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On the Evolution of the Mammalian Palate

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ON THE EVOLUTION OF THE MAMMALIAN PALATE

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I. Introduction

In spite of the fact that the possible homologies of the mammalian vomer have been under review for over fifty years, there still remain two strongly conflicting opinions. The original view that the paired "prevomers" of the reptile fused to form the single vomer of the mammal has been repeatedly attacked, and few writers maintain this homology to-day. Instead, it is usually believed that the mammalian vomer is a derivative of the reptilian parasphenoid, and that the reptilian "prevomers" are represented in the mammal only by the palatine processes of the premaxillae. But during the last few years doubts have been expressed about the validity of some of the evidence used, and it has been claimed that there is now good reason to return to the original homology.

Whether the mammalian vomer evolved from the parasphenoid or from the "prevomers" is not, in itself, a very important matter. But the current parasphenoid-vomer hypothesis is founded mostly on embryology, while the doubts of its validity have arisen from a consideration of recent palaeontological evidence, and the importance of the problem lies in the necessity of finding an explanation which satisfies both lines of evidence. To do this it has been necessary to re-examine both the facts and the lines of reasoning. The value of such an analysis lies in its promise to expose unreliable evidence and misleading methods.

In the first section of the following account the writers have attempted to give a concise summary of the available evidence on the problem, and the interpretations

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of other writers, and to resolve the apparent contradictions. It should be made clear that in this section no importance is attached to evidence about which there is any difference of opinion. It is the interpretation of some of the evidence which is held to be erroneous.

For the sake of clarity the terms prevomer and parasphenoid have been used in this section for the debated bones in the reptiles and lower vertebrates, and the term vomer only for the mammalian bone.

The consideration of the embryological evidence for the parasphenoid-vomer homology led to an examination of the current hypotheses concerning the homologies of the mammalian pterygoids which have also been claimed as derivatives of the reptilian parasphenoid. Here again there was a conflict between opinions based on embryology and those based on palaeontology, and it has been found possible to reconcile the two.

Finally, the revision of the homologies of these two mammalian bones makes it possible to discuss the probable stages by which the mammalian palate was derived from one similar to those of the advanced Theriodont reptiles, and to discuss these changes from the functional aspect. This section is much more hypothetical, and is offered as a basis for future discussion.

II. The vomer problem

(1) *Historical account*

Until towards the end of the last century morphologists had little hesitation in homologizing the mammalian vomer with the "paired vomers" of amphibians and reptiles. This was a natural interpretation in view of the relations of these bones and the fact that the "paired vomers" of reptiles may fuse and even support a false palate (Chelonia, Crocodilia).

The vomer of a mammal typically shows the following relations in the fully formed skull. It is a median element separating the true internal nares; it touches the premaxillae anteriorly, is clasped by the palatines posteriorly, and may touch the pterygoids; it lies antero-ventrally to the presphenoid region, and is normally quite anterior to the basisphenoid. Dorsally it clasps the nasal septum and ventrally extends towards the false palate.

The "paired vomers" of such a typical reptile as the lizard lie between the internal nares; they touch the premaxillae anteriorly, and are broadly in contact with the palatines postero-laterally; in unspecialized Reptilia they touch the pterygoids; they lie below the nasal capsules, mostly in front of the planum antorbitale, below the internasal septum, and have close relations with the paraseptal cartilages. They lie entirely in front of the basisphenoid, which is fused with the parasphenoid in the adult *Lacerta*.

The parasphenoid of the lizard is a membrane bone applied to the ventral surface of the basisphenoid; it is composed of a broad posterior plate, which extends laterally behind and ventral to the basipterygoid processes, and passes anteriorly into a narrow median processus cultriformis, which extends forward as far as the back of the orbits, below the interorbital septum and between the palatine rami of the pterygoids.

It will be clear from this account that the older morphologists, working on fully grown material, were justified in homologizing the mammalian vomer with the "paired vomers" in the reptiles. But Albrecht (1883) suggested that the homologues of the reptilian "paired vomers" were to be sought in the premaxillae; Bland Sutton (1884) found them in the anterior parts of the maxillae; while Parker (1885) regarded certain rudiments, which become the long palatine processes of the premaxillae in some mammals, as the equivalent of the reptilian "paired vomers". But the main argument of Bland Sutton, and of Smets (1885), was that the mammalian vomer is the homologue of the reptilian parasphenoid, or at least of its medial part. In 1895 Broom, in a paper dealing with Jacobson's organ and the relations of the neighbouring bones, argued that, since the Jacobson's organ of a lizard is undoubtedly homologous with that of such primitive mammals as *Ornithorhynchus*, their investing cartilages must be homologous, and also the bones which support them. This led to the conclusion that the "dumbbell" bone of *Ornithorhynchus*, already shown to be of paired origin by Wilson (1894) and Wilson and Martin (1893), must be homologous with the paired vomers of the lizard. It followed from this argument that the vomer of *Ornithorhynchus*, which developed behind the dumbbell, could only be the parasphenoid. Since the term vomer was to be used for the mammalian bone, Broom proposed the term "prevomers" for the paired or fused bones of lower forms. This term is now in general use; the homology of the palatine process of the premaxillae with the prevomers became accepted and also, though more slowly, the resulting parasphenoid-vomer homology. There has been little subsequent change in this embryological evidence. Support has been claimed in the discovery that the palatine processes in a bat *Miniopterus* (Broom 1895; Fawcett 1919) become separate from the rest of the bone, and in *Tatusia* (Fawcett 1921) ossify independently from the premaxillae and later fuse with them. But against this Green (1930) claimed that in a very young (122 mm.) embryo of *Ornithorhynchus* the dumbbell bone connected with the premaxillae by a thin thread of ossification. This was denied by de Beer and Fell (1936), though they admitted that both bones were enclosed in a continuous condensation of mesenchyme. The embryological evidence was summarized by Watson (1916):

> The most trenchant objection to the old view of the mammalian vomer lies in the "os paradoxum" of *Ornithorhynchus*. If the relations of a membrane bone to the chondrocranium mean anything in morphology, this bone is the fused prevomers. It is quite independent of the vomer, which hence cannot be homologous with the prevomers.

While the embryological evidence was being examined great progress was being made in the study of the Permian and Triassic Theriodontia, the reptilian order from which (it is generally agreed) the mammals evolved. Most of this work was done by Broom, who described numerous new forms, and by Watson, who was largely responsible for working out the basis for their classification into suborders, and for much of the detailed morphology. The Cynodontia, known since 1859, were admitted to be very close to the mammals in their general structure, and nobody hesitated to call the vomer-like bone of these forms the true vomer. Thus in his Croonian Lecture (1914) Broom said:

> In Cynodonts there is always a large median vomer which pretty certainly is the homologue of the mammalian vomer.

and

> Whether it ultimately turns out that the mammalian vomer is homologous with the paired vomers of most reptiles and the mammalian prevomer a neomorph, or that the dumbbell bone of *Ornithorhynchus* is the homologue of the lacertilian vomers, there can I think be little doubt that the Cynodont vomer is the homologue of the true vomer of the mammal.

The earlier suborders of the Theriodontia were less well known, and there were considerable differences of opinion as to the structure of the palate.

But about 1929 Broom discovered the parasphenoid in Theriodonts and in his book (1932) showed it fused under the basisphenoid in all the suborders, having the same position and relations as the parasphenoid of all typical reptiles.

That the bone should have remained unobserved for over forty years of critical study while it occupied its normal reptilian position illustrates the extent to which the parasphenoid-vomer theory dominated all observers' minds. They were seeking a bone in the snout in addition to the prevomers, and on several occasions its discovery in this region was announced—only to be denied later. Broom's discovery was immediately convincing because the bone was identical with the parasphenoid of all other reptiles. The discovery has been confirmed by sections made by Broom of a Gorgonopsid (1930) and of various Therocephalia (1936*a*), and independently by Parrington in a Cynodont (1933, 1935*b*), by Boonstra (1934*a*, *b*) in various Gorgonopsids and Therocephalia, and by Olson (1938) in a Gorgonopsid.

It is held by the present writers that the real importance of his discovery was overlooked by Broom. Instead of accepting the conclusion offered by what had now become a sound basis of direct evidence, Broom, assuming the problem to be already solved by embryology, interpreted the new evidence to fit the established theory. He called the Cynodont parasphenoid the vomer and, regarding the vomer-like bone as the product of the prevomers, and the Cynodont palatine processes as outgrowths of the premaxillae (for which there was by now good independent evidence), assumed the drastic reorganization required to evolve the mammalian skull (figure 1). If the parasphenoid-vomer hypothesis is correct, the palatine processes of the premaxillae of Theriodonts must have been abolished, and the specialized prevomers transformed into structures identical with them. At the same time the rostrum of the parasphenoid must have migrated forwards under the nasal septum, becoming fully disguised as the prevomers and acquiring identical major relations.

In 1933 Parrington called attention to the complete reversal of the evolutionary trends which the parasphenoid-vomer homology now implied. The resulting difficulty was ignored when Broom (1935) reviewed the whole question again. In this work Broom gave an account of the embryological evidence and added some account of the palaeontological data, but, as is shown later, without in any way meeting the new difficulties. Parrington later (1935*b*) illustrated the profound nature of the implied change by contrasting sagittal sections of a Cynodont and an Insectivore, in place of those of the Dicynodont and *Ornithorhynchus* used by Broom. The purpose of this was to compare forms as close as possible to the direct line of evolution rather than to compare the skull of a highly specialized type of synapsid reptile (admittedly aberrant) with that of a mammal which is so highly specialized that even the most recent critical work has failed to establish its relations with any other groups. In a review of recent work, Broom (1936*b*) admitted that Parrington's sections favoured the prevomer-vomer homology, but dismissed the matter by referring again to his own sections of specialized animals.

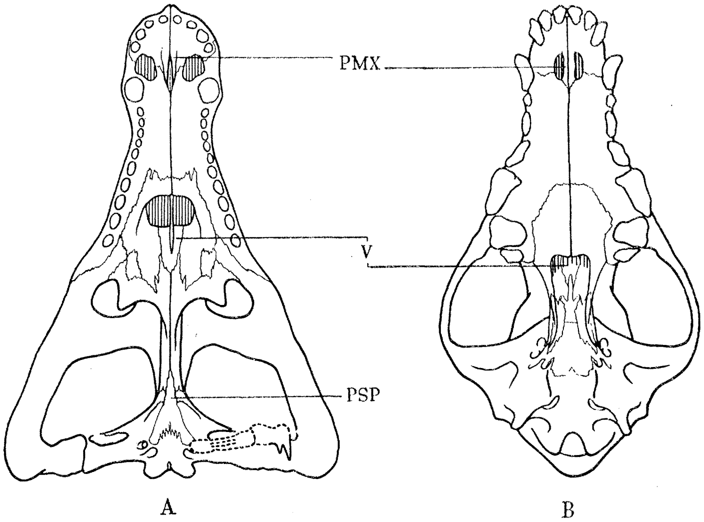

FIGURE 1. Palates of A, a Cynodont (*Cynognathus platyceps* Seeley, after Broili and Schröder), and B, a mammal (wolf). According to the parasphenoid-vomer theory, the palatine processes of the premaxillae (PMX) of the two forms are not homologous, nor are the vomers (V). Instead it is asserted that the mammalian palatine processes are homologous with the Cynodont "vomer", and the mammalian vomer is homologous with the Cynodont parasphenoid (PSP).

(2) *Palaeontological evidence*

For the purposes of this discussion it is necessary to consider only those forms which lie near to the line of evolution of the mammals. It is generally accepted that these are the Osteolepid fishes, the early Labyrinthodont Amphibia, the Cotylosaurs (in particular the Captorhinomorphs) and three orders of mammal-like reptiles—the Pelycosaurs, Theriodontia and Ictidosauria.

The palate in the Osteolepid Crossopterygians is best known from the work of Watson on *Eusthenopteron* (1926, p. 198, figure 4, and pp. 245 *et seq*.). A detailed anatomical study of some material of *Eusthenopteron* has been made by Jarvik (1937). The prevomers are fairly large tooth-bearing elements lying beneath the nasal capsules between the internal nares (figure 2A). The bones lie for the most part in front of the planum antorbitale, but send back thin pointed posterior processes which clasp the front of the parasphenoid. They are in contact anteriorly with the premaxillae, but may be separated from those bones mesially by a fossa apicalis (Jarvik 1937, figure 16). The primary upper jaw articulated with the planum antorbitale postero-laterally to the main mass of the prevomer. The dermal bones of the palate need little comment. The palatines and pterygoids meet the prevomers anteriorly, and the palatines form the postero-mesial margin of the internal nares. The basisphenoid lies far forward in the skull, and the basipterygoid processes are large scoop-shaped objects. The parasphenoid is a long narrow membrane bone applied to the floor of the interorbital septum and the basisphenoid. There is no development of lateral wings of the parasphenoid in the ordinary sense, though Romer (1937, p. 19) found it difficult to determine the lateral margin of the bone, and even reports a dermal sheath below the basipterygoid processes in the late form *Ectosteorachis* ("*Megalichthys*") *nitidus* Cope.

It is of some interest that Romer (1937, p. 22) records a mesial diverticulum in the walls of the nasal capsule of *Ectosteorachis*, which he suggests may have been occupied by structures homologous with the tetrapod Jacobson's organ.

The palate of the early Labyrinthodont Amphibia is best known from the work of Watson (1926, 1929). There are great differences in proportions in the skulls of Crossopterygians and Labyrinthodonts, as pointed out by Westoll (1938*a*, 1938*b*), but the morphological relationships of most of the palatal bones are very exactly maintained, as will be seen from figure 2A, B. The pterygoids, however, meet in the mid-line ventral to the anterior visible tip of the parasphenoid, and the interpterygoid vacuity is narrow. In those forms with a somewhat more open interpterygoid vacuity the paraphenoid is seen to extend farther forward, and in later Labyrinthodonts, in which the vacuities become steadily larger, the parasphenoid is clasped by the prevomers in the style of the Crossopterygians.

The structure of the palate of *Seymouria* is exactly comparable with those of the early Labyrinthodonts in which the interpterygoid vacuities are small (figure 2C). The main difference lies in the appearance of the vacuity in the palate for the jaw musculature, which has the shape more typical of the reptile, and cuts into the back of the ectopterygoid.*

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* A detailed account of the skull of *Seymouria* has been published since this paper was written (White 1939). The structure of the anterior part of the palate is shown to be rather more like that of *Baphetes* than the reconstruction used in this paper (figure 2C).

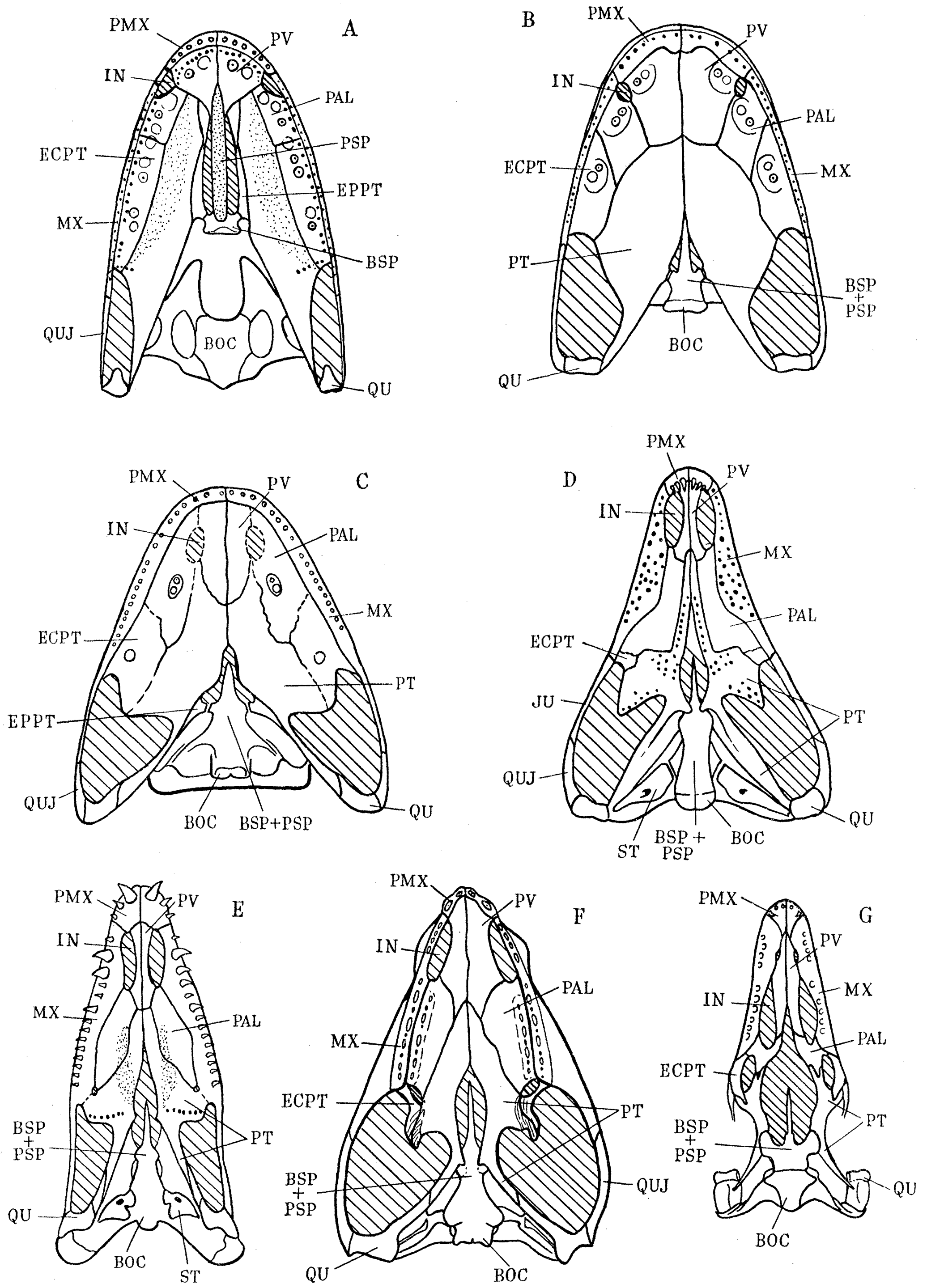

FIGURE 2. Palates of A, the Crossopterygian Fish *Eusthenopteron* (after Watson); B, the Labyrinthodont Amphibian *Baphetes* (after Watson); C, the primitive Cotylosaur *Seymouria* (after Romer and Watson); D, the Cotylosaur *Captorhinus* (after Romer); E, the Pelycosaur *Dimetrodon* (after Broom); F, the Rhynchocephalian *Sphenodon* (after Romer); G, the Lizard *Lacerta*.

