

Short Note

Microscopic Structure of the Skin, Heart, and Digestive Canal of the Pygmy Beaked Whale (*Mesoplodon peruvianus*)

Lorena Magallón-Flores,¹ Germán Garrido-Fariña,²
Alejandra Buenrostro-Silva,³ and Juan Meraz^{4*}

¹Biología Marina, Universidad del Mar Puerto Ángel, Oaxaca, México

²Departamento de Ciencias Biológicas, FES-Cuautitlán,

Universidad Nacional Autónoma de México, Cuautitlán Izcalli, México

³Instituto de Industrias, Universidad del Mar Puerto Escondido, Oaxaca, México

⁴Instituto de Recursos, Universidad del Mar Puerto Ángel, Oaxaca, México

*E-mail: sula@angel.umar.mx

Little is known about the Ziphiidae family of odontocetes (Rommel et al., 2006). They are considered small to medium in size (4 to 12 m), and their diet consists mainly of fish and squid (MacLeod et al., 2003; Baird et al., 2006). A remarkable characteristic of this group is their ability to dive to great depths (> 800 m) for periods of more than 1 h (Baird et al., 2006; Rommel et al., 2006).

Mesoplodon is the most diverse genus in the family, containing 14 morphologically cryptic species (Ellis & Mead, 2017), which often makes it difficult for identification (Dalebout et al., 1998). Sightings at sea are rare due to a faint blow that is practically invisible (Jefferson et al., 1993); also, they are elusive and difficult to observe and identify in the field. Considering these facts, much of what is known about their biology and distribution comes from studying stranded specimens (Mead, 1989; Rommel et al., 2006).

The pygmy beaked whale (*Mesoplodon peruvianus*) is one of the most recently described cetacean species (Reyes et al., 1991; Ellis & Mead, 2017), and it is also the smallest known ziphiid. *M. peruvianus* is distributed in the eastern tropical Pacific (Pitman et al., 1987; Reyes et al., 1991; Pitman & Lynn, 2001) in warm, tropical areas from the Gulf of California (Urbán-Ramírez & Auriolles-Gamboa, 1992; MacLeod et al., 2006; Hamilton et al., 2009), the Sonoran coast (Gallo-Reynoso, unpub.), the Mexican central Pacific (García-Grajales et al., 2017; Ortega-Ortiz et al., 2021), and Central America (Rodríguez-Fonseca, 2001; Bachara et al., 2020), down to north-central Chile (Sanino et al., 2007). There is a sighting report from New Zealand (Baker & Van Helden, 1999), which could be simply treated as the isolated case of a wandering individual.

Most of the available morphological information on the species has been obtained mainly from strandings reported from the coast of Peru (Reyes et al., 1991); La Paz Bay, Mexico (Urbán-Ramírez & Auriolles-Gamboa, 1992); Chile (Sanino et al., 2007); and recently in Oaxaca and Colima, Mexico (García-Grajales et al., 2017; Ortega-Ortiz et al., 2021).

Histological studies on marine mammals are focused mainly on delphinids (Bruce-Allen & Geraci, 1985; Vuković et al., 2005; Clark et al., 2008), being scarce on ziphiids. Detailed descriptions of the anatomy and histology of delphinid glands has been made on the pituitary gland (Vuković et al., 2011), adrenal gland (Suzuki et al., 2002; Clark et al., 2008; Vuković et al., 2010), lymph nodes (Vuković et al., 2005), and thyroid glands of harbour porpoises (*Phocoena phocoena*; Schumacher et al., 1993). Analysis of comparative anatomy and histology of the tracheobronchial tree and pulmonary parenchyma of several species of marine mammals have found that dolphins have a tracheal bronchus for the right lung, with rigid tracheas in beaked whales (Moore et al., 2014). At the respiratory system level, studies have focused on species such as bottlenose dolphins (*Tursiops truncatus*; Wislocki, 1929; Fanning & Harrison, 1974; Boyd, 1975), northern bottlenose whales (*Hyperoodon ampullatus*; Gouddappel & Slijper, 1958), bowhead whales (*Balaena mysticetus*; Henk & Haldiman, 1990), beluga and sperm whales (*Delphinapterus leucas* and *Physeter macrocephalus*; Belanger, 1940; Wislocki & Belanger, 1940), and Cuvier's beaked whales (*Ziphius cavirostris*; Otero-Sabio et al., 2020). Histological studies have also identified the high regeneration capacity of skin lesions of *T. truncatus* (Bruce-Allen & Geraci,

1985). The objective of this work is to contribute to the knowledge regarding the microscopic structure of different organs and tissue of *M. peruvianus*, being the first work of this kind for this species.

A specimen of *M. peruvianus* was found stranded on Zicatela Beach (15° 51' 43" N, 97° 04' 18" W; Figure 1), Oaxaca, Mexico, on 2 March 2016, where it died immediately. It was transported to the Biological Collections laboratory of the Universidad del Mar (UMAR) Puerto Escondido where samples from several organs were collected for histological analysis and preserved in 10% formalin. Histological analysis was carried out at the Histology and Biology Laboratory of FES-Cuautitlán, Autonomous National University of Mexico (UNAM). Samples were washed with running water to eliminate excess formalin. Subsequently, cuts of 1 cm³ were made and placed in labeled histocassettes. The first step was the dehydration of the tissues in alcohol (ethanol) at increasing concentrations (70 to 80%, 92 to 98%, and 98 to 100%) for periods of 15 min, radiating inside a microwave oven at medium power for periods of 2 min followed by 13 min of rest.

Subsequently, the samples were infiltrated, placing them in a xylene-chloroform solution as a binding reagent for 12 h. Afterward, the histocassettes were submerged into baths of ripe liquid paraffin at a temperature of 54 to 55°C for an hour in each of the histokinette jars. The inclusion was

done with the help of a paraffin dispenser, placing the samples inside Leukard bars to be filled with paraffin. The resulting blocks were placed in water and then frozen. The cuts of the blocks were made in a microtome with thicknesses of 4 and 5 μ and subsequently deposited onto slides, with alcohol (20 to 40%) applied to remove folds. The slides were placed in a flotation bath with water at 40°C with 0.1% grenetine. With the help of a brush, the tissue in the flotation bath was recovered onto slides previously smeared with Mayer's albumin. The resulting slides were placed in a thermal plate at 45°C to completely spread the tissues and remove the remaining water.

