

XVI.—*The True Shape, Relations, and Structure of the Alimentary Viscera of the Porpoise (Phocæna communis), as displayed by the Formal Method.* (With Lantern Demonstration of their Microscopic Structure.) By DAVID HEPBURN, M.D., F.R.S.E., Lecturer on Regional Anatomy, and DAVID WATERSTON, M.A., M.D., F.R.S.E., Demonstrator of Anatomy, University of Edinburgh. (With Three Plates.)

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*Introductory.*—Among the toothed whales (Odontoceti) the porpoise is the best-known representative of those members of the genus *Delphinus* or true dolphins which present a rounded muzzle as distinguished from a snout, and consequently it has already frequently been subjected to anatomical examination of a more or less detailed character. As in the case of all the Cetacea, however, the rapidity with which decomposition affects the various tissues and organs has hitherto proved a barrier to a prolonged and systematic examination of them, while, even under the most favourable conditions, the increasing putridity of the carcase has seriously militated against the recording of accurate observations.

Accordingly, when a porpoise, which had been captured in some fishing nets twenty-four hours previously, came into our possession last December, we took immediate steps for its perfect preservation, so that its dissection might be conducted at leisure under conditions of comfort as well as accuracy, and its various tissues "fixed" for reliable examination by the microscope.

*Method of Preparation.*—We therefore first recorded the measurements and external appearances of the animal, and then, having placed it upon its back in such a way as to remove all pressure from its dorsal fin, we opened a comparatively small vessel on its ventral aspect between the anus and the tail. Into this vessel—a small vein

immediately under cover of the blubber—we tied a fine canula having a lumen which would admit the stilette of a dissector's blowpipe. Through this vessel we injected, by means of a gravitation pressure of about four feet, about two gallons of an arsenical preservative to which 10 per cent. of formaldehyde had been added. The fluid took several hours to run into the animal, the body meanwhile becoming firm and rigid, but not in any way distended or deformed. The success of this method of preservation has been apparent at every stage of the dissection. After seven months, the carcase is still absolutely devoid of unpleasant odour, and no trace of decomposition is visible anywhere. The blood has been everywhere coagulated in the vessels, which are thus filled with a natural solid injection mass. The viscera have been fixed so as to retain their natural shapes and relationships. The tissues are all in perfect condition for undergoing further treatment in preparation for the microscope, with the exception of a slight desquamation of a few superficial cells from the mucous membrane of the alimentary canal. In our examination of this animal, therefore, we are in a position to present observations, made under conditions which we believe to be unique, which give results of a thoroughly reliable kind, besides being in many respects entirely novel and which no doubt account for differences between our results and those of former observers.

*External Appearances.*—The animal, which was a male, presented the characteristic features of its genus as regards its rounded muzzle, its teeth, the comparatively high position of its fore limbs upon its sides, the colour of its body and appendages, the tuberculated border of its dorsal fin, etc. The following measurements were recorded before the preservative fluid was injected:—

Length from tip of muzzle to centre of tail,	49½ inches	1.257 metres.
„ from muzzle to vent,	3½ „	.876 „
„ from vent to centre of tail,	15 „	.381 „
„ of oral cleft,	4 „	.102 „
„ from muzzle to anterior edge of root of flipper,	10½ „	.267 „
„ from muzzle to dorsal fin,	22¾ „	.578 „
„ of flipper,	6¾ „	.172 „
Width of tail,	10½ „	.267 „
Girth of tail at root,	6 „	.153 „
Distance between genito-urinary cleft and vent,	11½ „	.292 „
Length of base of dorsal fin,	8½ „	.216 „
Height of dorsal fin,	4½ „	.114 „
Distance from external angle of eye to external auditory meatus,	2 „	.051 „

There were nowhere any traces of hair, and no evidence of an external ear, while the external auditory meatus would not admit the stem of a wax vesta. As the adult porpoise is usually from four to five feet long, although it may reach a length of six feet, the present specimen may be regarded as slightly under its full growth.

In the present communication we desire to confine our attention to that part of the alimentary system contained within the cavity of the abdomen.

*Cavity of Abdomen.*—On opening the abdominal cavity by removing the ventral wall, it was found that the general shape of the cavity was oval, the anterior end was more obtuse than the posterior, and the greatest transverse diameter was opposite the lower or hinder border of the liver. The upper (anterior) part contained the liver and greater part of the stomach, while the posterior part was filled by the convoluted mass of the intestine.

The border of the liver extended across the cavity from a point opposite the eighth right costo-chondral junction to a corresponding point on the left side, in an almost transverse direction; and near the mesial plane of the body there was a triangular notch which was occupied by a small portion of the wall of one of the chambers of the stomach, while another small part of the stomach wall projected from below the border of the left lobe, but only for three-quarters of an inch. The coils of intestine were practically the same calibre throughout, and were suspended from the dorsal wall by a single mesial mesentery. There was no sign of a vermiform appendix, or cæcum, and no part of the tube showed to the naked eye any of the appearances characteristic of the large, as distinguished from the small, intestine.

The abdominal cavity measured 36·5 cms. in its long axis, and 19·5 cms. in its maximum transverse diameter, and at the posterior end it narrowed suddenly, and opened by a definite constricted orifice into an elongated tubular chamber, the representative of a pelvic cavity (Pl. I. figs. 1 and 2). The aperture was formed by a projecting margin of peritoneal membrane, over which the vasa deferentia turned in their course to the urethra. The diameters of this orifice were 2·5 cms. in the sagittal axis, by 1·5 cm. in the transverse, and the depth of the chamber was 7 cms. This tubular peritoneal recess passed between the pelvic bones ventrally, and the vertebral column dorsally, and formed the lining membrane of a chamber, which, from its position, contents, and boundaries, we regard as the representative of a pelvic cavity. The projecting margin on either side corresponded to the brim of a true pelvis. The relations of the viscera associated with the peritoneum confirm the analogy, as the urinary bladder lay between the peritoneum of its ventral wall and the pelvic bones and interpubic ligament, while the rectum descended in relation to the dorsal wall, being supported by a mesentery at its upper or anterior part, but gradually losing its peritoneal investment to end in the anal canal. Hitherto, this arrangement of the peritoneum does not seem to have been recognised as a pelvic cavity, although Turner\* in a description of the posterior end of the abdominal cavity of Risso's Dolphin (*Grampus griseus*), refers to the peritoneum as forming "four cæcal pouches," of which the dorso-mesial one apparently corresponds to the pelvic cavity which we have described.

*Peritoneal Folds and Reflections.*—The falciform ligament of the liver and the Ligamentum teres were both distinct, and were almost mesial in position. The former disappeared into a vertical slit, 5 cms. in length, in the ventral surface of the liver.

\* Sir WM. TURNER, *Jour. of Anat. and Phys.*, vol. xxvi. p. 264.

A peritoneal fold of the nature of a great omentum was represented by a short fold, not more than 6 cms. in length, depending from the curvature of the stomach, where it appeared from under cover of the liver, but did not contain any quantity of fatty tissue. The coils of intestine were suspended from the posterior or dorsal abdominal wall by a single mesial fold or mesentery, in which near the root there were large masses of lymphatic tissue, which diminished in size towards the caudal end. The lower end of the intestine passed into the pelvic chamber mesially, and was suspended by a continuation of the mesentery.

The absence of any intestinal coil corresponding in position to the colon rendered the arrangement of the peritoneum about the stomach and pancreas somewhat unusual.