BSP, basisphenoid; BOC, basioccipital; EPPT, epipterygoid; ECPT, ectopterygoid; IN, internal nares; JU, jugal; MX, maxilla; PAL, palatine; PMX, premaxilla; PSP, parasphenoid; PT, pterygoid; QU, quadrate; QUJ, quadratojugal; ST, stapes; PV, "prevomer".

In *Captorhinus* the structural pattern is only slightly modified; the prevomers are laterally compressed, but still separate the internal nares and retain the old relations to premaxillae, palatines and pterygoids. The parasphenoid is short, and apparently does not reach forward to the prevomers (figure 2D).

The mammal-like reptiles appear in the Lower Permian where they are represented by the Pelycosauria, an order which includes a number of genera very close in many features to the Captorhinomorph Cotylosaurs. These forms have been studied by many writers, notably Williston, Broom, Watson and von Huene, and there is no debate as to the identity of the palatal bones.

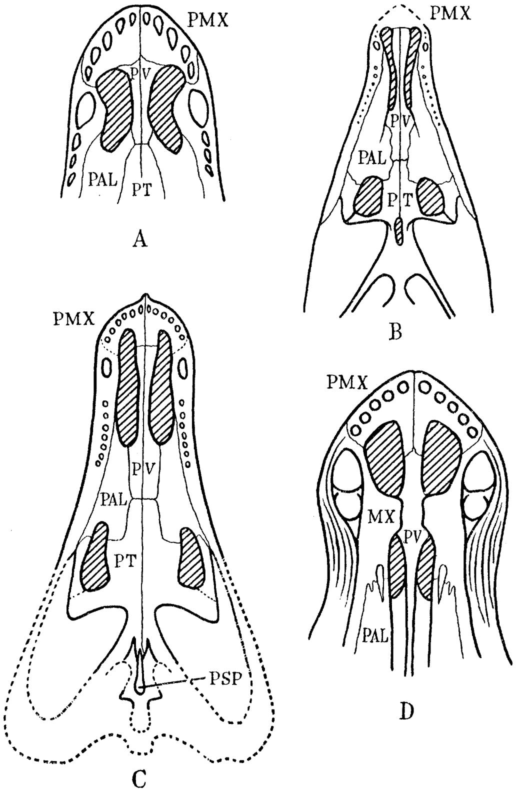

FIGURE 3. Palates of four Therocephalia to show evolution of "prevomers", palatine processes of the premaxillae, and false palate. A, *Scymnosaurus ferox* Broom (after Broom); B, *Ictidosuchoides longiceps* Broom (after Boonstra); C, *Pristerognathus minor* Haughton (after Broom); D, *Whaitsia* sp. mx, maxilla; psp, parasphenoid; pal, palatine; pmx, premaxilla; pt, pterygoid; pv, "prevomer".

A comparison of Broom's drawing of the palate of *Dimetrodon* (figure 2E) with those of more primitive Cotylosaurs on the one hand, and recent reptiles such as *Sphenodon* and the lizards on the other, illustrates the similarity of the bones and the certainty of their identifications (figure 2C–G). The prevomers are paired bones which divide the anteriorly placed internal nares and extend only a short distance backwards to meet the palatines and pterygoids. The parasphenoid is represented by the processus cultriformis, which projects forwards between the pterygoids, and a basal plate which is fused to the basisphenoid. The transition from this typical reptilian condition to a structure clearly resembling the mammals can be traced in the various suborders of the Theriodonts.

Identical prevomers are known in an early Theriodont, the Therocephalian *Scymnosaurus ferox* Broom (figure 3 A), but in the majority of Therocephalians the prevomers have grown backwards to meet the pterygoids at least half-way along the inner border of the palatines and in a few (e.g. *Scylacosaurus sclateri* Broom, and *Pristerognathus minor* Haughton (figure 3 C), etc.) the premaxillae have developed short palatine processes which project backwards between the internal nares. Our knowledge of the basisphenoid-parasphenoid complex of these forms is due to Broom and Boonstra, who have figured median sections which show that it projects forwards only a short distance (figure 3 B, C).

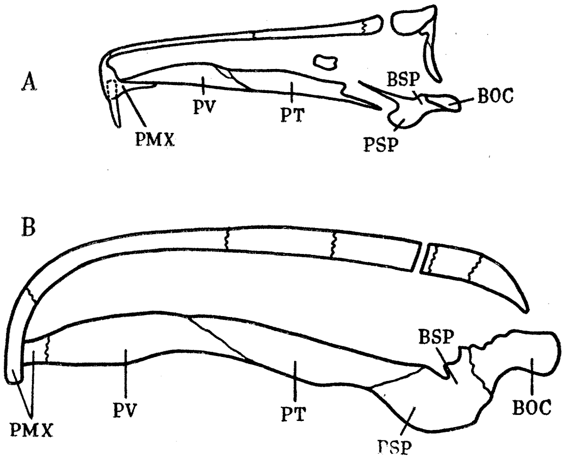

FIGURE 4. A, Diagrammatic median section of a Therocephalian skull, the anterior parts from sections of *Pristerognathus minor* Haughton, the posterior third from *Lycedops scholtzi* Broom (after Broom). B, Reconstructed median section of the Therocephalian *Theriognathus microps* Broom (after Boonstra).

BOC, basioccipital; BSP, basisphenoid; PSP, parasphenoid; PMX, premaxilla; PT, pterygoid; PV, "prevomer".

A few Therocephalia have developed a rudimentary false palate (e.g. *Whaitsia*, figure 3 D), and here the prevomers are fused and have a median septum which must have divided the nasopharyngeal passages, while the parasphenoid remains at the back of the skull (Broom 1932) (figure 4).

The Triassic descendants of the Therocephalia were the Bauriamorphs. In the two best-known forms, *Bauria cynops* Broom and *Ericiolacerta parva* Watson, there is a well-developed false palate formed by extensive processes of the premaxillae anteriorly and by the maxillae, or the maxillae and palatines, posteriorly (figure 5). In both forms the main component of the fused prevomers consists of a thin vertical sheet of bone which separates the nasopharyngeal passages and which extends backwards to form an extended plate almost exactly in the centre of the skull. In *Ericiolacerta* the prevomers have an expanded portion which forms part of the false palate (figure 5A). Recently Boonstra has shown that in *Bauria* the posterior end of the fused prevomers is grooved, and that the keel of the anterior end of the sphenethmoid lies in this groove exactly as the presphenoid-orbitosphenoid of the mammal rests in the mammalian vomer (figure 6).

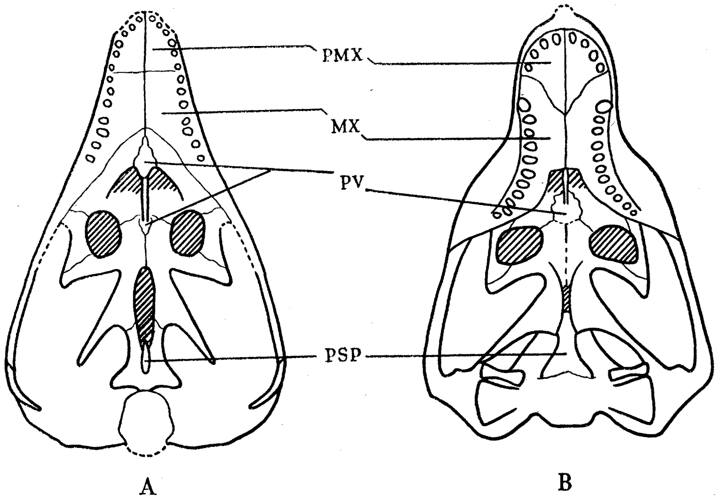

FIGURE 5. Palates of A, *Ericiolacerta parva* Watson (after Watson), and B, *Bauria cynops* Broom (after Boonstra), to show the false palate supported by the fused "prevomers" and the small size and posterior position of the parasphenoid in the Bauriamorphs. Lettering as in figures 3 and 4.

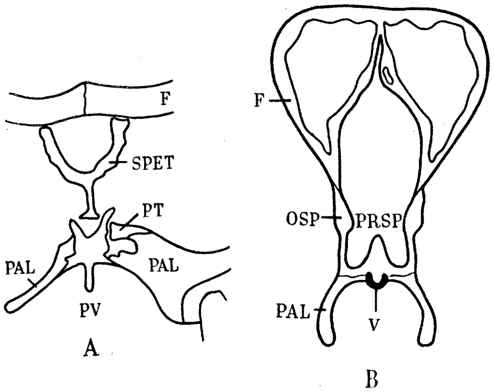

FIGURE 6. Section through the skulls of A, *Bauria* (after Boonstra), and B, a wolf, to show the relations of the "prevomer" and mammalian vomer to the sphenethmoid and presphenoid-orbitosphenoid respectively.

F, frontal; OSP, orbitosphenoid; PAL, palatine; PRSP, presphenoid; PT, pterygoid; PV, "prevomer"; SPET, sphenethmoid; V, vomer.

In both forms the parasphenoid is small and projects forwards only a short way into the interpterygoid vacuity (Watson 1931; Boonstra 1938). So far as the other Bauriamorphs are known they agree in essential points with these two forms.

In the Permian Gorgonopsia the premaxillae again have palatine processes projecting backwards between the internal nares (figure 7A). The prevomers, which are always fused, form an internasal bar, and extend posteriorly to meet the pterygoids about the centre of the palate, though the junction is hidden by the palatines which meet in the midline. The parasphenoid has the same structure as before and has been shown in section by Broom (1930), Boonstra (1934*a*) and Olson (1938) (figures 7B, 10B, C). The Triassic Cynodonts are generally believed to be descendants of the Gorgonopsia, though Boonstra has maintained that they are probably of Therocephalian origin. In them a false palate has been developed by the premaxillae, maxillae and palatines, and this is supported by a medium septum formed from the fused prevomers (figure 1A). The whole appearance of the structure of the anterior half of the skull is so like that of a mammal that it was not until Broom discovered the parasphenoid was still present at the back of the skull that there was any question as to the homologies of the vomer-like bone. The only drawings of medium sections so far published are those of Parrington (1935*b*) and Broom (1935). Both are of the Cynodont *Thrinaxodon liorhinus* Seeley, the former drawn directly from a sagittal section (figure 7C) and the latter restored from a series of transverse sections. The two differ but little, though Broom's section shows the parasphenoid extending rather farther forward and the prevomers extending rather farther backwards. Comparison with the Gorgonopsia shows that there is little, if any, difference in the relations of these bones in the two forms.

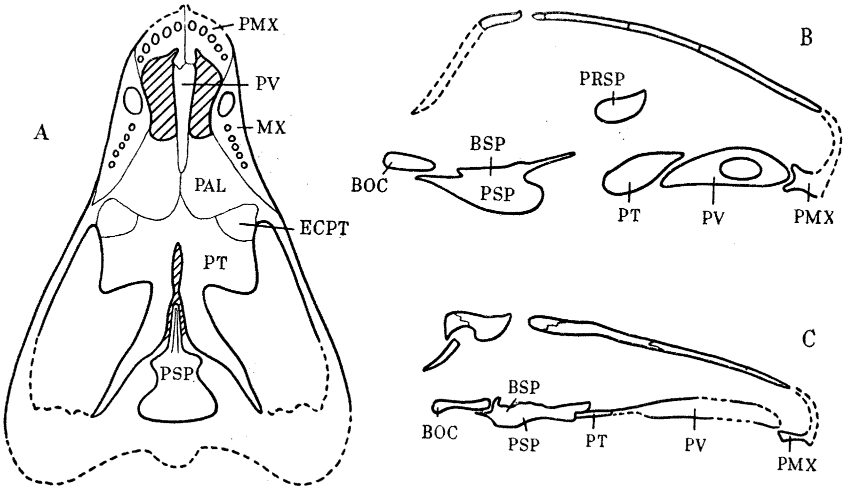

FIGURE 7. A, Palate of the Gorgonopsid *Cynarioides gracilis* Broom (after Broom). B, Reconstructed median section of *C. gracilis* Broom (after Broom). C, Median section of the Cynodont *Thrinaxodon liorhinus* Seeley (after Parrington). Lettering as in figures 3 and 4, with addition of ECPT, ectopterygoid; PRSP, presphenoid.

The order Ictidosauria was founded by Broom for two small reptiles from the Stormberg beds (Upper Trias) of South Africa, which appear to be closer to the mammals than any previously discovered form. They have not yet been described by their discoverer, Dr van Hoepen, and so can only be referred to as the Ictodosauria A and B as was done by Broom (1932).

These forms are more advanced than the Theriodonts in such features as the loss of the pre-frontal and post-orbital bones, the extreme reduction of the post-dentary bones of the lower jaw, and the structure of the palate.

According to Broom's figures specimen A shows nothing of the posterior part of the palate (figure 8A). Anteriorly there is a median process resembling the palatine processes of the premaxillae of Cynodonts, but which Broom labels "prevomer". Specimen B shows nothing of the snout, but posteriorly there is figured a bone, lying in the position of the mammalian presphenoid and vomer, which Broom claims is the true vomer derived from the reptilian parasphenoid (figure 8B). It differs from the Theriodont parasphenoid in that it does not extend below the basisphenoid posteriorly, and from the Theriodont prevomers in extending as far back as the basisphenoid. Unfortunately, the specimens are not very well preserved and their structures are difficult to determine. But assuming that the bone is a membrane bone, and is as figured by Broom, there is still no evidence that it is the parasphenoid which has migrated anteriorly rather than the prevomers which have continued their already well-established backward growth. To call the bone parasphenoid is to beg the whole question. But there is an even greater objection to this interpretation. When later (1935) Broom published a section of the skull, the position of the critical sutures of this bone are quite different (figure 8C). Here the parasphenoid is shown underlying the basisphenoid, and not extending so far forward as in the earlier figure. In fact, the section is an entirely hypothetical one, as is indicated by the dotting of the lines, and does not supply the critical evidence of the forward migration of the parasphenoid.

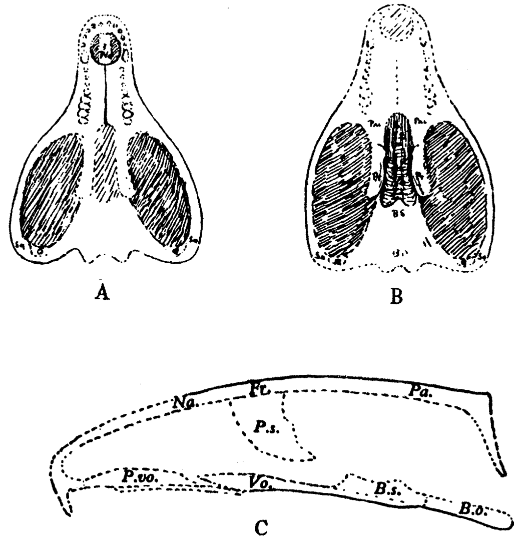

FIGURE 8. A, B, palates of the "Ictidosaurians A and B". C, hypothetical median section of an Ictidosaurian. (All from Broom.)

B.o., basioccipital; *B.s.*, basisphenoid; *Pal.*, palatine; *P.s.*, presphenoid; *Pt.*, pterygoid; *P.vo.*, "prevomer"; *Vo.*, "vomer" of Broom.

