The side wall of the braincase in cynodont therapsids, and a note on the homology of the mammalian promontorium

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The side wall of the cynodont braincase is not sufficiently well understood to form a sound basis for morphological or phylogenetic inference. This paper describes in detail the trigeminal region of a series of cynodonts from lateral and mesial aspects. Genera dealt with are *Thrinaxodon, Trirachodon, Diademodon* and *Tritylodon*. A reinterpretation of aspects of the braincase of the tritylodontid *Bienotherium* is presented. Attention is drawn to a fundamental dichotomy between herbivorous cynodonts and the carnivorous line leading to mammals. Homology between the cynodont parasphenoid wing and mammalian promontorium is demonstrated.
S. Afr. J. Zool. 1986, 21: 136 – 148

Die sywand van die sinodontbreinkas is tot dusver nog nie na behore bestudeer nie, daarom ontbreek 'n grondige kennis daarvan waaruit morfologiese en filogenetiese afleidings gemaak kan word. In hierdie artikel word in fyn besonderhede die laterale en mesiale aansigte van die trigeminiese streek van 'n reeks sinodonte beskryf. Genera wat bespreek word is *Thrinaxodon, Trirachodon, Diademodon* en *Tritylodon*. 'n Herbeskouing van die eienskappe van die tritylodontied *Bienotherium* se breinkas word ook aangebied. 'n Fundamentele tweedeling tussen die herbivore sinodontgroep en die karnivore sinodontgroep (wat oorsprong aan die soogdiere gegee het), word beklemtoon. Daar word bewys dat die promontorium van soogdiere ontstaan het uit die parasfenoied van die sinodonte.
S.-Afr. Tydskr. Dierk. 1986, 21: 136 – 148

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Received 15 June 1985; accepted 3 October 1985

Hopson (1964) recognized three regions in the side wall of the braincase of the tritylodontid *Bienotherium* which represent modifications of the typical cynodont condition. These, with some introductory comments, are as follows. (i) The anterior lamina of the periotic which overlaps the posterior margin of the epipterygoid: this he defined as the region lying lateral to the cavum epipterycum, and suggested it is probably an intramembranous ossification rather than an extension of neurocranium. The new material of *Tritylodon* described herein confirms such an origin for the structure so defined and demonstrates the presence of neurocranial anterior lamina as well. (ii) The ventrolateral flange is less happily defined as that part which contacts the quadrate ramus of the epipterygoid and is notched anteriorly for the second and third branches of the Vth cranial nerve and is penetrated by a small foramen for the *vena cerebralis media*. The foramen assigned to a medial head vein is in fact the exit for the third branch of the Vth cranial nerve and possibly a *vena capitus lateralis*, while the connected pair of anterior foramena represent V(2) and the *vena cerebralis media*, V(1) is probably covered laterally by membrane bone in *Bienotherium*. (iii) The posterolateral flange is a laterally directed process of prootic component of periotic projecting in front of the pterygoparoccipital foramen, it is penetrated near its base by a foramen for the *vena capitus lateralis*. Hopson's material did not show that it is also penetrated more dorsolaterally by a foramen for a branch of the stapedial artery. The various components of the cynodont prootic which combine in the tritylodontid lateral flange are apparent in *Thrinaxodon*.

More recently, Presley & Steel (1976) have presented a convincingly argued case for extending Hopson's membrane bone hypothesis to the whole of the cynodont anterior lamina, basing their case on what is known of the braincase of *Thrinaxodon*. These authors propose that the mammalian alisphenoid is homologous with anterior lamina of periotic plus quadrate ramus of epipterygoid. This proposal is attractive as far as anterior lamina is concerned but ignores the fundamental control exerted by neurocranial periotic over the position of the trigeminal nerve foramena. Also much of their speculation is based on inadequate data. These are the reasons for the present work.

This paper presents descriptions of lateral and mesial surfaces of the side wall of the braincase for an evolutionary grade series of cynodonts which it is hoped will increase understanding of these animals and improve the factual basis of conclusions which may be made from them concerning the origin of the morganucodontid grade mammalian braincase and dispel notions of a close relationship between morganucodontids and tritylodontids. Attention is also drawn to the obvious homology between cynodont parasphenoid and mammalian promontorium of petrosal.

Materials and Methods

Thrinaxodon

Two skulls with good braincases prepared in acetic acid by the author many years ago were available for study. From one of these the epipterygoid, prootic and opisthotic have been dissected out as a unit.

Trirachodon

A badly eroded skull originally preserved in a nodule was selected, as the ascending ramus of the dentary was missing on the right side allowing access to the braincase. The lateral surface of the braincase was prepared first, using an air hammer. The specimen was then embedded in plaster and cut saggitally and the mesial surface of the left side of the braincase prepared with the air hammer.

Diademodon

An isolated braincase from a large individual was selected. The lateral surfaces had been naturally exposed. The specimen was backed with plaster, saggitally cut and the mesial surfaces of the braincase prepared with the air hammer.

Tritylodon

A fairly complete mechanically prepared skull was available. As trigeminal foramena are preserved on the left side only it was possible to expose the sphenethmoid bones on the right. A well-preserved isolated braincase was saggitally cut and prepared in an acid mixture of 2,5% thioglycollic and 2,5% formic. Rinsing in bicarbonate of soda before washing was necessary to remove residual sulphur. A third specimen with the trigeminal region well preserved on the right side was mechanically prepared.

All consolidation was done with dilute Glyptal cement.

Stereophotographs of most of the material are presented to supplement the diagrammatic figures made using a Wild drawing mirror, which has the considerable advantage of allowing one to view the object in three dimensions while drawing.

Descriptions

Therocephalia

It is necessary to preface descriptions of cynodont braincases by reference to the primitive condition seen in the therocephalians. Mendrez' (1972) description of *Regisaurus* is a good starting point. She clearly described and illustrated the morphology and relationships of the entirely neurocranial prootic. The anterodorsal process and pila antotica (anteroventral process of Mendrez) lie deep to the epipterygoid and demarcate the prootic incisure (exit of the trigeminal nerve). Between the prootic incisure and the pterygoparoccipital foramen is a lateral process of the prootic (central process of Mendrez) which Kemp (1972) has recognized as the precursor of the cynodont lateral lamina.

In whaitsiid therocephalians (Kemp 1972 and personal observation) the epipterygoid exhibits some interesting developments. It sends a process backward, overlapping onto the anterodorsal process of the prootic. (I can confirm that the anterodorsal process is incomplete in Kemp's specimen.) A dorsally directed process of epipterygoid below this surrounds and encloses a foramen in the epipterygoid. Kemp states this must have transmitted maxillary and mandibular branches of the trigeminal: in view of the small size of this foramen and the large trigeminal notch below and behind it, this is unlikely. This epipterygoid foramen may have been unique to whaitsiids, but its anterior border corresponds well with the notch in the posterior border of the epipterygoid of cynodonts.

In cynodonts such as *Thrinaxodon* where the prootic and opisthotic are separated by a clear suture the prootic is referred to as such. In more advanced cynodonts these two bones fuse to form the periotic.

Thrinaxodon (Figures 1 & 2)

Presley & Steel (1976) state that in cynodonts the epipterygoid and prootic meet edge to edge. This is a misleading simplification. Fourie (1974) correctly described this contact in *Thrinaxodon* but did not discuss its potential significance. In

