アカボウクジラ類における胃部構造の分類学的意義

ジェームズ G. ミード

THE SYSTEMATIC IMPORTANCE OF STOMACH ANATOMY IN BEAKED WHALES

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ABSTRACT

The stomachs of Cetacea are generally uniform in their anatomy. The stomach of a bottlenose dolphin differs only in size from the stomach of a blue whale. The stomach chambers consist of the forestomach, main stomach, connecting channel and two pyloric stomach compartments. The only known exceptions to this general scheme are some of the river dolphins and the beaked whales. The forestomach is lacking and the pyloric stomach compartments number greater than two in all five genera of beaked whales. The functional significance of this is unknown but it may lead to a better understanding of beaked whale relationships.

Two summers were spent in Wadaura, Chiba Prefecture, where there was an active fishery for Baird's beaked whales. A detailed examination of the stomachs of 29 specimens was done. Examination of the scientific literature for the count of pyloric compartments in beaked whales gave conflicting results due to the lack of standardized terminology. Most of the conflicts seem to arise from differences in defining the compartments at the proximal and distal ends of the pyloric chambers.

INTRODUCTION

Beaked whales form the odontocete family Ziphiidae. The systematic

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relationships of this family to other whales are uncertain. In addition, the relationships of members of this family to one another are unclear. This study presents anatomical data that may shed light on the relationships of the beaked whale species to one another.

Cetacea are conservative in the arrangement of their stomachs, there being a forestomach, main stomach, two connecting chambers and a pyloric stomach. The only diversion from this pattern being in the beaked whales (Fig. 1). It was recognized by John Hunter in 1787 that the stomach of the bottlenose whale (*Hyperoodon ampullatus*) was divided into more compartments than the four recognized in other whales.

William Turner later found that the forestomach was absent in the beaked whales, but the main stomach and pyloric stomachs were of the normal cetacean pattern. It was in the connecting chambers, which he termed the "intermediate stomach", that he found additional differences.

Various other anatomists dealt with the cetacean stomach but they suffered from a lack of standardization of definitions. They also had problems with availability of specimens. Most anatomists only had access to stranded animals. The availability of stranded specimens and conditions under which they occurred were not generally conducive to detailed studies of the digestive system.

MATERIALS AND METHODS

One of the first problems that presented itself was that an extremely fresh animal may appear to have one count when the stomachs were probed externally and an entirely different count when the stomach was slit (Table 1). In addition poorly defined compartments tended to disappear with the post mortem breakdown of tissues.

I decided that the best plan was to obtain fresh stomachs and inflate them with formaldehyde to fix the membranes that divided the compartments. The stomachs could then be cut open and the anatomy studied at leisure.

I compared the number of compartments that I had estimated from an external examination of the stomach with the actual number. The mean ratio of external/actual compartments was 0.66 (N=17, SD=0.20, range 0.22-1.0). That result makes it essential that an internal examination be done.

There are many cases in which this procedure is not practical. I found that I could do consistent counts on fresh stomachs if I allowed the compartments to remain intact and explored the interior of the compartments by hand. This manual exploration was good for relatively large animals, like *Berardius*, but was unsuited for stomachs that were too small for the passage of a hand, like *Mesoplodon*.

I then begin to wonder about the variation in the number of compartments within a single species. It could be correlated to age or sex. Previous anatomists had only dissected one or two specimens. Given the problems with lack of standardized definitions, there was not enough data to answer these questions.

RESULTS

I visited Japan in the summers of 1985 and 1986 to work with *Berardius* specimens that were being taken in Wadaura. One of my projects was to examine as many stomachs as possible with the goal of determining the variation in number of compartments.

The stomach of *Berardius* lacks a forestomach and consists of two main stomach chambers which communicate via a wide aperture (Fig. 2). They are subequal in size with the proximal compartment being larger. The connecting chambers are extensive and vary in number between 7 and 10. Of the 29 stomachs examined, 10 were from females and 19 were from males. The animals ranged in age between 6 and 75 years. There appeared to be no correlation between either sex or age and number of connecting chambers.

Following the summer of 1986, I have investigated a number of other species of beaked whales and have come to the following tentative conclusions:

Forestomach: Is completely lacking in all the beaked whale genera.

Main stomach: Commonly divided into two compartments in *Ziphius, Berardius, and Mesoplodon* (Fig. 1). In Ziphius and *Berardius* the two main stomach compartments are in series, the connecting chambers opening off the distal compartment.