The great omentum, already described as depending from the stomach, was composed of four layers of peritoneum—two ventral and two dorsal. On tearing through the ventral layers, a lesser sac of peritoneum was opened, whose boundaries were as follows :—

Ventrally, the wall of the stomach ; dorsally, pancreas ; on the left, the first chamber of the stomach ; and on the right side, the last part of the stomach and the duodenum.

No aperture corresponding to a foramen of WINSLOW could be found, and the arrangement of the peritoneal membrane was more clearly brought out by examining it from behind, after removing the viscera *en bloc*.

The lesser sac was then seen to be completely closed in by the peritoneum, which had the following attachments :—

The anterior layers of the great omentum, attached to the greater curvature of chamber No. 2 of the stomach, were prolonged on the left side to the posterior surface of chamber No. 1, from which they were reflected off along an oblique line from the centre of its ventral border to the spleen.

Above the spleen, the two layers separated to envelop the œsophagus. The two posterior or dorsal layers pass dorsally to the border of the pancreas, where they diverge, one passing on the anterior ventral surface, and the other to the inferior caudal surface of that viscus.

On the right side, the layers passed on to the duodenum, and then backwards on to the posterior abdominal wall and pancreas, and thus on the right side the lesser sac became completely closed.

. The apex of the pancreas was in contact with the under surface of the liver.

The absence of an aperture into the lesser sac \* may be explained by reference to the relative positions of the stomach, liver, and pancreas. The pancreas, instead of lying

\* In a monograph entitled, "Recherches sur le développement de la cavité hépato-entérique de l'Axolotl et de l'arrière cavité du péritoine chez les mammifères (Lapin), par Albert Brachet, *Archives de Biologie*, tome XIII., 1893, pp. 559-618 (Plates XXIV. to XXVII.), the following passage occurs :—"La fermeture de cet hiatus" (de WINSLOW) "chez l'amphibien, provient de ce que le bord postérieur du méso-latéral est très peu étendu, et que dans son intérieur ne pénètre pas le foie. Ce bord, se continuant dans le mésoduodénum à son extrémité inférieure, se soude peu à peu à lui, de bas en haut. L'union entre les deux, progressant dans ce sens, amène l'occlusion de l'hiatus."

behind the lesser sac, with its head in the concavity of the duodenum, was found between the duodenum and the liver projecting to the left side, so as to be related to the first and second chambers of the stomach within the folds of the lesser omentum. The alteration in the peritoneal relations is best realised by supposing the pancreas to have moved to the right and forwards (ventrally), and then upwards (anteriorly) between the upper border of the duodenum and the liver, thereby separating the layers of the gastro-hepatic omentum, and pressing its posterior or dorsal layer into contact with the peritoneum covering the dorsal wall of the abdomen, until these two opposite walls of the lesser sac have fused together. That there has been an alteration of this kind is shown by the fact that the bile-duct has no free course, but from the under surface of the liver enters the head of the pancreas and remains in it, until it pierces the wall of the duodenum, and by the further fact that there is a reflection of peritoneum from the under surface of the liver to the back of the head of the pancreas, completely occluding any communication between the sac which lies on the dorsal aspect of the stomach and the general or great peritoneal cavity. Furthermore, that part of the liver bounded by the obliterated ductus venosus and the inferior vena cava (*Lobulus spigellii*), was situated on the dorsal aspect of the liver, and was entirely devoid of peritoneal covering. On the other hand, the *Lobulus caudatus*, situated on the dorsal aspect of the hilum of the liver, was associated with a blind digital process of peritoneum.

Between the layers forming the ventral part of the omentum, there was a curious arrangement of lymphoid tissue. There was a large number of bloodvessels in the peritoneal membrane, and these vessels passed through small nodules of lymphoid tissue, so that they produced the appearance of a bunch of grapes on a stalk, and the arrangement closely resembled the condition present in the human spleen when the vessels are isolated from the spleen tissue. A similar condition was not found in the other parts of the peritoneum.

*Stomach.*—As is well known, the stomach of this animal has been the subject of much debate. Observers have agreed that it presented four compartments, but they have differed as to the homologies and the sequence of these chambers, and, therefore, their special interest in the present instance is due to the fact of their having been fixed in a normal position so that they show their natural shapes, and consequently their homologies can readily be understood.

The different chambers composing the complex stomach had the following positions and relations:—1. The first and second chambers lay side by side, the first being situated on the dorsal aspect of the other compartments, and somewhat to the right side of the second compartment. *The first compartment* received the œsophagus at its anterior end, and formed a somewhat conical bag, not unlike a cardiac ventricle, measuring about five and a half inches (14 cms.) in the antero-posterior or long diameter, and three and a half inches (9 cms.) in the dorso-ventral direction. The axis of the chamber was a direct continuation of that of the œsophagus. It had two borders and two surfaces. The one border was dorsal in position, straight in character, and carried,

about its middle, a small spleen and an accessory mass of lymphoid tissue. The other border, ventral in position, was curved, and was in two parts. The anterior part was blended with the coats of the second chamber, while the posterior half was free, and united only by a peritoneal fold to the second chamber in the anterior half.

The surfaces were left dorsal, and right ventral. The former was free and entirely invested by peritoneum. The latter was flat, and in its upper part was in contact with the left surface of the pancreas, which here projected into the angle between chambers 1 and 2. This surface was crossed obliquely by the line of reflection of the peritoneum. The interior was filled with food consisting of fish which had been crushed and triturated so that the flesh was entirely removed from the bones, while the latter were, for the most part, disarticulated from each other. The food was moist, but not at all wet or pulpy, so that the treatment to which it had been subjected in this chamber might be called "dry mastication." The interior of this "kau-magen" presented appearances which quite corresponded with its apparent functions. Its walls were covered by a thick, white, almost porcellaneous lining, which was everywhere thrown into bold, prominent rugæ. On the ventral wall of the chamber, and immediately behind the œsophageal opening, the rugæ were thrown into a cauliflower-like projection, and in the centre of this mass a careful examination revealed the outlet of the chamber. The inlet and outlet were thus remarkably close to each other, but, besides being situated at right angles to each other, the manner in which the outlet was concealed within a mass of prominent rugæ made it quite impossible for food to enter indiscriminately from the œsophagus into the second, as well as the first, compartment. In the first instance, it was only possible for food to enter the first chamber. To the naked eye, the lining membrane was continuous with, and of the same nature as, the lining membrane of the œsophagus.

Under the microscope (Pl. II. fig. 3), the lining membrane was found to be situated upon a well-marked layer of loose areolar tissue in which numerous capillary blood-vessels ramified. Its vertical thickness measured almost 1 cm. The free surface was extensively but not deeply corrugated, while its deep surface was interrupted by numerous narrow clefts extending towards the free surface for varying distances, but usually not more than half-way. The whole arrangement was closely suggestive of the rete malpighi and stratified epithelial layers of skin, while the areolar tissue and vascular prolongations, which occupied the subjacent furrows or clefts, bore a close resemblance to the arrangement of the papillæ of the true skin. In the deeper layers, the cells of this lining membrane presented rounded nuclei, which stained deeply. Nearer to the free surface the nuclei stained less distinctly, but their rounded character was well maintained. Comparatively close to the surface, the nuclei became markedly flattened, and, at the same time, the cell stratification became pronounced. At this level also, and onwards to the free surface, the tissue was distinctly paler because it absorbed less of the staining agent. At no part of the membrane was there any trace of any arrangement for secretion.

