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MORPHOLOGY OF THE DROMEDARY CAMEL STOMACH WITH REFERENCE TO PHYSIOLOGICAL ADAPTATION

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Abstract: Dromedary camels (*Camelus dromedarius*) are adapted to their desert habitat where they are able to survive and reproduce despite very high temperatures, little vegetation, and limited water availability. The mechanism of thermoregulation in camels is highly efficient, which makes them maintain the appropriate body temperature to carry out their physiological activities. Compared to other mammals, camels are environmentally tolerant as they can be bred for milk and meat production in areas with scant natural resources depending on their unique physiological, anatomical and behavioral characteristics. The camel's digestive system has unique morphological features that make it highly adapted to its natural environment. Although the stomach of camels is divided into compartments, as in ruminants, they are referred to as pseudo-ruminants because they do not have the clearly divided four-chambered stomach found in true ruminants. However, their stomach is larger and more efficient in dealing with dry, tough, and fibrous food. Therefore, the current study aimed to review the gross anatomical and histological peculiarities and characteristic features of the dromedary camel stomach with respect to their physiological importance. The morphological characterization of the dromedary camel stomach might elucidate the functions of its different compartments. Thus, this review could add to our understanding of the physiology of the digestive system in dromedary camels.

Key words: dromedary camel stomach; morphology; desert habitat

Introduction

The worldwide population of camels is about 18 million, and about 16.5 million of them are dromedary or one-humped camels (1). Dromedary camels (*Camelus dromedarius*) are reared mainly in North and East Africa as well as in the eastern and western parts of Central Asia. They are economically important to low-income families in many countries of Africa and Asia as they are raised for the production of meat, milk, wool, and hides, as well as for transportation and as draft animals (2, 3).

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Dromedary camels are uniquely adapted to the harsh environment of arid and sub-arid regions, which are characterized by shortage of vegetation and water, high ambient temperatures, and other harsh conditions (4, 5). The ability of dromedaries to withstand adverse conditions is attributed to their morphological features, physiological adaption mechanisms, and behavioral attitudes (6). It has been reported that dromedary camels are able to cope with dehydration due to their efficient urinary (4) and digestive systems (7). Camels are able to withstand high ambient temperature, hunger, and thirst for long durations (6, 8). This ability has been attributed to their adaptive homeostatic mechanisms (8) and their high potential for converting the scanty resources of the desert environment into milk, wool, and meat (9, 10, 11). Thus, camels are considered as a good source of food in areas where the performance of other animals is adversely affected (2).

The digestive system of dromedary camel is highly adaptive to its natural habitat. The lips are long and thick with the upper one being split, which assists in selection and prehension of food when grazing on thorny desert bushes and shrubs (12). The esophagus is long (13) and protected by keratinized stratified squamous epithelium and mucous glands (13, 14). The long intestines in camels results in an increased surface area that enables better nutrient and water absorption (12, 15). The large size of the camel liver facilitates better digestion and blood detoxification than the livers of other species (12). However, the stomach is believed to play the most important role in the adaptation mechanism of the dromedary camel digestive system. The stomach is large and has a great capacity for digesting cellulose, specific and differentiated motility, very active microflora, and significant food mixing ability (11). Additionally, the camel stomach plays an important role in the maintenance of water balance during dehydration and rehydration (16).

This study reviews the gross anatomy, light microscopy, and electron microscopy of the dromedary camel stomach in relation to its physiological activity. The review might be helpful in understanding the digestive physiology of dromedary camels and their ability to withstand desert conditions.

Gross anatomy of camel stomach

The anatomical structure of the camel stomach is shown in Figures 1, 2 and 3.

Camels belong to the order Artiodactyls (even-toed ungulates), sub-order Tylopoda (pad-footed), and family Camelidae (17, 18, 19). Camelids and ruminants are taxonomically and behaviorally different (18, 19). Species of the two sub-orders independently underwent parallel evolution to develop a compound stomach with large cranial part (forestomach). The specific design of the stomach in Tylopoda and Ruminantia together with its related function and physiological actions confirm their non-homologous parallel evolution (20). In this respect Camelids are called modified- or pseudo-ruminants as they have segmented stomach like that found in true ruminants, but their stomach is segmented into three compartments: compartment 1 (C1), compartment 2 (C2) and compartment 3 (C3) rather than four (rumen, reticulum, omasum and abomasum) in true/typical ruminants (21, 22, 23; 24; 25). The stomach of adult camels extends from the diaphragm to the pelvic inlet, occupying the major part of the abdominal cavity (26). The categorization of the different parts of camel stomach seems to be controversial (25). According to many studies the stomach is divided into three compartments C1, C2 and C3 in dromedary camels (21, 22, 23, 25, 27), *Lama glama* (12, 28) and alpaca (20, 29). On the other hand, some other authors recorded four compartments (C1, C2, C3, and C4) in dromedary camel stomach (30, 31). Furthermore, the stomach in Bactrian camels has been considered as a single cavity with multiple different cardiac glands (24). It seems that most of the recent studies believe in the three compartment categorization of camel stomach depending on its morphological, histochemical and functional characteristics. Thus, the current review adopts the three-compartment segmentation of camel stomach i.e. compartment 1 (C1), compartment 2 (C2) and compartment 3 (C3).

