SOME OBSERVATIONS ON THE CETACEAN STOMACHS, WITH SPECIAL CONSIDERATIONS ON THE FEEDING HABITS OF WHALES

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ABSTRACT

Macro- and microscopical observations on the sei, fin, blue and sperm whale stomachs are described and discussed on the base of comparative-anatomical and functional viewpoint. The compartmentalization of the cetacean stomach is a unique character in the animal kingdom and it must be attributed to the aquatic life of the group. An attempt has been made to establish the relationship between the anatomical features of the cetacean stomach and its physiological function.

INTRODUCTION

In the latter half of the seventeenth century Tyson (1680) described the complicated stomach of the common porpoise. About one hundred years later Hunter (1787) remarked that the cetacean stomach revealed generally a highly characteristic feature of this group of animals, divided into several compartments. He noticed, furthermore, that it resembled very closely those of cattles and sheep, and he supposed the whales probably belonged to the ruminants, or had at least an intimate phylogenetical relationship with the ungulata. Thereafter, many anatomists directed their attention to the cetacean stomach and numerous reports were published, dealing directly or incidentally with this special feature of cetacean anatomy. Though it was soon ascertained that the cetacean stomach was, in spite of its resemblance to the ruminant one, quite different from the latter, its extraordinarily complicated structure remained for a long time without a clear comparative-anatomical explanations, not to speak of its physiological interpretation. The specifical differences in form of stomachs among all different kinds of whales were so extreme that it was very difficult to abstract the standard figure of them. We will quote here, for example, various numbers of stomach-chambers recorded by many authors for Mystacoceti. In most cases, the research materials of these authors were adult or fetal minke whale (*Balaenoptera acutorostrata*), though some of them studied the blue whale (*B. musculus*) or fin whale (*B. physalus*). Schulte alone used a fetus of the sei whale (*B. borealis*).

Hunter (1787) 5, Cuvier (1805) 4, Meckel (1829) 3,

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Eschricht (1849) 3, Murie (1865) 4, Carte & Macalister (1868) 5,
Perrin (1870) 4, Weber (1888) 3*, Pilliet (1891) 4,
Turner (1892) 5, Schulte (1916) 4*, Slijper (1962) 3*.
*without counting the duodenal ampulla.

At the end of the nineteenth century, however, Weber (1888) and Jungklaus (1898) published very splendid works on this problem and the macroscopic anatomy of the cetacean stomach was brought to a general conclusion. Thus, Weber classified the stomach of toothed whales, based on the development of its first compartment covered with the oesophageal mucous membrane, into the following 5 types: 1) Ziphiidaes-type, 2) Hypothetic intermediate-type, 3) Phocaena-type, 4) Globicephalus-type and 5) Lagenorhynchus-type, and he explained that these types had developed one by one in the order of their number from the most primitive Ziphiidaes type. On the other hand, according to Jungklaus, who endeavoured to use generally the comparative-anatomical characteristics of the cetacean stomach, not only of the toothed whales but also of the baleen whales, the most remarkable peculiarity of the cetacean stomach distinguishing itself from the same of other mammals did not lie in its mere complexity caused by the compartmentalization but consisted in the fact that the glandular stomach itself was separated into two divisions, one of those being provided with the peptic or fundus glands and the other with the pyloric glands. The latter divisions were, moreover, apt to be divided into two or more secondary compartments. On the difference between the Odontoceti and Mystacoceti stomachs he stated that in the latter the constrictions between each divisions or compartments were not so sharp as in the former. Jungklaus's conclusion of the characteristic feature for cetacean stomach is quite right from the comparative-anatomical standpoint, as was confirmed afterwards by Beddard (1900). From the physiological standpoint, however, we suppose that the complexity of the cetacean stomach, which is caused not only by the compartmentalization of the glandular portions but also by the oesophageal dilatation etc. has a great significance. Against this background information we will, in the present paper, try to present a detailed histological picture of the cetacean stomach.

MATERIALS

Baleen whale:

Sei whale (*Balaenoptera borealis*): 14.0 m male, 14.6 m female, 15.7 m female, 16.2 m female.
Fin whale (*Balaenoptera physalus*): 21.3 m female.
Blue whale (*Balaenoptera musculus*): 23.8 m male.

