Stomach Anatomy and Use in Defining Systemic Relationships of the Cetacean Family Ziphiidae (Beaked Whales)

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ABSTRACT

Members of the Cetacean family Ziphiidae (Beaked whales) exhibit surprising diversity in stomach anatomy, particularly in the number of connecting chambers between the main and pyloric stomachs. Sixty-one stomachs of five beaked whale species were examined, including *Berardius*, *Hyperoodon*, *Mesoplodon*, *Tasmacetus*, and *Ziphius*. Specimens were obtained post mortem from beach-stranded individuals, with the exception of 30 *Berardius* specimens that were taken at a whaling station in Japan. Most specimens were collected by the Marine Mammal Program of the National Museum of Natural History, with the exception of one specimen of *Mesoplodon steinegeri*, which from the Los Angeles County Museum and one specimen of *Tasmacetus* from the Museum of New Zealand. Additional data are included from published accounts. A single species was examined for all of the genera but *Mesoplodon*, where there was material for 7 of 13 known species. The sample of *Berardius bairdii* was sufficient (n = 30) to determine species-specific variation in compartment counts. Chamber anatomy was explored by means of manual palpation. Results indicate that ziphiid stomachs can be separated into at least three principal groups: generalized ziphiid stomach (one main stomach, one pyloric stomach), derived stomach type I (two main stomachs, one pyloric stomach), and derived stomach type II (two main stomachs, two pyloric stomachs). Generalized stomachs are found in *Hyperoodon*, *Tasmacetus*, *Ziphius*, *Mesoplodon densirostris*, *M. perrini*, and *M. stejnegeri*. Derived stomachs of type I are found in Berardius, and of type II are found in *Mesoplodon bidens*, *M. europaeus*, and *M. mirus*. The ziphiids clearly form a distinct group of cetaceans in their utilization of differences in stomach morphology. These anatomical differences may serve to elucidate systematic relationships among the ziphiids. Further study is necessary to establish whether these differences correlate with specialized adaptations related to an aquatic environment. Anat Rec, 290:581–595, 2007. © 2007 Wiley-Liss, Inc.

Key words: Ziphiidae; *Berardius*; *Hyperoodon*; *Mesoplodon*; *Tasmacetus*; *Ziphius*; anatomy; systematics; stomach

It has long been recognized that cetaceans have a complex multicompartmented (plurilocular) stomach as opposed to the simple (unilocular) stomach of humans and some other mammals (Tyson, 1680; Hunter, 1787; Home, 1807; Jungklaus, 1898). The plurilocular stomach is rather common in mammals, having been independently derived in such diverse orders as Rodentia, Artiodactyla, Perissodactyla, Hyracoidea, Proboscidea, Sire-

nia, Edentata, Primates, Marsupalia, Lagomorpha, and Chiroptera (Langer, 1985).

The ziphiids constitute a substantial portion of cetacean diversity, comprising 21 of 81 recognized species of whales and dolphins. The external body form of ziphiids is conservative. The most diverse genus, *Mesoplodon*, with 14 species appears to be diagnosed by differences in skull and tooth shape.

Cetaceans are generally thought to have a uniform system of stomach morphology, with the exception of the Ziphiidae (beaked whales) and Platanistidae (river dolphins). A project was embarked upon to define the variation in the ziphiids to shed some light on their systematic relationships (Mead, 1993). As this project progressed, it became apparent that there was appreciable variation in the morphology of the stomachs of all the families but it was confounded by lack of consistently comparable descriptions. At this point, it was decided to continue with the description of ziphiid stomachs and do an overview of the whole order Cetacea at a future time.

DEFINITION OF COMPARTMENTS

The literature is full of descriptions of cetacean stomach anatomy that refer to the compartment in the order that they are encountered, that is, first compartment, second compartment, etc. A more diagnostic nomenclature was preferred because the first stomach of ziphiids is not homologous to the first stomach of delphinids. There was a tendency to use nomenclature that is used by human anatomists and to designate the stomach compartments in Cetacea as cardiac, fundic, pyloric as they seemed to be composed histologically of tissues that were most similar to those regions of the human stomach. The cetacean stomach is sufficiently different histologically from the human stomach, with the exception of the term pyloric. The system used by Pernkopf and Lehner (1937) and subsequently by Slijper (1962) and Harrison et al. (1970) was used. Figure 1 of Harrison et al. is here simplified and presented as Figure 1.

Forestomach

The forestomach, also called the vormagen (forestomach; Pernkopf and Lehner, 1937) or esophageal stomach (Hunter, 1787; Turner, 1889; Harrison et al., 1970), is a chamber that lies between the esophagus and the mainstomach. It is lined with 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 seems to be homologous to the forestomach of ungulates (Langer, 1988:32). Turner (1889) and Weber (1886) both say that the forestomach in Cetacea is an esophageal dilation.

Mainstomach

The mainstomach, also called the cardiac stomach (Turner, 1889) or the second stomach (Hunter, 1787), is
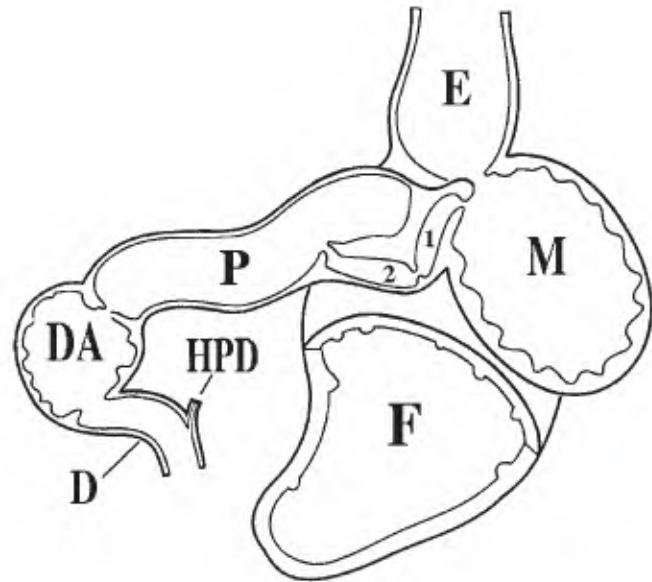

Fig. 1. Stomach of a typical odontocete, the delphinid *Stenella longirostris*, left lateral view (after Harrison et al., 1970). D, duodenum; DA, duodenal ampulla; E, esophagus; F, forestomach; HPD, hepatopancreatic duct; L, portion of liver; M, principal mainstomach compartment; MA, accessory mainstomach compartment; MD, distal mainstomach compartment; MP, proximal mainstomach compartment; P, principal pyloric stomach compartment; PA, accessory pyloric stomach compartment; PD, Distal pyloric stomach compartment; PP, proximal pyloric stomach compartment; 1, 2, etc., connecting chambers. Pyloric sphincters are the shaded areas between the pyloric stomach compartment and the duodenal ampulla.

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 approximately 3 mm thick in a specimen of *Delphinus delphis* (Harrison et al., 1970, page 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. Turner (1889) and Weber (1886) both arrived at the conclusion that the first stomach compartment (mainstomach) in ziphiids was homologous to the second in other cetaceans.

In cetaceans where the mainstomach is divided, if the compartments are in series, the compartment that communicates with the esophagus is the *proximal mainstomach compartment*. The second one that communicates with the connecting chambers is the *distal mainstomach compartment*. If the second compartment is blind, it is the *accessory mainstomach compartment*, and the first one is the *principal mainstomach compartment*.

