

XLI.—The Skeleton of a Sowerby's Whale (*Mesoplodon bidens*) stranded at St Andrews, and the Morphology of the Manus in *Mesoplodon*, *Hyperoodon* and the *Delphinidæ*.  
By Sir Wm. Turner, K.C.B., D.C.L., F.R.S., President of the Society.

(Read July 5, 1909. MS. received July 28, 1909.)

IN May 1908 an adult female Sowerby's whale, *Mesoplodon bidens*, was stranded in St Andrews Bay, about a mile from the clubhouse. Its capture and external characters were recorded by Professor W. C. McIntosh in the *Annals and Magazine of Natural History*, December 1908. The skeleton was obtained by him for the Gatty Marine Laboratory, and at his request I have examined and prepared this report on its characters.

The first observation on this interesting cetacean as a Scottish species was made by Mr James Sowerby \* on an animal stranded in the Moray Firth near Elgin in 1800; no record existed of another example in Scotland until 1872, when I described † the skull of a female in the Museum of Science and Art, now the Royal Scottish Museum. In 1881 I obtained from Messrs Anderson of Hillswick an imperfect skeleton ‡ of a male stranded in April in Urafirth Voe, North Mavine, Shetland, and in May 1885 the same gentlemen sent me the carcass of another male § captured at Voxter Voe, Delting, Shetland. In October 1888 a male was stranded in Dalgety Bay, on the north shore of the Firth of Forth, the characters of which I described at the time. || In April 1895 another male was captured in the Firth of Forth, at Morrison's Haven, Prestonpans, and its skull, some bones, and a limb were secured by my late assistant, Mr James Simpson, ¶ for the Anatomical Museum of the University. In drawing up the notes on the St Andrews animal, I have compared the skull and skeleton with the 1881, 1885, 1888 and 1895 specimens in the Anatomical Museum.

\* *The British Miscellany*, 1804-1806, vol. i., pl. i.

† *Trans. Roy. Soc. Edin.*, vol. xxvi. p. 759, 1872.

‡ *Journal of Anat. and Phys.*, vol. xvi., April 1882; *Proc. Roy. Soc. Edin.*, Jan. 1882.

§ "The Anatomy of a Second Specimen of Sowerby's Whale," *Journal of Anat. and Phys.*, vol. xx. p. 144, October 1885; *Proc. Roy. Soc. Edin.*, vol. xiii. p. 279.

|| *Proc. Roy. Phys. Soc. Edin.*, vol. x., 1888-1889.

¶ *Annals of Scottish Natural History*, October 1895, p. 250.

## MEASUREMENTS OF SKULLS.

	Royal Scottish Museum, 1872, ♀.	Shetland, 1881, ♂.	Shetland, 1885, ♂.	Dalgely, Firth of Forth, 1888, ♂.	Morrison's Haven, 1895, ♂.	St Andrews, 1908, ♀.
Greatest length of skull in straight line . . . . .	75 cm.	broken	76	77.3	broken	82.8
Length of rostrum . . . . .	49	broken	51.2	51	51	59
Height from vertex to ptery- goids . . . . .	24	26	27	27	broken	25.4
Breadth between upper mid- orbital borders . . . . .	28.5	28.5	28.4	29	...	29.1
Breadth across occipital condyls	11	10	11.1	10.3	10.5	11.2
Breadth between ant-orbital notches . . . . .	20	18.5	17.3	17.5	20.5	19.8
Premaxillæ, width behind anterior nares . . . . .	13	11.5	11.8	12.3	12.5	12.3
Premaxillæ, width in front of anterior nares . . . . .	10	10	11	9.2	10.5	9.9
Premaxillæ, width opposite anterior nares . . . . .	11	10	10.4	10	10.6	11
Width of anterior nares . . . .	4.5	5.5	5.6	5.4	4.8	6.2
Mandible, length of . . . . .	69	65	67	65.5	broken	73.8
"    "    symphysis . . . . .	24	broken	23.3	21	22.8	27.6
"    height of ramus . . . . .	11	10	10.7	11	broken	11.2

*Skull.*—The skull of the St Andrews specimen had the characteristic elongated, slender beak, and other general characters of the species. It was 82.8 cm. (32½ inches) in maximum length, and was the longest skull in the Table of measurements. The rostrum was not broken, and the slender tips of the superior and premaxillary bones as well as the mesial cartilage of the beak reached its free end. The length of the beak was 59 cm. (23¼ inches). The mes-ethmoid septum was prolonged into the upper end of the medio-rostral gutter for 8 cm., and was embraced anteriorly by the medio- (meso-) rostral bone, which occupied the gutter for 21 cm. This bone was divided on its upper surface into two lateral halves by a longitudinal groove, and in front of it the unossified medio-rostral cartilage extended to the tip of the beak.

In the 1881 specimen from Shetland, the mes-ethmoid was embraced by the medio-rostral bone, which was divided by a longitudinal groove into two distinct lateral halves as far as 24 mm. from the anterior pointed end, near which the surface of the bone was tuberculated. In the skull from Morrison's Haven the halves were fused together for 154 mm. from the pointed end, and the surface of the bone was smooth. The free end of the rostrum of this skull was somewhat curved to the right, and a

similar deflection was present in the tip of the mandible. In the Dalgety Bay cranium the longitudinal groove was present in the middle third and the lateral halves were distinct, the posterior and anterior thirds were not grooved, the surface of the medio-rostral bone was smooth and the anterior end was pointed.

In a paper on the development of the rostrum in *Mesoplodon*, H. O. Forbes regarded \* the meso-rostral consolidation as an upgrowth formed by the proliferation of the osseous tissue of part of the vomer and perhaps of the premaxillaries, and not as an ossification of the meso-rostral cartilage. The presence of a longitudinal groove, and the consequent indication of two lateral halves to the medio-rostral bone, favour to some extent, as regards its sides, this view, but I think that ossification of the mesial cartilage also participates in the production of the consolidated structure which occupies the medio-rostral gutter both in *Ziphius* and *Mesoplodon*.

In the female skull which I described in 1872 the medio-rostral gutter did not contain the corresponding bone, which I thought might be a female character, but its extensive ossification in the adult female now described showed that the absence of the bone in the previous specimen was an age, and not a sexual feature.

The two halves of the St Andrews mandible were not fused at the symphysis; the alveolus for the tooth was situated immediately in front of the hinder end of the symphysis, and the apex of the tooth projected for only 9 mm. beyond the alveolus; the retention of the crown within the alveolus indicated the female sex. In the mandible of the skull from Morrison's Haven the two halves were in process of fusion, the teeth were lost, but the large sockets extended for about half their extent behind the symphysis.

*Ear Bones.*—In the St Andrews specimen the tympanic bullæ and petrous bones were lodged in the hollow near the mastoid. The bulla was bilobed inferiorly and posteriorly, characteristic of the genus *Mesoplodon*.†

*Hyoid Apparatus.*—The hyoid proper consisted of a body with which the two great cornua were fused. At its anterior border was a notch bounded by a pair of short processes, each with an articular facet, to which the cerato-hyals had doubtless been attached. A well-marked pair of stylo-hyals was anterior to and separated by an interval from the thyro-hyals.

*Spine.*—As the epiphyses were fully ankylosed to their respective

\* *Proc. Zool. Soc. Lond.*, 28th Feb. 1893.

† See my account of the tympano-petrous bones in the *Odontoceti*, *Proc. Roy. Soc. Edin.*, vol. xxiv. p. 423, 1903.

vertebræ, the specimen was an adult. The column consisted of forty-seven vertebræ.

*Cervical vertebræ* from the 1st to the 4th were fused together, and formed a massive bone, but the laminæ of the 4th were distinct and did not meet to form a neural spine. The 5th, 6th and 7th were separate and with flattened bodies; in the 5th and 6th the neural arches were incomplete and without spines, but the 7th had a short spine. The transverse processes were distinct; in the atlas and axis no foramen was present at the root of each process; in the 3rd to the 6th the transverse process was formed by the junction of the diapophysis and the parapophysis, between which was the vertebrarterial foramen; in the 7th these two processes had not joined and the boundary of the foramen was incomplete.

*Dorsal Vertebræ*.—The 1st and the 5th to the last were separate bones, but the bodies of the 2nd, 3rd and 4th were tied together by a strong bar of bone fused with the ventral surface of their bodies. The body of the 1st dorsal was flattened, as in the last cervicals, but behind it the bodies gradually increased in antero-posterior diameter until the last, which measured 10.9 cm. and possessed a median ridge on its ventral surface. From the lower part of the side of the body of the 1st dorsal a tubercle projected which resembled the parapophysis of a cervical. The laminæ and spines were complete in all the dorsals and increased in size from before backwards. The 1st dorsal, where it gave rise to the parapophysis (inferior tubercle), had a large costal facet for the head of the 1st rib, on the posterior surface of the tubercle which extended on to the body, but no costal facet was seen on the short pointed transverse process. The body of each vertebra from the 2nd to the 7th had a costal facet on each side at its junction with the pedicle. From the 1st to the 8th vertebræ, and close to the anterior zygapophysis, a transverse process sprang from the neural arch, which, except in the 1st, had a large costal facet for the tubercle of a rib. In the terminal dorsals the transverse process did not project from the neural arch, but from the anterior part of the side of the body; zygapophyses were present in the 1st to the 8th dorsal; strong metapophyses projected from the laminæ of the terminal dorsals which overlapped the laminæ of the vertebra immediately anterior, and short metapophyses were present in the 7th and 8th vertebræ. In this spine and in those of the two Shetland and the Dalgety Bay animals the 7th vertebra was the last to show costal facets for both head and tubercle; the dorsal vertebræ behind it had a facet only on the transverse process for the tubercle of the rib.

*Lumbar vertebræ* had no facets for articulation with the chevron bones. They were the largest of the vertebræ, and were characteristic of the

region. The body was keeled on its ventral surface; the transverse processes were spatulate and sprang from about the middle of the sides of the bodies; the spines were long, flattened plates of bone.

*Caudal Vertebrae.*—Eighteen vertebræ followed the last lumbar. They diminished in size from before backwards; the eight most posterior consisted only of a body, and that of the terminal vertebra measured only 20 mm. in its antero-posterior and 18 mm. in its transverse diameter. The ten anterior had facets on the ventral surface for the nine chevron bones, which had articulated with them and with the intervertebral discs.

