

THE METOTIC CARTILAGE AND THE METOTIC FISSURE IN THE PENGUIN.

M. J. TOERIEN

Department of Anatomy, University of Stellenbosch

INTRODUCTION

According to Crompton's (1953) description of the ontogeny of the chondrocranium of the jackass penguin (*Spheniscus demersus*), this form differs from other birds in certain aspects of the development of the metotic region; 1) The development of the metotic cartilage is unique as it appears to be a process of the ear capsule and 2) the vagus nerve leaves the skull through a foramen in the basal plate and not through the metotic fissure.

In view of the usual similarity in the mode of development of the chondrocranium of birds such wide divergence in the development of one form seems remarkable.

This paper describes an attempt to elucidate these problems by experimental means. The procedure adopted is that of suppression of the development of the cartilaginous auditory capsule by extirpation of the ear placode. Similar experiments are well known and have been carried out in a variety of vertebrates. In the absence of the ear capsule the relative contributions of the remaining structures to the configuration of the otic region can be analyzed.

MATERIAL AND METHODS

Fresh eggs of *Spheniscus demersus* were obtained from the Government Guano Islands Division during May to July 1965 and incubated for 72 hours at 99F. The upper auditory placode was then removed from each embryo. (Head torsion in the penguin embryo, unlike that of the chick, can be either to the left or to the right.) The very tough amnionic fold covering the greater part of the body had to be cut through to reach the ear placode. At this stage of development the placode forms a deep depression with vertical sides. It is easily removed by means of glass needles and sharpened watchmaker's forceps. Considerable bleeding was encountered but this did not affect the mortality unduly.

Six operated embryos were raised and sacrificed at various stages of development between 16 to 20 days of incubation. The normal incubation time is about 40 days. The heads were sectioned at 20μ and stained with chromotrope II and haematoxylin. Graphic reconstructions were made of the chondrocrania of some of the specimens.

RESULTS

- (1) The membranous and cartilaginous labyrinths and the acoustic nerve are absent on the operated side in all but one specimen in which the ear capsule is partly developed.
- (2) The footplate of the columella is deficient.
- (3) The metotic cartilage on the operated side equals in size that of the normal side.
- (4) The metotic cartilage is attached to the skull base and
- (5) the VIIth, IXth and Xth cranial nerves leave the braincase through separate foramina (Fig. 1).

DISCUSSION

The absence of the ear capsule and the deficiency of the columellar footplate is consistent with results obtained in the majority of other vertebrates where similar operations were performed and need not be discussed further (for references see Toerien 1965a and 1965b).