There has been much discussion as to whether this compartment should be regarded as a part of the stomach, or merely a post-diaphragmatic diverticulum of the œsophagus. We have already shown that it carries the gastro-splenic omentum, and possesses the general peritoneal relations which one associates with the stomach, and there can be no doubt that it acts simply as a triturator of the food. Moreover, since the outlet is situated at right angles to the inlet, it is highly improbable that food could pass from the inlet to the outlet without first of all making its way through the triturator. Again, as the food which was found in the compartment was not digested, there appears no reason to suppose that any digesting takes place in this chamber as the result of the regurgitation of gastric juice into it from the second compartment.

In consideration of the nature of the teeth with which the porpoise is provided—viz., tearing teeth and not grinding teeth—it appears highly advantageous that the stomach should be so specialised as to supply the necessary grinding or triturating apparatus through the action of a chamber which is able to crumble food exactly as a piece of bread might be reduced to powder by the crushing action of the hand. We do not regard the similarity between its lining membrane and that of the œsophagus as of itself a sufficient reason for concluding that it is a diverticulum of the œsophagus, from the fact that in a one-chambered stomach the œsophageal lining membrane may be prolonged for some distance upon the interior of the stomach—e.g., in the pig; while from the general, but, more especially, the splenic, relations of this first compartment, we are of opinion that it must be regarded as an undoubted specialisation of the stomach, and not of the œsophagus. The peritoneal mesenteric or omental connection between this chamber and the spleen gives a strong argument for recognising the chamber as stomach, especially as the spleen always develops within the mesentery which attaches the primitive stomach, and not the œsophagus, to the dorsal wall of the abdominal cavity. That this association of the spleen with the first compartment of cetacean stomachs is not peculiar to the porpoise, has been shown by Sir WM. TURNER, who has recorded\* a similar arrangement in the stomachs of *Hyperoodon rostratus*, *Delphinus delphis*, *Delphinus (Lagenorhynchus) albirostris*, *Monodon monoceros*, and *Grampus griseus*. We think that the term “kau-magen,” or masticatory stomach, would fairly express its function and its morphology.

The *second compartment*, which was situated on the ventral aspect of the first, and formed an acute angle with it, had very much the shape of the human stomach, and presented two surfaces, two borders, and two apertures, but the chief axis lay more in the long axis of the abdominal cavity than does that of the human stomach. The ventral surface, rounded and convex, was in contact with the liver and the anterior abdominal wall. The dorsal surface looked towards the lesser peritoneal sac, and was in contact with the pancreas and chamber 1. The greater curvature measured 16 cms., and had an omentum attached to it; the lesser border measured 12·5 cms. In contact

\* TURNER, *Jour. of Anat. and Phys.*, vol. xxiii. pp. 466–492, vol. xxvi. pp. 258–270.

with this border, from left to right, were the pancreas, a peritoneal fold, and the recurved tubular part of the stomach for a distance of 6 cms. The apertures were situated, not at the ends, but in the walls or curvature. When opened, it was empty, and its cavity was only slightly smaller than that of the first chamber. With the exception of the external layer of muscle, the mucous and muscular coats were raised into thick prominent rugæ, separated from each other by deep intervening furrows. Although these rugæ were indented by mutual pressure, yet they resembled cerebral convolutions on a small scale. Their general disposition was in the long axis of the cavity, but, though running for the most part parallel to each other, they converged around the inlet and outlet of the chamber.

As already indicated, the inlet was placed upon the dorsal aspect of the chamber, and was at right angles to the line of entrance of the œsophagus into the first compartment. The appearances might be simulated by making a tight constriction round a one-chambered stomach close below its œsophageal orifice, and then applying the long contiguous sides of the two parts closely together. However, the sharp angle between the two compartments was occupied by the loose folds of the great omentum, so that neither of the chambers was prevented from distending, by its peritoneal relationships. Thread parasites adhered to the lining membrane, which was smooth and of a rusty brown colour.

Under the microscope, the secreting mucous membrane was from 2 to 3 mms. thick (Pl. II. fig. 4 (A)), and it closely invested the strong muscular ridges, which, as already indicated, resembled cerebral convolutions or large columnæ carneæ. It consisted essentially of tubular glands (Pl. II. fig. 4 (B)) supported upon a very distinct muscularis mucosæ, which sent definite prolongations, accompanied by a fine fibrous stroma, among the closely arranged tubules. The intertubular tissue was plentifully provided with capillary vessels.

The glands occupied the entire thickness of the mucous membrane, and each gland presented two parts, distinguishable from each other by structural differences. First, each gland, from its mouth inwards for a distance of .04 mm., consisted of a delicate basement membrane lined by short columnar cells, which surrounded a circular lumen—the duct of the gland—and stained after the manner characteristic of duct cells. The cells which had covered the free surface of the mucous membrane had been mostly desquamated, but so far as could be ascertained, they were similar to those lining the ducts just described. The gland proper constituted the remainder and second part of the secreting apparatus. Each tubule appeared to become branched as it passed inwards from the surface, but, judging from the fact that transverse sections of the tubules were not found in the deeper levels of the mucous membrane, the amount of tortuosity was not great. Each tubule (Pl. II. fig. 4 (B)) presented magnificent examples of central and parietal cells. The central cells were large nucleated polyhedral cells, set closely together and bounding the irregular lumen of the tubule. Everywhere they stained very deeply. The parietal cells formed a continuous single layer of cells, globular in shape



and set in intimate contact with the basement membrane, which sent prolongations inwards between them towards the central cells. As a result, each of the parietal cells occupied a recess or pocket exactly as if it lay in one compartment of a honeycomb. The parietal cells were not quite so large as the central cells, and from the fact that the former separated quite readily from the latter, one judged that there was no very definite uniting medium. The products of the activity of the parietal cells would find their way into the lumen of the tubule through fine interstices between the central cells, and these interstices were visible or concealed according to the direction of the section. Each parietal cell might be regarded as a unicellular secreting gland. They were filled with coarse eosinophile granules. It is important to note that these cells formed an unbroken layer, and that they were situated next to the blood supply, and that, therefore, they intervened between the central cells and their direct blood supply. In presenting a continuous layer of parietal cells, these tubular glands differ from those with which they correspond in such animals as the dog, the bat, and even in man, in all of which they only occur at intervals in the walls of the tubules. It is also of interest to note that these oxyntic cells are definitely restricted to one compartment of the stomach of the porpoise, whereas in the single-chambered stomachs of the other mammals above referred to, they are specially characteristic of the fundus, although not exclusively confined to that region.

The intertubular stroma everywhere showed very well marked capillary vessels, and throughout the stroma, more especially towards the free side of the mucous membrane, numbers of lymph cells were scattered.

