MORPHOLOGICAL AND EXPERIMENTAL STUDIES ON THE DEVELOPMENT OF THE POSTERIOR WALL OF THE AVIAN FORAMEN MAGNUM

M. J. TOERIEN

*Department of Anatomy, University of Stellenbosch**

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ABSTRACT

In embryos of *Gallus*, *Anas* and *Spheniscus* the posterior wall of the foramen magnum (tectum synoticum) is formed by the fusion of the two independently developing supra-occipital cartilages. Fusion of the supraoccipital cartilage with the ear capsule precedes that between the supraoccipital cartilage and the occipital process. The supraoccipital cartilage intervenes between the occipital process and the ear capsule before fusion of these elements occurs. In *Gallus* the tectum synoticum is secondarily fused to the supracapsular cartilage.

INTRODUCTION

A survey of the literature on the development of the avian occipital region reveals that the formation of the posterior and lateral walls of the foramen magnum is subject to a great deal of variation (Toerien 1972). Two "elements" are usually regarded as being involved either separately or together in the development of a cartilaginous roof for the medulla oblongata: (1) a cartilaginous connection between the posterior poles (canalicular part) of the ear capsules (tectum synoticum) and/or (2) a connection between the occipital arches or processes (tectum posterius). These tecta are described as consisting of either independently developing (sometimes paired) elements (supraoccipital cartilages) or as outgrowths or continuations of the ear capsules and/or the occipital processes.

In an endeavour to analyse the relative contributions (if any) of the ear capsule and the occipital process, normal avian embryos and embryos from which one or both of these structures are absent (57 specimens in total – Table 1) were studied by means of serial sections. To determine the boundaries of the elements contributing to the tectum in all stages of development, is by no means straightforward and use was made of rather subtle ways to delineate the structures. The discreteness of elements was established by the presence of lines of demarcation consisting of layers of flattened mesenchyme and cartilage cells surrounded by relatively little intercellular substance, by differences in staining intensities of regions and by the presence of indistinct peripheries (absence of a perichondrium) of certain parts of the composite structures. The accompanying reconstructions, incorporating these indistinct but consistent boundaries between elements, therefore differ significantly from conventional reconstructions of the avian occipital region at corresponding stages of development.

* Present address: Department of Anatomy, University of the Orange Free State, Bloemfontein.

TABLE 1

	GALLUS DOMESTICUS					SPHENISCUS DEMERSUS		ANAS BOSCHAS	
Age in days	*I* *Normal embryos*	*II* *Both ear capsules absent*	*III* *One ear capsule absent*	*IV* *Occipital arch absent*	*V* *Occipital arch and ear capsule absent*	*VI* *Normal embryos*	*VII* *One ear capsule absent*	*VIII* *Normal embryos*	*IX* *One ear capsule absent*
8	2								
9	5		5	2	1				
10	2			8	2				
11	2		2						
12	2		2					1	1
13	2	1	2						
14	2		2						
15								1	
16						2			
17									
18						2	2		
19									
20						2	2		

MATERIAL AND TECHNIQUES

In Table 1 the numbers of specimens of each species which were available for study, are given.

The absence of the cartilaginous ear capsule and the occipital process is induced by the (usually unilateral) removal of the ear placode (to suppress the development of the ear capsule) and/or the anterior 3 to 6 occipital somites (inhibiting the development of the basal plate and occipital process) on the 3rd day (*Gallus*) or 4th day (*Anas*, *Spheniscus*) of incubation. Some of the specimens listed in columns IV and V (Table 1), were operated by Lamprecht who has described the operating technique (1968). In four only of the specimens listed, is the posterior part of the basal plate (posterior to the vagal nerve roots) completely absent on the operated side. In the remainder of the specimens the basal plate is deficient to a greater or lesser extent and the occipital process absent.

Serial sections, 20μ in thickness, of all the heads were prepared and stained with haematoxylin and chromotrope IIR. Graphic reconstructions of the occipital regions of some specimens were made. The unoperated sides of experimental animals do not differ significantly from those of normal specimens and separate reconstructions of normal animals (except for a 10 day chick) are therefore not given.

THE NORMAL DEVELOPMENT OF THE OCCIPITAL REGION IN *GALLUS DOMESTICUS*

Eight and nine days of incubation (Fig. 1)

The cartilaginous basal plate is in the process of fusion with the chondrified ear capsule. The extent of the fusion varies along the plane of contact. Anteriorly the lateral edge of the basal plate is medially separated from the ventral aspect of the ear capsule by a definite

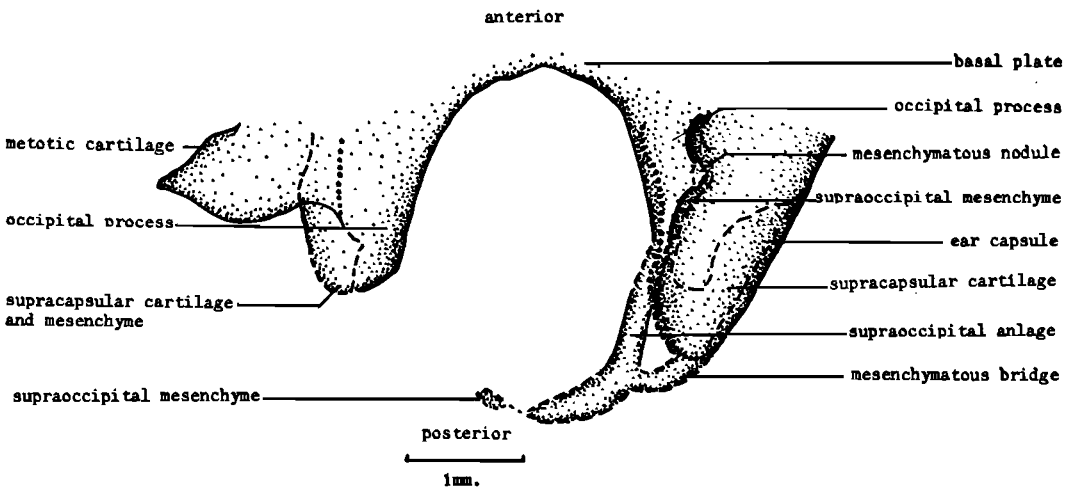

FIGURE 1
Ventral view of reconstruction of the posterior part of the chondrocranium of an 8-day *Gallus* embryo of which the development of the ear capsule has been suppressed unilaterally.

perichondrium whereas more laterally it is separated from the capsule by a relatively unstained layer of mesenchyme. Its extreme lateral edge is separated from the metotic cartilage by a layer of relatively compressed cartilage cells.