Connecting Chambers

The connecting chambers, also called the connecting channels (Harrison et al., 1970) or verbindungsstück (Pernkopf and Lehner, 1937), are the intermediate stom-
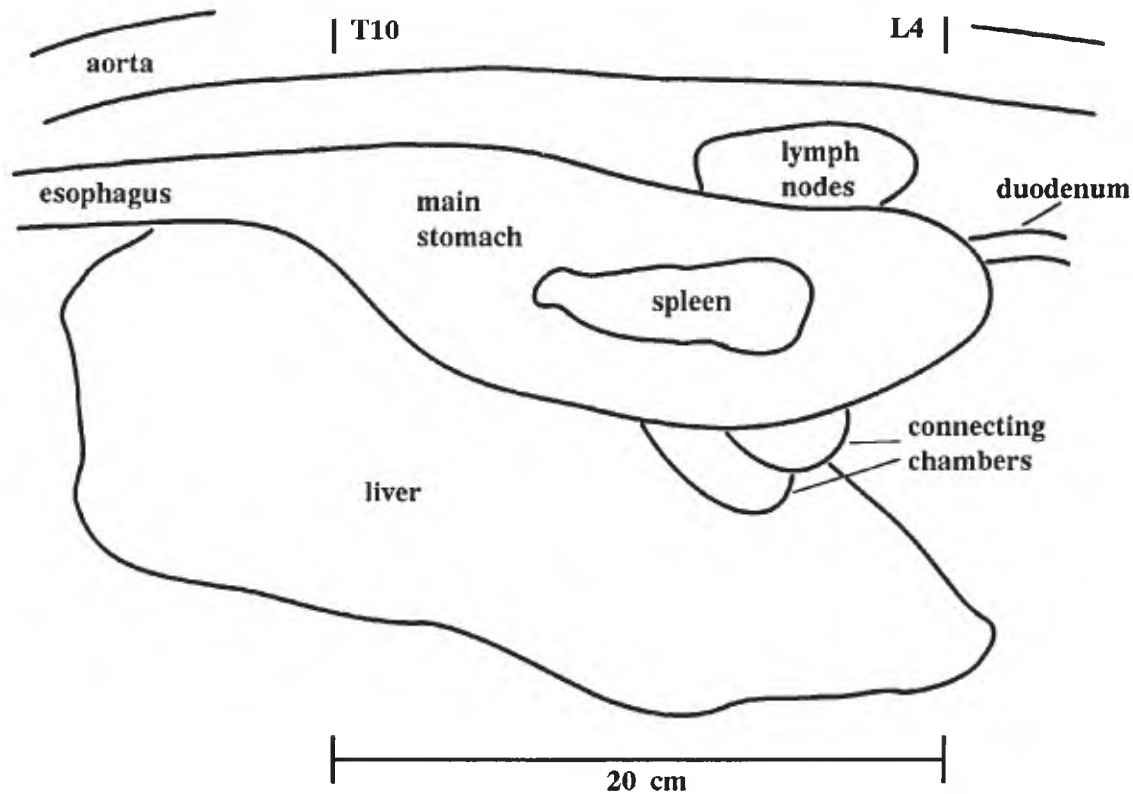
Fig. 2. Stomach of *Mesoplodon stejnegeri*, LACM 84299, left lateral view, showing the relationship of surrounding organs. T10 and L4 are the midpoints of the tenth thoracic and fourth lumar vertebrae.

ach (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 anatomists 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 stomach 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 in most cetaceans appears to be valvular (Harrison et al., 1970).

The connecting chambers are numbered starting with the one that communicates with the mainstomach, which is the *first connecting chamber.*

Pyloric Stomach

The pyloric stomach, also called the pylorusmagen (Pernkopf and Lehner, 1937), is the third and fourth stomachs (Home, 1807), fifth stomach (Turner, 1869), and the distal stomach (Turner, 1889). The first pyloric stomach compartment is noticeably larger than the preceding communicating chamber, often two or more times

as large. The epithelium is relatively thin and contains mucous cells that are organized into pits or pyloric glands. The epithelium is brown to yellowish in fresh specimens. 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.

In cetaceans that have the pyloric stomach divided into two compartments in series, the first compartment is the *proximal pyloric stomach compartment* and the second is the *distal pyloric stomach compartment*. If the second compartment is a blind opening of the first, the blind opening is called the accessory *pyloric stomach compartment* and the first is the *principal pyloric stomach compartment*.

Duodenal Ampulla

The duodenal ampulla is 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 usually 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. The presence or absence of the duodenal
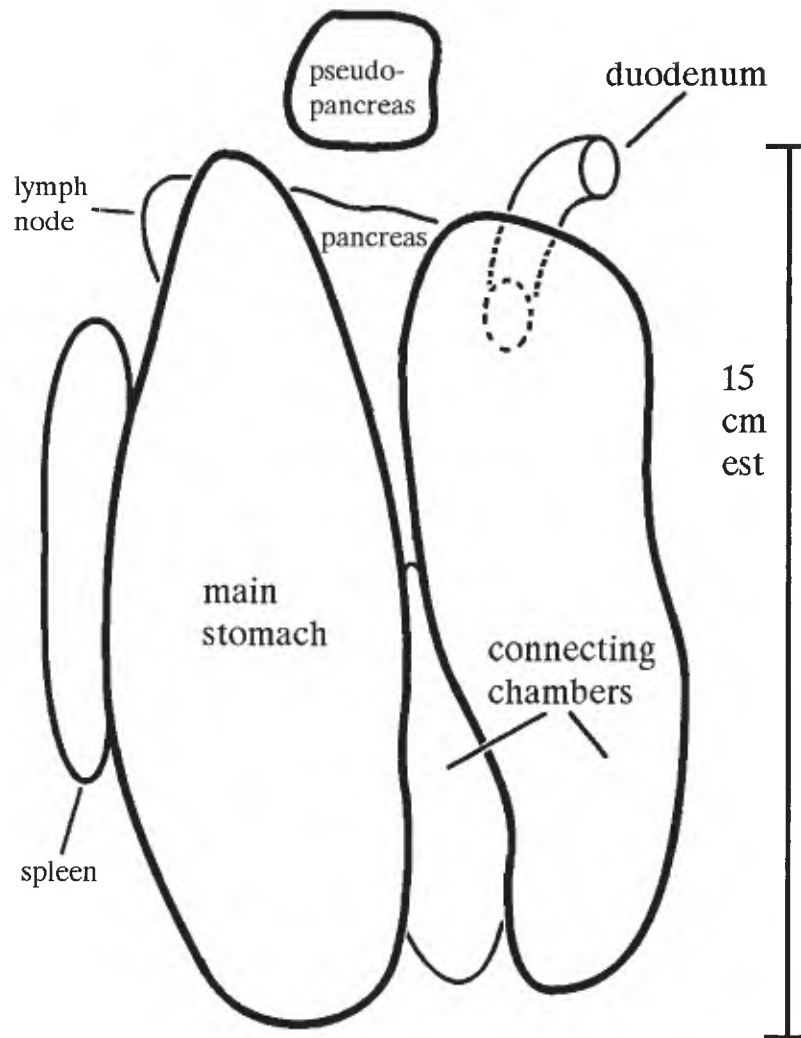
Fig. 3. Stomach of *Mesoplodon stejnegeri*, LACM 84299, posterior view, dorsal side up, showing the relationship in life of the stomach compartments, pancreas, and spleen.

ampulla seems to be variable. However, the presence of the pyloric sphincter and hepatopancreatic duct were constant and were used to define the distal margin of the stomach. Anterior, cranial, proximal, and oral are those compartments that the food passes through first, as opposed to posterior, caudal, distal, anal.

Measurements of Compartments

Because the orientation of the axis of the stomach is so complex, it was decided to give measurements of compartments in terms of length and width defined by the axis of that particular compartment. Length is the measurement parallel to the axis of food flow, and width is perpendicular to the axis of food flow.

Orientation of Illustrations

In the illustrations where the connecting chambers and pyloric stomach have been dissected free from the mainstomach (Figs. 4–6, 9–13), the anterior (esophageal) end of the mainstomach was put at the top left of the figure. Then the connecting chambers and pyloric stomach were unwound and the posterior (duodenal) end was positioned at the top right of the figure. In reality, the situation of the connection chamber is such that the duodenum opens posteriorly. Thus, the orientation of the figures is anatomically correct for the mainstomach and slowly becomes twisted to where the figure is 180 degrees in error for the duodenum.

The actual detailed orientation was determined in one specimen, a newborn male *Mesoplodon stejnegeri* (LACM 84299). The stomach was ventral to the thoracic aorta and dorsal to the liver, between the 10th thoracic and the 4th lumbar vertebra (Fig. 2). The mainstomach lay to the left and the connecting chambers and pyloric stomach compartments lay to the right. The duodenum exited from the dorsal right. The spleen lay along the right side of the mainstomach, and the pancreas lay on the dorsal surface of the stomach between the mainstomach and pyloric stomach compartments (Fig. 3).