Toothed whale:

Sperm whale (*Physeter catodon*): several adults, of which one 11.0 m long female and one 15.6 m long male were studied with special attention.

OBSERVATIONS

Stomach of the baleen whale

It is composed of four compartments arranged in series. The first compartment, into which the oesophagus opens, is nothing but a dilated sack at the lower end of the oesophagus and the fourth division is the extraordinarily developed duodenal ampulla, into which opens the combined duct of the liver and of the

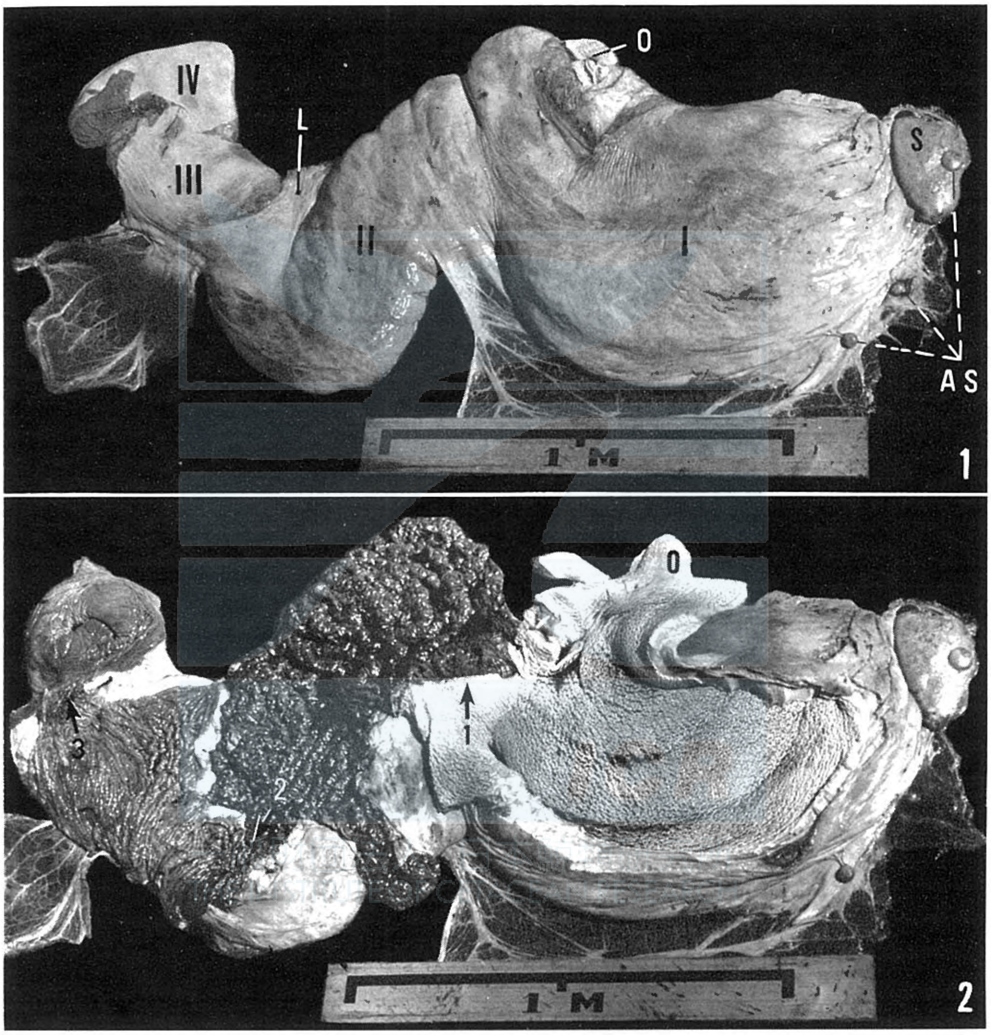

Fig. 1. Ventral view and frontal section of the stomach of a sei whale, 14.0 m male. The Roman numerals showing the first (I) to the fourth (IV) compartments and Arabic numerals with arrow showing boundary between the each compartments.
O: oesophagus S: spleen AS: accessory spleen L: gastro-phrenic ligament

