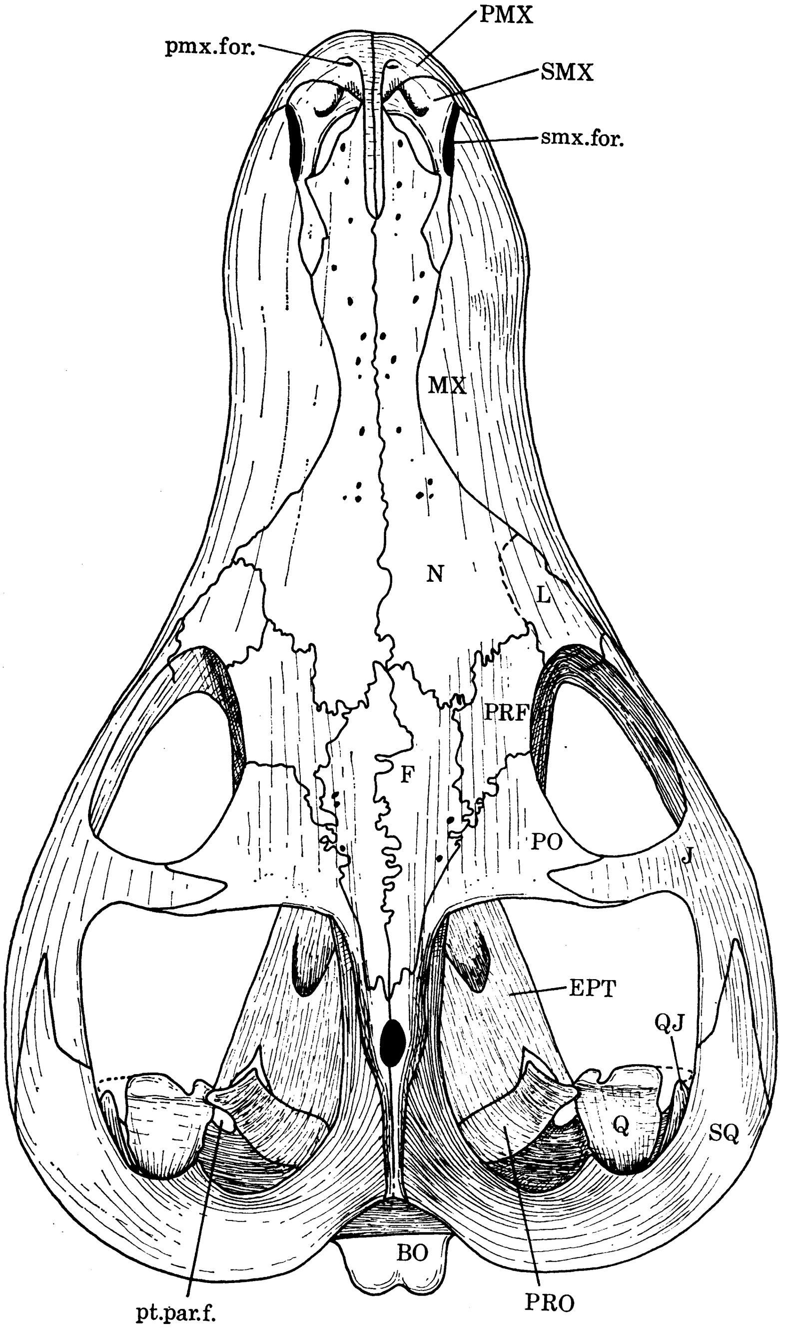

FIGURE 1. Skull reconstruction in dorsal view. (Magn. × 1.5.)

sagittal crest appears to be quite undamaged, and it lacks a dorsal extension so that the midline of the skull roof is a straight line (figure 3*a*). A very large pineal foramen is present.

The occiput is almost vertical and the squamosals show only a very limited posterior flaring, barely exceeding the level of the occipital condyle. The condyle itself is badly preserved but appears to have been double. The zygomatic arch rapidly attenuates from its connection with the occiput and is very narrow compared to later cynodonts. It does not flare laterally to any great extent.

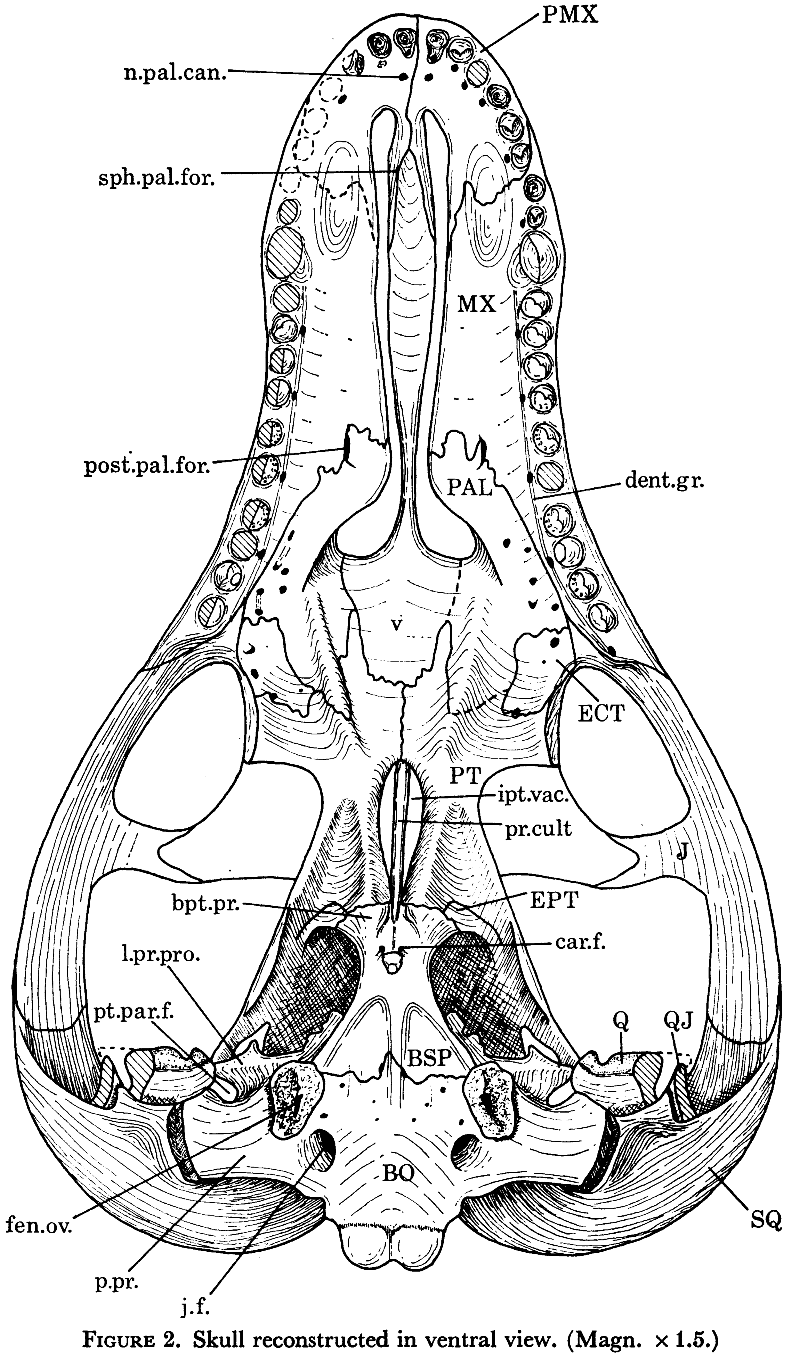

FIGURE 2. Skull reconstructed in ventral view. (Magn. × 1.5.)

In palatal view, the paired secondary palatal plates of the premaxillae, maxillae and palatines are fairly widely separated from one another in the midline. Behind them, the central area of the palate is bounded by a pair of pronounced ridges running postero-medially and defining a shallow mid-palatal vault. The lateral pterygoid flanges are very well developed. As in all typical primitive theriodonts, the base of the braincase is powerfully built, with the parasphenoid expanding broadly. The paroccipital processes are long and stout.

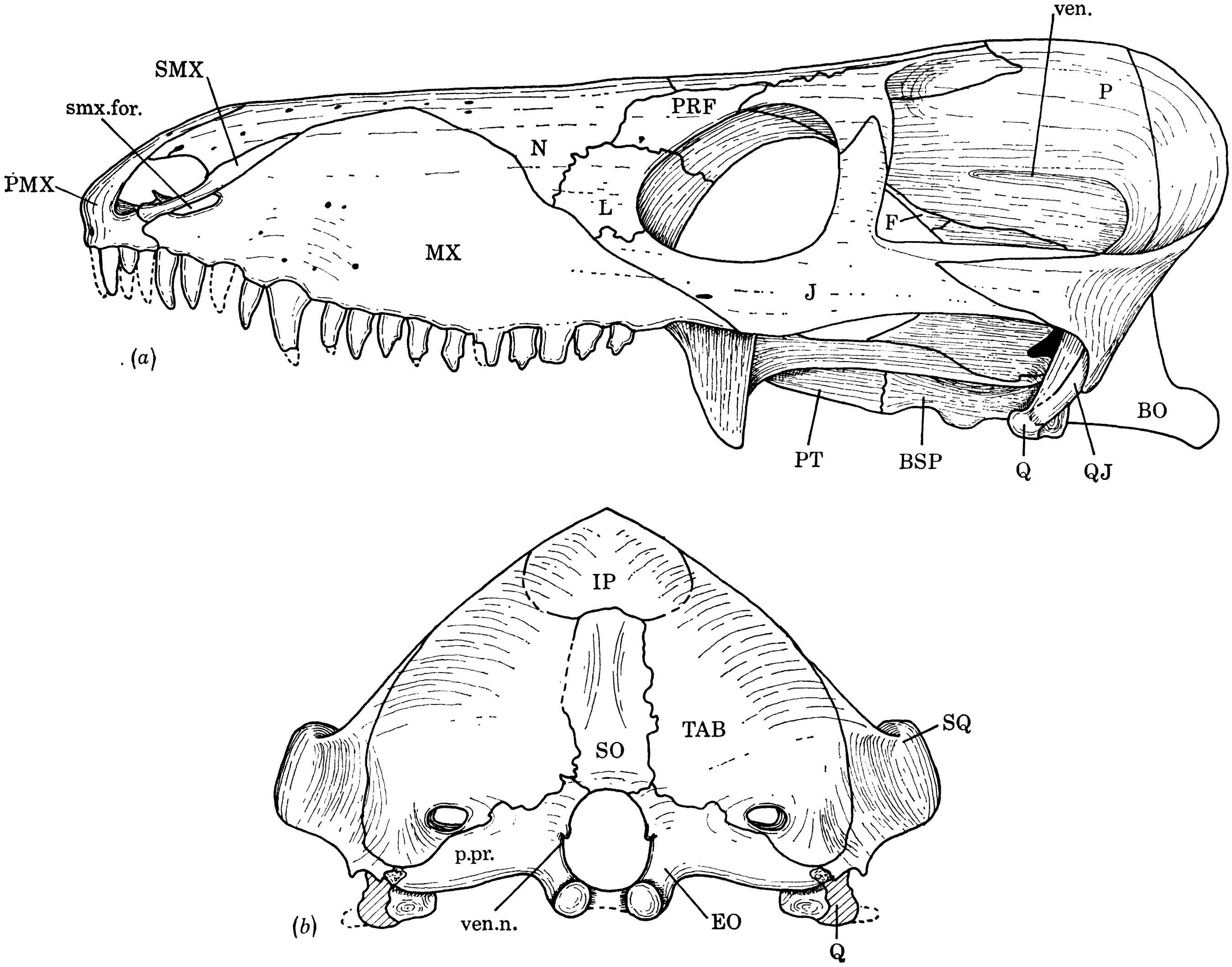

FIGURE 3. Skull reconstructed in (a) lateral view; (b) posterior view. (Magn. × 1.5.)

THE FEEDING APPARATUS

1. *The dentition*

Description

The complete postcanine dentition of all four tooth rows is preserved, although that of the upper right side has suffered from weathering laterally. The anterior regions are less well represented. The right upper side has only the empty alveoli of the first three incisors, the base of the last precanine and the base of the canine preserved. The left upper side has the complete dental margin but teeth are missing from positions 1, 4 and 7, and only the base of the tooth in position 3 remains. Incisor 2 is displaced from its alveolus. Both the lower precanine regions are intact but that of the left side lacks teeth altogether and that of the right is missing the first incisor.

The upper left dentition consists of five incisors within the premaxilla, an incisiform tooth whose alveolus is formed from the premaxilla internally and the maxilla externally, two incisiform teeth within the maxilla, a canine, and ten postcanine teeth. As the distinction between an incisor and a precanine rests on whether a tooth is housed in the premaxilla or maxilla, no unambiguous dental formula can be given in this case. The upper right dentition probably had the same arrangement of teeth and certainly there are ten postcanines. The dental formulae of the left and the right lower jaws differ from one another. That of the right dentary (figure 6) is four incisors, a canine, and thirteen postcanines. However the left dentary bears four incisors, a canine and positions for twelve postcanines, although two of these positions consist of alveoli lacking teeth, and temporarily plugged by bone pending the eruption of replacement teeth (figure 4). The tooth which is apparently completely missing on the left side is probably the first postcanine which has been shed but not replaced, as discussed below.

The form of the lower incisors is shown by the perfectly preserved second right tooth. The base of the crown is oval and set obliquely to the line of the jaw, and the crown tapers gradually to about halfway up, at which point there is a slight medial swelling. The distal part of the crown above the swelling curves posteriorly and bears two sharp, very finely serrated ridges along the antero-medial and postero-lateral edges, which run right to the sharp tip of the tooth. The bases of the two next posterior incisors are set almost perpendicular to the line of the jaw, and the orientation of the empty alveoli of the left jaw indicates that the lower incisors were somewhat procumbent. Of the upper incisiform teeth only the fifth, sixth and eighth on the left side are both present and well preserved. They show the same general form as the lower incisors but are more robustly built. The long axes of their oval bases all appear to be aligned antero-posteriorly and the teeth are perpendicular to the plane of the palate rather than procumbent. The lower canine is only present on the right side and is badly damaged. The base is oval in section and set antero-posteriorly. Only the tip of the crown is preserved, which shows a posterior curvature and sharp anterior and posterior ridges much like those of the incisors. The upper left canine is well preserved but lacks the tip. Like the lower canine, it has a longitudinally oriented oval base and sharp anterior and posterior ridges, and the whole crown curves backwards. It is somewhat larger than the lower canine.

The postcanine teeth of both the upper and the lower jaws are of two distinct types (figure 4), a relatively simple anterior type (A-type) and a more complex posterior type (P-type), which closely resemble the teeth of the procynosuchid referred to *Cyrbasiodon boycei* and described by Mendrez (1972). The A-type teeth are not unlike the incisors, with the crown rising to a medial swelling halfway up, from where two sharp ridges run up the crown to the very sharp tip. The crown curves posteriorly and the ridges are aligned along the antero-medial and postero-lateral margins so that the tooth may be described as 'facing' postero-medially. The more posterior A-type teeth tend to develop an incipient cingulum in the region of the medial swelling, in the form of a faint ridge beginning from the anterior ridge and crossing the medial swelling to the posterior ridge. It differs from a fully expressed cingulum in lacking cuspules and in its connection to the anterior ridge being nearer to the tip of the tooth than is its connection to the posterior ridge. The upper and the lower A-type teeth are similar but the uppers are slightly more heavily built. The P-type teeth have a well developed cingulum running horizontally round the lingual face of the tooth, about halfway up the crown, bearing from five to eight sharp cuspules. The anteriormost and posteriormost cuspules lie at the bases of the respective anterior and posterior ridges running up the edges of the large, sharp-pointed main cusp. They appear in lateral view as very small accessory cusps. The main cusp curves lingually to a small extent. Again, the upper and lower versions of the P-type teeth are virtually identical in form.

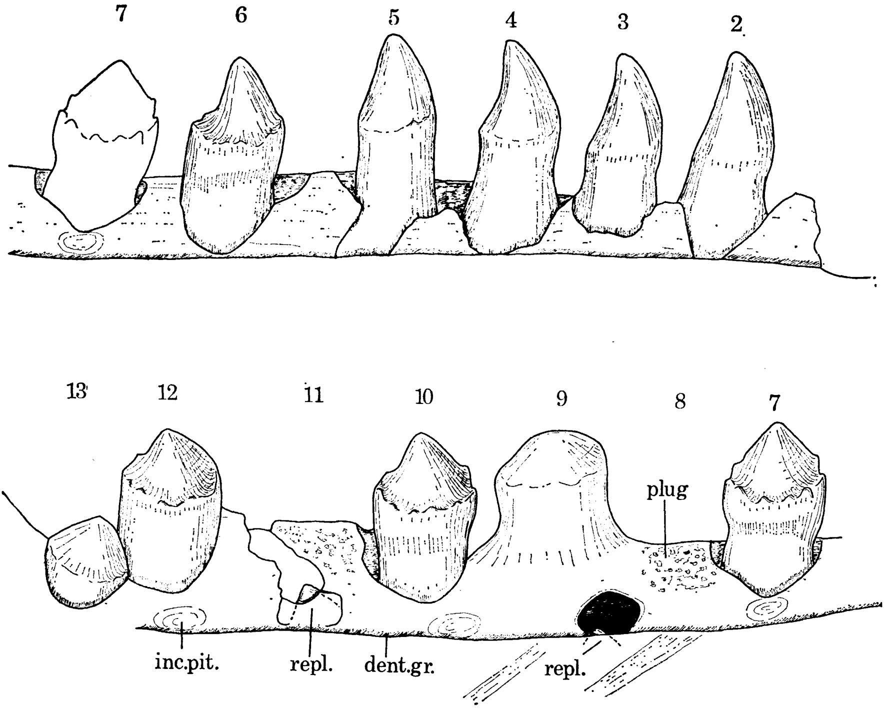

FIGURE 4. Lower left postcanine teeth in medial (lingual) view. The numbers refer to the tooth positions as interpreted in the text, and assuming that the first postcanine has been shed but not replaced. Based on a camera lucida drawing. (Magn. approx. × 4.)

Because the more posterior A-type teeth tend to develop an incipient cingulum, the transition along the tooth row is not strongly marked, certainly nothing like that described for *Dvinia* (Tatarinov 1968). Indeed there is a definite gradient of increasing complexity of tooth form from front to back in the A-type teeth. The upper and lower fourth left postcanines for example have discernible cingulum cuspules anteriorly and posteriorly, although not in the middle region and they may perhaps be described as transitional in form. The number of A-type teeth differs between the tooth rows, with four in both the upper and lower left sides, five in the lower right jaw and only three in the upper right (although the fourth upper right is rather simpler than the other P-types), a point discussed later.

The orientation of the individual teeth within the jaws shows a sharp transition for, with reference to the two ridges on the main cusp and the curvature of the cusp, the more anterior teeth 'face' postero-medially while the teeth behind 'face' medially. The change does not correspond with the change from A-type teeth to P-type teeth because in the case of both the lower jaws (figure 4) and the left upper jaw, the last of the postero-medial facing teeth is actually the first P-type, while in the right upper jaw it is the last A-type tooth.

Tooth replacement

Very active tooth replacement of a basically alternating type like that studied extensively in *Thrinaxodon* (e.g. Parrington 1936; Osborn & Crompton 1973) is manifest. The cycle of replacement of the posterior postcanine teeth is illustrated by a sequence of teeth in the lower left jaw (figure 4). The first stage is that of the sixth postcanine (interpreted as morphologically postcanine 7, as discussed below) with its cingulum cusps distinct but slightly worn and with a small, shallow depression in the dental groove, immediately lingual to the crown, marking the incipient development of a replacement crypt. The next stage is shown by the seventh extant postcanine (morphologically postcanine 9), where the medial edge of the alveolus has grown up around the base of the crown and become synostosed with it. The crown itself is severely worn, with the cingulum abraded off and the main cusp very low and blunted. A large replacement crypt opens from the dental groove, medial to the tooth, into a large cavity beneath the crown, from where the root of the tooth has already been resorbed. The crown of a small replacement tooth lies within this cavity, below the level of the jaw margin. Between the extant eighth and ninth postcanines (morphologically the site of postcanine 11) no crown is present and the alveolus is roofed over by a thin layer of rugose bone forming a plug. A break in the plug has exposed a replacement crown within the alveolus, further developed than that of the previous case and presumably soon to erupt. The next stage occurs in the last, tenth extant tooth position which is occupied by a half erupted postcanine tooth. No replacement crypt is present in the dental groove. Finally the eighth extant postcanine tooth (morphologically tooth 10) shows a young, fully erupted tooth with the main cusp, cingulum cusps and ridges sharp and well defined, and the medial wall of the alveolus low around the base of the crown. There is no replacement crypt, although a very faint, small depression in the dental groove indicates its future position.

Thus the cycle of posterior postcanine tooth replacement appears to consist of the wall of the alveolus growing up around the base of the crown and fusing with it to support it. The root is then resorbed. This is followed by growth of the bone into the crown from the walls of the alveolus and consequent shedding of the old crown and protective blocking of the alveolus. Meanwhile, a replacement tooth starts development in the replacement crypt in the dental groove, moves laterally into the alveolus, and finally erupts through the bony plug. It seems likely that this method of replacement allows the retention of a functional crown for a greater percentage of the time than would be the case if the whole tooth, including its root, were shed, as well as representing a saving of calcium phosphate.

