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By

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THE SKULL OF THE FOETAL NARWHAL, *MONODON MONOCEROS* L.

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(*Communicated by F. J. Cole, F.R.S.—Received* 12 *December* 1949)

CONTENTS

Understanding of the evolution of the mammalian orders and families, and of the relationships between members of an order, is often illuminated by a study of the development of the skull in the foetus. This account is the first description of the foetal narwhal. The material is extremely rare and the author is indebted to Professor L. R. Wager for the collection of the specimens when he was in Greenland as a member of the Courtauld Expedition in 1935–6. The chondrocranium and osteocranium of two early narwhal foetuses were investigated by dissection and by the preparation of models constructed from transverse sections of the head.

The narwhal is a highly specialized Cetacean. In the adult it differs from all other mammals in the complete absence of hairs, and from other Odontoceti in that instead of numerous similar teeth on both jaws, it has one very long straight tusk in the upper jaw in the male, and a pair of short tusks or none in the female, neither sex having teeth in the lower jaw. Sections of the younger foetus, however, exhibit hairs on each side of the mandible, indicating that the narwhal is a typical mammal in this respect. Continuous dental laminae in upper and lower jaws, with papillae for six pairs of teeth in the maxillae, and for two pairs in the mandibles, show that the specialized dentition of the adult is a modification of the more generalized foetal dentition.

The study leads to the conclusion that the narwhal is more closely related to the Delphinidae than to the Phocaenidae, and that it approaches the Delphinidae through *Globiocephala*.

INTRODUCTION

The material used for the present study consisted of two foetal narwhals, brought from Greenland by Professor L. R. Wager, who was the leader of the Courtauld Expedition to Kangerdlugssuak Fjord from 1935 to 1936. Knowing that I was interested in the foetal stages of rare mammals, Professor Wager undertook, before sailing, to look out for these specimens and bring back any he thought suitable for investigation. He was able to collect three seal and three narwhal foetuses. The Eskimo are accustomed to remove foetuses from female narwhals and take them home to their children, who wrap them up and carry them in their arms as dolls.

The narwhals were obtained just inside the mouth of the main fjord. The animals are of vital importance to the Eskimo, since the ivory of the tusk is an essential part of the harpoon, oil is extracted from the blubber for fuel, and the flesh is used for food for men and dogs. Wager writes; 'It is no easy matter to hunt successfully a large narwhal weighing about a ton, and two or three men have to collaborate. Towards the end of the second summer they had so much meat that they hunted only the male narwhal, and having killed it, took only the ivory tusk....In a year they killed 410 seals, 28 bears and 40 narwhals.'

No special method of preservation was employed; the foetuses were immersed in alcohol, the intense cold retarding putrefaction and giving excellent fixation of the tissues.

The data concerning the three specimens, henceforward called A, B and C, are as follows:

A. Mother shot at base, 29 May 1936. Female foetus 137 mm. long, 30 mm. broad at the widest part of the abdomen, 32 mm. high. Well preserved, but the colourless skin was torn in places. This specimen was sectioned and the skull was modelled.

B. Mother caught by Eskimos at Kangerdlugssuak, 28 June 1936. She had a young narwhal about 120 cm. long with her, but this was not caught. The uterus of the mother contained a foetus 150 mm. long, 24 mm. broad, 40 mm. high, and the specimen on arrival was much distorted by compression. The head of this specimen, which was also a female, was dissected.

C. Mother shot at base, 28 July 1936. Male foetus 280 mm. long, 60 mm. broad, 70 mm. high. This specimen has not yet been investigated, as it was considered too old for the present study.

HISTORICAL

Foetal narwhal material is very rare, and little has been written upon the few specimens known. The range of the species is very limited, few animals reaching farther south than 65° N latitude. The males are hunted for their ivory as well as for their flesh and blubber, but the female with its small and usually concealed tusk is of little value, and the Eskimo hunters leave it alone, unless they are short of meat. Narwhal tusks have been known since the twelfth century.

The first record of a narwhal foetus was made by Frederic Ruysch, the founder of a famous anatomical museum in Amsterdam. In his *Thesaurus Anatomicus* (1714) he figured a foetal narwhal suspended in a bottle. It had hairs on the top of its head, nostrils and large round eyes! The umbilical cord was present.

About 1736 Anderson saw a narwhal taken in the Elbe at Hamburg. He described it as a female, with two tusks, 7 ft. 5 in. and 7 ft. long, and it contained a foetus, about which, however, he gave no details.

A century later Rapp (1837) referred to the teeth of a foetal narwhal, noting the two pairs of teeth in the upper jaw.

Sir William Turner wrote several papers on narwhals, describing in 1872 a male foetus of 181 mm. length, with two pairs of teeth in the upper jaw, and in 1878 another foetus 1625 mm. long, the teeth being again described. Between these two dates Gervais (1873) gave an account of a foetus 1150 mm. long and of its teeth. It was almost at term, the only reference to age in any of the above foetuses, though according to Turner's measurements it was 500 mm. too short for a full-term foetus. However, since the duration of the gestation period is unknown, it is not possible to estimate the age of foetuses by Mackintosh & Wheeler's graphical method (1929). In 1879 Wilson described the retia mirabilia of the narwhal from a partly decomposed specimen 1606 mm. in length.

Fraser (1938), in his paper on the vestigial teeth of the narwhal, examined a male foetus 520 mm. in length, and found two pairs of symmetrical teeth in the upper jaw, the first or tusk-forming pair being longer and better developed than the second pair. Neither showed signs of spiral structure. Comparison with an older foetus 1588 mm. long, and with post-natal stages, indicated that asymmetry in size and length occurred later in both sexes in the tusk-forming pair, but not usually in the second or vestigial pair, which abort from the posterior end of the alveolus, leaving a shallow depression in the maxilla. The vestigial tooth may fall out on one side or the other, but the left is not affected, as far as Fraser could determine, by the great development of the tusk on that side.

The American Museum of Natural History possesses two narwhal foetuses, one a full-term foetus, from which the skeleton has been prepared, measuring 1500 mm. in length. The second, said to be between 3 and 4 months old, was embalmed and is 225 mm. long.

Finally, Huber (1934) made a partial dissection of the head of a full-term narwhal foetus, working chiefly on the superficial muscles and the blow-hole mechanism.

Thus the knowledge derived from these twelve foetuses amounts to little more than an account of the teeth and of the blow-hole mechanism.

METHODS

Foetus A, the better preserved and smaller specimen, was sectioned. The head, measuring 32 mm. in length, was cut off, decalcified, embedded in celloidin, and sectioned at 40μ by Dr Keith Richardson, of University College, London. The sections were then stained as follows:

Ehrlich's acid haematoxylin, 2 % in distilled water, for 12 hr. Rinsed in distilled water, differentiated in weak acid alcohol, blued in tap water, rinsed again in distilled water.

Counterstained in orange G erythrosin* for 30 min.

Dehydrated in 30, 50, 90 % alcohol, and transferred to a mixture of absolute alcohol 3 parts, chloroform 1 part.

Cleared in the following mixture, made up to soften, but not to dissolve, the celloidin:

creosote	40 ml.
bergamot oil	30 ml.
xylene	20 ml.
origanum oil	10 ml.

Each section was coaxed on to the surface of a slide, drained of oil, rinsed quickly in xylene from a drop bottle, and mounted in Canada balsam under a weighted cover-slip.

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* Tischutkin's formula: orange G, 4% aq., 10 ml.; erythrosin 10% aq., 2 ml.

I am grateful to Dr Richardson for cutting the sections and for suggesting the method of staining, which proved successful.

The skeletal parts of the head were drawn under the Edinger projection apparatus, using a Zeiss planar lens, giving a magnification of 12·5. Beeswax plates 1 mm. thick were employed for the models. Separate models of the chondrocranium and combined chondrocranium and osteocranium were made, also an enlarged model, magnified twenty-five times, of the membranous labyrinth and auditory ossicles.

Foetus B was dissected. The head was distorted by pressure and parts of the body had been damaged, but it was possible to make a fair dissection of the skull.

FOETUS A

The eye is closed. The single blow-hole is almost transversely placed on the anterior aspect of the head, so that it is directed straight forwards. The mouth is ventral and not quite terminal. The flippers are sufficiently transparent to show the fingers through the skin. The posterior apertures are sunk in a median elongated depression and consist of an anterior swollen vulva and immediately posterior to it the anus. On either side of the outer wall of the vulvar area is a mammary slit. Thus the female external genitalia are well developed.

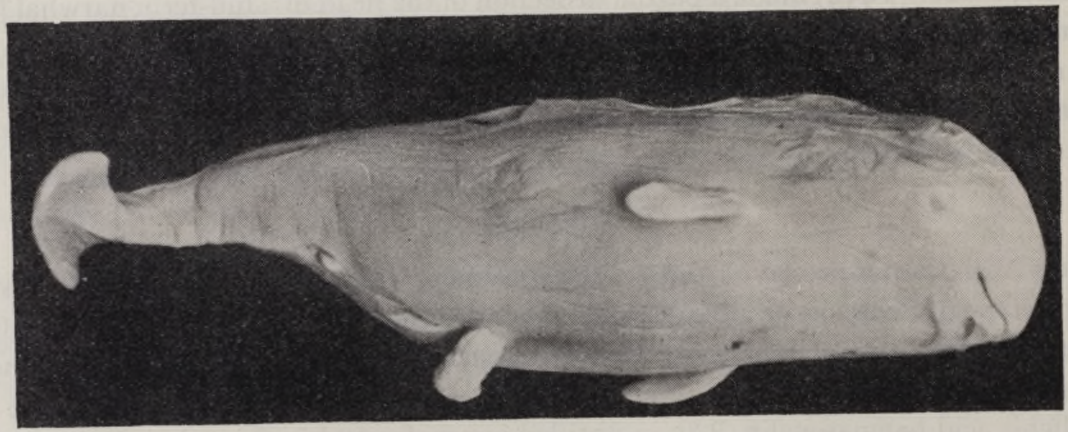

FIGURE 1. Foetus A in right ventro-lateral view. Note the severed umbilical cord, posterior to which are the vulva and the anus. The skin is torn in places. (Magn. × 1).

The tail has the horizontal fluke formed, but there is only a trace of division into two halves. The vertebral portion is laterally compressed with a mesial skin fold on dorsal and ventral sides. Ventrally this skin fold extends forwards almost to the anus, dorsally it fades out just over half-way up the back, its total length being 71 mm. There is no dorsal fin.

The age of the foetus is unknown. According to Turner (1878) a full-term specimen would be about twelve times the length of this foetus. This is the youngest foetus recorded.

Skull model

Although this was the youngest specimen, calcification was well advanced and the general characters of the genus were developed. The basi-cranial axis is almost flat, the basi-facial axis sloping upwards to the nasals and making an angle of about 135° with the former.

Owing to the high position of the external nares the basi-facial line is thus raised above the basi-cranial axis instead of being below it as in most other mammals. The upper jaw, however, is dropped, and whereas the brain case curves upwards anteriorly, the palate curves downwards. The anterior part of the nasal tube is thus almost vertical, and the nasal septum long and upright. The occipital plane makes an angle of 70° with the basis cranii. The roof of the skull is smoothly rounded, with a large anterior fontanelle, and there are lateral vacuities where ossification is imperfect.

Chondrocranium (figures 2, 3 and 4)

The basis cranii (*p.*) is thick and solid, and is flanked by two large occipital condyles (*oc.*), which, although more ventrally placed than in most mammals, do not quite meet. The pars lateralis (*pl.*) of the occipital cartilage meets its fellow to form a tectum posterius (*tp*) over the foramen magnum, though the paired supraoccipital portions of the arch are discernible. A small fenestra is present anterior to the fusion. There is an extensive ossification of the supraoccipital cartilages, forming a median supraoccipital bone (*sob*), with paired posterior prolongations on either side of the fenestra. In section the bone is wedged into the cartilage and appears capstan-shaped. The paracondylar process (*pcp*) is large and inflated; it exhibits an ossification centre (exoccipital) which is broadened out on the outer face of the skull, but is of small size intracranially. The styloid process of the hyoid apparatus is attached to the paracondylar process. In a recess postero-ventral to the intracranial ossification lies the hypoglossal foramen (*hf*), single on each side as in *Phocaena*. The large jugular foramen (*fj*) is the jagged gap between the auditory capsule and the occipital