pancreas. The other two, namely the second and the third, are real gastric compartments providing with digestive glands. Between these two, however, there is another small division developed especially in the fetal stage. In the female sei whale of 15.7 m length the largest compartment is the third one, measuring 110 cm and 85 cm respectively in the transverse and longitudinal diameters in relation to the axis of the digestive canal, followed by the fourth (85×75 cm) and the second (80×80 cm) in that order, and the first compartment is still smaller. Communication between the first and the second chambers is through a not so strong constriction. Where the second chamber leads into the third through the small connecting division, there exist two semilunar valves separating the two compartments. The third compartment opens into the fourth through the narrow passage constricted sharply by the pyloric sphincter (Fig. 1).

Macroscopical features of the mucous membrane: (Plate I)

The mucous membrane of the oesophagus is lined by the thick, graywhite and cornified epithelium folded with numerous longitudinal, fine furrows. The same epithelium clothes the inner surface of the first compartment too, and there are many reticular folds of several millimeter in width, which are ramified and anastomosed to each other. These reticular folds disappear, when the wall of the stomach is stretched, so that they are formed by the undulation of the whole wall. It is clear, therefore, that this compartment is able to contract and dilate to a considerable extent by the aid of the mural muscle strata. Where the first compartment leads into the second one, the mucous membrane changes its character abruptly, there is a distinct lineal boundary between the oesophageal epithelium of the former and the gastric lining of the latter (Plate I-1). This is covered by the soft, mucous epithelium of dark gray colour with some tone of yellow. Its surface is smooth for 2–3 cm from the line separating the oesophageal epthelium and the gastric lining referred to above, followed by thick reticular folds, about 1 cm in width, resembling the convolution of the human cerebrum. These folds do not disappear even when the stomach is stretched; that is to say that they are formed in the mucous membrane itself merely for the purpose to increase the inner surface of the stomach. The second compartment has, therefore, no anatomical feature to contract or dilate itself extensively. In the lower half of the second compartment the reticular folds are reduced as the compartment approaches the third one, in which the surface of the mucous membrane is quite smooth and without any furrows or folds. It is coloured yellowish gray, with some tone of pink. The duodenal ampulla is clothed also with smooth, soft membrane, coloured brownish red and it continues with that of the small intestine, without any constriction or valve. For the female sei whale (15.7 m long) the first compartment has the thickest wall measuring 2.5 (–3.0) cm, containing very well-developed muscular strata. The wall of the remaining three are somewhat thinner and measure about 1.2 (1.0–1.5) cm. The wall of the small intestine is 0.8–1.0 cm thick. For the male blue whale of 23.8 m length the walls of the first, second, third and fourth compartments were 4.0 cm, 2.0 cm, 1.5–2.0 cm (mucosa: 0.5, muscularis: 0.9, serosa: 0.1) and 1.3 cm (mucosa: 0.3, muscularis: 0.7, serosa: 0.3) respectively.

Histological structure: (Plate II)

Oesophagus is lined by an extensively stratified flat epithelium of about 1 mm in thickness. The most superficial layer of the epithelium (25–30 μ) is completely cornified and the cells have no trace of nucleis in contrast to the case in humans. The next layer of about 25 μ has cells containing rudimentary nuclei. These two layers are followed by a third layer, 4–5 cells in thickness the cytoplasm of the cells staining deep red with eosin and the nuclei are shriveled, indicating probably the commencement of the cornification of cells. The next layer is composed of several strata of large cells, occupying the greater part of the epithelium. While the cells of the upper portion of this layer are situated with their axis almost parallel to the surface of the epithelium, those of lower part make a right angle with the same especially in the areas between the papillae. While the nuclei of the former are smaller and stain deeply, those of the latter are larger and stain lightly. The deepest layer is bounding to the propria, and composed of crowded cells of small size. The connective tissue, propria, of about 3–4 mm in thickness, contains many vessels and fat-cells and forms high papillae, which are very well-developed, and the thickness reaches as high as 95% of the total thickness of the epithelium (in the case of humans oesophagus it is only 50%). The density of the papillae is also larger in the cetacean oesophagus than in the human case.

