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Vascularization of the gastrointestinal tract of the bottlenose dolphin (*Tursiops truncatus*, Montagu 1821)

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Abstract

Odontocetes primarily rely on fish, cephalopods, and crustaceans as their main source of nutrition. In the digestive system, their polygastric complex exhibits similarities to that of their closest terrestrial relatives such as cows, sheep, and giraffes, while the entero-colic tract shares similarities with terrestrial carnivores. The morphology, caliber, and structure of the odontocete intestine are relatively constant, and, since there is no caecum, a distinction between the small and large intestine and their respective subdivisions is difficult. To address this issue, we used the intestinal vascularization pattern, specifically the course and branching of the celiac artery (CA) and the cranial and caudal mesenteric arteries (CrMA and CdMA). A series of pictures and dissections of 10 bottlenose dolphins (*Tursiops truncatus*) were analyzed. Additionally, we performed a cast by injecting colored polyurethane foam in both arteries and veins to measure the caliber of the arteries and clarify their monopodial or dichotomous branching. Our results showed the presence of multiple duodenal arteries (DAs) detaching from the CA. The CrMA gave origin to multiple jejunal arteries, an ileocolic artery (ICA), and, in six cases, a CdMA. In four specimens, the CdMA directly originated from the abdominal aorta. The ICA gave rise to the mesenteric ileal branches (MIB) and mesenteric anti-ileal branches and the right colic arteries (RCA) and the middle colic arteries. From the CdMA originated the left colic and cranial rectal arteries (LCA and CrRA). The measurements revealed a mixed monopodial and dichotomous branching scheme. The analysis of the arteries and their branching gave us an instrument, based on comparative anatomy, to distinguish between the different intestinal compartments. We used the midpoint of anastomoses between MIB and RCA to indicate the border between the small and the large intestine, and the midpoint of anastomoses between LCA and CrRA, to tell the colon from the rectum. This pattern suggested an elongation of the duodenum and a shortening of the colic tract that is still present in this species. These findings might be related to the crucial need to possess a long duodenal tract to digest prey ingested whole without chewing. A short aboral part is also functional to avoid gas-producing colic fermentation. The rare origin of the CdMA on the CrMA might instead be a consequence of the cranial

thrust of the abdominopelvic organs related to the loss of the pelvic girdle that occurred during the evolution of cetaceans.

1 | INTRODUCTION

The macroscopic subdivision of the different intestinal tracts in mammals is based on anatomical and topographical landmarks, that is, the short duodenum is characterized by its topographical relationship with the pancreas; the duodeno-jejunal flexure is marked only by an abrupt lengthening of the mesentery (that indicates the start of the mesenterial intestine in man); the terminal part of the ileum is well distinguished from the jejunum only by the presence of the ileocecal fold; the different tracts of the large intestine are broadly defined by the conformation of the viscera and their topography. However, the said landmarks and anatomical differences may not be obvious and therefore easy to identify in all mammals (International Committee on Veterinary Gross Anatomical Nomenclature, 2017). A rational comparison of the digestive tract in different species could be based on the identification of the arterial supply of the respective parts. The major divisions of the celiac, cranial (= superior) mesenteric, and caudal (= inferior) mesenteric arteries have a well-defined distribution area, identified also by their nomenclature (International Committee on Veterinary Gross Anatomical Nomenclature, 2017; FIPAT, 2019; see also below).

Odontocetes are marine mammals whose diet is mostly based on fish but also includes cephalopods and crustaceans (Trites & Spitz, 2018). Their stomach complex shares some morphological characteristics with that of the closely related ruminants, even if their diets are completely different. The number of stomachs varies greatly among toothed whales, and—as a general rule—at least the first gastric chamber is a muscular stomach that acts mechanically (Cozzi et al., 2017; Yamasaki et al., 1974). On the other hand, the post-gastric parts of their intestine are similar to those of carnivores, possibly because of their animal protein-based diet. The intestine of toothed whales is a long and relatively uniform tube in which the caecum is missing, except in *Platanista gangetica* (Takahashi & Yamasaki, 1972). As a consequence, a macroscopic division between small and large intestine results is difficult or impossible to make (Yablokov et al., 1972).

Figure 1 schematically represents the intestine of a dog (a well-known representative of carnivores) and the human (the species whose anatomy is most studied). The blood supply to the postdiaphragmatic digestive tract is similar in the two examples; the only difference is that the human middle and right colic arteries (MCA and RCA) originate from the superior mesenteric artery, while in the dog they derive from the ileocolic artery (ICA). The names "cranial mesenteric artery" (CrMA), "caudal mesenteric artery" (CdMA), "cranial pancreaticoduodenal artery" (CrPDA) and "caudal pancreaticoduodenal artery" (CdPDA) conform to the *Nomina*

Anatomica Veterinaria (International Committee on Veterinary Gross Anatomical Nomenclature, 2017) and correspond, respectively, to the human superior mesenteric artery, inferior mesenteric artery, superior pancreaticoduodenal artery, and inferior pancreaticoduodenal artery (FIPAT, 2019).