The anterior postcanine teeth do not appear to have been replaced by the same mechanism, for there are no examples of synostosis of the alveolar wall with the tooth. Replacement pits in the dental groove are present medial to postcanines 2 and 4 in both the upper jaws, and postcanine 5 in both the lower jaws (in the case of the left lower jaw, this is the fourth extant postcanine, figure 4). Incipient pits are present medial to the other postcanines. Active tooth replacement is therefore in progress, but although there is some rather irregular variation in the height of the alveolar wall around the teeth, there appears to have been no plugging and root reabsorption. The anterior postcanines were less important in the feeding mechanism (and less subject to wear), and therefore the mechanism of synostosis and root reabsorption to decrease the time that an alveolus remained empty was unnecessary.

Replacement of the incisiform teeth also appears to have been simple, since again there is no indication of synostosis of the crown and alveolus, or of plugging of the alveolus. Replacement teeth, when present, lie immediately lingual to the base of the crown in a replacement crypt confluent with the alveolus rather than separated from it by a bony wall.

The overall pattern of replacement is more or less alternate but does not show a rigorously accurate pattern. The right lower jaw shows evidence of alternate replacement of the incisors (figure 6*c*). The first incisor is missing and only the medial wall of the alveolus remains, but an apparent fragment of a replacement tooth lies attached to it. The third incisor has the tip of a replacement tooth lying at the medial side of the base of the tooth, and the canine has a shallow, incipient crypt at its base suggesting replacement activity. On the other hand neither the second nor fourth incisors shows any sign of replacement. Postcanines 1 to 4 are not showing replacement but from postcanine 5 backwards simple alternate replacement is in progress. Postcanine 5 itself, which is the posteriormost A-type tooth, has a replacement crypt in the dental lamina and was observed during preparation to have an actual replacement tooth within it, although unfortunately it was subsequently destroyed. Postcanines 7, 9 and 11 are all old teeth, synostosed to the wall of the alveolus, and with large replacement crypts. Postcanine 13 is not synostosed but does nevertheless have a replacement crypt, covered medially by the coronoid bone. Postcanines 6, 8, 10 and 12 are all young, relatively unworn teeth, each with a low medial alveolus wall and no replacement crypt.

The left lower jaw differs in several respects from its fellow because it is at a different phase of tooth replacement. The incisors and canine are missing, but a small round pit lying anteromedial to the third alveolus, and an even smaller one adjacent to the first, represent developing replacement crypts. There is certainly no sign of replacement associated with the canine alveolus. Behind the canine (figure 4) there are but four A-type teeth instead of the five of the right side, followed by positions for eight P-type teeth (positions 7 and 10 are plugged alveoli as described above) as in the other jaw. The discrepancy in the number of A-type teeth may be due to one of two possible causes. One of the A-type teeth of the left side, presumably the first, may have been shed but not replaced. Alternatively, the first of the P-type teeth of the right side, may have been replaced by a morphologically simpler A-type tooth making five A-types, and at the same time a P-type would have had to be added at the hind end of the postcanine series. Both these phenomena are known to occur in the replacement pattern of *Thrinaxodon* (Osborn & Crompton 1973). Direct comparison of the teeth supports the first view, for in both jaws the last postcanine tooth is distinctive in being more oval, and having a less well developed cingulum, than the more anterior P-type teeth. Also, in the region of the A-type teeth, the posteriormost A-type which is the fourth postcanine on the left but the fifth on the right is very similar on both sides with about the same degree of incipient cingulum development. An equivalent comparison holds good for the fourth right and the third left A-type teeth. Finally the phase of tooth replacement in the two respective jaws is much more similar if loss of the first left postcanine is assumed. However, if true, then some degree of tooth repositioning must also have occurred because there is no gap between the canine and the first extant postcanine on the left side, and in fact the total length of the tooth row is almost exactly the same on the two sides.

Granted this interpretation of the left postcanine series, then the tooth replacement pattern is similar to that of the right side, but is variably a little out of phase at different tooth sites. None of the first three postcanines (i.e. p.c.2 to p.c.4) show replacement but, as on the right, postcanine 5 has a replacement crypt. As already described, the teeth posterior to this show

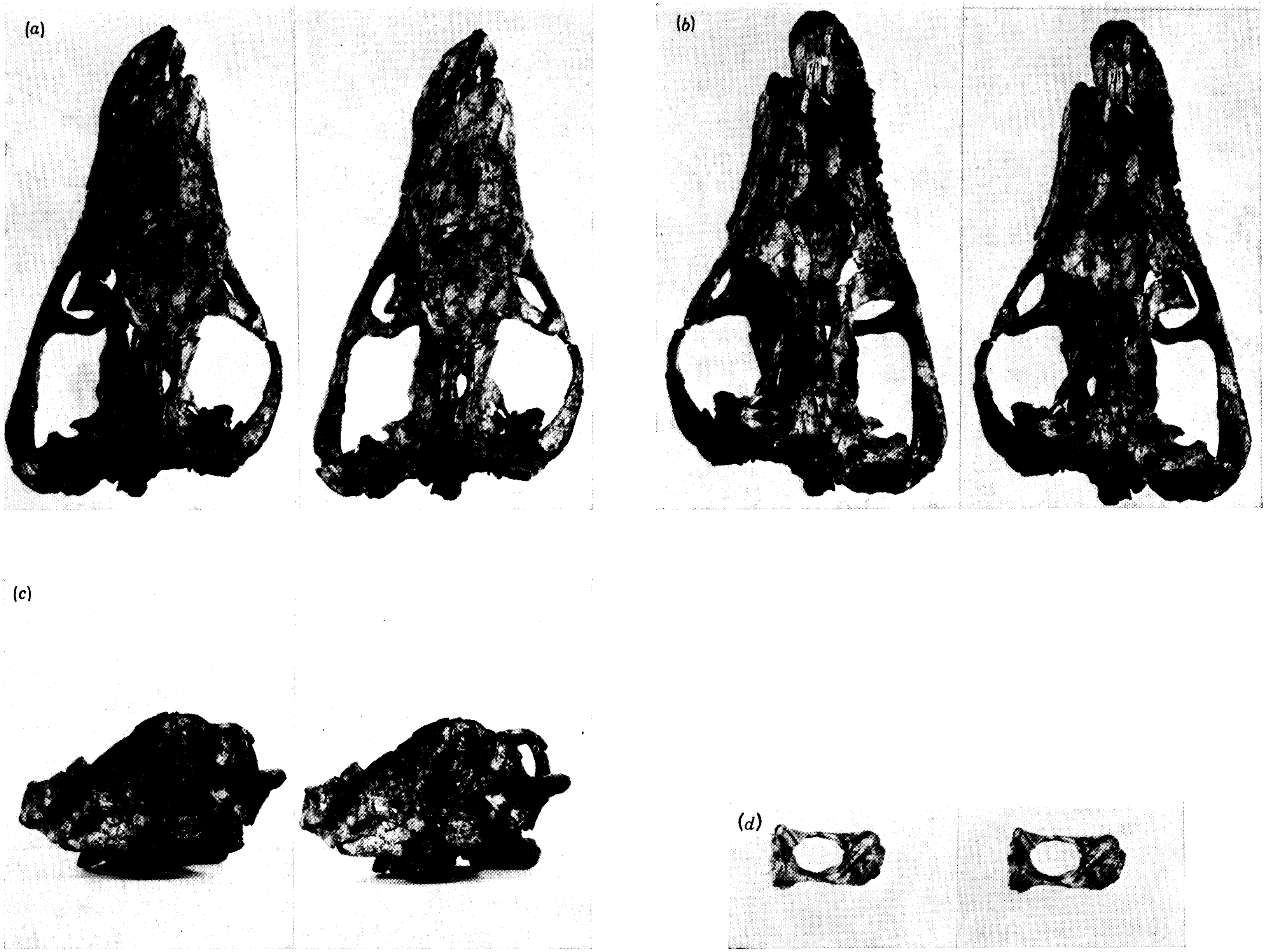

FIGURE 19. *Procynosuchus delaharpeae*: stereophotographs of the skull. (*a*) Dorsal view. (Magn. × 0.75.) (*b*) Ventral view. (Magn. × 0.75.) (*c*) Posterior view. (Magn. 0.75.) (*d*) Left stapes in dorsal view. (Magn. × 2.)

DESCRIPTION OF PLATE 2

FIGURE 20. *Procynosuchus delaharpeae*: stereophotographs of the skull. (*a*) Internal view of left side of the braincase. (Magn. × 1.) (*b*) Internal view of the right side of the braincase. (Magn. × 1.) (*c*) Left side of skull. (Magn. × 0.75.) (*d*) Right side of skull. (Magn. × 0.75.) (*e*) Right quadrate in anterior view. (Magn. × 2.) (*f*) Right quadrate in posterior view. (Magn. × 2.)

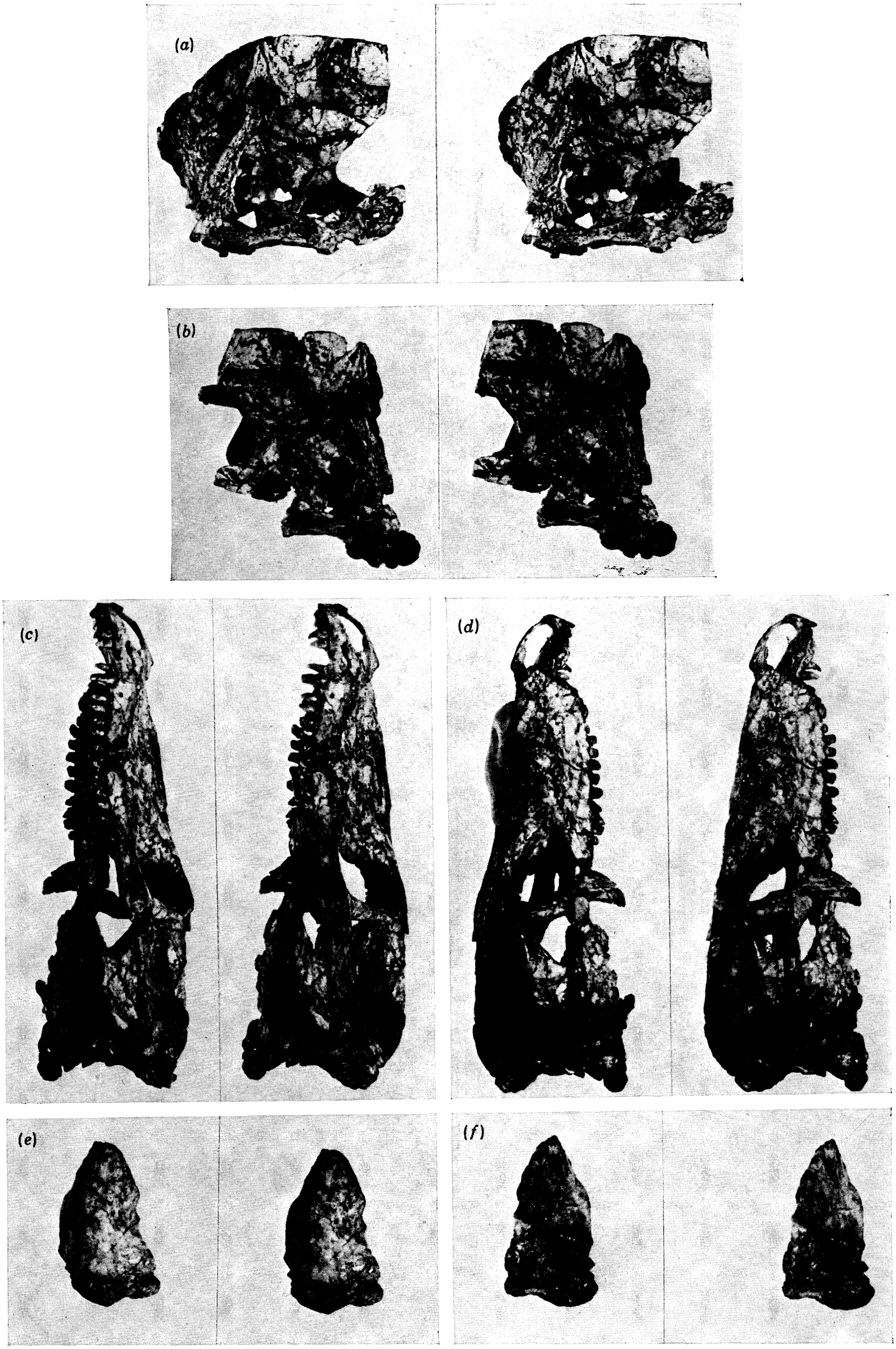

FIGURE 20. For description see opposite.

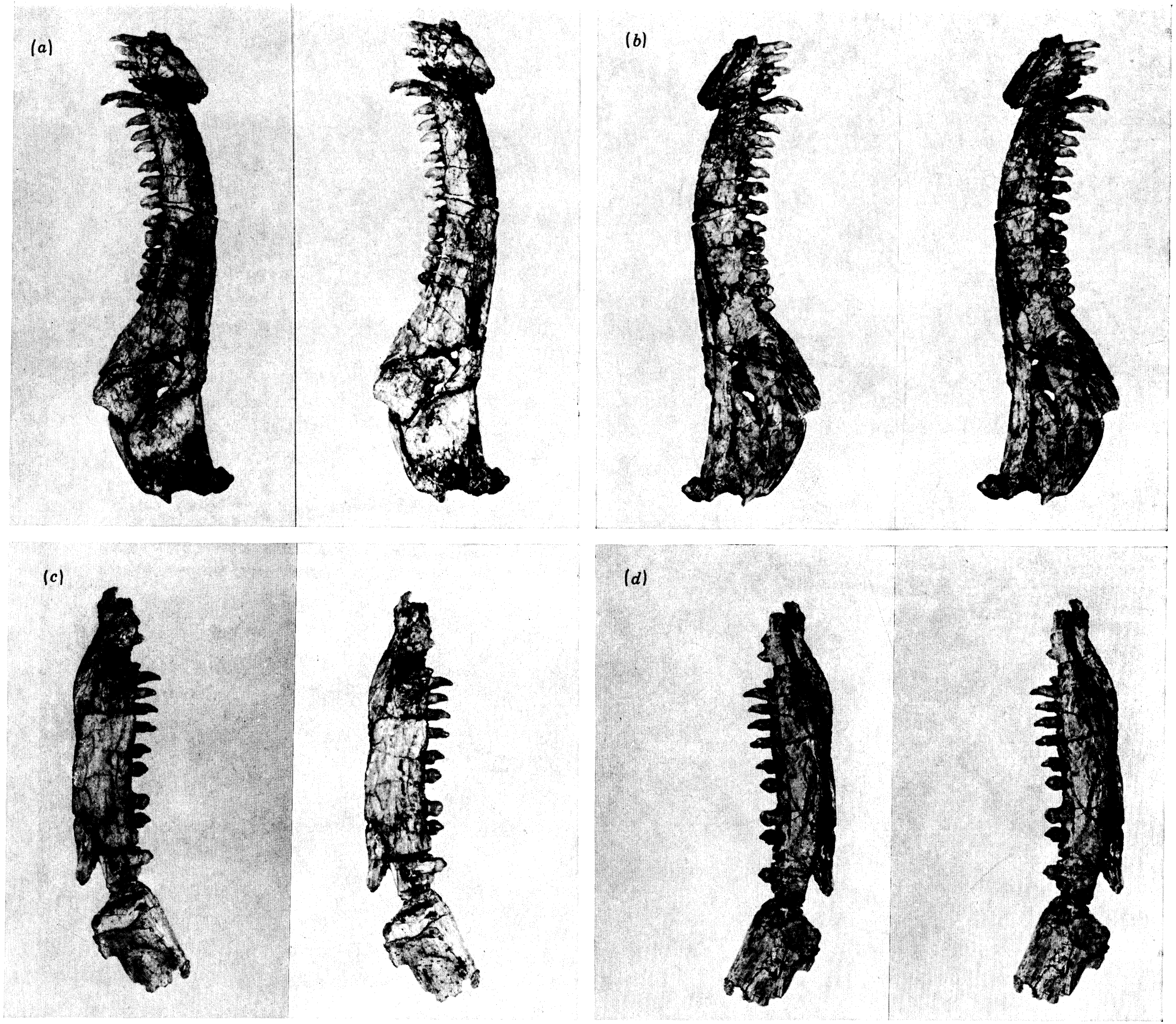

Figure 21. *Procynosuchus delaharpeae*: stereophotographs of the lower jaws. (*a*) Right jaw in lateral view. (Magn. × 1.) (*b*) Right jaw in medial view. (Magn. × 1.) (*c*) Left jaw in lateral view. (Magn. × 1.) (*d*) Left jaw in medial view. (Magn. × 1.)

a replacement wave in alternate positions with increasingly further developed teeth. Postcanine 7 is a fairly young tooth with an incipient crypt, postcanine 9 is an old synostosed tooth with a large crypt, postcanine 11 is a plugged socket with replacement tooth below, and postcanine 13 is a half erupted tooth with no crypt. Although these are the same positions as those showing replacement on the right side, they differ in that the equivalent right teeth are all at about the same stage in the replacement cycle rather than showing a younger to older gradient. The intervening left teeth, 10 and 12 are young and have no crypts, but postcanine 8 is anomalous since there is only a plugged socket with no crown. Presumably replacement at this site has been delayed.

Active replacement is also affecting the upper dentitions (figure 2). All the incisiform alveoli of the left side except for number 7 show replacement crypts and only alveoli 2 and 5 lack preserved replacement teeth. On the right side, the alveoli of teeth 5, 6 and 7 have been lost and that of tooth 8 is damaged. Replacement is in process at incisors 1 to 4 with small replacement teeth present at positions 1 and 4, an incipient crypt at position 2, and an almost erupted replacement tooth occupying alveolus 3. Both the left and the right upper canines have shallow crypts on their medial sides, but no preserved replacement teeth.

In the postcanine region simple alternate replacement is occurring on either side, with postcanines 2, 4, 6, and 8 having replacement crypts, and postcanines 1, 3, 5, and 7 being young teeth without crypts. As in the case of the lower right dentition, replacement of each of these postcanines is at about the same stage. Neither of the 10th postcanines has a replacement crypt although in both of them the medial wall of the alveolus seems to be in the process of growing around the base of the tooth. A small crypt lies in the dental groove posterior to the tenth left postcanine. This probably indicates the first stage towards the addition of a new postcanine tooth at the posterior end of the row. No such feature is apparent on the right side.

No full analysis of the tooth replacement pattern is possible from a single specimen and must await a series of suitably prepared individuals. Nevertheless a number of features of the pattern are indicated and may be summarized thus: (i) Replacement of incisors is so rapid that a simple alternation is obscured in the upper jaws, although still apparent in the lowers. (ii) Replacement in the more anterior postcanines is slow. (iii) At least the anteriormost postcanine can be shed without being replaced. (iv) Teeth can be added *de novo* at the posterior end of the tooth row, as indicated by the upper left dentition.

All these are features of the replacement pattern of *Thrinaxodon* (Osborn & Crompton 1973) and suggest that a similar arrangement exists in procynosuchids. It is not however known whether a relatively complex P-type tooth can be replaced by the relatively simple A-type as occurs in *Thrinaxodon*. This remains a possible but less likely alternative to (iii) above as the explanation for the discrepancy in tooth number of the right and left lower jaws respectively.

Tooth function

The evolution of a lingual cingulum on both the upper and lower posterior postcanine teeth appears to be the first step away from the primitive single-cusped reptile type of tooth towards the ultimate mammalian multi-cusped, occluding tooth. The form of these teeth has been described above, but what remains to be described is the presence of matching tooth wear facets on certain of the upper and lower postcanines. Such evidence of direct tooth to tooth contact has not been reported previously in procynosuchids nor even in the more advanced galesaurids like *Thrinaxodon*, and is of considerable significance in appreciating the functioning of these kinds of teeth. Postcanine 8 on the upper left side is an old, generally worn tooth synostosed to the walls of the alveolus and it has a single large flat facet facing medially and oriented almost vertically in the region of the cingulum (figure 5*a*). It is matched by a similar large, flat facet occupying most of the antero-posterior length of the lateral face of the main cusp of lower left postcanine 9 (i.e. the 8th extant postcanine), also a synostosed tooth. The adjacent upper postcanines, 7 and 9 on this side are young teeth but both have a small, round wear facet on the cingulum very slightly anterior to the middle of the tooth. The teeth adjacent to lower postcanine 9 which must have caused these smaller wear facets are not apparent, since postcanine 8 has shed its crown, and postcanine 10 is a very young tooth which must have only recently erupted. Similar wear facets are present on the right hand side of the jaws. The upper postcanine 9 has a large flat facet which corresponds with a facet on the anterior half of the crown of lower postcanine 11, both these being old, synostosed teeth. Upper postcanine 8 is badly damaged but upper postcanine 7, a young tooth, has a small round facet on the cingulum cusps between the middle and the front of the tooth, which corresponds to a large facet on the back of the old postcanine 9 of the lower dentition. Upper postcanine 6, also an old tooth, has wear on the cingulum cuspules in the middle of the tooth but the coresponding lower tooth, postcanine 8 is a very young tooth with no wear. Finally upper postcanine 4 has what may be a large wear facet, although this could be no more than damage. Again the lower tooth with which it corresponds is a very young tooth, postcanine 6.

