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Comparative anatomy of the stomach of the Cetacea. Ontogenetic changes involving gastric proportions – mesenteries – arteries

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Abstract

This study discusses three aspects of the comparative anatomy of the stomach in seven species of odontocete cetaceans: ontogenetic changes in the proportions of four gastric regions, the lines of fixation of the mesogastria to the stomach and the mode of branching of arteries that supply the organ.

An interspecific comparison revealed a considerable postnatal increase in the relative volume of the forestomach, however, in the harbour porpoise (*Phocoena phocoena*) there is a constant decrease in the size of the forestomach during the time period when the total length of the embryo lies between 7% and 12% of the neonatal length. The forestomach, which is not differentiated in species of the cetacean family Ziphiidae (*Mesoplodon densirostris* was investigated here), is completely differentiated on the ontogenetically left side of the stomach anlage, a situation that has only been found once – in the Bradypodidae or tree sloths – in terrestrial mammals.

The branching mode of the arterial supply of the stomach showed only one synapomorphy between *Stenella longirostris* and *Tursiops aduncus*, where the A. gastrica sinistra is a branch of the A. hepatica communis. In all other comparisons only symplesiomorphies could be discerned; between *Mesoplodon densirostris* and *Grampus griseus* in as many as three cases. This relatively high number of symplesiomorphies indicates that the gastric arterial system in both species did not change significantly from the basic situation at the beginning of cetacean evolution.

Introduction

Most of the published studies on the anatomy of the stomach of the Cetacea deal with only one species. The number of comparative investigations is limited (Weber 1888; Pernkopf and Lehner 1937; Slijper 1962). Due to this deficit, the present author attempted to consider material from different cetacean species. This study deals with three main aspects of comparative anatomy of the cetacean stomach.

1. The changes in relative size of the four gastric compartments are dealt with in an interspecific comparison. According to findings in terrestrial mammals (Langer 1988) it is assumed that changes in volume allow an extrapolation to the functional importance of the gastric chambers.
2. The lines of fixation of the Mesogastrium dorsale and the Mesogastrium ventrale to the stomach are discussed. With the help of these fixation-lines an idea can be obtained about the gastric regions that increased in size to form separate compartments.
3. The arterial supply of the gastric regions and their modes of branching were investigated. Interspecific comparisons allow differentiation between plesiomorphic ("basal", "primitive", or "ancestral") and apomorphic ("derived") branching modes. In a second step differentiation was made between symplesiomorphic and synapomorphic characters of arterial branching. Synapomorphies are characters that differentiated in the same direction in different species (Mayr 1975, 1976; Hennig 1982).

Material and methods

Specimens of cetacean species from the Indian Ocean were made available through the Centre for Dolphin Studies, Port Elizabeth Museum (PEM), South Africa (taxonomy according to Ross 1984 and Evans 1987). Species marked with an asterisk (*) are depicted in figure 1:

Superfam.: ZIPHOIDEA
Fam.: ZIPHIIDAE
*) *Mesoplodon densirostris* (Blainville, 1817) – Blainville's beaked whale, PEM 1022, PEM 1451,

Superfam.: DELPHINOIDEA
Fam.: DELPHINIDAE
Subfam.: Globicephalinae
*) *Grampus griseus* (Cuvier, 1812) – Risso's dolphin, PEM 1658, PEM 1858,
Subfam.: Delphininae
Delphinus delphis Linneus, 1758 – Common dolphin, PEM 1848, PEM 1850, PEM 1855, PEM 1856,
*) *Tursiops aduncus* (Ehrenberg, 1832) – Indian Ocean bottlenosed dolphin, PEM 1178, PEM 1849, PEM 1854, PEM 1857, PEM 1959,
Stenella longirostris (Gray, 1828) – Spinner dolphin, PEM 1030, PEM 1319,
Subfam.: Steninae
Sousa plumbea (Cuvier, 1829) – Humpback dolphin, PEM 963, PEM 1586.

The above-mentioned material originated either from specimens stranded on the Cape and Natal Coasts of the Republic of South Africa, or from individuals that were accidentally caught and drowned in shark-nets off swimming beaches of the coast of Natal. The material was either collected directly by the Port Elizabeth Museum or by the Natal Sharks Board, Umhlanga Rocks, Na-