In *Mesoplodon* (Fig. 3) the distal (second) main stomach compartment opens blindly off the proximal compartment and the connecting chambers communicate with the proximal compartment. The single *Tasmacetus* specimen was decayed such that I was unable to ascertain the details of the main stomach. It appeared to have one compartment. The main stomach of *Hyperoodon* also appears to be not divided.

Connecting chambers: The number varies throughout the family from

3 to 11. The proximal one or two compartments can be very weakly developed and are likely to be overlooked. Due to the additional problems of definition, I am extremely cautious about counts made by past authors.

The mean number of connecting chambers in *Berardius* is 8.24, with a modal value of 8 and a standard deviation of 0.69. Eight seems to be the general value for most *Mesoplodon* species, although it varies from 7 *(Mesoplodon europaeus)* to 11 (*Mesoplodon mirus*). The only exceptions to this are the one count of 3 in *Mesoplodon hectori* and the range from 3 to 5 in *Mesoplodon densirostirs.*

Hyperoodon appears to have 5-8 connecting chambers, although there are problems with various author's definitions of the chambers. The single *Tasmacetus* examined appeared to have at least 5 or 6 connecting chambers.

Pyloric compartments: The primitive number appears to be one (Fig. 1), as in *Ziphius*, with two variations.

In *Berardius* and *Mesoplodon stejnegeri* (Fig. 2) there is a small pyloric chamber developed distal to the main pyloric chamber, between it and the pyloric sphincter.

In the remainder of the *Mesoplodon* species examined (Fig. 3), the second pyloric compartment is a blind chamber opening off the main pyloric chamber. As far as can be determined from the literature, *Hyperoodon* has a single pyloric compartment. There was no evidence in the single *Tasmacetus* examined of more than one pyloric compartment.

In summary it seems probable that *Tasmacetus* is the most generalized, followed by *Hyperoodon, Ziphius* and *Berardius* in that order. The most highly derived stomachs are seen in *Mesoplodon.*

Much more detailed examination needs to be made before the tentative conclusions drawn from this investigation can be substantiated. Particular emphasis should be given to:

1. the nature of the division of the forestomach, how definite is it, does a septum exist in the distal compartment and out of which compartment do the connecting chambers open;
2. the precise arrangement of the first 3 connecting chambers must be noted because some of the variance may be due to miscounting these;
3. the arrangement and number of the pyloric stomachs must be noted; is

there 1 or 2 and are they arranged in series or is the second compartment blind?

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Table 1
Number of connecting chambers in *Mesoplodon* specimens in the United States National Museum of Natural History.

Species		Specimen number	External estimation connecting chambers	Actual connecting chambers*	
M. bidens		550414	8	8+2	
M. carlhubbsi		504128	5?, 6		
M. densirostris		486172	2	5+1	mean 4.2
		504217	0, 1, 2		SD 0.84
		550338	2	3+1?	N=5
	NY-203-86	550754		4+1?	
	DLR 011	571379		5+1	
		571470		4+1?	
M. europaeus		504256	?, ?, 8	7+2	mean 8.33
		504349	9	10+2	SD 1.21
		504610	7	7+2	N=6
	JGM 343	504738	7(9)	8+2	
		550390	7	9+2	
		550824		9+2	
M. hectori		504260			
		504853	2	3+1	
M. mirus		504612	8	9+2	mean 9.67
		504724	9	11+2	SD 1.15
		571459		9+2?	N+3
M. stejnegeri		504329	5	8+2?	mean 6.8
		504330	2+	6?+2?	SD 1.10
	(Adak #3)	504331	4	6+2?	N=5
		504865	2	8+1?	
	LA	84239	8	6+2	
T. shepherdi		484878	8?		
Z. cavirostris		504094	0, 1, 8		mean 8.67
		504327	7	8+1	SD 0.58
	(JGM 361)	504756	8(9)	9+1	N=3
		550735		9+1	

* The first number indicates connecting chambers, the second indicates pyloric chambers. If only one number is present, the two were not distinguished.

? The actual count was X+Y but the distinction into connecting and pyloric compartments was questionable.

Appendix 1. Glossary of stomach compartment terminology, largely taken from Harrison, Johnson and Young (1970).

Forestomach: also called the esophageal stomach (Hunter 1787, Turner 1889, Harrison *et al.*, 1970); a chamber that lies between the esophagus and the mainstomach. It is lined white stratified squamous epithelium, which is continuous with the esophageal epithelium. There is a complete absence of glands including mucous cells. The muscular lining of the forestomach is prominent and thick. It is highly distensible and functions as a holding compartment which is of importance in animals that feed opportunistically. Some digestive activity takes place in the forestomach due to reflux of stomach juices from the mainstomach. The communication between the forestomach and mainstomach is relatively wide and open. It is homologous to the forestomach of ungulates.