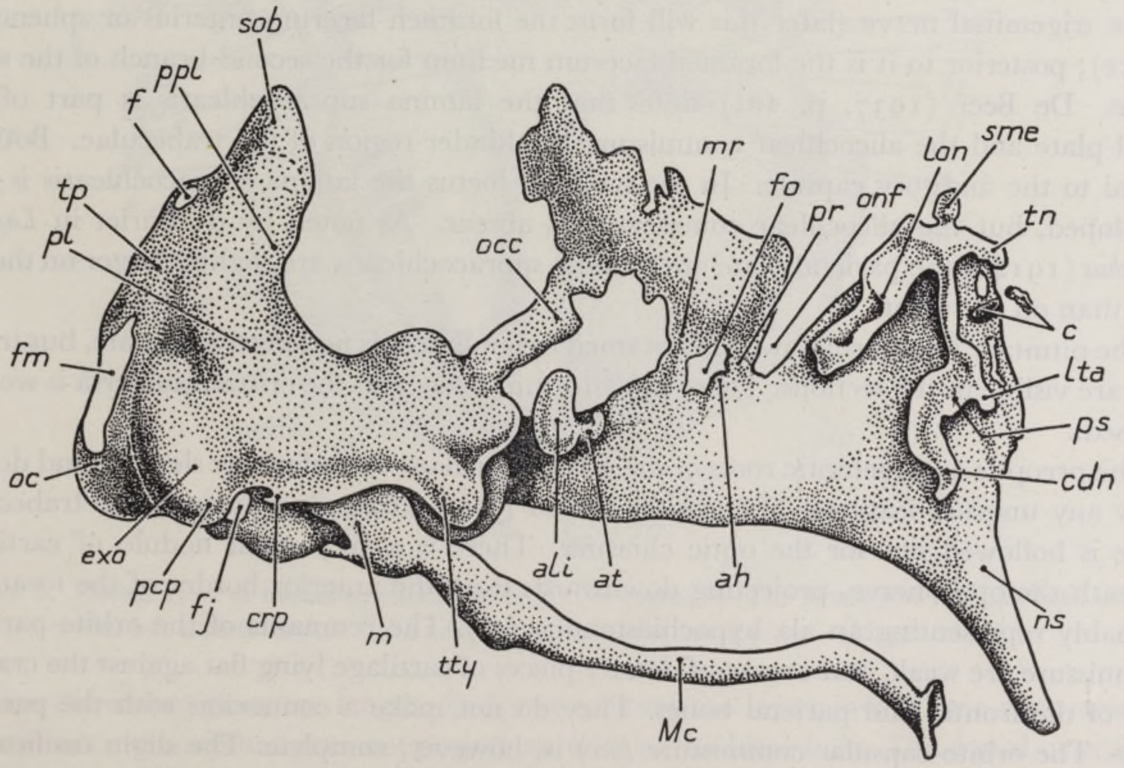

FIGURE 2. Right lateral view of wax plate reconstruction of the chondrocranium of foetus A. (Magn. × 4·5.)

cartilage. The parietal plates are joined to the auditory capsules by the prefacial and postfacial (parieto-capsular) commissures, and there is a vestige on the left side of an orbito-parietal commissure (*copv*). The wall of the skull laterally is substantial, and the tegmen tympani reinforces the prefacial attachment by forming a lateral prefacial commissure. The orbital cartilages are linked with the auditory capsules by orbito-capsular commissures (*occ*). The basal plate narrows between the auditory capsules and is strongly ossified ventrally as the basi-occipital bone (*bo*). This bone is, as it were, wrapped round the cartilage, so that it appears laterally in cranial view, while its posterior portion sends out a pair of bony extensions which partly overlap the auditory capsule on its ventral face. The notochord is intrabasal, but takes a sinuous course through the cartilage. Each basicochlear fissure (*bcf*) is well defined; in its middle part the sides are parallel, but it broadens posteriorly, where the basi-occipital ossification shows on the brain-case floor, forming an ovate hole, lateral to which lies the basivestibular commissure (*bvc*).

The lamina supracochlearis (*lsu*), or dorso-lateral projection of the basal plate, is short, and extends like a shelf over the anterior portion of the auditory capsule, but without attachment to it, the capsule being sunk below it. There is thus no alicochlear commissure, and the lamina supracochlearis merely links the trabecular and parachordal portions of the chondrocranium. The processus alaris (*pal*) has united with the ala temporalis (*at*) to form a club-shaped structure, ossified at its free end as the alisphenoid bone (*ali*). The ala temporalis is imperforate, and there is therefore no alisphenoid canal for the orbital artery. The alisphenoid is a cartilage bone and there is no trace of membrane bone in this region. The root of the processus alaris is pierced by the carotid foramen (*fc*), which is well within the basal plate. Anterior to the processus alaris is the large gap transmitting the first branch of the trigeminal nerve (later this will form the foramen lacerum anterius or sphenoidal fissure); posterior to it is the foramen lacerum medium for the second branch of the same nerve. De Beer (1937, p. 401) states that the lamina supracochlearis is part of the basal plate and the alicochlear commissure the hinder region of the trabeculae. Both lie dorsal to the auditory capsule. In the narwhal foetus the lamina supracochlearis is well developed, but the alicochlear commissure is absent. As noted by de Burlet in *Lagenorhynchus* (1914*b*) the parietal plate and lamina supracochlearis are slightly larger on the left side than on the right.

The pituitary fossa is shallow. The foramen hypophyseos is no longer perforate, but traces of it are visible in the sections. There is no dorsum sellae and the crista transversa is weakly defined.

The preoptic and metoptic roots of the orbital cartilage are relatively slender, and do not show any unusual features. The optic foramen (*fo*) is large, and mesially the trabecular plate is hollowed out for the optic chiasma. There is a very small nodule of cartilage beneath the optic nerve, projecting downwards from the anterior border of the foramen, probably representing an ala hypochiasmatica (*ah*). The remnants of the orbito-parietal commissure are weak, and consist of slender pieces of cartilage lying flat against the cranial face of the frontal and parietal bones. They do not make a connexion with the parietal plate. The orbito-capsular commissure (*occ*) is, however, complete. The slight ossification on the edge of the optic foramen postero-mesially is the anlage of the orbitosphenoid bone (*ors*).

The orbito-nasal fissure (*onf*) is large and ovate, but there is no sphenethmoid commissure.

The most remarkable portion of the chondrocranium is the nasal region, which is compressed laterally and truncated anteriorly, giving the skull a flat, depressed front, partly concealed in the flesh by a cushion of connective tissue, loaded with fat, which rounds it off. Its support is the massive cartilage of the septum nasi (*ns*) approximately triangular in shape, with its long axis almost vertical, but sloping slightly forwards at its ventral end. The height is twice the antero-posterior length, and it overhangs the lower jaw. There is no cranial rostrum since the septum does not project anterior to the blow-hole. The dorsal or cranial end of the septum is narrow; the foramen olfactorium advehens (*fol*) forming a longitudinal slit on each side of it. (There are no olfactory lobes in the brain, or olfactory nerves, and

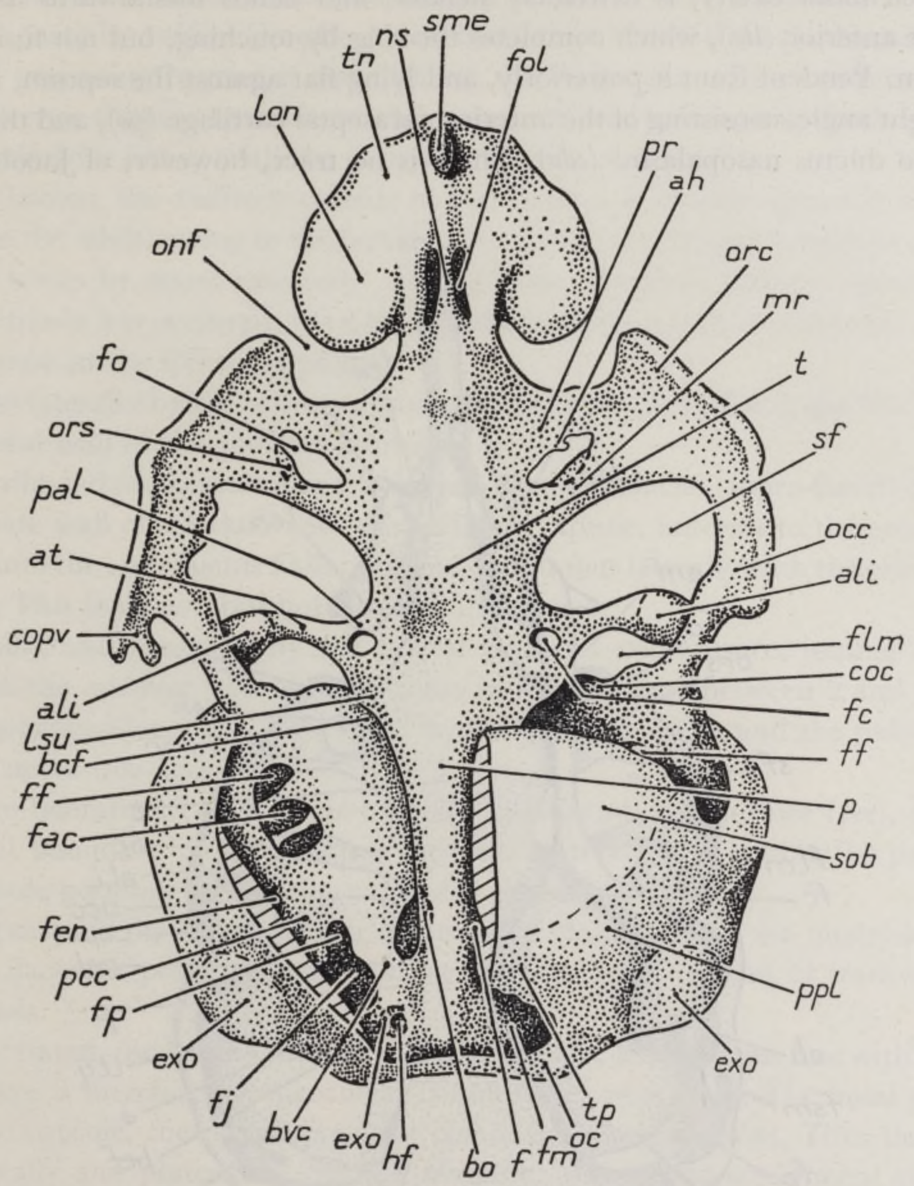

FIGURE 3. Dorsal view of model of chondrocranium of foetus A. The *tectum posterius* has been cut on the left side to expose the auditory capsule and basal plate. (Magn. × 4·5.)

a cribriform plate is absent). The lamina orbito-nasalis (*lon*) lies parallel with the septum nasi, and has the form of a flat plate projecting laterally, and turned ventralwards and mesialwards on its edge as a vestigial lamina transversalis posterior, which does not, however, reach the septum nasi. The latter and the pair of orbito-nasal cartilages unite anteriorly and rise up in a crest surmounted by a median spina mesethmoidalis (*sme*). The tectum nasi (*tn*) forms a shallow roof over the nasal cavities, directing the blow-hole forwards and slightly upwards. No epiphanial foramen is present. The paries nasi (*pns*), figure 8, flanking each nasal cavity, is extremely slender, and bends mesialwards as the lamina transversalis anterior (*lta*), which completes the ring by touching, but not fusing with, the nasal septum. Pendent from it posteriorly, and lying flat against the septum, is a cartilage bent at a right angle, consisting of the anterior paraseptal cartilage (*ps*), and the remnant of the cartilago ductus nasopalatini (*cdn*). There is no trace, however, of Jacobson's organ.

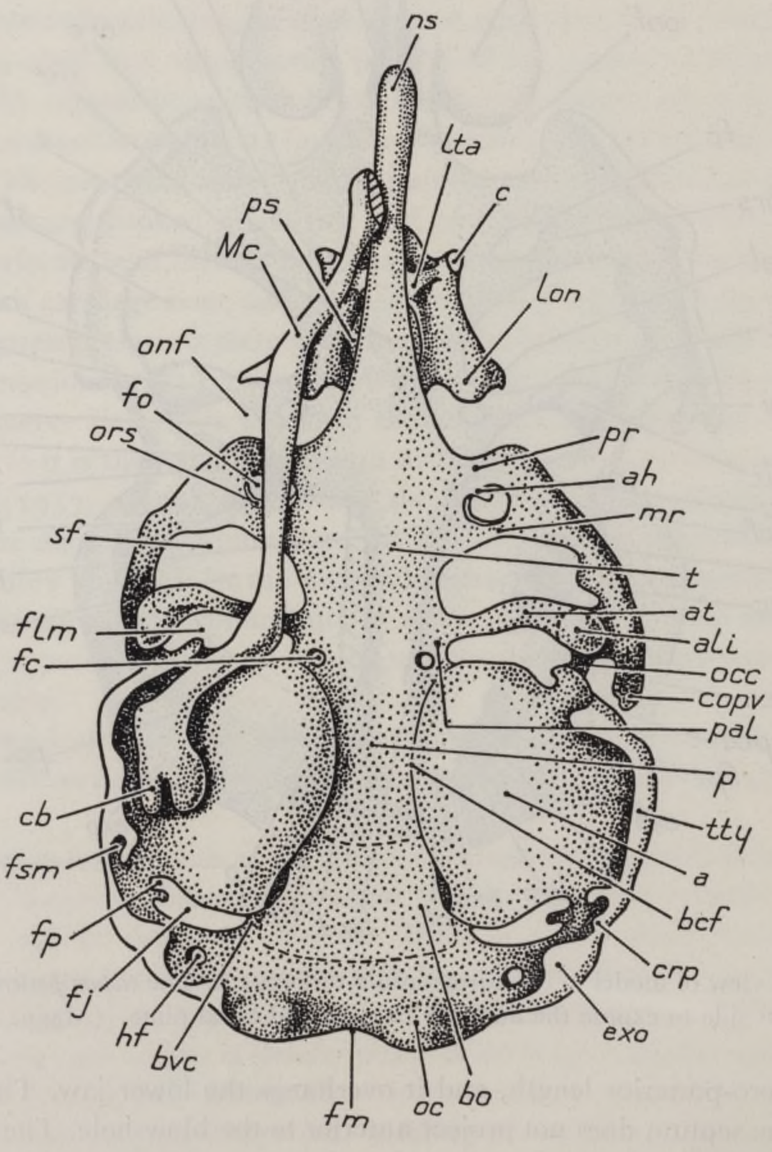

FIGURE 4. Ventral view of model of chondrocranium of foetus A. Meckel's cartilage has been removed on the left side of the specimen. (Magn. ×4·5.)