From the ventral aspect of this compartment, and about one inch (2·5 cms.) in front of its most dependent part, a small constricted passage, wide enough to transmit the handle of a rod 5 mms. in diameter, led into the *third compartment* (Pl. III. fig. 10B). This passage was quite concealed among the thick muscular rugæ of the second chamber, and its exact position would scarcely be suspected from an examination of the second chamber. Viewed from the third compartment, however, it presented the appearance of a small firmly constricted aperture opening backwards. We feel assured that this is nothing more than a mural passage from the second to the third chamber. It has been regarded by JUNGCLAUS as a separate chamber, supplying in itself the third chamber, which has long been sought for in order to complete the analogy between the stomach of the porpoise and that of other cetacea. But the necessity for doing this disappears, since the method we have employed reveals the presence of a distinct globular third chamber, entirely separate from the second and fourth compartments, and outside of the mural passage, which is required as an outlet from the second to the third compartments. The third compartment was situated somewhat behind and on the ventral aspect of the second, to which it was closely adherent by the surface next the inlet without the intervention of peritoneum; but on its dorsal and ventral surfaces the peritoneum was prolonged from the second compartment without interruption, and, moreover, it had the great omentum attached to the hinder border of

its free surface. This globular chamber was marked off from the distal tubular part by a constriction visible externally, and well marked internally. The walls of this chamber were little more than one-sixteenth of an inch (less than 2 mms.) in thickness. The lining mucous membrane was pale, very slightly rugose, and at frequent intervals it presented pin-point depressions surrounded by slightly raised rings of the mucous membrane. This chamber was found empty, but it appeared capable of holding, without distension, material equal in bulk to the size of a small orange. While the inlet opened backwards to the second compartment, the outlet opened forwards into the fourth compartment. The adjacent margins of these two openings were about three-eighths of an inch (9 mms.) apart. The outlet was not so firmly constricted as the inlet, and could transmit the tip of a little finger without being unduly stretched.

Examined microscopically (Pl. II. fig. 5), the mucous membrane was found to rest upon a thick layer of muscularis mucosæ, which everywhere sent prolongations into the intertubular intervals. As in the preceding compartment, the surface layer of epithelium had been desquamated, but otherwise the tissue was in a satisfactory condition. It formed a layer averaging about 5 mms. in thickness, and throughout it presented large numbers of tubular glands. At intervals in its deeper half spherical nodules of lymphoid tissue appeared, while all through the intertubular stroma, which was considerable in amount, large numbers of lymph corpuscles were visible. These were most numerous in the immediate vicinity of the lymph nodule. The tubular glands appeared to be fairly simple in their arrangement, and in all probability they do not always branch as they descend into the substance of the mucous membrane. When they do divide, it is probably not oftener than once. Towards their deeper ends they appear to follow a sinuous course, and they may there be somewhat convoluted. The end next the surface tends to be straighter and less wavy. A delicate basement membrane supported the cells which lined the glands. These cells were somewhat cubical in shape, and, while their nuclei were always quite distinct, yet those pertaining to the superficial part of the tubules stained much more deeply than those belonging to the deeper part of the gland. A transverse section of the deep end of a tube examined under a higher power (Pl. II. fig. 6) revealed a small circular lumen surrounded by a close-fitting layer of nucleated cells. There was no trace of any arrangement corresponding to parietal cells. The tubules of this and of the succeeding compartment may very fairly be likened to the pyloric glands of other mammals, but instead of being scattered among oxyntic glands and only predominating near, or being exclusively found in the vicinity of the pylorus, they are restricted to the third and fourth compartments, and are not intermingled with oxyntic glands.

Vessels of different sizes were readily visible in the submucous layer, but the penetration of capillaries into the intertubular stroma was not very great, as in the case of the second compartment. It would therefore appear as if the vascularity of this mucous membrane was not a prominent characteristic of its structure.

The succeeding or *fourth compartment* was shaped like an inverted V ( $\Lambda$ ), of which

the proximal limb was rather shorter than the distal one. A small amount of constriction was observed at the angle of the  $\Lambda$ , while at its termination it was bent slightly forwards. It would be possible to describe this segment of the stomach as *two* chambers, but that seems to be uncalled for, in view of the fact that the microscopic characters of its mucous membrane did not, in any special manner, differ from those detailed for the third compartment. Indeed, there is reason to believe that this entire segment is, in reality, one chamber of nearly uniform cylindrical appearance, capable of being divided into a larger or smaller number of subdivisions by means of septa or circular constrictions more or less pronounced. It is this chamber which is so frequently divided in the narwhal. They might very well correspond to the pyloric half of the human stomach subdivided by constrictions. The proximal limb of the  $\Lambda$ -shaped compartment was situated in front of the third chamber and in close apposition with the lesser curvature of the second, to which it was intimately connected by direct prolongations of the peritoneum upon their free surfaces. The great omentum was also continued into the angle formed by the limbs of the V. Like the preceding compartment, it was empty. From its inlet to the slight constriction at the angle of the V measured three and a half inches (9 cms.) in length by one and a half (38 mms.) in width. The general form of this segment of the chamber was an elongated oval.

Its walls, as regards thickness, were similar to those of the preceding chamber. The mucous membrane was pale, showing only a faint amount of rugosity; thereby indicating that it did not require to undergo much distension. At intervals pin-point depressions like those already noted in the preceding chamber were observed. At the point of the V—i.e., at the acute angle—there was a certain narrowing of the lumen which might be described as constriction, or might be referred to the mere acute bending. The microscopic features of the mucous membrane did not differ in any marked way from those already described in connection with the third compartment, but the tubules were probably rather shorter, and the mucous membrane slightly thinner.

The distal limb of the inverted V extended to the pylorus. It virtually formed a cylindrical tube measuring about five inches (13 cms.) in length, and directed backwards and to the right. Within one inch (2.5 cms.) of the pylorus it underwent a slight dilatation on its hinder aspect, forming an Antrum pylori. At the same time it turned forwards with considerable abruptness, to end at the pylorus. Along its anterior and somewhat concave aspect it afforded attachment for the gastro-hepatic omentum. Between the laminae of this omentum, masses of lymphatic gland were found towards its left end, and the head of the pancreas occupied a similar position in relation to the pylorus at the right end.

The mucous membrane was very slightly rugose, and presented numerous pin-hole depressions, each of which, as in the places already mentioned, was surrounded by a slightly raised ring of the mucous membrane. Microscopically the mucous membrane did not present any variation upon what has been stated in connection with the last two compartments (Pl. III. figs. 7A and B). Apparently the pin-hole depressions may be associated with the nodules of lymphoid tissue which are everywhere embedded in the

mucous membrane of the second and subsequent compartments. Whether these nodules communicate directly with the lumen of the intestine we cannot say, but we have not found any trace of surface epithelium superficial to these nodules in any part of the alimentary canal, where they occur embedded in the mucous membrane. There is plentiful evidence that these nodules push their way entirely through the stratum of tubular and intertubular tissue of which the mucous membrane consists. If they are covered over by a layer of surface cells, as is generally supposed, there are certainly no glandular structures between them and the lumen of the canal. In their whole structure they present a remarkable similarity to the faucial tonsils of man, and they may serve a similar purpose.

*The Pylorus.*—The pyloric orifice was a tightly constricted passage which, with some pressure, would admit a rod 5 mms. in diameter. It was situated in the middle of a projection somewhat like an exaggerated nipple. The actual orifice was found on the summit of this nipple, which was directed into the interior of the compartment backwards and to the right side.

Every one of these constricted passages was placed as if with the definite object of making the onward progress of the contents as difficult as possible, and only attainable after the most complete circuit of the compartment. The length of this canal was rather more than half an inch (16 mms.). In its general arrangement and appearance it resembled the canal which formed the passage of communication from the second to the third compartments. Still no one has ever proposed that the pyloric passage should be adduced as a separate chamber, and so we regard JUNGKLAUS' statement upon the third chamber as an error in homology.