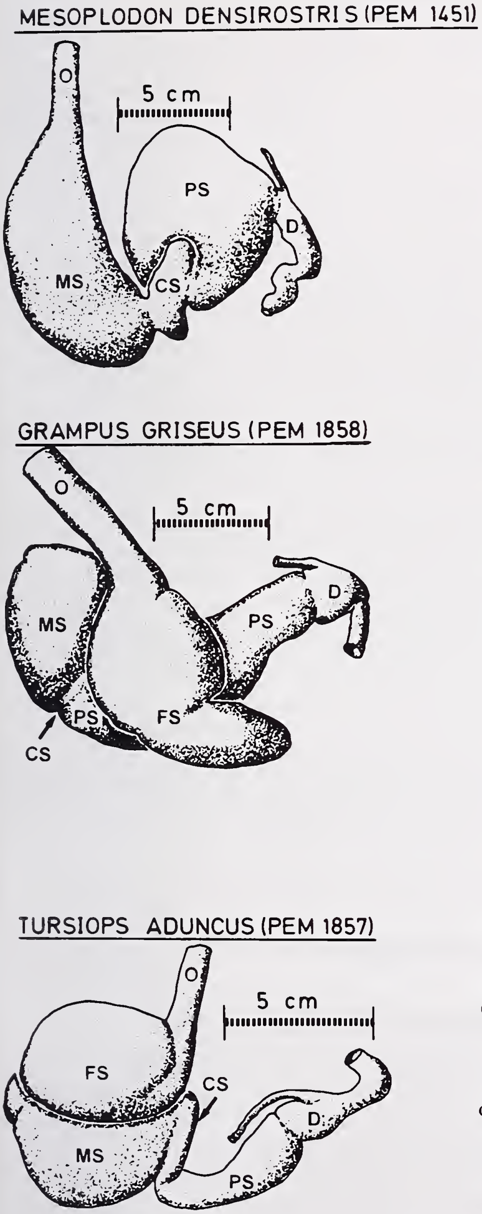


Fig. 1. Stomachs of three odontocete species. In *Mesoplodon densirostris* (Ziphiidae) a forestomach is not differentiated and in the two delphinid species *Grampus griseus* and *Tursiops aduncus* it is of different relative size and position. In *Grampus griseus* the connecting stomach cannot be distinguished from outside.
In all three species the Ductus hepatopancreaticus opens into the proximal duodenum, which in *Grampus griseus* and *Tursiops aduncus* is dilated to an ampulla duodeni.
Abbreviations: O = oesophagus, FS = forestomach, MS = main stomach, CS = connecting stomach, PS = pyloric stomach, D = duodenum.

tal, and then transferred to the collections of the Port Elizabeth Museum. The above-mentioned cetacean specimens where stored in toto in formalin solution, all of them with opened abdominal and thoracic cavities. The conservation of the in situ position of the organs thus remained undisturbed.

The studies were started by fenestrating the body wall either from the left or the right side to document photographically the position of the internal organs. After stepwise removal of the ribs, liver, and diaphragm, the digestive tract was totally removed and immersed in 5% formalin solution. The material was sealed in strong plastic bags and sent via Air Cargo to Giessen, Germany, where it arrived in good condition and was stored in cooled containers filled with 5% formalin solution. After rinsing the specimens and their arterial vascularisation were studied macroscopically.

The material from the Port Elizabeth Museum (PEM) consisted not only of specimens belonging to different species, but also to different developmental stages. The changes of relative volumes of the four gastric compartments, comparing all available material, were determined. The "baseline" of reference was the total length of the neonatal animal (Ln) as well as the total volume of the stomach (forestomach [FS] + main stomach [MS] + connecting stomach [CS] + pyloric stomach [PS]). The present author is fully aware that results of such interspecific comparisons can be biased because of considerable differences in gastric proportions, even in very young animals. The following procedure to determine volumes was applied: After different gastric portions (forestomach, main, connecting, and pyloric stomachs) were opened, cleaned of the contents and after the Tunica mucosa was removed (!) they were tightly filled (but not over-filled!) with moist cellulose pulp, which was pliable into any possible shape. The volumes of pulp were determined by packing them tightly (but not compressed!) into volumetric cylinders. The volumes of the forestomach (FS), main stomach (MS), connecting stomach (CS), and pyloric stomach (PS) were expressed as percentage of total gastric volume.

The total body length (Lt) of each specimen had already been determined when the animal was salvaged by the museum crew. From Ross (1984) the length of a newborn (Ln) of the species was known and the relative body length of each specimen could be expressed as a relative value (100 Lt/Ln).

To obtain an idea of the length of the weaning period, body length at weaning (Lw) and at birth (Ln) (raw data from Tomilin 1967 and Ross 1984) were compiled and body length at weaning relative to birth length (100 Lw/Ln) could be calculated; its value ranged from 113% in *Grampus griseus* to 194% in *Stenella longirostris.*

Additionally, serial sections (thickness 10 µm) of harbour porpoises embryos (*Phocoena phocoena*, collection M. Klima [MK]) were supplied by Professor Dr. Helmut A. Oelschläger, Frankfurt/M. The total length of the five specimens were as follows: MK 70: 42 mm, MK 67: 51 mm, MK 64: 60 mm, MK 62: 70 mm, MK 61: 95,5 mm. From these sections models of the external shape of the stomach were reconstructed from plates of "Styropor" (average thickness 2 mm). Secondly, the perimeters of the internal gastric lumina were traced with a "Videoplan" (Kontron Elektronik, München) to reconstruct three-dimensional shapes from serial sections. From the data of the luminal perimeters the "topological skeleton" of the six stomachs, i. e., the connecting lines of the "centres of gravity" of the respective cross-sections were processed with "3D-Top", a topological object processing program developed by T. Schwebel and Dr. A. Kriete, Giessen, and distributed by IMA-TEC, Bad Tölz, Germany. The length of the forestomach (Lf) as well as the length of the main stomach (Lm) from the end of the oesophagus to its tip were compared and it was possible to determine the relative length of the forestomach (Lf) as compared to the combined lengths of the forestomach plus main stomach (Lf + Lm).

Results and discussion

Ontogenetic development of stomach compartments in Cetacea

Relative volumes of the four gastric compartments in five odontocete species were plotted against relative body length and the following relationships became visible (Fig. 2): After birth the forestomach volume increases strikingly and the pyloric stomach volume decreases. The volume of the main stomach decreases but later shows a tendency to increase. These changes take place during the weaning period. The bar on top of the diagram in figure 2 represents the range of the weaning period. Increase in the relative volume of the main stomach is advantageous during the later part of the weaning period