The base of the occipital process is distinct from the ear capsule (exoccipitocapsular fissure) and surrounded by a perichondrium. The distal tip of the process consists of a cluster of concentrated (well-stained) cells devoid of intercellular substance. Posteriorly these cells are rather indistinctly (as far as can be determined by means of the transverse sections) separated from that of the anlage of the supraoccipital cartilage which more posteriorly is chondrified. This mesenchymatous connection between the cartilaginous supraoccipital and the occipital process represents the anlage of the occipitosupraoccipital commissure.

The occipital process and the cartilaginous supraoccipital anlage as well as the commissure between them is separated from the medial aspect of the ear capsule by a mass of relatively unstained mesenchyme which passes over imperceptibly into the cartilage of the ear capsule and the supraoccipital cartilage. Near the anterior part of this latter element a few procartilaginous cells seem to be in continuity with both this structure and the ear capsule – anlage of the supraoccipitocapsular commissure. In the region of this commissure, neither the anterior part of the supraoccipital cartilage nor the adjoining (ventral) part of the ear capsule are surrounded by definite perichondria. More laterally the mesenchyme intervening between the ear capsule laterally and the occipital process and supraoccipital chondrification medially, thins out considerably but is nevertheless continuous with a more massive layer of mesenchyme on the postero-lateral aspect of the ear capsule – the anlage of the supracapsular cartilage. Laterally the supracapsular mesenchyme is very diffuse but medially it merges imperceptibly with the capsular cartilage. Between the posterior pole of the ear capsule and the chondrified part of the supraoccipital cartilage, the intervening mesenchyme is deficient. The external occipital vein passes through this hiatus which represents a remnant of the supraoccipitocapsular fissure. The supraoccipital element ends posteriorly near the mid-sagittal plane as a diffuse mesenchymatous tract.

On the lateral edge of the middle part of the occipital process a distinct mesenchymatous nodule is found. A layer of compressed cells which is continuous with the perichondrium around the base of the occipital process separates the nodule from this process. Laterally the peripheral cells of the nodule are very diffuse and become indistinguishable from those of the mesenchymatous mass lying between the occipital process and the ear capsule.

10 days of incubation (Fig. 2)

The fully chondrified occipital process is anteriorly surrounded by a distinct perichondrium whereas posteriorly it is separated from the ear capsule by a zone of relatively unstained cartilage cells. The extent of the posterior tip of the process can be determined by its more intensely stained appearance relative to the surrounding tissue. The anterior part of the chondrified supraoccipital cartilage is continuous with the relatively unstained cartilage cells separating the occipital process from the ear capsule. Posteriorly the two supraoccipital elements are in cartilaginous continuity with each other posterior to the medulla (tectum synoticum). The supracapsular cartilage is chondrified in continuity with the postero-lateral part of the ear capsule but the element can be identified by its indistinct lateral periphery

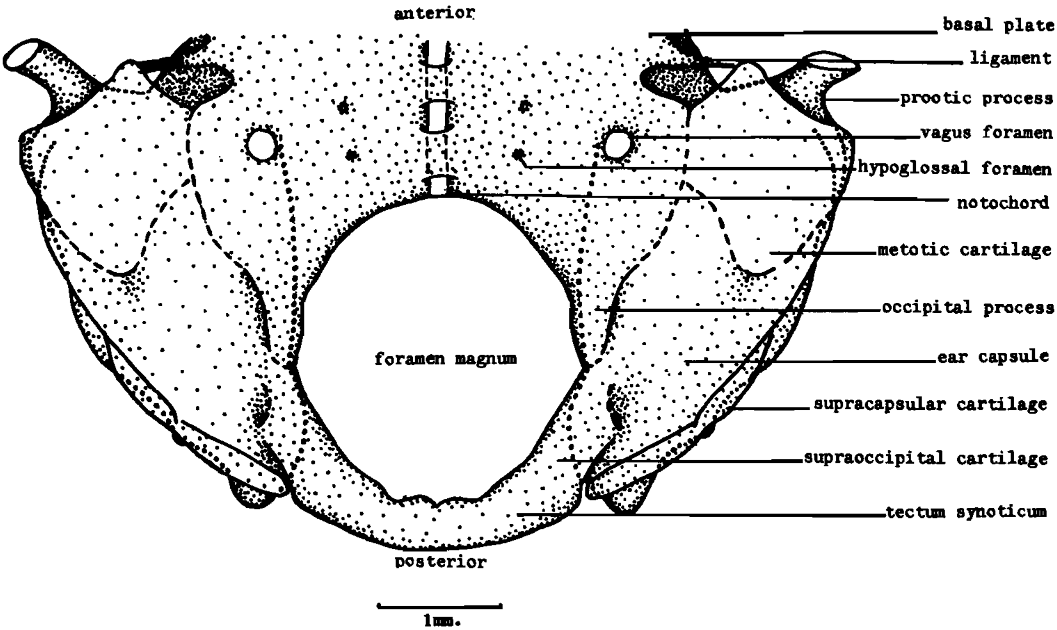

FIGURE 2
Ventral view of reconstruction of the posterior part of the chondrocranium of a normal 10-day *Gallus* embryo.

and its paler colour. The posterior "process" of the supracapsular cartilage reaches the supraoccipital cartilage posterior to the external occipital vein but it is not in cartilaginous continuity with it.

