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PEABODY MUSEUM OF NATURAL HISTORY
YALE UNIVERSITY
NEW HAVEN, CONNECTICUT, U.S.A.

Number 87 **December 10, 1964**

THE BRAINCASE OF THE ADVANCED MAMMAL-LIKE REPTILE *BIENOTHERIUM*

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INTRODUCTION

Recent discoveries of well-preserved cranial material of Mesozoic mammals, previously known almost exclusively from jaws and teeth, have yielded extremely interesting and unexpected information on the early evolution of the mammalian braincase. K. A. Kermack and his co-workers (D. M. Kermack et al., 1956; K. A. Kermack and F. Mussett, 1958) have described the periotic of the probable docodont *Morganucodon* which possesses an "anterior lamina," i. e. a prominent forward extension of the periotic on the side wall of the braincase, resembling the anterior periotic process of living monotremes. This structure forms a large part of the wall of the monotreme braincase in place of the ascending lamina of the alisphenoid which is characteristic of the braincase of marsupial and placental mammals. The presence of an anterior lamina in the periotic of *Morganucodon* led D. M. Kermack et al. (1956) to postulate a relationship between it and monotremes.

More recently, however, with the discovery of an anterior lamina in the periotic of the Upper Jurassic triconodont *Trioracodon,* K. A. Kermack (1962, 1963) has concluded that this structure may have occurred in several probably unrelated groups of Mesozoic mammals and therefore does not necessarily indicate a special relationship among any forms possessing it. He suggests that the expansion of the brain in these early mammals led to a concomitant expansion of the anterior margin of the periotic to form a protective cover for the brain. He believes that an anterior lamina was present in the late therapsids *Diarthrognathus* and *Oligokyphus,* which would indicate to him that the expansion of the periotic had begun at a pre-mammalian stage and had progressed independently in a number of lineages which crossed the reptile-mammal grade boundary.

The periotic has been described in only two other genera of Triassic and Jurassic mammals. A very fragmentary periotic of *Triconodon* was described by Simpson (1928) and redescribed by Kermack (1963), but it is essentially identical with the better preserved specimen of *Trioracodon.* Patterson and Olson (1961) have referred a fairly complete but badly crushed braincase to *Sinoconodon,* a triconodont-like mammal from the latest Triassic of Yunnan, China, but the structure of the anterior part of the periotic in this specimen cannot be determined with certainty. Rigney (1963) has recently given a short preliminary notice of a complete skull of *Morganucodon* from near the type locality of *Sinoconodon,* but nothing on the braincase has yet been published. Rigney believes that the braincase referred by Patterson and Olson to *Sinoconodon* actually belongs to *Morganucodon.*

The discoveries of these cranial remains are extremely significant in the amount of light they have shed on the "Dark Ages" of mammalian history. However, their great rarity and usually fragmentary nature introduces major difficulties in interpreting them correctly in the absence of structural series linking them with more completely known and better understood forms. For example, Kermack (1962, 1963) has drawn inferences as to the morphological relations of the alisphenoid with respect to the periotic in Mesozoic mammals, yet in only three genera of mammal-like reptiles from above the Middle Triassic has the side wall of the braincase been described, and in only one, the ictidosaur *Diar-*

thrognathus, (Crompton, 1958), is the contact of the alisphenoid with the periotic preserved. In the other two, the tritylodonts *Oligokyphus* (Kühne, 1956; Crompton, 1964) and *Likhoelia* (Ginsburg, 1962), both elements are incompletely preserved and their mutual contacts are unknown. I am presently studying the Upper Triassic tritylodont *Bienotherium* in which the braincase is almost completely preserved. The epipterygoid and prootic (reptilian homologues of the alisphenoid and anterior part of the periotic of mammals) in this genus indicate that in previous descriptions of tritylodonts and in Kermack's descriptions of *Morganucodon* and *Trioracodon* the mutual relations of these elements have been incorrectly interpreted. Consequently, Kermack's interpretation of the evolutionary history of the mammalian braincase during the Mesozoic requires some modification.

The prootic and epipterygoid of *Bienotherium* are described below. Comparisons are made with the homologous elements in cynodonts in order to indicate the ways in which the tritylodont braincase has been modified from the well-understood Early and Mid-Triassic therapsid pattern. New interpretations of the side wall of the braincase in other genera of tritylodonts and in the Mesozoic mammals described by Kermack and his co-workers are advanced, and a revision is offered of Kermack's (1962, 1963) theory of the evolutionary history of the orbito-temporal region of the skull in the earliest mammals.

ACKNOWLEDGMENTS

This paper is part of a work to be submitted to the Committee on Paleozoology, the University of Chicago, in partial fulfillment of the requirements for the degree of Doctor of Philosophy. I gratefully acknowledge the guidance of Dr. E. C. Olson during the course of this study. Thanks are due Dr. A. S. Romer of the Museum of Comparative Zoology, Harvard University, for permission to borrow comparative material, and to Dr. A. W. Crompton for permission to examine undescribed cynodont skulls in his possession. Dr. Olson and Drs. A. W. Crompton, J. H. Ostrom, D. A. Russell, and E. L. Simons read the manuscript; their suggestions and criticisms are appreciatively acknowledged.

MATERIALS AND METHODS

The description of the braincase of *Bienotherium yunnanense* Young (1940) is based primarily upon the posterior half of an adult skull which was sectioned serially using the method described by Olson (1944). In addition, several fragmentary specimens of the ear region and part of the braincase were utilized for this description. These specimens are part of the Yunnan, China, Fossil Collection of the Fu Jen Catholic University of Peking, China, and are designated by the abbreviation CUP. This collection is presently on loan to the Department of the Geophysical Sciences of the University of Chicago.

The collection of fossils of which these specimens of *Bienotherium* comprise a small part was made under the direction of Father Edgar Oehler in 1948 near the village of Lufeng in Yunnan Province, China. The *Bienotherium* material is from the lower Lufeng Series of latest Triassic age.

The braincase was sectioned at intervals of 1.5 mm (sections 1-14) and 0.5 mm (sections 14-71), nitrocellulose peels being made of each section. Enlarged graphic reconstructions were made of the specimen from several views, two of which are illustrated here (Figs. 2 and 3). Proportions were checked against a plaster cast of the specimen made prior to sectioning.

Comparative material includes the sections of *Thrinaxodon liorhinus* described by Olson (1944) as "Cynodont B," a complete skull of this species (No. 4282), which served as the basis for Fig. 1, from the South African Museum, Cape Town, and a skull of *Belesodon neidermeyeri* (No. 1533) from the Museum of Comparative Zoology, Harvard University.

THE EPIPTERYGOID AND PROOTIC OF *Thrinaxodon*

Before describing the braincase of *Bienotherium,* it is perhaps useful to review the morphology of the epipterygoid and prootic of a cynodont such as the well-known Lower Triassic species *Thrinaxodon liorhinus* (Figs. 1, 5A, 6A). The skull of *Thrinaxodon* has been well described by Parrington (1946), and Olson (1944) has given a detailed account of the braincase and ear region.