For the present study, stains were performed using the following techniques: Hematoxylin-Eosin, Gomori's Trichomics, Schiff's Periodic Acid, Alcian Blue, Van Gieson's Trichromic, and Casson's Trichromic. They were observed under the microscope at 10 \times , 20 \times , and 40 \times , and photographs were taken. The images were processed with *Picasa 3* software.

In the skin, cylindrical cells are observed in a pseudostratified arrangement in the basal stratum, along with adipose connective tissue with smooth muscle fibers and lots of collagen fibers. In the hypodermis and basal membrane of the dermis, uninucleated adipose cells can be seen. In addition to abundant collagen fibers, structures with characteristics of

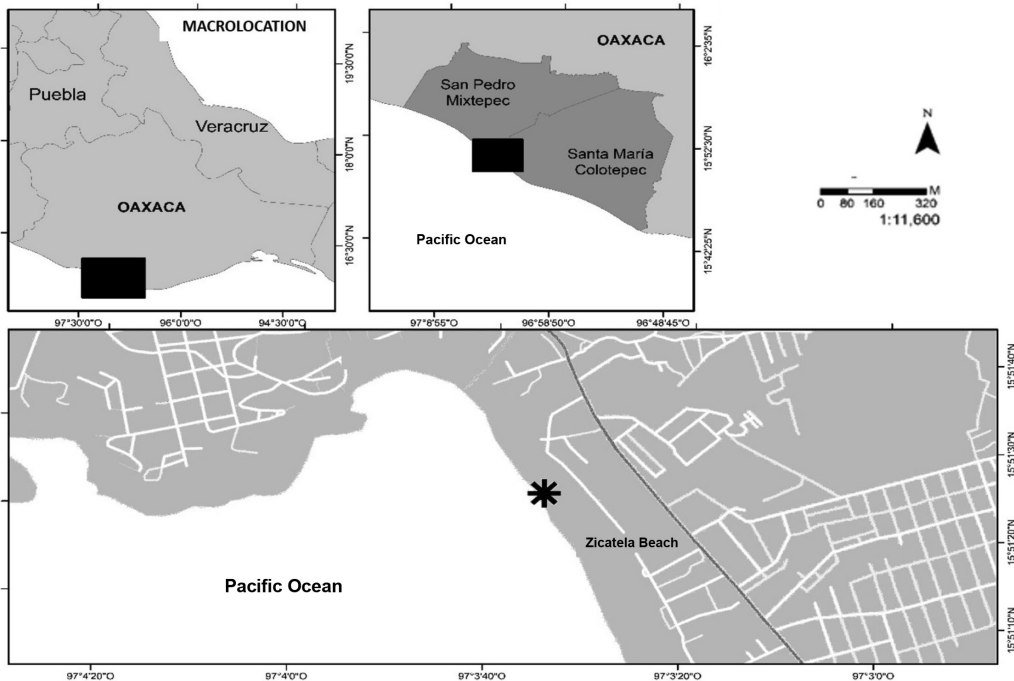


Figure 1. Location of Zicatela Beach at Puerto Escondido, Oaxaca, Mexico, where the stranded *Mesoplodon peruvianus* was found

nerve beams that pass through the organ in different directions can also be observed. This significantly highlights the density and length of the dermal papillae, reaching more than 50% of the length of the epidermis (Figure 2). A large number of vascular components are also seen (Figure 3).

The heart has epicardium, myocardium, and endocardium with general characteristics, distinguishing the central nuclei of the cardiomyocyte and intercalated disc. A large number of conductive cardiomyocytes, veins, venules, arteries, and arterioles are observed (Figure 4). Numerous arteries are noted to



Figure 2. A histological cut of *M. peruvianus* skin showing the epidermis, dermis, and tela subcutanea. Epithelium (Ep), adipose tissue (At), and sensory corpuscles (Sc) are indicated (staining with the Gomori's Trichomics technique).

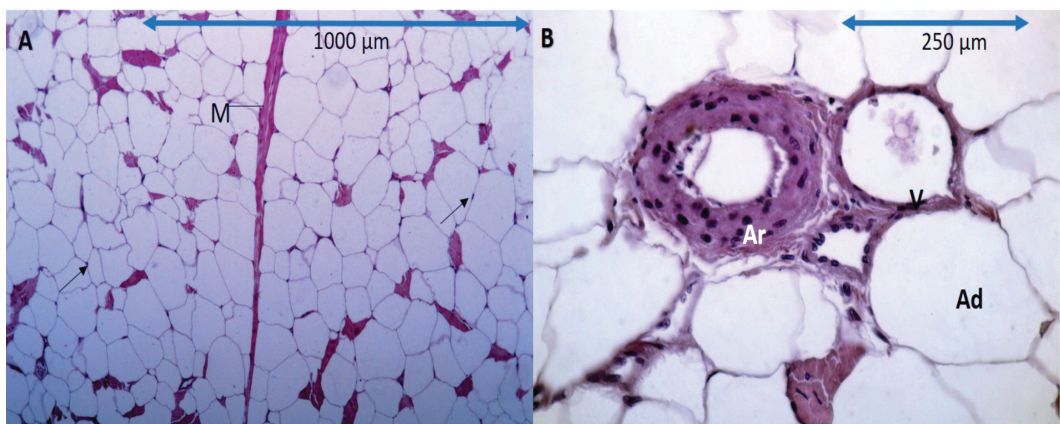


Figure 3. *M. peruvianus* fat cut: (A) adipocytes with a nucleus marked with an arrow and muscle (M); and (B) blood vessels showing artery (Ar), vein (V), and adipocytes (Ad) (staining with the Hematoxylin-Eosin technique).

be surrounded by a greater amount of connective tissue. Large blood vessels distinguishing the adventitious tunica in the arteries, as well as large tunica media and endothelial, are observed. A large amount of red blood cells are present in addition to a very apparent endothelium (Figure 5).