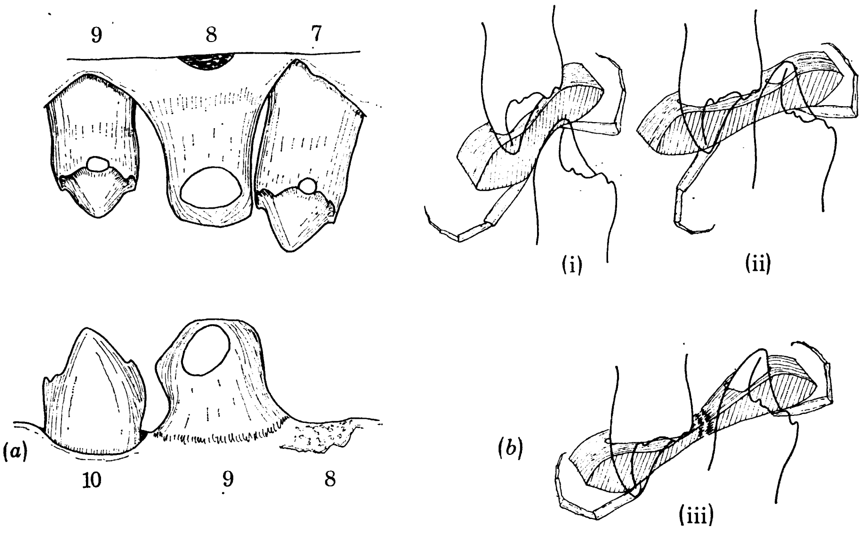

FIGURE 5. Functioning of the posterior postcanine teeth. (*a*), matching wear-facets on opposing upper (medial) and lower (lateral) left postcanines. (*b*), sequence of movement of a lower postcanine tooth relative to the corresponding upper postcanine when masticating an insect.

This evidence of tooth wear indicates that the lower postcanines did not interdigitate with the uppers as indicated by Crompton (1972*b*) but rather that each lower tooth worked against a particular, single upper tooth. This in turn shows that the teeth did not function by shearing action of the matching crests of the main cusps. However, it seems that the direct tooth to tooth wear was not an adaptation of the dentition but only an undesirable consequence of the actual mode of action of the teeth. In most cases one of the opposing teeth is young and recently erupted, whereas if large opposing facets were desirable, it might be supposed that the tooth replacement pattern would be such as to cause old, opposing teeth to remain together for as long as possible, and then be shed more or less simultaneously. It might be expected, too, that the rate of replacement would have slowed down, as occurs in later cynodonts. It is more probable that the wear indicates merely that the lower tooth passed as closely as possible to the cingulum of the upper tooth, so that occasional, more or less accidental abrasion between the teeth occurred.

Taking into account the form of the teeth, an explanation of their action may now be suggested (figure 5*b*). The sharp point of the main cusp will allow easy penetration of a relatively tough material, and the anterior and posterior crests of the main cusp will cause the tooth to make a hole which is oval in shape with acute anterior and posterior ends, giving rise to areas of high stress concentration. The effect of the cingulum will be greatly to increase the resistance of that side of the tooth to further penetration of the material. From the evidence of the tooth wear it has been shown that the tip of the main cusp of the lower tooth passed very close to the cingulum of the upper tooth. The biting action therefore was penetration of the material by the upper main cusp, followed by locking of the material against the cingulum. Meanwhile, the main cusp of the lower tooth penetrated the material immediately adjacent to the upper cingulum and the substance locked against the cingulum of the lower tooth. Further movement of the lower tooth past the upper tooth caused an increased distance between the cingula of the upper and lower teeth respectively, and assuming the material being chewed was of a suitable nature, tearing would occur, starting at the areas of high stress concentration noted above. The movement of the lower tooth away from the upper tooth appears to have had two components. First, since the cingula lie well above the bases of the crowns, further dorsal movement of the lower teeth was possible, past the uppers, to the fully closed position. There is also evidence, however, that the lower tooth underwent a degree of medial movement after contact with the upper tooth, mediated by a small amount of rotation of the whole lower jaw about its long axis. The orientation of the lower postcanine tooth row (figure 6*c*) is unusual. Behind the canine the dentary twists so that whereas the more anterior teeth point slightly laterally, the more posterior ones come gradually to point slightly medially. Thus if, as the jaw was closing, it rotated slightly about its long axis, the left jaw, for example, rotating clockwise as viewed from behind, successively anterior lower teeth would adopt a vertical orientation with respect to the opposing upper teeth, ready for occlusion. Meanwhile those lower teeth further back which had already met the upper teeth would turn medially, to further increase their final separation from the upper teeth. The degree of long axis rotation of the jaw could only be small because of the presence of the lateral pterygoid flanges. However, it could quite reasonably have caused a further 1–2 mm separation of upper and lower teeth after contact with the food, which would be very significant. The loose symphysis would allow such a jaw rotation, and the fact that the jaw closing musculature had a considerable medial component acting above the level of the lower teeth indicates the availability of suitable muscle forces for powering the rotation. The quadrate was capable of rotation about its own long axis as discussed later (page 94), which would provide the necessary motion of the lower jaw. As described earlier, the more anterior postcanine teeth face postero-medially, while the posterior teeth face medially. Since long axis rotation of the lower jaw was probably completed before the more anterior teeth had met, these latter teeth could not have functioned by the same mechanism as the posterior teeth. This explains their different design, for they were probably used only for prey retention, for which simple, sharp, postero-medially curving teeth are required.

The particular food material which would be appropriate for a dentition of the design suggested would be fairly hard, thin enough to be penetrated, and with a high stiffness (i.e. high modulus of elasticity) so that it ruptured rather than merely stretched. Insect cuticle would seem to fall comfortably into this category and it is suggested therefore that procynosuchids were the first reptiles to adapt successfully to mastication of insects, as opposed to merely capturing them and swallowing them whole.

No wear facets are present on the incisors, canines, or A-type postcanines, although at least in the case of the incisors, this could be for want of adequately preserved teeth. The presence of eight upper incisiform teeth, but only four lower incisors is related to the somewhat procumbent nature of the lowers. Since their tips are widespread, they occupy a greater length than would the same number of tips of upper incisors. In modern mammals, procumbency of the lower incisors often indicates a grooming function and it is interesting to speculate that this may have been the case in *Procynosuchus*. Otherwise, the single-cusped nature of all the anterior teeth must be assumed to indicate their food catching function. The canines are particularly suggestive of small active prey.

2. *The adductor jaw musculature*

Crompton (1963) attempted a reconstruction of the jaw muscles of procynosuchids, and considered that they approached a basic mammalian arrangement. There was a temporalis muscle from the medial wall of the temporal fossa (sagittal crest), a deep masseter from the medial surface of the zygomatic arch to the dorsal surface of the postdentary bones and to the small adductor fossa of the lateral face of the coronoid process, and a superficial masseter from below the orbit to the reflected lamina of the angular, the latter following Parrington (1955; but see Crompton & Hotton 1967). He also believed that the pterygoideus musculature from the region of the lateral pterygoid flange wrapped around the ventral edge of the postdentary bones to insert on the lateral face of the angular, behind the reflected lamina.

Barghusen (1968) considered the muscle arrangement in more detail, with particular respect to the condition of modern reptiles. He agreed that the adductor mandibuli externus muscle (temporalis plus masseter of mammals) was modified towards the mammalian condition, by having gained an insertion on the lateral surface of the lower jaw, that is to the adductor fossa of the coronoid process. He pointed out that by comparison with living forms, the postero-dorsal edge of the coronoid process was probably the site of attachment of an aponeurotic sheet ('bodenaponeurosis'), which rose up into the temporal fossa. Adductor externus muscle fibres which inserted into the lateral surface of the aponeurosis and onto the adductor fossa of the coronoid process represented the developing masseter muscle. He suggested that they may have had an origin either from the medial surface of the zygomatic arch or from the underside of an aponeurotic sheet covering the temporal fossa. In his figures Barghusen used the latter concept. He rejected the idea of a superficial masseter muscle having evolved, suggesting that it did not appear until much later on in cynodont evolution, but he accepted Crompton's interpretation of the pterygoideus muscle inserting on the lateral surface of the angular.

Kemp (1972*a*) concluded that in therocephalians part of the adductor musculature ran from the posterior part of the zygomatic arch, to insert on the lateral surface of the angular bone within and behind the recess that was formed by the large reflected lamina of these forms. Further (Kemp 1972*b*), such a muscle could be regarded as the forerunner of the masseter musculature of cynodonts by assuming an anterior migration of the site of the origin along the length of the zygomatic arch, and a shift in the insertion to the newly enlarged dentary. A somewhat similar suggestion by Crompton is quoted in an addendum to the paper by Barghusen (1968).

Allin (1975) has recently proposed that the angular region of the lower jaw, along with the jaw articulation, was much more closely involved in the hearing mechanism than is generally believed. In particular, he proposed that the fossa of the lateral surface of the angular in cynodonts carried an air-filled chamber acting as a tympanic cavity, and was overlain by a tympanic membrane, partly composed of the reduced reflected lamina itself. This would probably (although not necessarily, according to Allin) preclude the angular bone from major muscle attachments. Allin's concept is discussed in more detail in the section on hearing (page 114).

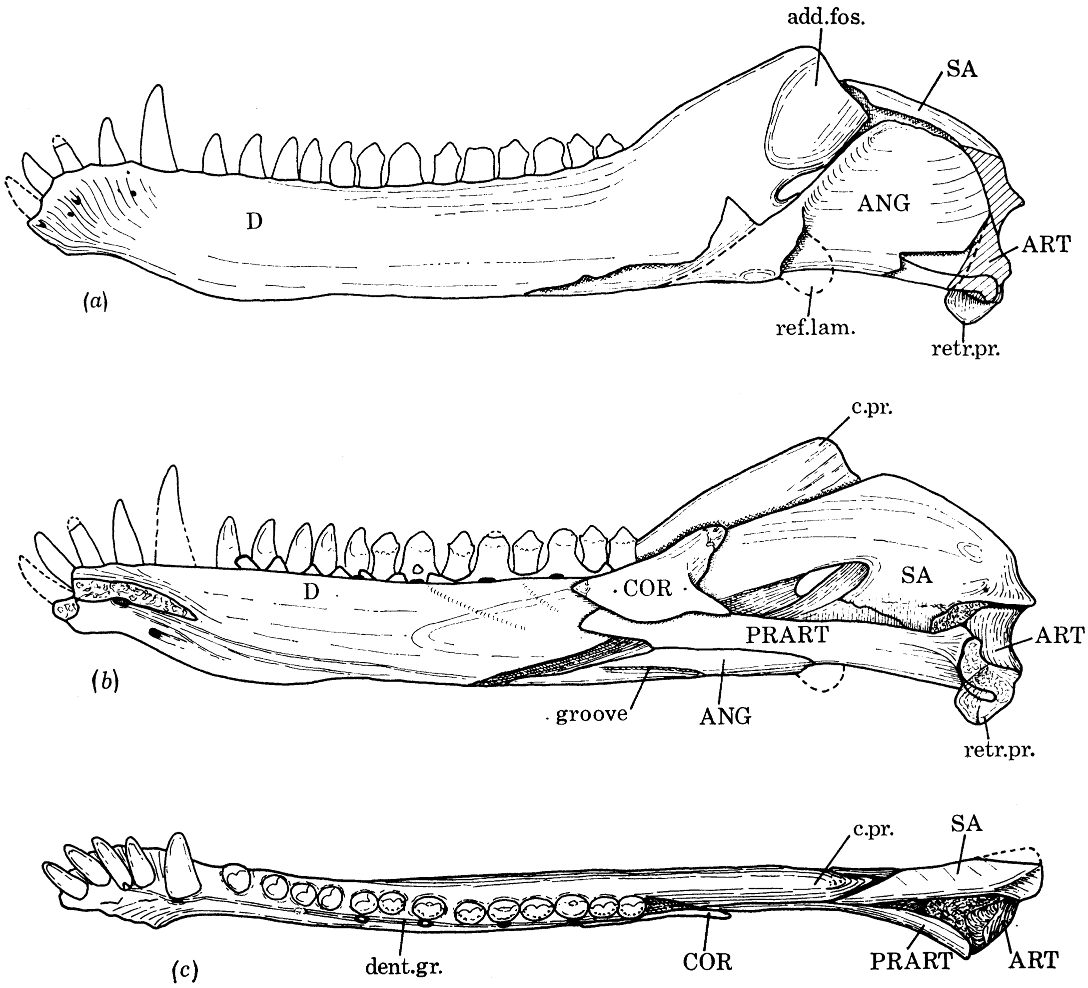

FIGURE 6. Lower jaw reconstruction in (*a*) lateral view, (*b*) medial view, (*c*) dorsal view. The dentition is based on the right mandible. (Magn. × 1.5.)

The anatomy of the present specimen of *Procynosuchus* (figure 8) confirms Barghusen's conclusions about the general nature of the temporalis muscle, but suggests some alternative views about the masseter. The medial and posterior edges of the temporal fenestra are marked by fine, short rugosities perpendicular to the edges, which indicate the attachment of a temporal aponeurotic sheet. However, neither the postorbital bar nor the zygomatic arch are so marked and it appears, therefore, that the temporal aponeurosis did not cover the temporal fenestra completely, but that it descended from the medial and posterior edges into the temporal fossa in association with the temporalis musculature. The posterior edge of the coronoid process of the dentary (figure 6) is also marked by fine perpendicular rugosities, showing that a bodenaponeurosis-like structure attached to it and extended postero-dorsally into the temporal fossa. The adductor mandibuli externus muscle was divided into a medial temporalis muscle and a lateral masseter muscle. The temporalis presumably originated from the undersurface of the temporal aponeurosis, as well as by a fleshy attachment to the extensive medial wall of the temporal fossa, formed from the postorbital and parietal bones. The anterior extent of the origin is indicated by a slight hollowing of the medial wall of the fossa immediately behind the level of the postorbital bar (figure 3*a*), which coincides with a marked change in the density of the minute nutritive foramina emerging on the surface of the bone. The medial surface of the postorbital bar, and the immediately adjacent areas, have a very high density of such pores, but the medial wall of the temporal fossa from the anterior hollowing backwards carries very few. The biological significance of the difference is not clear but it does seem likely to coincide with whether musculature attached to the bone or not. The ventral limit of the attachment of the temporalis muscle is probably defined by the lateral swelling of the medial wall of the temporal fossa along a near-horizontal line some one centimetre below the sagittal crest and just above the venous groove (figure 3*a*). The whole area above the swelling is a shallow fossa. Posteriorly the area of muscle attachment runs smoothly round onto the anterior face of the squamosal, which is slightly concave and faces anteriorly and slightly dorsally. The ventral limit of this part of the temporalis muscle attachment is a continuation of the ventral limit of the medial attachment, and is formed by the rounded edge of the squamosal overhanging the post-temporal fenestra, quadrate and quadratojugal. The large temporalis muscle, as defined by the extensive area of origin, presumably inserted onto both the medial and lateral surfaces of the bodenaponeurosis. The insertion of the temporalis must also have extended onto the adductor fossa of the coronoid process, as interpreted by Barghusen (1968). This is because

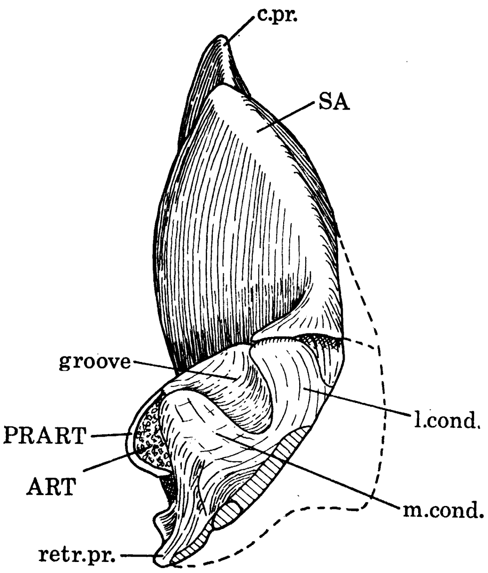

FIGURE 7. Posterior view of right lower jaw, as preserved. (Magn. × 3.)

the adductor fossa is a simple ventral extension of the presumed plane of the bodenaponeurosis, and because, as discussed below, muscle fibres from the zygomatic arch could not reasonably have inserted into the fossa. Yet undoubtedly the adductor fossa was an area of insertion of adductor musculature. The dorsal and dorsomedial parts of the surangular also appear to have been a site of insertion of temporalis muscle fibres as suggested by both Crompton (1963) and Barghusen (1968). A broad, horizontal fossa occupying the dorsal half of the medial surface of the surangular (figure 6*b*) appears to indicate the extent of a fleshy insertion of temporalis musculature. The somewhat broadened dorsal surface of the surangular is smoothly continuous with the medial surface and is also continuous with the posterior part of the adductor fossa of the coronoid process (figure 6*a*). In contrast, the lateral surface of the postdentary bones, formed from the angular, is separated from the dorsal surface of the surangular by a sharp ridge and therefore temporalis musculature does not appear to have invaded the lateral surface of the lower jaw posterior to the coronoid process.

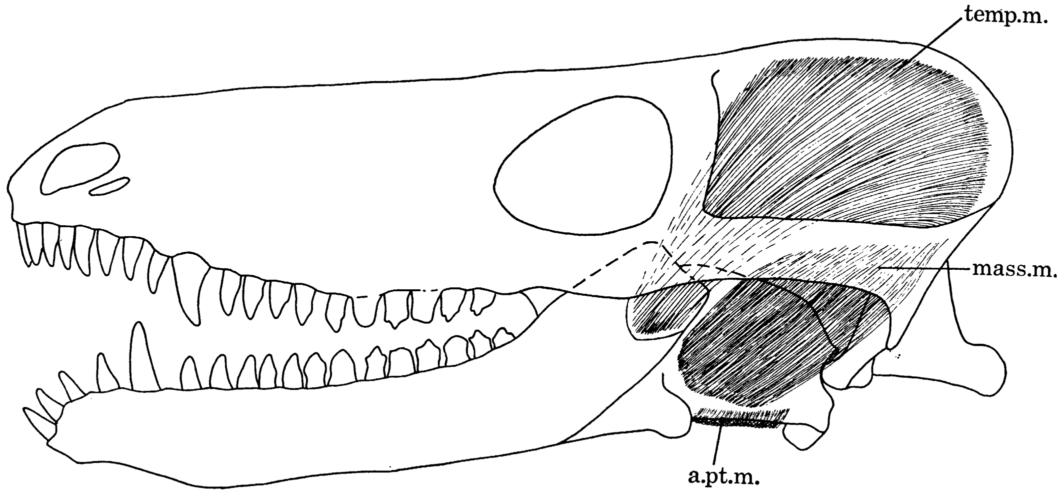

FIGURE 8. Reconstruction of the main adductor jaw musculature.

There is evidence in this specimen that muscle fibres originated from the medial surface of the zygomatic arch. In the first place, the lateral bowing and high position of the arch, although less marked than in later cynodonts, is more than can be accounted for simply in terms of making space for temporalis muscle fibres to attach to the lateral surface of the coronoid process of the dentary. It seems, rather, to be designed to allow musculature to run from the zygomatic arch itself to the lower jaw. More direct evidence comes from the surface of the medial face of the zygomatic arch, for there is an abrupt change about one centimetre from its anterior end. The anteriormost part has a very high density of minute nutritive foramina, but for most of its length there are very few such foramina and instead there is a series of very fine more or less horizontal striations, running back to the region of the quadratojugal. This striated area is in the form of a very shallow fossa occupying the lower half of the medial surface and facing ventro-medially. It may be recalled that a similar change in surface features of the bone apparently indicated the limit of the origin of the temporalis muscle. The muscle from the zygomatic arch, which may be considered homologous to the mammalian masseter, could not have inserted in the adductor fossa of the coronoid process. The adductor fossa lies approximately level with, and at the anterior end of the zygomatic arch when the jaws were closed (figure 8). Therefore the muscle would have produced a very small torque at the jaw hinge but an enormous, purely posteriorly directed force; and the more anterior part of the muscle would have had fibres so short that they would have restricted the gape to what would probably have been an intolerable extent. There is no evidence that muscles attached to the dentary ventral to the adductor fossa, for this surface does not differ from the rest of the lateral surface of the dentary, indicating that it was covered by thin dermis. Thus the only possible area to which the masseter could have attached is the lateral surface of the angular bone. This (figure 6*a*) is a broad, shallow fossa bounded antero-dorsally by a pronounced crest and dorsally by a crest of the surangular. The surface of the bone is smooth but bears extremely fine striations running approximately horizontally. Therefore, both the gross morphology and the nature of the surface of the bone of the zygomatic arch and angular bone respectively indicate the presence of a masseter muscle of the arrangement suggested (figure 8). There are however certain other considerations which support this interpretation. The nature of the jaw articulation, discussed later, suggests that the net medial component of the adductor musculature was significantly less than in therocephalians. This implies the presence of a well-developed lateral muscle, whose lateral component of its force would partly counteract the medial component of the large temporalis musculature. The phylogeny of cynodonts also adds support. The direct antecedents of cynodonts are not known but a close relationship to therocephalians seems well established (Kemp 1972*b*), and in these forms there is good evidence for a muscle attachment between the posterior part of the zygomatic arch and the angular recess between the body of the angular and its reflected lamina (Kemp 1972*a*). The proposed masseter of the cynodont would have evolved by a degree of anterior extension of the origin of the therocephalian muscle along the zygomatic arch, associated with reduction of the reflected lamina of the angular. The progressive increase in size of the dentary at the expense of the postdentary bones, in later cynodont evolution, can be interpreted as a progressive increase in the percentage of adductor muscle fibres attaching to a single strong bone, the dentary, in order to reduce the stresses across sutures between the lower jaw bones (Kemp 1972*b*). The presence of a pre-existing muscle attaching to the angular, which the dentary could progressively 'capture' by postero-ventral enlargement, is a necessary assumption of this view.

It will be noted that in the procynosuchids the temporalis muscle and the masseter muscle are quite distinct from one another, particularly as reflected in the discontinuity between their insertions on the dentary and angular respectively. This contrasts with the condition seen in the primitive mammal *Didelphis*, where there is no such clear cut distinction (Hiiemae & Jenkins 1969). However, it is not difficult to envisage the origin of the mammalian arrangement resulting from 'capture' of the masseter by enlargement of the dentary, coupled with an increase in the size of both temporal and masseter muscles, so that the two muscles become closely apposed to one another, as a single adductor complex.