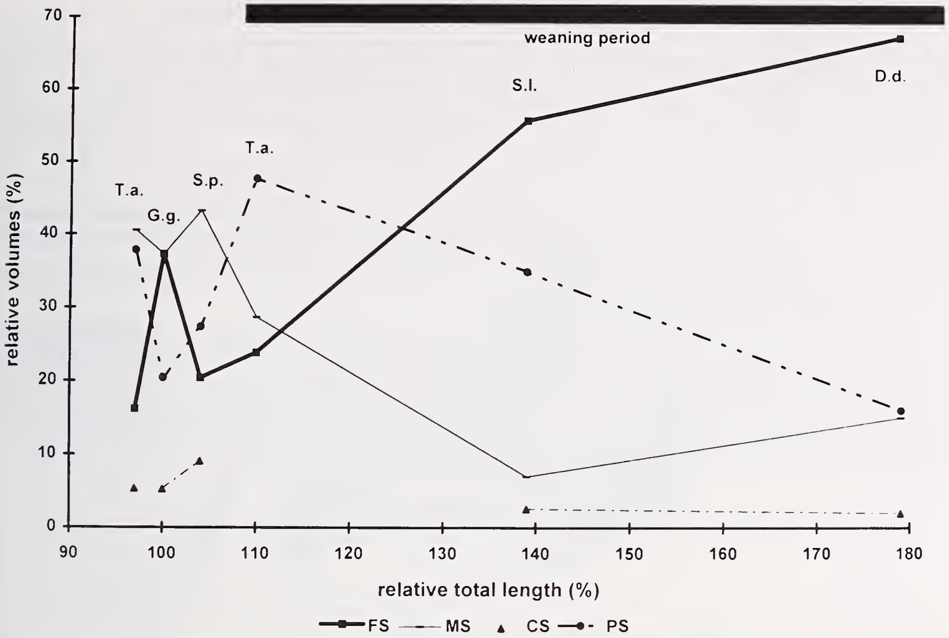


Fig. 2. Relationships between the relative total length, expressed as percentage of the length of the newborn animal (from Ross 1984), versus the relative volume of gastric compartments, expressed as percent of the total gastric volume. Material from six specimens, belonging to five odontocete species was used. An interspecific comparison is made possible, but results of such a study can be biased because of considerable differences in gastric proportions of different species.
Four gastric compartments were considered: FS = forestomach, MS = main stomach, CS = connecting stomach, PS = pyloric stomach.
Abbreviations: T. a. = *Tursiops aduncus*, G. g. = *Grampus griseus*, S. p. = *Sousa plumbea*, S. l. = *Stenella longirostris*, D. d. = *Delphinus delphis.*

because during this time the adult digestive process begins to develop. Autoenzymatic digestion (Langer 1988) of protein, i. e., digestion with the mammal's own proteolytic enzymes, becomes increasingly important. Milk, which in cetaceans is extremely rich in fat (Flindt 1985; Oftedal 1993) is later replaced by adult food, consisting of cephalopods, fish and, to some small extent, crustaceans, which are all rich in protein. The forestomach is the region where the massive Tunica muscularis of the gastric wall is able to compress the ingested food into a semi-liquid mass, which passes into the main stomach (Cockcroft pers. comm.).

The relative length of the forestomach of the harbour porpoise (*Phocoena phocoena*), expressed as a percentage of the combined lengths of both forestomach plus main stomach, increases, but later decreases. This prenatal "overshoot" might document different growing intensities in the compartments of the stomach. In cattle (*Bos primigenius*) Auernheimer (1909) and Becker et al. (1951), as well as in red deer (*Cervus elaphus*) Drescher-Kaden (1981) showed that the ruminoreticulum is relatively larger during the first half of the gestation period than during the second half. For the gastric gland of *Trichechus manatus* (West Indian manatee) Langer (1988) showed a similar "overshoot" in relative size.

It is interesting to compare the data of the considered gastric sections in the above-mentioned odontocets with data from the same regions of a mysticete species, the minke whale (*Balaenoptera acutorostrata*). The three animals investigated by Olsen et al. (1994) had a body length of about 200 to more than 400% of their neonatal length of 2.7 m (Norman et al. 1963) and 2.1 m to 2.74 m according to Tomilin (1967). The forestomach volume of the minke whale ranges from 44 to about 70% of the total gastric volume, the main stomach ("fundic chamber" according to Olsen et al. 1994) from about 22 to 44%, and the pyloric stomach from 8.5 to 12%. Only the values for the main stomach lie well above those depicted for *Delphinus delphis* (PEM 1848) in figure 2. It can be speculated that there is further increase in the relative volume of this gastric compartment during the post-weaning period of all cetacean species.

The above-mentioned discussion refers to born cetaceans. In the case of material from the harbour porpoise (*Phocoena phocoena*) some information on prenatal changes of gastric proportions can be gained. The length of the forestomach (Lf) was expressed as a percentage of the sum of both forestomach and main stomach (Lm) lengths (100 Lf/Lf + Lm) and plotted against the total length (Lt) of the five specimens, expressed as percentage of neonatal length (Ln) of the animals (100 Lt/Ln) (Fig. 3).

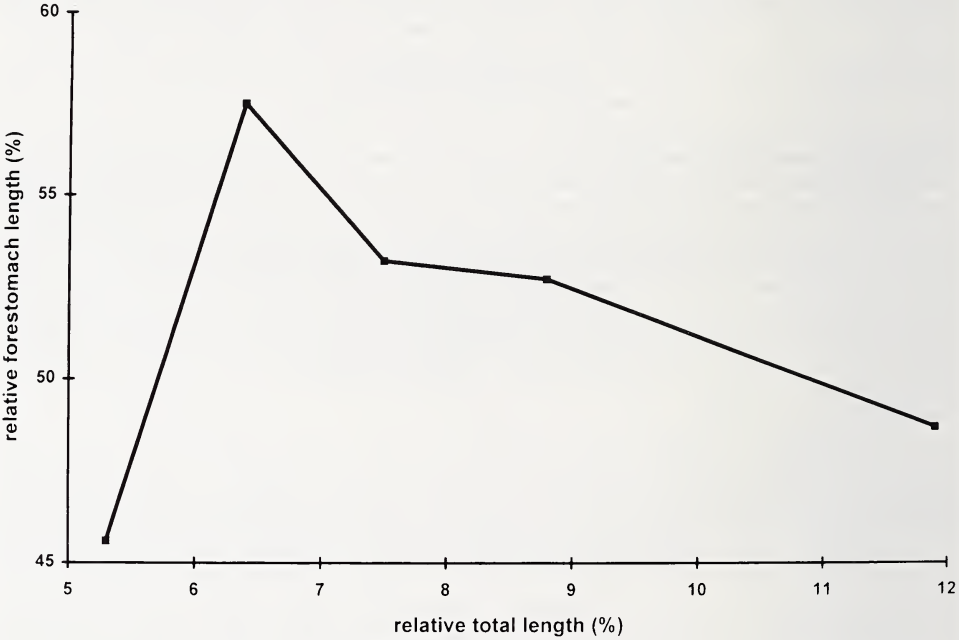


Fig. 3. Relationship between the total length, expressed as percentage of the length of the newborn animal of the habour porpoise, *Phocoena phocoena*, versus the relative forestomach length, expressed as the sum of the length of the forestomach plus the length of the main stomach.