The epipterygoid is greatly expanded dorsally, being in broad contact with the parietal and just meeting the frontal. Its postero-

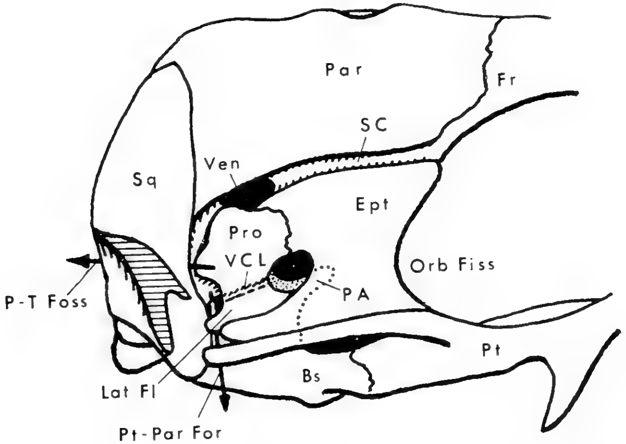

Fig. 1. *Thrinaxodon liorhinus* Seeley. Lateral view of braincase. Squamosal cut across depression which housed the quadrate. The outline of the anterior border of the prootic medial to the epipterygoid is indicated by the dotted line. Abbreviations on p. 29-30 ×2.

dorsal margin is in sutural contact with the prootic (Olson, 1944). Anteriorly, it has a broadly emarginated border which forms the edge of the large orbital fissure (*Orb Fiss*, Fig. 1), the opening through which cranial nerves II, III, IV, V_1, and VI left the braincase. Ventrally, the epipterygoid contacts the pterygoid which sends a slender quadrate ramus back to contact the quadrate (which is missing in Fig. 1). A posteroventral process of the epipterygoid also extends back toward the quadrate but does not reach it (Parrington, 1946). Between the posterior margin of the epipterygoid and the front of the prootic is a large foramen through which passed the maxillary and mandibular branches of the trigeminus nerve and a vein, probably homologous with the vena cerebralis media of sauropsid reptiles (see Cox, 1959).

The prootic forms the wall of the braincase in front of the ear region, contacting the squamosal and parietal dorsally and the rear margin of the epipterygoid anteriorly. Ventrally, the prootic bears a thin lateral sheet which supports the quadrate ramus of the epipterygoid and which is referred to here as the "lateral flange" (*Lat Fl*, Fig. 1, 6A). The anterior end of the lateral flange lies lateral to the trigeminal foramen. Its posterior end extends back beyond the hind margin of the epipterygoid to contact the paroccipital process so as to enclose the pterygo-paroccipital foramen (*Pt-Par For,* Fig. 1).

The prootic component of the foramen for the trigeminus nerve is somewhat complex and requires a detailed description, based in part on the sections of "Cynodont B." The notch in the anterior border of the prootic is the prootic incisure. From the anteroventral corner of this notch a process, the pila antotica (*P A,* Fig. 1), extends anterodorsally. It lies medial to the epipterygoid and is barely visible in side view. Between the pila antotica and the medial rim of the prootic incisure on the inside and the epipterygoid and the lateral flange on the outside is a narrow space, the cavum epiptericum (*Cav Ep,* Fig. 6A). In living reptiles this space contains the semilunar ganglion of the trigeminus nerve (see De Beer, 1937, p. 430). In *Thrinaxodon* that part of the prootic which forms the posterior border of the prootic incisure is very slightly hollowed, presumably for the posterior part of the semilunar ganglion. This hollow, though extremely shallow, has significance in the interpretation of *Bienotherium*. The paths of the three branches of the trigeminus nerve in *Thrinaxodon* were undoubtedly as in modern reptiles: the ophthalmic branch (V_1) passed forward within the cavum epiptericum and left the skull in front of the epipterygoid; the maxillary (V_2) and mandibular (V_3) branches passed out of the skull behind the epipterygoid, directly lateral to the prootic incisure. This is illustrated in Fig. 5A.

Along the dorsal margin of the prootic and epipterygoid is a gutter for the protection of a vein. This is the so-called "sinus canal" (*S C,* Fig. 1). A prominent foramen enters the braincase from the sinus canal above the prootic-epipterygoid contact. The posterior end of the gutter lies at the anterior opening of the post-temporal fossa (*P-T Foss,* Fig. 1) which transmitted a vein forward from the occipital region (see Cox, 1959). The prootic forms a short protective flange in front of this opening. A slight channel leads forward from the pterygo-paroccipital foramen to the trigeminal foramen which Watson (1920) has interpreted in other cynodonts as being for the vena capitus lateralis (*V C L,* Fig. 1).

THE EPIPTERYGOID AND PROOTIC OF *Bienotherium*

The only first-hand studies of the skull of *Bienotherium* are those of Young (1940, 1947), though Watson (1942) has contributed a very important interpretation of this material based on Young's earlier publication. The side wall of the braincase in Young's two skulls is largely unpreserved, and those parts which are present have proved difficult to interpret.

The lateral wall of the braincase (Fig. 2) is formed by the ascending lamina of the epipterygoid and the anterior part of the prootic, although ventrolateral wings of the frontal and parietal form a small part of the wall dorsally. In the cerebral region the frontal wing extends far down, medial to the epipterygoid, to a point below the floor of the cranial cavity (which, in front of the pituitary fossa, lies well above the base of the skull). In this region the floor and wall of the braincase proper are formed by a well-developed orbitosphenoid which largely excludes both the epipterygoid and the frontal from participating in the formation of the cranial wall (Fig. 3).

The epipterygoid has a high, broad ascending lamina extending well above the level of the cranial cavity to overlap the frontal and the anteroventral edge of the parietal. Its anterior margin is broadly incised by the orbital fissure. A slender process of the epipterygoid passes below the orbital fissure medial to the transverse flange of the pterygoid. The posterior border of the ascending lamina has a continuous overlapping contact with the prootic above the trigeminal foramen. The nature of this contact is described in greater detail below.

The inferolateral margin of the epipterygoid anterior to its quadrate ramus is overlapped by the pterygoid. The epipterygoid has a well-developed sutural contact with the basipterygoid process of the basisphenoid (*Bpt,* Fig. 4B). The quadrate rami diverge behind this point at an angle of about 45 degrees from the midline. Their posteroinferior border is bluntly rounded and forms a thickened out-turned rim. The quadrate ramus is more vertically oriented and much deeper than that of any cynodont. Furthermore, it lies entirely below the level of the cranial cavity and also below and largely medial to the paroccipital process (Fig. 4A). It does not contact the paroccipital process nor could it have reached the quadrate (the probable position of which is discussed below). Its suture with the prootic is seen in section to be deeply interdigitating (Fig. 4A, B).

The prootic of *Bienotherium* has a relatively greater exposure on the lateral surface of the braincase than does that of cynodonts, a fact due in large part to the presence of a thin lamina which extends well up on the lateral surface of the parietal to partially cover a deeply incised channel in the latter (*S C*, Fig. 2, 4A). This channel, the homologue of the sinus canal of cynodonts (Watson, 1911), is covered more extensively by a short lappet of the parietal. In cynodonts the sinus canal usually lies on or slightly above the prootic-parietal suture and, in advanced forms, is often

