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SOME FEATURES IN THE ANATOMY AND LATER DEVELOPMENT OF THE HEAD OF *DELPHINUS DELPHINUS* LINNÉ.

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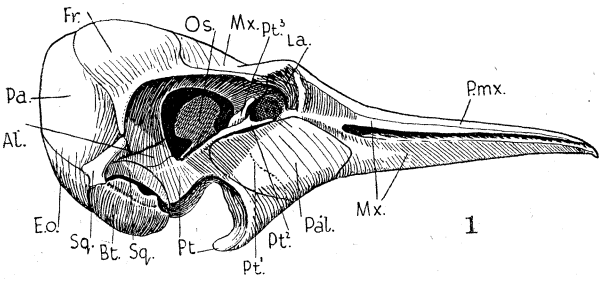
(Figures 1–29.)

Part I.—Osteology.

This part of the work is based on two foetal heads which I received from the New South Wales Fisheries Commission some years ago.

The larger of these was converted into a skull by careful dissection, and it has now been extensively disarticulated as the work proceeded. It measured seventy-eight millimetres from tip to occiput.

The smaller was decalcified and cut into serial sections along the sagittal plane after straining in alum carmine. This specimen measured fifty-two millimetres from



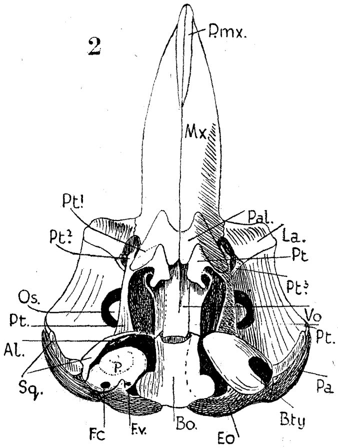


Fig. 1.—*Delphinus delphinus* Linné. The skull of a 78 mm. embryo, lateral view.
Fig. 2.—The same, ventral view.

Abbreviations used on illustrations to Part I.

A[1] & A[2], Accessory tympanic ossicle. Al., Alisphenoid. A.o., Ala orbitalis. Aq.coch., Aqueductus cochleae. Bo., Basioccipital. B.s., Basisphenoid. Bs.o., Basisphenoid ossific centre. Bt. & Bty., Basitympanic. C.n.l.d., Cartilage of the naso-lachrymal duct. E.o., Exoccipital. Fen.c., Fenestra cochleae. F.o., Fenestra ovale. Fr., Frontal. F.v., Fenestra vestibuli. I., Incus. La., Lachrymal. Le., Lateral ethmoidal plate of the vomer. L.t.a. & L.t.p., Lamina transversalis anterior and posterior. M., Malleus. Me., Mesethmoid. Mx., Maxilla. Na., Nasal. Os., Orbitosphenoid. Pa., Parietal. P., Pet. & Petr., Petrosal. Pl.e., Planum ethmoidale. P.mx., Premaxilla. Po., Postorbital process of the frontal. Ps., Presphenoid. Ps.a. & Ps.p., Anterior and posterior paraseptal cartilages. Ps.o., Presphenoidal ossific centre. Pt., Pterygoid.. Pt., Pterygoid and Palatine suture. Pt., Pterygoid, processus anterior. Pt., Pterygoid, processus anterior, lower limb. Pt., Pterygoid, processus anterior, upper limb. R., Rostrum. Sn., Septum nasi. Sq., Squamosal. St., Stapes. T.n., Tectum nasi. Ty., Tympanic bone. Vas., Vascular foramina. Vo., Vomer. VII, Facial canal.

tip to occiput. For this fine series of sections I am indebted to Professor C. W. Stump of the Department of Embryology and Histology, University of Sydney, and to him my sincere thanks are tendered.

In the larger specimen all the bones are completely ossified, whilst in the smaller much of the chondrocranium is still present. In fact, so much is this so that it has been possible to make comparisons between this chondrocranium and that of *Phocaena* as described by de Burlet (1913).

The chondrocranium resembles closely that of *Phocaena*; such differences as have been noted will be mentioned in the course of the description of the osseous skull.

THE SKULL.

Descriptive.

The general contours of the skull will be gathered from the drawings.

The Premaxillae (P.mx., Figures 1, 2 and 4) are elongated bones which fit in between the maxillae; superiorly they extend back the full length of the snout and bound the external nostril laterally. Inferiorly they appear as splints on either side of the midline, extending back somewhat less than half the length of the snout. The lateral face of the bone articulates with the maxilla. The lateral nasal process of the bone overlaps the frontal process of the maxilla, and its tip reaches the antero-lateral corner of the little nasal bone and lies upon the antero-medial corner of the frontal bone.

Upper and lower margins suture with the similar edges of the opposite bone. Between these edges the median face of the bones is concave and the anterior prolongation of the septum nasi lies between them.

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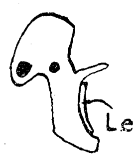

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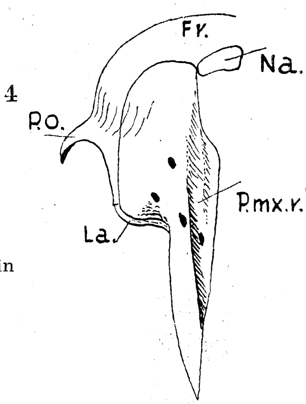


Fig. 3.—The maxilla, tranverse section just in front of the lachrymal bone.

Fig. 4.—The same, dorsal view.

The Nasal Septum, fairly thick behind, where it is attached to the upturned face of the mesethmoid crest and the anterior superior edge of the vomer, becomes thinned as it extends forward and is attached above and below to the sutures between maxillae and premaxillae. This cartilaginous septum nasi has been termed the rostral cartilage by previous workers, but, inasmuch as its attachment behind to the mesethmoid crest and vomer and its situation between the two lateral ethmoid plates of the vomer definitely establish its identity as the septum nasi, it would appear a pity to hide that identity under another designation.

The Maxilla (Mx., 4*) presents for examination a body and an expanded frontal process. The cross section of the body just in front of the lachrymal bone is shown in Figure 3; for the rest the shape of the bone may be gathered from Figures 1, 2 and 4. The body of the bone is divided into upper, facial, and lower palatine portions by the very conspicuous dental sulcus (Figure 1). This sulcus is continued back by a canal which carries the posterior dental nerve from the pterygo-palatine fossa. A second branch of the maxillary division of the fifth nerve, apparently the combined anterior and median dental, enters the back of the maxilla by a canal placed more medially

* Numbers such as these refer to the structure as seen in the sagittal sections illustrated in Figures 24 and 25.

than the last and emerges into the dental sulcus about half-way along its length. A third canal from the same fossa enters the back of the bone and appears on the floor of the premaxillary recess (P.mx.r., Figure 4) behind the position of the transverse section; its opening in that recess is shown in Figure 4. The other two canals are cut across in the section. This third canal transmits a branch of the superior maxillary nerve.

The frontal process of the maxilla is a thin lamina which is spread over an extensive area of the anterior portion of the frontal bone (Figure 11) and covers most of the lachrymal. It bounds the external nostril laterally under the premaxilla, and there reaches the corner of the nasal bone. It is perforated by four foramina from the pterygo-palatine fossa, of which it forms the roof. These foramina transmit branches of the infraorbital nerve.

The sutures between the maxilla and the premaxilla, palatine, lachrymal and frontal bones are obvious in the drawings. Medially the lateral ethmoid plate of the vomer (Le.) is plastered to the face of the maxilla below the premaxillary recess. Posteriorly the body is hollowed out beneath the base of the frontal process to form the roof, anterior and posterior walls of the pterygo-palatine fossa, and the median wall makes sutural contact with the median limb of the anterior process of the pterygoid bone high up at the back of the fossa, immediately in front of the anterior margin of the frontal bone.

Posteriorly, between the ascending lamina of the palatine and the lateral ethmoid plate of the vomer, the maxilla forms the front wall of the nasal cavity and a median portion of its frontal process forms the roof of that same cavity.

The form and situation of the Palatine bone (Pal., 60) and its ascending lamina are clearly shown in the drawings, as also are all its sutures, with the exception of the common suture of both bones with the inferior margin of the vomer.

The Pterygoid (58) is a complex bone which calls for special illustration to cover adequately its form and relations (Figure 5). One may recognize, for descriptive purposes, a body, internal and external plates, a lamina dorsalis, and anterior, palatine, hamular and posterior processes.

The body is a relatively stout lamina which lies behind and is slightly overlapped by the posterior margin of the ascending lamina of the palatine bone. It is narrower, antero-posteriorly, above than below, and inferiorly turns into the horizontal plane and is continued backward a little way as the palatine process. The internal and external pterygoid plates are attached to the posterior margin of the body. Inferiorly these two plates are attached to the upper surface of the palatine process, and this, thus

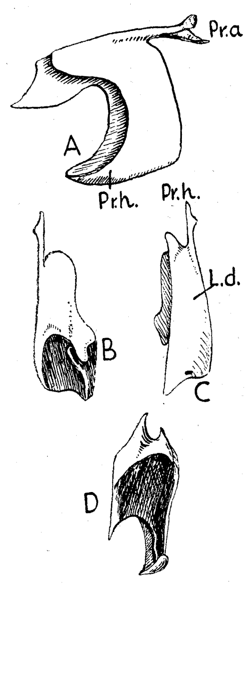


Fig. 5.—Pterygoid bone. A. lateral, B. ventral, C. dorsal, and D. posterior views.

strengthened, is continued backward and slightly downward, broadening somewhat, as the hamular process. Superiorly the plates are united by the lamina dorsalis, a horizontal lamina which lies beneath, and is sutured to, the basicranial alae. The lamina is narrow in front, where it underlies the base only of the ala orbitalis, and widens as it extends back so that it underlies practically the whole width of the alisphenoid ossification. The external plate does not extend so far posteriorly as the internal; it terminates where it sutures with the lower end of the pterygoid process of the squamosal bone. The lamina dorsalis is obliquely truncated at this point and the internal plate is continued back to suture with the lateral-down-turned edge of the basioccipital bone. The pterygoid plates, as they extend upward and backward from the hamular process and palatine lamina, arch inward, medially. This is more marked in the internal plate than in the external, and more pronounced posteriorly than in front. When the internal plate reaches the under side of the basicranial alae it turns mediad into the horizontal plane, adding to the width of the lamina dorsalis. Although the lamina dorsalis extends mediad of the dorsal edge of the internal plate anteriorly, and though that dorsal edge passes inward as it extends backward till it reaches the median margin of the dorsal lamina, the lamina itself is broader behind than in front because the dorsal edge of the external plate is here further from the midline.