The relative length of the forestomach increases up to a total length (Lt) of 51 mm, which is 6.4% of neonatal length and decreases in longer fetuses. This "overshooting" of the forestomach size could also be observed in some mammals with a voluminous gastric section that is "set off" from the direct connection between oesophagus and duodenum, such as in the red deer (*Cervus elaphus*, Ruminantia) (Drescher-Kaden 1981) and the Caribbean manatee (*Trichechus manatus*, Sirenia) (Langer 1988).

Lines of fixation of the dorsal and ventral mesogastrium

Two of the investigated species were used to depict the lines of fixation of the Mesogastrium dorsale et ventrale to the stomach: *Grampus griseus* (PEM 1858) (Fig. 4) and *Delphinus delphis* (PEM 1856) (Fig. 5). All other species showed a principally similar situation.

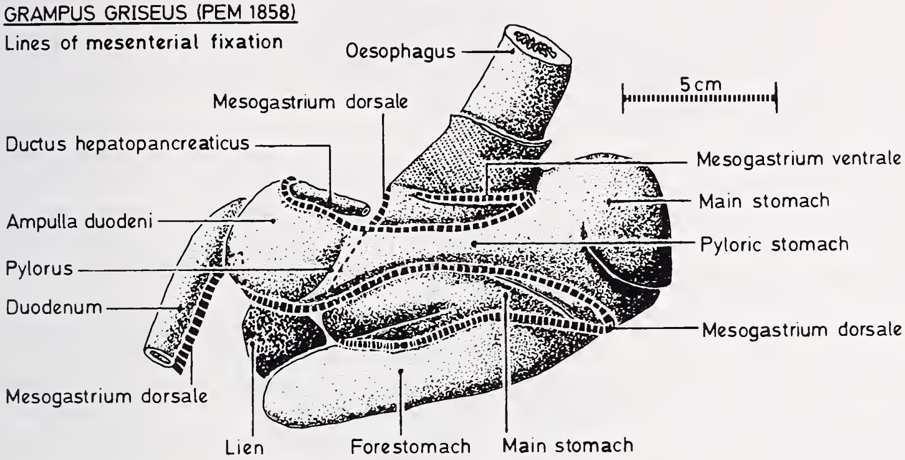


Fig. 4. Line of fixation (bold broken line) of the dorsal and ventral mesogastria to the stomach of *Grampus griseus.* The line of fixation of the dorsal mesogastrium is partly hidden behind the pyloric stomach, where it is represented by a thin broken line. The stippled area at the base of the oesophagus is the zone of tight fixation of this region to the diaphragm.

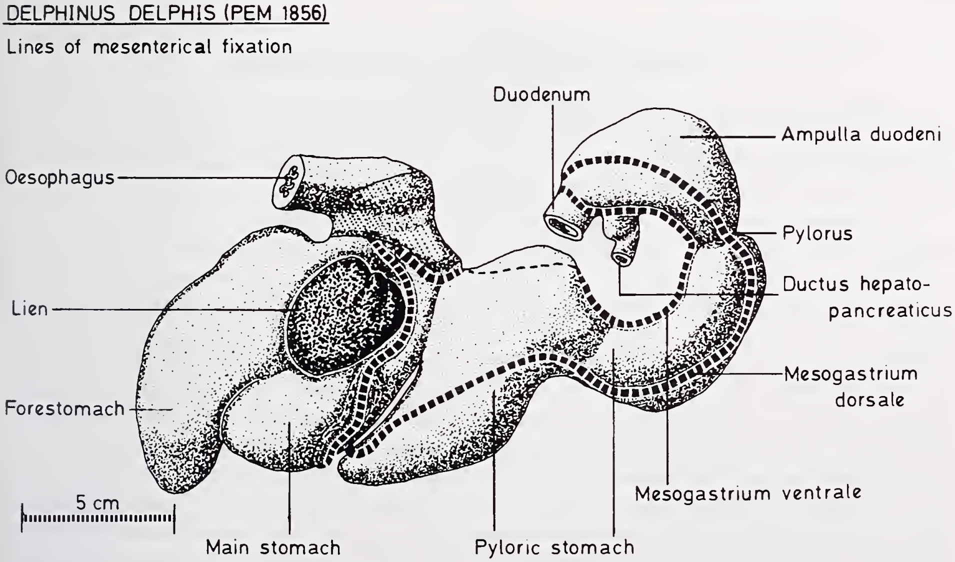


Fig. 5. Line of fixation of the mesogastria to the stomach of *Delphinus delphis.* For further details see legend to Fig. 4.

The Mesogastrium ventrale is attached at the gastric wall close to the oesophageal opening where the stomach is tightly connected with the diaphragm (Figs. 4 and 5). It runs over the oral part of the main stomach, follows the lesser curvature of the pyloric stomach and the pylorus and ends at the opening of the Ductus hepatopancreaticus into the Ampulla duodeni.