C1:

This is the first and largest compartment which comprises 83 % of the total stomach volume (32) and is considered as the analogous to the rumen in true ruminants (29, 31, 32). C1 is round in shape and located on the left part of the abdominal cavity, extending from the diaphragm at the level of the seventh rib to the caudal border at the level of the twelfth rib (31). External transverse groove and internal transverse muscular ridge divide C1 into a cranial portion (cranial sac) and a caudal portion (caudal sac) (29, 31, 32, 33). The opening separating C1 from C2 and that separating C2 from C2 are small in dromedary and alpaca camels compared to true ruminants (29). However, the relatively small C2 is not entirely separated from Cl in camelids (27). The interior of C1 contains two glandular sacs: the cranioventral glandular sac and the caudodorsal glandular sac (22, 26, 27, 29, 31, 34, 35, 36, 37). The cranioventral and caudodorsal glandular sacs are denoted by a crescent-shaped pillar internally that is corresponding to the transverse groove. Each sac contains glandular chambers formed by four walls (pillars); the caudodorsal sac is larger, irregular, and more sacculated, as compared to cranioventral sac (31). Recently, two sacculated regions in C1 and a third comb-like one have been reported in C2 (20). It has been stated that there are two regions in C1 of dromedary camel: non-glandular region and glandular regions; the non-glandular region is large and relatively smooth and constitutes 53.2% of the entire gastric mucosa (25). A ventricular muscular groove, like that found in true ruminants connecting C1 and C3, is also present in Llama and dromedary camels; during the neonatal period, fluid ingesta bypass C1 and C2 via this groove to enter C3 (29, 36).

C2:

C2 is the second and smallest gastric compartment constituting 6% of the total gastric volume (32). It is situated on the right part of abdominal cavity in dromedary camels (27, 30, 31, 36) and guanaco and llama (28). C2 is described as pear- (26) or kidney- (25) shaped in dromedary camels. Wang *et al.* (2000) described it as elliptically concave that continues cranially with the pro-ventriculus and the caudal glandular sac (38). Lechner-Doll *et al.* (1995) showed that in dromedary camels C2 is not completely separated from C1 (27). In *Llama and Guanaco*, C2 empties into C3 through a short and thick muscular tube that controls the rate of material movement into C3 (28).

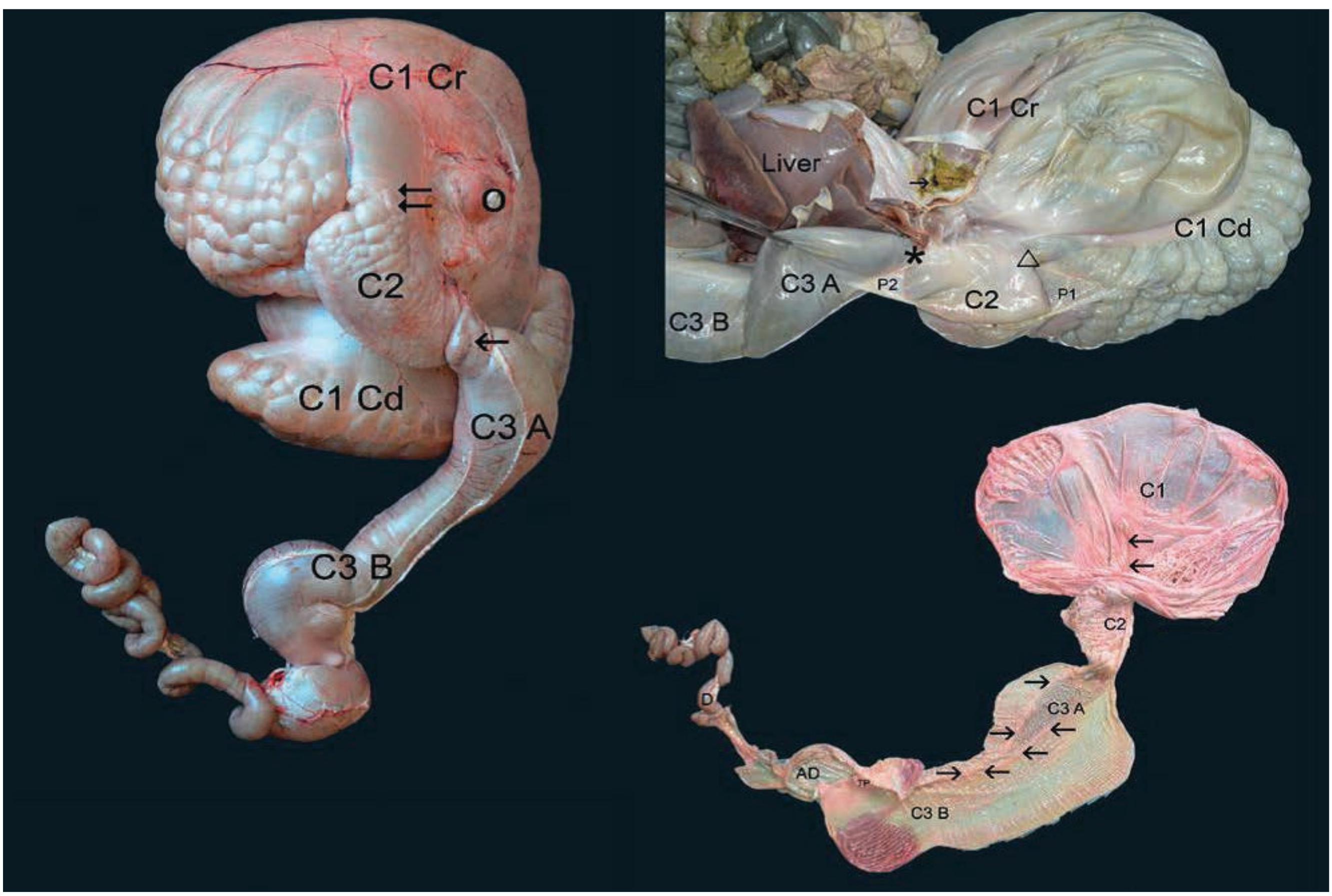

Figure 1: (From Pérez et al., 2016 after getting permission):