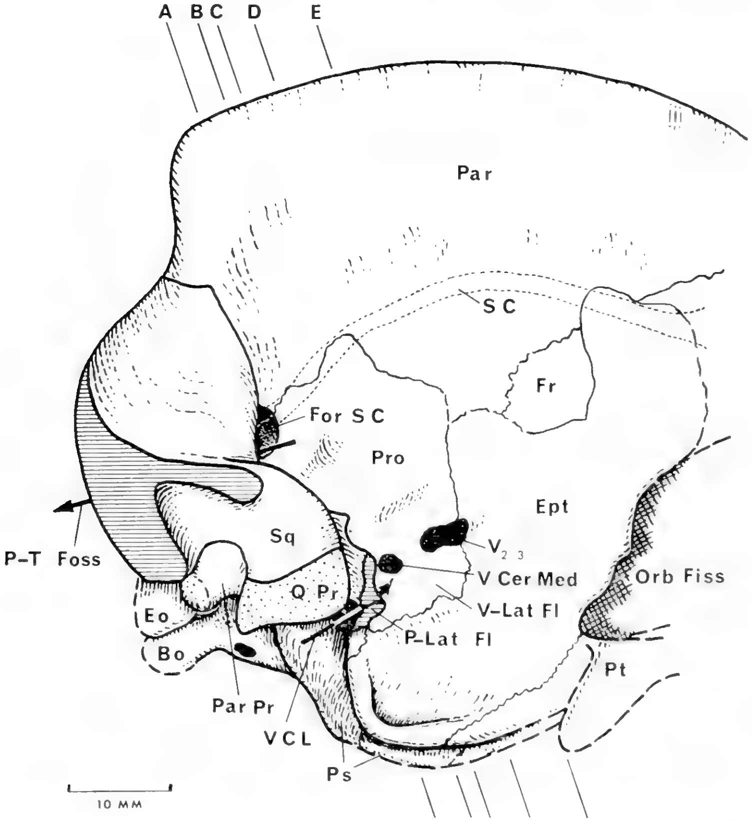

Fig. 2. *Bienotherium yunnanense* Young. Lateral view of braincase reconstructed from serial sections. Pattern of horizontal lines indicates cuts across squamosal and distal part of posterolateral flange. Sagittal crest partially restored. A-E, positions of sections A-E in Fig. 4. Abbreviations on p. 29-30.

covered by thin laminae from these elements. It marks the course of a vein (cf. Watson, 1920) possibly homologous with the parietal vein of living lepidosaurs (Cox, 1959). Between the posterodorsal margin of the prootic and the cranial process of the squamosal is a foramen in the parietal (*For S C,* Fig. 2) which marks the posterior terminus of the "sinus canal."

Anteriorly, the prootic forms a thin lamina overlapping externally the entire posterior margin of the ascending process of the epipterygoid, except where both elements are emarginated by the

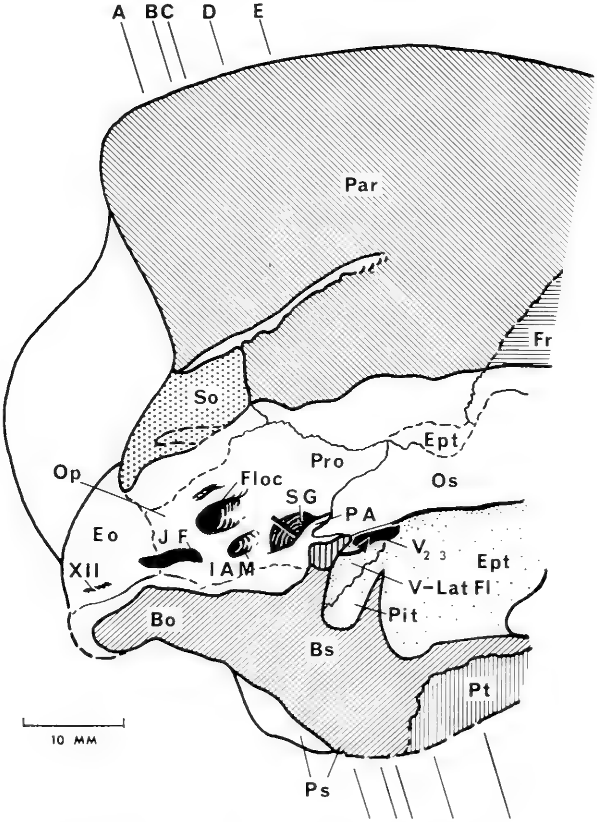

Fig. 3. *Bienotherium yunnanense* Young. Internal aspect of braincase in sagittal section. Basicranial process of prootic indicated by heavy vertical lines. The foramen for the vena cerebralis media lies lateral to the basicranial process and is thus not visible in this figure. A-E, positions of sections A-E in Fig. 4. Abbreviations on p. 29-30.

trigeminal foramen (*$V_{2,3}$*, Fig. 2-4). This is the reverse of the usual reptilian condition in which the prootic lies medial to the epipterygoid; its significance will be dealt with at greater length below.

Below the trigeminal foramen the prootic extends ventrally as a vertical flange in sutural contact with the quadrate ramus of the epipterygoid. This flange is homologous with at least part of the thin lateral sheet of the prootic of cynodonts which supports the quadrate wing of the epipterygoid, and which has been variously termed the "lateral lamina" (Kühne, 1956; Crompton, 1958) or "lateral flange" (Kermack, 1963). I shall use the latter term in this paper in order to avoid confusion with the "anterior lamina." In *Bienotherium* this vertical flange is homologous with only the anterior part of the lateral flange of cynodonts and so will be distinguished as the "ventrolateral flange" *(V-Lat Fl)* in subsequent discussion. It is vertically rather than ventrolaterally inclined as it is in cynodonts, and so is not clearly distinguishable from the side wall of the braincase proper. In cross-section (Fig. 4A-C), however, it is seen to lie below the floor of the braincase. It extends back to a point level with and medial to the anterodistal extremity of the paroccipital process.

In tritylodonts the anterior half of the distal end of the paroccipital process is turned downward to form a prominent boss (*Q Pr,* Fig. 2, 4A). In *Bienotherium* this boss may be seen to lack a cover of periosteal bone on its lateral surface (Fig. 4A). Young (1947, p. 549) identified this surface as "the medial contact with the quadrate," but did not specify which element of the skull forms it. Kühne (1956) believes this process supports the hyoid, the quadrate lying entirely posterior to it, but Crompton (1964) has convincingly argued that it indeed does support the quadrate. A single specimen (CUP 2268) of *Bienotherium,* in which this process is extremely well preserved, suggests that both Kühne and Crompton are correct, for the downturned process has both a broad antero-lateral surface which I believe certainly supported the quadrate and a medially-directed posterior process which I believe provided attachment for the hyoid.

Immediately in front of the paroccipital process the prootic is drawn out into a prominent laterally-directed process which is pierced by a single large foramen (*P-Lat Fl,* Fig 2, 4A). This process is not preserved in its entirety in any of the available specimens of *Bienotherium,* and some details of its structure cannot be determined. In the sectioned skull, its lower wing, that part below

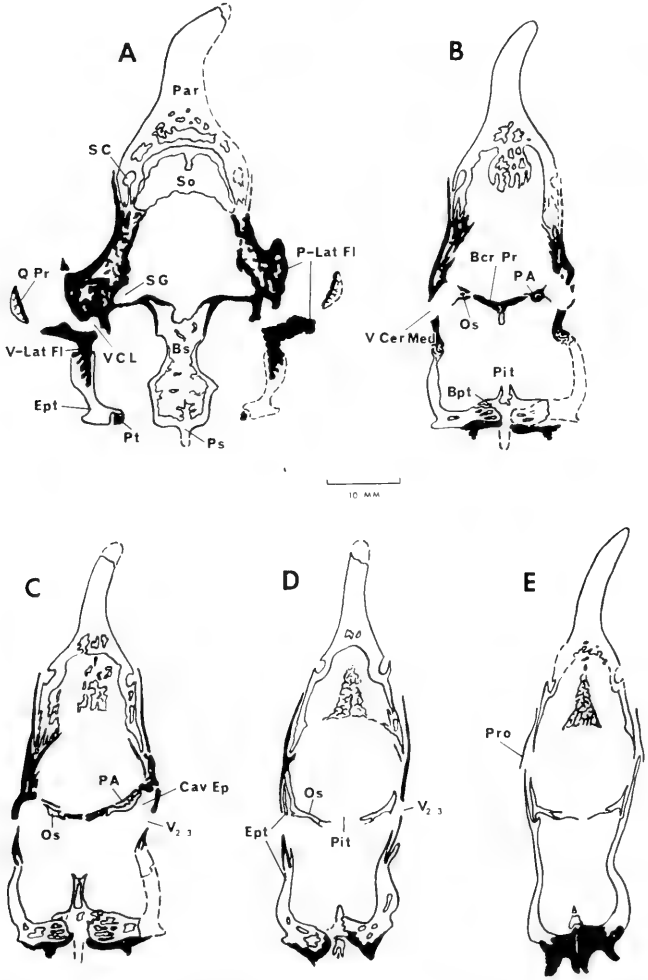

Fig. 4 *Bienotherium yunnanense* Young. Transverse sections across braincase in positions indicated in Figs. 2 and 3. A, through posterior part of depression for semilunar ganglion; B, through pila antotica and basipterygoid joint; C, through trigeminal notch in ventrolateral flange; D, through posterior end of ascending lamina of epipterygoid which lies medial to prootic; E, through anterior end of prootic. Note that the sections are obliquely oriented to vertical axis of skull. Prootic and pterygoid indicated in black. Abbreviations on p. 29-30.