The course of the line of fixation of the Mesogastrium dorsale is much more complicated because of the formation of a forestomach and the increase in volume in the region of the main stomach. Once again, the mesentery starts at the zone of fixation between the cardiac region and the diaphragm. From here it runs on the topographically left side of the main stomach. The round (*Grampus griseus*) or slightly triangular (*Delphinus delphis*) spleen is fastened to the main stomach via the dorsal mesogastrium. This passes over the greater curvature and follows the fold between the main and pyloric stomach regions. With a sharp bend the mesenterial fixation line crosses over to the pyloric stomach, which it follows towards the greater curvature, then passes over the pylorus and the duodenal ampulla to the tube-like part of the duodenum. In all investigated cetaceans the small greater omentum was small; in *Delphinus delphis* (PEM 1856), for example, this omentum just connects the main stomach with the oral end of the pyloric stomach and does not form an omental pouch.

In previous studies (Langer 1973, 1988) it was shown that the plurilocular stomachs of mammalian herbivores lies on the ontogenetically left side of the Fornix (= Fundus) ventriculi. It is highly probable that a hypothetical plane through the two lines of fixation of the mesogastria separates the ontogenetically right from the left part of the stomach. The forestomach in Cetacea belongs completely to the ontogenetically left side of the Fornix ventriculi, whereas the main stomach is partly derived from it.

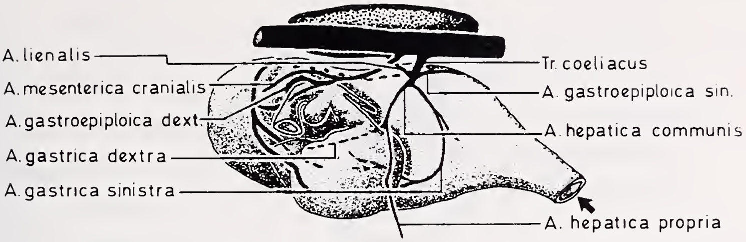
In terrestrial mammals it was possible to show that the different forestomach regions are generally partly derived from the ontogenetically left and right sides of the organ (Langer 1988). Only in tree sloths (Bradypodidae) the position of the total forestomach pouch on the ontogenetically left side of the stomach could be demonstrated. This similarity does, of course, not indicate a close relationship between Bradypodidae and Cetacea.

Arterial branching in the vicinity of the stomach

The arterial supply to the stomach and its surrounding organs was dissected in five species: *Mesoplodon densirostris* (PEM 1451) (Fig. 6 a), *Grampus griseus* (PEM 1858) (Fig. 6 b), *Delphinus delphis* (PEM 1856) (Fig. 6 c), *Tursiops aduncus* (PEM 1178) (Fig. 6 d), and *Stenella longirostris* (PEM 1319) (Fig. 6 e).

The arterial branching was not only documented in drawings, but also in schematic diagrams that generally list the Aorta abdominalis plus ten branches Tab. 1 a, b. A compilation of the information obtained by the schematic graphs of the branching mode gave the following information (Tab. 2): The Aa. hepatica communis, lienalis, gastrica sinistra et dextra, gastroepiploica sinsistra et dextra, and duodenalis can be branches of the Truncus coeliacus. On the other hand, the A. hepatica communis can give off the following branches: Aa. hepatica propria, gastrica dextra et sinistra, gastroepiploica dextra, duodenalis, mesenterica cranialis, and lienalis. Four of these above-mentioned vessels, the Aa. gastrica sinistra et dextra, lienalis and gastroepiploica sinistra represent either branches of the Truncus coeliacus, the A. hepatica communis, or the A. lienalis. In *Mesoplodon densirostris*, *Grampus griseus*, and *Delphinus delphis*, the Aa. lienalis and gastrica sinistra are branches of the Truncus coeliacus. This is the usual situation in unilocular stomachs such as in man (Lippert and Pabst 1985), horse and dog (Koch and Berg 1985). Only in *Delphinus delphis* the A. gastrica dextra branches from the Truncus coeliacus, in the four other species the right gastric artery a)

MESOPLODON DENSIROSTRIS (PEM 1451)



b)

GRAMPUS GRISEUS (PEM 1858)

Fig. 6 a, b

c)

DELPHINUS DELPHIS (PEM 1856)

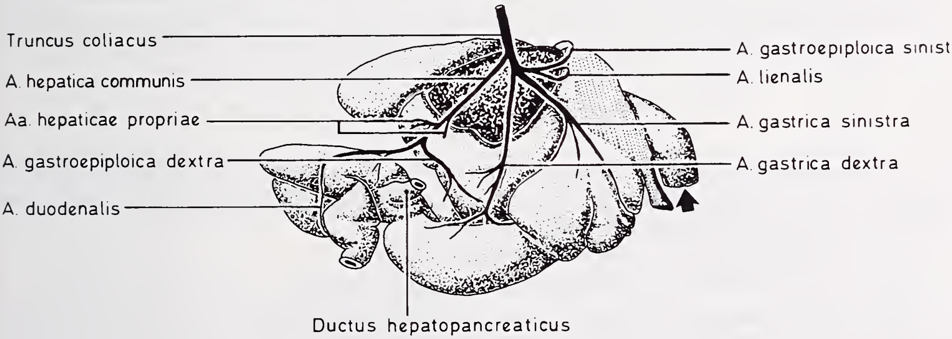


Fig. 6 c

is a branch of the A. hepatica communis. This latter situation can also be found in land mammals, such as man (Lippert and Pabst 1985), horse, pig, and dog (all with a unilocular stomach), as well as in three ruminant species, cattle, sheep, and goat (Koch and Berg 1985). In the three species of the subfamily Delphininae the A. gastroepiploica sinistra is a branch of the A. lienalis, just as in the unilocular stomachs of man, horse, pig, and dog.

