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Whaitsiid Therocephalia and the Origin of Cynodonts

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WHAITSIID THEROCEPHALIA AND THE ORIGIN OF CYNODONTS

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CONTENTS

The conclusion reached in this paper is that the cynodonts evolved from a therocephalian ancestor, and that among the known therocephalians, the whaitsiids are the forms closest to cynodont ancestry. Certain superficial specializations of the feeding apparatus, however, debar the known whaitsiids from a position of actual cynodont ancestry.

The evidence for this thesis lies in new detailed morphology of certain points of the whaitsiid skull, along with reassessment of much of the established cranial anatomy of the relevant groups. It is presented in the form of a series of comparisons of the skulls of whaitsiids, primitive cynodonts, other therocephalians and primitive therapsids respectively, and a summary of this is given in table 1.

The morphology of the whaitsiid skull is then discussed from a functional point of view, with particular reference to the design of bones as adaptations to resist the forces involved in the use of the jaws. The changes which must have occurred in the evolution of the cynodonts from a whaitsiid-like therocephalian are considered in this same context and it is argued that the organization of the cynodont skull can be seen as a logical functional development from the more primitive condition. In particular, the streptostylic nature of the jaw articulation, the enlargement of the dentary and reduction of the postdentary bones, and the reduction of the reflected lamina of the angular may all be correlated with the development of a masseter muscle.

INTRODUCTION

Since their earliest descriptions during the last century (Owen 1876; Seeley 1895) the cynodont reptiles have attracted interest because of their unmistakable relationship to mammals. Subsequent work, notably by Broom (e.g. 1915) and Watson (1911, 1913) served to demonstrate in even greater detail the appearance of essentially mammalian features within the group, although during this period knowledge of the earliest mammal groups of the Mezozoic was so scanty that very little could be said about the precise nature of the transition between reptiles and mammals. However, in recent years the discovery of abundant Upper Triassic mammal faunas (Kermack, Kermack & Mussett 1956; Kermack 1967; Parrington 1967, 1971) has stimulated a great increase in interest in cynodonts, for most workers in the field agree that these stem-mammals can be traced directly from the primitive, galesaurid (thrinaxodontid) cynodonts. A series of detailed studies of the dentition (Crompton & Jenkins 1968), the jaw musculature (Barghusen 1968), the braincase (Hopson 1964; Hopson & Crompton 1969) and the postcranial skeleton (Jenkins 1969, 1971) all indicate that the Upper Triassic mammals are closely comparable with cynodonts. The major dissenter from this view is Kermack (1967) who believes that the structure of the cynodont braincase is not appropriate for an ancestor of the mammals. Brink (1956*a*) has also doubted the cynodont ancestry of mammals.

The exact point of origin of cynodonts themselves from earlier therapsid reptiles is however still a matter of dispute. It has become difficult to accept the classic view of Watson (1921) that the cynodonts were derived from the Upper Permian gorgonopsid therapsids since the latter have been shown to be highly specialized towards a restricted mode of life, that of 'large-prey' carnivores. Their structural modifications in no way anticipate the cynodonts and they appear to have evolved quite independently from the very primitive synapsid level represented by the sphenacodont pelycosaurs (Kemp 1969*a*).

A second theory about cynodont ancestry was initiated by Broom (1938) when he described the first known members of the Procynosuchidae (figure 1*b*). These are undoubtedly cynodonts but of a very primitive type having, for example, an incompletely formed secondary palate and a relatively small dentary bone. Broom compared them rather superficially with the Therocephalia, a diverse Upper Permian group of therapsids. Brink has been the strongest supporter of this view of a therocephalian origin of the cynodonts and in particular he has drawn attention to a series of small, inadequately known forms called silphedestids which he regards as intermediate between cynodonts and therocephalians, although closer to the cynodonts (Brink 1951). Subsequently Brink (1960) has described in great detail a form called *Scalopocynodon* (figure 1*a*), which he regards as linking the silphedestids to the procynosuchids and at the same time showing a close affinity with therocephalians.

Romer (1969) has criticized Brink's analysis on the grounds that, while *Scalopocynodon* must be accepted as a true primitive cynodont, the similarities which it bears towards the therocephalians are either irrelevant to typical cynodonts because they are specializations of *Scalopocynodon* itself (e.g. absence of the postorbital and zygomatic arches) or else they are primitive features retained in both *Scalopocynodon* and the therocephalians from a much earlier therapsid level. On the other hand, Romer continues, the therocephalians possess a number of features that are absent from both cynodonts and *Scalopocynodon*, such as a suborbital fenestra in the palate, which positively debar the therocephalians from a position of cynodont ancestry. Thus Romer has proposed the third important theory of cynodont origin, that they evolved independently from a very early therapsid stock, the Phthinosuchia (figure 2*b*) of the early Middle Permian of Russia, forms which retained a number of pelycosaurian features.

There is, in fact, some confusion regarding the interrelationships of the primitive Russian therapsids, of which there are two groups of relevance here:

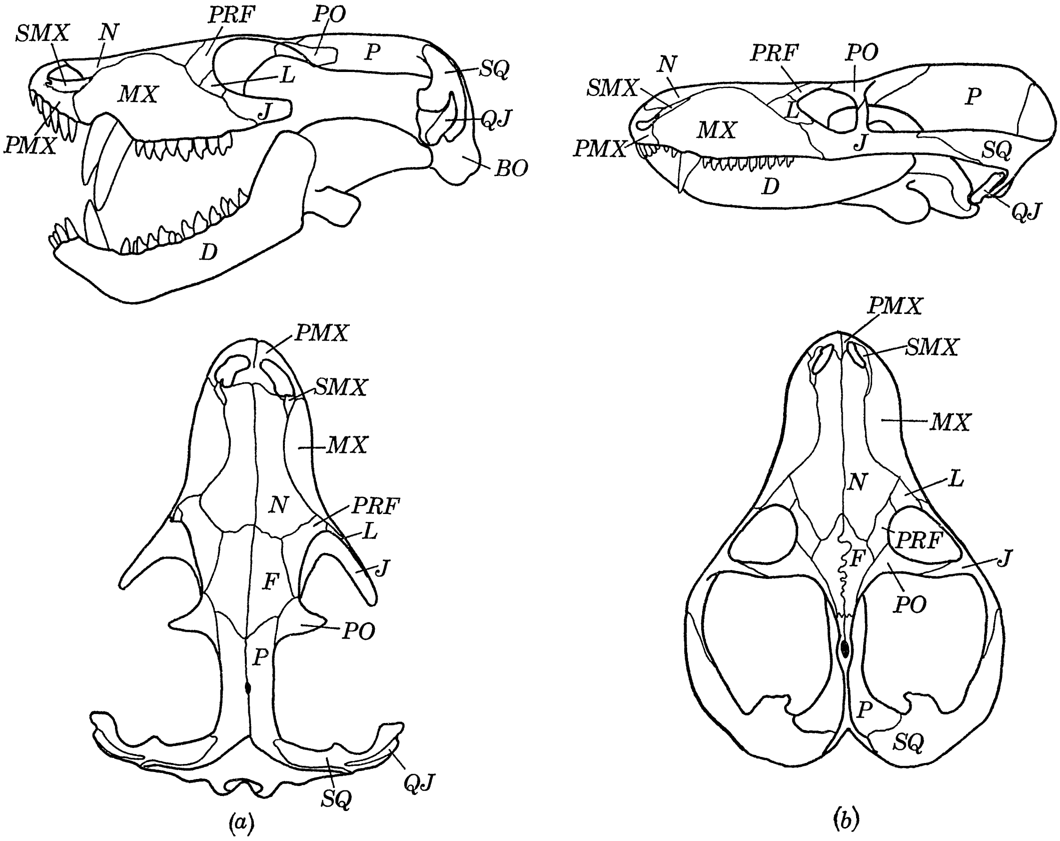


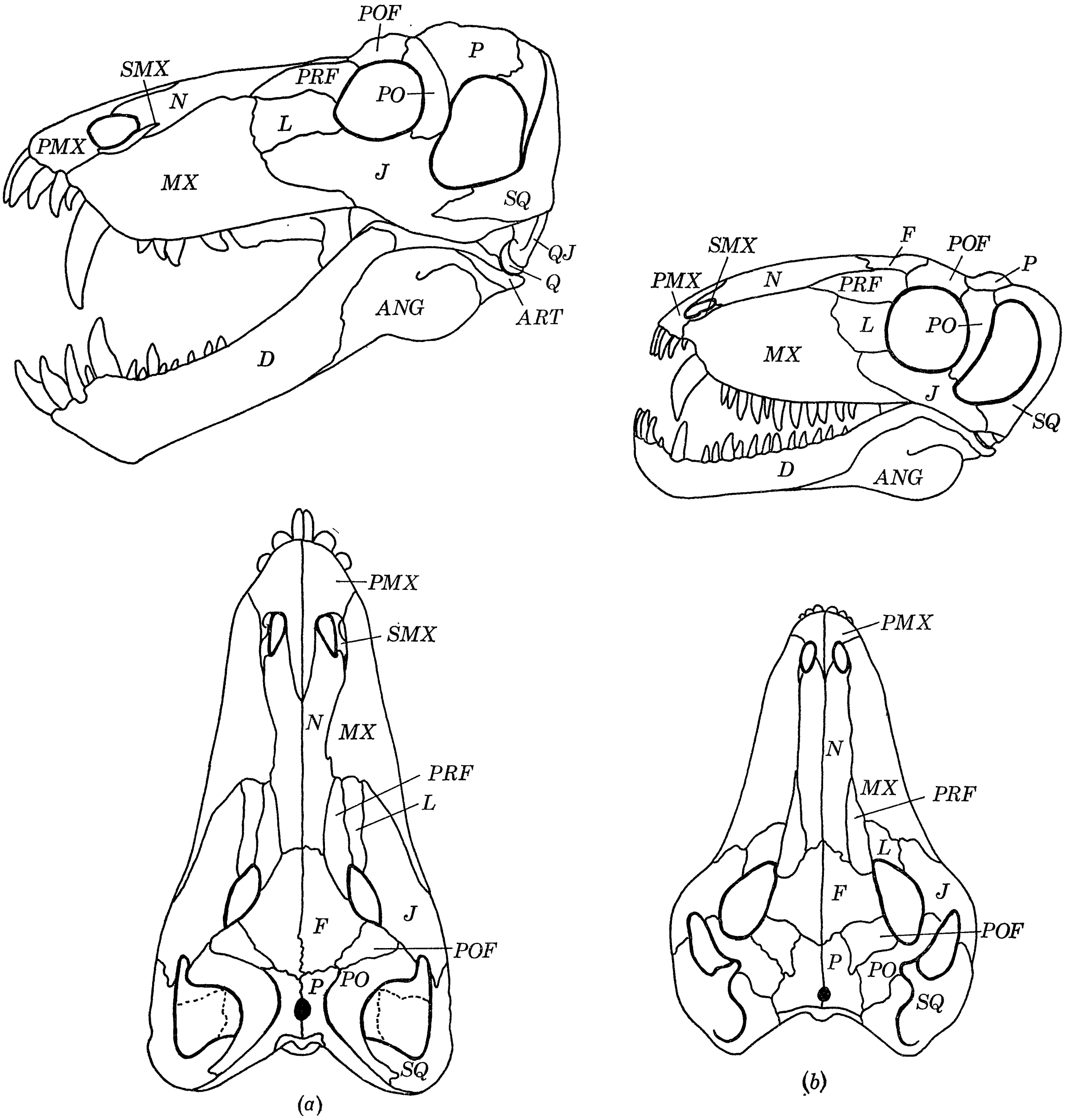
FIGURE 1. Procynosuchids. (*a*) *Scalopocynodon gracilis* Brink (incomplete restoration after Brink 1960). (*b*) *Leavachia duvenhagei* Broom (after Brink 1963 *b*).

(i) The Phthinosuchia (= Eotitanosuchia of Boonstra 1963) (figure 2*b*), which includes the genera *Phthinosuchus*, *Phthinosaurus* (Efremov 1954) and *Eotitanosuchus* (Chudinov 1960), and possibly *Biarmosuchus* and *Biarmosaurus* (Chudinov 1960).

(ii) The Brithopodidae (figure 2*a*), which includes the genera *Titanophoneus*, *Syodon* and *Doliosaurus* (Orlov 1958).

In 1956, Watson & Romer placed the phthinosuchians within the gorgonopsids as the most primitive members of that group, and they placed the brithopods together with the primitive carnivorous therapsids of South Africa, as the Titanosuchia which they regarded as an early specialized line of carnivorous theriodont therapsids. Boonstra (1963), however, suggested that the brithopods (and indeed all the titanosuchids of Watson & Romer) were an early branch of the herbivorous anomodont therapsids. He believed that the phthinosuchians (which he termed eotitanosuchians) were a 'relict infertile branch not ancestral to either the Theriodonta or the Anomodontia, but morphologically near the level from which these two sub-orders commenced their distinct lines of development' (Boonstra 1963, p. 186). Romer (1966) has since followed Boonstra and in particular he has stressed that the phthinosuchians lie close to the common ancestry of all the later theriodont groups.

Olson (1962) has classified both the primitive Russian groups together as the Eotheriodonta to be regarded as representing the basal stock from which all therapsids evolved. I have



(*a*) (*b*)

Figure 2. Eotheriodonts. (*a*) *Titanophoneus potens* Efremov (after Orlov 1958). (*b*) *Phthinosuchus discors* Efremov (after Efremov 1954).

suggested briefly that the phthinosuchids show a specific affinity towards the gorgonopsids and that if an ancestor of the therocephalians is to be sought amongst known forms, then the brithopods appear to be the nearest (Kemp 1969*a*). However, this is perhaps to overstate the difference when the most striking thing about the phthinosuchids and the brithopods

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respectively is the great deal of common structure that they demonstrate, structure which is primitive with respect to all later therapsids. For this reason, it has proved most useful here to adopt Olson's approach and use the term Eotheriodonta to embrace both of these primitive groups.

To return to the two current views on the origin of cynodonts, Romer's criticisms of Brink are well founded, for Brink has failed to find a single feature of the therocephalians that is both a modification of the primitive condition and also typical of cynodonts. Moreover, Romer has pointed to certain specializations of the therocephalians that are not to be expected in a cynodont ancestor unless positive evidence of an evolutionary reversal could be demonstrated, which it cannot. He cites the long snout with a long tooth row, the lack of well-differentiated canines and the presence of a suborbital fenestra, all therocephalian features absent from cynodonts.

At this point, however, it must be stressed forcibly that both the theory of Brink and the dissention of Romer are based almost exclusively upon a comparison of cynodonts with the scaloposaurid branch of the Therocephalia (figure 3*c*). These, along with certain related genera, are small, superficially cynodont-like forms that appear fairly early in the therapsid record (*Tapinocephalus*-zone of the South African Upper Permian), and they are also the best known therocephalians (Watson 1931; Crompton 1955; Sigogneau 1963).

In fact the Therocephalia form a rather diverse group. There is no final agreement about the division of the genera into families, although work currently being undertaken by Dr Ch. H. Mendrez of Paris should resolve much of the confusion that exists at present. In general, two groups of Therocephalia may be recognized. First there is a series of more or less large, primitive forms among which the Pristerognathidae and Whaitsiidae are the best-known families. Secondly, there are numerous smaller, generally more advanced forms which include the scaloposaurs and their allies, along with the advanced group Bauriidae. Some authors have regarded the differences between these two groups as significant at a high taxonomic level and have thus restricted the taxon Therocephalia to the former, more primitive group. Watson & Romer (1956), in particular, follow this course, and create a second infraorder, Bauriamorpha, for the scaloposaurid-like forms (which they divide into several families) along with the bauriids. Brink (1965), too, has classified the more advanced forms together, as the infraorder Scaloposauria, which he divides into three families, Ictidosuchidae, Scaloposauridae and Bauriidae, of increasing degrees of advancement. On the other hand, Haughton & Brink (1954) retained both the more primitive and the more advanced forms within the Therocephalia, contenting themselves with division into a series of families.

For the purposes of this paper I have used the term Therocephalia in the sense of Haughton & Brink, to include both the primitive and advanced forms, and have recognized the following five families. This is to ignore a number of genera which clearly deserve familial status but which are so imperfectly known that they have served no use in the elucidation of the problems discussed. Thus I do not present this as by any means a definitive classification of the Therocephalia, but only as a basis for the present work.

Pristerognathidae (figure 3*a*). Large but fairly generalized forms, tending to reduce both the size and number of postcanine teeth. The interparietal region of the skull particularly narrow. An early group, known only in the *Tapinocephalus*-zone of the Upper Permian of South Africa.

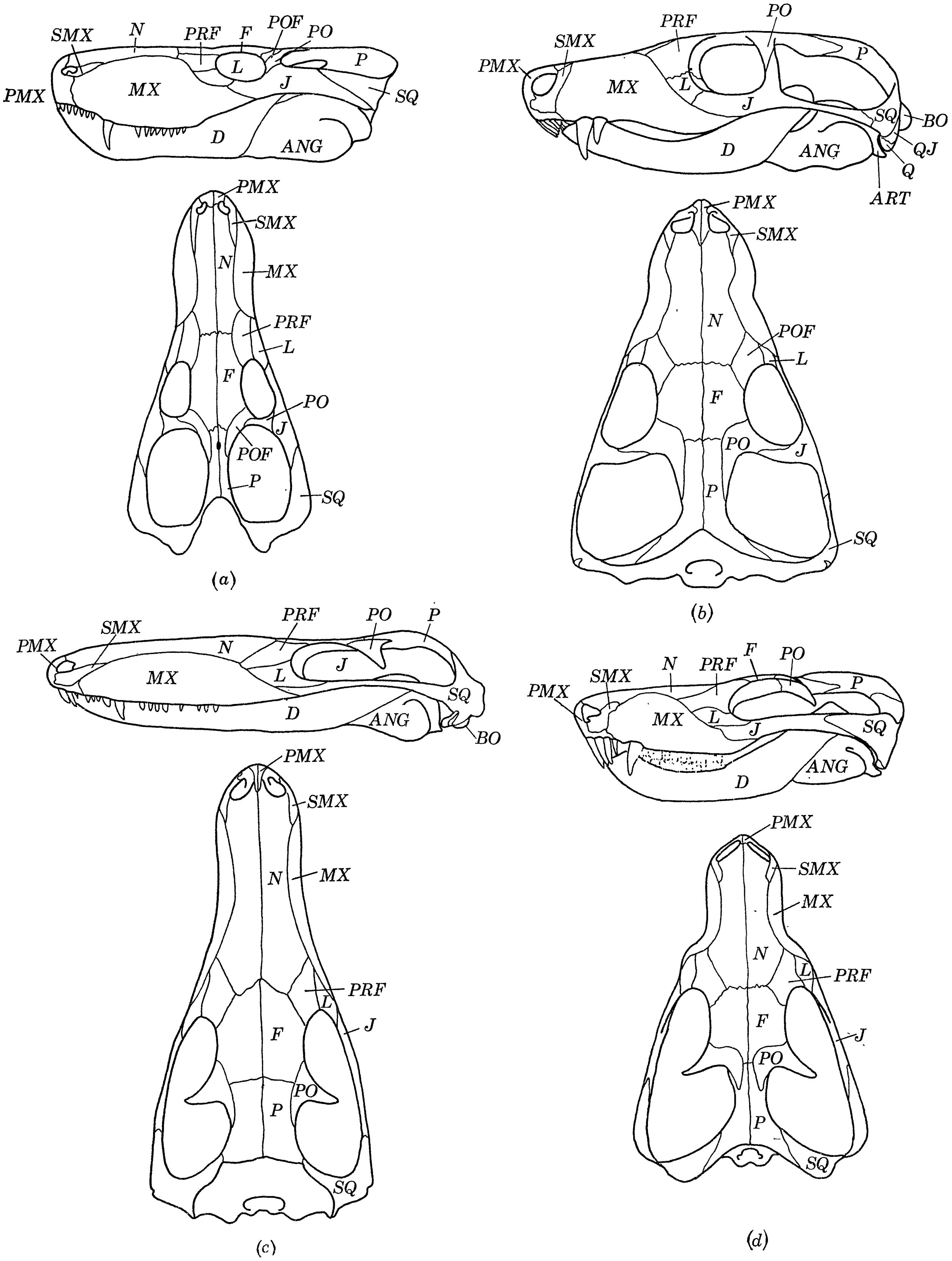


FIGURE 3. Therocephalians. (*a*) *Scylacosaurus sclateri* Broom (after Boonstra 1954). (*b*) *Aneugomphius ictidoceps* Broom & Robinson (after Brink 1956*b*). (*c*) *Tetracynodon darti* Sigogneau (after Sigogneau 1963). (*d*) *Bauria cynops* Broom (after Brink 1963*a*).

Whaitsiidae (figure 3*b*). Universally regarded as a highly specialized group, with complete loss of the postcanine teeth usual. A rather late group appearing only in the *Cistecephalus*-zone at the top of the Upper Permian of South Africa. Also known from contemporaneous Russian (Tatarinov 1963) and East African (Huene 1950; Kemp 1972) deposits.

Ictidosuchidae. Scaloposaurid-like forms but with the postorbital bar complete. Known from the *Cistecephalus*-zone to the *Lystrosaurus*-zone at the base of the Trias, in South Africa.

Scaloposauridae (figure 3*c*). Small, fairly advanced forms with long snouts, incomplete postorbital bar and a complete postcanine dentition. Appear early, in the *Tapinocephalus*-zone of the Upper Permian of South Africa, and survive into the Lower Trias.

Bauriidae (figure 3*d*). The most advanced of all therocephalians, paralleling the cynodonts in several respects, including a secondary palate, multicusped teeth, and expansion of the epipterygoid. The latest group, appearing in the *Cynognathus*-zone of the Lower Triassic of South Africa.

In the course of a detailed investigation into the cranial anatomy of certain specimens of whaitsiids, part of which has been published (Kemp 1972), I have been struck by an impressive series of resemblances between whaitsiids and cynodonts. In several cases the condition of the feature in question appears to differ from that shown in other therocephalian groups. In other cases the feature is to be found in such therocephalian groups as the scaloposaurs but has been overlooked in previous attempts to compare cynodonts with therocephalians. For quite a number of the characters it is simply not possible to determine from the literature their status in various therocephalian groups, and it is hoped that one result of this paper will be a closer examination of the detailed anatomy of such groups as the pristerognathids, for which there is no modern account at all.

I believe that a strong case may be presented that the cynodonts originated from within the Therocephalia, and that among the latter the whaitsiids bear the closest relationship to the cynodonts of all the *known* forms. In order to facilitate judgement of this perhaps rather surprising hypothesis, the first part of the paper consists of a comparative section where the characters that support the case are described for the whaitsiids and then compared in turn with primitive cynodonts to demonstrate the resemblance, with other therocephalians to show the range of the character, and finally with more primitive mammal-like reptiles to demonstrate that the character in question truly represents an evolutionary advance rather than a mere retention of the primitive condition. A summary of the comparisons is given in table form (p. 32).

The second part of the paper presupposes acceptance of the hypothesis that the cynodonts evolved from a whaitsiid-like therocephalian, and attempts to account for the evolution of the cynodont skull from therocephalians in functional terms.

No consideration has been afforded the postcranial skeleton because information about this region of whaitsiids, and indeed of therocephalians in general is exceedingly scant. I am not aware of any features of the postcranial skeleton which seriously contradict the views advanced here.

List of material figured or referred to in the text

CUMZ T 357. *Whaitsia* sp. Posterior half of skull prepared in acetic acid. *Cistecephalus*-zone, Upper Permian. South Africa (exact locality unknown). From the D. M. S. Watson Collection, former No. DMSW R 232.

CUMZ T899. Undetermined whaitsiid. Snout and anterior part of dentaries. Kawinga Formation, Upper Permian. Ruhuhu Valley, Tanzania. From the F. R. Parrington Collection, former No. FRP 89.

CUMZ T900. *Whaitsia* sp. Skull. *Cistecephalus*-zone, Upper Permian. Doornplaas, Graaf-Reinet, South Africa. From the F. R. Parrington Collection, former No. FRP 1964/30.

CUMZ T901. Indeterminate whaitsiid. Isolated posterior end of lower jaw. Kawinga Formation, Upper Permian. Ruhuhu Valley, Tanzania. From the F. R. Parrington Collection, former No. FRP 44.

CUMZ T902. Undetermined whaitsiid. Skull prepared in acetic acid. Kawinga Formation, Upper Permian. Ruhuhu Valley, Tanzania. From the F. R. Parrington Collection, former No. FRP 92.

CUMZ T815. *Thrinaxodon liorhinus*. Skull. *Lystrosaurus*-zone, Lower Trias. Harrismith, South Africa.

CUMZ T817. ?*Thrinaxodon* sp. Skull. *Lystrosaurus*-zone, Lower Trias, Harrismith, South Africa.