Broom's drawing of the palate suggests a different interpretation. The animal is a small one, and if, as might be expected from its advanced skeletal structures, the brain has become larger than that of its more primitive ancestors, then the "presphenoid" would have had to move down to provide the necessary accommodation. This would bring it in contact with the front of the basisphenoid (a position which it must reach sooner or later) and the hind end of the fused prevomers, resulting in a condition identical with that of a mammal by a very simple process. Once the "presphenoid" became attached to the basisphenoid there would no longer be any need of a parasphenoid for support, and it might be expected to disappear.

It is not argued that this interpretation provides good evidence for the prevomer-vomer homology. It is made to show that the Ictidosauria provide no evidence which supports the parasphenoid-vomer homology, and can, in fact, be interpreted just as easily to support the original view.

It will be seen from the foregoing account that the palaeontological evidence shows the gradual evolution of a skull which is very similar to that of a generalized mammal, the outstanding difference (apart from the structure of the ear) being the relatively small brain case of the Theriodont. There is general agreement about the identity of the bones in terms of those of more primitive forms, and the late Theriodonts were contemporaneous with *Tritylodon longaevus* Owen, the first known mammal.

If the problem of the origin of the mammalian vomer is considered solely from the palaeontological evidence, therefore, there can be no doubt that it is the product of the fused "prevomers" of their primitive ancestors.

(3) *Embryological evidence*

The embryological evidence for the parasphenoid-vomer theory rests largely on the assumption of the fixed relations of certain ossifications to the cartilages of the nose, but independent centres of ossification have also been used as indications of homologies.

It has been claimed that the "dumbbell" bone of *Ornithorhynchus* has the same relationships to the paraseptal cartilages as the prevomers of a lizard. The general law of the constancy of morphological relation leads naturally to the conclusion that the two ossifications must be homologous. If this is so, then it leaves only the parasphenoid of the lizard to account for the vomer of the mammal.

Now the rostrum of the parasphenoid of the lizard develops in the embryo just in front of the hypophysial fenestra and grows forwards, while the vomer of *Ornithorhynchus* appears below the nasal septum and grows backwards. This means that by assuming fixed relations for the prevomers, profound changes in relations are deduced for the vomers. In fact, the centre of ossification is held to have migrated so far forward that it is necessary for the bone to grow backward in order to occupy its final position (figure 9A, B). Moreover, it will be shown later that other important changes are implied if the paraseptal cartilages alone are used as guides to identification.

It is perfectly clear that there must have been a change of relations in at least one bone contributing to the nose, despite the general law of the fixity of relations,* and it becomes necessary to examine the value of the embryological evidence on which the parasphenoid-vomer theory rests. The logical course is to accept the explanation which involves the least change, particularly if this interpretation fits the palaeontological evidence and a reasonable explanation can be found for it.

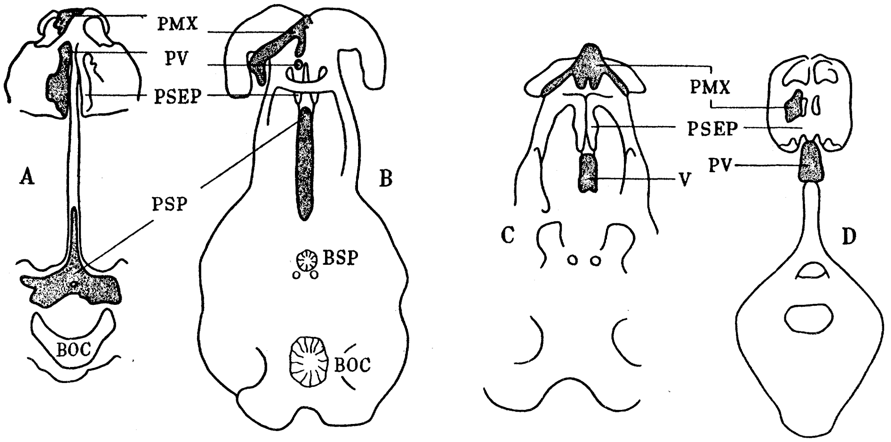

FIGURE 9. Simplified ventral views of embryos of A, *Lacerta* (47 mm.); B, *Ornithorhynchus* (122 mm.); C, *Ornithorhynchus* (28 mm.); D, the Chelonian *Emys* (11 mm. carapace-length). All figures simplified from de Beer (A after Gaupp, B and C after de Beer and Fell, D after Kunkel). In A and B the corresponding elements on the parasphenoid-vomer theory are indicated.

BOC, basioccipital; BSP, basisphenoid; PSP, reptilian parasphenoid, mammalian vomer; PMX, premaxilla; PSEP, paraseptal cartilage; PV, reptilian "prevomer", "os paradoxum" of *Ornithorhynchus*; V, mammalian vomer.

It is convenient to deal first with the use of centres of ossification as criteria in determining the independence, or the dual or single nature, of a bone. This is because, though widely held to be most unreliable by embryologists, it has constantly cropped up in discussions of this particular problem and has reappeared even in the most recent comments (Olson 1938).

First, the fact that the palatine processes of some mammals ossify from separate centres was the reason for regarding them as separate bones and the basis on which they were homologized with the prevomers. But de Beer (1937) says:

> The attempt might be made to define a bone according to embryological criteria as the product of a single embryonic centre of ossification, but this leads into serious difficulties. In the first place, many single bones may arise from more than one centre of ossification.

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* de Beer (1937, p. 494) says: "It is to be concluded from this discussion, therefore, that while morphological relations between different structures are remarkably constant, this constancy must not be taken as implying a hard and fast rule."

and

> The parietal in Man must, therefore, be regarded as affording evidence of the sub-division of an originally single bone, further examples of which are provided by the squamosal, tympanic, malleus, stapes, and certain Wormian ossifications in Man, or the suborbital and opercular ossicles in *Lepidosteus*.

and again

> In other words, *it is not possible to arrive at a satisfactory definition of what constitutes a bone along embryological lines, in terms of separate centres of ossification.* (Italics de Beer's.)

It is clear therefore that there are no reliable grounds on which the independence of the palatine processes in mammals can be asserted.

Again, in early papers much weight was placed on the fact that the vomer of *Ornithorhynchus* ossified from a single centre by comparing it with typical parasphenoids. The use of this argument was destroyed utterly when it was shown that the vomer of the allied *Echidna* ossified from two centres, particularly since this occurs also in other mammals (man, pig). Yet the argument has since been reversed and a double origin used as evidence in favour of the prevomer-vomer homology. Also quite recently it has been claimed that if two centres of ossification should be found in the parasphenoid of a Dicynodont reptile the whole problem would be solved (Olson 1938, p. 169).

Taking into account this history, and the considered opinions of such workers as de Beer, it is plain that paired or unpaired centres of ossification are valueless as criteria in this problem at least, and cannot be used for identifying homologues of either the palatine processes of the premaxillae or the vomer.

Since centres of ossification are useless in this problem, the only evidence provided by embryology is that of the relations of the debated bones to the surrounding structures, in particular to the cartilaginous neurocranium. The fact that the embryological evidence as interpreted by most previous writers is in direct conflict with the palaeontological evidence makes it important that comparisons should be made on as wide a scale as possible, both in regard to the number of forms which are compared, and also with regard to the number of "landmarks" which are used as points of reference.

Up to the present the embryological evidence has been drawn largely from a comparison of the embryos of *Ornithorhynchus* and *Lacerta*, but, since the form and relations of the mammalian vomer are undoubtedly associated with the formation of a false palate, it is worth while examining the structure of the nose in the Chelonia because in this group a false palate may be developed and there is no debate as to the identity of the premaxillae and prevomers.

The work of Kunkel shows that the prevomer of *Emys* develops from paired rudiments which soon fuse. It lies along the nasal septum and grows posteriorly towards the position of the parasphenoid. The prevomer has the normal reptilian relations to the palatines and pterygoids but ossifies *behind* the paraseptal cartilages. The premaxillae ossify on the ventral side of the nasal capsule, beneath the paraseptal cartilages. Hence if *Ornithorhynchus* is compared with *Emys* instead of a lizard, the law of fixity of relations implies that the monotreme "os paradoxum" is homologous with part of the premaxilla and the monotreme vomer is homologous with the reptilian prevomers. These homologies have been decided by exactly the same method as the parasphenoid-vomer homology (figure 9 C, D).

The important criterion used by embryologists is the relation of certain bones to the paraseptal cartilages and it is worth while calling attention to the consequences of accepting this evidence at its face value. The very different relations of the prevomer and palatine process of the premaxilla, and of the parasphenoid rostrum and the vomer, have already been mentioned (pp. 306, 317). Further, it should be pointed out that while the processus cultriformis of the reptilian parasphenoid is applied to the hinder part of the interorbital septum, the mammalian vomer clasps the lower margin of the nasal septum. If the relations of the prevomers and vomer to the floor of the nasal capsule are considered instead of the relations to the paraseptal cartilages alone, great morphological resemblances are found between them. The prevomers of the lizard, and in fact of all the non-mammals which have been considered, arise beneath the floor of the nasal capsule and extend only slightly, if at all, behind the lamina orbitonasalis. In the fully formed skull they lie between the internal nares and touch anteriorly the premaxillae, posteriorly the palatines and also, except in a few forms such as *Lacerta*, the pterygoids; and they may clasp the anterior tip of the processus cultriformis in Crossopterygians and Amphibia.

The mammalian vomer arises beneath the septum nasi; it may extend slightly behind the equivalent of the lamina orbitonasalis, and separates the anterior parts of the internal nasal passages. Anteriorly it touches the premaxillae, posteriorly the palatines and, in some forms, the pterygoids. In certain mammals it may even touch the anterior part of the basisphenoid.

These morphological relations of the reptilian prevomers and the mammalian vomer are so nearly parallel that it becomes necessary to examine the value of the paraseptal cartilages as criteria for homologizing the related bones, particularly since there are great differences between the paraseptal cartilages of *Ornithorhynchus* and those of a lizard.

In the lizard the paraseptal cartilages are long and extend posteriorly as far as the lamina orbitonasalis. The first stages of the ossification of the prevomers have not been figured, but at an early stage the bones lie along the whole length of the paraseptal cartilages. In *Sphenodon* Howes and Swinnerton have figured an early rudiment under the most *posterior* part of the paraseptal cartilage. On the other hand, in *Ornithorhynchus* the paraseptal cartilages are very greatly abbreviated and extend back only a short way from the "lamina transversalis anterior" towards the hinder part of the nasal capsule. The vomer begins to ossify beneath the septum nasi, *in front of* the planum antorbitale, but behind the paraseptal cartilages. The "dumbbell" bones ossify beneath the most anterior part of the paraseptal cartilages; according to Green they are co-ossified with the premaxillae, and though de Beer and Fell deny this, they admit that the premaxilla and "dumbbell" bone ossify from the same mesenchyme condensation. In some other mammals, particularly *Dasyurus* (see Fawcett 1917, 1918, 1919), the paraseptal cartilages have a more extensive posterior development, and it is found that in early stages the vomer is related to the posterior parts of the paraseptal cartilages, while the palatine processes of the premaxillae have come into relation with the most anterior parts.

Two points are clear. The abbreviated paraseptal cartilages of *Ornithorhynchus* and other mammals cannot be used as criteria of homology of related elements without paying strict attention to other features; and the relationships of the cartilage to the vomer and palatine processes of the premaxillae are equivocal, and do not provide the evidence necessary for the establishment of either the parasphenoid-vomer homology or the prevomer-palatine homology.

If, instead of relying entirely on relationship to the paraseptal cartilages, the developmental relationships of the various ossifications of the palate are considered to each other and to the nasal capsule as a whole, the conclusion that the reptilian prevomers are homologous with the mammalian vomer is inescapable.

(4) *Discussion*

The approach to the vomer problem may be made by way of the study of adults, of fossil forms, or of early growth stages; but in each case the interpretation of the evidence depends on the principles of comparative anatomy. The first method, which is the oldest, suffers from several disadvantages, notably the lack of living forms intermediate between organisms which it may be desirable to compare, and the frequency with which such structures as bones lose their individuality in the adult. The palaeontological method provides a series of individuals which may be arranged in order of their geological age, and from this it may be possible to work out many stages showing a gradual change from one structural pattern to another. The disadvantages to this method lie in the fragmentary, crushed or disturbed nature of most fossils, which necessitates more or less uncertain reconstruction and arduous preparation, and in the great gaps in the geological record of any group. The approach by using the techniques of embryology is very important, since the thin serial sections demonstrate the mutual relations of many of the structural parts with great clarity. But to be of great use it is often necessary to study many growth stages of an animal, and the method is open to the same fundamental objection as the study of adult living material, that intermediate forms between interesting structural patterns may not be available. Further application of embryological studies can only be made by using extraneous assumptions, such as some variety of the Biogenetic Law, and this in particular has been greatly discredited of late. But in spite of the growing opposition among embryologists to the recapitulation theory, some of the deductions which many embryologists make from their studies are implicitly based on its acceptance; thus the conditions found in the early stages of development of bones in mammals may not only be compared with those of other vertebrates, but are often treated uncritically as evidence of some ancestral conditions.

In the matter of the vomer problem, it has been shown that the palaeontological evidence is in accordance with a perfectly straightforward series of changes in the Theriodont reptiles. The prevomers fuse, and come to support the secondary palate in a manner indistinguishable from that of the mammalian vomer; the palatine processes of the premaxillae become more important, and attain mammal-like proportions; and the parasphenoid remains in its normal reptilian position fused to the basisphenoid, becomes reduced in some of the later Theriodonts, and is apparently lost in most mammals (see below).

The embryological evidence for the parasphenoid-vomer theory is shown to be very unsatisfactory. On the contrary it is argued that the evidence shows that the prevomer of reptiles and the vomer of mammals have the same morphological relationships at early growth stages if reference is not confined to the variable paraseptal cartilages. The methods of the comparative embryologist are based on the relationship of structures to nerves, blood vessels, cartilages, etc., which are presumed to be invariable; all that is claimed here is that the paraseptal cartilages in *Lacerta* and mammals cannot be regarded as reliable guides in this problem.

Broom (1935) has attempted to co-ordinate the evidence of embryology and palaeontology by dotting in the presumed position of Jacobson's organ in sagittal sections of a Gorgonopsid and a Therocephalian. But he ceased to do this just when the attempt becomes illuminating. The position is not indicated in the section of a Cynodont, presumably because, as Broom remarks, the prevomers have lost the lateral processes which supported Jacobson's organ and the organ itself may have been lost.

But the attempt is worth making since, *because the whole of the Cynodont nose is underlain by the premaxillae and maxillae, it follows that, if Jacobson's organ were present, it must have been underlain by one of them.* The obvious conclusion is that Jacobson's organ remained in approximately the same position that it occupies in all living mammals which possess it, and so was supported by the palatine processes of the premaxillae in the absence of lateral wings of the prevomers. This conclusion fits precisely the interpretation of the palatine processes of the mammal as homologous with the similar processes of the Theriodonts, and the identification of the dumbbell bone of *Ornithorhynchus* as fragments of the premaxillae is actually strengthened.

Some difficulties remain to be cleared up. Of these, undoubtedly the most pressing is the apparent support for the parasphenoid-vomer homology afforded by Broom's median longitudinal sections of *Dicynodon* and *Ornithorhynchus*. Without confirmatory evidence this comparison would hardly be sufficient basis for any theory, since both forms are very highly specialized, especially in palatal structures. Important characteristics of the Anomodonts, compared with other Synapsids, are the great shortening of the snout and the extension of the postorbital region, coupled with the great specialization of the premaxillae. The very great resemblance in snout proportions between a Gorgonopsian, Therocephalian or Cynodont and a mammal suggest that comparison should be made between these forms and a typical mammal, as Parrington has already done. Since the sagittal section is hardly affected by the formation of a secondary palate, it is permissible to consider any of these animals in the comparison. In all three Theriodont groups the pterygoids meet in the mid-line, which they do not in general in mammals; accordingly if the pterygoids (and palatines) are removed from the sagittal sections of, say, the Gorgonopsians *Cynariops robustus* (from Olson 1938, figure 3) and *Cynarioides gracilis* (from Broom 1930, plate 34, figure 35), the composite Therocephalian figured by Broom (1936 *a*, plate 8, figure 108), the Cynodont *Thrinaxodon* (from Parrington 1935 *b*, figure A) and the Anomodont *Dicynodon* (from Broom 1926, figure 1), it becomes possible more closely to compare the structures (figure 10 A–E) with those of various mammals from which the bones of the secondary palate have also been omitted (figure 10 F–K). When this is done the very clear similarity in the relations of the prevomer of the Theriodont and the vomer of the mammal becomes obvious. Since the *Dicynodon* condition is a very specialized one among the Synapsids, it may be pointed out that the parasphenoid rostrum extends only a little farther forward in the skull of that animal. In most Synapsids the processus cultriformis extends anteriorly beneath the posterior parts of the frontals, and the "sphenethmoid" elements lie beneath the frontals. Sollas and Sollas (1913, figure 5) have shown that in *Dicynodon* the anterior tip of the parasphenoid (which they regarded as basisphenoid) reaches as far as the most anterior part of the frontal, while Broom (1926) shows it underlying the hinder part of the nasal; the "sphenethmoid" elements retain their normal position. The prevomers in all forms lie ventrally to the main part of the nasal and the anterior parts of the frontal—the usual position of the mammalian vomer.

