ADDITIONAL OBSERVATIONS ON THE STOMACH IN THE ZIPHIOID AND DELPHINOID WHALES.

By Professor Sir Wm. Turner, M.B., LL.D., F.R.S.

From time to time I have communicated to this *Journal*[1] observations on the stomach in the Cetacea, more especially in certain species of the Delphinidæ and Ziphiinæ. Since the date of my last paper, October 1885, I have had opportunities of making some additional dissections of the stomach in certain species belonging to these families, and I propose in this communication to speak of the stomach in *Micropteron* (*Mesoplodon*) *bidens, Hyperoodon rostratus, Phocæna communis, Delphinus delphis, Delphinus* (*Lagenorhynchus*) *albirostris, Monodon monoceros, Delphinapterus leucas.*

Ziphiinæ.

Stomach of Micropteron bidens.—In my account of the specimen of Sowerby's whale captured in Shetland in 1885, I described the stomach of the animal, and discussed some points bearing on the morphology of that organ in the Cetacea generally. I came to the conclusion (*a*) that in Sowerby's whale the stomach was divided into a greater number of compartments than in any other known cetacean; (*b*) that the first gastric compartment, both in this and other Ziphioid whales, was not homologous with the œsophageal or 1st compartment of the stomach in the Dolphins; (*c*) that it was a true digestive chamber, and was homologous with the 2nd gastric compartment in the Dolphins; (*d*) that the œsophageal compartment of the stomach in the Delphinidæ is wanting in the Ziphioid whales.

In October 1888, I obtained another specimen of Sowerby's whale, which had been stranded in Dalgety Bay, on the north side of the Firth of Forth.[2] The stomach of this animal was

[1] "A Contribution to the Anatomy of the Pilot Whale (*Globiocephalus Svineval*)" (Nov. 1867, vol. ii.); "Further Observations on the Stomach in the Cetacea" (Nov. 1868, vol. iii.); "Anatomy of Sowerby's Whale" (Oct. 1885).

[2] I have given an account of the dimensions and external characters of this specimen in the *Proc. Roy. Phys. Soc. Edin.*, Dec. 19, 1888.

removed and inflated, and when in the distended condition a careful drawing was made of it (fig. 1). It was then dried, and its compartments subsequently opened into, so as to be preserved as a Museum specimen. It may be regarded as consisting of three chief divisions—proximal, intermediate, and distal.

The proximal or cardiac division (1), before it had somewhat shrunk in the act of drying, was 21 inches long and between 8 and 9 inches in its greatest transverse diameter. It

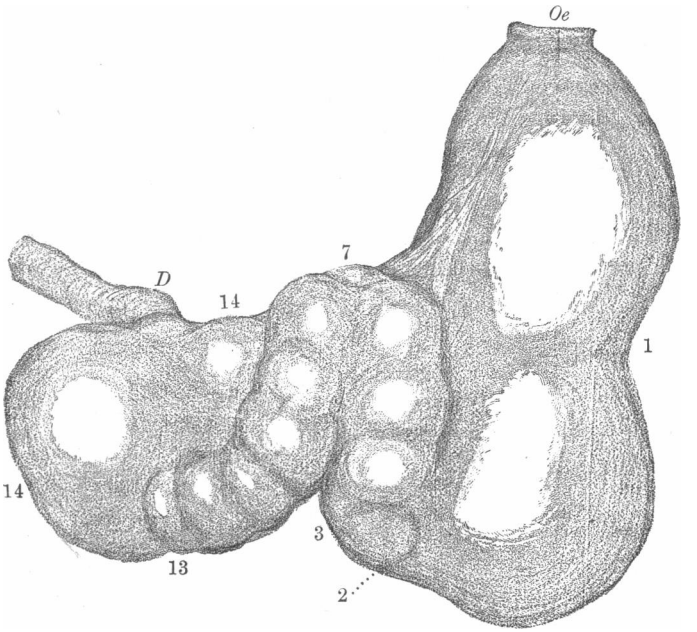

FIG. 1.—Ventral surface of stomach of *Micropteron bidens*. *Oe*, œsophagus ; *D*, duodenum. The numerals refer to the several compartments of the stomach. 2 points approximately to the 2nd compartment not visible in the figure. This and the following figures are from drawings of the stomach, by my pupil, Mr Harry G. Melville.

formed the left or cardiac bag of the stomach, and had about the middle of its surface an almost circular constriction, which divided it into two dilated parts nearly equal in size. The position of the constriction was marked in the interior by a projecting fold of mucous membrane, not so deep as to act as a valve, and permitting free communication between the two dilatations. At its anterior end it had a free communication

with the œsophagus. At its posterior end it opened by a short funnel-shaped passage into the 1st compartment of the intermediate division of the stomach, and a strong valvular fold of mucous membrane was situated at the opening. It possessed thicker walls than any of the other gastric compartments, principally owing to the thick folds of its mucous lining.

The intermediate division consisted of twelve subglobular compartments (2–13), varying in size from a small to a large orange. They were arranged so as to form a A-shaped figure with the apex directed forwards. The proximal limb of the A, which lay next to the cardiac division, consisted of five compartments. Another compartment was situated at the apex where the proximal and distal limbs became continuous with each other, and the distal limb was subdivided into six compartments. The separation between the different compartments was marked on the surface of the organ by a series of constrictions, which passed more or less circularly around the stomach; whilst internally a broad valve-like fold of mucous membrane projected both from the upper and lower walls, but did not meet in the axis of the lumen. An aperture of communication was therefore between each compartment and that on each side of it; the arrangement being somewhat like that of the foramen ovale in the auricular septum of the heart of the human fœtus. But further, I may state that in more than one of the globular compartments of this division a fold of mucous membrane projected from a part of the wall into the lumen, which, if it had been deeper and had extended farther round the wall, would have still further subdivided this portion of the stomach. The whole of the compartments of the intermediate division were visible on the ventral surface of the stomach, except that (2) which opened directly into the cardiac division (1), was placed on the dorsal aspect of that division a little in front of its posterior end, and is not seen therefore in figure 1, which gives the ventral aspect of the stomach.

The distal or pyloric division of the stomach (14) before being dried was 11 inches in its long diameter from right to left, and 9 inches in its antero-posterior diameter. It was marked by a circular constriction on the surface, with which a shallow ring-like fold of mucous membrane corresponded internally, so that

it possessed indications of a separation into two chambers, but as the communication between them was so wide they could not be regarded as distinct compartments. Of these two chambers the right was the larger, was almost globular in shape, and formed the right or pyloric end of the stomach. The left or smaller chamber was wedged in between the distal limb of the intermediate division and the proximal division of the stomach. Both the last compartment of the intermediate division and the duodenum communicated with the larger of these two chambers, so that the smaller chamber was as it were a wide diverticulum from the larger. The duodenum sprang abruptly from the posterior wall of the larger chamber, and its opening into that chamber was immediately opposite the opening of communication with the last compartment of the intermediate division. Both these openings were immediately to the right of the ring-like fold of mucous membrane which indicated the division of 14 into two chambers, and each opening was nearly in the centre of a strong and almost circular valve-like fold of mucous membrane.