The anterior process of the pterygoid (59) is a bifurcated continuation of the lamina dorsalis. The lower and lateral limb (Pt., 3) is a small pointed bar of bone which extends forward above the palatine bone, forming an incomplete floor to the hinder part of the pterygo-palatine fossa. The median limb is a shorter and stouter process which turns upward and mediad, and becomes applied along its superior margin to a ridge on the under side of the anterior margin of the frontal bone; the tip of the process makes contact with the maxilla on the inner wall of the pterygo-palatine fossa as already described. Behind the suture with the frontal bone the inner margin of the process sutures with the outer edge of the lateral ethmoid plate of the vomer (Figure 6, Pt. 4) in front of the orbitosphenoid bone. In this situation it forms the median boundary of the sphenoptic fissure in front of the orbitosphenoid and contributes a narrow area to the cranial floor.

Besides the sutural contacts already mentioned, the pterygoid bone is in contact with the vomer along the length of the median margin of the lamina dorsalis.

The Lachrymal (La.) is a roughly quadrilateral bone which is wedged in beneath the anterior portion of the frontal process of the maxilla in front of the frontal bone. It forms the outer part of the roof of the pterygo-palatine fossa and the fore part of the roof of the orbital fossa.

The Squamosal (Sq.) presents an irregularly pyramidal body which bears a small squamous lamina superiorly, a short stout laterally placed malar process and a long curved sickle-shaped pterygoid process in front. The body presents its longest face superiorly in the horizontal plane, and is coextensive with the lower margin of the parietal bone, to which it is sutured. The other two faces meet in a rounded angle, one looking anteriorly and a little ventrally, the other downward and a little posteriorly. The superior face of the bone is triangular and the malar process is attached along its outer edge. This process commences behind flush with the lateral margin of the exoccipital, by which it is slightly overlapped; as it extends forward it rises above the level of the body of the bone and is, by the body, carried out from the wall of the skull. It also projects below the antero-inferior face of the bone and extends forward and upward beyond the body of the bone. The pterygoid process (14) is a curved tapering anterior prolongation of the body which extends forward and mediad under the posterior margin of the alisphenoid bone, and then turns downward behind the posterior margin of the external plate of the pterygoid bone. Just where it turns downward away from the alisphenoid it carries the obliquely truncated posterior margin of the lamina dorsalis of the pterygoid bone with it.

The squamosal bone takes no part in the formation of the wall or floor of the cranial cavity, its squamous portion is quite small, and is applied to the outer aspect of the lower margin of the parietal above the body of the bone.

The Jugal is a little splint which extends between the postero-inferior corner of the supraorbital lamina of the frontal and the antero-superior corner of the malar process of the squamosal bone.

The Frontal (5 and 10) is an extensive bone, it forms the greater portion of the roof and anterior wall of the cranial cavity, and is quite thin except along the line of attachment of its supraorbital process. This latter is a relatively stout lamina which forms the roof of the orbital fossa, except for that small area supplied by the lachrymal. The anterior articulations of the frontal bone have already been detailed. Posteriorly the bone makes sutural contact with the interparietal and the parietal. Inferiorly it arches round the sphenoptic hiatus and behind this sutures with the anterior half of the outer margin of the alisphenoid bone.

The Interparietal is an irregular quadrilateral bone which is placed between the frontals anteriorly, the parietals laterally, and the exoccipital posteriorly.

The Parietals (Pa., 37) are a pair of narrow, curved, concave-convex bones wider below than above. They fit in between the frontal, interparietal, supraoccipital, exoccipital body of the squamosal and the posterior half of the lateral margin of the alisphenoid bone. So far are these bones curved round inferiorly that they share in the formation of the cranial floor lateral to the alisphenoid and the otic capsule. Behind the alisphenoid they lie lateral to the petrosal bone, but do not make contact therewith.

The Supraoccipital overlaps the hinder margin of the interparietal and on each side it sutures with the parietal above and the exoccipital below.

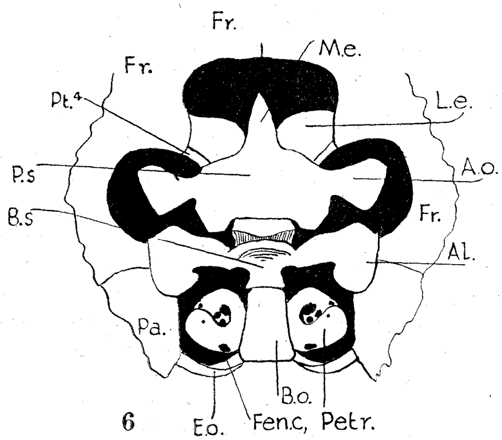
The Exoccipital (17) bone is sutured to the posterior face of the squamosal below, and above this to the hinder margin of the parietal. Above the foramen magnum it sutures with the supraoccipital and below with the basioccipital.

The Basioccipital (Figures 2 and 6, Bo.) presents a solid oblong body in the base of the cranial cavity and, on each side, a squamous process which extends downward and laterally beneath the canalicular portion of the petrous bone, but does not make contact with it, to suture with the inferior margin of the exoccipital bone.

The Basisphenoid (Figure 6, B.s., 55), in front of the basioccipital, is a little broader, but is neither as long nor as thick. The sella turcica on its dorsum is a shallow, relatively broad, depression. A carotid groove is impressed on the dorsum of the bone laterally and posteriorly at the point of attachment of the alisphenoid. The vomer is applied to its inferior surface.

The Presphenoid (Figure 6, P.s.) merges on either side into the orbitosphenoid and anteriorly into the ethmoid.

The form of Alisphenoid (Al., 15) and Orbitosphenoid (A.o. and Os.) is sufficiently shown in Figures 2 and 6, and they call for no further comment here.



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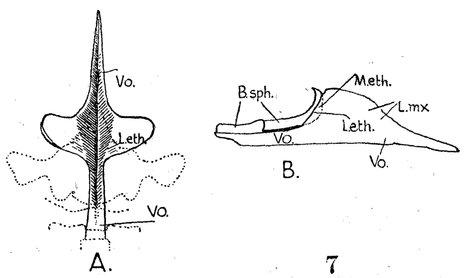

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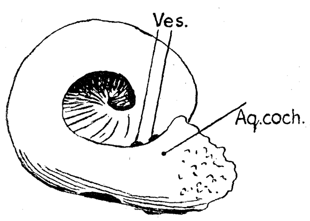
Fig. 6.—The cranial floor from above.

Fig. 7.—The Vomer. A. dorsal, and B. lateral views.

The Vomer (Figure 7) is an extensive bone which commences behind as a narrow flat plate applied to the under side of the basisphenoid. Beneath the presphenoid it becomes concave superiorly and keeled inferiorly; a little further forward it becomes V-shaped in cross section and then Y-shaped. The lower arm of the Y is fitted to the interpalatine suture. From the middle of the length of the presphenoid-mesethmoid ossification the limbs of the V get rapidly longer as the bone extends forward; they rise attached dorsally to the lateral edge of the forward bulging, upturned mesethmoid portion of the ossification. At the forward margin of the medial end of the orbitosphenoid bone the upper portion of the lateral wing of the vomer is reflected into the same plane as that bone, and its dorsal surface forms a small portion of the cranial floor in front of the orbitosphenoid and medial to the upper limb of the anterior process of the pterygoid bone. In Figure 7A, which depicts the vomer from above with the presphenoid-mesethmoid ossification and orbitosphenoid indicated in dotted lines over it, this lateral wing of the vomer is lettered L.eth. Forward of this point the two limbs of the Y rise a little higher still and become plastered to the inner face of the maxilla. At the posterior end of the intermaxillary suture the lower limb of the Y is dropped and the bone from here forward is once again V-shaped, the limbs of the V becoming shorter and shorter as the fore end of the bone is reached. The inferior margin of the vomer appears for a short distance between the maxillae on the palatine surface immediately behind the interpremaxillary suture. In Figure 7B the extensive limb of the bone applied to the medial face of the maxilla is lettered L.mx.

The resemblance of the Petrosal Bone to a discoid land shell with a dextral coil and a widely open umbilicus is very striking, and, continuing the simile, as it lies in position in the floor of the cranium the umbilicus is uppermost and the mouth of the shell on the outer, lateral, side and looking forward. By far the greater part of the bone is the cochlear portion; the vestibule and semicircular canals are lodged in the last quarter whorl of the shell. In my specimen the petrosal bone is not sutured to any bone, but is held in position by fibrous tissue only (Figure 2, P.)



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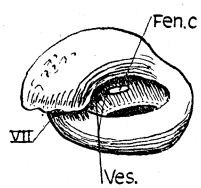

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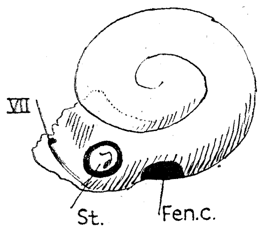

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Fig. 8.—The petrosal bone, dorsal view. Fig. 9.—The same, dorso-medial view.
Fig. 10.—The same, ventral view.