*Ribs.*—There were ten pairs of ribs. The 1st and the 10th were the shortest; they increased in length from the 1st (32 cm.) to the 6th (62 cm.) and then diminished to the last (16 cm.). The 1st, the broadest and most flattened, had a facet on the head and one on the tubercle; the right was marked by an oblique roughened groove on its surfaces, as if it had been fractured and afterwards repaired. The 2nd to the 7th had also vertebral facets on the head and tubercle, but the 8th and 9th had no head and articulated only with a vertebral transverse process. The 10th was an elongated flat bone 30 mm. in greatest width, pointed at both ends, and without head and tubercle.

The opportunity which I have had through the courtesy of Professor M'Intosh of studying the skeleton of the St Andrews Mesoplodon has led me to re-examine the skeletons of the two Shetland and the Dalgety Bay animals and to reconsider the mode of articulation of the ribs with the spinal column. In each skeleton the head or capitular process of the 1st rib was jointed to the body of the 1st dorsal vertebra, the transverse process of which was so slender and pointed that the large articular facet on the tubercle of the rib could not be adapted to it. In approximating the 1st rib to the spine its tubercle came into contact with the transverse process of the 2nd dorsal, with which it obviously had articulated. It consequently followed that from the 1st to the 7th rib the tubercle articulated with the transverse process of the vertebra immediately behind the body to which the head was jointed, and with which it was in numerical correspondence. As the tubercle of the 7th rib therefore articulated with the transverse process of the 8th dorsal, the 8th, 9th and 10th ribs, which had no capitular processes, articulated with the transverse processes of the 9th, 10th and 11th post-cervical vertebræ. It required therefore eleven vertebræ to articulate with ten pairs of ribs. In the St Andrews skeleton the transverse processes of the 11th post-cervical vertebra were broken, but they were entire in the corresponding vertebra in the other three skeletons, in each of which the free outer border

was marked by a distinct facet, so that provision existed for the articulation of the 10th rib with the 11th post-cervical vertebra.

*Vertebral Formula.*—The St Andrews skeleton had 47 vertebræ, and a similar number was found in the 1885 Shetland and the Dalgety Bay specimens, but the spines in the 1881 and 1895 animals were incomplete. The complete skeletons had 7 cervicals; 11 post-cervicals articulating with 10 ribs which were therefore dorsal vertebræ; 29 lumbo-caudal vertebræ, of which 11 may be termed lumbar and 18 caudal. The formula may be written  $C_7D_{11}L_{11}Cd_{18} = 47$ . Variations in the relative number of lumbar and caudal vertebræ may without doubt from time to time occur.

The length of the spine in the St Andrews skeleton, without allowing for the thickness of the intervertebral discs, was 12 feet 5 inches, and the length of the skull was 2 feet 8½ inches, together 15 feet 3½ inches. Professor M'Intosh estimated that the carcase was over 16 feet, and the length of the skeleton, allowance being made for the thickness of the discs, corresponded with this measurement. The Mesoplodon stranded in Dalgety Bay was 15 feet 1 inch in length; but, as the epiphysial plates of the vertebræ were not completely fused with the bodies, the animal was not fully grown, and although a male, the mandibular teeth projected only 2.6 cm. beyond the alveolus. The Shetland specimen, 1885, measured 15 feet 8 inches, the epiphysial plates were fused with the bodies, and the mandibular teeth projected 4.5 cm. beyond the alveolus. About 16 feet may therefore be regarded as the usual length of the adult Sowerby's whale.

*Sternum.*—It consisted of five transverse segments with four large intersegmental holes. The 1st, much the largest, 22 cm. long, was a broad plate, with two cornua in front, between which was a deep presternal notch. The two lateral halves of the 2nd segment were united mesially by a suture; the 5th or terminal segment was incomplete, and the hole between it and the 4th had an imperfect boundary behind; the 3rd and 4th segments were completely fused in the middle line. Each lateral border had articular facets for five costal cartilages: that for the 1st cartilage marked the anterior part of the 1st segment; those for 2nd, 3rd, 4th and 5th were opposite the line of articulation between the 1st and 2nd, 2nd and 3rd, 3rd and 4th, 4th and 5th sternal segments.

*Pelvic Bones.*—These bones were rudimentary; each consisted of a slender bar, 61 mm. long and 10 mm. in greatest width, faintly curved at the ends, which were attenuated. There was no sign of a rudimentary femur.

*Anterior Extremity.*—The *Scapulae* were plate-like, 32 cm. in diameter between the anterior and posterior angles, and 22 cm. between the glenoid



and vertebral borders. The coracoid was 10.6 cm. in length. The post-spinous fossa formed so large a proportion of the outer surface that the pre-spinous fossa was a mere groove. The spine was a sharp low ridge, but the large plate-like acromion was 11.2 cm. long and 4.6 cm. wide.

The *Humerus* was a short thick bone, only 15.5 cm. long. The head, neck and tuberosity were distinct; the shaft was somewhat flattened on its two surfaces, on the inner of which was a roughened depression, stronger in the left bone; the lower end had definite facets separated by a sharp ridge for the radius and ulna, and a concave surface on the inner border of the bone received the articular facet of the olecranon process.

The *Radius* and *Ulna* were parallel and not movable on each other. The radius was 16.5 cm. long, the shaft was 4.5 cm. wide at the middle, its surfaces were flattened. The humeral epiphysis was blended with the shaft; the carpal one was ossified, though not fused with the shaft. The ulna was almost the same length as the radius, the shaft was 3.2 cm. wide; the carpal epiphysis was ossified but not fused; the olecranon epiphysis was ossified but movable on the shaft, and in this respect it differed from the bone in the 1885 and 1888 specimens, in which the olecranon was completely fused with the ulna, though in them the carpal epiphysis was distinct.

*Manus*.—The manus was pentadactylous. It consisted of carpus, metacarpus and phalanges enclosed in a common tegumentary covering. The *Carpus* had a proximal row, *procarpus*, a distal row, sometimes called *mesocarpus*, a pisiform and an os centrale or ossa centralia. In the proximal and distal rows the bones were flattened on the palmar and dorsal surfaces and the cartilage between them was thin. The *procarpus* consisted of the three bones usually found in this row of the cetacean carpus, the relative position of which is indicated by their names, *radiale*, the smallest; *intermedium*, the largest; and the *ulnare*. The *intermedium* had a longitudinal groove on the palmar surface for the flexor digitorum ulnaris, and its upper border sent an angular prolongation between the carpal epiphyses of the radius and ulna.

In my memoir on the Sowerby's whale captured in 1885,\* I described its carpus and showed that the distal carpalia were only three in number, which I designated as follows: the smallest was *carpale*<sub>1</sub>, next to which was a large bone which represented *carpalia*<sub>2+3</sub>, and on the ulnar side a large bone which represented *carpalia*<sub>4+5</sub>. In the St Andrews example a similar arrangement existed. *C*<sub>1</sub>, 21 mm. in transverse diameter, articulated distally with the metacarpal of the pollex, *M*<sub>I</sub>, also with *M*<sub>II</sub>, and with the *radiale*, *centrale* and the conjoined *C*<sub>2</sub>+*C*<sub>3</sub>. *Carpalia*<sub>2+3</sub> formed a

\* *Journal of Anat. and Phys.*, vol. xx. p. 180.

bone 37 mm. in transverse diameter, which was grooved for the flexor digitorum, and articulated with  $M_{II}$  on one side of the groove and with  $M_{III}$  on the other, also with  $C_1$ , centrale, intermedium and  $C_{4+5}$ . Carpalia $_{4+5}$  formed a bone 42 mm. in transverse diameter, which articulated by its distal border with  $M_{IV}$  and  $M_V$ ; opposite the interval between these metacarpals its distal and proximal borders and the dorsal surface were notched as if the two halves of the bone were imperfectly united, so that



FIG. 1.—Right manus, palmar surface, Sowerby's Whale, St Andrews.

In this and other figures R means radius; U, ulna; *r*, radiale; *i*, intermedium; *u*, ulnare; *c* is a distal carpal, and the numeral associated with it is its number in the distal row; C is os centrale; the roman numerals are the metacarpal bones; P is pollex; *p* is the pisiform element.

it appeared that one part belonged to  $M_{IV}$ , the other to  $M_V$ ; it also articulated with  $C_3$ , ulnare and the pisiform cartilage. Both in the St Andrews and 1885 animals the three distal carpalia represented the five distinct elements found in Hyperoodon, in which a distal carpal occurs for the metacarpal bone of each digit. It is likely that the two elements which formed the bone  $C_{2+3}$ , as well as those of  $C_{4+5}$  had, as in Hyperoodon, been developed independently in the carpal cartilage, but thereafter became conjoined. In the St Andrews animal a narrow bar of cartilage formed the ulnar border of the carpus and a nodule of bone, the



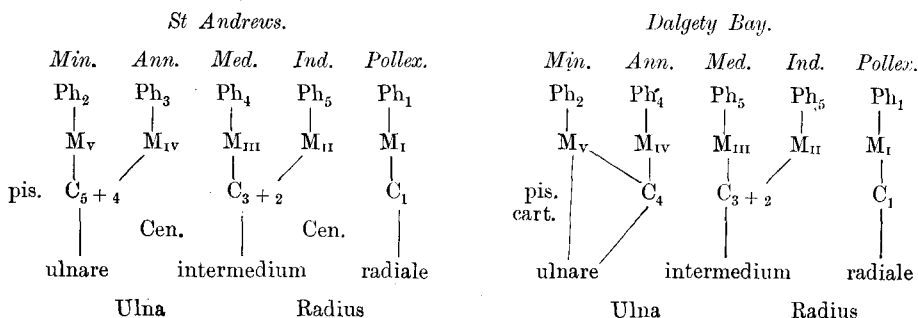


the St Andrews and 1885 specimens. Owing to its small transverse diameter the internal carpal articulated by its distal border only with  $M_{IV}$ , whilst  $M_V$  was jointed to its ulnar border and to the ulnare in the proximal row through an intermediate band of pisiform cartilage. The internal carpal represented perhaps only  $C_4$ , whilst  $C_5$  was not differentiated in the carpal cartilage, nor was a pisiform bone ossified in the cartilaginous inner border of the carpus.