In the dog, the celiac artery (CA), CdMA, and CrMA all derive directly from the abdominal aorta (AA) (König & Leibich, 2020; Nickel et al., 1992). The duodenum is supplied cranially by the CrPDA, originating from the CA, and by the CdPDA, from the CrMA. After the CdPDA, the CrPDA splits into multiple jejunal arteries (JAs) supplying all of the jejunum on one side, and the ICA on the other side. The ICA then detaches two MCA that vascularize the transverse colon, and one RCA, which supplies the distal part of the ascending colon. Subsequently, the ICA divides into the colic branch (CB), mesenteric ileal branch (MIB), and cecal artery. The CB supplies the first half of the ascending colon before anastomosing with the RCA. The MIB runs in the mesentery to supply the ileum and then anastomoses with the last jejunal artery. The caecal artery is the termination of ICA and continues cranially as the anti-mesenteric ileal branch (AMIB). The third and last major intestinal vessel, the CdMA, detaches the left colic artery (LCA) which supplies the descending colon, and the cranial rectal artery (CrRA) which supplies the rectum. To summarize, in both carnivores and humans, the ascending colon is supplied by branches of the CrMA, the descending colon by branches of the CdMA, and the transverse colon by both (although prevalently by CrMA).

In toothed whales, the duodenum is broadly recognizable by the presence of the duodenal ampulla and the outlet of hepatic and pancreatic ducts. The subsequent divisions between duodenum, jejunum, and ileum are very difficult (if not impossible) to tell apart either macroscopically or histologically (Cozzi et al., 2017; Huggenberger et al., 2019; Yablokov et al., 1972). The same applies to the ascending, transverse, and descending colon and most of the rectum, as their caliber and appearance remain uniform (Cozzi et al., 2017). To date, there are no in-depth studies on the intestinal vascularization of toothed whales. Only Slijper (1936) and Melnikov (1997) focused on the CrMA and CdMA, but they neither described their ramifications nor the subsequent intestine subdivision. On the other hand, Yamasaki et al. (1975) were able to identify in La Plata dolphins (*Pontoporia blainvillei*) the various parts of the postgastric tract. In these animals, as in other odontocetes, the subdivision between the jejunum and ileum is difficult. At the same time, the ileo-colic junction is easier to recognize due to the inner presence of longitudinal folds in the ileum, the external difference in thickness between the ileum and the colon, and the presence of the vasa recta. The colon

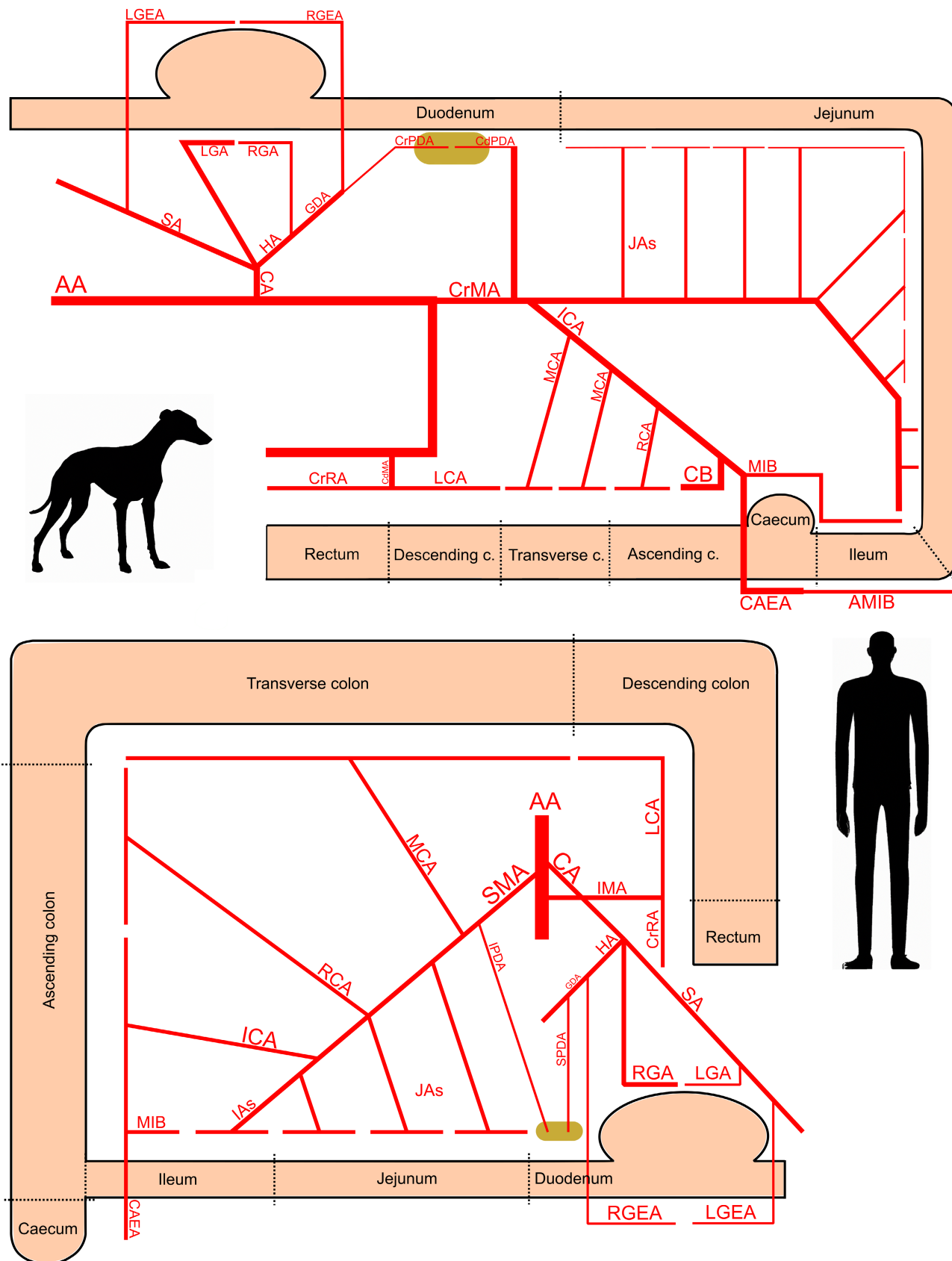**FIGURE 1** Scheme of the arteries of the digestive tract of the dog (as representative of terrestrial carnivores) and man. The oval brown shape represents the pancreas. AMD, superior mesenteric artery; IMA, inferior mesenteric artery; IPDA, inferior pancreaticoduodenal artery; SPDA, superior pancreaticoduodenal artery (International Committee on Veterinary Gross Anatomical Nomenclature (I.C.V.G.A.N.), 2017; FIPAT, 2019).