The nasal tube has thus no postero-ventral skeletal boundary, and posterior paraseptal cartilages are absent. Two isolated nodules of cartilage—*paranasals* (*c*)—are present on the side of each nasal tube, projecting forwards from the paries nasi. There are lateral ingrowths in the mucous lining of the nasal tubes, representing the maxillo-turbinal folds, but these contain no cartilaginous supports.

Meckel's cartilages (*Mc*) are slender twisted rods. Each lies along the mesial face of the dentary bone, the ventro-lateral border of which is cup-shaped to receive it. The anterior portion is curved downwards where the dentary narrows. Here it is enclosed by the bone and becomes partially ossified (?medio-Meckelian), then breaks through the anterior end of the dentary, projecting beyond it and forming the major part of the symphysis. The two cartilages diverge slightly anterior to the symphysis, and each ends freely. Posteriorly Meckel's cartilage is linked with the auditory region (see below).

As is well known, the auditory capsule in the Cetacea is readily separable from the rest of the skull in the adult, owing to the fact that the fused petrosal and tympanic are attached to the other bones by membrane only. In the foetus, however, before ossification in any part of the capsule has occurred, the cartilaginous capsule is linked with other parts of the chondrocranium at the following points:

(1) Antero-laterally by the orbito-capsular commissure (*occ*) joining the orbital cartilage with the lateral wall of the auditory capsule.

(2) Laterally and on the dorsal or cranial side by the prefacial (supra-facial) commissure, linking the side wall of the skull with the auditory capsule, anterior to the entrance of the facial nerve into the aqueductus Falloppii, and continuous laterally with the orbito-capsular commissure. This is shown, but not lettered, in figure 3.

(3) Laterally and ventrally by the lateral prefacial commissure, joining the tegmen tympani with the auditory capsule, the cavity in the cartilage between 2 and 3 known as the cavum supracochleare being occupied by the facial ganglion and the palatine branch of the facial nerve (see figure 4).

(4) Postero-laterally by the parieto-capsular (postfacial) commissure (*pcc*), forming the antero-lateral boundary of the foramen lacerum posterius, and joining the parietal plate and the capsule posterior to the internal auditory meatus.

(5) Posteriorly by the basivestibular commissure (*bvc*), forming the mesial boundary of the foramen lacerum posterius, and running longitudinally instead of transversely as in most mammals.

As already stated, the lamina supracochlearis overlaps, but does not fuse with the capsule wall, and there is therefore no alicochlear commissure, *sensu stricto*. The basal plate is also free from the capsule, the mesial prefacial commissure being absent. Thus the capsule is moored laterally and posteriorly, but not mesially, and has no attachment either to the trabecular plate (alicochlear commissure), or to the basal plate (mesial prefacial commissure).

The second peculiarity of the auditory capsule is its orientation. It has swung round to a more transverse position in the Cetacea, so that the cochlear sac is antero-ventral and has sunk to a position slightly ventral to the basal plate, being partly covered by the projecting edge of the latter (lamina supra-cochlearis), while the canalicular portion is elevated to a postero-dorsal position lateral to the cochlear part.

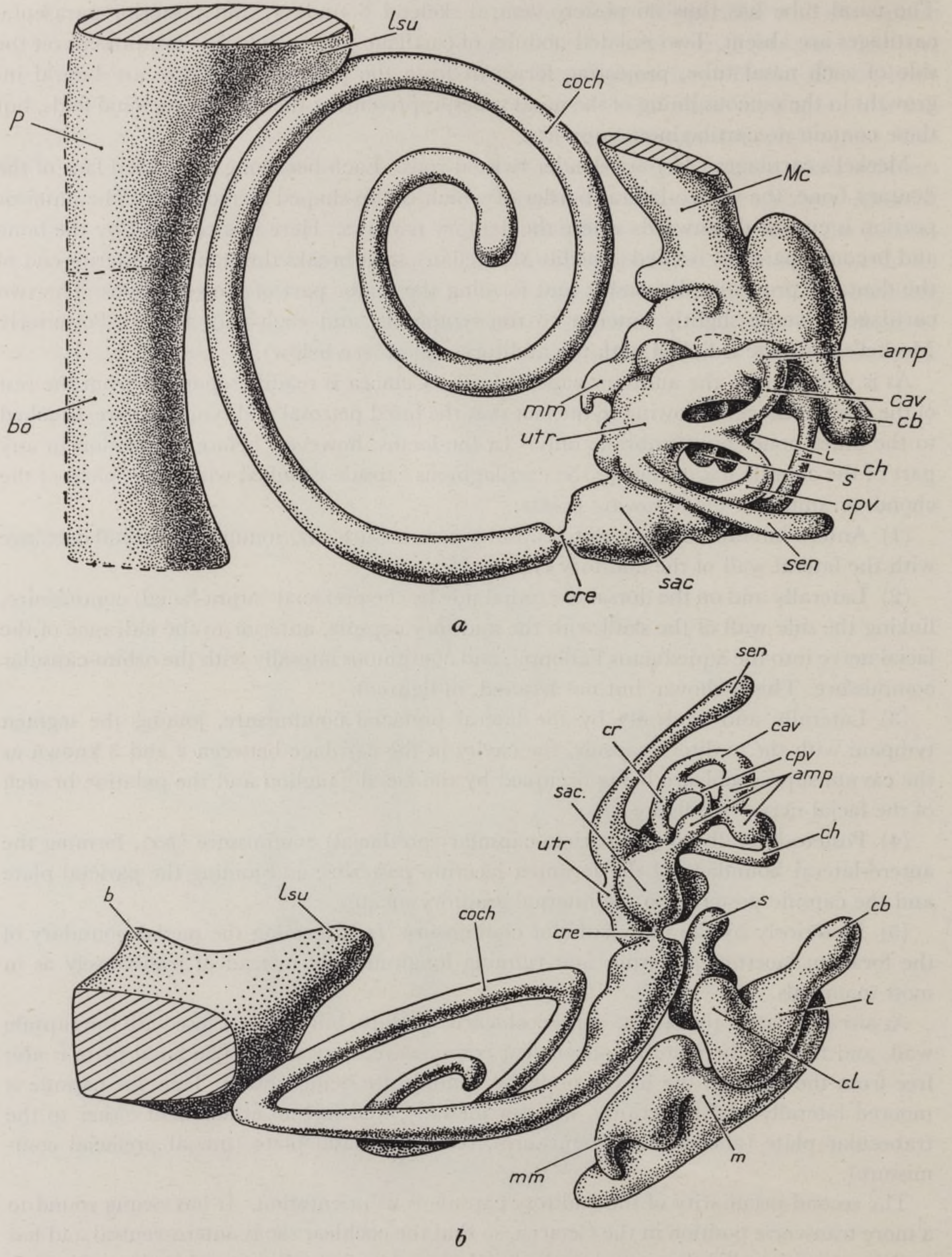

FIGURE 5. Two views of wax plate reconstructions of the membranous labyrinth and auditory ossicles of foetus A. (Magn. × 16.) *a*, Dorsal view to show the relative size of the canalicular and cochlear portions of the labyrinth. *b*, Posterior view to show the ossicles. A portion of the basal plate has also been modelled to illustrate the sunken position of the auditory capsule and its contents.

The foramen acusticum internum (internal auditory meatus) (*fac*) is a large irregular aperture situated between the cochlear and canalicular portions; it transmits the eighth nerve to the labyrinth, and is subdivided by a bar separating the cochlear and vestibular branches of the nerve. The foramen for the facial nerve (aqueductus Falloppii) (*ff*) is anterior to the foramen acusticum internum and is separated from it by cartilage. The foramen perilymphaticum (*fp*) lies on the anterior wall of the foramen lacerum posterius, (jugular foramen) appearing to be excavated from the latter. The small foramen endolymphaticum (*fen*) is antero-lateral to it.

The tegmen tympani (*tty*) is well developed at this stage, and extends downwards from the parietal plate, forming, as has been noted, the lateral prefacial commissure with the auditory capsule. Its free posteroventral portion curves round the exit of the facial nerve, then runs back as a short projecting shelf towards the attachment of the styloid process of the hyoid. This projection is the crista parotica (*crp*).

Auditory ossicles (figure 5)

These are at present pure cartilage. Meckel's cartilage ascends towards the auditory region and through the connexion between its posterior portion (the malleus (*m*)) and the incus (*i*), makes contact with the skull, but there is no condyle as yet on the dentary bone. Meckel's cartilage broadens posteriorly to form the globular head of the malleus for the socket on the body of the incus. There is little evidence as yet of a saddle-shaped articulation, though the cup-shaped socket on the incus is sinuous. At its posterior extremity there is continuity for a short distance with the incus, a condition that occurs in the early stages of development in other mammals. Antero-dorsally a short processus brevis (lateral process) is forming, but there is no narrowing in the future neck region towards the formation of a processus gracilis. The postero-ventral part bends sharply to form the arcuate manubrium (*mm*), which, even in the foetus, touches the small obliquely placed tympanic membrane by its tip.

The incus is a sturdy cartilage, with an anterior hollowed surface for articulation and partial fusion with the malleus. Its dorsal arm (crus breve) (*cb*) ascends dorso-laterally to fit into a depression, the fossa incudis, under the overhanging tegmen tympani of the skull, but there is no fusion of the cartilages. The crus longum (*cl*) passes backwards and mesialwards towards the head of the stapes and there is here a nodule of cartilage that may represent an os orbiculare (processus lenticulare), though it appears to belong to the stapes rather than to the incus, and is partly continuous with the former.

The stapes (*s*) is short and broad. Its base fits neatly into the fenestra ovalis (vestibuli). Externally it looks solid, but in the sections it exhibits a small hole between the crura, not traversed, however, even in the foetus, by a stapedial artery.

Rotation of the auditory capsule has brought the fenestra ovalis to a ventral position.

The membrane bone representing the pre-articular (goniale of Gaupp) is described on p. 17.

Cartilage bones represented at this stage are the supra-occipital, ex-occipitals, alisphenoids, orbitosphenoids and basi-occipital. The presphenoid and basisphenoid regions are not yet ossified.

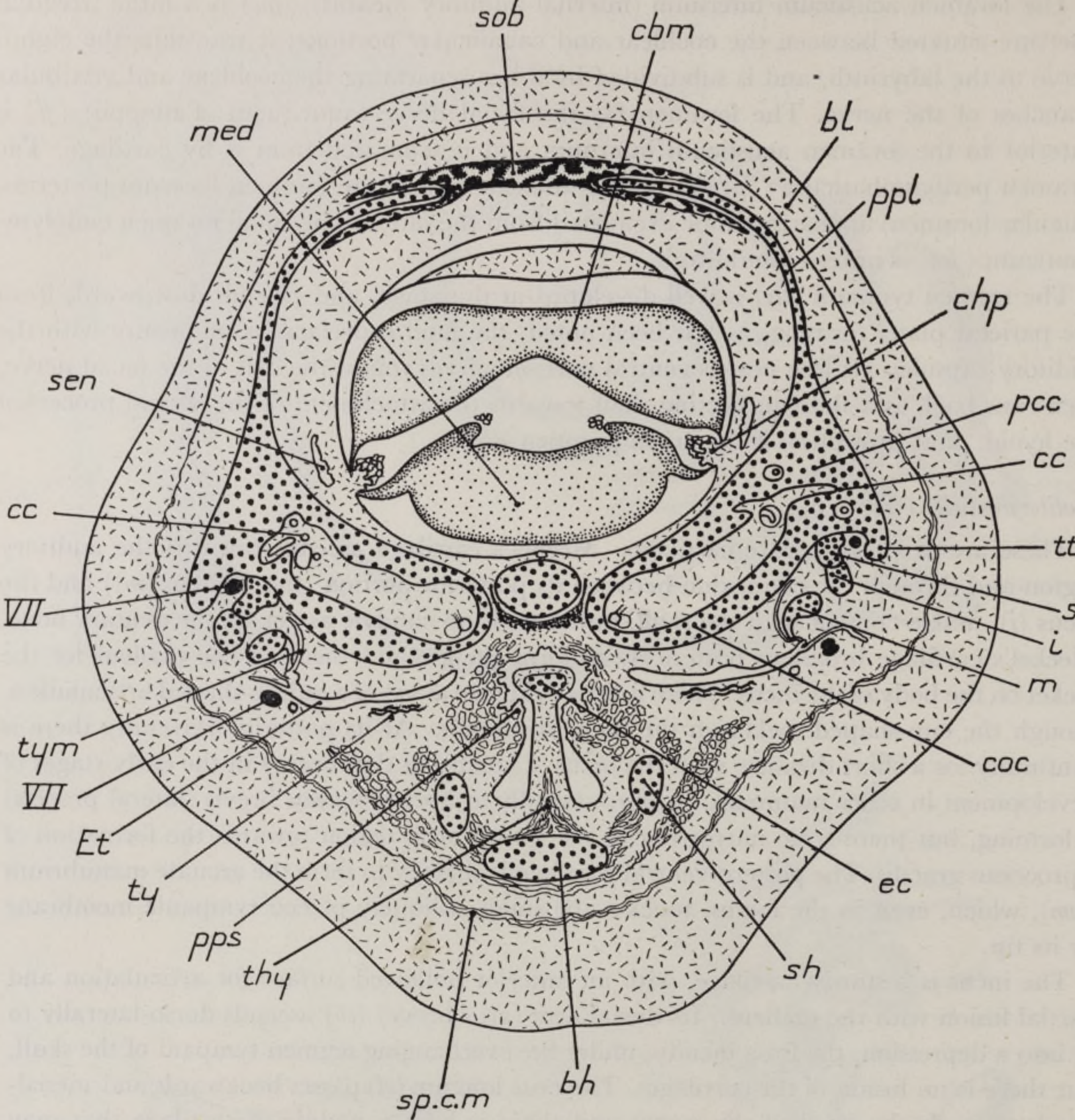

FIGURE 6. Foetus A. Section 550, through the canalicular and cochlear portions of the auditory capsule, the ear ossicles and the intra-narial epiglottis. Cartilage dotted, bone black dendritic, nerve solid black, muscle faintly lined, connective tissue and blubber with short, straight lines. (Magn. × 5·4.)