*Digits.*—Each of the five digits of the St Andrews animal consisted of a metacarpal bone  $M$ , and one or more phalanges,  $Ph$ . The metacarpal of the pollex  $M_I$  was a slender cylindrical bone 26 mm. long; at the free end was a nodule of cartilage which represented the phalanx. The metacarpals of the other digits were flattened;  $M_{III}$  was the longest, 51 mm.,  $M_V$  was only 25 mm. long, and was set at an angle to and articulated with the distal border of the carpal, which represented  $C_5$ . As some of the phalanges had been lost their exact number cannot be stated, but they were probably the same as in the 1885 specimen, viz.:  $D_{II}$ , five phalanges;  $D_{III}$ , four;  $D_{IV}$ , three;  $D_V$ , two, and the longest digit was the index.

In the Dalgety Bay specimen, however,  $D_{III}$  had five phalanges in one manus though only four in the other, and  $D_{IV}$  had four phalanges, of which the terminal was no bigger than a small shot.

The constitution of the manus in the St Andrews and Dalgety Mesoplodons may be expressed by the following formulæ, the number of phalanges in the St Andrews specimen being taken from the 1885 specimen:—



young, were stranded near Nairn. The mother was nearly 16 feet long, the young one about 9½ feet. Mr Taylor stated\* that in the upper jaw of the young animal 8 rudimentary teeth were concealed in the gum on each side, and in the lower jaw 17 on each side behind the normal tooth. Some years ago I described † a somewhat similar series of rudimentary teeth in the gum of the upper and lower jaws of a Hyperoodon upwards of 20 feet long. In March 1904 Mr Taylor obtained the head of a male specimen, 14 feet in length, stranded at Fraserburgh. ‡ It is obvious, therefore, that Sowerby's whale is not an uncommon species in the Scottish seas.

In my notice of the capture of Sowerby's whale in Dalgety Bay § the only English specimen to which I could refer was one recorded by Messrs Thomas Southwell and Eagle Clarke caught on the Yorkshire coast near Spurn Head in September 1885. || Since then, Messrs Southwell and Harmer have described a gravid female, 16 feet long, containing a foetus 5 feet long, captured in December 1892 at Overstrand, near Cromer, and purchased by the Hon. Walter Rothschild for his museum. ¶ In my previous memoirs on Sowerby's Whale, I referred to specimens caught on the French coast and to the descriptions by Reinhardt, Malm and Aurivillius of specimens stranded on the coast of Scandinavia. More recently J. A. Greig has described \*\* two specimens obtained in 1895 in the Scandinavian seas, one at the island Karmö, the other at the adjoining island Fæø. Mr Glover M. Allen has also recorded †† two recent specimens captured off the coast of North America, one at Annisquam, Massachusetts, in 1898; the other at Long Branch, New Jersey, in 1905. In a recent note (*Science*, vol. xxvi., 1907) F. W. True stated that, in his opinion, three species of *Mesoplodon* occur on the U.S. Atlantic coast, *bidens*, *europæus*, *densirostris*.

#### *Morphology of Manus in Hyperoodon and in the Delphinidæ.*

Since publishing in October 1885 my memoir on the Anatomy of Sowerby's Whale, in which I dwelt on the morphology of the manus in this cetacean, and compared it with the manus of *Hyperoodon* and *Globicephalus*, I have had the opportunity of dissecting several other specimens of the *Odontoceti*

\* The same *Annals*, p. 66, April 1900. The skeleton of the mother and the skull of the young animal are now in the Royal Scottish Museum.

† *Proc. Roy. Phys. Soc. Edin.*, vol. ix. p. 25, 1885-86.

‡ *Annals of Scottish Natural History*, p. 186, July 1904.

§ *Proc. Roy. Phys. Soc.*, vol. x., 1888-9.

|| *Ann. and Mag. Nat. Hist.*, ser. 5, vol. xxii. p. 53, 1886.

¶ *Ann. and Mag. Nat. Hist.*, ser. 6, vol. xi. pp. 275, 439, 1893.

\*\* *Bergens Museums Aarbog*, 1897, No. v., plates 1, 11, animal and skull.

†† *American Naturalist*, vol. xl. p. 357, 1906.

and of studying in fresh specimens the hand with the bones *in situ*, and not artificially articulated. I propose therefore to continue my account of the morphological constitution of the manus in the toothed whales.\*

#### HYPEROODON ROSTRATUS.

A young male 20½ feet long was stranded near Dunbar in November 1885. I secured the specimen and mounted the skeleton in the Anatomical Museum of the University. As the vertebral plates and the epiphyses of the long bones were not fused with their diaphyses the animal had not reached maturity. The carpal end of both radius and ulna had a well-marked epiphysial cartilage partially ossified. The carpalia were flattened on the surfaces and consisted of osseous nodules in masses of cartilage.

The *procarpus* or proximal row contained radiale, intermedium and ulnare. The radiale showed an osseous nodule 31 mm. in transverse diameter surrounded by cartilage which articulated with radius, intermedium and ulnare. In the intermedium the osseous nodule was 41 mm. wide, and with its surrounding cartilage articulated with radius, ulna, radiale, ulnare and carpalia<sub>2, 3, 4</sub>. The osseous nodule in the ulnare was 32 mm. wide, and with its cartilage articulated with ulna, intermedium, carpalia<sub>4, 5</sub>, and with the unossified pisiform cartilage, which formed the inner border of the carpus and was connected with the cartilage of the ulnare, carpale<sub>5</sub> and metacarpal<sub>v</sub>.

The distal row, *mesocarpus*, consisted of five distinct elements, three of which were partially ossified and two were unossified. Carpale<sub>1</sub> had an osseous nodule 17 mm. wide, and articulated with radiale, C<sub>2</sub> and M. Carpale<sub>2</sub> was unossified and articulated with radiale, intermedium, C<sub>1</sub>, C<sub>3</sub> and M<sub>II</sub>. Carpale<sub>3</sub> had an osseous nodule 24 mm. wide, and articulated with intermedium, C<sub>2</sub>, C<sub>4</sub> and M<sub>III</sub>. Carpale<sub>4</sub> had an osseous nodule 16 mm. wide, and articulated with intermedium, ulnare, C<sub>3</sub>, C<sub>5</sub> and M<sub>IV</sub>. Carpale<sub>5</sub> was unossified and articulated with ulnare, pisiform cartilage, C<sub>4</sub> and M<sub>V</sub>. The carpal elements in this Hyperoodon, though imperfectly ossified, corresponded in number and position with the bony carpus of the adult female previously described and a figure † of which is now reproduced on the next page; they showed that ossification did not proceed uniformly in the bones, for a needle passed through C<sub>2</sub> and C<sub>5</sub> failed to detect bone in the substance of their cartilage, whilst in C<sub>1</sub>, C<sub>3</sub> and C<sub>4</sub> the osseous nodule was visible on the surface. No os centrale was present in either carpus.

The hand was pentadactylous, the metacarpal of each digit articulated

\* In the *Proc. Roy. Soc. Edin.*, 1891-92, vol. xix. p. 70, I have discussed the morphology of the manus in the whalebone whale, *Balænoptera rostrata*.

† *Journ. of Anat. and Phys.*, October 1885, vol. xx. p. 184.

with its corresponding carpale, which belonged therefore to the same digit.  $M_I$  had an unossified phalanx;  $M_{II}$  had five phalanges in process of ossification;  $M_{III}$  had also five phalanges;  $M_{IV}$  had three phalanges and  $M_V$  had only two. The formula of the hand in *Hyperoodon* is as follows:—

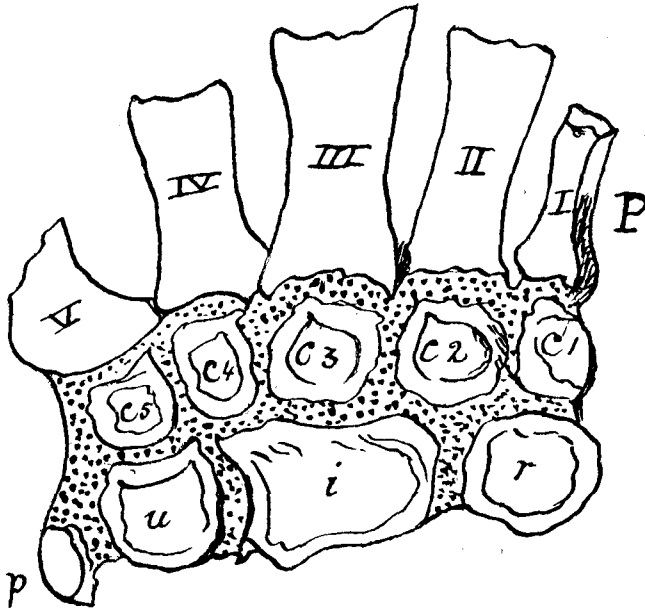
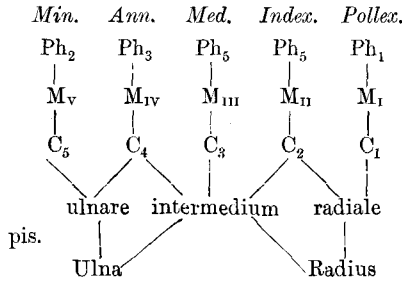


FIG. 3.—Carpo-metacarpal region of *Hyperoodon rostratus* enlarged from the figure in *Journ. Anat. and Phys.*, October 1885, vol. xx. p. 184. The dotted area represents cartilage.

The study of the manus in the younger animal confirmed the opinion, previously formed, from the examination of the *Hyperoodon* described and figured in my account of the Shetland *Mesoplodon*, that the distal row of the carpus in *Hyperoodon* possessed five distinct carpalia, one for each digit. In that memoir I referred to the generalised type of carpus described by Gegenbaur\* in the reptilian form *Chelydra serpentina*, in which five distinct distal carpalia were present. He contrasted this with the arrange-

\* Carpus and Tarsus, 1864.

ment in the mammalian carpus, in which the 4th and 5th metacarpals had together only one distal carpal, the os hamatum (unciform), a condition which he regarded as characteristic of the mammalia. My recognition of five distinct distal carpalia in *Hyperoodon* furnished, however, an example in a mammal of conformity in this respect with the earlier reptilian type.