the foramen, has its origin on the posterior end of the ventrolateral flange just above the suture with the quadrate ramus of the epipterygoid. Distally, it extends to within 2 mm of the "quadrate process" of the paroccipital process (Fig. 4A) and in undamaged specimens may have contacted it. The upper wing of the process is best preserved in a partial skull (CUP 2241), in which it does contact the anterior face of the "quadrate process," thereby completely enclosing the pterygo-paroccipital foramen.

The structure of the laterally-directed process of the prootic, as seen in the sections, strongly suggests that it may really be a compound structure formed by distinct dorsal and ventral moieties contacting one another distally to enclose the large foramen. In *Oligokyphus,* this process, called the "lateral lamina" by Kühne (1956) and Crompton (1964), appears in the published figures and descriptions to be a single deep lamina pierced by one large foramen and several smaller ones (see Kühne, 1956, p. 47, Fig. 13, and Pl. 7, Fig. 2). In an undescribed skull of *Tritylodon* (K405) from the South African Museum, Cape Town, the flange is too poorly preserved to allow a determination of its possible compound nature to be made, but it is clearly seen to be penetrated by two large foramina. In the available specimens of *Bienotherium* only a single foramen can be distinguished with certainty, but because of the incompleteness of the material, the definite absence of a second large foramen cannot be demonstrated. Despite this uncertainly, I believe that the homologies suggested below (and considered in greater detail on p. 17) between these structures in cynodonts and tritylodonts are essentially correct.

The laterally-directed process of the prootic in *Oligokyphus* has been homologized by Kühne (1956) with the "lateral lamina" (i. e. lateral flange) of cynodonts. However, as noted earlier, the ventrolateral flange of *Bienotherium,* which contacts the quadrate ramus of the epipterygoid, is homologous with at least the anterior part of the lateral flange of cynodonts. Therefore, the laterally-directed process of tritylodonts might best be called the "posterolateral flange."' I propose to use this name for both the upper and lower portions of this process although I shall try to show later that only the lower moiety appears to be homologous with part of the lateral flange of cynodonts. However, until this region of the skull of tritylodonts is better understood, I believe it preferable to refrain from further complicating the terminology used to describe it, at least for the present.

The trigeminal foramen, preserved only in the sectioned skull, lies about 10 mm anterior to the paroccipital process and about 5 mm in front of the posterolateral flange. It is about 5 mm long by 2.5 mm high and is slightly constricted at midlength so as to have a roughly "dumbbell"-shaped outline. Presumably this constriction represents the incipient subdivision of the single trigeminal foramen of reptiles into the separate foramina ovale and rotundum of mammals.

Some 2.5 mm behind and slightly below the trigeminal foramen is a second, much smaller, foramen *(V Cer Med)* lying completely within the prootic. It is immediately anterodorsal to the foramen in the posterolateral flange. Comparison with cynodonts suggests that the vena capitus lateralis *(V C L)* passed back through the latter foramen to the pterygo-paroccipital foramen, and thence to the middle ear cavity. In *Sphenodon* and some lizards a branch of the lateral head vein, the vena cerebralis media, leaves the skull through the trigeminal notch (O'Donoghue, 1920). In *Bienotherium* this vein probably passed out of the skull through the separate small foramen.

THE INTERNAL ASPECT OF THE BRAINCASE

Kühne (1956) and more recently Crompton (1964) have described the internal structure of the braincase of *Oligokyphus*. The cranial cavity of *Bienotherium* (Fig. 3) is nearly identical to that of *Oligokyphus,* so only the region anterior to the internal auditory meatus, which is largely unpreserved in the known material of the latter genus, will be described.

About 3 mm in front of the internal auditory meatus and slightly behind the level of the pituitary fossa is a deep hollow in the medial surface of the prootic (*S G,* Fig. 3, 4A). Kühne (1956) has interpreted this depression in *Oligokyphus* as the housing for the semilunar ganglion of the trigeminus nerve; in *Bienotherium* it surely served this function. In section (Fig. 4A), it may be seen that this hollow lies quite low in the wall of the cranial cavity and that it is floored by a very thin lamina of prootic which extends medially to join the deep basisphenoid-parasphenoid complex. Below this hollow is the great extracranial space enclosed laterally by the ventrolateral flange of the prootic and the quadrate ramus of the epipterygoid. Directly lateral to the semilunar depression is the posterolateral flange of the prootic.

Anteromedial to the depression for the semilunar ganglion is a short dorsoventrally flattened process of the prootic (*P A,* Fig. 3, 4B-C) which extends forward and upward. It has the same relations to the semilunar depression and the dorsum sellae as does the pila antotica of cynodonts (Olson, 1944; Brink, 1955) though it differs somewhat in appearance from that of *Thrinaxodon* (Fig. 6A). The lamina of the prootic which forms the outer wall of the braincase in this region extends forward approximately 8 mm beyond the level of the pila antotica, and thus conceals it from lateral view.

The braincase anterior to the pila antotica is completely floored by an extensive chondrocranial ossification here termed an orbitosphenoid (*Os*) though its relations are those of a compound laterosphenoid-orbitosphenoid. Posteriorly it contacts the pila antotica on either side of the pituitary fossa (Fig. 4B, C). A peculiarity of this skull is the pair of processes of the prootic which meet at the midline to form a portion of the dorsum sellae (*Bcr Pr,* Fig. 4B, C). "Basicranial processes" of the prootic have been described in gorgonopsians (Olson, 1944) but never in cynodonts. I believe they are not indicative of a close relationship with gorgonopsians but may merely represent a convergent structural modification correlated with the deepening of the braincase.

Lateral to the pila antotica the depression for the semilunar ganglion opens anteroventrally into the large subcranial space described above (Fig. 4B). At this point, the ventrolateral flange is pierced by the small foramen for the vena cerebralis media. This vein in *Sphenodon* passes down from the transverse sinus in the roof of the cranial cavity to leave the braincase through the prootic incisure (O'Donoghue, 1920). In *Thrinaxodon* it appears to have had a similar course, being enclosed in a special channel between the epipterygoid and the body of the prootic laterally and a special dorsally-directed lappet of the prootic medially (see Fig. 6A). In *Bienotherium* it would have left the braincase by way of the depression for the semilunar ganglion and the foramen in the ventrolateral flange.

The trigeminal foramen pierces the side wall of the skull on the contact of the epipterygoid and the ventrolateral flange about 8 mm anterior to the depression for the semilunar ganglion. Thus, the maxillary and mandibular rami of nerve V traversed about 8 mm of extracranial space before reaching the lateral surface of the braincase.