Membranous labyrinth (figure 5)

An enlarged model, magnified 25 times, was made of the membranous labyrinth and auditory cartilages of the right side. The labyrinth resembles that figured by Honigmann (1917) in *Megaptera*. The cochlea (*coch*) is very large, being twice the width and three times the length of the whole of the canalicular portion. Its two coils are widely spaced, and this is exaggerated in the model, since the scala tympani and scala vestibuli are not well defined, so that the ductus cochlearis alone was modelled. The canalicular portion is small but normal. The ampulla is as yet little wider than the canal it serves, but can be recognized by the presence of a crista ampullaris internally. The utricle has an elongated macula acustica, and contracts into a ductus utriculo-saccularis; into it opens the slender duct of the bulbous saccus endolymphaticus (*sen*), which curves dorsalwards to lie alongside the brain, under the connective tissue that will later form the dura mater. The saccule (*sac*) is small and has a macula acustica on its inner wall; it narrows and bends ventralwards as the canalis reuniens (*cre*), then expands into the ductus cochlearis, which performs two complete turns before ending blindly.

Osteocranium (figures 7, 8 and 9)

All the main membrane bones are present at this stage, though some are very thin.

The nasals (*nas*) are small bones, elliptical in contour, set on the summit of the head dorsal to the tectum nasi. The pair do not make contact mesially and between and behind them the spina mesethmoidalis projects upwards.

The premaxillae (*pmx*) are long, narrow shafts of bone, converging ventrally towards the nasal septum, but diverging dorsally where the maxilla forks round each premaxilla and runs alongside the nasal septum. The premaxilla hardly reaches the edge of the upper jaw at this stage but it does appear on the palatal surface for a small area anteriorly, though recessed. Since in the adult the premaxilla forms the lateral boundary of the nasal tube,

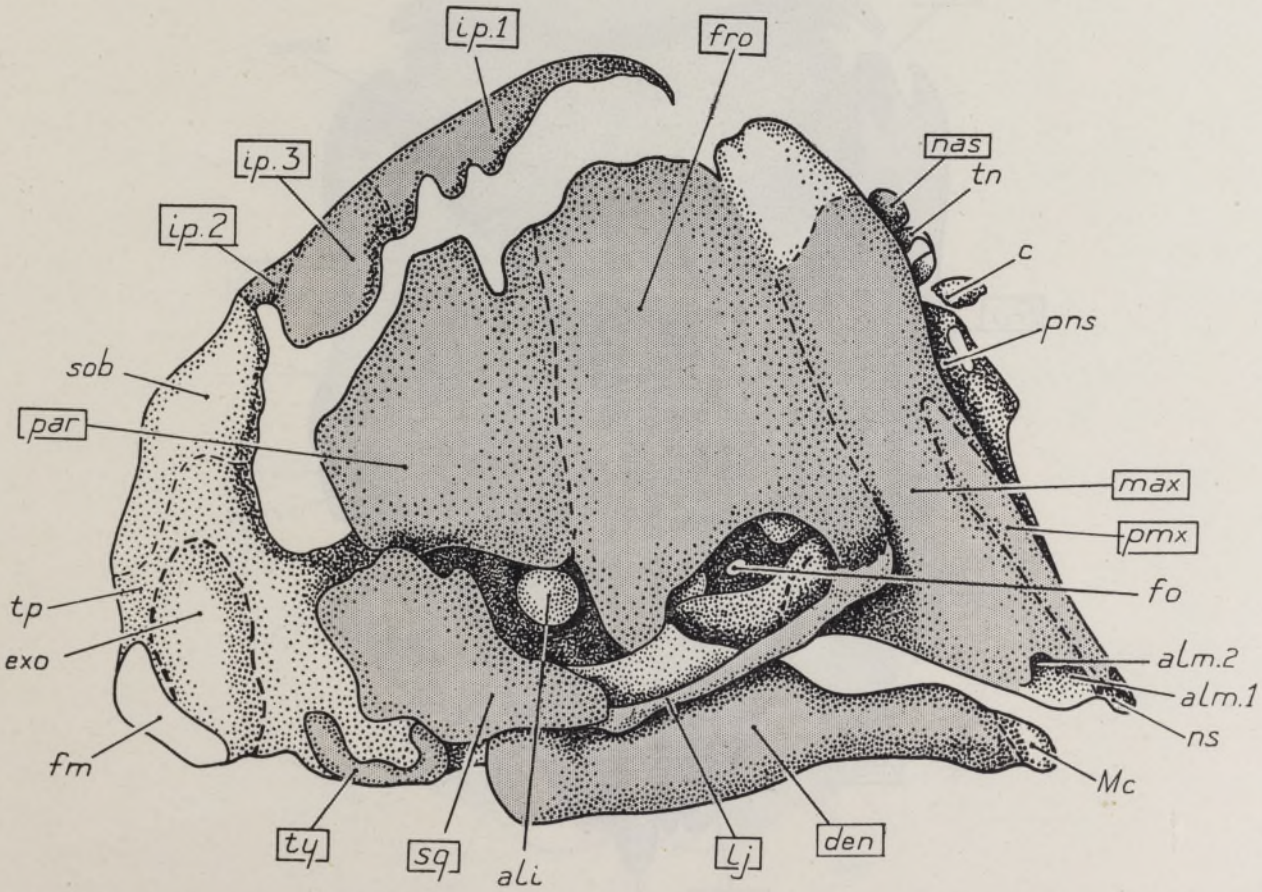

Figure 7. Foetus A. Right lateral view of wax plate reconstruction of the chondrocranium and osteocranium. The lettering for membrane bones has been enclosed in rectangles and the bones themselves finely stippled in this and some subsequent figures. (Magn. × 4·5.)

some rearrangement of the bony tissue must occur in this region, and it would appear to be brought about by the premaxilla growing upwards and covering part of the maxilla. See specimen B.

The maxillae (*max*) are massive bones commencing close to the paries nasi and extending ventralwards towards the nasal septum, making contact with the latter about midway along its length. Dorso-laterally each forms a very small part of the floor of the brain case, but it is more extensive on the face, where it overlaps the frontal, forks round the premaxilla as mentioned above, and reaches to the edge of the upper jaw, its palatal process forming the major part of the hard palate. It has no zygomatic process but meets the lachrymo-jugal alongside the pre-orbital process of the frontal. Antero-ventrally it is excavated to form two tooth sockets containing tooth papillae. Maxillae, premaxillae and nasal septum are prolonged downwards, overhanging the receding lower jaw.

The frontals (*fro*) are overlapped by the maxillae antero-ventrally but are free dorsally; they are therefore more extensive on the cranial than the facial aspect. On the face each

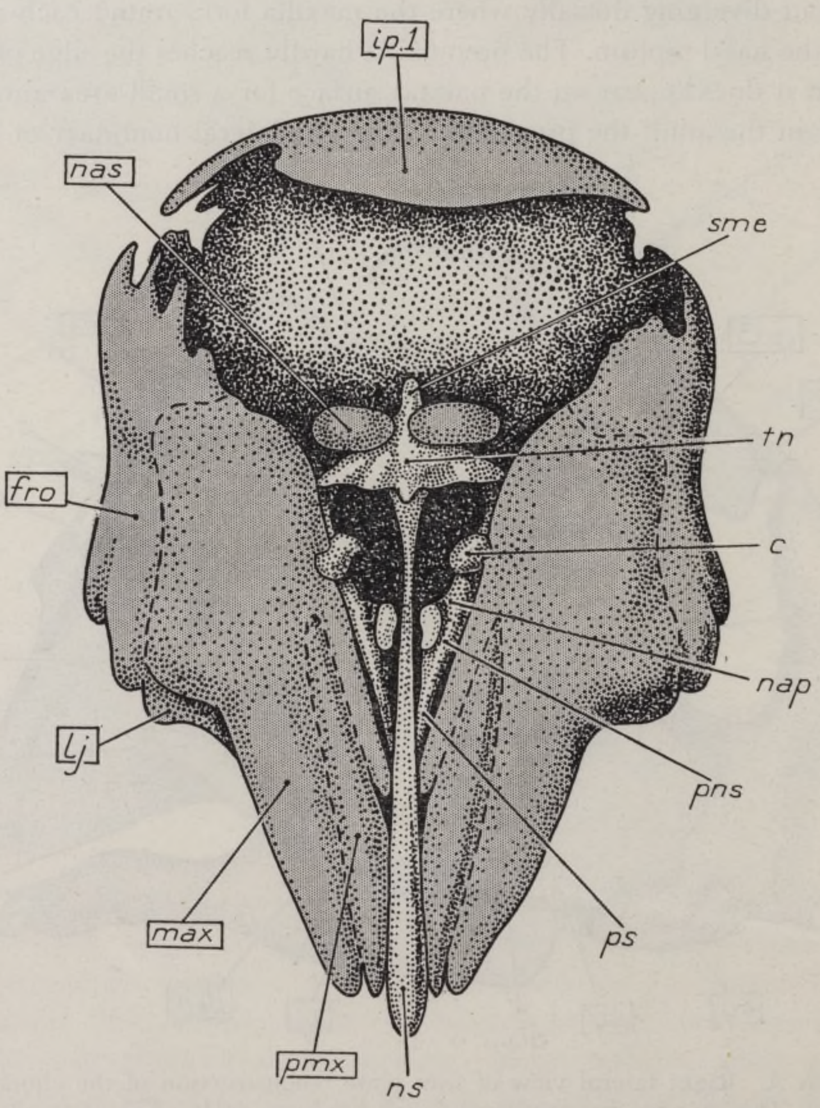

FIGURE 8. Foetus A. Anterior view of the same model as figure 7. (Magn. × 4·5.)

frontal is heavily built ventrally where it is hollowed out for the eye, and becomes thinner in the upstanding shaft, forming a jagged side boundary to the superior fontanelle. Pre- and post-orbital processes are well developed, the former meeting the maxilla and lachrymo-jugal, the latter hanging freely, the orbit being open posteriorly. The low position and downward direction of the eye are very marked, even at this early stage. On the cranial side the thin anterior shaft of the frontal reaches to the lamina orbito-nasalis, thus cutting off most of the maxilla from the brain case. The orbital cartilage and part of the orbito-parietal commissure lie flat against the cranial face of the frontal posteriorly.

The parietals (*par*) are small lateral bones making contact with the frontals on their anterior borders but otherwise surrounded by membrane. The two parietals are widely separated by the large inter-parietal, so that, as in other Odontoceti, they never reach the vertex of the skull. Ventro-laterally the parietal touches the bony alisphenoid. On the cranial side the thin bar of the orbito- capsular commissure is attached to it, running longitudinally across it, and there is a remnant of an orbito-parietal commissure on the left side.

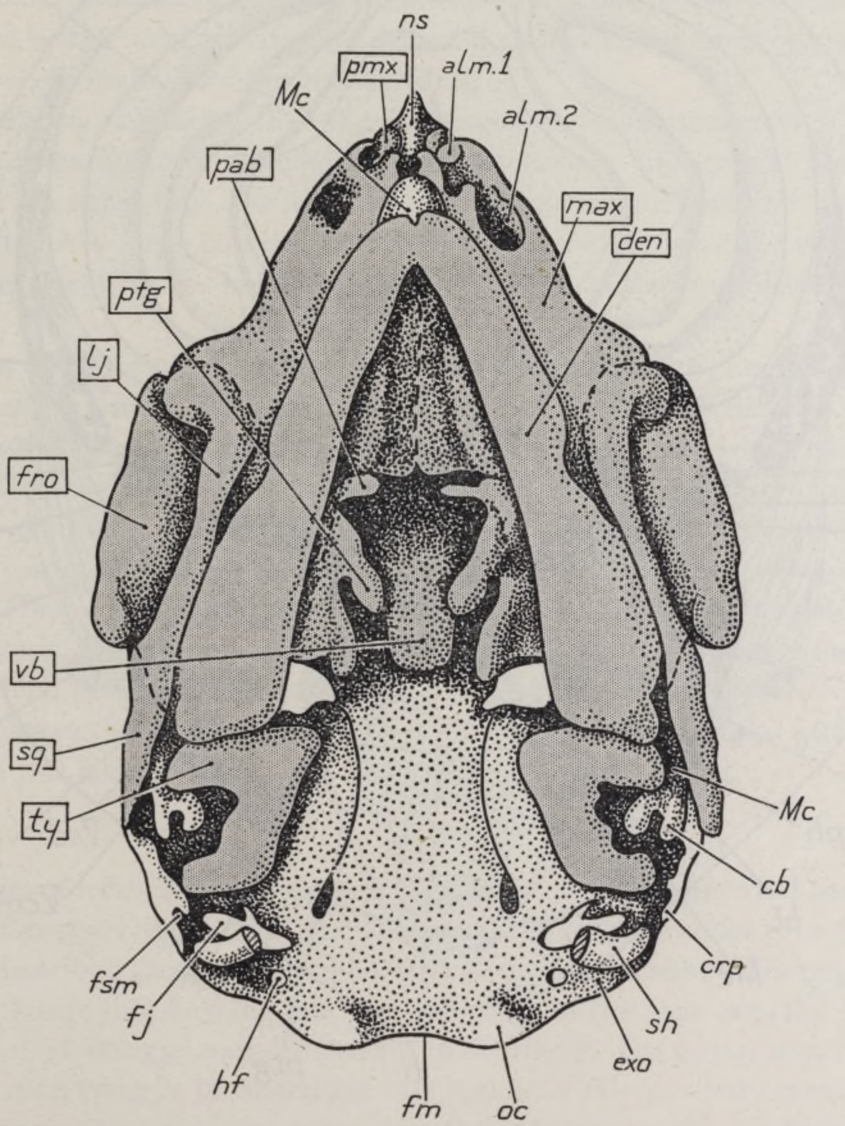

FIGURE 9. Foetus A. Ventral view of the same model as figure 7. (Magn. × 4·5).

