

## The Pterygoid and Ectopterygoid in Mammals

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**Summary.** A dorsal pterygoid element and a ventral ectopterygoid element can be recognised during the development of monotremes, marsupials and eutherian mammals. Their homology with the elements so named in fossils ancestral to mammals can be established by positional evidence. In monotremes the elements remain distinct and show specialised features, including a hamular cartilage in the ectopterygoid of one specimen of *Ornithorhynchus*. In most higher mammals the pterygoid element is much reduced and is replaced anteriorly by the perpendicular plate of the palatine. Posteriorly the pterygoid element fuses with the ectopterygoid, in many cases before the onset of ossification. The hamular cartilage arises by chondrification within the ectopterygoid element and shows no sign of being a separate morphological entity, but must be regarded as a specialised feature associated with the architecture of the palatal musculature. There is a strong case for the value of recognising that the 'pterygoid process' of higher mammals includes both a pterygoid and an ectopterygoid moiety.

**Key words:** Pterygoid – Ectopterygoid – Mammals – Cynodonts.

### Introduction

Since Fawcett (1905) described the embryology of the pterygoid bone (medial pterygoid plate) in man, it has been accepted that this structure is formed from separate dorsal and ventral elements, developing in membrane and cartilage respectively. This acceptance is reflected in standard textbook accounts of human anatomy (eg. Gray, 1973), but is not universally treated in recent texts on vertebrate structure and evolution (eg. Carter, 1967 p. 408; Alexander, 1975, Figs. 12/17). An obvious consequence of Fawcett's discovery is that the pterygoid of man cannot be adequately represented by its reptilian homonym, since the reptilian pterygoid is without question a single and very ancient structure which develops as a membrane bone.

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The homology of the two elements of the mammalian pterygoid is of interest not only to the academic anatomist, but also to the embryologist and to the palaeontologist. It is surprising, therefore, that there has been no attempt to reconcile the palaeontological account of Parrington and Westoll (1940) with the conflicting embryological treatment of de Beer (1937). The problem is given additional interest by the demonstration, by Gaupp (1908), of the existence of two separate pterygoid-like membrane bones in the monotreme *Tachyglossus aculeatus*. From that time onwards numerous attempts have been made to identify the primordia of the mammalian pterygoid not only with the two bones of the monotreme but also with separate ossifications in reptiles. Agreement was not easily reached, and the conclusions of different authors are summarised in Table 1, which is modified and extended from that of de Beer (1929).

Some of the difficulties may be initially clarified by considering the three heads of Table 1. Although at first sight these animal groups appear to be quite natural, we believe them to imply both *too sharp an antithesis between the three and too close a similarity within each group*, than the morphology of the region makes obvious. Thus the relative positions of the two elements of the pterygoid complex in *Ornithorhynchus* is arguably 'eutherian', whereas the larger, flatter plate of bone forming the ventral element in *Tachyglossus* gives a strong immediate impression of the 'reptilian' ectopterygoid. Within the eutheria the 'transpalatine' of *Dasyurus* advertises its claim to this identity so blatantly that it has been labelled accordingly (Broom, 1914). A visual presentation of the positions of the elements to be considered is given in Figure 1 (A–E).

It may be concluded from Fig. 1 that the pterygoid and ectopterygoid are represented as shown in all the three groups of tetrapods of Table 1; this was argued most cogently by Parrington and Westoll in 1940. At the time they wrote, they could reduce the possible homologues that were worthy of serious discussion to: the epipterygoid; the detached lateral wing of the parasphenoid (basitemporal); the pterygoid; and the ectopterygoid. They were then able to raise overwhelming objections to the claim that any part of the epipterygoid was included in the pterygoid complex. Thus the possibilities remaining were: that the dorsal element of all mammals was either the reptilian pterygoid or the lateral wing of the parasphenoid, and the ventral element of all mammals was the pterygoid or the ectopterygoid. They showed palaeontological evidence that the dorsal element was derived from the pterygoid of cynodonts, and that the ventral element must therefore be the ectopterygoid. In this paper we advance embryological reasons to support this view, to supplement the evidence of Parrington and Westoll. This confirms that there is value in recognising two elements in the pterygoid complex throughout mammals and that both of these elements are associated with the first visceral arch and not with the wall of the braincase, and both occupy homologous positions within that anlage throughout mammals.