The smooth muscle fibres of the lamina muscularis mucosae are arranged not so orderly as in other mammals, but are scattered irregularly. This unsystematic arrangement of the muscularis mucosae is noticed not only in the oesophagus but also in every compartment of the stomach and throughout the intestine, thereby losing the significance of the the name of " lamina ". The submucosa, formed by loose connective tissue, has nothing special to be described. The muscularis presents an inner, circular and an outer, longitudinal layer of muscle bundles. In the upper portion of the oesophagus it consists exclusively of striated fibres, but in the middle and lower parts the muscularis is composed wholly of smooth fibres. Between the inner and outer layers there are scattered nerve fibres and ganglia, analogous to Auerbach's plexus, which we come across in the intestines. The outer surface of the muscularis is covered with a thick membrane of connective tissue reinforced by elastic networks (adventitia).

The histology *the first compartment* of stomach is not very different from that of the oesophagus, in spite of the slight difference in the relative thickness of the corresponding layers or strata. It is quite obvious that this compartment is nothing but a dilated sack of the lowest part of the oesophagus.

The second compartment. The simple cylindrical epithelium lines the entire inner surface of this compartment, including the gastric pits. It is composed of light cells having distinct boundaries between each other. Nuclei of these cells are small-sized, deeply stained and are situated at the base of the cells. At the floor of the gastric pits open numerous gastric glands occupying the propria and we can discriminate two kinds of glands, the cardiac and the fundus glands.

The cardiac glands. Contrary to the earlier belief that the cetacean stomach is destitute of the cardiac glands, we found cardiac glands to exist in the stomach of a blue whale, occupying the narrow zone adjacent to the border-line at the junction between its first and the second compartments. They are quite like the pyloric glands of the third compartment in their structure, both being of the tubulo-alveolar nature and composed of light cells of one kind.

The fundus glands. This type of gastric glands, branched tubular in nature, are extended in the greater part of the mucous membrane of the second compartment, situated within the propria and are 2–3 mm in thickness (in humans it is at most about 1.0 mm). The zymogenic cells of this gland, 6–7 μ in diameter, are characteristic with the fairly coarse granules they contain, which stain with basic dyes in the same way as the chromatin of the nucleus. The second kind of cells found in this gland, the parietal cells, are much more developed than in the human stomach. They differ from the chief cells in being considerably larger (10–20 μ in diameter) and in their spherical or pyriform shape, containing sometimes two or more nuclei. Frequently, especially in the lower part of the gland, they do not reach the lumen of the tube, being connected with it by a narrow pedicle. The most striking characteristics of these cells are their strong affinity for acid dyes. Numeral ratio between the zymogenic and the parietal cells is about 3: 1 and this index shows, compared with that of 5–6: 1 in the human case, that the cetacean stomach has plenty of parietal cells, which are said to secrete hydrochloric acid. This peculiarity of the cetacean fundus glands must have some important meaning for the gastric function of this animal. Mucous neck cells are situated near the openings of the glands into the gastric pits and can be discriminated easily by their light cellular body and somewhat shriveled nucleus, lying aside at the bottom of the cells.

The propria consists mainly of reticulated tissue, containing many free cells or aggregated lymphatic cells.

The muscularis mucosae, which separates the propria from the underlying submucosa, does not form a well-defined layer and is divided into the following four groups of muscle bundles; 1) muscle-fibres scattered in the propria, some of which extend along the fundus glands up to the superficial layer underlying the epithelium, 2) fibre-bundles running in the same direction as the reticulated folds of the mucous membrane, 3) and 4) two muscle bundles in the deeper layer, which run independently of the direction of the reticulated folds, crossing each other at almost right angles.

In the loose connective tissue of the submucosa run arteries provided with very thick walls, just like the case in the cattle.

As muscularis was stripped of in our materials it was not possible to examine it histologically.

