Macroanatomical aspects of the gastrointestinal tract of the alpaca (*Vicugna pacos* Linnaeus, 1758) and dromedary (*Camelus dromedarius* Linnaeus, 1758)

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Abstract

Although camelids and taxonomic ruminants share fundamental convergent properties, such as microbial fermentation and a sorting mechanism in the forestomach with a resulting high degree of digesta particle size reduction, there are important differences in the capacity to process high amounts of food. We describe qualitative and quantitative characteristics of the gastrointestinal anatomy of alpacas (*Vicugna pacos*, 44.4±5.5 kg body mass), supplemented with some observations in dromedaries (*Camelus dromedarius*). The long large intestine of alpacas (610±128 cm) corresponds to the adaptation of camelids to arid environments. An important difference to taxonomic ruminants is the position of the second forestomach compartment (C2 vs. reticulum), which is not in line of the major forestomach axis in camelids, and the size of the corresponding orifice (C1-C2 vs. *Ostium rumino-reticulare*), which is distinctively smaller in camelids (alpaca: 3.2±0.3 cm width × 4.2±0.3 cm height, dromedary: 8.5±0.7 cm diameter) as compared to literature data for similar-sized ruminants. The opening between the second and third forestomach compartment (C2-C3 vs. *Ostium reticulo-omasale*) is of similar magnitude in camelids (alpaca: 2.2±0.7 cm diameter, dromedary: 3.1±0.5 cm diameter) and ruminants, but is opposite to the C1-C2 opening in camelids in a dorsal position. The generally smaller opening might represent a reason for the generally lower food processing capacity in camelids, and together with the arrangement of the openings might result in conditions during contractions of the C2 that are more favourable to (a low proportion of) larger particle escape into the C3. In contrast, the different arrangement of the openings and the larger connection to the preceding chamber might make such an escape of (a low proportion of) large particles from the reticulum to the omasum less likely in ruminants, giving their sorting mechanism a clear-cut anatomical threshold in the *Ostium reticulo-omasale*.

Kurzfassung

Kameliden und taxonomische Wiederkäuer (Ruminantia) weisen fundamentale Konvergenzen auf, wie mikrobielle Fermentation und einen Sortier-Mechanismus im Vormagen, mit einem entsprechend hohen Grad der Partikel-Zerkleinerung im Darminhalt. Dennoch existieren wichtige Unterschiede in der Fähigkeit, große Futteraufnahme-Mengen zu bewältigen. Wir beschreiben qualitative und quantitative Charakteristika der Magen-Darm-Anatomie von Alpakas (*Vicugna pacos*, 44.4±5.5 kg Körpermasse) sowie einige Beobachtungen bei Dromedaren. Der lange Dickdarm der Alpakas (610±128 cm) entspricht der Anpassung von Kameliden an aride Lebensräume. Wichtige Unterschiede zu taxonomischen Wiederkäuern sind die Position des zweiten Vormagen-Abteils (C2 der Kameliden im Vergleich zum Netzmagen der Wiederkäuer), das bei Kameliden nicht in der Hauptachse des Vormagens liegt, und die Größe der entsprechenden Öffnung (C1-C2 bzw. *Ostium rumino-reticulare*), die im Vergleich mit Literaturangaben ähnlich großer Wiederkäuer bei Kameliden deutlich kleiner ist (Alpaka: 3.2±0.3 cm × 4.2±0.3 cm, Dromedar: 8.5±0.7 cm Durchmesser). Die Öffnung zwischen dem zweiten und dritten Vormagen-Abteil (C2-C3 bzw. *Ostium reticulo-omasale*) ist bei Kameliden (Alpaka: 2.2±0.7 cm Durchmesser, Dromedar: 3.1±0.5 cm Durchmesser) und Wiederkäuern ähnlich, doch liegt sie bei Kameliden der C1-C2-Öffnung gegenüber in dorsaler Position. Die kleinere C1-C2-Öffnung könnte ein Grund für die generell niedrigere Futteraufnahme-Kapazität von Kameliden darstellen, und könnte zusammen mit der Position der C2-C3-Öffnung zu Bedingungen führen, die bei Kontraktion des C2 den Ausfluss (eines geringen Anteils) größerer Partikel in den C3 begünstigen. Die andersartige Anordnung der Ostia, und die geräumigere Verbindung von Pansen und Netzmagen, machen den Ausfluss (eines geringen Anteils) größerer Partikel aus dem Netzmagen ins Omasum bei Wiederkäuern weniger wahrscheinlich, so dass bei ihnen das *Ostium reticulo-omasale* eine klare anatomische Grenze hinsichtlich der Partikelgröße im Vormageninhalt darstellt.