A. Dromedary camel stomach. C1 Cr: Cranial part of first gastric compartment; C1 Cd: Caudal part of first gastric compartment; C2: Second gastric compartment C2; C3A and C3B: Proximal and distal parts of third gastric com-partment C3; O: Ostium car-diacum; Double arrow: Position of the orifice between C1 and C2; Arrow: Position of the orifice between C2 and C3A. B. Alpaca gastrointestinal tract showing external position of orifices of C2 and peritoneal folds that delimited C2. C1 Cr: Cranial part of first gastric compartment; C1Cd: Caudal part of first gastric compartment; C2: Second gastric compartment C2; C3A and C3B: Proximal and distal parts of third gastric com-partment C3; Triangle: Position of the orifice between C1 and C2; * Position of the orifice between C2 and C3A; P1: Peritoneal fold between C1caudal and C2; P2: Peritoneal fold between C2 and C3A. C. Internal view of the drome-dary stomach after dorsal incision. C1: First gastric compartment; C2: Second gastric compartment; C3A and C3B: Proximal and distal parts of third gastric compartment C3; TP: Torus pyloricus; AD: Ampulla duodeni; D: Duode-num; Arrows; Gastric groove. Scale bar = 10 cm

The internal surface of C2 shows several longitudinal and transverse muscular bands which form large and small chambers (31). The interior of C2 is similar to C1, except for the numerous bands and folds that form smaller and deeper chambers (26, 30). The entire gastric mucosa, except for the gastric groove, is found to be in the form of interconnected folds similar to, but smaller, than those found in glandular sacs (25).

C3:

C3 is described as a long tube located on the right part of the abdominal cavity under C2 (27, 29, 34, 31, 36). In dromedary camel and Alpaca it is composed of two parts: proximal and distal (29). The proximal part is the initial dilated part and the distal part is elongated and connects to the duodenum.

Internally, C3 is entirely lined by glandular and its mucosa is in the form of about 50 longitudinal folds that decrease craniocaudally and increase in the middle (27, 31, 34, 36). Like the abomasum in true ruminants, C3 in camels contains two regions: the fundic region and the pyloric region (22, 26, 31, 36, 39). The fundic region consists of thick longitudinal folds and the pyloric region is formed of thin longitudinal folds (30). However,