The conditions in *Ornithorhynchus* are also easily compared with more normal standards when it is realized that the vomer grows backwards during development; if the relations of the palatine bones be taken into account in *Dicynodon* and *Ornithorhynchus* the change in proportions becomes obvious (see figure 10).

The separate ossification of the palatine processes of the premaxillae is another important point which has to be accounted for. It is obvious that there is a general tendency for this separate ossification in mammals, for it has been reported in many genera; but *Ornithorhynchus* is remarkable in that the palatal processes remain separate in the adult as the "dumbbell bones". (In *Miniopterus* similar elements are secondarily detached.) There has been controversy over the real origin of the dumbbell bones; Green (1930) has indicated their connexion with the premaxillae by thin threads of ossification, but this has been denied by de Beer and Fell (1936), who, however,

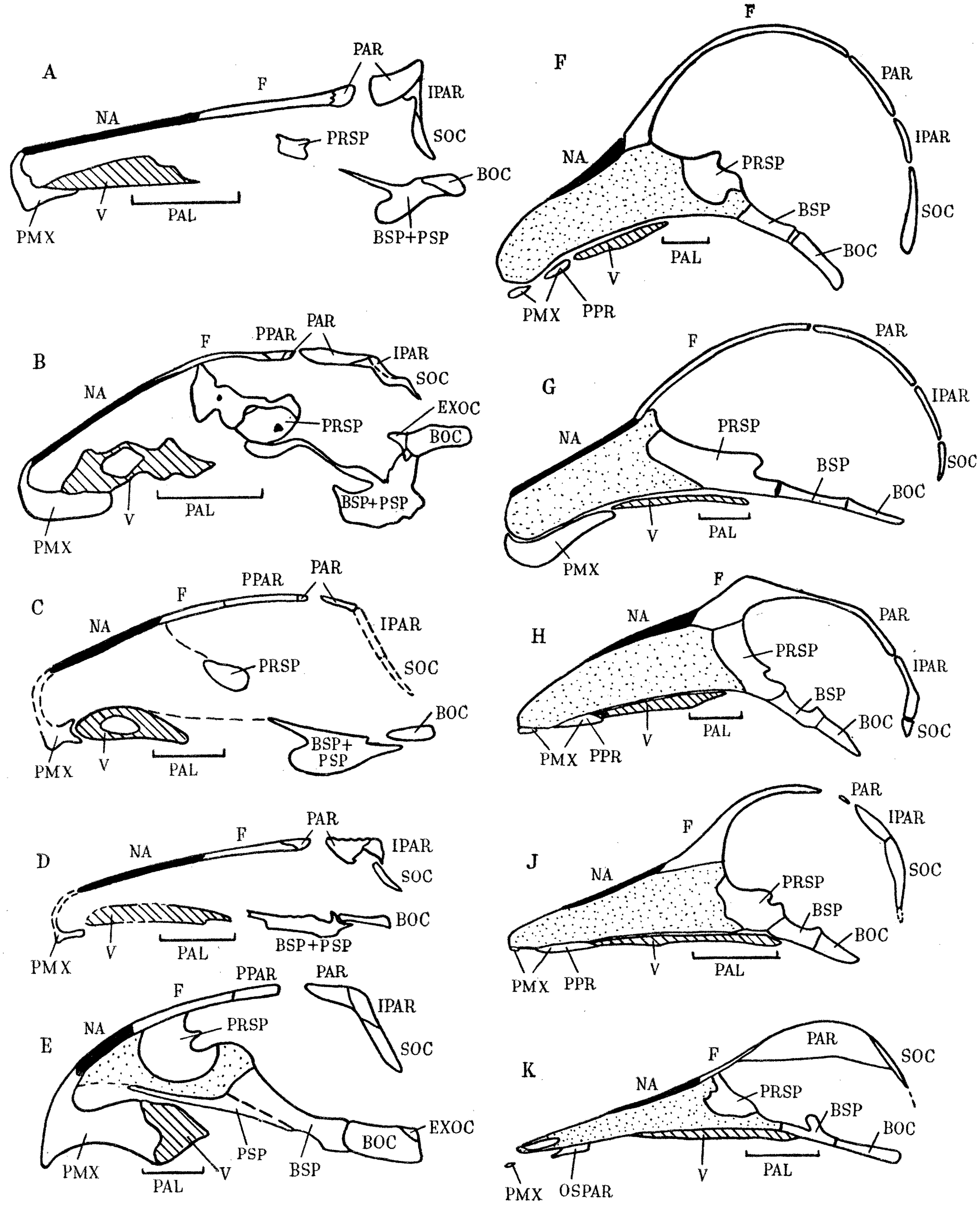

FIGURE 10. Median sections of Theriodonts (A–E) and Mammals (F–K) to demonstrate relations of the "prevomer" and vomer to the basis cranii. A, Therocephalian (compound—after Broom). B, *Cynariops*, a Gorgonopsian (after Olson). C, *Cynarioides*, a Gorgonopsian (after Broom). D, *Thrinaxodon*, a Cynodont (after Parrington). E, *Dicynodon*, an Anomodont (after Broom). F, Foetus of *Ovis* (after Broom). G, Pouch-young of *Macropus* (after Broom). H, Young *Cavia* (after Broom). J, Foetal *Bos* (after Broom). K, Young *Ornithorhynchus* (after Broom). In all cases any exposures of maxillae, palatines or pterygoids in the sections have been removed, but the approximate extent of the palatine is projected below each section.

BOC, basioccipital; BSP, basisphenoid; EXOC, exoccipital; F, frontal; IPAR, interparietal; NA, nasal; OS PAR, os paradoxum; PAR, parietal; PAL, palatine; PMX, premaxilla; PPR, palatine process of premaxilla; PPAR preparietal; PSP, parasphenoid; PRSP, presphenoid; SOC, supraoccipital; V, "prevomer" in Theriodonts, vomer in mammals.

admit a common mesenchyme condensation. The separate existence of the bones in the adult is very easy to understand. At the 28 and 122 mm. stages described by de Beer and Fell, the premaxillae are well ossified, meeting in a strong symphysis which bears the "os carunculae" and egg tooth. In the adult animal the symphyseal region has been resorbed, and the isolation of the palatine processes would follow directly. The frequent existence of separate ossification centres in the palatal processes of the premaxillary of mammals is not, in itself, good evidence that these parts represent once separate elements; in the pig (as summarized by de Beer 1937, p. 336) the maxilla ossifies from no less than five separate centres including two in its palatine process. In point of fact fragmentation of dermal bones is rare and the assumption that it occurs in *Ornithorhynchus* must be based largely on the relative simplicity of the resulting interpretation, set against the difficulties which arise if it is denied. There is some precedent to be found in the parietals of man which, unlike those of other mammals, ossify from two pairs of centres which occasionally fail to fuse in the adult.

So far evidence about which there is important difference of opinion has been avoided or discarded, but there is one set of observations which takes on a new importance at this stage. A slender splint of membrane bone, lying well behind the vomer and closely applied to the basisphenoid, has been recorded by Parker (1885, plate 37, figures 6, 8; plate 38, figure 7; plate 39, figure 8; see also p. 260) in *Galeopithecus* "*phillipensis*", and its presence has been confirmed by van Kampen (1922, p. 54). Both authors regard the bone as a parasphenoid. Fuchs (1910, p. 48, figure 14) has figured a similar parasphenoid in *Didelphys*. Neither Broom nor Töplitz found this element, but its existence has been reaffirmed by van Kampen (1922, p. 54). The relations of this slender element are entirely in favour of its homology with a typical reptilian parasphenoid, since it is applied to that part of the basisphenoid which in certain mammals is perforated by a hypophysial foramen (figure 11). It is clearly greatly reduced, and is no doubt very sporadic in its distribution; *Galeopithecus volans* seems to lack the bone, according to Parker (1885), and it is quite likely that it is present, if at all, only in certain individuals of any species of mammal. It is not unlikely that it could be found in other mammals by systematic searching, because the erroneous homologization of the mammalian vomer has diverted attention from this part of the roof of the mouth.

Bones known as "vomers" or "prevomers" occur in other groups of vertebrates besides those which have been considered. They are often paired elements, applied to the ventral side of the nasal capsule, and having the normal relations of the "prevomer" of primitive reptiles to the palatines, pterygoids and parasphenoid. Thus the Osteichthyes, with the exception of sturgeons and Teleostei, have a paired vomer, homologous with the so-called "prevomer" of non-mammalian tetrapods, and with the vomer of mammals. In *Acipenser* and Teleostei there is a median vomerine bone, which occasionally shows signs of a paired origin, and which may be regarded without doubt as homologous with the vomer.

The Amphibia need little comment; the so-called "prevomer" is certainly homologous with that of reptiles, and with the mammalian vomer. In Urodeles there is usually a long posterior tooth-bearing extension the development of which has been studied by Wintrebert. In *Salamandra* it extends very far back in the adult; but the bone is essentially a sheet applied to the floor of the nasal capsule.

The reptile "prevomers" are all easily homologized with the Synapsid "prevomer", and thus with the mammalian vomer. In Placodonts, Chelonia, etc., the bones are fused to form a median element which preserves the normal morphological relationships.

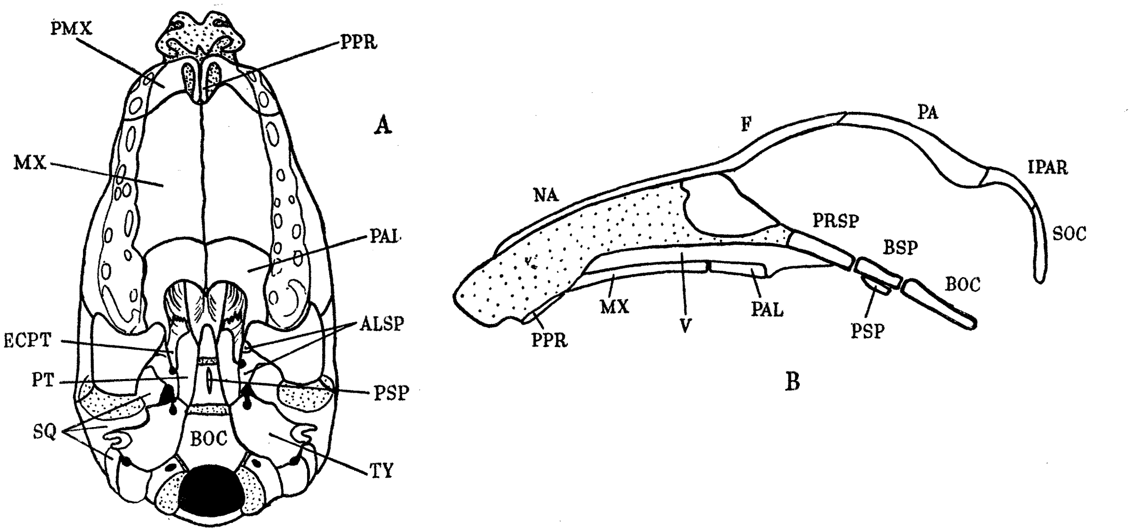

FIGURE 11. Young *Galeopithecus "phillipensis"* to show two pairs of pterygoids and the splint of bone representing the parasphenoid. A, palatal view; B, median section. (Both after Parker.)

ALSP, alisphenoid; BOC, basioccipital; BSP, basisphenoid; ECPT, ectopterygoid; F, frontal; IPAR, interparietal; MX, maxilla; NA, nasal; PSP, parasphenoid; PA, parietal; PAL, palatine; PMX, premaxilla; PPR, palatine process of premaxilla; PRSP, presphenoid; PT, pterygoid; SOC, supraoccipital; SQ, squamosal; TY, tympanic; V, vomer.

The birds show great variety in their palatal structure; the frequent separate ossification of the parasphenoidal rostrum and the lateral wings (basitemporals) might be used as evidence in favour of the parasphenoid-vomer homology, but the "prevomers", whenever they are certainly present, have normal relationships so far as they are allowed by the special modifications of skull-structure in the group.

It may be concluded, therefore, that there is full and satisfactory evidence that the elements now usually called "prevomers" in non-mammals are homologous with the mammalian vomer, and the former term must be discarded.

Finally the opinion of some leading morphologists may be mentioned. In his recent summary of the parasphenoid-vomer theory Broom (1935) claims the support of Goodrich, Watson, Gregory and von Huene, and quotes extensively from two of them. These remarks and quotations are most misleading. To the ordinary reader the support of four such eminent morphologists gives an overwhelming verdict in Broom's favour. But their opinions were formed and the passages quoted were written before the discovery of the parasphenoid in the Theriodonts, a discovery which, the writers maintain, has not only altered the whole position but has actually solved the problem by supplying the required direct evidence. Thus Goodrich (1930, p. 369), in the middle of his account of the problem, says, "Already in the more mammal-like Theriodontia the prevomers and parasphenoid assume much the same form and position as the premaxillary processes and median vomer of the mammal respectively", and he illustrates this from one of Broom's early figures in which reptilian prevomers are labelled "vomer", as the present writers maintain they should be.

It is to be hoped that these authorities will reconsider the problem, and, if possible, publish their opinions in the light of the recent evidence in order that one of the oldest problems in morphology may be satisfactorily settled.

III. The pterygoid problem

(1) *Historical account*

According to the scheme of homologies accepted by de Beer (1929, 1937, p. 435) the rostrum of the reptilian parasphenoid is represented by the mammalian vomer, and the wings of the parasphenoid of the lizard, or the equivalent "basitemporals" of the crocodile or bird, are represented by the "mammalian pterygoid" of monotremes, and by the main part of the pterygoid of other mammals. At first sight this is reasonable, since the "mammalian pterygoids" and vomer, taken together, do bear a certain general resemblance in shape to the parasphenoid of such a reptile as *Lacerta*. Moreover, it has been pointed out that the Vidian nerve passes between the "mammalian pterygoid" of monotremes, or the pterygoid of ditrematous mammals, and the basis cranii (Gaupp, de Beer), and this condition may be compared with that found in *Lacerta*, *Crocodilus*, etc., where the palatine nerve and internal carotid artery pass through a parabasal canal between the lateral wing of the parasphenoid (or basitemporal) and the basisphenoid.

Since it has been shown that the true homologue of the mammalian vomer is to be found in the reptilian "prevomers" and not in the parasphenoid, it becomes necessary to re-examine the validity of the homology of any mammalian pterygoid element with the wings of the reptilian parasphenoid. According to the evidence reviewed by de Beer, the apparently simple pterygoid of many ditrematous mammals ossifies from two distinct centres: a dorsal plate of membrane bone, and a ventral element which often arises from a nodule of cartilage, believed to be secondary cartilage. de Beer homologies these elements respectively with the "mammalian pterygoid" and "Echidna pterygoid" of the monotremes; but many different schemes of homology between mammals and reptiles have been set out by other workers, and are reviewed in tabular form by de Beer (1937, p. 436). The main homologies that have been proposed, so far as they affect this discussion, are set out below (for references see de Beer 1937):

A. Ditrematous mammal and Reptile.

Mammal's pterygoid =
- (*a*) Lateral wing of parasphenoid (Gaupp).
- (*b*) Reptilian pterygoid (Broom, Watson, Fuchs, Parker, van Kampen).
- (*c*) Lateral wing of parasphenoid + reptilian pterygoid (de Beer).
- (*d*) Ectopterygoid (= transverse) (Watson 1911).

B. Monotreme and Reptile.

"Mammalian pterygoid" =
- (*a*) Lateral wing of parasphenoid or basitemporal (Gaupp, van Kampen, de Beer).
- (*b*) Reptilian pterygoid (Watson, Broom).

"*Echidna*-pterygoid" =
- (*a*) Reptilian pterygoid (Gaupp, van Kampen, Fuchs, de Beer).
- (*b*) Epipterygoid (Watson).
- (*c*) Ectopterygoid (Transpalatine) (Broom).

(2) *The evolution of the pterygoids*

The palate of certain Crossopterygian fishes is now known through the work of Watson (1926, pp. 198, 245); the resemblance to that of early Labyrinthodonts is very strong, and the individual bones of the latter can be recognized without difficulty in the fish. Their relations to the premaxillae, maxillae, parasphenoid, prevomers and internal nares are identical (figure 2A, B). The extraordinary difference in proportion has been noted by Romer (1937, p. 46), and by Westoll (1936, p. 166, 1938*b*); certain Devonian forms afford a good series of links (Westoll 1938*a*).