Key words

Anatomy, Camelidae, intake, intestines, mesentery, stomach.

Introduction

Ruminantia and Camelidae families have a large compartmentalized stomach with extensive microbial fermentation. Functional ruminants – the phylogenetic ruminants as well as the camelids – combine simple foregut fermentation with peculiar sorting mechanisms that assure that larger digesta particles are regurgitated and ruminated (Lechner-Doll *et al.*, 1991; Dittmann *et al.*, 2015). This process of rumination is an obligatory physiological feature that facilitates a more efficient particle size reduction and higher digestive efficiencies (Foose, 1982; Fritz *et al.*, 2009; Clauss *et al.*, 2015). In taxonomic ruminants, this possibly also results in higher voluntary food intakes than in non-ruminant foregut fermenters (Clauss *et al.*, 2010).

However, in camelids, food intake is generally lower than in taxonomic ruminants, which also matches the camelids' comparatively lower metabolic rates (Dittmann *et al.*, 2014). It has been speculated that a possible reason for the difference in capacity for food processing could lie in morphophysiological differences between the respective forestomach particle sorting mechanisms (Dittmann *et al.*, 2015). In taxonomic ruminants, there is a clear-cut differences between the regions that contain both small and large particles (the rumen and the reticulum) and those that contain only small particles (from the omasum onwards), with the *Ostium reticulo-omasale* representing a concise threshold (Clauss *et al.*, 2009; Clauss *et al.*, 2016). In contrast, the transition from mixed to only small particles appears to be more gradual in camelids, occurring along a certain tubular stomach compartment (the so-called C3) (Lechner-Doll & von Engelhardt, 1989).

Possibly, the anatomy of the camelid forestomach contributes to this situation. However, apart from the general observation by Vallenas *et al.* (1971) that the C2 has an off-line position and appears relatively separated from the C1, this critical anatomical structure has not been investigated quantitatively, to our knowledge. Therefore, we used the opportunity of having access to carcasses of alpacas (*Vicugna pacos*) and dromedaries (*Camelus dromedarius*) to characterize the openings in the camelid forestomach in more detail. Additionally, we report further macroscopic measurements of the alpaca digestive tract for future comparative work.

Materials and Methods

Eight deceased alpacas, 4 males and 4 females, were obtained from a free-living alpacas population, located at the "Estancia Siglo XX", Punta del Este, Uruguay (34.4°S 55.0°W). Based on external appearance of the carcasses and rigor mortis, death had not occurred sooner than 24 h prior to carcass collection. The cause of death of the animals was not determined but did not appear to be related to the digestive tract. Animals were frozen immediately after being found for later dissection. The specimens were handled and treated according to the local Ethical Board guidelines of University of the Republic, Uruguay.

The body weight was 43.1 ± 7.3 kg in males, 45.8 ± 3.3 kg in females, and 44.4 ± 5.5 kg for all animals. For dissection, the ventral abdominal wall of each animal was cut, and the stomach was removed after sectioning the esophagus just prior to the diaphragm, and the pylorus just before the duodenum. Stomach contents were measured by weighing the unopened organ and re-weighing it after it had been opened and contents rinsed with tap water and dried with paper towels; this was performed for the whole stomach complex, and for each compartment individually. Anatomical measurements were taken following standard procedures for ruminants (e.g. Hofmann *et al.*, 1995; Pérez *et al.*, 2015; Sauer *et al.*, 2016). Briefly, the C1 was placed on its left side, and the height and length of the C1 and the C2, and the length of the curvature of C3A and curvatures of C3B were measured with soft measuring tape. For precise measurements of the curved structures, a flexible yarn was used firstly and then yarn was measured by calipers.

The intestinal tract was separated after sectioning the pylorus just prior to the duodenum, and dissecting it away from its attachments to the dorsal abdominal wall. The descending colon was tied off just prior the entrance of the pelvic cavity. After removal of all mesenteric attachments, the lengths of the different sections of the intestinal tract on the anti-mesenteric side were taken with a standard measuring tape. The full and empty weights of intestinal sections were also recorded. Pictures were taken with a digital camera (Nikon D7100, Nikon Corporation, Tokyo, Japan). As there were no evident differences between males and females, results are presented as mean ± SD for all eight animals.