COMPARISON WITH CYNODONTS

The epipterygoid and prootic of an early cynodont, *Thrinaxodon liorhinus,* have already been described. Some variation in this region of the skull exists in more advanced cynodonts, but the basic pattern is as in *Thrinaxodon.*

The lateral flange of the prootic, which occurs in cynodonts alone among pre-Upper Triassic therapsids, is a relatively simple structure in the well-known members of this group. In *Bienotherium* it is much more complicated and, as pointed out earlier, can be subdivided into two distinct parts which have been given the names "posterolateral flange" and "ventrolateral flange." Comparison with *Thrinaxodon* suggests that the lower process of the posterolateral flange (the upper process is discussed later) may be homologous with the hind portion which contacts the paroccipital process behind the quadrate wing of the epipterygoid. With the ventromedial migration of the anterior part of the lateral flange in tritylodonts, i. e. that part in contact with the quadrate ramus of the epipterygoid, the more posterolateral portion of the flange would have become progressively isolated as a conspicuous laterally-directed process. Its retention as a distinct entity, set well off from the ventrolateral flange (which serves the clear function of buttressing the epipterygoid), may have been related to the need for a protective cover for the anterior part of the middle ear cavity. As such it would be functionally equivalent to the partial bullae formed by the alisphenoid in didelphid marsupials or by the basisphenoid in some insectivores.

The progressive ventromedial migration of the anterior part of the lateral flange can be traced from *Thrinaxodon* (Fig. 1, 6A), in which it extends ventrolaterally at an angle of 45 degrees, through an advanced cynodont such as *Belesodon,* in which it is oriented at approximately 70 degrees to the horizontal, to *Bienotherium* (Fig. 2, 6B) in which it is essentially vertical. In this sequence the flange progressively deepens, as does the quadrate ramus of the epipterygoid.

The ventrolateral flange and, indeed, the entire anterior margin of the prootic of *Bienotherium* differ from these structures in cynodonts not only in their greater depth, but also in their much greater anterior extent. In cynodonts the lateral flange generally ends at the level of the prootic incisure (this is also true of *Diarthrognathus;* Crompton, 1958), and the inner surface of the prootic is only slightly hollowed for the semilunar ganglion so that the greater part of the prootic incisure is open laterally. In *Bienotherium* both the ventrolateral flange and the anterodorsal border of the prootic extend well forward of the prootic incisure, so that the incisure and the pila antotica are hidden from lateral view. Therefore, the prootic component of the trigeminal foramen in *Bienotherium* is not strictly homologous with the prootic incisure of cynodonts, for the former is merely a notch in the anterior border of the ventrolateral flange (compare Fig. 6A with Fig. 4D). What has happened in the tritylodont is that the lateral part of the prootic, mainly the ventrolateral flange, but also that part which in *Thrinaxodon* forms the outer and posterior border of the prootic incisure, has grown forward to close off the posterior part of the cavum epiptericum in which the semilunar ganglion lay. The cavum epiptericum in *Bienotherium* lies medial to both the epipterygoid and the anterior part of the prootic. This point is particularly significant in the interpretation of the braincase of Mesozoic mammals and will be returned to in the final section of this paper.

The posterolateral flange of *Bienotherium* differs from that of Lower and Middle Triassic cynodonts in that it is pierced by a large foramen which I have interpreted as having transmitted the vena capitus lateralis forward from the pterygo-paroccipital foramen. In Karroo cynodonts the side of the prootic above the lateral flange may bear a groove which extends between the pterygo-paroccipital foramen and the prootic incisure, and which has been interpreted by Watson (1916, 1920) as marking the course of the vena capitus lateralis. In *Diademodon* this groove may be overhung by a thin flange of prootic from the hinder and outer end of which "a special process is given off which runs outwards, lying parallel to and in front of the paroccipital process, to meet a similar special process of the squamosal" (Watson, 1916, p. 343). A similar structure is also seen in *Belesodon*. Were this special process of the prootic to move forward, away from the front of the paroccipital process, and downward to contact the distal end of the lateral flange lateral to the channel for the head vein, its relations would be the same as those of the upper half of the posterolateral flange of tritylodonts. As already pointed out, this flange is damaged in all available specimens of *Bienotherium,* so it is not possible to determine whether or not it is a compound structure. In *Oligokyphus* it appears not to be. However, the late Middle Triassic cynodont *Exaeretodon* from the Ischigualasto Formation of Argentina, recently described by Bonaparte (1962), has two well-developed and apparently distinct processes above and below the groove for the head vein. Bonaparte interprets the inferior process as being part of the epipterygoid ("aliesfenoide"), but inasmuch as sutures are not visible in this region of his specimen, it is perhaps better to interpret it as part of the prootic; its relations are those of the lateral flange of earlier cynodonts in which this structure invariably lies below the groove for the head vein. If this interpretation is correct, then conditions in *Exaeretodon* support the hypothesis that the posterolateral flange of tritylodonts is a composite structure formed by: (1) the posterior part of the lateral flange of cynodonts; and (2) the special process, developed in late cynodonts, which lies directly in front of the paroccipital process and above the groove for the lateral head vein.

Bienotherium differs from most cynodonts but, again, resembles *Exaeretodon* in having a distinct foramen in the lateral wall of the prootic for the middle cerebral vein. With the forward extension of the anterior part of the prootic lateral to the prootic incisure a separate foramen was developed in *Bienotherium,* probably so that the vein might retain its direct route from the braincase. Bonaparte has also interpreted the similar foramen in the prootic of *Exaeretodon* as being for the vena capitus lateralis (i.e. its middle cerebral branch). Possibly, then, the trigeminal notch in the prootic of this advanced cynodont may not represent the prootic incisure as would naturally be supposed from comparing it with Karroo cynodonts but may instead be a notch in the anterior border of the lateral flange. If such is indeed the case, this cynodont has progressed well along the way toward a tritylodont braincase structure. This, then, adds another piece of evidence to the by now well-documented theory of Watson (1942) that the tritylodonts arose from gomphodont cynodonts. However, because of the apparently great degree of parallelism seen in late cynodonts, I do not believe that this resemblance necessarily indicates a particularly close relationship between *Exaeretodon* and tritylodonts.

COMPARISON WITH OTHER TRITYLODONTS

The braincase has been described in only two other genera of tritylodonts: *Oligokyphus* from a Liassic fissure fill in Somerset, England, described by Kühne (1956) and Crompton (1964); and *Likhoelia* from the Red Beds of Basutoland, described by Ginsburg (1961, 1962). The latter is close to and may be generically inseparable from *Tritylodon*. In all specimens of both genera the prootic is incompletely preserved and the epipterygoid is known, albeit imperfectly, only in *Oligokyphus*.

Kühne (1956, Fig. 13) and Crompton (1964, Fig. 4-6) have illustrated the "lateral lamina" of *Oligokyphus* as a laterally-directed, obliquely-oriented sheet with the more anteroventral part of the sheet turned more horizontally and extending forward below the trigeminal notch. Crompton (1964, Fig. 14) has restored the epipterygoid as contacting only this horizontally-oriented ventral part of the "lateral lamina." Comparison with *Bienotherium* indicates that Crompton's restoration is correct and that the horizontal part of the "lateral lamina" corresponds to the ventrolateral flange and the oblique upper part to the posterolateral flange in the Chinese form. The ventrolateral flange of *Oligokyphus* thus differs considerably from that of *Bienotherium* in that it extends well outward from the braincase, as it also does in cynodonts, rather than being a vertical sheet in continuity with the lower part of the braincase wall.