A multichambered stomach is characteristic of cetaceans (Huggenberger et al., 2019). The stomach of *M. peruvianus* has four compartments: (1) proximal mainstomach, (2) distal mainstomach, (3) proximal pyloric stomach, and (4) distal pyloric stomach (following Mead, 2007). All four chambers have the mucosa composed of crypts,

as well as a large number of blood vessels (sometimes very large) associated with the basal lamina. The proximal mainstomach has the largest amplitude of the epithelium and well-defined crypts. The submucosal layer is fed by a large number of blood vessels and smooth muscle fasciae. The layer of the subserosa has a large number of congested blood vessels (Figure 6a). The distal mainstomach epithelium shows large blood vessels associated with the epithelial tunica and the well-defined submucosal tunica (Figure 6b).

Conversely, on the proximal pyloric stomach, there are a larger number of epithelial glands,

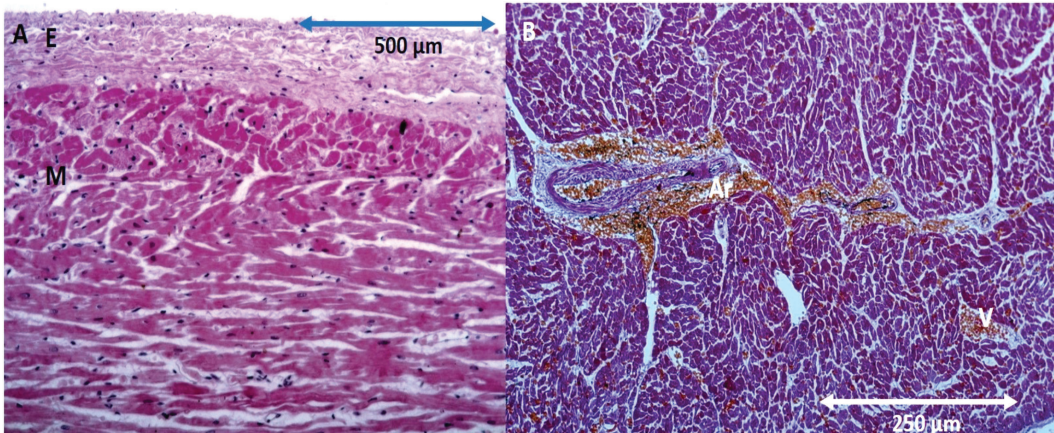


Figure 4. (A) Histological heart cut of *M. peruvianus* showing epicardium (E) and myocardium (M) (staining with the Hematoxylin-Eosin technique); and (B) striated heart muscle showing artery (Ar) and venule (V) (staining with the Gomori's Trichomics technique).

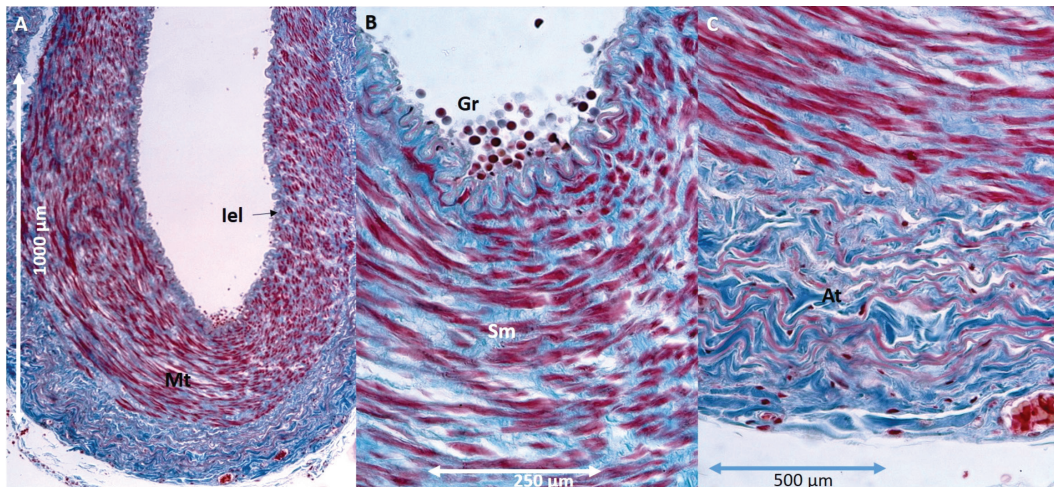


Figure 5. Cut of a blood vessel of *M. peruvianus*: (A) artery showing internal elastic lamina (Iel) and middle tunica (Mt); (B) red blood cells (Gr) and smooth muscle (Sm); and (C) detail of the adventitious tunica (At). All figures stained with the Gomori's Trichomics technique.

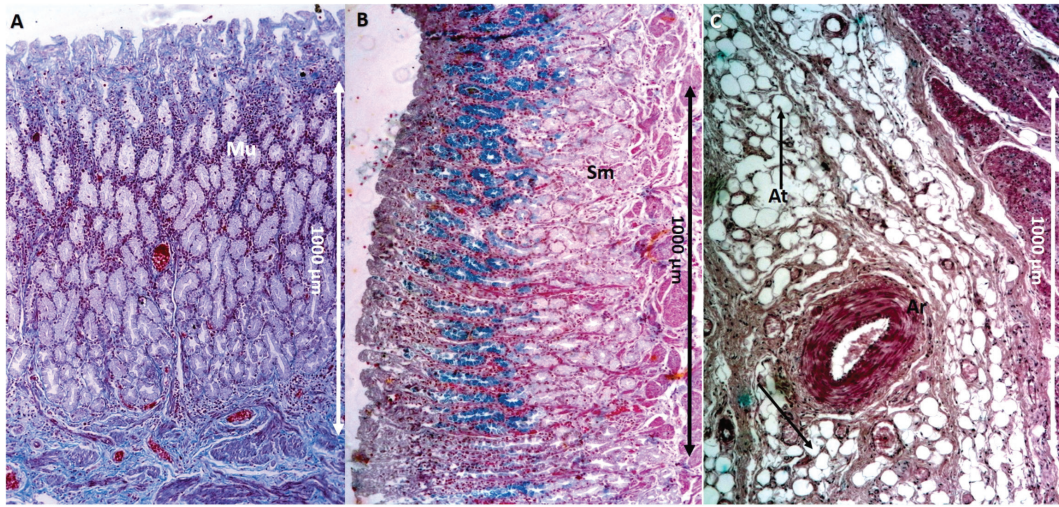


Figure 6. (A) Cut of the proximal pyloric stomach of *M. peruvianus* showing mucosa (Mu) (staining with the Gomori's Trichromics technique); (B) cut of the proximal mainstomach showing the smooth muscle (Sm) (staining with the Schiff's Periodic Acid technique); and (C) blood vessel, artery with red blood cells (Ar), and adipose tissue (At) (staining with the Hematoxylin-Eosin technique).