Additionally, the forestomach complexes of three 2-year-old dromedaries were available for inspection. These animals were obtained of a slaughterhouse of Tunisia. For dromedaries, no body mass measures were available.

Results

The stomach of both camelids was composed of the three classic compartments of the Camelidae (Fig. 1A, 1B). In the alpacas, the weight of the full stomach complex was 5.0 ± 1.9 kg. The C1 was the largest stomach compartment and weighed 4.0 ± 1.6 kg full, and 0.8 ± 0.2 kg empty. It had a sacculated form and was composed of two parts (the cranial and caudal C1). Its parietal surface was in
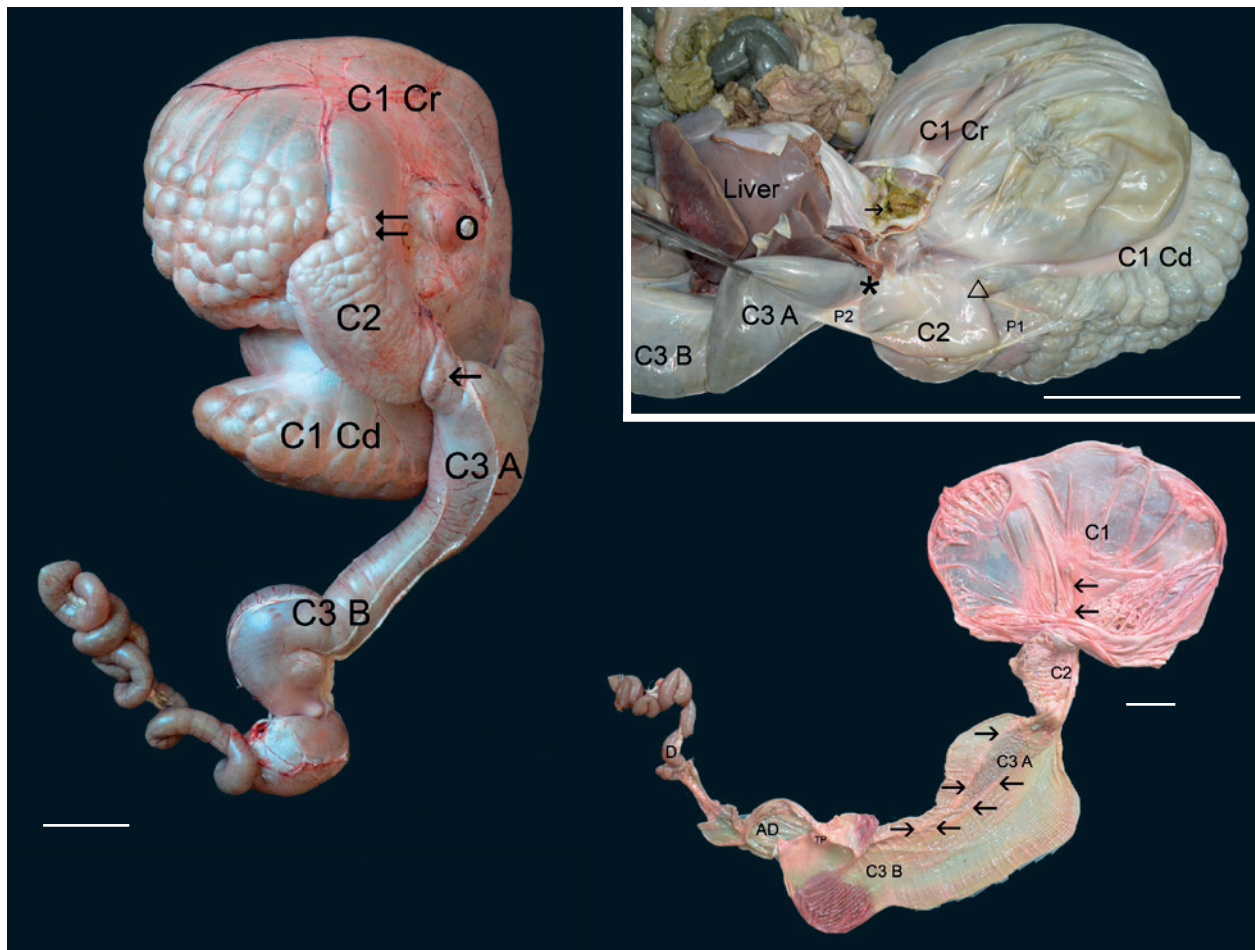
Fig. 1 A. Dromedary camel stomach. C1 Cr: Cranial part of first gastric compartment; C1 Cd: Caudal part of first gastric compartment; C2: Second gastric compartment C2; C3A and C3B: Proximal and distal parts of third gastric compartment C3; O: *Ostium cardiacum*; Double arrow: Position of the orifice 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; C1 Cd: Caudal part of first gastric compartment; C2: Second gastric compartment C2; C3A and C3B: Proximal and distal parts of third gastric compartment 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 dromedary 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: Duodenum; Arrows; Gastric groove. Scale bar = 10 cm.