11 and 12 days of incubation (Fig. 3)

The base of the tectum synoticum is chondrified in continuity with the mesenchymatous nodule found lateral to the occipital process in the early stage. This "nodule" which is also in incomplete cartilaginous continuity with the base of the occipital process forms a projection of the latter, lateral to and parallel with the process. Posteriorly the occipital process is almost completely fused to the ear capsule (i.e. to the intervening supraoccipital mesenchyme which has become chondrified in continuity with the ear capsule). The line of fusion is indicated by a layer of slightly compressed cells.

The anterior part of the supracapsular cartilage is discernible as a separate entity by its paler colour and diffuse lateral border but posteriorly it cannot be distinguished from the ear capsule. Posterior to the external occipital vein the tectum synoticum is fused to the ear capsule. This part of the capsule represents the posterior part of the supracapsular cartilage of the earlier stage. This connection between the capsule and the tectum forms an extensive portion of the dorsal part of the lateral wall of the foramen magnum. The occipital sinus is accommodated in the anteriorly directed concavity of the median part of the tectum synoticum.

13 days of incubation (Fig. 4)

The tectum synoticum can no longer on histological grounds be distinguished from the surrounding structures. Posteriorly the tectum has developed into an elaborate median cup-shaped structure. The major part of the lateral wall of the foramen magnum is formed by the connection between the tectum and the originally supracapsular part of the ear capsule.

THE DEVELOPMENT OF THE TECTUM SYNOTICUM IN THE ABSENCE OF THE EAR CAPSULE IN *GALLUS*

Eight and nine days of incubation (Fig. 1)

The occipital process is chondrifying. On the operated side it is laterally attached to a mass of tissue which is likewise in the process of chondrification. The line of demarcation is indicated by an abrupt change in the staining properties of the two structures. The paler stained lateral mass seems to represent the supracapsular cartilage. Laterally its cells are continuous with the metotic cartilage which can be distinguished by being more deeply stained. The supracapsular element extends anteriorly, dorsal to the basal plate and metotic cartilage and ends as a free process at the anterior level of the metotic cartilage. Posteriorly

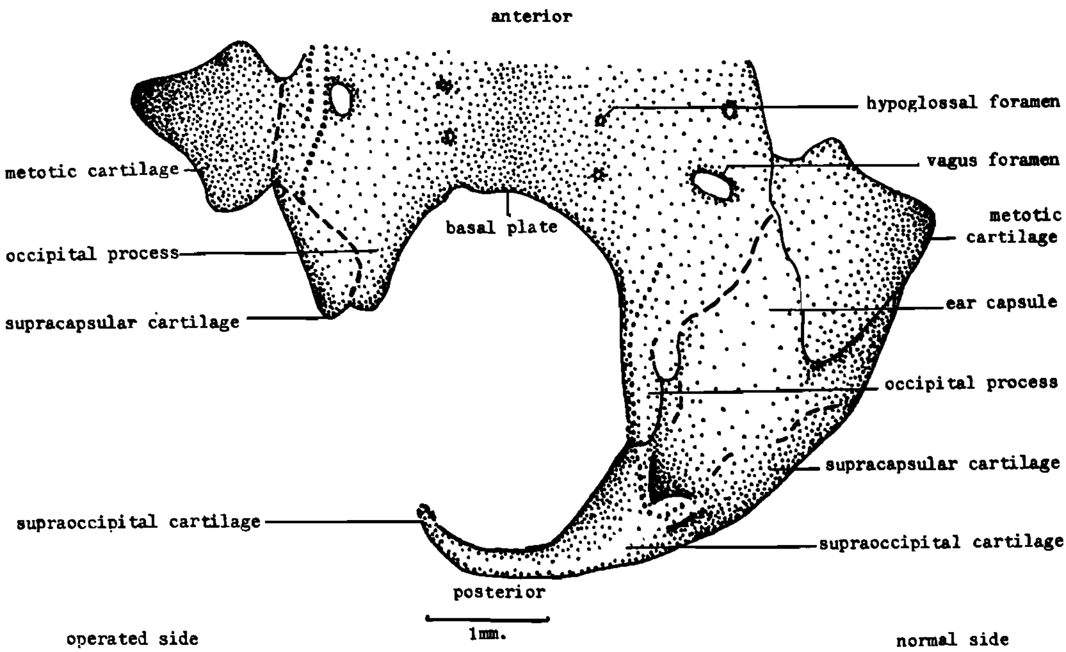

FIGURE 3
Ventral view of reconstruction of the posterior part of the chondrocranium of a 12-day *Gallus* embryo of which the development of the ear capsule has been suppressed unilaterally.

the more procartilaginous part of the supracapsular element does not extend beyond the posterior tip of the occipital process but a faint mesenchymatous continuation can be traced posteriorly for some distance.

Posterior to the medulla a mesenchymatous nodule is found on the operated side which is not clearly separated from the mesenchymatous posterior continuation of the supraoccipital anlage of the normal side. It will be argued that this nodule represents the supraoccipital element of the operated side.

12 days of incubation (Fig. 3)

On the operated side a mesenchymatous tract connects the supracapsular cartilage to the supraoccipital cartilage which is continuous with that of the normal side.

