THE DEVELOPMENT OF THE CHONDROCRANIUM OF SPHENISCUS DEMERSUS WITH SPECIAL REFERENCE TO THE COLUMELLA AURIS OF BIRDS

BY

A. W. CROMPTON, M.Sc.

(With 38 text-figures)

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PART I

PART I

I. INTRODUCTION

Apart from the works of W. K. PARKER (1866, 1869, 1875 a, 1875 b, 1891 a, 1891 b), T. J. PARKER (1892 a, 1892 b), SUSHKIN (1896, 1899), TONKOFF (1900), SONIES (1907), DE BEER and BARRINGTON (1934) and BROCK (1937) the avian chondrocranium has not received the same amount of attention as, for example, the reptiles, because it was tacitly assumed that the birds represent "a closed phylogenetic group".

Compared with the chondrocrania of other birds that of the penguin is typically avian. This lends no support to the view of LOWE (1933, 1942) that the penguins arose independently from other birds from a primitive reptilian ancestor devoid of the power of flight. CRAIGIE (1940, 1941) has shown that the cortical structure of the penguin cannot be considered more reptilian than avian. The palatal structure of the penguin skull (HUXLEY, 1867, CROMPTON, in press) indicates a close relationship between the penguins and the *Procellariiformes*. SIMPSON (1946) considers the penguins as a group closely related to the *Procellariiformes* which took directly to "submarine flying" from aerial flight, without the intervention of an intermediate terrestrial stage.

The first part of this paper is devoted to a study of the development of the chondrocranium and the second is concerned with related morphological problems.

Particular attention has been paid to the development and comparative anatomy of the avian columella auris. Only fragmentary descriptions of the development of this structure in birds have been given by SUSHKIN (1899) for the kestrel, SONIES (1907) for the duck and fowl, SMITH (1905) for the pigeon and DE BEER and BARRINGTON (1934) for the duck. Unfortunately it was not possible to obtain the work of SCHESTAKOWA (1934) on the development of the avian columella auris.

II. MATERIAL AND TECHNIQUE

The penguin embryos for this investigations were collected and sent to me by Mr. W. RAND of the Government Guano Islands. All specimens were fixed in 12 % formalin.

As the age of the embryos could not be ascertained, they were classified according to length (tip of beak to cloacal opening). In many cases, however, this did not prove to be a correct criterion of age, larger embryos proving on microscopical investigation to be younger than smaller ones.

Serial sections were made of a nestling, and embryos of the following lengths: 170 mm., 150 mm., 135 mm., 120 mm., 104 mm., 91 mm., 83 mm., 74 mm., 61 mm., 61 mm., 58 mm., 56 mm., 54 mm., 52 mm., 51 mm., 47 mm., 47 mm., 43 mm. and 34 mm. With the exception of the 56 mm., 54 mm., 51 mm., 47 mm. and 43 mm. embryos, these were all sectioned transversely.

Most young specimens were decalcified in Ebner's solution, while for several of the older embryos concentrated HNO_3 dissolved in 70 % alcohol in the proportion 6: 100 was employed.

The specimens were stained in toto with borax carmine, or Mayer's basic haemalum solution. In the younger stages counterstaining of the sections with azan was not a success, the entire section staining a homogeneous pale blue. The same applied, to a lesser degree, for the older embryos decalcified in Ebner's solution. However, in the older embryos decalcified in alcoholic HNO_3, excellent differential staining was obtained with azan.

In order to concentrate on the staining of cartilaginous tissue the Nowikoff method, redescribed by DE VILLIERS (1922) was employed. The embryo is stained in toto with borax carmine and the sections are counterstained with a strong solution of bleu de Lyon dissolved in 70 % alcohol and an aqueous solution of Bismarck brown. It is essential when employing this technique to control accurately the staining and differentiating times in the different solutions in order to obtain satisfactory results. In some cases, together with Bismarck brown and bleu de Lyon, the sections were lightly stained with carbol fuchsin which intensifies the brown colour given to the cartilage by Bismarck brown and stains the nerve fibres a light pink. Overstaining with carbol fuchsin should be avoided.

Fairly satisfactory results were obtained with embryos stained in toto with basic haemalum, and the sections stained with Bismarck brown and carbol fuchsin. The employment of carbol fuchsin in the staining technique is particularly helpful in the identification of procartilage. Together with Bismarck brown, this tissue stains a light reddish-brown.

The "projection method" of PUSEY (1939) was employed for the preparation of graphic reconstructions. Further, Pusey's contour method was frequently employed.

To elucidate many difficult features in the cranial morphology, wax-plate reconstruction models were prepared of the skull of the 58 mm. stage, the posterior region of the nasal capsule of the 74 mm. stage, the posterior region of the skull of the 91 mm. stage, the nasal capsule of the 150 mm. stage, and of the columella auris of the duck.

For comparative anatomical details of the avian columella auris, serial sections of a developmental series of the genus *Anas,* sectioned by F. J. GREWE, a young embryo of the South African nightjar (*Nyctisyrigmus pectoralis pectoralis*) sectioned by Dr. M. E. MALAN of the Zoological Institute Stellenbosch, a young embryo of *Stuthio* sectioned by Dr. G. T. BROCK, and a nestling starling sectioned by Prof. C. G. S. DE VILLIERS were available.

By the courtesy of Prof. H. STEINER of the Zoological Institute of Zürich it was possible to study serial sections of a 15 day embryo of the emu (*Dromiceius novaehollandiae*).

III. ACKNOWLEDGEMENTS

The present investigation was carried out under the supervision of Prof. C. G. S. DE VILLIERS, whom I wish to thank most sincerely for his constant assistance and advice. I am very grateful to Prof. C. A. DU TOIT for his personal interest and valuable criticism, especially during Prof. C. G. S. DE VILLIERS's absence.

I am further deeply indebted to the Council for Scientific and Industrial Research for a research scholarship, without which this work could not have been undertaken.

To the following I wish to record my cordial thanks: Mr. R. W. RAND, for the collection of penguin material, Prof. STEINER, for serial sections of a 15 day emu embryo, to Mr. D. N. S. VAN EEDEN, for assistance given in the preparation of wax-plate reconstruction models.

CHONDROCRANIUM OF SPHENISCUS DEMERSUS

IV. DESCRIPTION OF NINE DEVELOPMENTAL STAGES

A. STAGE I

(Figs. 1 to 4.)
Total length of embryo: 43 mm.

1. *The Basal Plate*

Arising from the anterior end of the parachordals ("Investing mass" of W. K. PARKER, 1869) is a high transverse bar of cartilage named by SONIES (1907) in the fowl and the duck, the acrochordal plate (*ACR. CAR.*, figs. 1, 2, 3). It forms an angle of approximately 130° with the parachordals; in younger stages this angle is even larger. The blastematous anlages of the acrochordal and the parachordals lie in the same horizontal plane. T. J. PARKER (1892 a) named the acrochordal plate in *Apteryx* the prochordal plate. JAGER (1924) showed that the acrochordal plate arose in connexion with the transverse commissure between the premandibular somites.

Contrary to all birds of which the cranial morphology has been described, the penguin shares a common characteristic with the *Dipnoi, Anura* and *Crocodilia* in that no fenestra basicranialis posterior is present. Although LUTZ (1942) makes no mention of it, no fenestra basicranialis posterior is found in the emu. SONIES (1907), DE BEER and BARRINGTON (1934) and LUTZ (1942) have shown that it is not possible to recognize the paired nature of the parachordals in birds. For this reason DE BEER (1937) suggests the term perichordal plate. However, T. J. PARKER (1892, a and b) claims that in *Apteryx* the parachordals remain distinctly paired until a late ontogenetic stage. Both the acrochordal plate and the perichordal one are traversed by the notochord. The anterior tip of the latter projects forwards a short distance through a small foramen in the anterior surface of the acrochordal plate; this surface is, in reality, its morphological ventral surface.

No attempt has been made in the present paper to investigate the cranial segmentation. However, it is possible in this stage to observe indications of the first and second occipital vertebrae that have become incorporated into the skull. This supports the findings of SONIES (1907), VAN WIJHE (1907, 1910) and DE BEER and BARRINGTON (1934). Three hypoglossal roots (*HYP. ROOTS.*, fig. 1) are present. Lying behind each hypoglossal root is a procartilaginous occipital arch (*OC. ARC.*, figs. 1, 2). These three occipital arches fuse dorsally with one another above the hypoglossal roots to enclose two of the roots in foramina. The anterior hypoglossal root is lodged in a shallow groove in the lateral surface of the basal plate. Later, when the occipital arch corresponding to the segment in front of the first hypoglossal root develops, the latter is also enclosed within a foramen.

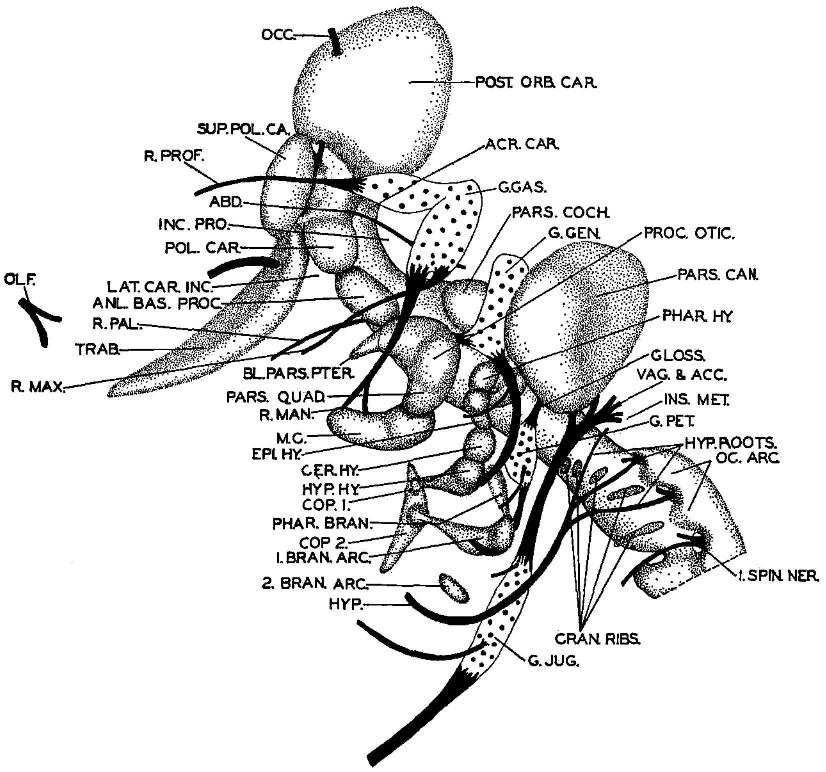


Fig. 1 (X ± 22.2). Stage 1. Reconstruction of chondrocranium and cranial nerves (norma lateralis).

Sushkin (1899) described three hypoglossal nerves in *Tinnunculus*. He claimed that the hypoglossal roots anterior to the posterior three disappeared during ontogeny. Sonies (1907) described only two hypoglossal roots and three hypoglossal foramina in the duck. De Beer and Barrington (1934) claim that up to four hypoglossal roots and five hypoglossal foramina exist in the early ontogeny. De Beer and Barrington's first hypoglossal root is associated with the ephemeral second metotic myomere. If younger stages of the penguin were to be investigated, indications of this first hypoglossal root would no doubt have been encountered. Lutz (1942) described three hypoglossal roots in a 15 day emu embryo, two of which are enclosed in foramina.

A further indication of the cranial segmentation is the presence of 5 cranial ribs (*CRAN. RIBS.*, fig. 1). They appear as areas of dense mesenchymatous tissue separating the myomeres below the perichordal plate. Each cranial rib lies behind the nerve corresponding to its segment. De Beer and Barrington (1934) observed four pairs of cranial ribs in the duck and claim that a connexion exists between the cranial ribs and the metotic cartilage. They, therefore, con-

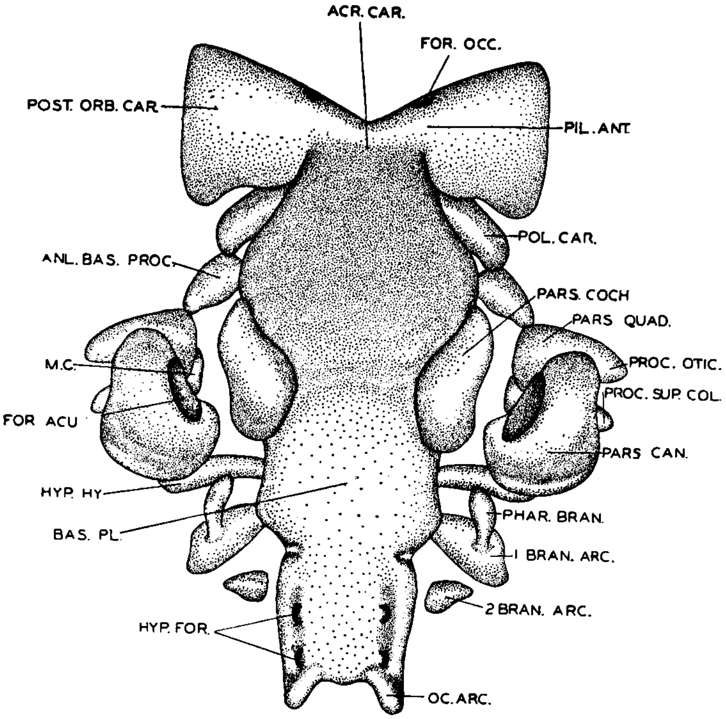


Fig. 2 (X ± 22.2). Stage I. Reconstruction of chondrocranium (norma dorsalis).

cluded that the metotic cartilage has arisen as the result of fusion of several cranial ribs. Sushkin (1899) described four pairs of cranial ribs in the kestrel. Sonies (1907) objects to the homologising of cranial ribs with true ribs, as the former never actually chondrify.

Two large masses of procartilaginous tissue which include the pila antotica (*PIL. ANT.*, fig. 2), (lamina antotica of Sonies, 1907) and the posterior orbital cartilage (*POST. ORB. CAR.*, figs. 1, 2, 3) (alisphenoid of W. K. Parker, 1866, T. J. Parker, 1892 a, and Parsons, 1932) arise on either side from the lateral surfaces of the acrochordal plate. It was not possible to observe the pila antotica and posterior orbital cartilage as two independent structures. However, Sonies (1907) has shown that the pila antotica and the posterior orbital cartilage arise from independent anlages in the fowl. The oculomotor nerve passes downwards between these two anlages. After the fusion of the two anlages in the fowl, the oculomotor nerve is lodged in a shallow groove which indicates the position where the pila antotica and the posterior orbital cartilage meet. In the penguin the oculomotor nerve (*OCC.*, fig. 1) is enclosed in a long canal, which probably represents the border between the posterior orbital cartilage and the pila antotica. An oculomotor canal is also found in *Apteryx* (T. J. Parker, 1892 a).

2. *The Auditory Capsule*

The procartilaginous anlage of the pars cochlearis (*PARS. COCH.*, fig. 2) of the auditory capsule, is situated on the latero-dorsal edge of the perichordal plate. Its postero-lateral edge projects laterally past the edge of the perichordal plate to form a shell-shaped roof to the medial region of the cochlear sac. The independence of the pars cochlearis from the perichordal plate supports the view of SONIES (1907) and DE BEER (1937) that the pars cochlearis in an independent structure and not a constituent part of the parachordal, as claimed by W. K. PARKER (1869), T. J. PARKER (1892 a) SUSHKIN (1899) and GAUPP (1900). SONIES named the earliest anlage of the pars cochlearis the cartilago basiotica. According to him it forms the connecting link between the parachordals and the acrochordal plate. In the penguin the pars cochlearis lies too far posteriorly to play the role claimed for it.

The basal plate (*BAS. PL.*, fig. 2) is made up of the following entities; the perichordal plate, the median acrochordal plate and the paired partes cochleares. SUSHKIN failed to observe the constituent parts of the basal plate and for this reason did not consider it to be a composite structure. It was designated by him the "Umhüllungsmasse".

Lateral to and separated from the pars cochlearis by a wide fissure is the procartilaginous anlage of the pars canalicularis (*PARS. CAN.*, figs. 1, 2). It is a cup-shaped structure with a large aperture directed medially. Faint indications of the semicircular canals are observable. The development of the auditory capsule from two independent anlages was observed in the duck by SONIES (1907), and DE BEER and BARRINGTON (1934), and in the starling and the fowl by SONIES (1907).

In the medio-anterior edge of the floor of the pars canalicularis there is a shallow groove lodging the facial nerve (*N.L.7. NER.*, fig. 6). The geniculate ganglion lies dorsal to the cochleo-canalicular fissure. Fused to the medio-ventral surface of the pars canalicularis is the pharyngohyal (*PHAR. HY.*, figs. 1, 4), which in later stages forms the rod and foot-plate of the columella auris. Also in later stages the pharyngohyal ("otostapes") breaks away from the pars canalicularis, with the result that a small circular foramen, the foramen ovale, remains in the side-wall of the pars canalicularis.

In the penguin, therefore, the foramen ovale is situated within the pars canalicularis region of the auditory capsule. SONIES (1907), considers the foramen ovale a remnant of the cochleo-canalicular fissure, while from DE BEER'S (1937) description it is not clear as to whether the foramen ovale develops within the pars cochlearis or pars canalicularis.

Extending ventrally from the latero-posterior edge of the pars canalicularis is a short, blunt procartilaginous process named by SONIES (1907), the cartilago metotica (*MET. CAR.*, fig. 4). He observed that it arose from an independent anlage in the duck and fowl. DE BEER and BARRINGTON (1934) also described the development of the metotic cartilage from an independent cartilaginous anlage in the duck and homologized it with the subcapsular process of the crocodile. As no connexion was observed in the penguin between the widely separated cranial ribs and the metotic cartilage, no support is given to the view of DE BEER and BARRINGTON (1934) that the metotic cartilage arises from the fusion of several cranial ribs. SUSSHKIN (1899) named the metotic cartilage the occipital wing and considered it an outgrowth of the "Umhüllungsmasse". T. J. PARKER (1892a) designated the metotic cartilage the "paroccipital process" and considered it an outgrowth of the auditory capsule. In the duck, (DE BEER and BARRINGTON, 1934, and SONIES, 1907) the metotic cartilage fuses firstly with the basal plate and secondly with the auditory capsule. In the fowl, (SONIES, 1907) on the other hand, it fuses firstly with the auditory capsule and secondly with the basal plate. In the penguin and in *Apteryx* it develops as an outgrowth of the auditory capsule. In the ostrich (BROCK, 1937) the metotic cartilage appears as a tract of mesenchyme continuous with the dorsal edge of the auditory capsule and free ventrally from the lateral edge of the basal plate. As the ontogeny of this structure varies from form to form it is not possible to determine its true nature.

An extremely wide incisura prootica (*INC. PRO.*, fig. 1), (incisura antotica of SONIES, 1907), is bordered anteriorly by the pila antotica and posterior orbital cartilage, ventrally by the parachordals and pars cochlearis, and posteriorly by the pars canalicularis. The incisura is not completely delimited posteriorly, as the pars cochlearis and pars canalicularis have not yet fused. The ganglion Gasseri (*G. GAS.*, fig. 1) is lodged in the incisura prootica. All the branches of the trigeminal nerve pass outwards through this incisure. The ramus profundus (*R. PROF.*, fig. 1) passes forwards below the posterior orbital cartilage. The abducent nerve (*ABD.*, fig. 1) passes outwards through the most anterior region of the incisura prootica and is not lodged in a notch at the base of the pila antotica as it is in the duck and the fowl (SONIES, 1907).

The incisura metotica (*INC. MET.*, fig. 1) is bordered incompletely anteriorly by the pars canalicularis and pars cochlearis, ventrally by the basal plate and posteriorly by the low occipital arches. The nervus glossopharyngeus (*GLOSS.*, fig. 1) passes downwards immediately behind the pars cochlearis and the composite nerve, (nervus vagus + nervus accessorius: *VAG + ACC.*, fig. 1) passes downwards behind the glossopharyngeus.

3. *The Anterior End of the Chondrocranium*

The polar cartilages (*POL. CAR.*, fig. 1, 3) are fused to the lateral surfaces of the acrochordal plate. Compared with the latter these structures are in an early state of chondrification and, as a result of this, it is possible to draw a line of demarcation between the two entities. The ventro-lateral region of each polar cartilage is directed ventro-laterally as a short blunt process, which, although it appears on lateral view to simulate an infrapolar process, must not be confused with it. A fairly wide lateral carotid incisure (*LAT. CAR. INC.*, figs. 1, 3) is formed between the acrochordal plate and the trabecular-polar bar. It is traversed by the internal carotids of either side which pass medially to reach the median foramen caroticum (*FOR. CAR.*, fig. 3).

The polar cartilages were first observed by SONIES (1907) in the duck, the starling and the fowl. In the fowl he shows that, as in the penguin, the polar cartilages originate in continuity with the acrochordal plate. According to SONIES (1907) the connexion between the polar cartilages and the basal plate takes place at the border between the pars cochlearis and the acrochordal plate. This is not the case in the penguin, where the partes cochleares lie far behind the acrochordal plate. SUSHKIN (1896, 1899) failed to differentiate the polar cartilages from the trabeculae in the kestrel.

The nature of the polar cartilages has been discussed by several authors. ALLIS (1923, 1924, 1931) claims that they represent pharyngomandibulars. DE BEER (1937) considers that it is possible that the polar cartilages arise from the mandibular arch, but is unable to prove his contention. MATVEIEV (1925) and HOLMGREN (1943) believe that the polar cartilages are of axial origin.

Situated between the ventro-lateral edge of the polar cartilage and the medial surface of the pars quadrata is an oval nodule of dense blastematous tissue, the anlage of the processus basitrabecularis (*ANL. BAS. PROC.*, figs. 1, 2, 3). Its topographical position, lateral to the nervus palatinus, supports the view that it is actually the anlage of this process. In later stages the anlage fuses to the skull base to form a small basitrabecular process. As this anlage occupies the same position as does the pharyngomandibular element in *Selachii,* described by SEWERTZOFF and DISLER (1924), it is not improbable that it represents a pharyngomandibular.

The trabeculae (*TRAB.*, figs. 1, 3) in this stage appear as two independent and widely separated procartilaginous bars. They are flattened in a horizontal plane and lie immediately below the forebrain. The posterior ends of the trabeculae are curved upwards and abut against the anterior surfaces of the polar cartilages. Connecting the posterior ends of the trabeculae with each other across the midline is a faint tract of procartilaginous tissue, the anlage of the precarotid commissure (*PRECAR. COM.*, fig. 3). No mention is made of this commissure in the literature on the avian chondrocranium. Faint indications of it are present in a 15 day emu embryo. LUTZ, however, does not mention it. In the penguin and the emu the large foramen basicranialis anterior is divided into two smaller foramina, a posterior foramen caroticum (*FOR. CAR.*, fig. 3) and an anterior foramen hypophyseos. The foramen caroticum is bordered anteriorly by the precarotid commissure, laterally by the polar cartilages and posteriorly

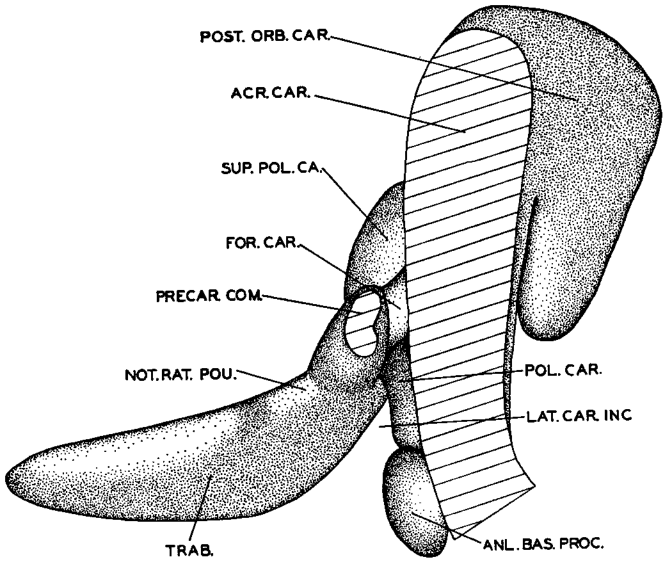


Fig. 3 (X ± 44.4). Stage I. Topography of the cranial flexure of the penguin.

by the acrochordal plate. The paired carotid arteries from either side pass medially through the lateral carotid incisure and fuse below the median foramen caroticum to form the median internal carotid which passes upwards through the foramen caroticum. Rathke's pouch, lying anterior to the precarotid commissure, passes upwards through the posterior region of the hypophysial fissure (*NOT. RAT. POU.*) which is bordered posteriorly by the precarotid commissure and laterally by the trabeculae. In later stages the trabeculae fuse in front of Rathke's pouch to form the trabecula communis.