contact with the left abdominal wall and its visceral surface was situated to the right side in contact with other viscera. The C1 did not show external grooves, and the most conspicuous characteristic of external conformation was the presence of glandular sacs. The biggest area of glandular sacs was situated on the visceral surface of the caudal sac (Fig. 1A). In the alpacas, the lengths of the cranial and caudal sacs of the C1 were 34.2 ± 6.7 cm and 35.1 ± 4.3 cm, respectively. The height of the C1 was 35.1 ± 5.9 cm. The distance between the cardia and the end of caudal sac of C1 was 37.5 ± 6.5 cm. The cardia opened into the cranial right part of the caudal C1, near to the orifice towards the C2.

The C2 was the smallest of the three stomach compartments (Figs. 1A, 1B). In alpacas, the full and empty C2 weighed 147 ± 38 g and 73 ± 40 g, respectively. The height and craniocaudal length of C2 were 10.4 ± 2.3 cm and 12.4 ± 3.5 cm. Whereas the transition of the C2 to

the C3 was evident in the external appearance of the stomach, the transition from C1 to C2 was less evident (Figs. 1A, 1B). Externally, C2 was in contact with the glandular sac of the caudal C1, and both structures were joined by a small serosal fold (Fig. 1B, P1). In addition, the C2 was joined to the proximal part of C3 (C3a) by another similar serosal fold (Fig. 1B, P2).