*The Duodenum.*—Beyond the pylorus, the intestine commenced with a marked dilatation, whose diameter at first resembled that of the adjoining part of the stomach. Very soon, however, it slightly increased in size, but after a course of two and a half inches (6.5 cms.), it suddenly dwindled and assumed the general characters of the remainder of the intestine.

Immediately before this dilatation became reduced to the proportions of the ordinary bowel, it received the bile-duct which penetrated its dorsal surface. Further, the pancreas was closely applied to this portion of the canal, but the pancreatic duct formed a tributary of the bile-duct, and so did not show a separate opening through the wall. This disposition of the pancreatic ducts was not surprising, since the bile-duct passed through, and was therefore surrounded by the head of the pancreas. From this disposition of these important ducts we are justified in regarding this section of the canal as the duodenum, which therefore corresponds to what are called the first and second parts of the human duodenum.

On being opened, the duodenum was seen to be lined by a mucous membrane considerably darker in colour than those which had lined the preceding compartments of the stomach. Whether this colour should be attributed to staining by bile we cannot say, as there was no gall-bladder, and therefore we saw no bile. It was thrown into promi-

nent rugæ, and presented a miniature copy of the interior of the second stomach chamber. Its capacity was about equal to that of the third compartment of the stomach. The opening of the bile-duct was situated on a papilla (*Papilla vateri*) on the dorsal wall of the duodenum, about half an inch (12 mms.) from the termination. This termination was not marked by any valvular constriction, but was merely indicated by a sudden reduction in calibre to the shape and proportions of the intestinal tube.

From such a distinct and precise disposition of this portion of the canal there can be no reasonable doubt that, so far as this animal is concerned, the duodenum should not be regarded as a section of the intestine, but rather as a separate and special chamber within which the liquid or peptonised food, having left the stomach, is subjected to the action of the biliary and pancreatic secretions. It was a contention of the late Professor GOODSIR that the duodenum of man ought to be considered as a separate segment of the bowel, on account of its attachments, structure, and functions. On these points, so far as the porpoise is concerned, this view is quite clearly supported.

Microscopically, the mucous membrane was remarkable for its negative as well as for its positive characters. Villi were entirely wanting from its surface, and there were no trace of Brunner's glands.

The rugæ already mentioned formed longitudinal ridges of muscularis mucosæ covered by the lining mucous membrane, which consisted of tubules similar to those found in the adjoining intestine.

The surface epithelium was, for the most part, denuded, but on some remaining patches the cells were short and cubical. Each gland was comparatively straight, the duct being lined by short columnar epithelium, while the deeper part of the gland presented a considerable number of chalice cells.

*The intestine*, which commenced at the end of the duodenum, extended to the anal aperture as a tube of uniform appearance and supported by a single mesentery. In calibre it appeared to be also fairly uniform, and although some parts were more firmly contracted than others, there was no outward evidence of division into large and small bowel. In its general appearance it resembled small bowel, and its least contracted parts were not larger than the diameter of an average digit. No diverticulum or appendix occurred anywhere. It measured rather more than fifty feet in length—i.e., nearly twelve times the length of the animal.

When we consider that the length of the human intestine is only from four to five times as long as the individual, we are probably justified in associating the unusual length of the intestine of the porpoise with the provision of an extended absorbing surface in compensation for the absence of villi from its lining mucous membrane. Transverse sections made at intervals along the entire length of the tube revealed the presence of eight or nine longitudinal and projecting folds which occupied the greater part of the lumen. These left very little free lumen, and in those places where the bowel was firmly contracted, the cut face appeared almost solid by reason of the longitudinal projections. In the first half or thereby of the bowel, these projections were fairly

evenly distributed round the interior of the tube (Pl. III. fig. 8A), but in the lower or hinder half those upon the mesenteric side of the gut were considerably reduced in size to make room for an increased prominence of those upon the side opposite to the mesentery (Pl. III. fig. 9A).

The microscopic appearances of the mucous membrane differed considerably in the upper and lower parts. At no point were villi discovered, but in the upper or anterior half the glandular arrangements were almost exactly similar to those of the duodenal mucous membrane (Pl. III. fig. 8B), except that in the bowel the glands were somewhat shorter than in the duodenum. Chalice cells were also prominent appearances. In the lower part of the bowel, the first noteworthy feature was the difference in the size of those ridges attached on the side next to the mesentery, as compared with the size of those on the side opposite to the mesentery. The latter set consisted of four thick and long projections. They occupied half of the circumference of the tube by their bases, but their projecting ends filled considerably more than half of the interior. The mucous membrane which lined the entire tube was very similar to that which has already been described for the upper part of the bowel, but the number of chalice cells now so greatly preponderated that the mucous membrane appeared like a network. The outstanding feature of the sections was the presence of globular masses of lymph tissue situated in the submucous layer (Pl. III. fig. 9B), but sending prolongations through the mucous covering apparently to discharge upon the free surface. We did not find a layer of epithelium covering those lymph nodules, but, as in other parts of the bowel, it may have been desquamated. This disposition of lymph tissue was confined to the three trenches which separated the four large ridges from each other, and these lymphoid patches were strictly limited to one side of the intestine, and no similar arrangement occurred on the mesenteric side of the intestinal wall. Nine or ten of these lymphoid masses were visible on the sides of a single ridge in each microscopic section, and the total amount of lymph tissue thus arranged must have been very great.

*The pancreas*, lying between the liver and stomach, was pyramidal in shape, measuring 8 cms. transversely, 7 cms. antero-posteriorly, and 6 cms. in height. The base was posterior, and looked towards the lesser sac, while the blunted apex was in contact with the under surface of the liver.

The left side was in contact with the first chamber of the stomach, the dorsal surface with the dorsal abdominal wall, but covered by peritoneum; the right surface was in contact with the terminal part of the stomach, pylorus, and duodenum; and the anterior surface, continuous with the right surface, looked towards the lesser sac, and was crossed by the tubular part of the stomach.

The tissue of which the gland was composed was folded round the bile-duct, which, therefore, passed through the gland.

*The liver* had two large lobes—right and left—which were prolonged anteriorly into two conical projections, between which there was a triangular depressed area, mesial in position.

These two projections coincided with the hollowed-out bases of the lungs, while the heart occupied the mesial depression, the diaphragm intervening in both cases.

There was no gall-bladder, and therefore no quadrate lobe to the liver, but indications of a spigelian and a caudate lobe have already been noted.

The microscopic structure of the liver, spleen, and pancreas did not materially differ from the appearances of those organs in man. The sections of the pancreas displayed the characteristic cells associated with acini and ducts.

From an examination of the sections, we are inclined to think that the cells described as "central acinar cells" are merely sectional views of the cells which line the commencement of ducts that chance to lie upon the side of the section next to the observer; and further, that the so-called paranucleus or "nebenkern" results from the same structures lying on the side farthest from the observer, and therefore less distinct. Otherwise it seems that in such clear and distinct sections these special structures should appear more frequently than they do.

It ought to be recorded that the tape-worm—*Bothriocephalus latus*—was found in the intestine. This parasite has not hitherto been observed in the alimentary canal of a marine mammal.

#### CONCLUSIONS.

(1) Although the porpoise, like other cetacea, is a mammal without hind limbs, and although its innominate bones are reduced to a couple of slender rods, yet, in the peritoneal arrangements associated with the posterior end of the abdominal cavity, there is evidence of a pelvic cavity which has not hitherto been recognised as such.