The interparietal (*ip*) is the largest element in the osteocranium. Posteriorly it ossifies from three centres, a pair of thin bony plates making contact with the supra-occipital, with a central plate partly overlapped by this pair. Anteriorly there is a median, wide, curved flap, roofing in the skull behind the anterior fontanelle. See specimen B and discussion on p. 27.

The lachrymo-jugals (*lj*) are slender bars of bone typical of the Cetacea, but differing from those of the porpoises and dolphins by being curved, as if they had been forced downwards and inwards by the overhanging eyeball. There is no trace of fusion between jugal

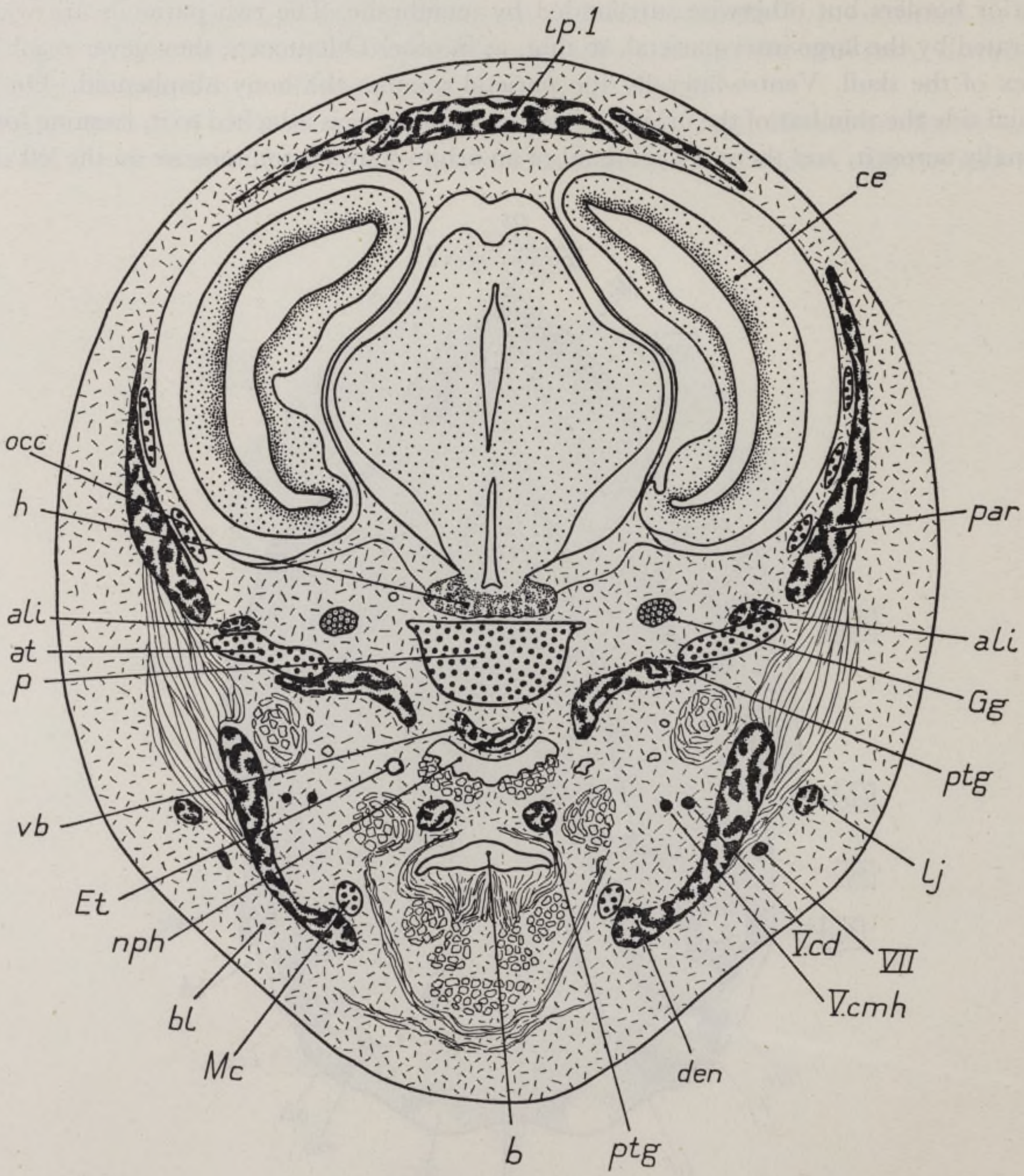

FIGURE 10. Foetus A. Section 388, through the pituitary region. (Magn. × 5·4.) Conventions as in figure 6.

and lachrymal, and the lachrymal portion is imperforate. Posteriorly there is a weak articulation with the forward shaft of the squamosal.

The squamosals (*sq*) are articulated with the lachrymo-jugals, but otherwise are linked only with the chondrocranium. They are small flat bones lying over the tegmen tympani. Although the dentaries are well ossified their condyles do not as yet make contact with the squamosals, the glenoid surfaces of which have not yet shaped themselves.

The tympanics (*ty*) are crescentic bones attached antero-laterally to the ventral side of the auditory capsules.

There is no periotic ossification at this stage.

Goniale. In close apposition to the antero-lateral horn of each tympanic crescent, and between it and the cartilaginous malleus (proximal end of Meckel's cartilage), is a small membrane bone, the pre-articular or goniale of Gaupp. In Cetacea this bone fuses with the tympanic, and from its close contact here there is every indication that it will do so.

The palatines (*pab*) form only a very small portion of the sides of the hard palate as in the adult. Their palatal processes extend mesialwards but do not meet mid-ventrally, and the vomer is exposed between them. They are deeper than broad, the anterior portions running forwards as tapering shafts dorsal to the maxillae.

The pterygoids (*ptg*) are larger than the palatines and act as supporters of the soft palate by means of their backwardly directed hamular processes. The lateral portion develops ventrally to the ala temporalis, the anterior portion touches the palatine.

The vomer (*vb*) is a large median bone closely pressed against the ventral side of the trabecular plate, dorsal to the palatal processes of the maxillae and hidden anteriorly by them.

The dentaries (*den*) are massive bones of typical Cetacean shape, i.e. flat and high, with weak condyles and coronoid processes. Anteriorly they become slender and curve ventralwards, stopping short opposite the alveolar region of the upper jaw, which overhangs them. The condyles have not reached the squamosals. Meckel's cartilages unite to form the anterior tip of the symphysis, but the dentaries join ventrally and form the posterior portion. The hollowing out of the mesial face of the dentary for Meckel's cartilage has been described above. The inferior dental nerve enters its foramen about halfway along the mesial surface of the bone. On the dorso-lateral surface of the dentary there is a shallow alveolar groove (*ald*), which becomes more pronounced in Stage B. See figures 12*c* and 14.

All the membrane bones present in the adult, except the periotic, are in process of development in this foetus.

Teeth

That two pairs of teeth are developed in the upper jaw of the narwhal has been known since C. Mulder discovered them in 1835, and several later writers refer to or describe them. Fraser (1938) described these teeth in the narwhal, and an account of his paper is given on p. 3. Both the future tusk-forming pair (the left tooth of this pair actually becoming the tusk) and the second vestigial pair are present in the foetus. The dental papillae for the first pair are equal, each lying in its dental sac in a hollow of the maxillary bone, and situated on the overhanging portion of the upper jaw (i.e. anterior to the symphysis rami). The second pair are also symmetrical in size and shape. Posterior to them the tooth band extends for a considerable distance, and can be traced through 65 sections. Thus the tusk forming pair occupy sections 111 to 132, the second pair 144 to 160, and the dental band continues to section 225. There are small dental papillae in the regions of sections 182, 191, 198 and 210, after which the band fades out. These are so regular that each probably represents the *anlage* of a tooth, making a possible six pairs on the upper jaw.

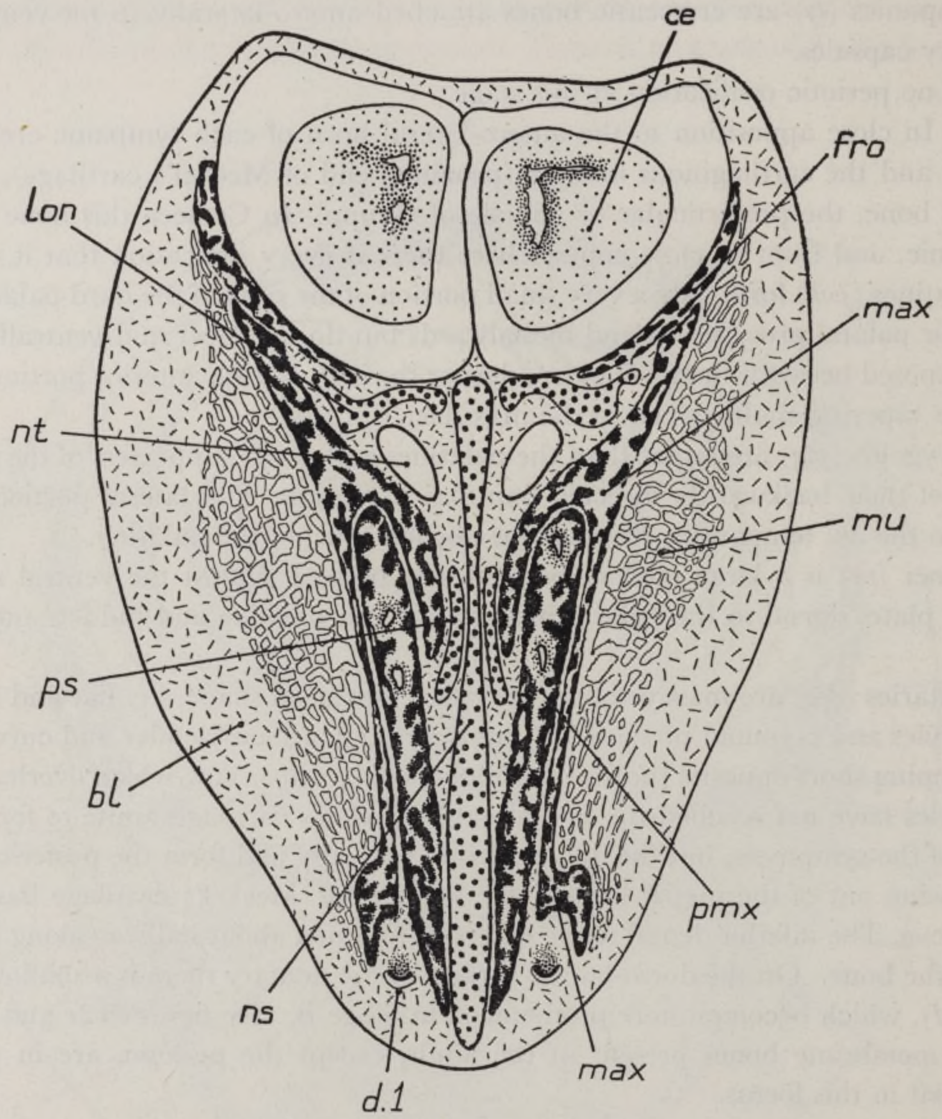

FIGURE 11. Foetus A. Section 120 through the lamina orbito-nasalis, nasal septum and the tusk-forming tooth. (Magn. × 5·4.)

On the lower jaw there is an invagination of the buccal epithelium running through 75 sections (162 to 237), with a dental papilla between sections 213 and 220, and another between 226 and 232. The model shows the corresponding alveolar groove on the dorso-lateral border of the dentary bone.

In the foetus, therefore, there are signs of six pairs of teeth in the upper jaw and of two pairs in the lower jaw, and the maxilla and dentary are excavated for their reception.