On looking into the open umbilicus (Figure 8) the first complete turn of the cochlear scala is found to be freely open, and this scala is seen to burrow into the vestibular portion of the bone and end blindly. Since this blind end is the commencement of the scala tympani, one should, perhaps, have said it commences here instead of ends blindly. Looking through the open commencement of the scala one can see the fenestra cochleae on its outer wall (Figure 9, Fen.c.). The inner wall of the vestibular portion of the bone is perforated by two canals, which lead right through the blind end of the vestibular scala and its outer wall to the vestibule which lies medial to and behind that blind end. Lateral to these two canals the bone is grooved just where the vestibular portion of the bone, the mouth of the shell as it were, is applied to the penultimate whorl of the cochlea. This groove may be traced out and round the bone; near the ventral surface it becomes converted into a canal for a short distance and is then continued on again as a groove lateral to the fenestra vestibuli. The groove lodges the facial nerve; it is in fact an incomplete aqueductus Fallopii, and the little spicule of bone which converts it into a canal for a short distance is all there is to represent the prefacial commissure at this stage of development. The widely open umbilicus is, of course, the internal auditory meatus.

Turning to the inferior surface of the bone (Figure 10), the fenestra vestibuli, neatly fitted by the circular base of the stapes, is an obvious feature.

On removing the stapes one opens into the vestibule, and a very complete opening it is, for one finds that one removed the whole of the floor of the recess when the stapes was removed. This recess is cup-shaped and in reading the description which follows it must be kept in mind that the depth of the recess is the roof, when it is correctly oriented. Immediately inside the vestibule on the anterior wall, but towards the median side thereof, a fairly large foramen opens into the vestibular scala near its tip. Laterally to this, a little higher, are two other foramina, the inner openings of the two foramina observed on the upper side of the bone. The one nearest the cochlear foramen transmits the branch of the vestibular nerve to the ampulla of the anterior vertical canal; the external aperture transmits as well cochlear twigs to the first portion of the ductus cochleae. The other foramen transmits the rest of the vestibular nerve. Opposite the cochlear foramen and a little higher in the vestibule there is a little recess which tends dorsad and laterally and ends in two tiny canals. The recess lodges the ampullae of the external and posterior vertical canals, which are those seen in its depth. The canal for the common limb of the two vertical canals opens into the vestibule high up on the antero-lateral wall. The recess for the ampulla of the anterior vertical canal and anterior end of the horizontal canal is in front of the last foramen slightly lower down. The aqueductus cochleae leaves the vestibule in the centre of the roof, and appears externally as shown in Figure 8.

The long axis of the vestibule, that is the line drawn through the centre of the stapes and on through the top of the roof, is oblique to both horizontal and sagittal planes of the skull, so that produced from above downward it passes forward and medially, whilst the ductus endolymphaticus and its aqueduct are at right angles to the horizontal plane.

The Stapes is a very simple little bone consisting of a discoid body and a short peg-like process. In the smaller head the stapes, like all the auditory ossicles, is cartilaginous, and the sections show the process to be a very small loop. It may be that in the larger head the process has been broken.

In the Incus (Figure 11) we have but half an "anvil", the pointed end and the foot of that side are missing. The short process of the incus is fitted to a groove on the under side of a spur which stands forward from the apex of the posterior process of the tympanic bone. In the smaller skull this process of the tympanic is continuous with the cartilaginous capsule. The long process turns inward and its apex lies immediately beneath the stapedial peg.

The Malleus (Figure 12) presents for examination a body, manubrium and two processes. The mass of the bone is roughly triangular, with the rounded apex below. The face depicted in Figure 12A looks backward and medially and has the fore end of the incus fitted to it by connective tissue. As viewed thus the bone appears as though

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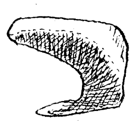

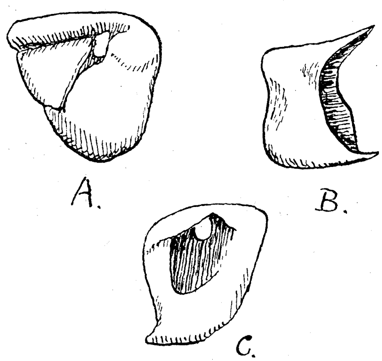

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Fig. 11.—The Incus.
Fig. 12.—The Malleus. A. posteromedial, B. posterolateral, and C. anterolateral views.

formed by the folding of the lower and medial portion round the upper and lateral, for a groove which looks like a suture divides the one from the other. This groove commences near the middle of the median margin and extends downward and laterally, deepening as it does so, and terminates in a foramen situated low down near the ventral margin of the bone, above the base of origin of the squamous horizontal process. The Manubrium is that portion of the bone above and medial to the groove. The foramen transmits the chorda tympani nerve.

Viewed from the side (Figure 12B), the body of the bone is oblong, with the short margins above and below. The anterior face of the bone is excavated as shown (Figure 12C). There is a triangular lamina which projects forward and laterally from the upper margin of the body. A similar, but smaller, lamina projects back from the inferior angle. Two Accessory Auditory Ossicles are present (Figure 13, A^1 and A^2). Each is a little flat plate of bone attached to the antero-lateral margin of the body of the malleus, above the inferior process. The antero-inferior angle of the smaller, lower, ossicle is attached to the tip of the pterygoid process of the squamosal.

In Figure 13 the auditory ossicles have been drawn *in situ*, seen from below. The position of the tympanic membrane below the malleus is indicated by the dotted lines.

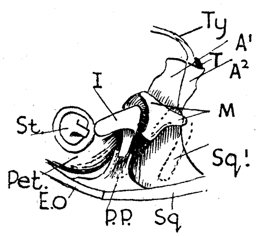


Fig. 13.—The tympanic ossicles in place, seen from below. The dotted line indicates the margin of the tympanic.

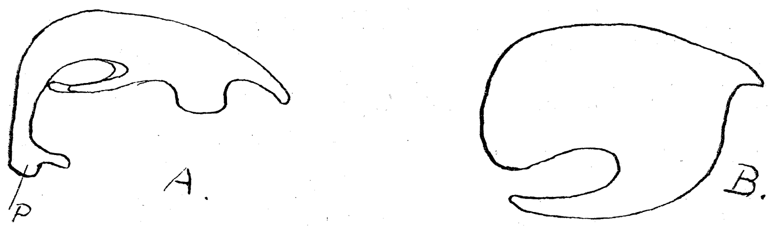


Fig. 14.—The Os tympani. A. lateral, and B. ventral views.

The Tympanic (Figure 14) is a spoon-shaped bone. The concavity is upward, and the long axis antero-posterior but slightly diagonally so that the fore end lies nearer the midline than the hind end. Four processes have to be described. The posterior arises from the full width of the posterior margin of the bone and turns abruptly upwards, and becomes wedged in in front of the sutures between the parietal, exoccipital and squamosal bones. At its apex the process bears a forwardly projecting spur, which is grooved on the under side for the reception of the incus. The posterior lateral process arises from the outer side of the bone. It is a thin, narrow bar of bone which, projecting back, becomes attached to the infero-lateral corner of the squamosal bone. The bay formed by this process and the margin of the main part of the bone is the annulus tympanicus, and it is filled in the fresh state by the tympanic membrane. The anterior-lateral process is a broader and much shorter lamina which extends upward from the lateral margin to gain attachment to the inferior margin of the smaller accessory auditory ossicle. The anterior process is a narrow prolongation of the bone which is attached to the tip of the pterygoid process of the squamosal bone along with the small accessory ossicle.

On comparing this young Odontocete skull with the young Mystacocete skulls described by Ridewood (1922), a general agreement is apparent, but there are observable differences in several places.

At the outset, one may express complete agreement with Ridewood's conclusion that the "alisphenoid bone of the whales . . . is but the ossified ala temporalis". There is no trace of any pterygoid wing.

The squamosal bone of our skull differs from that of the balaenoid skulls in not appearing in the cranial wall within, and also in the form of the falciform process. In those this process is flattened and bifid; in this it is rod-like and ends in a tapered point. This point certainly curves round the anterior margin of the periotic bone, but it also meets the pterygoid bone in this situation, forming, as it were, a strengthening bar to the under side of the posterior margin of the dorsal lamina of that bone. Ridewood (p. 259) states, on the authority of Beauregard, that the processus falciformis does not meet the pterygoid bone in the Odontocetes. In both my foetal skulls the conditions are as just described, but in an adult skull before me I find the pterygoid bone less extensive posteriorly, so that the two bones do not meet.

It should be mentioned here that in my foetal skulls the foramen through which the third division of the fifth nerve passes ventrally is confined to the dorsal lamina of the pterygoid bone; the pterygoid process of the squamosal bone takes no part in its formation. Seeing that this foramen is quite extra-cranial, it is hardly correct to designate it foramen ovale (*vide* Ridewood, p. 259).

The bifurcated anterior process of the pterygoid bone which I have described is not present in the pterygoid bone of the balaenoid forms (*vide* Ridewood, fig. 14c, p. 260).