TABLE 1. Data on specimens used in this paper and counts of their stomach compartments

Species, catalog no. or source	Field no.	Length (cm)	Sex	F	M	CC	P	Condition
Berardius bairdii								
571526	86-03	942	F	0	2	8	2	Fresh
571527	86-04	1075	M	0	2	7	–	Fresh
571528	86-05	965	M	0	2	7	–	Fresh
571529	86-06	1070	M	0	–	8	–	Fresh
571531	86-08	780	M	0	–	8	–	Fresh
571532	86-09	1040	F	0	2	9	2	Fresh
	86-10	960	M	0	2	8	2	Fresh
571533	86-11	1040	F	0	2	7	2	Fresh
571534	86-12	970	M	0	2	8	2	Fresh
	86-13	990	M	0	2	10	2	Fresh
	86-14	1010	F	0	2	8	2	Fresh
	86-15	950	M	0	2	9	2	Fresh
	86-16	960	M	0	2	–	2	Fresh
	86-17	1000	M	0	2	8	2	Fresh
	86-18	966	M	0	2	8	2	Fresh
571535	86-19	1010	M	0	2	8	2	Fresh
571536	86-20	910	F	0	2	8	2	Fresh
571537	86-21	1030	F	0	2	9	2	Fresh
	86-22	1030	M	0	2	8	2	Fresh
	86-23	1000	M	0	2	8	2	Fresh
	86-24	950	F	0	2	9	2	Fresh
	86-25	970	M	0	2	8	2	Fresh
	86-26	1020	M	0	2	9	2	Fresh
571538	86-27	950	M	0	2	8	2	Fresh
571539	86-28	970	M	0	2	9	2	Fresh
	86-31	950	M	0	2	9	2	Fresh
571542	86-32	990	F	0	2	9	2	Fresh
571543	86-33	1020	F	0	2	8	2	Fresh
571544	86-34	1030	F	0	2	8	2	Fresh
	86-35	920	M	0	2	8	–	Fresh
Hyperoodon ampullatus								
Vrolik, 1848		?	?	0	1	5?	1?	
Weber, 1886		?	?	0	1	7	1	
Bouvier, 1892		720	F	0	1	8	1	
Turner, 1889		?	?	0	1	5	1	
Mesoplodon bidens								
550414	RKB 1342	649	M	0	1	8	2	Fixed
Turner, 1889		460	M	0	2	12	2?	
Mesoplodon carlhubbsi								
504128	JGM 121	532	F	0	1	7	2	Fixed
Mesoplodon densirostris								
486172	JGM 009	349	M	0	1	5	1	Fixed
504217	JGM 137	397	F	0	1	2?	?	Fixed
550338	CWP 224	411	F	0	1	3	1?	Fixed
550754	NY-203-86	420	M	?	?	4	1?	Fixed
550746	JGM 442	397	F	0	1	5	1	Fixed
571379	DLR 011	405	?	0	1	5	1	Fixed
571470	JGM 464	408	F	0	1	4	1?	Fresh
Mesoplodon europaeus								
23346	------	381	M	0	2?	7+	2	Photograph
504256	JGM 142	473	F	?	?	7	2	Fresh
504349	JGM 166	420	F	0	1	10	2	Fixed
504610	JGM 332	458	F	0	1	7	2	Fixed
504738	JGM 343	456	M	0	1	8	2	Fixed
550390	JGM 433	447	F	0	1	9	2	Fixed
550824	WAM 090	208	F	0	1	9	2	Fixed
550853	WAM 099	460	F	0	2	10	?	Fixed
Mesoplodon perrini								
504853	JGM 391	390	M	0	1	3	1	Fixed
Mesoplodon mirus								
504612	JGM 334	483	F	0	1	9	2	Fixed
504724	JGM 336	456	M	0	1	11	2	Fixed
571459	JGM 460	493	F	0	1	9	2?	Fresh
Mesoplodon stejnegeri								
504329	JBB 1	448	M	0	1	8	2?	Fixed
504330	JBB 2	488	F	0	1	6	2?	Fixed
504331	JBB 3	457	M	0	1	6	2?	Fixed

TABLE 1. Data on specimens used in this paper and counts of their stomach compartments (continued)

Species, catalog no. or source	Field no.	Length (cm)	Sex	F	M	CC	P	Condition
504865	Sarvis	530 est	M	0	1	8	1?	Fixed
LA84299	HLR 90613	256	M	0	1	6	2	Fresh
Tasmacetus shepherdi								
484878	JGM 035	660	F	0	1	7	1?	Fresh
STR10549	Helden pers. comm.	600 est	M	0	1	10?	1	Fresh
Ziphius cavirostris								
Scott and Parker 1889		485	F	0	1	9	1	Fresh
504094	JGM 118	580	F	0	1	7?	1?	Fresh
504327	CWP 052	395	M	0	1	8	1	Fixed
504756	JGM 361	269	M	0	1	9	1	Fixed
550735	JGM 440	258	M	0	1	9	1	Fixed

F = forestomach; M = mainstomach; CC = connecting chambers; P = pyloric stomach. All specimens with catalog numbers were fixed in formalin and are held in the alcoholic collection of the Division of Mammals, National Museum of Natural History, Smithsonian Institution, with the exception of the *Berardius* specimens, which were dissected fresh and no whole stomach specimens taken, and LA84299, which was dissected fresh at the Los Angeles County Museum. STR10549 was dissected as a fresh specimen by Anton van Helden at the Museum of New Zealand.
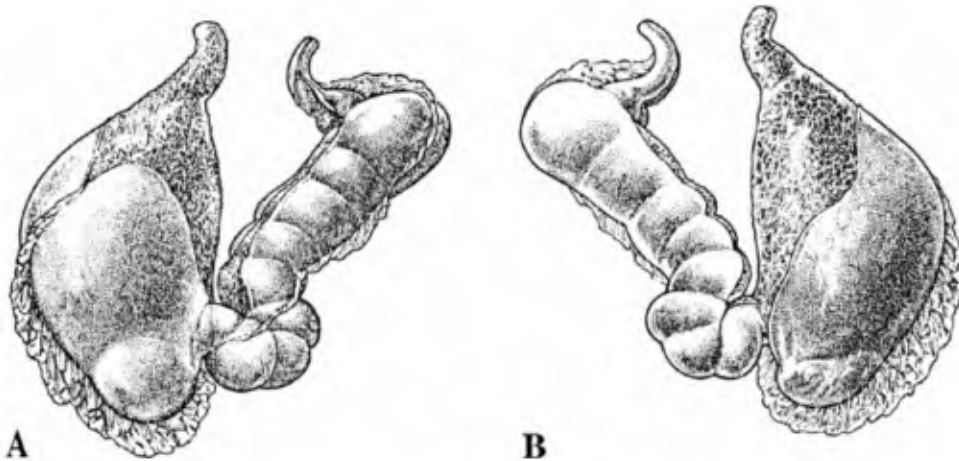
Fig. 4.   Generalized ziphiid stomach. **A:** Dorsal view of the stomach complex of *Ziphius cavirostris*, USNM 504756. The stomach chambers were dissected free and then fixed by inflating with formalin. The stippled texture represents the peritoneal membrane, the hatched texture around the esophagus represents the areas where the stomach was attached to the diaphragm or to the distal portions of the stomach (connecting chambers and pyloric stomach compartment) and the pancreas. Traces of the lacey omental membranes remain. **B:** Ventral view of the same. Labels as in Figure 1.

MATERIALS AND METHODS

Most of the material came from stranded animals that were collected by the Marine Mammal Program of the National Museum of Natural History. Those specimens are cataloged in the Division of Mammals and bear five- or six-digit United States National Museum (USNM) numbers. The stomach whose serial number begins with LA is a specimen that is housed in the Los Angeles County Museum (LACM). Some of the data were taken in the field and the stomachs not brought back to the museum. However, 24 stomachs were collected, fixed by filling them with formaldehyde and then preserving in alcohol. This is the most satisfactory technique for definition of compartments and results in specimens that one can refer to and confirm the anatomic details.

In compiling these data from stranded animals, it was realized that some of the variation in counts of stomach compartments was due to difficulties related to postmortem condition of the specimen and environmental conditions. It was then decided to go to Japan where beaked whales of the genus *Berardius* were taken commercially and to work in the controlled environment of a whaling station on fresh animals. This strategy would enable compilation of a statistically valid sample of specimens that were comparable in terms of freshness and method of counting.

Initially the compartments were counted by slitting them open. So much detail of definition was lost in a fresh specimen by cutting the walls of the chambers that it was nearly impossible to confirm a count. Manual palpation on the first connecting chamber and manually going through the connecting chamber system and counting the chambers was tried. In this manner, the counts could be repeated and the data confirmed. The partitions that separated the connecting chamber compartments were extremely flaccid and lost their resolution when they were slit. It was, therefore, easier to define the chambers manually rather than the visual method that had been used in slitting the stomachs. Table 1 summarizes the data on specimens examined.
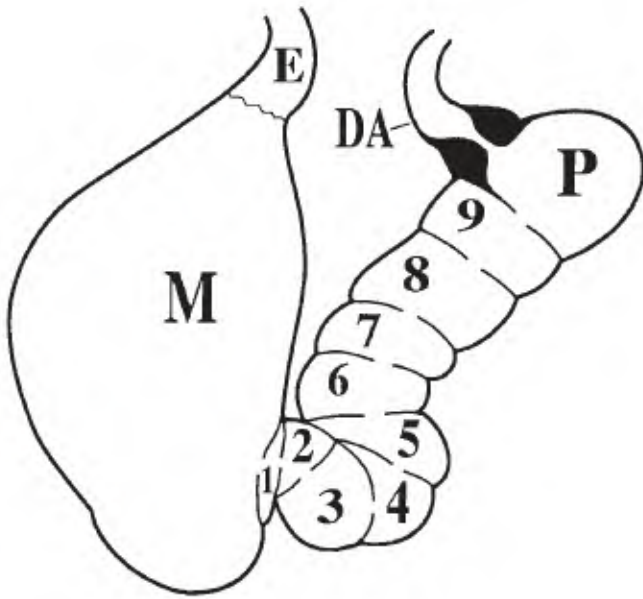
Fig. 5. Diagrammatic section of stomach of *Ziphius cavirostris*, 504756. Labels as in Figure 1.