The Duodenum, slightly dilated, was 2 inches in breadth at its commencement, and then almost immediately became a cylindrical tube. Its dilated end was prolonged as a short *cul-de-sac* about an inch to the left of its pyloric opening. The mucous lining of the *cul-de-sac* and of the anterior wall of the duodenum opposite the pyloric orifice was smooth. Immediately beyond the opening it was thrown into valvulæ conniventes, which were arranged circularly around the wall, and the intervals between them were occupied by reticulating folds of the mucous membrane.

This description of the stomach of Sowerby's whale differs in several particulars from my account of the stomach of the specimen (A) dissected in 1885. I have recognised in this more recent specimen (B) a subdivision of the organ into no fewer than 14 compartments, whilst in the previous example only 10 were described. The demarcation between the compartments was marked both by constrictions on the surface and by valve-like apertures of communication internally. In both examples the proximal and distal divisions corresponded respectively with each other, and the difference between the two

stomachs was in the number of compartments in the intermediate or Λ-shaped division. In A only eight were recognised, whilst in B as many as twelve were seen. It is possible that the difference in the number recognised may have been due to B having had a greater number of subdivisions than A; but it may also be due to B having been examined under more favourable conditions, both as regards the facilities for handling it and its comparative freshness; for, in the flaccid state which A was in when it reached me, it is possible that some of the smaller compartments of the Λ-shaped division may have been overlooked. The similarity in form and in the mode of internal communication of the twelve compartments of the Λ-shaped division leads me to regard them as homologous with each other, and as presenting a remarkable example of repetition of structure, so that I have grouped them together as forming a division of the stomach intermediate to the proximal and distal portions. But I would also point out that both the proximal and distal divisions, with their surface constrictions and projecting folds internally, exhibited a tendency to incomplete subdivision into smaller chambers, although the internal folds were not sufficiently deep to justify one in regarding these chambers as separate compartments.

In my description of A, I stated that the pancreatic duct was "about as large as the human femoral artery," and opened into the duodenum about 5 inches from the pylorus. From my more recent dissections I am of opinion that this large duct was the conjoined pancreatico-hepatic duct. My imperfect interpretation of its nature on that occasion, its connection with the liver having previously been cut through, was due to its being surrounded by the lobules of the pancreas at its duodenal end, which I am now satisfied is the rule in the Cetacea, so that it seemed to be the duct of the pancreas.

Stomach of Hyperoodon rostratus.—In my original account of the stomach of Sowerby's whale, I compared it with the published descriptions by John Hunter, Dr Jacob, Vrolik, and Eschricht of the stomach of Hyperoodon and with an inflated and dried specimen of the latter animal in the University Museum. A fresh specimen of the stomach of Hyperoodon was not at that time in my possession, but having preserved the

viscera of a young male captured at Dunbar in November 1885,[1] I have subsequently been able to examine the recent stomach of this animal, and to make a comparison between it and that of Sowerby's whale.

The Œsophagus was 4 inches in its transverse diameter a few inches in front of the stomach, but at its gastric end it was constricted to about an inch. Its entrance to the stomach was marked by an almost circular fold of mucous membrane, and its mucous lining presented a strong contrast in appearance to that of the cardiac division of the stomach.

The Stomach itself consisted of seven distinct compartments, arranged so as to form a proximal, an intermediate, and a distal division.

The proximal or cardiac division (1), somewhat pyriform in shape and directed backwards, was 21 inches long and $8\frac{3}{4}$ inches in greatest breadth. It was covered both ventrally and laterally by peritoneum; the spleen was attached to its left surface by a broad gastro-splenic omentum, and upon its posterior end a broad omental fold was prolonged backwards for upwards of 2 feet. At its anterior end it opened into the œsophagus. There was no constriction on its surface to indicate a partial division into two chambers. When this compartment was everted its mucous lining was seen to be elevated into strong folds similar to those which I described in Sowerby's Whale as containing numerous glands of the cardiac type of secreting glands.

The proximal was succeeded by the intermediate division, which consisted of five subglobular compartments (2–6), varying in size from a fœtal head to that of an adult. They were arranged so as to form a Λ-shaped figure, with the apex directed forwards. The two smallest compartments (2, 3) formed the ascending limb, the apex of the Λ consisted of compartment 4, about the size of an adult head, whilst the descending limb consisted of compartments 5 and 6, which were somewhat bigger than 4. All these compartments were seen on the ventral aspect of the stomach; they were differentiated from each other by circular constrictions, and were covered on the ventral sur-

[1] I gave an account of the external characters of this animal in *Proc. Phys. Soc. Edin.*, vol. ix., 1886.

face by peritoneum, a broad omental fold of which projected backwards from the posterior border of 6. The first compartment (2) of the intermediate division communicated with the right aspect of the proximal division by an opening situated about 15 inches from its œsophageal end, and therefore comparatively near to the posterior end of the proximal division. The several compartments of the intermediate division communicated successively with each other by openings in the

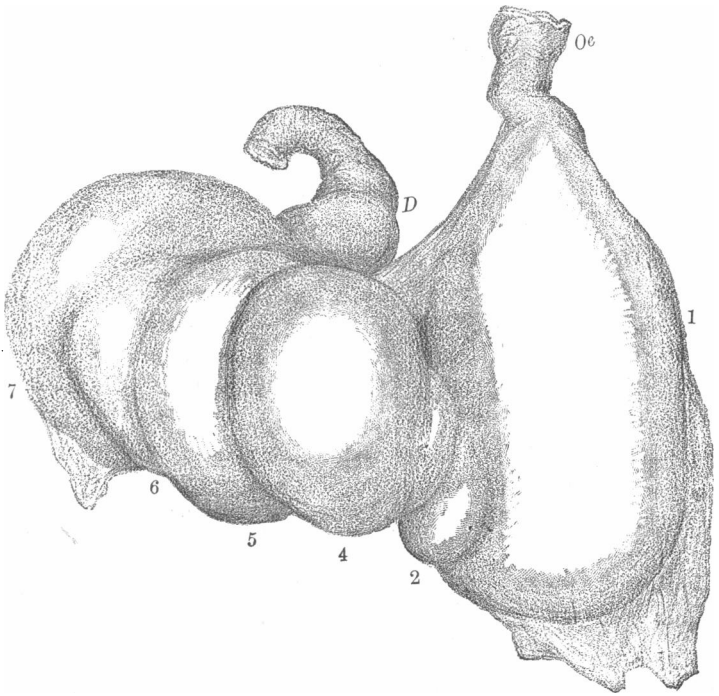

FIG. 2.—Stomach of *Hyperoodon rostratus*. *Oe*, œsophagus; *D*, duodenum. The numerals refer to the compartments of the stomach. The stomach was drawn so as to bring in the origin of the duodenum. The view-point, therefore, is somewhat forward, and the Λ-shaped form of the intermediate division is not distinctly shown in the figure.

valvular folds of mucous membrane which corresponded internally with the surface constrictions. These openings were not in the axis of the fold, but in proximity to the dorsal wall of the compartments.