is further divided only into an ascending and a descending part. This latter is also barely distinguishable from the rectum except by a shortening of the mesentery and the presence of internal longitudinal folds in the rectum (Yamasaki et al., 1975).

The present study examines the branching characteristics of the gut arteries of the bottlenose dolphin (*Tursiops truncatus*, Montagu 1821) and assesses the potential presence of monopodial and dichotomous branching vessels, which may have crucial implications for the efficiency and adaptability of the circulatory system. Monopodial and dichotomous branching are general biological terms that describe different patterns of growth or division in various organisms. Monopodial branching involves a main structure/trunk continuing to detach subordinate branches, while dichotomous branching involves a division into two equal branches. An understanding of these patterns is important in anatomy as it helps to clarify organ function based on blood distribution (Gordon et al., 2007; Labode et al., 2022).

Based on dissections, photographic database, and vascular injection of colored polyurethane foam in a dead specimen, here we describe the distribution of the vessels supplying the gut of the bottlenose dolphin. The analysis focused on the arterial vasculature, based on which we propose a tentative subdivision of the postgastric tracts of the bottlenose dolphin based on objective data. The description of the venous system that we report in the present article derives from the polyurethane cast.

2 | MATERIALS AND METHODS

2.1 | Specimens

A total of 10 bottlenose dolphins were used for the present study. The specimens were delivered to the Department of Comparative Biomedicine and Food Science (BCA) of the University of Padua (Italy) for *postmortem* necropsy and their tissues were then sampled for the *Mediterranean marine mammal tissue bank* (MMMTB; http://www.marinemammals.eu). The MMMTB of the Department of Comparative Biomedicine and Food Science (BCA) of the University of Padua is a biological tissue bank that hosts several 100 marine mammal specimens of different species. The MMMTB is a CITES-recognized (IT020) research center recognized by the Italian Ministry of the Environment. The MMMTB database also contains macroscopic and microscopic photographs of most dissections performed since the bank was established in 2002. Of these specimens, 5 were archival photographs of previous dissections, 4 anatomical dissections carried out for the purpose of the present study, and 1 to produce an anatomical cast of gastrointestinal vessels.

2.2 | Anatomical dissections

The gastrointestinal block was carefully dissected and removed from four bottlenose dolphins during diagnostic necropsies. Through these procedures, the AA and its branches in the craniodorsal part of the abdominal cavity were identified immediately after the aortic hiatus. Subsequently, the AA and the intestinal mesentery were followed in their caudal course to verify the presence of a CdMA detaching from the AA. Table 1 summarizes the information available for each specimen.

2.3 | Analyses of the photographic database

We searched our database for reliable photographic documentation of the intestine and relative blood supply. We identified five individuals (see Table 1) whose mesenteric and intestinal vascularization was captured photographically, and for which the images yielded data useful for the present study.

2.4 | Vascular cast

The vascular cast was obtained following the procedure described by De Sordi et al. (2014). Shortly, the stomachs and all the intestines until the anal opening were isolated, including the mesentery, the abdominal tract of the AA (Figure 2a), the spleen, the pancreas, and the venous system. The viscera were then positioned on a net, to facilitate transport in the following steps, with the intestinal loops in a single plane. Subsequently, all vessels were washed and rinsed with tap water using 60 mL syringes connected to plastic tubes inserted into the CA, CrMA, and portal vein (PV) and fixed with forceps. The process went on until all blood disappeared from the vessels.

To avoid excessive expansion of the veins, due to their elastic walls, and the compression of smaller terminal arteries, the cast of the arteries was made first. The cast of the veins was performed 2 h afterward, to allow for solidification of the polyurethane (see below) injected into the arterial system (Figure 2b). We injected also the arteries of the gastric chambers, but the blood supply of the stomach complex could not be described properly because of the changes induced on the viscera by postmortem diagnostic procedures.

TABLE 1 Origin of the specimens.

ID	Sex	Age class	Origin	Used for
# 9	F	Adult	Marine park	P
# 144	M	Newborn	Marine park	P
# 203	M	Adult	Wild	P
# 319	M	Adult	Wild	P
# 344	M	Subadult	Wild	P
# 496	F	Adult	Wild	D
# 537	F	Adult	Wild	D, P, C
# 571	F	Adult	Wild	D
# 616	M	Adult	Wild	D, P
# 636	F	Adult	Wild	D, P

Abbreviations: C, cast; D, dissection; F, female; M, male; P, pictures.