An exhaustive survey was done of the literature accounts that mentioned beaked whales and the few accounts (Bouvier, 1892; Turner, 1889; Vrolik, 1848; Weber, 1886) that gave quantifiable data were used. In addition, data are included from the stomach of a fresh *Tasmacetus*, dissected by Anton van Helden of the Museum of New Zealand.

RESULTS

Generalized Ziphiid Stomach: One Main, One Pyloric; *Ziphius, Hyperoodon, Tasmacetus, Mesoplodon densirostris, M. perrini, M. stejnegeri*

The generalized ziphiid stomach present in such diverse genera as *Ziphius, Hyperoodon, Tasmacetus* and certain species of *Mesoplodon* (*M. densirostris, M. perrini, M. stejnegeri*) lacks a forestomach and has a simple mainstomach with a tendency to form a distal mainstomach compartment. Leading off the mainstomach are a series of connecting chambers followed by the pyloric stomach compartments.

In *Ziphius cavirostris*, there is a distal bulge in the mainstomach that represents the beginning stages of
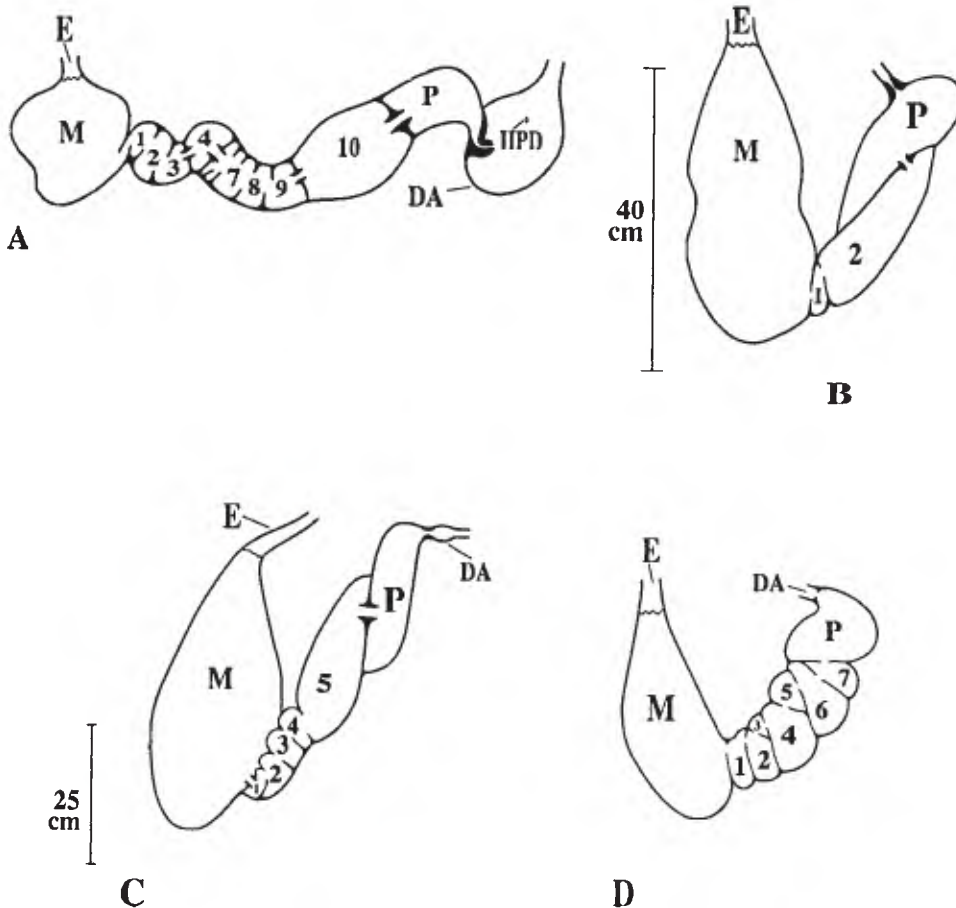
Fig. 6. Diagrammatic sections of other generalized ziphiid stomachs. **A:** *Tasmacetus shepherdi* STR10549. **B:** *Mesoplodon perrini* 504853. **C:** *Mesoplodon densirostris* 550746. **D:** *Hyperoodon ampullatus* (after Weber, 1886, page 59). Labels as in Figure 1.
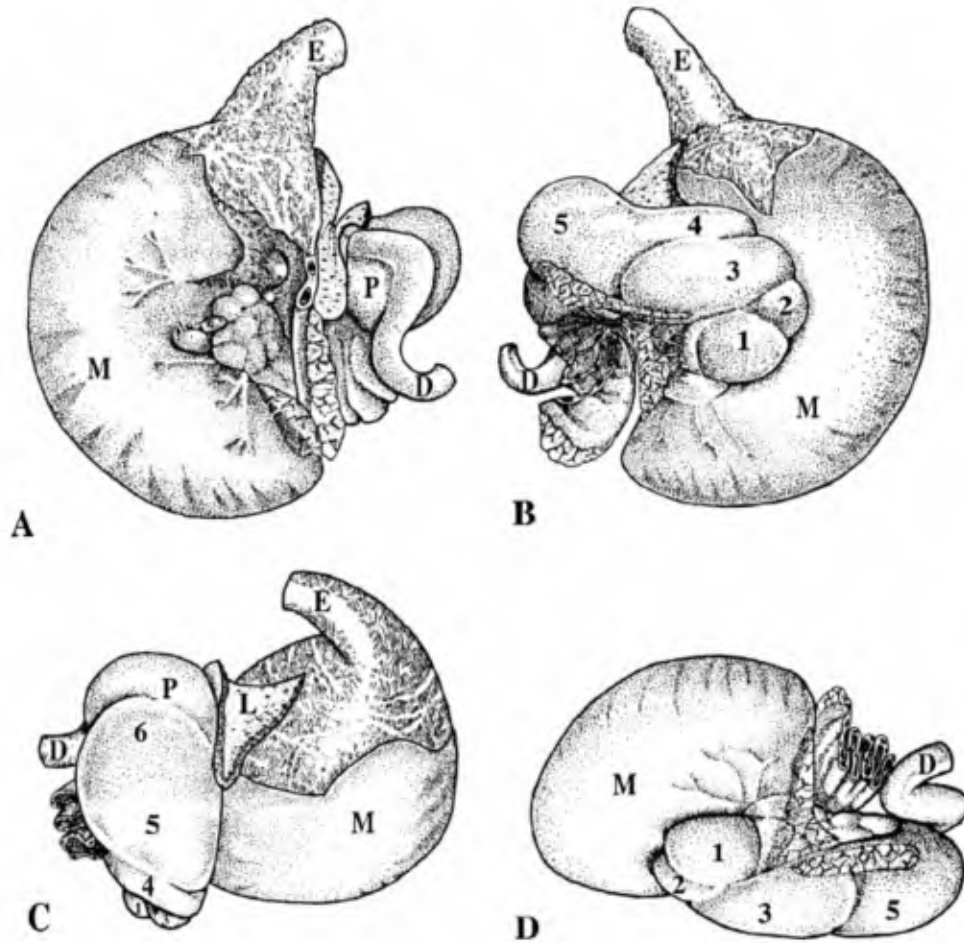
Fig. 7. Illustrations of the stomach compartments of a young *Mesoplodon stejnegeri* LACM 84299. The stomach chambers were dissected free and then fixed by inflating with formalin. **A:** Dorsal view. **B:** Ventral view. **C:** Anterior view. **D:** Posterior view. Labels as in Figure 1.

distal pouch (Figs. 4, 5). This is then followed by eight or nine connecting chambers, the first two of which are very small and difficult to define. There are nine in the specimen figured. The distal connecting chamber opens by means of a distinct sphincter into a single large pyloric stomach compartment. The pyloric stomach compartment then communicates by means of the pyloric sphincter with a small duodenal ampulla.