While investigating the dental lamina, hair germs were found in a regular series on each

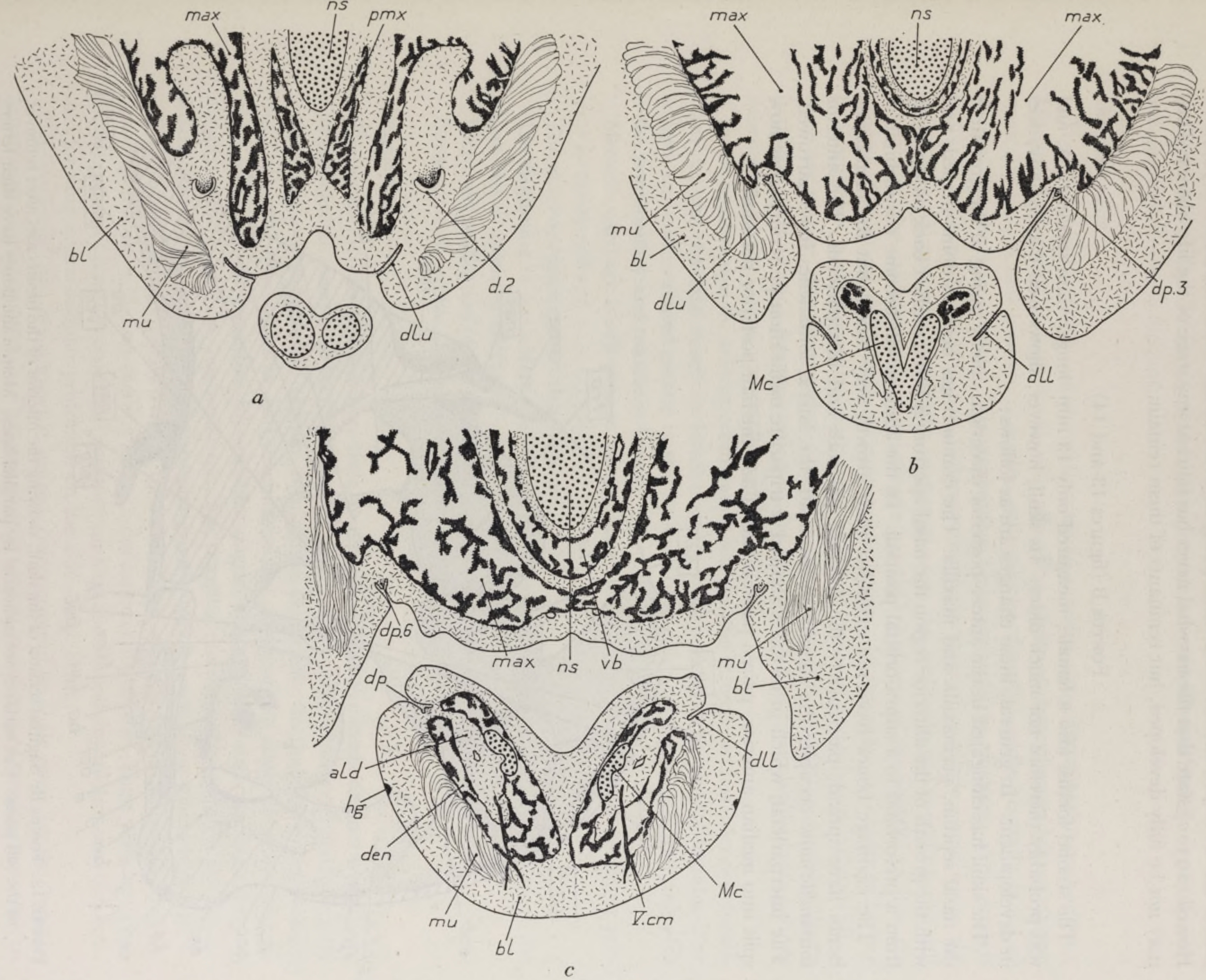

FIGURE 12. Foetus A. Three parts of sections to show teeth and dental laminae. For the tusk-forming tooth, see figure 11. *a*, Section 150. Second tooth and dental lamina in the upper jaw. (Magn. × 8·5.) *b*, Section 182. Dental lamina, with third dental papilla in the upper jaw, and lamina in the lower jaw. (Magn. × 8·5.) *c*, Section 215. Sixth dental papilla in the upper jaw. In the lower jaw note the alveolar grooves in the dentary bones, the dental laminae and a dental papilla on the left side of the section. Two hair germs are also present. (Magn. × 8·5.)

side of the lower jaw. There were seven pairs, one behind the other. Beddard (1900) and Howell (1930*a*) state that the narwhal never has hairs at any stage of the life history. They may not be fully developed, but remnants of them remain.

Foetus B (figures 13 and 14)

The second foetus, also a female, measured only 13 mm. longer than specimen A, and was probably therefore not much older. Its skull, however, shows well marked advances in development. In general, these changes are as follows:

The skull has elongated in the antero-posterior direction, chiefly owing to the growth of the nasal septum, premaxilla and maxilla. The cranium has become dome-shaped, and with the growth of the anterior region the nasal aperture is being pushed back on the head from a pre-orbital to a supra-orbital position. In the adult it will become post-orbital.

The cartilage bones have not extended their growth very much, but the membrane bones have spread, particularly the frontals, parietals and interparietals. The anterior fontanelle now occupies the summit of the head, the lateral fontanelles have narrowed. The interparietal, which in foetus A showed a tripartite ossification posteriorly, has now split into median anterior, paired postero-lateral and median posterior portions.

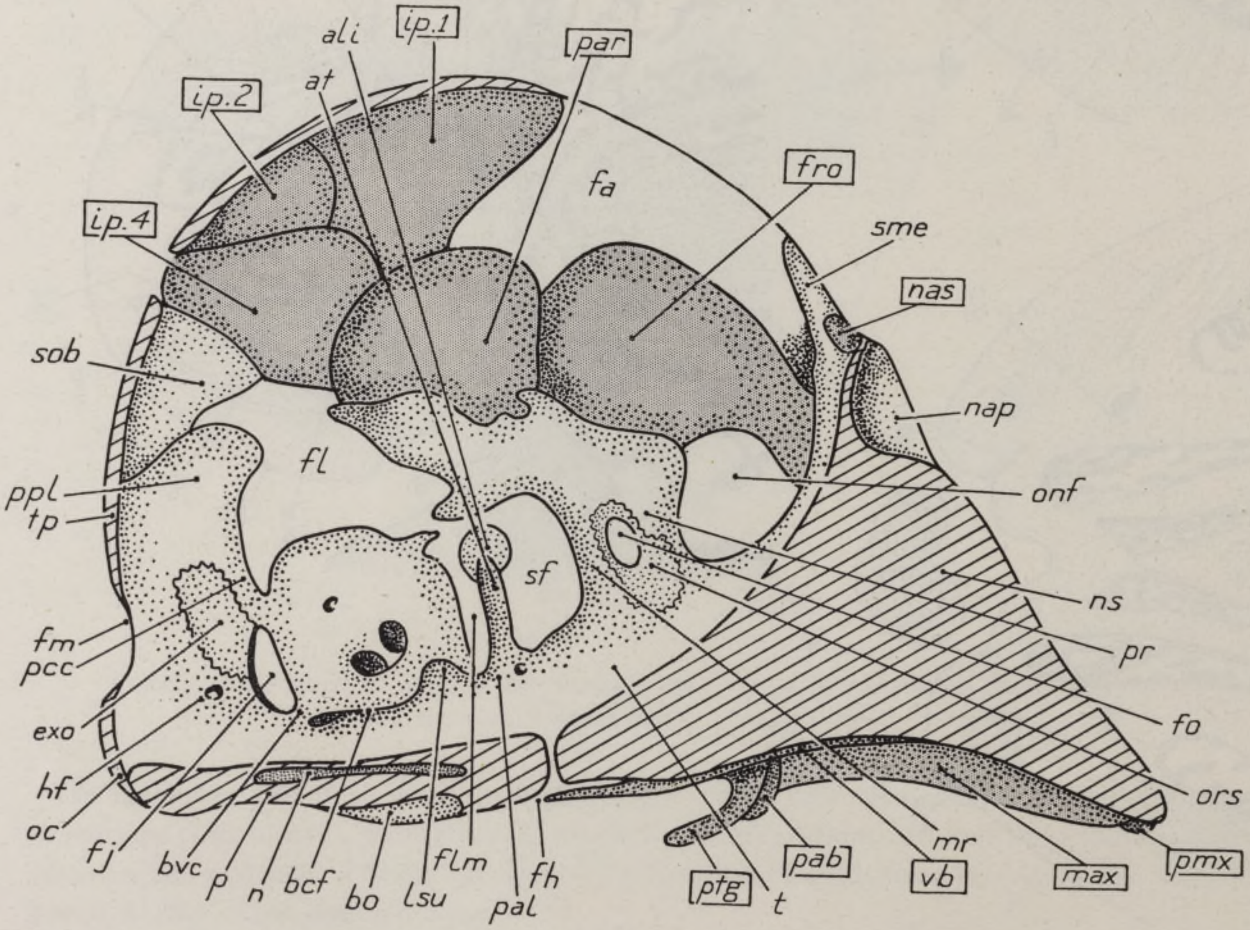

Figure 13. Foetus B. Sagittal section of the skull, showing the interior of the brain case, after removal of the soft parts. Cut surfaces are indicated by parallel lines. Membrane bones have their letters enclosed in rectangles. (Magn. × 4.)

After dissection the skull was bisected longitudinally and the brain removed to expose the remnants of the chondrocranium. Interpretation was facilitated by light staining with safranin (1 % in 50 % alcohol).

Chondrocranium

The basis cranii is thick and shows the curved remains of the intrabasal notochord (*n*). The occipital condyles have fused ventrally. The foramen hypophyseos (*fh*) is almost vertically placed and leads to a shallow sella turcica dorsally, while ventrally it is just covered by the bony vomer. The trabecular plate increases in thickness as it extends forwards to form the septum nasi, a large triangular mass of cartilage rising up to the external narial aperture. Laterally, in cranial view, the basivestibular commissure is still intact, but the orbito-capsular commissure has broken down at the middle, so that the process of isolation of the auditory capsule has begun. In this stage it is moored by the basivestibular, parieto-capsular, prefacial and lateral prefacial commissures, though all of these are weaker. The basicochlear fissure has narrowed, but the lamina supracochlearis is thicker. Ossification has proceeded in the preoptic root of the orbital plate—orbito-sphenoid bone (*ors*)—and the alisphenoid has spread.

In the nasal region the lamina orbitonasalis has become thinner but has extended dorsal-wards, so that the nasal bones are lower than the weak but tall spina mesethmoidalis. The septum nasi has increased greatly in size by forward and downward growth, carrying with it the premaxillary and maxillary bones.

Meckel's cartilage is still present on the inner face of the dentary, but it no longer projects at the symphysis.

The chief developments at this stage are:

The beginning of the isolation of the auditory capsules owing to the breakdown of the antero-lateral mooring cartilages.

Increased ossification of the orbital cartilage to form the orbito-sphenoid bone.

Great increase in size of the nasal septum.

Osteocranium

The nasals (*nas*) have grown very little, but the maxillae have made contact with them. The premaxillae (*pmx*) have become furrowed longitudinally; they have extended anteriorly with the growth of the nasal septum, but not yet posteriorly, so that the shafts running laterally to the nasal aperture and reaching to the nasals in the adult have not formed. Their palatal extent resembles that of older stages. The maxillary fork mesial to the pre-maxilla, seen in foetus A, has weakened. The maxillae (*max*) overlap the frontals; on the palatal aspect they exhibit a pair of alveolar grooves which reach along their whole length.

The frontals (*fro*) are partly covered by the maxillae, and overlap the parietals. They do not meet mid-dorsally and there is still a large anterior fontanelle. Their pre- and post-orbital processes have become more massive, pushing the eyeball downwards and outwards and forming a semi-tubular projection on the side of the head.

The parietals (*par*) are somewhat sunken, being covered on their edges by the frontals, squamosals and interparietals. They are entirely lateral in position. Dorsally they reach to the anterior fontanelle, posteriorly they form the anterior border of the lateral fontanelle.

The interparietal (*ip*) is the largest bone in the skull, and overlaps the parietals, but meets the frontals and supra-occipital, though development on the two sides of the head is not uniform. It shows division into four parts, anterior and posterior median bones and a pair of lateral ones. The lateral bones make contact with one another mid-dorsally. See foetus A, and Discussion, p. 27.