The distal or pyloric division (7) consisted of a large compart-

ment, 12½ inches in its longest diameter and 9 inches in its widest, being about equal in size to both 5 and 6. It projected by a large rounded end to the right of the last compartment of the intermediate division, and from this end a broad omental fold, continuous with that from the intermediate division, hung pendulous. The opposite end of the pyloric division was wedged in between the dorsal surface of the 5th and 6th compartments and the commencement of the duodenum. This

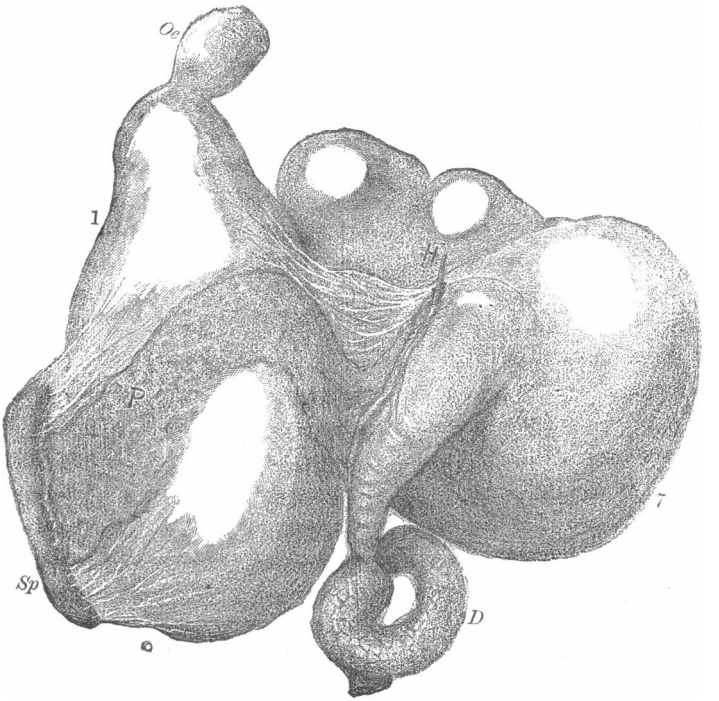

FIG. 3.—Dorsal surface of the stomach of *Hyperoodon rostratus*. *H*, hepatic duct; *Sp*, spleen; *P*, pancreas; *D*, cylindriform part of duodenum. The other lettering as in fig. 2.

division did not have any constriction on the surface to indicate either a partial or more complete separation internally into two or more chambers, but a well-defined constriction separated it on the one hand from 6, and on the other from the duodenum.

The Duodenum arose from the dorsal aspect of the pyloric division, so that its origin could not be seen from the ventral surface. It commenced as a funnel-shaped dilatation, which

was 12 inches long and 4½ inches in greatest breadth. It diminished in calibre as it passed away from the stomach, so that the narrow constricted end of the funnel was not more than 1 inch in diameter; here it became continuous with the cylindriform part of the duodenum, which widened out to a diameter of 2¾ inches. The mucous lining of the funnel was smooth on its surface, and valvulæ conniventes did not appear until close to its narrow end. The duodenum contained a quantity of the black horny beaks of the cuttle-fish on which the animal had fed.

The Hepatic Duct reached the dorsal wall of the funnel-shaped dilatation of the duodenum about an inch from the pylorus. It was almost as large as the human femoral artery, and was traced for nearly 4 inches in contact with the surface of the wall, where it was surrounded by lobules of the pancreas. It then pierced very obliquely the muscular and the mucous coats, its outline being visible without dissection, and opened into the duodenum about 5 inches from the narrow end of the funnel.

Pancreas.—This gland extended from the spleen to the commencement of the duodenum, where it surrounded the hepatic duct. It lay between the layers of the gastro-splenic omentum, across the dorsal aspect of the first compartment of the stomach, and on the dorsal surface of the funnel-shaped part of the duodenum. Its length was 15½ inches and its breadth was about 6 inches at the duodenal and 4 inches at the splenic extremity. In no part of its length had it any great thickness. It consisted of multitudes of dark brown lobules connected together by areolar tissue. The pancreatic duct was exposed on cutting into the substance of the gland, and was followed to its duodenal end to join the hepatic duct, where it was surrounded by lobules of the pancreas. The opening of the pancreatic into the hepatic duct was a little in front of the spot where the latter began to penetrate the duodenal wall, so that the terminal part of the duct and the orifice into the duodenum were common to both the pancreatic and biliary secretions.

Spleen.—The spleen was an elongated organ, 12½ inches in its antero-posterior diameter. It was widest about the middle, where it had a breadth of 2½ inches, and it was somewhat

attenuated at its two ends. Its connection with the proximal division of the stomach has already been stated.

This recent specimen of the stomach of Hyperoodon agrees with the dried specimen described in my paper of October 1885 in having seven compartments. In the dried specimen also they were arranged in proximal, intermediate, and distal divisions; the proximal and distal consisting each of a single compartment, the intermediate of five, two each in an anterior and a posterior limb, and one at the apex at the junction of the two limbs. It is now perfectly clear that the "elongated somewhat kidney-shaped sac," described in my previous paper, corresponds with the funnel-shaped dilatation of the recent specimen, and is therefore the commencement of the duodenum. John Hunter also described seven gastric compartments with a duodenal dilatation. Seven, therefore, is in all probability the usual number of compartments of the stomach of Hyperoodon, which possesses, therefore, only half the number of compartments present in Sowerby's whale. Occasionally, however, nine compartments are present, as in Eschricht's specimen, where, however, one of the nine was a sac-like dilatation of the œsophagus, and in a specimen recently described by Max Weber.

My recent dissections confirm the conclusions to which I arrived in my original paper on the stomach of the Ziphioid family of whales, that the first compartment does not correspond morphologically with the first compartment in the Delphinidæ, but with the second, and is a true digestive chamber, and that the first compartment in the Delphinidæ is absent in the Ziphiinæ.

Shortly after the publication of my former paper on the stomach of the Ziphiinæ, an admirable monograph on the Cetacea appeared by Professor Max Weber,[1] of Amsterdam, in which he gave an account of his dissection of the stomach of Hyperoodon.