In *Hyperoodon ampullatus* (Vrolik, 1848: Figs. 39, 40), there is a single mainstomach compartment followed by usually five connecting chambers and one pyloric stomach compartment. Weber (1886:59) found seven connecting chambers (Fig. 6D).

In one specimen of *Tasmacetus shepherdi* (USNM 484878), there was a mainstomach that did not appear divided and eight small distal compartments. This specimen was moderately decomposed making definitive observations impossible. These eight compartments were interpreted as representing seven connecting chambers and one pyloric stomach compartment.

A 6-m male *Tasmacetus* that stranded at Nelson, New Zealand, on the 20th of April, 1994, was dissected by Anton Van Helden of the National Museum of New Zea-

land (Van Helden, personal communication, 9 May 1994). He took notes and a drawing that formed the basis for Figure 6A. He indicated that there was no forestomach, an undivided mainstomach, five well-defined and six poorly defined distal chambers, and a duodenal ampulla. He was of the opinion that there was only one pyloric stomach compartment, which leaves us with approximately 10 connecting chambers in that specimen.

The stomach of a 397-cm female *Mesoplodon densirostris* (504746) was of the generalized ziphiid type (Fig. 6C). The mainstomach was approximately 50 cm in length and opened into a series of five connecting chambers. The fifth connecting chamber was much larger than the others. It measured approximately 25 cm in length and opened into a single pyloric stomach compartment. In a sample of five specimens of this species, the number of connecting chamber ranged from three to five.

The stomach of a 390-cm adult male *Mesoplodon perrini* was preserved. The mainstomach was approximately 40 cm long (Fig. 6B) and had a faint indication of a narrowing in the middle. This narrowing was not correlated with any internal structure as is seen in
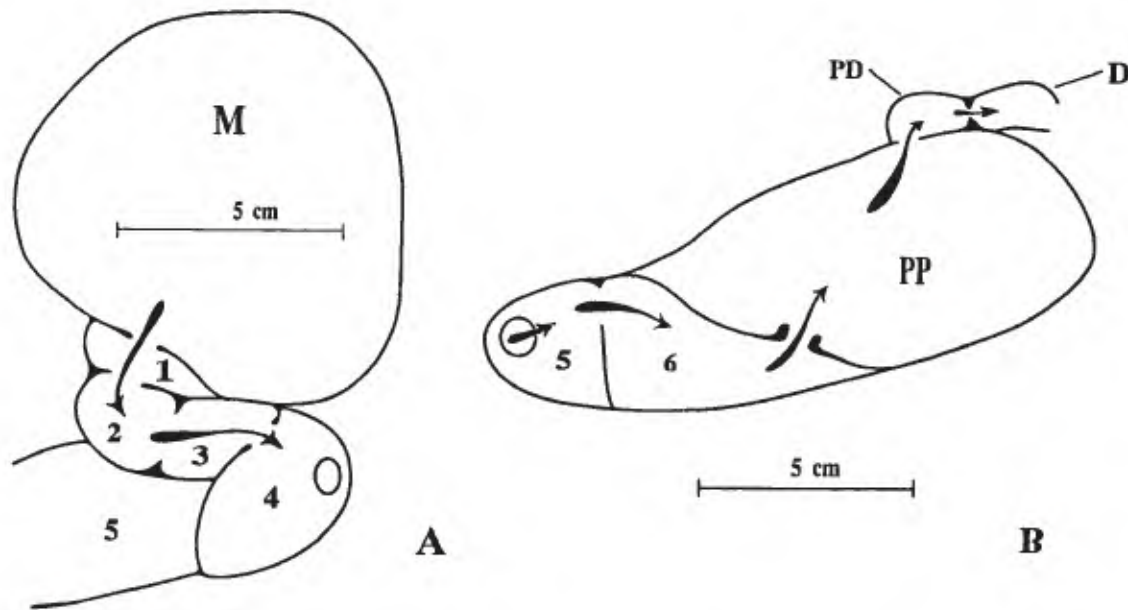
Fig. 8. Diagrammatic sections of the stomach compartments of *Mesoplodon stejnegeri* LACM 84299. **A:** Posterior view of principal mainstomach showing passages to connecting chambers 1–5. **B:** Lateral view showing passages from connecting chamber 5 through the duodenal ampulla. Labels as in Figure 1.

Berardius bairdii. The mainstomach opened into two connecting chambers, the second of which was much larger than the first. The second connecting chamber opened by means of a sphincter into the single pyloric stomach compartment.

The best specimen of *Mesoplodon stejnegeri* that was examined was a 256-cm newborn male (LACM 84299; Fig. 7). The mainstomach was approximately 20 cm in length. The first connecting chamber was 2.5 cm wide and 1 cm long. The orifice between the mainstomach and the first connecting chamber was simple (Fig. 8). The connecting chambers proceeded to gradually enlarge culminating in the sixth, which was 6.5 cm long. All of the connecting chambers communicated with one another with simple orifices. The orifice leading from the sixth connecting chamber into the proximal pyloric stomach compartment was sphincteric. The proximal pyloric stomach compartment was 6 cm wide by 10 cm long. It communicated with the smaller distal pyloric stomach compartment, which was approximately 2 cm long and 1 cm wide. There was a well-developed pyloric sphincter.

Derived Stomach Type I: Two Main, Two Pyloric (In Series); *Berardius*

The description of *Berardius bairdii* is based upon 29 specimens taken at a Japanese whaling station in 1985 and 1986. The figures of the stomach of *Berardius bairdii* are based on specimen 571526 (86-03), a 942-cm, sexually immature female taken on 26 July 1986 off Wadaura, Japan. The mainstomach was divided into two compartments by a fold that extends roughly one quarter of the way across the lumen of a moderately distended stomach (Fig. 9). This fold can form an effective valvular closure. This was demonstrated when a stomach was inflated with gas. The distal compartment was punctured and collapsed and the proximal compartment stayed inflated even with moderately heavy handling. The proximal mainstomach compartment was approximately 120 cm long by 65 cm wide in 86-03. The distal mainstomach compartment was not measured in this specimen but was approximately 70 cm long by 35 cm wide in another specimen (86-33).

The entrance to the first connecting chamber lies along the middle of the ventral portion of the left wall of the distal mainstomach. It lies somewhat off center relative to the main axis of the lumen of the first connecting chamber. The exact disposition of the connecting chambers is rather complex and is illustrated in Figure 10. Figure 10A is a diagrammatic representation showing the sections that Figure 10B are taken in. Connecting chambers 1 through 4 are in a straight line on one plane of the stomach complex. Connecting chamber 5 doubles back on itself and leads into connecting chamber 6, which is adjacent to connecting chamber 1. The complex then changes direction again and leads into connecting chambers 7 and 8. Figure 10C shows a sagittal section through most of the stomach compartments.

These connecting chambers range in volume from approximately 700 to 1,500 cc. and are lined by epithelium that was similar to the pyloric stomach compartments. The communications between the connecting chambers is free and permits passage of a fist. One of the apertures between the middle chambers, ranging from 3–4 to 5–6 cm, was smaller than the others. The communication between the last connecting chamber and the pyloric stomach compartment is a muscular sphincter that forcing two fingers through was difficult.