Evidence for a well developed adductor mandibuli posterior muscle, which in modern reptiles originates from the quadrate, is absent and the procynosuchid quadrate could not have had any substantial adductor musculature attaching to it. A vertical fossa on the lateral face of the prootic may well represent part of the area of origin of this musculature although it could not have been of great mechanical significance.

The adductor mandibuli internus muscle of modern reptiles includes the pseudotemporalis, with an origin mainly from the epipterygoid bone. The very smooth lateral surface of the broad procynosuchid epipterygoid (figure 16) suggests that it did indeed give origin to a pseudotemporalis-like muscle. Also part of the adductor mandibuli internus complex is the pterygoideus muscle. A very clear-cut site of origin of the pterygoideus muscle in this specimen is a pronounced posteriorly-facing fossa on the posterior surface of the lateral pterygoid flange (figure 11). It is discontinuous with the dorsal surface of the palate, suggesting that the latter region did not carry pterygoideus musculature. A second area for pterygoideus muscle attachment is the smooth, lateral-facing margin of the pterygoid bone in front of the basipterygoid articulation (figure 3*a*), which in turn is continuous with the epipterygoid. The quadrate ramus of the pterygoid is very delicate and could hardly have borne significant adductor musculature.

The insertion of the adductor mandibuli internus was presumably the smooth medial and ventral faces of the prearticular bone (figure 6*b*). In addition to a fleshy insertion here, there are two small, faint depressions on the ventral surface, a little way in front of the retroarticular process, suggesting points of ligamentous attachment. There is no clear indication in this specimen of whether pterygoideus muscles wrapped around the ventral edge of the lower jaw to insert on the lateral surface, because of the weathering of the postero-lateral part of the mandible. However, the fact that the fossa on the lateral face of the angular, interpreted as the area of insertion of a masseter muscle, does not have any ventral ridge delimiting it suggests that pterygoideus muscle fibres did indeed to some degree attach to the ventro-lateral part of the angular. It is impossible to tell whether adductor muscles inserted onto the anterior face of the rather poorly preserved retroarticular process of the articular.

Apart from its base, the reflected lamina of the angular is absent and it is not therefore possible to know whether any muscles inserted on it.

3. *The jaw opening musculature*

It is generally accepted that the retroarticular process of the cynodont articular bone was the site of insertion of a depressor mandibuli muscle, innervated by the facial nerve (VII), as in modern sauropsid reptiles. There are, however, difficulties associated with this interpretation, and in particular the condition in the monotreme and therian mammals respectively (Adams 1919). In monotremes a detrahens muscle, innervated by the trigeminal nerve (V), runs from the otic capsule region behind the jaw articulation, to insert on the ventro-medial part of the lower jaw. In contrast, the therian mammals have a digastric muscle formed from the intermandibularis muscle anteriorly with a trigeminal innervation, and from the interhyoideus musculature posteriorly with a facial innervation. The intermandibularis and interhyoideus muscles (Edgeworth's 1935 terminology) are developed normally in monotremes. Parrington (1974) followed Gegenbaur's early work in assuming that the posterior belly of the therian digastric muscle is homologous with the reptilian depressor mandibuli. The monotreme detrahens is seen as a neomorph. Parrington believed that the changes in the two respective mammal groups were consequent upon the change in function of the articular bone from jaw articulation to ear ossicle, and that the differences between monotremes and therians might indicate a separate origin of these two respective mammalian groups from within the cynodonts.

An alternative possibility is that the cynodonts themselves had a detrahens muscle attaching to the retroarticular process and innervated by the trigeminal nerve. The monotremes, with their relatively feeble jaws, have retained this ancestral condition, except of course that the insertion of the muscle has necessarily shifted onto the dentary. Only the therian stock changed radically, by losing the detrahens and coming to rely on the ventral musculature for jaw opening, thus forming the digastric muscle. Such ventral musculature is invariably present in tetrapods and is capable of jaw depression, and at least a part of its insertion is indicated in *Procynosuchus* by a longitudinal groove on the ventro-medial aspect of the angular bone (figure 6*b*). Also it is possible that the reflected lamina of the angular was involved with the insertion of ventral muscles, but in the present specimen the reflected lamina is missing.

Since the cynodonts shared a common ancestry with the sauropsid reptiles no later than the Middle Carboniferous, it is not unreasonable to draw a comparison between them with monotremes rather than with modern reptiles, and the view presented here offers a more simple explanation for the differences in jaw opening musculature between the two groups of living mammals. Also it accounts for the absence of embryological evidence of the one-time existence of a depressor mandibuli in mammals (Edgeworth 1935). Whether the tensor tympani muscle of the mammals, which inserts onto the medial face of the malleus (articular) is a derivative of the internal pterygoideus muscle as usually supposed, or of the proposed detrahens muscle of the cynodonts, cannot yet be decided.

4. *The jaw articulation*

The right quadrate, quadratojugal and articular bones were preserved in their natural positions, although the ventro-lateral region of the articulation has been lost due to weathering. The left articular region is missing altogether, but the recess in the squamosal that housed the quadrate and quadratojugal is preserved. The right quadrate was removed from the skull during preparation.

The reconstruction of the adductor jaw musculature (figure 8) indicates that there must have been substantial reaction forces generated at the jaw articulation during feeding. There were no large antero-dorsally directed muscles, and therefore a balance of the muscle forces in the antero-posterior line was not possible. Nor could the net dorsal component of the muscle force be centred upon the postcanine teeth, as can occur in later cynodonts and mammals (Crompton 1963). The masseter part of the musculature, acting with a lateral component to its force, was much smaller than the temporalis part with a medially directed component, and therefore there must have been an overall medial component of the muscle forces. It follows that the jaw articulation would have been subjected to a relatively large force directed postero-medially and dorsally, which would have to be resisted by the quadrate-articular joint and the quadrate attachment to the skull. In *Procynosuchus* there appears to be no way to avoid the paradox of large reaction forces being resisted by a quadrate bone which was only loosely attached. The quadrate readily came away from the skull in this acid prepared specimen, and the posterior face of the quadrate does not match at all closely the surface of squamosal recess against which it lay. Only the dorsal part of the posterior face of the quadrate actually contacts the squamosal (figure 9*d*). It is flat, faces somewhat medially, and is marked by a series of coarse ventro-laterally aligned ridges. The recess in the squamosal (figure 9*a*) for reception of the quadrate is a shallow pocket, separated from the quadratojugal by a pronounced vertical ridge against which the lateral edge of the quadrate lay. The deepest part of the recess is adjacent to the ridge and from here the recess is a fairly flat surface, facing antero-laterally and with no distinct dorsal or medial boundaries. The surface is smooth, periosteal bone showing no evidence that it was covered in cartilage in life. There is a series of very faint striations and minute foramina adjacent to the lateral ridge, and a slight rugosity on the medial side near to the apex.

In addition to the contact with the squamosal, which was probably ligamentous, the quadrate also meets both the quadrate ramus of the pterygoid and the lateral prootic process, at a common hemispherical facet halfway up the medial edge (figure 9*c*). The rugose nature of the facet indicates a moveable, ligamentous articulation rather than a rigid suture. A further point of ligamentous attachment of the quadrate is indicated by the small, oval facet at the dorsal tip of the bone (figure 9*d*), which faces postero-dorsally. Finally, there is no direct contact, at least above the level of the articulation, between the quadrate and the quadratojugal. These two bones are separated by the vertical ridge of the squamosal recess.

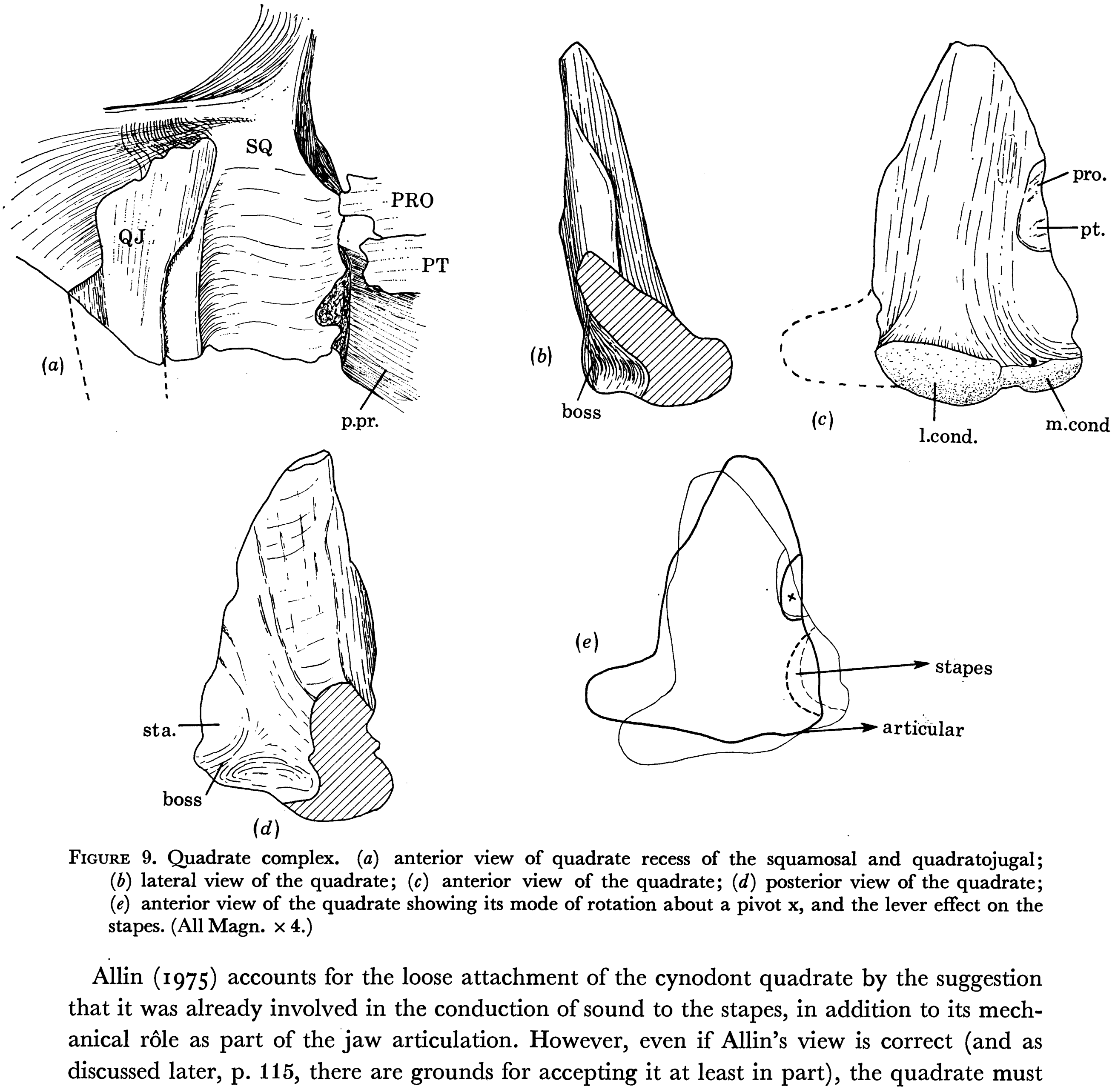

FIGURE 9. Quadrate complex. (*a*) anterior view of quadrate recess of the squamosal and quadratojugal; (*b*) lateral view of the quadrate; (*c*) anterior view of the quadrate; (*d*) posterior view of the quadrate; (*e*) anterior view of the quadrate showing its mode of rotation about a pivot x, and the lever effect on the stapes. (All Magn. × 4.)

Allin (1975) accounts for the loose attachment of the cynodont quadrate by the suggestion that it was already involved in the conduction of sound to the stapes, in addition to its mechanical rôle as part of the jaw articulation. However, even if Allin's view is correct (and as discussed later, p. 115, there are grounds for accepting it at least in part), the quadrate must still be interpretable in terms of its ability to transmit reaction forces arising from the muscle activities. The articulating surfaces of the quadrate and articular are incomplete laterally. The medial part of the articular condyle (figures 6 and 7) is a narrow surface, facing posteriorly and somewhat dorsally. It meets the narrow medial part of the quadrate condyle (figure 9*c*), which occupies the ventral and antero-ventral part of that bone. More laterally, the articular condyle is a deep fossa, facing posteriorly and only slightly dorsally. It lies postero-laterally to the medial condyle, from which it is separated by a deep, non-articulatory groove, and as far as the specimen is preserved, the lateral condyle extends postero-laterally. The lateral part of the quadrate condyle lies below the main body of the bone, and occupies the anterior as well as the ventral face of the bone. Thus, the axis of the hinge runs postero-laterally rather than simply laterally, and its articulating surface tends to be more vertical than horizontal. Kemp (1972*a* and *b*) analysed a jaw articulation of this design in therocephalians. It was shown that, in order for a hinge to operate when its axis lies obliquely to the transverse line, each quadrate must be capable of rotation about a longitudinal axis. If this condition is not met, then the jaws are unable to open without disarticulation of the articular bone from the quadrate. The purpose of the arrangement appears to be to allow the jaw hinge to resist muscles forces with a large medially directed component, without the articular bone being forced medially off the quadrate. The near-vertical orientation of the articulation reflects the requirement of resisting muscle forces with a large posteriorly directed force component. The same interpretation applies to *Procynosuchus*. The nature of the attachments of the quadrate to the skull indicates that it could have been perfectly free to rotate about a longitudinal axis, the contact with the pterygoid and prootic acting as the fulcrum (figure 9*e*). It is not known whether the quadratojugal was in contact with the quadrate at the level of the condyle, but even if it was, the quadratojugal appears to have been sufficiently freely held within the recess in the squamosal to be able to move with the quadrate.

A further feature of the quadrate region of the skull is the nature of the attachment of the stapes. The ventro-medial part of the posterior face of the quadrate carries a distinct boss, against which the distal end of the stapes rests (figure 9*d*). The stapes itself has a very large stapedial foramen (figure 17), which suggests that it was as light as possible, in connection with its sound conducting rôle. However, the fact that both anterior and posterior bars bounding the foramen are present suggests that the bone is also designed for considerable strength, and therefore that it was subject to large forces. Such forces could only be applied via its attachment to the mobile quadrate, and indeed, the more robust of the two bars of the stapes is the anterior bar lying immediately adjacent to the quadrate attachment. Thus, the stapes probably had a mechanical rôle in connection with the streptostyly of the quadrate, specifically to prevent excessive medial movement of the ventral end of the rotating quadrate. This rôle of the stapes may also account for the curious fact that the proximal end of the stapes is larger than the fenestra ovalis. There would be no tendency for the stapes to pierce accidentally the membrane of the fenestra ovalis. The possible rôle of the stapes and quadrate in sound conduction is discussed elsewhere (p. 114).

THE SNOUT

1. *External surface*

The pattern of the bones of the external surface is indicated in the figures. Much of the external surface of the snout is covered by a mass of minute nutritive foramina, often associated with tiny sulci, and the whole finely sculptured by ridging. There is however, a great deal of variation in different regions, between quite strongly sculptured and perfectly smooth, and this probably indicates variation in the fleshiness of the overlying skin. In the region of the external nostril, the alveolar border of the premaxilla is perfectly smooth and very poorly provided with nutritive foramina, as too is the alveolar region of the maxilla. This probably indicates that thick, fleshy, superficial tissue was present, presumably forming a muscular, mobile upper lip. The smooth type of bone surface curves gently round onto the floor of the external naris (figure 10), and is evidence for the existence of a valvular apparatus controlling the flow of air. In contrast, the external surface of the internarial process of the premaxillae is finely rugose, as is the more dorsal area of the maxilla. The most heavily sculptured bone is the nasal, particularly in the anterior region where it forms the dorsal border of the external naris. The frontal, prefrontal and lacrymal bones have the generalized type of light sculpturing and superficial foramina. Thus it appears that apart from the fleshy lips, the snout of *Procynosuchus* was covered by tightly applied, 'reptilian' skin.

As in therapsids generally, *Procynosuchus* is well endowed with foramina opening onto the external surface of the snout (figures 1 and 3*a*). Most of these probably form part of the infraorbital canal system (Tatarinov 1967). In the maxilla these are concentrated anteriorly around the canine region, and include one relatively large foramen, extending by a well developed sulcus from above the seventh precanine antero-ventrally to the level of the sixth precanine. Another well developed canal, exposed by damage to the anterior part of the maxilla, actually runs between the maxilla and the premaxilla to open anteriorly as a foramen on the external line of the suture between these two bones. The posteriormost of the maxillary foramina occurs at the level of the second postcanine teeth.

A single foramen emerges on the anterior face of the premaxilla, close to the ventral edge of the bone (figure 10). It leads into a dorsally directed canal whose entrance is presumably the foramen on the dorsal surface of the premaxilla immediately behind the base of the internarial process (figure 1).

A number of small foramina open onto the external surface of the nasal bone, each with a short, anteriorly-running sulcus. Unexpectedly, there are two large foramina opening near to the lateral margin of the right frontal bone (figure 1), and three similarly on the left frontal. All of them open in an anterior direction and the internal entrances lie in the roof of the olfactory lobe region of the dermal braincase (figure 14). Assuming that nerves at least emerged through these foramina, the roof of the skull appears to have been particularly sensitive.

2. *The septomaxilla and organ of Jacobson*

The significance of the septomaxilla with its associated medial process, canal, and septomaxillary foramen has been discussed by several authors, although no single widely accepted hypothesis has been proposed. Simpson (1933), presumably following Watson (1913), believed that the lacrymal duct emerged through the septomaxillary foramen, despite the fact that this duct opens anteriorly within the bony nasal cavity in living amniotes. Brink (1960) associated the septomaxillary apparatus with the organ of Jacobson and its associated glands and vascularization, in a rather vague way. Kemp (1969) suggested that in gorgonopsid therapsids the septomaxillary foramen was a special inhalent aperture for air going to the posterior part of the nasal capsule. Tatarinov (1965) proposed that the lateral ethmoidal nerve emerged from the septomaxillary foramen, despite the relatively enormous size of the foramen compared to other nerve foramina.

The very large external naris of *Procynosuchus* faces more laterally than anteriorly, and, as in all typical therapsids, the septomaxilla bounds it postero-ventrally and isolates the sizable septomaxillary foramen (figure 10). The anterior end of the bone expands as a large, flat plate lying upon the dorsal surface of the premaxilla and forming much of the floor of the external naris. The hind wall of this plate is produced dorsally as a more or less transverse wall, which curves antero-dorsally to define a prominent antero-laterally facing recess. It is proposed that Jacobson's organ lay within this recess and was bounded medially by a cartilaginous internasal septum rising from the median ridge formed by the paired premaxillae. Not only does this account for the recess, but it also corresponds to the position of Jacobson's organ in modern mammals. Many mammals have well-developed Jacobson's organs, including particularly the monotremes (Broom 1900; Wilson 1901). The organ is associated with the palatal process of the premaxilla and therefore lies anterior to the vomer. In the case of *Ornithorhynchus*, Jacobson's organ lies in a recess in the lateral face of the dumb-bell bone, which is now acknowledged as the homologue of the palatal process of the premaxilla (Parrington & Westoll 1940; Tatarinov 1965). Also in this particular animal, a septomaxilla is present, although it fuses with the dorsal surface of the premaxilla in the adult (De Beer & Fell 1936). It is also much simplified compared to cynodonts and lacks the medial process, the canal within it, and the septomaxillary foramen. Nevertheless its position is immediately lateral to Jacobson's organ, suggesting that at one time it could have been involved in the support of that organ. The septomaxillary foramen is manifestly too large to be accounted for solely as an exit for a nerve and blood vessels, particularly in view of the adequate foramina opening from the anterior region of the maxilla. On the other hand, the presence of fleshy lips would suggest that a mucous producing gland might have been present, in which case its duct could have emerged through the septomaxillary foramen. In support of this interpretation, there is a distinct fossa in the internal wall of the maxilla, immediately posterior to the septomaxillary foramen, which could have housed such a gland. The presence of a canal within the body of the septomaxilla has been demonstrated in most therapsids. *Procynosuchus* is possibly different in that there are three openings from the canal. The anterior one lies in the lateral region of the recess for Jacobson's organ. The middle one enters the canal from a recess in the ventral face of the septomaxilla, at the anterior end of the septomaxillary foramen. The posterior opening lies in the ventro-lateral surface of the septomaxilla, at the hindmost end of the septomaxillary foramen, immediately before the

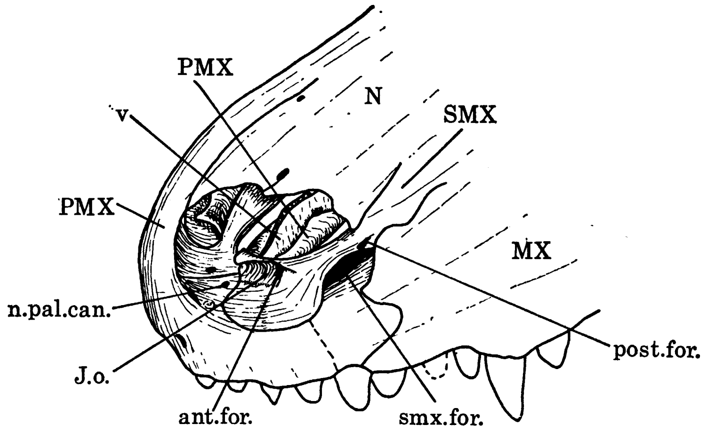

FIGURE 10. Antero-lateral and dorsal view of the region of the external nares. Based on a camera lucida drawing.

contact of the septomaxilla with the maxilla (figure 10). A possible interpretation of the canal is that it carried a branch of the mucous gland duct to Jacobson's organ, from the region of the septomaxillary foramen via the middle opening. At the same time it may have passed blood vessels to Jacobson's organ, from the infraorbital system in the maxilla via the posterior opening.