Weber describes his specimen as consisting of an elongated cardiac compartment and of a pyloric part divided into eight semi-globular chambers, making nine in all. His pyloric part includes both my pyloric and intermediate divisions. In his

[1] *Studien über Säugethiere. Ein Beitrag zur Frage nach dem Ursprung der Cetaceen*, Jena, 1886.

specimen, therefore, the part corresponding to what I have termed the intermediate division consisted of 7 chambers, instead of 5 as in both my fresh and dried specimens, whilst the distal division, to which alone I have applied the name pyloric, formed the last compartment much larger than any of the chambers of the intermediate division. Weber has also recognised that the mucous membrane of the cardiac compartment is rich in glands, and differs essentially from the 1st gastric compartment in other Cetacea with its lining of œsophageal epithelium, and he came to a similar conclusion to that which I had arrived at in the previous year, that the 1st division of the stomach of Hyperoodon corresponds with the 2nd compartment of other Cetacea, and that the 1st or œsophageal compartment in them is wanting in Hyperoodon and perhaps in other Ziphioids.

It is very satisfactory to me to find my conclusions on this matter confirmed by the independent observations of so accomplished a naturalist as Professor Max Weber.[1]

Delphinidæ.

Stomach of Phocæna communis.—Upwards of two centuries ago Edward Tyson gave an admirable account of the "Anatomy of a Porpess,"[2] and included in it a description, with a figure, of the stomach. Since then the anatomy of the organ in this animal has been described by various anatomists, including John Hunter, Sir Richard Owen, Robert Knox, J. B. S. Jackson, Arthur Jacob, and myself. It is unnecessary for me to say more in regard to the form of the stomach and the number of its compartments than that it consists, in succession from left to right, of a thin-walled, three-sided œsophageal compartment (1), lined by a squamous epithelium, with its base forward at the œsophagus, and its free apex directed backwards; of a

[1] Messrs John H. Scott and G. Jeffrey Parker have recently given a short description of the stomach of a Ziphius (sp. ?) caught in 1884 near Dunedin, New Zealand. The stomach consisted of ten compartments. The 1st or cardiac compartment was lined by a mucous membrane which they compare with the reticulum of the sheep's stomach. Eight compartments, mostly subglobular, made up what I have called the intermediate division, the first of which opened near the distal end of the cardiac compartment. The tenth compartment, next the duodenum, was elongated. The mucous lining of compartments (2–10) was soft and smooth.—*Trans. Zool. Soc. Lond.*, vol. xii. part 8, 1889.

[2] London, 1680.

cardiac compartment (2) not quite as large as the first, with numerous thick projecting folds of mucous membrane mostly running longitudinally; of a very small intermediate compartment (3) wedged in between 2 and 4; and of a long tubular pyloric compartment (4), which curves to the right, and becomes continuous with the subglobular dilated commencement of the duodenum.

This subglobular dilatation was lined by a smooth mucous membrane, but at the commencement of the cylindrical part of the canal the membrane was thrown into longitudinal folds. At the beginning of one of these folds was the mouth of the hepatico-pancreatic duct, through which a surgical probe could be passed along the duct as far as the transverse fissure of the liver. The hepatic duct was not dilated, and had no valve-like folding of its lining membrane.

As the microscopic characters of the mucous lining of the stomach are important factors in the comparison of the gastric compartments in the Ziphioid and Delphinoid whales, I have examined the mucous membrane of the three principal compartments of the stomach in the common Porpoise,[1] which may be taken as a type specimen of the Delphinidæ.

Vertical sections through the mucous lining of the 1st or œsophageal compartment, when examined under a low magnifying power, showed a thick layer of stratified epithelium, into the deeper part of which mucous papilla-like outgrowths of the corium projected. These were in all probability slender folds of the mucous membrane, which when vertically divided looked in section like papillæ. The sides and apices of these outgrowths were covered by numerous layers of epithelium.

Under higher powers the surface layers of epithelium were seen to consist of squamous cells, the nuclei in which were not very distinct. The deeper layers occupying the intervals between

[1] The examination was made on the mucous membrane of the stomach of an adult male. The œsophageal compartment was distended by a pultaceous mass of half-digested fish, the bones of which were in process of being "cleaned." Tyson states that Mr Ray found in the stomach of a Porpess "sand-eels, launces, or as called by Gesner *Ammodytæ*," also that Dan Major found the spines of fishes, small Tellinæ, particles of Testacea, Crustacea, and sand; whilst Tyson himself got in his specimen the spines of fishes and two or three nearly entire herrings. Tyson also saw the bones and spines of several fish in the œsophagus.

the outgrowths consisted of cells more polygonal in form, and the nuclei in which were very distinct. No glands were seen in the mucous lining of this compartment, which was obviously an extension of the mucous membrane of the œsophagus.

Vertical sections through the thick folds of mucous membrane of the 2nd or cardiac compartment showed it to be remarkably rich in elongated, tubular, branched glands containing peptic cells, so that, both in its general appearance to the naked eye and in its microscopic characters, it corresponded with the mucous lining of the cardiac compartment of the Ziphioid whales. The description which I gave in 1885 of the glands in the 1st gastric compartment of Sowerby's Whale (specimen A) applies almost verbatim to what I have seen in the 2nd compartment in the Porpoise. The glands are admirable examples of the "cardiac glands" of the stomach with their characteristic "peptic" cells.

Vertical sections through the mucous lining of the 4th or pyloric compartment showed it also to be highly glandular, but the glands differed in form and appearance from the cardiac glands. They were only about one-third their length, were less frequently branched, and the branching was apparently limited to the deep end. Their epithelial lining was so disintegrated that the shape of the cells could not be seen. The glands were of the type of "pyloric glands."

Stomach of Delphinus delphis.—Cuvier, in his *Leçons*,[1] describes the stomach of the Common Dolphin, which is in all probability this species. He speaks of five compartments, but his 5th compartment is apparently the same as what I shall describe as the subglobular commencement of the duodenum, whilst what he calls the long canal between his 2nd and 3rd compartments I shall name the 3rd compartment, so that his 3rd and 4th compartments are with me the 4th and 5th. Previous to Cuvier's description, Sir Everard Home had recorded[2] an account of the stomach of a small cetacean, which he names *Delphinus delphis* (Linnæus).[3] Dr J. B. S.

[1] *Leçons d'anatomie comparée*, t. iv., deuxieme partie, p. 79, 1835.

[2] *Phil. Trans.*, 1807.

[3] This animal was not *Delphinus delphis*, but probably either *D. tursio* or *D. albirostris*. From Home's figure and description, the stomach had only four chambers.

Jackson has also described and figured[1] the stomach of a fœtal Dolphin, the specific name of which he leaves in doubt, though in some respects he thinks it resembles *D. delphis*.