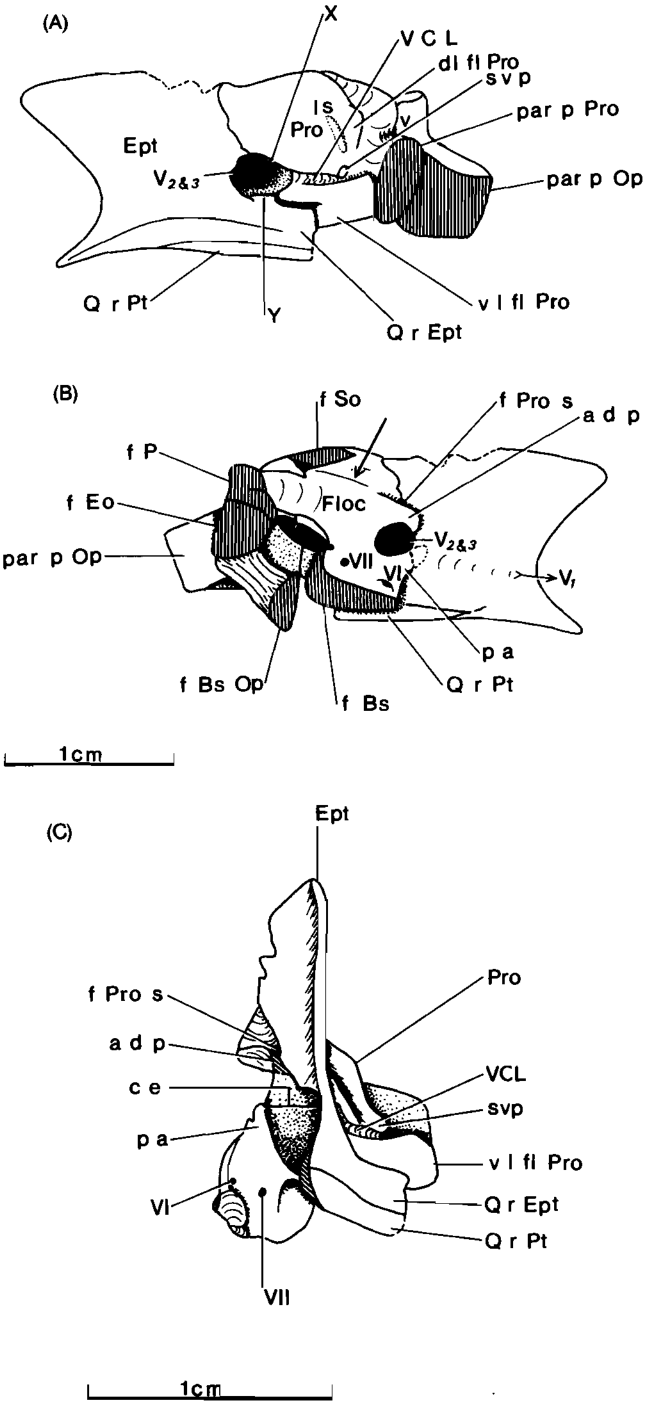

Figure 1 *Thrinaxodon*. Epipterygoid, prootic and opisthotic. (A) lateral, (B) medial, and (C) anterior views. (See list of abbreviations.)

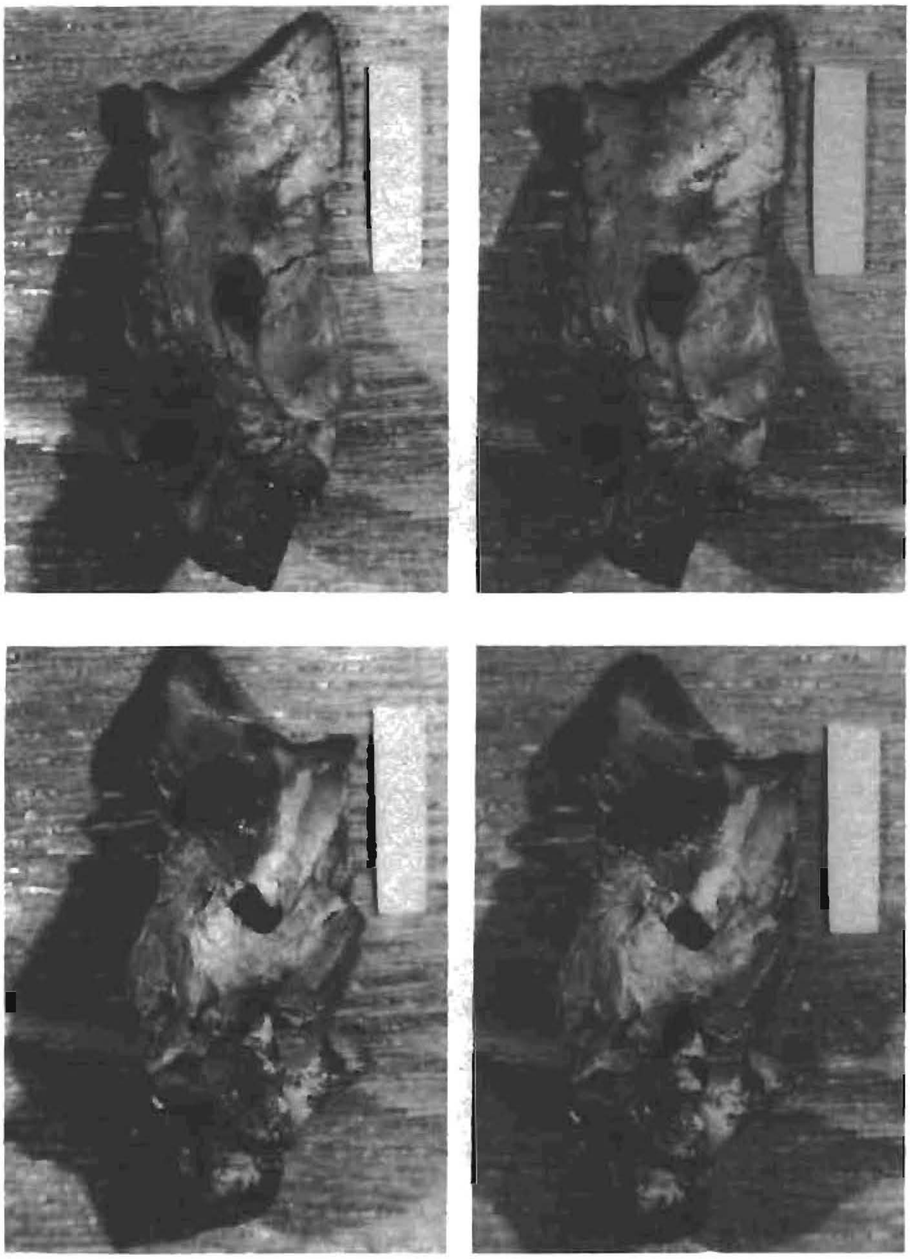

Figure 2 *Thrinaxodon*. Epipterygoid, prootic and opisthotic, in lateral view top and medial view bottom. Scale = 1 cm.

this animal both bones are rather thick in the contact region and the epipterygoid sends a vertical tongue into a deep groove in the prootic i.e. epipterygoid is overlapped laterally and medially by prootic; in addition, above the anterior border of the trigeminal foramen the mesial surface of the epipterygoid has a raised area providing support for the anterodorsal process of prootic (labelled anterior lamina by Crompton & Jenkins 1979). This process curves towards the tip of the pila antotica but still lies lateral to it. It is tempting to suppose that in tritylodontids and morganucodontids it is the anterodorsal process which makes sutural contact with the pila antotica, but this is unlikely.

The 'anterior lamina' of the *Thrinaxodon* prootic is more complex than supposed by Presley & Steel. This region is laterally thickened and has developed within it a venous sinus. This sinus cavity is seen in section in Fourie's figure 19B. The sinus was entered via a foramen tucked behind the anterodorsal process and drained through an opening behind the suture with the supraoccipital. It therefore seems certain that nearly the entire prootic in this animal was neurocranial.

The lateral wall of the *Thrinaxodon* prootic (Figure 1A) exhibits several other points of interest. The relationship of the ventral flange to the quadrate ramus of epipterygoid is somewhat variable. Essentially it lies medial to epipterygoid. In the specimen illustrated it abutts dorsally against a raised portion of epipterygoid (labelled Y); on the right side of the same specimen Y is replaced by a continuation of the prootic; in TM81 (TM = Transvaal Museum Pretoria) quadrate ramus of epipterygoid lies lateral to prootic right up to the canal for the *vena capitus lateralis*. In all specimens of *Thrinaxodon* examined, quadrate ramus of epipterygoid is as short as illustrated here. The tiny projection X in the figure is potentially significant as it may represent membrane bone more extensively developed in later cynodonts.

Before the posterolateral portion of the prootic is described it is necessary that an important venous foramen be dealt with. Kuhne (1956) very carefully prepared and described the course of a vein which penetrates the side wall of the braincase of *Oligokyphus*, running from deep within the floccular fossa to emerge low down in the channel occupied by the large vein which drained the sinus canal, which it joined before it passed out through the posttemporal fossa. Kuhne stated that this vein was absent in *Diademodon*. Kermack, Musset & Rigney (1981) have asserted that this arrangement is unique to tritylodonts. The course of this vein is difficult to get at without the use of acid or serial sectioning, and it cannot be prepared out in my specimens of *Trirachodon* and *Diademodon* to be described below. It must however be common to all cynodonts at this level as it is present in *Thrinaxodon*. In *Thrinaxodon* the foramen is in the suture between opisthotic and prootic anterior to the posttemporal fossa, as indicated (v) in Figure 1A. The prootic bears a deep notch leading to the foramen. Internally the vein has exactly the right relationship with the back of the floccular fossa.

It is now appropriate to consider posterolateral processes of prootic. The morphology of this region is somewhat variable. The dorsolateral flange borders the channel for the large vein from the sinus canal. An exactly homologous structure is present in *Tritylodon* and is distinct from the lateral flange in that animal, being linked instead with the quadrate process of periotic. Anterior to this dorsolateral flange in *Thrinaxodon* is a slight swelling of prootic (l.s.) and below it is a projection which I term the supravenous process. This process is somewhat variable in position but that illustrated is typical. The ventrolateral flange is large and unmistakable. It is the last three features which combine in the tritylodontid lateral flange, the supravenous process separating the foramena for *vena capitus lateralis* and stapedial artery, formed within the flange.

Trirachodon (Figures 3 & 4)

Discussion of the braincase of this animal has until now relied on a poorly illustrated description (Parrington 1946) of a specimen tentatively assigned to this genus. The specimen of *Trirachodon* illustrated herein, though somewhat crushed, confirms the presence of two trigeminal foramena as described by Parrington. The mesial view clearly shows how the two foramena are separated by a superficial bridge of membrane bone involving both prootic and epipterygoid, and how both lie lateral to the area occupied by the trigeminal ganglion cluster, bounded internally by the anterodorsal process and the pila antotica.