which are smaller compared to the first two chambers. A wide tunica mucosa can be seen in addition to the presence of adipose cells and a large number of blood vessels (Figure 6c). In the distal pyloric stomach, a wide, brush-edged epithelium can be distinguished. Paneth cells in the first third (attached to the basal lamina) are distributed along with the crypts, which are longer than the previous chambers. A large number of adipose cells are observed between the muscular cells of the organ and the serosa, with the presence of multiple blood vessels associated with the basal lamina.

Despite no evident differences in the caliber of the intestine, tissue samples were taken for the proximal and distal extremes. The proximal intestine shows a simple columnar pseudostratified epithelium with a large number of intercalated goblet exocrinocytes and a wide crypt (Figure 7). Very apparent large blood vessels are seen within the villi and in association with the epithelium. The duodenum with simple columnar pseudostratified epithelium with intercalated goblet exocrinocytes, along with villi larger than the proximal intestine, are observed. A wide tunica muscularis is seen, with a large number of blood vessels in the adipose tissue, associated with the serosa, which is different from that of other mammals (Figure 8). Extensions are observed in the epithelium into the light of the distal intestine. The tunica mucosa has more caliciform exocrinocytes than the proximal intestine, which appears to be the large intestine of a terrestrial mammal. A substantial amount of blood vessels are seen (Figure 9).

A large number of nerves and blood vessels were found in the studied organs, which may be associated with high energy needs for an organism living in extreme conditions, including the deep-sea areas where Ziphiidae are found (Baird et al., 2006). This relates to the efficient maintenance of vital conditions—not only at low temperatures and high barometric pressure, but also at a low respiration rate. When cetaceans dive to increasing depths, the temperature of the environment drops rapidly, blood pressure increases, and CO₂ levels increase due to apnea. The organization of the peripheral blood vessels contribute to the maintenance of body heat. This could explain the vascular structure found in all the organs analyzed in this study, with the presence of large blood vessels in large quantities and with a tunica muscularis more apparent than in other mammals, which are beneficial for withstanding internal and external pressure.

The complex and jagged interface between the dermis and epidermis is a characteristic of glabrous skin (Simpson & Gardner, 1972), which is evident in *M. peruvianus*. The numerous blood vessels and nerve endings found along the dermis can be related to the pelagic habits of the species. The remarkable length of the dermal papillae could be related to a greater efficiency in cell proliferation and skin surface replacement (Jones & Pfeiffer, 1994).

The adipose tissue of *M. peruvianus* presented abundant connective tissue and a large number of blood vessels, congested and of great size, which

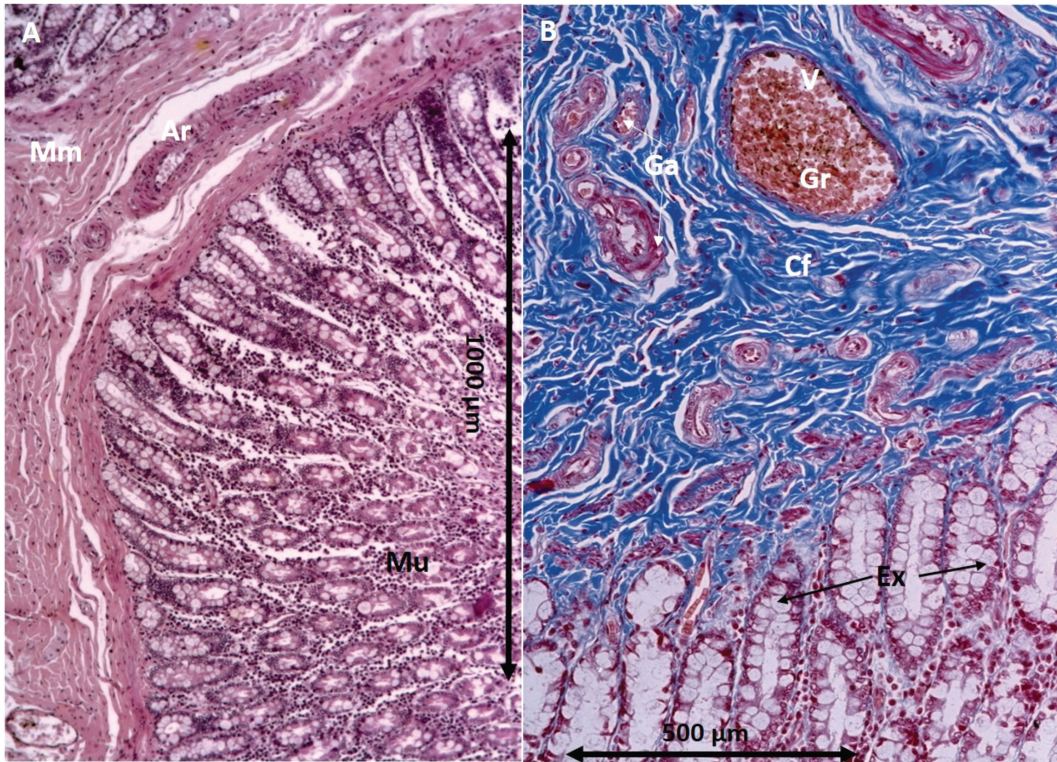


Figure 7. Cut of the proximal intestine of *M. peruvianus*: (A) musculature of mucosa (Mm), artery (Ar), and mucosa (Mu) (staining with the Hematoxylin-Eosine technique); and (B) vein (V) showing red blood cells (Gr), ganglia (Ga), collagen fibers (Cf), and goblet exocrinocytes (Ex) (staining with the Gomori's Trichomics technique).

may indicate a high capacity for thermoregulation. The presence of white adipose tissue (Figure 3) stands out, which serves mainly in the storage of energy in the form of triglycerides (Hashimoto et al., 2015). Ziphiids are the cetaceans with the highest concentration of wax esters, exceeding 80% in the fat layer (Koopman, 2018), while intramyocyte lipid droplets are observed at high densities in deep diving cetaceans (Sierra et al., 2015).