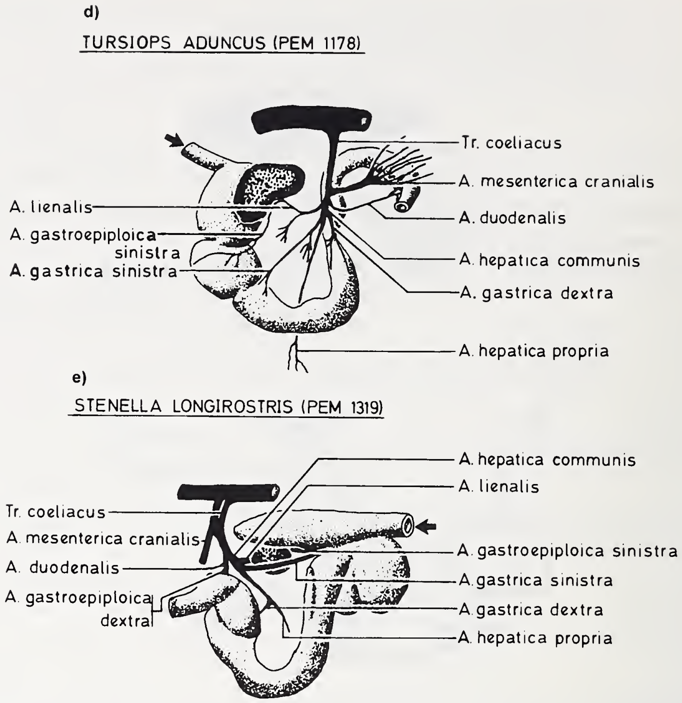


Fig. 6 d, e

Fig. 6. Arterial supply of the stomach of a) *Mesoplodon densirostris* (stomach seen from the right), b) *Grampus griseus* (stomach seen from dorsally and from the left), c) *Delphinus delphis* (stomach seen from dorsally and from the right, stippled area at base of oesophagus indicates the zone that is tightly fixed to the diphragm), d) *Tursiops aduncus* (stomach seen from left), and e) *Stenella longirostris* (stomach seen from the right). In all five cases the oesophagus is marked with an arrow.

A branching mode that can be found in the majority of the five investigated cetacean species, as well as in man, horse, and dog, is a plesiomorphic differentiation. The following four plesiomorphic modes can be documented:

1. A. lienalis is a branch of the Truncus coeliacus,
2. A. gastrica sinistra is a branch of the Truncus coeliacus,
3. A. gastrica dextra is a branch of the A. hepatica communis,
4. A. gastroepiploica sinistra is a branch of the A. lienalis.

The following four apomorphic branching modes can be listed:

I. A. lienalis is a branch of the A. hepatica communis,
II. A. gastrica sinstra is a branch of the A. hepatica communis,
III. A. gastrica dextra is a branch of the Truncus coeliacus,
IV. A. gastroepiploica sinstra is a branch of the Truncus coeliacus.

With the exception of *Grampus griseus* (PEM 1858) where technical reasons only allowed the comparison of three branching modes, it can be seen that the four remaining species each show at least one apomorphy: *Mesoplodon densirostris*: apomorphy No. IV, *Delphinus delphis*: apomorphy No. III, *Tursiops aduncus*: apomorphy No. III, *Stenella longirostris*: apomorphies Nos. I and II.

Table 1. Schematic illustrations for five cetacean species of the branching mode of arteries supplying the stomach. Arterial names with asterisks are either classified as plesiomorphic or apomorphic characters.

Table 1 a

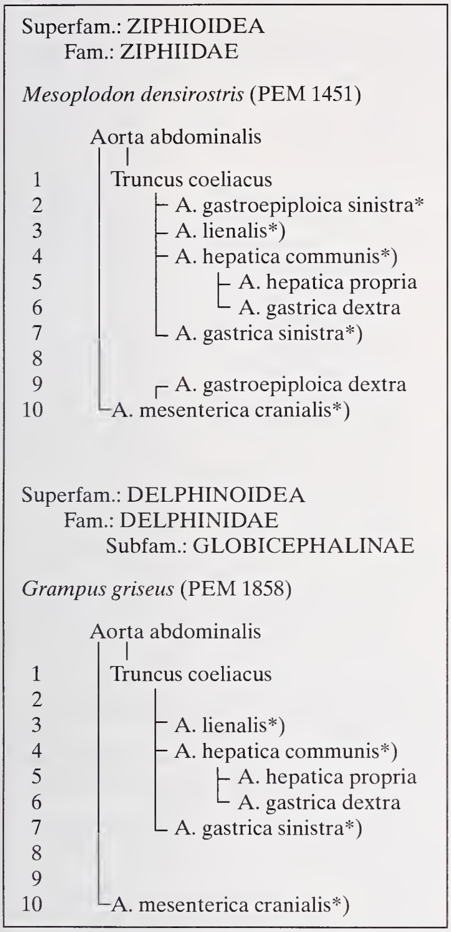
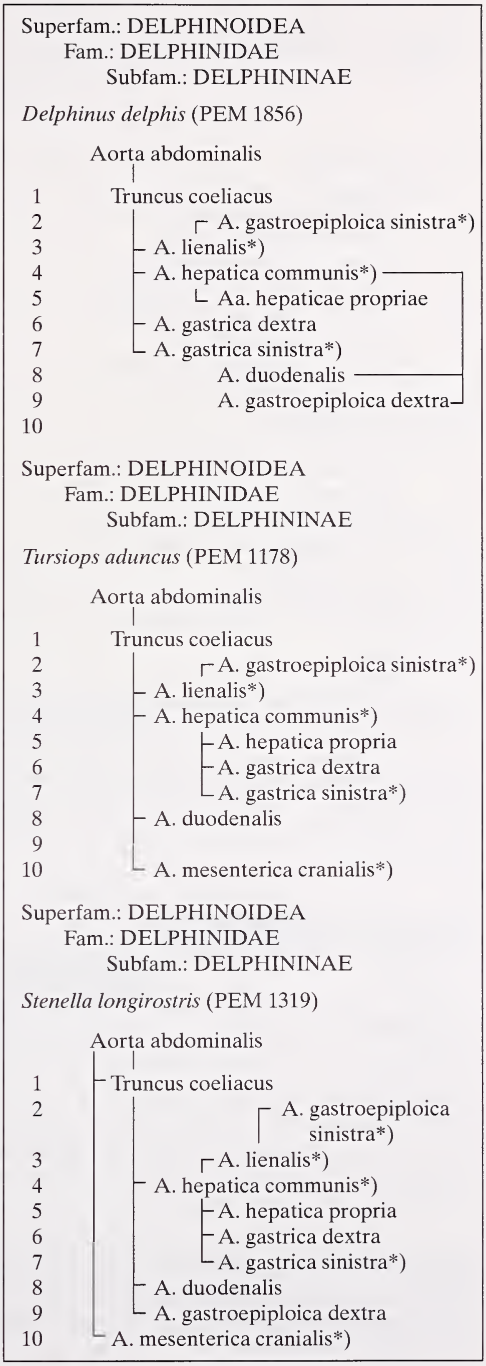