In the early Labyrinthodonts the palate is extensively ossified. The parasphenoid covers the ventral side of the basisphenoid, and extends forwards, in front of the basipterygoid processes, in the narrow interpterygoid vacuity (figure 2B); in the Carboniferous Embolomeri it seems to have been covered anteriorly and ventrally by the pterygoids, but in later forms, in which interpterygoid vacuities are broad, it clearly extends to the vomers. There are well-marked basipterygoid processes on the basisphenoid in early forms, making articulation with the epipterygoid; in later forms the pterygoid and parasphenoid meet in immovable sutural contact below this palatobasal articulation. The remaining dermal bones need no comment. The epipterygoid is an ossification of the cartilaginous upper jaw, and rests on the dorsal side of the pterygoid. Typically it rises towards the parietals, and may have three processes, the basal process (articulating with the basipterygoid process of the basisphenoid), the ascending process, and what Sushkin called the "processus prooticus". The profundus nerve (V_1) passed between the basal and ascending processes, while V_2 and V_3 passed between the ascending and pro-otic processes (Sushkin 1927, p. 272). The ramus palatinus of VII passed ventral to the basal process, and in advanced Labyrinthodonts was covered ventrally by the parasphenoid, near the suture with the pterygoid. Anteriorly, it certainly passed dorsally to the posterior margin of the vomer; and since the pterygoids form a great sheet, which is continuous with the plane of the vomers, and ventral to the processus cultriformis of the parasphenoid in, for example, *Orthosauriscus*, it may be presumed that the nerve ran immediately dorsal to the mesial parts of the pterygoid. In advanced amphibians the interpterygoid vacuities were remarkably broad, so that the nerve was probably not covered ventrally by any dermal bone between the expanded part of the parasphenoid and the prevomer (e.g. Säve-Söderbergh 1936, text-figure 4, etc.).

The palatal structure of *Seymouria* is remarkably like that of an Embolomerous amphibian, and the description given above fits it very well (figure 2C). Watson has described a small bone between the pterygoids and the basipterygoid processes, and compared it with the meniscus pterygoideus of *Sphenodon* and other reptiles; Olson, however, has stated that this element is not separate (Watson 1918, pp. 272–273, 287, figures 1, 5; and Olson 1936, p. 528). The parasphenoid, like that of Embolomeres, has no lateral wings covering the basipterygoid process, and the r. palatinus VII must have passed ventrally beneath the basipterygoid process, then dorsal to the pterygoid and prevomer.*

Captorhinus has been described by several workers, and quite recently Price (1935) has given a remarkably detailed account of the brain case. Compared with *Seymouria*, the most obvious modification in the palate is the reduction of the ectopterygoid, and the great development of the transverse bar of the pterygoid, which terminates in a deep flange applied to the interior of the mandible (figure 2A). Both these changes were probably connected with a change in angle of the jaw muscles indicated by the more nearly vertical position of the quadrate. The ectopterygoid is small, and situated on the pterygoid flange. The basis cranii, as described by Price, is of great importance in this discussion (figure 12). The parasphenoid is slightly expanded posteriorly, but has nothing at all like the wings of a lizard parasphenoid. The internal carotid artery pierces the lateral part of the parasphenoid just behind the basipterygoid process of the basisphenoid, and rises steeply to pass into the cranial cavity a little farther forwards. The ramus palatinus VII issues from a tunnel in the pro-otic and basisphenoid, and runs in a marked groove across the ventral face of the mesial part of the basipterygoid process; it is not at any time covered ventrally by the parasphenoid. Anteriorly the nerve must have run immediately dorso-mesial to the margins of the interpterygoid vacuity, lateral to the processus cultriformis (which Price has suggested

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* See Addendum, p. 352.

may be largely of cartilage bone and labels "presphenoid"—1935, p. 382); still farther forward it must have lain dorsally to the pterygoids and prevomers.

Dimetrodon, a typical Pelycosaur, has a palatal structure exactly similar to that of *Captorhinus*, though Broom (1910) did not figure a separate ectopterygoid (figure 2E). The pterygoids, like those of *Captorhinus*, bear teeth anteriorly where they meet in the mid-line just behind the prevomers, and so there can be no doubt that the palatine nerve ran dorsally to the bone.

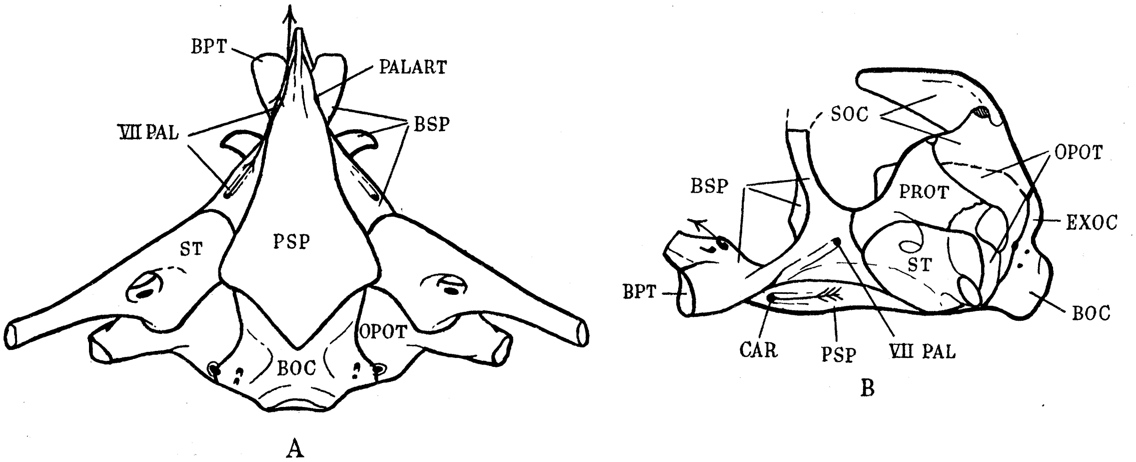

Figure 12. Brain case of *Captorhinus* (after Price). A, ventral, B, lateral view. In A, the arrow shows the course of the palatine nerve; in B, an arrow shows the course of the internal carotid artery.

bsp, basisphenoid; boc, basioccipital; bpt, basipterygoid process; car, groove and foramen for internal carotid artery; exoc, exoccipital; opot, opisthotic; psp, parasphenoid; palart, foramen for palatine artery; prot, pro-otic; soc, supraoccipital; st, stapes; vii pal, foramen and groove for ramus palatinus VII.

In the Theriodontia there was a very general tendency towards a closure of the interpterygoid vacuity. When this process is at all advanced the pterygoids meet in the mid-line, ventral to the processus cultriformis, in front of the basipterygoid processes, and behind the remnants of the interpterygoid vacuity. In all Theriodonts the parasphenoid is difficult to distinguish from the basisphenoid.

In all members of the group there can be no doubt of the homology of the pterygoid, epipterygoid, ectopterygoid, palatine and vomer elements (figures 1A, 3, 5, 7A).

In all forms the basipterygoid processes are situated near the front of the expanded part of the basisphenoid-parasphenoid complex. They have often been figured as elongated, dorsoventrally shallow structures, particularly in Gorgonopsia (e.g. Boonstra 1934*a*); but Olson (1938), working on a serially sectioned skull of *Cynariops robustus*, has found them to be comparatively rod-like and transversely directed. Immediately behind the basipterygoid process in Gorgonopsia, Watson and Boonstra have figured foramina which they regard as Vidian; but Olson shows conclusively that the corresponding foramina in *Cynariops* transmitted the internal carotids. In many Theriodonts the processus cultriformis was covered ventrally by the pterygoids. It is not remarkably long, usually extending anteriorly to a point beneath the hinder part of the frontal; it may be grooved dorsally for the reception of the "presphenoid". In some forms (e.g. Bauriamorphs) the processus cultriformis was probably greatly reduced.

In primitive Theriodonts the pterygoids have strong quadrate, transverse and palatal processes, and usually cover the palatobasal articulation of the palato-quadrate ventrally; in this way they frequently meet the parasphenoid, and may meet in the mid-line immediately in front of that bone, and behind the interpterygoid vacuity (e.g. many Therocephalia and Gorgonopsia (figure 3B, C)). The transverse process forms part of a deep vertical flange which was approximated to the inside of the mandible when the jaws were shut. The ectopterygoid or transpalatine usually forms part of the lateral face of this flange. In the Cynodonts, which are in some ways the most mammal-like Theriodonts, the quadrate process of the pterygoid is much reduced, and may finally be replaced functionally by a posterior extension of the epipterygoid ossification in the cartilaginous upper jaw (figure 1A). In this group, moreover, the interpterygoid vacuity closes, and the pterygoids meet in the mid-line as a strong beam in front of the palatobasal articulation, and expanding to the transverse processes.

The epipterygoid of Gorgonopsia and certain early Therocephalia is a comparatively slender element, lying dorsal to the pterygoid and against the basipterygoid processes. It rises up lateral to the brain case and usually reaches the roofing bones of the skull (parietal; often frontal and postorbital). In later Therocephalia and in Cynodontia the epipterygoid is much more expanded, and encloses a very typical cavum epiptericum. There are usually no foramina in the bone, but the posterior margin may be notched for $V_{2,3}$. It thus has the typical relationships of the reptilian epipterygoid but is also remarkably like the mammalian alisphenoid, except that it has no separate foramen rotundum (for V_2). In the Cynodont the epipterygoid makes contact with pterygoid and basisphenoid, posteriorly with the pro-otic, dorsally with the parietal and at least in some forms with the frontal and postorbital, while anteriorly it was probably separated from the brain case by an opening which was functionally a foramen lacerum anterium + foramen opticum.

The ectopterygoid is usually quite a small element, having a lateral contact with the maxilla, forming part of the outer face of the pterygoid flange, and making strong contacts with the palatine and pterygoid. In many forms there is a more or less extensive suborbital vacuity between the palatine, pterygoid and ectopterygoid. In certain Theriodonts (notably Cynodonts, and a few Gorgonopsia) the ectopterygoid does not meet the maxilla, and may be separated from it by part of the jugal. In Cynodonts, and probably in other groups, it seems to be a bone in process of reduction.

In many Therocephalia the palatal processes of the pterygoids bear teeth, and clearly lay well behind the internal nostrils. The same is true of the Gorgonopsia, in which the teeth extend also on to the palatines. But in those Theriodonts in which the formation of a secondary palate was well advanced (e.g. Whaitsidae in the Therocephalia, Bauriamorphs, Cynodonts, Ictidosauria) there are no teeth on the pterygoids or palatines. The Whaitsidae have deeply vaulted palates, and it is fairly certain that the internal nares were carried well back; the ectopterygoids here are placed rather postero-laterally to the presumed position of the internal nares. In the Bauriamorphs there is little doubt that the internal nares were distinctly mesial to the ectopterygoids, which can have played little or no part in their support. The Cynodont secondary palate includes a part derived from the palatines; posteriorly paired ridges on the palatines and pterygoids converge to the great beam posterior to the transverse processes, and are believed to have served for the attachment of the soft palate. However, *Cynognathus* has an equally marked ridge running from the palatine to the descending flange of the pterygoid, and the ectopterygoid forms part of this ridge. The morphological relationships of the ectopterygoid in Cynodonts are worth noting. The bone makes contact anteriorly with the palatine, posteriorly with the pterygoid, and may be excluded from the maxillary. It lies approximately at the level of the posterior tip of the vomer, is applied (with the pterygoid flange) to the inside of the closed mandible, and lies postero-mesially to the hindmost maxillary teeth.

In those Therocephalia and Gorgonopsia which bear teeth on the pterygoid, it is inconceivable that the r. palatinus VII should have run ventrally to this bone near the mid-line. It is almost certain that the nerve passed between the pterygoid bone and the brain case (including the parasphenoid) immediately in front of the basipterygoid process, and ran anteriorly for some distance dorsal to the pterygoids. This was no doubt true also of the Cynodonts; Professor D. M. S. Watson has recently found evidence to show that his published account of their course (1916, pp. 349 *et seq.*) is almost certainly erroneous.

The Ictidosauria are only known from rather poorly preserved material described by Broom. The palate is extraordinarily mammalian in appearance, particularly in the secondary palate and the arrangement of the maxillary teeth. Broom shows the side walls of the nasal passages carried much farther backwards than in Cynodonts, and careful consideration of his "Ictidosaurian B" (figure 8B) and of *Cynognathus* (figure 1A) shows that, if the ectopterygoid be present at all in the Ictidosaurian, it must lie posterior to the palatines, ventral (or ventro-lateral) to the pterygoids, and posteromesially to the maxillary teeth. This would place it on the side-wall of the choanal passage, retaining its old relations to the ascending ramus of the dentary. The main differences between the Cynodont and Ictidosaurian are in the greatly expanded basis cranii in the latter, which is bound up with the swelling of the whole brain case.

The Monotremes are in many ways extremely aberrant. The alisphenoid is very small, and is replaced functionally by a sheet of bone growing forwards from the periotic. There are two pterygoid elements on each side; a plate of bone (the "mammalian pterygoid") applied to the basis cranii, and a more ventral element, known as the "*Echidna*-pterygoid" (figure 13B, C). The latter touches the palatine anteriorly, but the hinder part of the naso-pharyngeal passage has also come into relationship with the otic region—a sign of the extraordinary change in proportion between any Theriodont and any mammal. The "mammalian pterygoid" underlies the basis cranii, extending back to the region of the ala temporalis (i.e. the alisphenoid), and the Vidian nerve transverses a canal between the "mammalian pterygoid" and the basis cranii. However, the internal carotids enter the cranial cavity *posterior* to the "mammalian pterygoids" in early growth stages, and are never enclosed by those bones.

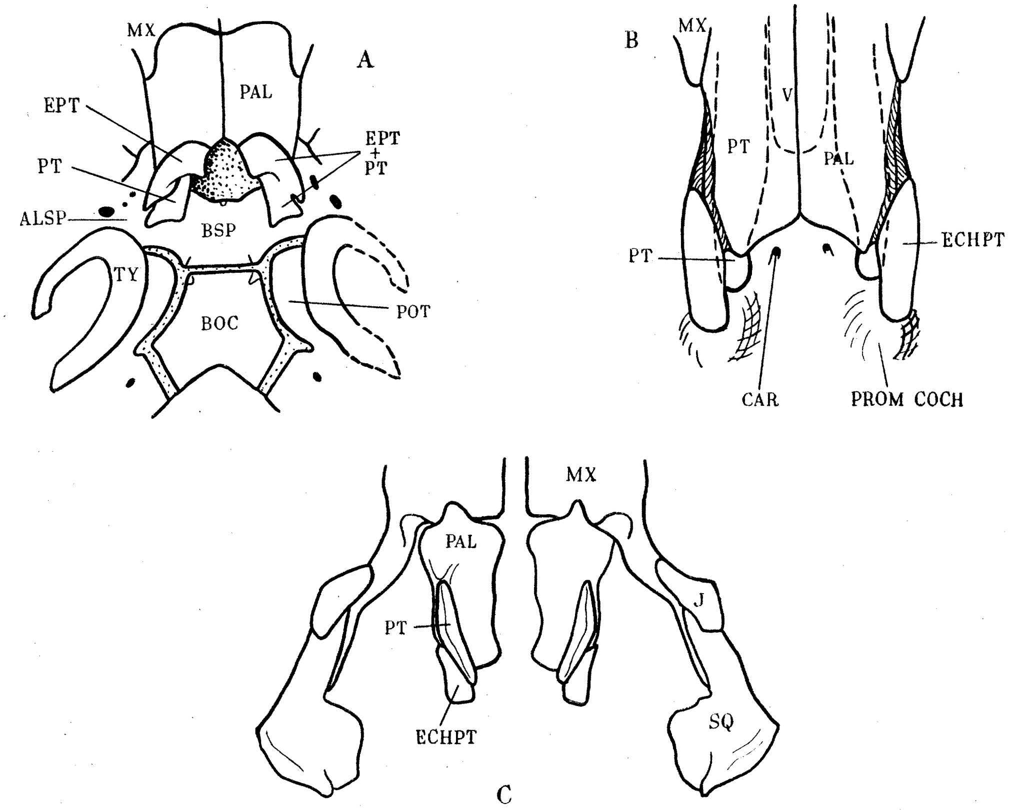

Figure 13. The posterior part of the secondary palate and related structures in some mammals. A, *Tatusia*, 40 mm. skull, ventral view. (After Broom.) B, *Ornithorhynchus*, 250 mm. total length, ventral view. (Adapted from Watson.) The position of the pterygoids and vomer under cover of the palatines is shown. C, *Ornithorhynchus*, 80 mm. total length. Dorsal view of dermal bones of palate. (Adapted from Watson.)

ALSP, alisphenoid; BOC, basioccipital; BSP, basisphenoid; CAR, foramen for internal carotid artery; EPT, ectopterygoid; ECHPT, *Echidna*-pterygoid; J, jugal; MX, maxilla; PAL, palatine; POT, periotic; PROM COCH, prominentia cochleae; PT, pterygoid ("mammalian pterygoid"); SQ, squamosal; TY, tympanic; V, vomer.