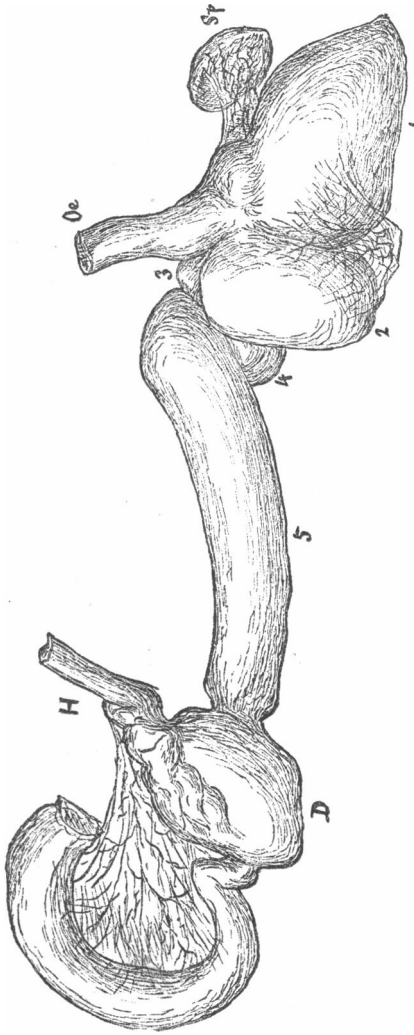

FIG. 4.—Ventral surface of stomach of *Delphinus delphis*. The lettering as in previous figures. The numerals refer to the compartments of the stomach.

The specimen which I examined was obtained from an animal shot in the Firth of Forth in 1887.[2] The stomach was removed

[1] *Boston Journal of Natural History*, vol. v. No. 2, October 1845.

[2] I have described the external characters of this animal in *Proc. Roy. Phys. Soc. Edin.*, vol. ix., 1887.

along with the surrounding viscera, the cavities were injected with spirit, and when the walls were hardened the compartments were opened into.

The Œsophagus, immediately after piercing the diaphragm, formed a pouch-like dilatation not unlike that described by Dr Jackson in his fœtal specimen. With this dilatation both the 1st and 2nd gastric compartments communicated. The mucous lining of the œsophagus was thrown into longitudinal ridges.

The Stomach consisted of five compartments. The 1st, or œsophageal, three-sided in form, with its base forward to the œsophagus and its free apex directed backward, was $5\frac{1}{4}$ inches long by 4 inches in greatest breadth. Its muscular wall was thin, and its mucous membrane was corrugated and formed narrow convolutions, covered by a thick layer of horny epithelium. The opening of this compartment into the œsophagus readily admitted two fingers.

The 2nd or cardiac compartment, subglobular in form, was to the right of the 1st compartment, from which it was separated by a deep cleft, but an omental fold passed from one to the other. It was $3\frac{1}{2}$ inches long by $2\frac{3}{4}$ inches in greatest breadth. Its mucous membrane was raised into numerous thick projecting folds, the general direction of which was longitudinal, though these were connected together by short oblique or transverse folds. This compartment had two openings at its anterior end, the one into the dilated part of the œsophagus, which admitted the middle finger; the other was separated from the œsophageal opening by a fold of mucous membrane, it communicated with the 3rd compartment, and only admitted the tip of the little finger.

The 3rd compartment was situated in the angle between the œsophagus and the 2nd compartment; it was not as big as a walnut, and its mucous membrane was smooth.

The 4th compartment was behind and to the right of the 3rd, and was as big as a walnut. It communicated with the 3rd by an opening readily admitting a thick probe, and was lined by a smooth mucous membrane.

The 5th or pyloric compartment formed the tubular part of the stomach. It was 10 inches long, and passed from left to right, where it joined the subglobular dilated commencement

of the duodenum. Its left end was in contact with the walls of both the 3rd and 4th compartments. Its mucous lining was mostly smooth, though with some faint ridges. The opening into the 4th compartment admitted a large probe, whilst a similar sized opening communicated with the duodenum.

The subglobular dilatation of the Duodenum was the size of a small orange, and was situated at the right end of the tubular part of the stomach. The cylindrical part of the duodenum arose from it at the back of its right surface, and the opening between the two was large enough to admit the little finger. The mucous lining of this dilatation was smooth, except at the orifice of the cylindriform tube, where it was longitudinally folded. Half an inch from this orifice was the mouth of the hepatico-pancreatic duct opening obliquely at the end of one of these longitudinal folds.

The Hepatic duct was traced from the portal fissure, where it was formed by the junction of two large ducts emerging from the liver. The hepatic duct ran parallel to the portal vein, and was almost as large as that vessel. It was surrounded by lobules of the pancreas, and then reached the duodenal dilatation, to the wall of which it was attached. At first it was covered by the serous coat of the duodenum, and then pierced the wall to open on the mucous surface as above described. A probe could not be passed along that part of the duct which was in contact with the duodenal wall, for the duct was tortuous at this spot. As is well known, the gall-bladder is absent in the Cetacea, but this remarkably wide duct would obviously serve as a reservoir for the bile; the tortuous part of the duct, where it was in contact with the duodenal wall, would act like the spiral valve in the neck of the human gall-bladder.

The Pancreas was situated in relation to the dorsal aspect of the stomach, and extended as far as the duodenum and the hepatic duct. The pancreatic duct was exposed on dissecting into the substance of the head of the gland, and was followed to the part of the bile-duct surrounded by the lobules of the pancreas, which it joined about $\frac{3}{4}$ inch from the duodenum.

The Spleen was attached to the dorsum of the 1st gastric compartment by a broad gastro-splenic omentum. The spleen

was almost disc-shaped, and measured 2 inches in antero-posterior by $1\frac{3}{4}$ in transverse diameter.

Stomach of Delphinus (Lagenorhynchus) albirostris.—The stomach of the white-beaked Dolphin has been described and figured by more than one naturalist, and I may refer to the memoirs of Messrs J. W. Clark,[1] Cleland,[2] and Max Weber[3] for an account of it.

It is unnecessary, therefore, to go into much detail; but as I have been able to compare the stomach of an adult with that of a suckling calf,[4] there are some points to which I shall briefly refer.

The Œsophagus, after piercing the diaphragm, was dilated, and directly communicated both with the 1st and 2nd gastric compartments.

The Stomach was divided into four compartments. The 1st or œsophageal was 19 inches long and $12\frac{1}{2}$ inches wide in the adult; $3\frac{1}{2}$ inches long by $3\frac{1}{4}$ inches wide in the suckling calf. It had in both the usual form of this compartment in the Delphinidæ, with the base forward and the apex pointing backwards. The wall was relatively thin, and the corrugated mucous membrane was covered by a thick, yellowish, stratified, squamous epithelium. This compartment contained in the adult a large quantity of clean fish bones, probably whiting or haddock, together with otoliths and a few limbs of a crustacean like the common shore crab. Similar clean fish bones were also seen in the œsophagus and mouth.