The tubular part of the stomach (C3) was composed of two parts (proximal and distal). The proximal part was the initial dilated part and the distal part was the subsequent elongated part (Fig. 1A). The proximal part of C3 was the smallest gastric compartment. In alpaca, its height was 8.7 ± 1.6 cm, and its craniocaudal length was 13.1 ± 2.7 cm. The curvature of the proximal part of C3 measured 22.1 ± 5.1 cm. For the distal part of C3 the curvature major and minor lengths were 52.5 ± 10.3 cm and 24.6 ± 4.0 cm, respectively. The whole full and empty C3 weighed 843 ± 279 g and 210 ± 59 g, respectively.
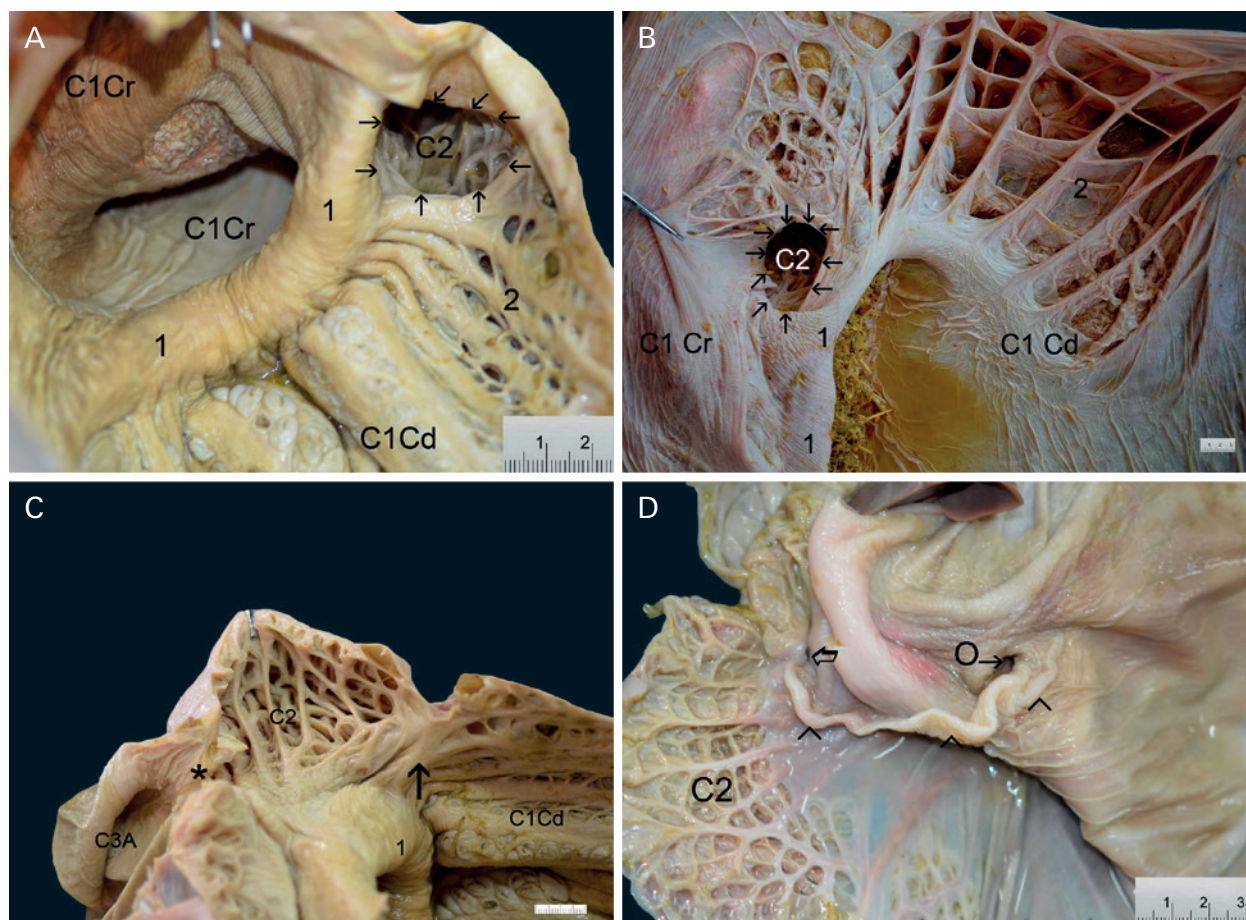
Fig. 2 A. Internal view of cranial part of C1 and C2 of alpaca stomach. C1Cr: Cranial part of first gastric compartment; C1 Cd: Caudal part of first gastric compartment; C2: Second gastric compartment C2; Arrows: Orifice between C1 and C2; 1: Transverse pillar of C1; 2: Glandular sac area of C1 Cd. **B** 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.

Internally, the C1 was structured by the typical pillars and glandular sac areas (Fig. 1C); the C2 was also characterized by the presence of a dense network of trabeculae that form the glandular sac areas (Fig. 1C). The orifice between the C1 and the C2 appeared comparatively small, measuring 3.2 ± 0.3 cm in width and 4.2 ± 0.3 cm in height in alpacas (Fig. 2A) and 8.5 ± 0.7 cm in diameter in dromedaries (Fig. 2B). Nevertheless, this opening still appeared large compared to the small canal that linked the C2 to the C3 with a diameter of approximately 2.2 ± 0.7 cm in alpacas and 3.1 ± 0.5 cm in dromedaries. Both orifices were positioned on opposing sides in the dorsal aspects of C2 (Fig. 2C). From the cardia in C1, a muscular lip extended across the C2 and ended in the orifice between C2 to C3 (Fig. 2D). In the proximal part of C3, the remains of the muscular ridges of the gastric groove were still visible (Fig. 1C).

The small intestine of alpacas measured 771 ± 140 cm (Fig. 3B). The gross intestine length was 610 ± 128 cm.