The third compartment. The simple cylindrical epithelium clothes the inner surface, where numerous gastric pits are developed. Glands of this compartment that extend into the propria are the pyloric glands. They are of the branched tubulo-alveolar nature, and the glandular epithelium here presents great differences from that of the fundus glands as these are composed of only one kind of cells. Although these cells differ slightly from the zymogenic cells of the fundus glands, they resemble the latter in all essential particulars so much so that we may take them for the same.

The propria of this compartment does not differ from that of the second chamber. The muscularis mucosae also resembles that of the second one, but the first group of muscle-bundles is more developed in this compartment and the second group is lacking, while the third and fourth groups are only weakly developed.

In the submucosa there are scattered fat-cells, vessels, nerve-cells and fibres. The muscularis is stripped off.

The fourth compartment (duodenal ampulla). The histology of the fourth compartment in the oral half is not very different from that of the third compartment and in the anal half in their structure leads into the small intestine.

Stomach of the sperm whale

As refered to in the introduction, the constrictions between adjacent gastric compartments in the sperm whale are marked more sharply than in the baleen whales, and we can easily discern four compartments. The first and second compartments are very large, each measuring 140×140 cm for an adult male of 15.6 m length, and the third and fourth are somewhat smaller, measuring 130×60 cm and 130×100 cm respectively.

The inner surface of the first compartment is covered with the same, yellowish white epithelium as is the case with that of the oesophagus. There are, however, no well-developed folds, the inner surface here being provided only with the irregular reticular fine furrows, especially in the region between the opening of the oesophagus and the passage into the second compartment. The oesophageal epithelium of the first compartment stands out distinctly from the soft, mucous membrane of the second one. The surface features of the latter resemble that of the sei whale, having been provided with the reticular folds, which diminish in the areas near the first and third compartments. The third and fourth compartments are clothed by a similar smooth membrane as in the sei whale, though in the fourth come into sight semilunar folds as it approaches the opening into the small intestine.

Thickness of walls of different compartments. The thickness of the wall of the first compartment is 2.5–3.0 cm (mucosa 0.7, muscularis 1.7, serosa 0.4) of the second compartment 2.5–3.0 cm (mucosa 0.8, muscularis 1.4, serosa 0.7), and each of the third and fourth compartments 1.0–1.5 cm. It was not possible to do histological studies of the stomach of this whale, as it is very difficult to get seasonably fresh materials to be used for microscopical work.

DISCUSSION

1. *Cetacean stomach seen from the comparative-anatomical viewpoint:*

To understand the physiological meaning of the complicated feature of the cetacean stomach, we may first briefly review the comparative anatomy of the stomach in the animal kingdom. Fishes have stomachs of various shapes. Amphibians and reptiles have also gastric sacks and the birds posses in addition to the crop, dilated sack of the oesophagus, glandular and muscular stomachs. As to the mammals though the monotremata and a small group of rodentia are said to have no glandular stomach, almost all others have glandular stomach, where three distinct regions or areas can be identified, namely the cardiac glandular, the gastric or fundus glandular and pyloric glandular. Besides, there very often are also the oesophageal, non-glandular region or expansions. According to the combinations of these regions among mammals, there are many types of stomachs, and Ellenberger (1926) classified them into the following groups:

1) Simple stomach composed merely of glandular regions
   a) simple form lacking in cardiac sacks
      i) shaped like a simple sack, e.g. phoca;
      ii) provided with swelling of fundus, e.g. carnivora, insectivora, many rodentia, chiroptera, apes and man;
   b) complex form provided with one or more cardiac blind sacks, e.g. sirenian, large kangaroos and pig;
2) Complicated stomach composed not only of glandular regions but also of oesophageal region or expansions (always possess the cardiac area).
   a) simple form . . . the glandualr and oesophageal regions make altogether a simple stomacheal sack.
      i) provided with not so large fundus, e.g. horse and tapir.
      ii) provided with conspicuously large fundus, e.g. mouse and rat.
   b) complex form . . . the oesophageal ampulla makes one or more forestomachs independently of the glandular, real stomach, e.g. cetacean and ruminantia.