Both Kühne and Crompton appear to have correctly identified the pila antotica in *Oligokyphus*. Crompton (*ibid.*, p. 76) has speculated on the possibility of a trigeminal foramen completely surrounded by the prootic although he notes that there is no conclusive evidence for such a reconstruction because of the incomplete preservation of the anterior border of the prootic in the available specimens. He suggests, however, that the anteroventral corner of the prootic above the trigeminal nerve may have extended downwards and forwards in life towards the pila antotica to thus enclose the nerve. In *Bienotherium* (Fig. 3, 4B, C) the pila antotica lies medial to the outer wall of the braincase which is formed by the anterodorsal part of the prootic and the ventrolateral flange. In order for a closed trigeminal foramen to be formed in *Oligokyphus,* the anteroventral corner of the prootic above the trigeminus nerve would have to extend downwards, lateral to the pila antotica and the semilunar ganglion, to contact the anteromedial border of the "lateral lamina." *Oligokyphus* may have had such a closed trigeminal foramen, as suggested by Crompton, but the deep notch or damaged foramen in the prootic of all known specimens of this genus may equally well represent a venous foramen as occurs in *Bienotherium,* with the trigeminal notch having lain further forward in that part of the prootic which is not preserved.

In the beautifully preserved braincase of *Likhoelia,* Ginsburg (1962) has identified as part of the epipterygoid ("alisphénoide") a portion of the posterolateral flange which in *Bienotherium* is formed entirely by the prootic. The groove or foramen which Ginsburg has identified as the "orifice du nerf trijumeau" appears to be the depression for the semilunar ganglion with its outer wall broken away. On this interpretation, the ventrolateral flange is almost entirely missing in this specimen.

THE CAVUM EPIPTERICUM OF TRITYLODONTS AND MESOZOIC MAMMALS

The cavum epiptericum, as described by De Beer (1937, p. 430), is an extracranial space situated laterally to the side wall of the orbitotemporal region of the skull and medially to the processus ascendens of the palatoquadrate cartilage. It lodges the ganglia of the trigeminal and facial nerves and is traversed by their branches. In reptiles, including cynodonts (Figs. 5A, 6A), the cavum epiptericum is bounded medially by the pila antotica and laterally by the epipterygoid. In marsupial and placental mammals (Figs. 5D, 6D), according to De Beer (1937), the expanded alisphenoid (mammalian homologue of the epipterygoid) has incorporated the cavum into the bony skull. The pila antotica is no longer present and the boundary between the cavum and the cranial cavity is indicated only by the dura mater, in which, however, may be embedded isolated nodules of cartilage, possible remnants of the pila.

The mammalian alisphenoid has expanded back even further than has that of cynodonts so that it surrounds the mandibular ramus of the trigeminus, which pierces it via the foramen ovale. The maxillary branch may pass forward medial to the alisphenoid or it may pierce it.

In monotremes (Fig. 5C, 6C), the cavum epiptericum is especially well defined, for its medial wall is clearly indicated by the persisting pila antotica (taenia clino-orbitalis) (Goodrich, 1930, p. 269). The alisphenoid is a small ossification fused to the basicranium, its place in the side wall of the skull having been taken by a large anterior process of the periotic (processus anterior perioticus; Watson, 1916). This anterior process ossifies in the membrana spheno-obturatoria which forms the outer wall of

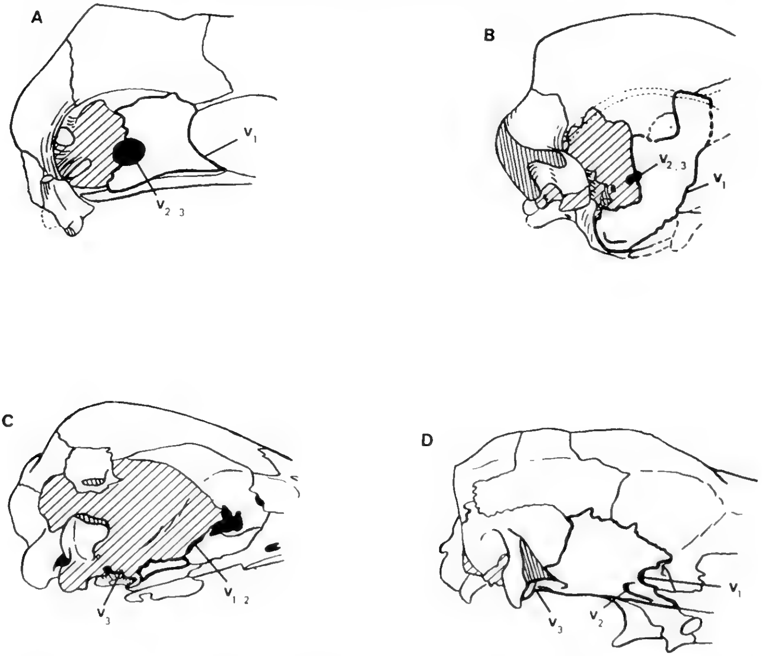

Fig. 5 Orbitotemporal regions of: A, *Thrinaxodon;* B, *Bienotherium;* C, *Ornithorhynchus;* D, *Didelphys.* Periotic indicated by oblique lines, epipterygoid-alisphenoid by heavy outline. Exits of branches 1 to 3 of the trigeminus nerve are indicated. (A after Parrington, 1946; C and D after Jollie, 1962.) Not to scale.

the cavum. It is notched ventrally to form with the basisphenoid a foramen pseudovale for the mandibular branch of the trigeminus nerve. The maxillary branch leaves the skull in front of the periotic process.

In the periotics of the Mesozoic mammals *Morganucodon* (see Fig. 8) and *Trioracodon,* described and figured by Kermack and Mussett (1958) and Kermack (1963), there is an anterior process pierced by a foramen pseudovale. This process is called the "anterior lamina" by these authors. On its medial side it bears a depression which Kermack interprets, undoubtedly correctly, as having housed the semilunar ganglion. Its ventral margin he interprets as forming a lateral flange of the sort seen in cynodonts.

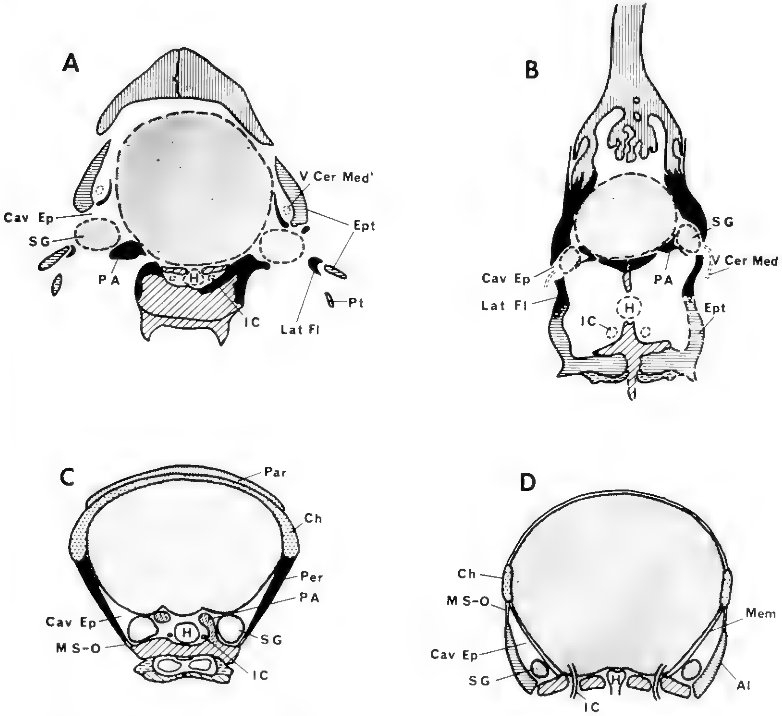

Fig. 6. Transverse sections across orbitotemporal regions of: A, *Thrinaxodon;* B, *Bienotherium;* C, embryo *Ornithorhynchus;* D, generalized therian mammal. Periotic indicated in black. In A and B the brain and other soft structures are restored in broken lines. Abbreviations on p. 29. (C modified from Watson, 1916; D modified from Goodrich, 1930.) Not to scale.