A foramen lies just anterior to the septomaxilla, close to the mid-line of the floor of the internal naris (figure 10). It leads into a short, vertical canal which opens ventrally on the palate, immediately behind the tooth-replacement pit of the first incisor (figure 2). This is interpreted as the naso-palatine canal, carrying the duct of Jacobson's organ. It lies in a position topologically corresponding to the anterior palatine fissure of modern mammals, which carries the naso-palatine canal in many members.

The interpretation of the septomaxilla and its associated structures presented here accounts for most of the observed features, and also indicates an arrangement reasonably similar to that in mammals. Derivation of the mammalian organization from that in *Procynosuchus* requires little more than a reduction of the septomaxilla along with the loss of its medial process and foramen.

3. *Nasal cavity*

The anterior part of the brain occupied a pronounced fossa on the internal surface of the frontal bones, bounded anteriorly by a semi-circular ridge (figure 14). The anteriormost part of the fossa is roughened and probably indicates the site of attachment of a mesethmoid cartilage, as suggested by Tatarinov (1963) in therocephalians. It would correspond to a median ossification present in gorgonopsids (Kemp 1969) and dicynodonts (Cox 1959). A well-developed system of longitudinal ridges runs forwards from the level of the mesethmoid cartilage, a feature universal in therapsids and regarded as the lines of attachment of a series of turbinal cartilages. On each side, a single, substantial ridge arises. Both the lateral and the medial edges of each ridge are sharp, but the medial edge soon peters out. The lateral edge becomes less prominent, but continues for the full length of the nasal cavity. Two pairs of foramina lie just medial to the lateral edge, but do not appear to be associated with the turbinal system. They are probably the internal openings of a canal system which terminates externally in the dorsal region of the nasal bone.

Another feature apparently typical of therapsids generally is a deep, conical recess between the turbinal ridges medially and the anterior wall of the orbit (figure 14). Tatarinov (1963) has referred to it as a mesethmoidal fovea, and suggested that it contained the labyrinth of the reticulate bone, as in modern mammals. A smooth notch between the turbinal ridge and the anterior boundary of the brain fossa may represent the point at which a branch of the olfactory nerve entered the fovea. The internal surface of the rest of the nasal cavity is smooth and featureless. The root of the upper canine tooth causes only a very slight medial bulging of the wall.

The vomer bears an ossified median septum about 3 mm high for its full length, and presumably was continued dorsally as a cartilaginous internasal septum.

4. *Internal nares*

From about the level of the canines backwards, paired medially directed flanges of the maxilla and palatine bones form an incomplete secondary palate (figure 2). The anterior part of the slit-like internal naris widens slightly, and the opposing edges, of the alveolar process and the palatal process of the premaxilla respectively, are flattened. This indicates that in life this part of the naris was probably not covered by soft tissue, but remained open as a palatal fissure. In contrast, the lateral edge of the rest of the choana is sharp and smooth, and appears therefore to have supported soft tissues completing the secondary palate. The definitive internal nares are formed by the palatine bones ventrally and laterally and the expanded vomer dorsally. Because the vomer is at a more dorsal level, the nares take the form of a pair of almost circular apertures, facing postero-ventrally, and separated from one another to some degree by a thin, vertical vomerine septum. A broad, shallow vault continues the air passage backwards from the internal nares, which is bounded by a pair of well developed ridges. The vault terminates abruptly just in front of the interpterygoid vacuity, which presumably corresponds to the level of the epiglottis.

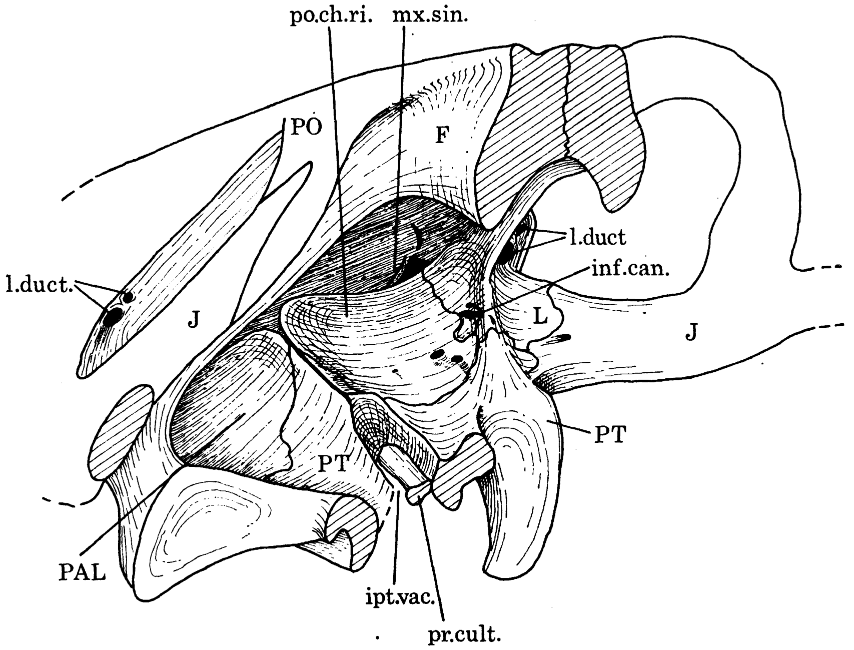

FIGURE 11. Postero-lateral and dorsal view of the palatal region. Based on a camera lucida drawing.

5. *Foramina of the snout*

Certain of the foramina of the snout have been mentioned already. Thus, the septomaxillary foramen with its associated septomaxillary canal, and the presumed naso-lacrymal duct in the premaxilla are discussed in connection with Jacobson's organ. The external foramina of premaxilla, maxilla, nasal and frontal bones have been considered in the context of the external surface of the snout.

The most extensive system for distributing nerves and blood vessels to the snout is the infraorbital canal system. Fourie (1974) described a maxillary antrum in the internal wall of the maxilla of *Thrinaxodon*, from which an infraorbital canal distributed branches of the maxillary nerve (V) and presumably branches of the infraorbital artery to various parts of the external surface of the snout. It is these canals which emerge as the external foramina of the premaxilla, maxilla and nasal bones. However, Fourie was unable to determine from his material the manner in which the nerves and blood vessels reached the maxillary antrum from behind. On the other hand, Kühne (1956) found a canal which he termed, slightly confusingly, the infraorbital canal in the tritylodont *Oligokyphus*. It runs from a foramen on the dorsal surface of the palate, between the lachrymal, maxilla and palatine bones, forwards within the suture between the lachrymal and maxilla. There is no equivalent of the maxillary antrum in *Oligokyphus*.

In *Procynosuchus*, a maxillary antrum is present, and it appears to be connected posteriorly with a canal corresponding to Kühne's infraorbital canal. The dorsal surface of the palate, behind the internal nares, is a broad, concave area consisting largely of the palatine bone, with components of the lachrymal laterally and the pterygoid postero-medially (figure 11). The anterior boundary is the post-choanal ridge, an elevated, transverse ridge meeting the internal surface of the side wall of the nasal cavity. The lateral part of the choanal ridge is formed from a medially directed plate of the lachrymal. Also near the lateral end of the post-choanal ridge is a vertical plate, probably of the palatine, which runs antero-laterally from the ridge to the internal surface of the nasal capsule. This anterior process and the post-choanal ridge between them form the walls of a deep recess in the maxilla, below the level of the lachrymal duct, which is the maxillary antrum.

Immediately alongside the lachrymal ridge which forms the lateral margin of the dorsal surface of the palate, there is a small exposure of, presumably, the maxilla between the lachrymal and the palatine (figure 11). A large foramen which is in fact a gap between the presumed maxilla and the palatine, leads into a forwardly running canal, and it is this canal which is taken to be the equivalent of Kühne's infraorbital canal. Without a sectioned skull it is impossible to be sure of the course of this canal, but it seems almost certain that it runs anteriorly through the bone to emerge in the maxillary antrum. If so, then it appears that this infraorbital canal is the route by which the maxillary nerve and infraorbital blood vessels reach the snout.

A second, much smaller foramen lies immediately above the infraorbital foramen, and is entirely within the lachrymal bone. It could be a separate opening for a canal carrying the lachrymal branch of the maxillary nerve. Such a canal is present in *Oligokyphus*, but opens from the infraorbital canal itself rather than separately (Kühne 1956). Alternatively, Kühne also describes an apparently vascular canal, close to but distinct from the infraorbital canal, running within the lachrymal bone. Yet another small foramen associated with the lachrymal lies on the crest of the lateral ridge, about 3 mm anterior to the lachrymal-pterygoid suture. It leads into an antero-medially directed canal, and this may correspond to Kühne's vascular canal just mentioned.

One final foramen probably to be regarded as part of the infraorbital system lies on the medial surface of the jugal just behind its suture with the lachrymal. It leads postero-laterally into the bone and exits, presumably, as the single relatively large foramen on the lateral surface of the jugal (figure 3*a*).

A second canal system serving the snout is found in *Procynosuchus*, which is absent from other cynodonts. Two large foramina penetrate the dorsal surface of the palatine bone medial to the infraorbital foramen (figure 11). They are associated with a short, posterior sulcus and lead into antero-ventrally directed canals. It is assumed that these canals open as the series of foramina on the palatal surface of the palatine and ectopterygoid bones (figure 2). A possible interpretation is that they carried branches of the pharyngeal artery and facial nerve to the palate. Kemp (1972*b*) suggested that they represent the remnant of a therocephalian-like suborbital fenestra, presumed to have been present in the ancestors of the cynodonts. In later cynodonts, as in mammals, these particular nerves and blood vessels reach the palate directly from behind the posterior palatal margin.

There are two other snout foramina, neither evidently connected with either the infraorbital or suborbital systems. The first is a narrow slit between the palatal process of the premaxilla and the vomer (figure 2), which has not been described in other cynodonts. It may perhaps have carried the spheno-palatine branch of the maxillary nerve, which in modern mammals supplies parts of the nasal cavity. The second is the prominent posterior palatal foramen, lying in the suture between the palatal processes of the maxilla and palatine bones (figure 2). It is large and lies in the middle of a short, antero-posteriorly oriented sulcus. All cynodonts possess this foramen, and presumably it is the homologue of the mammalian posterior palatal foramen, which carries the palatine artery of the internal carotid system, along with the palatine nerve of the maxillary branch of the facial nerve.

Finally mention should be made of the lachrymal canal, which opens posteriorly by the usual two foramina in the anteriormost region of the orbit (figure 11). The dorsal aperture is smaller than the lower one, and the latter is associated with a small depression on the floor of the orbit, probably for the lachrymal gland. The duct runs anteriorly through a longitudinal ridge on the inner surface of the lachrymal, to open about 10 mm anterior to the orbital wall, immediately above the maxillary antrum.

THE BRAINCASE

Following the establishment of the general structure of the braincase of *Thrinaxodon* by Watson (1920), the detailed anatomy of this form is virtually completely known as a result of the study of serially ground specimens by Olson (1944) and Fourie (1974). The braincase of the present specimen of *Procynosuchus* shows considerable resemblance to that of *Thrinaxodon* and therefore the following account concentrates on points of difference which do exist, and on problems of interpretation of the functional and morphological significance of the anatomy.

1. *Interpterygoid vacuity and basipterygoid articulation*

In contrast to later cynodonts, except possibly juveniles (Estes 1961, but see Fourie 1974), a relatively large interpterygoid vacuity exists between the pterygoids (figures 2 and 12). Its sides are deep and the anterior three quarters of the dorsal margin is a sharp crest. The posterior part of the dorsal margin is smoothly rounded. The processus cultriformis of the parasphenoid completely bisects the vacuity to insert for a very short distance between the pterygoids anteriorly. It is a slender rod, round in cross-section except that the dorsal surface is in the form of a groove which presumably supported an unossified interorbital septum.

The basipterygoid articulation is very similar to that of *Thrinaxodon* with powerful basipterygoid processes extending anterolaterally to buttress against the pterygoids (figures 2, 12 and 16). The dorsal surface of the pterygoid is overlaid by a thin medial sheet of the epipterygoid which contacts the dorsal, posterior and ventro-lateral surfaces of the basipterygoid process. The degree of ventral exposure of this part of the epipterygoid is rather less than in *Thrinaxodon.* A delicate mid-ventral septum, continuous with the processus cultriformis in front, lies between the basipterygoid processes. A little further back there is a short, round process on the ventral surface of the parasphenoid, immediately behind the ventral openings for the internal carotid artery, whose significance is not clear.

Undoubtedly the interpterygoid vacuity is a primitive character retained in *Procynosuchus* from therocephalian-like and ultimately pelycosaurian ancestors. It is unlikely that any nerves or blood vessels passed through the vacuity since in later cynodonts no foramen exists between the processus cultriformis and the pterygoid. The interpterygoid vacuity is perhaps best interpreted as a remnant of a cranial kinetic mechanism, subsequently locked in the line leading to cynodonts. There is evidence for cranial kinetism in scaloposaur therocephalians (Crompton 1955*a*), which involves mobility of the basipterygoid articulation. In cynodonts the structure of the basipterygoid articulation clearly precludes any possibility of movement of the braincase relative to the palatoquadrate. However, in many reptiles the form of the basipterygoid process of the basisphenoid is similar to that of *Procynosuchus* but differs in having a rounded antero-lateral end which connects moveably with a socket formed from the palato-quadrate. In cynodonts the formation of a suture between the components of the basipterygoid articulation appears to have locked this joint, and the insertion of the processus cultriformis between the pterygoids anteriorly has strengthened it. Further strengthening of the connection of the braincase to the palato-quadrate occurred in later cynodonts by closure of the now redundant interpterygoid vacuity.

Further evidence that cranial kinetism occurred in the ancestors of cynodonts is the absence of ossification at the top of the supraoccipital bone, described below (page 111; figures 13 and 14), suggesting that movement was formerly possible between the supraoccipital and the postero-dorsal bones above it.

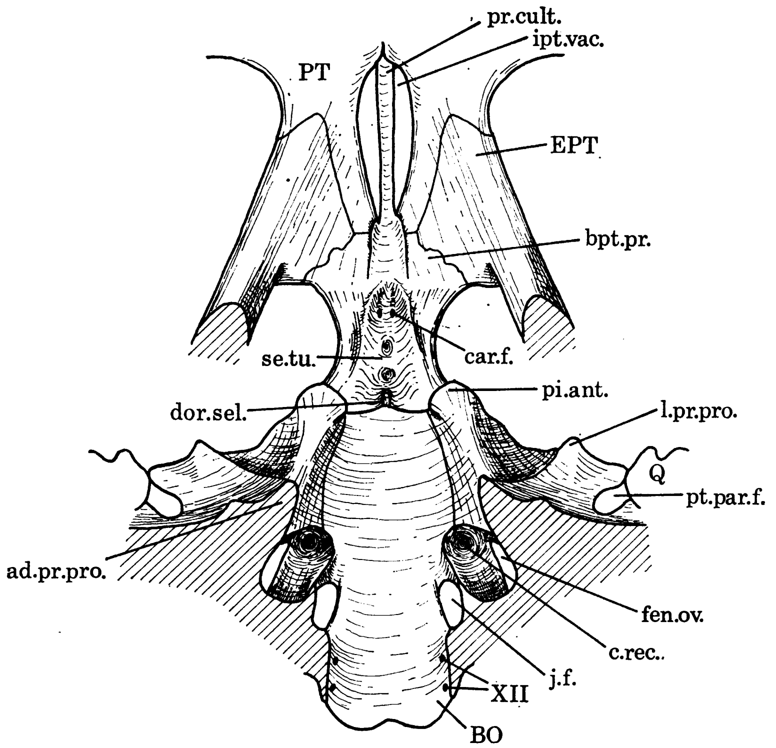

FIGURE 12. Reconstruction of the floor of the braincase in dorsal view. (Magn. × 2.)

2. *Sella turcica and unossified zone*†

Posterior to the interpterygoid vacuity, the dorsal surface of the para-basisphenoid bears a pair of rather irregular ridges, diverging slightly from the point of origin of the processus cultriformis, and between which the bone forms a shallow trough. Lateral to each ridge the

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† See figure 12.

bone surface is flat and horizontal, and forms the dorsal surface of the basipterygoid process, meeting the epipterygoid antero-laterally. From the level of the hind edges of the basipterygoid processes, a pair of high, narrow ridges arises, diverges posteriorly, and defines the lateral limits of the very long, but shallow sella turcica. The posterior boundary of the sella is marked by a small, squat, median dorsum sellae occupying the hindmost part of the basisphenoid, which appears to be slightly better developed than in *Thrinaxodon* where Fourie (1974) describes it as practically non-existent. A small depression lies immediately anterior to the dorsum sellae, and further forwards a second wider, but shallower depression is present. These two are quite distinct from one another and the floor of each has a series of minute nutritive foramina. It seems that the pituitary gland had two ventral lobes arranged in tandem and was not deeply inserted into the bony braincase floor.

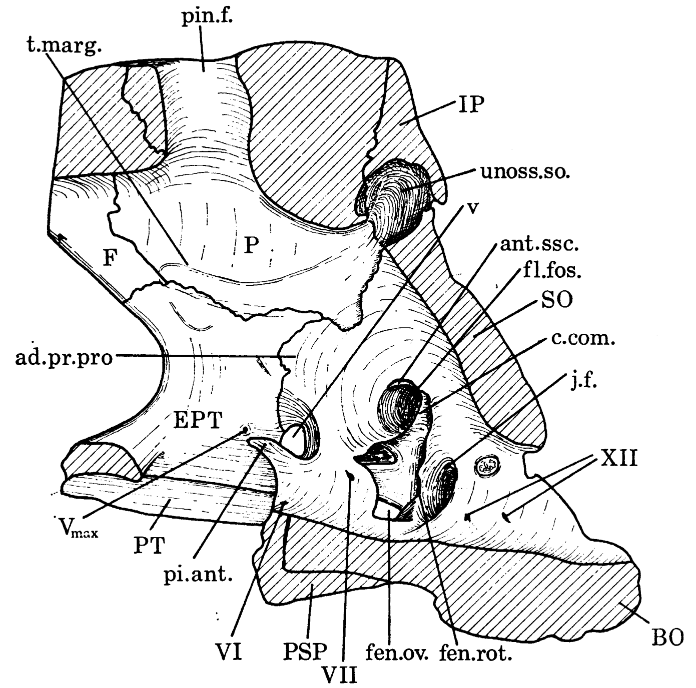

FIGURE 13. Internal view of the right side of the braincase as preserved but with details of the left side incorporated. (Magn. approx. × 2.)

The paired internal openings of the internal carotid canal lie right at the front of the sella turcica and a short groove runs anteriorly from each towards the front margin of the sella.

The posterior edge of the basisphenoid is straight and is separated from the basioccipital by a narrow fissure, the unossified zone of Olson (1944), which was presumably cartilage-filled in life. The postero-lateral corner of the basisphenoid makes a buttressing contact with the vertical anterior edge of the prootic, immediately below the pila antotica, and this suture too is open and in line with the unossified zone.

3. *Cranial nerves*

The exit for the trigeminal nerve is basically similar to that of other cynodonts. Medially (figure 13) it is a large notch between the antero-dorsal process of the prootic and the pila antotica (antero-ventral process of the prootic), and because the pila antotica does not contact the epipterygoid, this medial rim is incomplete anteriorly. The dorsal surface of the pila antotica extends laterally to form a delicate, concave floor to the cavum epiptericum (figure 12), almost but not quite reaching the epipterygoid laterally. It is smoothly continuous with the broad, anterior face of the main body of the prootic behind, and the latter in turn is continued dorsally by the almost equally broad underside of the antero-dorsal process of the prootic. Thus a relatively long tunnel runs postero-laterally from the medial rim of the trigeminal foramen, to carry the trigeminal nerve to the outside of the braincase (figure 16). The lateral rim of the tunnel is complete, being formed from the posterior edge of the epipterygoid in front, the root of the quadrate ramus of the epipterygoid ventrally, and the lateral prootic process postero-ventrally. The trigeminal tunnel is separated from the lateral prootic process by a sharp bend of the prootic, and it presumably housed the trigeminal ganglion.

A small, but distinct foramen pierces the epipterygoid about 2 mm in front of the trigeminal foramen, clearly present on the right side but more doubtful on the less well preserved left (figures 13 and 16). It probably represents a separate exit for the maxillary branch of the trigeminal nerve despite its small size. There is no evidence regarding the course of the branches of the trigeminal nerve after they leave the braincase.

A small foramen emerges from the ventral part of the prootic, about 4 mm from the anterior edge and immediately above the line of contact with the basisphenoid (figure 13). It corresponds to the position of a foramen described by Parrington (1946) in *Thrinaxodon* and is probably the exit for the cranial nerve VI. Fourie (1974) described a notch, rather than a foramen, immediately below the pila antotica for that nerve.

The single foramen for the facial nerve VII pierces the prootic immediately in front of the apex of the fenestra ovalis (figure 13). It runs antero-laterally through the thickness of the bone and emerges beneath the ridge forming the lateralmost part of the floor of the trigeminal canal (figure 16).

Because of the failure of ossification separating the inner ear from the brain cavity, no foramen for the acoustic nerve VIII is present, in contrast to *Oligokyphus* and mammals.