Table 1 b



In total, *Mesoplodon densirostris* and *Grampus griseus* have three symplesiomorphic branching modes, which is the highest number of symplesiomorphies seen in this study (Tab. 3). The lowest number of symplesiomorphies, namely one, can be found when comparing *Stenella longirostris* with *Mesoplodon densirostris*, *Grampus griseus*, and *Delphinus delphis*. It should be kept in mind that symplesiomorphies do not indicate that bearers of these characters are closely related to one another, thus forming a

Table 2. Symplesiomorphies (P), i. e., joint possession of ancestral characters, and synapomorphies (A), i. e., joint possession of derived characters (Mayr 1976), in the branching mode of arterial vessels are indicated in this compilation by multiple x's in a horizontal line. Five cetacean species are considered. Md: *Mesoplodon densirostris*; Gg: *Grampus griseus*; Dd: *Delphinus delphis*; Ta: *Tursiops aduncus*; Sl: *Stenella longirostris*.

Branches of the Aorta abdominalis and origin of arteries supplying the stomach in five species of the Cetacea					
	Md	Gg	Dd	Ta	Sl
Aorta abdominalis					
├ Truncus coeliacus	×	×	×	×	×
│ ├ A. hepatica communis	×	×	×	×	×
│ │ ├ A. hepatica propria	×	×	×	×	×
│ │ ├ A. gastrica dextra (P)	×	×		×	×
│ │ ├ A. gastrica sinistra (A)				×	×
│ │ ├ A. gastroepiploica dextra			×		
│ │ ├ A. duodenalis			×		
│ │ ├ A. mesenterica cranialis					
│ │ └ A. lienalis (A)					×
│ ├ A. lienalis (P)	×	×	×	×	
│ │ └ A. gastroepiploica sin. (P)			×	×	×
│ ├ A. gastrica sinistra (P)	×	×	×		
│ ├ A. gastrica dextra (A)			×		
│ ├ A. gastroepiploica sinistra (A)	×				
│ ├ A. gastroepiploica dextra					×
│ └ A. duodenalis				×	×
└ A. mesenterica cranialis	×	×			×

Table 3. The number of synapomorphies are depicted in the upper part of this table, symplesiomorphies can be found at the bottom.

Number of symplesiomorphies and synapomorphies in the arterial branching of gastric vessels in cetaceans					
			Synapomorphies		
	Mesoplodon	*Grampus*	*Delphinus*	*Tursiops*	*Stenella*
Mesoplodon		/	0	0	0
Grampus	3		0	0	0
Delphinus	2	2		0	0
Tursiops	2	2	2		1
Stenella	1	1	1	2	
			Symplesiomorphies		

monophyletic group. However, when two species show a common synapomorphic character, they are of monophyletic origin (Hennig 1982). Such a synapomorphy is found in *Stenella longirostris* and *Tursiops aduncus*, where the A. gastrica sinistra is a branch of the A. hepatica communis.

Table 4. Differentiations of the four gastric regions in 24 cetacean species are compiled from the literature; FS = forestomach, MS = main stomach, CS = connecting stomach, PS = pyloric stomach. Informations from the following publications have been considered: 1. Amasaki et al. (1989), 2. Berzin (1972), 3. Boulart and Pilliet (1884), 4. Cattaneo (1898), 5. Cave (1982), 6. Gaskin (1978), 7. Green (1972), 8. Harrison et al. (1970), 9. Home (1807), 10. Jungklaus (1898), 11. Kaiya et al. (1982), 12. Ohe (1951), 13. Pernkopf and Lehner (1937), 14. Ping (1926), 15. Rice and Wolman (1990), 16. Slijper (1962), 17. Smith (1972), 18. Tarpley et al. (1987), 19. Turner (1867), 20. Turner (1886), 21. Turner (1889), 22. Vrolik (1848), 23. Weber (1886), 24. Weber (1888), 25. Yamasaki and Kamiya (1981), 26. Yamasaki and Takahashi (1971).

	Gastric regions in 24 cetacean species					
Family	Genera and species	FS	MS	CS	PS	References
Platanistidae	*Pontoporia blainvillei*	–	+	+	+	6, 25, 26
	Inia geoffrensis	+	+	+	+	11, 25
	Lipotes vexillifer	(+)	(+)	(+)	+	25
	Platanista gangetica	+	+	+	+	25, 26
Delphinidae	*Sousa plumbea*	+	+	+	+	own
	Stenella longirostris	+	+	+	+	own
	Stenella roseiventris	+	+	+	+	8
	Delphinus delphis	+	+	+	+	3, 4, 9, 13, 21, own
	Tursiops truncatus	+	+	+	+	7, 13, 16, own
	Lagenorthynchus albirostris	+	+	+	+	13, 24
	Grampus griseus	+	+	+	+	own
	Globicephala melaena	+	+	+	+	13, 19, 20, 24
Phocoenidae	*Phocoena phocoena*	+	+	+	+	5, 6, 10, 17, 24, own
	Neophocaena phocaenoides	+	+	+	+	14
Physeteridae	*Kogia breviceps*	+	+	+	+	15
	Physeter catodon	+	+	+	+	2
Ziphiidae	*Mesoplodon bidens*	–	+	+	+	20, 21
	Mesoplodon densirostris	–	+	+	+	own
	Ziphius cavirostris	–	+	+	+	6
	Hyperoodon spec.	–	+	+	+	13, 22, 23
Balaenopteridae	*Balaenoptera acutorostrata*	+	+	+	+	1
	Balaenoptera physalus	+	+	+	+	6, 16
	Balaenoptera spec.	+	+	+	+	12, 13
Balaenidae	*Balaena mysticetus*	+	+	+	+	18