## Materials and Methods

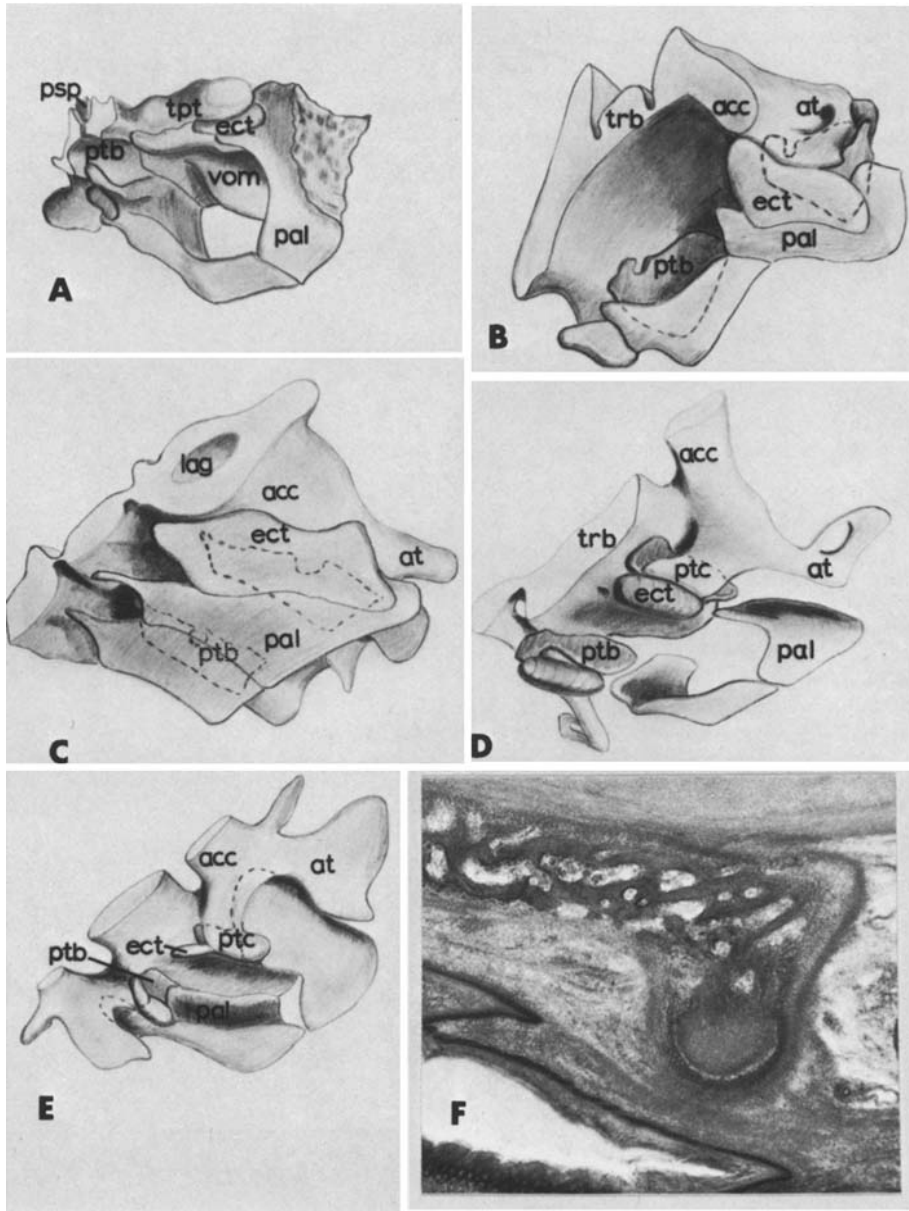
The material employed in this study consisted of serially-sectioned mammalian embryos or their heads. The sections were, in most cases cut transversely to the basicranial axis and were either 10 µm paraffin

Table 1

	Reptile			
	Monotreme	Ventral "echidna pterygoid"	Basitemporal (Laterobasal) (Lat. Wing of Parasphenoid)	
Ditrematous mammals			Epipterygoid	Ectopterygoid
	Dorsal "mammalian pterygoid"			Pterygoid
Pterygoid (Unitary)	Gaupp 1908 Kesteven 1918 Watson 1916	Fuchs 1910 van Kampen 1905	Gaupp 1908	Fuchs 1910 Kesteven 1918 Watson 1916 van Kampen 1905
Dorsal element of complex pterygoid	Broom 1914 de Beer 1929 Goodrich 1930 Jollie 1962 Kuhn 1971 Lubosch 1907 McIntyre 1967 Parrington and Westoll 1940 Stadtmüller 1936 van Bemmelen 1901 <i>Present paper</i>		de Beer 1929 Goodrich 1930	Broom 1914  Jollie 1962 Kuhn 1971 Lubosch 1907 McIntyre 1967 Parrington and Westoll 1940 Stadtmüller 1936 van Bemmelen 1901 <i>Present paper</i>

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Palatine (perpendicular plate)	Fuchs 1910					
Alisphenoid (tympanic wing)	van Kampen 1905	Kesteven 1918 Watson 1916	van Kampen 1905	Kesteven 1918 Watson 1916		
Entotympanic (or absent)	Gaupp 1908 Reimbach 1952					Gaupp 1908
Basitemporal of <i>Cavia</i>			Parker 1887			