Comparison between whaitsiids, cynodonts and other therapsids

The jaw articulation

The structure of the whaitsiid quadrate and quadratojugal (figure 4*a* to *c*) and their mode of attachment to the rest of the skull has been described in detail recently (Kemp 1972). Above the condyles, the body of the quadrate fits into a shallow pocket in the anterior face of the squamosal in a loose but more or less conformable manner and there is a characteristic notch (*q.n*) in the ventral border of the squamosal behind the quadrate which coincides with the position of the posterior opening of the quadratojugal canal. The medial face of the quadrate is in the form of a shallow concavity into which the distal end of the paroccipital process fits, forming a loose contact. The ventral part of the quadrate is swollen to form the articulating condyles and the lateralmost region is extended laterally to the rest of the bone. The quadratojugal rests upon this lateral extension, from which it rises dorsally as a thin lamina. The anterior edge of the lamina is in contact with the lateral edge of the body of the quadrate while behind the quadrate the quadratojugal lamina is held within a narrow slit in the squamosal. This slit is the most characteristic feature of the suspensory region of the skull. It opens both anteriorly and posteriorly as well as ventrally and is very narrow and deep, enclosing the quadratojugal for its full extent. In posterior view it is tilted dorso-medially and at the same time it slants antero-laterally.

The ventro-medial part of the quadrate is produced forwards as the pterygoid wing, which lies against the lateral face of the quadrate ramus of the pterygoid in a broad, overlapping contact. Apart from the articulating surfaces themselves, the only remaining contact of the quadrate is with the stapes which runs laterally from the fenestra ovalis to abut against a medially directed stapedial process of the quadrate.

The quadrate and quadratojugal of the cynodonts show a remarkable similarity to those of the whaitsiids (Parrington 1946; Crompton 1972). In the best-known galesaurid cynodont, *Thrinaxodon* (figure 4*d* to *f*), the notch in the ventral edge of the squamosal is present, although it is relatively larger than in the whaitsiids and has a small flange of the quadrate extending back into it. Lateral to the notch there is again a deeper slit for the reception of the blade-like quadratojugal, although in this case the squamosal is cut away lateral to the quadratojugal so that only the dorsal third or so of the quadratojugal is actually in contact with the outer edge of the slit. The relation between the anterior part of the quadratojugal and the lateral edge of the quadrate appears to be very similar to the whaitsiid condition. The main body of

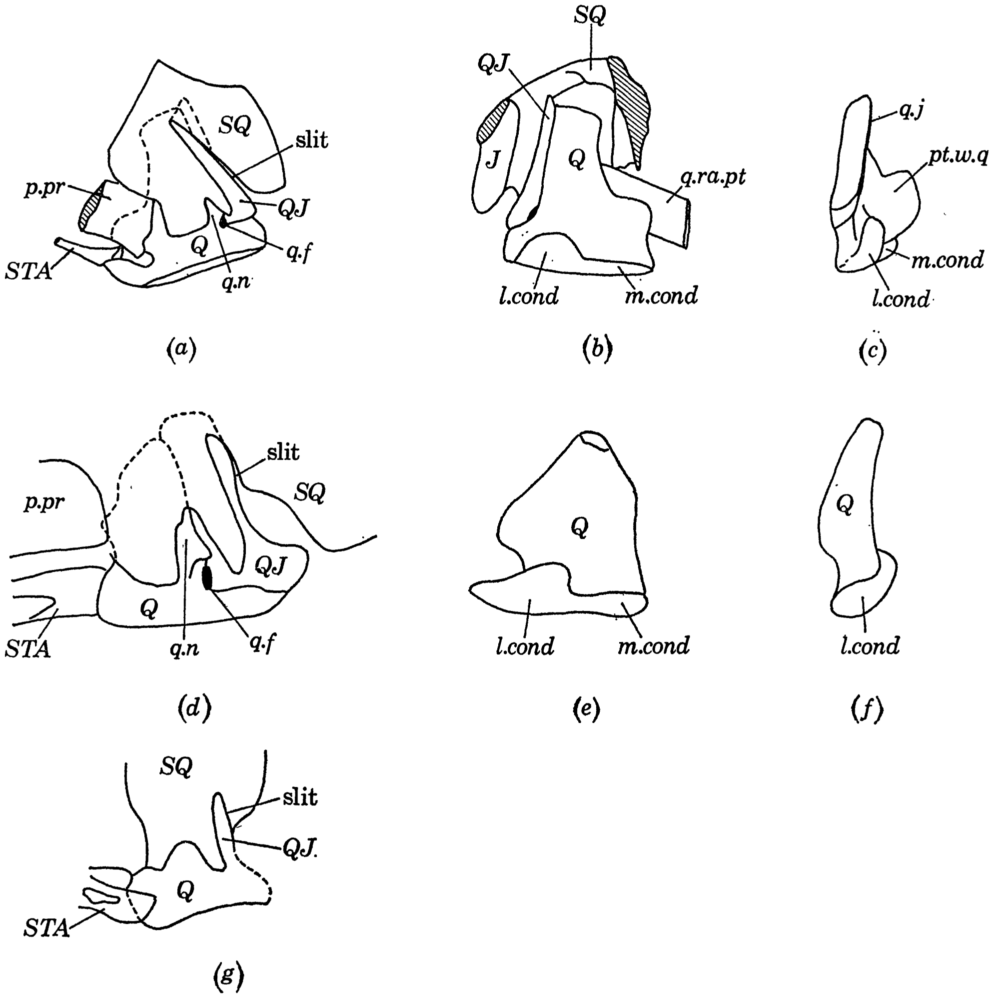


Figure 4. Quadrate complex of whaitsiids and cynodonts. (*a*) Unidentified whaitsiid (T 900), quadrate and quadratojugal *in situ*, posterior view. (*b*) The same in anterior view. (*c*) Quadrate of the same in lateral view. (*d*) *Thrinaxodon* quadrate and quadratojugal *in situ*, posterior view (after Crompton 1972). (*e*) *Thrinaxodon* quadrate, anterior view (after Parrington 1946). (*f*) *Thrinaxodon* quadrate in lateral view (after Parrington 1946). (*g*) *Leavachia* quadrate and quadratojugal *in situ*, posterior view (after Crompton 1972).

the quadrate is again transversely widened and set into a shallow pocket in the anterior face of the squamosal. Its pterygoid wing is not as well developed as in the whaitsiids but still overlaps the quadrate ramus of the pterygoid. The paroccipital process abuts against the medial face of the quadrate, although it is possible that in the cynodonts there is a thin flange of the squamosal interspersed between. The relationship between the stapes and the quadrate is more or less identical to the situation in the whaitsiids.

The detailed structure of this region is not very well known in the procynosuchids, although Crompton (1972) has attempted a reconstruction of *Leavachia* (figure 4*g*). He shows a quadrate notch in the ventral edge of the squamosal which is intermediate in size between the small whaitsiid notch and the larger *Thrinaxodon* notch. The slit for the quadratojugal is illustrated as less deep than in *Thrinaxodon* or the whaitsiids, but with the squamosal less cut away lateral to the slit than in *Thrinaxodon*, and thus more whaitsiid-like. Brink (1960) figures a cynodont-

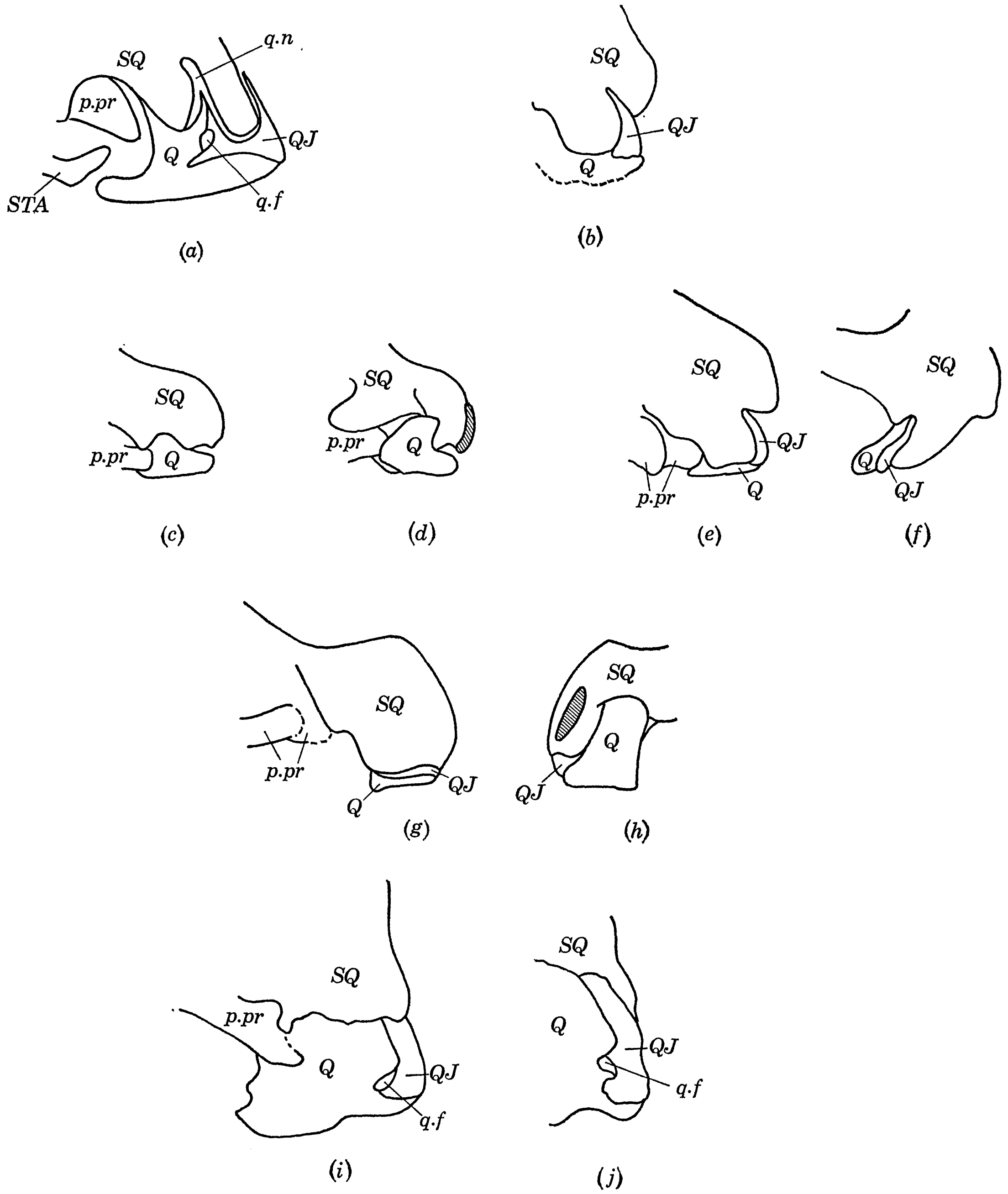


FIGURE 5. Quadrate complex of other therocephalians. (*a*) *Lycedops* (pristerognathid) quadrate and quadratojugal *in situ*, posterior view (after Broom 1936). (*b*) *Oliveria* (ictidosuchid) quadrate and quadratojugal *in situ*, posterior view (after Brink 1965). (*c*) *Ictidosuchops* (scaloposaurid) quadrate *in situ*, posterior view (after Crompton 1955). (*d*) The same in anterior view. (*e*) *Tetracynodon* (scaloposaurid) quadrate and quadratojugal *in situ*, posterior view (after Sigogneau 1963). (*f*) The same in lateral view. (*g*) *Bauria* (bauriid) quadrate and quadratojugal *in situ*, posterior view (after Crompton 1955). (*h*) The same in anterior view. (*i*) *Titanophoneus* (brithopod) quadrate and quadratojugal *in situ*, posterior view (after Orlov 1958). (*j*) The same in anterior view.

like arrangement of the quadrate-quadratojugal complex in *Scalopocynodon*, with the quadratojugal clearly lying within a slit in the secondarily reduced squamosal of this particular form (figure 1*a*).

To consider the nature of this region of the skull in the other therocephalian groups, Broom (1936) reconstructed the quadrate area of the skull from serial sections of the pristerognathid *Lycedops scholzi*, showing some resemblance to the whaitsiid condition (figure 5*a*). The squamosal bears a deep notch in its ventral border behind the quadrate, adjacent to the quadratojugal foramen. Further laterally the quadratojugal rests on the dorsal surface of the quadrate condyle and sends a spur dorsally. However, the full extent of this spur is not indicated and it is not clear whether it lay enclosed in a slit in the squamosal after the fashion of the whaitsiids, or whether it lay along the lateral and posterior faces of the quadrate, having been exposed only as a result of breakage of the squamosal bone. In Broom's figure, the relationship of the medial part of the quadrate of *Lycedops* to the paroccipital process and the stapes is very similar to the whaitsiids. Boonstra (1953, 1954) has described the articular region of several pristerognathids although none of them are well preserved. In certain of his specimens, notably *Theriodes cyniscus* (Boonstra 1953, Figure 2*b*), the notch in the ventral edge of the squamosal is indicated, but in none of them is there any indication of the quadratojugal fitting into an incision in the squamosal. A specimen of *Pristerognathus vanderbyli* in the Institüt für Geologie und Palëontologie of Tübingen University has the quadrate complex in place, but does not appear to have a slit in the squamosal for the quadratojugal. However, this specimen is being further prepared by Dr Ch. H. Mendrez in Paris, which should finally elucidate the detailed structure of the pristerognathid jaw articulation. On balance, it seems at present that this group of the therocephalians does not possess the highly specialized whaitsiid-cynodont type of quadrate-quadratojugal.

Among the ictidosuchid therocephalians, Mendrez's recent description of *Regisaurus jacobi* (Mendrez 1972) shows quite certainly the absence of a slit in the squamosal for the quadratojugal. The quadrate and quadratojugal have been lost from both sides of the skull without apparently causing any damage to the squamosal. The recess in the squamosal that housed these bones has been prepared completely showing it to be a simple concavity with no sign of a slit. This description of *Regisaurus* is slightly at variance with the account of Brink (1965) of *Oliveria parringtoni* (figure 5*b*) for which specimen he figures the quadratojugal wedged into a slit in the squamosal, in posterior view. The ventral edge of the squamosal however lacks the notch behind the quadrate. If Brink's figure be compared with figures of the same specimen by Findlay (1968) it appears that the specimen is not as whaitsiid-like as might be supposed since the quadratojugal does not emerge from an opening of a slit on the anterior face of the squamosal so that it seems likely that its appearance in posterior view is a result of a cutting away of the squamosal lateral to the quadrate-quadratojugal complex (as is the case of scaloposaurs, described below) and not to the existence of a whaitsiid-like slit running right through the squamosal from its posterior to anterior faces. Brink states that this region of the skull of *Oliveria* is unsatisfactorily displayed.

Turning to the scaloposaurs, there is no evidence for the features so characteristic of the whaitsiid quadrate complex. Crompton (1955) shows no incision in the squamosal for the quadratojugal even in the specimen of *Ictidosuchops* (figure 5*c*, *d*) which he serially ground at intervals as close as 285 μm. The quadrate is perfectly well preserved, even though the quadratojugal was evidently absent, and so it is not likely that so prominent a feature as the slit would be overlooked. *Tetracynodon darti* (Sigogneau 1963) is similarly well preserved in this region and yet does not show a slit in the squamosal (figure 5*e*, *f*), except that, as suggested above in *Oliveria*, the lateral part of the squamosal has been cut away, exposing the quadratojugal in posterior view and thus giving the superficial appearance of a slit.

The situation in the most advanced of the therocephalians, the bauriids, is clear from the account by Crompton (1955) of a well-preserved articulatory region of *Bauria* (figure 5*g*, *h*). The shape of the quadrate resembles that of the whaitsiids, but there is no slit in the squamosal for the quadratojugal, nor is there the notch in the ventral border of the squamosal behind the quadrate. These observations are confirmed by Brink (1963*a*) who described the skull structure of *Bauria* from several specimens. The quadratojugal wraps around the lateral and posterior face of the quadrate, separating it from the squamosal, and not entering a slit in the squamosal.

Therefore, with the possible but doubtful exception of the pristerognathids, the method of supporting the quadrate and the quadratojugal in whaitsiids is unique among those therocephalians which have been adequately described.

The more primitive synapsid arrangement of the jaw articulation is quite different. In the pelycosaurs (Romer & Price 1940) the quadrate is firmly sutured to the squamosal and the quadrate ramus of the pterygoid, while the quadratojugal has barely been reduced from its primitive role as part of the lower temporal arcade of the temporal fenestra. In the Eotheriodonta Orlov's (1958) figures of brithopods, particularly *Titanophoneus*, show an advance over the pelycosaur condition in that the quadratojugal is further reduced and has become intimately associated with the lateral edge of the quadrate (figure 5*i*, *j*). It does not, however, show any tendency to develop the special relationship with a slit in the squamosal as seen in whaitsiids and cynodonts. Equally, there is no notch in the ventral edge of the squamosal behind the quadrate. The quadrate itself was firmly sutured to the squamosal and to the quadrate ramus of the pterygoid. The quadrate and the quadratojugal of the phthinosuchids are not well known, but as far as comparison is possible are similar to the condition in brithopods (Efremov 1954).

Another feature of the region of the jaw articulation in which whaitsiids and cynodonts show a marked similarity is the form of the articulating condyles themselves. In the whaitsiids (Kemp 1972) the quadrate bears two condyles, lateral and medial, which are continuous with one another in their posterior regions (figure 4*a*) but are quite distinct anteriorly, where the lateral condyle is an almost hemispherical boss that rises up onto the anterior face of the quadrate (figure 4*b*, *c*). In contrast, the medial condyle is flatter and is restricted to the ventral surface of the quadrate. The condyles of the articular bone of the lower jaw correspond to the quadrate condyles, for the lateral articular condyle has a high dorsally directed process in front whilst the medial condyle is flatter and faces postero-dorsally. These two condyles of the articular bone together make an articulating surface whose axis is inclined markedly anteromedially, and which faces largely posteriorly (figure 6*a*). The retroarticular process of the articular bone is a large, ventrally directed process that arises from just behind the lateral condyle (figure 6*a*).

The structure of the quadrate condyles of *Thrinaxodon* have been figured by Parrington (1946), showing quite clearly the differentiation into lateral and medial parts, with the lateral one rising up on to the front face of the quadrate and the medial one restricted to the ventral surface (figure 4*d* to *f*), exactly as in the whaitsiids. The articular condyles of the lower jaw face largely posteriorly and, again as in whaitsiids, the lateral condyle rises more dorsally in front of the quadrate than does the medial condyle (figure 6*c*). The retroarticular process of

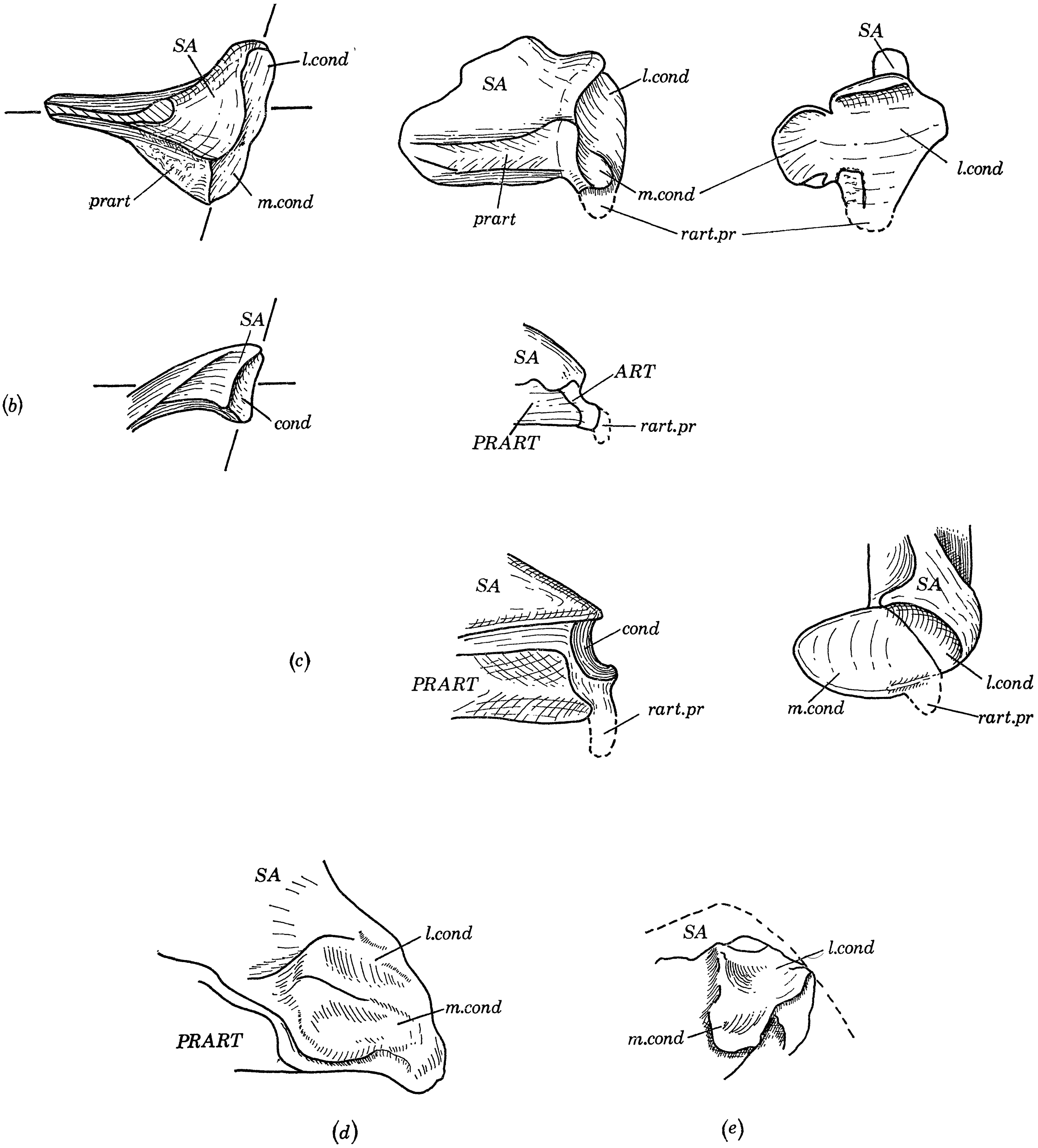


Figure 6. Articulation of the lower jaw. (*a*) Unidentified whaitsiid (T 901) hind end of lower jaw in dorsal, medial and posterior views. (*b*) *Leavachia* hind end of lower jaw in dorsal and medial views (after Brink 1963 *b*). (*c*) *Thrinaxodon* hind end of lower jaw in lateral and posterior views (after Crompton 1963). (*d*) *Syodon* (brithopod) hind end of lower jaw in medial view (after Orlov 1958). (*e*) *Phthinosaurus* (phthinosuchid) hind end of lower jaw in medial view (after Efremov 1954).

the cynodont articular bone (Crompton 1963) is ventrally directed and is directly continuous with the posterior part of the lateral articular condyle. Indeed, it is difficult to discern any features by which the condyles of *Thrinaxodon* differ from those of the whaitsiids, except for the angle that the axis of the hinge makes in a horizontal plane. In the whaitsiids this axis ran antero-medially while in the cynodont it is almost transversely oriented, although perhaps retaining a slight angular displacement (personal observation on specimen T815).

The structure of the articulating condyles of the procynosuchids is not well known, but the details which are available indicate a whaitsiid-like arrangement. In *Leavachia* (Brink 1963*b*) the quadrate condyles appear to have been divided into lateral and medial parts, and in lateral view Brink figures the articular condyle facing posteriorly and bearing against the anterior face of the lateral quadrate condyle. Most significantly, the axis of the articular condyles is alined strongly anteromedially as seen from above, at about the same angle as in the whaitsiids (figure 6*b*). Crompton (1972) reconstructs a ventrally directed retroarticular process in *Leavachia*, again resembling the whaitsiid condition.

In the procynosuchid *Dvinia* (Tatarinov 1968), the articular condyles of the lower jaw appear to face posteriorly and to have their axes alined antero-medially, much as in *Leavachia*. Unfortunately, the exact form of the condyles of *Scalopocynodon* (Brink 1960) is not clear.

Among the non-whaitsiid therocephalians, the detailed structure of the articulating condyles is not well known. The pristerognathid *Lycedops scholtzi*, as illustrated by Broom (1936) has a posteriorly facing articular condyle, with the lateral part rising dorsally to a greater extent than the medial part, but, comparing his figures of the lateral and the medial views of the lower jaw, the axis of the condyle appears transversely oriented. Boonstra's (1953, 1954) descriptions concur with Broom's but add no further details. On the other hand, the Tübingen specimen of *Pristerognathus vanderbyli*, referred to above (p. 11), suggests that the axis of the articulation was indeed alined antero-medially in the horizontal plane, as in the whaitsiids. A series of stereo-photographs of an acid prepared pristerognathid specimen in the South African Museum, Cape Town, have been made available to me by Professor A. W. Crompton. These demonstrate that the condyle of the articular resembles that of the whaitsiids in many respects. The lateral part of the condyle does indeed rise higher in front of the quadrate than does the medial part, and the two parts together make a posterior facing condylar surface with the axis alined antero-medially. The quadrate condyles are less clearly shown, but appear to be in two parts with the lateral part of the articulating surface rising on to the lower part of the anterior face of the quadrate, and the medial part restricted to the ventral surface of the quadrate.

The articular of the ictidosuchid *Oliveria* faced posteriorly as far as can be judged from Brink's (1965) figure of the side view of the skull. Finlay's (1968) illustration of the ventral view of the same skull shows that the axis of the jaw articulation ran markedly antero-medially. Thus the limited information about them suggests that again there are similarities between this group of therocephalians and the whaitsiids.