In ditremate mammals there are naturally many individual slight modifications of the structures of the palate, but the following generalizations may be made. There is usually no sign of a separate parasphenoid. The basisphenoid is exposed in the base of the cranium, and is followed anteriorly by a "presphenoid" (a cartilage bone), and by the vomer, which separates the nasal cavities and supports the bony false palate. In some Ditremata the vomer may extend back to the basisphenoid. The palatines have all the normal relations of the Cynodont elements, except that they have now a suture with the "presphenoid". The pterygoids rest on the basisphenoid and presphenoid, and each consists of a basal plate applied to those bones, enclosing a Vidian canal, and a vertical sheet forming the posterior part of the choanal passage. The pterygoids sometimes have the old reptilian contact with the posterior end of the vomer, but this contact is usually lost. Occasionally there are two paired elements forming the pterygoid; a dorsal plate, and a ventral element reaching forward to the palatines (e.g. *Tatusia* (figure 13A), *Tamandua*, *Choloepus* and *Galeopithecus* (figure 11A)) which clearly correspond respectively to the "mammalian pterygoid" and "*Echidna*-pterygoid" of monotremes. The alisphenoid has very variable relations in some ways; Gregory and Noble (1924) have given an account of the variability of nerve foramina, and have also pointed out the relations to the tympanic chamber in many forms. Otherwise it has so many points in common with the Cynodont epipterygoid that there can be little doubt of its homology with that element. Watson (1916, p. 354) pointed out that it differed from the Cynodont element in its relationship to V_2 and V_3; however, it seems not unlikely that the Cynodont epipterygoid (which is notched posteriorly for V_2 and V_3) could have grown a bridge between these two nerves, and thus acquired a separate foramen rotundum.

There can be no doubt of the homology of the palatine bone throughout this series, and the "mammalian pterygoid" is just as clearly the homologue of the reptilian pterygoid, which has already become greatly reduced in the Cynodontia and restricted to the region below, and in front of, the basipterygoid processes.

The parasphenoid was probably a separable element in the early Labyrinthodonts, but in the Synapsid reptiles it had become fused with the basisphenoid so as to be indistinguishable in the adult in many forms and appears to have been greatly reduced in some late Theriodonts. It has probably lost its identity altogether in most mammals (see pp. 325, 338).

There remains only the ectopterygoid. In certain Theriodonts it is apparently a bone in process of reduction; this is particularly noticeable in the case of advanced Cynodonts, and it has been shown above that the more ventral pterygoid element of *Tatusia*, etc., and the "*Echidna*-pterygoid" of monotremes, has anteriorly and dorsally the morphological relations of this bone. Also it has been possible to indicate the probable conditions in the Ictidosauria, forms which appear to have been intermediate between the reptiles and mammals in respect to this region. The general loss of the more ventral "pterygoid" of mammals as an independent element seems to follow the trend already noticed in Cynodonts, and it may be concluded that there is strong palaeontological evidence for the view that the reptilian ectopterygoid is homologous with the more ventral pterygoid element of *Tatusia* and other mammals, and with the *Echidna*-pterygoid of monotremes. But there is no evidence that the ectopterygoid habitually formed part of the side-wall of the naso-pharyngeal passage in normal theriodonts. The Ictidosauria indicate how this change may have occurred, but there is a need of more positive evidence of the position and relations of the bones and of the exact arrangement of the soft palate in all Theriodonts. A possible explanation of the change, based on the reduction of the reptilian adductor mandibulae musculature, is given below (see figures 14, 16).

(3) *Embryological evidence*

These suggested homologies of the mammalian pterygoid elements are contradicted by other suggestions based on the study of embryological material. Two of these views have gained rather wide support:

(i) The suggestion of Gaupp (followed by de Beer and to some extent by van Kampen) that the lateral wing of the reptilian parasphenoid is represented in the pterygoid elements of mammals.

(ii) The suggestion of Watson (1916) that the homologue of the *Echidna*-pterygoid is to be sought in the epipterygoid of the reptile.

The first theory may be dealt with quickly. No reptile near the mammalian line has enlarged parasphenoid wings like those of the lizard*; the conditions in *Captorhinus* and other forms show clearly that r. palatinus VII was not enclosed between the parasphenoid and the basis cranii, and this is probably true of all forms near the direct line, and also of the Crossopterygian fishes. In the advanced Labyrinthodonts the covering of the nerve by the parasphenoid may occur, but is clearly secondary. It is significant that neither *Youngoides romeri* Olson and Broom (figured Olson 1936, figure 1, as *Youngina capensis*) nor *Prolacerta broomi* (Parrington 1935*a*, figure 2) have expanded parasphenoid wings, and both forms must be on or near to the lacertilian line of evolution. The development of parasphenoid wings in bony fishes is probably also a secondary development in phylogeny (Westoll, unpublished). The greatly expanded parasphenoid wings of the lizard and other tetrapods must therefore be regarded as secondary modifications and not primitive structures which might survive in mammals.

But the theory could be controverted without regard to the detailed palaeontological evidence, because it depends on the equation of the Vidian canal of the mammal with the parabasal canal of *Lacerta*, etc. Now, the parabasal canal of *Lacerta* is situated behind the basipterygoid processes, and transmits the internal carotid artery as well as the r. palatinus VII. The internal carotid in mammals normally enters the cranial cavity through the foramen lacerum medium, behind the pterygoids, while the Vidian canal is at least mainly anterior to the processus alaris. Thus the homology invoked by Gaupp is based on an incomplete analogy, and depends on the relations of a bone

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* See Addendum, p. 352.

to a nerve which has a considerable caudo-rostral extent. The embryological reasoning is equivalent to saying that Doncaster must be York because both are on the same main line from London to Edinburgh, and lie between Manchester and the North Sea. Fuchs (1910) has already shown the falsity of Gaupp's homology, and compares the mammalian Vidian canal with the pterygoid canal of certain Chelonia. The homologies involving the lateral wing of the parasphenoid must therefore be discarded.

It remains to consider the homologues of the reptilian epipterygoid in mammals. Gregory and Noble (1924) have given a review of this problem; they concluded, with Broom, that the alisphenoid of *ditrematous* mammals represents the epipterygoid of the Cynodont reptile, and this homology has been accepted by Watson. The morphological relations of the elements are strongly in favour of this equation; the single difficulty is the course of V_2, which pierces the alisphenoid in ditrematous mammals (foramen rotundum), and apparently issued, with V_3, from a notch in the back of the bone in Cynodonts. This difficulty is easily surmounted, and it is now clear (especially after the analyses of Goodrich 1930 and de Beer 1937) that the alisphenoid, which ossifies in the true ala temporalis (or in membranes related to it), is in every important way equivalent to the epipterygoid. But Watson's comparison of the quadrate ramus of the epipterygoid of Cynodonts with the *Echidna*-pterygoid of monotremes (1916, pp. 352–353) is so suggestive of their homology that special attention must be given to his argument. There can be no doubt that the "*Echidna*-pterygoid" is the homologue of the "ectopterygoid" of *Tatusia*; the bones have identical morphological relationships except to the tympanic cavity, but a comparatively slight posterior growth of the bone in *Tatusia* would bring it to the same position. In *Tatusia*, moreover, the alisphenoid is well developed; it must ossify in the ala temporalis, and is certainly the homologue of the epipterygoid of reptiles. In *Ornithorhynchus*, too, de Beer and Fell (1936, p. 6) have shown the presence of a typical ala temporalis, which however remains very small; they have described ossifications in this cartilage, forming rudimentary alisphenoids which must fuse with the basisphenoid. Hence fragmentation of the Cynodont epipterygoid must be allowed if Watson's homology is to be upheld; and the relations of the mammalian pterygoid to the alisphenoid and "*Echidna*-pterygoid" are not what would be expected in such a case. Moreover, the "*Echidna*-pterygoid" is a membrane-bone, having anteriorly and mesially the normal relations of an ectopterygoid towards the palatine and pterygoid. In addition it lies in a plane immediately mesial to the tympanic cavity, preserving the Theriodont relations of the ectopterygoid to the bones at the posterior end of the reptilian mandible. Since even the palatine has come to have a contact with the alisphenoid in mammals, it cannot be considered very remarkable that the homologue of the ectopterygoid should also have this relationship, and lie still more posteriorly. The articulation of the *Echidna*-pterygoid with the pro-otic in *Ornithorhynchus* must be regarded as a secondary modification. It may be concluded that Watson's suggested homology, which was based on all the best evidence available at that time, has been overthrown by the subsequent discovery of the true ala temporalis and alisphenoid in developing *Ornithorhynchus* (de Beer and Fell 1936). The reading of the palaeontological and developmental evidence here put forward is certainly in favour of the homology of the "*Echidna*-pterygoid" with the reptilian ectopterygoid; the close comparison made by Watson between the "*Echidna*-pterygoid" and the quadrate ramus of the Cynodont epipterygoid is misleading. Actually, if the ectopterygoid of *Tatusia* were to extend back to the tympanic ring and periotic it would also have exactly the relations of the "*Echidna*-pterygoid"; the criteria used by Watson are not really sufficient to separate two bones with a parallel development in this region (cf. Watson 1916, pp. 352–353), for both the ectopterygoid and the ventral part of the alisphenoid could fulfil the conditions of the *Echidna*-pterygoid.

The homology of the "*Echidna*-pterygoid" in Ditremata is sometimes disputed. Watson (1916) believed it to be represented in the alisphenoid, for which we have seen the evidence is now removed. Gaupp thought it to be lost, with the possible alternative that it became the endotympanic; the latter view has been shown to be erroneous by van Kampen. Broom (1914) found a separable "transpalatine" (i.e. ectopterygoid) lying more or less ventral or ventro-lateral to the "pterygoids" in *Tatusia*, etc., and regarded it as the homologue of the "*Echidna*-pterygoid". Similar observations have been made on other mammals (e.g. *Choloepus*), and Parker (1885) figured such ventral elements in *Galeopithecus*, and regarded them as true pterygoids, the separate dorsal plates being called "*mesopterygoids*". In his summary of characteristic features of Marsupials (presumably based on dissections of foetal material) Parker (1885, p. 270) says: "The pterygoids are very small, and their basicranial part limited, on account of the constant separate development of a large mesopterygoid." In most Ditremata there is no distinct ventral bone, but a large separate nodule of secondary cartilage is usually found in early development in the appropriate position. This nodule later ossifies and fuses with the more dorsal "pterygoid" plate, to form the hamulus of the normal adult pterygoid bone. It seems that de Beer (1929, 1937) was justified in homologizing the more dorsal plate with the "mesopterygoid" of *Galeopithecus*, the "pterygoid" of *Tatusia*, and the "mammalian pterygoid" of monotremes respectively. The nodule of secondary cartilage would represent the "transpalatine" of *Tatusia* and the "*Echidna*-pterygoid" of menotremes, and thus the ectopterygoid of reptiles. It may therefore be concluded that certain Ditremata may retain an independent ectopterygoid into the adult (e.g. *Tatusia*); in others the bone may be separate in early post-natal life, and fuse later with the pterygoid; while in still others the homologue of the ectopterygoid is to be sought in the more ventral element which ossifies from a nodule of secondary cartilage found only in foetal stages. It is not impossible that the element may be lost altogether in some mammals.

de Beer (1929, 1937) has advocated the homology of the nodule of secondary cartilage with the pterygoid bone of reptiles. His view is partly based on his identification of the dorsal plate as the homologue of the lateral wing of the parasphenoid (which has already been controverted) and partly on the recognition of a procartilaginous continuity between the nodule and the processus alaris in *Sorex*. This is not at all satisfactory evidence. In the first place, it is difficult to see why a procartilaginous bridge between a cartilage and the accepted homologue of a *dermal bone* should have any phylogenetic significance, because it is clearly a secondary development. Moreover, even if the connexion be granted, it merely shows that the element in question is a bone of the palate, and the ectopterygoid would fulfil the necessary requirements.

The view of Fuchs (1910) that the entire pterygoid of Ditremata is equivalent to the *Echidna*-pterygoid, and this to the reptilian pterygoid, does not seem to be in accordance with the palaeontological evidence, or with the occasional presence of two pairs of pterygoid elements in certain forms, and the demonstrably compound nature of the pterygoid in most foetal Ditremata. He regarded the homologue of the "mammalian pterygoid" of the monotremes as included in the palatine of higher mammals, but his argument is not convincing.

As a result of this analysis, it is held that the embryological evidence, on which was based the homology of mammalian pterygoid elements with the lateral wing of the parasphenoid of reptiles, is fundamentally unsound, and is founded on a false, because partial, analogy. This demonstrates once more the difficulties which follow too rigid a comparison of young stages of animals which are not closely related.

IV. The parasphenoid

Since it has been shown that the presence of any part of the reptilian parasphenoid in the mammalian pterygoids or vomer is highly unlikely, there remains for consideration the fate of the bone in mammals. The vestigial splint in *Didelphys* and *Galeopithecus* "*phillipensis*" has already been mentioned in the discussion of the vomer problem. The relations of this element (figure 11) are completely in favour of its homology with the reptilian parasphenoid. In this respect it is only necessary to emphasize its position relative to the pterygoids, alisphenoid, basisphenoid (particularly the region pierced in some mammals by the hypophysial foramen) and the vomer. It is greatly reduced but is in the position of the median part of the reptilian parasphenoid, and in particular of the rudiment of the processus cultriformis in *Lacerta*. Hence any possible equivalents of reptilian basitemporals should lie postero-laterally to this bone, and probably behind the main part of the alisphenoid. Parker (1885, p. 260 footnote) mentions paired membrane bones added to the basisphenoid in Eutheria, represented by the lingulae sphenoidales in man, and goes on: "I strongly suspect that they are the 'basitemporals'—symmetrical remnants of the parasphenoid—so well seen in Birds and the Crocodilia." The morphological relations of the lingulae sphenoidales are not wholly out of accordance with this view, but they ossify from the cartilaginous alicochlear commissures which are derived from the true polar cartilages. Van Kampen (1922) has also identified mammalian homologues of the "basitemporals". (It is interesting to notice that he regards these elements as possibly having been derived from some pterygoid elements of fishes, and in such a case presumably incorporated by fusion into the normal reptilian parasphenoid. This view is almost certainly based on a consideration of the embryology and anatomy of Teleost fishes, which differ very greatly in the palatal structures from the Crossopterygian fishes.) Van Kampen controverts Parker's view of the homology of the lingulae sphenoidales in man, and instead (p. 55) regards the "ossicula Bertini" (conchae sphenoidales) as being probably the equivalent of the basitemporal, "wenigstens insoweit sie als Belegknochen entstehen". But the element in question is an ossification in the cartilage of the lamina orbitonasalis, which later fuses with the front of the presphenoid, and it is impossible for it to have anything to do with the basitemporal. In certain insectivores there is a strong "processus tympanici" of the basisphenoid, which van Kampen homologizes with the basitemporal. The process is not known to have a separate development, and occurs only in a few forms. In others, a similarly placed tympanic process of the alisphenoid may be developed instead, and van Kampen regards it as representing the same element. Although these processes are in the correct general position for basitemporals, there is no good evidence to suggest that they represent anything but specializations of the cartilage bones in some insectivores and marsupials. Elsewhere van Kampen (pp. 54–55) indicates the "mesopterygoids" of Parker's description of *Galeopithecus* as the basitemporals; this has been shown to be most unlikely.

It may therefore be concluded that the only satisfactory trace of any parasphenoid element in mammals, so far as is yet known, is the small splint of bone found applied to the basisphenoid in certain individuals of *Galeopithecus* and *Didelphys*. Considering the relations of this small bone, it is very remarkable that its claims to be the parasphenoid have been so often overlooked in favour of the extremely dubious claims of the vomer.

V. THE EVOLUTION OF THE MAMMALIAN PALATE FROM A THERIODONT CONDITION

While several points in the evolution of the mammalian palate are still doubtful, it is felt that the following homologies have been established on adequate palaeontological grounds and are not contradicted by embryological evidence:

Reptilian "prevomers" = mammalian vomer.

Reptilian pterygoid = "mammalian pterygoid" of monotremes, and at least the dorsal part of the pterygoid of ditrematous mammals.

Reptilian ectopterygoid = "Echidna-pterygoid" of monotremes, ectopterygoid of *Tatusia*, etc., and probably part of the pterygoid (hamulus) of the adults of most ditrematous mammals.

Reptilian parasphenoid = Vestigial splint bone in some *Didelphys* and *Galeopithecus*, lost in most mammals.

Reptilian epipterygoid = Mammalian alisphenoid, small or vestigial in monotremes.

It is well known that important differences between the skull of a mammal and that of a Theriodont lie in the enormous increase in the size of the brain-case, the loss of the post-dentary bones from the jaw and the incorporation of some of them into the middle ear, together with the reduction of the massive paroccipital processes. The homologies established in this paper enable a detailed comparison of the palates to be made, and this calls attention to the following less obvious differences:

(1) The posterior extension of the naso-pharyngeal passage.

(2) The reduction of the pterygoids and their separation in the mid-line.

(3) The reduction of the ectopterygoids, their more posterior position and their inclusion in the walls of the naso-pharyngeal passage.

(4) The morphological shortening of the ventral aspect of the skull in the orbito-temporal region, which has brought the palatines and the basipterygoid processes close together.

(5) The loss of the parasphenoid and the appearance of the presphenoid and basisphenoid in the palatal view of the skull.

(6) The anterior displacement in many forms of the anterior root of the zygomatic arch.