(2) From the present observations, we agree with those previous observers who have described the stomach of the porpoise as four-chambered, and we are in harmony with them as regards the homologies of the first and second compartments, although we regard the first compartment as developed from the primitive stomach, and not as a dilatation of the post-diaphragmatic oesophagus.

(3) We do not regard the "canal" or mural "passage," which lead onwards through the wall of the second compartment, as the third compartment, but look upon this "canal" as the inevitable association of the thick wall of the second compartment. Moreover, it is not quite so long as the "passage" of communication between the first and second chambers, and but little longer than the pyloric "passage," neither of which have ever been regarded as homologous with separate compartments.

(4) We find the third compartment in a distinct chamber beyond the wall of the second, and clearly demarcated from the fourth, both by its somewhat spherical shape and by its constricted outlet.

(5) Although JUNGCLAUS and other writers support the view that the third compartment of the adult porpoise is the mural "canal" or "passage" already referred to,

yet, in his plate, JUNGKLAUS figures several stomachs of foetal porpoises which apparently entirely agree with our description of the adult stomach.

We are therefore forced to conclude that, by our method of preservation, we have been able to retain the normal appearances and shapes of these stomach chambers, which have hitherto either been lost, or of such uncertain characters as to lead to error or difficulty in the determination of their true homologies.

(6) The fourth compartment, being tubular or cylindrical, is distinctly marked off from the spherical third chamber on the one hand, and from the duodenum on the other. The acute bend near the middle of this chamber, and the pre-pyloric dilatation (Antrum pylori), show how readily it might be still further subdivided.

(7) From these considerations, it would seem as if the stomachs of all cetacea were constructed upon a common plan of subdivision into a series of chambers, with such variations as regards the number, size, and particular shapes of the compartments as are explicable by reference to the porpoise, and are probably due to differences in the characters of the teeth and the nature of the food determining the presence or absence of that particular compartment which we have called the "kau-magen" or masticatory stomach, and which in the case of the porpoise forms the first of the series of compartments. Further, the homologies of these compartments among different members of the Cetacea should be established by their structure and anatomical relations rather than by numerical sequence.

(8) We regard the duodenum as that dilated part of the alimentary canal between the pylorus and a point immediately beyond the common entrance of the bile and pancreatic ducts.

(9) Intestine proper commences at the termination of the duodenum, and is suspended throughout in the mesial peritoneal mesentery.

(10) The small size of the spleen is probably compensated for by the unusual amount of lymphoid tissue distributed in the omentum and at different parts in the wall of the alimentary canal, especially towards its lower end.

(11) Throughout the entire length of the alimentary canal, villi were absent.

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#### LITERATURE.

The literature on the Cetacean Stomach is very extensive, but it has been brought up to date by Dr Friedrich Jungklaus, who quotes 63 memoirs in his paper "Der Magen der Cetaceen," *Jenaische Zeitschrift für Naturwissenschaft*, xxxii., 1898.

*Lehrbuch der Vergleichenden Mikroskopischen Anatomie der Wirbeltiere*, Oppel (Jena), 1896.



## EXPLANATION OF FIGURES.

- Fig. 1. Inlet of pelvic cavity of male porpoise (viewed from abdominal cavity).  
 Fig. 2. The hinder part of the abdominal cavity viewed from the side, showing inlet of pelvic cavity.  
 Fig. 3. Section of first compartment of stomach of porpoise stained in hæmatoxylin-eosin.  $\times 96$ .  
 Zeiss, oc. 4, obj. BB.  
 Fig. 4 (A). Outline of section of second compartment of stomach of porpoise,  $\times 20$ , to show thickness of mucous membrane.  
 Fig. 4 (B). Section of second compartment of stomach of porpoise stained in Benda's fluid.  $\times 270$ .  
 Zeiss, oc. 4, obj. DD, to show structure of secreting tubules.  
 Fig. 5. Section of third compartment of stomach of porpoise stained in hæmatoxylin-eosin.  $\times 96$ .  
 Zeiss, oc. 4, obj. BB.  
 Fig. 6. Section of a tubule (deep end) of third compartment stained in hæmatoxylin-eosin.  $\times 270$ .  
 Zeiss, oc. 4, obj. DD.  
 Fig. 7A. Section of fourth compartment stained in hæmatoxylin-picro-fuchsin.  $\times 96$ . Zeiss, oc. 4, obj. BB.  
 Fig. 7B. t.s. of one tubule.  $\times 470$ . Zeiss, oc. 4, obj. E.  
 Fig. 8. t.s. section of upper end of intestine stained in eosin-methyl-blue. (A) natural size. (B)  $\times 96$ .  
 Zeiss, oc. 4, obj. BB.  
 Fig. 9A. t.s. of lower end of intestine, natural size.  
 Fig. 9B. One ruga in transverse section stained in hæmatoxylin-eosin.  $\times 20$ . Zeiss, oc. 4. Beck, obj. 2".  
 Fig. 10. Scheme of compartments of stomach of porpoise.

## A. After Jungklaus.

- O. Œsophagus.  
 I. First compartment.  
 G. Epithelial boundary between first and second compartments.  
 II. Second compartment.  
 III. Third „  
 IV. Fourth „  
 P. Pylorus.  
 Ad. Ampulla duodenalis.  
 P.v. Papilla vateri.  
 D. Duodenum.

## B. Hepburn and Waterston.

- O. Œsophagus.  
 I. First compartment (Kaumagen).  
 II. Second „  
 III. Third „  
 IV. (a) Proximal part of fourth compartment.  
 (b) Distal „ „ „  
 (c) Antrum pylori.  
 P. Pylorus.  
 D. Duodenum.  
 P.v. Common entrance of bile and pancreatic ducts, Papilla vateri.  
 Int. Intestine.

We desire to express our indebtedness to Sir WM. TURNER and Professor SCHÄFER for much friendly criticism and suggestion during the preparation of this paper.