**Fig. 1A–F.** Graphic reconstructions to show the posterior palates of **A** *Thrinaxodon* (from sections in Fourie, 1972), **B** *Ornithorhynchus* 122 mm CR, **C** *Tachyglossus* 27 mm HL, **D** *Rattus* 16 mm CR, **E** *Sorex* 11 mm CR. Abbreviations: *acc* alicochlear commissure; *at* ala temporalis; *ect* ectopterygoid; *pal* palatine; *ptb* pterygoid bone; *psp* parasphenoid; *ptc* pterygoid cartilage; *tpt* transverse process pterygoidei; *trb* trabeculae cranii. **F** shows a parasagittal section through the ectopterygoid of *Ornithorhynchus* (295 mm snout-tail) to illustrate the cartilaginous hamulus present in this specimen

series, stained by Masson's Trichrome technique or, in the case of larger embryos, the head was bulk-stained with Haematoxylin and Eosin and sectioned in low-viscosity nitrocellulose at 60  $\mu\text{m}$ .

Graphic reconstructions were made using Peter's (1922) oblique-view method. Specimens used in this study, with collector's synonyms in parentheses.

### 1. Monotremes

*Tachyglossus aculeatus*: H.L. 14 mm/38 mm CR; H.L. 21 mm/56 mm CR; H.L. 27 mm/78 mm CR; 98 mm CR.

*Ornithorhynchus anatinus* (snout-tail lengths): 28 mm; 56 mm; 80 mm; 122 mm; 140 mm; 170 mm; 200 mm; 225 mm; 250 mm; 295 mm.

### 2. Marsupials

*Didelphys virginiana*: (crown-rump length (straight)): 33 mm CR; 42 mm CR; 14 mm CR; 24 mm CR; 49 mm CR; 35 mm CR.

*Macropus sp.*: 8 mm H.L./25 mm CR.

*Trichosurus vulpecula*: 12 mm H.L./32 mm CR; 27 mm H.L./65 mm CR.

### 3. Eutherian mammals

*Erinaceus europeus*: H.L. 7 mm; 9 mm; 13 mm; 14.5 mm.

*Felis catus*: Newborn.

*Mustela domestica*: 15 mm H.L.

*Meriones unguiculatus*: 6 mm H.L.; 12 mm H.L.

*Hipposideros puttalam*: CR: 8 mm; 10 mm; 13 mm.

*Mus musculus*: aet. 11, 12, 14 days and 14 mm CR.

*Myotis tricolor*: CR 7.5 mm; 10 mm; H.L. 12 mm/CR 24 mm.

*Sus scrofa*: CR. 4.8 mm; 8 mm; 12 mm; 15 mm; 20 mm; 32 mm; 36 mm; 40 mm; and 7 somite; 16 somite.

*Potamogale velox*: 11 mm/24 mm; 13 mm/29 mm; 16 mm/?C.R.L.

*Rousettus leschenaulti* (*Pteropus seminudus*): 8 mm/15 mm; 9 mm/17 mm.

*Oryctolagus cuniculus*: preosseus.

*Rattus norvegicus*: CR 16 mm; newborn.

*Tadarida sp.* (*Nyctinomus sp.*): CR 3 mm; 4.5 mm; 7 mm; 8.5 mm; 10 mm; 11 mm; 12 mm; 14 mm; 15 mm; 16 mm; 18 mm.

*Sorex araneus* (*Sorex vulgaris*): 4.5 mm; 6.5 mm; 7 mm; 8.5 mm; 9.5 mm; 11 mm; and juvenile male H.L. 20 mm.

*Talpa europea*: 8 mm/16 mm; 13 mm/28 mm.

*Dasyptes hybridus* (*Tatusia hybrida*): 32 mm CR.

## Embryological Findings

### a) Evidence for Two Elements

In each of the specimens examined it is possible to recognise a dorsal element (pterygoid of this paper) and a ventral element (ectopterygoid of this paper) by shape and position but in many specimens these elements are fused. The dorsal element is lamelliform, lies parallel to the wall of the nasopharyngeal duct and has its dorsal edge in contact with the basicranium behind the palatine. The ventral element is in all cases thicker and rounder in overall shape. It lies ventral to the pterygoid element, whose ventral edge makes contact and often fuses with its upper surface. Its more ventral position brings it into the plane of the sides of the soft palate, just caudal to the horizontal part of the palatine bone (palatine process) and

medial to the tensor veli palatini muscle. In the Ditre mata, with the exception of *Dasy pus*, the ventral element contains hyaline cartilage, often a very large proportion of its substance; an endochondral ossification centre occurs ventrally in it but addition of perichondral membrane bone occurs more dorsally, near the junction with the pterygoid element.