The scaloposaurs too had a posterior-facing articular condyle, with the axis inclined antero-medially, but it is not known whether the quadrate condyle was divided into lateral and medial components (Crompton 1955; Sigogneau 1963). In the case of the bauriids (Brink 1963*a*), the quadrate may have been divided into lateral and medial parts, although this is far from clear and virtually nothing is known of the exact form of their condylar surfaces.

Among the eotheriodonts, the condyles of the brithopods are quite different from whaitsiids and cynodonts, and are probably rather specialized. While the quadrate condyle is divided into lateral and medial parts, these are arranged approximately along a transverse line in *Titanophoneus* (Orlov 1958), and together they form a screw-shaped articulating surface. The lateral part of the condyle (figure 5*j*) does not extend onto the anterior face of the quadrate as in whaitsiids. In the brithopod *Syodon* (figure 6*d*), the articular condyle is double, but is quite unlike the whaitsiid type because the lateral condyle is dorsal to the medial condyle somewhat like the sphenacodont pelycosaur articular condyle (Watson 1948). It does not seem likely that this particular group of eotheriodonts demonstrates the primitive arrangement of the articulating condyles. Virtually nothing is known of the structure of the condyles in the phthinosuchids, except that in *Phthinosuchus* (Efremov 1954) there is some indication that the articular condyle faced dorsally and not posteriorly, quite unlike the therocephalian-cynodont type (figure 6*e*).

In summary therefore, it is clear that the method of supporting the quadrate, including a sheet-like quadratojugal inserted into a deep slit in the squamosal, is closely similar in the whaitsiids and cynodonts respectively, but quite different in the other therocephalian groups (with the possible exception of the pristerognathids) and in the more primitive therapsids. Secondly, the articulating condyles of both the quadrate and the articular bones are very nearly identical in whaitsiids and primitive cynodonts, although in this case there are some definite similarities to other therocephalians as well. The nature of the condyles in the latter, however, is not yet sufficiently known to be certain just how far the similarity extends. The known eotheriodont groups possessed a totally different form of jaw articulation.

Lower jaw

The postdentary bones of the lower jaw of whaitsiids (figure 7*b*) have been figured in both internal and external views by Brink (1956*b*) and Kemp (1972), and they show a very significant reorganization compared to more primitive synapsids, a reorganization that is also demonstrable in primitive cynodonts and still recognizable in galesaurids. In the whaitsiids, the surangular forms a broad, thin sheet of bone that runs forward over the medial face of the dentary in the region of the coronoid process, and is strongly curved. The ventral region of the postdentary bones consists of a stout strut formed from the prearticular and angular, which runs forward horizontally to insert between the splenial and the dentary. The anterior ends of the surangular and the prearticular-angular units respectively are connected by the flat, L-shaped coronoid bone, while between these two units there is a very large intramandibular fenestra passing right through the jaw. The lateral opening of the fenestra is partially occluded by the posterior part of the dentary, and the latter bone rises above the surangular as a discrete coronoid process.

Exactly the same pattern of the bones of the lower jaw may be seen in the procynosuchids (figure 7*c*, *d*). *Leavachia* (figure 7*d*) (Brink 1963*b*) and *Dvinia* (Tatarinov 1968) have both been figured in medial as well as lateral view, and it is difficult to see differences from the whaitsiids except that enlargement of the dentary has further occluded the lateral opening of the intramandibular fenestra. The surangular forms a curving sheet applied to the upper part of the medial surface of the dentary while the prearticular and angular together form a stout ventral rod.

In *Thrinaxodon* (Crompton 1963) the arrangement of the postdentary bones has become more modified as a result of the yet further enlargement of the dentary, but at the same time the basic pattern of the earlier forms can be recognized (figure 7*e*). The prearticular and the angular form a stout rod ventrally and the surangular a broader sheet applied to the inner dentary surface. Between them, there is a relatively large intramandibular fenestra opening medially. The lateral opening of the fenestra is almost, but not quite completely, occluded by the posterior growth of the dentary. The coronoid bears a similar relationship to the other postdentary bones as in the whaitsiids.

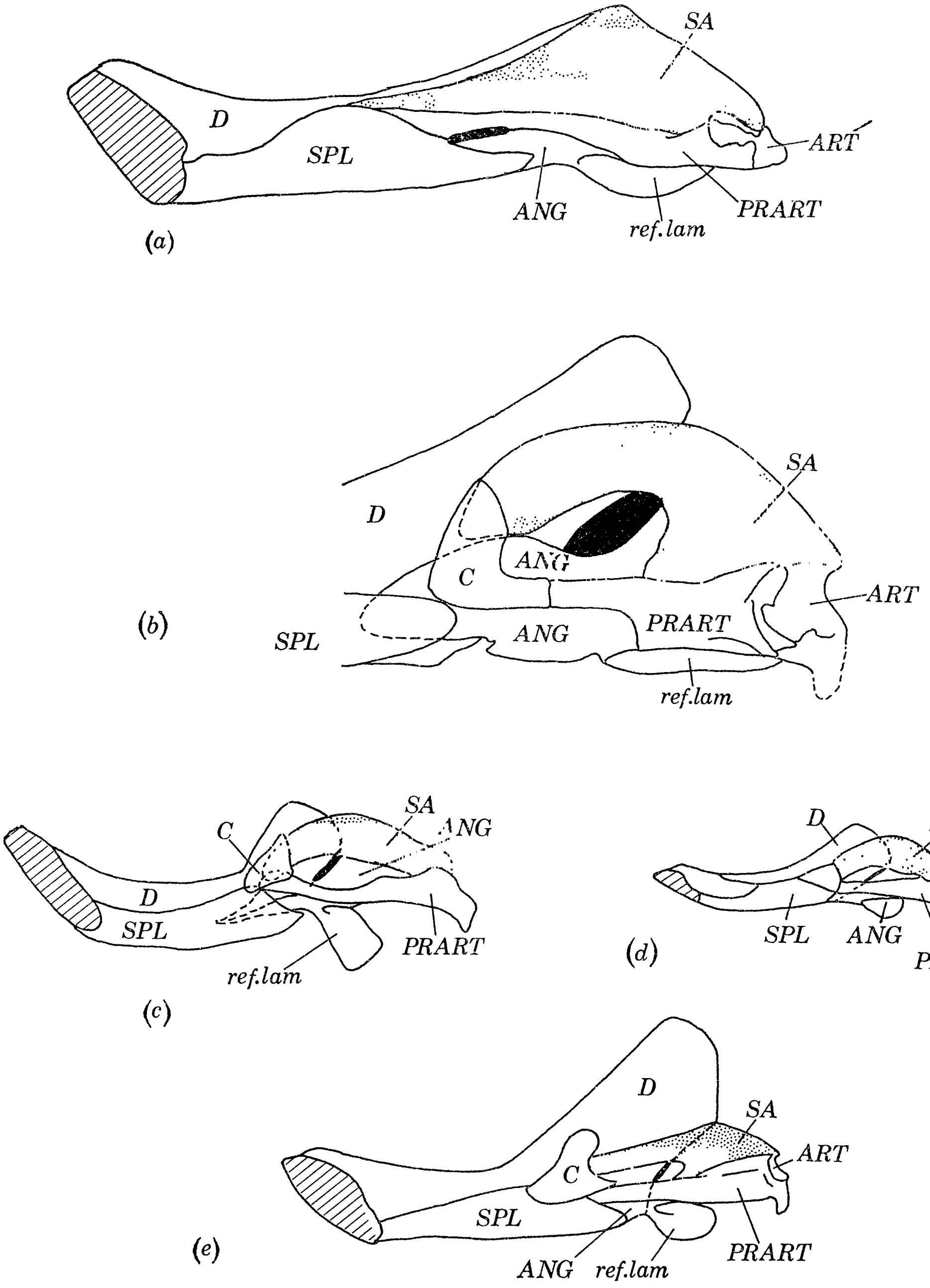


FIGURE 7. Internal view of lower jaw. (*a*) *Titanophoneus* (after Orlov 1958). (*b*) Unidentified whaitsiid (T 900) (*c*) Scalopocynodon (after Brink 1960). (*d*) *Leavachia* (after Brink 1963*b*). (*e*) *Thrinaxodon* (after Crompton 1963).

Among the other therocephalian groups, the ictidosuchids (Brink 1965), scaloposaurs and bauriids (Crompton 1955) and their close relatives appear to have an essentially similar arrangement of their postdentary bones, with a large intramandibular fenestra right through the jaw, although there is a strong tendency to exaggerate the size of the fenestra and to reduce the surangular and prearticular-angular units to relatively delicate rods. The pristerognathids are quite different in the organization of their postdentary bones as they appear to lack the intramandibular fenestra altogether, for in the stereophotographs of the acid prepared skull mentioned earlier, there is clearly no opening in the lower jaw. The surangular is in contact with the prearticular-angular unit for the full length of the postdentary bones. Further, the upper edge of the surangular meets the posterior edge of the coronoid process of the dentary, and thus does not overlap it extensively as in the whaitsiids. This is true also of the specimen of *Pristerognathus vanderbyli* in Tübingen.

In the more primitive synapsids, the pattern of the bones of the lower jaw differs from the whaitsiid condition. The prearticular of *Dimetrodon* runs high up towards the dorsal surface of the lower jaw and in the ophiacodont pelycosaurs there is actually a median foramen below the prearticular (Romer & Price 1940). The brithopods too have the prearticular running almost to the dorsal margin of the jaw (figure 7*a*) and there is a small fenestra below it. The surangular of these forms does overlap the medial surface of the dentary but it also extends ventrally to meet the prearticular along the whole of its ventral margin (Orlov 1958). While this arrangement could be regarded as ancestral to the whaitsiid type, it completely lacks their modifications.

The inner face of the lower jaw of *Phthinosaurus* has been figured by Efremov (1954). It is not well preserved but appears to resemble the brithopods in having the prearticular high up with a small fenestra below it, and in having the surangular meeting the prearticular along its full ventral edge.

A second feature of the lower jaw in which the whaitsiids resemble the early cynodonts is of course the development of the coronoid process, a feature lacking in the eotheriodonts.

Palate

One of the principal objections to the theory of the origin of cynodonts from therocephalians is the absence of a suborbital fenestra in the cynodont palate (Watson 1921; Romer 1969). In all typical therocephalians this fenestra is a large perforation on either side of the posterior part of the palate, bounded by the palatine, pterygoid and ectopterygoid bones and associated with it is a characteristically narrow, rod-shaped ectopterygoid. The only members of the Therocephalia which lack the fenestra are the whaitsiids, although certain of them do retain it, at least in a reduced form (e.g. *Moschowhaitsia*, Tatarinov (1963) (figure 8*c*)). Even those whaitsiids in which the fenestra is absent have a narrow, elongated ectopterygoid bone (figure 8*d*) which indicates that they have been derived from fenestra-bearing forms, because the primitive shape of this bone was roughly quadrilateral, as seen, for example, in pelycosaurs and brithopods (figure 8*b*).

Nevertheless, the whaitsiids may be regarded as a group in which the function of the suborbital fenestra had become redundant and thus it tended to be lost. If then it could be established that the cynodonts went through a stage in their evolution when the fenestra was present, but that it had subsequently been lost, they too could be considered as a group in which the function of the fenestra was reduced, which could be taken as evidence for a whaitsiid–cynodont relationship. The actual evidence for a suborbital fenestra at some stage of cynodont ancestry is not strong, but there are certain indications. In the procynosuchids there is a small foramen in the palate in the region where the fenestra lies in typical therocephalians. It is between the ectopterygoid and the palatine in *Scalopocynodon* (Brink 1960) (figure 8*e*), while in *Dvinia* (Tatarinov 1963) (figure 8*f*), the foramen lies in the suture where the ectopterygoid, palatine

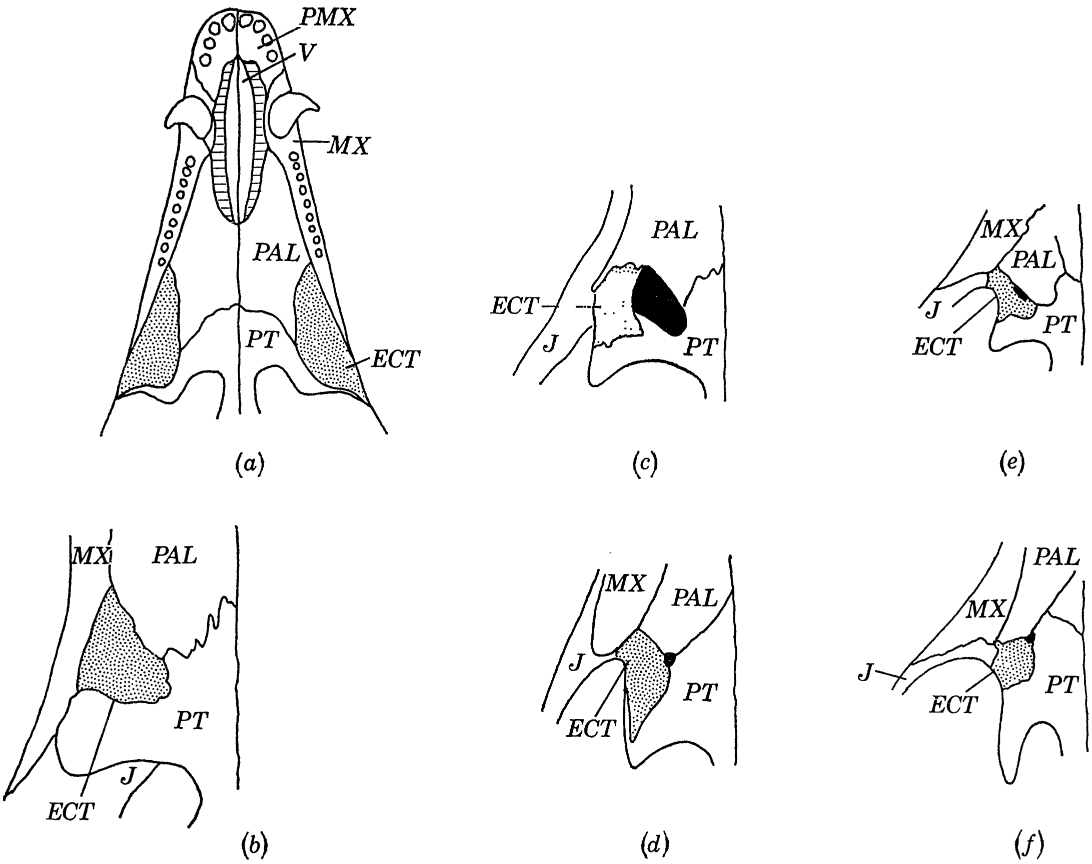


FIGURE 8. Palate in ventral view. Ectopterygoid stippled. (*a*) *Eotitanosuchus* (phthinosuchid) (after Chudinov 1960). (*b*) *Titanophoneus* (after Orlov 1958). (*c*) *Moschowhaitsia* (after Tatarinov 1963). (*d*) *Aneugomphius*(after Brink 1956*b*). (*e*) *Scalopocynodon* (after Brink 1960). (*f*) *Dvinia* (after Tatarinov 1968).

and pterygoid all meet, and thus it resembles closely a similar foramen in the whaitsiid *Aneugomphius* (Brink 1956*b*) (figure 8*d*). The association of the foramen with the sutures, and its apparent variability in position, suggests that it exists in procynosuchids as a remnant of a larger aperture. Possibly the main function of the fenestra was lost, but a secondary function was the transmission of a nerve or blood vessel and the small foramen remained to serve in this limited capacity.

As Brink (1960) has pointed out, the ectopterygoid of the procynosuchids is larger than in later cynodonts, but Romer (1969) has argued that this is merely the retention of a primitive feature that has no necessary relevance to possible relations to the therocephalians. In fact, the procynosuchid shape of the ectopterygoid is both narrower and shorter than the corresponding eotheriodont bone. It might be argued that the procynosuchid shape of the bone resulted from an overall reduction in its size, and that it never had the characteristically narrow form associated with a suborbital fenestra. Equally, however, it could be claimed that the ectopterygoid of procynosuchids owed its narrowness to the one-time presence of a fenestra and that, after the loss of the fenestra, it subsequently shortened as well. It would be a small step to convert a whaitsiid ectopterygoid as shown in figure 8*d* to a procynosuchid ectopterygoid of the form shown in figure 8*f*. It may thus be argued that the absence of a suborbital fenestra in cynodonts cannot be considered as evidence against a therocephalian origin of that group, and it is to the whaitsiids in particular that the comparison of this region of the palate points, for no other therocephalians show any tendency to reduce the suborbital fenestra, while in some of them at least, e.g. the scaloposaurs (*Tetracynodon*, Sigogneau 1963), the ectopterygoid is particularly specialized for it contacts only the pterygoid and the lachrymal bones, and neither it nor the pterygoid, contact the jugal.

The whaitsiid palate shows a number of other similarities to the cynodont palate which are also modifications away from the eotheriodont condition. The vomer is a single, median bone which is deep and narrow for much of its length and thus quite unlike the paired flat bones of all the more primitive therapsids, including the pristerognathids. The ictidosuchid vomers are approaching this condition (Mendrez 1972) for they are fused anteriorly, although still paired posteriorly, while the scaloposaurs and bauriids possess completely fused vomers with a deep, narrow section between the internal nares, and thus they resemble the whaitsiids in this respect.

Behind the vomer, the palate of the whaitsiids is deeply vaulted (figure 20, plate 2) along the midline, and the edges of the vault are bounded by sharp ridges which have been presumed to support a soft palate (Tatarinov 1963). This is closely comparable with the condition in procynosuchids where flanges on the maxillae and palatines pass medially to floor incompletely the palatal vault. In both these cases, the palatal vault terminates posteriorly by a wide, low exit onto the surface of the palate. Somewhat similar conditions are found in the other therocephalian groups, with the exception of the pristerognathids in which the palatal vault is barely developed at all. Among the eotheriodonts, the palate of phthinosuchids (figure 8*a*) is virtually flat with no vault, while in the brithopods where there is some degee of vaulting, the posterior termination is quite unlike that of the whaitsiids for it is deep and very narrow, a condition reminiscent of the gorgonopsids (Kemp 1969*a*).

In all the therocephalian groups there has been a great reduction of the palatal dentition, which is to be expected in the ancestors of the cynodonts. In contrast, the eotheriodonts are primitive in retaining well-developed palatal teeth. The brithopods have a number of relatively massive teeth on the palatine and to a lesser extent on the pterygoid (Orlov 1958), and in the case of the phthinosuchids there are broad dentigerous areas on both palatines and pterygoids.

Epipterygoid

The broadly expanded epipterygoid has always been known as a characteristic of the whaitsiids, although no detailed description of its form has yet been given. Two specimens available to me show this bone to advantage, specimens T 357 (figure 18, plate 1) and T 902, and the resemblance to the cynodont epipterygoid is astonishing.

The whaitsiid epipterygoid is widely expanded to form a broad, thin sheet lying between the pterygoid of the palate and the parietal region of the skull roof (figure 9*a*). The anterior edge is deeply concave in lateral view and is rounded except for its upper one-third or so which is thin and sharp. Behind this anterior edge, the bone is curved in a complex manner; the upper part stands almost in a parasagittal plane except for a slight lateral flaring immediately below its contact with the skull roof, while the ventral part of the bone turns to run postero-laterally alongside the quadrate ramus of the pterygoid and at the same time it curves slightly medially in a ventro-dorsal direction.

A most prominent feature of the posterior part of the epipterygoid is the large foramen (*for.v*) which must have transmitted the maxillary and mandibular branches of the trigeminal nerve. It is formed from a narrow posteriorly directed process running from the hind edge of the epipterygoid just below the level of the epipterygoid-parietal contact which meets a second process running dorsally from the quadrate ramus of the epipterygoid. Although these two processes contact one another, they do not fuse and together they meet the antero-dorsal process of the prootic. (In specimen T 357, the foramen is not completed behind because the posterior of the two epipterygoid processes has been broken.)

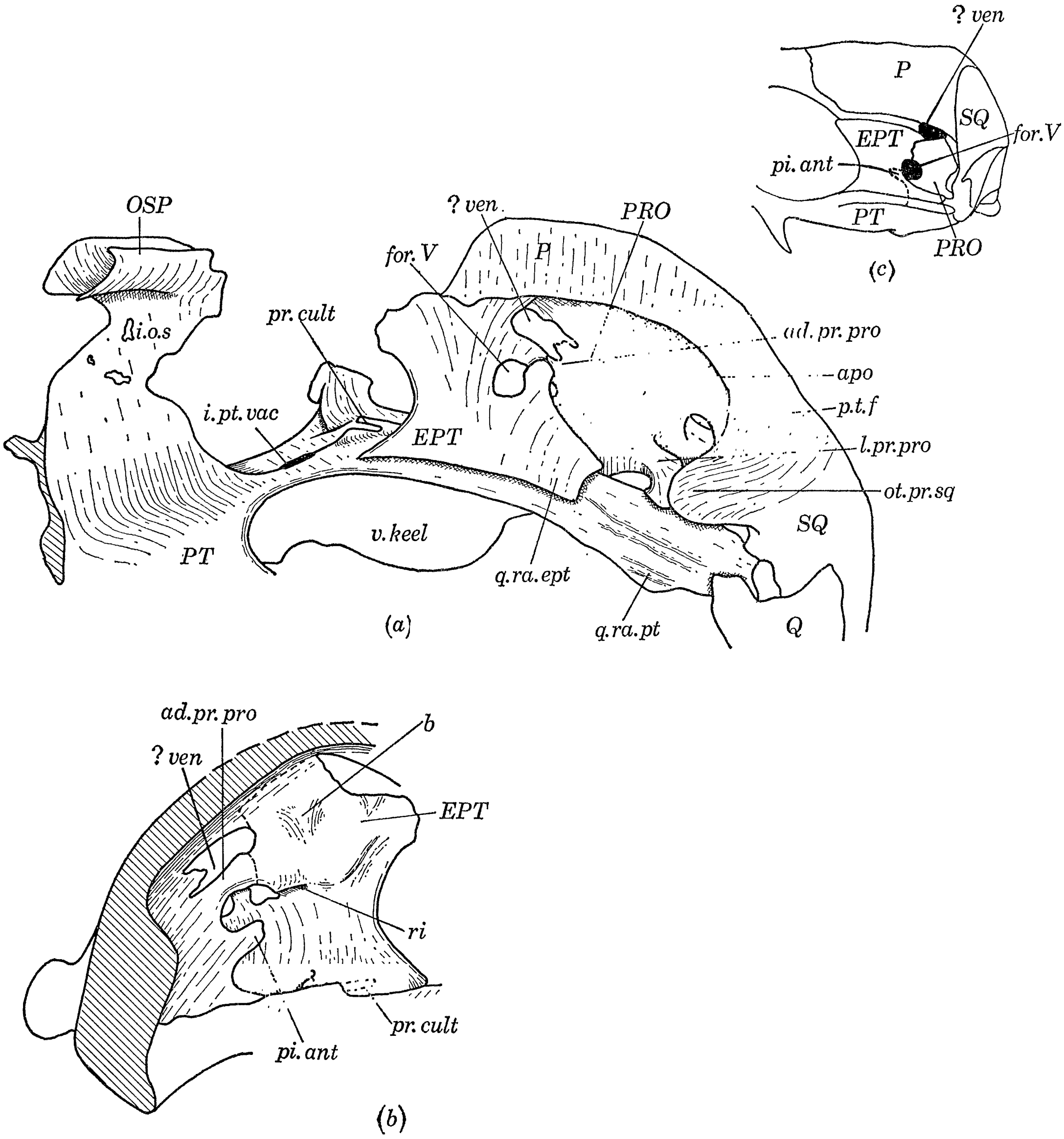


FIGURE 9. Braincase and associated structures. (*a*) Unidentified whaitsiid (T 902) in lateral and slightly antero-dorsal view, × $\frac{3}{4}$. (*b*) Inner view of the epipterygoid of the same specimen. (*c*) *Thrinaxodon* in lateral view (after Parrington 1946; Hopson 1964).

A feature of the more dorsal of the processes is a sharp, slightly out-turned upper edge. This process lies well below the level of the parietal and there is therefore a second large foramen bounded by the parietal and supraoccipital above, and the epipterygoid anteriorly and ventrally, and the prootic posteriorly. A small process of the prootic runs across this foramen for a short distance.

The quadrate ramus of the epipterygoid is a very thin sheet of bone that is slightly convex in outer view between its upper and lower edges. It runs towards the quadrate but terminates well before reaching that bone. The posterior edge of the ramus is sharp and irregular. The external surface of the whole of the epipterygoid is smooth and featureless.