Kermack (1963) has given an extended discussion of the probable evolution of the braincase in Mesozoic mammals, based on the above-mentioned periotics and a sphenoid of *Triconodon* (earlier described by Simpson, 1928), with additional evidence provided by the braincases of late therapsids, notably *Oligokyphus.*

The anterior lamina of the periotic, according to Kermack's interpretation, is "an ossification within the wall of the neurocranium itself" (p. 97) which has grown forward internal to the alisphenoid. His explanation for this expansion is that the alisphenoid in advanced therapsids "played no part in the formation of the wall of the braincase proper, from which it is separated by the cavum epiptericum. In this condition, should an expansion and an extension forward of the brain occur in evolution, the corresponding ossification of the braincase to give it protection could only have been an ossification within the wall of the neurocranium itself: in other words a forward extension of the petrosal" (p. 97). As the semilunar ganglion comes to lie medial to the anterior lamina, as it does in monotremes, Kermack supposes that *part* of the cavum epiptericum must have been incorporated within the expanding braincase. Thus he interprets the cavum as having been subdivided by the formation of the anterior lamina, with part of it enclosed within the neurocranium and part of it left outside of the braincase proper but still medial to the alisphenoid. Kermack's conception, as understood here, of the braincase of a Mesozoic mammal such as *Morganucodon* is illustrated in Fig. 7A.

As *Oligokyphus* has a depression for the semilunar ganglion on the inner surface of its prootic, Kermack believes that the anterior lamina began to form at the therapsid structural level. *Oligokyphus* has a much wider "lateral flange" than have *Morganucodon* and *Trioracodon;* therefore, Kermack concludes that the space between the anterior lamina and the alisphenoid has become progressively narrower, undoubtedly as a result of brain expansion in the mammals. At some time above the Upper Jurassic the anterior lamina would come into contact with the alisphenoid, and "the cavum epiptericum would finally vanish" — squeezed out of existence by the expanding brain. At this stage one or the other of the two elements participating in the skull wall would be suppressed: in the monotreme line it would be the alisphenoid, in the therian line the anterior lamina. This basic differentiation of the braincase in the

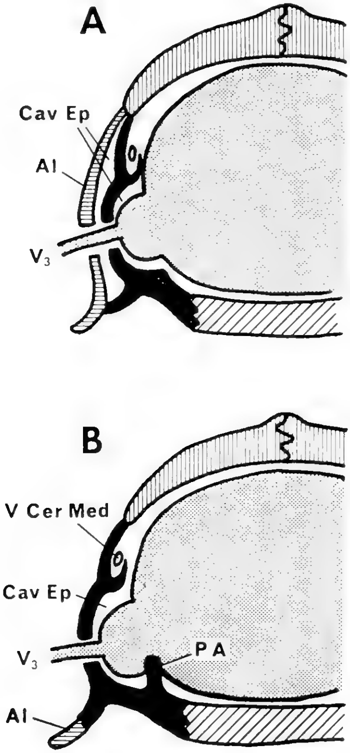

Fig. 7. Hypothetical transverse sections through the braincase of a Mesozoic mammal. A, Kermack's (1962, 1963) interpretation, as it is understood by the writer, in which the cavum epiptericum lies primarily lateral to the anterior lamina; B, the writer's interpretation, in which the cavum epiptericum lies medial to the anterior lamina and lateral to a persisting pila antotica. Periotic indicated in black. Abbreviations on p. 29.

two main higher categories of living mammals, the Prototheria and the Theria, need not have been accomplished until after the Late Jurassic.

Despite Kermack's belief that the anterior lamina is an ossification of the neurocranium, the origin of the processus anterior perioticus of monotremes as an intramembranous ossification strongly suggests a similar mode of origin for the anterior lamina of both tritylodonts and the Mesozoic mammals. With this in mind, a comparison of the periotics of *Morganucodon* and *Trioracodon* with the prootic of *Bienotherium* suggests the following interpretations of braincase structure in the Mesozoic mammals: (1) the lateral flange (probably the "anterior part" only) supported only a persisting quadrate ramus of the alisphenoid; (2) the ascending lamina of the alisphenoid lay primarily rostral to the anterior lamina, the entire anterior margin of which it probably contacted except perhaps at the foramen for the maxillary branch of the Vth nerve which may have lain between the two elements; and (3) the cavum epiptericum lay entirely *medial* to both the anterior lamina of the periotic (posteriorly) and the alisphenoid (anteriorly). Further, because of the primitive structure of the described braincases of Triassic aand Jurassic mammals, I believe they quite probably retained a pila antotica, as still persists in monotremes. In Fig. 7B, is illustrated my conception of the braincase of a Mesozoic mammal such as *Morganucodon.*

In Fig. 8, the periotic of *Morganucodon* (drawn from the stereophotograph in Kermack, 1963) is figured with the periotic (prootic + opisthotic) of *Bienotherium,* and a number of features in the former are reinterpreted in the light of information obtained from the latter. For a more complete discussion of the morganucodont periotic, see Kermack (1963).

In both genera the depression for the semilunar ganglion has a well-developed floor formed by a thin shelf of the periotic. In

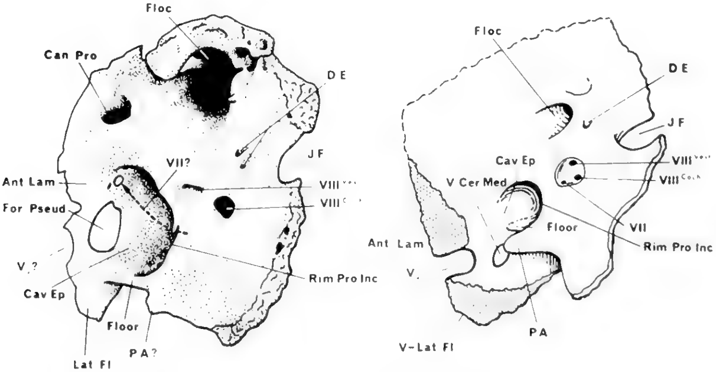

Fig. 8. Left: *Morganucodon.* (After Kermack, 1963.) Right periotic viewed medially and probably somewhat anterodorsally. Right: *Bienotherium.* Right periotic viewed medially and somewhat anterodorsally; details of internal auditory meatus added from *Oligokyphus;* stippling indicates areas of contact with epipterygoid. Not to scale. Abbreviations on p. 29.

cynodonts the space in which the semilunar ganglion lay is open ventrally, as is usual in reptiles. But, as noted above on p. 6, there is in *Thrinaxodon* a very slight hollowing of the posterior border of the prootic incisure, and it seems reasonable to assume that this hollow has been deepened in *Bienotherium* and *Morganucodon* by a relative forward movement of the neurocranial portion of the periotic both lateral to and below that part of the cavum epiptericum which housed the semilunar ganglion. This would account for the well-developed floor of this hollow and the fact that its lateral wall in *Bienotherium* clearly has the appearance of having been ossified in cartilage (see Fig. 4A), though further forward this wall seems to be an intramembranous ossification. The hollow has a semicircular medial border (*Rim Pro Inc,* Fig. 8) which corresponds to the medial border of the prootic incisure of *Thrinaxodon.*

As in a cynodont, the medial border of the prootic incisure of *Bienotherium* is terminated anteriorly by the pila antotica. In *Morganucodon* there is a short process in the corresponding location which may represent an ossified pila antotica (*P A*?., Fig. 8).