Mainstomach: also called the cardiac stomach (Turner, 1889) or the second stomach (Hunter, 1787); the active digestive chamber which is lined with reddish-purple, highly convoluted, sometimes trabeculate epithelium. The muscular lining of the mainstomach is relatively thin, being about 3 mm thick in s specimen of *Delphinus delphis* (Harrison *et al.*, 1970:381). The epithelial lining of the mainstomach contains mucous, parietal and chief cells. It is the active, secretory portion of the stomach complex producing mucus, digestive enzymes and hydrochloric acid. It communicates with the connecting chambers by a small opening that may be capable of being closed by muscular action.

Connecting chambers: also called the connecting channels (Harrison *et al.*, 1970), the intermediate stomach (Turner, 1889) or the third stomach (Hunter, 1787). This is a narrow, tortuous passage, provided with a valve and sphincter at either end and usually a third one in the middle (Harrison *et al.*, 1970). Many anatomist have not recognized the complexity of this compartment which has led to differing counts of the total stomach chambers. The epithelium lining the connecting chamber is thin and contains pyloric glands, hence it could be considered functionally a division of the pyloric stomach. The connecting chambers communicate with the pyloric stomach by a narrow sphincter that often is slightly everted into the pyloric chamber and is very different from the more proximal communications. This sphincter is centrally located in the distal wall of the last communicating chamber.

The function of the connecting chamber is most cetacea appears to be valvular (Harrison *et al.*, 1970).

Pyloric stomach: also called the third and fourth stomachs (Home, 1807), fifth stomach (Turner, 1869), and the distal stomach (Turner, 1889). The first pyloric compartment is noticeably larger than the preceding communicating chamber, often two or more time as large. The epithelium is relatively thin and contains mucous cell which are organized into pits or pyloric glands. The muscular wall of the pyloric stomach is thinner that any of the other compartments. The pyloric stomach communicates with the duodenal ampulla by means of the heavily muscular pyloric sphincter. The pyloric stomach in most cetaceans seems to be a holding and neutralization chamber for partly digested food.

Duodenal ampulla: a dilation of the proximal segment of the duodenum which can be mistaken for a stomach compartment. The lining is smooth proximally, grading into heavy trabeculae or folds as it narrows down. The hepatopancreatic duct courses distally on the external wall and opens into the ampulla where it narrows down. The distal end of the ampulla does not have any structure that could be mistaken for the pyloric sphincter.

Anterior, proximal, oral: Those compartments that the food passes through first as opposed to posterior, distal, anal.

Appendix 2. Preliminary bibliography of works dealing with the anatomy of cetacean stomachs.

Anderson, J. 1879. Anatomical and zoological researches: comprising an account of the zoological results of two expeditions to western Yunnan in 1868 and 1875; and a monograph of the two cetacean genera, *Platanista* and *Orcaella*. 2 vols, B. Quaritch, London.

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Burmeister, H. 1867. Preliminary observations on the anatomy of *Pontoporia blainvillii*. *Proc. Zool. Soc. Lond.* 1867:484-489.

Carleton, M. C. 1973. A survey of gross stomach morphology in New World Cricetinae (Rodentia, Muroidea), with comments on functional interpretations. Misc. Publ., Mus. Zool., Univ. Mich. 146, 43pp.

Carleton, M. C. 1981. A survey of gross stomach morphology in Microtinae (Rodentia, Muroidea). Zeitschrift f. *Säugetierkunde* 46(2):93-108.

Eschricht, D. F. 1845. Undersogelser over Hvaldyrene; Fjerde Afhandling, om Naebhvalen. Kgl. Danske Videnskbernes Selskabs, naturvidenshabelige og mathematiske Afhandlinger, llte Deel, pp. 1-58, pls 5-8.

Fischer, P. 1867. Note sur un cetace (*Grampus griseus*) echoue sur les cotes de France. *Annales des Sciences Naturelles,* 8: 363-373.

Gihr, M. and Pilleri, G. 1969. On the anatomy and biometry of *Stenella styx* Gray and *Delphinus delphis* L. (Cetacea, Delphinidae) of the western Mediterranean. *Investigations on Cetacea* 1:15-65.

Harrison, R. J., Johnson, F. R. and Tedder, R. S. 1967. Underwater feeding, the stomach and intestine of some delphinids. *J. Anat.* 101:186-187.