In many of our series of embryos the collection is not sufficiently complete to establish the developmental sequence of events leading to the ossification and fusion of these elements, but we can confidently assert the following patterns:

(i) Two blastemata, ossifying separately and never fusing: *Ornithorhynchus Tachyglossus*.

(ii) Two blastemata, fusing after ossification or chondrification: *Talpa; Erinaceus, Sorex, Meriones, Rattus*.

(iii) Two blastemata, fusing before ossification or chondrification: *Trichosurus, Didelphys, Rousettus, Hipposideros, Tadarida*.

In each case the boundary between ectopterygoid and pterygoid was as distinct as that between the palatine and the two former bones. We regard this as strong evidence that there are two morphological elements to be considered throughout the mammals.

The relationships of the palatine, pterygoid and ectopterygoid to the palatine nerve and the floor of the chondrocranium are shown in Fig. 3. The positional equivalence of the ectopterygoid in each case is clear. In ditremes its posterior extent is less than in monotremes. In the latter, the pterygoid is extensive, though with different relations to the braincase in platypus and echidna (Kuhn, 1971). Its anterior part, related to the sphenopalatine ganglion, is replaced by the perpendicular plate of the palatine in ditremes (Fuchs, 1910). Its posterior part varies considerably in extent, and seems to include the 'basitemporals' of Parker (1885).

#### *b) Evidence that Both Elements Belong to the Upper Jaw Anlage*

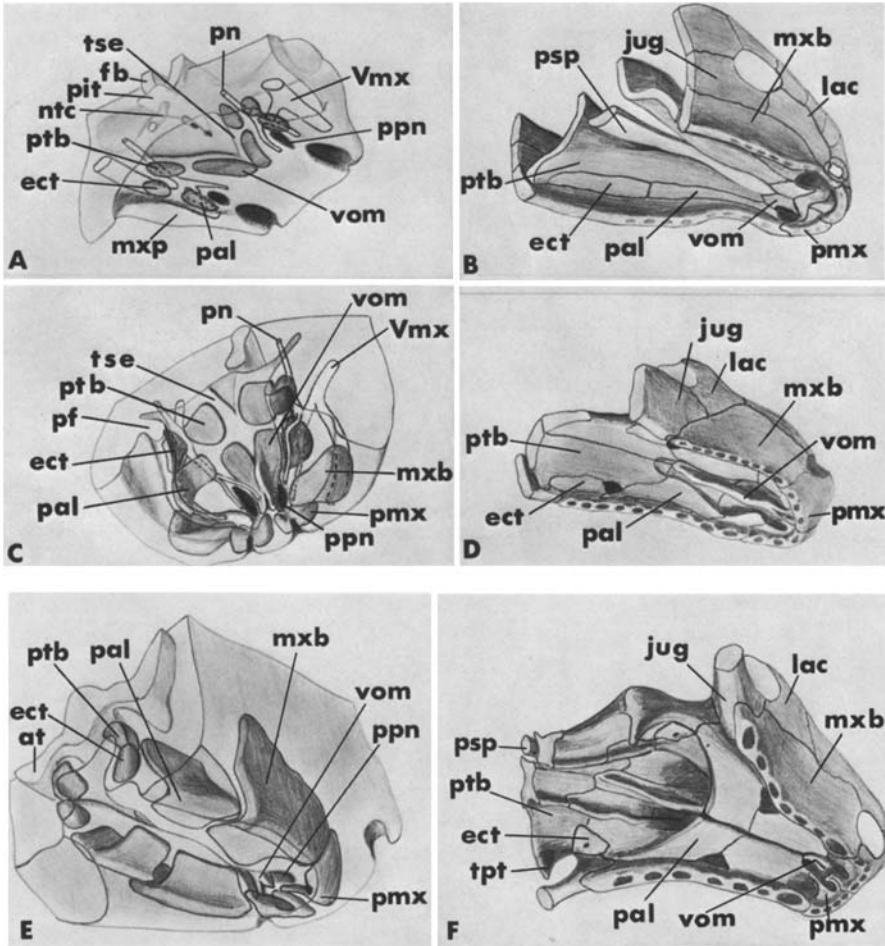
In our series of *Mus, Sus, Tadarida* and *Sorex* we have been able to confirm the existence of, and trace the fate of, the tecto-septal extension of the maxillary process of first arch mesoderm, described by Frazer (1931). The roof of the stomatodaeum of the early embryo has a thin layer of diffuse mesoderm, derived from the prochordal plate, covered by a low epithelium. One tecto-septal extension appears from the inner aspect of the maxillary process and grows to the mid-line to meet the other first in the region of the primitive nasal septum and then gradually further back to form a complete extra layer of mesoderm in the roof of the mouth as far as the tubo-tympanic recess, so closing off the mouth of Rathke's pouch. In the early embryo this mesoderm may be recognised as more dense than the prochordal mesoderm, and by the thicker oral epithelium which covers it.