The proximal pyloric stomach compartment is capacious, equal in volume to the mainstomach. This was 110 cm long by 60 cm wide in another specimen (86-33).
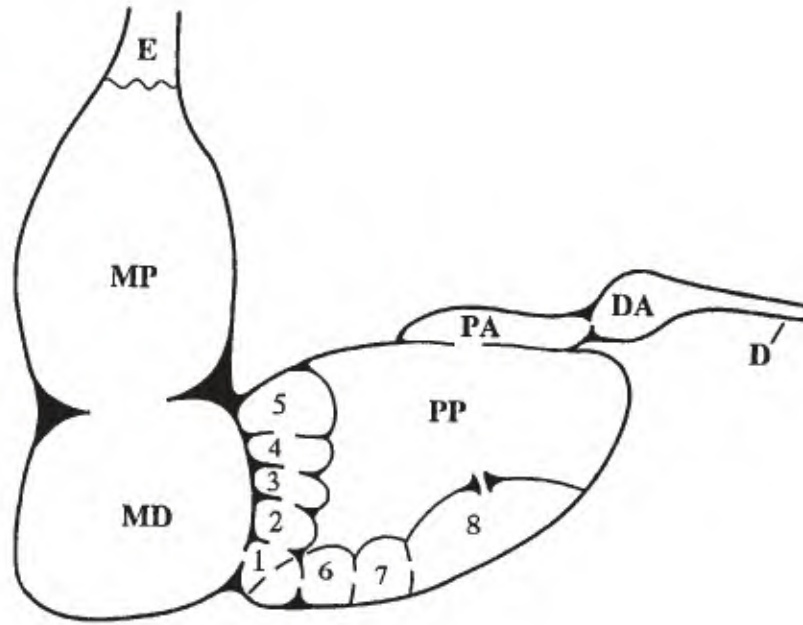
Fig. 9. Diagrammatic view of Derived Stomach Type I, *Berardius bairdii*, 571526. Labels as in Figure 1.
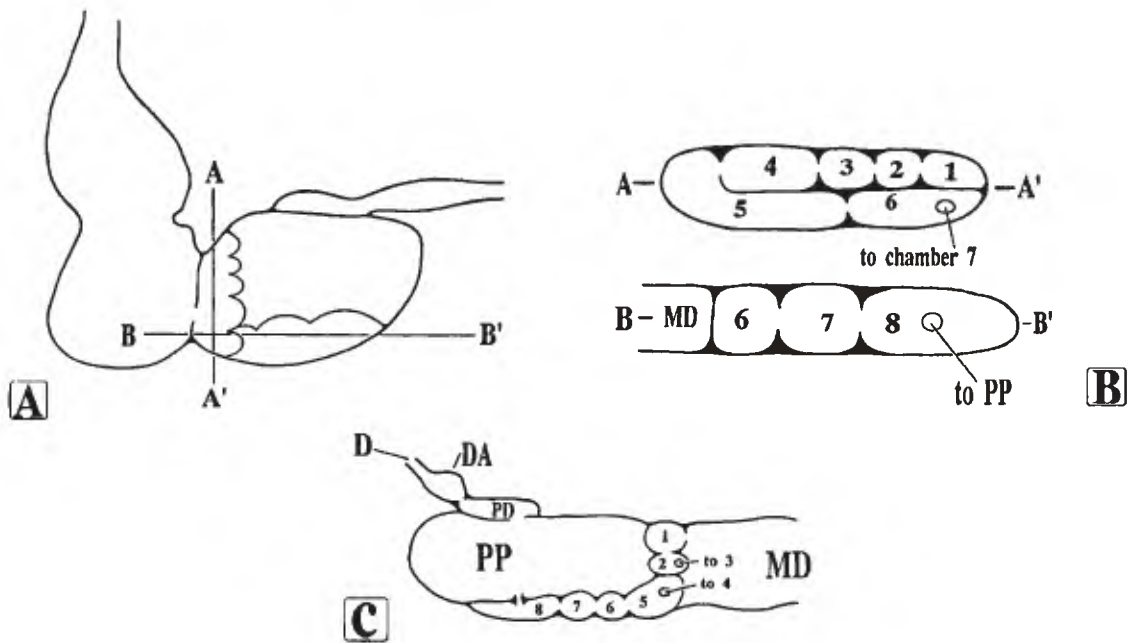

Fig. 10. Diagrammatic view of Derived Stomach Type I, *Berardius bairdii*, 571526. **A:** Same view as in Figure 9, showing orientation of sections A– A′, B–B′. **B:** Cross-sections taken along lines A-A′, B-B′. **C:** View in a plane perpendicular to A and B. Labels as in Figure 1.

It communicates freely with an extremely small distal pyloric stomach chamber.

The pyloric sphincter is pronounced. The hepatopancreatic duct opens into the duodenal ampulla approximately 5 cm distal to the pyloric sphincter. The duodenal ampulla is approximately the size of the distal pyloric stomach compartment.

Derived Stomach Type II: Two Main and Two Pyloric (Proximal and Blind Accessory); *Mesoplodon bidens, M. europaeus, M. mirus*

***Mesoplodon bidens*: two main (in series), two pyloric.** Turner (1889) described the stomach of a 460-cm male *Mesoplodon bidens*. Figure 11A is based on his description. The mainstomach was 53 cm in length and
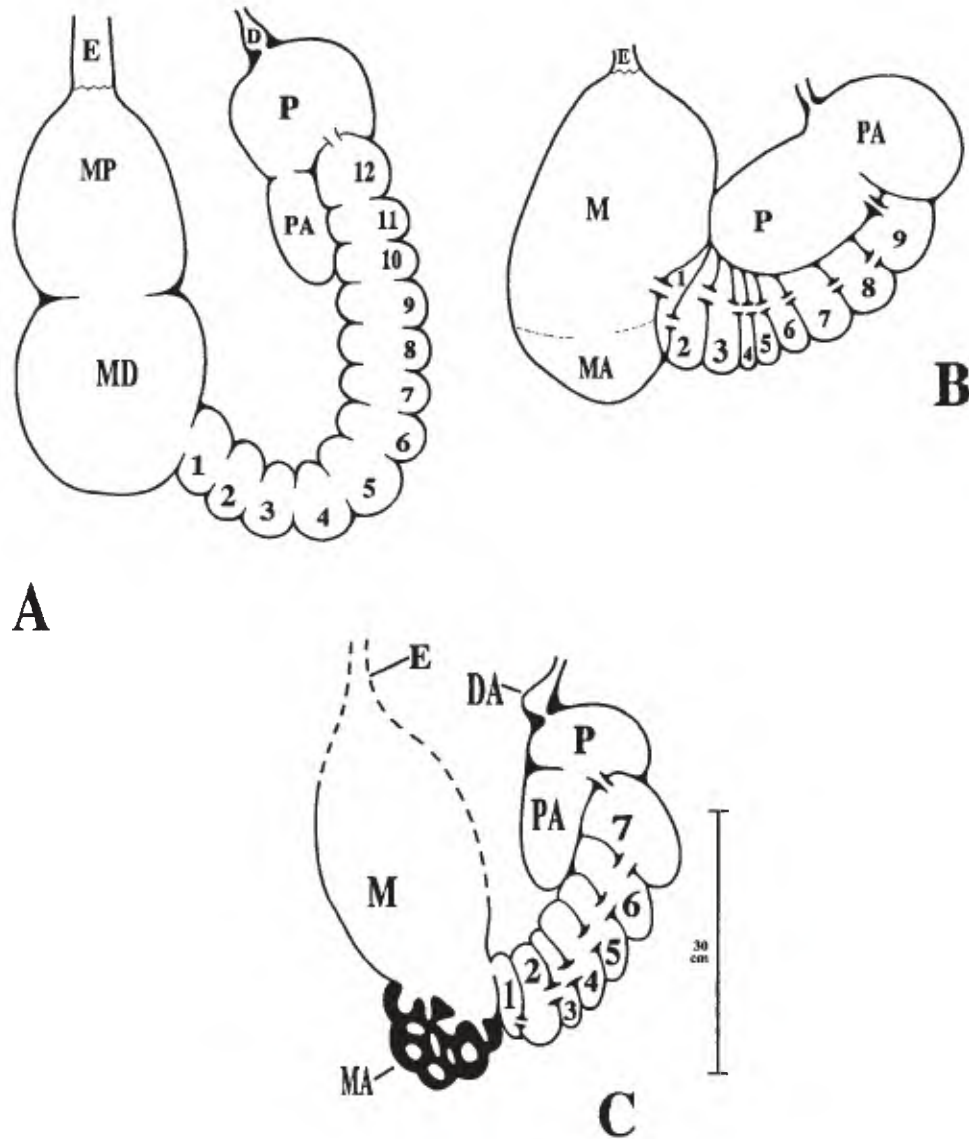
Fig. 11. Diagrammatic view of Derived Stomach Type II. **A:** *Mesoplodon bidens*, STR01068 (after Turner, 1889). **B:** *Mesoplodon mirus*, 571459; *Mesoplodon carlhubbsi*, 504128. Labels as in Figure 1.

was divided into two compartments by a constriction and an internal membrane. This then opened into a series of 12 connecting chambers varying in size from a "small to a large orange." The last connecting chamber opened by what was assumed to be a sphincter into the *principal* pyloric stomach compartment. A blind *accessory* pyloric stomach compartment was formed by a shallow membranous fold. The stomach of an earlier 468 cm male (Turner, 1885) had eight connecting chambers. It did not have its mainstomach divided into two, but did have a crescentic membrane dividing the pyloric stomach compartments.

Mesoplodon europaeus, mirus: two main (one blind), two pyloric (one blind). In *Mesoplodon europaeus* (550390 (Fig. 12) the esophagus empties into

the large mainstomach, as in the generalized ziphiid type. It is lined by thick glandular epithelium, which is thrown into transverse folds. The folding is probably to increase the epithelial surface area and does not indicate distensibility of the stomach.