The contact between the epipterygoid and the parietal extends from the postero-dorsal corner of the epipterygoid forwards along a horizontal line but the more anterior part of the epipterygoid appears to have been free of the skull roof, as indicated in specimen T 902. (In specimen T 357, the antero-dorsal part of the epipterygoid is missing.) Where the two bones do contact, the suture is interdigitating and the epipterygoid overlaps internally to a slight extent. Ventrally the epipterygoid is intimately associated with the pterygoid. The quadrate ramus of the epipterygoid overlaps the quadrate ramus of the pterygoid, although the contact is restricted to the upper half of the pterygoid, and appears to have been a ligamentous connexion only, since the opposing faces of the two bones are slightly separated in specimen T 902. More anteriorly the pterygoid becomes plate-like and horizontal but it retains a low, vertical ridge along its lateral margin continuous with the vertical quadrate ramus. Anteriorly to the quadrate ramus the epipterygoid is still in contact with the lateral face of the margin of the pterygoid, but it also sends a horizontal process medially over the dorsal surface of the pterygoid, adjacent to the basipterygoid articulation (figure 10*b*). It is probable, although not entirely certain from the present specimens, that the horizontal process of the epipterygoid actually contacts the basipterygoid process of the basisphenoid. The anterior part of the horizontal process runs medially over the pterygoid towards the processus cultriformis of the parasphenoid, but a flange of the pterygoid rises dorsally from alongside the processus cultriformis and turns laterally to enclose the epipterygoid in a slit.

The inner surface of the left epipterygoid of specimen T 902 is particularly well preserved (figure 9*b*). Immediately above the inner opening of the trigeminal foramen there is a sharp ridge of bone which continues the line of the antero-dorsal process of the prootic forwards for a short distance (*ri*). The ridge curves downwards around the antero-dorsal margin of the foramen and then turns to run anteriorly from the front of the foramen for a short distance before fading out. Thus there is a small pocket under the ridge lying just in front of the inner opening of the trigeminal foramen, which presumably housed the semilunar ganglion of the trigeminal nerve. A second, much less prominent ridge runs antero-dorsally from the region of termination of the first ridge, almost to the antero-dorsal limit of the epipterygoid. The medial surface of the epipterygoid is also marked by a distinct boss (*b*) in the middle of the dorsal part of the bone.

The antero-ventral process of the prootic (pila antotica, Olson 1944) lies a long way medial to the epipterygoid and is thus not at all involved in the epipterygoid-braincase relationships.

There is a profound similarity between the epipterygoid of the whaitsiids, as just described, and that of the cynodonts among which the epipterygoid region of *Thrinaxodon* is particularly well known (Parrington 1946). The lateral aspect of the bone (figure 9*c*) shows the deeply concave anterior margin and the complex curvature, with the quadrate ramus turning to run postero-laterally while the main part remains in a parasagittal plane. The trigeminal foramen of the cynodont epipterygoid is formed by a meeting of a posterior spur of the epipterygoid and the antero-dorsal process of the prootic, although in this case the two bones meet along a fairly long suture. The ventral completion of the foramen also differs in the cynodont because the ventral border is formed from the quadrate ramus of the epipterygoid rather than from a distinct spur rising from this ramus, and posteriorly the rim of the foramen is formed from the lateral prootic process discussed below (p. 28). The second large foramen that was noted in the whaitsiids also occurs in *Thrinaxodon*, between the parietal, epipterygoid and prootic bones. The nature of the ventral attachment of the epipterygoid to the pterygoid is similar in cynodonts and whaitsiids. In *Thrinaxodon*, the quadrate ramus of the epipterygoid overlaps the pterygoid laterally and again the attachment is restricted to the more dorsal part of the pterygoid and is loosely preserved. More anteriorly, the epipterygoid again sends a medially directed horizontal process over the pterygoid which is clasped in a slit in the pterygoid in the manner described for the whaitsiids. This is particularly clearly shown in a specimen of *?Thrinaxodon* (T 817) where the dorsal surface of the basicranial axis has been prepared mechanically. The posterior part of the horizontal process of the epipterygoid of *Thrinaxodon* clearly contacts the basipterygoid process of the basisphenoid and the pterygoid has been reduced in this region so that the overlying epipterygoid is exposed in ventral view adjacent to the basipterygoid articulation (figure 10*c*).

The inner surface of the epipterygoid is clearly demonstrated in a series of stereophotographs of an acid-prepared specimen of *Thrinaxodon* in the South African Museum (the photographs were given to Cambridge University Museum of Zoology by Mr C. Gow). The pila antotica is not involved in the contact of the epipterygoid with the braincase because, as in whaitsiids, it lies well medial to the epipterygoid. There is an interesting condition of the pila antotica seen on one side of the specimen for it curves upwards to meet the antero-dorsal process of the prootic and thus converts the trigeminal notch of the prootic into a complete foramen, medial to the trigeminal foramen of the epipterygoid. This is reminiscent of the condition in a particularly well-ossified gorgonopsid specimen, *Arctognathus* sp. (Kemp 1969*a*), where the ossification of the prootic is continued forwards in front of the trigeminal notch, converting the latter into a complete foramen. Since in the gorgonopsids the epipterygoid is completely unexpanded, it suggests that in the cynodonts the presence of a complete prootic foramen for the trigeminal nerve has no relevance to the expansion of the epipterygoid, but is the result of ossification of cartilage that is primitively always present. However, it does demonstrate a further similarity between whaitsiids and cynodonts because there appears to be a small recess between the epipterygoid and the prootic in the antero-dorsal region of the trigeminal foramen, which corresponds to the recess noted in the whaitsiids which probably housed the semilunar ganglion. If the pila antotica of the whaitsiid, which is unfinished and therefore probably continued in cartilage, were to have been completed as in the cynodont so that it met the antero-dorsal prootic process, it would in fact bear exactly the same relationship to the presumed recess for the semilunar ganglion as appears to be the case in *Thrinaxodon*.

The ridges noted on the medial face of the whaitsiid epipterygoid are not apparent in either the South African specimen of *Thrinaxodon* or in specimen T 817.

To summarize, the epipterygoids of whaitsiids and cynodonts are basically very similar, and differ only in the following apparently trivial respects:

(*a*) In cynodonts there is a relatively long sutural contact between the epipterygoid and the antero-dorsal process of the prootic, instead of the simple, limited overlap in whaitsiids.

(*b*) The posterior border of the trigeminal foramen is formed from the lateral process of the prootic in cynodonts and from the epipterygoid in whaitsiids.

(*c*) The horizontal process of the epipterygoid probably has a more extensive contact with the basipterygoid process in cynodonts than in whaitsiids.

The detailed form of the epipterygoid is much less well known in the procynosuchids. In *Scalopocynodon*, Brink (1960) describes a very whaitsiid-like condition with a 'feeble overlap of the prootic' by the epipterygoid and no apparent suture formation between these two. The base of the epipterygoid is clearly like that of the whaitsiids with a medially directed horizontal process reaching towards a dorsal crest of the pterygoid alongside the parasphenoid (in his specimen, the epipterygoid has evidently been displaced slightly and no doubt in life the epipterygoid actually met the pterygoid crest). In *Leavachia* (Brink 1963*b*) the epipterygoid again merely overlaps the antero-dorsal process of the prootic without forming a suture. It seems therefore that the extensive sutural attachment of the epipterygoid to the prootic was not achieved in the cynodonts until the galesaurid level of evolution.

In other therocephalian groups there is some tendency towards expansion of the ascending process of the epipterygoid, but in none of them except the bauriids does it approach the degree of development found in the whaitsiids. In both the pristerognathids, and ictidosuchids (Mendrez 1972), the dorsal and ventral parts of the epipterygoid are a little expanded, but there is no formation of a trigeminal foramen or any close approach towards contact with the prootic. The bauriids do form a broad sheet of the epipterygoid but, according to the description of Brink (1963*a*), there is still no trigeminal foramen, or even a notch representing an incomplete foramen; no contact with the prootic; and no well-developed quadrate ramus. Thus it cannot be considered as at all cynodont-like.

The epipterygoid is not known in either the phthinosuchids or the brithopods, which fact alone suggests that it was not enlarged. The primitive condition of the ascending process of the epipterygoid, as represented in the pelycosaurs (Romer & Price 1940) and also the gorgonopsids and dicynodonts, is a simple, slender rod.

In the form of the epipterygoids, therefore, the whaitsiids and the cynodonts show a very detailed resemblance to one another, a condition not met with in any other therapsid group.

The basicranial axis

There are several features of this region of the skull of whaitsiids that resemble the cynodont structure, particularly the manner in which the pterygoid is associated with the parabasisphenoid complex, the reduction of the interpterygoid vacuity and the reduction of the processus cultriformis of the parasphenoid.

In the whaitsiids, the pterygoids form a very deep, narrow keel behind the palate and they clasp the equally deep keel of the parasphenoid posteriorly and so form a three-layered sheet of bone (figures 9*a*, 10*a*). The posterior termination of each pterygoid is at about the level of the ventral opening of the carotid canal and in fact, in specimen T357, the anterior borders of these apertures are clearly formed from the pterygoid itself. Along the base of the keel each pterygoid expands as a horizontal girder alongside the basicranial axis of the skull, which completely underlies the basipterygoid process of the basisphenoid (cf. figure 10*a* with 10*b*). (In *Aneugomphius* (Brink 1956*b*), the posterior edges of the basipterygoid processes are just visible in ventral view.) In dorsal view the basipterygoid process is a triangular, horizontal plate as shown on the right side of specimen T 902 (figure 10*b*), and the probability of the epipterygoid contacting the process has been noted earlier (p. 21). Between the basipterygoid processes, the processus cultriformis of the parasphenoid arises as a low, median septum flanked on either side by the medial edges of the pterygoids, while anterior to the base of the processus cultriformis the medial edges of the pterygoids rise dorsally as flanges that turn medially to enclose the foot of the epipterygoid as described above (p. 21). There is a deep, narrow cleft between the medial edges of the pterygoids in this region (*i.pt.vac*, figures 9*a* and 10*b*), which does not quite penetrate through to the ventral surface of the skull. Morphologically the cleft is a remnant of the interpterygoid vacuity which is thus completely closed in this particular specimen. In certain other whaitsiid species, e.g. *Moschowhaitsia* (Tatarinov 1963) and *Aneugomphius* (Brink 1956*b*) the cleft does continue ventrally between the pterygoids right to the ventral surface of the skull and thus the interpterygoid vacuity persists, although in a reduced form.

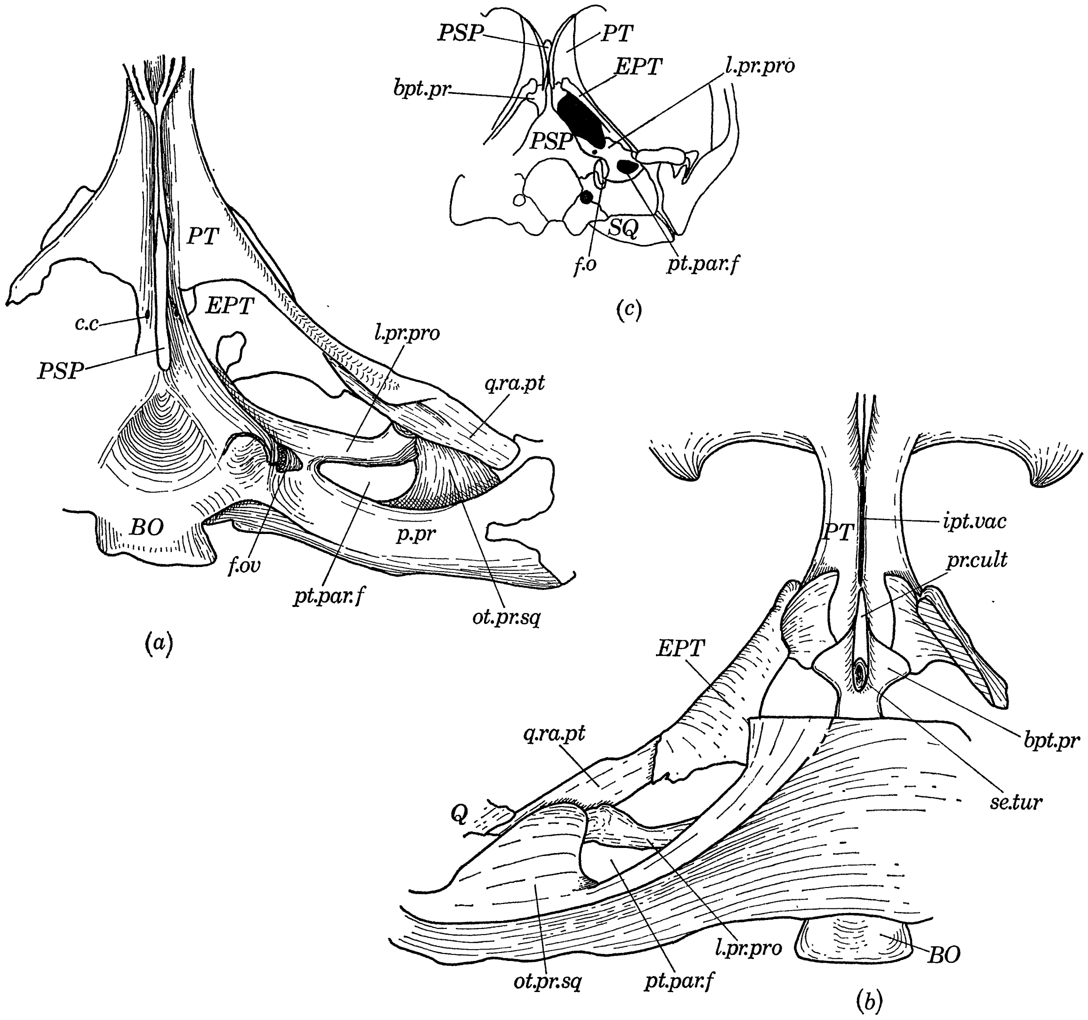


FIGURE 10. Braincase and associated structures. (*a*) Unidentified whaitsiid (T 902) in ventral view, $\times \frac{3}{4}$. (*b*) The same specimen in dorsal view. (*c*) *Thrinaxodon* in ventral view (after Parrington 1946).

The processus cultriformis was unfortunately lost during the preparation of specimen T 902, but it had been observed as a very short anteriorly directed spur of bone running forwards from the remaining basal region. The dorsal surface was in the form of a sulcus and the bone was very thin dorso-ventrally. No other whaitsiid specimen available to me has the processus cultriformis preserved (which alone is evidence of its delicate, reduced nature). However, the orbitosphenoid of specimen T 902 is very well ossified and has been isolated from the rest of the skull along with the median septum upon which it rested (figure 9*a*). The septum is a paired structure for most of its height and is formed from the pterygoids acting as an interorbital septum. Above the pterygoid part of it, the septum is unpaired and rather poorly ossified and is continuous with the orbitosphenoid itself. There is quite definitely no anterior extension of the parasphenoid inserted between the pterygoid and the orbitosphenoid parts of the median septum and therefore, at least with respect to the known condition in pelycosaurs (Romer & Price 1940) and gorgonopsids (Kemp 1969*a*) the processus cultriformis has been reduced, for in these more primitive forms the processus extends antero-dorsally to underlie the orbitosphenoid, while being itself supported ventrally by the pterygoid septum.

In *Thrinaxodon* the median ventral keel of the pterygoids and parasphenoid is practically absent (figure 10*c*). However, the form of the pterygoid just behind the palate is very whaitsiid-like for there is a ridge curving postero-medially from the lateral pterygoid process of the palate, below the level of the main, horizontal part of the pterygoid. The ridges from each side meet and continue posteriorly as far as the level of the basipterygoid articulation and presumably represent a vestigial ventral keel. The pterygoids of *Thrinaxodon* do not extend so far posteriorly as in the whaitsiids so that each basipterygoid process with its contact with the epipterygoid is exposed in ventral view. If, however, it were imagined that the pterygoids had a ventral keel, and that they extended a little further posteriorly, then they would be more or less indistinguishable from those of whaitsiids.

The organization of the basipterygoid articulation in the cynodonts is basically the same as in the whaitsiids, for the pterygoid runs forwards as a horizontal girder alongside the basicranial axis for a considerable distance while the epipterygoid, as noted earlier (p. 22), sends a medially directed horizontal plate above the pterygoid to contact the basipterygoid process and, more anteriorly, to be enclosed by the medial part of the pterygoid alongside the processus cultriformis.

As in most whaitsiids, the interpterygoid vacuity of *Thrinaxodon* has been suppressed as a result of the medial edges of the pterygoids approaching one another anterior to the parasphenoid, although Estes (1961) has described a small interpterygoid vacuity persisting in a juvenile specimen. Thus it appears that in both the whaitsiids and the cynodonts there was a tendency, not always fully achieved, to close the interpterygoid vacuity.

The processus cultriformis has been described by Parrington (1935; Parrington & Westoll 1940) on the basis of a bisected skull of *Thrinaxodon*. As in the whaitsiids it appears to be short and, although the orbitosphenoid of this cynodont is not ossified, it seems unlikely that the processus cultriformis was long enough to have played a role in the ventral support of the orbitosphenoid.

The detailed structure of the basicranial axis of procynosuchids is mostly limited to knowledge of the ventral aspect. In the case of *Scalopocynodon* (Brink 1960) there is a moderately large interpterygoid vacuity, although the pterygoids bounding it are thickened and are apparently tending to close it. The rostrum of the parasphenoid too is well developed compared to *Thrinaxodon*, but has nowhere near the anterior extent found in the pelycosaurs and gorgonopsids referred to above. In both *Leavachia* (Brink 1963*b*) and *Dvinia* (Tatarinov 1968) moderate-sized interpterygoid vacuities persist, but the nature of the processus cultriformis of neither of these types is known. In all these procynosuchids the form of the pterygoid resembles that of *Thrinaxodon* and the whaitsiids in having marked ridges curving postero-medially from the palate to form the vestigeal pterygoid keel. Indeed, they more closely resemble the whaitsiids for they extend farther posteriorly and so conceal the contact of the epipterygoid with the basipterygoid process, and in *Leavachia* at least the pterygoid keel is still to some extent present.

In all the other groups of Therocephalia the relationship of the pterygoids to the basicranial axis is similar to that described in the whaitsiids, with crests on the pterygoids curving postero-medially from the back of the palate to meet in the midline and run backwards alongside the basicranial axis. The interpterygoid vacuity separating the pterygoids just behind the palate persists in all of them however. The ventral keel is still present, although somewhat reduced, in ictidosuchids and scaloposaurs, and is probably even more reduced in bauriids (Brink 1963*a*). The extent of the keel in pristerognathids is not certain.

The basipterygoid articulation of the other therocephalians resembles the whaitsiids in that the pterygoid extends sufficiently far back to cover any contact of the epipterygoid with the basipterygoid articulation.

The detailed structure of the basicranial axis beyond external features is known only in the case of the scaloposaurs, which Crompton (1955) investigated by means of serial-grinding. He showed that the interpterygoid vacuity was fully persistent and that the rostrum of the parasphenoid extended right across it, both features differing from the whaitsiid-cynodont condition. The basipterygoid articulation itself is apparently very specialized in scaloposaurs, being movable, which could not possibly be the case in either whaitsiids or cynodonts with their extensive contact between the pterygoid and the parabasisphenoid.

In the case of the pristerognathids, mention has already been made of their small, but apparently persistent, interpterygoid vacuity. Olson (1944) describes an extensive rostrum of the parasphenoid which supports the orbitosphenoid ossification, which if true is a considerable difference from the whaitsiid-cynodont condition.

So little information is available about the basipterygoid region of eotheriodonts that it is possible that they resembled the whaitsiid-cynodont condition. All the phthinosuchid specimens described have been extensively damaged in this region. Brithopods, as figured by Orlov (1958), show a rather different arrangement of the basicranial region. The pterygoids have a very short length of contact with the basicranial axis and the basipterygoid processes are massive and fully exposed in ventral view, and have a very long contact with the pterygoids that is quite unlike the corresponding contact in whaitsiids and cynodonts. The interpterygoid vacuities are completely closed, a precocious development compared to whaitsiids and cynodonts. No information is available concerning the nature of the processus cultriformis.

Mention has already been made of the nature of the processus cultriformis of gorgonopsids and pelycosaurs, which presumably indicates the primitive synapsid pattern. It is sufficiently extensive to underlie the orbitosphenoid region of the skull and the same is true of the dicynodonts (e.g. Cox 1959) and apparently also the pristerognathid therocephalians as seen above. In view of this, it must be regarded as probable that the eotheriodont processus cultriformis was similarly unreduced, and thus unlike that of the whaitsiids and cynodonts.

Thus comparison of the basicranial region of the skull is less than satisfactory on account of lack of detailed information for many of the groups. However, there are marked similarities between the whaitsiids on the one hand and the cynodonts on the other. And there are a number of indications that this overall similarity cannot be extended to either the other therocephalians or the more primitive therapsids.

The squamosal and lateral prootic process

The whaitsiid squamosal may be described in terms of a number of processes as Brink (1956*b*) has done for *Aneugomphius*.

(1) The ventral process that runs down behind the quadrate. This process has been described in the context of the jaw articulation and shown to be similar in both whaitsiids and cynodonts.

(2) The zygomatic process arising lateral to the quadratojugal and meeting the jugal to form the zygomatic arch.

(3) The parietal process that runs medially over the anterior face of the occiput to meet the parietal and, together with that bone, to form the occipital crest.

(4) The otic process that runs ventrally over the front face of the occiput, medial to the quadrate (figures 9*a*, 10*a*, *b*, *ot.pr.sq*).

Processes 1 to 3 are universal in synapsids but process 4 is not to be found in eotheriodonts and is thus the most interesting. It is a fairly thin sheet of bone that originates by a wide base from the rest of the squamosal medial to the quadrate, at about the level of the dorsal edge of the quadrate, and it runs antero-ventrally as a free process as far as the quadrate ramus of the pterygoid which it just contacts. At the same time it runs slightly medially. The distal end is a convex edge and from here there is a bony bridge running medially to connect it with the prootic bone. In specimen T902, the bridge is evidently a narrow, laterally-directed process of the prootic in contact both with the otic process of the squamosal and also touching the quadrate ramus of the pterygoid. It is quite free of the anterior face of the occiput, with the result that there is a large foramen (figure 10*a*, *pt.par.f*), equivalent to the pterygo-paroccipital foramen of cynodonts (Parrington 1946; Hopson 1964) bounded by the lateral prootic process in front, the otic process of the squamosal laterally, and the anterior face of the occiput posteriorly. This foramen faces ventrally and lies immediately in front of the posttemporal fenestra. In specimen T357, (figure 18, plate 1) the connexion between the squamosal and the prootic is present in exactly the same way, although in this case it is difficult to decide whether it is a laterally directed process of the prootic or a medially directed process of the squamosal which forms the anterior border of the foramen. The process is smoothly continuous with the squamosal on its anterior surface although posteriorly there is some evidence of a sutural connexion between the distal end of the process and the squamosal. The connexion of the process to the body of the prootic is damaged slightly in this specimen. It is of course possible that these two specimens differ in that the process is formed from the prootic in one and from the squamosal in the other, but most probably there are components of both bones involved and the relative contribution of each is variable. Mendrez (personal communication) has confirmed that in *Whaitsia* the process is formed from the squamosal, backed medially by a lateral process of the prootic.

This region of the skull in *Leavachia*, as described by Brink (1963*b*), bears a striking resemblance to the whaitsiid condition. The otic process of the squamosal (process 4) is present, and in contact with the prootic. Although there is no mention of a pterygo-paroccipital foramen behind the contact, this could easily be the result of incomplete preparation as appears to be the case in previously described whaitsiids. The condition in *Scalopocynodon* (Brink 1960) is difficult to interpret because of the great reduction of the squamosal. There is a contact between the squamosal and the prootic, medial to the quadrate, but not evidently by a distinct otic process of the squamosal.

As pointed out by Hopson & Crompton (1969), the presence of a laterally directed process of the prootic is probably universal in cynodonts. In *Thrinaxodon* (Parrington 1946) there is no large otic process of the squamosal, but the squamosal extends slightly downwards just medial to the quadrate as a very small process. The lateral process of the prootic contacts the squamosal at this point, and with reference to the condition in *Leavachia* particularly, it seems that this small process of the squamosal in *Thrinaxodon* is a vestige of a true otic process. The other major difference between cynodonts and whaitsiids is the expansion in the former of the lateral process of the prootic to form a sheet of bone (figure 10*c*) with a long contact with the quadrate ramus of the epipterygoid which, as noted earlier (p. 22), constitutes the posterior border of the trigeminal foramen of the epipterygoid.

Among the other therocephalian groups, the ictidosuchids have a very similar arrangement to that of the whaitsiids. In *Regisaurus*, Mendrez (1972) describes a whaitsiid-like otic process of the squamosal (which she terms an antero-ventral process), which is in contact with a lateral process of the prootic (her central process). These two, together with the anterior face of the occiput, form a pterygo-paroccipital foramen which, as in whaitsiids and cynodonts, lies anterior to the posttemporal fenestra.

A well-developed otic process of the squamosal is also to be found in the scaloposaurs (Crompton 1955; Sigogneau 1963, who both refer to it as 'squamosal process 3'). However, neither a lateral process of the prootic nor a pterygo-paroccipital foramen have been described in this group. On the other hand, bauriids (Brink 1963*a*) appear to have a sutural contact between an otic process of the squamosal and a lateral process of the prootic which presumably forms a pterygo-paroccipital foramen, although Brink's figure is not clear on this latter point.