The cast procedure was explained as follows: acetone was poured into a container and mixed with red or blue-colored nitro dyes (PebeoCeramic®—Pebeo, Gemenos Cedex, France) to better distinguish the arterial from the venous system. Polyurethane foam (diphenylmethane-4,4-diisocyanate; Soudafoam—Soudal N.V., Turnhout, Belgium) was then added slowly while stirring until a homogeneous semi-liquid compound was obtained. A 4 g to 1 mL ratio was kept, as per the protocol used by De Sordi et al. (2014). The compound was then injected by means of a 60 mL syringe and the pressure was maintained until the most distal arterioles were colored.

The sample was left to dry in refrigerated storage at 4°C for 24 h, then immersed in a 10% NaOH solution for 3 weeks in a designated container, until full corrosion of the organic matter (Figure 2c). Subsequently, the sample was gently washed and allowed to dry for several days before analysis, counting, and diameter measurements.

Arteries and their diameters were counted at their origin with a 0.1 mm precision caliper and at their first, second, and third divisions, when possible, as the overlapping between arteries and veins made the counting of some hidden vessels difficult. Diameter calculations were carried out to estimate the monopodial or dichotomous branching of the intestinal vascularization.

3 | RESULTS

A series of pictures and the cast allowed us to study the vascularization of the gastrointestinal tract. The cast revealed a well-defined net of arteries and arterioles. However, distal veins and small arterioles were incompletely filled possibly due to the presence of venous valves or blood clots (see also below).

3.1 | Arterial system

In all analyzed samples, the arterial system of the abdominopelvic digestive tract was composed of a CA, a CrMA, and a CdMA. The CrMA detached from the AA. The CdMA, on the other hand, originated either from the CrMA (Figure 3a) or eventually directly from the AA at the level of the caudal mesenteric lymph nodes (CdML) (Figure 3b). The cast revealed a CA detaching (*i*) a splenic artery

FIGURE 2 Casting procedure of the gastrointestinal tract. (a) Arteries of the gastrointestinal tracts, (b) cast preparation, (c) cast after the corrosion process and before the final wash. RA, renal artery.
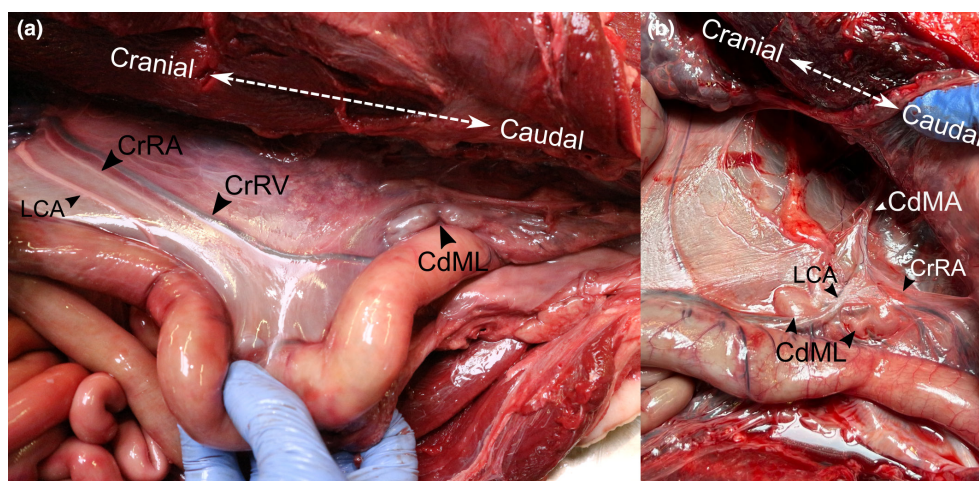