The heart tissue of *M. peruvianus* showed a large number of nerve cells and blood vessels, which would help the body maintain its functions during bradycardia (Noren et al., 2004) and long periods of apnea, which can exceed 60 min (Baird et al., 2006; Rommel et al., 2006). The lymph nodes had numerous arteries surrounded by a large amount of connective tissue, with the germination centers surrounded by their external crown.

Ziphiids can be considered polygastric animals, having four stomachs or a tetra-cameral stomach. The purpose of this anatomical structure is to compensate for the absence of mastication through grinding and compression in the first chamber before absorption takes place in the subsequent

compartments, where there is a difference between the mucous membranes from the various chambers (Cozzi et al., 2017). *Mesoplodon* genus presents two mainstomachs and two pyloric stomachs, with some variations in the compartments according to the species (Mead, 2007). For *M. peruvianus*, it was found that the four compartments of the stomach have the mucosa composed of crypts in addition to a large number of blood vessels, sometimes very large, associated with the basal lamina, indicating that digestion requires a large amount of energy.

Histological analysis of the proximal mainstomach of *M. peruvianus* shows well-defined crypts with large amounts of acidophilus granules, which coincides with the literature (Harrison et al., 1970). On the other hand, a large muscular layer was found as mentioned by Cozzi et al. (2017), accompanied by the submucosal tunica and the serosa, both fed by a large amount of blood vessels. The distal mainstomach is rounder and smaller than the proximal mainstomach, coated with glandular epithelium and with gastric juice production. By performing a histological analysis of the distal mainstomach, it was possible

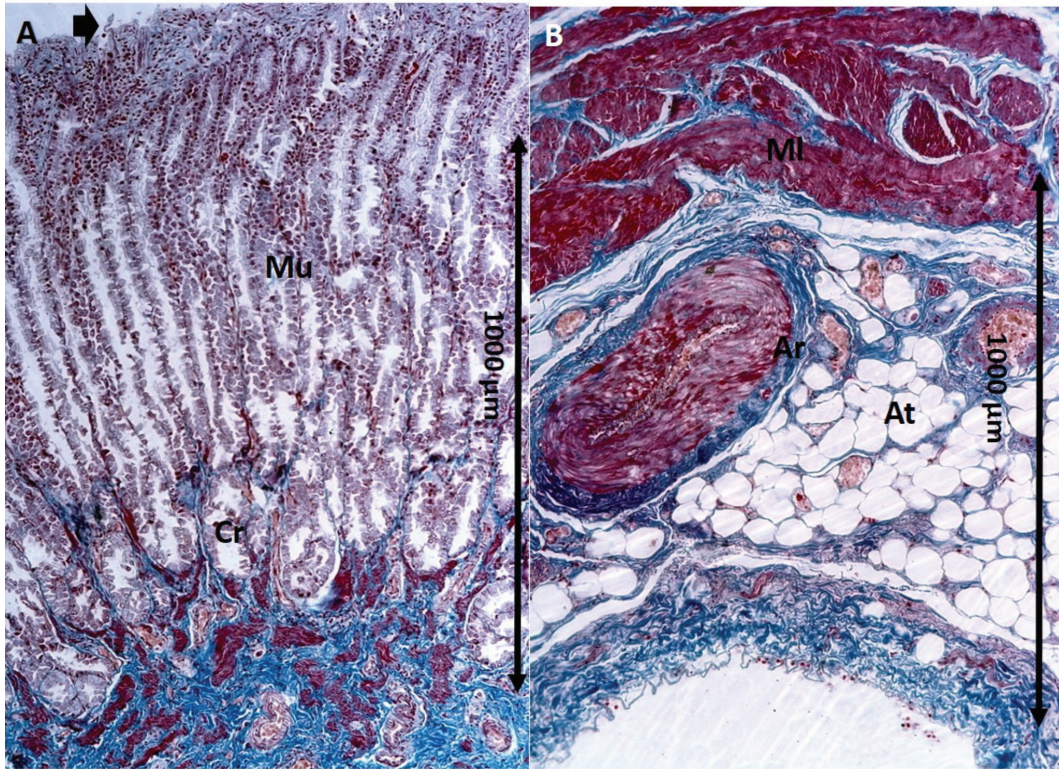


Figure 8. A histological cut of the duodenum of *M. peruvianus*: (A) mucosa (Mu) and crypts (Cr)—the arrow shows the villi; and (B) smooth muscle (MI), artery (Ar), and adipose tissue (At). Both (A) and (B) were stained with the Gomori's Trichomics technique.

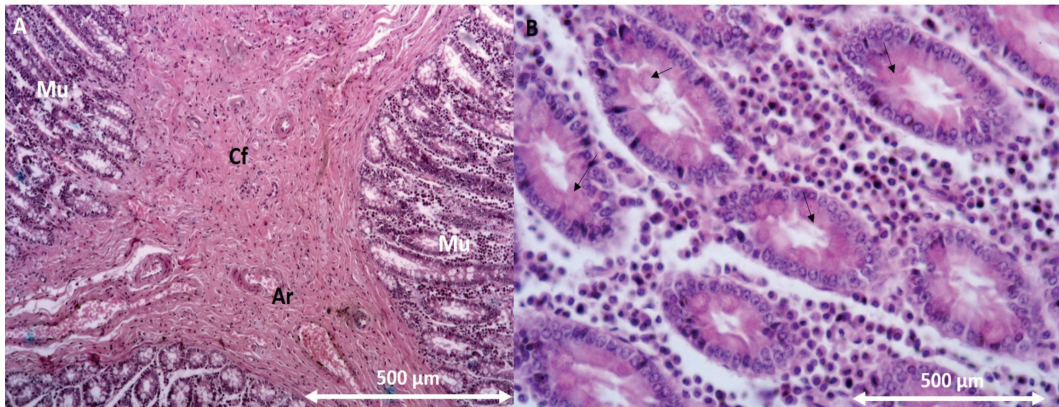


Figure 9. Cut of the distal intestine of *M. peruvianus*: (A) mucosa (Mu), arteries (Ar), and collagen fibers (Cf); and (B) detail showing the goblet exocrinocytes (black arrows). Both (A) and (B) were stained with the Hematoxylin-Eosine technique.

to distinguish a glandular epithelium with wide crypts (Cozzi et al., 2017).