The anterior lamina and ventrolateral flange are much better developed in *Bienotherium* than in *Morganucodon.* In the tritylodont they broadly overlap the outer surface of the epipterygoid, which is a strong piece of evidence for their being intramembranous rather than neurocranial ossifications. The thin anterior part of the anterior lamina in *Morganucodon* which meets in front of the foramen pseudovale is also most likely to be an intramembranous ossification.

The differences in the foramina for the trigeminus nerve and the vena cerebralis media are such as one might expect in two forms at their respective evolutionary levels, with *Morganucodon* the more advanced in a mammalian direction.

As pointed out above, the "anterior lamina" of the periotic of monotremes is an intramembranous ossification within the membrana spheno-obturatoria which lies completely lateral to the cavum epiptericum. Goodrich (1930, p. 269) points out that the alisphenoid in therian mammals may also be partly ossified within the membrana spheno-obturatoria. In *Didelphys,* for example, the entire ascending lamina of the alisphenoid is ossified in this membrane (De Beer, 1937, p. 439). The ascending lamina of the epipterygoid of *Bienotherium* is a thin, solidly-ossified sheet of bone which, like the anterior lamina of the prootic, may have ossified at least partly intramembranously. If this is so, it might have been a matter of relatively slight functional and, perhaps, developmental significance if one element were to expand at the expense of the other.

The history of the monotreme orbito-temporal region, as interpreted here, has mainly involved the progressive extension forward of the periotic into the membrana spheno-obturatoria and the concomitant regression in front of it of the ascending lamina of the alisphenoid. *Morganucodon* and *Trioracodon* represent an intermediate structural stage in which there was still an ascending lamina of the alisphenoid, but in which the mandibular ramus of the trigeminus nerve was surrounded by the periotic. *Sinoconodon* (Patterson and Olson, 1961) possesses an alisphenoid, but the presence of an anterior lamina of the periotic cannot be determined in the single braincase referred to this genus.

Morganucodon, if it is indeed a docodont, and the Triconodonta and Monotremata are all generally acknowledged to be non-therian mammals (see Simpson, 1961), and the Tritylodontia are reptiles which almost certainly left no mammalian descendants. Therefore, the anterior lamina of the periotic as presently known occurs only in lines which did not lead to the living Theria. Inasmuch as nothing is known of the cranial structure of symmetrodonts or pantotheres, nothing can be said about the possible presence of an anterior lamina in the ancestry of the marsupials and placentals. I do not believe, as Kermack (1962, 1963) has argued, that the early ancestors of the Theria more likely than not did possess an anterior periotic lamina.

Concerning the therapsid ancestry of the different lines of early mammals, many of which appear to have evolved independently from a reptilian structural grade, the Cynodontia are the best candidates for the ancestry of those which possess an anterior periotic lamina. The presence of a lateral flange and various protective laminae (probably of membranous origin) overlying venous channels suggests that the prootic of cynodonts might easily have formed an expanded intramembranously-ossified anterior lamina. Indeed, in one descendant group, the Tritylodontia, it has actually done so. The common possession of cheek teeth with three main longitudinally-oriented cusps by carnivorous cynodonts, triconodonts, and *Morganucodon* lends support to this hypothesis. Ictidosaurs, which possess a lateral flange but not an anterior lamina, and bauriamorphs, which possess neither, would appear to be less likely ancestors for these mammals. Further speculation, however, must await the discovery of cranial material of symmetrodonts and pantotheres, and also of a greater variety of Upper Triassic therapsids than is presently known.

SUMMARY

The braincase of the Upper Triassic tritylodontid *Bienotherium yunnanense* (Therapsida; Reptilia) is characterized by: (1) the *anterior lamina,* a forward extension of the anterior portion of the prootic which overlaps externally the posterior margin of the epipterygoid; (2) the *ventrolateral flange,* a deep vertical sheet of the prootic which extends below the level of the braincase to contact the quadrate ramus of the epipterygoid and which is notched anteriorly for the exit of the second and third branches of the Vth cranial nerve and is penetrated by a small foramen for the vena cerebralis media; and (3) the *posterolateral flange,* a laterally directed process of the prootic which closes the pterygo-paroccipital foramen and is penetrated by a foramen for the vena capitus lateralis.

The ventrolateral flange is homologous with only the anterior part of the lateral flange of cynodonts. The posterolateral flange appears to be a composite structure, formed by: (a) the posterior part of the cynodont lateral flange; and (b) a special process developed in late cynodonts which lay above the channel for the vena capitus lateralis.

The anterior lamina of the prootic of *Bienotherium* lies lateral to the cavum epiptericum and is probably an intramembranous ossification rather than an anterior extension of the neurocranium. A similar condition is seen in the periotic of living monotremes. The notch in the anterior margin of the prootic is, therefore, not homologous with the prootic incisure of typical reptiles, which is a notch in the neurocranial part of the prootic.

Kermack's (1962, 1963) theories on the evolution of the mammalian braincase during the Mesozoic do not conform with what is known of the developmental anatomy of living mammals,

and are contradicted by the structure of the braincase in *Bienotherium*. It is probable that the cavum epiptericum in *Morganucodon* and *Trioracodon* lay entirely medial to both the alisphenoid and the anterior lamina of the periotic, and that both of these elements were largely ossified intramembranously. It is also likely that these Mesozoic mammals retained a pila antotica, as do monotremes.

The cynodonts appear to be the best candidates for the ancestry of those mammals which possess an anterior lamina of the periotic, i.e. morganucodonts, triconodonts and monotremes. No evidence exists as to the possible ancestry of the Theria.

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ABBREVIATIONS

Al	Alisphenoid
Ant Lam	Anterior Lamina
Bcr Pr	Basicranial Process of Prootic
Bo	Basioccipital
Bpt	Basipterygoid joint between Basisphenoid and Epipterygoid
Bs	Basisphenoid
Can Pro	Prootic Canal for Vena Cerebralis Media
Cav Ep	Cavum Epiptericum
Ch	Chondrocranial Wall
D E	Endolymphatic Duct
Eo	Exoccipital
Ept	Epipterygoid
Floc	Floccular Fossa
Floor	Floor of Depression for Semilunar Ganglion

For Pseud	Foramen Pseudovale
For S C	Foramen of Sinus Canal
Fr	Frontal
H	Hypophysis
I A M	Internal Auditory Meatus
I C	Internal Carotid Artery
J F	Jugular Foramen
Lat Fl	Lateral Flange
Mem	Membranous Side Wall of Braincase
M S-O	Membrana Spheno-Obturatoria
Op	Opisthotic
Orb Fiss	Orbital Fissure
Os	Orbitosphenoid
P A	Pila Antotica
Par	Parietal
Par Pr	Paroccipital Process
Per	Periotic
Pit	Pituitary Fossa
P-Lat Fl	Posterolateral Flange
Pro	Prootic
Ps	Parasphenoid
Pt	Pterygoid
P-T Foss	Post-Temporal Fossa
Pt-Par For	Pterygo-Paroccipital Foramen
Q Pr	Quadrate Process of the Paroccipital Process
Rim Pro Inc	Medial Rim of Prootic Incisure
S C	Sinus Canal
S G	Semilunar Ganglion of Trigeminus Nerve
So	Supraoccipital
Sq	Squamosal
V Cer Med	Vena Cerebralis Media
V C L	Vena Capitus Lateralis
Ven	Venous Foramen
V-Lat Fl	Ventrolateral Flange
$V_{1\text{-}3}$	Branches 1-3 of Trigeminus Nerve
VII	Facial Nerve
$VIII^{Coch}$	Cochlear Branch of Auditory Nerve
$VIII^{Vest}$	Vestibular Branch of Auditory Nerve
XII	Hypoglossal Nerve