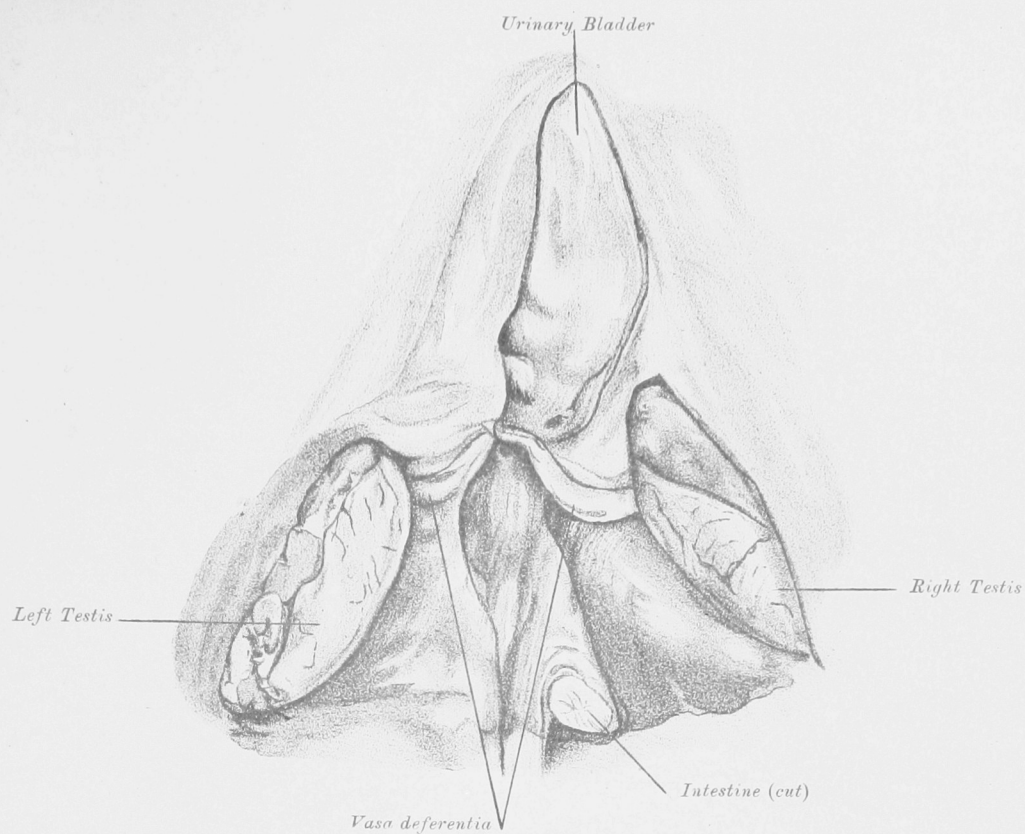


Fig. 1. INLET OF PELVIC CAVITY OF MALE PORPOISE VIEWED FROM ABDOMINAL CAVITY.

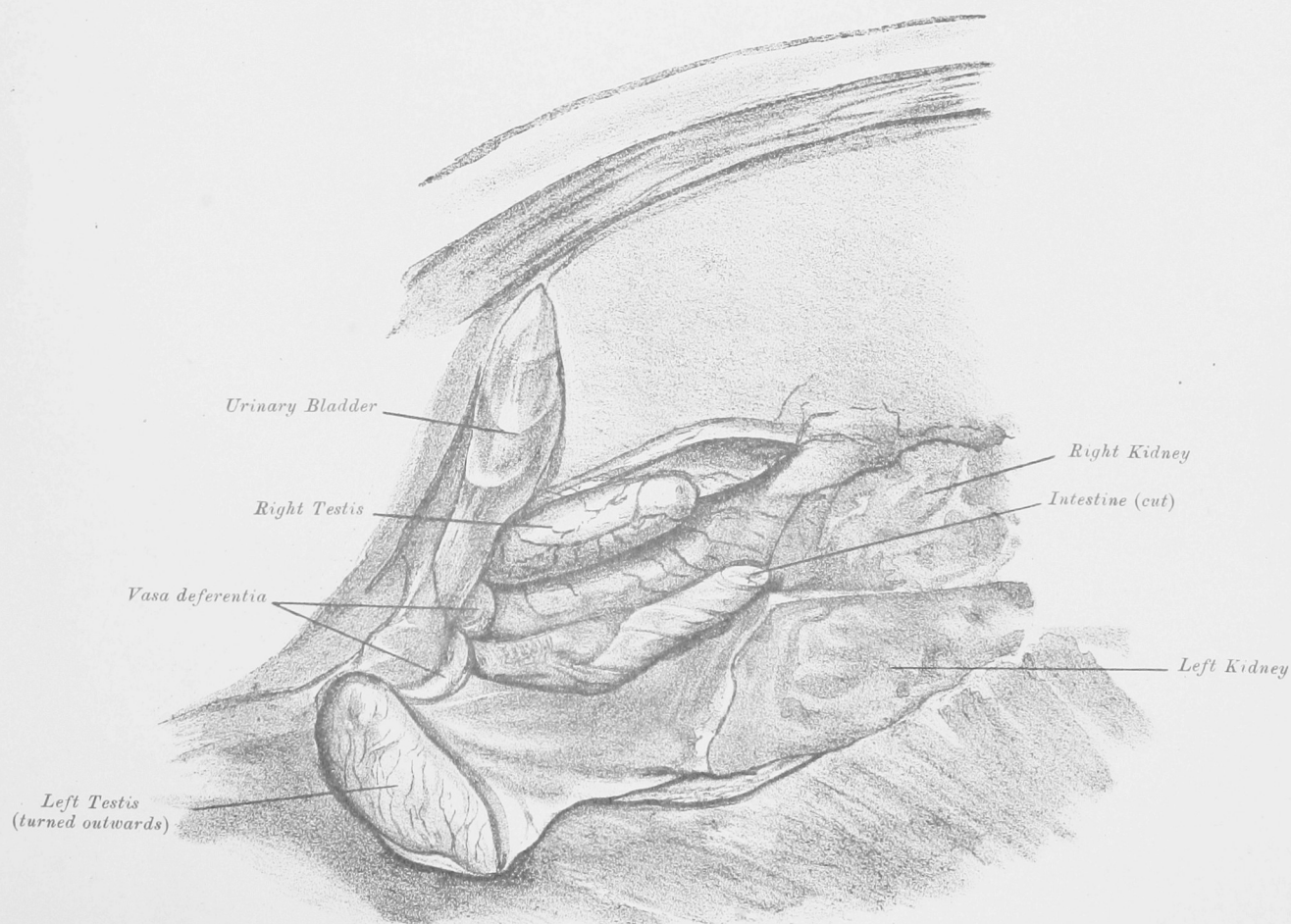


Fig. 2. THE HINDER PART OF THE ABDOMINAL CAVITY VIEWED FROM THE SIDE.

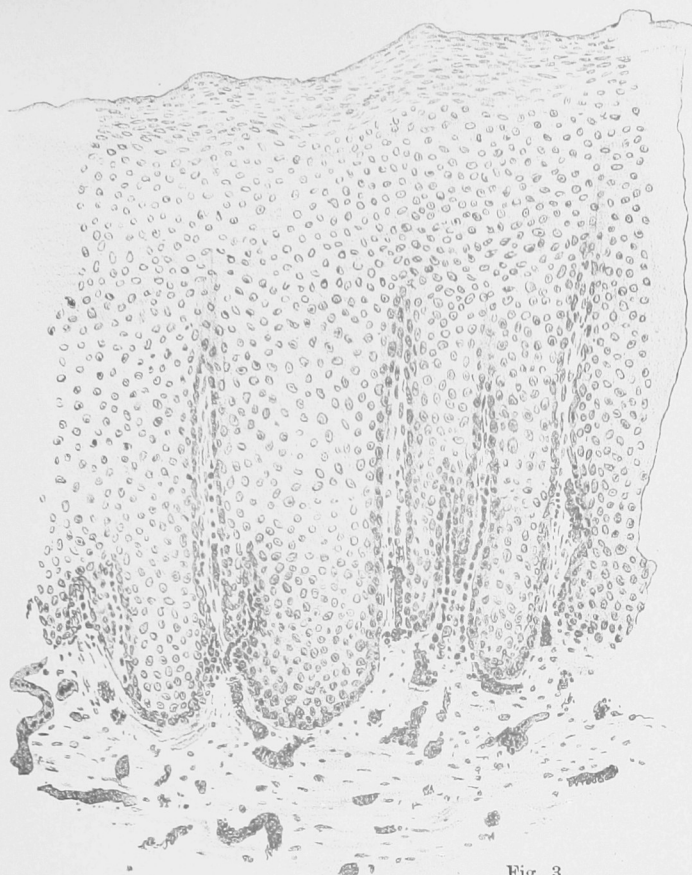


Fig. 3.