The situation in the pristerognathids is not satisfactorily known yet. In the Tübingen specimen of *Pristerognathus* there seems to be a well-developed otic process of the squamosal running ventrally alongside the quadrate and meeting the prootic. This region of the skull is a little obscure but there is a hint of a pterygo-paroccipital foramen as well. In the stereophotographs of the South African Museum specimen too there appears to be an otic process of the squamosal, although in this case it is not possible to discern a lateral process of the prootic meeting it.

There is no otic process of the squamosal or lateral process of the prootic in either of the eotheriodont groups, nor in pelycosaurs, gorgonopsids or dicynodonts.

It seems on balance that the organization of this particular region of the skull, characterized by the otic process of the squamosal, the lateral process of the prootic and the pterygo-paroccipital foramen is a common, if not universal, feature of therocephalians. The cynodont condition can be regarded as deriving from it and so, while it cannot be taken as an indication of a specific whaitsiid-cynodont relationship, it nevertheless adds support to a belief in a therocephalian ancestry of the cynodonts, when compared with the primitive condition.

Temporal fenestra

Perhaps the most immediate similarity between the therocephalians and the cynodonts lies in the form of the temporal fenestra, for in both groups the fenestra has increased in size by a medial expansion, resulting in a narrow intertemporal region, and by an increase in length resulting in a complete change in the preorbital:postorbital ratio of the skull (figures 1 to 3).

Although a similar increase in size of the temporal fenestra has occurred in other therapsid groups, the exact method of the expansion differed, so that the detailed form of the bones is not closely comparable with the therocephalian-cynodont arrangement. In the whaitsiids, the intertemporal region is very narrow, with a fairly sharp dorsal edge, and the sides are near to vertical and deep, giving a wide, laterally facing area for the origin of temporalis muscle fibres. The ventral limit of this area is marked by a horizontal ridge running posteriorly and sweeping round behind onto the anterior face of the occiput some way below the dorsal edge of the occiput (figure 9*a*, *apo*). Above the ridge, the anterior face of the occiput is a broad, antero-dorsally facing area that is continuous with the lateral face of the intertemporal region. The actual dorsal edge of the occiput is a sharp occipital crest.

Much the same form of the fenestra appertains in cynodonts, with the parietal and occipital crests continuous and the ridge delimiting the muscle areas of the intertemporal and occipital regions similarly continuous.

Among the non-whaitsiid therocephalians these characters are similarly developed in pristerognathids (figure 3*a*), ictidosuchids and bauriids (figure 3*d*). The scaloposaurs (figure 3*c*) differ however because their intertemporal region is flatter, broader and lacks the deep near-vertical lateral faces. The occiput too lacks the broad, anterior-facing surface (Crompton 1955; Sigogneau 1963). It is possible that the scaloposaur arrangement is correlated with the small size of the animals.

In the case of the eotheriodonts there has been little expansion of the temporal fenestra above the pelycosaur level, particularly in the phthinosuchids (figure 2*b*), where the temporal region is still very wide and the postorbital skull length small. In the brithopods (figure 2*a*) there is some tendency to narrow the intertemporal region so that the lateral faces start to carry temporalis muscle fibres, but this lateral region still faces largely dorsally. As in phthinosuchids, the postorbital skull length has remained relatively small compared to the preorbital length.

One final minor point about the temporal region of the skull is the loss of the postfrontal bone in whaitsiids, along with ictidosuchids, scaloposaurs and bauriids. This is the case in cynodonts but pristerognathids (Mendrez 1965) along with all the more primitive therapsids have retained it.

The occiput

In considering the origin of cynodonts from the Therocephalia, perhaps the most disquieting feature of all is the structure of the occipital surface (figure 11), for the Therocephalia (including whaitsiids) show a number of characters which differ markedly from the cynodonts:

(i) The occiput is relatively lower and broader.

(ii) The supraoccipital is also low and broad, so that it forms or at least almost forms part of the border of the posttemporal fenestra. In cynodonts the supraoccipital is narrow and relatively high.

(iii) The posttemporal fenestra is very large and leads into a deep recess lying above the dorsal surface of the paroccipital process (figure 18, plate 1). In cynodonts the posttemporal fenestra is a small round aperture.

(iv) The posttemporal fenestra is surrounded by the tabular, supraoccipital (at least almost), the squamosal and the paroccipital process. In cynodonts it is formed exclusively by the tabular, at least superficially.

But despite these differences from whaitsiids, the cynodont occiput cannot be compared directly with the primitive condition as seen in the eotheriodonts for example. In the case of *Titanophoneus* (figure 11*a*) or *Phthinosaurus* (Efremov 1954), the height to width ratio (ignoring the squamosals which are secondarily expanded laterally in cynodonts) is intermediate between therocephalians and cynodonts. The supraoccipital is therocephalian-like in being low, and broad enough to form part of the edges of the posttemporal fenestrae, and the posttemporal fenestra is surrounded by the paroccipital process, tabular and supraoccipital (although not apparently by the squamosal). On the other hand, the posterior opening of the posttemporal fenestra is small and cynodont-like.

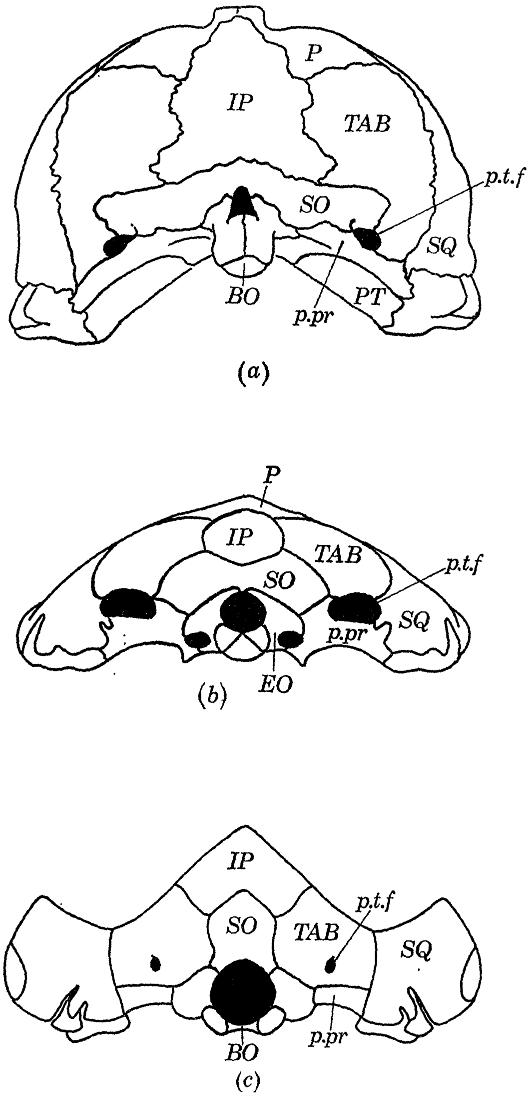


Figure 11. Occipital views of skulls. (*a*) *Titanophoneus* (after Orlov 1958). (*b*) *Aneugomphius* (after Brink 1956*b*). (*c*) *Thrinaxodon* (after Parrington 1946).

The true extent of the differences in the bone patterns cannot be certain until sectioning of the skulls has revealed whether, for example, the cynodont supraoccipital is in fact broad and only overlain superficially by the tabulars. Nevertheless, on the basis of external appearance it is clear that whether the cynodonts evolved from an eotheriodont-level directly, or via a therocephalian level, there was a considerable reorganization of the structure of the occiput.

Two hypotheses may reasonably be suggested.

(1) The cynodont condition was achieved by a medial extension of the tabular at the expense of the supraoccipital, from the eotheriodont condition. Accompanying this was an increase in height of the supraoccipital at the expense of the interparietal. The posttemporal fenestra remained more or less unchanged in size.

(2) The cynodonts went through a therocephalian stage, involving a relative broadening of the skull, which would account for the low interparietal of cynodonts compared to eotheriodonts. Correlated with this broadening of the skull was a great increase in the size of the posttemporal fenestra. This is reasonable since one of the prime functions of the posttemporal fenestra was probably to produce a posterior facing recess into which occipital musculature could insert (Cox 1959). In controlling a broad head, it would be the lateral occipital musculature which would have to become more powerful. The evolution of the cynodonts from this level of organization involved a subsequent re-narrowing of the occiput, correlated with the expansion laterally of the squamosals to form flared zygomatic arches. The narrowing was achieved principally by narrowing of the supraoccipital and paroccipital processes. A course of evolution such as this would account for the otherwise inexplicable difference in bone patterns in eotheriodonts and cynodonts respectively. Reduction of the posttemporal fenestra in the cynodonts, compared to the therocephalians could well be correlated with improvements in the atlas-axis complex which led to a more stable arrangement and thus presumably reduced the need for such large stabilizing musculature (Kemp 1969*b*).

On the basis of present information it is not possible to decide with confidence between these two hypotheses, although the first one does suffer from the need to postulate changes for which there is no obvious reason. Thus the structure of the occiput cannot be quoted as evidence denying the possibility that the cynodonts arose from a therocephalian ancestor.

Summary of the comparisons

The accompanying table (table 1) summarizes the previous discussion, although it does not of course attempt to show degees of similarity and difference, for which the text should be consulted. Cynodont characters which are not, to the best of our current knowledge, found in the eotheriodonts but which are known in the whaitsiids are listed in the order in which they were described. The further distribution of the characters among pristerognathids and scaloposaurs is indicated. In contrast to this list, I am not aware of any cynodont characters which are also found in eotheriodonts but not in at least certain therocephalians (with the exception of the small posttemporal fenestra discussed above).

Taken as a whole therefore, the table presents the case for accepting that the common ancestor of the cynodonts and the therocephalians had evolved a sufficient suite of therocephalian characters as to be itself included in the Infraorder Therocephalia. Secondly, the table indicates that among the known therocephalian families the Whaitsiidae bears the closest relationship to this postulated common ancestor. The characters which support this latter contention are marked 'W' in the table, indicating their presence exclusively in cynodonts and whaitsiids. Other characters, marked 'w' are technically present in other therocephalian groups but are manifestly most cynodont-like within the whaitsiids. Present detailed knowledge about the pristerognathids is unsatisfactory and it remains possible that they, like the whaitsiids, bear a close relationship to the cynodonts. It is particularly clear, however, that the scaloposaurs and related groups are the least cynodont-like forms of the therocephalians, and this fact explains the weakness of previous attempts to derive cynodonts from therocephalians, particularly that of Brink (1960).

Table 1

	eotheriodonts	pristerognathids	scaloposaurs	whaitsiids	cynodonts	
jaw articulation						
quadratojugal in a slit in the squamosal	–	–	–	+	+	W
notch in squamosal behind quadrate	–	?+	–	+	+	w
articular condyles set at angle to transverse axis of skull	–	+	+	+	+	.
lateral quadrate condyle partly on front face of quadrate	–	+	–	+	+	.
lower jaw						
surangular above and prearticular-angular below a large fenestra	–	–	+	+	+	w
coronoid process of dentary	–	+	+	+	+	.
ventrally directed retroarticular process†	–	?	–	+	+	W
palate						
tendency to close completely a suborbital fenesta	–	–	–	+	+	W
median vomer with narrow ventral edge	–	–	+	+	+	.
well-developed palatal vault along midline	–	–	+	+	+	.
loss of palatal teeth	–	–	+	+	+	.
epipterygoid						
greatly expanded, with trigeminal notch, etc.	–	–	–	+	+	W
basicranial axis						
form of pterygoid alongside parabasisphenoid	–	+	+	+	+	.
strong tendency to close interpterygoid vacuity	+‡	–	–	+	+	W
reduction of processus cultriformis	–	–	–	+	+	W
squamosal region						
otic process of squamosal	–	+	+	+	+	.
lateral prootic process and pterygo-paroccipital foramen	–	?	–§	+	+	.
temporal fenestra						
intertemporal region narrow, with vertical lateral faces	–	+	–	+	+	w
large, anterior facing occipital crests	–	+	–	+	+	w

† Hopson (personal communication) suggests that this may be the normal therapsid condition.
‡ Probably a specialized condition in eotheriodonts.
§ Present in ictidosuchids.

It is appropriate here to consider two important points. The first is that despite the similarities between whaitsiids and cynodonts, *the known whaitsiids themselves cannot be seriously considered as*

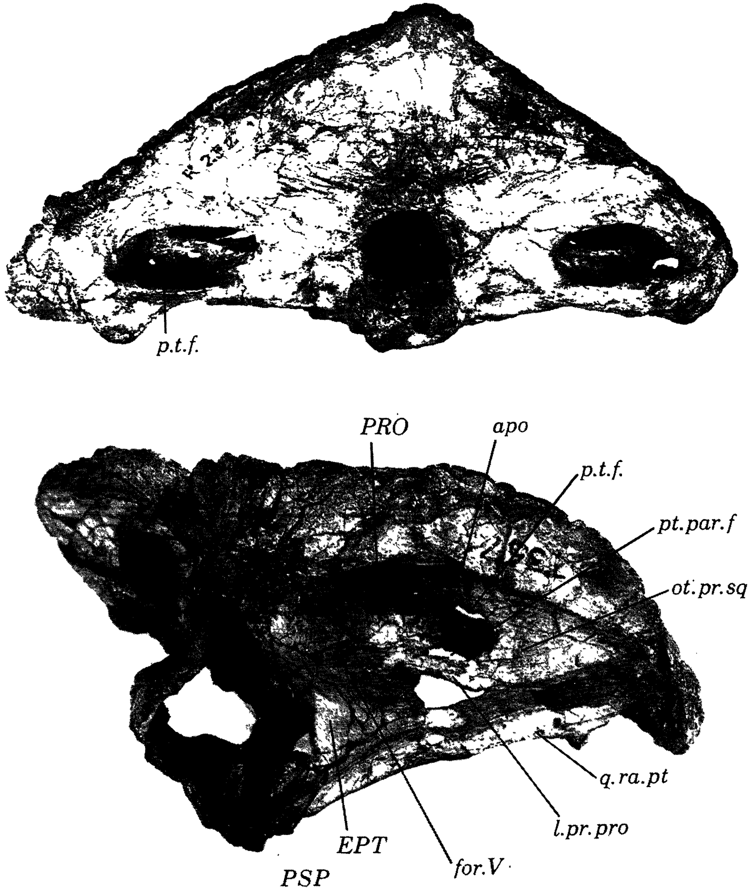


FIGURE 18. Unidentified whaitsiid, No. CUMZ T357. Above, occipital view. Below, posterior part of skull viewed from in front and slightly dorsolaterally. (Photograph by Mr William Lee.) (Magn. × 1.)

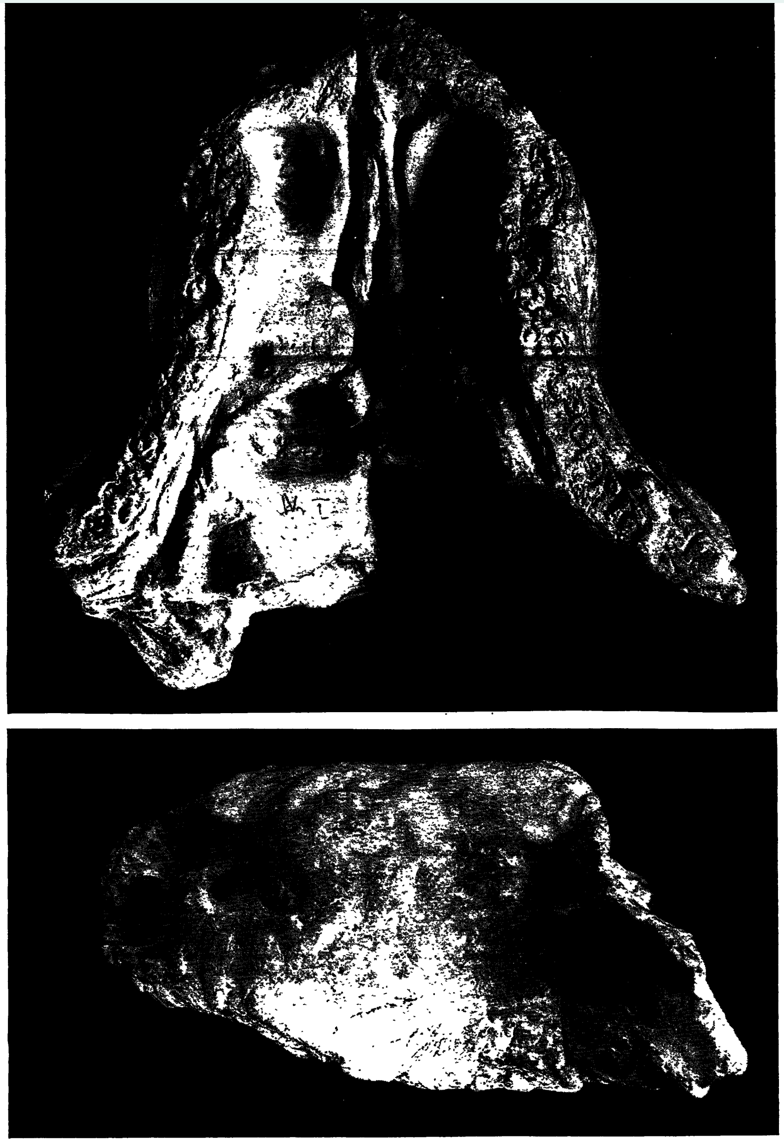


FIGURE 19. Plaster cast of a possible whaitsiid-cynodont in the South African Museum, Cast No. CUMZ T980. Anterior part of the skull in palatal and lateral views. (Photograph by Mr William Lee.) (Magn. × 1.)

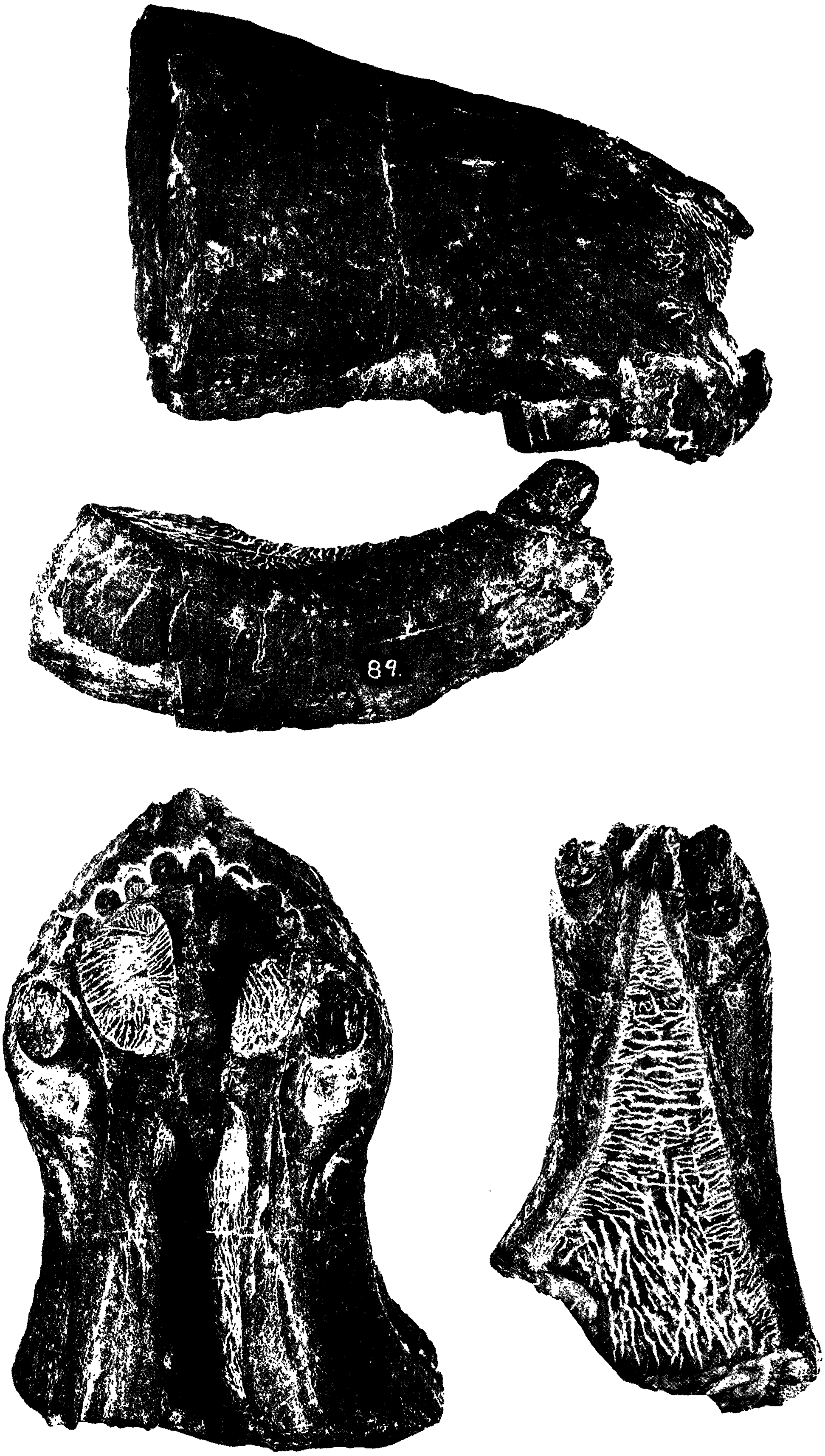


FIGURE 20. Unidentified whaitsiid snout and dentaries, No. CUMZ T 899. Above, lateral view of skull and lower jaw. Below, palatal view of skull, and lower jaw in dorsal view. (Photograph by Mr William Lee.) (Magn. × 1.)

cynodont ancestors because of their possession of several peculiarities which in no way anticipate cynodont structure. This is further discussed in the next section.

The second point is the possibility of the similarities between whaitsiids and cynodonts having resulted from convergent evolution. The process of judgement between convergence and genetic relationship as alternative explanations of observed similarities must be a subjective assessment of probability. The greater the number of similarities, and the greater the degree of similarity of these characters, then the greater is the probability that they result from phylogenetic relationship. The exact point at which the similarity is sufficiently marked to make the hypothesis of phylogenetic relationship the more probable is a matter of personal opinion; in my opinion the facts of the present case make the hypothesis that cynodonts arose from therocephalians, and that among the latter the whaitsiids are the closest known forms to the actual cynodont ancestor, overwhelmingly preferable to the alternative hypothesis of convergence.

There are two ways in which confidence in this conclusion could be increased. The first would be the discovery of forms that are structurally intermediate between therocephalians and the early cynodonts. This method must await fortune. The second way is to analyse the differences between the two groups in functional terms. If it can be shown that the changes which must have occurred in the derivation of the cynodonts from the therocephalians have functionally desirable significance, then the postulated evolutionary step gains increased credence. This is the subject of a subsequent section (p. 36).

Specializations of the whaitsiid skull

In the past the Whaitsiidae have been regarded as no more than an aberrant family within the Therocephalia, on the basis of several specialized features absent from other therocephalian families. At most some of their characters, particularly the expanded epipterygoid and perhaps the closure of the suborbital fenestra, have been seen as points of convergence towards cynodont structure. Now, however, we have a changed situation for the known features in which the whaitsiids and the cynodonts specifically resemble one another are sufficiently numerous and detailed that the probability of the resemblances being due to phylogenetic relationship greatly exceeds the probability that they are due to convergent evolution.

Nevertheless, there remains a series of whaitsiid characters which are modifications away from the basic therocephalian organization in a direction divergent from that leading towards cynodonts, and in the absence of evidence of reversal of evolution these characters must indicate that the whaitsiids themselves could not have been the actual cynodont ancestors. The characters in question (figure 20, plate 2) are principally related to the dental apparatus and the most important ones are:

Dentition consisting of well-developed incisors, large canines but complete loss of postcanine teeth, except in a few forms where a reduced number of small postcanine teeth persist (e.g. *Moschowhaitsia*, Tatarinov 1963).

Bulbous muzzle, resulting from the pinching inwards of the maxillae immediately behind the upper canines.

Broad, rather shallow muzzle.

Dentary with a strongly concave dorsal margin.

In many forms a process of the maxilla runs medially across the palate to contact the vomer and thus divides the internal nares into anterior and posterior parts.

Watson & Romer (1956) have suggested that the postcanine dentition of whaitsiids may have been replaced by horny tooth-plates, and certainly a number of the features of this region of the skull can be explained by such a hypothesis. The pinching in of the maxillae behind the canine teeth leads to the direct opposition of a broad, roughened area of the maxilla, lateral to the palatal vault, with the wide dorsal surface of the dentary. A similar skull form is seen in the gomphodont cynodonts and in bauriid therocephalians where the effect is to oppose the upper and lower postcanine tooth rows on both sides simultaneously. Furthermore, the curious concave form of the dorsal surface of the dentary makes little sense if there were no dental structure at all present. On the other hand, there is not the mass of nutrient foramina piercing either the maxilla or the dentary in the region of the presumed tooth-plates which might be expected by comparison with other animals that had such plates, particularly chelonians and dicynodonts (Crompton & Hotton 1967). But the lateral surface of these bones are well provided with foramina (Tatarinov 1964) and it is possible that it was from these that the tooth-plates received nourishment. On the whole it seems most probable that tooth-plates were in fact present. The exact form that they took is however obscure. Sharp cutting plates would be expected to attach to a fairly sharp edge of bone as, for example, the anterior end of the dicynodont beak. Thus it is probable that in whaitsiids the plates were broad and used for crushing.