FIGURE 3 Vascularization of the caudal part of the intestine. (a) Absence of a CdMA detaching from AA at the level of the CdML, (b) single case where the CdMA was detaching from the AA with its division in LCA and CrRA. AA, abdominal aorta; CdMA, caudal mesenteric artery; CdML, caudal mesenteric lymph nodes; CrRA, cranial rectal artery; LCA, left colic artery.
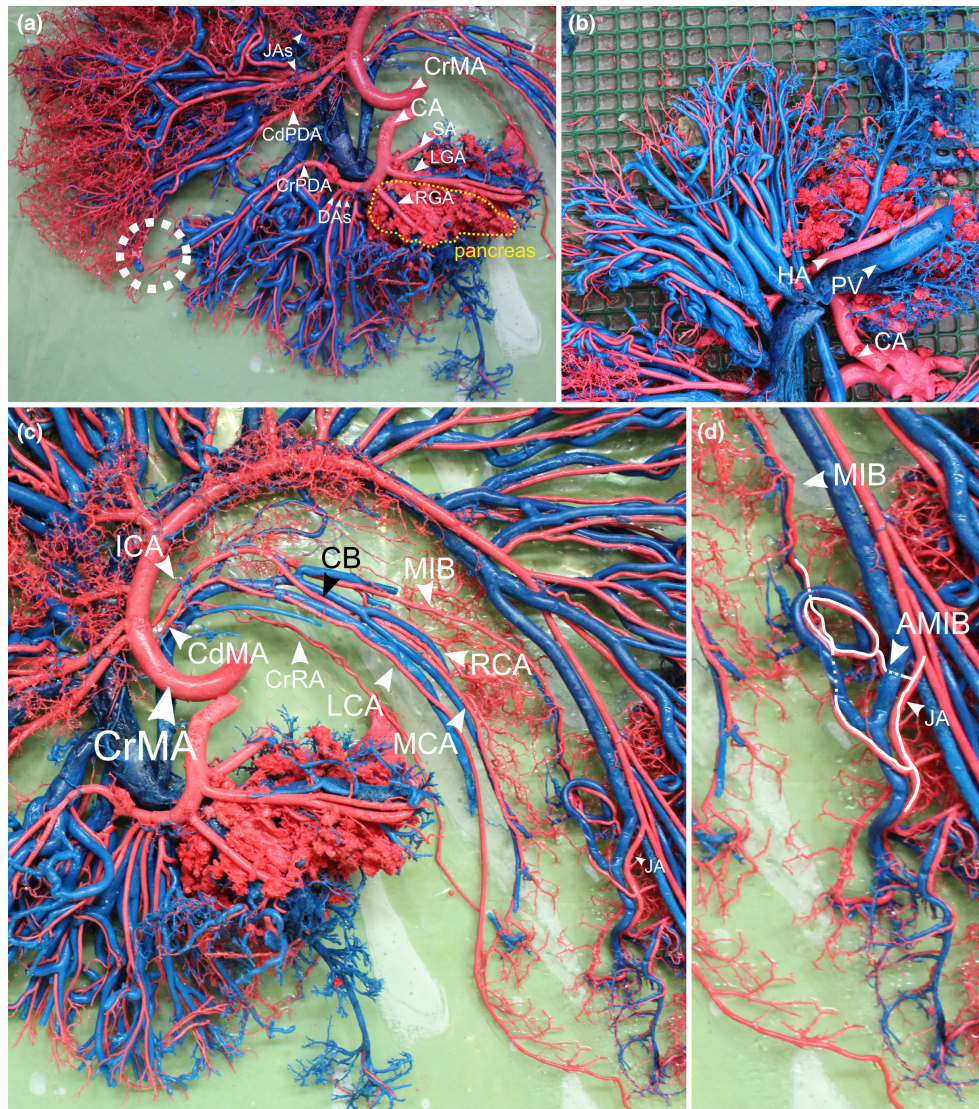
FIGURE 4 Arterial system. (a) First part of the arterial vasculature focusing on the CA. The dotted circle marks the anastomoses between the CrPDA and CdPDA. (b) Other aspect of the cast focusing the course of the HA. (c) Arteries originating from the CrMA. (d) Detail of the loop and anastomoses (white line) of the MIB and AMIB with the last JA. AMIB, anti-mesenteric ileal branch; CA, celiac artery; CrMA, cranial mesenteric artery; CdPDA, caudal pancreaticoduodenal artery; CrPDA, cranial pancreaticoduodenal artery; HA, hepatic artery; JA, jejunal arterie; MIB, mesenteric ileal branch.

(SA) reaching the spleen; (*ii*) a left gastric artery (LGA) and right gastric artery (RGA) going to the stomach chambers and the pancreas (Figure 4a); and (*iii*) a hepatic artery (HA) running alongside the PV (Figure 4b). The cast showed that after the RGA, the CA detached five duodenal arteries (DAs) and then terminated into the CrPDA. The latter anastomosed with the CdPDA after detaching from the CrMA (Figure 4a). Several JAs originated from the intestinal side of the CrM after the CdPDA (Figure 4a). The CdMA and then the ICA branched out roughly at the same level of CrMA but on the opposite (parietal) side. The CdMA detached the CrRA after separating from the CrMA and continued as the LCA (Figures 3a and 4c). In the cast, the ICA detached an MIB which anastomosed with the last JA. There a small artery, presumably the AMIB, was also found joining the MIB and the last JA (Figure 4d). The ICA also gave origin to a CB, which branched right away into RCA and MCA (Figure 4c).