The first deviation from the generalized ziphiid type comes in the division of the mainstomach into a **principal mainstomach** and a blind **accessory mainstomach**. This can be readily seen from an external examination (Fig. 12B) but is most striking in a sectional view (Fig. 13A,B). The principal mainstomach of 550738 was approximately 35 cm in anteroposterior length and 24 cm in width, and the accessory mainstomach was 7 cm in anteroposterior length and 12 cm in width. The accessory mainstomach portion was separated from the principal mainstomach by partition in which there was a circular opening 6 cm wide. The cavity of the acces-
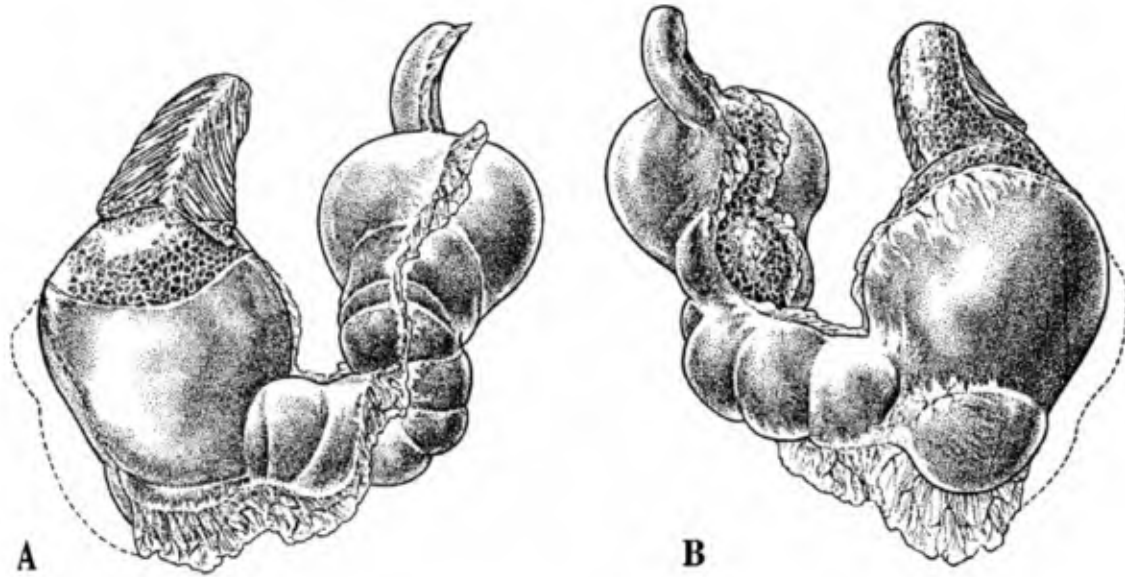
Fig. 12. Views of Derived Stomach Type II, *Mesoplodon europaeus*, 550390. The stomach chambers were dissected free and then fixed by inflating with formalin. **A:** Dorsal view. **B:** Ventral view. Structures are labeled in Figure 13.
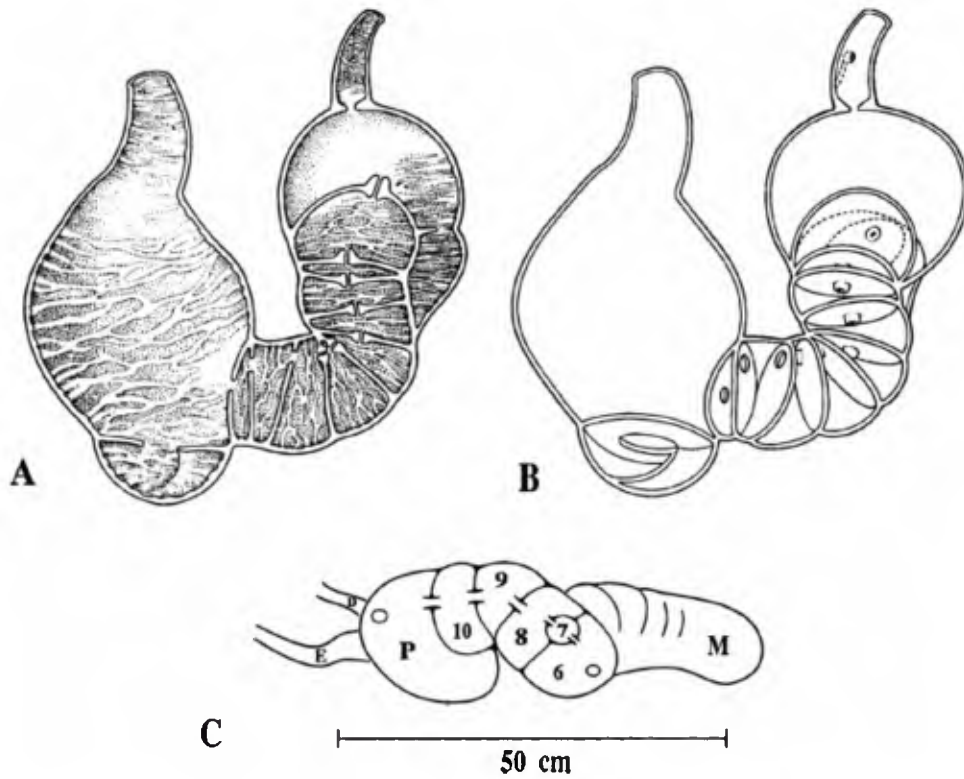

Fig. 13. Semidiagrammatic views of Derived Stomach Type II, *Mesoplodon europaeus*. **A:** Dorsal view showing texture of internal lining and an accurate rendition of communications between connecting chambers (550390). **B:** Three-dimensional dorsal section showing the shape of partitions between the connecting chambers and the presence or absence of sphincters and their orientation (550390). **C:** Diagrammatic lateral view of stomach showing the relationship between connecting chamber 7 and the other connecting chambers (550853). Labels as in Figure 1.

TABLE 2. Summary of numbers of stomach compartments

Taxon	Main stomach	Connecting chambers range	Mean	Mode	Pyloric stomach range	N
Ziphius	1	8–9	8.5	—	1	4
Berardius	2	7–10	8.3	8	2	30
M. bidens	2	8	8	8	2*	1
M. carlhubbsi	1	5?	5?	5?	–	1
M. densirostris	1	3–5	4.3	5	1	7
M. europaeus	2*	7–10	8.8	9–10	2*	7
M. perrini	1	3	3	3	1	1
M. mirus	2*	9–11	9.6	9	2*	3
M. stejnegeri	1	7–8	6.8	6	2	5

An asterisk denotes that the additional compartment is a blind accessory compartment.

sory mainstomach was partially divided by a crescentic fold.

The first connecting chamber opens off the principal mainstomach approximately 28 cm from the esophageal opening. The first connecting chamber is small and difficult to define from the second. The first connecting chamber could have been conceived of as just a minor dilation of an extremely complex valvular system between the mainstomach and the second connecting chamber. It was only when the specimen was fixed that the anatomy became evident. The epithelial lining of all of the connecting chambers is very similar to the lining of the pyloric stomach compartment.

The communication between the mainstomach and the first connecting chamber and between the first and second, and second and third are simple openings without muscular sphincters (Fig. 13A,B). The communications between the remainder of the connecting chambers and the terminal connecting chamber and the pyloric stomach compartment are sphincteric (Fig. 13A,B). This is particularly true of the connection between terminal connecting chamber and the proximal pyloric stomach compartment.

Care must be taken when counting the connecting chambers to probe the communication thoroughly. Sometimes, as in specimen 550853 (Fig. 13C), a small internal chamber appears that is not evident from an external view. This happened in the seventh connecting chamber of this specimen.

The second deviation from the generalized ziphiid type comes in the pyloric stomach compartment. The terminal connecting chamber opens by means of a pronounced sphincter into the side of the principal pyloric stomach compartment. A blind accessory pyloric stomach compartment then opens laterally off the principal pyloric stomach compartment. The accessory pyloric stomach compartment lies proximal to the principal pyloric stomach compartment. The principal pyloric stomach compartment is the larger of the two, measuring 16 cm in length and 16 cm in width in 550738. The accessory pyloric stomach compartment measured 11 cm in length and 8 cm in width.

Both pyloric stomach compartments were lined by typical cetacean pyloric epithelium. The pyloric sphincter was well developed and opened into a modest duodenal ampulla. There appeared to be no hepatopancreatic ampulla (Ampulla of Vater). The hepatopancreatic duct opened into the ampulla 7 cm distal to the pyloric

sphincter in 550738. The hepatopancreatic papilla was 4 mm high.