The tecto-septal mesoderm becomes subdivided into anlagen consistently associated with one another and with the regional nerves (Fig. 2):

The vomer lies medially placed and anteriorly, deep to the nasopalatine nerve. Its blastemata are at first bilateral, but before ossification fuse across the mid-line.

The pterygoid lies medially, caudal to the sphenopalatine ganglion, with the Vidian nerve deep to it.

The palatine lies lateral to the vomer, anterior to the ganglion and ventral to the greater palatine nerve.



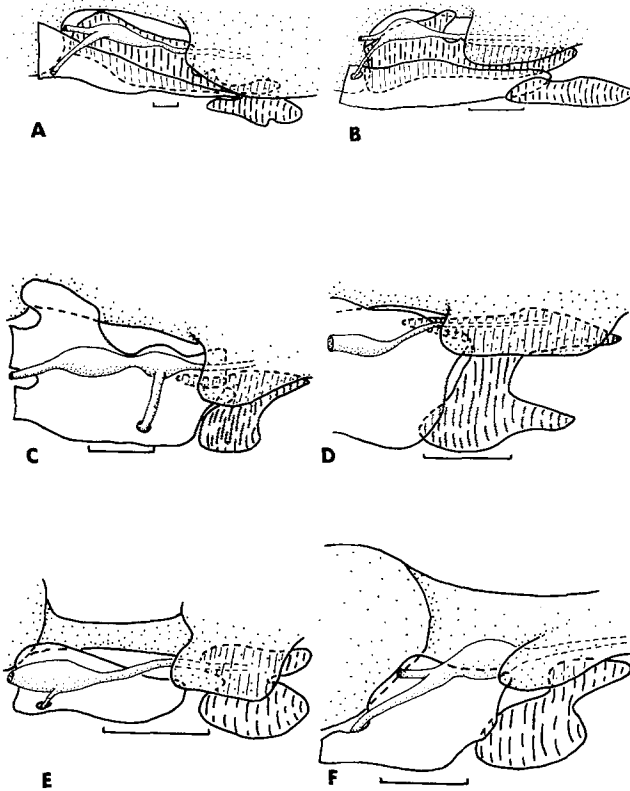
**Fig. 2A–F.** Three stages of palate formation in pig embryos are compared with the structure of fossil skulls. **A** 12 mm pig, **B** *Eusthenopteron* – an osteolepid crossopterygian, **C** 20 mm pig, **D** a theriocephalian, **E** 36 mm pig, **F** a galesaurid cynodont. *Abbreviations:* *at* ala temporalis; *ect* ectopterygoid; *fb* forebrain; *jug* jugal; *lac* lacrymal; *mxb* maxilla (bone); *mxp* maxillary process; *npd* nasopharyngeal duct; *pal* palatine; *pf* palatine fold; *pit* pituitary; *pn* palatine (nerve); *pmx* premaxilla; *ppn* posterior primary naris; *psp* parasphenoid; *ptb* pterygoid (bone); *tse* tecto-septal exterior; *vom* vomer; *Vmx* maxillary nerve (V)

The ectopterygoid lies lateral to the pterygoid, posterior to the ganglion, dorsal to the lesser palatine nerves and with its dorsal edge ventral to the pharyngeal rami of the ganglion.

*c) Evidence that the Parasphenoid is Not Associated with the Pterygoid Element*

A small parasphenoid is recognisable in each of our *Didelphys* specimens. The pterygoid element has a medial edge which is continued in fibrous connective tissue





**Fig. 3A–F.** Graphic reconstructions showing from the lateral aspect the outlines of the posterior end of the palatine (white), pterygoid (dorsal element, hatched) and ectopterygoid (ventral element, hatched), and the Vidian nerve, sphenopalatine ganglion and some of its branches. The outlines of the deepest portion of the chondrocranium, nasal capsule and ala temporalis (pterygoid process) are indicated (coarse stipple). Scale line: 1 mm. **A** *Ornithorhynchus*. **B** *Tachyglossus*. **C** *Trichosurus*. **D** *Didelphys*. **E** *Meriones*. **F** *Erinaceus*. Note that where pterygoid and ectopterygoid are fused, no boundary between the elements may be drawn with accuracy, although a constriction in the outlines indicates the boundary approximately in each case.

to the mid-line to meet its fellow. Although the bone of the parasphenoid lies in the same plane as the bone of the medial edge of the pterygoid, the tissue connecting the pterygoids curves ventrally as it approaches the mid-line, to pass beneath the parasphenoid. This shows that the pterygoids do not lie in the same morphogenetic plane as the median parasphenoid.