In a valuable memoir, "Die Hand der Cetaceen,"\* the first part of which appeared in 1889, W. Kükenthal described the hand of a young *Hyperoodon* in which five distinct distal carpalia, "corresponding," he said, "with the carpus described by Turner," were present. They were approximately of equal size; one was associated with the radiale, one with the ulnare, and three with the intermedium; each carpale carried the metacarpal of a digit. Only the intermedium, radiale and carpale<sub>1</sub> possessed ossific nuclei. In an older animal five distal carpalia were seen, each with an osseous nucleus. In it an os centrale was also present. In the second part of the memoir, 1893, Kükenthal described a section of the hand of *Hyperoodon* in the Museum of the Royal College of Surgeons, London, in the carpus of which were three proximal carpals, five distal carpalia, and an os centrale. He had also two foetuses of this animal 55 and 15·8 cm. long respectively, in both of which carpale<sub>5</sub> was distinct from carpale<sub>4</sub>; in the larger foetus carpale<sub>2</sub> was partially fused with carpale<sub>3</sub> and an os centrale was present.

The hands in the two specimens which I have personally examined and the carpal regions in the five animals described by Kükenthal prove conclusively that *Hyperoodon* possessed five distal carpalia in a large proportion of individuals. At the same time it should be stated that a smaller number of distal carpalia has been described in some skeletons. Thus Vrolik's example had four bones; Van Bambeke spoke of four bones, C<sub>1</sub> and C<sub>2</sub> separate, C<sub>3+4</sub> conjoined; Max Weber stated that in one specimen in Amsterdam four distal carpals were found, viz. C<sub>1</sub> to C<sub>4</sub>, C<sub>5</sub> not being represented; † whilst in a smaller animal only three bony distal carpalia had been developed, the fourth probably not having reached the stage of ossification.

### *Delphinidæ.*

#### DELPHINUS DELPHIS—*The Common Dolphin.*

I have dissected two females of this dolphin; one, 5 feet 5½ inches in a straight line, was shot in the Firth of Forth in February 1887; ‡ the other,

\* *Vergleich. Anat. Entwicklungsgeschichte untersucht an Wahlthieren*, Jena, Erster Theil 1889, Zweiter Theil 1893; also in *Denksch. der medic.-natur. wiss. Gesellsch. zu Jena*, Dritter Band, 1889 and 1893.

† *Morphologisches Jahrbuch*, May 1888, Bd. xiii., Taf. xxvii. fig. 4, p. 626.

‡ *Proc. Roy. Phys. Soc. Edin.*, 1887, p. 346.



taken in Shetland in February 1895,\* was 5 feet 8 inches long. The smaller specimen was not adult, as the epiphyses were only partially ossified, but in the longer animal the radial and ulnar epiphyses were ossified, though not fused with the shafts. The hand was pentadactylous. The *procarpus* consisted of an osseous radiale 15 mm. wide, an intermedium 20 mm. wide, and an ulnare 16 mm. wide in the longer, though with smaller osseous nodules and more cartilage in the younger animal. The radiale articulated with radius, intermedium, carpale<sub>1</sub> and C<sub>2</sub>; the intermedium with radius, ulna, radiale, ulnare and two distal carpalia. The ulnare articulated with ulna, intermedium, a third carpal and metacarpal<sub>V</sub>.

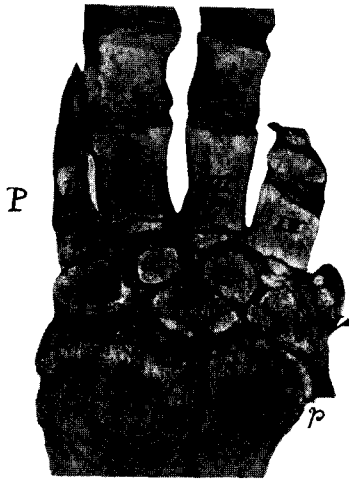


FIG. 4.—Dorsal surface, right manus, *Delphinus delphis*.

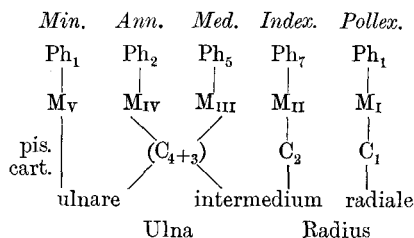
Only three bones were present in the distal row. At the radial end of this row was the bone which I have designated carpale<sub>1</sub>, though some writers regard it as the metacarpal of the pollex. In the older animal it was 9 mm. in transverse diameter and articulated with radiale, largely with metacarpal<sub>I</sub> and slightly with metacarpal<sub>II</sub>; it obviously belonged to the pollex. The bone next to it I name carpale<sub>2</sub>; it was 13 mm. wide and articulated with radiale, intermedium, largely with M<sub>II</sub> and slightly with M<sub>III</sub>; it belonged to the index digit, and may be regarded therefore as carpale<sub>2</sub>. The third bone in the row, 13 mm. wide, probably represented two carpalia; it articulated with intermedium, ulnare, and in almost equal proportions with M<sub>III</sub> and M<sub>IV</sub>; it seemed to belong, therefore, to both medius and annularis, and was probably formed by the fusion of carpalia<sub>3</sub> and 4. No other osseous

\* I am indebted to Mr Thos. Anderson of Hillswick for this specimen.

nodule was in the distal row, but in the younger specimen a piece of cartilage intervened on one border between  $C_{3+4}$  and the ulnare, and on the other between  $C_{3+4}$ ,  $M_{IV}$  and  $M_V$ : it possibly represented an unossified carpale<sub>5</sub>. Neither specimen showed an os centrale. The pisiform cartilage extended on the border of the carpus from the ulna to the fifth metacarpal. In the digits the metacarpals and phalanges had both proximal and distal epiphyses.  $M_I$  the pollex had one phalanx;  $M_{II}$  had seven phalanges;  $M_{III}$  five phalanges;  $M_{IV}$ , two, and  $M_V$  only one phalanx; owing to the absence of carpale<sub>5</sub>  $M_V$  was connected through the intermediate cartilage with the ulnare and was rudimentary.

Max Weber in his very suggestive memoir "Ueber den Carpus der Cetaceen" \* figured the manus of this dolphin; he considered that only two distal carpalia were present, which he numbered  $C_{2+3}$  and  $C_4$ ; they corresponded to the carpalia that I have named  $C_2$  and  $C_{3+4}$ , whilst the bone named in my description  $C_1$  he regarded as the metacarpal of the pollex. Kükenthal inclined to the same view, though he thought this bone might be carpale<sub>1</sub>, or that  $C_1$  might have blended with  $M_I$ , or with radiale, or had perhaps disappeared.

The formula of the hand of *Delphinus delphis* is as follows:—



#### DELPHINUS ACUTUS (*Lagenorhynchus leucopleurus*).

In April 1906 a white-sided dolphin was stranded near Dunrobin Castle, and the external characters and skeleton were described by me in June of the same year.† I may refer to that description for details regarding the animal, and I reproduce a radiograph of one flipper (fig. 5).

The animal was a female and was not adult, for the skeleton was imperfectly ossified, and the radio-ulnar epiphyses were not fused with the shafts. The *procarpus* consisted of radiale, intermedium and ulnare. Two relatively large bones were present in the middle of the mesocarpus, one of which articulated with  $M_{II}$  and  $M_{III}$ , and obviously represented  $C_2 + C_3$ ,

\* *Morphologisches Jahrbuch*, May 1888, Taf. xxvii. fig. 7.

† *Proc. Roy. Soc. Edin.*, vol. xxvi. p. 310, 1906.

the other articulated with  $M_{III}$  and  $M_{IV}$ , and represented without doubt  $C_4$ , though possibly also  $C_5$  was fused with it, as no separate  $C_5$  was present. On the radial side of  $C_2 + C_3$  a bone which I regarded as  $C_1$  was in series with the radiale and the pollex. The pisiform cartilage was unossified, and there was no sign of an os centrale. The metacarpals were five in number, and that of the fifth articulated with the ulnare. The metacarpals and phalanges had proximal and distal epiphyses, but the phalanges of the pollex and minimus were not ossified.

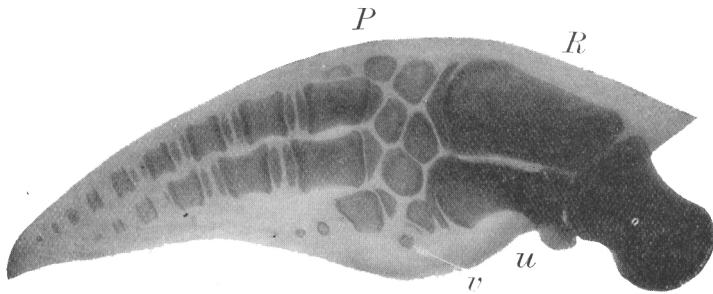
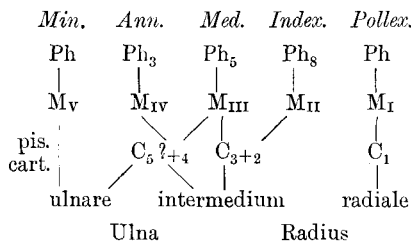


FIG. 5.—Radiogram of flipper of *Delphinus acutus*.

Kükenthal has described an embryo of this dolphin 45.5 cm. long, in which he recognised two cartilaginous distal carpalia comparable with the relatively large bones above described. A third cartilage distal to the radiale similar to my  $carpale_1$  was present, but Kükenthal left it an open question whether it should be regarded as  $carpale_1$  or the metacarpal of the pollex; in the latter case  $carpale_1$  had either disappeared or become fused with the radiale.

I suggest the following formula for the hand of *Delphinus acutus*:—



LAGENORHYNCHUS ALBIROSTRIS (*Delphinus albirostris*).

In 1888 I obtained an adult female white-beaked dolphin, and had the skeleton mounted in the Anatomical Museum. The manus was carefully dissected. The radial and ulnar epiphyses and the metacarpal and phalangeal epiphyses were fused with their respective shafts. The carpal

bones were fully ossified. In the *procarpus* the radiale, with a transverse diameter 25 mm., articulated with radius, with a distal carpal which I regard as  $C_{2+3}$ , and with metacarpals I and II. The intermedium 30 mm. wide articulated with radius, ulna, ulnare and the two distal carpalia. The ulnare 24 mm. wide articulated with ulna, intermedium, distal carpal<sub>4</sub>, with the metacarpal of digit V, but was separated from  $M_{IV}$  by an interval occupied by cartilage.

