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Abstract

We describe the macroscopic anatomy of the intestine of the giraffe (Giraffa camelopardalis). The small intestine was divided into duodenum, jejunum and ileum as usual. The caecum was attached to the ileum by a long ileocaecal fold, and to the proximal ansa of the ascending colon by a caecocolic fold. The ascending colon was the most developed portion of the gross intestine and had the most complex arrangement with three ansae: the proximal ansa, the spiral ansa and the distal ansa. The proximal ansa completely encircled the caecum, describing a 360° gyrus, and represented the widest portion of the intestine. The spiral ansa was formed by three and a half centripetal gyri, a central flexure and three centrifugal gyri. The last centrifugal gyrus left the spiral and described nine flexures of different form and direction over the left side of the mesentery. The two portions that formed each of these flexures ran parallel to each other. The last part of this gyrus ran parallel to the jejunum. When compared with domestic cattle, giraffe had a comparatively short small intestine and a comparatively long large intestine, with a resulting small ratio of small:large intestine. Reasons are presented why this should be considered a peculiarity of cattle-like ruminants rather than a different representative of a browser-grazer dichotomy in general.

Gross anatomy of the intestine in the giraffe (*Giraffa camelopardalis*)

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Running head: Giraffe intestine

With 3 figures and 1 table.

Summary

We describe the macroscopic anatomy of the intestine of the giraffe (*Giraffa camelo-pardalis*). The small intestine was divided into duodenum, jejunum and ileum as usual. The cecum was attached to the ileum by a long ileocecal fold, and to the proximal ansa of the ascending colon by a cecocolic fold. The ascending colon was the most developed portion of the gross intestine and had the most complex arrangement with three ansa: the proximal ansa, the spiral ansa, and the distal ansa. The proximal ansa completely encircled the cecum, describing a 360° gyrus, and represented the widest portion of the intestine. The spiral ansa was formed by three and a half centripetal gyri, a central flexure and three centrifugal gyri. The last centrifugal gyrus left the spiral and described nine flexures of different form and direction over the left side of the mesentery. The two portions that formed each of these flexures ran parallel to each other. The last part of this gyrus ran parallel to the jejunum. When compared to domestic cattle, giraffe had a comparatively short small and a comparatively long large intestine, with a resulting small ratio of small:large intestine. Reasons are presented why this should be considered a peculiarity of cattle-like ruminants rather than a difference representative of a browser-grazer dichotomy in general.

Key words: anatomy, intestine, peritoneum, abdomen, gut, mesenteria

Introduction

The giraffe (*Giraffa camelopardalis*) is both the largest extant ruminant (Owen-Smith, 1988) and a strict browser (Leuthold and Leuthold, 1972, Pellew, 1984, Codron et al., 2007). In the debate whether body size alone (Gordon and Illius, 1994) or adaptations to the natural diet in terms of a browser-grazer-classification (Hofmann, 1989) are the major influence factors on the digestive anatomy and physiology, the giraffe has therefore been considered an ideal research model (Clauss and Lechner-Doll, 2001). The existing evidence indicates that, when compared to large grazing ruminants, the giraffe has a smaller rumen with weaker rumen pillars (Clauss et al., 2003b), lower reticular crests (Hofmann, 1973), a smaller omasum (Clauss et al., 2006a), less developed masseter muscles (Clauss et al., 2008), average-sized parotis and larger mandibular glands (Hofmann et al., 2008), a uniform rumen papillation indicative for an absence of stratification of the rumen contents (Clauss et al., 2009), and a less distinct selective particle retention in the forestomach (Clauss et al., 2006b). The teeth of the giraffe are different from those of grazing ruminants (Janis, 1995), which results in a reduced chewing efficiency on artificial diets in captivity (Clauss et al., 2002) as compared to the natural diet (Hummel et al., 2008a). In summary, these results gained from giraffes indicate that feeding adaptations most likely play also an important role in shaping the digestive morphology and physiology of ruminants, not only body size. Among the predictions made by Hofmann (1989) that have not been tested so far is that grazing ruminants have a higher ratio of small intestine vs. large intestine (on a length measurement basis, with ratios of 1.9-2.7 being typical for browsing and 4.0-4.5 typical for grazing ruminant species). To our knowledge, length measurements of the intestinal tract of the giraffe have not been published so far, and therefore, we wanted to use the opportunity of two giraffe dissections to determine the according ratio in this species.

Additionally, given deviations observed in the intestinal tract of cervids from the pattern usually seen in domestic ruminants (Pérez et al., 2008), we wanted to test whether the giraffe – as a representative of a comparatively old ruminant family – showed similarities to cervids in this respect.

Other objective of this work is to give a description of the anatomy of the intestine of the giraffe, including its arteries in order to improve the existing knowledge on this species.