In addition, two differences concerning the back of the skull will be mentioned:

(7) The great reduction in size of the squamosal.

(8) The different attitude of the occiput.

It is possible to offer explanations for some of these changes which are correlated with changes in the relations of the jaw muscles with the skull. In this section of the paper views are advanced which are admittedly largely hypothetical, but which lead to some consideration of functional implications of the structural changes. In this attempt to put flesh on dry bones the authors have necessarily felt less closely bound to factual evidence, and there is little doubt that some of their suggestions will be challenged. It should be insisted therefore that this section of the paper is not intended as additional support for the previous conclusions, but is intended to direct attention to certain new or little-understood problems in the transition from the Theriodont to the mammal. In certain cases deliberate emphasis has been placed on hypotheses which seem to be at present incapable of proof, in the hope that other workers may have a concrete case to argue.

Notes on jaw musculature

It is well known that the areas of origin and insertion of muscles are variable, so that evidence of homology of bones derived from the study of muscles is not very reliable, and their use has been made difficult by a confused nomenclature. Also, since fossil material seldom gives adequate evidence of muscle attachments, discussions concerning them must be based on living animals and are liable to the difficulties consequent upon comparisons made between animals which are only distantly related. The conclusions of recent workers on jaw muscles, however, fit very closely to those made in this paper, and their application is of considerable help.* Since the findings of the workers on jaw musculature are based on quite independent grounds, the reliability of each line of approach is strengthened.

Both Adams (1919) and Brock (1939) regard the m. tensor tympani and m. tensor palati of mammals as derivatives of the original adductor muscles of the jaw, and agree in deriving them from the same reptilian muscle—the pterygoideus division of the adductor internus (Brock) (=pterygoideus anterior of Adams) (see table 1). In young Geckos this muscle is inserted round the posterior lower border of the mandible, and is attached to the pterygoid bone (Brock 1939, p. 742). In certain other reptiles it has a more extensive attachment and may extend on to the palatines, ectopterygoids, pterygoids, maxillae, parietals, pro-otic and quadrate. The insertion into the posterior part of the mandible is also variable, but the muscle is usually wrapped round the under parts and inserted on the angular, articular and prearticular. The equivalent muscles in mammals also have rather variable relations, but they have their origin on the pterygoid bone (sometimes also on the processus alaris or the auditory capsule) and are usually inserted on the malleus or tympanic. These homologies are in keeping with the now generally accepted view that the mammalian ear ossicles are derivatives of the post-dentary bones of the reptilian lower jaw. The slender remnant of the old pterygoideus muscle of the reptile may remain in some mammals as the tensor tympani, but it usually subserves another function as the tensor palati (see figure 14A, B, AIPT; figure 14C, TTY).

TABLE 1. HOMOLOGIES OF SOME JAW MUSCLES

Reptiles		
Adams' scheme	Brock's scheme	Mammals
Pterygoideus anterior	Adductor internus, pterygoideus	Tensor tympani (or Tensor palati)
Capiti-mandibularis profundus	Adductor internus, pseudo-temporalis	Pterygoideus internus (sometimes called Adductor internus) Pterygoideus externus†
Capiti-mandibularis medius Capiti-mandibularis superficialis	Adductor externus group	Temporalis Zygomatico-mandibularis Massetericus

† According to certain authors the pterygoideus externus of mammals is derived from the same mass as the temporalis, etc., i.e. from the reptilian adductor externus [adductor (or levator) mandibulae externus]. The acceptance of this view would not greatly modify the discussions herein.

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* The most recent general work on jaw muscles (Edgworth 1935) is difficult to apply because of the unorthodox views of the author, who, moreover, neglects palaeontological evidence of phylogeny in favour of a reliance on recapitulation.

The pterygoideus externus and the pterygoideus internus (=adductor anterior) of mammals are apparently derived from the reptilian adductor internus (pars pseudotemporalis) of Brock's notation (=capiti-mandibularis profundus, Adams). In mammals these muscles usually arise on the alisphenoid and the lateral face of the pterygoid plate, and are inserted on the inner side of the mandible. In the Geckos

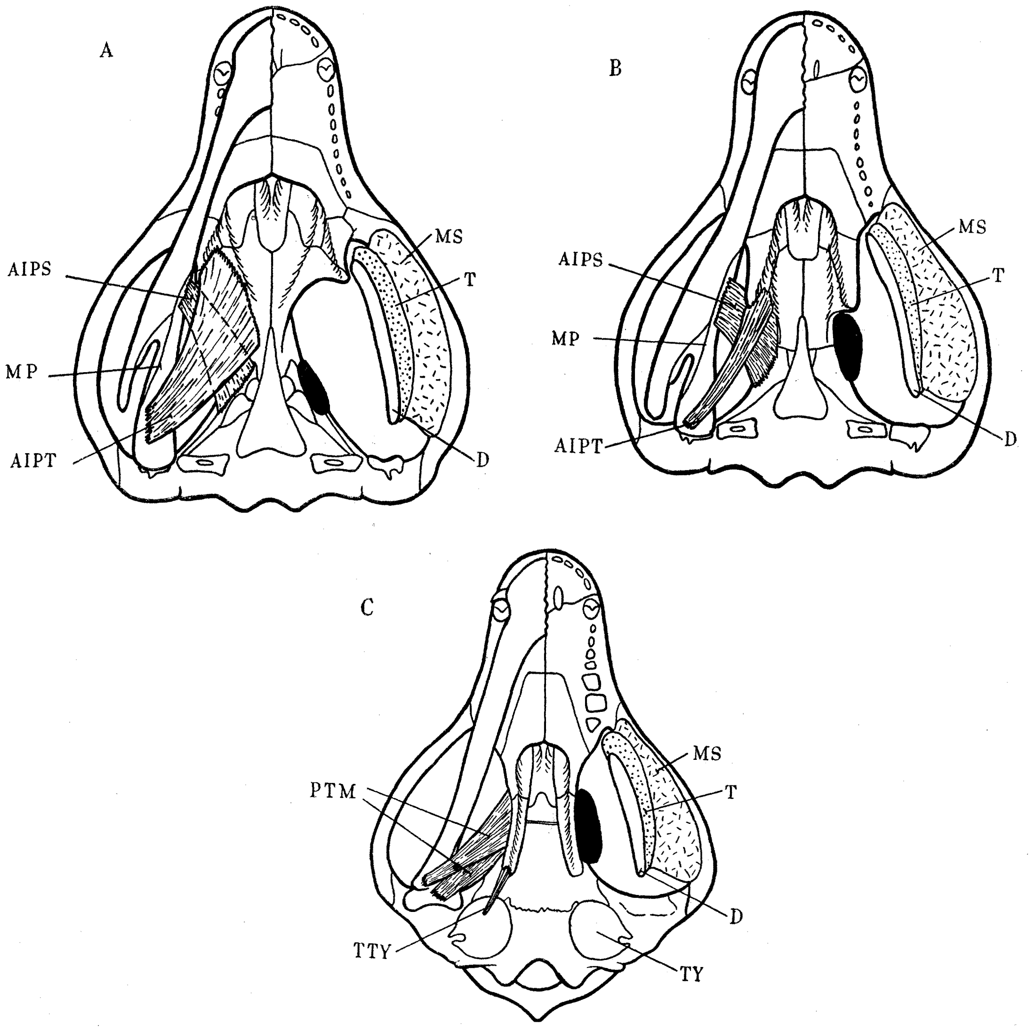

FIGURE 14. Schematic representation of differences in musculature, mandible, and palate in A, a Cynodont; B, an Ictidosaurian-like stage; C, a mammal. Based on outlines of figure 16A, C, F (*q.v.*). In each drawing the right ramus of the mandible is in place, and the muscles of the adductor internus group (Brock) are shown on the same side. On the opposite side of each figure the pseudotemporal muscle is sectioned near its origin and shown in black; the ascending ramus of the dentary is cut through and shown in relation to the main mass of the adductor externus group, which is shown very diagrammatically in section.

AIPS, adductor internus, pseudotemporalis (reptile); AIPT, adductor internus, pterygoideus (reptile); D, dentary; MP, post-dentary bones of the reptilian mandible; MS, masseter of mammal; PTM, pterygoideus externus and internus of mammal; T, temporal of mammal; TTY, m. tensor tympani; TY tympanic.

(Brock 1939, p. 742) the pseudo-temporal muscle is attached to the epipterygoid and outer face of the pterygoid, and extends up on to the orbito-temporal part of the cranium. It has been shown by Adams to have similar general relations in other reptiles, and to be inserted on the inner face of the mandible, often on the coronoid. It will be seen that the general relations of these muscles are in favour of their homologous nature, and, moreover, agree with the writer's interpretation of the "mammalian pterygoids", "*Echidna*-pterygoids" and alisphenoids as the reptilian pterygoids, ectopterygoids and epipterygoids respectively.

In reptiles the pseudotemporalis part of the adductor internus (Brock) passes obliquely across the outer face of the pterygoideus part of the same mass, internal to the adductor externus. It might be expected, therefore, that in Cynodonts the pseudotemporalis passed anteroventrally from the expanded epipterygoid and side of the brain case to the region of the coronoid, or the ascending process of the dentary, a course which would probably take it immediately outside, or posterior to, the corner of the pterygoid flange (figure 14A, AIPS). Similarly the pterygoideus portion was probably attached to the margin of the pterygoid in front of the epipterygoid, and possibly to the ectopterygoid as it may have extended on to the ventral surfaces of the bony sheet formed by these bones (figure 14A, AIPT).

The reduction of the pterygoideus muscles of the reptile left the adductor externus group as the dominant jaw muscles, and in the mammalian ancestors the group was probably already differentiated into the equivalents of the masseter, temporal, etc. of the mammal. In reptiles the muscles of this group are usually inserted on the coronoid, sometimes on other post-dentary bones, and occasionally on the posterior part of the dentary. In mammals the masseter is typically inserted on the outer face of the posterior angle of the dentary, the temporal on the coronoid process. A certain morphologically anterior migration of the insertion is indicated.

Change in attitude of the pterygoid and ectopterygoid

If these suggestions are approximately correct, then the small size of the pterygoid elements in mammals is probably correlated with their functional obsolescence. Their reduction may be expected to have taken place with the reduction of the reptilian pterygoideus muscle when the post-dentary bones lost their share of the jaw articulation and were transformed into auditory ossicles. From this point of view the great median beam formed by the Cynodont pterygoids is a structural necessity because of the nature of the pterygoideus musculature (AIPT), and the fact that the greatly reduced pterygoids in mammals do not normally meet in the mid-line readily becomes intelligible. The remnants of the pterygoids, however, have a new importance in forming the side walls of the nasopharyngeal ducts.

The stages by which the laterally extended Theriodont pterygoids were transformed into the typical "mammalian" condition are unknown in any fossil forms, but the Ictidosauria had apparently attained the mammalian condition. The functional aspect of the problem has been dealt with briefly by Gregory and Adams (1915, p. 765). They noted the correlation between the reduction and separation of the reptilian pterygoid bones and the reduction of the reptilian "pterygoideus anterior" muscle (=pterygoideus of Brock); but their recognition of the homologues of the reptilian pterygoid and ectopterygoid in the basal portion of the alisphenoid and the "true mammalian pterygoid" respectively follows an earlier opinion of Watson's, which was greatly modified by his later work on the Monotreme Skull, and is not in agreement with the evidence for the homology of these mammalian bones reviewed in preceding sections. Adams (1919) follows essentially the same scheme, and in his discussion of the mammalian pterygoid muscles says that "the condition of the pterygoid region has probably been very much modified by their action, as a comparison with the reptilian condition shows that the pterygoid region is pinched in and pulled to the rear. We assume that this condition has been brought about largely by the action of pterygoid muscles" (p. 103). This explanation is not in itself satisfactory, as it immediately raises the question, Why did the musculature not exercise this force in earlier forms? Moreover, while the attitude of the pterygoid muscles might be correlated with a backward movement of the pterygoid bones, their pull would oppose any "pinching in". The lateral relations of the pterygoid flange in Theriodonts therefore have to be considered; it abuts against the inside of the mandible, near the hinder end of the lower limb of the dentary, and near the front of the post-dentary bones. It is therefore necessary also to discuss the relations of the lower jaw.

It must be decided first whether the dentary bone has increased in size relative to the rest of the skull. If the dentary length be compared with the snout-occipital crest length in primitive mammals, the ratio is found to vary somewhat, but is about 3/4. The same is true of Cynodonts. Comparison of the skull of a Cynodont with that of a mammal shows that one of the main differences in the posterior part is the much smaller size of the squamosals in the mammal; the Cynodont squamosals are large, more or less laterally directed from the brain case, and lie largely behind the inner ear, while the mammalian squamosals are more forwardly directed and lie largely in front of the inner ear. It may therefore be accepted, as a first approximation, that the new jaw articulation came about by the forward movement of the squamosals, rather than by the posterior enlargement of the dentaries. The great reduction of the post-dentary bones must have occurred *pari passu* with a very considerable disturbance of the jaw musculature; the obsolescence of the once important pterygoideus part of the adductor internus has already been emphasized. The reduction of the posterior part of the lower jaw means that, for a new mechanical equilibrium, the main musculature must be shifted forward on to the dentary, and it is not improbable that this change took place rapidly.

Forward movement of the adductor externus muscle mass might be expected to result in changes in the areas of origin and insertion, and also in the anterior margin of the fossa, internal to the jugal and quamosal, through which most of the musculature passes. In advanced Theriodonts the adductor externus mass was probably already differentiated into the equivalents of the masseter, temporal, etc. of the mammal, and these must have acquired more extensive insertions on the dentary, with a more anterior distribution. These changes were no doubt associated with minor changes in the shape and structural importance of the coronoid process of the dentary. They are also indicated in the anterior displacement of the root of the zygomatic arch in mammals, in which the coronoid process and the masseter muscle come to lie outside the posterior part of the maxillary dentition. This movement, trivial in itself, would bring the side wall of the palatine, the pterygoid and the ectopterygoid into a plane mesial to the important jaw musculature. It may be suggested that these elements would become, in effect, laterally compressed, so that they came to stand more or less vertically in the skull; this would allow the reptilian pseudo-temporalis musculature to expand forward on the side of the brain case and palatal elements, to form at least part of the mammalian pterygoid muscles. An important corollary of this process is that the ectopterygoid would be brought into close relations with the side wall of the nasopharyngeal passage, and the mammalian conditions would thus be reached. Most of these changes had, apparently, been accomplished in the Ictidosauria, judging from Broom's figures (see this paper, figures 8, 14B, 16C; cf. *Trithelodon*, figured by Broom 1932, figure 104 E).

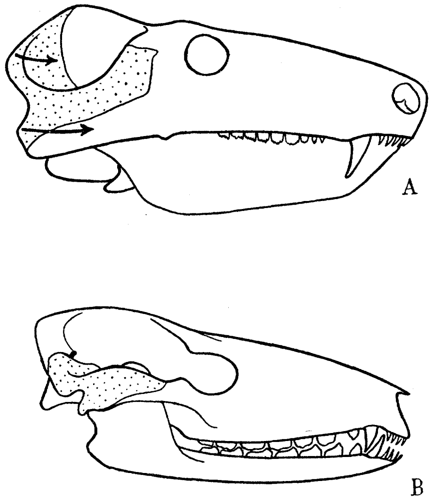

FIGURE 15. Lateral view of heads of A, a Cynodont, and B, a mammal (both generalized), to show the reduction and forward movement of the squamosal in the mammal and suggesting the absence of any marked increase in the size of the dentary.

The breakdown of the reptilian post-orbital bar is a logical consequence of this change, because the origins of the "adductor externus" mass would be moved forward against it. In one group of Therocephalia, the Scaloposaurids leading to the Bauriamorphs, the post-orbital bar is broken down at the lower end, probably by the action of the more lateral parts of the adductor externus mass (e.g. masseter and zygomatico-mandibularis). It is probable that there was an independent breakdown of the post-orbital bar in the mammalian line, and it is even possible that it did not take place at the lower end of the post-orbital bar, but at the upper end, through the greater action of the temporalis musculature.

A possible explanation of the evolution of the mammalian pterygoids, based on a survey of functional changes, has now been attempted. Before proceeding to a consideration of regional effects of the same functional changes a remaining important character of the ventral aspect of the mammalian palate may be discussed.

Appearance of presphenoid

The basis cranii in front of the basioccipital was covered ventrally in Theriodonts by dermal bones—parasphenoid and conjoined pterygoids. The reduction of the pterygoids has already been dealt with, and the complete loss of the parasphenoid in most mammals has been demonstrated. Removal of these elements would be expected to expose the basisphenoid and the sphenethmoid complex, but there has also been some descent of the latter, correlated with the expansion of the brain case. The appearance of the mammalian elements (presphenoid, orbitosphenoid, and mesethmoid if present) is thus easily explicable.