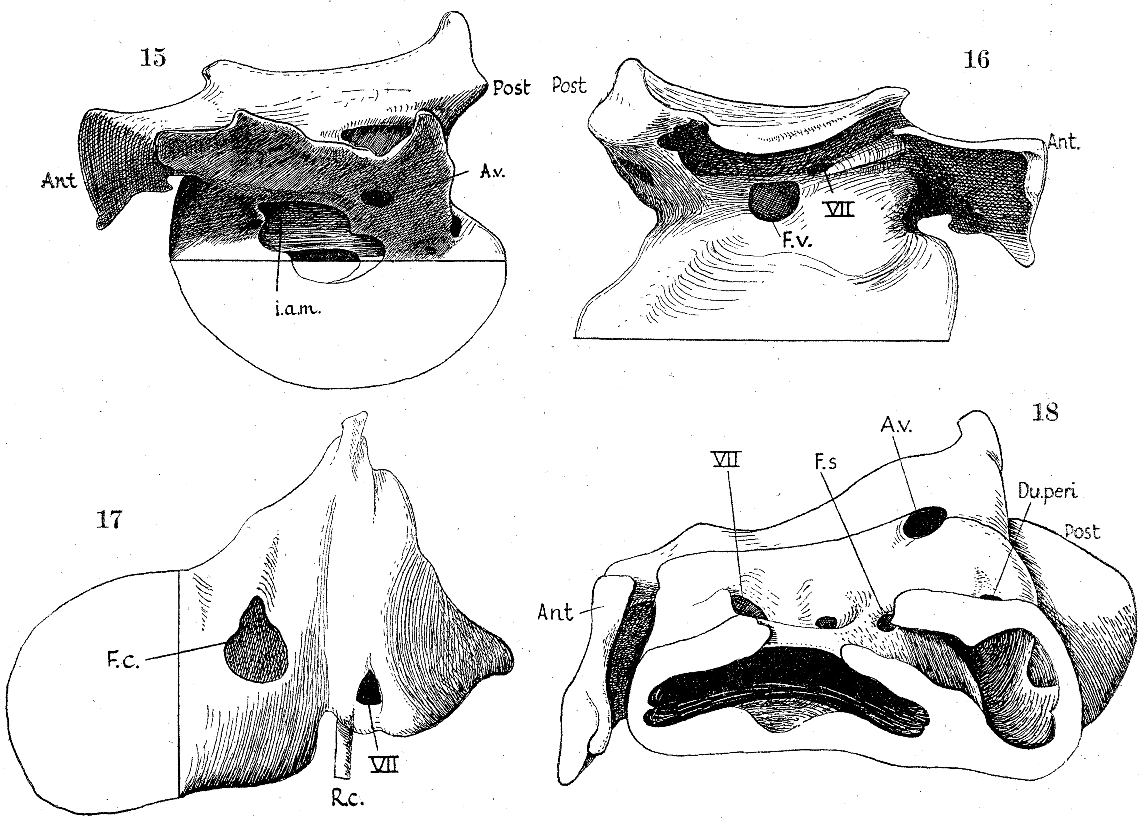
The palatine process of the frontal bone which Ridewood figures (fig. 15, p. 263) is not present in the foetal dolphin skull. Above the posterior end of the pterygoid the outer end of the alisphenoid bone intervenes between it and the parietal and frontal above and the squamosal behind (see Figure 1).

I hesitate to compare the tympanic bone of my little skull with those of the balaenoid forms, because it is an exceedingly fragile bone and so dissimilar that I have thought it well may have been mutilated in the process of disarticulation. It would, however, seem that, firstly, Ridewood's posterior pedicle (fig. 10, p. 241) corresponds with my posterior process, that his sigmoid process is my anterior lateral, and, secondly, his ossiculum accessorium is the anterior, and the facial process of the gonial is the posterior of the two accessory ossicles which I describe. If this be so, then that which I describe as the posterior lateral process of the tympanic bone is the "posterior conical process" which develops later in the balaenoid forms.

The cartilaginous otic capsule is of particular interest, and the better to study it a wax plate model has been made from the serial sections. This model comprises the whole of the vestibular and part of the cochlear portion, together with the attached tegmen tympani. In Figures 15, 16 and 17 the model is shown as seen from above, below and behind. In the first and last of these the part of the capsule not included in the model is indicated. The line along the unfinished edge of the model is the medial side of it and that face is in the sagittal plane, for it was from sagittal sections that the model was reconstructed. The dorsal line of the model corresponds to the horizontal plane along the long axis of the head. It will be observed that the model is thicker in front than behind; therefore, since the dorsal line is in the horizontal plane, the ventral slopes downwards from in front.

The marked difference between this cartilaginous capsule and the slightly older ossified capsule is due mainly to the attached massive tegmen tympani, but also, to a lesser degree, to an upstanding boss above the vestibular portion. The anterior portion of the tegmen later becomes ossified continuously with the os tympani, forming the anterior process thereof. The posterior portion, behind the sulcus incudis, becomes the posterior process of the same bone. Both portions lose their continuity with the capsule. The dorsal boss is, for the most part, absorbed later.

At no point is this otic capsule in continuity with the chondrocranium. The prefacial commissure is represented by the irregular mass of cartilage attached antero-laterally and dorsally to the pars cochlearis, and it is to this that the tegmen tympani is attached anteriorly. Confining the term tegmen to the horizontal portion of the tympanic processes, its attachment is continued along the dorso-lateral edge of the capsule and it projects well beyond the capsule both in front and behind. Anteriorly the lateral projection of the tegmen is not marked, but increases towards the back of the capsule. Along its length the lateral edge of the tegmen carries a vertical flange. In front of the capsule this is in the transverse plane; beside the capsule the vertical flange is in the sagittal plane. Posteriorly the tegmen and its flange constitute the large irregular mass which Ridewood (1922) designated the crista parotica. The vertical flange ends posteriorly in a curved margin which rises towards the lateral margin of the fenestra vestibuli. To the outer side of it there is attached a stouter ridge which merges



Figs. 15-18.—A model of part of the otic capsule and attached parts.
15. Dorsal view. 16. Ventral view. 17. Posterior view.
18. Medial section.

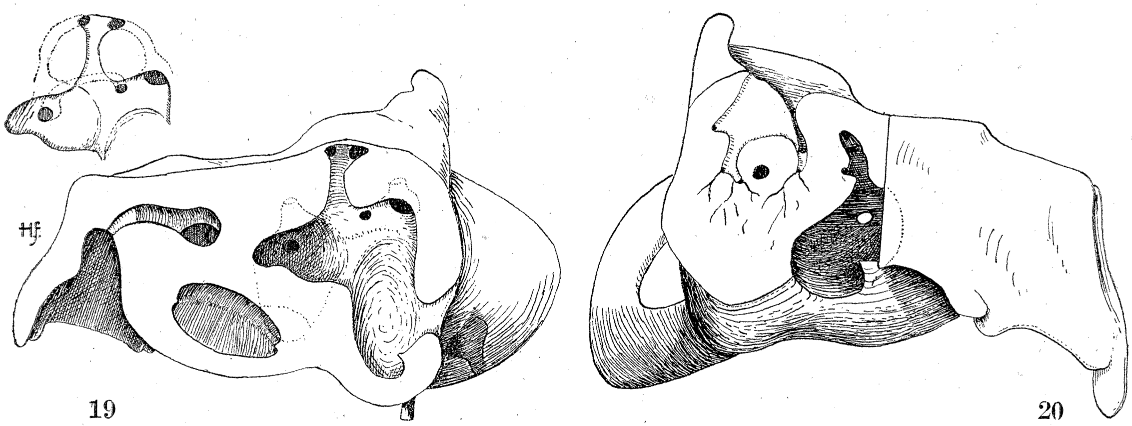
superiorly into the contour of the capsule, but inferiorly curves up and backward forming a solid, low flange which overhangs the fenestra. The body of the malleus is fitted to these two curved margins. Near the centre of its length the inferior edge of the lateral flange is embayed to form the sulcus incudis. At this point its dorsi-ventral depth is small, but behind this point it swings ventrally, increasing in depth, to join the anterior face of the crista parotica as a fairly stout flange. The parotic crest is excavated medially to this last, and at the depth of this excavation the posterior wall of the capsule is perforated by a fairly large foramen. This is the posterior facial foramen, and it is seen in the postero-medial and inferior face of the parotic process. The cavity is largely filled by the stapedius muscle, which arises from its walls; the facial nerve runs backwards along its medial wall.

The fate of the tegmen and its processes may be mentioned here. The tegmen itself is largely absorbed setting its processes free from the capsule. The anterior transverse flange becomes the processus anterior of the os tympani. The longitudinal vertical flange becomes one of the accessory auditory ossicles, and the solid process immediately behind and to the outer side of it becomes the other. The processus posterior of the tympanic bone is formed from the crista parotica and the portion of the ridge bearing the sulcus incudis.

Turning our attention next to the dorsal surface of the capsule (Figure 15), the most obvious feature is the large internal auditory meatus. In the antero-lateral corner of this, the internal aperture of the canalis facialis is readily recognisable. One cannot, however, recognise the usual superior and inferior acoustic foramina so readily. On the other hand the areas and foramina of human osteology are not difficult of identification. A crista transversa very obviously separates a superior, lateral from an inferior, medial fossula.

The foramen for the nerves to the utricle and the ampullae of the anterior and external semicircular canals is placed in the lateral wall of the superior vestibular area in the posterior part of the superior fossula. The canalis centralis and tractus spiralis foraminosa are completely continuous in one large circular aperture and the inferior vestibular area is but faintly differentiated from the area cochlea of the inferior fossula. The foramen singulare in the lateral wall of the inferior vestibular area is not quite comparable with that canal in the human skull, for it transmits a twig of the cochlear nerve as well as that for the ampulla of the posterior vertical semicircular canal. These three canals in the lateral wall of the meatus acusticus internus are clearly shown in my drawing of the medial view of the model (Figure 18).

Posterior to the internal auditory meatus, quite close to the medial edge of my model, there is a small foramen which opens into the labyrinth close to the junction of cochlear and vestibular portions. In the sections this little canal is filled with loose connective tissue, and communicates with the similar tissue between the scala vestibuli and the cartilaginous wall above it. Quite definitely, it does not transmit any blood vessels, and, although it opens dorsally instead of ventrally, I incline to the view that this is a canal for the ductus perilymphaticus.