This specimen shows that the quadrate ramus of epipterygoid of *Trirachodon* is a little shorter than in *Thrinaxodon*, terminating just behind the trigeminal foramen.

The mesial surface of the braincase shows a notch in the dorsal border of the periotic which probably indicates the point of entry of a vein to the periotic sinus. Periotic anterior to a line between this notch and the tip of the anterodorsal process of periotic is neomorphic for *Trirachodon*. The epipterygoid sends a mesial process towards the anterodorsal process of periotic, reminiscent of its behaviour in whaitsiids.

Diademodon (Figures 5 & 6)

Very little is known of the braincase of *Diademodon* apart from the work of Watson (1911, 1913). The braincase is robustly constructed. There are two trigeminal foramena, the upper transmitted V maxillary and the lower shows distinct channels in its ventral border for V mandibular and the lateral head vein. In lateral aspect periotic and epipterygoid meet in a complex suture and an impression is created of the epipterygoid having captured the trigeminal foramena, but from the accurately superimposed position of the prootic incisure and pila antotica (Figure 5A) the relationship of trigeminal ganglia to neurocranial structures is seen to be conventional, indicating that the epipterygoid has spread back across the lateral surface of periotic, whose internal anterior lamina is therefore neurocranial.

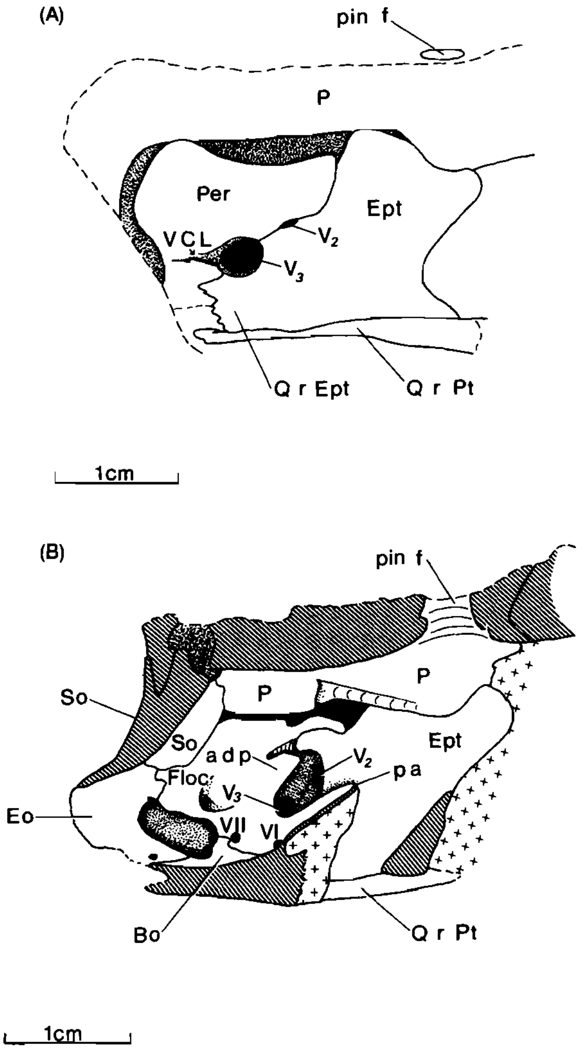

Figure 3 *Trirachodon*. BP/1/5050 Braincase. (A) lateral view, (B) medial view. (See list of abbreviations.)

Not shown by the figures is the fact that in *Diademodon* the quadrate ramus of the epipterygoid is long (Brink 1955 figure 3A), and seems to reach the quadrate (personal observation).

The mesial view shows the unusual orientation of the braincase. The venous foramen v(i) may be the same as that described by Watson (1913): it lies on the suture between supraoccipital and periotic, v(ii) lies at the junction between supraoccipital and parietal. Straddling the same suture is a depression above a crisply demarkated ridge which would have housed the lateral lobe of the cerebellum. A topographically identical ridge is present in *Thrinaxodon* (arrowed in Figure 1B). An anterodorsal process of prootic could not be distinguished on either side of the specimen.

Tritylodon (Figures 7 – 16)

External features of the trigeminal region will be described first, starting with the left side of BP/1/4261 (Figures 7 & 8). There are two important features of this specimen which help to unravel its complexity. A bar of periotic is in overlapping sutural contact with a posteriorly directed process of epipterygoid: this must be homologous with the more extensive contact seen in *Trirachodon*. Above this a neurocranial process of periotic runs mesial to epipterygoid and has a laterally directed channel above its ventral edge, clearly for V opthalmic. The foramen defined by these features thus provides a window onto the course of V(1) and the exit of V(2).

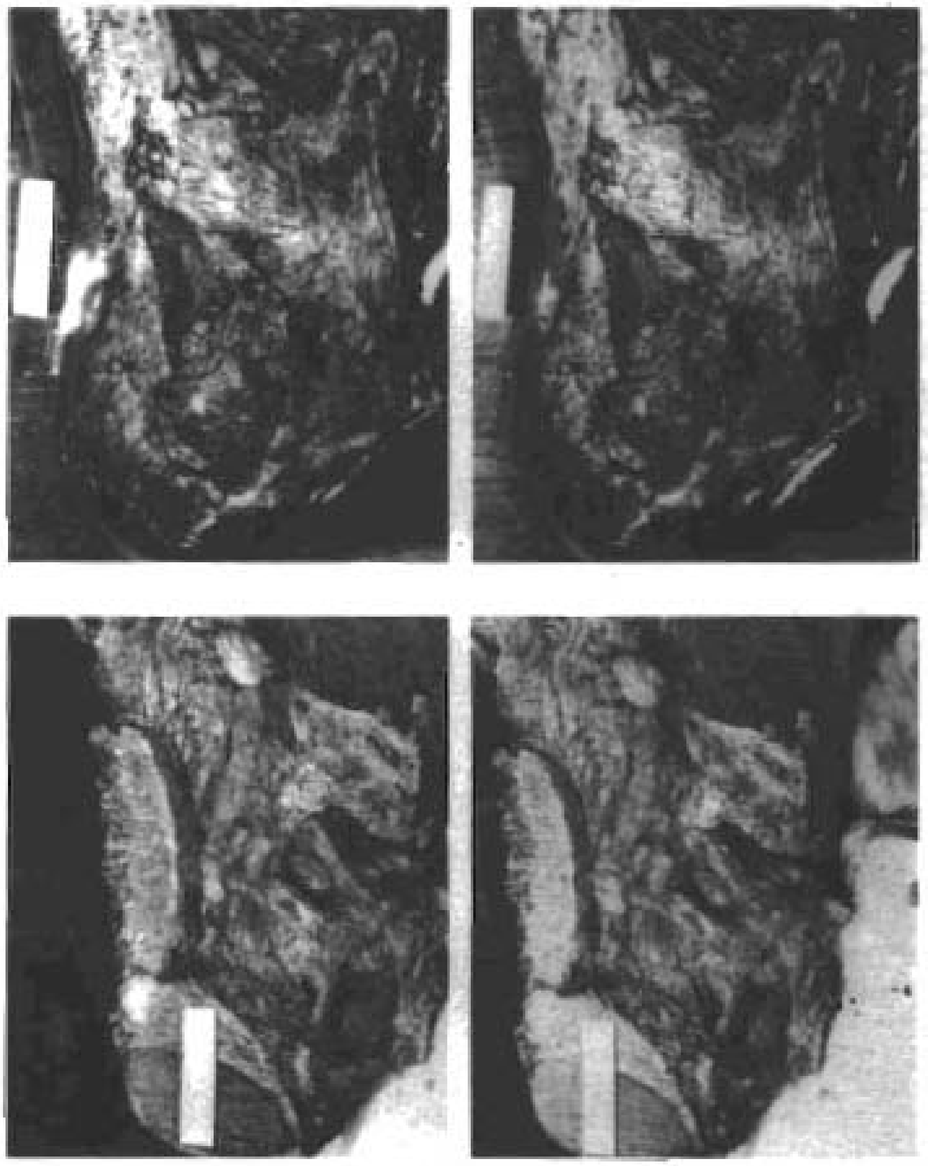

Figure 4 *Trirachodon.* BP/1/5050. Braincase in lateral view top and medial view bottom. Scale = 1 cm.