3.2 | Venous system

The veins were almost all satellites of the arteries. In the cast, we identified a PV that collected blood returning from the cranial mesenteric vein (CrMV) and the splenic vein (SV). It was also possible to detail and better identify the veins forming the CrMV. Multiple jejunal veins, together with the caudal and cranial pancreaticoduodenal veins, the duodenal veins, and the right gastric vein, joined to constitute the CrMV (Figure 5). The SV, on the other hand, collected blood from the left gastric vein (LGV) (Figure 5a,b). The cast also revealed that the right and middle colic veins merged to form the CB, later joined by the ileal vein. The latter and the CB formed the short ileocolic vein, which later joined the left colic vein (LCV). Together with the cranial rectal vein, they contributed to forming the caudal mesenteric vein (Figure 5c,d).
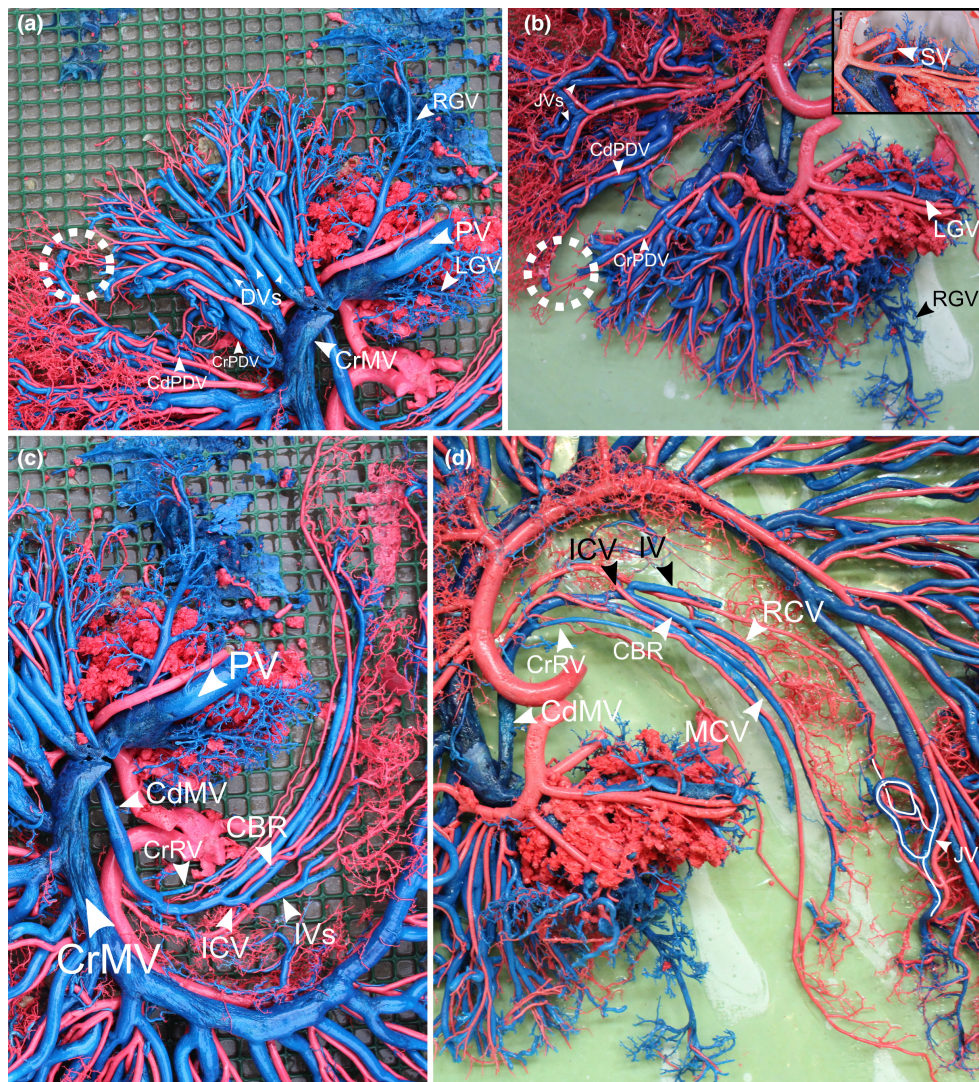
FIGURE 5 Venous system. (a) First part of the veins which joined together to become PV. (b) Other aspect of the cast to better identify some other veins. In both (a) and (b), the dotted circle indicated incomplete anastomoses between the CrPDV and CdPDV. (b inset) Particular of the LGV joining the SV. (c) Second part of the veins collects residual blood to become PV. (d) Other aspect of the cast to show the caudal veins. The white line follows the loop and the anastomoses of the IVs and AMIB (venous part) with the last JV. AMIB, anti-mesenteric ileal branch; CdPDA, caudal pancreaticoduodenal artery; CrPDV, cranial pancreaticoduodenal vein; IV, ileal vein; JV, jejunal vein; LGV, left gastric vein; SV, splenic vein.

Unfortunately, the presence of valves and some blood clots prevented a detailed casting of the finer veins, and as a consequence a precise comparison with the corresponding arterial ramifications was impossible.

A general summarizing scheme of the dolphin gastrointestinal vascularization is shown in Figure 6. Diameter calculations are shown in Table 2.

4 | DISCUSSION

The present work reports the vascularization of the gastrointestinal tract of the bottlenose dolphin through dissections, picture analysis of nine specimens, and a polyurethane foam cast. Our results

confirmed that a macroscopic subdivision of the intestine of this species is difficult due to the lack of morphological clues and the absence of most of the topographical landmarks used in other mammals. Unlike in human, a subdivision of the abdominal cavity into a supramesocolic and an inframesocolic space, based on the transverse mesocolon (Blackburn & Stanton, 2014; Solass et al., 2016) is impossible. However, the branching, distribution patterns, and relative caliber of the arteries allowed the identification of the key vessels and thus established a basis for comparison.

The CA gave rise to multiple vessels which, listed from their origin were (a) the HA, which ran close to the PV, and supplied the liver; (b) the LGA and (c) the RGA both of which supplied the stomachs; and (d) the SA which supplied the spleen. The CA then detached multiple DAs that reached the duodenum and terminated into the CrPDA.

FIGURE 6 General scheme of the vascularization of the gastrointestinal tract of the bottlenose dolphin. Dotted lines indicate the possible presence of a CdMA detached directly from the AA, with its division in LCA and CrRA. The oval brown shape represents the pancreas. AA, abdominal aorta; CdMA, caudal mesenteric artery; CrRA, cranial rectal artery; LCA, left colic artery.