Figs. 19-20.—A model of the otic capsule and attached parts.
19. Medial section. 20. Lateral section.

The Aqueductus Vestibuli for the ductus endolymphaticus is situated at a higher level lateral to the inferior vestibular area of the internal auditory meatus.

A large triangular orifice lateral to the aqueductus vestibuli gives entrance to the nutrient pit and fissure shown in section in Figure 20.

In a posterior view of the model one notes the position of the large fenestra cochleae, which can be seen from the internal auditory meatus as in the osseous capsule; and the smaller posterior facial foramen (Figure 17) with the proximal end of Reichert's cartilage attached to the crista parotica below it.

Inferiorly the fenestra vestibuli is an obvious feature. Lateral and anterior to this is the tympanic orifice of the facial canal. The facial sulcus runs along the base of attachment of the tegmen tympani, lateral to the fenestra vestibuli, and on into the fossa for the stapedial muscle in the parotic process and so through the posterior facial foramen (Figure 16).

The Hiatus Fallopii will be found at the fore end of the capsule, high up, lateral to the root of the tegmen tympani, behind the medial extension of the transverse lamina thereof (Figure 19).

The Facial Canal expands almost at once to accommodate the geniculate ganglion; it then continues laterally and ventrally beneath the commissura prefacialis, and then turns posteriorly, burrowing along the attachment of the vertical longitudinal lamina of the tegmen tympani.

The form of the cochlear labyrinth calls for little comment. It is a flattened helix, and the lamina spiralis is but indicated.

The shape of the vestibular portion of the labyrinth and the position of its various diverticula will be gathered by reference to Figures 19 and 20. These are illustrations of the model in section, and in the former of the two drawings I have indicated with dotted lines the recesses which lie lateral to the plane of section. The widely open communication between the vestibular and cochlear portions of the labyrinth has been cut across in Figure 19, and the recess for the common arm of the vertical semicircular canals cut along its length. The recess for the ampullae of the external and anterior vertical canals has been partly opened into, and the orifice of the anterior end of the (future) bony horizontal canal shown in its lower part. The recess for the ampulla of the posterior vertical canal is also partly opened into. The lower portion of the saccular cavity (shown in Figure 20 along with half of the fenestra vestibuli) is indicated in Figure 19 by dotted lines.

Had the plane of section of Figure 19 been two sections further from the mid-line, the roof of the recess for the crus commune would have been found to give way as the aqueductus vestibuli, and in the section itself the passage is found occupied by the endolymphatic duct. In the little drawing above Figure 19 I have indicated the situation of the three semicircular canals.

It will be noted that in the osseous capsule the widely open communication between the vestibular and cochlear portions of the cartilaginous labyrinth has been reduced to quite a relatively small foramen.

It will be noted that the attachment of Reichert's Cartilage is not to the body of the parotic process, but to the floor of the cavum musculi stapedei (Figures 17 and 19).

The Tympanic Cavity is nearly co-extensive with the inferior surface of my model, but extends rather further medially. It is a dorso-ventrally flattened space whose roof medially is a thin membranous and epithelial covering of the inferior surface of the otic capsule, and whose floor is the upper surface of the os tympani similarly covered.

Looking for the tympanic cavity in the sections, beginning with the more lateral, one finds it first as two nearly oval cavities, which enlarge towards the midline, the posterior one more rapidly than the anterior; next the posterior cavity acquires a dorsal extension and again contracts and the partition between anterior and posterior portions peters out and the two communicate uninterruptedly. The dorsal extension of the posterior division, however, continues mediad as a triangular recess in a thickening of the tissue between the capsule and the cavity. This recess still further medially is found to be supported on the manubrium of the malleus and finally to end blindly with the last little segment of the manubrium in front of it. The point of communication of this recess with the rest of the cavity is immediately below the incudo-stapedial joint. The tensor tympani muscle passes forward from that part of the manubrium mallei which thus supports the anterior wall of this little epitympanic membranous recess (recessus manubrii).

The cartilaginous Incus is essentially the same "half anvil" as the bone in the larger specimen; on the other hand, the model I have made of the cartilaginous Malleus presents a different appearance from the bony malleus of the larger specimen. It completely explains the appearance of a suture across the anterior face of the bony specimen. Relatively the cartilaginous specimen is narrower from side to side, and the manubrium is found folded round from the inferior edge of the body, which is laterally compressed below, and is joined to the lower edge of the thicker upper portion of the body. I am just a little doubtful as to whether this union actually does take place, for unfortunately my section number 36 is exceedingly thick, and a section is missing between this and section numbered 37. There is, however, little room for doubt. In the cartilaginous specimen the lower portion of the body is not so thick as the bony specimen, and the space between the body and the manubrium is not so much filled in. Anteriorly the body of the malleus is produced in ossifying tissue. This is found as a forward continuation of the medial half of the body only and to a lesser distance of the horizontal portion of the manubrium. The plate of ossifying tissue does not expand horizontally to any appreciable extent above, though there is here a slight ridge on its medial face, so that whilst one may say that the inferior horizontal plate of the bony specimen is foreshadowed, one can hardly say that for the smaller superior plate. The proximal end of Meckel's cartilage lies against the concave medial face of this plate of ossifying tissue.

The rounded upper and medial contour of the body of the malleus fits neatly to the posterior curved edge of the longitudinal vertical plate of the tegmen tympani.

The Nasal Capsule.

The correct interpretation of the component parts of the nasal capsule will be made with confidence only by the examination of earlier stages of development than that we are now studying. Already in our specimen the capsule has undergone those changes which result in the peculiar situation of the cavities and nostrils.

That which follows is therefore offered as presenting the probable interpretation of the structures.

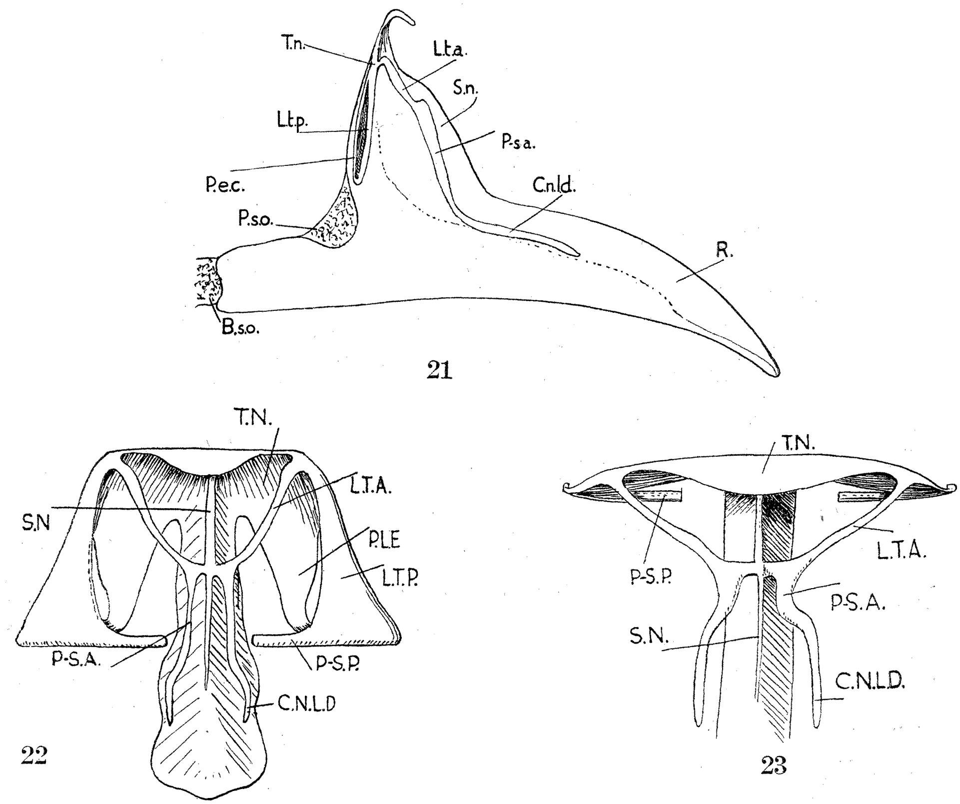
In the drawing of the model from the side (Figure 21) the ethmoidal crest, nasal septum, rostral cartilage and presphenoidal cartilage are all readily recognisable.

From either side of the upper portion of the ethmoid crest (Figure 22) a vertical plate of cartilage extends laterally. The vertical width of this plate increases as it extends. The lateral margin is sinuate, and it terminates below in a pointed piece which projects beyond the rest of the plate. The tip of the point is joined to the lower corner of the backward-turned lateral edge of a narrow triangular plate which is parallel to, and whose tip is attached to, the larger plate near the dorsal margin thereof. This smaller recurrent plate is placed just in front of the larger. From its infero-medial angle, just in front of the point of attachment to the larger plate, a little cylindrical rod extends horizontally inward towards the mesethmoid crest, but does not reach the crest.

There is a fissure between the lateral margin of the major plate and the inner margin of the smaller, recurrent plate. Through this fissure the olfactory nerves enter the nasal capsule, to reach the sensory epithelium, which is confined to the lateral recess of the nasal cavity.

Turning now to the front of our model (Figure 22), a solid little pellicle of cartilage is found attached to the nasal septum near its anterior margin, high up, on both sides. This branches almost at once into sinuate dorsal and ventral limbs. The dorsal limb curves upward, backward and laterally to join the major and recurrent transverse plates at their point of union. The ventral limb extends downward till it almost comes into contact with the outbulging of the solid rostral cartilage below the septum nasi; it then turns outward parallel with the curve of the rostral cartilage, and then abruptly forward a little distance from the rostral cartilage (Figure 23). In the sections it is found that this ventral limb terminates in front, just medial to and behind the spheno-palatine fossa.