13 days of incubation (Fig. 4)

The supracapsular cartilage of the operated side is in cartilaginous continuity with the supraoccipital cartilage of the same side and the posterior wall of the foramen magnum is completed. As in the preceding stage, the supraoccipital cartilage is less well-developed on the operated side. In a single specimen of which the development of both ear capsules had been

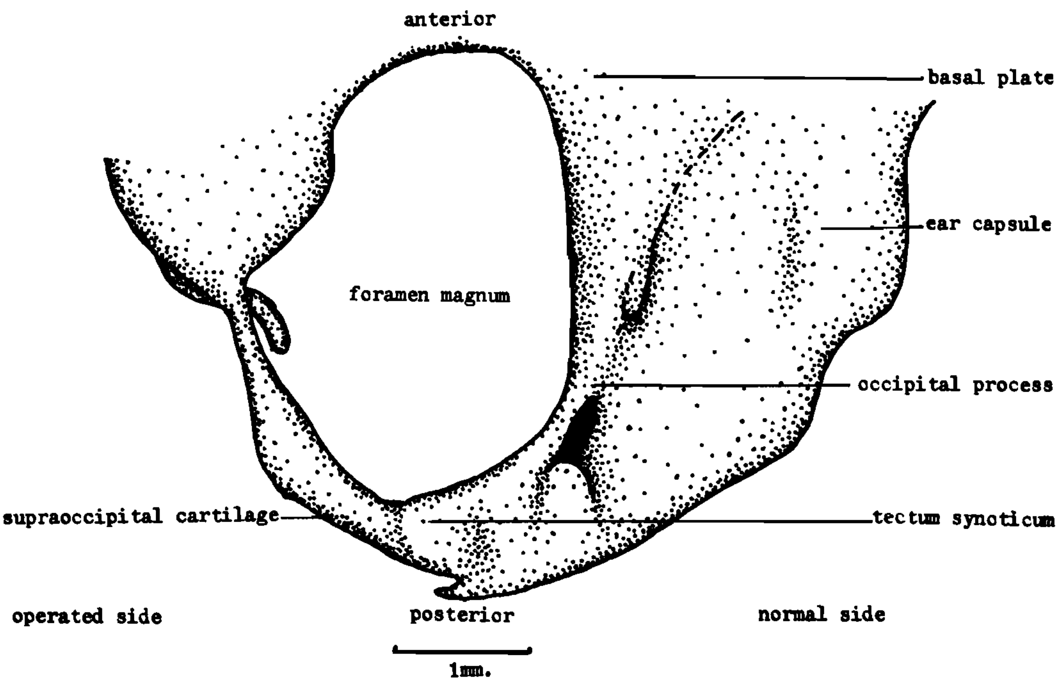

FIGURE 4
Ventral view of reconstruction of the posterior part of the chondrocranium of a 13-day *Gallus* embryo of which the development of the ear capsule has been suppressed unilaterally.

inhibited, the fused supraoccipital cartilages are in cartilaginous continuity with both supracapsular cartilages. In the mid-sagittal plane the tectum is developed into the large anteriorly concave structure which accommodates the occipital sinus.

The lines of demarcation between the supracapsular cartilage, occipital process and metotic cartilage are almost completely obliterated at this stage.

THE DEVELOPMENT OF THE OCCIPITAL REGION IN THE UNILATERAL ABSENCE OF THE OCCIPITAL PROCESS IN *GALLUS*

Nine and 10 days of incubation (Fig. 5)

The ten specimens in this group are not all identical, particularly since the development of the basal plate is not suppressed to the same extent in all specimens. Another variable factor is the extent of the encephalocoel which results from this operation (see below).

A complete cartilaginous posterior wall for the foramen magnum was not encountered in any of the specimens. The width of the gap in the posterior wall is associated with the extent of the encephalocoel. Where the encephalocoel is large the tectum is virtually absent on the operated side while in cases where there is little protrusion of the brain a tectum is better developed. No correlation was found between the size of the tectal remnants and the amount of basal plate cartilage present.

In the specimen figured (Fig. 5, one of four similar specimens) the development of the basal plate (and occipital process) is suppressed to such an extent that the vagus nerve roots pass around the posterior edge of the skull base remnant of the operated side. The encephalocoel is relatively mild and the gap in the posterior wall of the foramen magnum relatively

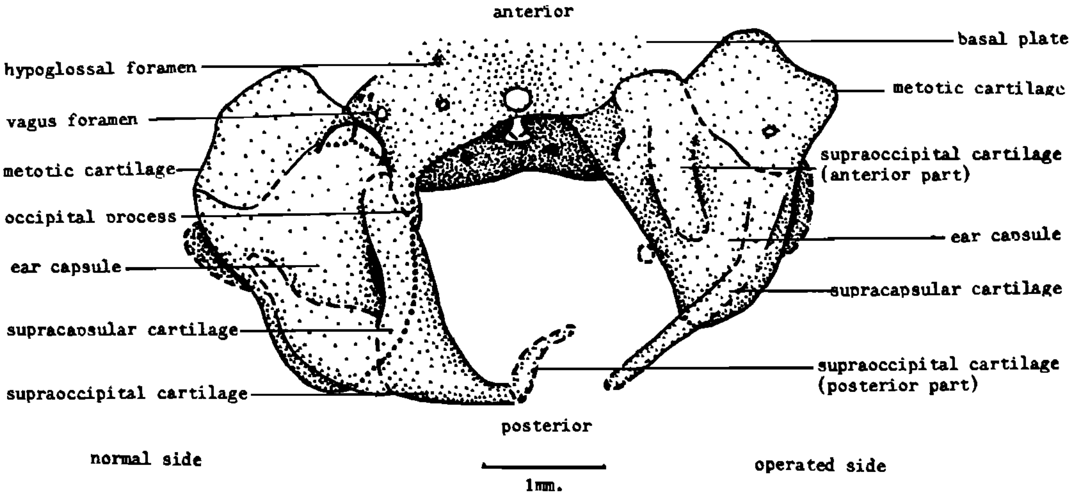

FIGURE 5
Ventral view of reconstruction of the posterior part of the chondrocranium of a 10-day *Gallus* embryo of which the development of the posterior part of the basal plate and occipital process have been suppressed unilaterally.

narrow. The supraoccipital element on the operated side is reduced and seems to consist of an anterior cartilaginous part and a posterior mesenchymatous part continuous with the supraoccipital element of the normal side.