We did not identify any left or right gastroepiploic artery. It is possible that the RGA supplied the pancreas, based on its respective position close to the pancreas and distant from the so-called CrPDA. The latter name was kept owing to its anastomoses with the CdPDA, which was the first artery detaching from the CrMA (Figure 4; TA, NAV; International Committee on Veterinary Gross Anatomical Nomenclature, 2017). The anastomosis between the cranial and caudal pancreaticoduodenal arteries is topographically related to the caudal duodenal flexure in terrestrial mammals, in which the end of the duodenum is defined by the anastomosis between the CdPDA and the first JA (König & Leibich, 2020; Nickel et al., 1992). Applying the same concept to the bottlenose dolphin, the duodenum would receive more arteries than its terrestrial relatives. Our results indicate that both cranial and caudal pancreaticoduodenal arteries have lost their role functional to supply the pancreas and that the latter organ could instead receive its blood from either the RGA and/or the LGA. This is probably because the right lobe of the pancreas of the bottlenose dolphin is more cranial than in carnivores and does not extend along the descending part of the duodenum (Figure 4a, for reference, see Cozzi et al., 2017).

One of the roles of the duodenum is to buffer the acidity of the gastric contents and regulate the transition of the ingesta from the stomach to the small intestine. The pancreatic and hepatic secretions contribute to the digestion of carbohydrates, lipids, and proteins (Reece et al., 2015). The gut of carnivores is adapted to a very protein-rich diet with absorption-ready complex molecules. Therefore, the intestine of carnivores is shorter than that of omnivores, and much shorter and simpler than that of herbivores, because these latter need to ferment simple sugars from plants through the microbiota, generally (Duque-Correa et al., 2021; Karasov et al., 2011; Slijper, 1979). Toothed whales do not chew their prey but swallow them whole. One key difference in the digestive process between terrestrial carnivores and toothed whales is the presence, in the latter group, of at least one muscular forestomach that helps mechanically mince the food before forwarding it to the subsequent gastric chambers and the duodenal ampulla (Cozzi et al., 2017). The relatively longer duodenal tract of the bottlenose dolphin might be necessary to increase postgastric absorption, which would require a consistent and adequate blood supply. This may explain the presence of several DAs and veins.

TABLE 2 Diameter measurements.

Name of the principal artery	Diameter (mm)	First order branching diameters (mm)	Second order branching diameters (mm)
CA	8	–	–
LCA	5.5	–	–
RCA	4.92	(1) 3.04 (2) 2.94	– –
HA	5.34	–	–
SA	4.24	3.11 –	– –
DAs	2.68 ($\pm$0.77 SD of 8 vessels)	(1) 2.138 ($\pm$0.55 SD of 5 vessels) (2) 2.19 ($\pm$0.60 SD of 5 vessels)	(1a) 1.99 ($\pm$0.33 SD of 3 vessels) (1b) 1.77 ($\pm$0.2 SD of 3 vessels) (2a) 2.43 ($\pm$0.61 SD of 3 vessels) (2b) 2.35 ($\pm$0.49 SD of 3 vessels)
CrPDA	2.14 (end of CA)	(1) 1.98 (2) 1.85	– (2a) 1.59 (2b) 1.44
CrMA	11.10	–	2.75 (last JA)
CdPDA	4.34	(1) 3.93 (2) 4.00	(1a) 2.59 (1b) 2.56 –
JAs	4.42 ($\pm$1.12 SD of 14 vessels)	(1) 3.71 ($\pm$0.92 SD of 8 vessels) (2) 3.04 ($\pm$0.84 SD of 8 vessels)	(1a) 2.55 ($\pm$0.67 SD of 8 vessels) (1b) 2.58 ($\pm$0.34 SD of 8 vessels) (2a) 2.74 ($\pm$0.23 SD of 6 vessels) (2b) 2.66 ($\pm$0.37 SD of 6 vessels)
CdMA	2.04	(1) LCA=2.04 (2) CrRA=1.26	– –
ICA	3.27	(1) MIB=2.54 (2) CB=2.45	(1a) AMIB=2.11 (1b) MIB=2.27 (2a) RCA=2.09 (2b) MCA=1.75

Note: Principal vessels detached from the AA are labeled with bold characters. The primary and secondary branches of CdMA are indicated as LCA and CrRA. In case of multiple arteries supplying the same tract (like the duodenum or jejunum), we reported the mean value derived from the measurement of all vessels involved ($\pm$SD).

Abbreviations: AA, abdominal aorta; AMIB, anti-mesenteric ileal branch; CA, celiac artery; CdMA, caudal mesenteric artery; CdPDA, caudal pancreaticoduodenal artery; CrMA, cranial mesenteric artery; CrRA, cranial rectal artery; CrPDA, cranial pancreaticoduodenal artery; DAs, duodenal arteries; HA, hepatic artery; ICA, ileocolic artery; JAs, jejunal arteries; LCA, left colic artery; MCA, middle colic arteries; MIB, mesenteric ileal branch; RCA, right colic arteries; SA, splenic artery.

In the cast, the CdPDA and multiple JAA arose from one side of the CrMA, while the CdMA and the ICA were derived from the opposite side. We identified the CdMA as such for two reasons: (*a*) it was possible to follow its course through all the intestinal mesenteries and (*b*) we did not find any artery, except in four cases (Figure 3b), in which an artery arose from the AA at the level of the CdML, as common in other mammals (König & Leibich, 2020; Nickel et al., 1992). The terminations of the JAs anastomosed within each other, as commonly observed in other mammals and man (Berta et al., 1979; Conley et al., 2010; Eisberg, 1924; Grandis et al., 2021; Noer, 1943; Smodlaka & Henry, 2014; Sommerová, 1980). We noted that the ICA soon divided into MIB and CB. The MIB first detached a small branch, corresponding to the AMIB, then terminated

anastomosing with the last JA and the RCA. We identified the CB splitting into the RCA and the MCA. The former anastomosed with MIB and MCA, the latter anastomosed with the RCA and LCA. We noted that, based on its diameter (Table 2), the LCA was the continuation of the CdMA after giving rise to the CrRA (Figure 4). In both the RCA, MCA and LCA we did not observe any *vasa recta*, as described in La Plata dolphin (Yamasaki et al., 1975).