The jugular canal for cranial nerves IX, X and XI is developed normally and is separated from the internal auditory meatus by a ridge (figure 13). There is a broad, shallow sulcus running antero-medially across the floor of the braincase from the internal opening of the canal, well shown on the right side (figure 12). Two separate hypoglossal canals leave the brain cavity posterior to the jugular foramen, to open into the medial wall of the jugular canal just before its external termination.

4. *Blood vessels*

Very little can be deduced about the course of the arteries in the braincase region. The size of the stapedial foramen of the stapes may indicate that the stapedial artery was well developed, branching off the internal carotid artery. The course of the latter artery cannot be determined until it reaches a groove on either side of the parasphenoid, which runs antero-medially for about three millimetres to the internal carotid foramen (figures 2 and 16). The groove is consistent with a course of the artery from high up in the tympanic cavity, antero-ventrally along the side of the para-basisphenoid. A small, narrow foramen leads off this path into the lateral wall of the para-basisphenoid anterior to the lower part of the fenestra ovalis (figure 16). The ventral emergence of such a branch of the internal carotid artery is probably the series of small foramina on the ventral surface of the parasphenoid and anterior part of the basioccipital (figure 2). The ventral openings of the paired internal carotid arteries into the braincase lie close together, separated by a very fine ridge. The dorsal openings of the carotid canals lie a little further anterior, in the anterior region of the sella turcica, and from each a short groove runs antero-dorsally to the front of the sella (figure 12).

Other foramina in the braincase region which are probably also arterial, although possibly for nerves as well, leave the internal surface of the frontal bone. One lies in the dorsal part of the process that descends to meet the antero-dorsal corner of the epipterygoid (figure 13), and another (figure 14) pierces the braincase roof medial to the postorbital bar, just medial to the ridge marking the anterior part of the brain. On the right side a further foramen lies 4 mm posterior to the latter, and is represented on the left side by two much smaller foramina. These foramina cannot be followed through the bone, but they probably represent the blood supply which emerges onto the external roof of the skull through the foramina of the interorbital region (figure 1). One possible implication of this arrangement is that these foramina were supplied from the internal carotid system within the braincase, which was thus a better developed system than in modern mammals, where practically the entire external surface of the skull is supplied by the external carotid artery system.

The course of the main veins in the head of cynodonts has been discussed by Watson (1911) for *Diademodon* and by Fourie (1974) for *Thrinaxodon*. They agree that a persistent vena capitis lateralis ran from the trigeminal foramen back across the lateral surface of the prootic, to leave the skull via the pterygo-paroccipital foramen (between the lateral process of the prootic, the quadrate ramus of the pterygoid, and the paroccipital process). A vein also ran forwards through the post-temporal fenestra from the occipital region to join the vena capitis lateralis, and another vein, occupying the dorsal gutter between the parietal and prootic, ran ventrally down the posterior part of the prootic, also to join the vena capitis lateralis. A foramen is described by both authors along the course of the dorsal gutter, lying between the epipterygoid, the prootic, and the parietal and opening into the braincase. Following Cox (1959) who considered the veins of dicynodonts, Fourie (1974) regards the vein in the gutter as equivalent to the vena capitis dorsalis of modern reptiles and a further vein, anterior to the foramen, is described as the vena capitis parietalis, also found in modern reptiles. There are minor disagreements between Watson, Cox and Fourie on the arrangement of the connections between these veins.

The anatomy of *Procynosuchus* does not accord with this general scheme on a number of points. In the first place, the gutter for the supposed vena capitis dorsalis and parietalis, while prominently developed (figure 16), lies well above the line of the suture of the parietal with the epipterygoid and the prootic, and there is no foramen opening into the cranial cavity along its course. It commences abruptly anteriorly and runs horizontally backwards, widening towards its posterior end. Here it joins a wide vertical channel down the prootic, as in other cynodonts, and terminates at the pterygo-paroccipital foramen. The smooth, round post-temporal fenestra opens anteriorly into the vertical channel close to the pterygo-paroccipital foramen.

The second major difference is that there is no indication of a channel running across the lateral face of the prootic for the vena capitis lateralis. Certainly the anterior edge of the vertical channel is not interrupted at any point above the pterygo-paroccipital foramen. On the other hand, a groove runs anteriorly from the ventral rim of the pterygo-paroccipital foramen, immediately below the lateral prootic process, towards the facial foramen (figure 16). Thus the vena capitis lateralis, if present, must have run ventral to the lateral prootic process. There is no positive evidence that it continued past the facial foramen to the trigeminal foramen, but this would nevertheless be expected. A third difference (or possibly a point not considered before) is the relatively large size of the jugular foramen, which is about 3 mm in diameter and clearly gave exit to a well developed internal jugular vein of a mammalian kind. Relevant points on which *Procynosuchus* agrees with other cynodonts are the size of the trigeminal foramen, suggesting a major outlet for a vein in addition to the nerve, and the presence of a notch on either side of the foramen magnum (figure 3*b*), presumably for a vertebral vein.

Comparatively speaking, the venous system of the head of modern reptiles is dominated by a persistent vena capitis lateralis, running laterally to the otic capsule, and fed by a vena cerebralis media emerging through the trigeminal foramen. A vena cerebralis posterior leaves the cranial cavity via the foramen magnum to reach the jugular vein, and in some forms a branch of the latter emerges through the jugular foramen (Bruner 1907; O'Donoghue 1920). Those reptiles which have a vena capitis dorsalis use it to drain blood into the cranial cavity, where it links up with the vena cerebralis media. In mammals, the vena capitis lateralis is more or less lost (except in monotremes). Blood draining from the well developed dural sinuses within the cranial cavity leaves via a series of emissary veins to the external jugular vein (Butler 1967). There is a great deal of variation among different mammals, but generally the important emissary veins are the prootic emissary via the trigeminal foramen, the postglenoid emissary via the spheno-parietal fontanelle (the foramen jugular spurium of the adult), the vertebral vein through the foramen magnum, and the internal jugular vein through the jugular foramen, which is relatively small in most forms.

Because of the great variation among living reptiles on the one hand and among mammals on the other, there is no reason to suppose that there was a single pattern of head drainage in cynodonts, even less that cynodonts can be expected to demonstrate an intermediate stage between living reptiles and mammals, in any detail. From the evidence available, *Procynosuchus* appears to have had the following system. The vena capitis lateralis, if present at all, was not well developed and ran back from the cavum epiptericum (between the prootic and the epipterygoid, near to the trigeminal foramen), passed close to the facial foramen and ran immediately below the lateral prootic process. In accordance with living reptiles and mammalian embryos, the vena capitis lateralis left the head by running postero-ventrally below the paroccipital process. A large vein, perhaps the homologue of the reptilian vena capitis dorsalis, drained the temporal fenestra, collected in the gutter along the parietal bone, and descended down the posterior part of the prootic to the pterygo-paroccipital foramen (figure 16). It was joined by a vein from the occipital region which entered the head through the post-temporal fenestra. Presumably the dorsal-plus-occipital vein connected up with the vena capitis lateralis ventral to the pterygo-paroccipital foramen, together forming what might be regarded as an internal jugular vein. Several veins emerged from the cranial cavity, through the large trigeminal foramen, possibly through the smaller but still substantial facial foramen, through the very large jugular foramen, and through the foramen magnum. Since what evidence there is indicates that a large vena capitis lateralis was not present, at least some of the emerging veins must have fed directly into an external jugular system and must therefore have been functional equivalents of the emissary veins of mammals. The size of the trigeminal foramen in particular, suggests that the homologue of the mammalian prootic emissary vein had developed, running through the cavum epiptericum. That the head venous system shows these signs of a significant approach to a mammal-like system is an indication of the possibility that intracranial dural sinuses of a mammal-like form had also evolved (Butler 1967), although there is no direct evidence for them from the internal surfaces of the bones of the braincase. Another possible correlation with elaboration of the blood system is enlargement of the brain, and as discussed below, there is direct evidence for this.

5. *The brain*†

Reconstruction of the gross morphology of the brain is difficult because, by comparison with living reptiles, there is no certainty that it filled the cranial cavity, unlike the case in mammals. There is the added difficulty that in certain respects the therapsid brain differed from all extant vertebrates and therefore direct assumptions about the relative size and position of constituent parts may be unreliable. Nevertheless, certain facts about the brain anatomy can be established and there are some assumptions that can be reasonably made. With these, a restoration of the brain of *Procynosuchus* is attempted and the result is a picture of a brain which certainly could have fitted into the braincase and is probably the best approximation presently available.

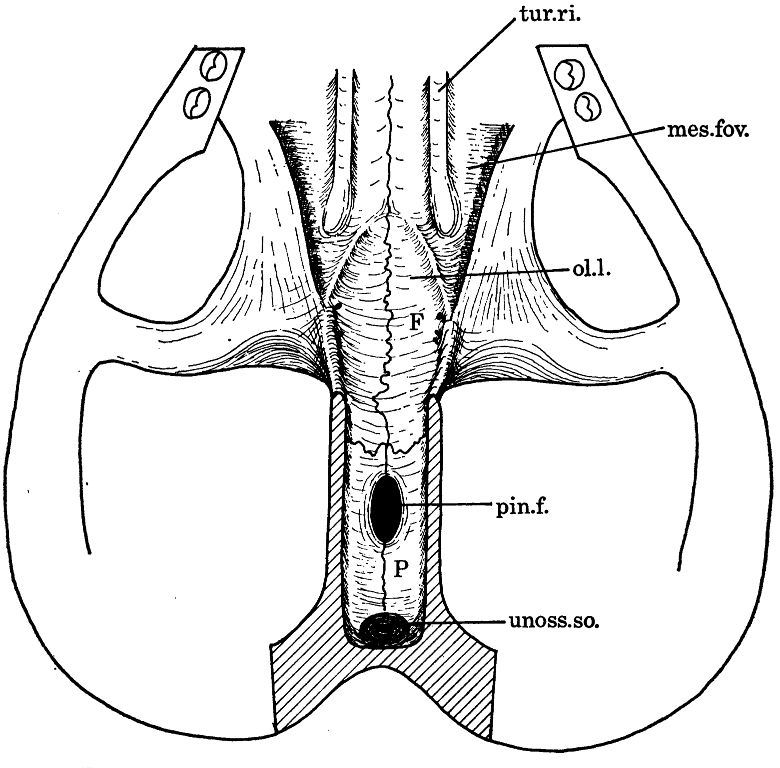

FIGURE 14. Reconstruction of the internal surface of the skull roof. (Magn. × 1.5.)

Four parts of the brain can be restored fairly confidently.

1. The olfactory lobes occupied the fossa on the ventral surface of the frontal bones (figure 14). The fossa is incipiently double, for there is a slight median ridge. It is bounded antero-laterally by well developed ridges, which reduce in height anteriorly, but just meet in the midline in a rugose area which probably marks the attachment of an unossified mesethmoid element. Immediately anterior to the ridges are the pair of turbinal ridges, a clear indication that this fossa housed the anteriormost part of the brain, which must have been the olfactory lobes. The fossa is concave both from side to side and antero-posteriorly, indicating that the

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† See figure 15.

lobes were bulbous. The depth of the lobes is not known, and the length can only be approximate since there is no definite posterior boundary. However there is a change from concave to slightly convex just behind the level of the postorbital bar, which presumably marks the limit of the lobes and gives them a length of about 13 mm. The maximum width of the fossa, which occurs about halfway along it, is about 10 mm.

2. The position and approximate dimensions of the cerebellum are indicated by a marked concavity in the medial wall of the posterior part of the braincase (figure 13). The floccular fossa lies in the centre of this area. Anteriorly, the concavity occupies the dorsolateral process of the prootic and dorsally it reaches to the top of the supraoccipital part of the braincase. Posteriorly, it is continuous from one side of the braincase to the other across the supraoccipital bone. Ventrally, it is not well defined because of the widely open internal auditory meatus. The minimum dimensions indicated for the cerebellum are 11 mm from front to back, 11 mm dorso-ventrally and, allowing for the slight crushing of the braincase, about 15 mm wide. In addition, the floccular fossa is very prominent indeed as a hemispherical pocket about 4 mm deep. It runs posterio-medially and, as described later, has a typically close relationship with the semicircular canals.

3. The position of the pituitary, and hence presumably the overlying hypothalamus, is indicated by the sella turcica (figure 12). As described, the sella turcica is a long, narrow but fairly shallow pocket, with two small separate depressions in the midline. The fact that these depressions are formed may be taken as evidence that this part of the brain did in fact lie within the sella.

4. The brain stem, including the medulla oblongata, is indicated by the form of the floor of the braincase (figure 12). It is transversely concave, showing that the brain was in contact with it (as Olson (1944) concluded). The width increases between the level of the fenestra ovalis and the trigeminal opening, which may indicate the development of a mammal-like pons. Olson (1944) found evidence for a pons in cynodonts and other therapsids in the form of a paired depression in the floor of the braincase at about the level of the floccular fossa. These depressions are connected by a transverse depression at their anterior ends. In *Procynosuchus* there is such a depression in the floor immediately antero-medial to the right jugular foramen. It is not evident on the left side, presumably due to distortion, and there is no bridge apparent.

5. Since the base of the brain apparently filled the lower part of the braincase, and yet there are no indications of the course of the cranial nerves on the internal surfaces of the bone, it can be assumed that these nerves connected to the brain at least fairly close to the positions of their respective foramina in the braincase.

There is very little direct evidence about the structure of the brain between the olfactory lobes, the cerebellum, the brain stem and the pituitary and certain assumptions must be made to allow completion of the brain reconstruction. The first assumption is that the cerebrum was substantially larger than the cerebellum. This is true of all groups of living tetrapods and there is certainly no reason to suspect that cynodonts were highly aberrant in this regard. Thus it becomes clear that most of the space between the olfactory lobes and the cerebellum was occupied by the cerebrum. The optic lobes could not have been very large and may well have been reduced almost to mammal-like corpora quadrigemina. A second assumption is that the brain could have extended anteriorly to the epipterygoid. There is no indication that the front of the epipterygoid had any particular relationship to the brain, and it certainly could not

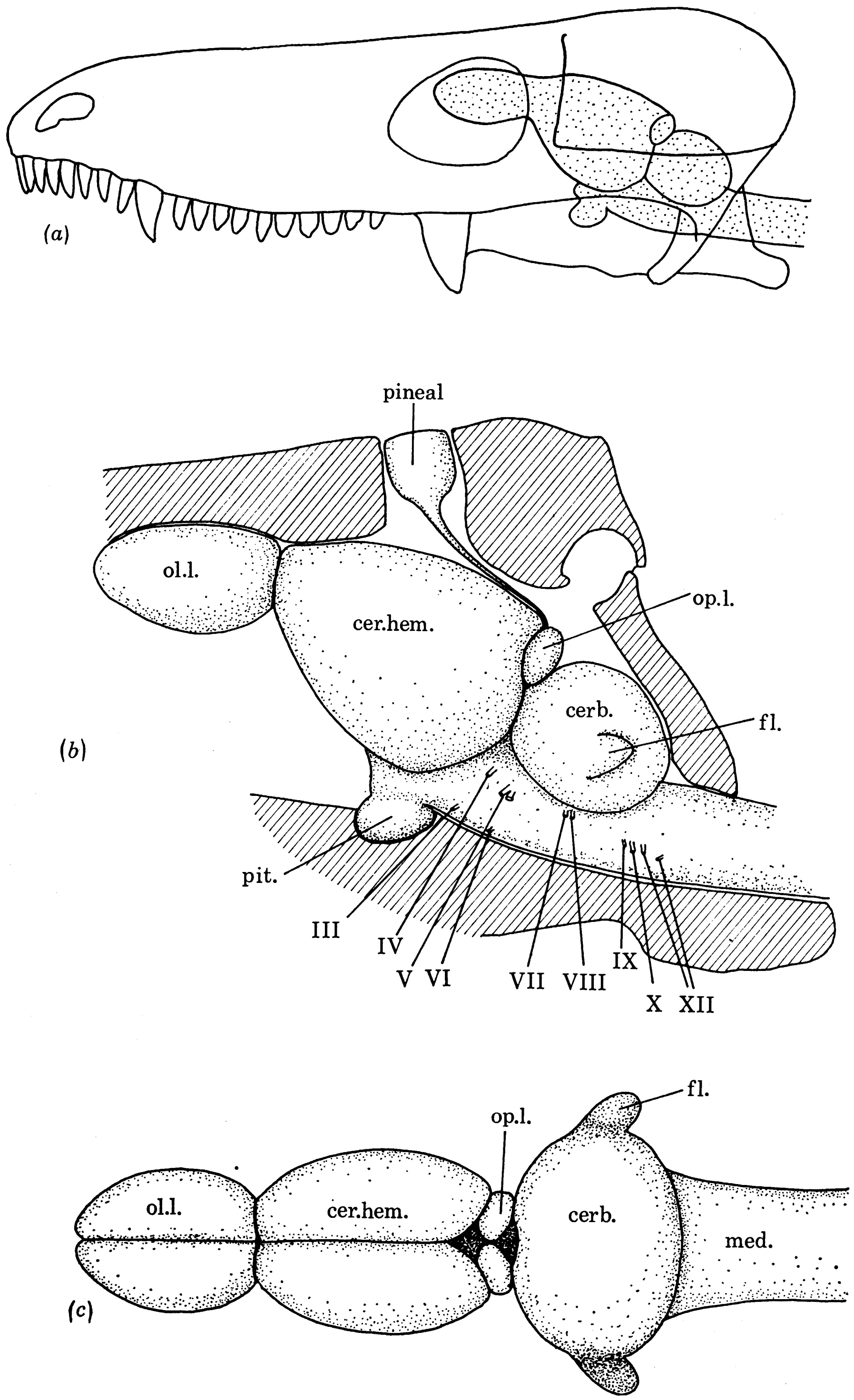

FIGURE 15. Reconstruction of the brain. (*a*) position of the brain in the skull. (Magn. × 1.) (*b*) **lateral** view of the brain. (Magn. × 2.) (*c*) dorsal view of the brain. (Magn. × 2.)

have reflected accurately the lateral profile of the cerebrum. There is no reason why the brain should not have been protected only by connective tissue or cartilage in front of the epipterygoid since it lies deep within the skull. The only possible direct evidence on the anatomy of the cerebrum is a shallow, concave area in the inner face of the parietal bone below the pineal canal (figure 13). Given the need for a cerebrum larger than the cerebellum, there is no other part of the brain that could have occupied this hollowing. Further ventrally however, there is no indication on the side wall of the epipterygoid of the brain. Within the context of these remarks, the dimensions of the cerebrum can be assessed as a maximum width, occurring towards its ventral part, of about 13 mm, a length of perhaps 19 mm, and a vertical height of some 15 mm.

The relatively enormous pineal foramen indicates the presence of a fully developed pineal eye, presumably complete with lens and retina. Although this organ is associated with the epiphyseal region of the diencephalon of the brain, those modern reptiles in which it persists have the pineal eye connected by a long stalk, and presumably the same was true here. The epiphysis must have lain deep down between the paired cerebral hemispheres, much as it does in modern mammals, which have lost the functional pineal eye.

The reconstruction of the brain based on this discussion is particularly surprising in its size and generally mammal-like proportions (figure 15*a*). Indeed, compared to the brain of a similar sized *Didelphis* skull, there is not very much difference. The mammal has a somewhat wider cerebrum, although the lateral appearance of the brain of the two is similar. An endocranial cast of this particular *Didelphis* skull fits into the brain case of *Procynosuchus* comfortably, apart again from being a little too wide in the cerebrum. It seems likely therefore that the brain of cynodonts has been under-rated hitherto and, in keeping with much else of its anatomy, cynodonts are far more mammalian than reptilian as far as comparisons with living forms are concerned.

6. *The inner ear*†

The structure of the inner ear corresponds closely to that of *Thrinaxodon* as described by Olson (1944), Estes (1961) and Fourie (1974). The internal auditory meatus is freely open medially into the brain cavity. It is bounded posteriorly, and thus separated from the jugular foramen by a prominent ridge of bone, presumably of the opisthotic part of the braincase, in which there is a notch where the foramen rotundum probably opened into the jugular canal. The sacculo-cochlea recess is indicated both anteriorly and posteriorly by the concave impressions in the periotic bone immediately internal to the antero-ventral and postero-ventral margins of the fenestra ovalis (figure 12). Where these two walls meet ventrally, immediately internal to the lowest point of the fenestra ovalis, there is a cochlea recess in the braincase floor. It is about 3 mm in diameter and 4 mm deep.

The posterior ampulla of the semi-circular canals is high and narrow, lying postero-laterally to the hind margin of the internal auditory meatus. The apertures for the posterior and horizontal canals lie deep within it. As in other cynodonts, the anterior and external ampullae are confluent, together forming a deep, low space with the entrance overhung by a well developed shelf of the prootic (figure 13). With reference to the skull base, this recess lies at about the same level as the posterior ampullary recess. Above this level, the internal auditory meatus narrows to a vertical groove behind the floccular fossa, which indicates the crus communis. The postero-dorsal part of the anterior canal runs around the top of the floccular fossa,

† See figure 13.

unossified medially, to the crus communis. The dorsal aperture of the posterior vertical canal is also seen at the top of the crus communis. This has evidently been misinterpreted by Watson (1913) and Simpson (1933) as a ductus endolymphaticus.

The large foramen ovalis lies ventro-laterally to the internal auditory meatus.

7. *The morphology of the side wall of the braincase*

The composition of the side wall of the cynodont braincase between the otic capsule and the orbit is of particular interest because of the fundamental differences between mammals and reptiles in this feature, and because of the difference that exists between the therian mammals and the non-therian mammals (monotremes, eozostrodonts, triconodonts and multituberculates) respectively (Kermack 1967; Kermack & Kielan-Jaworowska 1971).