In the moderately decomposed stomach of a 493-cm *Mesoplodon mirus* (571459), there was found traces that suggested a blind accessory compartment in the mainstomach. It could not be definitely determined due to the state of decomposition. The epithelium in the mainstomach seemed to be unusually thick, but that may have been due to decomposition. The indentation of the mainstomach shown in (Fig. 11B) did not correspond to any internal features. This type of indentation seems to be common in *Mesoplodon* stomachs.

The orifice between the mainstomach and the first connecting chamber was extremely complicated in that there were numbers of layers of epithelium involved in it. One could have defined a second small compartment in the orifice. The first and second connecting chambers were small relative to the third. There were a total of nine connecting chambers in this specimen.

The last connecting chamber opened into a large proximal pyloric stomach compartment. This communicated freely with a second distal pyloric stomach compartment which, in turn, communicated with the duodenal ampulla.

***Mesoplodon carlhubbsi*: two main (one blind, trabeculated), two pyloric (one blind).** The only specimen of *M. carlhubbsi* that was able to be examined (Fig. 11C) was damaged. The proximal portion of the main stomach had been cut off and the connecting chambers, although complete, had been badly mutilated. The stomach resembled *M. europaeus* grossly, but the accessory portion of the main stomach had been modified.

It appeared as though there was an internal partition separating the principal mainstomach from the accessory and that the epithelium in the accessory portion had developed a network of interconnected trabeculae. There was no grossly noticeable difference in the epithelium of both main stomach compartments. The trabeculae were composed of moderately loose fibrous connective tissue.

The first connecting chamber appeared to be relatively long and tubular. All of the connecting chambers communicated with rather pronounced sphincters. Table 2 summarizes the anatomical data on the ziphiid species examined.

TABLE 3. Potential relationships of species of
***Mesoplodon* based on stomach morphology**

Generalized ziphiid stomach	(1-0-09-1-0-0)
M. perrini	(1-0-02-1-0-0)
M. stejnegeri	(1-0-06-1-0-0)
M. densirostris	(1-0-04-1-0-0)
M. bidens	(1-1-12-1-1-0)
M. europaeus	(2-0-07-1-1-0)
M. carlhubbsi	(2-0-07-1-1-0)
M. mirus	(2-0-09-1-1-0)

The numbers in parentheses are the number of mainstomach, accessory mainstomach, connecting chambers, pyloric, accessory pyloric, and distal pyloric stomach compartments.

Undescribed Ziphiids

Berardius arnuxii is extremely similar to *B. bairdii* in external morphology and osteology and may be conspecific with it. There is no reason to assume that *B. arnuxii* differs appreciably in stomach morphology from *B. bairdii*. On the other hand *Hyperoodon planifrons* differs from *H. ampullatus* in its osteology and in the development of adult sexual dimorphism, which is taken to extremes in *H. ampullatus*. These differences lead Moore (1968) to establish a new subgenus, *Frasercetus*, for *H. planifrons*. It would be expected that the two species may differ in stomach morphology.

Mesoplodon bowdoini is extremely similar to *M. carlhubbsi* in other aspects of their anatomy, and it is to be expected that they share a common stomach morphology. What the morphology of the remaining species of *Mesoplodon* are remains to be determined.

DISCUSSION

The systematic relationships of the ziphiid genera are still unresolved. Moore (1968) has made the only attempt to resolve the question. This is an exceedingly difficult group to work with systematically. Moore separates *Berardius* and *Ziphius* into the tribe Ziphiini and *Tasmacetus*, *Indopacetus*, *Hyperoodon*, and *Mesoplodon* into the tribe Hyperoodontini. Based on the retention of a primitive ziphiid stomach anatomy in *Tasmacetus*, moving it into the tribe Ziphiini seems warranted. The genera *Berardius*, *Tasmacetus*, and *Ziphius* are sufficiently different to warrant classification into different subtribes as Moore has done. The data on the stomach morphology do not disagree with this placement, as *Ziphius* and *Tasmacetus* appear to have the basic generalized ziphiid stomach. *Berardius* is more derived but clearly not especially related to *Hyperoodon* and *Mesoplodon*.

That leaves the tribe Hyperoodontini with the genera *Hyperoodon*, *Mesoplodon*, and *Indopacetus*. Moore (1968) appears justified in his establishment of a subgenus *Frasercetus* to contain *Hyperoodon planifrons* and his establishment of *Indopacetus*.

Several species groups based on stomach anatomy are evident (Table 3). *Mesoplodon perrini* differs from the generalized ziphiid stomach only in the reduction of connecting chambers. *M. stejnegeri* and *M. densirostris* differ from the generalized ziphiid stomach in having the development of another pyloric stomach compartment in series with the original. *M. bidens* differs from the gen-

eralized pattern in having developed a second main compartment in series with the first and a blind accessory pyloric stomach compartment. *M. europaeus* and *M. mirus* form a group in that they have a blind accessory compartment opening off the main compartment and a blind accessory pyloric stomach compartment.

The ziphiids clearly form a distinct group of cetaceans in their utilization of differences in stomach morphology. What these differences mean in terms of function is impossible to say. Functional conclusions cannot even be assigned to the differences in stomach morphology of domestic animals like the cow and sheep, much less animals about whose physiology and diet infinitely less is known. Ziphiids feed on a variety cephalopods and deep water fishes (Clarke, 1996), but there does not seem to be any pattern to their diet that would explain their diversity in stomach anatomy. The importance of this study is to demonstrate that there is a morphological system whose variance is relatively low that may serve to elucidate systematic relationships among the ziphiids.

LITERATURE CITED

Bouvier EL. 1892. Anatomical observations on hyperoodon rostratus lilljeborg. Ann Nat Sci Zoo 13:259–320, 257–258.
Clarke MR. 1996. The role of the cephalopods in the world's oceans. Philos Trans R Soc Lond Biol Sci B 351:977–1112.
Harrison RJ, Johnson FR, Young BA. 1970. The oesophagus and stomach of dolphins (*Tursiops, Delphinus, Stenella*). J Zool 160:377–390.
Home E. 1807. Observations on the structure of the different cavities, which constitute the stomach of the whale, compared with ruminating animals, with a view to ascertain the situation of the digestive organ. Philos Trans R Soc Lond MDCCCVII:93–102, pls III, IV.
Hunter J. 1787. Observations on the structure and economy of whales. Philos Trans R Soc Lond 77:306–351, pl. 5.
Jungklaus F. 1898. Der magen der Cetaceen. Jenaische Zeitschrift Naturwissenschaften 32:1–94, pls 1, 2.
Langer P. 1985. The mammalian stomach: structure, diversity and nomenclature. Acta Zool Fennica 170:99–102.
Langer P. 1988. The mammalian herbivore stomach: comparative anatomy, function and evolution. Stuttgart: Gustav Fischer. xvii +557 p.
Mead JG. 1993. The systematic importance of stomach anatomy in beaked whales. [International Marine Biology Research Institute, Kamogawa, Japan]. IBI Reports 4:75–86.

Moore JC. 1968. Relationships among the living genera of beaked whales with classifications, diagnoses and keys. Fieldiana: Zoology 53:209–298.

Pernkopf E, Lehner J. 1937. Vorderdarm. Vergleichended Beschreibuung des Vorderdarmes bei den einzelnen Klassen der Kranioten. In: Bolk L, Göppert E, Kallius E, Lubosch W, editors. Handbuch der Vergleichenden Anatomie der Wirbeltiere. Band III, Berlin: Urban and Schwarzenberg. p 349–476.

Scott JH, Parker TJ. 1889. On a specimen of *Ziphius* recently obtained near Dunedin. Trans Zool Soc Lond 12:241–248, pls xlviii–l.

Slijper EJ. 1962. Whales. London: Hutchinson and Co. 475 p.

Turner W. 1869. Further observations of the stomach in the Cetacea. J Anat Physiol 3:117–119.

Turner W. 1885. The anatomy of a second specimen of Sowerby's whale (*Mesoplodon bidens*) from Shetland. J Anat Physiol 20:144–188, pl. 4.

Turner W. 1889. Additional observations of the stomach in the ziphioid and delphinoid whales. J Anat Physiol 23:466–492.

Tyson E. 1680. *Phocaena*: or the anatomy of the porpus, dissected at Gresham College. London: B. Tooke.48 p, 2 pls.

Vrolik W. 1848. Natuur- en ontleedkundige beschwouwing van den *Hyperoodon*. Natuurkundige Verhandlingen van de Hollandsche Maatschappij der Wetenschappen te Haarlem, Tweede Verzameling, 5e Deel, 1e Stuk. p 1–128, pls. I–XV.

Weber M. 1886. Studies of more saugethiere. A contribution to the question of the origin of the cetacean. Jena, Gustav Fischer, viii, 248.