Materials and Methods

The intestinal tracts of two giraffes were used in this study. At a Zoological Garden of Uruguay, a juvenile male giraffe (25 months of age) weighing 754 kg was died of acute traumatic pericarditis. The animal was dissected at the Veterinary Faculty of the University of Montevideo. After removal of the intestinal tract from the abdominal cavity, the mesenteric insertion sites and arterial blood supply were studied and documented by digital photography (Nikon D200, Nikon, Paris, France). After dissection of all mesenteric attachments, the lengths of the different sections of the intestinal tract were taken on the anti-mesenteric side with a standard measuring tape. Similar procedures were used for an adult, female giraffe (17 years of age) weighing 946 kg from a European Zoo. The animal had to be euthanized due to bilateral fractures of the distal phalanx of the forelimbs. It was pregnant, and the foetus, uterus and associated fluids had a total weight of 146 kg. In this animal, length measurements were performed on the small and large intestine. For comparison, data from the other extant giraffid species, the okapi (*Okapia johnstoni*), was taken from Clauss et al. (2006c), and data for domestic cattle was collated.

Terms are used in agreement with the Nomina Anatomica Veterinaria (2005), and the different intestinal sections were defined according to the Nomina Anatomica Veterinaria (2005) and Barone (1997).

Results

In both giraffes investigated, the small intestine had about twice the length of the large intestine (Table 1). The small intestine (Fig. 1) was divided into duodenum, jejunum and ileum. The ileum (Fig. 3) opened into the large intestine through the ileal ostium, which was found at the junction of the cecum with the ascending colon. The cecum (Fig. 3) was attached to the ileum by a long ileocecal fold, and to the proximal ansa of the ascending colon by a cecocolic fold (Fig.3). Both the cecum and the colon were smooth externally and had no sacculations or bands. The ascending colon was the most developed portion of the whole intestine and it had the most complex arrangement. The ascending colon (Figs. 1, 2) had three ansae: the proximal ansa, the spiral ansa, and the distal ansa. The proximal ansa completely encircled the cecum, describing a 360° gyrus (Fig. 1). This was the widest portion of the intestine. The spiral ansa was formed by three and a half centripetal gyri, a central flexure and three centrifugal gyri (Fig. 2). The last centrifugal gyrus left the spiral and was found loose over the left side of the mesentery (Fig. 2), describing nine flexures of different form and direction. The two portions that formed each of these flexures ran parallel to each other. The last part of this gyrus, after describing the nine flexures, was straighter and ran parallel to the jejunum. This last part, once it reached the root of the mesentery, was placed within the concavity of the proximal ansa, where it became the distal ansa of the ascending colon. The distal ansa of the ascending colon lies medial to the proximal ansa and ascending duodenum and was continued cranially by the transverse colon, at the level of the right colic flexure. At the level of the left colic flexure, the transverse colon was continued by the descending colon. The latter continued as rectum at the entrance of the pelvic cavity. The arterial blood supply of the giraffe's intestine was provided mainly by the cranial mesenteric artery. The celiac and caudal mesenteric arteries supplied blood to the cranial and caudal portions of the intestine, respectively. The first two branches of the cranial mesenteric artery were the caudal pancreaticoduodenal artery for the pancreas and duodenum, and the middle colic artery for the transverse colon. The last centrifugal gyrus that appears intermingled with the jejunum was supplied by the jejunal arteries, which go to the jejunum. The cranial mesenteric artery gave off the ileocolic artery, which was directed caudally. The spiral ansa of the ascending colon was supplied by the colic and right colic branches of the ileocolic artery. This ileocolic artery also gave branches for the proximal ansa of the ascending colon, and the mesenteric ileal branch for the ileum. It then continued as the cecal artery. The cecal artery went in the ileocecal fold to the ileum, giving off branches to both cecum and ileum. These branches form a very thin and diffuse antimesenteric ileal branch within the ileocecal fold. The ileum was also supplied by the ileal arteries.

Discussion

The ascending colon of the giraffe had three ansae (proximal, spiral and distal) as it is described for bovines, ovines and caprine (Smith, 1955b, Smith, 1955a, Smith and Meadows, 1956, Smith, 1959, Barone, 1997), *Ozotoceros bezoarticus* (Pérez et al., 2008) and for other deer (Westerling, 1975). Also in agreement with the literature of the domestic ruminants, the spiral ansa consisted of centripetal gyri, a central flexure and centrifugal gyri (Barone 1997; Nomina Anatomica Veterinaria 2005).

In the giraffe the most conspicuous finding is that the last centrifugal gyrus of the spiral ansa that was found loose over the left side of the mesentery, describing several flexures, with a last part that was straighter and ran in parallel to the jejunum. In the cow, the last centrifugal gyrus accompanies the spiral, but in sheep, this gyrus runs in parallel to the jejunum on the left side of the mesenterium. This last centrifugal gyrus of the giraffe was supplied by the jejunal arteries in similar form to descriptions in sheep (Barone 1997). In accordance with the established knowledge (Barone 1997; Nomina Anatomica Veterinaria 2005), the transverse colon was found cranial to the root of the mesentery and the cranial mesenteric artery, and it was supplied by the middle colic artery.

We observed in the giraffe one additional peritoneal fold (cecocolic fold) that we only observed in the pampas deer (Pérez et al., 2008), and that was not described in other ruminants, such as bovines, ovines, and caprines (Barone 1997; Nomina Anatomica Veterinaria 2005), or other deer species (Westerling, 1975).