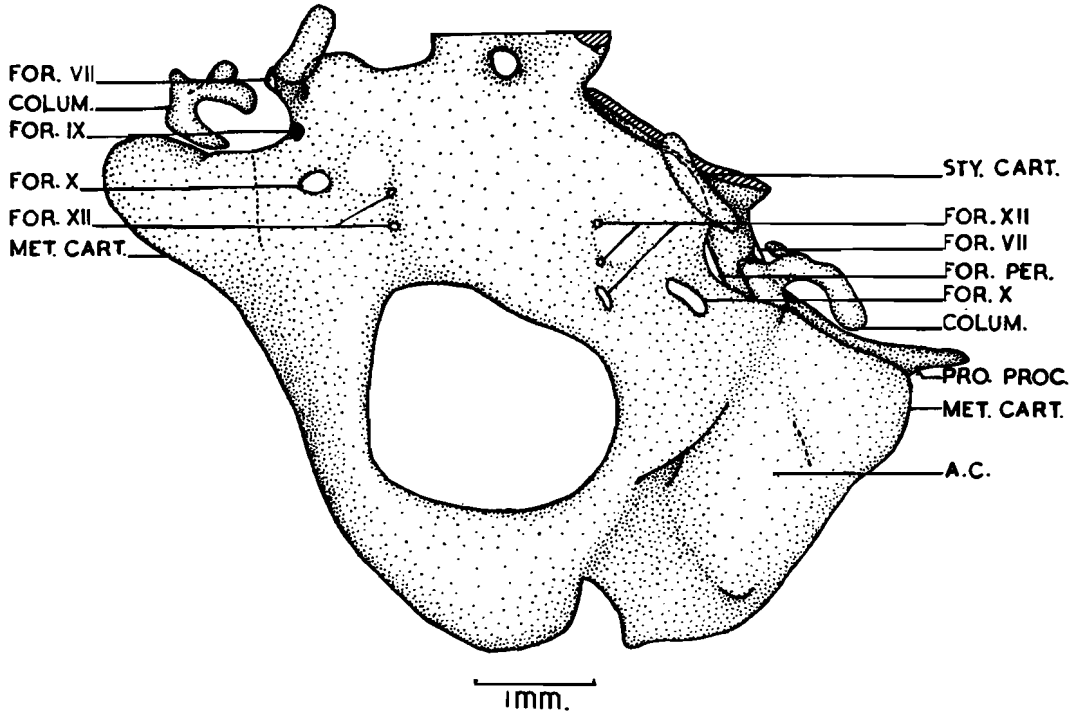


Figure 1. Ventral reconstruction of skull base of 18 day embryo of *Spheniscus demersus*. The lines of demarcation between metotic cartilage and skull base are indicated by broken lines. Colum., columella auris; A.C., auditory capsule; For. VII–XII, foramina for cranial nerves; For. per., periotic foramen; Met. cart., metotic cartilage; Pro. proc., prootic process; Sty. cart., stylohyal cartilage.

THE METOTIC CARTILAGE

This structure is a characteristic feature in birds but has also been identified in crocodiles (de Beer and Barrington 1934) and chelonians (Toerien 1965a). Several avian morphologists give detailed descriptions of the development of this structure.

In *Anas*, *Gallus* and *Sturnus* (Sonies 1907) and *Struthio* (Frank 1954) it develops as a separate anlage. De Beer and Barrington (1934) suggested that the metotic cartilage is probably a modification of a number of cranial ribs. Suschkin (1899) regarded it as a lateral development of the occipital plate in *Tinnunculus* whereas Crompton (1953) described it as a process of the auditory capsule in *Spheniscus*. According to Engelbrecht (1958) *Pyromelana* presents yet another mode of development. Two separate anlagen are found which eventually fuse. The medial anlage develops in continuity with the occipital region and the lateral part in conjunction with the floor of the otic capsule.

In the later stages of development in birds the metotic cartilage is attached to the auditory capsule, occipital arch and basal plate. It forms the lateral and posterior walls of the cavum metoticum which opens anteriorly towards the middle ear. Ventrally it also forms the floor of the recessus scalae tympani (de Beer and Barrington 1934).

Benoit (1955, 1960) found that the metotic cartilage develops after suppression of the cartilaginous ear capsule in the domestic fowl. Furthermore, judging by his figures, the size of the structure appears not to be affected by the operation. It would therefore seem that in the domestic fowl the cartilage develops independently of the ear capsule as it does in chelonia (Toerien 1965a).

The present experiment shows that in *Spheniscus* too, the metotic cartilage is not of capsular origin and thus disproves Crompton's claim (1953).

The present material does not allow of pronouncing on the validity of the cranial rib theory but this will be dealt with by Lamprecht (in preparation).

THE METOTIC FISSURE

During the early stages of development the glossopharyngeal and vagus nerves leave the brain-case between the skull base and the ear capsule. This (metotic) fissure is later obliterated by a more extensive fusion between capsule and skull base and by the attachment of the base of the metotic cartilage to the occipital plate.

According to de Beer and Barrington (1934) the foramina of the glossopharyngeal and vagus nerves in the fowl and the duck serve to indicate the position of the original fissura metotica and of the line of fusion between the metotic cartilage and the lateral edge of the basal plate. Soies (1907) claims that in these animals the nerves pierce the base of the metotic cartilage. This view was also put forward by Brock (1937) for the ostrich although Frank (1954) states that from the earliest stages the metotic cartilage and skull base are joined in this animal and that it is therefore impossible to decide whether the single foramen for the two nerves lies in or between the two structures.