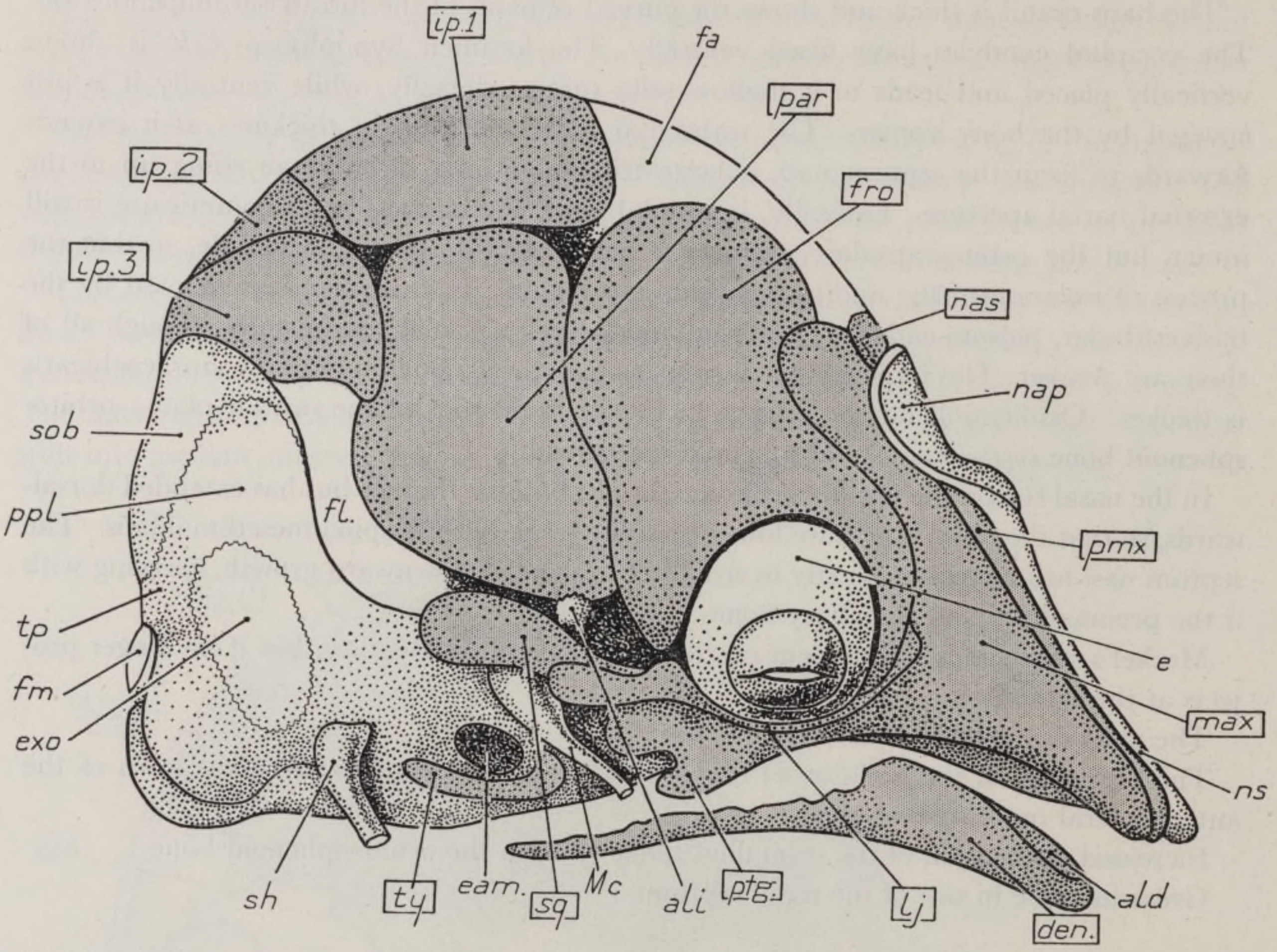

FIGURE 14. Foetus B. Lateral view of the dissected skull. Meckel's cartilage and the stylo-hyale have been cut short. A portion of the dentary has been drawn to indicate its position and down-turned symphysial end. (Magn. × 4.)

The lachrymo-jugals (*lj*) are still pressed in and under the eye. Posteriorly each almost touches the post-orbital process of the frontal.

The squamosals (*sq*) have developed glenoid surfaces for the condyles of the dentary.

The tympanics (*ty*) are closing the gap in the crescent as they broaden.

The palatines (*pab*) approach one another but do not quite meet on the palate. The pterygoids (*ptg*) show little further development.

The vomer (*vb*) is less exposed owing to the growth of the maxillae and palatines.

The dentaries (*den*) have shaped themselves and show a curved alveolar groove on the antero-dorsal border of each.

The chief bony developments at this stage are:

The growth of the premaxillae and maxillae in relation to the extension of the nasal septum.

The partial covering of the vomer by palatal processes of the maxillae and the palatines.
The enlargement of the alveolar groove in each dentary.

DISCUSSION AND CONCLUSIONS

Characters of the order, suborder and family

The foetal narwhal exhibits many of the characteristics of the adult animal. Externally the blow-hole, small, downwardly directed eyeball, minute external auditory meatus without a pinna, paddle-like fore-limbs, tail fluke and external genitalia are sufficiently well developed to distinguish not only the order and sub-order to which the two foetuses belong, but their genus and sex. It is unfortunate that no younger specimens are available and also that no accurate estimate of the age of these two foetuses could be made, owing to the scarcity of the material and the almost entire absence of data regarding the duration of the gestation period.

If the specimen in the American Museum of Natural History, measuring 225 mm. is between three and four months old, as has been suggested, then these two specimens are considerably younger, and are the youngest yet recorded.

Internally the restriction of the hair germs to the region of the mouth and the continuous sheet of blubber beneath the skin are features of the Cetacea, as also are the rounded skull, with depressed front and high, domed brain case, the weak zygomatic arch and mandible, laterally restricted frontals and parietals, and greatly developed supra-occipital and interparietal.

The narwhal agrees with other members of the Odontoceti in the presence of teeth. Like them it has small nasal bones not roofing in the nasal passages. The olfactory lobes of the brain and the olfactory nerves have disappeared with degeneration of the olfactory organ, and turbinal bones are absent. The maxilla overlaps the frontal, and both the latter and the parietal are pushed back on the skull, neither reaching the vertex. The lachrymal is fused with the jugal and there is no naso-lachrymal canal. The auditory capsule has rotated to a transverse position, with a very large antero-ventral cochlear portion and small postero-dorsal canalicular portion. The result is that the internal auditory meatus faces dorsalwards, the fenestra ovalis antero-ventrally. The flat rami of the mandible unite in a mental symphysis.

In the Monodontidae the head is rounded and not prolonged forwards as a rostrum, though in the adult the skull is elongated anterior to the blow-hole by the extension of the premaxilla and maxilla, carrying with them the nasal septum, bearing the tusk or tusks, but this is largely hidden by blubber. The adult has no hair, but the foetus exhibits seven pairs of hair germs on the lower jaw. The dentition is reduced, in the male only one tooth or a pair of teeth being visible in the form of a straight, tapering tusk usually on the left side, or more rarely a pair of tusks. This tusk may attain a length of more than half that of the body (9 ft. in a 15 ft. body), and is spirally coiled sinistrally. The tooth on the right side may remain concealed, or it may also form a sinistrally coiled tusk. In the female, two short tusks may be formed, or one or none. It has been known for the past century that two pairs of teeth are formed in the upper jaw, the second pair aborting or falling out. The lower jaw does not produce teeth. The foetus, however, exhibits dental papillae, equal on both sides, for both the above pairs of teeth, and in addition four small dental papillae on a diminishing dental lamina on each side, the whole of the tooth band lying in a groove in the maxilla. On the lower jaw the foetus shows traces of two pairs, with the corresponding continuous alveolar groove, in the short, down-turned dentary.

Comparison of foetal and adult narwhal skulls (figure 15)

The skulls from foetal narwhals A and B were compared with a young adult skull in the British Museum (Natural History):

	A	B	young adult
length of pre-orbital region to total length	1:3·75	1:3·2	1:2·5
position of blow-hole	antorbital	antorbital	postorbital
length of brain case to total length	1:1·05	1:1·4	1:3·9
height to length	1:1	1:1·4	1:1·65

Although therefore the narwhal characteristics are pronounced in the foetal stage, the proportions show a progressive change with age. Briefly these involve an elongation of the cranial rostrum in order to carry the weight of the tusk, the pushing back of the blow-hole to a post-orbital position and its elevation from an anterior to an antero-dorsal position, the shortening of the brain case relative to the total length of the skull, and a small relative increase in height, chiefly due to the development of the brain case floor in the exoccipital and squamosal regions. The overlapping and telescoping of the bones, which are so marked a feature of adult cetaceans, has only just begun in the foetus. The short, down-turned mandible lengthens relatively and straightens itself with age.

Comparison with other members of the Odontoceti

The relationship of the narwhal to other members of the Odontoceti has been assessed chiefly on the external characters of the adult. Earlier workers recognized four families: Physeteridae, +Squalodontidae, Platanistidae and Delphinidae, but some of these have now been split up. The Ziphiidae have been taken out of the Physeteridae, two new fossil families have been added (+Eurhinodelphidae and +Acrodelphidae), the Platanistidae remain untouched, and the Delphinidae have been divided into Monodontidae (for *Monodon* and *Delphinapterus*), Phocaenidae (for *Phocaena* and *Phocoenoides*) and Delphinidae for all the remainder. This cuts across the older classification based on the length of the rostrum.

The question then arises: to which of these families is the Monodontidae most nearly related? In bodily contour it has resemblances to the Ziphiidae and some Platanistidae, in which the dorsal fin is reduced, the pectoral fin is small and broad, the neck vertebrae are free or nearly so, and the number of vertebrae is in the neighbourhood of fifty. In the Ziphiidae the teeth are reduced to one or two in the lower jaw, the opposite of the condition in *Monodon*. No information on the foetal stages of members of these families is available, and consequently relationships cannot be established.

There remain the Delphinidae and Phocaenidae, and in these families investigation of both adult and foetal stages has been more extensive. The foetal skull has been studied in *Phocaena* (de Burlet 1913*a*; Ridewood 1922; Slepzov 1940), *Globiocephala* (Schreiber 1916), *Lagenorhynchus* (de Burlet 1914*b*), *Delphinus* (Kesteven 1941; Slepzov 1940), and *Delphinapterus* (Slepzov 1940). Matthes (1921, 1923) has summarized the work done by observers up to those dates.

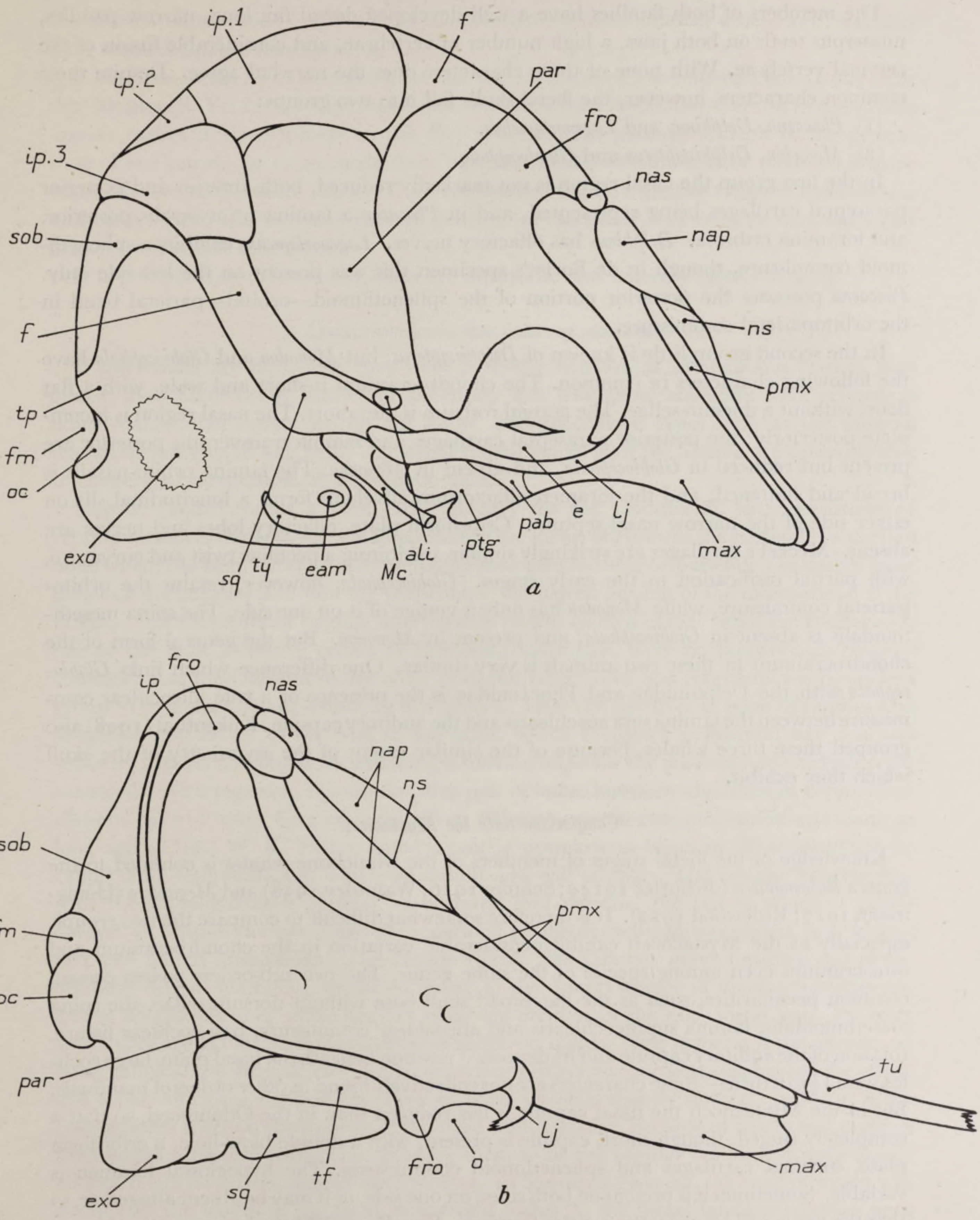

FIGURE 15. Comparison of foetal and adult skulls. The skulls have been drawn to the same length of base, and in lateral view. *a*, Foetus B. (Magn. × 4.) *b*, Young adult, from a specimen in the Natural History Museum, South Kensington. The lachrymo-jugal and the tusk are broken off. (Magn. × $\frac{1}{4}$.)