The independent origin of the trabeculae was observed in the duck by SONIES (1907), and DE BEER and BARRINGTON (1934). In this stage of the penguin ontogeny the trabeculae are continuous with the polar cartilages, but a clear line of demarcation may be observed between the two structures. The sagittal bar of cartilage dividing the foramen hypophyseos of the sparrow into right and left halves (DE BEER, 1937), is not present in the penguin. HUXLEY (1874), DE BEER (1931, 1937), PLATT (1897), HOWES and SWINNERTON (1901), and ALLIS (1923, 1924, 1931) consider the trabeculae to be of visceral origin. ALLIS went so far as to claim that the trabeculae are homologous with the pharyngo-premandibulars. GOODRICH (1930) considers the trabeculae as "structures sui generis developed to support and protect the forebrain and nasal sacs." HOLMGREN (1943) claims that the trabeculae are of axial origin. No attempt has been made in this paper to determine the morphology of the trabeculae. Nevertheless, it is interesting to note that in this stage these cartilages lie practically parallel to the other visceral arches. DE BEER (1923) considers this fact relevant to this theory that the trabeculae represent the premandibular arches.

Lying above the polar cartilage and the posterior end of the trabecula, is a large nodule of procartilaginous tissue, the anlage of the suprapolar cartilage (*SUP. POL. CA.*, figs. 1, 3). Posteriorly it abuts against the anterior surface of the acrochordal plate, and ventrally it is separated from the trabeculae by a narrow fissure through which the ophthalmic artery passes outwards. The suprapolar cartilages were first observed in the kestrel by SUSHKIN (1899), who designated them "supratrabecular cartilages". SONIES (1907) pointed out that these structures lie dorsal to the polar cartilages, and for this reason he introduced the term suprapolar cartilages. DE BEER (1937) homologizes the suprapolar cartilages with the supratrabecular bar of *Lacerta* and *Sphenodon.*

4. *The Palatoquadrate and Meckel's Cartilage*

The pars quadrata (*PARS. QUAD.*, fig. 1) has a sickle-shaped form. The anlage of the basitrabecular process is syndesmotically connected to the medial surface of the antero-dorsal region of the pars quadrata. No definite corresponding cartilaginous basal process is found upon the pars quadrata. Anterior to the attachment of the basitrabecular process the pars quadrata is continued forward by a short dense blastematous process, the posterior region of the pars pterygoidea (*BL. PARS. PTER.*, fig. 1). In later stages this blastematous process chondrifies in continuity with the pars quadrata to form the processus orbitoquadratus. Anterior to the blastematous processus pterygoidea a faint tract of blastematous tissue extending forward into the ethmoidal region is observable. This probably represents the anterior region of the pars pterygoidea.

SONIES (1907) says the following concerning the processus orbitoquadratus of birds, "— — — und ist mit dem Processus pterygoideus des Palatoquadratums der Reptilien und dem langen Processus palatinus der Knorpel-Fische zu homologisieren". DE BEER and BARRINGTON (1934) also consider the processus orbitoquadratus as homologous with the pars pterygoidea, and for this reason employ the term processus pterygoidea for this process. The work of PRINS (in press) on the musculus orbitoquadratus of the penguin supports the view, that the processus orbitoquadratus represents a remnant of the pars pterygoidea.

A short blunt process, the processus oticus (*PROC. OTIC.*, figs. 1, 2) arises from the postero-dorsal surface of the pars quadrata and is directed in a laterodorsal direction. It does not, however, reach the lateral surface of the auditory capsule. Ventrally the pars quadrata is syndesmotically joined to the posterior region of Meckel's cartilage (*M. C.*, figs. 1, 2, 4) which has the form of a short rod. Posteriorly in the region of the pars quadrata it expands laterally.

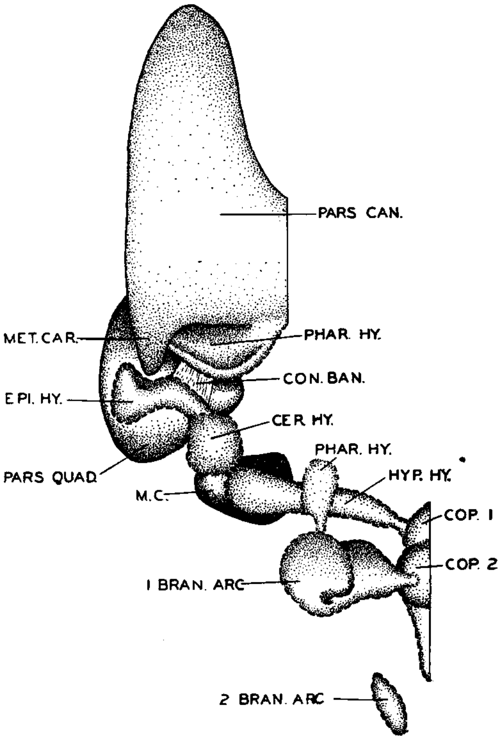


Fig. 4 (X ± 44.4). Stage 1. Reconstruction of hyoid arch (norma posterior).

5. *The Hyoid Arch*

The hyoid arch of this stage is constituted by four blastematous anlages. For the sake of convenience they have been named the pharyngohyal, epihyal, ceratohyal and hypohyal, but, as to whether they are homologous with the similarly named divisions in the piscine hyoid arch, is by no means certain. De Beer (1936) suggests that the visceral arches of fishes and of higher vertebrates may have acquired segmentation independently.

The pharyngohyal (*PHAR. HY.*, figs. 1, 4) appears in syndesmotic continuity with the ventro-medial surface of the pars canalicularis. In later stages the pharyngohyal forms the foot-plate and the major portion of the rod of the columella auris. The epihyal (*EPI. HY.*, figs. 1, 4) lies ventro-caudal to the pharyngohyal. Its lateral region is extended ventro-dorsally past the ventrolateral surface of the pharyngohyal to form the processus supracolumellaris lateralis (*PROC. SUP. COL. LAT.*, figs. 5, 9). In most birds two dorsal processes, a medial and a lateral, arise from the columella auris. The terms processus supracolumellaris lateralis and medialis have been introduced here to designate these two processes. No processus supracolumellaris medialis is found in the penguin.

The proximal region of the epihyal is connected by means of a tract of connective tissue (*CON. BAN.*, fig. 4) to the ventral edge of the pharyngohyal. Following upon the epihyal in a ventro-caudal and slightly medial direction is a spherical nodule of blastematous tissue, the ceratohyal (*CER. HY.*, figs. 1, 4). A blastematous hypohyal has the form of a long slender rod connecting the ceratohyal to copula 1 (*COP. 1.*, figs. 1, 4).

The ramus hyomandibularis of the facial nerve passes backwards dorsal to the epihyal and medial to the processus supracolumellaris lateralis. Immediately behind the epihyal the chorda tympani is given off from the hyomandibular. This nerve passes forwards lateral to the processus supracolumellaris lateralis. Anterior to the hyoid arch it passes downwards towards the lower jaw.

6. *The Branchial Arches*

Situated medially below the skull and lying almost at right angles to the long axis of the parachordals, is a dense mass of blastematous tissue containing the anlages of copula 1 and 2. These appear as local concentrations within this blastematous mass. SUSHKIN (1899) described a similar condition in the early ontogenetic stages of *Tinnunculus*.

The connexion between the hypohyal (ventral end of the hyoid arch) and copula 1 has not previously been observed in birds, and it indicates that copula 1 is a basihyal.

Behind the hyoid arch and in connexion with copula 2 is the blastematous anlage of the first branchial arch (*I BRAN. ARC.*, figs. 1, 4). Its attachment to copula 2 indicates that the latter is a basibranchial. W. K. PARKER (1866) considered copula 1 to be part of the hyoid arch and for this reason designated it the "urohyal".

Attached to the postero-dorsal edge of the first branchial arch is a faint tract of blastematous tissue. In later stages it proves to be the site of an independent chondrification which has been named the pharyngobranchial (*PHAR. BRAN.*, figs. 1, 4). This term must not be taken to imply that the anlage is homologous with the piscine pharyngobranchial. No subdivision of the rest of the branchial arch was observed.

A remnant of the second branchial arch (*2 BRAN. ARC.*, figs. 1, 4) of birds in the form of dense blasteme, is found behind the first branchial arch, between the second and third branchial pouches. Whereas in reptiles it develops further, in birds it atrophies in the later ontogeny. KALLIUS (1905) describes a similar condition to that of the penguin in the duck and in the sparrow.

B. STAGE II

(Figs. 5 to 9.)
Total length of embryo: 47 mm.

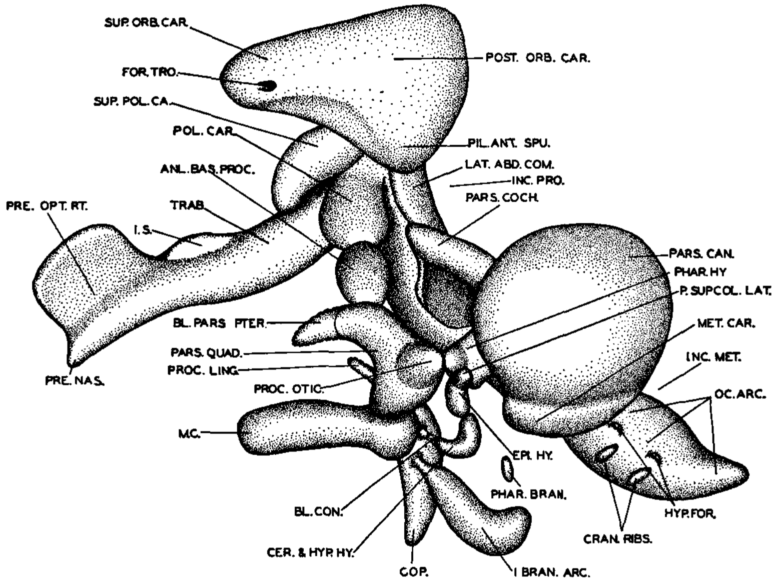


Fig. 5 (X ± 22.2). Stage 2. Reconstruction of the chondrocranium (norma lateralis).

1. *The Basal Plate and Auditory Capsule*

Considerable lateral expansion of the basal plate in the occipital region is observable in this stage. The occipital arch corresponding to the segment in front of the first hypoglossal root has now developed. This arch fuses with the occipital arch behind, dorsal to the hypoglossal root, to enclose the latter in a foramen. The posterior occipital arch has grown in height. In contrast to stage I, where the hypoglossal foramina were directed laterally, they now open in a latero-ventral direction. Only the posterior three cranial ribs of stage I remain.

A blunt process, separating the glossopharyngeal and vagal nerves, arises from the lateral surface of the basal plate, with the result that the nervus vagus is lodged in a shallow depression on the lateral surface of the basal plate (*N. L. 10 NER.*, figs. 6, 7). A similar condition was observed by Sonies (1907) in the duck.

The posterior orbital cartilage has expanded laterally to enclose the trochlear nerve in a long horizontal canal (*FOR. TRO.*, figs. 5, 6, 8). Parsons (1932) observed the trochlear canal in a young embryo the gentoo penguin (*Pygoscelis papua*). The latero-anterior region of the posterior orbital cartilages is extended forwards over the eyes by means of a long procartilaginous process, the supra-orbital cartilage (*SUP. ORB. CAR.*, figs. 5, 6, 8). A flange of slightly differentiated procartilaginous tissue, the anlage of the pila antotica spuria (*PIL.*

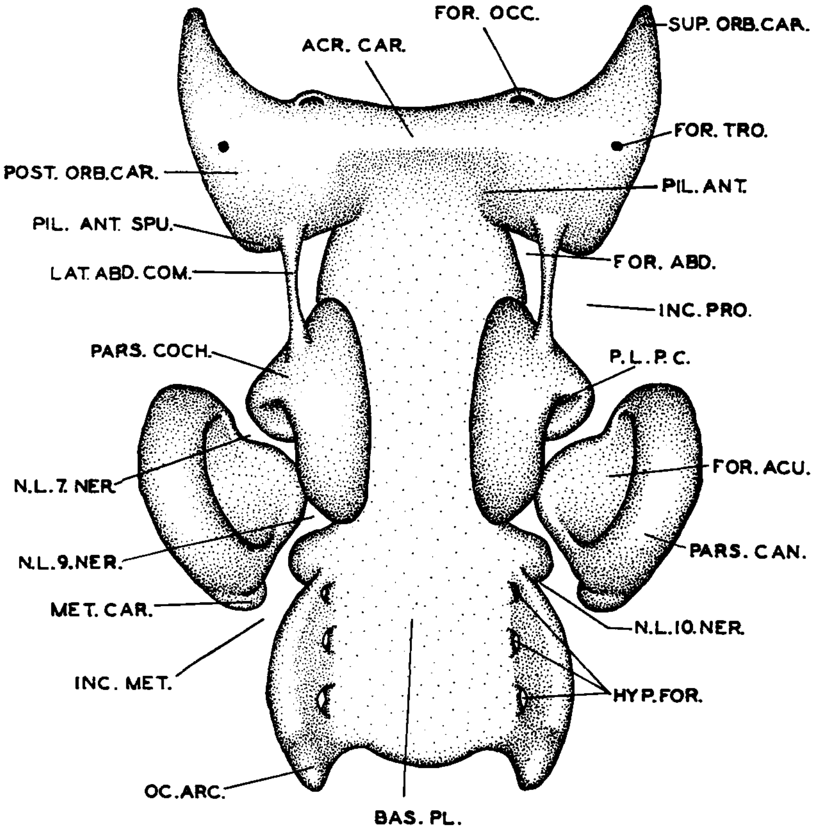


Fig. 6 (X ± 27.5). Stage 2. Reconstruction of basal plate and auditory capsule (norma dorsalis).

ANT. SPU., figs. 5, 6) which lies lateral to the ramus profundus, extends downwards from the latero-ventral region of the posterior orbital cartilage. This supports the findings of De Beer and Barrington (1934) and Brock (1937). Although the presence of a pila antotica spuria is a feature common to most birds, Kesteven (1942) has pointed out that it does not develop in the emu or the grebe (*Podiceps*).

A procartilaginous lateral abducent commissure (*LAT. ABD. COM.*, figs. 5, 6, 7) stretching between the posterior surface of the posterior orbital cartilage and the latero-anterior surface of the pars cochlearis, lateral to the abducent nerve, has developed at this stage. The abducent nerve is now enclosed within its own foramen (*FOR. ABD.*, fig. 6). According to De Beer and Barrington (1934) and Sonies (1907) the abducent foramen is formed by the encroachment of the pila antotica upon the abducent nerve.

It is still possible in this stage to distinguish the pars cochlearis as an in-

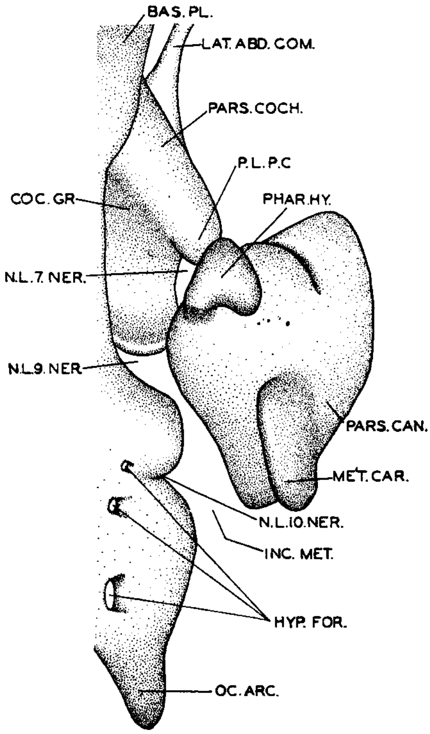


Fig. 7 (X ± 36.6). Stage 2. Reconstruction of auditory capsule (norma ventralis).

dependent structure. As in stage I, it is separated from the pars canalicularis by means of a narrow fissure. The pars cochlearis has increased in length, so that a broader base is apposed to the perichordal plate. The postero-lateral roof of the pars cochlearis has grown further laterally to form an effective roof to the cochlear region of the auditory sac (*COC. GR.*, fig. 7). A short blunt process, the processus lateralis partis cochlearis (*P. L. P. C.*, figs. 6, 7), lying in front of the facial nerve, grows out from the antero-lateral region of the pars cochlearis. The facial nerve passes upwards through the cochleocanalicular fissure towards the geniculate ganglion. A similar course for the facial nerve was described by Brock (1937) in the ostrich. "The facial nerve emerges through a groove situated anteriorly between the cochlear and canalicular portions of the otic capsule, its foramen is not separated from the trigeminal incisure." In later ontogenetic stages of the penguin, the processus lateralis partis cochlearis fuses with the anterior surface of the pars canalicularis and forms an anterior border to the facial nerve foramen. As the pars canalicularis and the pars cochlearis have not yet fused, neither the incisura metotica nor prootica is completely delimited.

The metotic cartilage has increased considerably in size. Its dorsal edge is fused to the latero-dorsal region of the canalicular portion of the otic capsule, while the ventral edge appears as a broad flange directed in a ventro-medial direction towards the lateral edge of the basal plate. Thus a space, the cavum metoticum, is enclosed between the metotic cartilage, laterally, and the auditory capsule, medially.

2. *The Anterior End of the Chondrocranium*

It is still possible to distinguish between the trabeculae and the polar cartilages. The medial regions of the polar cartilages are wedged between the trabeculae and the acrochordal plate. Consequently the medial regions of the polar cartilages are narrow, while laterally each expands to form a broad blunt process. With the exception of the narrow distal region, which remains blastematous, the entire blastematous basitrabecular process anlage of the previous stage has chondrified. In the emu and the ostrich the entire anlage of the basitrabecular process chondrifies.

In stage I the posterior ends of the trabeculae were curved dorsally, so that they lay practically parallel to the acrochordal plate. In the intermediate period between stages I and II the trabeculae have straightened out and rotated dorsally to form a horizontal bar lying practically at right angles to the acrochordal plate. The trabeculae have fused with each other in the midline to form the trabecula communis (*TRAB. COM.*, fig. 8). With the formation of the trabecula communis, the foramen hypophyseos (*FOR. HYPOP.*, fig. 8). is now completely delimited.

T. J. PARKER (1892 a, and b) described three basicranial foramina in the skullbase of *Apteryx:* a posterior, a middle and a anterior basicranial foramen. The anterior two appear to be homologous with the foramen hypophyseos and the foramen caroticum of the penguin. The boundary between the two foramina is formed in *Apteryx* by a commissure connecting the posterior regions of the trabeculae. Anteriorly the trabecula communis is extended forwards as a short prenasal process (*PRE. NAS.*, figs. 5, 8). Two flat plates of procartilaginous tissue, the preoptic roots of the orbital cartilage (*PRE. OPT. RT.*, figs. 5, 8) directed dorsally and slightly laterally, arise from the antero-lateral surfaces of the trabecula communis. The interorbital septum (*I. S.*, figs. 5, 8) grows upwards from the centre of the trabecula communis behind the preoptic roots. BROCK (1937) in her description of the ostrich chondrocranium claims that the interorbital septum is formed by the fusion of the preoptic roots with each other in the midline. The present, and the later ontogenetic stages of the penguin clearly show that the interorbital septum and the preoptic roots are two distinct structures. The preoptic roots may in later ontogenetical stages be cemented to the anterior region of the interorbital septum, but they certainly do not represent the latter.

W. K. PARKER (1891), SUSHKIN (1899), and FILATOFF (1906) claim the

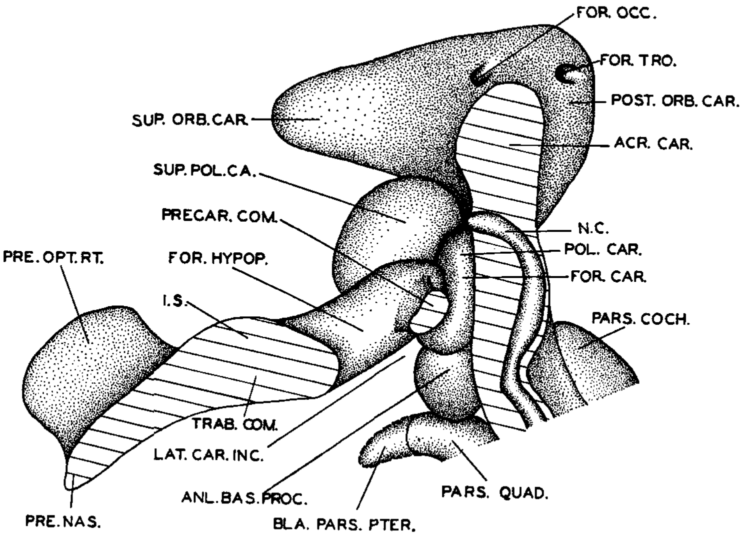


Fig. 8 (X ± 30). Stage 2. Topography of the cranial flexure of the penguin.

existence of an intertrabecular bar in the fowl, kestrel and pigeon respectively. According to these authors the interorbital septum develops out of this structure. No indication of an intertrabecular bar is found in the penguin. The trabeculae fuse with each other without the intermediation of an intertrabecular bar to form the trabecula communis. Although the central tissue constituting the trabecula communis is in a less advanced state of chondrification than the laterally situated tissue, this central portion cannot be considered a separate structure.

3. *The Visceral Arches*

The processus oticus of the pars quadrata has increased considerably in length, but it has not yet reached the auditory capsule. The pars pterygoidea is still in a blastematous condition. Meckel's cartilage has increased in length.

The blastematous pharyngohyal has grown in an antero-medial direction to form a short blunt process. In later stages this will constitute the major part of the columella auris rod. The blastematous processus supracolumellaris lateralis is directed in a more dorsal direction than in the previous stage. Continuous with the dorsal end of this process is a nodule of blastematous tissue (not shown in the reconstruction) lying between the processus oticus and the metotic cartilage. This nodule is probably homologous with the intercalary of reptiles. The increased growth of the pharyngohyal has shortened the distance separating the pharyngohyal and the epihyal.

In the rest of the hyoid arch the ceratohyal and the hypohyal have fused to

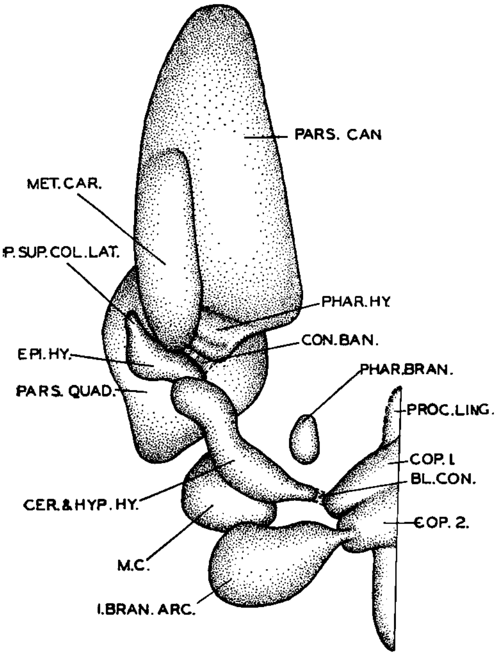


Fig. 9 (X ± 36.6). Stage 2. Reconstruction of the hyoid arch (norma posterior).

form a long blastematous rod. The slender connexion formerly existing between the hyoid arch and the basihyal, has atrophied so that only a faint tract of blasteme (*BL. CON.*, fig. 9) remains to indicate its earlier presence.

Copula 1 and 2 have chondrified to form a single copula, but a demarcation may still be observed between the two structures. A short, blunt process directed towards the ventral end of the hyoid arch arises from the lateral surface of copula 1. Kallius (1905) named this process the lateral wing of the copula. Copula 1 is extended forward by a blastematous process (*PROC. LING.*, figs. 5, 9). It is not improbable that this process is homologous with the processus lingualis of reptiles and the "glossohyal" (Sushkin, 1899). In later stages it atrophies, and the anlage of the paraglossum develops dorsally to it. It was not found possible to ascertain whether any part of the processus lingualis contributes to the formation of the paraglossum.

The first branchial arch is still in a blastematous state. Proximally it has a slender attachment to a short, laterally directed process of copula 2 (basibranchial). This process is serially homologous with a similar process on the lateral surface of the basihyal. The blastematous pharyngobranchial is found occupying the same position as it occupied in stage I. However, as a result of the extensive backward growth of the first branchial arch, the previous slender connexion between the two structures is broken down.

The blastematous second branchial arch has atrophied.

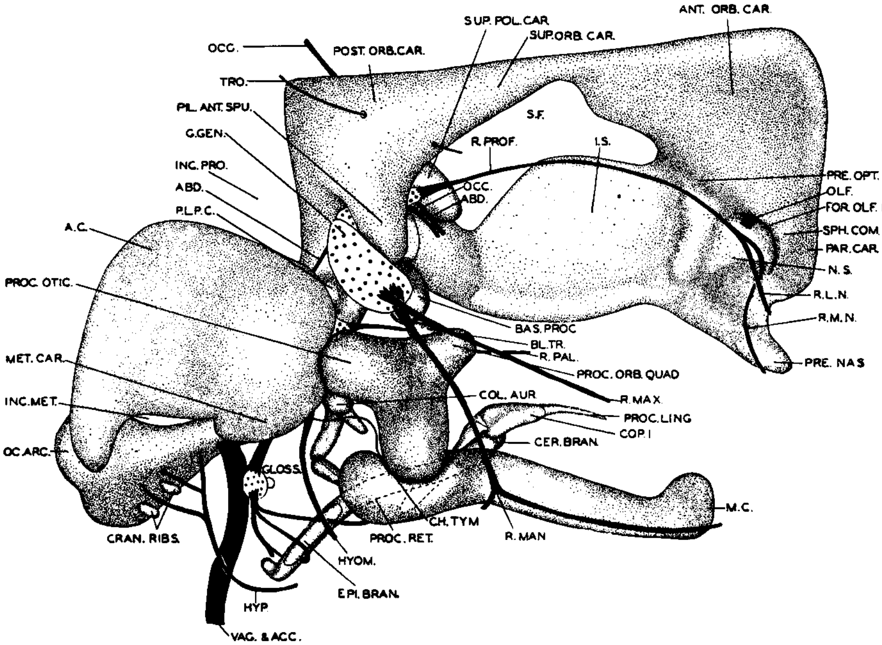


Fig. 10 (X ± 20.5). Stage 3. Reconstruction of chondrocranium and cranial nerves (norma lateralis).