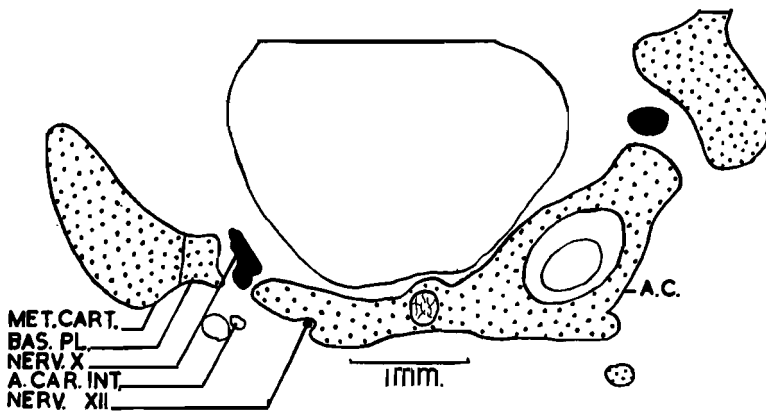


Figure 2. Section through skull base of 18 day embryo of *Spheniscus demersus*. The line separating the metotic cartilage from the skull base is indicated. A. car. int., internal carotid artery; Bas. pl., basal plate; Nerv. X & XII, vagus and hypoglossal nerves. Other abbreviations as in Text—figure 1.

Crompton (1953) describes in detail how the foramen for the vagus nerve in the penguin becomes enclosed by cartilage which proliferates from the basal plate between the vagus and glossopharyngeal nerves. The metotic cartilage is therefore completely excluded from partaking in the formation of the foramen for the vagus nerve. The foramen for the glossopharyngeal nerve is presumably formed by the ear capsule laterally and the basal plate medially and posteriorly. Anteriorly the wall is formed by a fusion of basal plate and ear capsule.

Benoit (1955, 1960) has found that in the absence of the ear capsule in the fowl the IXth and Xth cranial nerves pass through foramina which mark the lateral limit of the basal plate. The other walls are not mentioned but judging from his figures the metotic cartilage plays no part in enclosing the nerves, the lateral wall being formed by the occipital arch.

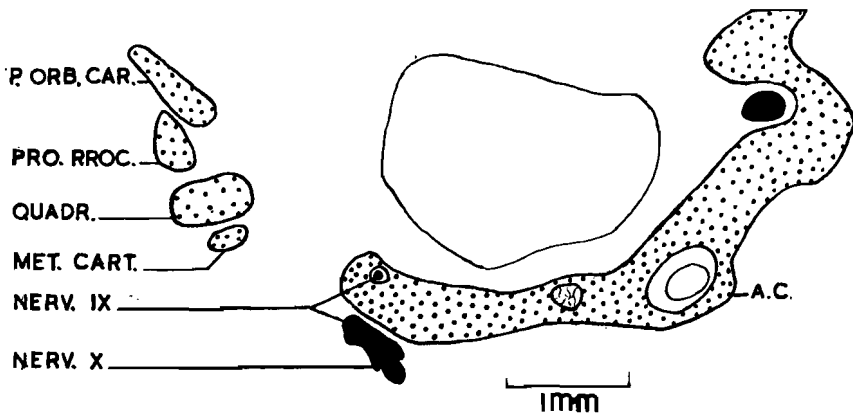


Figure 3. Section through skull base of 18 day embryo of *Spheniscus demersus*. Note the foramen for the glossopharyngeal nerve. P. orb. car., post orbital cartilage; Quadr., quadrate. Other abbreviations as in Text—figures 1 and 2.

In the absence of the ear capsule the relations in the penguin are similar to those in the operated chick as figured by Benoit (1955, 1960). In the embryos sectioned, a fairly definite line of demarcation is found between the metotic cartilage and skull base (Figs. 1 & 2). On the operated side (left side in figures) this line, in conformity with Crompton's description, runs some distance lateral to the lateral border of the foramen for the vagus nerve. On the normal side it is also present but more pronounced posteriorly (Figs. 1).

On the operated side the glossopharyngeal nerve is surrounded by a few cartilage cells where it crosses the lateral border of the basal plate (Figs. 1 & 3). If the boundary between basal plate and metotic cartilage is correctly identified, the cartilage lateral to the nerve cannot be of metotic process origin. In the absence of the ear capsule the nerve must therefore be bare where it crosses the edge of the basal plate as in the turtle (Toerien 1965a) or surrounded by basal plate cells as is presumably found around the vagus nerve. The enclosure of the glossopharyngeus by cartilage could, of course, be the result of the operation and therefore of no morphological significance.