The situation of the olfactory foramen would seem to indicate that the true posterior area of the capsule lies between the recurrent and major transverse cartilages. There is no doubt that the anterior nares have acquired a dorsal situation, and my interpretation of the capsule is based on the assumption that the whole structure has shared in the turning movement which placed those apertures in their dorsal situation; not only this, but that as the capsules were thus rotated, they were also, so to speak, squashed back, so that the posterior end of the capsule was pushed from the midline on each side.



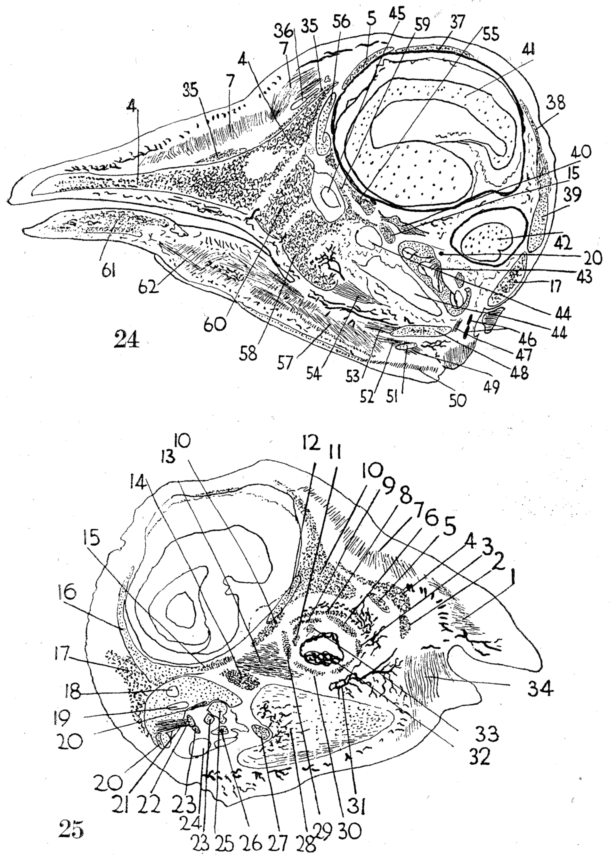
Figs. 21-23.—A model of the nasal capsule and rostral cartilage.
21. Lateral view. 22. Anterior view. 23. Dorsal view.

If this be the fact, then the major transverse plate at once becomes recognisable as the tectum nasi and transverse planum ethmoidale. The superior limb of the anterior sinuate cartilage is the lamina transversalis anterior, the inferior limb is the anterior paraseptal cartilage, and its anterior continuation is the cartilage of the naso-lachrymal duct. The recurrent transverse cartilage is the lamina transversalis posterior, and the cylindrical rod attached to its lower corner is the posterior paraseptal cartilage.

The little forward-turned edge of the tectum nasi alone has heretofore been regarded as the tectum nasi (de Burlet, 1916; Ridewood, 1922).

It will, perhaps, be somewhat difficult to realise how a transversely placed rod can be regarded as a paraseptal cartilage. It appears to me that this cartilage has been pushed outward and rotated into the transverse plane by the backward and lateral movement of the posterior end of the capsule.

Figure 23, a view of the capsule from above, will help one to recognise the superior limb of the anterior sinuate cartilage as the lamina transversalis anterior. The anterior direction of the cartilage of the naso-lachrymal duct is due to the fact that it has retained its relation to the medial, here anterior, corner of the orbit. In view of the fact that the naso-lachrymal duct itself is not developed, this constancy and the persistence of its cartilage at all are of peculiar interest, taken in conjunction with the fact that little remains of what was, in all probability, in the ancestral form a typical mammalian nasal capsule.



1. M. nasolabialis. 2. Lachrymal. 3. M. rectus internus. 4. Maxilla. 5. Frontal. 6. M. obliquus superior. 7. The muscle which opens the blow hole. 8. M. levator palpebrae superioris. 9. M. rectus superior. 10. Frontal. 11. M. rectus superior. 12. Commissura orbito-temporalis. 13. M. pterygoideus internus. 14. Pterygoid process of the squamosal. 15. Alisphenoid. 16. Lamina parietalis. 17. Exoccipital. 18. Nutrient canal. 19. External semicircular canal. 20. Facial nerve. 21. Stapedial muscle. 22. Stapes. 23. Incus. 24. Cavum tympani. 25. Malleus. 26. Manubrium mallei. 27. Meckel's cartilage. 29. M. rectus externus. 30. M. rectus inferior. 31. M. obliquus inferior. 32. Choroid. 33. Optic nerve. 34. M. buccinatorius. 35. Premaxilla. 36. Lateral recess of the blow hole. 37. Parietal. 38. Supraoccipital. 39. Taenia synoticum. 40. Gasserian ganglion. 41. Cerebrum. 42. Medulla. 43. Cochlear branches of the eighth nerve. 44. Lateral pharyngeal recess. 45. Dorso-lateral recess of the naso-pharynx. 46. XI-XII nerves. 47. M. jugulo-hyoideus. 48. Styloid process. 49. M. sternohyoideus. 50. Panniculus carnosus. 51. Hyoid cornu. 52. M. geniohyoideus. 53. M. stylohyoideus. 54. M. tensor palati. 55. Basisphenoid. 56. Planum ethmoidale. 57. M. hyoglossus. 58. Pterygoid bone. 59. Processus anterior ossis pterygoidei. 60. Palatine. 61. Dentary. 62. M. genioglossus.

Figs. 24 and 25.—Sagittal sections Nos. 22 and 38. Embryo measuring 52 mm. from tip of snout to occiput.

Part II.—Myology.

This portion of the work is based upon the examination of one foetal and two young dolphin heads, for which I have to thank Mr. E. Le G. Troughton and the Trustees of the Australian Museum, and also the head of one fully-grown specimen which was kindly procured for me by Mr. McArthur, of the Red Funnel Trawlers Proprietary, Limited, Sydney, and to him also my thanks are tendered.

The Superficial Facialis Musculature.

For the most part the superficial facial muscles are embedded in the deep layer of the superficial subcutaneous fat and fascia. It is, therefore, quite impossible to dissect out the muscles as may be done in the great majority of other vertebrates. It was found, however, that these muscles could be very clearly demonstrated by carefully shaving off the skin and subcutaneous tissues in successive thin layers parallel to the surface. The method gave excellent results, the various muscles being brought very clearly into view layer by layer. In the early trials it was found that the layers removed were too thick, as shown by the fact that the whole of the fibres on the deep side of some of the slices were running in directions different from those on the surface of the slice. This method has the very real drawback that it does not permit the determination of the course of the motor nerves. The innervation of the muscles, however, can be determined on one side of the head, the muscles having been demonstrated on the other.

Before proceeding to the description of the true facialis muscles, it appears advisable to describe the more superficial panniculus carnosus (Figure 26). This has, in part, been regarded by Huber (1934) as portion of the facialis musculature, and certainly does invade the area of the head usually supplied by the platysma. It lies more superficially than the true facial muscles and, unlike those, is not permeated by the connective tissue; but, like the great majority of muscles throughout the vertebrates, presents clean definite cleavage planes between the contiguous tissues and its surfaces, both superficial and deep. The muscle also differs strikingly from the true facial muscles in that its fasciculi are bound in coarse, readily separable, bundles.

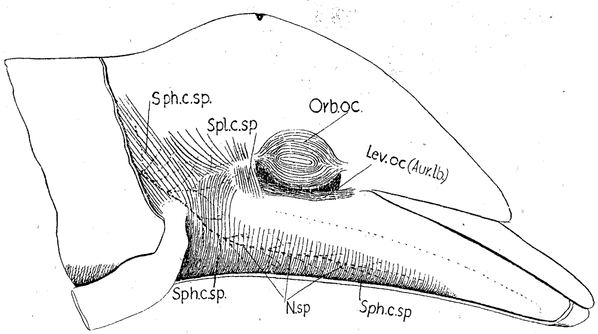


Fig. 26.—The most superficial muscles.

The portion of the panniculus carnosus (50) in which we are interested is that in front of the shoulder girdle. It arises from the superficial fascia a short distance dorsal to the mid-lateral line in uninterrupted continuity with the panniculus of the body generally. There are actually only a few fasciculi having this origin anterior to the shoulder girdle, and these few are continued right round the ventrum to a similar origin on the other side of the body. In front of these, the origin of the dorsal panniculus fasciculi drops to a lower level and the insertion is into the superficial fascia along a line at a slightly lower level than the mid-line of the eye. This small sheet of short fibres extends from the long fibres to the posterior margin of the orbicularis oculi. From the posterior half of the line of insertion of these fasciculi a ventral sheet of fasciculi arises; these are continued round to the other side. In front of these, arising from the same line, there is a small sheet of short fibres which end in the superficial fascia at and a little lower than the level of the ventral margin of the orbicularis oculi. This little sheet of fasciculi lies ventrally to the root of the zygoma.

Immediately below it, and medial to the posterior end of the mandible, the ventral, intermandibular continuation of the panniculus commences. This is a long narrow sheet of fasciculi which arise in the subcutaneous tissues between the jaws along a line which, commencing behind just a short distance within the ventral line of the mandible, gradually approaches the midline to terminate a short distance behind the symphysis menti. The insertion of the fibres is into a similar line on the other side of the intermandibular area.

Explanation of the abbreviations used on Figures 26-29.