*d) Evidence that the Mammalian Vomer is Not a Parasphenoid*

Our series of platypus show that the dumb-bell bone of this species, which has been alleged to be the vestige of the reptilian (pre-) vomer (de Beer and Fell, 1936), is in origin a palatine process of the premaxilla. There is clear continuity between the premaxilla and the dumb-bell bone in our series of S.T. length 80, 122, 170 and 200 mm, but in specimens of S.T. length 140, 225, 250 mm the attenuated

connection between the body of the premaxilla and the dumb-bell bone breaks down, leaving the two elements separate in the adult. Our specimens include the series of a 122 mm embryo examined by de Beer (1936) and our interpretation of this series is that while there is a short break between the bony lamellae in the connecting strand, as described by those authors, there is no break in the periosteum: thus in this specimen the two components may be just about to separate, but no evidence is provided for the view that each element is, prior to this, a distinct developmental entity. We therefore support the view of Green (1930) in this matter, contrary to the opinion of de Beer.

*There is therefore in no mammal an additional pair of elements between the vomer and the premaxilla, and thus the vomer(s) in all mammals occupy an homologous position to those of reptiles.*

*e) Secondary Cartilage in the Ectopterygoid of the Platypus.*

One specimen (295 mm S.T. length, one side of head only available) shows a small rounded projection from the ventral surface of the ectopterygoid. Its histological appearance is very similar to that of the hamular cartilage of ditrematous mammals (Fig. 1F).

## Discussion

### *General*

The establishment of homology between elements requires consideration of four lines of evidence: homology of anatomical position, homology of developmental anlagen, homology (within the fossil evidence available) of common phylogenetic origin and, where potentially metameric structures are being compared, of serial homology in metameres. In the case of the pterygoid problem, the last consideration arises only if elements are recognised both within the first visceral arch (eg. pterygoid or ectopterygoid) and outside the anlage of that arch (eg. parasphenoid). In the present paper we seek to establish by use of the first three lines of evidence that in mammals pterygoid and ectopterygoid lie within first arch tissue: if that demonstration proves valid then the question of serial homology needs no formal discussion.

### *The Existence of Two Elements*

The chief fascination of the problem is brought into sharp relief by reading Table 1, or the account and table in Stadtmüller. It becomes clear that many of the older authors, including Gaupp, treated the pterygoid of ditrematous mammals as a single morphological entity. Although many subsequent writers have discussed this problem in terms of two elements (following the pioneering work of Lubosch (1907), Broom (1914) and Fawcett (1905)) wherever phylogeny has been considered, it must be recognised that excellent comparative embryology papers such as Roux (1947), Reinbach (1952), Schneider (1955) join Gaupp, at least by implication, in treating the ditrematous pterygoid as a single entity.

Consideration of our embryological findings shows why this should be. If an author is describing elements after the onset of ossification and chondrification, then only the monotremes and possibly some specimens of edentates (Broom, 1914) will show obviously discrete elements for an appreciable period. In the ditremata an early fusion of the two elements is the rule, and in very many species this fusion takes place prior to any formation of bone or cartilage. In reconstructions of the cranium in subsequent stages both elements will be within a single periosteum and the only indication of the 'dual' nature of the pterygoid will be where a distinction between bone and cartilage is made: *this is probably not the true boundary*. Since the majority of papers on the developing cranium concentrate on the analysis of differentiated anlagen it is reasonable that description of this region should treat only 'the pterygoid' of ditrematous mammals.

Our embryological findings show the disadvantages of this classical treatment: in the pre-cartilaginous stages of many of our specimens it is clear that two distinct aggregates of mesoderm arise in the caudal part of the tecto-septal mesoderm and, although they fuse early, the more dorsal and medial anlage gives rise to the flat, membrane-bone, component of the pterygoid, while the ventral anlage gives rise to the more rounded hamulus which (with exceptions, eg. *Dasypus*) contains a large proportion of cartilage. All the authors cited in this paper recognise these two components of the pterygoid descriptively and we take this recognition as meaning that their prime observations were in no way in conflict with ours. We therefore maintain that it is valid, for the purposes of morphological analysis, to regard the pterygoid of ditrematous mammals as a composite of two elements.

### *Histogenesis of the Elements*

Until late in development both elements in our monotremes are membrane bones. It is of interest, however, that there is secondary cartilage in that part of the ectopterygoid of our largest platypus which is related to the tensor veli palatini muscle. In our *Dasypus*, where the two elements are fused in a tiny posterior isthmus of synostosis (Edgeworth, 1923), each is membrane bone. In the advanced stages of all our other specimens the ectopterygoid element contains a substantial amount of cartilage. When mature, we can find no criterion by which this cartilage might be judged to be 'secondary cartilage' on histological grounds (contra de Beer, 1937). However, in a number of early specimens (especially clearly in a 16 mm rat), the matrix in each element stains in an identical manner, and in this rat each anlage has undoubtedly appeared as a core of membrane bone before any cartilage in the ventral element.