The epipterygoid (figures 13 and 16) has a characteristically cynodont form, with the broad processus ascendens making flush, finely inter-digitating sutures with the frontal and parietal bones dorsally. The processus ascendens of *Procynosuchus* is lower relative to the total skull height than in *Thrinaxodon*. The extensive posterior contact of the epipterygoid with the dorso-lateral process of the prootic is slightly damaged by crushing on both sides. The ventral part of the suture, above the trigeminal foramen, is a flush, slightly interdigitated suture between two bones of equal thickness. However the dorsal half of the suture consists in addition of a thin, short, anterior extension of the prootic plastered to the medial face of the epipterygoid. It would seem to correspond to the process actually referred to as the dorso-lateral process in *Thrinaxodon* by Fourie (1974), although here it is less well defined. There is no venous foramen between the parietal, epipterygoid and prootic as described in other cynodonts. A short ridge lies on the inner surface of the epipterygoid immediately in front of the antero-dorsal process and oriented antero-dorsally (figure 13).

The epipterygoid forms the anterior margin of the large trigeminal foramen. Immediately in front of it there is a second, much smaller foramen which can only be for the maxillary branch of the trigeminal nerve (v_2). It lies entirely within the epipterygoid, as described earlier (page 103). The ventral part of the epipterygoid contributes to the basipterygoid articulation as described earlier (page 100). Further back the base of the epipterygoid lies against the lateral surface of the quadrate ramus of the pterygoid, but sends a low flange a short distance down the medial face of the pterygoid as well. The posterior ramus of the epipterygoid ends abruptly at the level of the posterior edge of the trigeminal foramen, and only the pterygoid continues backwards to contact the quadrate.

The second bone contributing to the side wall of the braincase is the prootic. The ossified pila antotica (antero-ventral process) lies well medial to the epipterygoid and does not contact it, and the pair of pilae antoticae are well separated from each other by the broad basisphenoid. Each is pierced near its base by the foramen for the abducens nerve (see page 103). The manner in which the dorsal surface of the pila antotica expands laterally to form a partial floor to the canal through which the trigeminal nerve left the braincase has been described on page 103. The antero-dorsal process, or anterior lamina, of the prootic is a broad sheet in sutural contact with the epipterygoid. The lateral process of the prootic is a broad flange at the base of the lateral surface of the bone, which curves smoothly round from the vertical body of the prootic to its almost horizontal lateral part, which is in sutural contact with the quadrate ramus of the pterygoid (figure 2). Possibly its anterior tip met the posteriormost part of the epipterygoid, but because of some degree of disarticulation of the bones this is not certain. The distal edge of the lateral process runs postero-laterally and contacts a facet on the quadrate, immediately above the contact between the pterygoid and quadrate bones.

A feature of the braincase not described in other cynodonts is a shallow but very distinct trough on the medial surfaces of the parietal and epipterygoid bones (figure 13). It commences abruptly along the line of suture between these two bones, a little way behind the anterior margin of the epipterygoid, then runs backwards to reach the large medial space lying above the supraoccipital at the postero-dorsal corner of the skull. The anterior part of the trough has a ventral extension, behind which it narrows. It then gradually increases in height backwards. The dorsal edge is sharply delimited, as is the ventral edge along the epipterygoid part of its course. However, there is no distinct ventral margin at the level of the prootic and supraoccipital bones. The trough appears to be the site of attachment of the cartilaginous taenia marginalis (dorso-lateral wall of the chondrocranium) connected posteriorly with an unossified tectum synoticum occupying the space above the supraoccipital bone. The swollen anterior end of the supposed taenia marginalis lies along an antero-dorsal projection of the pila antotica and thus probably indicates the region where these two cartilages met.

The standard interpretation of the side wall of the therapsid braincase is that of Olson (1944) who regarded the antero-ventral process of the prootic as an ossified pila antotica, a view universally accepted on the grounds of its relationship to the trigeminal foramen, the abducens foramen, and the basicranium. Olson regarded the antero-dorsal process of the prootic as an ossification of the taenia marginalis. Although accepted for therapsids generally, there is some doubt about this interpretation for cynodonts, in which the process is much broader and has developed a sutural contact with the epipterygoid. Most recently, Presley & Steel (1976) compared the antero-dorsal process of cynodonts with the anterior lamina of the monotreme skull, which is a membrane bone ossifying in the lamina obturans, morphologically in the same plane as the epipterygoid. As such it lies lateral to the cavum epiptericum, whereas the taenia marginalis is in a plane medial to the cavum epiptericum. They consequently suggest that the antero-dorsal process of cynodonts is a neomorph and not homologous with the structure of the same name in other therapsids. The condition in *Procynosuchus* described here indicates that at least the inner part of the antero-dorsal process is an ossification in the same plane as the taenia marginalis. This is shown by the continuity of the trough for the taenia marginalis with the antero-dorsal process, by the lack of any form of discontinuity between the antero-dorsal process and the pila antotica, and possibly by the small, but definite medial overlap of the epipterygoid by the antero-dorsal process. On the other hand, there is some support for the idea that the prootic also had a membrane component, fused to its lateral surface, in the flush sutural contact laterally between the antero-dorsal process and the processus ascendens of the epipterygoid. If the suggested membranous component is regarded as an ossification in the lamina obturans, which has become fused to the chondrocranial ossification forming the true antero-dorsal process, then it is simple to achieve the subsequent non-therian mammal condition by expansion of the membranous component, much as Hopson (1964) has proposed.

Presley & Steel (1976) also doubted the homology of the cynodont processus ascendens of the epipterygoid with the ala temporalis of therian mammals, because in the former both the maxillary nerve (V_2) and the mandibulary nerve (V_3) emerge behind the processus ascendens, while in the mammals the ala temporalis separates the exits for these two nerves. The present specimen of *Procynosuchus* evidently has a separate exit for V_2, lying completely within the epipterygoid. Thus it seems possible for the ossification of the epipterygoid ascending process itself to form a foramen rotundum for this nerve, and there is no need to deny that the ala temporalis is a simple derivation of the processus ascendens of the epipterygoid.

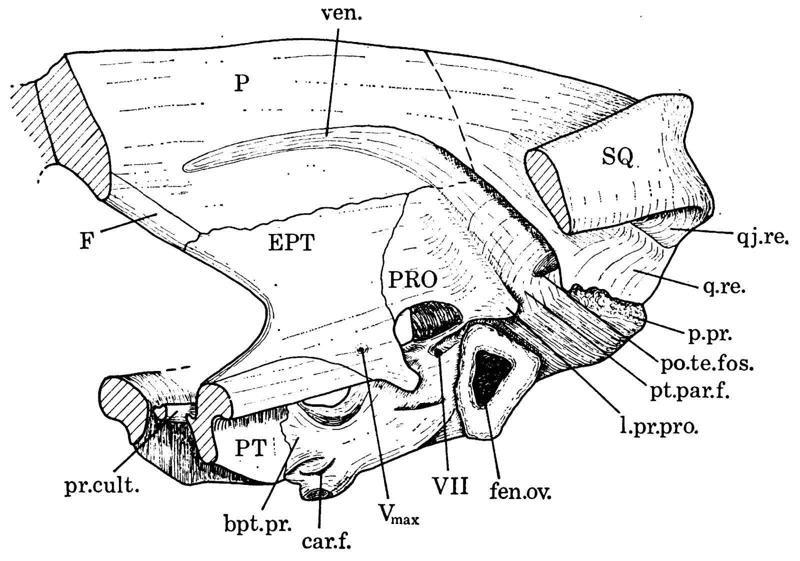

Figure 16. Antero-lateral and ventral view of the posterior half of the skull. Based on a camera lucida drawing.

The middle ear

1. *Description*†

The left stapes (figure 17) alone is present and was preserved isolated, close to the left orbit of the skull. It is extremely well-preserved, although the distal end was apparently completed by cartilage. The orientation is based on the descriptions of *Thrinaxodon* by Parrington (1946), Estes (1961) and Fourie (1974), who all agree that the stapedial foramen faced ventrally and the more slender of the two edges lay posteriorly. The dorsal surface is presumed to be indicated by an oblique ridge distal to the foramen (figure 17*a*), which is interpreted as an ill-developed dorsal process. The proximal face (figure 17*b*), which fits into the fenestra ovalis, lacks a periosteal layer and is about twice as long as high. It decreases in height towards the back, but is close to oval in shape. The bar of bone anterior to the foramen is both thicker and deeper than the posterior bar, and the foramen itself is relatively huge. Distally, the ventral surface is concave (figure 17*c*), suggesting a possible site for attachment of a small muscle. The dorsal surface is marked by a sharp, but low ridge running postero-laterally from the front to the hind margins. With the stapes held in place, this oblique ridge contacts the overlying paroccipital process and thus is probably the homologue of the more prominent dorsal process of the stapes seen in other cynodonts. Distal to the ridge, the dorsal surface lacks a periosteal layer, as does the distal end itself (figure 17*d*), and was therefore probably completed in cartilage. The stapes must have contacted the quadrate distally. A perfectly preserved boss occupies the posterior face of the right quadrate (figure 9), in the ventromedial region and defines a small, oval, concave area lateral to it. Medial to the boss, the quadrate is very thin and oriented almost transversely, and the medial edge is sharp.

† See figures 16 and 17.

Because of the small size of the boss, the stapes could only have made a very limited contact with the quadrate, certainly less than half the width of the distal end of the stapes actually touching the quadrate. The greater part of the distal end must have projected posteriorly behind the level of the quadrate.

The fenestra ovalis (figure 16) is well-preserved on both sides, although a little distorted on the right. It approximates to an equilateral triangle with one apex antero-dorsal, one antero-ventral and the third posterior. Each side is slightly convex and is formed from a thick ridge of bone lacking a periosteal layer. The plane of the fenestra faces laterally and slightly antero-ventrally. The proximal end of the stapes is a little longer than the maximum dimension of the fenestra, but is substantially lower. Thus the stapes more than fills the upper part of the fenestra, but leaves the lower part, particularly the antero-ventral region, clear.

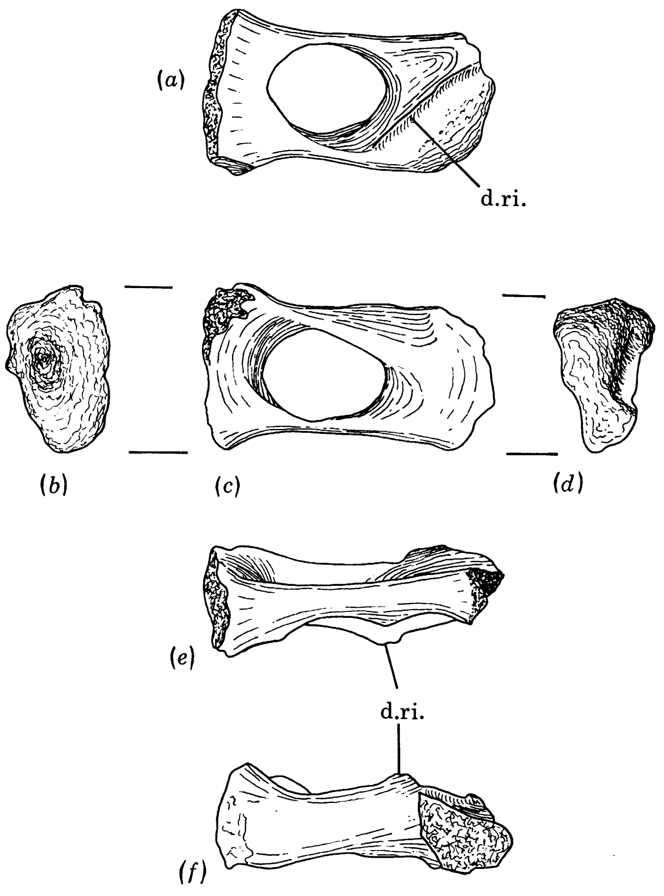

Figure 17. Left stapes in (*a*) dorsal view, (*b*) proximal view, (*c*) ventral view, (*d*) distal view, (*e*) posterior view, (*f*) anterior view. (Magn. × 4.)

The tympanic cavity is not defined in bone except for the ventral surface of the paroccipital process, which forms the postero-dorsal wall. Its plane coincides with the postero-dorsal rim of the fenestra ovalis and it is slightly concave from both front to back and medial to lateral.

Unlike the later cynodonts, *Procynosuchus* lacks any obvious osteological sign of an external auditory meatus. The equivalent of the bony meatus is no more than a slight depression on the lateral part of the occiput, occupying the squamosal and, to a small extent, the tabular (figure

3*b*). (Also there is no narrow, deep groove present similar to that described by Tatarinov (1968) in *Dvinia.*) This is probably because the squamosal has not expanded posteriorly in connection with increasing musculature in the temporal fenestra.

2. *Functional interpretation*

A great deal of controversy has surrounded interpretation of the cynodont middle ear, much of which has been reviewed recently by Allin (1975). Very briefly, there are three basic views. The first is that cynodonts had a middle ear essentially comparable to that of modern reptiles, with a tympanic membrane behind the quadrate bone which actuated the stapes directly (or via a simple cartilaginous extrastapes). Parrington (1946), Hopson (1964) and Tatarinov (1968) among others have adopted this idea. It is based largely on the interpretation of the sulcus on the back of the squamosal as the site of an external auditory meatus, which terminates behind the quadrate, immediately lateral to the distal end of the stapes. A second view is that cynodonts lacked a tympanic membrane and could only detect ground-borne (or possibly low frequency air-borne) sound, by direct transmission through the lower jaw bones to the quadrate and stapes. Evidence for this theory is the lack, supposedly, of any appropriate site for a tympanum. The third view is that a tympanum occupied the angular bone, which is the homologue of the tympanic bone which supports the tympanum in mammals. The most recent exposition of this view is Allin's (1975) study. In a carefully argued discussion, Allin concludes that an air-filled mandibular recess occupied the fossa in the lateral surface of the angular bone, and that the superficial tissues of the recess acted as the tympanic membrane. The angular bone itself was part of the vibrating structure (as is the tympanic bone of the monotremes), and sound was conducted via the postdentary bones and the quadrate to the stapes. His principal anatomical argument is the broad abuttment of the distal end of the stapes onto the quadrate, along with reinterpretation of the squamosal sulcus as the site of origin of the depressor mandibuli muscle. By his hypothesis, Allin accounts for the reduction of the postdentary bones in the cynodonts as progressive improvement of the hearing ability, and he also points out that his proposed mechanism for cynodont hearing is essentially the same as the method in mammals, and thus the transition from the one to the other is readily accounted for functionally.

Certainly the middle ear apparatus of a cynodont possesses several features not to be expected in a simple 'sauropsid'-like ear. In the case of *Procynosuchus*, the form of the stapes is paradoxical. On the one hand the huge stapedial fenestra suggests that it was as light as possible, presumably in relation to the detection of relatively high frequency sound. On the other hand, the bone as a whole appears to be designed for greater strength than would be expected. The presence of a complete bar of bone, both anterior and posterior to the foramen, would be expected to give the bone a high strength to mass ratio, but at the same time involves a greater mass than a simple, single rod would have. Therefore it is likely that the stapes was subjected to relatively large forces which could only be applied via the quadrate. The fact that the stapes contacts the quadrate by a bony attachment, another unexpected feature of the middle ear, supports this interpretation, as does the fact that it is the more robust anterior arm of the stapes which is in line with the quadrate contact, rather than the more delicate posterior arm. It was argued earlier (page 94), on the grounds that the quadrate was mobile, as well as on the shape of the stapes, that the stapes had a mechanical rôle in supporting and controlling the quadrate from the medial side, in addition to any sound-conducting rôle it may also have had. Further evidence is the fact that the medial end of the stapes is larger than the fenestra ovalis and therefore the danger of the stapes piercing the membrane of the fenestra ovalis is avoided. There was also seen to be an *a priori* requirement for support of the quadrate from the medial side, and the stapes is seen to be in an appropriate position to do this job.

The question remains of the rôle of the stapes in sound reception. Given the suggested organization of the articulation region of the skull, it would perhaps be inevitable that vibrations of the lower jaw, be they substrate borne or low frequency airborne, would be transmitted from the articular to the quadrate and from the quadrate to the stapes. The geometrical arrangement of these bones is suitable and in fact there would be a small, but possibly significant, gearing effect (figure 9*e*). Vibration of the articular bone in a transverse direction would be passed to the quadrate condyle. This in turn would cause the quadrate to vibrate in the transverse plane about a fulcrum formed by the contact of the quadrate to the pterygoid and prootic. The stapes runs medially from its attachment to the quadrate and this attachment lies between the respective points of contact of the quadrate with the articular (below) and the pterygoid/prootic (above). The lever effect would decrease the amplitude but increase the pressure of movement as applied to the stapes. In addition there would be the possibility, difficult to prove for certain, that the stapes did not move in a simple piston manner but rocked to and fro in a horizontal plane, giving a further gearing ratio. Allin has argued for an air-filled chamber lodged in the lateral face of the angular bone, whose superficial tissues acted as an ear drum. This does not seem likely in *Procynosuchus*, where evidence discussed earlier (page 90) indicates that the lateral fossa of the angular was occupied by the masseter muscle insertion. However, an air cavity and tympanic membrane are not necessary for the functioning of an apparatus of the kind proposed, as is seen in a number of modern reptiles which lack a tympanum of any kind.

Even though this route for sound vibrations probably existed, it does not exclude the possibility of a more conventional arrangement for hearing being present as well. Indeed, there is some evidence for this in *Procynosuchus*, for unlike later cynodonts, the distal end of the stapes has only a partial contact with the quadrate. As described, the posterior half at least of the distal end of the stapes lies posterior to the quadrate and faces freely laterally. There is no reason why it should not have contacted a tympanum of a generally 'postquadrate' type by means of an unossified (or at least unpreserved) extrastapes. The absence of a defined external auditory meatus in *Procynosuchus* prevents any accurate assessment of where such a tympanum might have been. In later cynodonts which do have the meatus set into the back of the squamosal, such a tympanum would appear to have been immediately postero-lateral to the quadrate. Allin's interpretation of the meatus as the site of origin of the depressor mandibuli muscle is not convincing because of its tortuous course and the enormous size of depressor mandibuli that it would imply. On the other hand, Presley (1977 and personal communication) has compared the cynodont squamosal sulcus with the mammalian external auditory meatus, showing a great similarity in its course, but also suggesting that the cynodont meatus carried on below and forwards from the ventral termination of the bony meatus. This would suggest a tympanic position in these later cynodonts, and also therefore in *Procynosuchus*, rather antero-ventral to the quadrate.

Thus it is concluded that in *Procynosuchus* sound conduction directly from the lower jaw, via the quadrate passed to the stapes and that this picked up low frequency airborne or ground-borne sound. There was also a conventional tympanic membrane actuating the stapes via an extrastapedial process, although the material does not permit us to be sure of the exact position of the tympanum.

PROCYNOSUCHUS AND THE PHYLOGENY OF CYNODONTS

In order to understand the relationship of *Procynosuchus* to the other cynodont taxa, it has proved necessary to reconsider the overall phylogeny within cynodonts, since present concepts are unsatisfactory in a number of respects. It is not intended to present an exhaustive reclassification of the group at the present time and attention is only given to the phylogenetic relationships of the pre-Middle Triassic forms. In recent years, a profound reappraisal of the logical basis and methodology of taxonomy has occurred. The strictly phyletic approach associated particularly with Hennig (1966) has proved useful in its application to certain kinds of organisms, including fossil vertebrates. Since this method demands an appreciation of the polarity of character transitions, i.e. a distinction between the ancestral (plesiomorphic) and derived (apomorphic) states of the characters, it works best with those fossil groups whose individual specimens have a high morphological content, and whose record is sufficiently extensive to allow comparisons to be made of a wide range of forms. Whether or not a phyletic approach results in a more satisfying classification than more traditional methods, it does at least have the merit of indicating with great clarity exactly how the classification has been derived. This is because it is based on two simple tenets, first defining monophyletic taxa exclusively on possession of shared derived (synapomorphic) characters, and second arranging the constituent taxa wherever possible as a dichotomous hierachy. Schaeffer, Hecht & Eldridge (1972), Løvtrup (1977) and Patterson & Rosen (1977) have among others discussed the phyletic approach in detail.

The idea of extensive parallel evolution, particularly of the lower jaw, has coloured recent approaches to cynodont taxonomy, and is epitomized by the widely accepted classification of Hopson & Kitching (1972). These authors recognize two superfamilies of cynodonts thus:

Cynognathoidea	Procynosuchidae (including *Procynosuchus* and *Dvinia*
	Galesauridae (including *Thrinaxodon*)
	Cynognathidae
	Chiniquodontidae
	Trithelodontidae (essentially diarthrognathids)
Tritylodontoidea	Diademodontidae (including trirachodonts)
	Traversodontidae
	Tritylodontidae

Parallel evolution of the 'advanced' cynodonts from, at the latest, a procynosuchid grade is implied in this arrangement. Indeed it reflects a belief that parallel evolution continued all the way to the virtually mammalian condition of trithelodonts and tritylodonts respectively (Hopson & Crompton 1969; Crompton & Jenkins 1973). In view of the considerable interest in cynodonts as a classic example of the phenomenon of parallel evolution, and its implication in ideas of patterns of macroevolution, it is important to establish whether this hypothesis of parallelism is well founded. This may be done by a consideration of the phylogenetics of the following well known genera as representatives of the pre-Middle Triassic families: *Diademodon*

(Broili & Schröder 1935; Brink 1955), *Cynognathus* (Broili & Schröder 1934), *Thrinaxodon* (Parrington 1946; Fourie 1974), *Dvinia* (Tatarinov 1968) and *Procynosuchus*. The postcranial skeletons of all these forms except *Dvinia* and *Procynosuchus* have been described in detail by Jenkins (1971). Konjukova (1946) briefly mentions part of the skeleton of *Dvinia*. The postcranial skeleton of the present specimen of *Procynosuchus* is being described and where necessary will be referred to.