From this classification it is clear that the complexity of the mammalian stomachs is caused mainly by two reasons by the expansion of the fundus or cardiac blind sacks, and by the oesophageal forestomach that can be divided again into two or more compartments. In view of these facts, the cetacean stomach, of which the complexity lies in the subdivisions of the glandular stomach itself, is an exceptional case in the animal kingdom. Though Ellenberger in his classification grouped the cetacean stomach with the ruminantia, we see now that there is a distinct difference between these two. In the latter, though it is composed also of four compartments, the first three, rumen, reticulum and omasum, are clothed with the oesophageal epithelium and only the last one, abomasum, represents the real digestive part of the stomach. Thus in the ruminantia the stomach may be regarded as being primarily divided into two regions, the last of which only is the digestive region, and the first, non-digestive, being again sharply divided up into three compartments. In the cetacea, on the other hand, the stomach, although divided primarily into two parts like that of the ruminantia, shows a further subdivision of the digestive region which may be exceedingly complicated in the Ziphiidae, while the non-digestive region is not divided at all.

2. *On the function of the cetacean stomach, with considerations on its interrelation to the food-catching modus of whales:*

Anatomical features of various organs in the animal body are generally formed and elaborated by two components, the external or the environmental and the internal or the hereditary. While the latter moment defines the hereditary features, the former modifies often the anatomical structures so as to be adapted to the environments of the animal. And such organs, under the influence of the environment, can get strongly modified in their shape, size and structure. We consider the stomach to furnish an example of this latter kind, as this organ is apt to be modified according to the alimentary life of its possessor.

From this view-point the complicated stomach of the cetaceans seems to be intimately related to its alimentation, especially with its mode of food-catching in the aquatic environment. Weber (1885) mentioned already that the complexity of the stomach of the cetaceans was caused by the impossibility of their chewing in the aquatic medium, which seemed to be quite acceptable to us. He, however, did not explain the reason for the cetacean inability to masticate food. We would therefore, like to put forward our view-point here to explain this.

Judging from the anatomy of the cetacean oral cavity, it is evident that the whales do not masticate their food. To say nothing of the baleen of Mystacoceti, the numerous teeth of Odontoceti are also far from being suited for mastication, for they are conical homodont teeth, not to adapted for chewing, although aparently well-suited for biting foods. The case of sperm whale and *Ziphius* also is not much different from that of Mystacoceti, as the former has only ten and several teeth in the mandible and that with wide diastema in between the teeth, and the latter possess only one or two pairs of teeth in the rostral end of the mandible. The mandibular articulation and masticatory muscles of whales, together with the poor development of their lips also lend support to the above view, which is further augmented by the poor development of the salivary glands indicating that the cetacean mouth is not anatomically and physiologically meant for mastication. Thus deprived of the function of mastication, the cetacean mouth is devoted, we believe, exclusively to prehension of food.

Of the two major functions of mouth in higher animals, namely prehension and salivary digestion, the cetacean mouth seems to be primarily concered with the former function. This can be explained by the aquatic environment and food-habit of these animals, as they require a large quantity of food, and like the ruminantia, they cannot be expected to waste their time between catching and swallowing of food. This feature needs a large stomach with compartments given to different functions like storing, grinding and digestion. Thus the complex stomach of whales with its four compartments is very well adapted for their aquatic life.

SUMMARY

Some of the notable findings on the anatomy of the cetacean stomach are summarized as follows:

1. The cetacean stomach is composed of four serially arranged compartments, of which the first one is a oesophageal sack, the second one has numerous fundus glands, the third one possesses many pyloric glands and the last one represents a well-developed duodenal ampulla.

2. Between the second and the third compartments there is, moreover, a small communicating division, which is prominent especially in the fetal stages.

3. The first compartment is clined with an extensively stratified flat epithelium, of which the superficial layer is completely cornified and the cells have no trace of nucleus, just like in the oesophagus.

4. The wall of the first compartment is the thickest of the four, and contains very well-developed muscular strata. This compartment has undoubtedly a considerable contractibility.

5. Despite the general belief that the cetacean stomach is destitute of cardiac glands, we found them in an adult blue whale stomach in the narrow region adjacent to the boundary between the first and the second compartments.