The arterial supply of the intestine of the giraffe has more similarities with that described for sheep than for the cow (Barone 1997). Still, there are differences in the arrangement of the arteries that go to the ileum and to the proximal ansa of the ascending colon. Because the last centrifugal gyrus in sheep is simpler and shorter (Barone 1997) than in the giraffe, there are more branches from the jejunal arteries for this gyrus in the giraffe. In the cow, there is a collateral branch of the cranial mesenteric artery that does not exist in sheep (Barone 1997) or in the giraffe studied.

When comparing the ratios of the small vs. the large intestine length in giraffe and okapi to that of domestic cattle, the observation of Hofmann (1989) that ruminants of different feeding types have different intestinal length ratios appears to be supported. At 1.3-2.0, the ratio of giraffe and okapi is mostly even below the range of 1.9-2.7 given for typical browsing species. In contrast, domestic cattle – as a representative of grazing species – achieves ratios of 4.0-5.5 (Table 1), which is even higher than the range of 4.0-5.0 given by Hofmann (1989) for typical grazers. This high ratio is due to both a particularly long small intestine, and a particularly short large intestine, including a short caecum (Table 1). It has been known for a long time that cattle have, for their body size, short large intestines (Hecker and Grovum, 1975).

The reasons for this difference between cattle and giraffids can only be speculated upon. Cattle have significantly shorter fluid retention times than giraffids (Clauss et al., 2006b), which might lead to a particularly high yield of microbial protein from the cattle forestomach (see Hummel et al., 2008b). As this protein is not as easily digested as protein of plant origin (Van Soest, 1994), the long small intestine of cattle might represent an adaptation to this presumptive high influx of microbes. The short large intestine, on the other hand, could be a consequence of intra-abdominal space competition between organs. Mortolaa and Lanthier (2005) speculated that the observed, unusually high breathing frequency in cattle-like ruminants could stem from the fact that the particularly voluminous forestomach in these animals reduced the space available for the lung, thus necessitating compensatory high breathing frequencies. Similarly, Clauss et al. (2003a) had speculated that the high water content in the feces of large cattle-like ruminants – which defecate in 'pies' and therefore have a higher faecal moisture than species defecating in pellets, like the giraffids (Clauss et al., 2004) - could also be caused by the fact that the voluminous forestomach reduces the space available for the water-absorbing colon. These speculations would support the concept of Hofmann (1989) that in particularly adapted grazers, particularly high ratios of small vs. large intestines can be observed. However, long large intestines, and low faecal moisture contents, have also observed in several grazing wild ruminant species

(Woodall and Skinner, 1993, Hofmann, 1999, Clauss et al., 2004, Clauss et al., 2005, Pérez et al., 2008). Therefore, rather than characterizing a difference between feeding types, the observed differences in intestinal ratios more likely set cattle-like ruminants apart from other ruminant species.

References

Legends of figures

Figure 1: Left view of the intestine of the giraffe (*Giraffa camelopardalis*)
J: jejunum; C: Caecum; APC: ansa proximalis coli; Cp: centripetal gyri of the spiral ansa; Cf: centrifugal gyri of the spiral ansa LCG: last centrifugal gyri of the spiral ansa. The scale bar represents 10 cm.

Figure 2: Left view of the ascending colon of the giraffe (*Giraffa camelopardalis*)
M: mesenterium; J: jejunum; APC: ansa proximalis coli; Cp: centripetal gyri of the spiral ansa; Fc: flexura centralis; Cf: centrifugal gyri of the spiral ansa LCG: last centrifugal gyrus of the spiral ansa. The scale bar represents 10 cm.

Figure 3: Peritoneal folds of the caecum of the giraffe (*Giraffa camelopardalis*)
IL: ileum; C: Caecum (extended towards the bottom of the figure); APC: ansa proximalis coli; PI: ileocecal fold; CCF: caecocolic fold. The scale bar represents 10 cm.

Table 1. Intestinal measurements in giraffids (giraffe and okapi) as compared to domestic cattle.

Organ	*Giraffa camelopardalis*		*Okapia johnstoni*[1]		Domestic cattle[2]
	Juvenile	Adult	Juvenile	Adult	Adult
Body mass (kg)	754	800	-	231	-
Duodenum (cm)	100	-	-	98	-
Jejunum (cm)	2630	-	-	2025	-
Ileum (cm)	52	-	-	54	-
Small intestine (SI) (cm)	2782	4740	1981	2177	3760-6300
Caecum (cm)	44	96	31	46	32-75
Ansa proximalis coli (cm)	120	277	127	166	-
Ansa spiralis coli (cm)	1018	-	478	894	-
Colon transversum & descendens (cm)	1200	-	479	527	-
Rectum (cm)	50	-	135	80	-
Large intestine (LI) (cm)	2432	2383	1250	1713	730-1200
Total intestinal length (cm)	5214	7123	3231	3890	-
Ratio SI:LI	1.1	2.0	1.6	1.3	4.0-5.5

[1] (Clauss et al., 2006c)

[2] (Zietzschmann et al., 1943, Habel, 1975, Barone, 1997, Baldwin et al., 2004; and W. Pérez, pers. obs.)