The important differences between *Diademodon* and *Cynognathus* which lead to the view that they separated at a very early stage in cynodont evolution are the morphology of the postcanine teeth and the structure of the occiput. *Diademodon* teeth are expanded across the jaw to form a multi-cusped, grinding dentition, with crown to crown occlusion between the upper and lower teeth (Crompton 1972*b*). *Cynognathus* postcanine teeth consist of a single longitudinal row of sharp cusps, which act by shearing between the uppers and the lowers. However, as Crompton (1955*b*) first demonstrated, certain growth stages of *Diademodon* possess very cynognathid-like sectorial teeth at the back of the jaw, which are subsequently replaced by characteristic *Diademodon* teeth. Hopson (1971) has confirmed this in detail. In view of this fact, separation of *Cynognathus* from *Diademodon* at the superfamily level on dental grounds hardly seems justified, particularly since as Osborn (1973) suggested, different tooth-form at different stages in the development of a dentition is probably related simply to the age of the dental lamina. Presumably therefore, a change from one tooth type to the other would be a simple evolutionary event. The second major difference is that the dorsal margin of the occiput of *Diademodon* is deeply incised, while that of *Cynognathus* is high. Superficially the latter condition resembles that of the Procynosuchidae, since even in *Thrinaxodon* there is some emargination. However, the cynognathid occiput does resemble that of *Diademodon* in the existence of a very deep, pronounced groove for the external auditory meatus in the back of the squamosal. This is virtually absent in procynosuchids and only incipiently developed in *Thrinaxodon*, and it probably results from a posterior extension of the temporal fenestra related to increased temporalis jaw musculature. Thus both the cynognathid and the diademodontid occiputs appear to have evolved to an advanced stage in a similar manner, a stage well beyond that represented by *Thrinaxodon*. The absence of the dorsal incision of the occiput in *Cynognathus* would seem therefore to be a secondary condition, related possibly to the adoption of a carnivorous habit and the need for a large postero-dorsal component of the temporalis muscles. Thus neither of the characters regarded as widely separating these two genera are reliable. Indeed one could go further and suggest that the possession at some stage of development of cynognathid-like teeth, and the possession of an advanced occiput with a deep external auditory meatus are two synapomorphic characters, shared by these two forms. At any event, these supposed differences must be set against an impressive array of detailed similarities in features that are certainly apomorphic relative to *Thrinaxodon* and the procynosuchids. These features include the structure of the lower jaw, with a very detailed resemblance between the reduced, rod-like postdentary bones and between the shapes of the dentaries. The reduction in the width of the basicranial axis and in the size of the gap between the braincase and the epipterygoid is identical in the two genera. Both have a narrowed snout and teeth which occlude, upper to lower. In the postcranial skeleton, the similarities are so marked that it is frequently impossible to distinguish one from the other on isolated bones. Jenkins (1971) mentions the detailed similarity in the form of the expansions of the ribs, and the shape of the bones of the pelvis, both these examples contrasting with *Thrinaxodon* and even more so with procynosuchids.

All these and several other similarities would have to have evolved in parallel if Hopson & Kitching's classification is accepted. Parallel evolution can of course occur, but it can be demonstrated either by a lack of particularly close resemblance on detailed inspection of the characters in question, or else by a substantial number of other characters indicating true affinity. Neither of these conditions apply in the present case, and so it must be concluded that *Diademodon* and *Cynognathus* have a primary sister-group relationship to one another, relative to *Thrinaxodon* and the procynosuchids (figure 18).

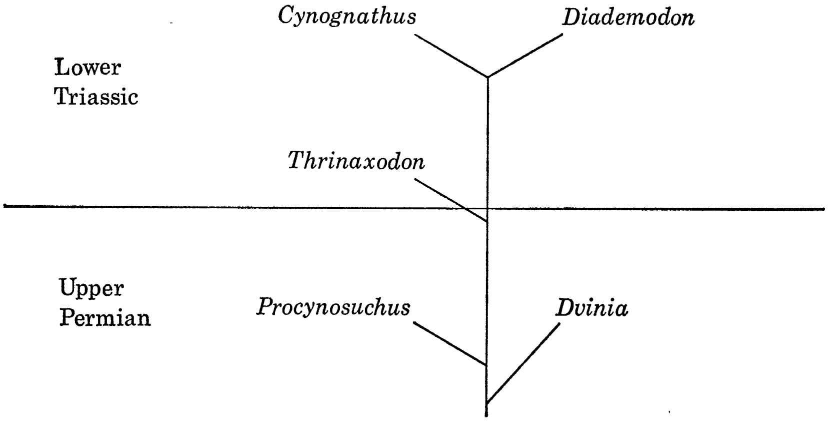

FIGURE 18. Phylogeny of pre-Middle Triassic cynodonts.

Taken together, *Cynognathus*, *Diademodon* and *Thrinaxodon*, form a monophyletic group, the three genera sharing the following probably apomorphic characters compared to the procynosuchids: reduction of the number of incisors and loss of the precanine teeth; the adductor fossa of the lateral surface of the dentary reaching the ventral margin of the jaw; reduction in size of the postdentary bones; reduction of the ectopterygoid; loss of the interpterygoid vacuity (Estes (1961) describes a vacuity in a juvenile form of *Thrinaxodon*, although Fourie (1974) failed to find one); many features of the postcranial skeleton, including expansion of the ribs and of the ilium. *Thrinaxodon* is structurally close to the point of divergence of the cynognathid/diademodontid line and has few unique apomorphies. The relatively anterior position of the quadrates, and the low number of postcanine teeth are probably in this category however.

Procynosuchus lacks the apomorphic characters which are shared by *Cynognathus*, *Diademodon* and *Thrinaxodon*, listed above. It also shows none of the apomorphies shared by any two of the three advanced genera. It follows therefore that *Procynosuchus* is the sister group of those three taken together. Certainly, as in the case of *Thrinaxodon*, the structure of the skeleton of *Procynosuchus* is close to the expected structure of the common ancestral form of all the cynodonts that followed it, and none of its features can be regarded confidently as apomorphic.

The phylogenetic position of the aberrant Upper Permian genus *Dvinia* is less easy to determine, since most of its characteristic features are either probable specializations unique to itself, or else primitive features shared with *Procynosuchus* but of no value in assessing its relationships. Stressing the former type of characters, Tatarinov (1968) placed *Dvinia* in a separate family, Dviniidae, while Hopson & Kitching (1972) were evidently more impressed by the primitive characters and consequently included *Dvinia* in the Procynosuchidae. Tatarinov's approach creates a sound monophyletic family but fails to indicate its phyletic position, while

Hopson & Kitching's view results in the creation of a grade rather than a correctly indicated monophyletic family.

In fact, *Dvinia* has certain superficial similarities to *Diademodon*, although none of these stand up to close scrutiny. For example, the large temporal fenestra of *Dvinia* has about the same relative size of that of *Diademodon*, but its expansion has been achieved by extending postero-medially, so that the posterior end of the sagittal crest is the posteriormost point of the skull, and antero-medially between the orbits. In *Diademodon* the large size of the fenestra has been achieved largely by expansion of the postero-lateral part of the fenestra instead. In both genera the postcanine teeth are transversely expanded, but they have no detailed similarity of cusp arrangement, and of the two only in *Diademodon* is there tooth to tooth occlusion. Thus *Dvinia* cannot be interpreted as the sister group of *Diademodon*, and equally it shares no derived characters with either *Cynognathus* or *Thrinaxodon*. Similarities between *Dvinia* and *Procynosuchus* which are not present in the other genera are particularly: extra incisors and precanines; somewhat comparable postcanine teeth with a single, dominant main cusp; relatively small dentary with restricted adductor fossa, and relatively very large postdentary bones; interpterygoid vacuity; relatively large ectopterygoid; lack of expanded ribs; little anterior development of the ilium. When considered in the context of therapsid reptiles in general, and particularly the smaller therocephalians, all these features appear to be primitive for cynodonts as a whole. Characters of *Dvinia* which are shared with none of these other cynodonts included the following: complex posterior postcanine teeth, with numerous extra cuspules around the main cusp, which are sharply distinguished from the very simple anterior postcanine teeth; upper tooth rows parallel to one another rather than diverging; postero-medial part of the temporal fenestra expanded; no pineal foramen; basipterygoid processes reduced; narrow base to braincase, with no lateral expansion of the parasphenoid; pterygoids meet in the midline behind the basipterygoid articulation; basioccipital not forming part of the fenestra ovalis; extensive posterior exposure of the quadrate. All these characters are probably specializations of *Dvinia* alone and thus constitute a series of apomorphic features defining the taxon. In addition however there are a few other characters unique to *Dvinia* amongst the known cynodonts which are possibly plesiomorphs for cynodonts in general, namely: paired vomer; supraoccipital bone slightly wider than the postparietal, rather than much narrower; six lower incisor teeth rather than four in *Procynosuchus* or three in later genera. These three characters are to be found, if not comprehensively, amongst therocephalian therapsids and suggest therefore that *Dvinia* diverged phylogenetically before the dichotomy of *Procynosuchus* and the other cynodonts.

Figure 18 summarizes the phylogeny of cynodonts proposed here. The Middle and Upper Triassic members of the Cynodontia have not been considered in detail. None of them appear to share significant derived characters with *Dvinia*, *Procynosuchus* or *Thrinaxodon* and therefore they are all derivable from the *Cynognathus*/*Diademodon* lineage and are not relevant to the problem of the primitive cynodonts. No attempt at a formal classification of cynodonts is made at this stage, but it is clear that a new one is due which reflects the phyletic arrangement presented.

The problem of the origin of the cynodonts has been discussed at length previously (Kemp 1972*b*), when it was concluded that the Therocephalia are closely related to the Cynodontia, and that amongst the subtaxa of therocephalians, the Whaitsiidae are the closest of all. In more up-to-date terminology, the whaitsiids are the sister group of all the cynodonts, sharing with them a number of uniquely derived characters such as the expanded epipterygoid and loss of the suborbital vacuity. No evidence has appeared in the course of this present study which requires modification of that view.

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List of abbreviations used in the figures

add. fos.	adductor fossa
ad. pr. pro.	antero-dorsal process of the prootic
ANG	angular
ant. for.	anterior foramen of the septomaxillary canal
ant. ssc.	anterior semicircular canal
a. pt. m.	anterior pterygoideus muscle
ART	articular
BO	basioccipital
bpt. pr.	basipterygoid process
BSP	basisphenoid
car. f.	carotid foramen
c. com.	crus communis
cerb.	cerebellum
cer. hem.	cerebral hemisphere
COR	coronoid
c. rec.	cochlea recess
c. pr.	coronoid process
D	dentary
dent. gr.	dental lamina groove
dor. sel.	dorsum sellae
d. ri.	dorsal ridge
ECT	ectopterygoid
EO	exoccipital
EPT	epipterygoid
F	frontal
fen. ov.	fenestra ovalis
fen. rot.	fenestra rotunda
fl.	flocculus
fl. fos.	floccular fossa
inc. pit	incipient replacement pit
inf. can.	posterior opening of infraorbital canal
IP	interparietal
ipt. vac.	interpterygoid vacuity
J	jugal
j. f.	jugular foramen
J. o.	position of Jacobson's organ
L	lachrymal
l. cond.	lateral condyle
l. duct.	lachrymal duct
l. pr. pro.	lateral process of the prootic
mass. m.	masseter muscle
m. cond.	medial condyle
med.	medulla oblongata
mes. fov.	mesethmoid fovea
MX	maxilla
mx. sin.	maxillary sinus
N	nasal
n. pal. can.	nasopalatine canal
ol. l.	olfactory lobe
op. l.	optic lobe
P	parietal
PAL	palatine
pi. ant.	pila antotica
pin. f.	pineal foramen
pit.	pituitary
PMX	premaxilla
pmx. for.	premaxillary foramen
PO	postorbital
po. ch. ri.	post-choanal ridge
post. for.	posterior foramen of the septomaxillary canal
post. pal. for.	posterior palatine foramen
po. te. fos.	post-temporal fossa
p. pr.	paroccipital process
PRART	prearticular
pr. cult.	processus cultriformis
PRF	prefrontal
PRO	prootic
pro.	attachment of the prootic
PSP	parasphenoid
PT	pterygoid
pt.	attachment of the pterygoid
pt. par. f.	pterygo-paroccipital foramen
Q	quadrate
QJ	quadratojugal
qj. re.	quadratojugal recess
q. re.	quadrate recess
ref. lam.	reflected lamina
repl.	replacement tooth
retr. pr.	retroarticular process
SA	surangular
se. tu.	sella turcica
SMX	septomaxilla
smx. for.	septomaxillary foramen
SO	supraoccipital
sph. pal. for.	sphenopalatine foramen
SQ	squamosal
sta.	attachment of the stapes
TAB	tabular
temp. m.	temporalis muscle
t. marg.	taenia marginalis
tur. ri.	turbinal ridge
unoss. so.	unossified part of the supraoccipital
v	vomer
ven.	venous channel
ven. n.	venous notch
V	trigeminal nerve
$V_{max.}$	maxillary branch of the trigeminal nerve
VI	abducens nerve
VII	facial nerve
XII	hypoglossal nerve

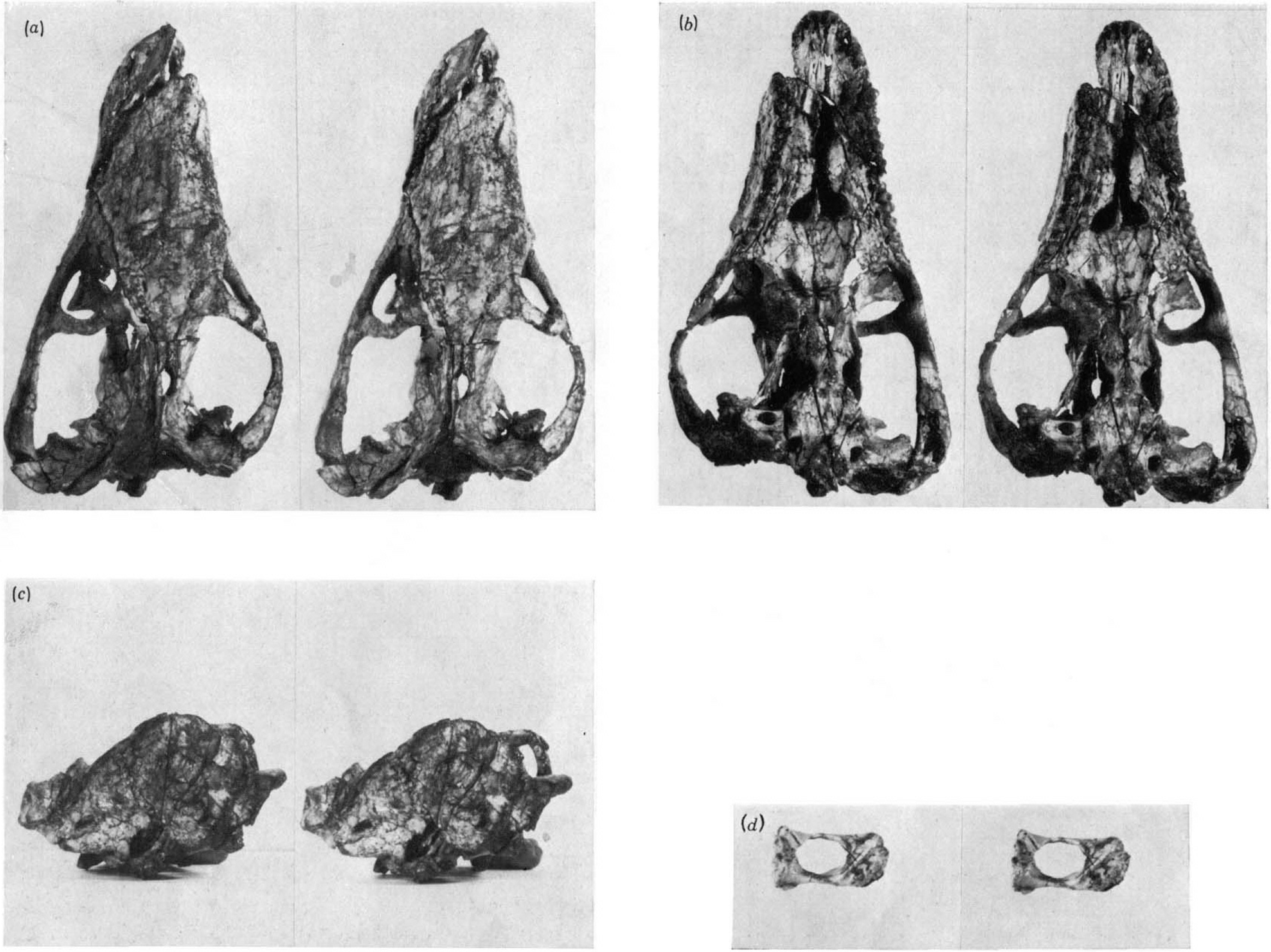

FIGURE 19. *Procynosuchus delaharpeae*: stereophotographs of the skull. (*a*) Dorsal view. (Magn. × 0.75.) (*b*) Ventral view. (Magn. × 0.75.) (*c*) Posterior view. (Magn. 0.75.) (*d*) Left stapes in dorsal view. (Magn. × 2.)

FIGURE 20. For description see opposite.

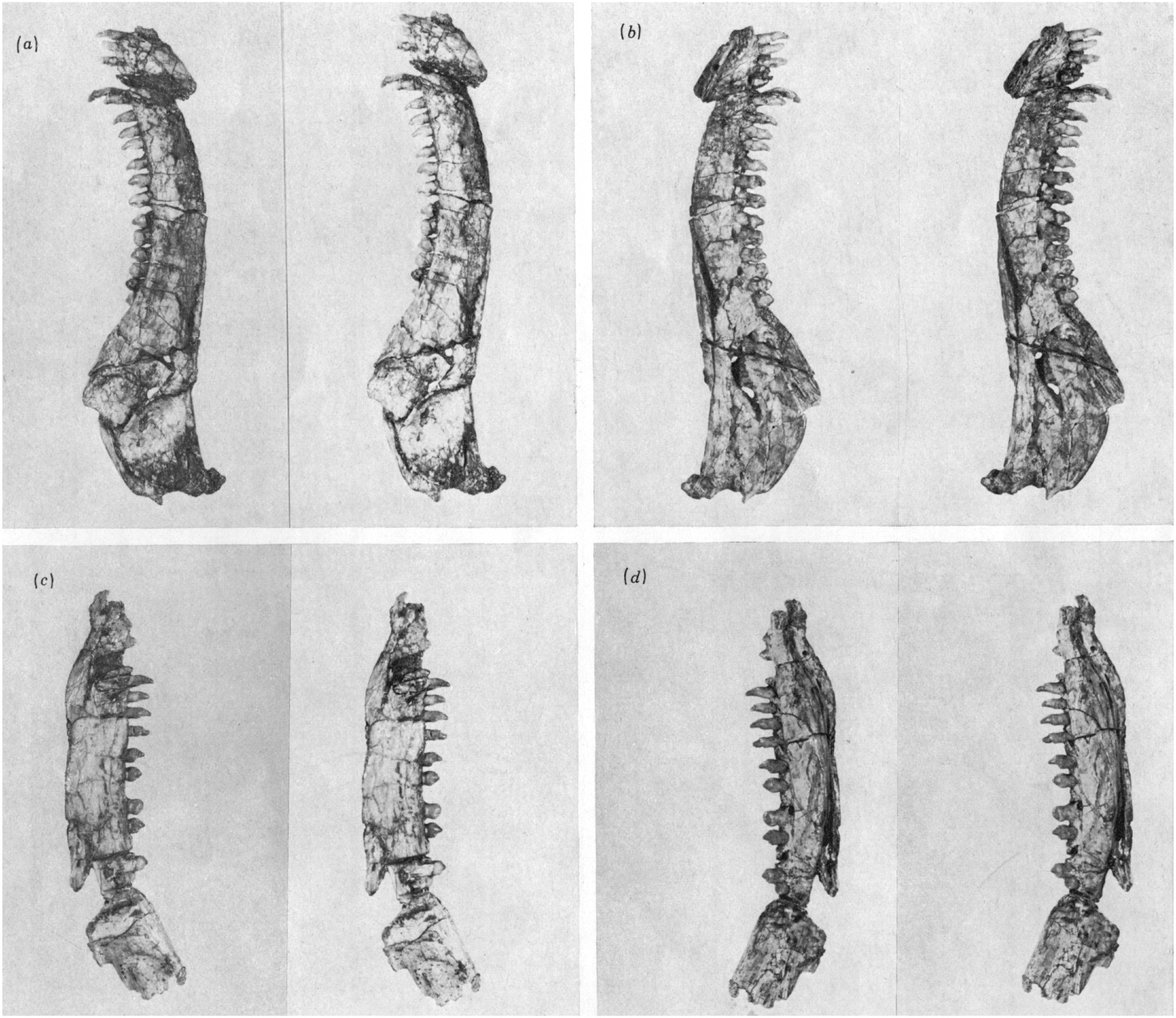

FIGURE 21. *Procynosuchus delaharpeae*: stereophotographs of the lower jaws. (*a*) Right jaw in lateral view. (Magn. ×1.) (*b*) Right jaw in medial view. (Magn. ×1.) (*c*) Left jaw in lateral view. (Magn. ×1.) (*d*) Left jaw in medial view (Magn. ×1.)