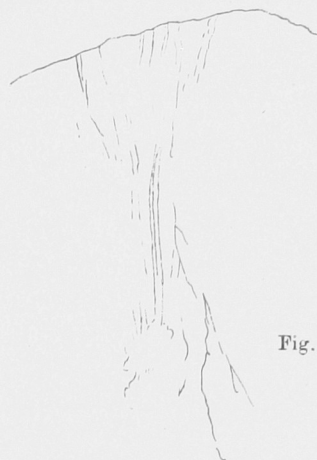


Fig. 4 (A).

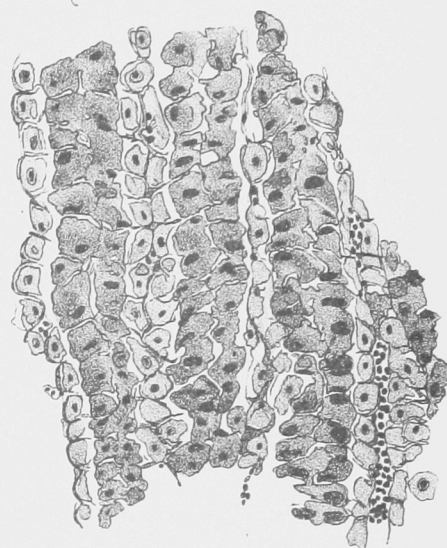


Fig. 4 (B).

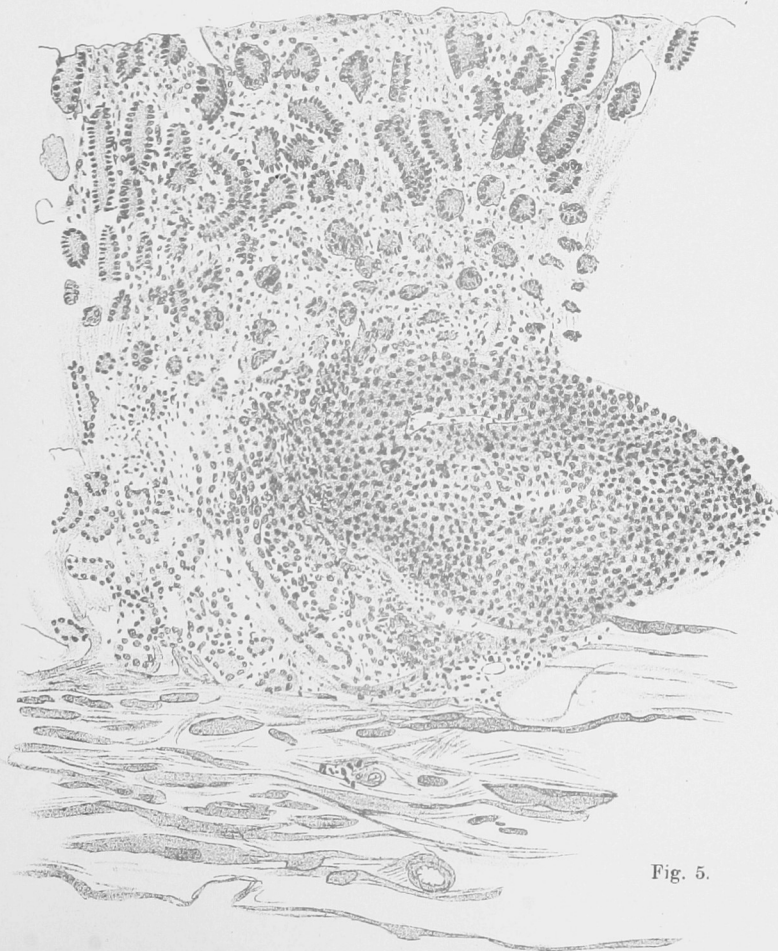


Fig. 5.

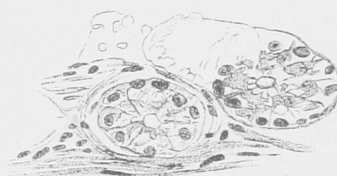


Fig. 6.



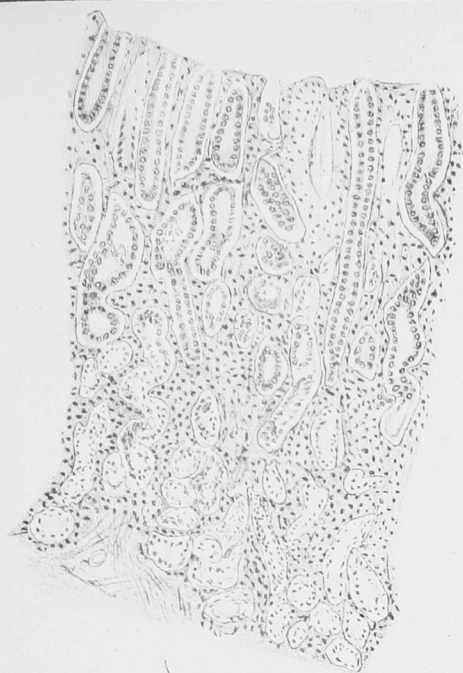


Fig. 7 (A)



Fig. 8 (A).



Fig. 8 (B).



Fig. 7 (B).



Fig. 9 (A).



Fig. 9 (B).

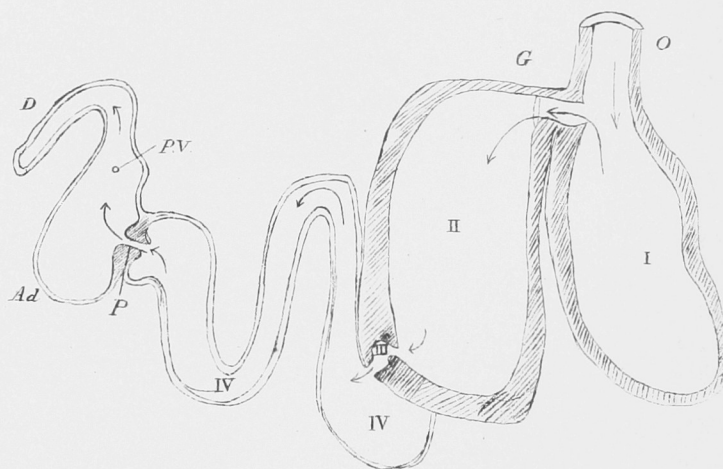


Fig. 10 (A).

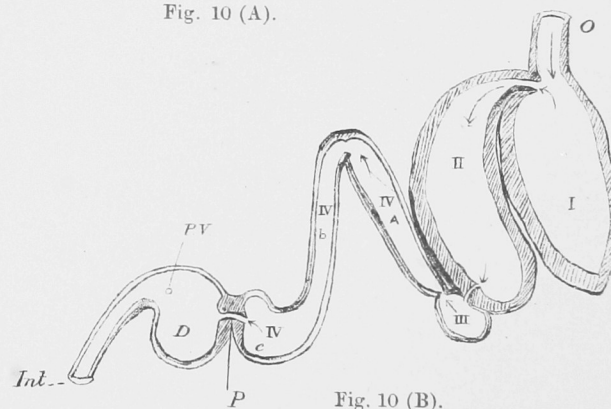


Fig. 10 (B).