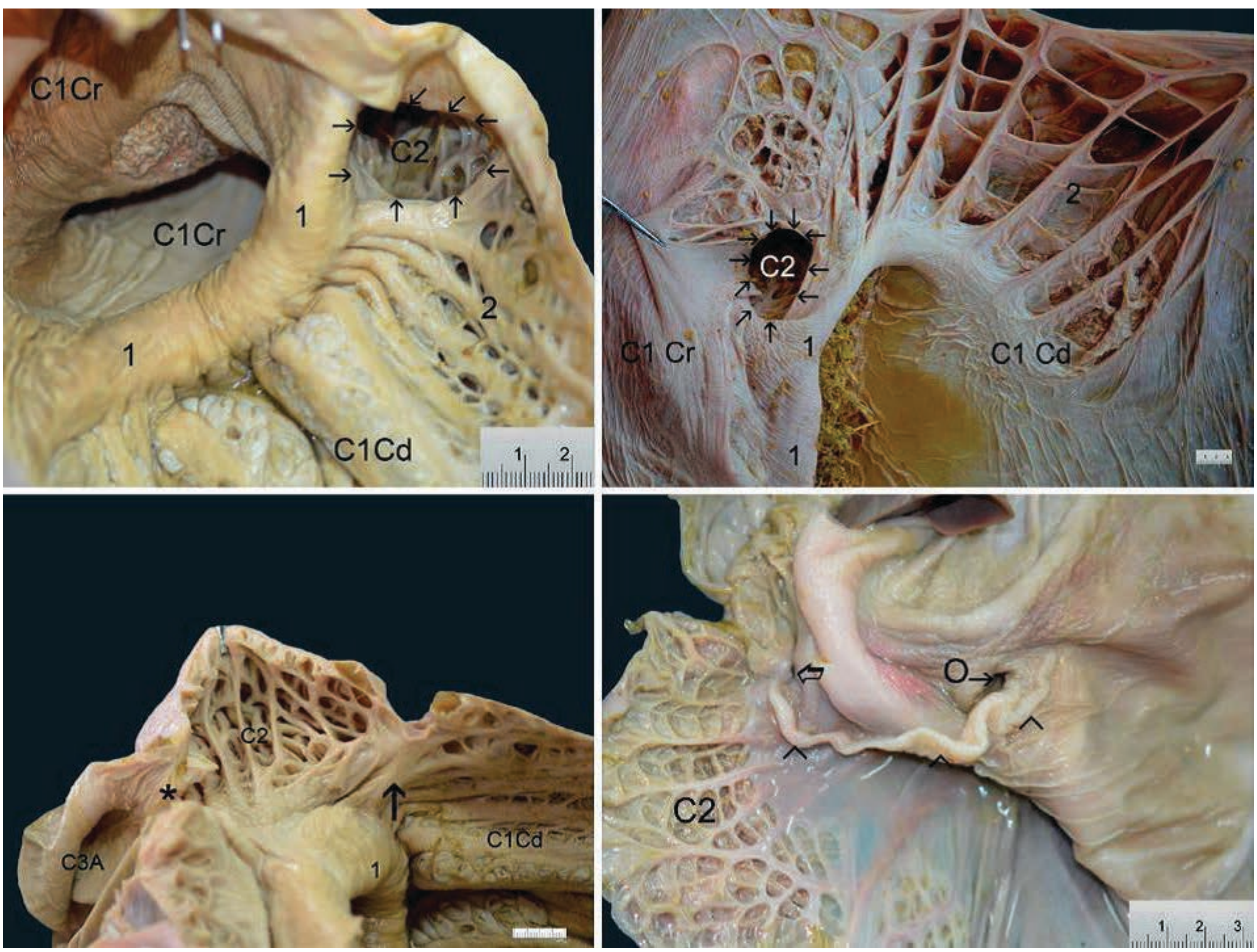

Figure 2: (From Pérez et al., 2016 after getting permission):

A. Internal view of cranial part of C1 and C2 of alpaca stomach. C1Cr: Cranial part of first gastric compartment; C1 Cd: Caudal part of first gastric compartment; C2: Second gastric compartment C2; Arrows: Orifice between C1 and C2; 1: Transverse pillar of C1; 2: Glandular sac area of C1 Cd. B. Internal view of cranial part of C1 and C2 of dromedary camel stomach. C1Cd: Caudal part of first gastric compartment; C2: Second gastric compartment C2; Arrows: Orifice between C1 and C2; 1: Transverse pillar of C1; 2: Glandular sac area of C1Cd. C. Internal view of cranial part of C1 ventral, C2 and C3 A of alpaca stomach after dorsal incision of C1 dorsal and the dorsal walls of orifices between C1 to C2 and C2 to C3. C1 Cd: Caudal part of first gastric compartment; C2: Second gastric compartment C2; C3 A: First part of the third gastric compartment; Arrow: Opened orifice between C1 and C2; Asterisk: Opened orifice between C2 and C3 A; 1: Transverse pillar of C1. D. Internal view of cranial part of C1 and C2 of alpaca stomach.O: Ostium cardiacum; C2: Second gastric compartment C2; Arrow: Orifice between C2 and C3A; Arrowheads: Sulcus ventriculi in the inner side of C2. Scale bars in cm.

three regions have been reported in the interior of C3 in dromedary camel: cranial region with slender tortuous folds, middle region with tight folds and distal region with characteristic thick wavy folds like those found in true ruminant's abomasum (25).

Histology of camel stomach

The different compartments of the dromedary camel stomach consist of four tunics: tunica mucosa, tunica submucosa, tunica muscularis, and tunica serosa (30, 31). All compartments in dromedary stomach are glandular except C1 which exhibits both glandular and non-glandular mucosae (Fig. 4A, B) (40). The latter authors stated that the glandular mucosa in C1 is only found in the regions of glandular sacs, whereas the non-glandular mucosa is present elsewhere. Similar findings have also been reported in other camelids (27, 28, 33, 41). However, eight histological regions are found in dromedary camel stomach (25). The first region, which constitutes about 53.2% of the stomach, is non-glandular and occupies the body of the first compartment. The other seven regions have glandular mucosae. Whereas keratinized stratified squamous epithelium lines the mucosa of the entire true ruminant's forestomach (rumen, omasum, abomasum), it is only restricted to the dorsal parts of Cl and C2 in camelids (27, 41, 42). The latter authors mentioned that the ventral part of C1, C2 and the entire internal surface of