Therefore, the length ratio of the small intestine vs. large intestine was 1.26. The cecum length was 14.8 ± 2.6 cm, and its full and empty weights were 59 ± 15 g and 18 ± 3 g. The cecum was attached to the ileum by a narrow ileocecal fold. Both, the cecum and the colon were smooth externally, and did not have sacculations or bands. The ascending colon was the most developed portion of the whole intestine, and it had the most complex arrangement (Fig. 3B). The ascending colon had three ansae: the proximal ansa, the spiral ansa and the distal ansa. The cecum and the proximal ansa were the widest portion of the intestine. The proximal ansa described a 360° gyrus and was followed by the spiral ansa. The length of the proximal ansa was 88 ± 23 cm, and its full and empty weights were 636 ± 226 g and 105 ± 21 g, respectively.

The spiral ansa of alpacas was formed by 5.5 centripetal gyri, a central flexure, and 5.5 centrifugal gyri. The proximal ansa surrounded the spiral ansa completely. The spiral ansa was visible as a mass in the form of a

Fig. 3 A. Intestine of the alpaca without mesenterium. 1: Duodenum; 2: Jejunum; 3: Ileum; 4: Cecum; 5: *Ansa proximalis* of ascending colon; 6: *Ansa spiralis* of ascending colon; 7: *Ansa distalis* of ascending colon; 8: Descending colon. **B.** Abdominal digestive organs of the alpaca. 1: Liver; 2: Stomach; 3: Duodenum; 4: Jejunum; 5: *Ansa proximalis* of ascending colon; 6: *Ansa spiralis* of ascending colon; 7: Ascending mesocolon; 8: *Ansa distalis* of ascending colon; 9: Transverse colon; 10: Descending colon. Scale bars in cm.

truncated cone and was fixed to the mesenterium of the *Colon ascendens* (Fig. 3B). The last centrifugal gyrus of the spiral ansa was followed by the distal ansa with an S-shaped disposition; the first curve was open caudally and the second was open cranially (Fig. 3B). At the level of the right colic flexure the second part of the *Ansa distalis* was followed by the short transverse colon that forms a simple curve around cranial mesenteric artery continuing in the descending colon. The latter continued as rectum at the entrance of the pelvic cavity. The length of the rest of the ascending colon (spiral and distal ansae), transverse, descending colon and rectum was 508±118 cm, and its full and empty weights were 593 ± 109 g and 234 ± 39 g, respectively.

Discussion

To the best of our knowledge, this is the first anatomical description of the gastrointestinal tract of the alpaca compared with dromedary camel. Smuts & Bezuidenhout (1987) described the anatomy of the stomach of the dromedary (*Camelus dromedarius*), and Wang *et al.* (2000) that of the Bactrian camel (*Camelus bactrianus*). Vallenas *et al.* (1971) described the anatomy of the stomach of two llamas (*Lama glama*) and one guanaco (*Lama guanicoe*), and Alzola *et al.* (2004) described the topography and morphology of stomach of llama (*Lama glama*), so that the only camelid species not described with respect to digestive anatomy remains the vicuña (*Vicugna vicugna*). So far, no apparently relevant differences in the digestve tract anatomy between camelid species have been noted.

In camelids, the stomach is composed of only three compartments (Vallenas *et al.*, 1971; Langer, 1988; Clayton *et al.*, 1996; Wang *et al.*, 2000). The names of C1, C2 and C3 are used by most authors (e.g. Cummings *et al.*, 1972; von Engelhardt & Sallmann, 1972; Luciano *et al.*, 1979; Yarbrough *et al.*, 1995; Van Hoogmoed *et al.*, 1998; Wang *et al.*, 2000). Galotta *et al.* (1994) used the terms proximal, intermediate and distal for C1, C2 and C3, and this nomenclature was adopted in anatomical textbooks (Barone, 1997), but camelids never were added to Nomina Anatomica Veterinaria (2012).

In broad terms, the three forestomach compartments of camelids can be functionally compared to the rumen, reticulum and omasum of ruminants (Clauss & Hofmann, 2014). Similar to the rumen, the C1 is the main location of fermentative digestion, and the typical stratification of rumen contents (Clauss *et al.*, 2009; Hummel *et al.*, 2009) has also been described qualitatively in camelids (Vallenas *et al.*, 1971), including its visualization by computer tomography (Stieger-Vanegas & Cebra, 2013). In contrast to taxonomic ruminants, the C1 of camelids is not papillated, but both the C1 and the C2 contain sacculated areas that do not have a direct counterpart in the reticulorumen of taxonomic ruminants (Vallenas *et al.*, 1971). Although the contractions of the forestomach show qualitative differences between ruminants and camelids corresponding to the anatomical differences (Lechner-Doll *et al.*, 1995), there is no indication that differences in motility could be linked to a lower food processing capacity in camelids.