The distal row of the carpus contained only two bones. The larger was wedged between and separated the radiale and intermedium from each

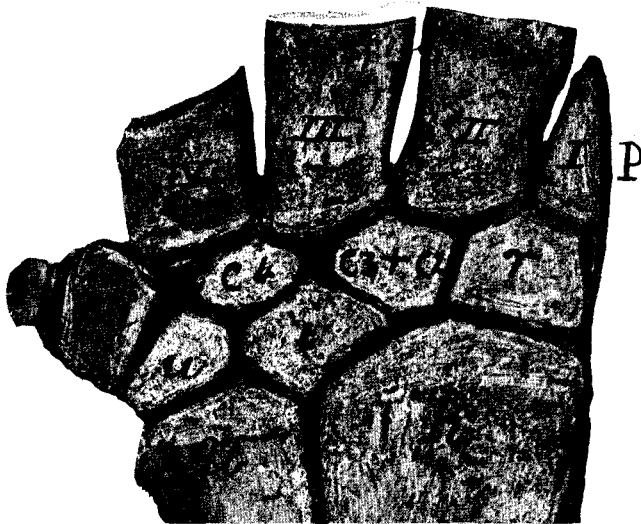


FIG. 6.—Left manus, dorsal surface, *Lagenorhynchus albirostris*.

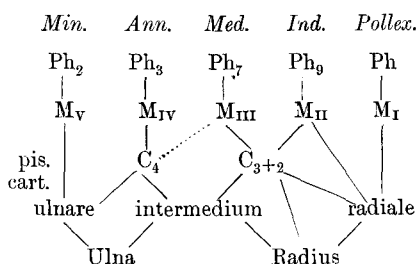
other; it was 27 mm. wide, and articulated with both these bones, slightly with the carpal end of the radius, extensively with metacarpals II and III, and also with the smaller disto-carpal; it was obviously carpal<sub>2+3</sub> fused together. The intermedium and the larger carpale were marked by a shallow groove on both palmar and dorsal surfaces, which was in line with the interosseous space in the forearm and with the interval between  $M_{II}$  and  $M_{III}$ ; the groove was doubtless for a tendon, or an artery. The smaller carpale was 24 mm. wide and articulated with intermedium, ulnare, almost equally with  $M_{III}$  and  $M_{IV}$ , and with the larger disto-carpale; to its ulnar side a piece of unossified cartilage separated it from  $M_V$ ; it is marked  $C_4$  in fig. 6, and the unossified cartilage may represent an undeveloped  $C_5$ . A plate of pisiform cartilage was at the ulnar border of the carpus, and extended from the lower end of the ulna

to the base of  $M_V$ . No ossific nodule had been formed in it. The carpus did not contain an os centrale.

In digit I, the pollex, the metacarpal was elongated and somewhat conical; it articulated directly with the radiale, for carpale<sub>1</sub> was not developed, and also with carpale<sub>2+3</sub>; the phalanx was not ossified. In the other digits the metacarpals were flattened. Metacarpal<sub>II</sub> articulated for more than a third with radiale and the rest with carpale<sub>2+3</sub>; it had nine osseous phalanges. Metacarpal<sub>III</sub> articulated almost equally with carpalia<sub>2+3</sub> and  $C_4$ ; it had seven osseous phalanges. Metacarpal<sub>IV</sub> articulated with carpale<sub>4</sub> and with the cartilage between it and the ulnare; it had three osseous phalanges. Metacarpal<sub>V</sub> was marked by a groove on the dorsal surface which passed obliquely between the two lateral borders; the bone projected at the ulnar border of the manus, and was set at an angle to  $M_{IV}$ ; it articulated with ulnare and  $M_{IV}$  and it joined the pisiform cartilage; two rudimentary osseous phalanges were embedded in cartilage.

Max Weber gave figures of the manus in two specimens of *Lagenorhynchus albirostris*. In the older the three bones of the procarpus were represented, whilst only two disto-carpalia were figured, which he interpreted as  $C_2 + C_3$  and  $C_4$ , giving a significance like that which I have also attached to them. His conception of the metacarpus and phalanx of digit V corresponded with the conclusion to which I have subsequently arrived. From the figure of the carpus in the younger specimen it would seem that he recognised in it three distinct disto-carpalia, whilst a fourth was to be found in a bone occupying the position of the ulnare: the ulnare proper had either disappeared or become blended with the intermedium.

I suggest the following formula for *L. albirostris*:—



#### PHOCENA COMMUNIS (*Delphinus phocena*).

The manus of the common porpoise was dissected in an adult female in December 1892, and has also been examined in other specimens.

In the adult the radial and ulnar carpal epiphyses were united with the

shafts. The *procarpus* contained the three customary bones. The radiale, 14 mm. in transverse diameter, articulated with radius, intermedium, the carpal cartilage associated with the pollex and with  $M_{II}$ . The intermedium was 14 mm. wide, grooved on the palmar surface, and articulated with radius, ulna, radiale, ulnare and the two distal carpalia. The ulnare was 7 mm. wide and articulated with ulna, intermedium, the more ulnar distal carpal,  $M_V$ , and with the pisiform cartilage. This cartilage was only 5 mm. wide and 7 mm. long, and extended from the ulnar epiphysis to  $M_V$ ; it did not contain an ossified nucleus. No *os centrale* was seen.

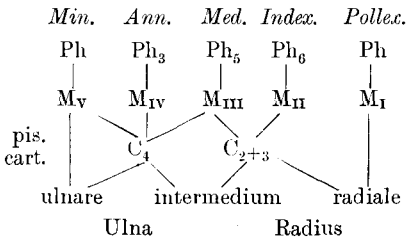
Two distal-carpalia were situated in the mesocarpus. The more radial was a small bone 9 mm. wide, with a groove in line with that on the intermedium opposite the interval between  $M_{II}$  and  $M_{III}$ , with both of which the nodule articulated, as well as with the radiale, intermedium, and the more ulnar distal carpal. The last-named bone was 12 mm. wide, and articulated with ulnare, intermedium, the radial distal carpal, and  $M_{III}$ ,  $M_{IV}$  and  $M_V$ . The more radial bone apparently represented  $C_{2+3}$ , and the more ulnar  $C_4$ , or it may be  $C_{4+5}$ . Both  $C_1$  and  $C_5$  were absent as independent units.

The hand was pentadactylous. Digit I, the pollex, was so close to the radial border and so slender that it might easily have been overlooked. It was connected with a band of cartilage on the radial border of the carpus extending to the radiale, which, though no ossific nodule was found in it, might perhaps represent carpal<sub>1</sub>.  $M_I$ , 12 mm. long, was very slender, and had at its distal end an unossified phalanx. Digit II, the longest, consisted of  $M_{II}$ , 21 mm. long, and six small osseous phalanges, the terminal of which was no bigger than a very small shot; it was connected with the carpal cartilage of the pollex, the radiale, and the outermost distal carpal. Digit III had a metacarpal 20 mm. long and five small phalanges;  $M_{III}$  articulated with both distal carpals. Digit IV had a metacarpal 13 mm. long and three small phalanges. Digit V projected from the ulnar side of the carpus;  $M_V$ , 8 mm. long and 11 mm. wide, was connected with  $M_{IV}$ , the ulnar distal carpal, the ulnare and the pisiform cartilage.

The presence of three bones in the procarpus of the porpoise and of only two disto-carpalia has been generally described by anatomists. Both Weber and Kükenthal numbered them as  $C_1$  and  $C_2$ . Kükenthal considered that  $C_1$ , as described in this memoir on the radial border of the carpus, was either absent or blended with  $M_I$ , or with the radiale; his  $C_1$  would therefore represent my  $C_2 + C_3$  conjoined, whilst his  $C_2$  might be the conjoined  $C_4 + C_5$ , though more likely from its position only  $C_4$ , whilst  $C_5$  had either not developed or had blended with the ulnare.



The following formula is given for *Phocæna communis* :—



### GLOBICEPHALUS MELAS (*Pilot Whale*).

In my previous memoir on *Mesoplodon*,\* so frequently referred to, I gave a short description of the carpus of *Globicephalus melas*. I have again studied this specimen, compared it with the descriptions which were subsequently published by Max Weber and by Kükenthal, and have been led to modify the opinion which I had previously expressed on the morphology of certain of its disto-carpalia.

In the two hands of my specimen the radial and ulnar epiphyses were ossified, but not fused with the shafts. The bony elements of the carpus were well formed and dominated the cartilaginous matrix. The radiale was 47 mm. in transverse diameter, the intermedium 40 mm. and the ulnare 24 mm.

The bone on the radial border of the carpus, which I had previously spoken of as carpale<sub>2</sub>, I now regard as carpale<sub>1</sub>, which necessarily modifies the numerical order of the other disto-carpalia, so that the former carpale<sub>3</sub> now becomes C<sub>2</sub>, and the former C<sub>4</sub> becomes carpale<sub>3</sub>. Again, the bone situated in the plane of the proximal ends of the metacarpals, which from its rounded form and roughened surface I had regarded as distal carpal C<sub>1</sub>, is now described as the metacarpal of the pollex. This change in opinion of the morphology of these bones is based on a fuller recognition of the position of the os centrale, which in the original description was regarded as placed between carpalia<sub>2</sub> and <sub>3</sub>, whereas its true position is between carpale<sub>1</sub>, C<sub>2</sub>, the radiale and the intermedium. The present description follows, therefore, the amended view of the morphology of the bones.

Carpale<sub>1</sub>, 34 mm. in transverse diameter, articulated with radiale, an os centrale in right carpus, and about equally with M<sub>I</sub> and M<sub>II</sub>: carpale<sub>2</sub>, the bone of which was 33 mm. wide, articulated with intermedium, os centrale in right carpus, radiale in left, carpale<sub>3</sub>, and about equally with M<sub>II</sub> and M<sub>III</sub>: carpale<sub>3</sub>, the bony part 31 mm. wide, articulated in right carpus with inter-

\* *Journ. Anat. and Phys.*, Oct. 1885, vol. xx. p. 185.

medium, ulna, ulnare, carpale<sub>2</sub>, and about equally with M<sub>III</sub> and M<sub>IV</sub>; in this carpus it was distinct from the ulnare, but in the left hand it was fused with it and formed a conjoined bone (compare fig. 7 with fig. 8). No separate carpale<sub>4</sub> or <sub>5</sub> existed, though possibly C<sub>3</sub> may contain the element C<sub>4</sub>, and carpale<sub>5</sub> may potentially be present as a part of M<sub>V</sub>, for the ulnare was relatively small, so that C<sub>5</sub> could scarcely be regarded as fused with it.

In the interval between carpale<sub>1</sub>, C<sub>2</sub>, the radiale and the intermedium was shrunken cartilage containing in the right carpus a small osseous nodule, which may be regarded as an os centrale, but in the left carpus the corresponding cartilage was unossified. Unossified and shrunken pisiform cartilage



FIG. 7.—The right carpus of *G. melas*.