The members of both families have a well developed dorsal fin, long, narrow paddles, numerous teeth on both jaws, a high number of vertebrae, and considerable fusion of the cervical vertebrae. With none of these characters does the narwhal agree. Despite these common characters, however, the foetal skulls fall into two groups:

(1) *Phocaena*, *Delphinus* and *Lagenorhynchus*.

(2) *Monodon*, *Delphinapterus* and *Globiocephala*.

In the first group the nasal region is not markedly reduced, both anterior and posterior paraseptal cartilages being represented, and in *Phocaena* a lamina transversalis posterior, and foramina cribrosa. *Delphinus* has olfactory nerves. *Lagenorhynchus* exhibits a sphenethmoid commissure, though in de Burlet's specimen this was present on the left side only. *Phocaena* possesses the posterior portion of the sphenethmoid—orbital—parietal band in the orbitoparietal commissure.

In the second group little is known of *Delphinapterus*, but *Monodon* and *Globiocephala* have the following characters in common. The chondrocranium is short and wide, with a flat floor, without a dorsum sellae. The cranial rostrum is also short. The nasal region is incomplete posteriorly; the posterior paraseptal cartilages and lamina transversalis posterior are present but reduced in *Globiocephala*, and absent in *Monodon*. The lamina orbito-nasalis is broad and flattened, and the foramen olfactorium advehens forms a longitudinal slit on either side of the narrow nasal septum. Cribriform plate, olfactory lobes and nerves are absent. Meckel's cartilages are strikingly similar, exhibiting a peculiar twist and curvature, with partial ossification in the early stages. *Globiocephala*, however, retains the orbito-parietal commissure, while *Monodon* has only a vestige of it on one side. The spina mesethmoidalis is absent in *Globiocephala*, and present in *Monodon*. But the general form of the chondrocranium in these two animals is very similar. One difference which links *Globiocephala* with the Delphinidae and Phocaenidae is the presence of a true alicochlear commissure between the lamina supracochlearis and the auditory capsule. Kükenthal (1908) also grouped these three whales, because of the similar extent of the asymmetry of the skull which they exhibit.

Comparison with the Mystacoceti

Knowledge of the foetal stages of members of the whalebone whales is confined to the genera *Balaenoptera* (de Burlet 1914*a*; Schulte 1916; Walmsley 1938) and *Megaptera* (Honigmann 1917; Ridewood 1922). It is therefore somewhat difficult to compare the two groups, especially as the Mystacoceti exhibit considerable variation in the chondrocranium and osteocranium even among species of the same genus. The two sub-orders possess certain common peculiarities, such as the flat broad skull base without dorsum sellae, the spina mesethmoidalis, lamina supracochlearis and alicochlear commissure, basi-cochlear fissure, rotation of the auditory capsule and its depressed position beneath the basal plate, large cochlea with 1½ to 2 turns—these characters are not collectively found in other orders of mammals. But in the Mystacoceti the nasal capsule is less reduced than in the Odontoceti, so that a completely ringed, though short, capsule is present, with a double blow-hole, a cribriform plate, turbinal cartilages and sphenethmoid commissures. The hypoglossal foramen is variable. Sometimes it is present on both sides, on one side, or it may be absent altogether, so that the nerve will leave by the jugular foramen. Equally variable is the interparietal bone, described by Ridewood (1922) as large in *Balaenóptera borealis*, small or absent in *B. musculus*. This requires further investigation.

It has been stated by palaeontologists that the Mystacoceti are younger geologically than the Odontoceti. Yet embryology shows that the specialized distinctive features of the whales appear earlier in development in the Mystacoceti. It is perhaps difficult in the present state of our knowledge to reconcile these two statements, which might be modified if more material were available for study. Until we can investigate a greater range of fossil whales and earlier foetal specimens of modern genera, we can place little reliance on conclusions drawn from so few specimens.

It is possible that the two suborders are diphyletic and not very closely related.

Comparison with other orders of mammals

If the whales are diphyletic they were probably derived, as Honigmann (1917) suggested, from carnivorous Eutherian ancestors. But how those ancestors were related to other mammalian orders we do not know, and specialized types such as the modern whales do not give us any help. Apparent resemblances with the Sirenia are probably due to convergent adaptations to an aquatic habit.

Slepzov (1940) claims a very early ancestry for the Odontoceti, with persistence of reptilian features in the skull. He states that in the foetus of *Phocaena* the parietal is a median bone which has been wrongly interpreted by zoologists as the interparietal. The paired bone they call the parietal is to him the postfrontal, the paired portion of the interparietal is the tabular, and the posterior median interparietal retains its own name. Since the Insectivora, one of the most primitive orders of Eutherian mammals, have no postfrontals, Slepzov considers that the Odontoceti are older than the Insectivora and represent a very ancient group. There are two objections to this theory. First the postfrontal bone of reptiles and amphibia had access to the wall of the orbit, which Slepzov's postfrontal has not, and secondly there is no ground for assuming a median *origin* for the parietal bone in Eutherian mammals. With regard to the tabular, this pair of bones has been identified in *Chrysochloris* (Broom 1916; Forster Cooper 1928), *Phoca* (Watson, verbal communication 1916)and as long ago as 1885 W. K. Parker noted a pair of postparietal bones in *Microgale* which he called supra-temporals, but which we should now call tabulars. The tabular has relations with the supra-occipital, parietal, ex-occipital and periotic, the last of which it partly covers. In reptiles the two bones are separated by the dermal supra-occipital, now identified as a paired interparietal (von Huene 1912). The tabulars move forwards out of the occipital ring in mammals, probably owing to the disappearance of the supra-temporals, but in no case do they make contact with one another in the mid-dorsal line. In other words they are in the longitudinal plane of the ex-occipitals. Now in foetus A the membrane bone, called above interparietal, ossifies from four centres, two median, one behind the other, and a pair alongside the posterior median bone, which is slightly sunken. In foetus B the pair of bones meet on the summit of the head mid-dorsally. Because of this dorsal position there seems little justification for claiming them to be the tabular bones, and accordingly all four bones have been named interparietal. In Slepzov's *Phocaena*, the head of which was about half the length of the head of narwhal foetus A, the bones labelled tabulars were lateral in position. It would be interesting to ascertain whether in older porpoises these lateral elements grew over towards the mid-dorsal line, as they do in the narwhal. If they do, they are probably not tabulars.

SUMMARY

1. The heads of two narwhal foetuses from Greenland were investigated for the structure of the chondrocranium, early osteocranium and the membranous labyrinth. Until this work was undertaken, nothing was known of the development of the skull in the narwhal.

2. Specimen A (137 mm. long) was sectioned transversely and models were prepared by the wax plate method of the chondrocranium, the complete skull, the brain and the membranous labyrinth. The skull of specimen B (150 mm.) was exposed by dissection, and cut in sagittal section.

3. Although so young, the foetuses exhibited the generic characters of the narwhal, and their sex was determinable, both being females. The chief external difference was the position of the blow-hole, which was directed forwards in the smaller foetus, antero-dorsally in the older one.

4. One pair of hypoglossal foramina and large inflated paracondylar processes are present.

5. The auditory capsule, free in adult Cetacea, is moored to the chondrocranium by true and lateral prefacial, orbito-capsular, postfacial and basivestibular commissures. There is no alicochlear commissural attachment, or other connexion with the basal plate, and the capsule is sunk below the level of the latter, the lamina supracochlearis extending like a shelf over it. The basicochlear fissure is continuous and well defined. The complete isolation of the auditory capsule mesially confirms the view that the cochlear portion of the capsule is a true part of it and is not a derivative of the parachordal plate.

6. The ala temporalis is imperforate; the alisphenoid is a cartilage bone.

7. There is no dorsum sellae. Preoptic and metoptic roots of the orbital cartilage and an ala hypochiasmatica on the anterior border of the foramen are present.

8. There is no trace of a sphenethmoid commissure.

9. The lamina orbitonasalis is broad and flat, as in *Globiocephala*, and the foramen olfactorium advehens forms a longitudinal slit on either side of the narrowed nasal septum.

10. A spina mesethmoidalis is present.

11. The nasal capsule is greatly reduced, the tectum and paries nasi are weak. There is a lamina transversalis anterior but not posterior. No posterior paraseptal cartilage. A remnant of the cartilago naso-palatini lies close against the nasal septum, but there is no trace of Jacobson's organ. The only remnant of the posterior portion of the capsule is the reflected edge of the lamina orbitonasalis.

12. Meckel's cartilages are slender and twisted, and resemble in shape those of *Globiocephala*.

13. The tegmen tympani and crista parotica are well developed.

14. There is some continuity between the malleus and the incus. In sections the stapes exhibits a small hole between the crura, but this is not visible externally.

15. A pre-articular (goniale of Gaupp) is present.

16. The interparietal, ossifying from four centres, forms the main part of the roof of the skull. No evidence that it represents more than a compound interparietal can be adduced.

17. There is no separate lachrymal.

18. The upper jaw has two teeth on each side and dental papillae for four others, all in an alveolar groove in the maxilla. The lower jaw shows dental papillae for two teeth on each side and a well developed alveolar groove in each dentary. These teeth are never cut.

19. Seven hair papillae are present on each side of the lower jaw. These also are vestiges. The adult narwhal has no hairs.

20. The study of the foetal skull leads to the conclusion that the Monodontidae are related to the Delphinidae more closely than to the Phocaenidae, and approach the Delphinidae through *Globiocephala*.

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Reference Letters

(Wherever possible, the reference letters are the same as those used by Professor de Beer in *The Vertebrate Skull*)

a, auditory capsule
ah, ala hypochiasmatica
ald, alveolar groove in dentary bone
ali, alisphenoid bone
alm. 1, alveolus in maxilla for first tooth
alm. 2, alveolus in maxilla for second tooth
amp, ampulla
at, ala temporalis

b, buccal cavity
bcf, basicochlear fissure
bh, basihyale
bl, blubber
bo, basioccipital bone
bvc, basivestibular commissure

c, isolated cartilage near blow-hole
cav, anterior vertical semicircular canal
cb, crus breve of incus
cbm, cerebellum
cc, canalicular part of auditory capsule
cdn, cartilago ductus nasopalatini
ce, cerebral hemisphere
ch, horizontal semicircular canal
chp, choroid plexus
cl, crus longum of incus
coc, cochlear part of auditory capsule
coch, cochlea
copv, vestige of orbito-parietal commissure
cpv, posterior vertical semicircular canal
cr, crus commune
cre, canalis reuniens between saccule and cochlea
crp, crista parotica

d. 1, first or tusk-forming tooth
d. 2, second tooth
den, dentary bone
dll, dental lamina of lower jaw
dlu, dental lamina of upper jaw
dp. 3, third dental papilla
dp. 6, sixth dental papilla

e, eyeball
eam, external auditory meatus

ec, epiglottal cartilage
Et, Eustachian tube
exo, exoccipital bone

f, fontanelle
fa, anterior fontanelle
fac, foramen acusticum internum
fc, carotid foramen
fen, foramen endolymphaticum
ff, foramen for facial nerve
fh, hypophysial foramen
fj, jugular foramen
fl, lateral fontanelle
flm, foramen lacerum medium
fm, foramen magnum
fo, optic foramen
fol, foramen olfactorium advehens
fp, foramen perilymphaticum
fro, frontal bone
fsm, stylomastoid foramen

Gg, Gasserian ganglion

h, hypophysis
hf, hypoglossal foramen
hg, hair germ

i, incus
ip. 1, median anterior interparietal bone
ip. 2, median posterior interparietal bone
ip. 3 and 4, paired lateral interparietal bones

lj, lachrymo-jugal bone
lon, lamina orbitonasalis
lsu, lamina supracochlearis
lta, lamina transversalis anterior

m, malleus
max, maxillary bone
Mc, Meckel's cartilage
med, medulla oblongata
mm, manubrium of malleus
mr, metoptic root of orbital cartilage
mu, muscle

n, notochord
nap, nasal aperture
nas, nasal bone
nph, naso-pharynx
ns, nasal septum
nt, nasal tube

o, orbit
oc, occipital condyle
occ, orbito-capsular commissure
onf, orbito-nasal fissure
orc, orbital cartilage
ors, orbitosphenoid bone

p, parachordal or basal plate
pab, palatine bone
pal, processus alaris
par, parietal bone
pcc, parieto-capsular commissure
pcp, paracondylar process
pl, pars lateralis of parietal plate
pmx, premaxillary bone
pns, paries nasi
ppl, parietal plate
pps, palato-pharyngeus sphincter
pr, preoptic root of orbital cartilage
ps, paraseptal cartilage
ptg, pterygoid bone

s, stapes
sac, saccule
sen, saccus endolymphaticus
sf, sphenoidal fissure
sh, stylohyoid cartilage
sme, spina mesethmoidalis
sob, supra-occipital bone
sp.c.m, sphincter colli muscle
sq, squamosal bone

t, trabecular plate
tf, temporal fossa
thy, thyrohyoideus muscle
tn, tectum nasi
tp, tectum posterius
tty, tegmen tympani
tu, tusk
ty, tympanic bone
tym, tympanic membrane

utr, utricle

vb, vomer bone

V *cm*, mental branch of trigeminal nerve
V *cd*, inferior dental branch of trigeminal nerve
V *cmh*, mylohyoid branch of trigeminal nerve
VII, facial nerve

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