C. STAGE III

(Figs. 10 to 15.)

Total length of embryo: 56 mm.

A large gap in the development exists between stages II and III but, despite this, the advance from the former to the latter may be accurately followed.

1. *The Basal Plate and Auditory Capsule*

The occipital region of this stage is characterized by the extensive growth of the posterior occipital arch. It rises steeply from the posterior region of the basal plate to form a high posterior wall to the fissura metotica.

In this stage four hypoglossal foramina are found in the left side of the basal plate. No hypoglossal nerve traverses the anterior hypoglossal foramen. Only the two posterior cranial ribs remain in this stage.

The laterally directed process of the basal plate anterior to the nervus vagus has fused with the basal plate behind the nervus vagus to enclose the latter within its own foramen (*FOR. VAG.*, figs. 10, 11, 12). The metotic cartilage plays no role in the formation of this foramen. De Beer and Barrington (1934) claim that, in the duck, the fissura metotica is divided into two by the metotic

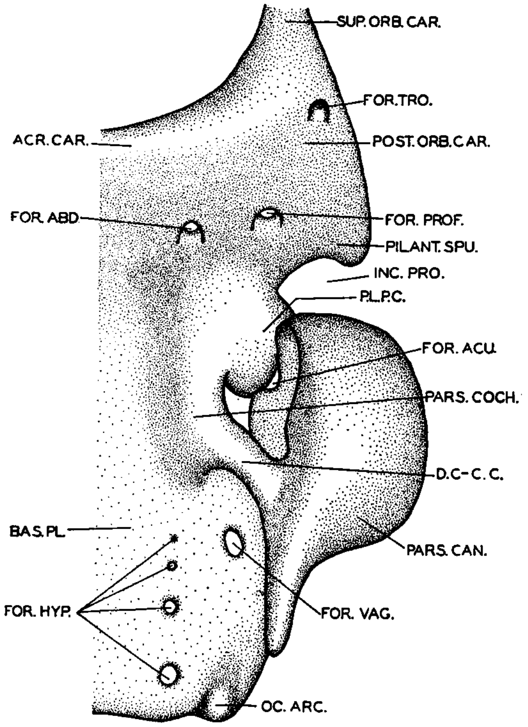


Fig. 11 (X ± 27.3). Stage 3. Reconstruction of basal plate (norma dorsalis).

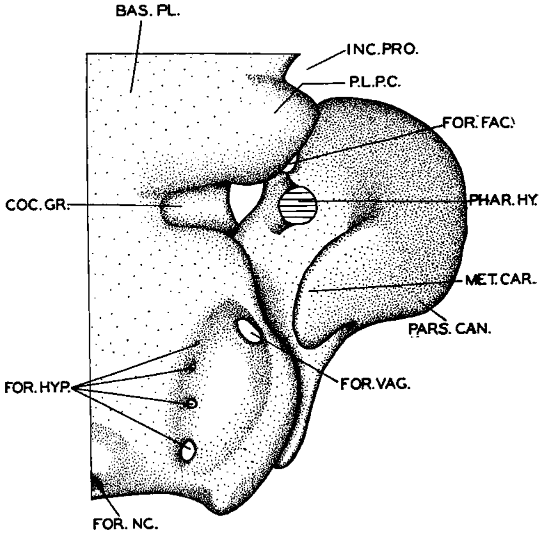


Fig. 12 (X ± 27.3). Stage 3. Reconstruction of auditory capsule (norma ventralis).

cartilage which fuses with the basal plate between the nervus vagus and the nervus glossopharyngeus. They do not make it clear whether the nervus vagus is enclosed within a foramen in the basal plate or whether it passes outwards through a remnant of the fissura metotica. According to Sonies' (1907) description for the duck, the metotic cartilage fuses with the basal plate behind the notch lodging the nervus vagus and then spreads forwards to cover the groove laterally. Brock (1937) claims that in the ostrich both the nervus vagus and the nervus glossopharyngeus are surrounded by the metotic cartilage.

Above the eyes a slender connexion is developed in this stage between the supraorbital cartilage and the anterior orbital cartilage. The anterior surface of the posterior orbital cartilage presents a concave surface to the posterior surface of the eye-ball.

The pila antotica spuria is now fully formed; below the ramus profundus it fuses with the lateral abducent commissure to enclose the ramus profundus in its own foramen (*FOR. PROF.*, fig. 11). An independent foramen for the ramus profundus was observed in *Apteryx* by T. J. Parker (1892 a) and in the fowl and the duck by Sonies (1907). De Beer and Barrington (1934), who

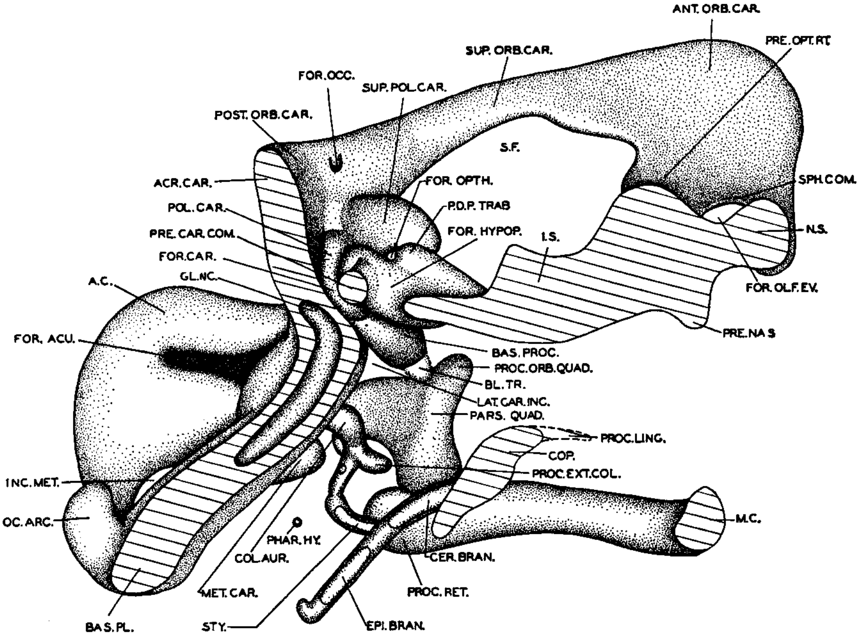


Fig. 13 (X ± 27.3). Stage 3. Disposition of cranial entities as viewed from a median sagittal section.

described the development of the pila antotica spuria in the duck, were the first to realize its significance.

The anterior wall of the oculomotor canal now appears as a thin cartilaginous lamella. This clearly indicates that the anterior wall is undergoing degeneration.

Fusion between the lateral abducent commissure and the basal plate behind the abducent nerve has considerably reduced the size of the foramen for the abducent nerve.

The partes cochleares have now fused completely with the perichordal plate. Further, the perichordal plate has extended laterally to fuse with the free latero-posterior region of the pars cochlearis, forming a roof to the cochlear region of the auditory sac. All that now remains to indicate the presence of the partes cochleares are two shallow grooves in the ventral surface of the basal plate. The grooves lodge the cochlear sacs of either side. The processus lateralis partis cochlearis has grown further laterally to abut against the pars canalicularis. The dorsal surface of this process is syndesmotically fused to the antero-ventral surface of the pars canalicularis in front of the facial nerve. The posterior surface of this process abuts against the ventral floor of the pars canalicularis postero-medial to the groove lodging the facial nerve. As a result the facial nerve is wedged between the processus lateralis partis cochlearis and the canalicular portion of the otic capsule (*FOR. FAC.*, figs. 11, 12, 14). That part of the processus lateralis partis cochlearis lying in front of the facial nerve may be considered homologous with the prefacial commissure described by DE BEER and BARRINGTON (1934) for the duck. In the young ontogenetic stages of the penguin the facial nerve has to pass through the cavity of the auditory capsule in order to reach the geniculate ganglion.

A broad cartilaginous commissure stretches between the postero-dorsal region of the pars cochlearis and the ventro-lateral surface of the pars canalicularis. The term dorsal cochleo-canalicular commissure (*D. C.-C. C.*, figs. 11, 14) has been introduced in this paper to designate this commissure.

The fusion of the processus lateralis partis cochlearis with the pars canalicularis anteriorly, and the development of the dorsal cochleo-canalicular commissure posteriorly, form the anterior and posterior borders of the acustic foramen (*FOR. ACU.*, figs. 11, 13, 14), the lateral border of which is formed by the pars canalicularis, and the medial, by the pars cochlearis. The acustic foramen must therefore be considered a remnant of the cochleo-canalicular fissure. With the fusion of the two regions of the otic capsule with each other, the posterior border of the incisura prootica and the anterior border of the incisura metotica are now completed.

The pars canalicularis is extended backwards as a broad conical process lying above the basal plate. The metotic cartilage has grown further in a medio-ventral direction towards the basal plate.

2. *The Anterior End of the Chondrocranium*

In this stage the polar cartilages are indistinguishably fused to the trabeculae anteriorly, and to the acrochordal plate posteriorly. The anlage of the basi-trabecular process is fused to the antero-ventral surface of the polar cartilage, but a line demarcating the two entities is still observable. A tract of blastematous tissue (*BL. TR.*, figs. 10, 13, 14) still connects the basitrabecular process (*BAS. PROC.*, figs. 10, 13, 14) with the pars quadrata.

The ventral region of the acrochordal plate has migrated forwards to come to lie beneath the polar cartilage. As a result, the formerly wide, lateral carotid incisure has been narrowed down considerably.

Fusion between the suprapolar cartilage and the trabeculo-polar bar has enclosed the ophthalmic artery in a small foramen (*FOR. OPTH.*, fig. 13). In front of the ophthalmic artery the suprapolar cartilage fuses with a postero-dorsally directed process of the trabeculae (*P.D.P. TRAB.*, fig. 13). Behind the ophthalmic artery the suprapolar cartilage fuses with the dorsal surface of the polar cartilage and the anterior surface of the acrochordal plate. The ventral opening of the oculomotor canal lies laterally to the upper end of the suprapolar cartilage.

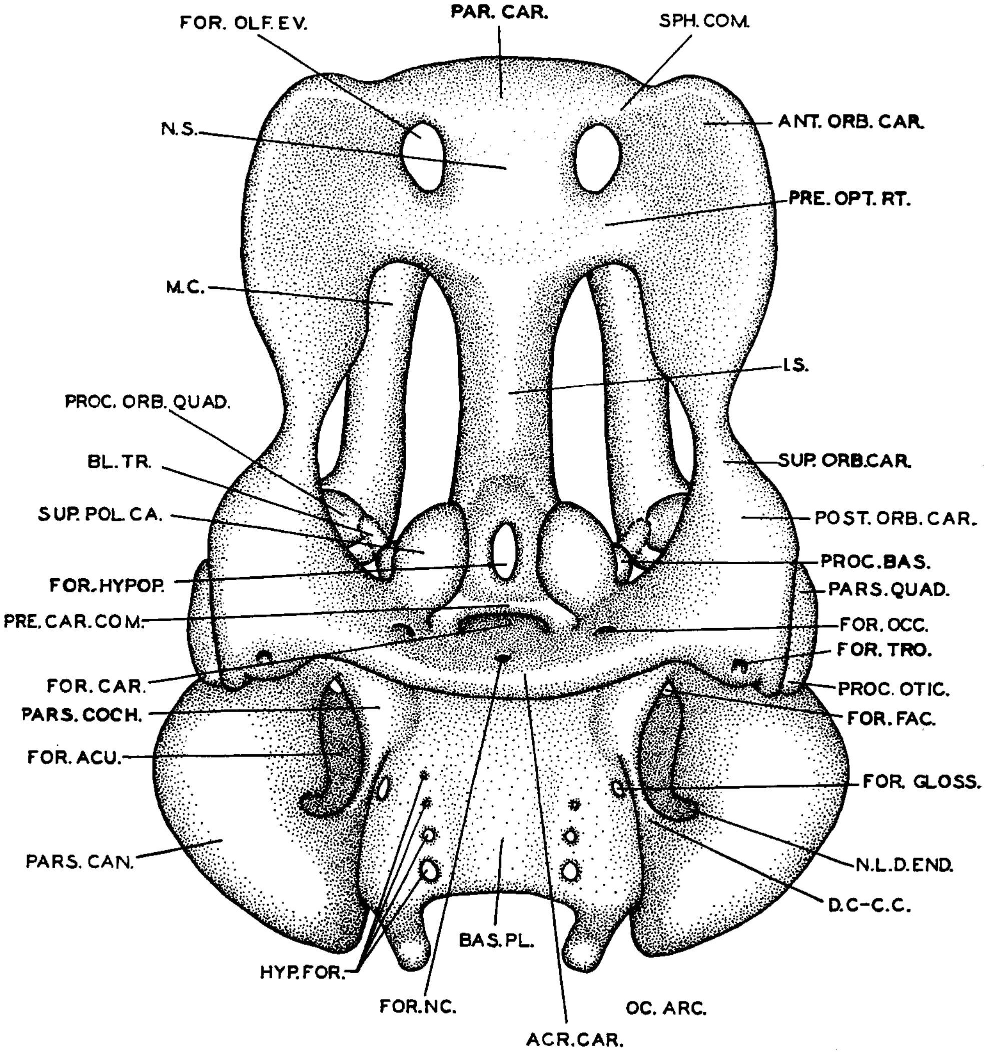


Fig. 14 (X ± 25). Stage 3. Reconstruction of chondrocranium (norma dorsalis).

As a result of the degeneration of the tubular duct connecting Rathke's pouch to the stomodaeum, the hypophysial foramen has begun to close.

The prenasal process, seen for the first time in Stage II, has greatly increased in length. Appearing as a new structure in this stage is the nasal septum (*N. S.*, figs. 10, 13, 14). It is formed as an upward growth of the postero-dorsal surface of the prenasal process, and is continuous with the interorbital septum behind. At its base the septum is narrow, but dorsally it expands sidewards to form the parietotectal cartilage (*PAR. CAR.*, figs. 10, 14). Consequently the nasal septum seen in transverse section presents a triangular shape. The interorbital septum has increased considerably in height, mainly between the preoptic roots. A transverse section of this stage shows that the preoptic roots arise from the lateral surface of the trabecula communis and extend upwards, parallel to the interorbital septum. At a point level with the upper end of the septum, the preoptic roots expand into two large cartilaginous plates, the anterior orbital cartilages (*ANT. ORB. CAR.*, figs. 10, 13, 14), (orbitosphenoids of T. J. PARKER, 1892 a). These cartilages extend backwards, lateral to, but widely separated from, the interorbital septum, to achieve a slender connexion with the posterior orbital cartilage. A large sphenoid fontanelle (*S. F.*, figs. 10, 13) is now enclosed on each side, through which the optic nerves pass outwards. With the interorbital septum as a base and the orbital cartilages as the side walls, a deep trough is formed which lodges the forebrain.

A sphenethmoid commissure (*SPH. COM.*, figs. 10, 13, 14) has developed connecting the anterior surface of the orbital cartilage with the parietotectal cartilage of the nasal capsule. This commissure forms the lateral border of the foramen olfactorium evehens (*FOR. OLF. EV.*, figs. 10, 13, 14), which is further bordered medially by the nasal septum, posteriorly by the preoptic root and anteriorly by the posterior edge of the parietotectal cartilage. The nervus olfactorius passes through the foramen olfactorium evehens to reach the nasal sac. Below the large foramen olfactorium evehens, the ramus profundus divides into two branches; the ramus medialis nasi and the ramus lateralis nasi. While the ramus medialis nasi passes downwards alongside the medial surface of the nasal septum and follows the prenasal process forwards, the ramus lateralis nasi passes forwards in an antero-lateral direction. It will be seen in later stages that the ramus medialis nasi passes through the cavity of the nasal capsule.

3. *The Visceral Arches*

In the pars quadrata, the processus oticus has reached, and articulates with, the auditory capsule and the antero-dorsal surface of the metotic cartilage. The blastematous pars pterygoidea has chondrified in continuity with the pars quadrata to form the processus orbitoquadratus (*PROC. ORB. QUAD.*, figs. 10, 13, 14).

Meckel's cartilage has increased considerably in length; it extends backwards beyond the pars quadrata to form the processus retro-articularis (*PROC. RET.*, fig. 10).

Extensive changes have taken place in the hyoid arch. The epihyal and pharyngohyal elements have chondrified and fused to form the columella auris (*COL. AUR.*, figs. 10, 13), and the pharyngohyal now exists in cartilaginous continuity with the pars canalicularis. The processus supracolumellaris lateralis has chondrified, and the blastematous intercalary has atrophied. Of particular

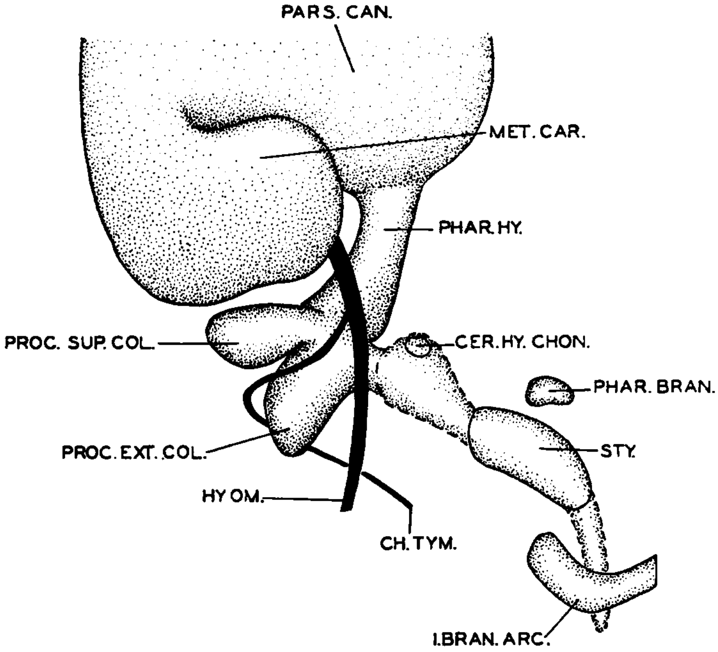


Fig. 15 (X ± 66.6). Stage 3. Reconstruction of the hyoid arch (norma posterior).

importance in this stage is the development of the processus extracolumellaris (*PROC. EXT. COL.*, figs. 13, 15). It develops from the base of the epihyal and is directed in an antero-ventral and slightly lateral direction. Following upon the proximal region of the epihyal, in a medio-ventral direction, is the rest of the hyoid arch which is still to a large extent in a blastematous state. The connexion between the ventral end of the hyoid arch and copula 1 has atrophied completely. When the hyoid cornu is viewed from the lateral aspect, it presents a semicircular shape with both the dorsal and ventral extremities directed forwards. Within the blastematous hyoid cornu two centres of chondrification may be observed. One of these (*CER. HY. CHON.*, fig. 15) is found in the dorsal region of the cornu, and from its topographical position it may be concluded that it represents a chondrification of the ceratohyal blasteme. Similarly the chondrification in the ventral region of the hyoid cornu appears to be a chondrification of the hypohyal blasteme. This chondrification is generally designated as the "stylohyal" (*STY.*, figs. 13, 15). In several birds, for example the duck and the fowl, the entire hyoid cornu chondrifies from a single centre. The chorda tympani in its forward course from behind the columella auris passes lateral to the processus supracolumellaris lateralis and dorsal to the processus extracolumellaris.

During the intervening development, between stages II and III, the median copula has migrated forwards and has come to lie below the trabeculae. The processus lingualis is still in a blastematous condition.

Within the blasteme of the first branchial arch two centres of chondrification are present, the ceratobranchial (*CER. BRAN.*, figs. 10, 13) and the epibranchial (*EPI. BRAN.*, figs. 10, 13). W. K. PARKER (1866) originally named these two divisions of the branchial arch the "thyrohyals" but, in a later work (1869), introduced the terms ceratobranchial and epibranchial. Most of the modern workers on the avian chondrocranium employ PARKER'S (1869) terminology. However, GAUPP (1900) homologized the divisions of the avian branchial arch with those of the *Urodela* and consequently designated them hypo- and ceratobranchials. According to KALLIUS (1905), the cerato- and epibranchials arise in the duck by segmentation of a solid cartilaginous branchial arch. This is contrary to the findings of SONIES (1907), and DE BEER and BARRINGTON (1934), who describe the branchial arch of the duck as developing from two independent cartilaginous centres. As no subdivision was observed in the penguin branchial arch in the blastematous state, PARKER'S (1869) terminology will be retained.

The blastematous pharyngobranchial has now chondrified and appears as a small nodule lying close to the geniculate ganglion. A dorsally directed blastematous process situated at the extreme distal end of the first branchial arch is reminiscent of the earlier ontogenetic connexion between the pharyngobranchial and the rest of the first branchial arch.

D. STAGE IV

(Figs. 16 and 17.)

Total body length of embryo: 51 mm.

Although this stage is somewhat smaller than the previous one its development is slightly more advanced.

1. *The Basal Plate and Auditory Capsule*

The incisura metotica is almost completely obliterated in this stage by the fusion of the auditory capsule with the basal plate below, and with the occipital arch behind. Only the anterior region of the recessus scalae tympani (*REC. SCA. TYM.*, fig. 21), through which the nervus glossopharyngeus passes outwards, remains. The fusion between the two regions of the auditory capsule has proceeded further. Anteriorly it is no longer possible to distinguish between the processus lateralis partis cochlearis and the pars canalicularis. In addition, a further cartilaginous commissure has developed connecting the postero-ventral surface of the pars cochlearis with the ventral surface of the pars canalicularis. The term ventral cochleo-canalicular commissure (*V. C.-C. C.*, fig. 21) has been introduced here to designate this commissure; it lies vertically below the

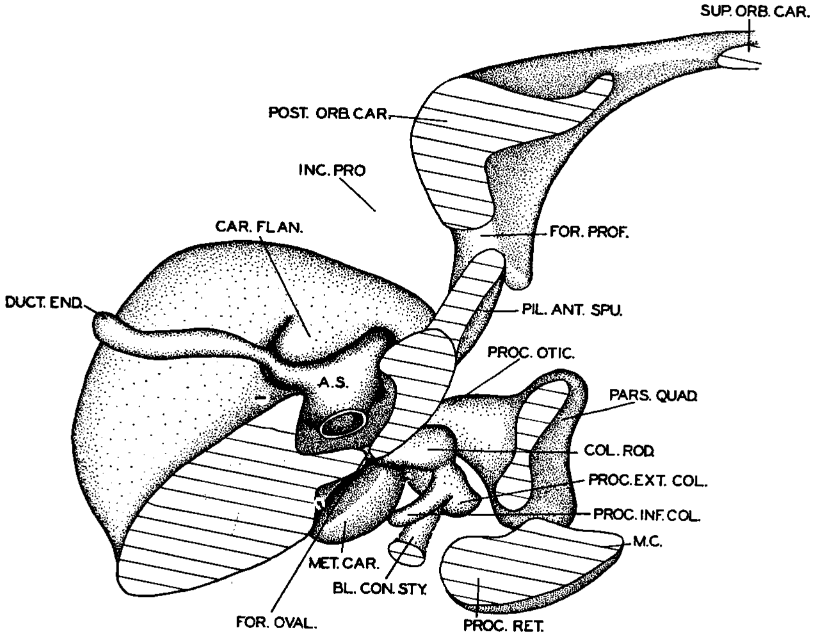


Fig. 16 (X ± 23.3). Stage 4. Topography of the suspensorial region.

dorsal cochleo-canalicular commissure. With the development of the ventral commissure the foramen perilymphaticum (*FOR. PER.*, figs. 20, 21) is delimited. It is bordered dorsally and ventrally by the dorsal and ventral cochleo-canalicular commissures respectively, laterally by the pars canalicularis and medially by the pars cochlearis. Anteriorly this foramen opens into the cavity of the auditory capsule, and posteriorly into the recessus scalae tympani.

A cartilaginous flange (*CAR. FLAN.*, fig. 16) now grows downwards from the central portion of the lateral edge of the auditory foramen, medial to the ductus endolymphaticus (*DUCT. END.*, fig. 16). As a result, the ductus endolymphaticus is lodged in a deep notch in the posterior corner of the auditory foramen.