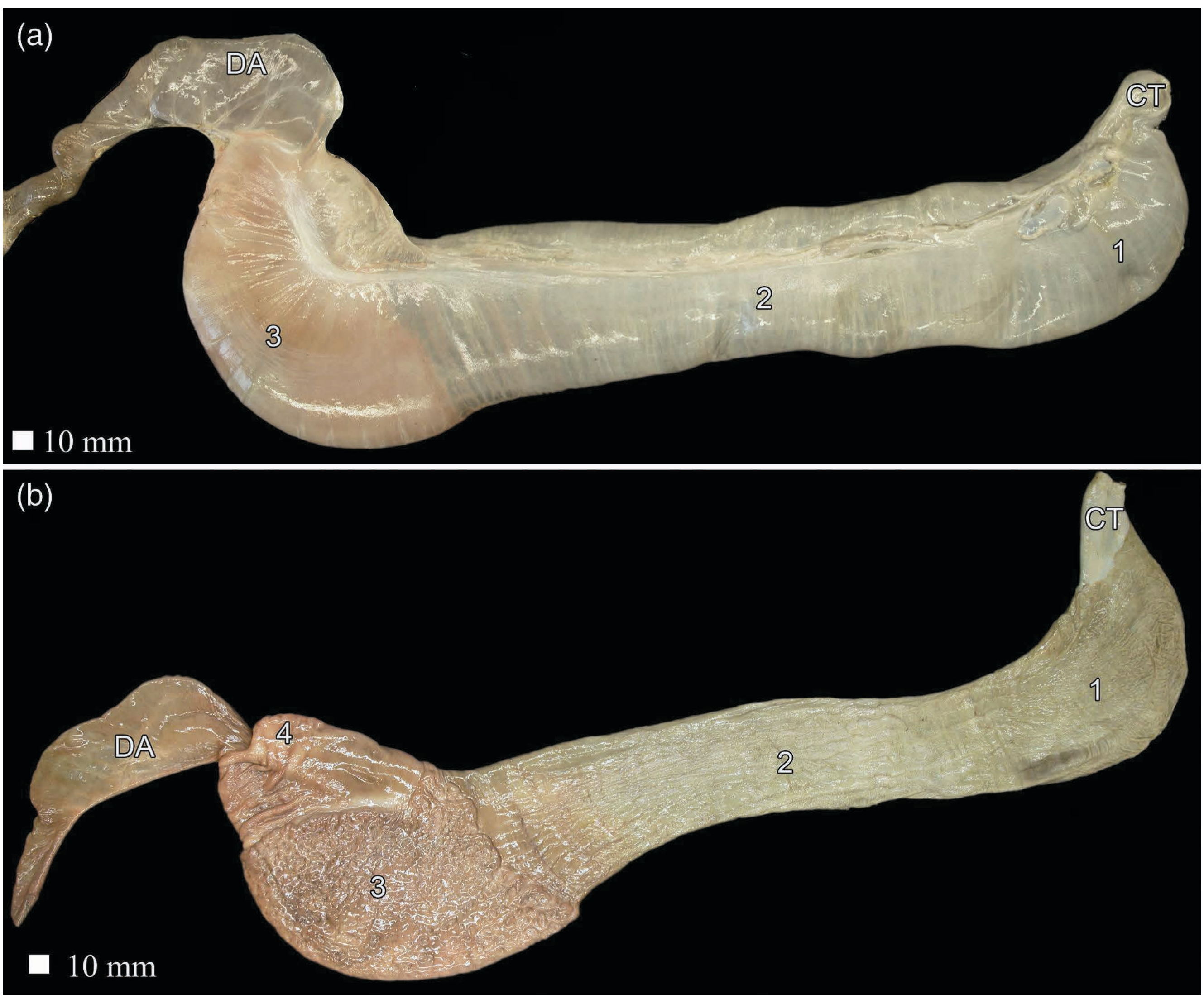

Figure 3: (From Vater et al., 2021 after getting pretermission)

External (a) and internal (b) morphology of C3. CT, Connection tube; DA, duodenal ampulla. 1: Initial bend of C3; 2: straight part of C3; 3: caudal loop of C3; 4: torus pyloricus

C3 are lined by simple columnar epithelium with deep tubular glands underneath. They conclude that this region is similar to the cardiac region of true ruminant's abomasum. The mucosal lamina propria is in the form of loose connective tissue which contains gastric glands in glandular regions (30, 31, 43). While muscularis mucosa is absent in the non-glandular region, it constitutes a thin layer of circular smooth muscle fibres in the glandular region (30, 31). However, the muscularis mucosa is totally absent in glandular sacs of dromedary camels (35). The tunica submucosa of dromedary camel stomach is formed of connective tissue with some blood vessels as well as nerve and smooth muscle fibres; the tunica muscularis which follows the submucosa is in the form of smooth muscle fibers arranged as an inner circular layer and an outer longitudinal layer and it is followed by serosa which is a thin layer of connective tissue covered by mesothelium (30, 31).

In C1 of the camelids stomach, including dromedaries, the epithelium of the non-sacculated region is keratinzed stratified squamous, whereas it is simple columnar in the glandular sac area (27, 30, 31). However, it has been reported that the glandular sacs in dromedary camel have only keratinized stratified squamous epithelium (35). The lamina propria of C1 consists of loose connective tissue with simple branched glands (30, 31, 33, 42). These glands have also been described as deep tubular in shape (41- 43).

In C2, whereas the walls and floors of the glandular saccules are lined by simple columnar epithelium, longitudinal bands, which are non-glandular, are lined by keratinized stratified squamous epithelium (30, 31,). Both stratified squamous and simple columnar epithelia in C2 have also been reported in other camelids (27). On the other hand, the stratified squamous epithelium of C2 is found to be non-keratinized (30). Moreover, the entire mucous membrane of C2 is reported to be lined by simple columnar lining (43). The muscularis mucosa in C2, which is in the form of circular smooth muscle layer separating the lamina propria from the submucosa, is only found in the glandular region, (30, 31). In C2 the muscularis mucosa of the bands consists of a longitudinal layer of smooth muscle fibers, whereas it is in the form of a smooth muscle bundle in the upper regions of the primary folds (30).

The mucosa of C3 in camels is highly folded and entirely glandular; it is lined by simple columnar epithelium followed by a lamina propria which