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Hunter, J. 1787. Observations on the structure and economy of whales. *Phil. Trans. Roy. Soc. Londo.* 77:371-450, pls xvi-xxiii.

Jackson, J. R. S. 1845. Dissection of a spermaceti whale. *Boston Jour. Nat. Hist.* 1845(5):236.

Jacob, A. 1825. Account of a whale which was found floating in the Atlantic ocean on the north-west coast of Ireland, with some observations respecting its generic characters and anatomical structure. *Dublin Phil. Jour. Sci. Rev.* 1-2(1825-26):333-350

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Turner, W. 1889. Aditonal observations on the stomach in the ziphioid and delphinoid whales. *J. Anat. Physiol.* 23(n.s.) 3:466-492.

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Watson, M. and Young, A. H. 1879. The anatomy of the northern beluga. *Trans. R. Soc. Edinb.* 29:393-434.

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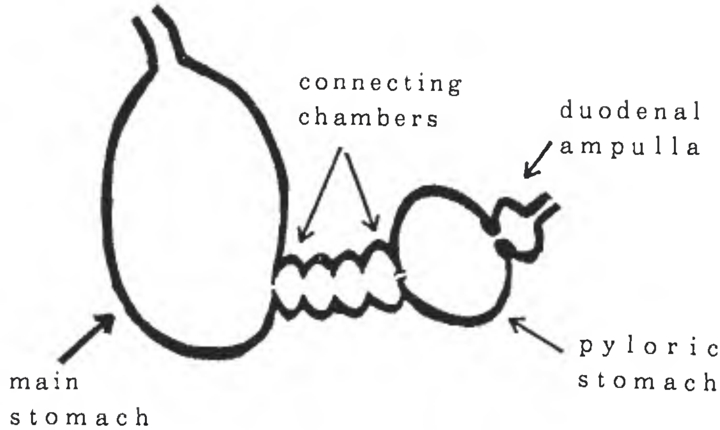

Fig. 1. Generalized ziphiid stomach *Ziphius, Hyperoodon, Tasmacetus.*

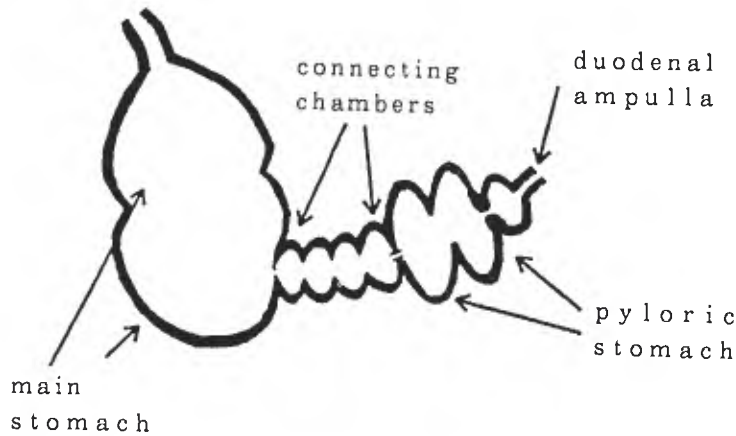

Fig. 2. Derived stomach type I *(Berardius).*

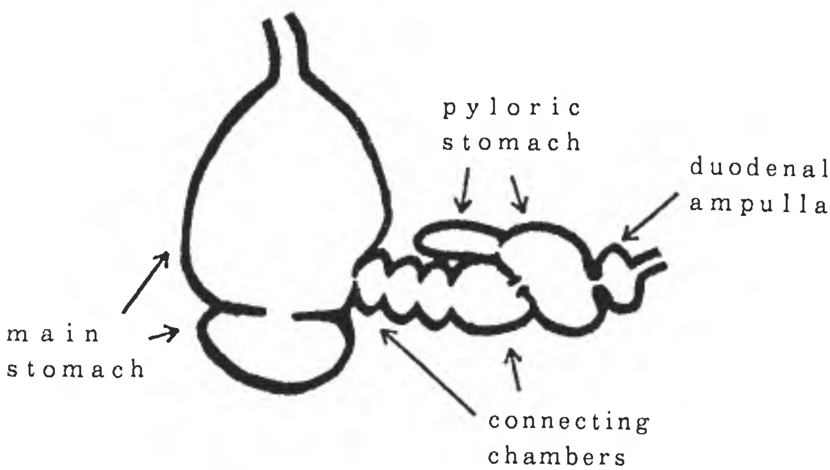

Fig. 3. Derived stomach type II *(Mesoplodon).*