The anterior, relatively unstained supraoccipital element, is partly fused both anteriorly and posteriorly to the darkly stained ear capsule – the line of fusion being indicated by the change in colour of the cartilage cells. The central part of the supraoccipital element is surrounded by a perichondrium.

The supracapsular cartilage extends far postero-medially and partly closes the gap in the posterior wall of the foramen magnum.

THE DEVELOPMENT OF THE OCCIPITAL REGION IN THE ABSENCE OF THE EAR CAPSULE AND THE OCCIPITAL PROCESS IN *GALLUS*

Nine and 10 days of incubation

In the absence of both the occipital process and the ear capsule the supracapsular cartilage and the supraoccipital element seem to be absent as anatomical entities. Neither could remnants of these elements be recognised histologically. The metotic cartilage is much less affected by this operation (Lamprecht 1968).

The encephalocoel is very extensive in these specimens. This feature was found to be directly related to the reduction of the tectal element in those specimens from which only the occipital somites had been removed (see above).

THE NORMAL DEVELOPMENT OF THE OCCIPITAL REGION IN *SPHENISCUS DEMERSUS*

16 days of incubation

The chondrifying occipital process lies on the ventro-medial aspect of the ear capsule. The base of the process can be clearly distinguished from the ear capsule which consists of more mature cartilage cells. The distal part of the process is mesenchymatous and lies on the medial aspect of the posterior pole of the ear capsule and ventral to the anlage of the supraoccipital cartilage. The supraoccipital element can be distinguished from the medial aspect of the posterior pole of the ear capsule by a lesser content of intercellular substance.

Posteriorly the procartilage of the supraoccipital element is replaced by mesenchyme which is continuous with its counterpart of the opposite side, posterior to the medulla. Laterally, ventral to the ear capsule, the diffuse peripheral (mesenchyme) cells of the supraoccipital element pass over into the procartilaginous supracapsular element which lies on the lateral aspect of the posterior pole of the ear capsule. More posteriorly the tectum is separated from the posterior pole of the ear capsule by a deep incisura which is occupied by the external occipital vein. No tectal mesenchyme is found posterior to this vein.

18 days of incubation (Fig. 6)

The cartilaginous occipital process can be clearly distinguished from the ear capsule by a perichondrium anteriorly, whereas posteriorly it is separated from the ear capsule by a zone

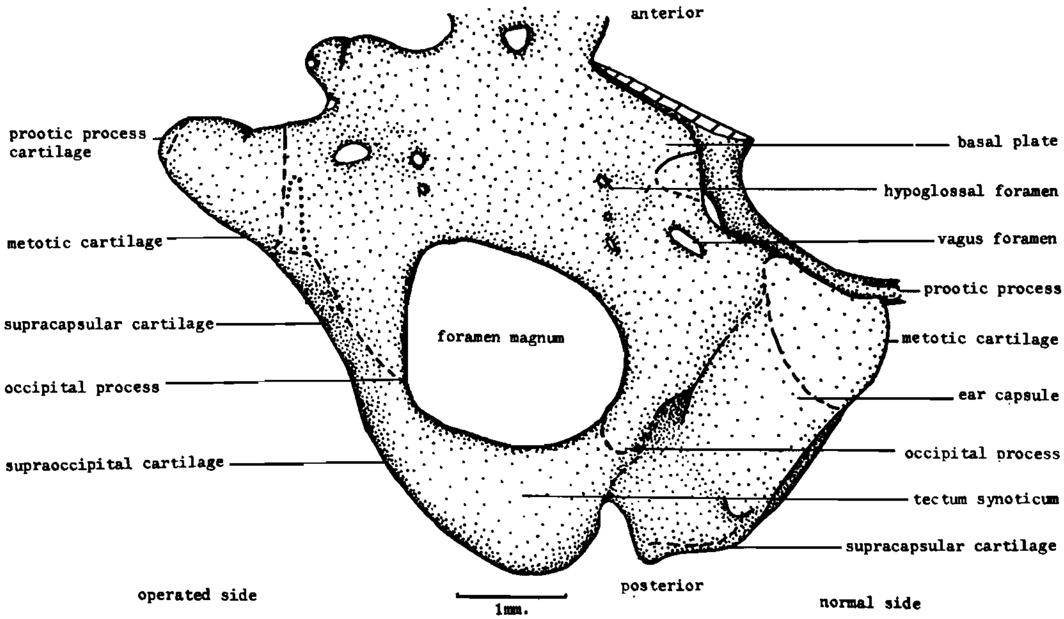

FIGURE 6
Ventral view of reconstruction of the posterior part of the chondrocranium of an 18-day *Spheniscus* embryo of which the development of the ear capsule has been suppressed unilaterally.

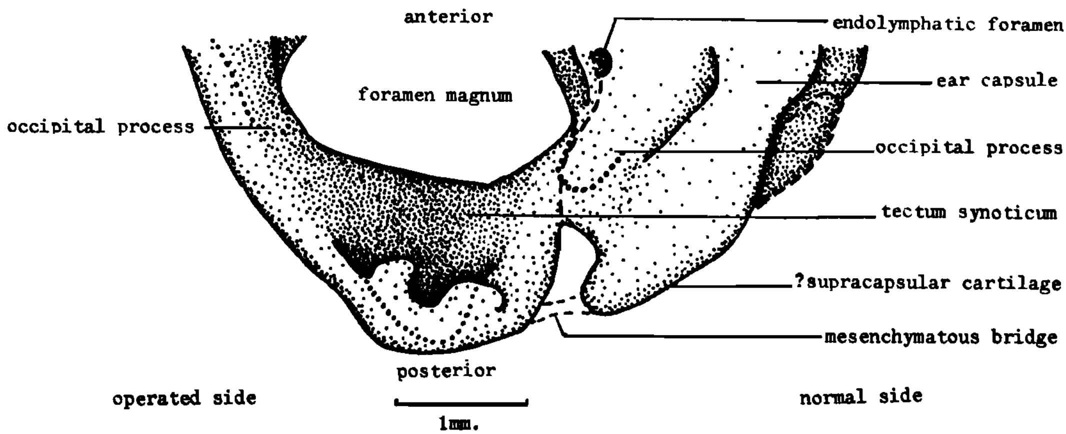

FIGURE 7
Dorsal view of reconstruction of the posterior part of the chondrocranium of a 20-day *Spheniscus* embryo of which the development of the ear capsule has been suppressed unilaterally.

of concentrated cells not surrounded by intercellular substance. These cells pass over into the cartilaginous part of the supraoccipital element dorsally. The latter structure can be readily distinguished from the ear capsule which is more intensely stained.