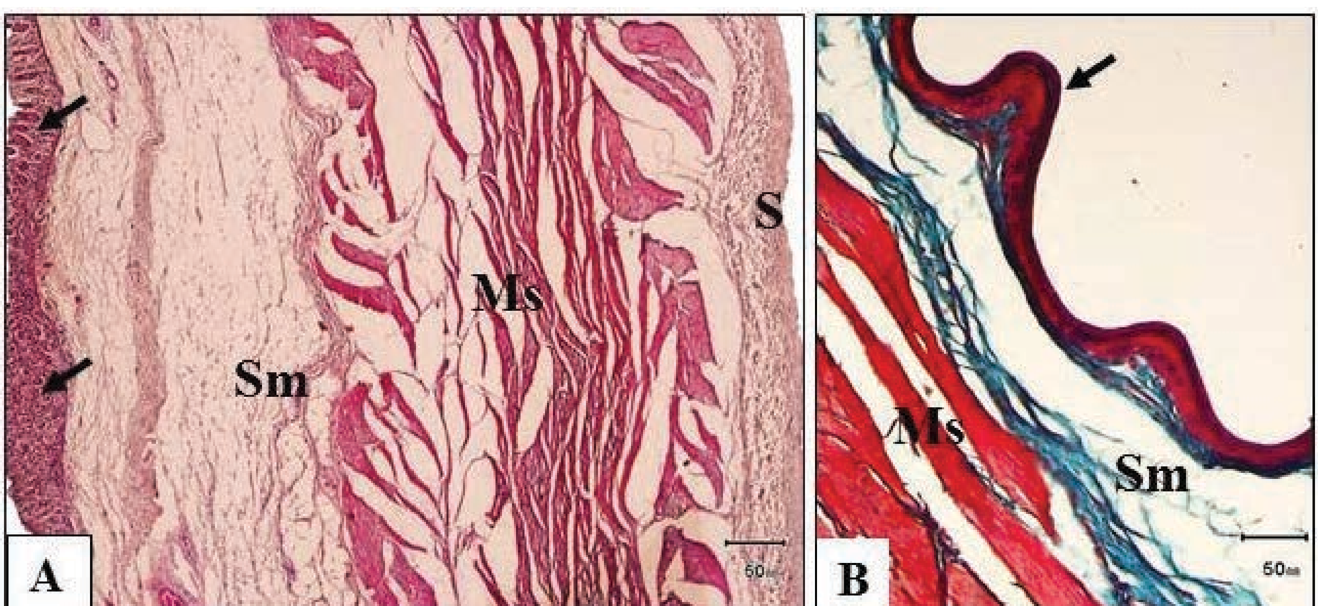

Fig. 4

Figure 4: (From Abuagla, 2014, PhD thesis)

A: Glandular area of C1 showing simple columnar epithelium and mucosal gastric glands (Arrows); submucosa (Sm), tunica muscularis (Ms) and serosa (S). H&E stain. X4. **B:** Non-glandular area of C1 showing keratinized stratified squamous epithelium (Arrows), submucosa (Sm) and tunica muscularis (Ms). Massons' trichrome stain. X10.

contains gastric glands (20, 27, 33). Similar findings have also been noted in ruminant abomasum (27, 43). Large gastric glands are observed in dromedary camel C3 which are continuous with numerous gastric pits (39). The greater curvature of tunica mucosa of the terminal dilated part of C3 bears very thick folds which divide the mucosa into nearly regular region with gastric areas; this region contains the proper gastric glands (fundic glands) which are somewhat different from those in the true ruminants (22). However, the terminal distended part of C3 considered as a separate fourth compartment, named C4 (30, 31). While in one study C4 is divided into three histological regions: cardiac, fundic, and pyloric regions (31), other two studies divided it into two regions: fundic and pyloric regions, considering the cardiac region as a narrow band between the fundic region and C3 (30, 34). The mucosa in the cardiac region of C4 is folded and the epithelial lining is simple and columnar, whereas the lamina propria contains simple branched tubular glands with mucus secreting cells (30, 31, 34). The lamina propria is surrounded by a thin muscularis mucosa of circular smooth muscle fibers (30, 31, 34). Osman (1999) stated that the smooth muscle fibers of muscularis mucosa do not reach the folds or laminae of C3 as it does in ruminants (30). The gastric glands of C4 in dromedary camel are lined by three types of cells: mucous cells, parietal cells, and chief cells (31). These cell types have previously been reported in the same species (30, 34). The mucous cells are tall and found in the glandular neck region. The chief cells are basophilic and mainly basally located. The parietal cells are numerous compared to the chief cells. They are rounded and acidophilic and located in the basal and parietal regions (30, 31). The gastric glands in the basal part mainly contain mucus-secreting cells with some parietal cells (21, 30, 31). However, the pyloric glands have been observed with mucous cell types that with spherical or flat nuclei occupying the glandular basal part (30).

Ultra-structurally, the dromedary saccular area is folded and studded with numerous glands of various sizes and shapes including cup-shaped, cap-shaped and flower-shaped which are lined by folded cells (Fig. 5A, B) (40). Also in Llama guanaco, transmission electron microscopy reveals glandular sac epithelial cells with tiny microvilli (42). In dromedary camels the columnar cells lining the glandular sacs are closely packed together and they present basal rounded or oval nuclei and rich