In this stage the first indications of the foramen ovale (*FOR. OVAL.*, fig. 16) can be observed. Anteriorly and posteriorly to the proximal region of the pharyngohyal, the cartilaginous wall of the pars canalicularis has begun to atrophy. The lateral and medial portions of the pharyngohyal are still fused to the otic capsule.

2. *The Anterior End of the Chondrocranium*

As a result of further increase in height of the interorbital septum, the sphenoid fontanelle is smaller. In this stage the maximum development of the supra-

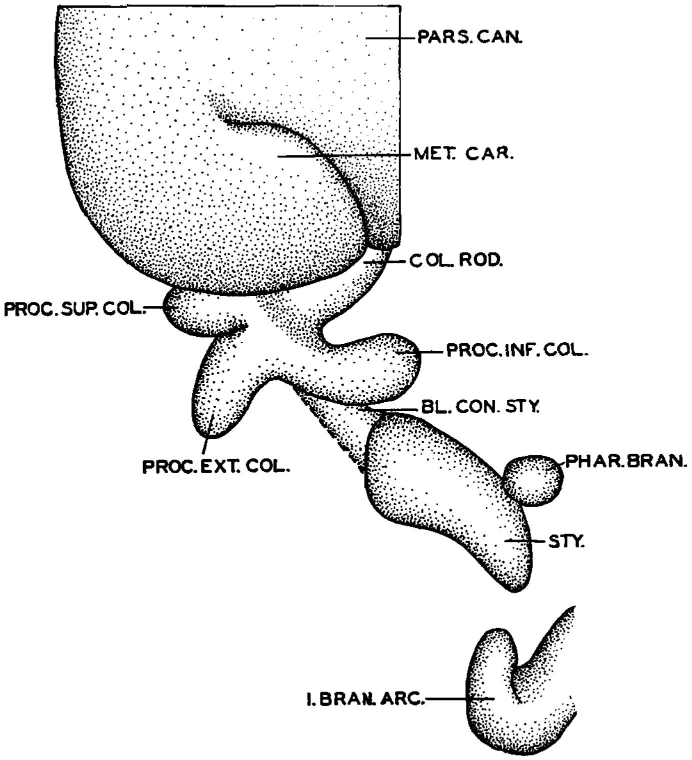


Fig. 17 (X ± 55). Stage 4. Reconstruction of the hyoid arch (norma posterior).

orbital cartilage is encountered. It appears as a broad horizontal plate underlying the forebrain.

3. *The Visceral Arches*

In the hyoid arch the ceratohyal cartilage has fused to the medial surface of the epihyal. Further, the medial region of the ceratohyal has extended medially as a short blunt process to form the processus infracolumellaris (*PROC. INF. COL.*, fig. 17). A blastematous connexion (*BL. CON. STY.*, fig. 17) is still found between the stylohyal and the columella auris. In most birds the processus infracolumellaris is considered to represent a remnant of the earlier connexion between the hyoid cornu and the columella auris. This is not the case in the penguin, in which the processus infracolumellaris is found together with the above connexion.

E. STAGE V

(Figs. 18 to 22.)
Total length of embryo: 58 mm.

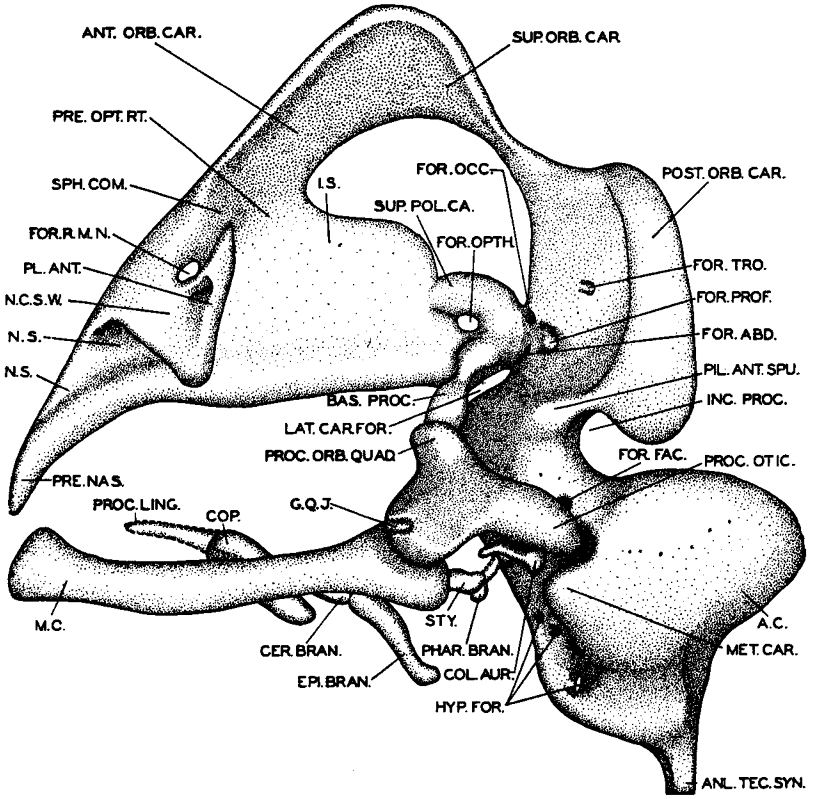


Fig. 18 (X ± 16.2). Stage 5. Reconstruction of chondrocranium (norma lateralis).

As a result of the extensive development of the ethmoidal region, the skull is now beginning to assume a typical avian appearance.

1. *The Basal Plate and Auditory Capsule*

The posterior orbital cartilage has grown considerably sideways and upwards to form a thick transverse concave plate forming the posterior wall to the orbit. Together with the above-mentioned growth, a corresponding degeneration of the anterior and posterior regions of the posterior orbital cartilage has taken place. The lateral expansion of the posterior orbital cartilage is well illustrated by the position of the trochlear canal. Whereas in the previous stages it was lying near the lateral surface, it now lies relatively nearer the medial surface. The supraorbital cartilage has atrophied, so that only a slender connexion remains between the two regions of the orbital cartilage. The oculomotor nerve is still covered by a thin strip of cartilage.

A blastematous tract, the anlage of the tectum synoticum (*ANL. TEC. SYN.*,

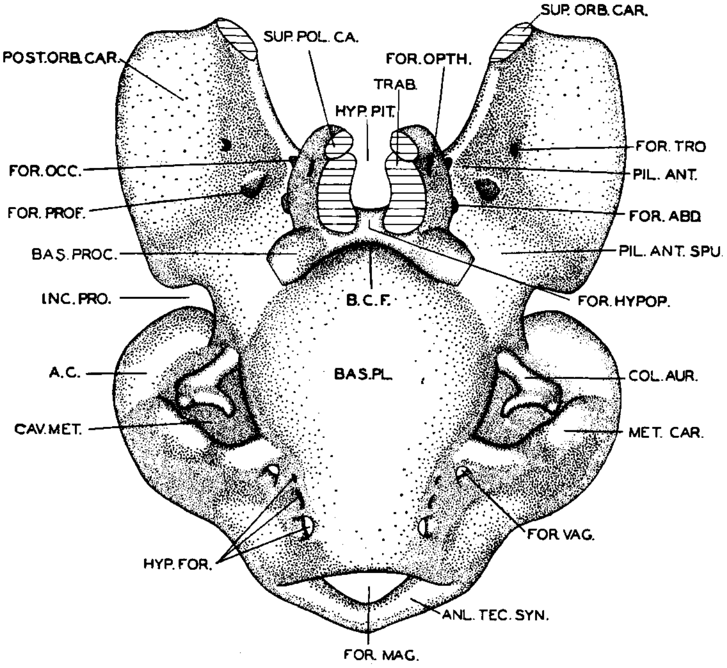


Fig. 19 (X ± 16.6). Stage 5. Reconstruction of the basal plate (norma ventralis). The anterior region of the chondrocranium has been removed.

figs. 18, 19, 21), connects the posterior ends of the auditory capsule with each other behind the medulla oblongata to form the posterior border for the foramen magnum (*FOR. MAG.*, figs. 19, 21).

In this stage the postero-lateral edge of the posterior orbital cartilage closely approaches the dorsal surface of the auditory capsule, with the result that the wide incisura prootica has been narrowed down considerably.

In the auditory capsule a cartilaginous plate has developed which forms the floor to the cochlear groove. Laterally this floor is continuous with the pars canalicularis. All that now remains to indicate the double origin of the auditory capsule is the position of the foramen for the facial nerve. This nerve still passes through the cavity of the auditory capsule, but there is a tendency for it to be enclosed in a canal formed by the further fusion of the two regions of the auditory capsule behind the facial nerve.

The flange of cartilage which was lying medially to the ductus endolymphaticus, has fused with the dorsal cochleo-canalicular commissure so as to form a separate foramen for the ductus endolymphaticus. The auditory foramen now assumes a circular shape.

The recessus scalae tympani opens medially into the cranial cavity through the apertura medialis recessus scalae tympani (*A. M. R. S. T.*, figs. 20, 21) and

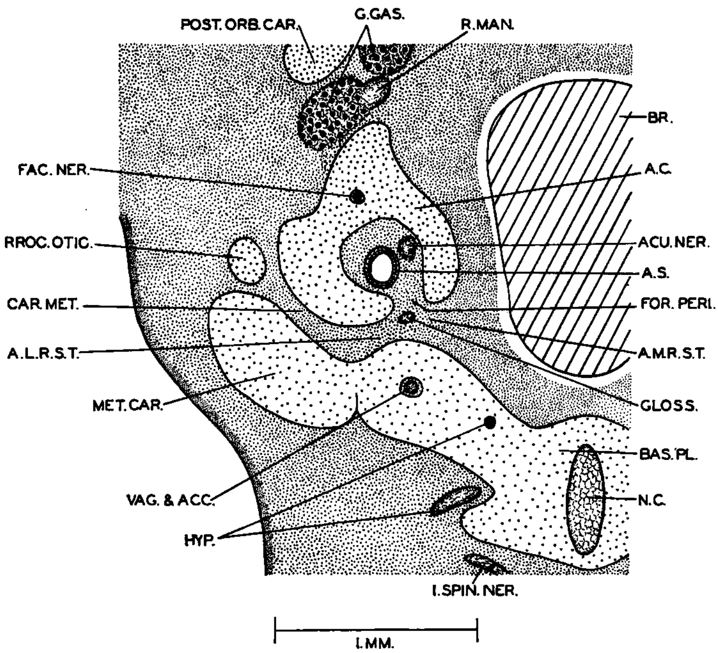


Fig. 20. Stage 5. Transverse section through the auditory capsule.

laterally into the tympanic cavity through the apertura lateralis recessus scalae tympani (*A. L. R. S. T.*, fig. 20).

In earlier stages a growth of the metotic cartilage towards the lateral edge of the basal plate was observed, but in this stage the metotic cartilage has fused with the lateral edge of the basal plate, lateral to the fusion of the auditory capsule with the basal plate.

In the penguin therefore, the metotic cartilage plays no role in the dividing up of the fissura metotica. The posterior edge of the metotic cartilage has fused to the lateral surface of the auditory capsule, while the thick anterior edge remains free and forms a lateral wall to the apertura lateralis recessus scalae tympani. The cavum metoticum opens forwards into the tympanic cavity. The medial region of the metotic cartilage is continued forwards as the subcapsular process, which fuses to the lateral edge of the basal plate, thereby forming a floor to the recessus scalae tympani. In birds only does the recessus scalae tympani possess a floor. The secondary tympanic membrane is stretched over the fenestra pseudorotunda, which is bordered dorsally by the ventral edge of the foramen perilymphaticum and ventrally by the lateral edge of the subcapsular process.

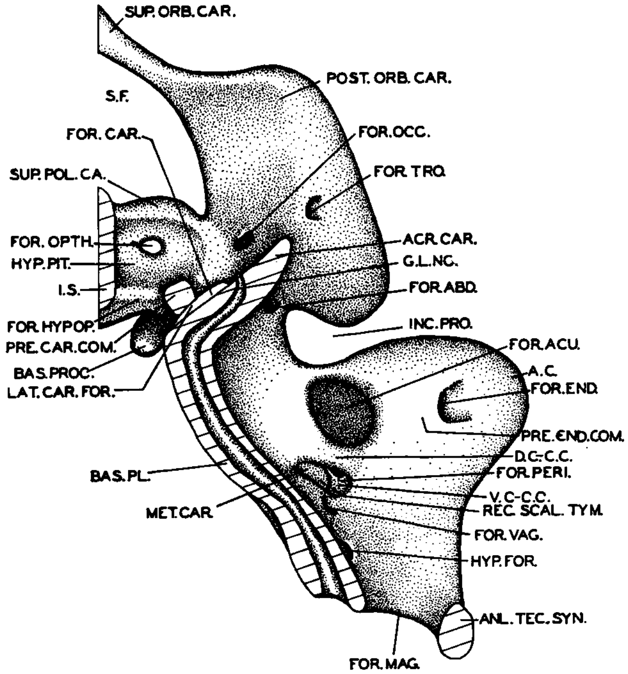


Fig. 21 (X ± 16.6). Stage 5. Disposition of cranial entities as viewed from a median sagittal section.

2. *The Orbital Region*

The most marked development of the interorbital septum in this stage is immediately in front of the hypophysial region. The anterior ends of the suprapolar cartilages have fused with the latero-posterior surfaces of the interorbital septum. All that now remains to indicate the original independence of the suprapolar cartilages are the large ophthalmic foramina. A deep hypophysial pit (*HYP. PIT.*, figs. 19, 21) bordered posteriorly by the acrochordal plate, anteriorly by the posterior edge of the interorbital septum, laterally by the suprapolar cartilages, and ventrally, incompletely, by the precarotid commissure, lodges the hypophysis cerebi. Two median foramina, the foramen caroticum and the foramen hypophyseos open ventrally into this pit.

The dorso-medial region of the basitrabecular process is fused to the antero-ventral surface of the polar cartilage. The medial region of the basitrabecular process is extended slightly medially so as to lie directly beneath the precarotid commissure. Simultaneously, the base of the acrochordal plate has migrated forwards, so that syndesmotic continuity is established between the lateral regions of the acrochordal plate and the ventro-medial regions of the basitrabecular processes. The result is that the lateral carotid incisure is transformed to a lateral carotid foramen (*LAT. CAR. FOR.*, figs. 18, 21). This foramen, through which the carotid artery of the same side passes in order to reach the median foramen caroticum, is bordered dorsally by the polar cartilages, ventrally by the lower end of the acrochordal plate, posteriorly by the fusion between the acrochordal plate and the polar cartilage, and anteriorly by the medial region of the basitrabecular process. It is of particular importance to note that the lateral carotid foramen is formed without the intervention of an infrapolar process, a characteristic typical of most avian chondrocrania.

Between the basitrabecular processes of either side, the precarotid commissure dorsally, and the acrochordal plate ventrally, remains a small basicranial foramen (*B. C. F.*, fig. 19), opening forwards. This foramen cannot be considered homologous with the posterior basicranial foramen as it lies anterior to the acrochordal plate. However, it will be seen that in later stages the foramen occupies a position simulating the posterior basicranial foramen of other forms.

Together with the formation of the lateral carotid foramen, a narrow cavum is enclosed between the acrochordal plate and the polar cartilage. Four foramina open into this cavum: the two lateral carotid foramina, the basicranial foramen and the foramen caroticum. The connexion between Rathke's pouch and the stomadaeum has now atrophied completely, with the result that only a very small foramen hypophyseos remains.

3. *The Ethmoidal Region*

The side-wall of the nasal capsule (*N. C. S. W.*, fig. 18) makes its appearance in this stage as a simple procartilaginous plate, lying lateral to the nasal sac, which grows downwards from the edge of the parietotectal cartilage. In the ontogeny of the duck, DE BEER and BARRINGTON (1934) describe two independent cartilaginous centres for the side-wall of the nasal capsule, the paranasal cartilage and the planum antorbitale. Such independent anlages were not observed in the penguin, neither did BROCK (1937) observe them in the ostrich. A small transverse plate, the planum antorbitale (*PL. ANT.*, figs. 18, 22) develops out of the lower posterior region of the capsular side-wall and forms an incomplete posterior wall to the capsule.

The ramus medialis nasi enters the nasal cavity by passing in an antero-medial direction over the dorsal edge of the planum antorbitale. A broad vertical plate of cartilage arises from the dorsal edge of the planum antorbitale postero-medially to the ramus lateralis nasi and fuses dorsally with the sphenethmoid commissure to enclose the ramus medialis nasi in its own foramen. No mention is made of this commissure in the literature, and for this reason the term postprofundal commissure (*POST. PROF. COM.*, fig. 22) is introduced in this paper. The profundus foramen is bordered dorsally by the parietotectal cartilage, anteriorly by the posterior edge of the side-wall of the nasal capsule,

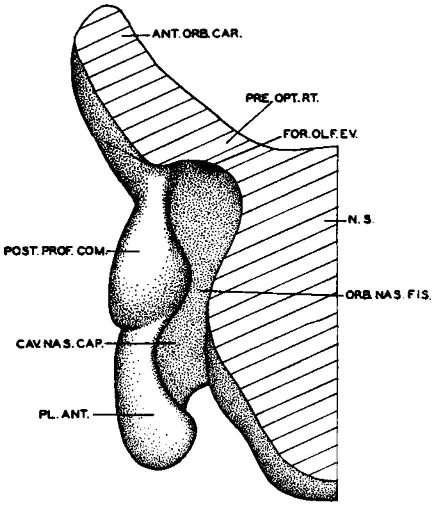


Fig. 22 (X ± 33.3). Stage 5. Reconstruction of a portion of the hinder region of the nasal capsule.

ventrally by the dorsal edge of the planum antorbitale and posteriorly by the postprofundal commissure. Although this latter postprofundal commissure develops out of the planum antorbitale, it cannot be considered as homologous with the latter structure, as it lies medial to the ramus medialis nasi.

The cavity of the nasal capsule is confluent with the orbit behind on account of the presence of the orbitonasal fissure (*ORB. NAS. FIS.*, fig. 22) which is bordered dorsally by the sphenethmoid commissure, medially by the nasal septum and laterally by the postprofundal commissure and the medial edge of the planum antorbitale.

4. *The Visceral Arches*

A shallow groove which lodges the posterior end of the quadratojugal ossification has now developed on the lateral surface of the antero-ventral region of the pars quadrata.

Meckel's cartilage has further increased in length to keep pace with the forward growth of the prenasal process.

In the previous stage it was seen that the anlage of the processus infracolumellaris had fused with the epihyal. Although the present stage is considerably older than the 51 mm stage, it is still possible to observe the processus infracolumellaris as a separate entity. It is separated from the epihyal by means of a narrow connective tissue disc. A broad band of dense connective tissue still connects the stylohyal with the columella auris.

F. STAGE VI

(Figs. 23 to 26.)

Total length of embryo: 61 mm.

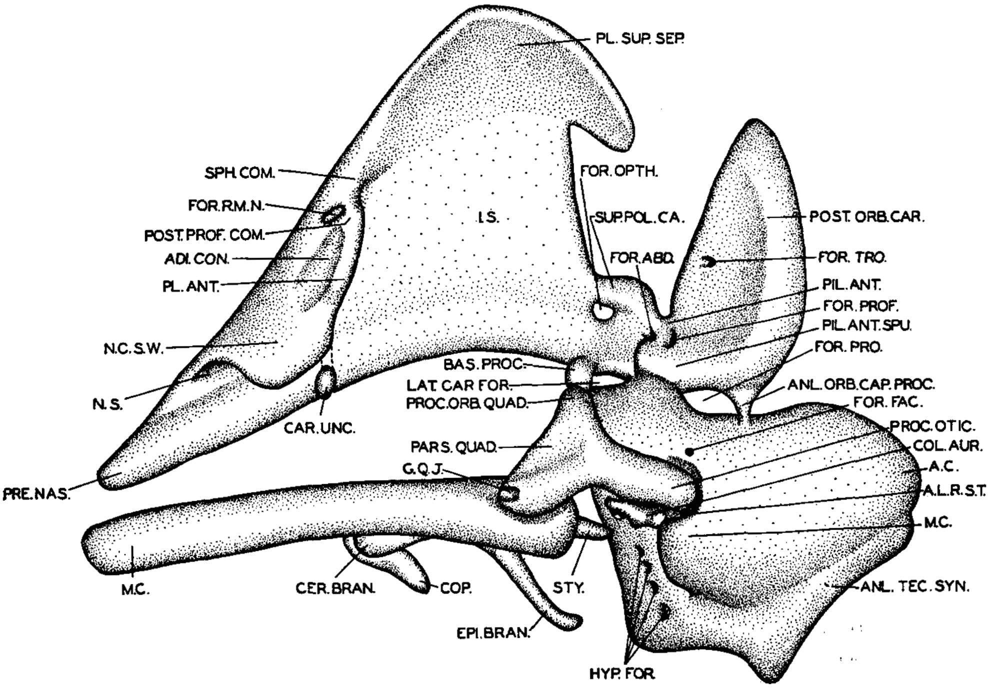


Fig. 23 (X ± 13.8). Stage 6. Reconstruction of the chondrocranium (norma lateralis).

1. *The Basal Plate and Auditory Capsule*

The narrow blastematous tectum synoticum of earlier stages has developed further to form a broad band of tissue, connecting the posterior regions of the auditory capsules.

The posterior orbital cartilages are further reduced in thickness to form a thin, transversely disposed concave plate. Together with the further extention of the posterior orbital cartilage dorsally and laterally, there is an accompaning degeneration of the medial region of this cartilage. As a result the trochlear nerve passes through the cartilage near to its medial edge.

A narrow strip of early procartilaginous tissue, the anlage of the orbitocapsular process (*ANL. ORB. CAP. PROC.*, fig. 23), stretches from the ventro-lateral edge of the posterior orbital cartilage to the dorsal surface of the auditory capsule. With the development of this process, the incisura prootica is transformed into a foramen prooticum (*FOR. PRO.*, fig. 23), bordered anteriorly by the pila antotica spuria, dorsally by the ventral edge of the posterior orbital cartilage, ventrally by the dorsal surface of the auditory capsule and posteriorly by the anlage of the orbitocapsular process. In the duck, De Beer and Barrington (1934) were able to distinguish in this region two independent processes which grew towards each other and fused to form the posterior

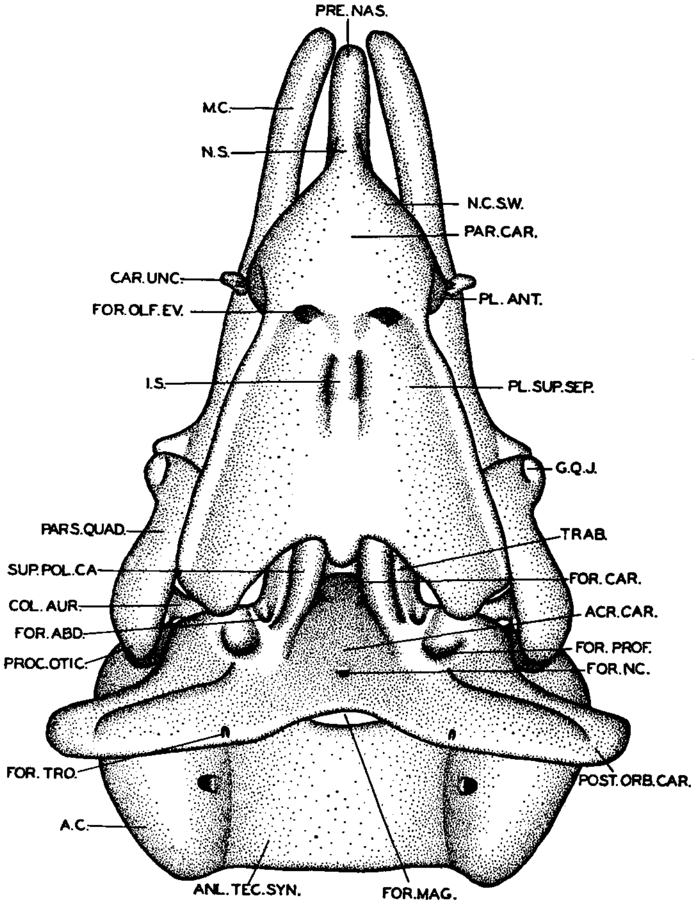


Fig. 24 (X ± 13.8). Stage 6. Reconstruction of chondrocranium (norma dorsalis).

border of the foramen prooticum. They are: (1) the orbitocapsular process from the orbital cartilage and (2) the prootic process from the auditory capsule. As a clear demarcation may be drawn between the anlage of the orbitocapsular process and the dorsal surface of the auditory capsule, there is no reason to assume that a prootic process is present in the penguin.

The anterior wall of the oculomotor canal has completely atrophied with the result that the nerve passes downwards to the eye-muscles in a shallow groove in the anterior surface of the region of the pila antotica and of the posterior orbital cartilage.

Narrow strips of atrophied cartilaginous tissue still connect the proximal region of the pharyngohyal with the pars canalicularis. The facial nerve canal is now fully formed, and in consequence, the facial finally passes outwards without traversing the cavity of the auditory capsule.