The 2nd or cardiac compartment was $10\frac{1}{2}$ inches long in the adult, and subglobular in shape. In the calf it measured about 3 inches both in length and breadth, and was separated from the 1st compartment by a deep cleft. Its mucous lining was elevated in strong folds, which to some extent were arranged longitudinally, but as short intermediate folds were numerous, and intersected each other, the arrangement was more reticulated than in the Porpoise. Max Weber, in his memoir, has given a figure of them, and states that the mucous membrane

[1] *Proc. Zool. Soc. Lond.*, June 20, 1876.

[2] *Jour. of Anat. and Phys.*, vol. xviii., 1884.

[3] *Tijdschrift den Ned. Dierkundige Vereeniging*, 1887.

[4] I have described the external characters of these animals in *Proc. Roy. Phys. Soc. Edin.*, December 19, 1888.

contains numerous tubular branched glands in which "peptic" cells are found. The 2nd compartment communicated with the 3rd by an opening situated in proximity to the œsophageal opening of the 2nd compartment.

The 3rd or intermediate compartment was in the adult as big as a small pear; in the calf about the size of a large hazel-nut. It was situated in relation to the dorsal surface of the 2nd compartment between it and the commencement of the 4th compartment, with which it communicated by a distinct opening.

The 4th or pyloric compartment formed the tubular stomach. In the adult it was about 12 inches long; in the calf only 4 inches. In both it curved to the right, and ended in the dilated commencement of the duodenum. The left end of this compartment projected into the angle of separation between the œsophagus and the 2nd compartment, where it formed a dilated cul-de-sac not unlike 4*a* in Max Weber's figure. The mucous lining both of the 3rd and 4th compartments was smooth.

The Duodenum was separated from the 4th compartment by a constriction, and the opening between them, large enough to admit a quill, was in the centre of a well-defined pyloric valve. It commenced by a large funnel-shaped dilatation, which was lined by a smooth mucous membrane. In the calf the hepatico-pancreatic duct opened on the surface of this mucous membrane, 2 inches from the pyloric orifice, on the summit of a ridge-like papilla. Immediately beyond the mouth of the duct the mucous membrane was elevated into valvulæ conniventes.

The Hepatic duct was attached to the wall of the dilated part of the duodenum for about 2 inches before it began to pierce its coats, and was enclosed by peritoneum. It was as large in the calf as the humeral artery, and in the adult as the common iliac artery of Man, and the lumen was much dilated. It was easily probed both from the hepatic and duodenal ends, but the probe could not be made to pass through that part which was in contact with the surface of the duodenal wall, apparently on account of the mucous lining being thrown into spiral folds. The hepatic duct was surrounded in the usual way by the pancreas, and the pancreatic duct opened into it close to the duodenum. Clark has figured the dilated hepatic

duct in his drawing of the stomach, and Cleland refers to its sacculated condition in his specimen.

The Spleen was attached to the dorsal surface of the 1st gastric compartment by an omentum. It was 2¼ inches long in the calf, much attenuated at its anterior end, and 1 inch in breadth near the posterior end.

Stomach of Monodon monoceros.—Very little apparently has been published on the stomach of the Narwhal. Dr Fleming, in his account[1] of a specimen, 12 feet long, stranded early in the century in Shetland, states that the stomach was divided into several compartments, and that the extent of its inner surface must be greatly increased by numerous cylindrical papillæ, some of them more than 2 inches long, which were dispersed over it. Meckel,[2] from the examination of a small fœtus, states that the 1st compartment was roundish, much smaller than the 2nd, and with the inner surface set with numerous strong, teeth-like projections arranged in compact longitudinal rows. He does not state the number of compartments, but I infer that he thinks there were three or five.

In September 1887, I received from Captain John Gray, of the whaling ship "Hope," a fœtal Narwhal, 5 feet 1 inch long, and therefore approaching the full term of utero-gestation. It had been preserved in salt, and was in good condition. I removed the stomach along with the surrounding viscera from the abdomen, injected the cavities with spirit, and, after it was hardened, opened into the several compartments.

The Œsophagus pierced the diaphragm, and 1½ inch beyond that muscle it opened into the 1st compartment of the stomach.

The Stomach consisted of five compartments. The 1st or œsophageal was 6½ inches long and 3½ inches in its greatest breadth. It was somewhat three-sided in outline, with its base forward at the œsophagus and the apex at the free posterior end. When opened into by a longitudinal incision, yellowish, horny cuticular-looking flakes of epithelium, often of considerable size, which had peeled off the surface, were lying loose in the cavity. When examined microscopically, they were seen to consist of stratified squamous epithelium. The surface exposed

[1] *Memoirs Wernerian Society*, vol. i., 1811.

[2] *System der Vergleich. Anatomie*, 527, vol. iv., 1829.

was smooth except for sparingly scattered papillary projections from $\frac{1}{8}$th to $\frac{1}{4}$th of an inch in length; but in proximity to the opening of communication with the œsophagus and to that into the 2nd compartment, the papillæ were crowded together in considerable numbers. These are probably the papillæ referred to both by Fleming and Meckel in their descriptions. The opening into the 2nd compartment was close to that into the œsophagus, a fold of mucous membrane covered with the papillæ alone separating them from each other. These openings were almost equal in diameter, and each readily admitted two fingers.

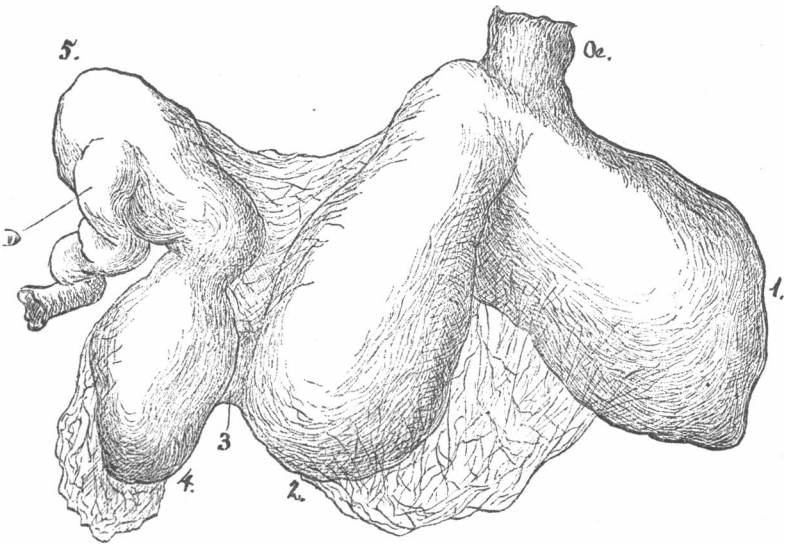

FIG. 5.—Stomach of a large fœtal *Monodon monoceros*. The letters and numerals are as in the preceding figures.