The palatal process of the maxilla runs medially across the internal nares, dividing the latter into anterior and posterior parts. The lower canine enters the anterior part when the jaws closed and the function of the palatal process is related to this. In the acid prepared skull T 902, the palatal process is seen to be the base of a transverse wall of bone rising up to isolate partially the anterior part of the nasal cavity from the posterior part. Thus an anterior recess is formed into which the lower canine fits, which is only in continuity with the large posterior part of the cavity dorsally. A similar condition exists in the gorgonopsids (Kemp 1969*a*), where the palatine bones form an antero-dorsally directed wall of bone isolating a recess for the lower canine from the main part of the nasal cavity. In both cases the function was no doubt to protect the large sensory part of the nasal capsule from food particles carried on the lower canine.

On the strength of these rather superficial specializations of the whaitsiid feeding apparatus, it is clear that cynodonts, with their full complement of postcanine teeth, could not have arisen directly from whaitsiids. On the other hand, the very fact that whaitsiids and cynodonts both appeared to have developed a method of feeding that involved powerful use of the postcanine region of the jaws, with tooth plates and multicusped teeth respectively, is suggestive. For it indicates that both groups had evolved modifications of the jaw apparatus that allowed a greater force to be developed. It is likely that the common ancestor of these two groups had incipiently developed such improvements, and that in order to realize the potential of the new arrangement, one of them developed tooth plates and the other multicusped teeth, reflecting presumably somewhat different dietary habits.

No described specimen has the characters to be expected of a whaitsiid-like ancestor of the cynodonts, but there is a specimen of a theriodont snout in the South African Museum, Cape Town, which has a number of very suggestive features. There is a cast of this specimen in the Cambridge Museum of Zoology (T 950) presented by Professor A. W. Crompton (figure 19, plate 1). The form of the snout is very whaitsiid-like, being rather broad and flat with the maxillae somewhat pinched in behind the canines. However, there are eleven postcanine teeth on the left and probably eleven on the right, which is a greater complement than in any described whaitsiid. The single canine is large and there appear to be five left incisors. The number of right incisors is not clear. All the teeth have broken off at their bases so it is not possible to know whether the postcanines were multicusped. A further cynodont feature is the false palate formed from the maxilla and palatine. The two sides of the false palate do not meet along the midline (a procynosuchid character) and it is rather short. The perforation of the palate which housed the lower canine when the jaws were closed is very cynodont-like since it appears to be surrounded medially as well as posteriorly and laterally, by the maxilla. A detailed description of this specimen is awaited with great interest.

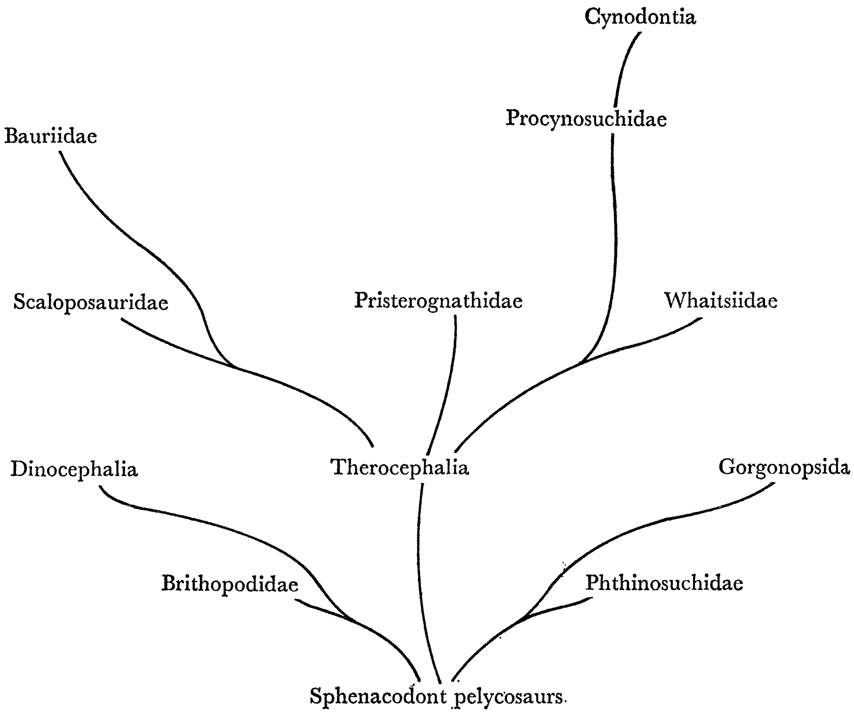
The stages in the evolution of cynodonts

The evidence presented in the foregoing sections of this paper leads to the hypothesis that the whaitsiids are representatives of a real stage in the phylogenetic line from eotheriodonts to cynodonts, relict in that they are contemporaneous with the earliest cynodonts, and superficially specialized in their dental apparatus. Acceptance of this hypothesis means that the following are the *known* stages in the evolution of cynodonts:

(1) Eotheriodont: characterized by the absence of those features listed in table 1.
(2) Whaitsiid (therocephalian): characterized by possession of those features listed in table 1.
(3) Procynosuchid: characterized by the following additional features:
  (i) Nasal and lachyrmal bones meeting.
  (ii) Frontal bone excluded from the orbital margin.
  (iii) Posterior end of frontals narrow to a point.
  (iv) Zygomatic arch heavier and more flared laterally.
  (v) Dentary larger and with adductor fossa laterally.
  (vi) Reflected lamina of the angular reduced.
  (vii) Multicusped postcanine teeth.
  (viii) Quadratojugal less extensively held by squamosal.
  (ix) Secondary palate more complete.
  (x) Some reduction of pterygoid flange of the palate and of the ectopterygoid.
  (xi) Reduction of posttemporal fenestra.
  (xii) Double occipital condyle.
  (xiii) Reduction of the parasphenoid-pterygoid keel.
(4) Galesaurid level: characterized by the following additional features:
  (i) Dentary still larger and with a much more extensive adductor fossa.
  (ii) Reflected lamina further reduced.
  (iii) Quadratojugal still less firmly held by the squamosal.
  (iv) Axis of the jaw hinge transversely oriented.
  (v) Ligamentous connexion between the quadratojugal and the postdentary bones (Crompton 1972).
  (vi) Secondary palate completed medially.
  (vii) Epipterygoid forming a suture with prootic.

The morphological gap between the whaitsiid and the procynosuchid levels is sufficiently large for it to be retained as the conventional division between the Infraorders Therocephalia and Cynodontia respectively, so the current concept of the Cynodontia need not be altered. However, the formal definition of the cynodonts must be reformulated because several of the characters traditionally regarded as cynodontid also characterize the lower level of organization. No longer can the expanded epipterygoid, the arrangement of the jaw hinge, the lateral process of the prootic, etc. be used in the cynodont definition. At the present time those features noted above as procynosuchid provide the basis for the definition of the Cynodontia, although subsequently no doubt intermediate forms between the whaitsiid and cynodont levels will be described and the diagnosis of the cynodonts will need a further revision.

Table 2. Phylogeny of the therapsids discussed



The phylogenetic conclusions reached as a result of the comparative morphology presented here may be summarized by the accompanying diagram (table 2). The exact position of the pristerognathids is debatable and elucidation of this point must await detailed anatomical description of the group. Equally, the detailed relationships of the primitive eotheriodonts (Phthinosuchidae and Brithopodidae) is open to alternative interpretation (see Introduction).

FUNCTIONAL CONSIDERATIONS

The functional organization of the whaitsiid level

It is now apparent that the characters of the cynodont skull did not all appear simultaneously but that they evolved to some extent sequentially. In order to understand the primary functional significance of a given feature it is necessary to look at it in the context of the organization of the skull in which it first appeared, since it was then that its original nature was determined. Further modification of the function of the feature may subsequently occur, but there must be functional continuity between the original and subsequent roles it plays in the skull, and therefore only with an understanding of the functional history of the feature can its significance in the later stage be fully appreciated. Ideally one should have a complete morphological series of

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forms in order to know fully the sequential order in which characters appeared, and whether any of the characters appeared simultaneously and therefore perhaps in functional correlation, but none the less it is useful to have even a single intermediate stage and thus to know at least something of the pattern of appearance of the characters. In the present case, for example, the pattern of the postdentary bones of the cynodont cannot be seen solely as functionally correlated with increase in size of the dentary or reduction of the reflected lamina of the angular, since these features appeared at different stages. The meaning of the arrangement of the cynodont postdentary bones can only be appreciated fully by interpreting its significance in the skull in which it first appeared. Thus no understanding of the organization of the cynodont skull can be complete without first appreciating the organization of the ancestral skull-type.

The jaw musculature and functioning of the jaw articulation of the whaitsiid skull have been discussed elsewhere (Kemp 1972), and these will be reviewed briefly here. It is probable that the major factor determining skull architecture is the pattern of mechanical forces related to the use of the jaws. Other functions of the skull such as housing the brain and special sensory apparatus are probably less closely correlated with overall skull form. The magnitude of the forces generated by the contraction of the jaw muscles against food appear to have been sufficiently large to place a high adaptive premium on designing the skull to resist them without disarticulation of the bones, and without excessively increasing their mass. Application of this hypothesis leads to a meaningful analysis of the architecture of the bones, which in itself justifies the assumption.

Jaw muscles (figure 12)

The anatomy of the skull and lower jaw indicates that there were three principal jaw closing muscles (see Kemp 1972 for detailed arguments). By far the largest was the temporalis (figure 12, *temp.*), originating from the broad lateral surface of the intertemporal region of the skull (sagittal crest) and the anterior facing surface of the upper part of the occiput (occipital crest). These two surfaces form a continuous muscle-bearing area that is bounded ventrally by a sharp edge, probably representing the line of attachment of an aponeurotic membrane. The occipital site of origin extends ventrally as the otic process of the squamosal (figures 9*a*, 10*b*), medial to the quadrate. The absence of the crest presumed to be for attachment of an aponeurotic membrane in this region suggests that some temporalis muscle fibres did in fact originate from the otic process. The temporalis fibres inserted high up on the lower jaw on the internal face of the coronoid process and the dorsal and internal faces of the surangular and there is no osteological evidence of the division of this muscle into discrete slips.

A second jaw closing muscle was the zygomatico-angularis, probably derived from the lateral-most part of the temporalis (figure 12, *Z. Ang.*), which originated from the inner and ventral surfaces of the posterior part of the zygomatic arch and inserted on the lateral surface of the lower jaw, on the angular bone above and internal to the reflected lamina. A strong crest on the angular marks its principal site of insertion.

The third jaw closing muscle was the anterior pterygoideus (figure 12, *A. Pt*) with an origin from the posterior surface of the lateral pterygoid flange of the palate and possibly from more posterior areas such as the ventral keel of the pterygoid. The insertion of the anterior pterygoideus muscle was probably within the angular recess, the space between the reflected lamina and the body of the angular, the muscle wrapping around the ventral edge of the jaw.

This proposed reconstruction of the musculature is based on direct anatomical observations

(Kemp 1972) and it accounts directly for certain of the whaitsiid characters, particularly the arrangement of the *temporal fenestra*, the *otic process of the squamosal* and the *coronoid process* (table 1). The three muscles together form an integrated jaw closing complex with certain properties not found in earlier synapsids or in other reptiles in general. The primary effect was the polarization of the muscles into two, one running postero-dorsally and the other antero-dorsally from the lower jaw. The first one, the temporalis, inserts high up on the jaw and the second one, the anterior pterygoideus, inserts low down. Because the latter actually inserts on the lateral surface of the jaw within the angular recess, it effectively exerts itself along the ventral margin of the jaw. In the case of both these muscles, both the length of the muscle fibres and the length of the moment arm about the hinge are increased and so both the size of the effective gape and the moment they produce are enlarged. And their geometrical properties are such that the temporalis is more effective at low gapes and the anterior pterygoideus at high gapes. The size of the gape over which an adequate moment can occur is therefore increased too (Kemp 1972). One of the consequences of this polarization of the muscles however is the danger of the anterior pterygoideus muscle causing disarticulation of the lower jaw at the jaw hinge, at high gapes, by pulling the lower jaw forwards. The zygomatico-angularis muscle functioned to prevent this because it always has a high force with a large posteriorly directed component.

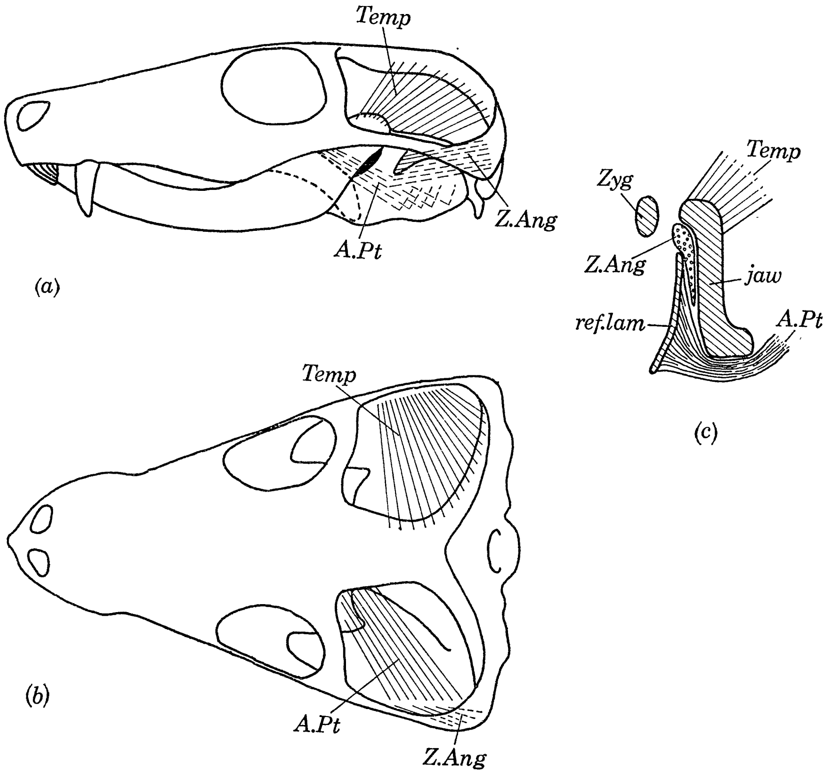


FIGURE 12. Reconstruction of whaitsiid jaw musculature, skull outline based on *Aneugomphius* (after Brink 1956*b*). (*a*) Lateral view. (*b*) Dorsal view. (*c*) Transverse section through the lower jaw in the region of the reflected lamina of the angular. Muscles indicated are the temporalis (*temp*), the anterior pterygoideus (*A. Pt*) and the zygomatico-angularis (*Z. Ang*).

Jaw articulation (figure 13)

Thus there are definite primary advantages in this reorganization of the jaw musculature but there are also a number of secondary problems raised and several of the whaitsiid skull characters may be interpreted as reflecting functional devices to overcome such problems. Perhaps most striking is the radical design of the *jaw articulation* which has been analyzed in detail (Kemp 1972). To summarize the conclusions reached, the temporalis muscle was much the largest jaw-closing muscle and its force was directed largely posteriorly. Thus, except at wide gapes the articular bone had to bear against the anterior face of the quadrate. Moreover, the increase in size of the temporalis muscle was by a medial expansion of the temporal fenestra so that most of its fibres would have had a significant medially directed component of their force. Add to this the fact that the anterior pterygoideus muscle too had a medially directed component and it is clear that there must have been a very large net force tending to pull the articular off the quadrate in a medial direction. This is overcome by the axis of the articulation being alined antero-medially (figure 6*a*). But on geometrical grounds the lower jaw could not rotate about such inclined axes unless the quadrate became streptostylic in such a way that it could rotate about a longitudinal axis. Thus the nature of the *attachment of the quadrate*, both

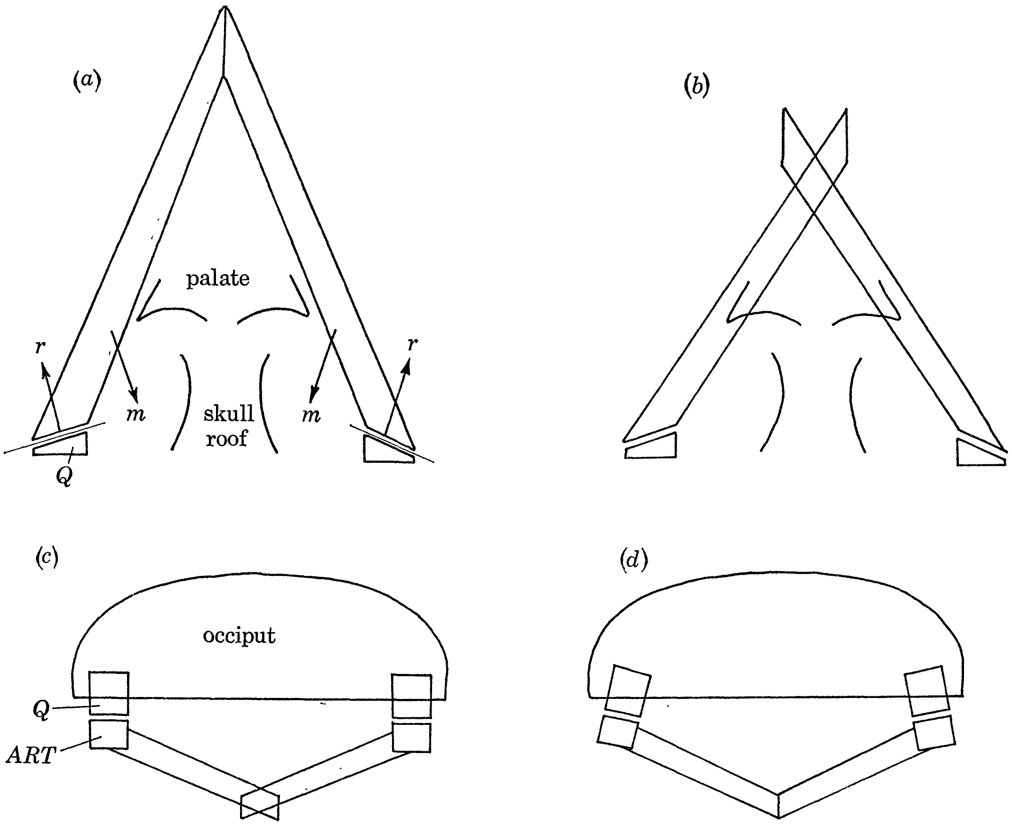


Figure 13. The whaitsiid hinge mechanism. (*a*) Diagrammatic representation of the skull and lower jaws as seen from above. The axis of the jaw hinge is inclined in the horizontal plane so that the reaction (*r*) produced by the net muscle force (*m*) is at right angles to that axis. (*b*) The same but with the jaws open; the effect of the inclined axes is to tend to force the anterior ends of the lower jaws medially. (*c*) As for the previous figure but seen from posterior viewpoint. (*d*) Correction of the tendency to displace the anterior ends of the lower jaws medially, by rotation of the quadrate complex about a longitudinal axis.

directly and indirectly via the quadratojugal in a slit in the squamosal, is to be explained as allowing just such a streptostylic movement.

The forces on the lower jaw

The increase in the magnitude of the forces generated by the jaw muscles led to problems of transmission of the forces between the points of attachment of the muscles and, ultimately,

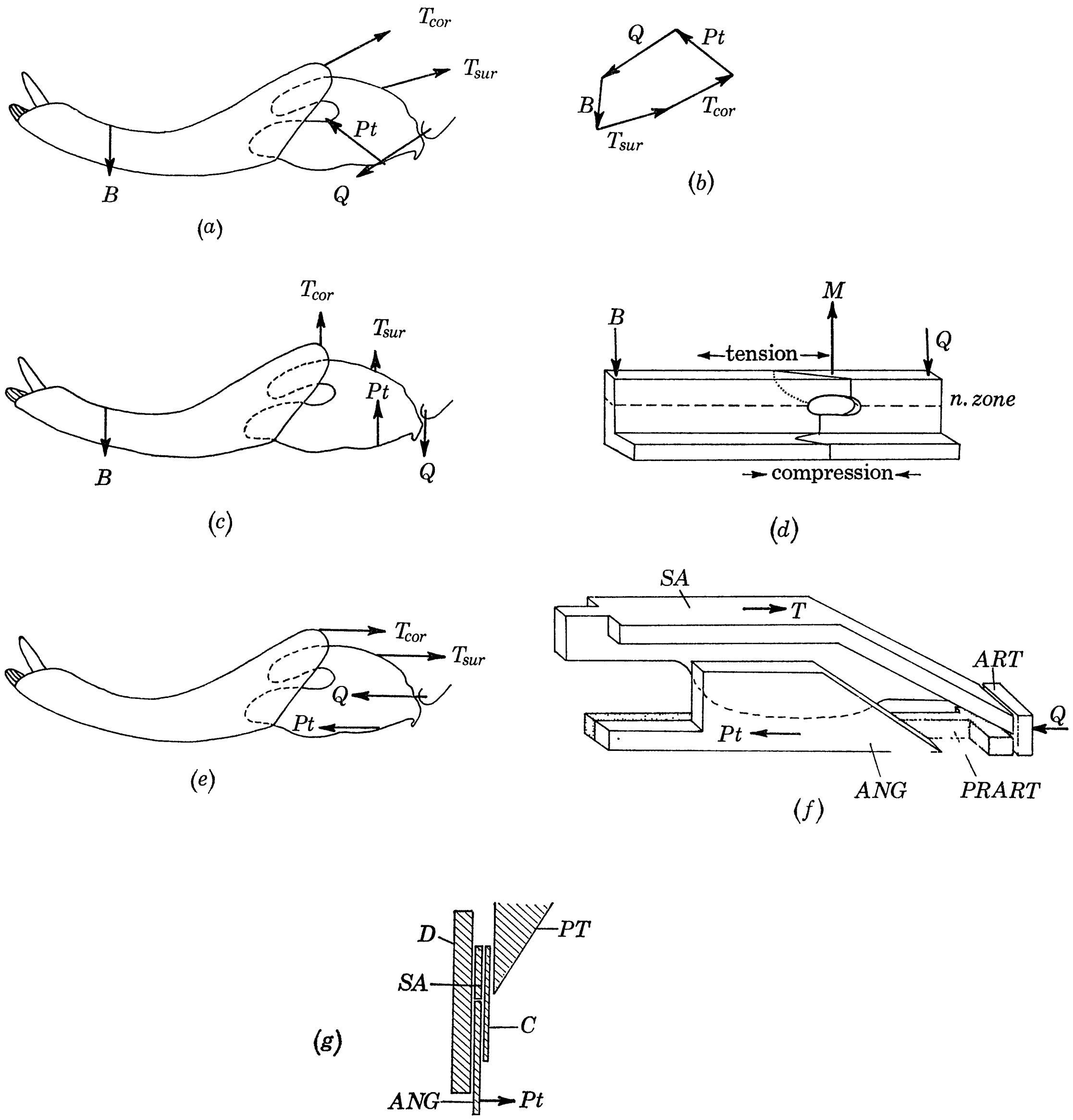


FIGURE 14. Mechanics of the whaitsiid lower jaw. (*a*) The external forces acting on the lower jaw, shown as vectors of assumed values. The method of calculation of the reaction force at the dentition (*B*) is indicated in the text. (*b*) Force polygon, used to calculate the magnitude and direction of the hinge reaction (*Q*). (*c*) The vertical components of the external forces. (*d*) The effect of the vertical components in producing a bending moment, and the principles of jaw design to resist it. Note the broad overlap of bones in the region of tension, the interdigitation of thickened bones in the region of compression, and the position of the intramandibular fenestra in the neutral zone. (*e*) The horizontal components of the external forces. (*f*) Principles of the design of the lower jaw to resist the stresses due to the horizontal components (prearticular stippled). (*g*) The role of the coronoid bone (*C*) in preventing medial disarticulation of the ventral post-dentary bones (*ANG*) from the dentary (*D*).

the dentition. The characteristic design of the bones of the *lower jaw* (figure 7*b*) can be interpreted as an arrangement which withstands better the stresses imposed upon the jaw. In an analysis of the structural properties of the jaw it is necessary to distinguish clearly between two aspects. First we may consider the jaw as a single, rigid unit with forces applied at certain points and reactions to the forces being generated at the points of contact of the jaw with the rest of the skull, namely the quadrate and the dentition. Secondly, we may consider the pattern of stresses within the jaw resulting from these forces and reactions, and note the manner in which the bones and sutures are designed to withstand such internal stresses. For simplification, the jaw musculature as reconstructed has been reduced to three muscles, each regarded as acting at a point on the lower jaw (figure 14*a*). The temporalis muscle has been divided into a part attaching to the coronoid process (T_{cor}) and a part to the surangular (T_{sur}), and the third muscle is the anterior pterygoideus (Pt). Compared to these three muscles, the zygomatico-angularis probably had a small force and certainly produced only a small moment about the articulation and has thus been ignored.

Each of these three muscles produces a force which may be resolved into vertical, horizontal and transverse components. For the moment it is convenient to ignore the transverse components since these are not involved in the production of movement of the jaw. Each of the three muscles produces a moment about the jaw hinge which tends to cause clockwise rotation of the jaw, oriented as figured (figure 14*a*). With the jaws closed upon food, an anticlockwise moment will develop of equal magnitude in the form of a reaction force (B) acting at the contact of the teeth, a distance (a) from the jaw hinge.