The proximal pyloric stomach was not observed to be separated by a sphincter into the duodenal ampulla since this species has an additional

chamber before the ampulla. On the other hand, coinciding with Cozzi et al. (2017), the tunica mucosa is quite wide and, thus, its epithelium can be distinguished with numerous mucosal cells. The distal pyloric stomach demonstrated that the

stomach of *M. peruvianus* is similar to that possessed by ruminants. Compared with the previous chambers, the distal pyloric stomach shows a lot of adipose cells and obvious Paneth cells, and its main distinction is a well-differentiated brush edge.

Obvious Paneth cells were found in the glands of the proximal intestine (Lieberkun crypts; Harrison et al., 1970). The mucosa shows the typical coating found in terrestrial mammals, with absorbent cells with microvilli, goblet cells, and enterochromaffins (Cozzi et al., 2017). Exocrine glands and large crypts and villi with simple columnar pseudostratified epithelium are observed accompanied, as the duodenum, by intercalated goblet exocrinocytes.

Unlike the proximal intestine, the distal intestine has a large presence of muscle, and collagen fibers can be observed in the bulk, potentially supporting the voluntary and involuntary bowel movements associated with suction feeding (Pfeiffer, 1993). The tunica mucosa is found to have a large number of goblet exocrinocytes compared to the previous section (Simpson & Gardner, 1972), and an absence of villi (Simpson & Gardner, 1972; Russo et al., 2012). Similar to other deep diving cetaceans, *Mesoplodon* genus has a small stomach and intestine in relation to the total body mass due to the high metabolic cost of viscera as compared with shallow divers (Pabst et al., 2016).

Of the techniques used for the staining of tissues, those that exhibited the best results for showing the various histological components were the staining with Gomori's Trichomics technique and the staining with the Hematoxylin-Eosine technique.

It is important to mention that there is limited information on the histology of cetaceans, and practically none for ziphiids, making it difficult to construct a detailed comparison with other marine mammals. The descriptions reported herein, despite being derived from one single individual, represent the first approximation of its kind regarding *M. peruvianus*.

Acknowledgments

Appreciation to PROFEPA and UMAR authorities, Jesús García Grajales and Pablo Torres Hernández, for the comments and fieldwork. Some volunteers in Zicatela Beach helped in the recovery of the whale, while UMAR students and Valentina Islas assisted with laboratory work, and Carmen Alejo provided some ideas. Tonatiuh Magallón and Daniela Bernot helped with translation and revision of the English version. Many thanks to David Rosen and two anonymous reviewers for improving this short note.

Literature Cited

- Bachara, W., Ibarra Portillo, R., Martínez de Navas, E., & Pineda, L. (2020). Beaked whales strandings in El Salvador. *Latin American Journal of Aquatic Mammals*, 15(1), 41-44.
- Baird, R. W., Webster, D. L., McSweeney, D. J., Ligon, D. A., Schorr, G. S., & Barlow, J. (2006). Diving behaviour of Cuvier's (*Ziphius cavirostris*) and Blainville's (*Mesoplodon densirostris*) beaked whales in Hawai'i. *Canadian Journal of Zoology*, 84, 1120-1128. <https://cdnsiencepub.com>; <https://doi.org/10.1139/z06-095>
- Baker, A. N., & Van Helden, A. L. (1999). New records of beaked whales, genus *Mesoplodon*, from New Zealand (Cetacea: Ziphiidae). *Journal of the Royal Society of New Zealand*, 29(3), 235-244. <https://doi.org/10.1080/03014223.1999.9517594>
- Belanger, L. F. (1940). A study of the histological structure of the respiratory portion of the lungs of aquatic mammals. *American Journal of Anatomy*, 67(3), 437-461. <https://doi.org/10.1002/aja.1000670305>
- Boyd, R. B. (1975). A gross and microscopic study of the respiratory anatomy of the Antarctic Weddell seal, *Leptonychotes weddelli*. *Journal of Morphology*, 147(3), 309-336. <https://doi.org/10.1002/jmor.1051470306>
- Bruce-Allen, L. J., & Geraci, J. R. (1985). Wound healing in the bottlenose dolphin (*Tursiops truncatus*). *Canadian Journal of Fisheries and Aquatic Sciences*, 42(2), 216-228. <https://doi.org/10.1139/f85-029>
- Clark, L. S., Cowan, D. F., & Pfeiffer, D. C. (2008). A morphological and histological examination of the pantropical spotted dolphin (*Stenella attenuata*) and the spinner dolphin (*Stenella longirostris*) adrenal gland. *Anatomia Histologia Embryologia*, 37, 153-159. <https://doi.org/10.1111/j.1439-0264.2007.00821.x>
- Cozzi, B., Huggenberger, S., & Oelschläger, H. (2017). *Anatomy of dolphins: Insights into body structure and function*. Academic Press.
- Dalebout, M. L., Van Helden, A., Van Waerebeek, K., & Baker, C. S. (1998). Molecular genetic identification of southern hemisphere beaked whales (Cetacea: Ziphiidae). *Molecular Ecology*, 7(6), 687-694. <https://doi.org/10.1046/j.1365-294x.1998.00380.x>
- Ellis, R., & Mead, J. G. (2017). *Beaked whales: A complete guide to their biology and conservation*. Johns Hopkins University Press.
- Fanning, J. C., & Harrison, R. J. (1974). The structure of the trachea and lungs of the South Australian bottle-nosed dolphin. In R. J. Harrison (Ed.), *Functional anatomy of marine mammals* (pp. 231-252). Academic Press.
- García-Grajales, J., Buenostro-Silva, A., Rodríguez-Rafael, E., & Meraz, J. (2017). Biological observations and first stranding record of *Mesoplodon peruvianus* from the central Pacific coast of Oaxaca, Mexico. *Therya*, 82(2), 179-184. <https://doi.org/10.12933/therya-17-451>
- Goudappel, J., & Slijper, E. (1958). Microscopic structure of the lungs of the bottlenose whale. *Nature*, 182, 479. <https://doi.org/10.1038/182479a0>