The 2nd or cardiac compartment passed backwards to the right of the 1st compartment, but was separated from it by a deep cleft. It was cylindriform in shape, $6\frac{1}{2}$ inches long, and 2 inches broad. When opened into, the mucous lining was seen to form projecting folds, some of which were longitudinal, but others were shorter and intermediate in direction. The folds were not so strong or numerous as in Phocæna or Delphinus, and a portion of the mucous surface was comparatively free from them. They were crowded with branched tubular glands of the cardiac type in form and arrangement. The contained

cells were relatively large and granular, and obviously would become peptic cells in a stomach functionally active.

The 3rd compartment, about as big as a small walnut, was situated between the right side of the posterior end of the 2nd and the middle of the left side of the 4th compartment. It was scarcely visible on a surface view, and was only distinctly recognised after it had been opened into. It communicated with the 2nd compartment by an opening situated only 1½ inch from the free posterior end of the latter, and by the 4th compartment about midway between its opposite ends. The mucous lining was smooth.

The 4th compartment was situated immediately to the right of the 3rd, and passed from behind forwards. It was 3¼ inches long, 1½ inch wide, and generally cylindriform in shape. Its mucous lining was smooth.

The 5th or pyloric compartment proceeded from the anterior end of the 4th forwards and to the right, curving somewhat on itself, so that it had a convexity forwards. It was tubular in shape, and between 4 and 5 inches long. Its mucous lining was smooth, and it opened into the anterior end of the 4th compartment by an aperture which admitted a quill.

The Duodenum arose from the right and posterior aspect of the 5th compartment. It was somewhat dilated at its commencement, but soon became a cylindriform tube. Its opening into the 5th compartment readily admitted a quill. The mucous lining of the dilated portion was smooth, that of the cylindriform tube was elevated into valvulæ conniventes. Close to where the cylindriform part of the duodenum began was a semi-lunar fold of mucous membrane which bounded the orifice of the hepatico-pancreatic duct.

The Hepatic duct passed backwards and was not dilated as in *D. albirostris;* it became surrounded by lobules of the pancreas before it reached the wall of the duodenum. The Pancreas was in contact with the dorsal surface of the stomach from spleen to duodenum. The Spleen was attached to the dorsal aspect of the 1st gastric compartment by a broad gastro-splenic omentum. It was 2½ inches long and only ½ inch in breadth.

Stomach of Delphinapterus leucas.—Messrs Barclay and

Neill published in 1816[1] an account of the stomach of a White Whale (*Beluga*) killed in the Firth of Forth. They described four compartments, and pointed out the œsophageal character of the first. More recently descriptions of the stomach in this Cetacean have been given both by Professor Wyman and by Drs Watson and Young, and its division into five compartments has been recognised.

The specimen which I dissected was obtained from a young fœtus, only 13½ inches long, which was presented to me by Captain Phillips, of the whaling ship "Nova Zembla." From its small size I can do little more than record the dimensions and relative position of the five chambers of which it was composed.

The 1st compartment was of the usual form met with in the Delphinidæ. It was 1 inch long, and opened into the bottom of the œsophagus: its mucous membrane was corrugated.

The 2nd or cardiac compartment was closely attached to the right side of the 1st. It opened into the 1st compartment near to its œsophageal orifice. Its mucous lining was elevated into folds. Immediately to the right of the posterior end of the 2nd was the 3rd compartment, about the size of a large pea. The 4th compartment was placed ventrally, and to the right of the 3rd. It was about ¾ths of an inch long. The 5th or pyloric compartment commenced at the anterior end of the 4th, and extending for about 1 inch to the right, formed the tubular part of the stomach; it was bent on itself at its pyloric end, and joined the dilated commencement of the duodenum.

The stomach of this fœtus, that of the more advanced fœtal Monodon, and that of the calf White-beaked Dolphin all accord with what I stated some years ago in describing the stomach of Globiocephalus,[2] that in the fœtus and young stomach the paunch or œsophageal compartment is of about the same size as the 2nd compartment, whereas, when one of these Cetaceans acquires its nourishment independently of the mother, the paunch attains a great increase in relative magnitude.

From the foregoing description of the stomach in so many species of the Delphinidæ it is obvious that, whilst this organ

[1] *Memoirs Wernerian Soc.*, vol. iii., 1816.

[2] *Jour. Anat. and Phys.*, vol. iii. p. 118, 1869.

throughout the series is in many particulars constructed on a common plan, yet that there are differences amongst the different species. Each species possesses (*a*) an œsophageal or 1st compartment, lined by a prolongation of the squamous epithelium of the œsophagus, which has no representative in the Ziphiinæ; (*b*) a cardiac or 2nd compartment, with a richly folded mucous membrane closely packed with "cardiac glands"; it is a true digestive chamber, and corresponds with the 1st or cardiac division of the stomach in the Ziphiinæ; (*c*) a tubular, more or less elongated pyloric compartment continuous with the dilated commencement of the duodenum, and the mucous lining of which is packed with "pyloric glands"; it corresponds with the pyloric division of the stomach in the Ziphiinæ. The three compartments—œsophageal, cardiac, and pyloric—are constant in the Delphinidæ, and form the chief chambers of the stomach.

But interposed between the cardiac and pyloric compartments is a variable number of small compartments, which are, I think, to be regarded as corresponding with the intermediate division of the stomach in the Ziphiinæ. In *Phocæna communis* and *Lagenorhynchus albirostris* only one such compartment is interposed, so that the maximum number of gastric chambers in these animals is four. In the Porpoise this intermediate compartment communicates with the second or cardiac compartment much nearer to its posterior than its anterior end; but in the White-beaked Dolphin the 3rd or intermediate compartment opens into the 2nd at its anterior end. In *Orcella brevirostris* Dr John Anderson describes[1] three compartments with "a narrow funnel-shaped channel between the 2nd and 3rd sacs," and this "channel" opens into the 2nd compartment in proximity to its communication with the 1st. I regard this "channel" as an intermediate compartment, so that the stomach of Orcella is of the same type of construction as that of the White-beaked Dolphin. The non-glandular structure of the œsophageal compartment, and the abundant glands in the mucous lining of the cardiac and pyloric chambers, are described by Dr Anderson.

In *Globiocephalas melas* (as I showed in my previous papers), *Delphinus delphis*, *Monodon monoceros*, *Delphinapterus leucas*,

[1] *Anatomical and Zoological Researches*, London, 1878.