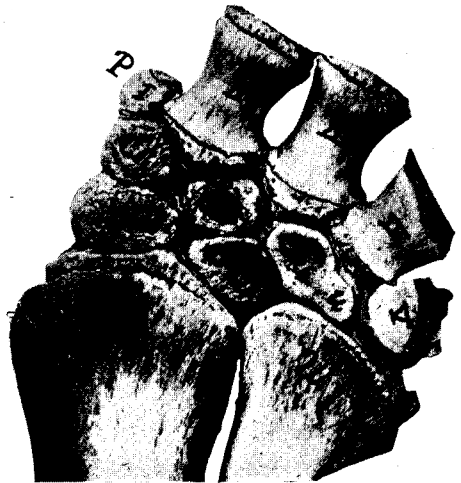


FIG. 8.—The left carpus of *G. melas*.

formed the ulnar border of the carpus. In their articulations the metacarpals were arranged as follows:—M<sub>I</sub>, the rounded bone with roughened surface for the pollex above referred to, articulated with carpale<sub>1</sub>: M<sub>II</sub> with C<sub>1</sub> and C<sub>2</sub> about equally, and with the cartilage of the os centrale: M<sub>III</sub> with C<sub>2</sub> and C<sub>3</sub> about equally: the carpal ends of M<sub>II</sub> and M<sub>III</sub> were bifaceted, the facets separated by a mesial ridge were inclined laterally, so that the corresponding distal carpalia were not opposite to the ridge, but to the lateral facets and to the interval between two metacarpals: M<sub>IV</sub> with carpale<sub>3</sub> and the ulnare: M<sub>V</sub> with ulnare, the ulna and the pisiform cartilage.

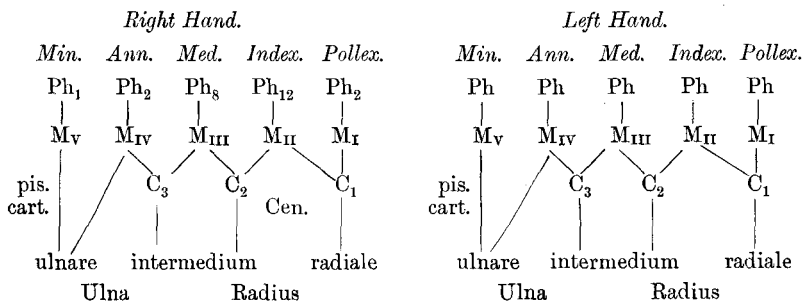
In Max Weber's figure of the hand of *Globicephalus melas* three distinct disto-carpalia were recognised:—carpale<sub>1</sub>, the most radial, jointed with M<sub>I</sub> and M<sub>II</sub>: a bone which he regarded as representing carpale<sub>2+3</sub> jointed with the bases of M<sub>II</sub> and M<sub>III</sub>: next to it a bone lettered C<sub>4</sub> which articulated

with  $M_{III}$  and  $M_{IV}$ . No carpal<sub>5</sub> was present, and both  $M_{IV}$  and  $M_V$  articulated with the ulnare and the latter also with the ulna. An os centrale occupied the position described above in my specimen.

Kükenthal had the opportunity of studying several embryos of *G. melas*. He recognised only three separate distal carpalia. Carpal<sub>1</sub> in the larger embryos was the biggest and had a short metacarpal<sub>I</sub>; carpal<sub>2</sub> was associated with  $M_{II}$  and  $M_{III}$ , though principally with  $M_{II}$ ; carpal<sub>3</sub> with  $M_{III}$  and  $M_{IV}$ ; whilst carpal<sub>5</sub> was directly fused with the ulnare with which  $M_V$  articulated. He referred to an os centrale described by me as present in the well-grown *G. melas*, but in the majority of the hands of his embryos the centrale was not visible. He stated that the foetal carpus corresponded in the number and position of its elements with that of the well-grown animal. The pisiform cartilage was well formed in the embryos, and in all a small, rounded piece of cartilage projecting from the radial border of the radiale represented the præpollex of von Bardeleben.

As is well known, *G. melas* is distinguished by the number of the phalanges in the second and third digits and by the great length of the digits, the index being the longest.

The formulæ of the carpus in my specimen are appended, and that in the right hand corresponds with formula No. 2 in Kükenthal's memoir, p. 34.



#### GRAMPUS GRISEUS (*Risso's Dolphin*).

In September 1899 a school of Risso's dolphin was captured near Hillswick, Shetland, and specimens were sent to me by Dr Charles Anderson.\* I dissected the hands in two animals. From the state of the ossification neither had reached maturity, though one was more advanced than the other: the radio-ulnar epiphyses were ossified, though not fused with the shafts.

\* See my account in *Proc. Roy. Phys. Soc. Edin.*, vol. xi. p. 192, 1891-92; also my description of the Viscera in *Journ. Anat. and Phys.*, vol. xxvi. p. 258, 1892. Two of the skeletons are mounted in the Anatomical Museum of the University.

In the more advanced specimen the carpal bones were well ossified, but in the other the cartilage was more abundant. The *procarpus* had radiale, intermedium and ulnare. In the older animal the radiale was 33 mm. in transverse diameter, the intermedium 40 mm. and the ulnare 28 mm. The radiale articulated with radius, intermedium, carpalia<sub>1</sub> and<sub>2</sub>. The intermedium was grooved on its palmar surface; its proximal border mostly articulated with radius and only slightly with ulna; it also articulated with radiale, C<sub>2</sub> and C<sub>3+4</sub>, the latter of which intervened between intermedium



FIG. 9.—Dorsal surface, left manus, *Grampus griseus*.

and ulnare. The ulnare articulated with the inner half of the ulnar epiphysis, with C<sub>3+4</sub>, with M<sub>IV</sub> and M<sub>V</sub>, and with the pisiform cartilage, which contained no osseous nodule.

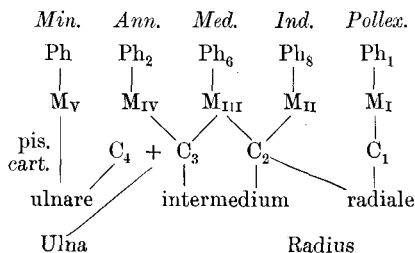
The distal row had three separate carpalia. Carpale<sub>1</sub> was 25 mm. wide and articulated with radiale, C<sub>2</sub> and the epiphysis of M<sub>I</sub>. Carpale<sub>2</sub> was 31 mm. wide and articulated with radiale, intermedium, C<sub>3</sub>, largely with M<sub>II</sub> and slightly with M<sub>III</sub>. Carpale<sub>3</sub>, 29 mm. wide, was grooved on palmar surface, and articulated with intermedium, ulnare, epiphysis of ulna, largely

with  $M_{III}$  and less so with  $M_{IV}$ ; carpale<sub>4</sub> was probably fused with it. No os centrale was present, and the pisiform cartilage extended from ulna to 5th metacarpal.

The manus was pentadactylous. Digit I had its metacarpal 25 mm. long, somewhat conical and articulating by its proximal epiphysis with carpale<sub>1</sub>, whilst distally it was continuous with an unossified phalanx. The other metacarpals were flattened bones, which as well as the phalanges had proximal and distal epiphyses. The second metacarpal articulated with  $C_2$  and very slightly with  $C_1$ ; its digit was the longest and had eight phalanges. The third articulated with carpalia<sub>2</sub> and <sub>3</sub>, and had six phalanges. The fourth, whilst 31 mm. in transverse diameter, was only 20 mm. long; it articulated with carpale<sub>3</sub> and with the ulnare; its two phalanges were short and flattened. The fifth metacarpal consisted of a bony nodule 24 mm. wide and 13 mm. long, which was imbedded in cartilage continuous with the pisiform, and there was no bony phalanx.

A feature in this manus was the rudimentary condition of the fifth digit, the absence of carpale<sub>5</sub>, and no separate  $C_4$ , though this element may have blended with the ulnare, or rather with carpale<sub>3</sub> (fig. 9), which articulated with both  $M_{III}$  and  $M_{IV}$ . From the close relation of the fifth metacarpal with the ulnare,  $C_5$  had either never been developed or had disappeared very early, either by atrophy, or by fusion with the ulnare or with  $M_V$ . So rudimentary was the fifth digit that in the manus of the younger of the two dolphins it was scarcely recognisable, and the manus almost seemed as if it were tetradactylous.

The formula in the well-ossified manus of Risso's dolphin was as follows:—

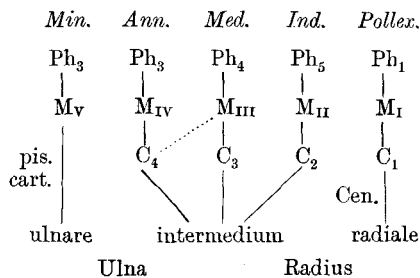


*DELPHINAPTERUS LEUCAS (Beluga or White Whale).*

In his memoir "On the Hand in the Cetacea," W. Kükenthal described and figured the characters in an adult Beluga and in a number of embryos at various stages of development. The *procarpus* was typical. The *mesocarpus* was variable. In the youngest embryo five cartilaginous disto-carpalia  $C_1$  to  $C_5$  were recognisable. Carpale<sub>5</sub> however disappeared early,

so that at a later stage only four cartilaginous distal carpalia were present. A fusion of carpale<sub>3</sub> with C<sub>4</sub> might also occur and the number be reduced to three carpalia, C<sub>1</sub>, C<sub>2</sub>, C<sub>3+4</sub>. He thought that carpale<sub>5</sub> probably became a part of the ulnare. He saw sometimes two centralia, one of which might remain, though usually both fused with adjoining bones.