- Hamilton, T. A., Redfern, J. V., Barlow, J., Balance, L., Gerrodette, T., Holt, R. S., Forney, K. A., & Taylor, B. L. (2009). *Atlas of cetacean sightings for the Southwest Fisheries Science Center Cetacean and Ecosystem Survey: 1986-2006* (NOAA Technical Memorandum NMFS 440). U.S. Department of Commerce, National Oceanic and Atmospheric Administration.
- Harrison, R. J., Johnson, F. R., & Young, B. A. (1970). Oesophagus and stomach of dolphins (*Tursiops Delphinus*, *Stenella*). *Journal of Zoology*, *160*(3), 377-390. <https://doi.org/10.1111/j.1469-7998.1970.tb03088.x>
- Hashimoto, O., Ohysuki, H., Kakizaki, T., Amou, K., Sato, R., Doi, S., Kobayashi, S., Matsuda, A., Sugiyama, M., Funaba, M., Matsuishi, T., Terasawa, F., Shindo, J., & Endo, H. (2015). Brown adipose tissue in cetacean blubber. *PLOS ONE*, *10*(2), e0116734. <https://doi.org/10.1371/journal.pone.0116734>
- Henk, W. G., & Haldiman, J. T. (1990). Microanatomy of the lung of the bowhead whale, *Balaena mysticetus*. *The Anatomical Record*, *226*(2), 187-197. <https://doi.org/10.1002/ar.1092260208>
- Huggenberger, S., Oelschläger, H., & Cozzi, B. (2019). *Atlas of the anatomy of dolphins and whales*. Academic Press.
- Jefferson, T. A., Leatherwood, S., & Webber, M. A. (1993). *Marine mammals of the world*. United Nations Food and Agriculture Organization (FAO).
- Jones, F. M., & Pfeiffer, C. J. (1994). Morphometric comparison of the epidermis in several cetacean species. *Aquatic Mammals*, *20*(1), 29-34.
- Koopman, H. N. (2018). Function and evolution of specialized endogenous lipids in toothed whales. *Journal of Experimental Biology*, *221*(Suppl. 1), jeb161471. <https://doi.org/10.1242/jeb.161471>
- MacLeod, C. D., Santos, M. B., & Pierce, G. J. (2003). Review of data on diets of beaked whales: Evidence of niche separation and geographic segregation. *Journal of the Marine Biological Association of the United Kingdom*, *83*(3), 651-665. <https://doi.org/10.1017/S0025315403007616h>
- MacLeod, C. D., Perrin, W. F., Pitman, R. L., Barlow, J., Balance, L., D'Amico, A., Gerrodette, T., Joyce, G., Mullin, K. D., Palka, D. L., & Waring, G. T. (2006). Known and inferred distributions of beaked whale species (Ziphiidae: Cetacea). *Journal of Cetacean Research and Management*, *7*(3), 271-286.
- Mead, J. G. (1989). Beaked whales of the genus *Mesoplodon*. In S. H. Ridgway & R. Harrison (Eds.), *Handbook of marine mammals* (pp. 349-430). Academic Press.
- Mead, J. G. (2007). Stomach anatomy and use in defining systemic relationships of the cetacean family Ziphiidae (beaked whales). *The Anatomical Record*, *290*(6), 581-595. <https://doi.org/10.1002/ar.20536>
- Moore, C., Moore, M., Trumble, S., Niemeyer, M., Lentell, B., McLellan, W., Costidos, A., & Fahlman, A. (2014). A comparative analysis of marine mammal tracheas. *The Journal of Experimental Biology*, *217*, 1154-1166. <https://doi.org/10.1242/jeb.093146>
- Noren, S. R., Cuccurullo, V., & Williams, T. M. (2004). The development of diving bradycardia in bottlenose dolphins (*Tursiops truncatus*). *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology*, *174*(2), 139-147. <https://doi.org/10.1007/s00360-003-0398-9>
- Ortega-Ortiz, C. D., Díaz-Torres, E. R., Llamas-González, M., Cuevas-Soltero, A. B., Martínez-Romero, A. G., Meza-Yáñez, R., Martínez-Sánchez, D., Olivos-Ortiz, A., Liñán-Cabello, M. A., Verduzco-Zapata, M. G., Aguilar-Olguín, S., Rivera-Rodríguez, M. C., & Bachara, W. (2021). Sightings and strandings of beaked whales from the Mexican Central Pacific. *Aquatic Mammals*, *47*(2), 114-126. <https://doi.org/10.1578/AM.47.2.2021.114>
- Otero-Sabio, C., Centelleghé, C., Corailn, L., Graïc, J. M., Cozzi, B., Rivero, M., Consoli, F., & Peruffo, A. (2020). Microscopic anatomical, immunohistochemical, and morphometric characterization of the terminal airways of the lung in cetaceans. *Journal of Morphology*, *282*, 291-308. <https://doi.org/10.1002/jmor.21304>
- Pabst, D. A., McLellan, W. A., & Rommel, S. A. (2016). How to build a deep diver: The extreme morphology of mesoplodonts. *Integrative and Comparative Biology*, *56*(6), 1337-1348. <https://doi.org/10.1093/icb/icw126>
- Pfeiffer, C. J. (1993). Neural and muscular control functions of the gut in odontocetes: Morphologic evidence in beaked whales and beluga whales. *Journal of Physiology*, *87*(6), 349-354.
- Pitman, R. L., & Lynn, M. S. (2001). Biological observations of an unidentified mesoplodont whale in the eastern tropical Pacific and probable identity: *Mesoplodon peruvianus*. *Marine Mammal Science*, *17*(3), 648-657. <https://doi.org/10.1111/j.1748-7692.2001.tb01010.x>
- Pitman, R. L., Aguayo, A., & Urbán-R., J. (1987). Observations of an unidentified beaked whale (*Mesoplodon* sp.) in the eastern tropical Pacific. *Marine Mammal Science*, *3*(4), 345-352. <https://doi.org/10.1111/j.1748-7692.1987.tb00321.x>
- Reyes, J. C., Mead, J. G., & Van Waerebeek, K. (1991). A new species of beaked whale *Mesoplodon peruvianus* sp. N. (cetacean: Ziphiidae) from Peru. *Marine Mammal Science*, *7*(1), 1-24. <https://doi.org/10.1111/j.1748-7692.1991.tb00546.x>
- Rodríguez-Fonseca, J. (2001). Diversidad y distribución de los cetáceos de Costa Rica (Cetacea: Delphinidae, Physteridae, Ziphiidae y Balaenopteridae) [Diversity and distribution of the cetaceans of Costa Rica (Cetacea: Delphinidae, Physteridae, Ziphiidae and Balaenopteridae)]. *Revista de Biología Tropical*, *49* (Suppl. 2), 135-143.
- Rommel, S., Costidos, A. M., Fernández, A., Jepson, P. D., Pabst, D. A., McLellan, W. A., Houser, D. S., Cranford, T. W., Van Helden, A. L., Allen, D. M., & Barros, N. B. (2006). Elements of beaked whale anatomy and diving physiology and some hypothetical causes of sonar-related stranding. *Journal of Cetacean Research and Management*, *7*(3), 189-209.