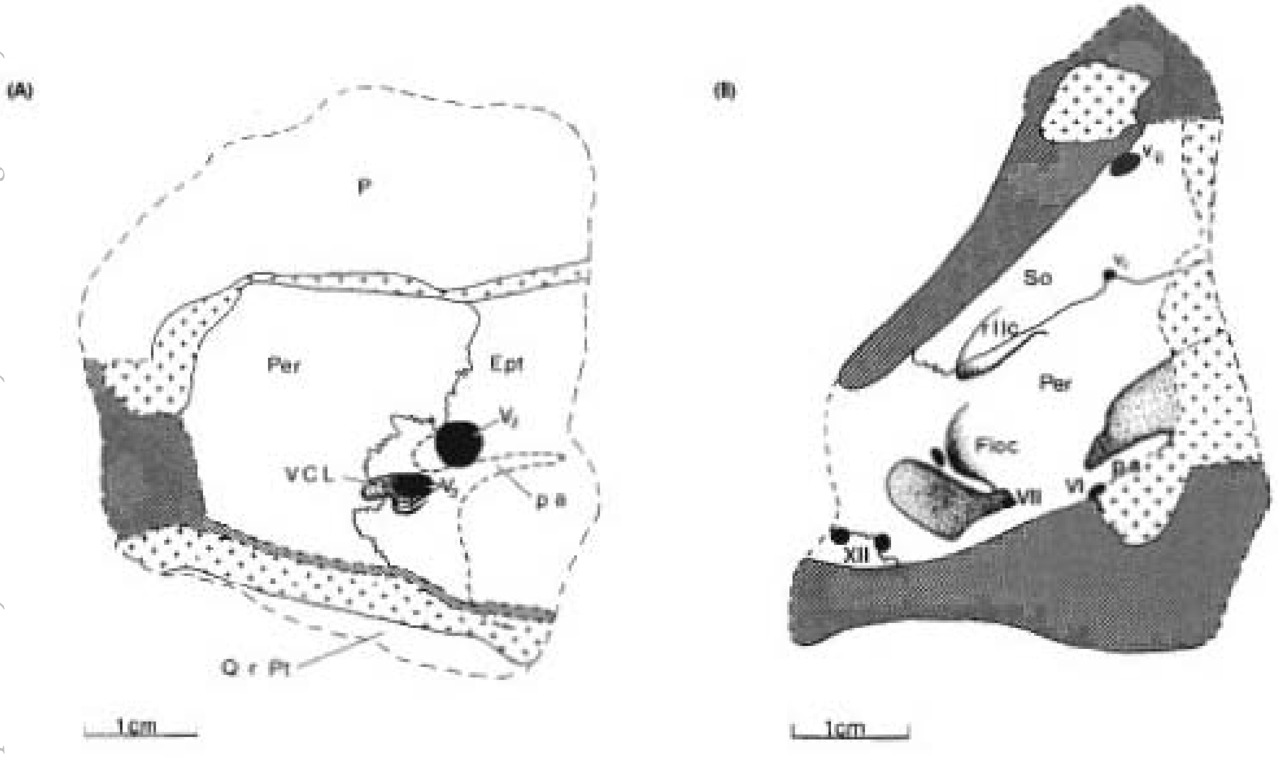

Figure 5 *Diademodon.* BP/1/4677 Braincase. (A) lateral view, (B) medial view. (See list of abbreviations.)

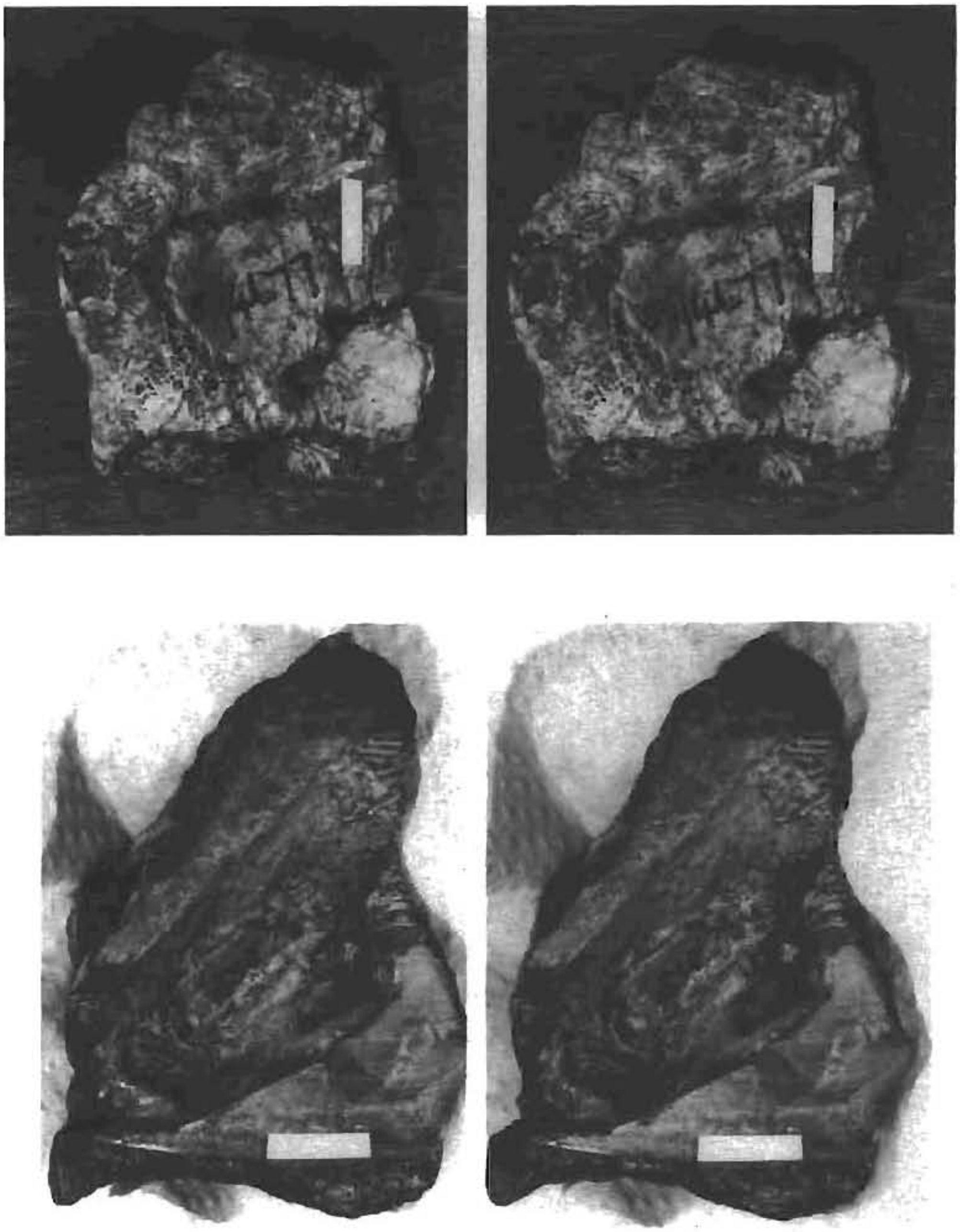

Figure 6 *Diademodon*. BP/1/4677. Braincase in lateral view top and medial view bottom. Scale = 1 cm.

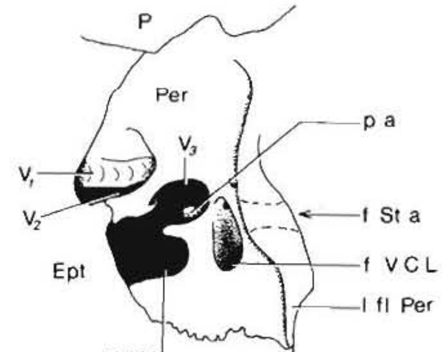

Figure 7 *Tritylodon*. BP/1/4261 Trigeminal region, left lateral view. (See list of abbreviations.)

The second important feature is the floor which is formed below the recess for the semilunar ganglion by pila antotica and anterior lamina (Figures 9 & 10) noted by Hopson (1964). The semilunar ganglion and the foramen directly lateral to it represent the remnant of the cynodont single trigeminal opening which transmitted all three branches of the trigeminal plus the lateral and median head veins. There is a possibility that a vein, the *vena capitus lateralis* emerged with V(3) from the foramen directly lateral to the semilunar ganglion. The foramen at the base of the lateral flange immediately behind the trigeminal region is undoubtedly formed from the open channel for the *vena capitus lateralis* of cynodonts like *Thrinaxodon*. The course of this vein is separated dorsally from the exit of V(3) by a sharp edge; a branch must therefore have run superficially across the periotic above the trigeminal region. This leaves the large ventral foramen (Figures 7 & 9): this must have transmitted a vein draining the cranial region below the brain (floored here by laterosphenoid), which ran forward with V(1). This vein, the *cerebralis media*, joined the *capitus lateralis* anterior to the foramen for the latter in the