The loss of the parasphenoid as a normally occurring well-developed bone is a problem not yet open to an easy solution. In Cynodonts and other Theriodonts the conjoined pterygoids and parasphenoid form a structural unit which must be significant in the mechanics of the jaw musculature. It may well be that the changed conditions in mammals, notably the inferred forward shift of the main musculature with the reduction of the post-dentary bones, did away with the necessity for the continuance of a strong parasphenoid. The mechanical value of a strong dermal structure in Theriodonts probably lay in its buttressing action against muscular stress during those early growth stages when the chondrocranium remained comparatively unossified; the almost indistinguishable fusion between parasphenoid and basisphenoid in the mammal-like reptiles may be construed as evidence for this "doubling" nature of the bones.

Changes in cranial proportions

If the skulls of an advanced Theriodont and a mammal be compared (e.g. a Cynodont and a Carnivore—see figure 1) certain remarkable differences in proportion may be observed. In the former the brain case behind the basipterygoid processes is short and narrow compared with the snout, from which it is separated by a long narrow region floored by the pterygoids. In the mammal the posterior part of the brain case is much swollen in comparison, and lies comparatively far closer to the snout. The enlargement in size of the brain case is a well-known feature of mammalian evolution, and need not be further discussed. But the morphological implications of the closer approximation of the basisphenoid-basioccipital region to the snout have not hitherto been realized. In discussing this, full allowance must be made for the comparatively superficial effects already referred to as the "pulling-back" and "pinching-in" of the pterygoid portion of the palate. Further analysis of the change may be made on the following grounds, which are believed to be good "first approximations" to a true general statement:

(i) The proportional length of the snout to the skull length is not greatly different in the two forms; since the relative immobility of the basis cranii is suspect, the length of the whole skull is measured between the anterior tip of the snout and the occipital crest, or, perhaps better, half way between the occipital crest and the condyles. The "snout" implies the skull in front of the orbits, and is normally bounded in ventral view by the back of the palatines and vomer in both forms.

(ii) If this snout be taken as a relatively unmodified structural unit, the proportional length of the remainder of the ventral aspect of the skull is much decreased in the mammal.

(iii) On the other hand the Theriodont basis cranii behind the basipterygoid processes is certainly not significantly longer in proportion than the corresponding region in mammals; in general it seems to have retained much the same proportional length.

The effective shortening in the mammal must therefore be regarded as confined between the posterior end of the snout and the region of the basipterygoid processes. Thus it would affect precisely those parts of the Cynodont skull which have already been shown to be a most important part of the structural pattern in relation to the musculature, namely, the strong posterior median part of the joint pterygoids. This morphological shortening is also indicated in the mammal by the close approximation and normal contact of the palatine and alisphenoid bones. Unfortunately the cranial foramina in the Theriodonts (especially in Cynodonts) are still imperfectly known, but in the mammal the very close approximation of the optic foramen and foramen lacerum anterior, and the foramina rotundum and ovale, and the reduction in the orbitosphenoid, point to the same conclusion.

This analysis implies that the mammalian basis cranii has been moved forwards towards the snout. It seems possible to account in part for another great difference between Theriodonts and mammals through this change, i.e. the change in the occipital slope. In a Theriodont the occiput slopes upwards and forwards from the condyles; in a mammal the slope is upwards and backwards. It would be dangerous to ascribe all this difference to the forward movement of the basis cranii, because the occiput is such an important structural region that the major moulding forces may be expected to pertain to the neck musculature and the mechanics of the neck joint; but the change in shape is certainly in full harmony with the changes in the basis cranii and palate.

The changes in the evolution of the palate are indicated diagrammatically in figure 16; in the preparation of this figure a number of assumptions are made, which are not necessarily absolutely true, namely:

(i) The evolution is represented as from a recognizably Cynodont-like form (figure 16A) through Ictidosaurian-like stages (figure 16C, D) to a recognizable Eutherian (Carnivore) type (figure 16F).

(ii) The snout is modified in proportions as little as possible.

(iii) The basis cranii behind the basipterygoid processes is progressively more swollen, but does not greatly vary in length, and it moves forward steadily as a unit.

The changed attitude of the pterygoid and ectopterygoid bones, the shortening of the cranium, and the transfer of the post-dentary bones to the middle ear are shown to fit reasonably into the picture based on these assumptions; it can hardly be denied that figure 16A is quite recognizably a Cynodont, and figure 16F is just as clearly a mammal. The diagram is not intended to give unqualified support to the derivation of the mammals from the Cynodonts; other groups of Theriodonts could be used to provide similar diagrams based on slightly different assumptions. However, many of the distinguishing features between Cynodont and mammal skulls may now reasonably be regarded as structural features correlated with differences in musculature, and the mammalian jaw musculature must have passed through stages at least very similar to the Cynodont equipment, no matter which Theriodont group may be regarded as including mammalian ancestors. Since the morphological differences between Cynodonts and Mammals are largely functional, the above analysis indicates that they are not in themselves sufficient to disprove the contention that some generalized Cynodont may be a mammalian ancestor, the evolutionary line passing through some Ictidosaurian-like form.

A further important feature may perhaps be correlated with these changes in the basis cranii. The Cynodont brain cavity is known from certain natural casts (see Watson 1913), and shows considerable differences from that of any mammal. The mammalian brain is usually considered to be "advanced" in that the cerebral hemispheres have grown very considerably, and largely cover the mid-brain. It would be of great interest to search for any evidence of a morphological shortening of the brain in mammals; it is of possible significance that the ventral part of the mammalian brain, as compared with that of almost any reptile, shows a great crowding together of structures in the general region of the pituitary. These questions, however, must be left for discussion by those more familiar with problems of brain morphology.

Examination of the mutual spatial relations between the pterygoid region of the palate and the lower jaw in the Theriodonts and mammals indicates a marked degree of resemblance. The lower jaw of advanced Theriodonts, such as Cynodonts, is rather closely applied to the pterygoid and ectopterygoid, so that the lateral flange formed by these elements is immediately internal to the foot of the ascending ramus of the

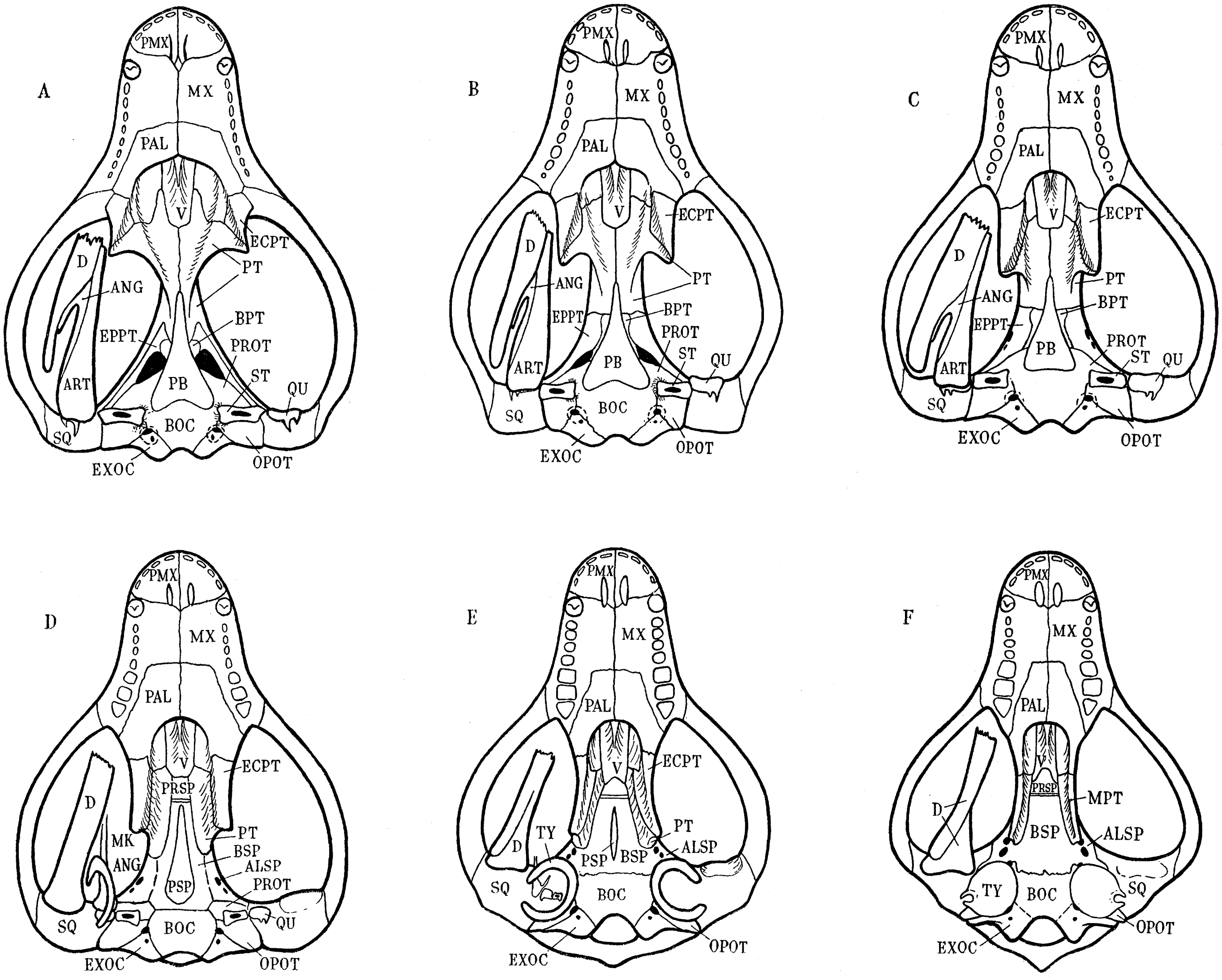

FIGURE 16. Diagram to show six possible stages in the evolution of a mammalian palate from that of an unspecialized Cynodont (A). Certain features of (B) are known in other Cynodonts. Stage (C) is, in shape and proportions, represented by the Ictidosauria. Stage (D) hypothetical. Stage (E) is largely realized in *Galeopithecus*. In stage (F) the typical compound mammalian pterygoid is formed. In each case the posterior part of the lower jaw is seen on the left of the figure.

ANG, angular; ALSP, alisphenoid; ART, articular + prearticular, etc.; BOC, basioccipital; BPT, basipterygoid process; BSP, basisphenoid; D, dentary; ECPT, ectopterygoid; EPPT, epipterygoid; EXOC, exoccipital; MK, Meckel's cartilage; MPT, compound pterygoid; MX, maxilla; OPOT, opisthotic; PSP, parasphenoid; PAL, palatine; PB, parasphenoid + basisphenoid; PMX, premaxilla; PRSP, presphenoid; PROT, pro-otic; PSP, parasphenoid; PT, pterygoid; QU, quadrate; ST, stapes; SQ, squamosal; TY, tympanic; V, vomer.

dentary just above the ventro-posterior angle in the margin of that bone, and at the same transverse plane with the anterior tips of the surangular, prearticular and angular (cf. sections of Gorgonopsia—Broom 1930, plate 31, sect. 16–20; Therocephalia—Broom 1936*a*, plate 7, figure 96). The pterygoid elements in mammals retain this relation, which is particularly clearly shown in late foetal stages of, for example, Marsupials.

Consideration of the probable evolution of the mammalian palate, lower jaw, basis cranii and brain case from the Theriodont condition has thus suggested the following conclusions:

(i) The snout region and the dentary have been comparatively little modified, and may be regarded as fixed references for other movements.

(ii) The posterior part of the basis cranii has moved forwards relative to the snout.

(iii) The squamosals have been reduced in size and moved forwards.

(iv) There has been some posterior movement of the pterygoid and ectopterygoid.

(v) There has been a notable morphological shortening of the post-dentary region, the posterior part of the pterygoids, and the orbitosphenoid, but this shortening does not extend to the skull roof.

(vi) The changes in jaw and palate are such that the spatial relations between the remnants of the pterygoid flange and the postero-ventral part of the dentary are little changed from the Theriodont conditions, and in foetal mammals the relations of the pterygoid elements to the remnants of the post-dentary bones are very Theriodont-like.

The changes mentioned in (v) above are particularly interesting, since they are strongest ventrally and slight or absent on the dorsal aspect of the skull. There has been a plastic compression of a natural region of the skull, lying between the snout and dentary in front, and the basis cranii and squamosals behind. It is possible to regard this in two ways. On the one hand there may be perceived a change of growth gradients in the evolutionary sequence; on the other, functional changes of more or less definable character may be correlated with the structural difference. From the embryological point of view a most significant feature is the small sign of such proportional changes during ontogeny; the mammal skull is "mammalian" in proportion at an early stage.

Whatever degree of correlation may be inferred between changes in skull structure and musculature, it should be emphasized that neither change can yet be regarded as consequent upon the other; the causation of the changes almost certainly involves many other factors.

In conclusion, the main changes in structure of the mammalian palate may be tabulated, and tentatively correlated with one another and with functional changes (see table). In this way the interdependence of many apparently distinct processes is emphasized.

TABLE 2

	Evolutionary changes in palatal view of mammalian skull	Correlated with
(1)	Expansion of brain case	Growth in size of brain
(2)	Changes in jaw musculature, including (*a*) reduction of reptilian pterygoideus (*b*) forward movement of reptilian adductor externus	See (3), (4), (5), (7), (10), (12), etc.
(3)	Reduction of pterygoid bones	(2*a*), (8), (12)
(4)	Anterior displacement of anterior root of zygomatic arch	(2*b*)
(5)	Movement of ectopterygoid to form *Echidna*-pterygoid, and finally part of the pterygoid bone of ditremata	(2*a*), (2*b*); posterior movement correlated with (2*a*), mesial movement with (2*b*) (see text)
(6)	Posterior extension of bony walls of naso-pharyngeal passage	See (5); probably also correlated with need for protection of the naso-pharyngeal passage against pressure of muscle bellies
(7)	Reduction of reptilian postorbital bar	(2*b*), (4)
(8)	Forward movement of posterior basis cranii with respect to the snout	(3)
(9)	Change in attitude of the occiput	(8); probably also neck musculature
(10)	Forward movement and reduction in size of squamosal	(8)
(11)	Formation of new squamoso-dentary articulation	(10)
(12)	Reduction in post-dentary bones	(11)
(13)	Loss of parasphenoid	Descent of presphenoid? Lack of necessity of strong dermal buttress?
(14)	Appearance of sphenethmoid complex (presphenoid) in palatal view	(1), (3), (13)

VI. SUMMARY

1. The direct evidence of palaeontology shows that the Triassic Theriodonts possessed vomers and palatine processes directly comparable with those of mammals, and that these were developed from the reptilian prevomers and premaxillae respectively.

2. It is claimed that there is no evidence to show that the structures evolved in the Theriodont nose were ever changed.

3. It is shown that the fundamental assumptions on which the embryological evidence for the parasphenoid-vomer homology rest are quite untenable in the light of the resulting conclusions; or when the embryology of the Chelonia is taken into account; or when other structures besides the paraseptal cartilages are used as guides. The whole theory therefore rests on an entirely unreliable basis.

4. The embryological data can be interpreted more easily to fit the original "prevomer"-vomer homology.

5. The term "prevomer" is synonymous with vomer, and must lapse.

6. The homology of any mammalian pterygoid element with the lateral wing of the reptilian parasphenoid is similarly analysed and shown to be erroneous.

7. The "mammalian pterygoid" and "*Echidna*-pterygoid" of monotremes are shown to be homologous respectively with the pterygoid and ectopterygoid of the Theriodonts and other reptiles.

8. The pterygoid of ditrematous mammals is found to include the homologue of the reptilian pterygoid; the ectopterygoid is occasionally represented separately, usually it is fused with the pterygoid. In some it may possibly be absent.

9. The fate of the reptilian parasphenoid in mammals is discussed, and it is concluded that the element is probably reduced altogether in normal mammals. Median splints present in certain forms are regarded as true parasphenoid vestiges.

10. The mutual relations of the palate and lower jaw are considered, with special reference to musculature and to changes in proportion.

ADDENDUM (*April* 26*th*, 1940)

Since this paper was written there has been published a detailed account (White 1939) of the osteology of *Seymouria*, which has long been regarded as an almost perfect transitional stage between the Labyrinthodont Amphibia and the Cotylosaurian Reptiles. The new account differs from previous ones in important respects. The front of the palate is now known to be less aberrant than is indicated in our figure 2C; the interpterygoid vacuity is closed; and the shape of the ectopterygoid is somewhat different. The most important changes concern the parasphenoid, which has large laterally directed processes reaching to the fenestra ovalis. In spite of the apparent similarity to the wings of the lizard parasphenoid, the lateral extensions in *Seymouria* are of a different nature. They are not applied to the postero-ventral surfaces of the basipterygoid processes, and do not cover the Vidian nerve or internal carotid artery; they do not meet the pterygoids. Indeed, the conditions in *Seymouria* would closely resemble those in *Captorhinus* (figure 12A) if the fenestra ovalis in that form were to be carried far laterally, carrying the pro-otic, opisthotic and parasphenoid in unchanged mutual relations. These conditions do not, therefore, oppose the views advanced above. Instead they show that lateral extensions or wings of the parasphenoid have probably been derived independently in different groups of reptiles. White regards *Seymouria* as a specialised archaic form which did not give rise to any higher reptiles.

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