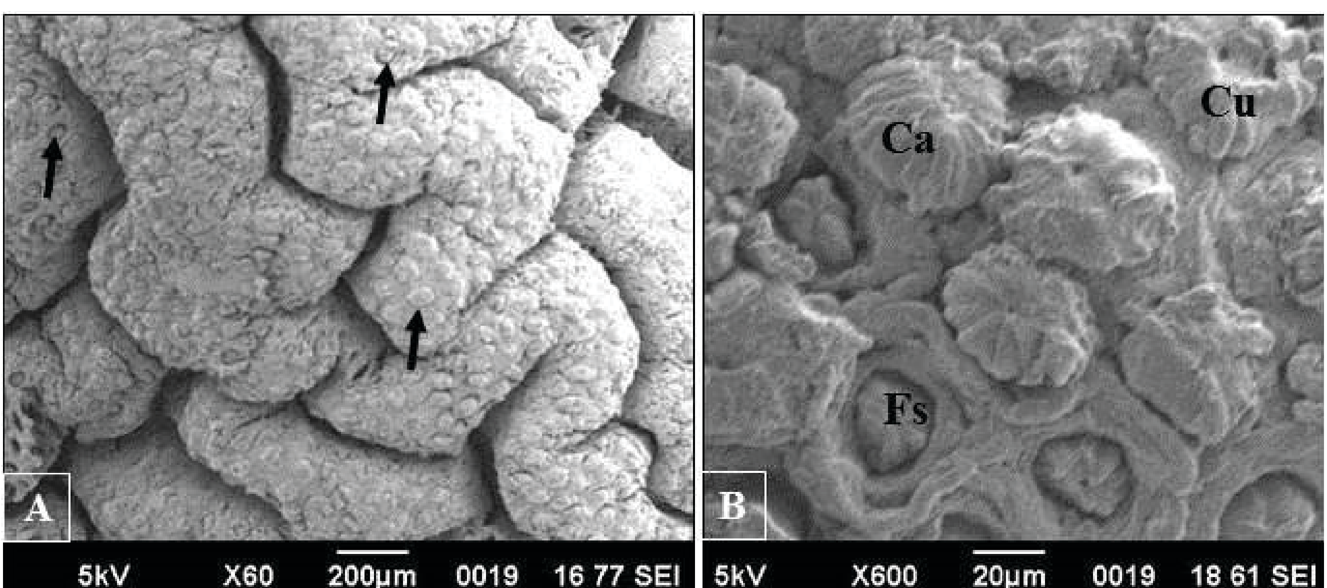

Fig. 5.

Figure 5: (From Abuagla, 2014, PhD thesis)

A: Scanning electron microphotograph of glandular area of C1 showing folded mucosa with different gastric glands (Arrows). X60. B: Scanning electron microphotograph of glandular area of C1 with cup-shaped (Cu), cap-shaped (Ca) and flower-shaped (Fs) glands. X600.

in mitochondria, rough endoplasmic reticulum, Golgi apparatus, numerous secretory granules and several dense bodies, especially in their apical cytoplasm (Fig. 6A,B) (40). It has also been stated that the plasma membrane of abomasal glands shows prominent enfolding in some epithelial cells of dromedary (31) and Llama (41, 42) camels. The mitochondria are numerous and mainly occupying the supra-nuclear cytoplasm of many cells in the epithelium of cranioventral and caudodorsal sacs in dromedary camels (31). The mitochondria are numerous and mainly occupying the supra-nuclear cytoplasm of many cells in the epithelium of cranioventral and caudodorsal sacs in dromedary camels (31). In llama, the mitochondria are slender or elongated in shape with a dense matrix filling wide parts of the upper cytoplasm (41). Additionally, the dromedary camel (31) and *Llama guanaco* (41) have well-developed Golgi apparatuses as well as numerous secretory granules and dense bodies in the apical cytoplasm and glandular cells of the cranioventral and caudodorsal sacs. It has also been noted that in Bactrian camels the glandular cells in the sac area have low- and high-density granules in the supra-nuclear cytoplasmic region (24).

Adaptation of camel stomach

Physiologically, camel stomach is similar to true ruminants in several aspects, including microbial fermentation, re-gurgitation, re-chewing, and re-swallowing of ingested food (18, 19). It has been reported that slow circular movements between the cranio-ventral and caudo-dorsal sacs of rumen facilitates microbial activity (27). The large size of the dromedary C1 and C2 and true ruminant's rumino-reticulum results in increased storage capacity and efficient digestion of forage rich in crude fiber (12). Gastric differentiation of camels enables using C1 and C2 as a fermentation vat because it offers complex media for anaerobic bacteria (44). Moreover, the large forestomach in grazers and browsers like dromedary camels could be linked to the fact that they require more retention time for the digesta (45). It has been mentioned that the relatively small orifice between C2 and C3 can only allow for passage of a certain size of food particles which ensures adequate food fermentation and absorption in forestomach in camels and cattle (45 46). However, two important morphological differences between the forestomach in camels and true ruminants