- Russo, F., Gatta, C., De Gioramo, P., Cozzi, B., Giurisato, M., Lucini, C., & Varrichio, E. (2012). Expression and immunohistochemical detection of leptin-like peptide in the gastrointestinal tract of the South American sea lion (*Otaria flavescens*) and the bottlenose dolphin (*Tursiops truncatus*). *The Anatomical Record*, 295(2), 1482-1493. <https://doi.org/10.1002/ar.22532>
- Sanino, G. P., Yáñez, J. L., & Van Waerebeek, K. (2007). A first confirmed specimen record in Chile and sightings attributed to the lesser beaked whale *Mesoplodon peruvianus* Reyes, Mead and Van Waerebeek, 1991. *Boletín del Museo Nacional de Historia Natural, Chile*, 56, 89-96.
- Schumacher, U., Zahler, S., Horny, H. P., Heidemann, G., Skirnisson, K., & Welsch, U. (1993). Histological investigations on the thyroid glands of marine mammals (*Phoca vitulina*, *Phocoena phocoena*) and the possible implications of marine pollution. *Journal of Wildlife Diseases*, 29(1), 103-108. <https://doi.org/10.7589/0090-3558-29.1.103>
- Sierra, E., Fernández, A., Espinosa de los Monteros, A., Díaz-Delgado, J., Bernaldo de Quirós, Y., García-Álvarez, N., Arbelo, M., & Herráez, P. (2015). Comparative histology of muscle in free ranging cetaceans: Shallow versus deep diving species. *Scientific Reports*, 5, 15909. <https://doi.org/10.1038/srep15909>
- Simpson, J. G., & Gardner, M. B. (1972). Comparative microscopic anatomy of selected marine mammals. In S. Ridgway (Ed.), *Mammals of the sea – Biology and medicine* (pp. 277-319). Charles C. Thomas.
- Suzuki, M., Ishikawa, H., Otani, S., Tobayama, T., Katsumata, E., Ueda, K., Uchida, S., Yoshioka, M., & Aida, K. (2002). The characteristics of adrenal glands and its hormones in cetaceans. *Fisheries Science*, 68(Suppl. 1), 272-275. https://doi.org/10.2331/fishsci.68.sup1_272
- Urbán-Ramírez, J., & Aurióles-Gamboa, D. (1992). First record of the pygmy beaked whale *Mesoplodon peruvianus* in the North Pacific. *Marine Mammal Science*, 8(4), 420-425. <https://doi.org/10.1111/j.1748-7692.1992.tb00058.x>
- Vuković, S., Lucić, H., Živković, A., Đuras Gomerčić, M., Gomerčić, T., & Galov, A. (2010). Histological structure of the adrenal gland of the bottlenose dolphin (*Tursiops truncatus*) and the striped dolphin (*Stenella coeruleoalba*) from the Adriatic Sea. *Anatomia Histologia Embryologia*, 39, 59-66. <https://doi.org/10.1111/j.1439-0264.2009.00981.x>
- Vuković, S., Lucić, H., Gomerčić, H., Đuras, M., Gomerčić, T., Škrtić, D., & Curković, S. (2005). Morphology of the lymph nodes in bottlenose dolphin (*Tursiops truncatus*) and striped dolphin (*Stenella coeruleoalba*) from the Adriatic Sea. *Acta Veterinaria Hungarica*, 53(1), 1-11. <https://doi.org/10.1556/avet.53.2005.1.1>
- Vuković, S., Lucić, H., Đuras Gomerčić, M., Galov, A., Gomerčić, T., Curković, S., Škrtić, D., Domitrián, G., & Gomerčić, H. (2011). Anatomical and histological characteristics of the pituitary gland in the bottlenose dolphin (*Tursiops truncatus*) from the Adriatic Sea. *Veterinarski Arhiv*, 81(1), 143-151.
- Wislocki, G. (1929). On the structure of the lungs of the porpoise (*Tursiops truncatus*). *American Journal of Anatomy*, 44(1), 47-77. <https://doi.org/10.1002/aja.1000440103>
- Wislocki, G., & Belanger, L. (1940). The lungs of the larger Cetacea compared to those of smaller species. *Biological Bulletin*, 78(2), 289-297. <https://doi.org/10.2307/1537779>