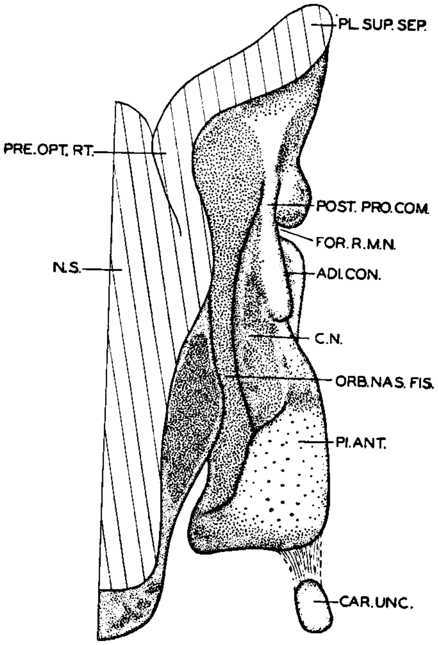


Fig. 25 (X ± 27.3). Stage 6. Reconstruction of a portion of the hinder region of the nasal capsule.

2. *The Orbital Region*

Owing to the large size of the eyes, the slender connexion between the two regions of the orbital cartilage has atrophied.

The lower lateral regions of the acrochordal plate have fused to the ventromedial portions of the basitrabecular processes. The anlage of the pterygoid bone, which lies near to the distal termination of the basitrabecular process, has now appeared. As a result, the blastematous connexion between the pars quadrata and the processus basitrabecularis has broken down.

A marked developmental feature of this stage is the dorsal growth of the interorbital septum. The posterior regions of the anterior orbital cartilages seen in previous stages as two plates of cartilage lying alongside the interorbital septum, have migrated medially. Their ventral halves are cemented to the dorsal region of the interorbital septum (fig. 25), while their dorsal halves extend laterally to form a horizontal plate, the planum supraseptale (*PL. SUP. SEP.*, figs. 23, 24, 25). Consequently the anterior orbital cartilage seen in transverse section is L-shaped. A remnant of the former connexion between the two regions of the orbital cartilage appears as a short blunt process directed backwards from the planum supraseptale towards the posterior orbital cartilage.

3. *The Ethmoidal Region*

Considerable progress may be observed in the nasal capsule of this stage. However, the anterior portion is as yet poorly chondrified. The side-wall of the nasal capsule has increased in length, mainly by addition to its anterior region. As a result of the increased height of the posterior region of the nasal septum, the postprofundal commissure has been lengthened to form a long vertical plate, lying practically parallel to the nasal septum. Ventrally the postprofundal commissure passes into the planum antorbitale with a gentle curve. Owing to the excessive development of the postprofundal commissure, the planum antorbitale remains rudimentary and forms an incomplete posterior wall to the nasal capsule. The postero-ventral edge of the side-wall is turned inwards to form a rudimentary floor (*RUD. FLOOR.*, fig. 29) to the nasal capsule (solum nasi).

The concha nasalis has made its appearance in this stage. It is formed by a folding of the nasal capsule side-wall into the cavity of the nasal capsule in a medial and slightly forward direction. Consequently, the "turbinal" of the concha nasalis develops in the penguin as a simple folding of the side-wall of the capsule. A wide aditus of the concha nasalis (*ADI. CON.*, figs. 23, 25) opens posterolaterally. The concha nasalis stretches from the postero-dorsal region of the nasal capsule downwards and sligthly forwards. The dorsal end of the concha nasalis lies in the postprofundal commissure behind the profundus foramen, with the result that, together with the formation of the concha nasalis, the profundus foramen is displaced sideways so that it now opens not laterally, but latero-posteriorly.

Ventral to the posterior edge of the nasal capsule a small independent nodule of cartilage, the cartilago uncinata (*CAR. UNC.*, figs. 23, 25) is found. Although it is difficult to be positive, the nodule appears to chondrify in the anterior remnant of the pars pterygoidea. The cartilago uncinata is connected to the ventral edge of the planum antorbitale by means of a short ligament.

4. *The Visceral Arches*

The independent anlage of the processus infracolumellaris seen in the previous stage has now fused with the medial region of the epihyal. Only a slender tract of blastematous tissue remains between the stylohyal and the columella auris.

The branchial arch is now completely chondrified. A diathrosis has developed between the ceratobranchial and the epibranchial, and between the ceratohyal and the copula. The posterior ends of the epibranchials are flexed laterally.

A short blastematous process, the remnant of the processus lingualis, stretches forwards from the anterior end of the copula. A narrow blastematous plate,

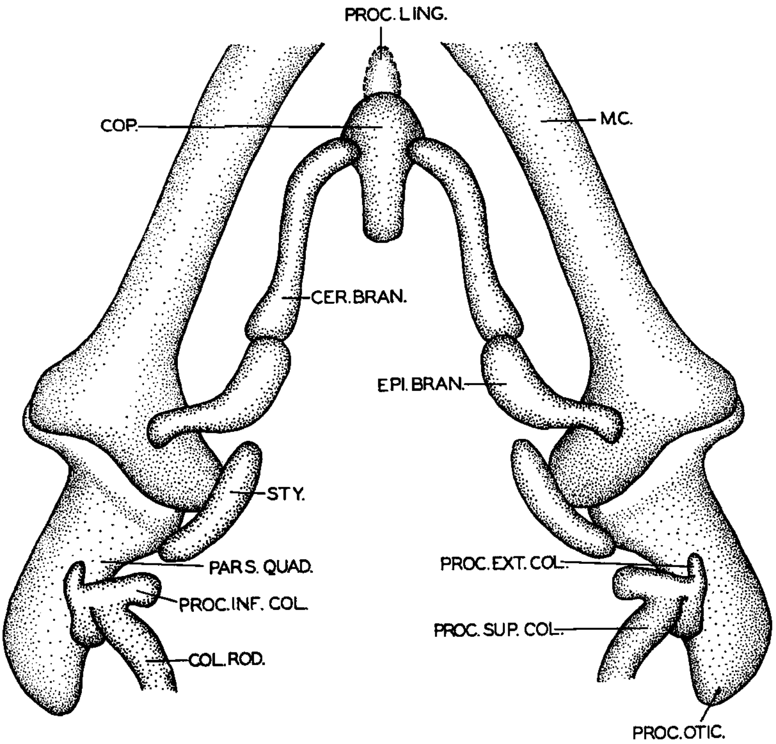


Fig. 26 (X ± 23.6). Stage 6. Reconstruction of the visceral arches (norma ventralis).

the anlage of the paraglossal cartilage, is situated dorsally to the anterior region of the copula. On either side of this plate a centre of condensation of the tissue is observable. These indicate the paired nature of the paraglossal cartilage. Anteriorly the anlage of the paraglossal cartilage merges into the blasteme of the entoglossal process.

G. STAGE VII

(Figs. 27 to 30.)

Total length of embryo: 74 mm.

The main characteristic of this stage is the straightening out of the cranial flexure.

1. *Basal Plate and Auditory Capsule*

All that now remains of the medial region of the acrochordal plate is a narrow strip of disentegrated cartilage which does not completely surround the notochord. Ventrally the anterior surface of the notochord (*N. C.*, fig. 27 c) traverses the posterior region of the basicranial foramen. The reduction of the dorsal region of the acrochordal plate is indicated by the proximity of the foramen, through which the anterior tip of the notochord projects, to the dorsal surface of the acrochordal plate. In earlier stages the acrochordal plate was continued for a considerable distance, dorsally, above the notochord foramen.

Further reduction of the medial region of the posterior orbital cartilage has freed the trochlear nerve. As a result of this reduction, the medial edge of the posterior orbital cartilage presents a serrated contour.

Owing to the disentegration of the cartilage previously forming the groove for the oculomotor nerve, the nerve now passes forwards, out of the cranial cavity, dorsal to the surrounding cartilaginous structures.

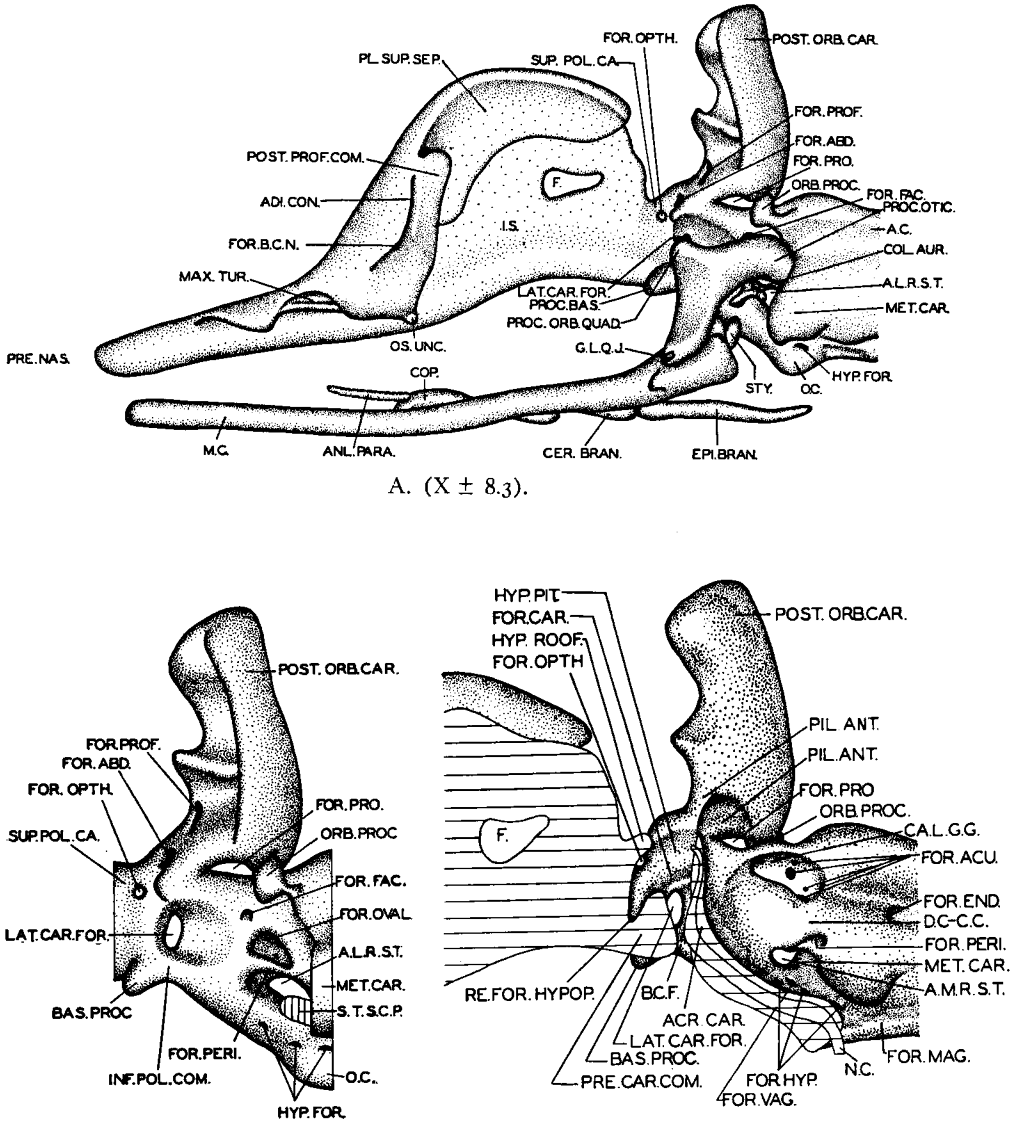
The large acustic foramen observed in earlier stages has been subdivided into four small foramina. However, the extent of the original large foramen is indicated by a shallow depression (*CA. L. G. G.*, fig. 27 c) lodging the geniculate ganglion. The internal foramen of the facial nerve canal opens into the anterior region of this depression. In this stage the cartilage of the pars canalicularis surrounding the proximal region of the pharyngokyal has atrophied completely, so that a small foramen ovale is formed. It is probable that part of the pars canalicularis, to which the pharyngohyal was fused, contributes to the formation of the foot plate of the columella auris.

Postero-ventrally, where the metotic cartilage is fused to the lateral region of the auditory capsule, resorbtion of cartilage has been responsible for a short canal which connects the cavum metoticum with the exterior. The free anterior end of the metotic cartilage has grown further forward. The anlage of the orbitocapsular process has chondrified (*ORB. PROC.*, fig. 27) and fused to the lateral surface of the auditory capsule, dorsal to the articulatory facet of the processus oticus.

2. *The Orbital Region*

As a result of the straightening out of the cranial flexure, the posterior edge of the trabeculae, the medial region of the basitrabecular process, and the lower lateral regions of the acrochordal plate have been stretched to form a broad infrapolar commissure (*INF. POL. COM.*, fig. 27 b) which serves as a ventral border to the lateral carotid foramen. This simulates the infrapolar process of other avian chondrocrania. However, it was shown in previous stages that no infrapolar process, strictly homologous with the infrapolar process of other birds, is found in the penguin. As a further result of the straightening out of the cranial flexure, the basicranial foramen comes to lie vertically below the medial foramen caroticum and opens downward, and not forwards, as in the previous stage.

Fusion of the trabecular bars with each other in the midline, and with the



A. (X ± 8.3).

B. (X ± 13.3).

C. (X ± 13.3).

Fig. 27. Stage 7.

A. Reconstruction of chondrocranium (norma lateralis).

B. Reconstruction of the hypophysial region (norma lateralis). Pars quadrata and metotic cartilage have been removed.

C. Median view of the posterior region of the auditory capsule.

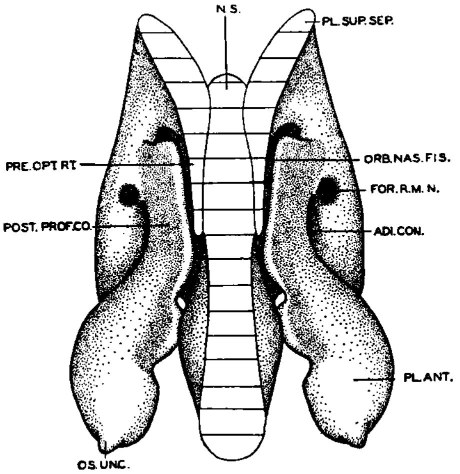


Fig. 28 (X ± 11.0). Stage 7. Reconstruction of the nasal capsule (norma posterior).

precarotid commissure behind, now occludes the hypophysial foramen. In a sagittal section the dorsal remnant (*RE. FOR. HYPOP.*, fig. 27 c) of this foramen may be observed as a narrow cavum lying anterior to the dorsal region of the precarotid commissure.

The region of the supratrabecular cartilage lying dorsal to the ophthalmic foramen, has begun to atrophy. A short horizontal roof (*HYP. ROOF.*,. fig. 27 c) overlying the anterior region of the hypophysial pit, has developed from the posterior surface of the interorbital septum. The optic chiasma lies immediately above this roof. The optic nerves are lodged in a shallow notch in the posterior region of the interorbital septum.

The basitrabecular process, which now articulates with the pterygoid, extends laterally and slightly forwards.

A large fontanelle (*F.*, fig. 27 a, b) has developed in the posterior region of the interorbital septum. The planum supraseptale has undergone reduction and now remains as a narrow horizontal plate. However, it may still be distinguished from the interorbital septum as a separate entity (fig. 27 a).

3. *The Nasal Capsule*

The anterior region of the nasal capsule is still in an early state of chondrification. A very long prenasal process stretches beyond the anterior limit of the nasal capsule.

A small oval fenestra septi nasi posterior (*F. S. N. P.*, fig. 34) has made its appearance in the nasal septum. In a sagittal section of the latter the anterior region of the nasal septum is low, while posterior to the fenestra septi nasi posterior it rises rapidly to attain a height equal to that of the interorbital

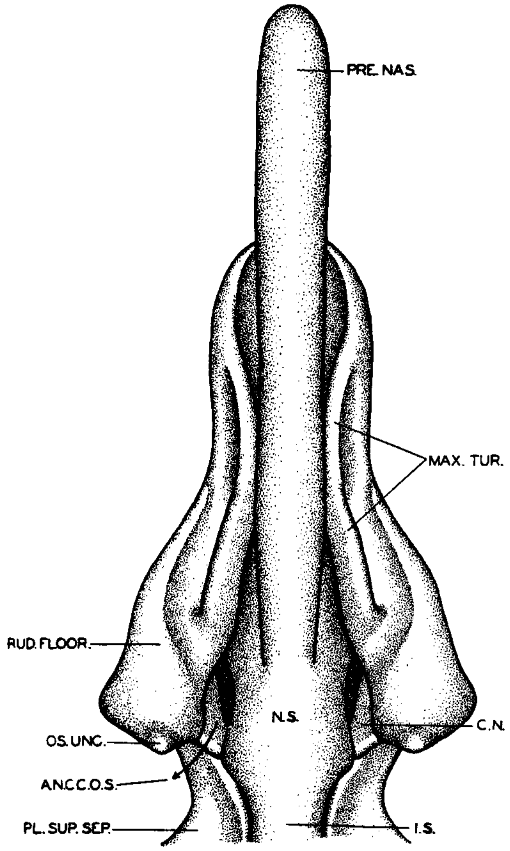


Fig. 29 (X ± 16.6). Stage 7. Reconstruction of the nasal capsule (norma ventralis).

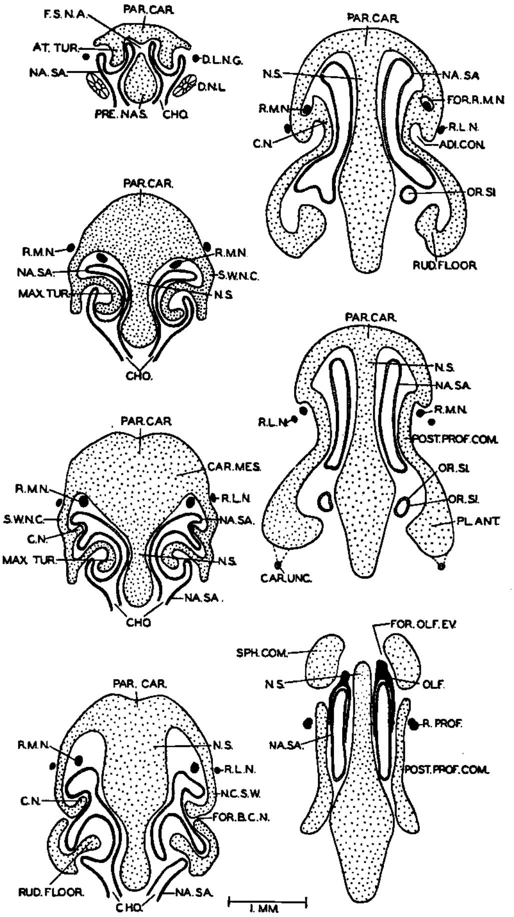


Fig. 30. Stage 7. Series of transverse sections through the nasal capsule.

septum. The dorsal region of the septum immediately behind the fenestra septi nasi posterior is triangular in shape. It is in this large cartilage mass that the mesethmoid ossification arises. Posterior to the mesethmoid cartilage (*CAR. MES.*, fig. 30) the septum nasi narrows to merge into the interorbital septum. Ventral to the mesethmoid cartilage, a small area of the septum has begun to atrophy. This is the first indication of the craniofacial foramen.

The postprofundal commissure has grown backwards to form a broad plate, the posterior edge of which closely approaches the nasal septum, with the result that the orbitonasal fissure is narrowed down considerably. The fissure may be divided into two regions: a narrow dorsal, and a broad ventral region. The latter allowing for the passage of the orbital sinus from the nasal cavity (*A. N. C. C. O. S.*, fig. 29), is bordered incompletely: dorsally by the ventral edge of the postprofundal commissure, medially by the nasal septum, and laterally by the medial edge of the planum antorbitale.

As a result of the further deepening of the concha nasalis, the foramen for the ramus medialis nasi now opens directly backwards. Ventrally the aditus conchae is obliterated, because the side walls of the concha nasalis fuse with one another to form a solid turbinal. Dorsally, however, the concha nasalis still has the form of a simple fold of the side wall. A narrow fissure in the side wall of the nasal capsule is found directly behind the turbinal of the solid concha nasalis (*FOR. B. C. N.*, fig. 30).

The maxilloturbinals have made their appearance in this stage. They appear as two long cartilage plates which grow inwards and downwards from the side wall of the nasal capsule. Anteriorly they arise from the ventral edge of the side wall, while posteriorly they are covered laterally by the lower region of the side wall. Posteriorly the maxilloturbinals form a rudimentary floor to the nasal capsule. In order to elucidate the anatomy of the nasal capsule, a series of transverse sections through the capsule is given in fig. 30.

The independent cartilago uncinata found ventrally to the planum antorbitale in the 61 mm stage has now ossified. The os uncinatum is embedded in the ventral edge of the planum antorbitale.

4. *The Visceral Arches*

All three processes of the columella auris: the processus supracolumellaris lateralis, the processus infracolumellaris and the processus extracolumellaris lie in the same plane and are embedded in the tympanic membrane. The connexion between the columella auris and the stylohyal has atrophied.

The first branchial arches have increased considerably in length so that their posterior regions now lie at a point level with the foramen magnum. A small pharyngobranchial is still present.

The paraglossal cartilage has developed further, but is still in an early state of chondrification. Its anterior end is directed forwards as a sharp process lying in the tongue, while its postero-ventral end articulates with the antero-dorsal surface of the copula. A small medial foramen in the posterior region of the paraglossal cartilage still indicates its paired nature.

H. STAGE VIII

(Figs. 31 to 34.)
Total length of embryo: 91 mm.

1. *The Basal Plate and the Auditory Capsule*

The medial region of the acrochordal plate has now completely atrophied. As a result, the notochord projects upwards from a small medial foramen

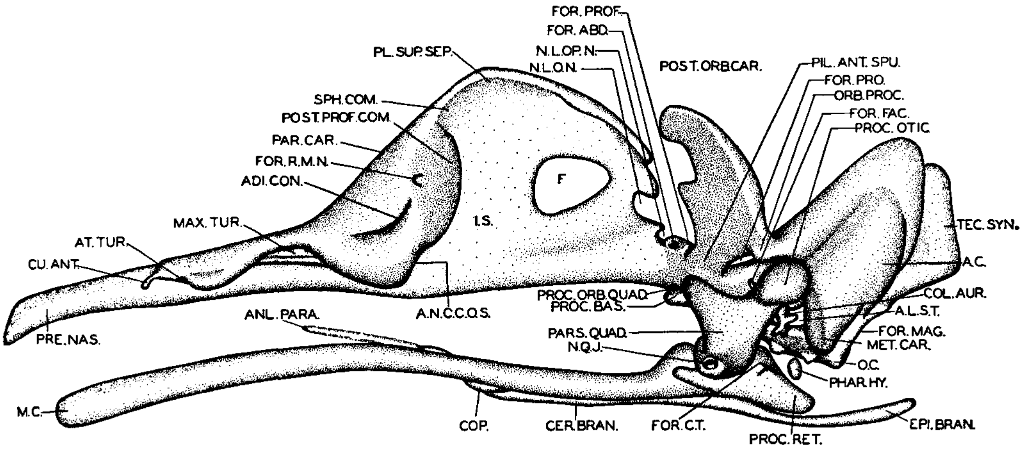


Fig. 31 (X ± 7). Stage 8. Reconstruction of chondrocranium (norma lateralis).

(*FOR. N. C.*, figs. 32, 33) in the antero-dorsal surface of the basal plate. Whereas in earlier stages the anterior region of the notochord was surrounded by the acrochordal plate, it is now embedded in a thick membrane (*MEM.*, fig. 33), the remnant of the acrochordal plate. In the nestling, a bony lamella, forming the posterior wall to the hypophysial pit, develops in this membrane.

Atrophy of the acrochordal plate was described by T. J. PARKER (1892 a) in *Apteryx:* "the medial portion of the dorsum sellae is formed of connective tissue in which the upturned end of the notochord is embedded." SONIES (1907) described the degeneration of the acrochordal plate till only a narrow bridge remains, forming the anterior border to the fenestra basicranialis. In the sparrow and the starling, according to SONIES (1907), the acrochordal atrophies completely, with the result that the fenestra basicranialis posterior and the fenestra hypophyseos become confluent. SONIES claims that no atrophy of the acrochordal plate is found in the fowl. However, TONKOFF (1900) showed that part of the medial wall actually does atrophy, although not as extensively as in the duck.

Only two hypoglossal foramina now remain in the basal plate. A reconstruction of the posterior orbital region shows a slender pila antotica and an extremely well-developed, broad pila antotica spuria. In the adult skull the pila antotica ossifies to form a slender pleurosphenoid lying medial to the ramus profundus.

The tectum synoticum is fully chondrified in this stage. It consists of a broad plate of cartilage connecting the ventro-posterior edges of the auditory capsule. Posteriorly it projects backwards as a short cylinder between the posterior regions of the auditory capsule.