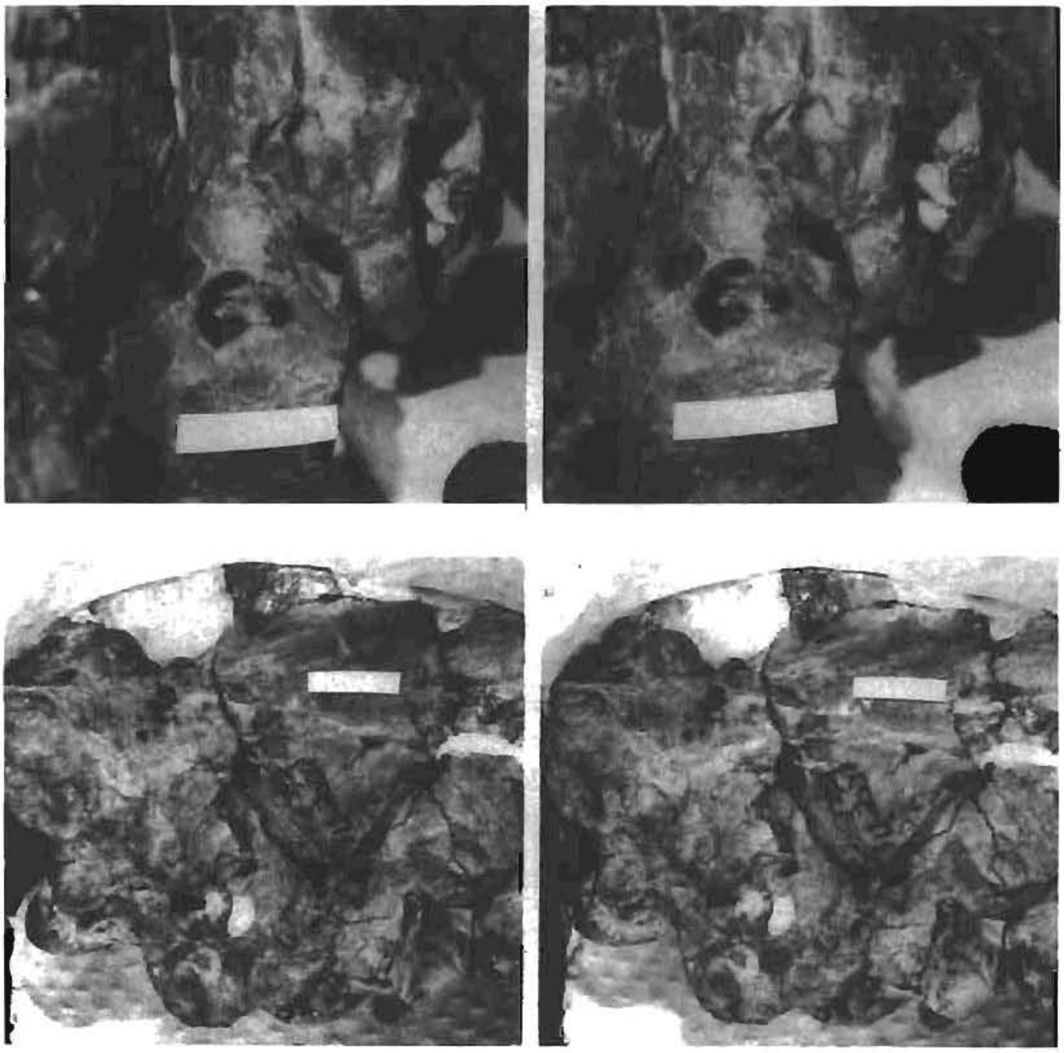

Figure 8 *Tritylodon*. BP/1/4261. Left trigeminal region in lateral view top, and bottom, right side showing orbitosphenoid. Scale = 1 cm.

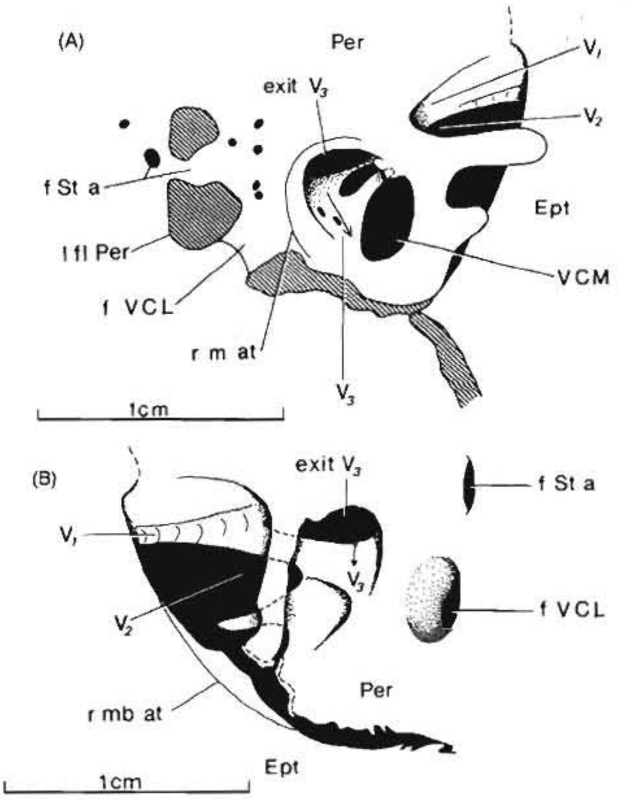

Figure 9 *Tritylodon*. BP/1/5104a. Lateral views of trigeminal region. (A) right side, (B) left side. (See list of abbreviations.)

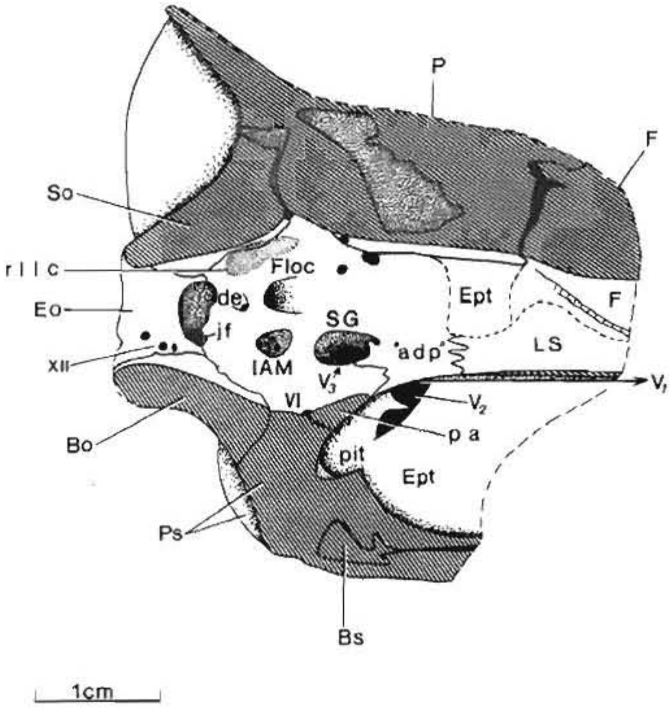

Figure 10 *Tritylodon*. BP/1/5104a. Internal view of left side of braincase. (See list of abbreviations.)

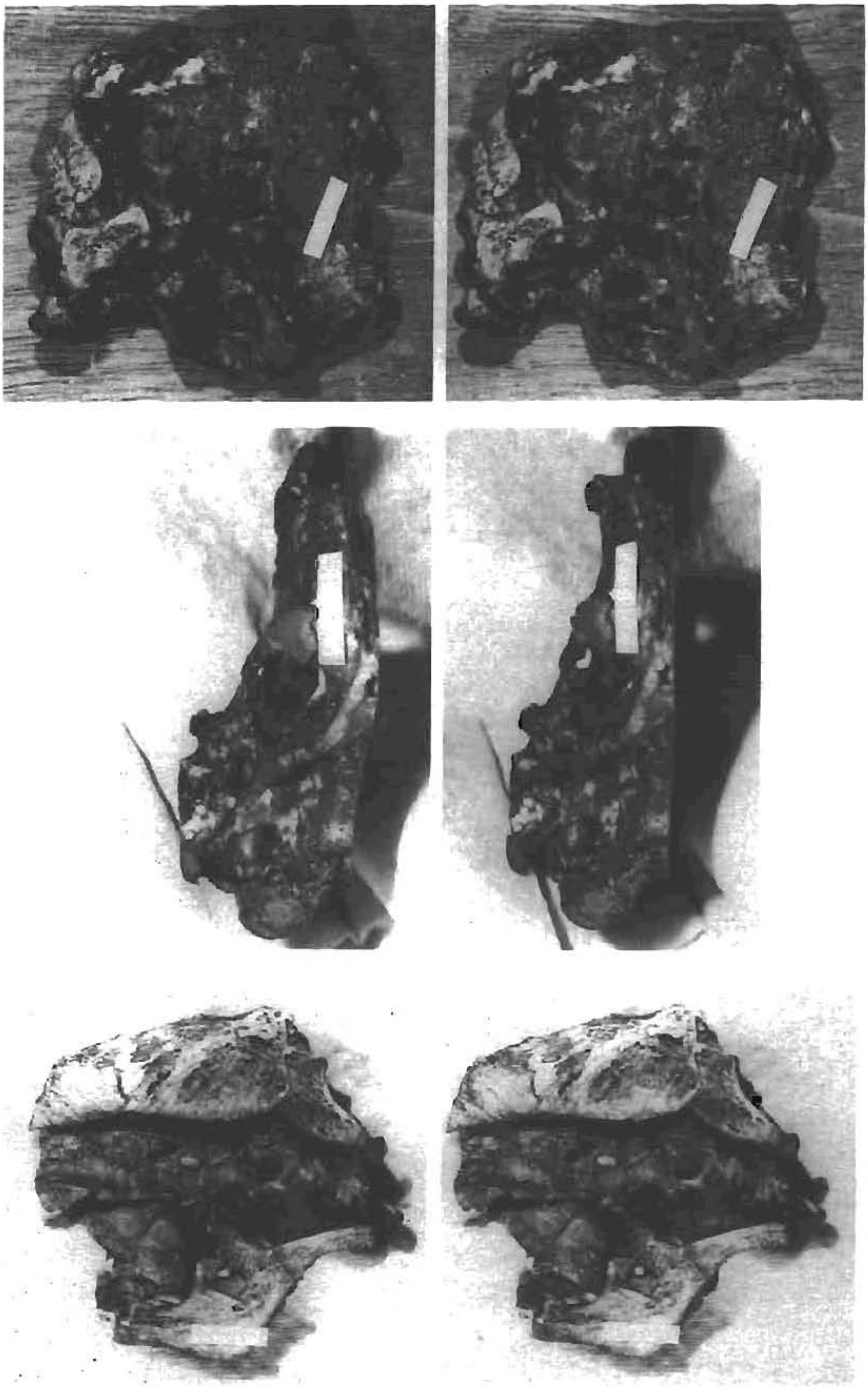

Figure 11 *Tritylodon*. BP/1/5104a. Right side of braincase in, from top to bottom, lateral, ventral and medial views. Scale = 1 cm.

lateral flange. Kermack *et al.* (1981) have argued that the *vena cerebralis media* ran mesial to the lateral flange in *Morganucodon*. This is because they believe that the foramen for the head vein transmitted the VIIth nerve.