Crompton (1953) states that the medial region of the metotic cartilage is extended forward as a subcapsular process forming the floor of the recessus scalae tympani. However, the

exclusion of the metotic process in forming the walls of the foramina for the vagus-accessory and glossopharyngeal nerves would then also imply that that part of the floor of the recessus scalae tympani traversed by the glossopharyngeus, must be of basal plate origin (Fig. 1).

The facial nerve leaves the skull on the operated side through a foramen similar to that of the glossopharyngeus (Fig. 1). In the fowl (Benoit 1955, 1960) and the turtle (Toerien 1965a) the nerve crosses the edge of the basal plate in the absence of the ear capsule. According to Crompton (1953) the facial nerve of the penguin runs through the wall of the ear capsule (indicating the boundary between the originally separate cochlear and canalicularanlagen). He also states that the prefacial commissure separating the facial canal from the incisura prootica is entirely of capsular origin. It therefore seems that the presence of cartilage cells lateral to the facial nerve is of no morphological significance. It is, however, possible that the prefacial commissure which might be partly supported by the skull base in the ostrich (Frank 1954) is also involved in the formation of the foramen.

CONCLUSIONS.

The present experiment shows that the metotic cartilage of the penguin is not of capsular origin as Crompton maintains but develops independently of the ear capsule as in other birds and in chelonia. On the other hand it tends to bear out Crompton's contention that the vagus nerve passes through a foramen in the skull base. The exit of the facial and glossopharyngeal nerves through foramina on the operated side, probably has no morphological significance.

ACKNOWLEDGEMENTS.

The work reported here was supported by grants from the U.S. National Institutes of Health and the S.A. Council for Scientific and Industrial Research. I am much indebted to Mr. Bosman of the Government Guano Islands Division for help in procuring the eggs and to Mr. de V. B. Lamprecht, Miss H. E. le Roux and Mrs B. van der Walt of this department for technical assistance.

SUMMARY

Some unique features of the otic region of the penguin (*Spheniscus demersus*) skull as described by Crompton (1953) are reinvestigated in the experimentally produced absence of the ear capsule. The origin of the metotic cartilage and the morphology of certain cranial nerve foramina are discussed.

REFERENCES

- BENOIT, J.-A.-A. (1955). De l'excision de l'otocyste chez l'embryon de Poulet, et ses conséquences sur la morphogénèse de la capsule otique cartilagineuse. *C. R. Soc. Biol.*, 149: 988-1000.
- BENOIT, J.-A.-A.- (1960). Etude expérimentale des facteurs de l'induction du cartilage otique chez les embryons de Poulet et de Truite. *Ann. Sci. nat. Zool.*, 12: 323-385.
- BROCK, G. T. (1937). The morphology of the Ostrich chondrocranium. *Proc. zool. Soc. Lond.* 107: 2.
- CROMPTON, A. W. (1953). The development of the chondrocranium of *Spheniscus demersus* with special reference to the columella auris of Birds. *Acta zool., Stockh.*, 34: 71-146.

- DE BEER, G. R. and BARRINGTON, E. J. W. (1934). The segmentation and chondrification of the duck. *Phil. Trans.*, 223: 411–467.
- ENGELBRECHT, D. v. Z. (1958). The development of the chondrocranium of *Pyromelana orix orix*. *Acta zool., Stockh.*, 39: 115–199.
- FRANK, G. H. (1954). The development of the chondrocranium of the Ostrich. *Ann. Univ. Stell.* 30: 181–248.
- SONIES, F. (1907). Ueber die Entwicklung des Chondrocraniums und der knorpligen Wirbelsäule bei den Vögeln. *Petrus Camper*, 4: 395–486.
- SUSCHKIN, P. P. (1899). Zur Morphologie des Vogelskelets. Schädels von *Tinnunculus*. *Nouw. Mem. Soc. Nat. Moscou.*, 16: 1–163.
- TOERIEN, M. J. (1965a). An experimental approach to the development of the ear capsule in the turtle, *Chelydra serpentina*. *J. Embryol. exp. Morph.*, 13: 141–149.
- TOERIEN, M. J. (1965b). Experimental studies on the columellacapsular interrelationship in the turtle *Chelydra serpentina*. *J. Embryol. exp. Morph.*, 14: 265–272.