The clockwise moment $= T_{cor}x + T_{sur}y + Ptz$ (T_{cor}, T_{sur} and Pt are the three respective muscle forces and x, y and z are their respective mean perpendicular distances from the jaw hinge).

The anticlockwise moment developed $= B.a$. Therefore

$$B = \frac{T_{cor}x + T_{sur}y + Ptz}{a}.$$

It is impossible to get accurate assessments of the magnitudes of the forces of the muscles, but a very rough estimate of their relative sizes is that each one is 1 unit of force. Equally approximate is that their respective mean distances from the hinge are in the ratio:

$$x = 2 : y = 1 : z = 1 : a = 6.$$

On this basis, the relative magnitude of $B = 0.67$ unit of force.

The direction and magnitude of the reaction at the hinge (Q) can be derived from these figures by construction of a link polygon (see any text-book of structural mechanics for a discussion of this method, e.g. Reynolds & Kent 1965) as in figure 14*b*. Under the conditions considered here, the reaction is seen to be directed forwards and slightly downwards, and to have a magnitude of roughly one unit of force.

Having established the pattern of external forces acting upon the jaw in the parasagittal plane, we may now consider the pattern of stresses which they produce within the jaw itself, and the nature of the adaptations to resist them. For this purpose it is easiest to apply the principle of comparability which states that each force can be resolved into three components mutually at right angles to one another (vertical, longitudinal and transverse in this case) and each component be considered independently in terms of the stresses it produces. Consider first the vertical components. The lower jaw may be thought of as analogous to a beam supported at either end by the quadrate and dentition, with a series of three upwards forces applied at points between the supports. The supports themselves develop downwards support reactions (figure 14*c*). The main effect of these forces is to produce a bending moment in the beam, which tends to bow it upwards, resisted by a moment of resistance in the form of tension along the dorsal part of the jaw and compression along the ventral part (figure 14*d*). Between these two zones is the neutral layer in which there is no stress (see Alexander 1968 for a simple account of this effect).

The strength of bone under both tension and compression is high, of the order of 6×10^7 g/cm^2. The tensile strength of collagen fibres is considerably lower, roughly 7×10^5 g/cm^2 and the strength of the attachment of collagen fibres to bone is even less. However, as long as the lower jaw consists of separate bones, the sutural connexions between bones must be of connective tissue, principally collagen fibres and thus it is the sutures which tend to be the weakest areas of the jaw, under stress. In regions where the stress is compressive the bones can buttress against one another and so the compressive strength across the suture will be that of bone itself. In the case of tension, however, it is necessary to rely on the tensile strength of collagen to prevent disarticulation. In the present case, the connexion of the dentary to the postdentary bones in the dorsal region of the jaw is by means of a broad sheet of surangular extensively overlapping the internal surface of the dentary which allowed a large area of collagenous connexion but not direct abutment of the bones. This suture therefore appears to be designed to resist the tension arising in the dorsal region of the jaw. Conversely, the ventral connexion of the postdentary bones to the dentary is by means of a thickened strut, formed of both the angular and the prearticular which inserts anteriorly between the dentary and the splenial. The splenial in turn has a great overlap with the dentary all the way forwards to the symphysis. This thickening and interdigitation of the bones may be interpreted as an arrangement resistant to the compression in the ventral part of the jaw. The neutral zone of the jaw lies somewhere about half way up and it is here that the intramandibular fenestra lies. It would seem that the fenestra represents no more than a reduction of weight in a region of the jaw which is subjected to very little stress and it does not therefore weaken the jaw significantly. Figure 14*d* demonstrates these principles as a mechanical model, showing how the lower jaw is designed to resist the vertical components of the forces.

The longitudinal components of the forces acting on the jaw are shown in figure 14*e*. The posteriorly directed component of T_{cor} will tend to place the suture between the dentary and the surangular under compression. It is not possible to be accurately quantitative, but it is clear that the effect of this compression will be partly to offset the tension across this suture resulting from the effect of the vertical components of the jaw muscles, as just discussed. The posteriorly directed component of T_{sur}, on the other hand, will increase the tension across this suture. Both T_{sur} and T_{cor} will place the suture between the surangular and the articular under both compressive and shear stresses. The suture is a broad more or less transverse buttress apparently resistant to compression, and the shear involved will be small because the jaw articulation is not very far below the level of these muscles. The longitudinal component of Pt is anteriorly directed and will tend to place the angular upon which it acts under tension with respect to the posterior part of the jaw (principally the surangular) and compression with respect to the anterior part. The angular has a very broad overlapping suture with the surangular and indeed the posterior termination of the intramandibular fenestra is due to the extent of this overlap. Thus again we see the characteristic form of suture that resists tension. The attachment of the angular anteriorly has already been seen to be designed to resist the compression due to the vertical force components. The final longitudinal force is the anteriorly directed reaction at the articulation, which accounts for the broad, anteriorly facing contact between the two hinge bones. Farther forwards, the articular makes a broad buttress with the surangular, as noted, and also a similar medial buttress with the prearticular, again a compression resistant suture. This latter bone particularly was probably responsible for transmitting the hinge reaction forwards to the dentary as compression. Figure 14*f* shows the basic design of these bones in terms of resistance to the horizontal forces.

The final force components to consider are those directed transversely. With the exception of the zygomatico-angularis, these were all directed medially and their consequence upon the design of the jaw hinge has been seen. As far as the design of the lower jaw is concerned, the problem of resistance to the transverse forces is largely avoided as a result of the massive lateral pterygoid flange of the palate. In the case of the vertical force components, the anterior and posterior supports of the jaw are of necessity far apart and thus the jaw has to be deep in order to resist bending. It would not be feasible to make the jaw particularly broad in a transverse direction as well, to resist medial bending due to the transverse components of the muscle forces, and so an extra support is used in a position close to the points of insertion of the muscles. The bending moments produced by the transverse components between the pterygoid and the jaw hinge are thus very small, and are probably not critical. At wider gapes, the jaw loses support from the pterygoid flange, but the geometrical arrangement of the muscles is such that the magnitude of the transverse components of the forces falls off rapidly as the gape increases. The most critical region would have been the ventral edge of the jaw because it will be clear of the pterygoid flange at quite low gapes. This region is thickened considerably compared to the more dorsal regions. There would be a tendency for the transverse component of Pt to pull the ventral postdentary bones medially away from the dentary, and the coronoid bone was probably involved in resisting this (figure 14*g*). It has a broad overlapping contact with both the ventral and the dorsal postdentary bones and lies exactly adjacent to the pterygoid flange. Thus with a small gape it would remain wedged between the pterygoid flange and the upper part of the jaw and would tend to hold the bones of the lower part of the jaw in place.

In this discussion it has been assumed that the teeth were actually biting on food and thus the lower jaw was static and effectively supported on either side of the points of muscle attachment. Another condition in which large stresses would have been generated within the jaw would be when the muscles were contracted forcibly to impart a rapid angular acceleration to the jaw. However, the pattern of stresses under such conditions would be similar to those found in the static case since the centre of inertia of the jaw lies well forwards of the muscle insertions. At any given instant during acceleration, the jaw could be regarded as experiencing a downwards reaction force at the centre of inertia, instead of at the dentition.

It may be concluded that the reorganization of the bones of the lower jaw that was characteristic of many of the Therocephalia, including the whaitsiids was a functionally significant redesign correlated with the radical increase in the jaw muscle forces.

The forces on the skull

A number of other characters of the skull may similarly be interpreted in mechanical terms, related to the pattern of stresses set up by the action of the jaw muscles.

The intertemporal region of the skull between the postorbital bar and the occiput behaves as a loaded beam supported at either end. The load is principally the force of the temporalis muscle fibres which originate from it, and these have a vertical component which will be especially large when the jaws are open, so part of their effect will be to produce a bending moment. However, in order to increase the size of the temporal fenestra and thus the number of muscle fibres, the intertemporal bar has become narrower and thus potentially weaker and less resistant to bending. Its strength and rigidity have been increased partially by deepening it, and also by connecting it functionally to a second beam, the basicranial axis, via the *expanded epipterygoid* (figure 15). This region of the skull, therefore, has the properties of a box with four rigid walls and presumably adequate resistance to prevent bending or disarticulation by the force of the temporalis muscle. The deep parasphenoid-pterygoid keel of the basicranial axis will further increase the resistance of the basicranial axis against bending. The actual stresses acting across the epipterygoid contacts under these conditions will be principally dorso-ventral compression as some of the force tending to bend the intertemporal bar will be used now to bend the basicranial axis and thus some of the force acting perpendicularly downwards on the intertemporal bar will be transmitted vertically down the epipterygoid to act on the basicranial axis. The sutural contacts of the epipterygoid both dorsally (direct abutment) and ventrally (a horizontal foot overlying the basicranial axis) may be interpreted as compressive-resistant.

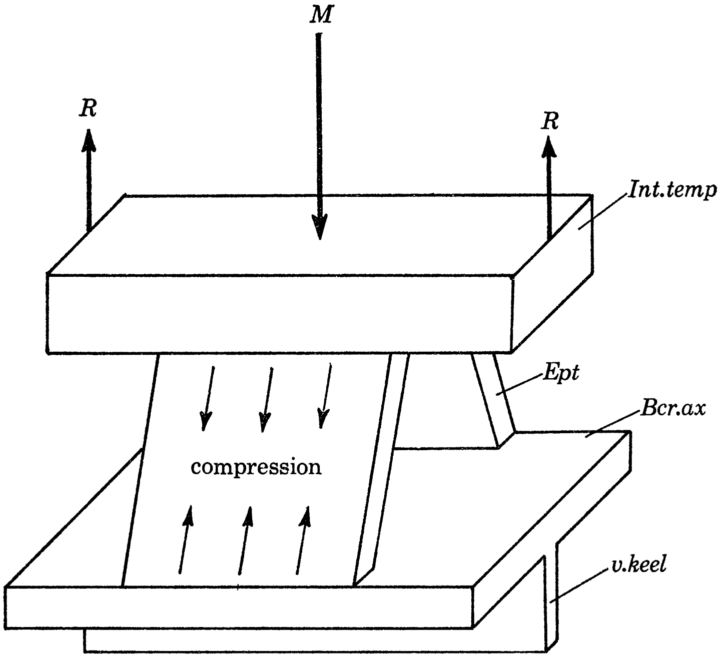


FIGURE 15. The mechanical role of the expanded epipterygoid. The stresses produced by the action of the muscle force (M) and the end reactions (R) are resisted by the box-section beam formed from the intertemporal region (*Int. temp*), the epipterygoids and the basicranial axis (*Bcr. ax*).

There are other possible functions of the epipterygoid and it is not possible to know at present which is of initial significance. There may have been muscle fibres originating from it, perhaps part of the temporalis muscle complex, although there is no clear indication from the bone surface that this was so. And in any case muscle fibres between the epipterygoid and the lower jaw would be directed almost laterally and would not produce a very big moment except at wide gapes. Another possible function is of course protection of the brain since the epipterygoid ultimately comes to form part of the side wall of the braincase, although the extent to which it protects the brain in whaitsiids must have been minimal. A ridge described on the inner surface of the epipterygoid (p. 21, figure 9*b*) is probably indicative of the attachment of persistent cartilage. It runs from the point where the antero-dorsal process of the prootic meets the epipterygoid to form the trigeminal foramen, and continues vaguely in the direction of the orbitosphenoid ossification. Its course is that which might be expected to have been the line of attachment of the unossified braincase floor to the epipterygoid, marking the ventralmost extent to which the brain reached down the medial side of the epipterygoid. With a brain restricted to a position as high as this evidence would indicate, most of the expanded epipterygoid is too far ventro-laterally placed to afford any direct protection, and the main region of bulging of the temporalis muscle fibres lay well below and lateral to the brain cavity and would not therefore be hazardous to the brain itself. And in the case of gorgonopsids, at least, the side wall of the braincase can become ossified directly with no need for expansion of the epipterygoid (Kemp 1969*a*). On the whole, therefore, it seems most probable that expansion of the epipterygoid occurred originally for the mechanical purpose suggested.

The development of a rigid *basicranial axis* by close and extensive attachment of the pterygoids with the parabasisphenoid, associated with loss of both the interpterygoid vacuity and the movable basipterygoid articulation must partly be correlated with the strengthening of the basicranial axis for resistance to the muscle forces. There is, however, a second possible significance. Crompton (1955) has described a series of kinetic joints between various bones of the skull of scaloposaurs. The meaning of cranial kinetism in mammal-like reptiles is not clear and the explanation of Crompton that it is for shock absorption is not entirely satisfactory (see Frazzetta (1962) for a discussion of the problem of cranial kinetism). In the case of lizards, at least, kinetism seems to be a method of more efficiently using obliquely oriented muscles (Kemp MS.), and possibly the same was true in scaloposaurs. Equally speculatively, perhaps this condition was a basic therocephalian feature lost in the whaitsiids and other groups. Accepting both these possibilities, the loss of the kinetism would presumably have occurred when the muscles became reorganized in the pattern suggested here and thus became more efficiently used without the need for the special kinetic movements. Indeed, in a skull with very powerful muscles, kinetism might be a positive disadvantage due to the tendency to disarticulate completely some of the movable joints. The changes in the basicranial axis, the suppression of the interpterygoid vacuity and the reduction of the rostrum of the parasphenoid may all be explicable in this way.

The *lateral process of the prootic* (figure 10*a*, *b*) is a stout, rather narrow rod which braces the posterior end of the quadrate ramus of the pterygoid against the braincase. There is no evidence from the embryology of modern vertebrates of its homologue and it is probably a neomorph developed to strengthen the quadrate ramus of the pterygoid. When the quadrate became streptostylic, its attachment to the quadrate ramus of the pterygoid had to be movable and thus the major support of the free end of the quadrate ramus was reduced in effectiveness. Yet it was important to hold the ramus steady, as part of the medially directed force applied to the quadrate from the lower jaw was probably transmitted to the skull via the pterygoid. Thus the process can be interpreted as a compression member, transmitting the medially directed force directly to the braincase.

The reason for the closure of the *suborbital fenestra* is enigmatical. Possibly it can be correlated with an increase in size of the anterior pterygoideus muscle and thus a need to strengthen the postero-lateral region of the palate from which this muscle originates. However, until an adequate explanation for the existence of the fenestra is forthcoming, the mystery of its subsequent disappearance is hardly likely to be solved.

Thus the series of morphological characters presented in table 1 as features shared by whaitsiids and cynodonts can be accounted for in functional terms as manifestations of the overall functional morphology of the skull at the whaitsiid level of organization.

The origin of the cynodont skull

If it be true that the cynodonts evolved through a state similar in organization to the whaitsiids, then the novel features of the cynodont skull should be explicable as logical functional modifications from the whaitsiid condition. This appears to be so.

Jaw musculature

In many ways the jaw musculature of cynodonts resembles that of whaitsiids, with a large temporalis muscle originating from the medial and posterior edges of the temporal fenestra

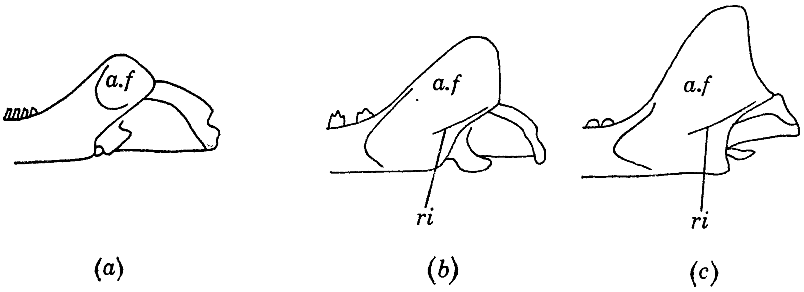


Figure 16. The adductor fossa of cynodonts (after Barghusen 1968). (*a*) Procynosuchid; (*b*) *Thrinaxodon*; (*c*) Advanced cynodont.

and inserting on the coronoid process of the dentary (Adams 1919; Parrington 1934; Crompton 1963). The anterior pterygoideus muscle too was probably reasonably large, at least in early cynodonts. However, as Barghusen (1968) has stressed, one of the most characteristic features of cynodonts is the development of an adductor fossa on the lateral surface of the dentary. The fossa is a concave area restricted to the lateral surface of the coronoid process in procynosuchids (figure 16*a*), but extending more and more ventrally in later cynodonts (figure 16*b*, *c*) and by comparison with mammals Barghusen concludes that it marks the region of insertion of a masseter muscle originating from the zygomatic arch. Correlated with the masseteric fossa is a lateral bowing of the zygomatic arch. Barghusen suggested two possible sources for the masseter muscle, either by a ventral extension of the insertion of part of the temporalis muscle complex from an aponeurotic sheet, connecting to the dorsal edge of the jaw, on to the lateral surface of the jaw itself; or by anterior extension along the jaw of the lateral slip of the temporalis which formerly inserted on the surangular region of the lower jaw. In view of the probable existence of a zygomatico-angularis muscle in whaitsiids which ran between the posterior part of the zygomatic arch and the upper part of the angular, the most likely way in which the masseter evolved is a simple anterior migration of both the origin and the insertion of this muscle. The attachment of the zygomatico-angularis to the angular bone in whaitsiids was probably correlated with the large reflected lamina of the angular (Kemp 1972). A shift of its insertion on to the dentary would account for the reduction of the reflected lamina in cynodonts, since the anterior pterygoideus muscle would no longer be in competition for the lateral surface of the lower jaw behind the dentary.

Jaw articulation

The appearance of the masseter muscle in this form had a number of very significant effects. In the first place of course it would have increased the total closing moment produced by the jaw musculature. Further, however, it would have had a significantly large laterally directed component which would tend to oppose the medially directed component of the rest of the musculature and thus the need for the complex design of the jaw articulation preventing medial disarticulation of the articular would disappear. The axis of the jaw hinge could become transversely oriented and orthal rotation of the jaws would be possible without the need for the quadrate itself to rotate about a longitudinal axis any longer (see p. 39). However, instead of the quadrate of cynodonts reverting to the primitive condition of immovable fixture to the squamosal it appears to have modified its streptostylic ability to allow antero-posterior (propalinal) movements of the lower jaw. The evidence for propalinic streptostyly of the cynodont quadrate is threefold. Parrington (1946) has drawn attention to the loose nature of the quadrate attachment in *Thrinaxodon*. As described earlier (p. 8) the same basic attachments of the quadrate are present in cynodonts as in whaitsiids and the main difference is that the quadratojugal is less deeply inserted into a slit in the squamosal. In whaitsiids it is the form of the quadratojugal-squamosal attachment that is principally responsible for preventing the quadrate complex from shifting anteriorly (Kemp 1972) and thus it appears as if the cynodonts have reduced this particular constraint. Secondly, Brink (1955) has indicated a pattern of tooth wear in *Diademodon*, a fairly advanced cynodont, which is consistent with propalinic movements of the lower jaw. The third evidence is the recent demonstration by Crompton (1972) in *Thrinaxodon*, of a ligamentous attachment between the quadratojugal and the surangular of the lower jaw, alongside the bony articulation between the quadrate and the articular. This particular feature appears to have evolved at least as early as *Thrinaxodon*, and Crompton accounts for it as a device to strengthen the jaw joint that became necessary when the post-dentary bones became reduced (see below). He sees it as a forerunner of the secondary bony articulation of later cynodonts. However, it is difficult to see just how a ligament running anteriorly from the quadratojugal to the lower jaw could strengthen the joint against the normal forces to which it would be subjected, since these forces would be backwards and upwards. It is more probable that the ligament was involved in the streptostylic movements of the quadrate complex, functioning to pull the quadrate forwards when the jaw muscles protracted the lower jaw. At least in early cynodonts the net force of the jaw closing muscles must have had a large posteriorly directed component, for the temporalis was still the largest muscle. Thus the articular bone must continue, as in whaitsiids, to bear against the anterior face of the quadrate. In order to maintain a reasonable potential gape therefore, it would not be possible for the articular bone to develop a dorsal process behind the quadrate as well, and so during the protractive phase of the lower jaw there would be a tendency for the articular to become disarticulated from the quadrate in an anterior direction. The development of Crompton's ligament to overcome this danger is only to be expected.

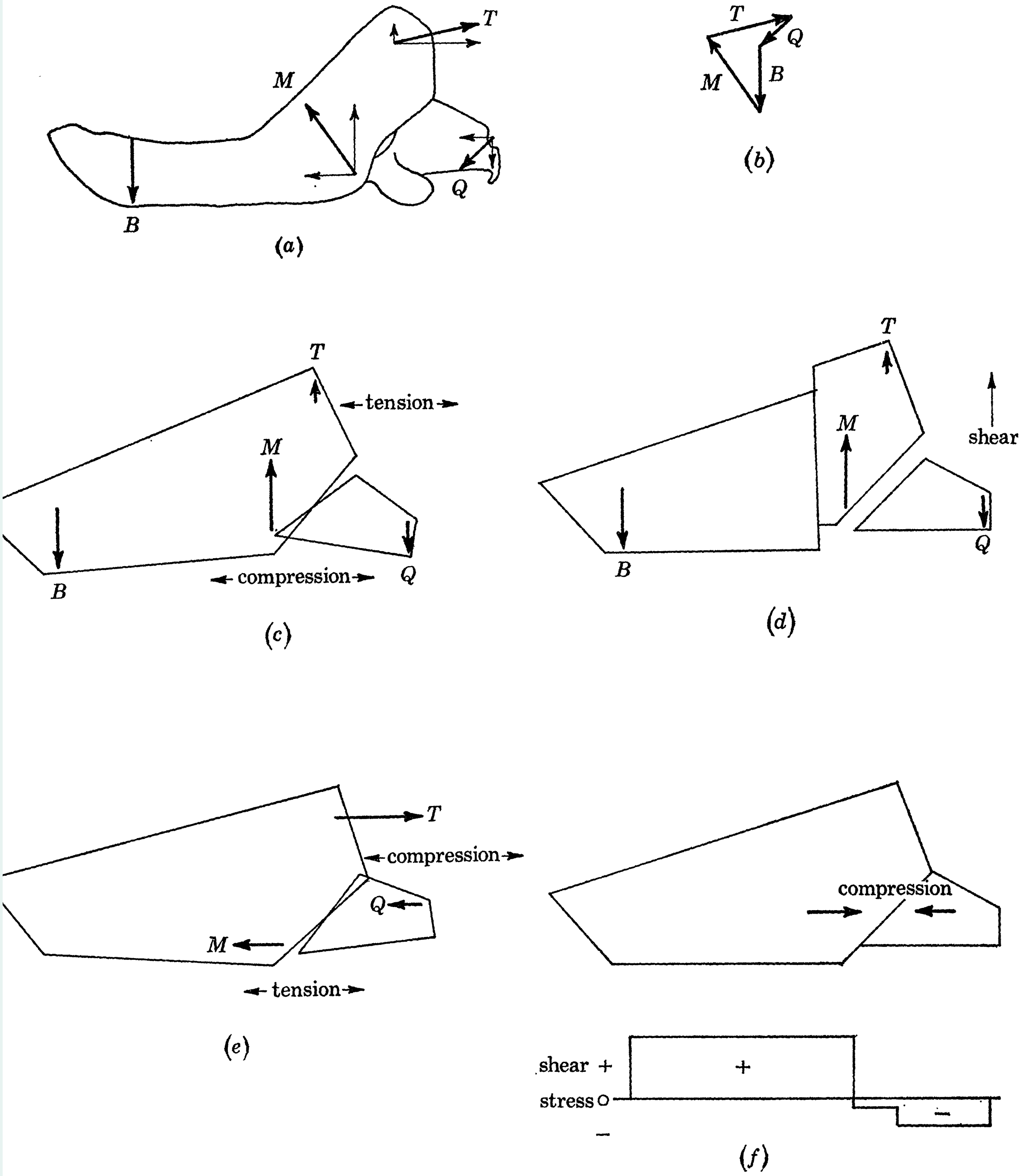
In the procynosuchids the axis of the jaw hinge is still inclined antero-medially (figure 6*b*) so that the rotational type of streptostyly of the whaitsiids was probably still present. This corresponds with the small size of the masseteric fossa of the dentary in that group, for the masseter muscle must have been too small to balance effectively the other muscles at this stage. In the galesaurids, however, the masseteric fossa is greatly enlarged and the axis of the jaw hinge is very nearly transverse. By this stage the muscles must have been more or less balanced transversely and the rotational type of streptostyly had given way to the propalinic type.

The forces on the lower jaw

Another consequence of the development of the masseter muscle is part of the general phenomenon of the increase in size of the dentary and the increasing extent to which the jaw muscles gain insertion on that bone. Correlated with this is the relative reduction of the postdentary bones and their apparent weakness. Parrington (1934) pointed out the trend towards more anterior insertion of the jaw muscles with a resulting increase in the force of the bite and decrease in hinge reaction. Crompton (1963) presented a more detailed analysis and showed how theoretically the hinge reaction could be abolished completely, by polarizing the muscles into antero-dorsal and postero-dorsal units and extending the dentition posteriorly. In the advanced therapsid *Diarthrognathus* it is possible that the point of intersection of the lines of action of the closing muscles lay vertically above the dentition, in which case the total closing force could be resisted entirely by the teeth, with no reaction at all at the hinge. Crompton showed how this state is progressively approached from the earliest cynodonts through later types, with a continuous tendency towards reduction of the reaction at the hinge. Following Watson (1912) and Adams (1919), he argued that it is this reduction in hinge reaction that allows the reduction in relative size of the postdentary bones.