In the latter the foramen perilymphaticum and the recessus scalae tympani have increased considerably in size. A narrow slit-like foramen places the tympanic cavity and the cavum metoticum in communication with each other. Projecting into the cavum metoticum is a short diverticulum of the middle

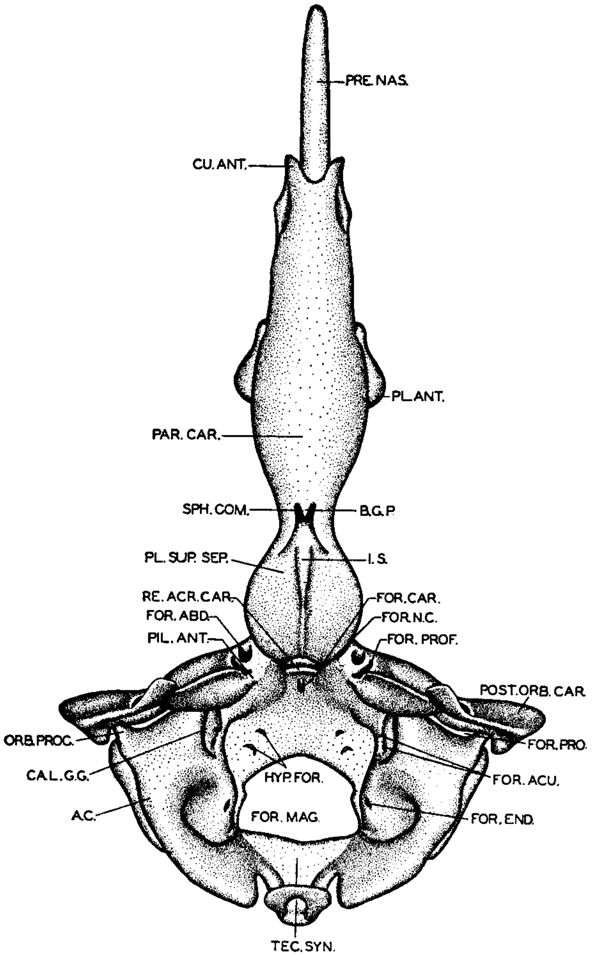


Fig. 32 (X ± 7). Stage 8. Reconstruction of chondrocranium (norma dorsalis).

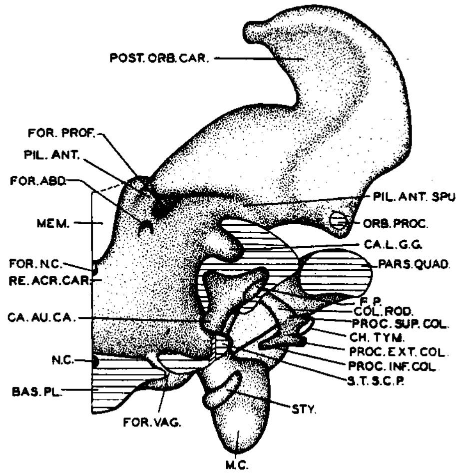


Fig. 33 (X ± 9). Stage 8. Auditory region of the skull.

ear. The rest of the cavum is filled with loose connective tissue. In the adult skull, however, the diverticulum completely fills the cavum.

The columellar rod is directed outwards and downwards so that a fairly sharp flexure occurs.

2. *The Orbital Region*

In contrast to the previous stage the hypophysial foramen is still open. Fusion of the infrapolar commissures of either side with each other in the midline, has closed up the basicranial foramen. On the right side the suprapolar cartilage remains as a slender cartilage bridge above the ophthalmic artery, but on the

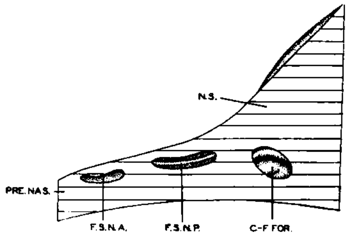


Fig. 34 (X ± 14). Stage 8. Disposition of the foramina of nasal septum.

left it has atrophied, with the result that the ophthalmic artery is lodged in a deep notch. The groove lodging the optic arteries has deepened considerably.

Two small processes projecting forward from the skull base are all that remain of the once extensive basitrabecular processes. It has been shown in an earlier work (Crompton, in press) that these processes ossify later. However, when the joint between the pterygopalatine arcade and the parasphenoid becomes functional late in ontogeny, the ossified basitrabecular processes atrophy into thick ligaments stretching from the skull base to the pterygoid.

The fontanelle in the interorbital septum is now larger. During the further development of the skull, the size of this fontanelle continues to increase until only the small anterior region of the interorbital septum persists in the adult skull. Further reduction of the planum supraseptale is observable in this stage.

3. *The Nasal Capsule*

Three foramina are now found in the nasal septum, the fenestra septi nasi anterior (*F. S. N .A.*, fig. 34), the fenestra septi nasi posterior (*F. S. N. P.*, fig. 34) and the craniofacial foramen (*C-F. FOR.*, fig. 34).

The postprofundal commissure has extended its area of fusion with the sphenethmoid commissure above and has fused with the nasal septum behind, to obliterate the dorsal region of the orbitonasal fissure. A broad ventral fissure remains for the passage of the orbital sinus. The fusion of the side walls of the concha nasalis has spread dorsally. A long fissure in the side wall of the nasal capsule, co-extensive with the concha nasalis, is found immediately behind the turbinal.

In the duck the maxilloturbinal gyrates up to 1 ½ times. In contrast to this, the maximum gyration found in the penguin is ¾ of a turn. The anterior region of the side wall is fully formed. Stretching downwards from the dorsal surface of the anterior parietotectal cartilage is a long cartilaginous curtain, the atrioturbinal (*AT. TUR.*, fig. 31). Its posterior end overlaps the anterior edge of the maxilloturbinal. An anterior wall to the fenestra narina, the cupola anterior (*CUP. ANT.*, fig. 31), has developed from the anterior parietotectal cartilage. In the duck (De Beer and Barrington, 1934) and the kestrel (Sushkin, 1899) the lamina transversalis stretching from the cupola

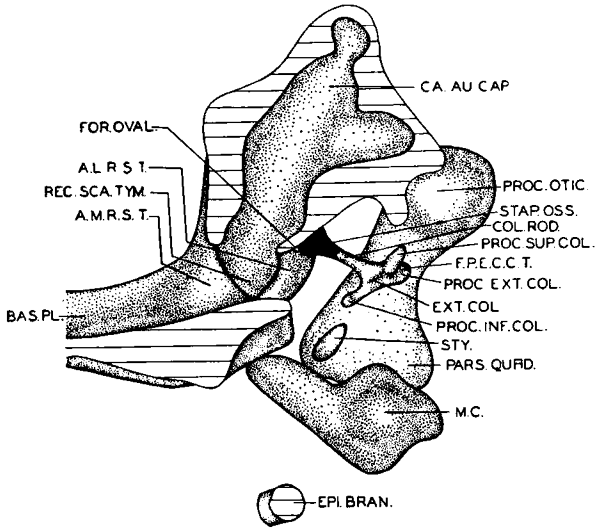


Fig. 35 (X ± 7). Stage 9. Columella auris viewed from behind.

anterior to the median septum forms a floor to the anterior region of the nasal capsule. No such structure is found in the penguin.

I. STAGE IX

(Figs. 35 to 36.)

Total length of embryo: 150 mm.

No complete description of the chondrocranium will be given for this stage.

In the columella auris of the right side, a slender bar of cartilage stretches between the lateral surface of the p. supracolumellaris lateralis and the dorsal surface of the p. extracolumellaris, to form the lateral border of a small foramen traversed by the chorda tympani. This cartilage bar must not be confused with the laterohyal, (see later section) as it lies lateral and not medial to the chorda tympani. The flexure of the columella auris has straightened out. As the medial portion of the rod, including the foot plate, has ossified to form the stapes, it is now possible to divide the columella auris into two portions, an ossified stapedial and a cartilaginous extracolumellar. The columella auris chondrified as a single structure before ossification set in, so it is impossible to ascertain whether the two divisions of the columella auris are co-extensive with the pharyngohyal and the epihyal. No joint develops between the stapes and the extracolumella. A small stylohyal persists ventral to the p. infracolumellaris.

In the nasal capsule the three foramina have increased considerably in size

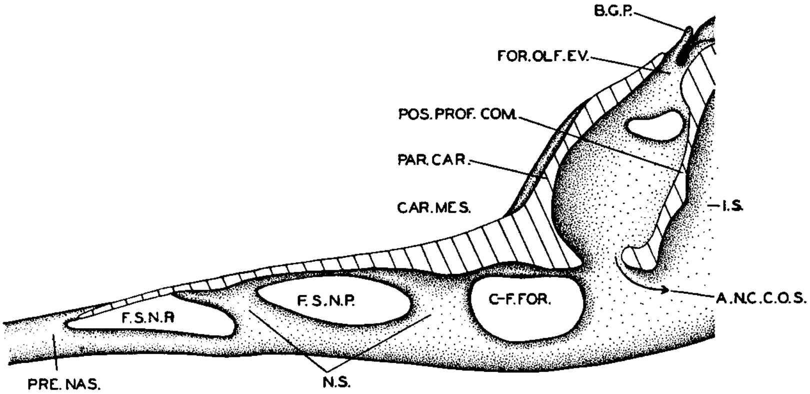


Fig. 36 (X ± 7). Stage 9. Reconstruction of median view of nasal capsule.

so that little of the original nasal septum remains. Below the foramen olfactorium evehens an additional foramen has appeared in the nasal septum.

In the nestling penguin the mesethmoid cartilage ossifies and the entire anterior region of the nasal capsule remains cartilaginous throughout life. Within the postprofundal commissure and the planum antorbitale the second ossification of the nasal capsule, the ectethmoid, develops. This latter bone is synostotically joined to the mesethmoid medially and dorsally. The membrane bones of the beak are syndesmotically connected to the anterior region of the nasal capsule and the prenasal process. As a result of the above attachment, common to adromoeognatic birds, the anterior region of the nasal capsule together with the membrane bones of the beak shift upwards during kinesis. In order that this may take place in the penguin, the ventral border of the craniofacial foramen atrophies, thus transforming the foramen into a craniofacial fissure which lies vertically below the mesokinetic line of flexure, situated between the mesethmoid posteriorly and the cartilaginous nasal capsule anteriorly. A craniofacial foramen is found in all adromoeognathic birds, but its development has only been described by Swart (1946) for the duck. Swart pointed out that the craniofacial fissure develops, not from a special craniofacial foramen as in the penguin, but from the fenestra septi nasi posterior.

De Villiers (1946) has shown that in the dromoeognathic birds the entire nasal septum ossifies in continuity with the orbitosphenoid. During the kinesis the dorsal membrane bones of the beak are lifted away from the dorsal edge of the ossified nasal septum.

A small process (*B. G. P.*, fig. 36) which is directed backwards arises from the posterior central edge of the parietotectal cartilage. In the fowl and the duck this process is so large that it covers the anterior part of the interorbital septum.

The aditus conchae is now completely obliterated by the fusion of the side walls of the concha nasalis with each other.

PART II

I. RÉSUMÉ AND DISCUSSION

A. COLUMELLA AURIS

1. *Development of the Columella Auris of the Penguin*

Before discussing the avian columella auris in detail, a short summary of its development in the penguin will be given.

In the first stage four blastematous anlages constitute the hyoid arch. For convenience sake the anlages are named the pharyngo-, epi-, cerato-, and hypohyal elements. These divisions are not necessarily homologous with the similarly named ones in the hyoid arch of the fish. The epi-, cerato- and hypohyal elements abutt against one another, while the pharyngohyal, which is fused to the auditory capsule, is connected to the epihyal by a strand of connective tissue. The p. supracolumellaris lateralis develops from the lateral surface of the epihyal and projects dorso-laterally past the ventro-lateral surface of the pharyngohyal. In stage II the hypohyal and the ceratohyal have fused to form a long blastematous rod. The pharyngohyal grows ventrally as a short process to form the rod of the columella auris. In stage III the pharyngo- and epihyal have chondrified and fused to form the columella auris. From the ventral region of the epihyal, the p. extracolumellaris develops. Continuous with the dorsal end of the p. supracolumellaris lateralis is a nodule of dense blasteme situated between the p. oticus and the metotic cartilage. This nodule is probably homologous with the intercalary of reptiles. An amphistylic jaw suspension is therefore represented in the early developmental stages of the penguin. However, this amphistylic condition cannot be considered homologous with the amphistylic jaw suspension of the crossopterygians, where it is found as a result of the connexion between the processus quadratus of the hyomandibular and the posterior surface of the quadrate (WESTOLL, 1943). The processus quadratus is homologous with the processus internus of reptiles, a process not found in birds. With the disappearance of the blastematous intercalary in stage III an autostylic condition is effected.

The p. infracolumellaris develops as an outgrowth of an independent chondrification developing within the ceratohyal blasteme. This ceratohyal chondrification later fuses with the epihyal. In other avian orders that have been investigated, the p. infracolumellaris represents a remnant of the proximal region of the interhyal, i.e. the connexion between the hyoid cornu and the columella auris. In the penguin apparently the interhyal completely disappears without giving rise to any adult structure. VERSLUYS showed that in *Lacerta* the p. infracolumellaris represents a proximal remnant of the interhyal while in *Geckonidae* the processus develops medial to the interhyal as in the penguin.

In the crocodile, where the p. internus does not develop, the ventral end of the hyoid cornu is fused to the posterior surface of Meckel's cartilage. This connexion led PETERS (1874) and OWEN (1846) to believe that the hyoid cornu in the crocodile was homologous with the processus internus of other reptiles. They went even further and also considered the hyoid cornu of birds as homologous with the processus internus. HUXLEY (1869) named the hyoid cornu, which in *Gallus* is fused to the columella auris, the p. infrastapedialis and also considered it homologous with the p. internus. However, both the work of VERSLUYS (1903) and my own observations on the developmental history of the hyoid arch in the penguin, make it quite clear that the p. internus of PETERS and OWEN and the infrastapedial of HUXLEY, represent the ventral end of the hyoid arch.

Within the hypohyal blasteme, the large stylohyal cartilage develops. The cartilaginous continuity existing between the stylohyal and the columella auris in several birds is not found in the penguin.

In all tetrapods the columella auris develops from two centres, here named the pharyngo- and epihyal elements, but generally designated "otostapes" and "hyostapes". In some forms e.g. *Lacerta agilis* (HOFFMANN, 1889 and VERSLUYS, 1903), *Crocodilia* (GOLDBY, 1925), *Sphenodon* (WYETH, 1924), *Struthio* (BROCK, 1937), *Tinnunculus* (SUSHKIN, 1899), *Columba* (SMITH, 1905) and *Speniscus demersus,* a continuity, either blastematous or cartilaginous, is found between the otostapes and the auditory capsule during the ontogeny. Because of this HOFFMANN (1889) named the proximal region of the columella auris the "otostapes", thereby implying that it developed from the auditory capsule, and the distal portion the "hyostapes", which he believed represented the dorsal portion of the hyoid arch. REICHERT (1837), HUXLEY (1869), VERSLUYS (1903), GOODRICH (1930) and DE BEER 1937) all, however, consider that the entire columella auris is a derivative of the hyoid arch, and this view has been supported by recent palaeontological findings. In the above-mentioned forms the cartilage of the auditory capsule to which the pharyngohyal ("Otostapes") is fused, atrophies in the later ontogeny to form the foramen ovale. It is possible, therefore, that the auditory capsule contributes to the formation of the footplate. VERSLUYS (1903) explains the continuity existing between the columella auris and the auditory capsule as the result of the blastematous anlages of both the auditory capsule and the "otostapes" arising simultaneously and developing together. In a form such as *Platydactylus,* for example, where the blastematous anlages of the auditory capsule and the otostapes do not arise together a distinction may be drawn between the two entities, throughout the ontogeny.

The chorda tympani of the penguin follows a typical course. It passes forwards from behind the stapes; lateral to the p. supracolumellaris lateralis and dorsal to the p. extracolumellaris. BROCK (1937) described the following course for the chorda tympani in the penguin: "The chorda tympani branches from the hyomandibular immediately above the columella shaft and then passes forward in a precolumellar course towards the trigeminal ganglion." But what BROCK here describes is not the chorda tympani but probably one of the numerous sympathetic nerves found in this region.

2. *Development of the Columella Auris in the Duck*

The development of the columella auris of *Anas* was described by DE BEER and BARRINGTON (1934), but, as it was not studied in detail, an investigation of the development of this structure was undertaken.

In the 4 ½ day embryo the columella auris consists of two distinct procartilaginous centres lying against each other: the "otostapes" and the "hyostapes". Neither DE BEER and BARRINGTON (1934) nor SONIES (1907) observed this division. These cartilaginous centres are homologous with the blastematous anlages, epihyal and pharyngohyal, found in the penguin but, whereas the demarcation between the pharyngo- and epihyal in the penguin is lost when chondrification sets in, the distinction is retained in the duck. Proximally the "otostapes" of the duck is in a blastematous state, but may be distinguished from the blasteme of the auditory capsule. A thin tract of procartilaginous tissue, the interhyal, connects the stylohyal with the hyostapes. No independent ceratohyal chondrification is present. In DE BEER's description of the duck he claims the appearance of the stylohyal as an independent chondrification in the 8 ½ day embryo. SONIES (1907) also described a separate cartilaginous centre for the stylohyal. A supracolumellar arcade, the "suprastapedial arcade" of SUSHKIN (1899) consisting of dense blastematous tissue stretches from the dorso-lateral edge of the "hyostapes" to the dorso-lateral edge of the "otostapes" to enclose a small "foramen of Huxley" (*HUX. FOR.*, fig. 37). The dorsal surface of the "hyostapes" forms the ventral border to this foramen. Dorsally within this arcade a separate nodule of cartilage is present.

GOLDBY (1925) described how the p. dorsalis develops from the "otostapes" in the crocodile. VERSLUYS (1903) describes a similar development for this process in the lizards. The chondrification found in the supracolumellar arcade of the duck may possibly be homologous with the independent chondrification in the p. dorsalis of reptiles.

In the 5 ½ day embryo the medial region of the "otostapes" has chondrified

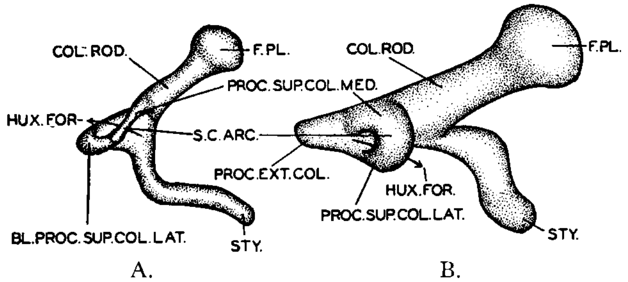


Fig. 37. The columella auris of the duck.
A. 6 1/2 day embryo. B. 9 1/2 day embryo.

to form a footplate and the chondrification within the supracolumellar arcade has increased in size.

In the 6 ½ day embryo (fig. 37 a) the chondrification within the supracolumellar arcade has spread medially and fused to the "otostapes". The side wall of the auditory capsule has chondrified, and a foramen ovale, lodging the footplate of the columella auris, is formed.

In the 9 ½ day embryo (fig. 37 b) the "oto-" and "hyostapes" have fused. A p. extracolumellaris develops from the lateral surface of the hyostapes. The cartilage in the supracolumellar arcade has spread laterally to fuse with the "hyostapes", so that a cartilaginous arcade "stretching" between "otostapes" and "hyostapes" is formed. The medio-dorsal region of this arcade projects dorsally as a short process. Two dorsal processes are thus found in the duck: a medial process developing from the "otostapes", homologous with the p. dorsalis in reptiles and a lateral process developing from the hyostapes, homologous with the p. supracolumellaris lateralis of the penguin. Dorsally they fuse with each other to enclose Huxley's foramen.

The relationship between the p. dorsalis of reptiles and the medial process of birds was pointed out by Huxley (1869), Versluys (1903) and De Beer (1937). Huxley (1869) named the dorsal process of reptiles and the medial process of birds the p. "suprastapedialis".

De Beer (1937) is aware of the existence of two dorsal processes and their affinities in the different groups, but uses the same nomenclature to cover both processes: "the lateral prong of the hyoid" or the "suprastapedial process". He does, however, observe that the medial process develops from the "otostapes" and the lateral process from the "hyostapes".

Stresemann (1927—34) mentions only one process in birds, the p. supracolumellaris which has to include both the medial and the lateral processes of the columella auris. Wyeth (1924) has named the lateral process in *Sphenodon* the p. suprastapedialis and the medial process the "recurrent process".

In order to avoid confusion the medial process will be named the p. supracolumellaris medialis and the lateral the p. supracolumellaris lateralis.

3. *Columella Auris of the Fowl, Kestrel, Starling, Nightjar and Ostrich.*

The development of the columella auris of the fowl was investigated by SONIES (1907). As in the penguin, he found an independent cartilaginous anlage for the p. infracolumellaris which later connects the stylohyal to the columella auris. He describes a foramen intracolumellare (Huxley's foramen), but like HUXLEY (1869) considers it to be a foramen within the p. extracolumellaris; its development is not described.

SUSHKIN (1899) investigated the development of the columella auris of the kestrel. Correctly, he homologizes the three processes of the columella auris with the three similar processes of the reptilian columella auris. SUSHKIN (1899) describes a blastematous suprastapedial arcade lodging an independent cartilaginous nodule.

He considers this nodule as representing a remnant of the operculum of fishes. However, SUSHKIN does not recognize a lateral process.

The columella auris of the starling has a well-developed p. supracolumellaris medialis. Fused to its lateral surface is the upper end of the p. supracolumellaris lateralis. An exceptionally long p. extracolumellaris is developed but there is no indication of the p. infracolumellaris. The stylohyal appears as two independent chondrifications.

The columella auris of the South African nightjar (*Nyctisyrigmus pectoralis pectoralis*) is rather similar to the columella auris of the duck. The p. supracolumellaris medialis and the p. supracolumellaris lateralis fuse dorsally to form a short process thus enclosing "Huxley's foramen". A long interhyal connects the columella auris with the stylohyal.

W. K. PARKER (1875 a) describes two suprastapedial processes in the columella auris of the woodpecker (*Picus vividis*).

BROCK (1937) accurately described the columella auris of the ostrich in which only the p. supracolumellaris medialis chondrifies. The p. supracolumellaris lateralis is found as a ligament stretching from the hyostapes to the tip of the p. supracolumellaris medialis. In a younger ostrich embryo (age unknown) a blastematous supracolumellar arcade containing an independent nodule is found. In the 16 day embryo the cartilaginous anlage has grown medially to fuse with the "otostapes" to form a cartilaginous p. supracolumellaris medialis. An analogous condition is found in the 6 ½ day duck columella auris but, whereas in the later development of the duck a p. supracolumellaris lateralis chondrifies, this process remains ligamentous in the ostrich.

The ostrich and the penguin thus represent opposite extremes in the avian columella auris. In the latter only the p. supracolumellaris lateralis develops, while in the ostrich only the p. supracolumellaris medialis chondrifies. In other birds both processes chondrify and fuse dorsally to enclose "Huxley's foramen". In *Lacertilia* and the ostrich, only the p. supracolumellaris medialis (p.

dorsalis) develops. In this respect the columella auris of the ostrich appears to be primitive, but it is equally possible that the ostrich condition is neotenic. It has already been pointed out that the adult condition of the columella auris of the ostrich is similar to an embryonic stage of the apparatus in the duck. A retention of the latter condition may possibly explain the condition in the ostrich.

4. *Comparative Anatomical Survey of the two Dorsal Processes in the Vertebrate Classes.*

WESTOLL (1943), PARRINGTON (1949), ROMER (1941) and EATON (1939) all share the opinion that the p. supracolumellaris medialis (p. dorsalis) of reptiles is developed from the dorsal articulatory facet of the crossopterygian hyomandibular. The ventral facet, according to them, forms the footplate and medial portion of the columella auris in all tetrapods.

In *Anura* the columella auris develops from two centres of chondrification (the "otostapes" and "hyostapes") as in birds an reptiles. Arising from the "hyostapes" (pars externa plectri) in some *Anura,* e.g. *Rana,* is an ascending process which is directed towards the crista parotica with which it fuses. There is good reason to believe that it is homologous with the processus supracolumellaris lateralis of birds, as they both arise from the "hyostapes". DE BEER (1937) employs the term laterohyal for both the p. ascendens in the *Anura* and the corresponding process in *Sphenodon* and birds. No p. supracolumellaris medialis develops from the "otostapes" (pars interna plectri) in *Anura.* It is interesting to note that REINBACH (1950) does not consider the hyostapes of *Amphibia* and *Amniota* as being homologous. According to him the p. dorsalis (p. supracolumellaris medialis) of reptiles and birds is homologous with the hyostapes of *Amphibia.*

In the *Gymnophiona* and *Urodela* the "hyostapes" does not appear to chondrify (DE BEER, 1937). WESTOLL (1943) remarked upon the shortness of the columella auris in both these orders and suggests that the tympanic process (p. extrastapedialis) is included within the p. quadratus (p. internus) of the *Gymnophiona.* As the p. internus develops from the ostostapes and appears to be homologous in all groups in which it is found, the view of DE BEER that the distal part of the columella auris (hyostapes) does not chondrify in the *Gymnophiona,* is more acceptable. In the *Urodela* WESTOLL (1943) considers that the tip of the stylus represents a greatly reduced p. tympanicus.