In an important memoir on the Anatomy of a Beluga the late Sir John Struthers gave a detailed account with figures\* of the structure of the manus. The procarpus consisted of the three customary bones, whilst the other bones were regarded as four distal carpalia C<sub>1</sub> to C<sub>4</sub>, a small os centrale, and a pisiform, the ulnare, centrale, C<sub>3</sub> and pisiform not being ossified. As Sir John Struthers had presented to me for the Anatomical Museum this and other specimens from his collection of cetacea, I have examined the manus, and I concur in his interpretation of the carpal elements. Thus carpale<sub>1</sub> belonged to the pollex: C<sub>2</sub> was mainly for M<sub>II</sub>, though with a slight articulation with M<sub>III</sub>: C<sub>3</sub> was for M<sub>III</sub>, though C<sub>4</sub> was divided equally between M<sub>III</sub> and M<sub>IV</sub> and its distal angle intervened between these two metacarpals: no independent C<sub>5</sub> existed, for M<sub>V</sub> articulated directly with the ulnare, which was relatively large and probably included, though still in the cartilaginous stage, C<sub>5</sub>, and its dorsal angle also reached the base of M<sub>IV</sub>. The area of cartilage interposed between radiale, intermedium, C<sub>1</sub> and C<sub>2</sub>, which Struthers regarded as an os centrale, holds the position of that carpal element and may be regarded as its unossified representative. The formula of this carpus corresponds with No. 4 of the formulæ of Beluga given by Kükenthal on p. 28 of his memoir, except that there is only one os centrale.



#### MONODON MONOCEROS (*Narwhal*).

In 1887 and 1889 Professor Leboucq of Ghent published an account of his researches on the morphology of the hand in marine mammals,† and described the constitution of the carpus in four foetuses of the Narwhal.

\* *Journ. Anat. and Phys.*, vol. xxx., Oct. 1895.

† *Anatomischer Anzeiger*, 16th March 1887; *Archives de Biologie*, t. ix. p. 571, 1889.



In all the specimens the three cartilaginous proximal elements, radiale, intermedium, and ulnare, were present. In one the intermedium and ulnare were in process of fusion with each other, but the pisiform cartilage was recognised in only the two smallest. In three specimens (B, C, D) five disto-carpalia were seen, of which  $C_1$  was blended with the base of  $M_I$ , but the fusion was not sufficient to obliterate the primitive separation;  $C_2$  articulated with  $M_{II}$ ;  $C_3$ , usually the largest, articulated with  $M_{III}$ ;  $C_4$  with  $M_{IV}$ ;  $C_5$  for  $M_V$  was distinct in specimen (C), but in B and D it was in process of fusion with carpal $_4$ . In the smallest foetus (A)  $C_1$  was distinct from  $M_I$ , but  $C_5$  was not differentiated, and possibly had not been developed as an independent unit. A and B had an os centrale in the interval between the radiale, intermedium, and carpal $_2$  and  $_3$ , which in B had the form of a rounded nodule continuous with the distal border of the intermedium. In the largest foetus (D) the centrale was most distinct and in process of fusion with  $C_2$ , though the original line of separation was apparent. In a paper on the carpus of Beluga, published in 1893, Kükenthal referred to an embryo of *Monodon monoceros*, 24 cm. long, in which he saw two centralia.\*

I may also state that Leboucq in his memoir described three foetuses of Beluga, in each of which he found a well-formed centrale; in one it was free between the radiale, intermedium, and  $C_2$ ; in another it was in process of fusion with  $C_2$ ; in the third it was partially fused with the radiale.

In the collection of cetacean limbs presented to me by Sir John Struthers were three specimens of the Narwhal, in one of which, an adult, the radio-ulnar epiphyses were fused with their respective bones; but in the other two the ossification was not so complete. The adult was dissected by Professor Struthers, who, so far as I know, did not publish a description of it.† Radiograms of the three hands were taken for me by Mr Ernest Henderson. That of the adult has greatly assisted me to determine the constitution of the carpus: in it the bony radiale was 26 mm. in transverse diameter; the intermedium, deeply grooved on both surfaces, was 37 mm.; the ulnare was 26 mm. wide. In the distal row a piece of cartilage separated the radiale from  $M_I$ ; in the radiogram it was seen to have in its substance a small nodule of bone, and it probably represented  $C_1$ , which was

\* *Morphologisches Jahrbuch*, vol. xix. p. 63, 1893.

† At the Aberdeen meeting of the British Association, September 1885, Professor Struthers exhibited the carpal bones and cartilages of several cetacea, including the Narwhal, but his description was not published. See Report of meeting, p. 1056. In the *Journal of Anat. and Phys.*, vol. vi. p. 115, 1872, he referred in a footnote to the fibrous arrangements replacing muscles in the hand of the Narwhal, but did not speak of the bones.

only partially ossified; so that this element of the carpus was not fused with  $M_I$ , but resembled the foetus A in Leboucq's collection, in which  $C_1$  formed an independent unit. To its ulnar side was a well-defined bony carpale, 25 mm. wide, which articulated with the cartilage of  $C_1$ , with the intermedium, os centrale,  $C_4$ ,  $M_{II}$  and  $M_{III}$ ; it should be regarded as  $C_2$  conjoined with  $C_3$ .  $C_4$ , 21 mm. wide, articulated with intermedium, ulnare,  $C_{2+3}$ ,  $M_{III}$ , and  $M_{IV}$ , also with a piece of cartilage on its disto-ulnar border

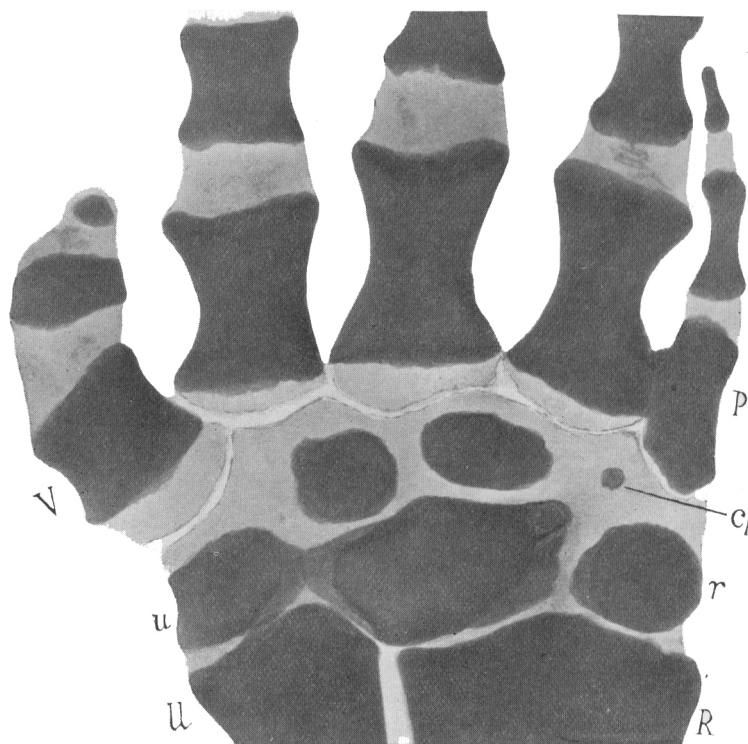


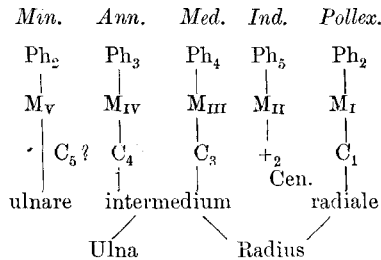
FIG. 10.—Radiogram of manus of adult *Monodon monoceros*.

which was situated between the ulnare,  $M_{IV}$  and  $M_V$ , and may possibly represent an unossified  $C_5$ . Projecting from the disto-radial border of the intermedium, and continuous with it by a narrow neck, was a nodule of bone 7 mm. in transverse diameter, which articulated with the radiale,  $C_{2+3}$ , and the cartilage with its nodule described as  $C_1$ ; it was obviously an os centrale fused with the intermedium; in its relations and intimate association with that bone it corresponded with the arrangement in the foetus B in the Leboucq collection.  $M_I$  articulated with the probable  $C_1$  and with the radiale;  $M_{II}$  with  $C_1$  and  $C_{2+3}$ ;  $M_{III}$  with  $C_{2+3}$  and  $C_4$ ;

$M_{IV}$  with  $C_{IV}$  and the cartilage of the possible  $C_V$ ;  $M_V$  slightly with that cartilage, but mostly with the ulnare.

The two less advanced specimens had in the distal row the bony carpalia which I have designated  $C_{2+3}$  and  $C_4$ ; no ossific nodule was seen in the radiograms in the cartilage between the radiale and  $M_p$ , or in that between the ulnare and  $M_V$ . In both a process of bone projected from the disto-radial border of the intermedium, like that which I have interpreted in the adult as an os centrale.

The formula of *Monodon monoceros* is as follows:—



#### MORPHOLOGICAL SUMMARY.

It will have been seen from the foregoing description that in the Ziphioid whales, *Hyperoodon* and *Mesoplodon*, and in the Delphinidæ, whilst the three bones of the proximal row of the carpus, and the pisiform cartilage either unossified or only partially so, are constant in number and correspond generally in their arrangement, yet that the distal carpalia vary in number, and in their articulations with the procarpus and with the metacarpal bones; also that the ossa centralia are inconstant. *Hyperoodon* should, as I stated in 1885, be regarded as the type in which each of the five digits has its corresponding distal carpal, for articulation with the metacarpal of the digit to which it belongs. In other genera and species, however, a smaller number of distal carpalia are present, and the question naturally arises which members of the type-number have remained and which have disappeared as independent units. The range in number varies from five in *Hyperoodon* to four, or three, or even two in other species. In my memoir on the Shetland *Mesoplodon*, 1885, I discussed the question of the diminution in the type-number from five distal carpalia, and stated that it "may be due either to one or more centres of ossification not having formed in the carpal cartilage, or to the fusion with each other of ossific nuclei which were distinct in the younger condition of the same carpus." The terminology of the carpal bones introduced

by Gegenbaur, and their substitution for the older descriptive terms (adopted from human anatomy in the writings of anatomists as eminent as Owen, van Beneden and Flower), have greatly facilitated the description of this region; the graphic formulæ employed by Leboucq, Max Weber, and Kükenthal, which I have also used in this memoir, enable the eye to follow the description and assist one in recognising the morphology of the carpal bones in the manus of the Cetacea.

The guide to the solution of this problem is to be found in a manus in which the number of disto-carpalia corresponds with that of the digits; whilst in specimens in which some carpalia are wanting, it is important to study the articulations of those which are present with the metacarpal bones.

As previously stated, Hyperoodon provides us with the necessary key, for in this carpus each metacarpal, in the majority of specimens examined, has a definite disto-carpal for articulation with it. The researches of Kükenthal and Leboucq into the development of embryos of several species of Cetacea have shown that, in the early stages of Beluga and Monodon, a fifth differentiated cartilage existed in the distal row, which was not represented by a bony  $C_5$  in the fully formed carpus, so that in the progress towards ossification this carpal element had disappeared.\* A similar defect has also been observed in the carpus of a few specimens of Hyperoodon; the missing bone was carpal<sub>5</sub>, and the formula of the distal row was reduced in them to carpalia<sub>1, 2, 3, 4</sub>.