From this we infer that it is reasonable to homologise the vicinity of the hamulus of the 'pterygoid' with an ancestral membrane bone. Support for this is found not in its mature histology but in the contrast, soon after its chondrification, between it and the adjacent ala temporalis, a true component of the chondrocranium. This contrast is seen even in de Beer's specimen of *Sorex* (1929), cited by Reinbach (1952) in support of the possibility that the hamulus is a detached portion of the pterygoid process of the ala temporalis.

### *The Position of the Elements*

Inspection of the figures clarifies the skeletal relationships to be considered. Of the recent animals, in each case the 'pterygoid' or dorsal element lies medial to a ventrally and medially projecting portion of the ala temporalis (processus pterygoideus or 'pterygoid cartilage'). In the monotremes this association is very close and the ossification spreads from the pterygoid into the subjacent cartilage of the ala temporalis. Comparison with the cynodont *Thrinaxodon* shows that membrane bone in this position could very well be derived from that portion of the pterygoid which lies above the pharynx and includes the pharyngeal ridges of the fossil. (It is tempting to go further and to speculate on the relationship between the prominent transverse process of the pterygoid in cynodonts and the pterygoid cartilage of the ala temporalis of mammals: this will be discussed in a future treatment of the ala temporalis.)

Concerning the ventral element, demonstrably a reptilian ectopterygoid in the cynodont by the evidence of a phylogenetic series (Parrington and Westoll, 1940), the similarity between it and the flat 'ectopterygoid' of *Tachyglossus* is striking, as is also the case in Broom's edentates (1914). By position and development there can be no doubt that the ectopterygoids of *Tachyglossus* and the platypus are homologous; and the similarity of position between the latter and the eutheria is quite clear. Further evidence of the positional similarity is provided by the relationship of the elements to the Vidian nerves. The problem of the Vidian nerve and canal has been discussed extensively by Fuchs (1910). In the monotreme the nerve is medial to the pterygoid at the caudal end, but passes between the dorsal edge of the pterygoid and the neurocranium to lie lateral to the pterygoid as it runs forward to the sphenopalatine ganglion. In ditremes the usual course of the Vidian nerve is, as in Man, entirely dorsal and lateral to the pterygoid, but in the rodents where the pterygoid develops caudally, close to the level of the otic ganglion, the Vidian nerve lies on the medial or pharyngeal surface of the early pterygoid. This suggests that within the Ditremata there may have been divergences from a basic pattern similar to that of the monotremes.

De Beer (1929) showed that in *Sorex* the ventral element fuses at a procartilaginous stage with the pterygoid cartilage of the ala temporalis, while the dorsal element remained a discrete membrane bone. He argued from this that there was a close association in development between the ventral element (his reptilian pterygoid) and the cartilage of the upper jaw as represented by the ala temporalis, proving the ventral element to be a pterygoid. But since he considered this to be an advanced character in *Sorex*, it is not clear why the same argument could not equally support the case for the ventral element being an ectopterygoid, a possibility which de Beer mentions and does not exclude in his subsequent discussion. We have examined de Beer's specimens, and agree entirely with his descriptive findings, but differ from him in interpretation. The elements concerned are distributed at the time of early ossification very similarly in the shrew and the rat (with the proviso that at this stage the ventral element is membrane bone in the rat and cartilage abutting on the pterygoid process of the ala temporalis in the shrew). Fig. 1 shows this similarity of position: there can be no case for doubting the homology of the respective elements in the two cases, but the rat shows that at least

in one mammal both elements are histologically equivalent at this stage: in the shrew the subsequent histological differentiation is proceeding more rapidly. This shows the danger inherent in generalising from one species. It must be presumed that the rat is displaying a more primitive state at this stage of development and thus that each element is equally likely to have been, phylogenetically, a membrane bone related closely to the cartilage of the upper jaw.

### *The Homology of the Anlagen of the Elements*

With the recognition of the existence of two elements, and the demonstration of their reasonable positional resemblance to the pterygoid and ectopterygoid of mammal-like reptiles, it remains to establish whether the development of these anlagen follows a pattern which might reasonably have been followed in the embryos of their fossil ancestors, and whether any ambiguity in homologies can be excluded. We regard the association of both elements with the tecto-septal extension of maxillary process mesoderm as very important in this respect. In his commentary on the osteological significance of this anlage, Frazer (1931) notes that it may be expected to give rise to the vomer and pterygoid medially, and to the palatine and ectopterygoid (transpalatine) more laterally, and we here confirm that this is the case. Although it seems clear from his text that Frazer recognised the phylogenetic importance of this observation, he did not illustrate a phylogenetic series, and so we present here our Fig. 2 in which the position of the anlagen at three stages of development of this roofing mesoderm may be compared with the roof of the mouth of three fossils which may reasonably be regarded as representing stages close to the actual evolution of the mammalian mouth, nasal septum, and palate. The correspondence in position of the elements is very striking: *it is indeed tempting to postulate that each fossil shows the limit of the tecto-septal extension reached in its own ontogeny*. The different behaviour of the roofing mesoderm in the different classes of vertebrates and its correlation with the structure of the skeleton in this region is a large question which will be extensively treated elsewhere, but we state here with confidence that in all the vertebrates we have studied both the pterygoid and the ectopterygoid arise within the posterior part of the tecto-septal extension. It is therefore probable that these elements arose within that anlage in the vertebrates ancestral to mammals, and this is an embryological reinforcement of the argument of homology by position.