BP/1/5104a illustrated in Figures 9A, 11 & 12 would have been more difficult to interpret in isolation because there is no epipterygoid process meeting the periotic bar. Otherwise this specimen is not much different except that the periotic bar (clearly itself of membrane origin) is extended ventrally by membrane bone which links up with the ventrolateral flange. The anterior foramen between this new membrane bone and the epipterygoid is probably variable and of no consequence. The left side of the specimen (Figure 9B) is a little damaged and the periotic bar has been deflected ventrad

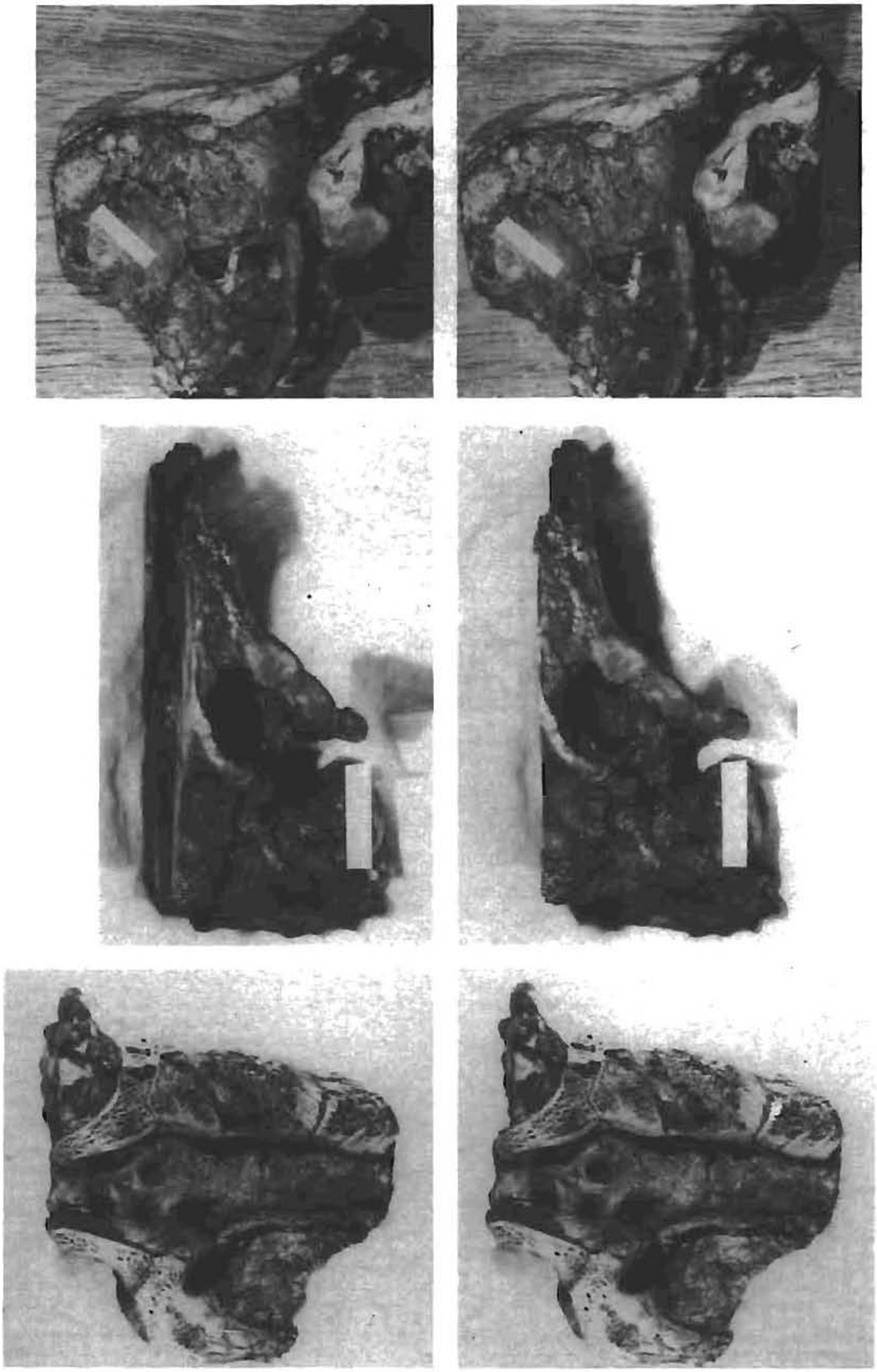

Figure 12 *Tritylodon*. BP/1/5104a. Left side of braincase in, from top to bottom, lateral, ventral and medial views. Scale = 1 cm.

during fossilization.

BP/1/4876 (Figures 13 & 14) has a more completely ossified trigeminal region than the previous two specimens. A lateral overgrowth of periotic protects the course of V(1) and the foramen for the *vena cerebralis media* is reduced. Immediately behind the foramen in the lateral flange for the stapedial artery is a small foramen for a branch of this artery leading in to the internal auditory meatus. This foramen is also seen in Figure 9A.

Clearly the trigeminal region of *Tritylodon* has undergone considerable remodelling which has necessitated a secondary overgrowth of membrane bone to protect the nerves and blood vessels. The result of the same process is seen in *Bienotherium*. Hopson's foramen for the *vena cerebralis* *media* lies lateral to the pila antotica and would have communicated directly with the semilunar ganglion; this then is clearly the exit of V(3) and the *vena capitus lateralis*. Regarding the other foramena in *Bienotherium* I suggest that the course of V(1) may be covered by membrane bone so that foramena assigned to V(2) and V(3) are for V(2) and the *vena cerebralis media* respectively.

Internal anatomy of the periotic is much as described by Crompton (1964) in *Oligokyphus* but shows important points of difference from Hopson's (1964) interpretation of *Bienotherium*. The anterodorsal margin of the periotic is difficult to interpret and is therefore conservatively shown as a dashed line; emerging at and just behind the suture dorsally is a cluster of venous foramena leading to the periotic sinus: these constitute a useful marker for comparison with *Thrinaxodon* and *Trirachodon*. Hopson described and figured the orbitosphenoid (= laterosphenoid) in contact with the pila antotica. I am reasonably certain that a dorsal neurocranial periotic component is interposed between these elements in *Tritylodon* ('a.d.p.' Figure 10). There is no indication as to whether this neurocranial 'anterodorsal process' represents the true anterodorsal process as seen in *Thrinaxodon* and *Trirachodon*. The fact that the process is not recognizable in *Diademodon* suggests that its development was suppressed in *Diademodon* and this may thus be the case in *Tritylodon*.

The right side of BP/1/4261 (Figures 15 & 8) is damaged and has lost much of the periotic and epipterygoid, this allowed preparation of the sphenoid bones. Part of a laterosphenoid is present in contact with periotic. A substantial orbitosphenoid is ossified in the pila metotica in front of the pituitary fossa. This element has a channel in its dorsal margin marking the course of V opthalmic. A similar bone is present in *Diarthrognathus* (Crompton 1958) and I suggest that the bone identified as epipterygoid in *Luangwa* (= *Scalenodon*?) by Kemp (1980) may also be an orbitosphenoid: it is an unlikely looking epipterygoid and was found deep within the specimen. In *Tritylodon* the paired latero- and orbitosphenoids

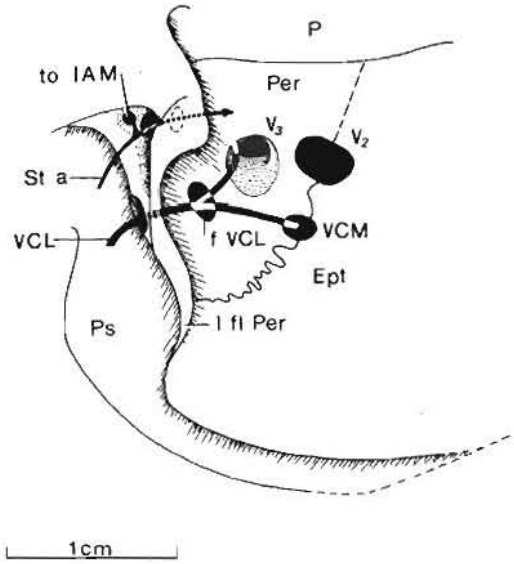

Figure 13 *Tritylodon*. BP/1/4876. Braincase, right lateral view. (See list of abbreviations.)