The posterior part of the broad continuous tectum synoticum is much enlarged and is concave anteriorly. Mesenchyme no longer connects the tectum synoticum (supraoccipital element) to the supracapsular cartilage which can only be recognised as a crest of immature cartilage cells on the postero-lateral aspect of the posterior pole of the ear capsule.

20 days of incubation (Fig. 7)

The line of demarcation separating the supraoccipital cartilage from the occipital process and the ear capsule is indistinct. The weakly stained cells of the supraoccipital element gradually pass over into the more heavily stained cells of the ear capsule. The tectum synoticum is posteriorly produced into a large cup-shaped, mid-line structure which houses the occipital sinus. Posterior to the external occipital vein, mesenchyme connects the supraoccipital cartilage to the posterior pole of the ear capsule. This part of the capsule presumably represents the supracapsular cartilage which in this region can no longer be identified as a distinct entity.

THE DEVELOPMENT OF THE OCCIPITAL REGION IN THE ABSENCE OF THE EAR CAPSULE IN *SPHENISCUS*

18 days of incubation (Fig. 6)

On the operated side the supracapsular cartilage is medially fused to the occipital process and dorso-laterally to the metotic cartilage. The lines of fusion indicated in Fig. 6 are based on the change of staining intensity of the cartilage cells, occurring along these lines. Anteriorly the paler stained supracapsular cartilage is produced into a free process dorsal to the boundary between the basal plate and the metotic cartilage. Posteriorly the supracapsular cartilage is continuous with the supraoccipital which forms with its counterpart, a complete tectum synoticum. On the operated side the tectum is, however, not as well developed as on the normal side.

20 days of incubation (Fig. 7)

The tectum synoticum is extensively developed into an anteriorly directed cup-shaped structure. The line of fusion between the supraoccipital and the supracapsular cartilages is no longer perceptible.

THE NORMAL DEVELOPMENT OF THE OCCIPITAL REGION IN *ANAS BOSCHAS*

12 days of incubation (Fig. 8)

The cartilaginous base of the occipital process is separated from the surrounding tissue by a perichondrium. The cells of the central part of the process are, however, indistinctly separated from a mass of mesenchyme which merges with the cartilage cells of the ear capsule.

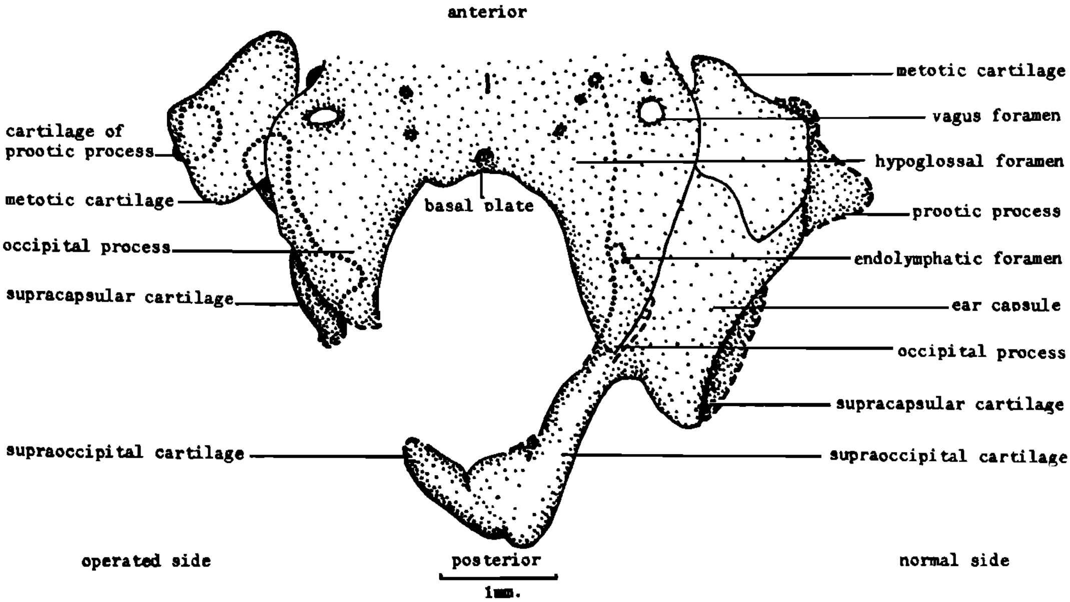

FIGURE 8
Ventral view of reconstruction of the posterior part of the chondrocranium of a 12-day *Anas* embryo of which the development of the ear capsule has been suppressed unilaterally.

Anteriorly the mesenchyme cells extend as far as the endolymphatic foramen and seem to participate in the formation of the superficial part of its posterior wall. Posteriorly the mesenchyme passes over into the chondrified supraoccipital anlage. A lateral continuation of these cells linking up with the supracapsular cartilage could not be definitely established. At this stage of development only the lateral edge of the supracapsular cartilage can be identified. It consists of weakly stained cartilage cells not surrounded by a perichondrium.

The mesenchymatous distal part of the occipital process is clearly distinguishable posteriorly from the cartilaginous supraoccipital element, dorsally from its procartilaginous anterior continuation and laterally from the chondrified ear capsule.