The parasphenoid, both in those mammals which possess it (Fuchs, 1910, Starck, 1967), and in those other classes which have it, does not develop from the tecto-septal extension: indeed it seems, at least in all tetrapods, to arise from the prochordal mesoderm which underlies the basicranium and is therefore probably not a derivative of the first visceral arch (or indeed any visceral arch). This seems to us conclusively to exclude such a parasphenoid from the ancestry of any part of the mammalian pterygoid.

There remains, however, the possibility that some of the bone which in the fossil antecedents of mammals is regarded as a parasphenoid, could have developed in the tecto-septal extension and therefore, while not being the homologue of the parasphenoid of modern reptiles, could have given rise to a median vomer (not the reptilian vomer) and left its more posterior and lateral portions as the dorsal

component of the pterygoid complex in mammals. The only support for this far-fetched concept, which seems implicit in de Beer's homologies if seen in the light of our own findings, would be the existence of a separate median or paired entity, representing the reptilian vomer, in the front part of the tecto-septal extension in mammals, between the mammalian vomer and the premaxilla. De Beer (1936) recognised such an element in the dumb-bell bone of the platypus and argued that since it was homologous by position to the reptilian 'pre-vomer' it was indeed a vestige of that structure and the mammalian vomer was thereby a 'parasphenoid' (median); the dorsal pterygoid element the lateral wings of the 'parasphenoid', and the ventral element therefore the reptilian pterygoid. However, on examining de Beer's specimens and a number of others, we can find nothing to support de Beer's (1936) rejection of the view of Green (1930) that the dumb-bell bone is at first a portion of the anlage of the premaxilla. If this be the case, then the mammalian vomer is by position a reptilian vomer and similarly pterygoid and ectopterygoid fall into place both by position and development. No need remains, either, to explain why the therapsids leading to mammals should have developed a 'parasphenoid' within their maxillary mesoderm, in distinction to all other vertebrates.

#### *Homology by Phylogeny*

The paper by Parrington and Westoll (1940) reviews commandingly a great deal of palaeontological evidence in support of the homologies being advocated in this paper. We are not aware of more recent findings which throw doubt on their overwhelming case for these homologies, and their demonstration of the improbability of the 'parasphenoid' argument which had become, at the time they wrote, the only serious alternative. How serious an alternative it is can be understood by reading the almost contemporary reviews of Stadtmüller (1936) and de Beer (1937). We do not propose to present any further comment on the evidence of Parrington and Westoll than to state that the principal purpose of the present paper is to show that the embryological support for their case is very strong indeed.

#### *Evolutionary Implications*

It is impossible to comment with certainty on the significance of the possession by cynodonts of a separate pterygoid and ectopterygoid. At that stage in therapsid evolution the pterygoid is still an extensive element in the upper jaw whose structure, and especially the persistence of a basipterygoid joint, suggest the possibility of kinesis; while palatine fenestrae, bounded by pterygoid medially and ectopterygoid posterolaterally, are large in primitive therapsids, although typically absent in cynodonts. The retention of two distinct elements in monotremes may therefore be regarded as a primitive feature. However, while the pterygoid itself may retain its primitive relations to surrounding skeletal elements and to the Vidian nerve, it is interesting that the ectopterygoid of *Tachyglossus* has specialised along lines broadly resembling those of the armadillo, while that of the platypus is much more like those of true mammals, even possibly to the extent of showing cartilage in relation to the tensor palati muscle. We regard it as significant that wherever the

tendon of that muscle is so placed as to change its angle of pull around the hamulus, the hamulus is cartilaginous. We therefore attribute the origin of the secondary cartilage in the ectopterygoid to its special role in the mechanics of the secondary palate: specifically to act as a "pulley". Where the ectopterygoid serves mainly as an element of the hard part of palate, it remains a membrane bone. It follows that the membrane bone is the primitive state of the ectopterygoid, and the cartilaginous hamulus represents an advanced character-state in mammalian evolution.

It is also clear that the pterygoid proper has been much reduced in extent between cynodont and mammal. During this reduction it has been replaced anteriorly by the palatine, and posteriorly has become fused with the ectopterygoid. This fusion may provide firmer support between the braincase and the palate for the tensing action of the palatal muscles.

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