6. The fundus glands of the second compartment have extraordinarily numerous parietal cells. They may have some intimate relation with the gastric function of whales.

7. The smooth muscle fibres of the lamina muscularis mucosae of all the four compartments are scattered irregularly, and as such do not deserve to be called " lamina ".

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EXPLANATION OF PLATES

Plate I.

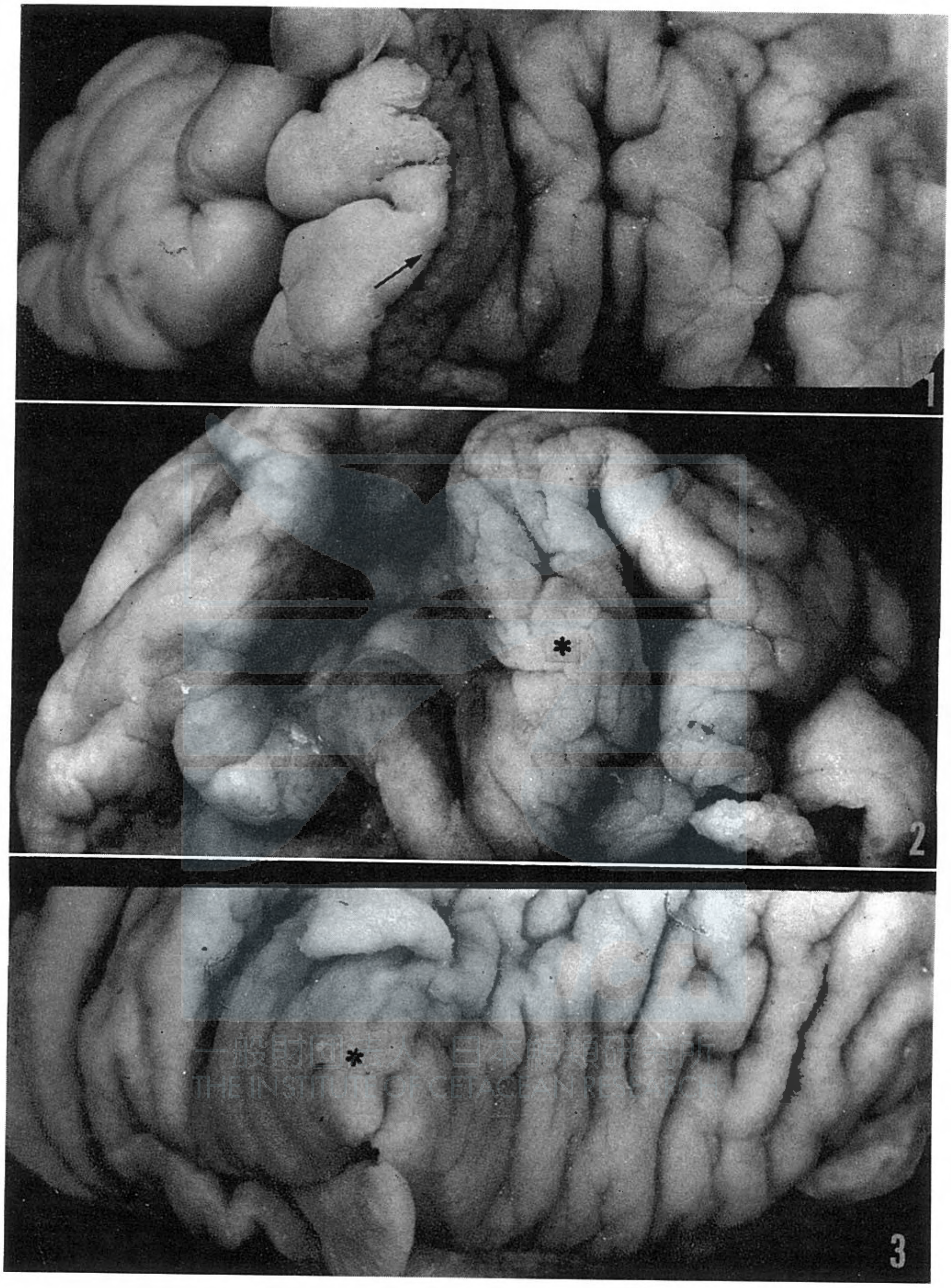
Mucous membrane of the stomach of a fin whale, 21.3 m long female. (×3 natural size)

Fig. 1. Boundary between the first (left) and the second compartments.
Fig. 2. Boundary between the second (left) and the third compartments.
Fig. 3. Boundary between the third (left) and the fourth compartments.