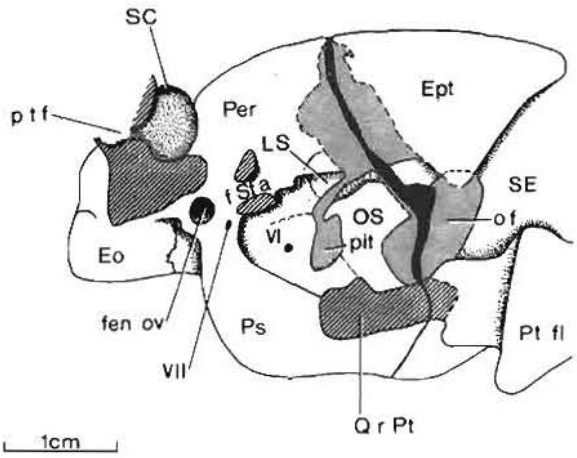

Figure 15 *Tritylodon*. BP/1/4261. Right side of braincase showing orbitosphenoid. (See list of abbreviations.)

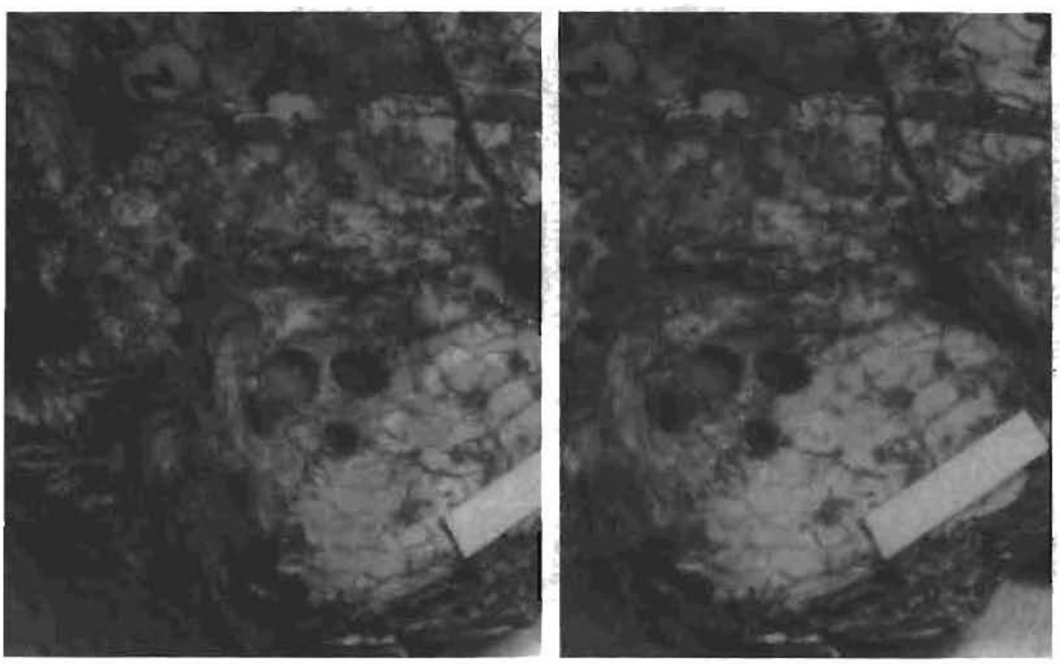

Figure 14 *Tritylodon*. BP/1/4876. Trigeminal region of right side. Scale = 1 cm.

channelled V opthalmic forwards and met an extensive median sphenethmoid medial to the epipterygoid above the optic foramen.

Homology of the mammalian promontorium

Kuhne (1956) and Crompton (1964) misidentified the paraspehnoid of *Oligokyphus*, calling it basisphenoid. This notion has been perpetuated, most recently by Kemp (1983), in spite of the fact that Hopson (1964) correctly identified the parasphenoid wings in *Bienotherium*. Kermack *et al.* (1981) consider the petrosal of *Morganucodon*, including the promontorium, to be a simple fusion of opisthotic and prootic.

In some lizards the parasphenoid is known to ossify from three centres, for the rostrum and the parasphenoid wings (Gaupp 1900; van Pletzen 1946). Strangely however both Gaupp and de Beer (1937) equated the reptilian parasphenoid wings with the mammalian pterygoids.

In *Tritylodon* the parasphenoid encloses the posterior portion of the basisphenoid (Figures 10 & 11). Basisphenoid is exposed in ventral view in the region of the basal articulation, here fused (Figure 16). The parasphenoid has sutural contact with periotic, exoccipital, basioccipital, and basisphenoid, and it forms the anterior border of the fenestra cochleae — exactly as does the promontorium of *Morganucodon*. Immediately anterior to the fenestra vestibulae there is a small foramen in the suture between periotic and parasphenoid; this undoubtedly communicated with a foramen in the posterior wall of the recess for the semilunar ganglion. This foramen therefore corresponds exactly with the description by Kermack *et al.* (1981) of the *foramen stylomastoidium primitivum* of *Morganucodon*. Contrary to Kermack *et al.* this foramen is here interpreted as the exit for the facial nerve VII. These authors believe that VII was transmitted in *Morganucodon* by a foramen which pierced the lateral flange. This latter foramen in fact transmitted the head vein. In *Morganucodon* a chain of small foramena anterior to this form a line of weakness between the promontorium and the rest of the petrosal.

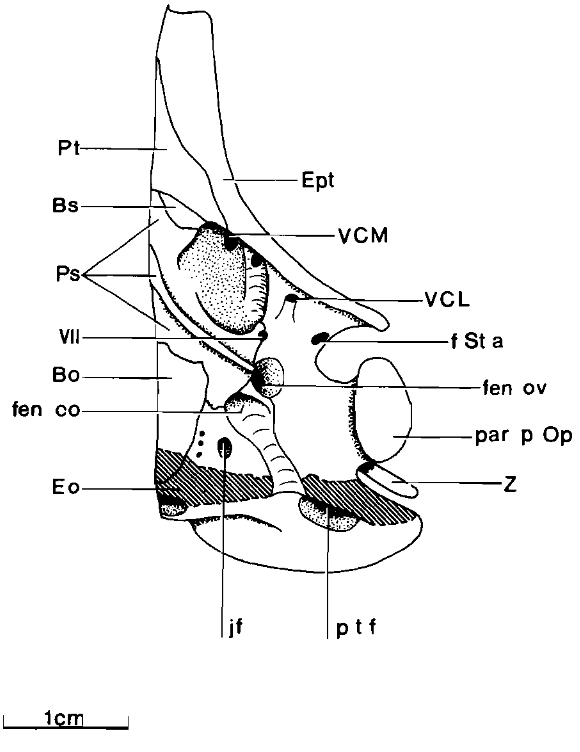

Figure 16 *Tritylodon*. BP/1/5104a. Left side of braincase, ventral view. (See list of abbreviations.)

There can be no doubt that the morganucodontid petrosal represents a fusion of neurocranial periotic with the cynodont parasphenoid wing which is membrane bone.

Summary

The anterior lamina of the cynodont periotic is neomorphic with respect to the condition in *Thrinaxodon*. It is best defined on internal structures as the region anterior to a line between the foramen for V(3) and a venous foramen or cluster of foramena at or near its dorsal border which enter the periotic sinus. Neomorphic extension of the prootic had already begun in *Thrinaxodon* as shown by the complex nature of the relationship between prootic and epipterygoid: the epiterygoid is sandwiched between processes of prootic. The anterodorsal process overlaps the epipterygoid mesially, as to a lesser extent, does prootic above it: this must be considered to be neurocranial bone. Posterior border of epipterygoid is overlapped laterally by prootic as well, and this can be considered a membrane bone component. After the *Thrinaxodon* grade a split can be postulated into herbivorous forms (*sensu lato*) in which the anterior lamina has an extensive neomorphic neurocranial component (*Diademodon* and tritylodontids) and carnivorous forms in which the anterior lamina is composed entirely (or nearly so) of membrane bone. *Trirachodon* represents a structural grade near the base of the herbivore line.

In the *Trirachodon/Diademodon* grade the epipterygoid is modified to meet periotic between the foramena for V(2) and V(3). *Trirachodon* is the last of the cynodonts considered here to retain a recognizable anterodorsal process of periotic. The anterior lamina overlaps laterally a posteriorly directed spur of epipterygoid reminiscent of that seen in some of the therocephalians. Lateral to the prootic incisure anterior lamina meets in sutural contact a neomorphic extension of epipterygoid.