KINGSBURY and REED (1909) and SCHMALHAUSEN (1923) describe a ligament in the *Urodela* stretching dorsally from the tip of the stylus ("otostapes") to the squamosal. As the p. supracolumellaris medialis develops from the otostapes in birds and reptiles, it is probable that the ligamentum squamoso-columellare of the urodeles is homologous with this process and the dorsal arti-

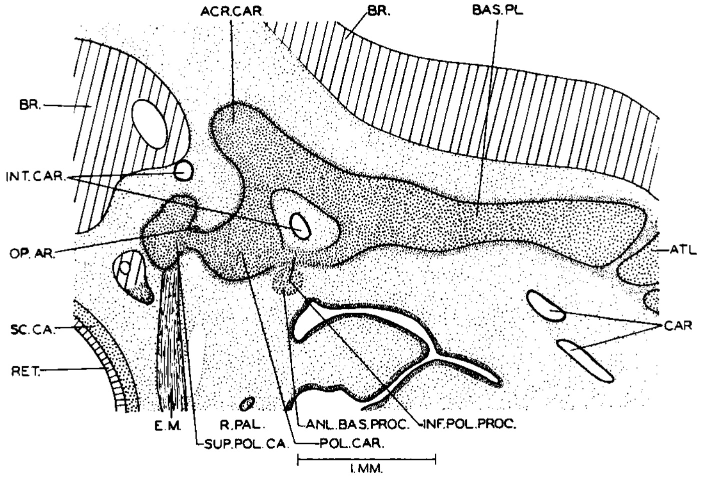


Fig. 38. Sagittal section through the infrapolar process of the emu.

culatory facet of the crossopterygian hyomandibular. Westoll (1943) does not support or refute this view. He does, however, claim a dorsal process in the typical *Stegocephalia: Eryops* and *Edops,* near the distal termination of the columella auris. Romer points out that the stapes of the earliest amphibians is not well-known and that, although a dorsal process may be found, it is not as pronounced as it is in primitive reptiles and crossopterygians. It is not unlikely that this distal process of the *Stegocephalia* is homologous with the p. supracolumellaris lateralis (p. ascendens) found in the *Anura,* and not with the p. supracolumellaris medialis (p. dorsalis) of reptiles.

Amongst these latter a chondrified p. supracolumellaris lateralis reaching the dorsal end of the p. supracolumellaris medialis, is found only in *Sphenodon.* The dorsal ends of these processes lie between the p. oticus of the pars quadrata and the p. paroticus and are thus homologous with the intercalary found in *Lacertilia. Sphenodon* has no p. extracolumellaris or tympanic membrane. This led Huxley (1869) to believe that the foramen in the columella auris of *Sphenodon* was bordered laterally by the extracolumellaris which had rotated upwards to fuse with the p. supracolumellaris medialis. Versluys (1903), however, makes it quite clear that the p. supracolumellaris lateralis (his "laterale Spange") of *Sphenodon* is homologous with the same process in birds where it is formed by the dorsal growth of the hyostapes towards the dorsal end of the p. supracolumellaris medialis. The development of the columella auris of *Sphenodon* was investigated by Howes and Swinnerton (1901) and Wyeth (1924). None of these authors observed the division of the columella auris into "oto"- and "hyostapes". All, however, share the opinion that the suprastapedial process (p. supracolumellaris lateralis) develops from the extracolumellar cartilage.

Young developmental stages of the columella auris of *Sphenodon* are similar to those of the penguin in that only the p. supracolumellaris lateralis is developed. WYETH (1924) describes the development of a "recurrent process" (p. supracolumellaris medialis) in later stages and states, "a conspicious recurrent process is borne on the medial surface of the suprastapedial cartilage just ventral to the intercalary and extends in a ventro-medial direction almost to the dorsal surface of the medial (stapedial) extremity of the extrastapedial cartilage, to which it is firmly attached by a band of ligamentous fibres." In later stages the cartilaginous region of the recurrent process extends ventrally to fuse with the extracolumellar plate. A similar development of the medial process is described in the ostrich and the duck in this paper.

In crocodiles the p. supracolumellaris lateralis does not chondrify. Within the hyoid cornu two chondrifications commonly designated as the epi- and ceratohyals are found, which may possibly be homologous with topographically similar chonrifications found in the hyoid cornu of the penguin and which are here termed ceratohyal and hypohyal (stylohyal). During the ontogeny of the crocodile GOLDBY (1925) describes a cartilaginous continuity between the hyoid cornu (epihyal) and the columella auris. This connexion is later broken down, but a ligament stretching from the free dorsal end of the hyoid cornu to the columella auris remains to indicate the earlier connexion. A further ligament (HUXLEY and GOLDBY) is developed stretching from the epihyal (dorsal end of the hyoid cornu) to the dorsal tip of the p. supracolumellaris medialis (intercalary). A triangular foramen is thus formed, which is bordered laterally by this ligament, medially by the p. supracolumellaris medialis and ventrally by the "hyostapes" and the ligament stretching between the "hyostapes" and the "epihyal". VERSLUYS (1903) considered the ligament between the epihyal and the intercalary to be homologous with the p. supracolumellaris lateralis of *Sphenodon* and birds. The enclosed foramen would consequently be homologous with Huxley's foramen. Although this is possible, it is improbable, as the ligament arises from the free end of the hyoid cornu and not from the "hyostapes".

In lizards the conditions are obscure. According to VERSLUYS (1903) an extracolumellar ligament stretches from the insertion plate to the intercalary. Superficially this ligament appears to be homologous with the p. supracolumellaris lateralis, but BROCK (1932) gives an interpretation to this tendon which would appear to invalidate this view. VERSLUYS (1903) divides the insertion plate of the lizards into two regions. A larger pars inferior and a smaller pars superior which is represented by a small, dorsally directed process. Both these processes lie within the tympanic membrane and both develop from the hyostapes early in the ontogeny. The pars inferior appears to be homologous with the p. extracolumellaris, while it is not improbable that the pars superior represents a short p. supracolumellaris lateralis.

B. THE PARAGLOSSUM

The tongue of all birds is supported by a long slender structure, the paraglossum, which articulates posteriorly with the dorsal surface of copula 1. It may ossify completely or partially or remain cartilaginous throughout life. The anatomy of this structure in the different avian orders was admirably treated by Gaupp (1905). Many theories have been advanced over the last 110 years to explain the true nature of this structure. With the exception of Kallius (1905) all the authors who worked on the paraglossum considered in to be a modification of the ventral end of the hyoid cornu.

Before Reichert, the paraglossum was called either the os linguale or the os entoglossale. Reichert (1837) and Owen (1846, 1866) considered that the postero-lateral aspects of the paraglossum (their glossohyal) were ceratohyals, while the anterior unpaired region was considered as homologous with the glossohyal (basihyal) of fishes.

Nomenclature Employed for the Two Dorsal Processes of the Columella Auris in Sauropsida.

	p. supracolumellaris lateralis (penguin, author) Develops as an outgrowth of the epihyal (hyostapes)	p. supracolumellaris medialis (penguin, author) Develops as an outgrowth of the pharyngohyal (otostapes)
Penguin	present	absent
Duck, Fowl, Kestrel, Nightjar and Starling	"laterale Spange" (Versluys) laterohyal (De Beer)	p. suprastapedialis (Huxley) p. supracolumellaris (Stresemann) laterohyal or p. dorsalis (De Beer)
Ostrich	ventrally directed tip of p. dorsalis (Brock) ligamentous p. supracolumellaris lateralis of author (penguin)	p. dorsalis (Brock)
Sphenodon	"laterale Spange" (Versluys) p. suprastapedialis (Wyeth, Howes and Swinnerton) laterohyal (De Beer)	p. suprastapedialis (Huxley) p. dorsalis (Versluys) recurrent process (Wyeth)
Lizards	pars superior (Versluys)	p. dorsalis (Versluys) — also the term generally employed

W. K. PARKER (1866, 1869) claimed that the entire paraglossum was formed by the fusion of the ventral ends of the hyoid arch. However, in a later work (1891) he considered that the paraglossum also contained a basihyal. T. J. PARKER (1892) designated the paraglossum the "Y-shaped cartilage". He considered the arms of the "Y" to be ceratohyals and the medial stem a basihyal. GEGENBAUR (1898) claimed that the ventro-posterior regions of the paraglossum were formed by the hypohyals.

Up to the time of SUSHKIN (1899) the medial copula was considered a single structure. However, SUSHKIN (1899) showed that in the anlage of this structure two centres of chondrification may be observed: the copula 1 and 2. He further claimed that the paraglossum (his entoglossal) was formed by the fusion of the two ceratohyals.

KALLIUS (1905) introduced the term paraglossum and considered the bone to be a new structure in birds. GAUPP (1905) basing his argument on comparative anatomy, claimed that the paraglossal cartilage was homologous with the basihyal. SONIES (1907) and DE BEER and BARRINGTON (1934) consider the paraglossum to be formed by the fusion of the ceratohyals. DE BEER and BARRINGTON (1934) however, are prepared to accept the view of KALLIUS that the anterior copula is a basihyal.

In the youngest stage of the penguin investigated a connexion is found between the hyoid cornu and copula 1. Although this connexion has never before been described in birds, its appearance was anticipated by KALLIUS (1905). This connexion clearly indicates that the paraglossal cartilage cannot be considered a derivative of the hyoid arch as it develops in front of it, further, it indicates that copula 1 is a basihyal. Extending forwards from the anterior point of copula 1 in the early stages of the ontogeny there is a blastematous process which is probably homologous with the processus lingualis and the glossohyal of SUSHKIN (1899). However, it never chondrifies, but atrophies during the later ontogeny.

The anlage of the paraglossum appears in stage VI as a connective tissue plate lying dorsal to the anterior region of copula 1. It is probable (though this was not actually observed) that the processus lingualis contributes to the formation of the posterior region of the paraglossum.

It may be concluded, firstly, that the paraglossal cartilage in birds does not develop from the hyoid cornu, but is a de novo structure, and secondly, that copula 1 is a basihyal.

C. THE NASAL CAPSULE AND THE OS UNCINATUM

The nasal capsule of the penguin is peculiar for two reasons: firstly, the olfactory nerve enters the nasal capsule directly through the foramen olfactorium evehens, a feature found only in the *Selachii, Polypterus, Acipenser,* *Gadus, Dipnoi* and *Amphibia* and secondly the ramus medialis nasi of the n. profundus enters the nasal capsule through its own foramen in the side wall of the nasal capsule.

In all forms, with the exception of those mentioned above, the foramen olfactorium evehens does not open directly into the nasal cavity, but into a extracranial space, the cavum orbitonasale. De Beer (1937) describes this condition as follows: "In some forms a relative shifting of position has taken place between the lamina orbitonasale and the preoptic root of the orbital cartilage, the former moving forward (or/and) the latter backwards. The result is that the foramen olfactorium evehens then no longer opens directly into the nasal cavity, but into a space, the cavum orbitonasale, which may be regarded as either an aquisition to the orbit or a loss to the nasal cavity." In the duck and the fowl the extensive development of the interorbital septum carries the preoptic roots dorsally, with the result that, after the olfactory nerve has passed through the foramen olfactorium evehens, it finds itself for a short distance in the orbit (cavum orbitonasale). It leaves the orbit and enters the nasal cavity through the foramen olfactorium advehens. In the further development of the duck and the fowl the orbital cartilage (planum supraseptale) separating the olfactory nerve from the orbit and lying behind the foramen olfactorium evehens, atrophies. This further increases the length of the course of the olfactory nerve through the orbit. Further there is an extensive posterior development of the parietotectal cartilage, which forms a roof to the cavum orbitonasale and the foramen olfactorium advehens. The degeneration of the orbital cartilage and sphenethmoid commissure does not take place so extensively in the penguin as to expose the olfactory nerve. The foramen olfactorium evehens is not carried dorsally as in the duck and the fowl, with the result that it opens directly into the nasal capsule. Had the preoptic roots of the penguin developed further dorsally, the conditions prevailing in the duck and the fowl would result.

In the swallow (De Beer and Barrington, 1934) as in the penguin, the orbital cartilage and the sphenethmoid commissure do not atrophy. As a result of the extensive fusion between the interorbital septum and the preoptic root in the swallow, the olfactory nerve is enclosed within a long canal which opens directly into the nasal cavity. In the ostrich (Brock, 1937) an extremely short cavum orbitonasale appears to develop.

The extensive posterior development of the parietotectal cartilage, so characteristic of the fowl, ostrich and duck, is not found in the penguin. Here the backward growth of the parietotectal cartilage is represented by an extremely short median process directed postero-dorsally from the posterior central region of the parietotectal cartilage. It only appears in the late stages of the ontogeny.

In birds and reptiles the ramus medialis nasi enters the nasal capsule through the foramen orbitonasale. This foramen is bordered dorsally by the sphenethmoid commissure, ventrally by the dorsal edge of the lamina orbitonasale, medially by the nasal septum and laterally by the parietotectal cartilage. In the penguin, however, the ramus medialis nasi passes through a foramen in the side wall of the nasal capsule. In the early developmental stages of the nasal capsule of the penguin, the fissura orbitonasalis is divided into two: a foramen for the ramus lateralis nasi and a medial orbitonasal fissure. This is effected by means of a vertical plate of cartilage, the postprofundal commissure, which grows upwards from the dorsal edge of the planum antorbitale medially to the ramus medialis nasi and fuses with the sphenethmoid commissure. In later stages the postprofundal commissure grows obliquely backwards to form a broad plate which later fuses with the preoptic root and the nasal septum to form an oblique posterior wall to the nasal capsule. As a result of the extensive development of the postprofundal commissure, the planum antorbitale is poorly developed, forming only a rudimentary posterior wall to the nasal capsule.

In conclusion it may be said that the foramen for the ramus medialis nasi is a remnant of the originally wide, orbitonasal fissure.

In the 61 mm. stage a small independent cartilago uncinata connected to the lamina orbitonasalis by means of a thick strand at connective tissue, is found ventral to the lamina orbitonasalis. As this nodule appears to develop within the blasteme of the pars pterygoidea, it probably represents a chondrification of the anterior end of the palatoquadrate. In later stages it is found as a small ossification embedded in the ventral region of the planum antorbitale. Stretching between this ossicle and the jugal bone is a thin ligament. Towards the end of the ontogeny the ossicle atrophies, but the ligament remains to indicate its former position.

Without doubt this transitory ossification is homologous with the lacrimo-palatine ossicle or the uncinate ossicle which is found in many birds, where it extends from the ectethmoid (lateral ethmoid) to the jugal. In the penguin, however, it is smaller, and its ventral portion is represented by a ligament. Pycraft (1900) described a particularly well-developed uncinate ossicle in the ostrich. According to W. K. Parker (1875 b), the os uncinatum develops from a cartilaginous bud arising from the trabeculae. De Beer (1937) suggests that it develops from a portion of the ectethmoid that has become segmented off. Grewe (in press) describes a ligamentum lacrimo-jugale which stretches between the ventro-medial edge of the lacrimal and the jugal. He attempts to show that this ligament is preceded in the ontogeny by a cartilaginous bud which arises from the antorbital plate. Judging from the topographical position which it occupies, it appears to be homologous with the uncinate cartilage of the penguin. Although Brock makes no mention of this structure in her description of the development of the chondrocranium of the ostrich, she indicates a similar process, directed ventrally from the lamina orbitonasalis, in the figures illustrating stage III and IV. However, as the development of the uncinate ossicle of the ostrich has not yet been described, the above suggestion is necessarily tentative.

De Beer (1937) describes a long process, the processus maxillaris posterior arising from the ventro-lateral corner of the lamina orbitonasalis. Concerning this process he says: "In many *Urodela* in *Gymnophiona, Lacertilia, Sphenodon, Chelonia, Crocodilia* and birds, the pterygoid process ends freely, but it is not impossible that the processus maxillaris posterior may represent its extreme anterior end, fused to the lamina orbitonasalis." It is possible that the uncinate ossicle of birds is homologous with the processus maxillaris posterior of Lacerta, firstly because of its topographical position and secondly because of its relationship with the blasteme of the pars pterygoidea. However, in contrast to the reptiles this structure ossifies to form the os uncinatum, whereas in reptiles it remains cartilaginous. The birds are peculiar among the *Sauropsida* in that the lamina orbitonasalis ossifies to form the ectethmoid. The lamina orbitonasalis which is homologous in all groups ossifies only in fishes and birds. In the fishes the anterior end of the palatoquadrate ossifies to form the autopalatine. This ossification is not found in the *Amphibia* or the reptiles. It is not improbable that the os uncinatum of birds is homologous with the autopalatine of fishes.

Two cartilages of flat and oval shape lying in the ventro-medial periosteum of the pterygoid, ventral to the parasphenoid, are found in an embryo of a body length of 120 mm., and have an approximate length of 0.4 mm. That they develop in situ is certain, as the connective tissue anlages of these cartilages may be seen occupying the same position relative to the pterygoid in younger stages. There are two possible explanations for these cartilages; either they represent neomorphic structures without phylogenetic importance, or they are remnants of the pars pterygoidea. As neomorphic cartilages develop in response to stress and strain the latter explanation is more probable.

D. THE BASITRABECULAR PROCESS, INFRAPOLAR PROCESS AND PRECAROTID COMMISSURE

A striking characteristic of the dromoeognathic birds is the well-developed basitrabecular process of the adult skull. In the adromoeognathic birds there is a tendency for this process to atrophy as a result of the articulation which arises between the palato-pterygoid arcade and the parasphenoidal rostrum. The basitrabecular process is found, however, in the embryos of all adromoeognathic forms. A particularly well-developed basitrabecular process is found in the ontogeny of the penguin. In the nestling this process dwindles to a ligament. This confirms the findings of Pycraft (1898, 1910) for a nestling of *Pygoceles papua.* Simpson (1946) in his description of the fossil penguin, *Pareptenodontes antiarticus* finds no indication of a basitrabecular process.

In the penguin the basitrabecular process develops from an independent anlage, which lies between the pars quadrata and the polar cartilage. In later stages it fuses with the ventral surface of the polar cartilage. The distal region of the anlage of the basitrabecular process does not chondrify. A similarly developing basitrabecular process was described by SUSHKIN (1899) in the kestrel and by LUTZ (1942) in a 15 day old embryo of the emu. In the latter, in contrast to the penguin, the entire anlage of the processus basitrabecularis chondrifies, so that the lateral surface abuts against the pars quadrata. A large processus basitrabecularis, which reaches the pars quadrata, was observed by BROCK (1937) in the ostrich. However, no independent anlage for this process was described. In fig. 92 of T. J. PARKER'S (1892 a) description of the development of the kiwi skull, an independent anlage for the basitrabecular process is indicated, but no mention is made of it in the text. In the early ontogenetic stages of the duck, DE BEER and BARRINGTON (1934) describe a band of procartilaginous tissue stretching between the polar cartilage and the pars quadrata. They consider it to be a remnant of the basal articulation. It is probable that this band is homologous with the independent anlage for the basitrabecular process found in the penguin and the emu.

KESTEVEN (1941, 1942) considers that the basitrabecular process of birds is not homologous with the similarly named process of the reptiles as this process develops from the polar cartilage in birds and from the trabeculae in the reptiles. For this reason he suggests the term basipolar process for the process found in birds. KESTEVEN claims that the course of the ramus palatinus in reptiles and birds offers further support to his view that the basitrabecular processes are not homologous in the two classes. According to him the main body of the ramus palatinus in birds passes forwards dorsal, to the processus basitrabecularis while only a small branch passes forwards below this process. In reptiles the characteristic position for the ramus palatinus is below the basitrabecular process. However, the division of the ramus palatinus into two branches passing forwards, one dorsal and the other ventral to the basitrabecular process, was described by ENGELBRECHT (in press) in *Microsaura pumila* and by FRANK (in press) in *Rhampholeon platyceps*. The condition of the palatine nerve, as described by KESTEVEN for the birds cannot, therefore, be considered a characteristic peculiar to the class.

In the early stages of the penguin ontogeny it is clearly seen that the ramus palatinus passes forwards below the basitrabecular process, and no branch dorsal to this process is found. In the late embryonic stages a stout sympathetic nerve accompanies the ramus palatinus forwards. Behind the basitrabecular process, the sympathetic component separates from the ramus palatinus and passes forwards dorsal to the process. In front of the basitrabecular process the greater part of the sympathetic nerve rejoins the ramus palatinus. It is probable that KESTEVEN, FRANK & ENGELBRECHT confused this sympathetic component with the true ramus profundus.

It has already been pointed out that in the penguin the processus basitrabecularis arises from an independent anlage. It may fuse with either the trabeculae or the polar cartilage without affecting the homology of this process in different groups. If, however, the independent anlage of this process in the emu and the penguin is a secondary characteristic the process may still be considered homologous in both groups, whether it develops from the trabeculae or the polar cartilage as the polar cartilages are probably derivatives of the trabeculae.

In birds two processes, directed backwards towards the basal plate below the internal carotid arteries of either side, develop from the ventral surfaces of the polar cartilages. The posterior tips of these processes fuse with the ventral surfaces of the basal plate to form a ventral border to the lateral carotid foramen. The term infrapolar process was introduced by SONIES (1907). As SONIES could find no indication of the processus basitrabecularis in the duck or in the fowl, he considered the infrapolar process to be homologous with the basitrabecular process. LUTZ (1942) described both a basitrabecular and a basipterygoid process in the emu. The work of DE BEER (1937) and GOODRICH (1930) has shown quite conclusively that the processus basitrabecularis and the processus basipterygoideus are two names for the same structure. Serial sections of a 15 days emu embryo show that the so called processus basipterygoideus of LUTZ (1942) is homologous with the basitrabecular process anlage of the penguin and that the processus basitrabecularis of LUTZ is homologous with the infrapolar process in other forms. LUTZ apparently makes the same mistake as SONIES (1907) in considering that the infrapolar process and basitrabecular process are homologous. DE BEER and BARRINGTON (1934) make it quite clear that the processus basitrabecularis and the infrapolar process are two distinct structures.

In the penguin and the ostrich (BROCK, 1937) no definite infrapolar process developing from the polar cartilage is found. In the early stages of the penguin ontogeny a wide incisura, traversed by the lateral carotid artery of either side, is formed between the acrochordal plate and the ventral surface of the trabeculopolar bar. In the later ontogenetic stages the ventral edge of the acrochordal plate migrates forwards and fuses with the ventral portion of the basitrabecular process. As a result the lateral carotid incisure is transformed into a lateral carotid foramen without the intervention of an infrapolar process. Together with the straightening out of the cephalic flexure, the connexion between the medial region of the basitrabecular process and the acrochordal plate is stretched to form a ventral border to the lateral carotid foramen. This border simulating an infrapolar process of other birds must not be confused with a true infrapolar process.

The absence of the infrapolar process in the penguin is associated with the acute cranial flexure. Where the cranial flexure is not so large, e.g. the starling (SONIES, 1907), the fowl (SONIES, 1907, TONKOFF, 1900, BROCK, 1937), the kiwi (T. J. PARKER, 1892 a, b) and the emu, a well-developed infrapolar process has to be formed in order to reach the basal plate below the internal carotid arteries.

The penguin is peculiar in possessing a precarotid commissure which develops from the proximal ends of the trabeculae and divides the large hypophysial foramen into two foramina. Rathke's pouch passes through the anterior foramen hypophyseos, while the internal carotid passes through the posterior foramen caroticum. Contrary to the description of LUTZ (1942) of the emu skull, faint indications of a precarotid commissure in a 15 day emu embryo were observed. However, older embryos were not available to ascertain whether this commissure actually chondrifies in the later ontogeny. A commissure similar to that of the penguin was described by T. J. PARKER (1892 a, b) in the kiwi. No precarotid commissure is found in any of the other avian chondrocrania that have been described.

In *Selachii* a precarotid commissure was described by DE BEER (1937) and ALLIS (1923). It does not, however, develop from the trabeculae as in the penguin, but from the medial surfaces of the polar cartilages. ALLIS (1923) considers the precarotid commissure of the *Selachii* as homologous with the infrapolar processus of birds. Instead of these processes fusing with each other to form a precarotid commissure as they do in the *Selachii*, ALLIS claims that they fuse with the basal plate to form the infrapolar process in birds. As no infrapolar process or precarotid commissure is found in either the reptiles or the amphibia this view is hardly tenable.

II. SUMMARY

1. No fenestra basicranialis posterior is found in the penguin.
2. Five cranial ribs are present in the early ontogeny, all however disappear during the later stages.
3. During the early ontogeny the oculomotor nerve is enclosed in a long canal situated between the pila antotica and the posterior orbital cartilage.
4. The auditory capsule arises from two centres, the pars canalicularis and the pars cochlearis.
5. The pharyngohyal ("otostapes") arises in continuity with the pars canalicularis.
6. The cartilago metotica develops as a process of the auditory capsule.
7. The basitrabecular process arises from an independent anlage lying below the polar cartilage. It is syndesmotically connected to the medial surface of the pars quadrata and lies dorso-lateral to the palatine nerve.
8. The trabeculae arise as two independent bars below the fore-brain. Their posterior ends are connected by a precarotid commissure, which later divides

the foramen basicranialis anterior into two foramina: a foramen caroticum and a foramen hypophyseos.