Orca gladiator (Hunter), *Grampus rissoanus* (Murie), and *Grampus griseus* (Fischer), two compartments are interposed between the cardiac and pyloric chambers (though some writers speak of one of these compartments as if it were only a passage), so that there are five in all. These intermediate compartments are numbered in my description 3 and 4. Compartment 3 does not open into the 2nd or cardiac chamber at the same place in these various species. In *Globiocephalus melas* and *Delphinus delphis* it communicates with that chamber close to its anterior end, and a similar arrangement, according to Dr Murie, is found in *Grampus rissoanus*. In *Monodon monoceros* and *Delphinapterus leucas*, on the other hand, the opening is in proximity to the posterior end. The relation of compartment 4 to the pyloric chamber presents also some modifications. In Beluga and the Narwhal the pyloric chamber arises from the anterior end of compartment 4, and has no direct relation either to the wall of compartment 3 or to the anterior end of the cardiac compartment 2. In Globiocephalus and Delphinus, on the other hand, the left end of the pyloric chamber is in close relation to the walls of both these compartments. The Narwhal and Beluga, therefore, in their gastric arrangements, are more closely allied to each other than they are to the Common Dolphin and the Pilot Whale. The question also arises whether compartments 3 and 4, in such stomachs as those of Globiocephalus and Delphinus, strictly correspond with 3 and 4 in the Narwhal and Beluga. In the two latter it is evident that compartment 3 corresponds in position with compartment 3 in the Porpoise; whilst 3 in the Pilot Whale and Common Dolphin is in correspondence with 3 in the White-beaked Dolphin.

In the Delphinidæ there are also modifications in the relations of the œsophagus to the 1st and 2nd compartments of the stomach. In Phocæna, Monodon, and Beluga the œsophagus opens directly into the 1st compartment only, into the latter of which the cardiac chamber also directly opens. In *Delphinus delphis*, *Globiocephalus melas*, and *Delphinus albirostris*, both the 1st and 2nd compartments open directly into the bottom of the œsophagus. It seems possible, therefore, in these last named, for the food to pass directly into the cardiac chamber without entering into the œsophageal compartment.

In both forms, however, the anatomical arrangements would permit the regurgitation into the 1st or œsophageal compartment either of the gastric juice secreted by the glands of the cardiac mucous membrane, or of the constituents of the food after it has passed into the 2nd compartment, or of both. In *Delphinus albirostris*, for example, perfectly clean fish-bones have been found by several observers, including myself, in the œsophageal compartment. Now, as the mucous lining of this chamber is not glandular, the flesh can only have been removed from these bones by the action of the secretion of the cardiac glands, which probably had been poured into this chamber for the purpose; and the flesh soaked with and rendered pultaceous by the gastric juice had then entered the cardiac chamber in the furtherance of the digestive process, the bones being left behind. Or, as is, I think, less probable, the fish swallowed as food may have passed directly into the cardiac chamber, the flesh being there dissolved off the bones, and these latter, when clean, regurgitated into the œsophageal compartment. In either case the cleaned bones would be collected in that compartment, and then, by a further process of regurgitation, expelled by the œsophagus, pharynx, and mouth. The presence of clean fish-bones in the mouth of the adult White-beaked Dolphin which I dissected is evidence of the mode in which the animal gets rid of the undigested skeletons of the creatures on which it lives, a process which is more simple than if they had to travel along the several compartments of the stomach and the great length of intestine.

But the most remarkable instance of the mode in which those Cetacea which live on food containing indigestible or difficultly digestible substances, get rid of them, is furnished by the *Orca gladiator* dissected by Eschricht,[1] who found the skin of one of the many seals which it had swallowed partly hanging out of the mouth and partly contained in the mouth and throat. The animal had died whilst in the act of regurgitating the skin. In the œsophageal compartment of its stomach the remains of thirteen porpoises and thirteen seals were found, and the bodies of all

[1] "On the Northern Species of Orca," translated in the *Memoirs on Cetacea*, published by the Ray Society, 1866. In an Orca previously dissected by Professor Nilsson the stomach contained four seals with the skins on.

the seals were skinned, though slight traces of flayed skins were found in the stomach itself. Some of the animals appeared to be fresh flayed; most of them were half digested or already fallen to pieces, some only remaining in the shape of loose parts of the skeleton. A fourteenth seal, very small in size, much decomposed by digestion, had slipped into the 2nd compartment, though Eschricht thinks not until after death.

It is obvious that in this animal, as well as in the Porpoise which I dissected, referred to in the footnote on p. 477, the process of digestion was actively going on in the 1st or œsophageal compartment. This could only have been effected through the regurgitation of the secretion of the cardiac glands into that compartment. I agree, therefore, with the opinion expressed by Tyson, Sir Richard Owen,[1] and some other subsequent writers, that the 1st compartment in the Dolphins serves not only as a reservoir, but that the food undergoes a considerable change in it, due to the action of the gastric secretion regurgitated from the 2nd cavity. The food converted into a pultaceous mass can then pass readily into the 2nd and succeeding compartments, and the process of gastric digestion is completed by the action of the secretion of the glands of the pyloric chamber. It is obviously an advantage for the Dolphins, which swallow entire fish and other marine vertebrates, and where certain of the gastric compartments and apertures are small in size, to have a macerating chamber at the commencement of the stomach, in which the flesh can be separated from the skin and skeleton, and these indigestible materials at once placed in a position to be rejected at the mouth.

Hyperoodon, Sowerby's Whale, and the other Ziphiinæ do not have such a "macerating chamber" at the commencement of the stomach. With them the food, which is apparently largely composed of Cuttle-fish, passes at once into the cardiac compartment, to be subjected in it to the action of the gastric juice. The horny beaks, which are the only indigestible structures, are not regurgitated, but, as was shown by my specimen, pass through the several compartments of the stomach, and reach the intestine.

Both Cuvier and Meckel, in their systematic treatises on

[1] Note on p. 359 to John Hunter's article "On the Structure and Œconomy of Whales," *Collected Works*, vol. iv.

Comparative Anatomy, have remarked the variations in size of the Hepatic Duct. This was well shown in my dissections. In *Delphinus delphis* and *albirostris* the duct was so dilated as to serve as a reservoir for the bile, and the tortuous character of its canal before it pierced the duodenal wall would obstruct the rate of bile-flow into the duodenum. In Phocæna, Monodon, and Beluga the duct was not dilated. In Hyperoodon and Micropteron, although the duct was large, its lumen was not especially dilated.

(*Note.*—At the meeting of the Royal Society of Edinburgh, 18th March 1889, a paper was read, on the "Stomach of the Narwhal," by Dr Sims Woodhead and Mr Robert Gray, but the Proceedings of that date have not yet been published.)