Aur.lb., M. auriculo-labialis. Dig.ant. (Csv.lb.), M. digastricus anterior. G.gl., M. genioglossus. G.hy., M. geniohyoideus. H., Humerus. Hy., Hyoid cornu. Hy.gl.l., M. hyoglossus, Hy.gl.m., M. styloglossus. Mx.la., M. maxillo-labialis. My.hy., M. mylohyoideus (Csv.la.). Na.lb., M. nasolabialis. N.sp., A branch of the 4th cervical nerve. N.st.hy., Nerve to the M. sternohyoideus. N.tr., Nerve to the M. trapezius. O.h., M. occipito-humeralis. Orb. oc., M. orbicularis oculi. Orb.oris., M. orbicularis oris. S.-c.m., M. sterno-cleidomastoideus. S.l., Superior laryngeal nerve. Sp., Sensory and motor twigs of cervical nerves. Sph.c.sp., M. sphincter colli spinalis (panniculus). St.th., M. sternothyroideus. Sty.hy., M. stylohyoideus. Sty.hy.p., M. jugulo-hyoideus. Sty.ph., M. stylopharyngeus. Sty.pr., Styloid process. Tr., M. trapezius. V.i.d., Inferior dental nerve. V.my., Mylohyoid branch of the inferior dental nerve. VII.p.a., Preauricular branches of the facial nerve. VII.r.a., Retroauricular branches of the facial nerve.

It is impressed again that all the fibres of the muscle just described are arranged in those coarse, discrete fasciculi which differ so strikingly from the structure of the true facial muscles. This is stressed because it is, in some locations, the only feature on which the identification as panniculus carnosus rests.

Innervation.—The whole of the sheet, with the exception of the short fasciculi behind the eye, is very obviously innervated by one large branch of the fourth cervical nerve. This nerve leaves the anterior trunk of the brachial plexus quite close to the point of emergence of the trunk from the vertebral canal. The nerve becomes superficial below the inferior margin of the sterno-cleido mastoid muscle, but it gives off twigs deep to this muscle and the M. occipito-humeralis, which pass to the portion of the muscle dorsal to the mid-lateral line, and also a branch which passes to the upper ends of those long fibres which arise from the line behind the eye. The main nerve runs right forward on the deep surface of the pars intermandibularis giving off twigs to the muscle all the way along. No nerves were traced to the two short, partly separated, sheets immediately behind the eye (Figure 26).

These two sheets are, of course, right in the position in which reduced remnants of the auricular muscles might be expected, and there is, therefore, a temptation so to identify them. As against this identification the evidence of the similarity of the structure of the sheets and its marked difference from all the facial muscles is so strong as to preclude any other identification than that they are separated portions of the panniculus.

The whole of this sheet of muscle fibres must be regarded as being an anterior extension of the M. constrictor colli spinalis of the Reptilia, and it has been so labelled in the illustration (Figure 26).

In the posthumously published notes already referred to, Huber (1934) identifies the dorsal portion of this constrictor colli spinalis as the sphincter colli primitiva and the ventral portion as the sphincter colli profunda. This was in *Tursiops* and *Monodon*, and the resemblance of the muscles so identified is so close that there can be no doubt that the muscles in all three forms are identical. Huber's identification includes the muscle amongst the superficial facialis muscles; in other words he would regard it as homologous with the dorsal and ventral parts of the constrictor colli facialis of the reptilia, the Cs.2 of our numeration.

Whilst its situation is such as to justify Huber's identification, that evidence appears to be outweighed by the marked dissimilarity of the muscle to the rest of the superficial facialis muscles and by the innervation. One does not overlook the fact that it is quite common to find the posterior portion of the Cs.2 in the Sauria supplied with sensory fibres by the cervical nerves, and the implication that it may be that the innervation of this muscle by the fourth cervical may also be sensory. Admittedly this is a possibility, but the complete continuity of the muscle with the panniculus carnosus above, between and behind the shoulder girdle, together with the similarity of muscular structure, leads to the conclusion that we are in the presence of a peculiar anterior expansion of the spinal muscle.

The M. Orbicularis Oculi (Figures 26, 27).—As is usual in the Theria generally, this muscle extends into the deeper layers of the skin itself and is the most superficially placed of all the facial muscles. Its more centrally placed superficial fibres describe complete ovals around the eyelid; those placed further out diverge as indicated in Figure 26. In deeper layers the fibres again group themselves into two groups—those which complete the oval and those, more peripherally placed, which are inserted into anterior and posterior tendinous intersections which are firmly bound to the temporal bone anteriorly and to the zygoma posteriorly. The posterior superficial fibres which diverge both anteriorly and posteriorly present a peculiarity which appears to be *sui generis*, but it is possible that the most posterior of these are a 'rest' of the attrahens aureum.

The peripheral superficial fibres which run ventrad and rostrad to end in the skin immediately behind the gape, together with a small group of fibres arising in front of the eye (1), constitute a M. naso-labialis (Figure 27).

The M. orbicularis oris (Figure 27) is represented by a small set of fibres immediately in front of the last muscle. These are placed nearly as superficially as the M. orbicularis oculi behind and below the gape, but as they curve forward and dorsally above the angle of the gape they pass more deeply and come to underlie the muscle which is described next.

The M. maxillo-labialis (Figure 27) pars orbitalis arises from the maxilla medial to and in front of the orbit. These fibres pass forward with a ventro-lateral inclination and terminate in the superficial tissues of the cheek above the hinder end of the gape.

The pars profunda of this same muscle takes its origin from the premaxilla some distance further forward and its fibres pass laterally with a caudo-ventral inclination to terminate in the tissues of the lip deep to the pars orbitalis.

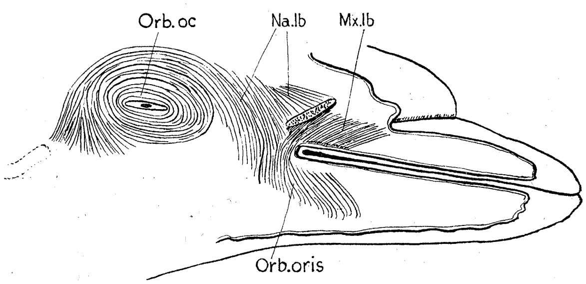


Fig. 27.—The superficial facialis muscles.

An incomplete M. buccinatorius (34) is formed by the anterior portion of the orbicularis oris and this pars profunda of the M. maxillo-labialis, but the two sets of fibres are separated by quite an appreciable distance.

Below the orbicularis oculi there is a muscle whose superficial fibres take their origin from the root of the zygoma, and from there run forward to terminate in the deep tissues of the cheek immediately behind the angle of the gape. These fibres may be regarded as constituting a modified M. auriculo-labialis (Figure 26). The fibres of this muscle, which lie more deeply, curve upward and forward below the orbit to be attached to the antorbital process of the frontal bone. They constitute an auriculo-temporalis and function as a levator bulbi oculi. The deepest of these fibres are parallel with and bound to the splint-like malar bone.

The mass of the 'melon' is largely made up of the two remarkably extensive muscles, one of these functioning to close the blow-hole, the other to open it.

The fibres of the opener of the blow-hole (7) are inextricably embedded in the dense connective tissue of the melon. The extent of the muscle and the direction of its fibres are best demonstrated by the shaving method used upon the other facial muscles; it can, however, be demonstrated by the ordinary dissection method. The muscle takes its origin from the maxilla and premaxilla in front of the blow-hole, and its fibres pass caudad, with increasing inclination dorsad in the more anterior fibres, to terminate in the tough subcutaneous tissues of the front wall of the blow-hole.

The occluder of the blow-hole is in two halves, right and left. Each half arises from the maxilla on either side of, but behind, the blow-hole. The fasciculi pass forward and mediad to be inserted into the side wall and lateral edge of the front wall of the blow-hole. The fasciculi radiate, so that those arising nearest the blow-hole are inserted low down, whilst those furthest away reach the external end of the hole. This is one of the most peculiar muscles I have seen throughout the whole vertebrate series. Its fasciculi are large and are very loosely knit together. Not only is this so, but they are arranged in layers parallel to the direction of their pull. In the result each half of the muscle is built up as a series of sheets of fasciculi which are vertically placed, but with an inclination mediad both from below up and from behind forward.

Previous investigators (Murie, 1874; Huber, 1934) have described this muscle as being composed of different numbers of leaves. I find that in the dolphin the number of component leaves is largely determined by the amount of patience and skill expended on their determination. As many as eighteen have been demonstrated in one half. The peculiar feature is that when the separation has been effected, the plane of separation is absolutely clean, resembling the typical cleavage plane between separate muscles with different origins or insertions but similar directions. Obviously this peculiar 'fasciculation' in sheets permits untrammelled differential pull, ensuring perfect closure of the blow-hole.

Whilst this muscular structure is without exact parallel elsewhere in the vertebrates, it recalls the divisions in some of the more massive quadrato-mandibularis muscles of the Selachii, and it is of interest to note that the division there was necessitated by the difference in the amount of contraction required to bring the jaws together by muscle parts which were inserted along their length.

The Stapedius muscle (21) arises in a fossa in the posterior part of the petrosal bone and passes directly forward to be inserted into the distal end of the small process of the stapes. The facial nerve issues from the facial canal in the fossa in question, and the nerve to the muscle is given off whilst the main nerve is in contact with the muscle.

THE MUSCLES INNERVATED BY THE FIFTH NERVE.

The M. digastricus anterior (Figure 28) arises from the lower edge of rather less than the posterior one-third of the mandible. The posterior fibres run nearly directly caudad and constitute the lateral edge of the muscle. The anterior fibres pass caudad and mediad and constitute the medial border of the muscle. The muscle is a flat, relatively thick sheet of fasciculi and is inserted into the superficial edge of the anterior face of the whole of the length of the hyoid.

The innervation is by a tolerably thick branch of the mylohyoid branch of the inferior dental nerve. This reaches its deep surface and immediately breaks up into three main and these into several smaller twigs before penetrating the muscle.