The posterior part of the supraoccipital element is in cartilaginous continuity with its counterpart from the opposite side to form a tectum synoticum. A deep incisura, containing the external occipital vein, is not closed off posteriorly by a mesenchymatous or cartilaginous bridge.

15 days of incubation

The anterior part of the occipital process is clearly separated from the ventral aspect of the ear capsule by a perichondrium. The chondrified distal part of the process is separated from the supraoccipital cartilage and from the ear capsule by a layer of darkly stained mesenchyme cells without or with very little intercellular substance. The supraoccipital cartilage is completely fused to the ear capsule but has lost the connection with its counterpart of the opposite side. The tectum is thus incomplete posteriorly.

The extreme posterior tip of the ear capsule has a diffuse periphery and extends far posteriorly. This region probably represents a part of the supracapsular cartilage since the posterior semicircular canal does not enter it. Posterior to the external occipital vein this posterior extension is in no way connected to the supraoccipital cartilage.

THE OCCIPITAL REGION IN THE ABSENCE OF THE EAR CAPSULE IN *ANAS BOSCHAS*

12 days of incubation (Fig. 8)

The basal plate and the occipital process of the operated side can readily be distinguished from the overlying supracapsular cartilage. The central part of the latter element is in cartilaginous continuity with the occipital process although the line of fusion can easily be determined by a difference in staining intensity. Anteriorly and posteriorly the supracapsular cartilage is completely detached from the occipital process.

A relatively poorly developed supraoccipital cartilage is fused to that of the normal side but it is not connected in any way to the supracapsular cartilage.

DISCUSSION

Normal development of the tectum synoticum in Gallus, Anas *and* Spheniscus

In the three species investigated the supraoccipital cartilage develops as a chondrification in a mass of mesenchyme situated on the medial aspect of the canalicular part of the ear capsule. The mesenchymal mass also lies between the capsule and the occipital process and in *Anas* it reaches the endolymphatic foramen anteriorly. In *Gallus* and *Spheniscus* this mesenchyme is laterally continuous with another mass of mesenchyme which chondrifies as the supracapsular cartilage. In the youngest stages the supraoccipital mesenchyme is not continuous with that of its counterpart of the opposite side.

The supraoccipital chondrification in *Gallus* therefore develops as an independent structure as was observed by Sonies (1907, tectum synoticum) in both *Gallus* and *Anas*. In later stages this chondrification spreads and comes into cartilaginous continuity with the ear capsule and still later also with the postero-ventral aspect of the occipital process. Although Sonies (1907) remarked that the supraoccipital cartilage (tectum synoticum) "früher mit den Ohrkapseln zusammenfliesst als mit den Occipitalplatten (Occipitalbögen)" this is not apparent from his description where it is merely stated that (in both *Gallus* and *Anas*) the supraoccipital (tectum synoticum) is fused to the same region of the ear capsule to which the occipital process becomes attached. De Beer and Barrington (1934) in *Anas* and Crompton (1953) in *Spheniscus* did not observe an independent supraoccipital anlage nor a fusion between the supraoccipital cartilage and the occipital process.

Posteriorly the two cartilaginous supraoccipital elements become continuous (preceded by a mesenchymatous connection) to form a tectum synoticum. In *Gallus* and *Spheniscus* the mid-sagittal part of the tectum, when maximally developed, consists of a cup-shaped structure which is sometimes perforated (Sonies 1907; Crompton 1953). In the duck, however, the tectum breaks down in the midline at an early stage as has also been observed by de Beer and Barrington (1934).

When the mesenchymatous bridge between the supraoccipital cartilage and the supracapsular cartilage (which is also fused to the ear capsule), posterior to the external occipital vein, chondrifies, a second lateral connection of the tectum synoticum is established. This seems to be the only connection between the tectum and ear capsule observed by Tonkoff (1900). He stated that the now cartilaginous tectum synoticum is attached to a narrow ridge of cartilage (presumably the supracapsular cartilage) on the posterior aspect of the dorsal arch of the anterior semicircular canal. De Beer (1937) mentioned both lateral roots of the tectum synoticum in his description of *Gallus* but stated that the hindmost (corresponding to the anterior root in the 12-day specimen, Fig. 3) "gives the impression of being a detached dorsal end of the occipital arch, now attached to the auditory capsule. The remainder of the occipital arch ends freely". In the oldest stages of *Gallus* investigated the posterior root (posterior to the external occipital vein) forms an extensive part of the lateral wall of the foramen magnum.

In *Anas* (Sonies 1907, de Beer and Barrington 1934) and *Spheniscus* (Crompton 1953) a cartilaginous connection between the tectum synoticum and the extreme posterior pole of the ear capsule (supracapsular cartilage) was not observed. However, in my 20 day stage (oldest) of *Spheniscus* a mesenchymatous bridge posterior to the external occipital vein is found which could presumably chondrify in later stages to establish a secondary cartilaginous lateral connection of the tectum with the ear capsule.

The development of a tectum in the absence of the ear capsule and the occipital process

The presence of the supraoccipital cartilage in the absence of the ear capsule shows conclusively that it is not a part of the capsule. In *Gallus* the supraoccipital chondrifies on the operated side in the mesenchymatous nodule posterior to the medulla and spreads anteriorly to become attached and later fused, to the supracapsular cartilage and the occipital process. This connection is relatively weaker than that of the normal side and is established much later. Two factors are probably responsible for this retardation in development: (1) The absence of an ear capsule leaves a much wider gap between the supraoccipital and the supracapsular cartilage to be bridged over. (2) It is possible that the full development of both the supracapsular and supraoccipital cartilages are dependent on (induced by) the normal ear capsule. In *Anas* too the supraoccipital cartilage develops posterior to the medulla on the operated side. In the only operated specimen available (12 day) it is not yet connected to the supracapsular cartilage or to the occipital process but this will doubtless have happened in older specimens.

In the penguin embryo of 18 days the supraoccipital cartilage of the operated side is extremely well-developed and connected to the supracapsular cartilage and occipital process. As is the case in *Gallus* the supraoccipital element will probably be separate from the supracapsular cartilage in younger specimens lacking an ear capsule.