Very probably, the interspecific differences of the branching types of arteries that supply the stomach and organs in its vicinity, represent a complex of morphological differentiations. In spite of the remarkable diversity of branching modes, it is possible to differentiate between "primitive" or plesiomorphic and "derived" or apomorphic characters. According to modern studies on ribosomal DNA sequenc and some morphological characteristics (Milinkowitch et al. 1993; Meyer 1993; Klima and Oelschläger 1994) the Ziphiidae in general are widely removed from the odontoces, and the genus *Mesoplodon* is perhaps the most primitive modern ziphiid (Duffield Kulu 1972). On the other hand, the branching of the A. gastroepiploica sinistra from the Truncus coeliacus has to be categorized as an apomorphy (No. IV). The genus *Grampus* belongs to the delphinid subfamily Globicephalinae (Evans 1987). Duffield Kulu (1972) concluded that *Grampus* belongs to the more primitive of the higher odontocetes.

A differentiation within the cetacean family Delphinidae becomes possible: The arterial supply of the stomach of *Grampus griseus* (Subfamily Globicephalinae) is more similar to that of *Mesoplodon* than to the three representatives of the subfamily Delphininae (*Delphinus delphis*, *Tursiops aduncus*, *Stenella longirostris*).

According to the literature all four gastric regions, the forestomach, the main stomach, the connecting stomach and the pyloric stomach can be identified in the Delphinidae, the Phocoenidae, the Physeteridae, the Balaenopteridae and the Balaenidae (Tab. 4)., i. e., they can be found in Odontoceti as well as in Mysticeti. The situation in the Platanistidae is ambiguous with *Pontoporia blainvillei* lacking a forestomach (GASKIN 1978; YAMASAKI and KAMIYA 1981; YAMASAKI and TAKAHASHI 1971), but two other species (*Inia geoffrensis* and *Platanista gangetica*) having a forestomach. In the Ziphiidae a forestomach is not differentiated. A recent illustration of a Cuvier's beaked whale, *Ziphius cavirostris*, published by PFEIFFER (1993), depicts a forestomach in this species, but it cannot be decided from this drawing whether the slight external groove is related with an internal separation between forestomach and main stomach.

The following conclusions can be drawn from the present observations: Although the external form of the stomach is variable, a forestomach is differentiated in most Cetacea. It increases in size after birth. However, there are some groups (Zipiidae and some Platanistidae) where a forestomach is not differentiated at all. It is assumed that this is an apomorphic character because all other Cetacea – Mysticetes included(!) – differentiate a forestomach. This section of the stomach developed on the ontogenetically left side of the stomach anlage, i. e., it lies to the left of the twisted area between the lines of fixation of the two mesenteries (mesogastria) of the stomach. The arterial supply of the stomach of different cetacean species shows symplesiomorphies between species with a forestomach and *Mesoplodon densirostris*, which does not have this differentiation.

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Zusammenfassung

Vergleichend-anatomische Untersuchungen am Magen der Cetacea. Ontogenetische Proportionsveränderungen – Mesenterien – Arterien.

In dieser Studie werden drei vergleichend-anatomische Aspekte des Magens von sieben Odontoceten-Arten behandelt: Die Veränderungen der Proportionen der vier Magenabschnitte im Laufe der Ontogenese, die Befestigungslinien der beiden Magenmesenterien an diesem Organ und der Verzweigungsmodus der den Magen versorgenden Arterien.

Bei einem interspezifischen Vergleich zeigt sich, daß das relative Volumen des Vormagens (bezogen auf das Volumen des Gesamtmagens) nach der Geburt beträchtlich zunimmt, daß aber beim Schweinswal (*Phocoena phocoena*) die Größe des Vormagens vor der Geburt abnimmt, und zwar in der Periode, in der die Gesamtlänge der Embryos zwischen 7% und 12% der Länge des Neugeborenen beträgt. Der Vormagen, der bei Arten der Familie Ziphiidae nicht ausgebildet ist (*Mesoplodon densirostris* wurde hier untersucht) entsteht in seiner ganzen Ausdehnung auf der ontogenetisch linken Seite der Magenanlage. Diese Situation wurde bei Landsäugetieren bislang nur ein Mal, und zwar bei den Bradypodidae, gefunden.

Nur bei *Stenella longirostris* und *Tursiops aduncus* ist die A. gastrica sinistra ein Ast der A. hepatica communis, ein Verzweigungsmodus der den Magen versorgenden Arterien, der als synapomorpher Charakter zu bezeichnen ist. Bei allen anderen Vergleichen konnten nur Symplesiomorphien nachgewiesen werden; zwischen *Mesoplodon densirostris* und *Grampus griseus* war dies sogar dreifach möglich. Diese relativ hohe Zahl von Symplesiomorphien läßt vermuten, daß sich das arterielle Versorgunssystem des Magens bei beiden Arten nicht weit von der Ausgangssituation, wie sie sehr wahrscheinlich zu Beginn der Cetaceen-Evolution herrschte, entfernt haben dürfte.

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