However, in procynosuchids and galesaurids the arrangement of the muscles is still far from the ideal as exemplified by *Diarthrognathus* and there would still have been a significant reaction at the jaw hinge. And even in advanced cynodonts, use of the more anterior teeth would require either a hinge reaction or else only partial use of the closing muscles. Thus the pattern of the postdentary bones must be expected to be designed to resist by no means insignificant stresses. The same method that was applied to the whaitsiid jaw may be used once again in order to show the stresses acting on the jaw (see p. 41). In figure 17*a* the lower jaw of *Thrinaxodon* is shown with appropriate muscle forces representing the temporalis (T) and masseter-plus-anterior pterygoideus (M), on the assumption that both insert exclusively on the dentary. Taking moments about the jaw hinge, the relative magnitude of the reaction at the teeth (B) can be found assuming unitary force for each of the muscle groups, T and M and their positions as shown on the diagram. The reaction at the quadrate (Q) is found by completion of the force polygon (figure 17*b*) constructed from the muscle forces and the reaction at the teeth. (The position of the bite has been placed well forward so that there is a significant hinge reaction, since this is the condition under which the postdentary bones are subjected to the greatest stresses.)

The reaction at the hinge (Q) is seen to be directed antero-ventrally which is in accord with the observation that the articular bone bears against the anterior as well as the ventral face of the quadrate, and it can only be assumed that the support of the quadrate by the squamosal is adequate to prevent disarticulation of the quadrate. This seems likely since the squamosal supports the back and the top of the quadrate directly and thus the stress between the two is solely compressive. The strength of the union will depend only on the considerable compressive strength of bone. A more serious problem is the apparent reduction in the contact between the



IGURE 17. Mechanics of the cynodont lower jaw. (*a*) The external forces acting on the lower jaw, resolved into vertical and horizontal components. Derivation of the vector reactions (*B* and *Q*) was by the same method as for figure 14. (*b*) Force polygon of the external forces. (*c*) The effect of the vertical components of the external forces in producing a bending moment. (*d*) The effect of the vertical components of the external forces in producing shear stress. (*e*) The effect of the horizontal components of the external forces, producing stresses that tend to cancel those in (*c*). (*f*) The net stresses acting across the dentary-postdentary boundary. These are reduced to a small compressive force in the ventral region, and a vertical shear force. The magnitude and direction of the latter is indicated in the shear diagram below, for each point along the jaw.

dentary and the postdentary bones compared to the whaitsiids. However, if the external forces acting on the jaw are resolved into vertical and horizontal components (figure 17*a*) the manner in which the stresses across this boundary are reduced becomes clear. Consider first the vertical forces. As in the whaitsiids, we may regard the jaw as a beam supported at either end (by the teeth and the quadrate respectively) with perpendicular forces acting between the supports (the vertical components of the muscle forces). Two types of stress will arise in the beam, a bending moment (figure 17*c*) which will be resisted by the development of tension across the dorsal part of the dentary-postdentary contact, and compression along the ventral part; and secondly, a shear force which acts vertically upwards, tending to pull sections of the jaw directly upwards away from the rest of the jaw (figure 17*d*) (this stress was ignored in the discussion of whaitsiids since it is probably of much less significance to them).

Consider now the horizontal components of the external forces acting upon the lower jaw (figure 17*e*). There is a posteriorly directed force of the temporalis muscle, and anteriorly directed forces from the masseter-plus-pterygoideus muscle complex and from the quadrate reaction. (The couple formed by this system of horizontal forces, which tends to rotate the jaw in a clockwise direction about a point between the points of application of T and M, is balanced by a couple tending to rotate the jaw in an anticlockwise direction about the same point which arises as part of the reaction forces at the quadrate and the teeth. This is one way of explaining the reason why the vertical reaction force at the hinge is less than, and at the teeth more than, the reactions that would develop if the muscles pulled in a vertical direction.) The stresses which arise across the dentary-postdentary boundary as a result of the horizontal components of the external forces will take the form of compression dorsally due to the temporalis, and tension ventrally due to the masseter-plus-anterior pterygoideus, because all the muscles insert on the dentary. There will also be a compression ventrally due to the quadrate reaction.

To consider now both the vertical and the horizontal components together, the dorsal region of the dentary-postdentary boundary will be subjected simultaneously to tension because of the bending moment of the vertical forces (figure 17*c*), and compression because of the horizontal component of the temporalis (figure 17*e*). These will tend to cancel with one another leaving this region free of any horizontal stress. The ventral region of the dentary-postdentary boundary will be subjected simultaneously to compression due to the bending moment of the vertical forces (figure 17*c*) and tension due to the horizontal component of the masseter-plus-anterior pterygoideus (figure 17*e*). These will tend to cancel one another too, but since the temporalis has been assumed (as was probably the case at least in early cynodonts) to have a larger horizontal component than the antero-dorsally directed muscles, there is still the residual anteriorly directed component of the hinge reaction tending to compress the ventral region of the dentary-postdentary boundary. It would seem likely therefore that the net stress here is still compression. We may note now that the reduction of the postdentary bones in the cynodonts (figure 7*e*) takes the form of great reduction of the surangular overlap of the dentary high up on the jaw, which corresponds with the conclusion that the tension between these two (cf. whaitsiids, figure 14*d*) has been abolished. The ventral postdentary bones which in the whaitsiids functioned to resist compression still retain this function in cynodonts but to a reduced extent. They persist therefore as a stout ventral rod locking between the dentary and the splenial. Finally there is the shear stress acting on the lower jaw due to the vertical components of the external forces (figure 17*d*). The shear force does not involve bending of the jaw, and collapse due to shear would have to occur at two sections of the jaw simultaneously. Thus weakness of the dentary-postdentary boundary alone does not matter as long as the rest of the jaw is strong enough. The development of horizontal ridges on the dentary of cynodonts, adjacent to the postdentary bones, was probably to strengthen the dentary against the shear stress which thus adequately compensates for the weakness of the dentary-postdentary boundary. Figure 17*f* summarizes the net stresses acting across the dentary-postdentary boundary.

Overall therefore, we can account for the reduction of the postdentary bones in cynodonts as a logical development from a whaitsiid-like condition consequent upon a gradual increase in the percentage of the temporalis muscle, the anterior pterygoideus muscle, and the new masseter muscle insertions exclusively on to the dentary bone. The problem of weakness across sutures is quite overcome. At the procynosuchid level these changes had only just commenced and there must still have been a large tensile stress acting between the dentary and the surangular. Thus the postdentary bones of these skulls have retained a very whaitsiid like arrangement. However, by the galesaurid level as typified by *Thrinaxodon*, a great proportion of the musculature inserted upon the dentary with the resulting decrease in stresses across the dentary-postdentary boundary and significant reduction of the postdentary bones had commenced. Through the later cynodonts, as more and more still of the musculature inserted on the dentary and at the same time the geometrical arrangement of these muscles progressively reduced the stress at the hinge, the stress across the dentary-postdentary boundary would continue to decrease until all that remained was a small amount of compression. However, since the overall muscle force was still increasing, the shear stress on the jaw would continue to increase and thus the dentary itself had continuously to strengthen by increasing the horizontal strutting (figure 16*b*, *c*; *ri*). The posterior extension of the dentary alongside the postdentary bones may be seen as a manifestation of this gradually increasing strength of the dentary, necessary to resist the vertical shear stress.

Forces on the skull

The changes in the pattern of external forces acting upon the lower jaw of the cynodonts affect also the distribution of stress within the rest of the skull and to some extent novel features of the skull can be correlated with such changes. An obvious example is the dorsal bowing of the zygomatic arch, in order to resist better the force of the masseter muscle which attaches to it. Rather more difficult to explain is the reduction of the ventral keel of the parasphenoid and pterygoids. In the whaitsiids where there was a large reaction at the jaw hinge, the skull could be considered as a beam supported at either end with a force, in the form of the temporalis muscle, acting between the supports. As the situation of balance between the muscle forces and the reaction at the dentition is approached in cynodonts, the hinge reaction reduces and the skull is no longer acting as a simple beam supported at either end. The almost horizontal temporalis muscle will cause a forwardly directed force in the parietal region rather than a bending moment. The rôle of the ventral keel in whaitsiids was to strengthen the resistance of the posterior region of the skull to a bending moment so that in cynodonts it would have become redundant. Instead it was necessary to strengthen the intertemporal region against compression. Thus the relative cross-sectional area of the parietal and frontal increased, principally by increasing their depth, and the suture between them became more firmly interlocking, the frontals having sharp posterior edges which wedge between the parietals. One of the most characteristic of all cynodont features (Mendrez 1967) is the meeting of the nasal bone with the lachrymal (figure 1*b*) rather than the primitive condition seen in all earlier synapsids of the prefrontal meeting the maxilla. This change is probably correlated with the large increase in the reaction force through the posterior part of the dentition, vertically upwards just in front of the orbit. The lachrymal bone has a direct contact with the palate bones as well as with the bones of the skull roof and is thus in a key position for the distribution of a large stress on the posterior part of the maxilla over a wide skull area. It is to be expected, therefore, that the lachrymal bone should tend to persist, while the prefrontal bone which does not appear to be greatly involved in stress transmission is reduced.

The retention of the expanded epipterygoid of the cynodonts is perhaps a little unexpected in view of the comments made above regarding the loss of the ventral keel, to the effect that vertical forces acting in this region of the skull were reduced compared to whaitsiids. However, the skull of cynodonts is less flat than that of the whaitsiids, and thus the temporalis muscles tend to approach more closely the brain cavity. At the same time the brain appears to have enlarged (at least in *Thrinaxodon* compared to whaitsiids, although this might be a relative effect correlated with size, smaller animals having relatively larger brains, as pointed out by Watson (1931)). Thus the potential protective function of the epipterygoid may have had to be realized. The area of the internal surface of the epipterygoid which lies dorsal to the pila antotica, and which presumably therefore formed part of the functional wall of the braincase, is vastly larger in *Thrinaxodon* than in whaitsiids.

The lateral pterygoid flanges of the cynodont palate are reduced relative to those of whaitsiids, as a result no doubt of the increasing tendency to balance the lateral and medial force components of the jaw musculature.

The pattern of stresses acting upon the skull must have been immensely complex and variable. Nevertheless, many of the structural novelties of the cynodont skull appear to be explicable as logical modifications of a whaitsiid-like skull designed to resist more effectively the increased forces of the improved jaw musculature. As long as a self-consistent functional hypothesis along these lines can be maintained, the case for a therocephalian ancestry of cynodonts, which was based in the first instance on comparative morphology, must be regarded as strengthened.

LIST OF ABBREVIATIONS USED IN THE TEXT-FIGURES

ad.pr.pro	antero-dorsal process of the prootic
a.f	adductor fossa
ANG	angular
apo	site of attachment of aponeurotic sheet
A.Pt	anterior pterygoideus muscle
ART	articular
b	boss
B	reaction force at the dentition
Bcr.ax	basicranial axis
BO	basioccipital
bpt.pr	basipterygoid process
C	coronoid
c.c	carotid canal
cond	condyle articulating surface
D	dentary
ECT	ectopterygoid
EO	exoccipital
EPT	epipterygoid
for.V	trigeminal foramen
f.ov	fenestra ovalis
Int.temp	intertemporal region of the skull
i.o.s	interorbital septum
IP	interparietal
i.pt.vac	interpterygoid vacuity
J	jugal
L	lachrymal
l.cond	lateral condyle
l.pr.pro	lateral process of the prootic
M	masseter plus anterior pterygoideus muscle force
m.cond	medial condyle
MX	maxilla
N	nasal
OSP	orbitosphenoid
ot.pr.sq	otic process of the squamosal
P	parietal
PAL	palatine
pi.ant	pila antotica

PMX	premaxilla
PO	postorbital
POF	postfrontal
p.pr	paroccipital process
prart	site of attachment of prearticular
PRART	prearticular
pr.cult	processus cultriformis
PRF	prefrontal
PRO	prootic
PSP	parasphenoid
Pt	force of anterior pterygoideus muscle
PT	pterygoid
p.t.f	posttemporal fossa
pt.par.f	pterygo-paroccipital foramen
pt.w.q	pterygoid wing of the quadrate
Q	quadrate
q.f	quadrate foramen
q.j	site of attachment of quadratojugal
QJ	quadratojugal
q.n	quadrate notch
q.ra.ept	quadrate ramus of the epipterygoid
q.ra.pt	quadrate ramus of the pterygoid
rart.pr	retroarticular process
ref.lam	reflected lamina of the angular
ri	ridge
SA	surangular
se.tur	sella turcica
slit	slit in squamosal for quadratojugal
SMX	septomaxilla
SO	supraoccipital
SPL	splenial
SQ	squamosal
STA	stapes
T	force of temporalis muscle
TAB	tabular
T_{cor}	part of temporalis muscle inserting on coronoid process
Temp.	temporalis muscle
T_{sur}	part of temporalis muscle inserting on surangular
?ven	probable foramen for vein
v.keel	ventral keel
Z.Ang	zygomatico-angularis muscle
Zyg	zygomatic arch

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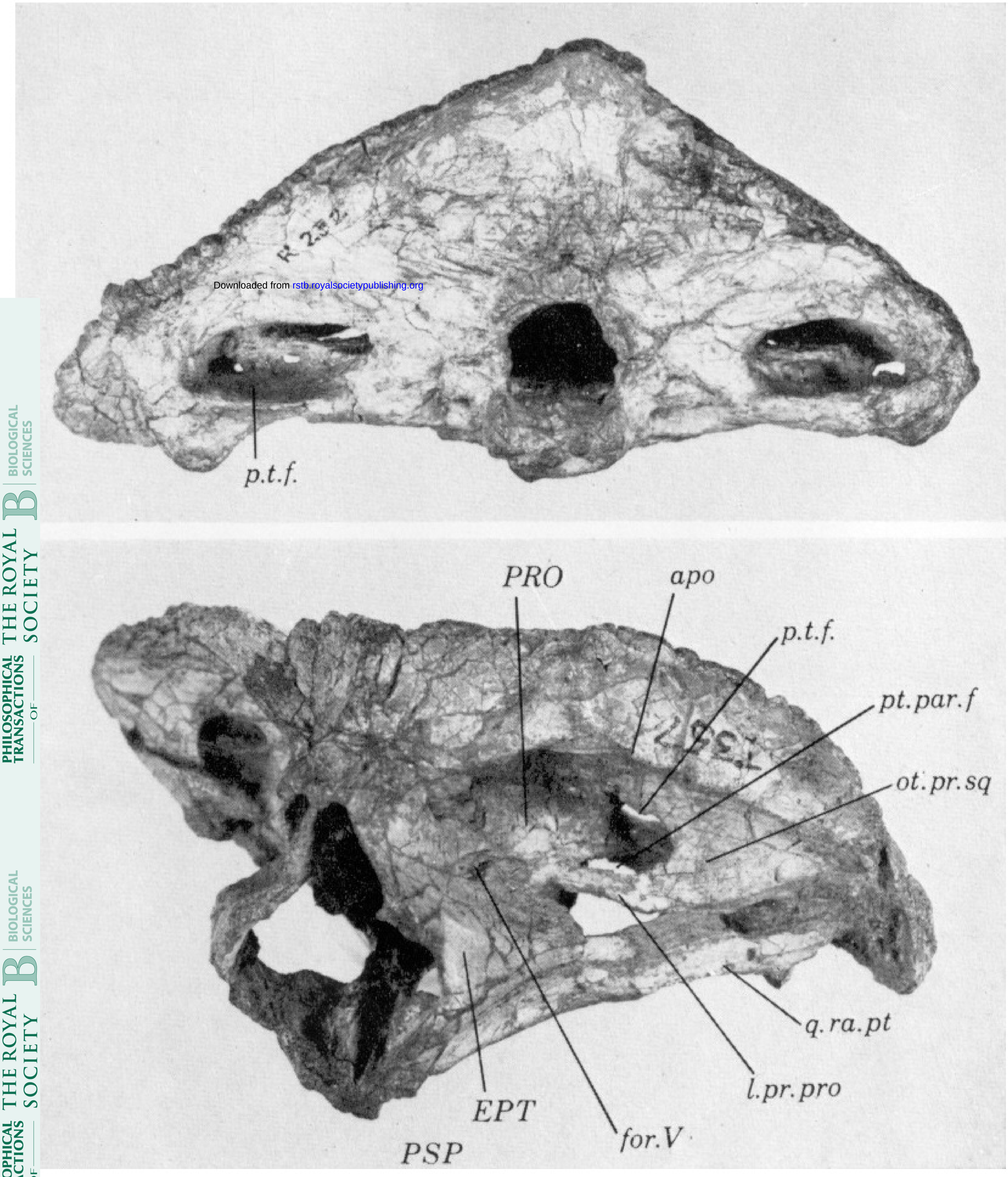


GURE 18. Unidentified whaitsiid, No. CUMZ T 357. Above, occipital view. Below, posterior part of skull viewed from in front and slightly dorsolaterally. (Photograph by Mr William Lee.) (Magn. ×1.)

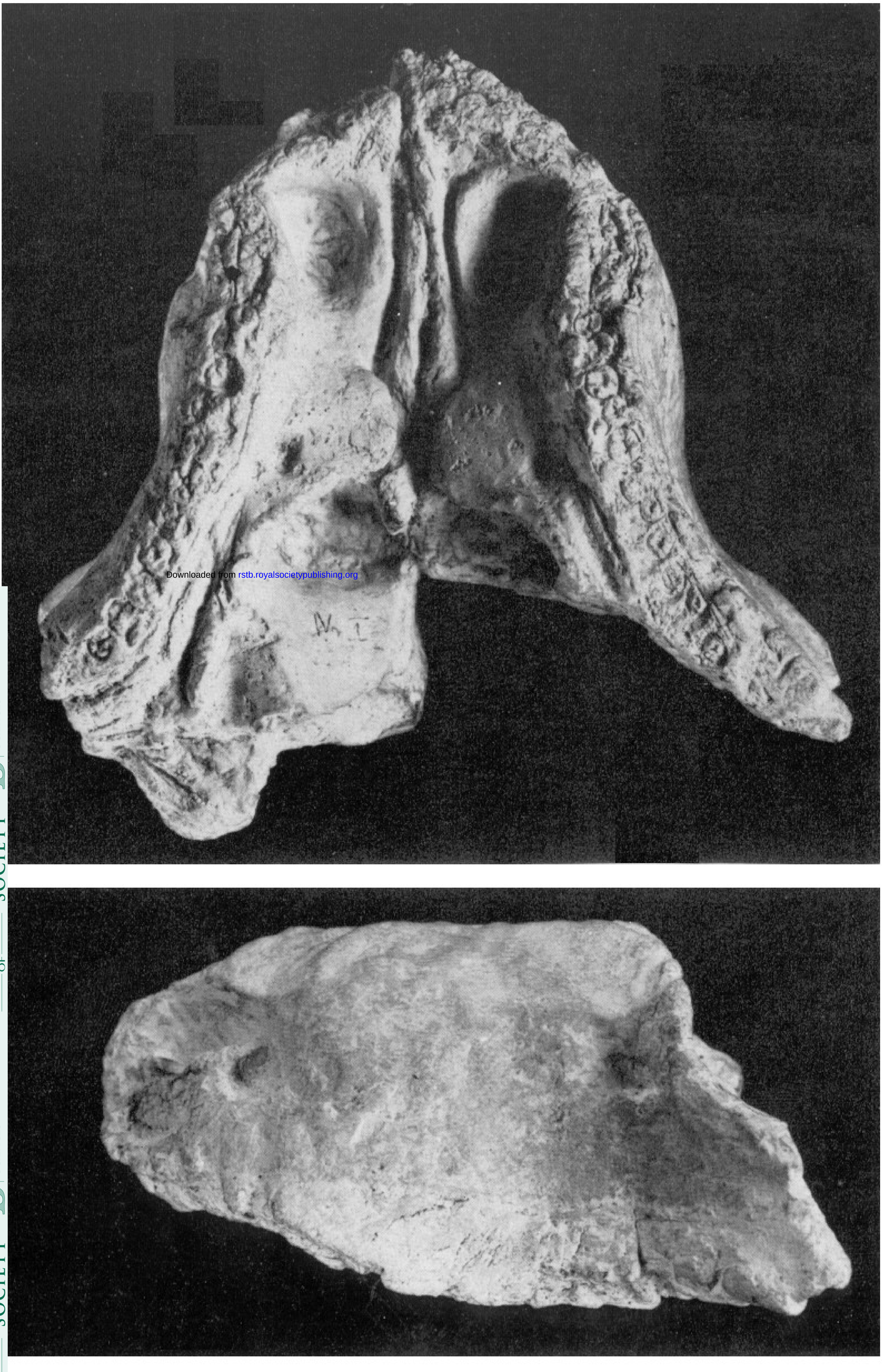
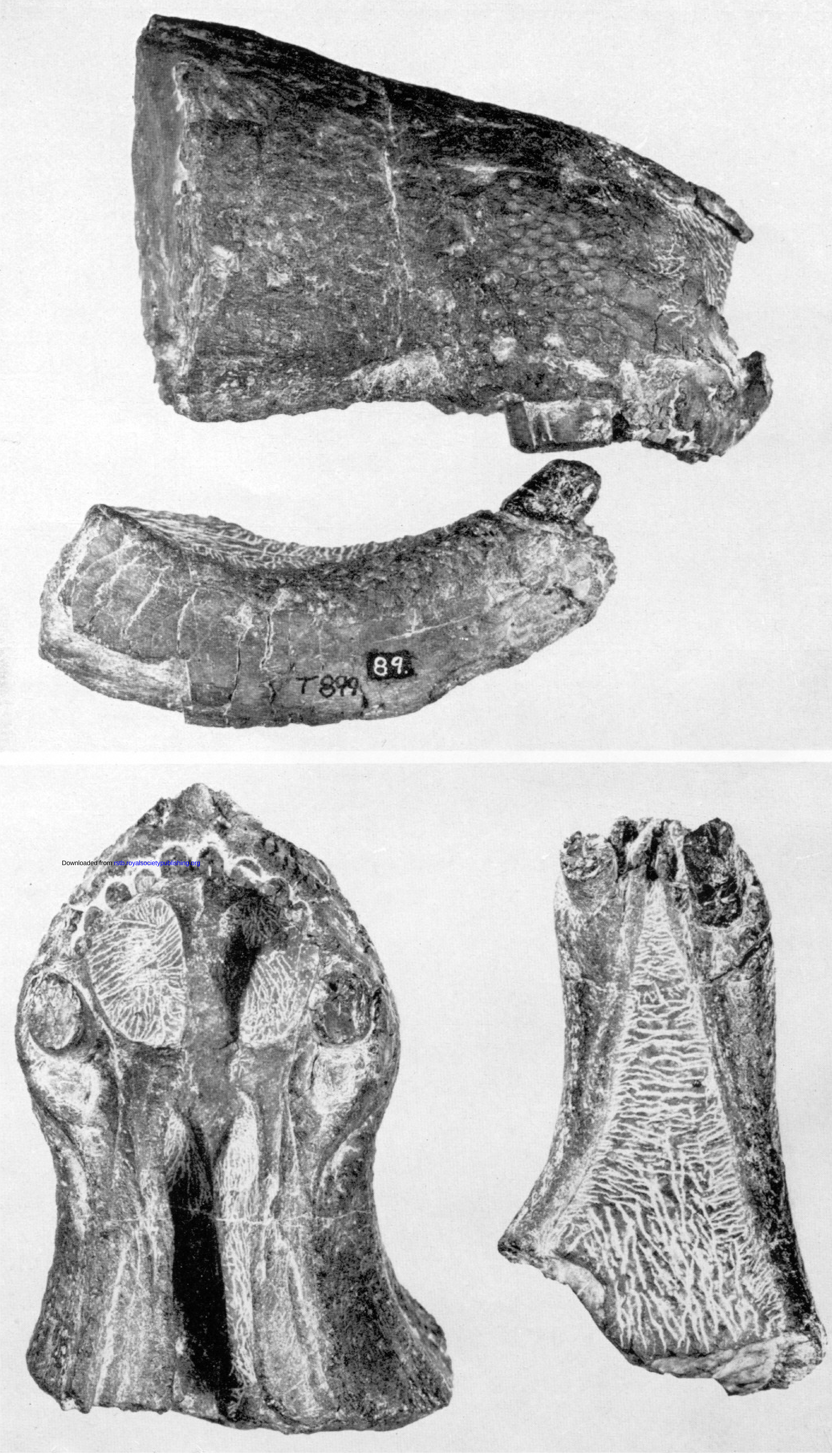


Figure 19. Plaster cast of a possible whaitsiid-cynodont in the South African Museum, Cast No. CUMZ T980. Anterior part of the skull in palatal and lateral views. (Photograph by Mr William Lee.) (Magn. ×1.)



IGURE 20. Unidentified whaitsiid snout and dentaries, No. CUMZ T899. Above, lateral view of skull and lower jaw. Below, palatal view of skull, and lower jaw in dorsal view. (Photograph by Mr William Lee.) (Magn. × 1.)