In *Diademodon* the anterodorsal process apparently does not ossify but a neomorphic extension of neurocranial periotic extends across the mesial surface of the epipterygoid. Membrane bone extension of the epipterygoid invests the lateral surface of the periotic well beyond the prootic incisure.

The important aspect of this grade is that the foramen for V(2) emerges above the opening for V(3) in membrane bone. This is closely comparable to the arrangement of trigeminal foramena in *Morganucodon* except that in the ancestors of the latter it is not necessary to postulate a stage when epipterygoid contacted periotic between V(2) and V(3). One can therefore suggest that the carnivorous cynodont ancestors of morganucodontids could have had a more conventional epipterygoid which did not become involved with the trigeminal foramena, but that these were gradually separated by periotic alone.

The tritylodontids represent the end of a trend in which the anterior lamina and epipterygoid formed a bar separating the exits of V(2) and V(3). In tritylodontids the recess for the semilunar ganglion is ringed by neurocranial bone medially but lateral to this the recess is open anteriorly for the passage of V(1) and V(2).

The parasphenoid wings in *Tritylodon* are parts of a single bone which ossify from separate centres during ontogeny, yet there is good evidence that they are the homologues of the paired promontoria of the *Morganucodon* petrosals. Particularly significant is the *foramen* for the facial nerve which in *Tritylodon* lies on the suture between parasphenoid and

List of abbreviations

a d p	anterodorsal process	pit	pituitary fossa	
'a d p'	neurocranial anterior lamina	P	parietal	
Bo	basioccipital	Per	periotic	
Bs	basisphenoid	Pro	prootic	
c e	cavum epipterycum	Ps	parasphenoid	
d e	ductus endolymphaticus	Pt	pterygoid	
dl fl Pro	dorsolateral flange of prootic	Q r Ept	quadrate ramus of epipterygoid	
Ept	epipterygoid	Q r Pt	quadrate ramus of pterygoid	
Eo	exoccipital	r mb at	rim for membrane attachment	
f Bs	basisphenoid facet of prootic	r l l c	recess for lateral lobe of cerebellum	
f Bs Op	basisphenoid facet of opisthotic	S C	sinus canal	
f Eo	facet for exoccipital	S E	sphenethmoid	
f P	facet for parietal	S G	recess for semilunar ganglion	
f Pro s	prootic sinus foramen	So	supraoccipital	
f So	facet for supraoccipital	s v p	supravenous process	
f St a	foramen for stapedial artery	v l fl Pro	ventrolateral flange of prootic	
f VCL	foramen for vena capitus lateralis	V C L	vena capitus lateralis	
fen. co.	fenestra cochleae	V C M	vena cerebralis media	
fen. ov.	fenestra ovalis	X	incipient process of membrane bone	
F	frontal	Y	aberrant process of epipterygoid	
Floc	floccular fossa	v	vein	
IAM	internal auditory meatus	v(i)	venous foramen	
jf	jugular foramen	v(ii)	venous foramen	
LS	laterosphenoid	V(1)	opthalmic	
l. s	lateral swelling	V(2)	maxillary	branches of trigeminal nerve
l fl Per	lateral flange of periotic	V(3)	mandibular	
OS	orbitosphenoid of optic foramen	VI	abducens nerve	
p a	pila antotica	VII	facial	nerves
p t f	posttemporal fossa	XII	hypoglossal	
par p Pro	paroccipital process of prootic	Z	squamosal process which in lower cynodonts lies between quadrate and quadratojugal.	
par p Op	paroccipital process of opisthotic			
pin f	pineal foramen			

periotic while in *Morganucodon* it lies between promontorium and periotic components of the petrosal.

Conclusions

This investigation was originally restricted in scope to the relationships between epipterygoid and prootic/periotic and the pattern of trigeminal nerve foramena in cynodonts. In this regard two important conclusions are possible: the first is that it is possible to suggest a middle Triassic dichotomy between a carnivorous cynodont line leading to mammals, and a herbivorous line which culminated in the tritylodontids. In both lines an extensive anterior lamina of periotic developed: in the carnivorous line the neurocranial component of the lamina was likely suppressed, while in the herbivorous line it was accentuated and associated with extensive ossification of ethmoid elements. The second important conclusion is that in respect of the characters examined, morganucodontid mammals show no significant advance over their cynodont ancestors.

One can therefore agree with Crompton & Jenkins (1979), Kemp (1983) and Presley (1981) that the morganucodontid braincase represents the primitive condition from which all later mammals were derived, but take issue with Kemp over his observation 'that tritylodontids show an intermediate condition of the braincase' (i.e. between cynodonts and mammals).

Secondly the suggestion of Presley & Steel (1976) that the mammalian alisphenoid which consists of membrane and cartilage bone, may in part be anterior lamina of petrosal rather than processus ascendens of epipterygoid, is supported by this investigation as it is always anterior lamina which transmits V(2) and V(3) in cynodonts and morganucodontids. The suggestion of these authors that the cartilage bone component may be derived from quadrate ramus of epipterygoid is attractive, but needs to be approached with caution from the cynodont perspective. It is only in *Trirachodon, Diademodon* and *Tritylodon* that epipterygoid is known to meet anterior lamina between V(2) and V(3) so that this situation would need to be separately derived in mammals.

A spin-off from this investigation is the conclusion that the parasphenoid wings of *Tritylodon* are clearly homologous with the promontoria of the *Morganucodon* petrosals. In view of the compound nature of the alisphenoid of recent mammals it is desirable to refer to epipterygoid in cynodonts and morganucodontids. The term periotic is to be preferred for cynodonts in which prootic and opisthotic are fused, while petrosal is appropriate for morganucodontids in which part of the parasphenoid fuses with the periotic to form the promontorium.

References

BRINK, A.S. 1955. A study on the skeleton of *Diademodon. Palaeont. afr.* 3: 3 – 39.

CROMPTON, A.W. 1958. The cranial morphology of a new genus and species of ictidosaurian. *Proc. zool. Soc. Lond.* 130: 183 – 216.

CROMPTON, A.W. 1964. On the skull of *Oligokyphus. Bull. Brit. Mus. (Nat. Hist), Geol.* 9(4): 70 – 82.

CROMPTON, A.W. & JENKINS, F.A. (Jr.) 1979. Origin of mammals. In: Mesozoic Mammals: the First two-thirds of Mammalian History. (Eds) Lillegraven, J.A., Kielan-Jawarowska, Z.

& Clemens, W.A. University of California Press, Berkeley. pp. 59 – 73.

DE BEER, G.R. 1937. The Development of the Vertebrate Skull. Clarendon Press, Oxford.

FOURIE, S. 1974. The cranial morphology of *Thrinaxodon liorhinus* Seeley. *Ann. S. Afr. Mus.* 65(10): 337 – 400.

GAUPP, E. 1900. Das Chondrocranium von *Lacerta agilis. Anat. Hefte, Arb.*, 15: 433 – 595.

HOPSON, J.A. 1964. The braincase of the advanced mammal-like reptile *Bienotherium. Postilla* 87: 1 – 30.

KEMP, T.S. 1972. Whaitsiid Therocephalia and the origin of cynodonts. *Phil. Trans. R. Soc. Lond. (B).* 264(857): 1 – 54.

KEMP, T.S. 1980. Aspects of the structure and functional anatomy of the Middle Triassic cynodont *Luangwa. J. Zool. Lond.* 191: 193 – 239.

KEMP, T.S. 1983. The relationships of mammals. *Zool. J. Linn. Soc.* 7: 353 – 384.

KERMACK, K.A., MUSSET, F. & RIGNEY, H.W. 1981. The skull of *Morganucodon. Zool. J. Linn. Soc.* 71: 1 – 158.

KUHNE, W.G. 1956. The Liassic therapsid *Oligokyphus*. 149 pp., 12 pls. British Museum (Nat. Hist.) London.

MENDREZ, C.H. 1972. On the skull of *Regisaurus jacobi*, a new genus and species of Bauriamorpha Watson and Romer 1956 (= Scalopsauria Boonstra 1953), from the *Lystrosaurus*-zone of South Africa. In: Studies in Vertebrate Evolution, (ed.) Joysey, K.A. & Kemp, T.S. Oliver and Boyd, Edinburgh.

PARRINGTON, F.R. 1946. On the cranial anatomy of cynodonts. *Proc. Zool. Soc. Lond.* 116: 181 – 197.

PRESLEY, R. 1981. Alisphenoid equivalents in placentals, marsupials, monotremes and fossils. *Nature* 294(5842): 668 – 670.

PRESLEY, R. & STEEL, F.L.D. 1976. On the homology of the alisphenoid. *J. Anat.* 121(3): 441 – 459.

VAN PLETZEN, R. 1946. The cranial morphology of *Cordylus* with special reference to the cranial kinesis. Annals Univ. Stellenbosch 24: 41 – 68.

WATSON, D.M.S. 1911. The skull of *Diademodon*, with notes on those of some other cynodonts. *Ann. Mag. Nat. Hist.* Ser. 9 8: 293 – 330.

WATSON, D.M.S. 1913. Further notes on the skull, brain and organs of special sense of *Diademodon. Ann. Mag. Nat. Hist.* Ser. 8 12: 217 – 228.