An objective division of the intestine of the bottlenose dolphin in its different components was therefore tentatively possible based on its vascular supply.

In the cast, there were five DAs after the duodenal ampulla, plus a CdPDA that anastomosed with the first JA. Unfortunately, it was not possible to precisely count these arteries and confirm the

findings through careful examination of our photographic collection. The point of anastomosis between the CdPDA and the first JA may mark the beginning of the jejunum. Here we also note that further studies are needed to verify whether the jejunum of the bottlenose dolphin is characterized by the presence of longitudinal folds, as described in *Platanistidae* (Yamasaki et al., 1975). The inosculation between the last JA and the MIB could identify the transition from the jejunum to the ileum. Finally, the passage from small to large intestine may be identified halfway between the MIB (first branch of the ICA) and the RCA (from the CB, second branch of the ICA) (Figure 6), as in the ferret (Grandis et al., 2022). The origin of the CrRA and LCA may help determine the beginning of the rectum and the end of the colon by identifying either (*a*) the midpoint between the anastomosis of the CrRA with the LCA, if the CdMA originates from the CrMA or (*b*) the point of branching of the CdMA, if this artery derives directly from the AA (Figure 6). We were not able to identify a clear macroscopical ileo-colic junction as the appearance and the intestinal thickness were always similar. Further studies in very fresh animals may help to verify if the transition from the small to the large intestine, as hypothesized here based on vascular anastomosis, eventually corresponds to relatively subtle changes in mucosal structure, hitherto undescribed in the literature relative to the bottlenose dolphin.

The number and arrangement of the vessels supplying the different segments of the gut is a natural consequence of the greater length of the small intestine compared to the large intestine, a typical condition in obligate carnivores, as reported in the ringed seal (Smodlaka & Henry, 2014).

The assessment of the caliber of the different vessels of the cast (Table 2) suggested a mixed of dichotomous and monopodial branching, as happens in other systems such as the bronchial tree (Aharinejad et al., 1998; Gordon et al., 2007; Kruszewski & Whitesides, 1998; Wang & Kraman, 2004). In particular, the CA started with a diameter of 8 mm and ended with the CrPDA with a diameter of 2.14 mm. The CrMA, in turn, started with 11.1 mm and ended with the last JA of 2.75 mm. During their course both CA and CrMA gave origin to multiple arteries that presented dichotomous branching, except for the CdMA. This is in accordance with the concept that monopodial branching is efficient to transport blood to long distances (CA, CrMA, and CdMA), while dichotomous branching works better in supplying larger areas (Gordon et al., 2007).

The veins clearly accompanied the arteries thus allowing to name them precisely, as shown in Figure 5. The caudal mesenteric vein, after collecting blood from the ileocolic vein, the LCV and cranial rectal vein flew into the CrMV as happens in other mammals (König & Leibich, 2020; Nickel et al., 1992). However, the CrMV originated only from the right gastric vein, which is not the case in other terrestrial mammals as the latter usually flows into the SV together with the LGV. In our case the SV was the continuation of the LGV only. After receiving these latter arteries, the CrMV finally joined the SV to form the PV. For a simpler and more schematic visualization (see also Figure 6).

The CdMA of land mammals originates from the AA at the mid lumbar level (König & Leibich, 2020; Nickel et al., 1992). In our experimental series, the CdMA of bottlenose dolphins inconstantly originates directly from the AA (4 times out of 10), possibly due to the great changes in the posterior part of the body, including the reduction of the pelvic bones and utter disappearance of the hind limbs. As a consequence, the CdMA may have been reduced to a simple branch of the CrMA. There are few comparative observations in other cetacean species: according to some former descriptions, the CdMA derives directly from the AA in the harbor porpoise (Slijper, 1936) and the fin whale (Walmsley, 1938).

Previous studies on the intestine of cetaceans concluded that a shortening of the aboral part of the gut is associated with a softening of the feces (Simpson & Gardner, 1972). The main functions of the colon include carbohydrates fermentation, microbial digestion, and water and electrolytes reabsorption. In terrestrial mammals the intestinal motility decreases from the ileum onward, to support the digestive action of the colic mucosa (Reece et al., 2015). This is not the case in cetaceans, most probably because increased fermentation could produce gases that could in turn hinder swimming and diving behavior because of the intense abdominal pain due to the thick, inextensible abdominal walls. In the end, the reduced development of the vessels destined for the last part of the intestine found in this study seems to be a natural consequence of the shape and function of the large intestine in this species.

The present data may represent a starting point for future investigations with traditional methods (anatomical dissections, casts, etc.) or advanced technologies (Computed Tomography scans with radio-contrast agents), and thus contribute to a more advanced understanding of the organization and blood supply of the cetacean intestine.

CONFLICT OF INTEREST STATEMENT
The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT
The data that support the findings of this study are available from the corresponding author upon reasonable request.

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