The experimental suppression of the occipital process similarly has no fundamental morphological effect (i.e. in contrast to its mechanical effect as a result of the encephalocoel) on the development of the supraoccipital cartilage and it is clear that the tectum is not a part or a derivative of the occipital process.

Other morphological problems

In *Anas*, *Gallus* and *Spheniscus* the mass of supraoccipital mesenchyme separating in early stages the occipital process from the ear capsule, chondrifies in later stages in continuity with the medial wall of the capsule. When Sonies (1907) therefore found that in *Anas* and *Gallus* the occipital processes are "verbinden" or "vereinigt" with the ear capsule or when Engelbrecht (1958) stated that in *Pyromelana* the dorsal tip of the occipital process is synchondrotically connected to the ear capsule (see, however, Müller 1961, p. 308), it would probably be more correct to state that the occipital process is laterally fused to the intervening supraoccipital cartilage which has already become a "part" of the ear capsule.

The extreme tip of the occipital process is in the stages investigated, not attached or fused to the intervening mesenchyme but to the supraoccipital element which has chondrified independently of the ear capsule and has become fused to it subsequently.

In the species investigated the fusion of the supraoccipital cartilage to the ear capsule precedes that between the supraoccipital cartilage and the occipital process. Sonies (1907) who also observed this sequence in *Gallus* and *Anas* therefore preferred the term tectum synoticum for the structure which forms the posterior wall of the foramen magnum. In most other birds where this region is adequately described the term tectum synoticum is also used to denote this structure (*Gallus:* Tonkoff 1907, Gaupp 1906, de Beer 1937; *Anas:* de Beer and Barrington 1934; *Struthio:* Brock 1937, Lang 1956; *Hirundo:* de Beer and Barrington 1934, de Beer 1937; *Spheniscus:* Crompton 1953; *Pyromelana:* Engelbrecht 1958; *Strix:* May 1961; and *Podiceps:* Toerien 1972). In the latter form the tectum synoticum is at a late stage fused to the occipital process. In *Strix* (May 1961) the tectum is supported (unilaterally at least) by the occipital process and possibly also in the late stages of *Pyromelana* (see Fig. 23 of Engelbrecht 1958) and *Spheniscus* (see Fig. 32 of Crompton 1953).

In another group of birds the occipital processes are joined by the structure which forms the posterior wall of the foramen magnum. Such a tectum posterius has been observed in *Tinnunculus* (Suschkin 1899) and *Apteryx* (de Beer 1937). De Beer (1937) also stated that in *Passer* "the tectum is a tectum posterius" (p. 285) but in the accompanying figure (Plate 102, Fig. 3) and in the earlier work of de Beer and Barrington (1934) the structure is labelled as a tectum synoticum.

In some forms the posterior wall of the foramen magnum is described as a combined tectum synoticum and tectum posterius. However, the posterius part of the combined tectum does not necessarily seem to represent actual outgrowths of the occipital processes. In the specimens described by Slabý (1951a, *Phalacrocorax*; 1951b, *Turdus* and *Ardea*) the tectum appears to be secondarily fused to the occipital process (and the ear capsule) whereas in specimens described by Frank (1954, *Struthio* and *Nyctisyrigmus*) and Müller (1961, *Rhea*) the possibility is mentioned that the cartilage connecting the occipital processes is a part of the tectum synoticum or has developed *in loco* between the occipital arches.

A (mesenchymatous) tectum posterius independent of the tectum synoticum has only been described by Slabý (1951b) in *Turdus*.

CONCLUSIONS

In view of the rather unspecific boundaries between the various developing elements of the occipital region, the widely different descriptions of previous workers are not surprising. However, in view of the almost identical development of this region in the three species here described it is possible that most of the differences between species described earlier will be found to disappear when these are subjected to new investigation.

From the present investigation the following points seem to be evident:

(1) A tectum posterius is not present as an anatomically discrete cartilaginous entity but it could conceivably be regarded as that part of the tectum synoticum which secondarily becomes fused to the tips of the occipital processes. The latter structures are not "prolonged" further postero-dorsally than the lateral walls of the foramen magnum.

(2) Fusion between the occipital process and the "ear capsule" occurs subsequently to the fusion of chondrifying intervening supraoccipital mesenchyme to the medial aspect of the ear capsule.

(3) The supraoccipital elements chondrify as discrete structures. The cartilage spreads posteriorly, preceded by mensenchyme, to become fused in the mid-sagittal plane. Anteriorly the mesenchyme spreads between the occipital process and the medial wall of the ear capsule in the direction of the endolymphatic foramen. This part of the supraoccipital mesenchyme chondrifies in continuity with the medial wall of the ear capsule and subsequently becomes fused to the occipital processes.

(4) In the earliest stage the supraoccipital mesenchyme is continuous with the supracapsular mesenchyme but chondrification does not seem to take place in continuity. Cartilaginous contact between these two elements in the chicken is established secondarily, posterior to the external occipital vein.

De Beer and Woodger (1930) found that in the rabbit the supraoccipital and supracapsular cartilage (parietal plate) develop independently but become fused to each other at an early stage, dorsal to the ear capsule. Müller (1961) stated that in *Rhea* the canalicular part of the ear capsule tends to separate the two elements so that no fusion occurs between them. The development of the avian occipital region as described here differs less from that of the mammal (rabbit) than was assumed by Müller (1961). As has been pointed out above the supraoccipital and supracapsular elements also become fused in the chicken and possibly also in a late stage of the penguin. However, the development of the avian tectum differs from that of the mammal in that in the latter the (originally also paired) supraoccipital elements are fused to the occipital processes prior to their fusion to the supracapsular cartilage (parietal plate). Although the term tectum posterius is therefore preferred for the posterior wall of the mammalian foramen magnum, it does not differ fundamentally from the avian tectum synoticum.

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