9. The processus orbitoquadratus chondrifies in the posterior region of the pars pterygoidea.
10. The hyoid arch develops from four independent blastematous anlages, the pharyngohyal ("otostapes"), epihyal, ("hyostapes"), ceratohyal, and hypohyal (stylohyal).
11. The processus supracolumellaris lateralis develops from the lateral surface of the epihyal.
12. The connexion in the early ontogeny between the hypohyal and copula 1, indicates that the latter is a basihyal.
13. The chorda tympani follows a typical reptilian course.
14. Copula 1 (basihyal) and copula 2 appear in the early ontogeny as two independent chondrifications. Later they fuse to form a single copula.
15. A remnant of the second branchial arch is found in the early ontogeny.
16. Throughout the greater part of the ontogeny the trochlear nerve is enclosed in a long horizontal canal within the posterior orbital cartilage.
17. The pila antotica spuria develops as a downgrowth from the posterior orbital cartilage. It fuses with the lateral abducent commissure to form the lateral border to the foramen for the ramus profundus.
18. A lateral abducent commissure stretching between the posterior orbital cartilage and the pars cochlearis, forms the lateral border to the abducent nerve.
19. The facial nerve is wedged in between the two portions of the otic capsule. In the early development the facial nerve passes through the cavity of the auditory capsule, but later it is enclosed in a cartilaginous canal.
20. The auditory foramen is the remnant of the cochleo-canalicular fissure.
21. The trabecula communis is extended forwards by a prenasal process.
22. The preoptic roots arise from the antero-lateral surfaces of the trabecula communis.
23. The interorbital septum grows upwards from the centre of the trabecula communis.
24. No intertrabecular bar is found in the penguin.
25. A transitory blastematous intercalary nodule situated between the metotic cartilage and the processus oticus appears in the early ontogeny.
26. Copula 1 is extended forwards as a blastematous process, the processus lingualis. It is possible that this process contributes to the formation of the paraglossum.
27. Up to four hypoglossal foramina appear in the left side of the basal plate during the ontogeny.
28. The nervus vagus traverses a foramen in the basal plate.
29. A supraorbital cartilage connects the two regions of the orbital cartilage.
30. The posterior regions of the auditory capsule are connected with each

other dorsally by the dorsal cochleo-canalicular commissure and ventrally by the ventral cochleo-canalicular commissure. These commissures form the dorsal and ventral borders of the foramen perilymphaticum.

31. The nasal septum grows upwards from the posterior region of the prenasal process.
32. The sphenethmoid commissure stretching from the postero-lateral surface of the parietotectal cartilage to the posterior orbital cartilage, forms the lateral border to the foramen olfactorium evehens. No foramen olfactorium advehens is found in the penguin.
33. The processus extracolumellaris develops from the lateral surface of the hyostapes.
34. The cartilage of the pars canalicularis, to which the "otostapes" is fused, atrophies and so the foramen ovale is formed. It is possible that part of the pars canalicularis contributes to the formation of the footplate of the columella auris.
25. The processus infracolumellaris develops from the ceratohyal chondrification. It is not formed from the interhyal as in most birds and reptiles.
36. The tectum synoticum chondrifies in a broad tract of blastematous tissue connecting the posterior edges of the auditory capsules with each other.
37. A cavum metoticum is enclosed between the auditory capsule and the metotic cartilage. In the late stages of the ontogeny, a diverticulum of the tympanic cavity grows into the cavum metoticum.
38. The medial region of the cavum metoticum is extended forwards as a subcapsular process forming a floor to the recessûs scalae tympani.
39. The free anterior edge of the metotic cartilage forms a lateral wall to the apetura lateralis recessûs scalae tympani.
40. The lateral carotid foramen is formed without the intervention of an infrapolar process. This is a result of the acute cranial flexure.
41. There is a basicranial foramen simulating the foramen basicranialis posterior of other forms, but it cannot be considered homologous with the latter as it lies anterior to the acrochordal plate.
42. In the nasal capsule an independent paranasal cartilage and an antorbital plate were not observed. These two structures arise in continuity with the side wall of the nasal capsule.
43. The orbito-nasal fissure is divided into two by a postprofundal commissure. The ramus medialis nasi passes into the nasal capsule through the lateral portion of the orbitonasal fissure. In the late ontogeny the postprofundal commissure forms the major portion of posterior wall of the nasal capsule. Owing to the development of a postprofundal commissure the planum antorbitale remains rudimentary.
44. The anterior orbital cartilage fuses with the dorsal region of the interorbital septum to form the planum supraseptale.

45. The concha nasalis is formed by a simple folding of the side wall of the nasal capsule. In later stages the aditus conchae is obliterated by the side walls of the concha nasalis fusing with one another to form a solid turbinal.
46. The os uncinatum is apparently homologous with the autopalatine bone of fishes.
47. In the late ontogeny the acrochordal plate dwindles to a membrane. In the nestling this membrane ossifies.
48. Simultaneously with the degeneration of Rathke's pouch the foramen hypophyseos closes.
49. Three foramina are found in the nasal septum: a foramen septi nasi anterius, a foramen septi nasi posterius and a f. craniofaciale. The latter is transformed into a craniofacial fissure by the degeneration of the ventral border of this foramen in order that kinesis may take place.
50. The paraglossal cartilage appears to be a de novo structure found only in birds.
51. In birds, in general, and in *Sphenodon,* two dorsal processes arise from the columella auris. A processus supracolumellaris medialis develops from the otostapes and appears to be homologous with the processus dorsalis of reptiles. A processus supracolumellaris lateralis develops from the hyostapes and appears to be homologous with the processus ascendens of the *Anura.* Dorsally they fuse with each other to enclose "Huxley's foramen".
52. In the penguin only the processus supracolumellaris lateralis is present, while in the ostrich only the processus supracolumellaris medialis chondrifies.

III. REFERENCES TO LITERATURE

ALLIS, E. P. 1923. Are the polar and trabecular cartilages of Vertebrate embryos the pharyngeal elements of the mandibular and premandibular arches? J. Anat., Lond. 58: 37.

— 1924. In further explanation of my theory of the polar and trabecular cartilages. J. Anat., Lond. 59: 333.

— 1931. Concerning the homologies of the hypophysial pit and the polar and trabecular cartilages of the fishes. J. Anat., Lond. 65: 247.

BROCK, G. T. 1932. Some developmental stages in the skulls of the geckos, Lygodactylus capensis and Pachydactylus maculosa, and their bearing on certain important problems in the lacertilian craniology. S. Afr. J. Sci. 29: 508.

— 1937. The morphology of the Ostrich chondrocranium. Proc. zool. Soc. Lond. Vol. 107. Ser. C. p. 2.

CRAIGIE, E. H., 1940. The cerebral cortex in palaeognathine and neognathine birds. J. comp. Neurol. 73: 179.

— 1941. The cerebral cortex of the penguin. J. comp. Neurol. 74: 353.

CROMPTON, A. W. Contributions to the craniogenesis of Spheniscus demersus (in press).

De Beer, G. R. 1930. Development of the chondrocranium of Lacerta. Quart. J. micr. Sci. 73: 707.

— 1931. On the nature of the trabecula cranii. Quart. J. micr. Sci. 74: 701.

— 1937. The development of the vertebrate skull. Oxford.

De Beer, G. R. and Barrington, E. J. W. 1934. The segmentation and chondrification of the skull of the duck. Philos. Tran. Vol. 223. Ser. B. p. 411.

De Beer, G. R. and Barrington, E. J. W. 1934. The segmentation and chondrification of the skull of the duck. Philos. Tran. Vol. 223. Ser. B. p. 411.

De Villiers, C. G. S. 1922. Neue Beobachtungen über den Bau und die Entwickelung des Brustschulterapparates bei den Anuren, insbesondere bei Bombinator. Acta. Zool., Stockh. 3: 1.

— 1946. The relations of the vomer and palatoquadrate bar to the cranial rostrum in the tinamou (Crypturellus species). Ann. Univ. Stellenbosch 24. A. 21.

Eaton, T. H. 1939. The crossopterygian hyomandibular and the tetrapod stapes. J. Wash. Acad. Sci. 29: 109.

Engelbrecht, D. van Z. Contributions to the cranial morphology of the chamaeleon, Microsaura pumila (in press).

Filatoff, D. 1906. Frage über die Anlage des Knorpelschädels bei einigen Wirbeltieren. Anat. Anz. 29: 623.

Frank, G. H. Contributions to the cranial morphology of Rhampholeon platyceps (in press).

Gadow, H. 1888. On the modifications of the first and second visceral arches with special reference to the homologies of the auditory ossicles. Philos. Trans. 179: 451.

Gaupp, E. 1898. Ontogenese und Phylogenese des Schall-leitenden Apparates bei den Wirbeltieren. Ergebn. Anat. Entwgs. 8: 990.

— 1900. Das Chondrocranium von Lacerta agilis. Anat. Hefte 1, abt., XLIX. Hefte (14. Bd. H. 3.) s. 435.

— 1904. Das Hyobranchiaskelet der Wirbeltiere. Ergebn. Anat. Entwgs. 14: 808.

Gegenbaur, C. 1898. Vergleichende Anatomie der Wirbelthiere. Leipzig.

Goldby, F. 1925. Development of the columella auris in Crocodilia. J. Anat., Lond. 59: 301.

Goodrich, E. S. 1915. The Chorda tympani and middle ear in reptiles, birds and mammals. Quart. J. micr. Sci., 61: 13.

— 1930. Structure and development of the vertebrates. MacMillan and Co., London.

Grewe, F. J. Nuwe gegewens aangaande die ontogenese van die neuskliere, die orgaan van Jacobson en die dekbene van die skedel by die genus Anas. (in press).

Hoffmann, C. K. 1889. Over de Ontwikkelingsgeschiedenis van het Gehoororgaan en de morphologische Beteekenis van het Gehoorbeentjie by de Reptilien. Verh. Akad. Wet., Amst. 28: 1.

Holmgren, N. 1943. Studies of the head of fishes. Part IV. Acta. Zool. Stockh. 24: 1.

Huxley, T. H. 1867. On the classification of birds and on certain cranial bones observable in that class. Proc. zool. Soc. Lond. p. 415.

— 1869. On the representatives of the malleus and the incus of the mammalia in other Vertebrata. Proc. zool. Soc. Lond.

Jager, J. 1926. Ueber die Segmentierung der Hinterhauptregion und die Beziehung der cartilago acrochordalis zur Mesoderm commissure Morph. Jb. 56: 1.

Kallius, E. 1905. Beiträge zur Entwicklung der Zunge. II Teil Vögel. Anat. Hefte. Bd. 28. H. 2/3 S. 305.

Kesteven, H. L. 1941. On certain debatable questions in cranioskeletal homologies. Proc. Linn. Soc. N.S.W. 61: 293.

Kesteven, H. L. 1942. The ossification of the avian chondrocranium with special reference to that of the emu. Proc. Linn. Soc. N.S.W. 67: 213.

Kingsbury, B. F. and Reed, K. D. 1909. The columella auris in amphibia. J. Morph. 20: 549.

Lowe, P. R. 1928. Studies and observations bearing on the phylogeny of the ostrich and its allies. Proc. zool. Soc. Lond. p. 185.

— 1933. On the primitive characters of penguins and their bearing on the phylogeny of birds. Proc. zool. Soc. Lond. p. 483.

— 1942. Some additional anatomical factors bearing on the phylogeny of the struthiones. Proc. zool. Soc. Lond. p. 1.

Lutz, H. 1942. Beiträge zur stammengeschichte der Ratiten. Vergleich zwischen Emu-Embryo und entsprechenden Carinatenstadium. Rev. suisse Zool. 49: 299.

*Matveiev, B. 1925. The structure of the embryonal axial skull of the lower fishes. Bull. Soc. Nat. Moscou. 34: 416.

Owen, R. 1846. Report on the archetype and homologies of the vertebrate skeleton. Transactions of the British Association.

— 1866. Anatomy of Vertebrates. Longmans, Green and Co. London.

Parker, T. J. 1892 a. Observations on the anatomy and development of Apteryx. Philos. Trans. 182: 25.

— 1892 b. Additional observations on the development of Apteryx. Philos. Trans. 183: 73.

Parker, W. K. 1866. On the structure and development of the skull in the Ostrich tribe. Philos. Trans. 156: 113.

— 1869. On the structure and development of the skull of the common fowl. (Gallus domesticus.) Philos. Trans. 159: 755.

— 1875 a. On the morphology of the skull in the woodpeckers (Picidae) and the Wrynecks (Yungidae). Trans. Linn. Soc. Lond. Zool. 1: 1.

— 1875 b. On the structure and development of the birds skull. Trans. Linn. Soc. Lond. Zool. 1: 99.

— 1891 a. On the morphology of the Gallinacaea. Trans. Linn. Soc. Lond. Zool. 5: 213.

— 1891 b. On the morphology of a reptilian bird Opisthocomus cristatus. Trans. zool. Soc. Lond. 13: 43.

Parrington, F. R. 1949. Remarks on a theory of evolution of the tetrapol middle ear. J. Laryng. 63: 580.

Parsons, C. W. 1932. Report on penguin embryos collected during the Discovery investigations. Discovery Reports. 6: 139.

*Peters, W. 1874. Ueber die Gehörknöchelchen und ihr Verhältniss zu den zungenbeinbogen bei Sphenodon punctatus. Mber. Akad. Wiss., Berlin.

Prins, F. X. Die "musculus orbitoquadratus" en Constrictor I — derivate van die pikkewyn (in press).

Pusey, H. K. 1939. Methods of reconstruction from microscopical sections. J. R. micro. Soc. 59: 232.

Pycraft, W. P. 1898. Contributions to the osteology of birds. Part II. Impennes. Proc. zool. Soc. Lond. p. 958.

— 1910. History of birds. Lond.

Reichert, C. 1837. Über die Visceralbögen der Wirbeltiere im allgemeinen und deren Metamorphosen bei den Vögeln und Saügetieren. Arch. Anat. Physiol., Lpz. p. 120.

Reinbach, W. 1950. Phylogenetische Wandlungen am Visceral-Schädel der niederen Wirbeltiere. Forsch. Fortsehr. dtsch. Wiss. 26 Jahrg. Hefte 15/16, s. 208.

Romer, A. S. 1941. Notes on the crossopterygian hyomandibular and braincase. J. Morph. 69: 141.

*Schestakowa, 1934. Die Entwicklung des Schalleitenden Apparates der Vogel. Bull. Soc. Nat. Moscou. 43: 225.

Schmalhausen, T. J. 1923. Der Suspensorialapparat der Fische und das Problem der Gehörknöchelchen. Anat. Anz. 56: 534.

Sewertzoff, A. N. and Disler, N. N. 1924. Das Pharyngomandibulare der Selachier. Anat. Anz. 58: 245.

Simpson, G. G. 1946. Fossil penguins. Bull. Amer. Mus. nat. Hist. 87: 7.

Smith, G. W. 1905. Middle ear and columella of birds. Quart. J. micr. Sci. 48: 11.

Sonies, F. 1907. Ueber die Entwickelung des chondrocraniums und der Knorpeligen Wirbelsaüle bei den Vögeln. Petrus Camper, 4. p. 395.

Stresemann, E. 1927—34. Sauropsida: Aves. Kükenthal—Krumbach'sches. Handbuch der Zoologie. V. 7. "Hälfe" 2. p. 1.

Sushkin, P. P. 1896. Zur Anatomie und Entwickelungsgeschichte des Schädels der Raubvögel. Anat. Anz. 11: 767.

— 1899. Zur Morphologie des Vogelskelets. I. Schädel von Tinnunculus. Nouw. Mem. Soc. Nat. Moscou. 16: 1.

Swart, P. J. 1946. Die ontogenese van die "desmognate" monddaktipe by Anas. Ann. Univ. Stellenbosch 24. A. 1.

Tonkoff, W. 1900. Zur Entwickelungsgeschichte des Hühnerschädels. Anat. Anz. 18: 296.

van Wijhe, J. W. 1907. Sur le développement du chondrocrâne des oiseaux. C. R. Ass. Anat. 9: 117.

— 1910. On the development of the chondrocranium of birds. 7. Int. Congr. Zool. p. 1.

Versluys, J. 1903. Entwickelung der columella auris bei den Lacertiliern. Zool. Jb. abt. 2. 19: 107.

Westoll, T. S. 1943. The hyomandibular of Eusthenopteron and the tetrapod middle ear. Proc. roy. Soc. Ser. B. 131: 393.

Wyeth, F. J. 1924. Development of the auditory apparatus in Sphenodon. Philos. Trans. B. 212: 259.

* Not seen in the original.

IV. ALPHABETICAL LIST OF ABBREVIATIONS USED IN THE FIGURES

ABD. Abducent nerve

AC. Auditory capsule

ACR. CAR. Acrochordal cartilage

ACU. NER. Acustic nerve

ADI. CON. Aditus concha

A.L.R.S.T. Apetura lateralis recessus scalae tympani

A.M.R.S.T. Apetura medialis recessus scalae tympani

ANL. BAS. PROC. Anlage of the basitrabecular process

ANL. C.-F. FOR. Anlage of the craniofacial foramen

ANL. ORB. CAP. PROC. Anlage of the orbitocapsular process

ANL. PARA. Anlage of the paraglossal cartilage

ANL. TEC. SYN. Anlage of the tectum synoticum

ANT. ORB. CAR. Anterior orbital cartilage

A.N.C.C.O.S. Apeture in the nasal capsule communicating with the orbital sinus

A.S. Auditory sac.

ATL. Atlas

AT. TUR. Atrioturbinal

B.C.F. Basicranial foramen

BAS. PL. Basal plate

BAS. PROC. Basitrabecular process

B.G.P. Backward growing process of the parietotectal cartilage

BL. CON. Blastematous connexion between the hyoid arch and Copula I

BL. CON. STY. Blastematous connexion between the columella auris and the stylohyal cartilage

BL. PARS. PTER. Blastematous pars pterygoidea

BL. PRO. SUP. COL. LAT. Blastematous processus supracolumellaris lateralis

BL. TR. Blastematous tract connecting the processes basitrabecularis with the pars quadrata

BR. Brain

1. BRAN. ARC. First branchial arch

2. BRAN. Arc. Second branchial arch

CA. AU. CA. Cavity of the auditory capsule

CA. L. G.G. Cavity lodging the ganglion geniculatum

CAR. Carotid artery

CAR. FLAN. Cartilaginous flange

CAR. MES. cartilage in which the mesethmoid ossification arises

CAR. UNC. Cartilage uncinata

CAV. MET. Cavum metoticum

CER. BRAN. Ceratobranchial

CER. HY. Ceratohyal

CER. HY. CHON. Ceratohyal chondrification

CER. HYP. HY. Fused ceratohyal and hypohyal blasteme

C.F. FOR. Craniofacial foramen

CHO. Choanae

CH. TYM. Chorda tympani

COC. GR. Cochlear groove

COL. AUR. Columella auris

COL. ROD. Columella rod

CON. BAN. Connective tissue band

C.N. Concha nasalis

COP. Copula

COP. I. First copula

COP. II. Second copula

CRAN. RIBS. Cranial ribs

CU. ANT. Cupola anterior of the nasal capsule

D.C.-C.C. Dorsal cochleo-canalicular commissure

DUCT. END. Ductus endolymphaticus

D.L.N.G. Duct of the lateral nasal gland

D.N.L. Ductus naso-lacrimalis

E.M. Eye-muscle

EPI. BRAN. Epibranchial

EPI. HY. Epihyal

EXT. COL. Extracolumella

F. Fontanelle.

FAC. NER. Facial nerve

F. PL. Footplate of the columella auris

FOR. ABD. Foramen for the abducent nerve

FOR. ACU. Foramen acusticum

FOR. B. CN. Foramen behind the concha nasalis

FOR. CAR. Foramen caroticum

FOR. C.T. Foramen in lower jaw for chorda tympani

FOR. END. Foramen for ductus endolymphaticus

FOR. FAC. Foramen for the facial nerve

FOR. HYPOP. Foramen hypophyseos

FOR. MAG. Foramen magnum

FOR. NC. Foramen for the tip of the notochord

FOR. OCC. Foramen for the oculomotor nerve

FOR. OLF. EV. Foramen olfactorium evehens

FOR. OPTH. Foramen for the ophthalmic artery

FOR. OVAL. Foramen ovale

FOR. PRO. Foramen prooticum

FOR. PERI. Foramen perilymphaticum

FOR. PROF. Foramen for the profundus nerve

FOR. R.M.N. Foramen for the ramus medialis nasi

FOR. TRO. Foramen for the trochlear nerve

FOR. VAG. Foramen for the vagus nerve

F.P.E.C.C.T. Foramen in the processus extracolumellaris for the chorda tympani

F.S.N.A. Fenestra septi nasi anterior

F.S.N.P. Fenestra septi nasi posterior

G. GAS. Ganglion Gasseri

G. GEN. Ganglion geniculatum

G. JUG. Ganglion jugulare

G.L.N.C. Groove lodging the notochord

GLOSS. Glossopharyngeal nerve

G. PET. Ganglion petrosum

G.Q.J. Groove in the pars quadrata for the quadratojugale

HYOM. Hyomandibular nerve

HYP. Hypoglossal nerve

HYP. FOR. Hypoglossal foramen

HYP. HY. Hypohyal
HYP. PIT. Hypophysial pit.
HYP. ROOF. Hypophysial roof
HYP. ROOTS. Hypoglossal roots
HUX. FOR. Huxley's foramen
INC. MET. Incisura metotica
INC. PRO. Incisura prootica
INF. POL. COM. Infrapolar commissure
INF. POL. PROC. Infrapolar process
INT. CAR. Internal carotid artery
I.S. Interorbital septum
LAT. CAR. FOR. Lateral carotid foramen
LAT. CAR. INC. Lateral carotid incisure
LAT. ABD. COM. Lateral abducent commissure
L.R. ACR. CAR. Lower region of the acrochordal plate
LS. Lens
MAX. TUR. Maxilloturbinal
M.C. Meckel's cartilage
MEM. Membrane
MET. CAR. Metotic cartilage
NA. SA. Nasal sac.
NC. Notochord
N.C.S.W. Nasal capsule side wall
N.L.D. END. Notch lodging the ductus endolymphaticus
N.L.O.N. Notch lodging the optic nerve
N.L. OP. N. Notch lodging the ophthalmic nerve
N.L. 7. N. Notch lodging the facial nerve
N.L. 9. NER. Notch lodging the glossopharyngeal nerve
N.L. 10. NER. Notch lodging the vagus nerve
NOT. RAT. POU. Notch for Rathke's pouch
N.S. Nasal septum
OC. ARC. Occipital arch.
O.C. Occipital condyle
OCC. Oculomotor nerve
OLF. Olfactory nerve
OP. AR. Ophthalmic artery
ORB. NAS. FIS. Orbitonasale fissure
ORB. PROC. Orbitocapsular process
OR. SI. Orbital sinus
OS. UNC. Os uncinatum
PAR. CAR. Parietotectal cartilage
PARS. CAN. Pars canalicularis
PARS. COCH. Pars cochlearis
PARS. QUAD Pars quadrata
P.D.P. TRAB. Postero-dorsally directed process of the trabeculae
PHAR. BRAN. Pharyngobranchial
PHAR. HY. Pharyngohyal
PIL. ANT. Pila antotica
PIL. ANT. SPU. Pila antotica spuria
P.L.P.C. Processus lateralis partis cochlearis
OL. SUP. SEP. Planum supraseptale
POL. CAR. Polar cartilage
POST. ORB. CAR. Postorbital cartilage
POST. PROF. COM. Postprofundal commissure
PRECAR. COM. Precarotid commissure
PRE. END. COM. Pre-endolymphatic commissure
PRE. NAS. Prenasal process
PRE. OPT. RT. Preoptic root of the orbital cartilage
PRO. EXT. COL. Processus extracolumellaris
PROC. INF. COL. Processus infracolumellaris
PROC. LING. Processus lingualis
PROC. ORB. QUAD. Processus orbitoquadratus
PROC. OTIC. Processus oticus
PROC. RET. Processus retroarticularis
PROC. SUP. COL. Processus supracolumellaris
P. SUP. COL. LAT. Processus supracolumellaris lateralis
PROC. SUP. COL. MED. Processus supracolumellaris medialis
RE. FOR. HYPOP. Remnant of the foramen hypophyseos
RE. ACR. CAR. Remnant of the acrochordal cartilage
RET. Retina
R.L.N. Ramus lateralis nasi
R. MAN. Ramus mandibularis
R. MAX. Ramus maxillaris
R.M.N. Ramus medialis nasi
R. PAL. Ramus palatinus
R. PROF. Ramus profundus
RUD. FLOOR. Rudimentary floor to the nasal capsule
S.C. ARC. Supracolumellar arcade.
SC. CA. Sclerotic cartilage
S.T.P.A. Section through the pila antotica

STAP. OSS. Stapedial ossification
S.T.S.C.P. Section through subcapsular process
S.F. Sphenoid fontanelle
S.P.H. COM. Sphenethmoid commissure
1. SPIN. NER. First spinal nerve
STY. Stylohyal cartilage
SUP. ORB. CAR. Supraorbital cartilage
SUP. POL. CA. Suprapolar cartilage
TEC. SYN. Tectum synoticum
TRAB. Trabeculae
TRAB. COM. Trabecula communis
TRO. Trochlearis nerve
VAG & ACC. Vagus plus accessory nerve