The C2 has been considered to be similar to the reticulum, as the location of particle sorting according to their buoyancy; correspondingly, Vallenas *et al.* (1971) state that similar to the reticulum (Clauss *et al.*, 2009; Hummel *et al.*, 2009), this compartment always contains relatively liquid contents. Finally, similar to the omasum, the C3 has been shown to re-absorb a large proportion of fluid (von Engelhardt *et al.*, 1979). The similarity in terms of the distribution of fluids and fluid reabsorption, typically considered a prerequisite for the particle sorting mechanism, is, however, apparently not matched by

a similar clear-cut threshold from which onwards only small particles are found in the forestomach (Lechner-Doll & von Engelhardt, 1989).

Potentially, an important difference in the overall morphology of the forestomach is the arrangement of the second as compared to the first chamber. Whereas in ruminants, the reticulum is located along the major axis of the rumen, namely cranial to it, the C2 is not aligned with the major axis of the C1 in camelids. In ruminants, the connecting opening (the *Ostium rumino-reticulare*) is clearly of a larger size, with 9 × 5.5 cm in a bushbuck (*Tragelaphus scriptus*) or 7 × 4 cm in a reedbuck (*Redunca redunca*) (comparable in body mass to the alpacas of this study, with an opening between C1 and C2 of 3 × 4 cm), and app. 22 × 8 cm in the African buffalo (*Syncerus caffer*) (Hofmann, 1973), comparable to the dromedaries of this study, with an opening between C1 and C2 of 8.5 cm diameter. Actually, the size of the opening between C1 and C2 in alpacas is of similar size as the *Ostium rumino-reticulare* in dikdik (*Madoqua* spp.) or suni (*Neotragus moschatus*) (Hofmann, 1973), some of the smallest ruminant species. Compared to the ruminant forestomach, the forestomach of camelids thus contains a bottleneck between C1 and C2, which might be one reason why camelids cannot process the high amounts of food taxonomic ruminants can.

The opening between the C2 and C3, with diameters of 22 – 31 mm, is of a similar dimension as the *Ostium reticulo-omasale* in ruminants of comparable body size, ranging from 20 mm in the impala (*Aepyceros melampus*) to 40 mm in the African buffalo (Hofmann, 1973). A hypothesis originating from the comparison of the openings in the present study is that due to the smaller connection between the C2 and the C1, and because both the opening between C2 and C1 and the opening between C2 and C3 are in a dorsal position, larger particles might more easily 'erroneously' pass on to the C3 during contractions of the C2, whereas in ruminants, similar incidences are less likely to occur due to the larger size difference between, and the different arrangement of, the *Ostium rumino-reticulare* and the *Ostium reticulo-omasale*.

With respect to the intestinal measurements, the ratio of small:large intestine was 1.26 in the alpaca of the present study, and 2.0 (40 m *vs*. 19.5 m) in dromedaries (Smuts & Bezuidenhout, 1987), which are both low compared to ratios typical for ruminants (Hofmann, 1989) and, in the case of the alpaca, distinctively lower than ratios typically reported in cervids (Pérez *et al.*, 2008). We had commented previously that this ratio is unlikely to be linked to feeding type (Pérez *et al*., 2008). Rather, the length of the large intestine is related to the water metabolism of a species (Woodall & Skinner, 1993). Camelids are particularly adapted to water conservation, and the number of turns of spiral ansae hence is higher than in domestic ruminants. The spiral ansa of alpacas consists of 5.5 centripetal gyri, 1 central flexure and 5.5 centrifugal gyri. According to textbooks (Barone, 1997; König & Liebich, 2015) there are, by contrast, only 3 to 4

gyri in each direction in small domestic ruminants. Unpublished studies about tolerance to restriction of water showed that water consumption is lower in alpacas and llamas compared to sheep (cited in San Martín, 1994), and Rübsamen & von Engelhardt (1975) showed that under water restriction, llamas reduce food intake to a lesser degree than goats.

To conclude, the results of this study give evidence from macroscopic anatomy about the capacity of camelids to conserve water and live in arid environments, and about a potential reason for their forestomachs' lesser capacity to process similarly high amounts of food with appropriate particle sorting as taxonomic ruminants.

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