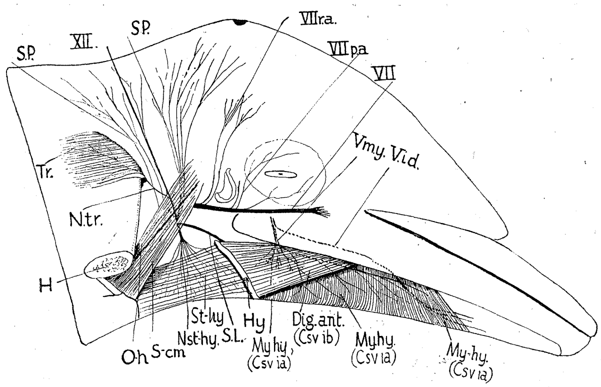


Fig. 28.—The muscles exposed by the removal of those shown in Figures 26 and 27.

The Mylo-hyoid muscle (Figure 28) is very extensive, recalling that of the Ungulata rather than any carnivore. Its fasciculi cross the midline without interruption. Posteriorly the muscle arises from a deeply placed mandibulo-hyoid ligament, which is really the anterior, thickened margin of a fascia which arises from the posterior end of the mandible and passes across, deep to the M. digastricus anterior, between that and the styloid muscles, to be bound to the cranial half of the styloid cartilage and the outer third of the hyoid cornu. Anterior to this ligamentous origin the muscle arises from the inner surface of the mandible some distance dorsal to its inferior edge. This line of origin extends forward to the junction of the anterior and middle thirds of the length of the mandible. Posteriorly the fasciculi have a slight caudal trend, anteriorly they have a fairly sharp inclination forward, and at the extreme anterior end the fibres interlace in the midline.

The muscle is innervated by numerous fine twigs from the long terminal branch of the mylo-hyoid nerve. These reach the muscle on its ventral surface—that is, of course, the superficial surface.

MUSCLES OF MASTICATION.

The Masseter is a relatively small muscle; its fibres arise from the inferior edge and inner surface of the malar process of the squamosal bone. Passing ventrad and rostrad these fibres are inserted directly into the superior margin of the dentary in front of the tip of the low coronoid process.

The Temporal muscle arises from the parietal bone and the superior surface of the squamosal. It supplies the greater part of the posterior wall of the orbit, and its fibres run forward, laterally and ventrally, gathering to a short stout tendon which is inserted into the tip of the coronoid process.

The External Pterygoid arises from the lateral plate of the pterygoid bone and from the ascending lamina of the palatine in front of it. It is inserted into the dentary medially to and in front of the M. massetericus.

The Internal Pterygoid (13) arises from the internal plate of the pterygoid bone and from the fossa between the two plates. It is inserted into the coronoid process just in front of and below the insertion of the M. temporalis.

The Tensor Tympani arises from the processus anterior of the tympanic bone. Its fibres run straight back and converge, to be inserted into the dorsal and medial edge of the anterior surface of the malleus.

The Tensor Veli Palatini (54) arises from the hamular process of the pterygoid bone. Its fibres radiate caudad and laterad into the soft palate and are inserted into the tough tissues thereof.

THE POST-HYOID LONGITUDINAL MUSCLES (Figures 28, 29).

The sterno-hyoideus muscle is an exceedingly massive muscle at its origin from the relatively deep anterior surface of the sternum deep, to the insertion of the sterno-cleidomastoid muscle. As this muscle extends to its insertion, along the whole of the posterior margin of the hyoid, it grows rapidly thinner.

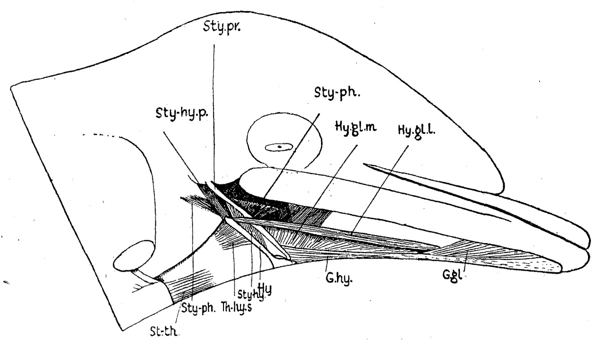


Fig. 29.—The deeper muscles of the pharynx and the tongue.

Innervation: This is from two sources. (1) A remarkably thick branch of the XII nerve breaks up into nine large nerves, all of which enter the muscle and break up into a brush of fine twigs within it. There are, in all, between forty and fifty of these fine nerves. (2) A fairly thick branch from the cervical plexus also terminates in this muscle, splitting into five branches after it enters the muscle.

This exceedingly lavish supply of nerves is apparently quite unique amongst the vertebrates; no other muscle even approaches this rich supply. The most careful dissection failed to discover any one of these many nerves emerging from the muscle again.

The Thyro-hyoid muscle is entirely covered ventrally by the M. sterno-hyoideus. The origin of the muscle is from the ventrum of the thyroid cartilage close to its lateral edge and not far posterior to the hyoid. The fasciculi run nearly straight forward, diverging slightly, so that the muscle is slightly broader at its insertion into the lateral half of the hyoid cornu than it is at its origin.

Innervation: This is by a twig from the division of the XII, which innervates the M. sterno-hyoideus.

The Sterno-thyroid muscle arises from the anterior face of the sternum deep to the M. sterno-hyoideus. Its fibres run straight forward to be inserted into the posterior edge of the thyroid cartilage on either side of the midline.

Innervation: by the same nerve as the last muscle.

THE PREHYOID LONGITUDINAL MUSCLES AND THE INTRINSIC MUSCLES OF THE TONGUE (Figure 29).

The Genio-hyoid muscle is divided into right and left halves anteriorly, but in the posterior half of their length the two halves are completely blended in the midline. The origin of the muscle is from the body of the hyoid and the medial end of the styloid process, and the insertion is by a fascial ribbon into the symphysis menti and into the inferior edge of both rami for a short distance behind the symphysis.

Innervation: This is by the anterior division of XII.

The Hyo-glossus is a long narrow muscle which arises from the extreme lateral end of the hyoid cornu and runs forward along the greater length of the ventro-lateral margin of the tongue and is inserted, deep to the posterior margin of the genio-glossus muscle, into the tissues of the ventrum of the tongue.

Innervation: Anterior division of XII.

The Genio-glossus muscle arises from the ventral edge of the rami of the jaws anteriorly and passes caudo-medially to be inserted into the tissues of the ventrum of the tongue deep to the fascial band of the M. genio-hyoideus.

Innervation: Anterior division of XII.

The Stylo-glossus is a relatively extensive muscle. It arises from the medial third of the length of the styloid process, in front of the hyoid. The most lateral fasciculi take an almost transverse direction around the base of the tongue, the most medial a nearly longitudinal. The intermediate fasciculi take up the intermediate directions. The insertion is into the dense tissues of the side and ventrum of the tongue.

Innervation: Anterior division of XII.

The Stylo-hyoideus muscle arises from the middle third of the length of the styloid process and is inserted into the greater part of the length of the hyoid cornu. The direction of the fasciculi is almost directly mediad.

Innervation: By a fine twig of the facial nerve.

The Jugulo-hyoideus muscle (47). That which has been thus identified is a comparatively small, nearly cylindrical muscle which arises from the basioccipital bone immediately to the medial side of the periotic and medial to and just behind the attachment of the styloid process to the periotic. The insertion is into the lateral tip of the hyoid cornu.

Innervation: Glosso-pharyngeal.

The Stylo-pharyngeus and the Superior Constrictor muscles of the Pharynx are both probably represented by a triangular sheet of fasciculi which arise from the base of the skull medially to the periotic and converge to be inserted into the fascial structures which bind the styloid process and the hyoid to one another and to the larynx. This insertion is deep to the Mm. stylo-hyoideus and jugulo-hyoideus.

Innervation: Glosso-pharyngeal.

THE 'ACCESSORY' MUSCLES (Figure 28).

The Mm. trapezius and Sterno-cleidomastoideus have been regarded as muscles properly innervated by the nervus accessorius. Their innervation has been made the subject of a series of studies by Howell and his colleagues. With Straus (1936, p. 398), he states that the accessory field of musculature is always present in mammals, "except in Cetacea there uniformly is a M. trapezius . . . a part representing a sterno-cleidomastoid always is present, even in Cetacea".

In the Dolpin there is apparently a normal sterno-cleidomastoid and two muscles representing the trapezius.

The M. Sterno-cleidomastoideus.—The origin of this muscle has been transferred from the petrosal to the exoccipital immediately medial to and behind it. It is a stout, flat muscle whose direction is caudad, mediad and ventrad from its origin to its insertion, without any division, into the anterior edge of the sternum and the clavicle close thereto.

The M. Occipito-humeralis probably represents that portion of the M. trapezius which arises from the occipital bone and from the neck. This also is a flat muscle. It arises from the exoccipital bone immediately above the line of origin of the last muscle, so that it overlaps the greater part of it at and close to their origins. The insertion is into a tubercle on the anterior surface of the humerus just distal to the head of that bone.

The rest of the M. trapezius is probably represented by a thin sheet of muscle fasciculi which arise from the lateral spine of the axis vertebra and from the fascial sheath of the lateral trunk muscles. These fasciculi run backwards horizontally and are inserted into the fascial sheath of the scapulo-humeral muscles. It may be remarked that there is no spine on the dorsal surface of the scapula of *Delphinus*, and this, probably, accounts for the insertion into the fascia.

Innervation: The sterno-cleidomastoid and the occipito-humeralis muscles are innervated by a branch of the vago-accessorius trunk which is given off just outside the cranial foramen. Doubtless this is composed largely, if not entirely, of fibres from the nervus accessorius.

The little trapezius muscle, however, appears to be innervated only by cervical nerve fibres. The nerve to the muscle is given off from the first trunk of the brachial plexus, but beyond the junction of the commissure from the cervical plexus, so that it cannot be determined by dissection whether the muscle is innervated by cervical or brachial plexus fibres.

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