Plate II.

Histological section of the stomach of a fin whale, 21.3 m long female. The Roman numerals showing the first to the fourth compartments. (×4 natural size)

Fig. 1. Boundary between the first and the second compartments.
Fig. 2. Boundary between the second and the third compartments.
Fig. 3. Boundary between the third and the fourth compartments.
S: sphincter muscle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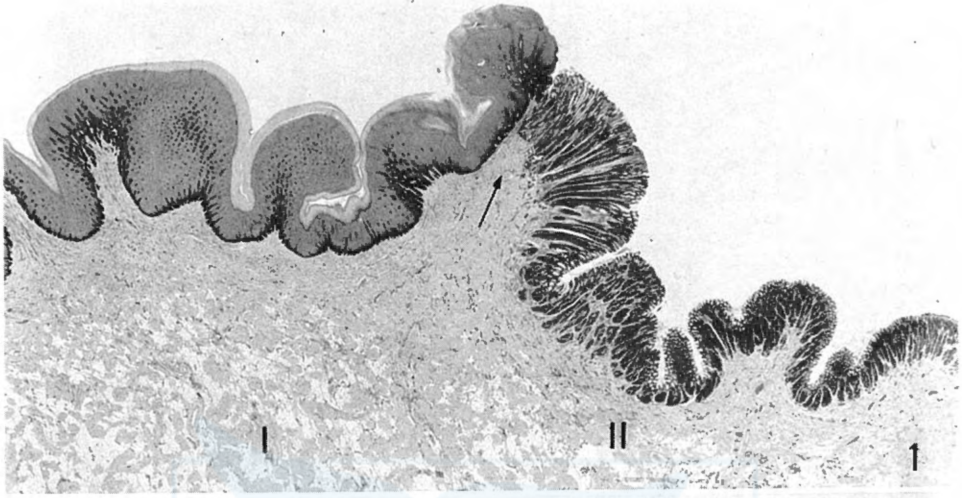
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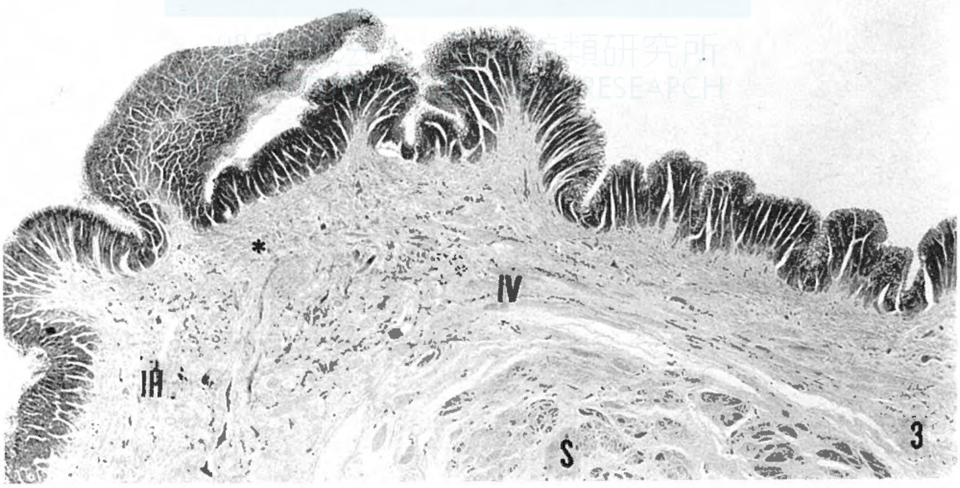
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