Are we to assume that either five carpalia constitute in the Cetacea generally the normal number of elements in the distal row in the very early stages of development; or that a carpus may be formed at its initial development in which the elements of the disto-carpalia are fewer than five? In the latter instance the diminution in number would be a fundamental developmental defect, and could only be satisfactorily determined by the study in a given species of a sufficient number of specimens at the commencement of and in the early stages of cartilaginous differentiation in the carpus. In the former case the deficiency would be due to the disappearance of the cartilaginous precursors of the bones, either by atrophy in the early stages of development, or by fusion between adjoining cartilages or bones at somewhat later stages. The fusion might take place: *a*, between cartilages or bones in the same row; *b*, between cartilages or bones in the distal with those in the proximal row; *c*, between the disto-carpalia and the metacarpals.

\* Gervais, in his part of the great *Ostéographie des Cétacés* by Van Beneden and himself, figured the manus of a foetal Hyperoodon in which five cartilages were present in the distal row, but he regarded the fifth of these as a pisiform.

Examples of fusion in the same row are not uncommon in the cetacean carpus, and their articulation with the metacarpals should be carefully noted in determining which of the bones are fused together. Of the species described in this communication there can be no doubt that the rule in *Mesoplodon bidens* is for  $C_2$  to fuse with  $C_3$ , and to articulate with  $M_{II}$  and  $M_{III}$ ; usually also  $C_4$  fuses with  $C_5$  and articulates with  $M_{IV}$  and  $M_V$ . The fusion of  $C_2$  and  $C_3$  constitutes the *ziphius* type of carpus of Kükenthal. In the Dalgety Bay *Mesoplodon* the small size of the most ulnar disto-carpal led me to think that it represented only  $C_4$  for articulation with  $M_{IV}$ ; whilst  $M_V$  was displaced from the proper distal border of  $C_4$ , and articulated with the ulnare;  $C_5$  was, on this view, possibly absent.

In *Lagenorhynchus albirostris*  $C_2$  and  $C_3$  were fused, and the conjoined bone articulated with  $M_{II}$  and  $M_{III}$ ;  $C_4$  was small, articulated with  $M_{IV}$  and not with  $M_V$ ;  $C_1$  and  $C_5$  were absent as separate bones or were perhaps combined with others.

In *Grampus griseus*  $C_3$  and  $C_4$  were fused and articulated with  $M_{III}$  and  $M_{IV}$ , whilst  $C_2$  remained as a separate bone for  $M_{II}$ , and  $C_1$  articulated with the pollex.

In *Delphinus acutus* and *Monodon monoceros*  $C_2$  and  $C_3$  were fused and articulated with  $M_{II}$  and  $M_{III}$ ;  $C_4$  was present, and articulated principally with  $M_{IV}$ ;  $C_1$  was also present, but  $C_5$  did not exist as a separate bone. *Phocaena communis* had only two disto-carpals, being the minimum number found in the Odontoceti; of these one apparently represented  $C_2$  fused with  $C_3$ , whilst the other was  $C_4$ ;  $C_1$  and  $C_5$  were not visible as independent units.

As a distinct example of fusion of a distal with a proximal carpal I may refer to fig. 8, the left carpus of *Globicephalus melas*, in which  $C_3$  had fused with the ulnare. The question of fusion between bones of the distal and proximal rows, or of the distal with the metacarpals, arises also in connection with the condition of  $C_1$  and  $C_5$  of the distal carpalia, which bones may in several species be absent as independent units; the possibility of fusion either with a bone of the proximal row or with a metacarpal has to be considered.  $C_5$  is the element which most frequently has no separate representative, and which cannot definitely be regarded as fused with  $C_4$ . In *Delphinus delphis* and *acutus*, *Grampus griseus*, *Lagenorhynchus albirostris*, *Globicephalus melas*, *Phocaena communis*, *Delphinapterus leucas* (Beluga), *Monodon monoceros*,  $M_V$  articulated directly with the ulnare without the interposition of a separate disto-carpale. Kükenthal regarded this as the *Beluga* type of carpus common in the Odontoceti. It might arise from fusion of the cartilaginous  $C_5$  with the ulnare, or from

fusion of  $C_5$  with  $M_v$ , or from an early atrophy and disappearance of the cartilaginous  $C_5$ .

The question whether  $C_1$  is present or absent in some species of cetacea has been a matter of discussion. There can be no doubt of its presence in Mesoplodon, Hyperoodon, Beluga and Grampus. In Lagenorhynchus and Phocœna it was absent, and  $M_I$  articulated directly with the radiale, with which  $C_1$  might have fused; though, as Leboucq has shown in *Monodon monoceros*, the fusion of  $C_1$  with  $M_I$  does at times undoubtedly take place. In Delphinus, again, the question has arisen whether the bone immediately distal to the radiale is to be regarded as  $M_I$  or  $C_1$ . If the former, then the pollex would possess two phalanges, and its metacarpal would articulate directly with the radiale. If the latter,  $C_1$  would be interposed between the radiale and  $M_I$ , and the carpus would possess three disto-carpals. I have adopted the latter interpretation and applied it also to the carpus of Globicephalus.

As regards the os centrale, Mesoplodon and Globicephalus furnished examples of the presence of an os centrale as an independent bone; in the right manus of the St Andrews Mesoplodon a second centrale had been developed, and in that from Dalgety Bay an os centrale had fused with the radiale. In Monodon the centrale was fused with the intermedium. In the Struthers collection of cetacea, already referred to, is the dissected hand of an adult cetacean which, though not marked, is I believe that of Hyperoodon.\* The carpus consisted of ten bones and cartilages, three in the proximal row; five separate disto-carpalia, of which  $C_1$  and  $C_4$  were well ossified,  $C_2$  and  $C_3$  partially so, whilst  $C_5$  and the pisiform were unossified. An almond-shaped unossified os centrale, 21 mm. in transverse and 14 mm. in vertical diameter, was intercalated on the palmar surface between the radiale, intermedium, carpalia  $_1$  and  $_2$ . In the presence of an os centrale this specimen corresponded with specimens of Hyperoodon, two well grown and a fœtus, as described by Kükenthal. In Beluga an unossified piece of cartilage probably represented the centrale. Kükenthal came to the conclusion from his observations on embryos that centralia are not unfrequently present in the early stages, but that they commence to disappear when other elements in the carpus lose their

\* This limb probably belonged to the Hyperoodon which Professor Struthers obtained in 1871, and the finger muscles of which he described in the *Journal of Anat. and Phys.*, vol. vi. p. 115. At the Aberdeen meeting of the British Association, 1885, he exhibited the carpus of Hyperoodon along with those of other cetacea, but no description was published. *Report*, p. 1056. The radio-ular epiphyses were fused with their shafts. The radiale, intermedium, and ulnare were respectively 43, 58 and 45 mm. wide; the disto-carpalia 1 to 5 were 39, 33, 35, 27, 30 mm. respectively.



independence. The disappearance may perhaps in some cases be due to atrophy of the cartilaginous centrale, or, as in *Mesoplodon* and *Monodon*, to its fusion with an adjoining carpal bone.

The pisiform element of the carpus seems to be constant in the cartilaginous stage, but in my specimens it was undergoing ossification only in *Hyperoodon* and the St Andrews *Mesoplodon*.

From the observations of Leboucq and Kükenthal on the development of the phalanges, their number in the adult is less than in that of the embryo of the same species, apparently by fusion with each other of pieces originally distinct, a condition which applies also to diminution in the number of pieces originally present in the carpus.

In this memoir I have purposely restricted myself to the consideration of the carpus in those *Odontoceti* that I have personally examined. The principles which have guided me in ascertaining the morphology of the bones can be applied to their determination in other species of whales; but as this paper has reached a length more than I had originally intended, I must leave for another occasion their further application.

As supplementary to my description and figures of the carpus of *Mesoplodon* I append a radiogram of the manus of that animal, which shows

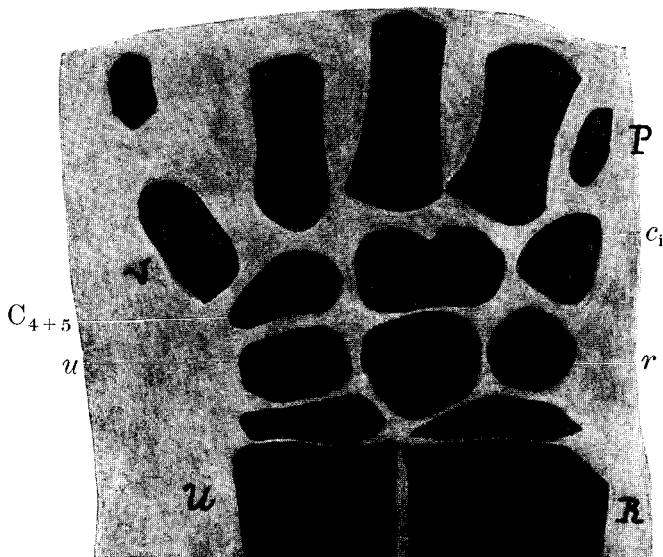


FIG. 11.—Radiogram of hand of *Mesoplodon bidens* from Morrison's Haven.

distinctly, in the undissected carpus, carpal<sub>1</sub> as a separate bone associated with the pollex; carpal<sub>2</sub> fused with C<sub>3</sub>, as indicated by the notch opposite the interval between M<sub>II</sub> and M<sub>III</sub>; carpal<sub>4</sub> fused with C<sub>5</sub> for M<sub>IV</sub> and M<sub>V</sub>.

The radio-ulnar epiphyses, though ossified, are not fused with the shafts of their bones.

All the illustrations, with the exception of fig. 3, are from photographs of the specimens made in the Anatomical Department of the University by the Museum assistants, Mr Ernest Henderson and Mr William Gill, to whom I would express my indebtedness.

For convenience of reference the lettering of the figures is as follows:—R, radius; U, ulna; *r*, radiale; *i*, intermedium; *u*, ulnare; *c*, with arabic numerals disto-carpalia; the roman numerals are the metacarpals; C, the os centrale; P, pollex; *p*, the pisiform element.

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(Issued separately October 14, 1909.)