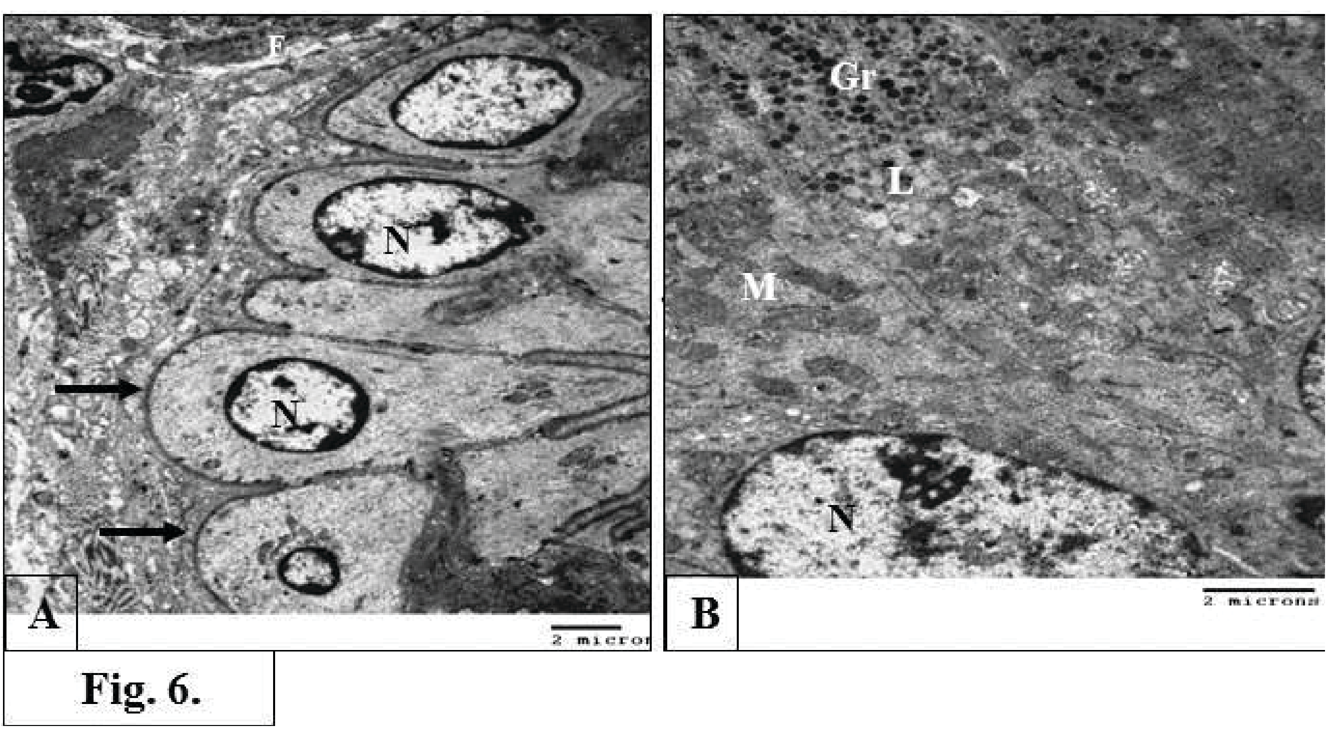

Figure 6: (From Abuagla, 2014, PhD thesis)

A: Transmission electron microphotograph of glandular area of C1 showing closely packed columnar or pyramidal epithelial cells (Arrows) with oval nuclei (N). X3600. B: Transmission electron microphotograph of glandular area of C1 showing oval nuclei (N), supra-nuclear mitochondria (M), lipid droplets (L) and secretory granules (Gr). X5800.

have been stated (29). Firstly, whereas in true ruminants the reticulum lies along the major axis of the rumen (cranial to it), the major axis of the C1 is not aligned with C2 in camelids. Secondly, in true ruminants, the opening between the rumen and reticulum is relatively larger as compared with the opening between C1 and C2. Thus, the forestomach of camels contains a bottleneck between C1 and C2 which might explain why they cannot process high amount of food compared to taxonomic ruminants. It has been mentioned that the glandular sacs in camels allows for increased gastric surface area which increases the absorption rate of volatile fatty acids (VFAs) 3 - 4 times that of other ruminants (47). Moreover, the glandular sacs might perform rapid absorption of water and solutes (41). The glandular sacs could also be considered as a means of protecting camels from dehydration in hot environmental conditions (12). It is reported that water-deprived sheep lose much more rumen water than camelids (46) which is related to the anatomical differences between camels and true ruminants. This could also be related to the extremely slower water turnover in camels (48). The later author concluded that water dynamics in the alimentary canal allows camels to survive and produce during dry periods (48). Similarly, the fatty acid absorption in the llama stomach is faster than in true ruminants (49, 50). The absorption of soluble particles and water in camel stomach occurs mainly in C3 (51). In this respect, the contents of C3 in the camel stomach are dry, which strongly suggests significant water absorption (52). The glandular microscopic structure of the camel gastric compartments is responsible for their high digestibility coefficient (32). The keratinized stratified epithelium of the upper digestive tract, including non-glandular parts of C1 and C2, enables camel to deal with dry and thorny forage in desert (53). The large gastric glands in C3 fundic region indicates that the camel stomach is more prepared for glandular digestion than fermentative digestion as compared to true ruminants (25). C3 parietal cells arrangement and chief cells behavior can preserve muco-substance during fastening or diminishing of the food (22). The columnar cell lining and prominent enfolding in the plasma membrane of the glandular sacs could be considered as an indication of the absorptive function in the surface and glandular epithelial cells. Despite the prominent differences in morphology between camels and true ruminants, both show similar dependence on salivary glands for provide the mucus, alkali, and fluid needed for the fermenting food in the forestomach (34). This indicates the dominance of the absorptive function of the camel stomach over its secretory function. It has also been shown that the mucus found in the surface epithelium of the camel stomach might mainly be a protective function (54). While the latter authors claim that that the function of the glandular endocrine cells in camel stomach is unknown, they are considered important in water-electrolyte balance during dehydration (55). It has been noted that the ruminal endocrine and secretory activity in camels could account for nitrogen retention (54). The latter authors claimed that nitrogen decline in both urine and feces together with sodium renal loss enable camels to maintain a relatively stable extracellular volume (54). It has also been stated that the flow of water urea-nitrogen in the same direction accounts for the lower water content in the feces and urine of camels compared to that of sheep (56). Thus, the camel has a far more efficient mechanism of nitrogen conservation than other ruminant animals (57). It has been reported that concerning the recycling of urea, 12 days of dehydration in camels are equal to 2 days of dehydration in sheep (56). Ultrastructure review shows that the gastric secretory activity in camels could be indicated by the presence of many mitochondria, well-developed Golgi bodies, and numerous secretory granules and dense bodies in the supra-nuclear cytoplasm of glandular epithelial cells (31).

Conclusion

The data reviewed in this work shows morphological and physiological adaptations of the dromedary camel stomach. These adaptive mechanisms of camel stomach reflect its capability to deal with limitations of food and water in harsh habitat compared to other mammalian species. Moreover, this review could be considered as a contribution toward a better understanding of the unique digestive system of the dromedary camel.

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