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Abstract

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2. A new interpretation of established findings regarding the digestive tract of sloths illustrates that the interplay of posture, anatomy, the density of ingesta, and gravity can provide a novel explanation of behavioural and morphological adaptations in herbivores, as the average particle size and dry matter content increases within their forestomach from its caudal towards its cranial portion. In sloths, this could be indicative of a stratification of ingesta occurring in the upright sitting posture adopted while resting, as opposed to their characteristic upside-down posture when foraging.

3. The sitting resting posture of sloths could therefore be an adaptation to exploit the tendency of the forestomach contents to stratify in order to pass larger, more difficult-to-digest particles faster from the fermentation chamber.
A potential interplay of posture, digestive anatomy, density of ingesta and gravity in mammalian herbivores, or why sloths do not rest upside down

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Running head: Digestive anatomy and gravity
ABSTRACT

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2. A new interpretation of established findings regarding the digestive tract of sloths illustrates that the interplay of posture, anatomy, the density of ingesta, and gravity can provide a novel explanation of behavioural and morphological adaptations in herbivores, as the average particle size and dry matter content increases within their forestomach from its caudal towards its cranial portion. In sloths, this could be indicative of a stratification of ingesta occurring in the upright sitting posture adopted while resting, as opposed to their characteristic upside-down posture when foraging.

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Keywords: digestive physiology, herbivory, particle size, particle density, resting posture
Mammalian herbivores have to adapt to the trade-offs inherent to their natural diet: Plant particles require time for bacterial fermentation; if the passage of ingesta is delayed for this purpose, then the capacity for intake of new food becomes limited. The most widespread digestive strategy to solve this problem is the selective retention of small, easier-to-digest particles and the selective, faster excretion of larger, more difficult-to-digest particles. This allows the digestive tract to be cleared of the less valuable, bulky and potentially intake-limiting fraction (Björnhag, 1989). This strategy is shared by marsupial foregut (Hume, 1984) and hindgut fermenters (Cork & Foley, 1991), rodents and lagomorphs (Björnhag, 1987), equids (Björnhag et al., 1984) and probably more animal groups yet to be investigated. The notable exceptions to this rule are ruminating herbivores; in these animals, the selective retention of the larger particles of ingesta is a viable strategy, as they can be reduced in size by repeated mastication. Ruminating herbivores can therefore make the greatest use of a given amount of forage, although their digestive strategy imposes certain restrictions on their potential range of adaptation because of the distinctive intake-limiting effect of the selective retention of large particles if ingesta (Clauss et al., 2003).

The selective retention of small particles in the hindgut or the macropod forestomach is predominantly achieved by a combination of taeniae and haustrae and peristaltic and antiperistaltic movement of the gut walls, although this general principle is achieved by slightly different anatomical designs in different animal species (Hume & Sakaguchi, 1991). In the majority of morphophysiological designs, the gut itself actively separates the fractions according to particle size. To date, another physiological principle has received little attention, other than in ruminating animals where it ensures the selective retention of large particles in the rumen (reviewed by
Lechner-Doll et al., 1991; c.f. Fig. 1): In a voluminous gastrointestinal compartment, ingesta particles tend to separate by gravity according to their different functional density, with denser particles sinking to the bottom and less dense particles floating. As larger particles in general tend to be lighter and smaller particles tend to be denser, this means that due to the density gradient alone, smaller and larger particles can separate themselves in a gastrointestinal chamber of sufficient volume and liquidity.

The propensity to separate, i.e. the functional density gradient, differs among different forages. It is most prominent in grass ingesta, as is notable in the distinct stratification of rumen contents of grazing ruminants (Hofmann, 1973; Sutherland, 1988). Browse, on the other hand, does not induce a detectable stratification of rumen contents, even though in browsing ruminants, a (probably less distinct) selective retention of large particles does occur in the rumen (Clauss et al., 2001). Investigations identifying those characteristics of forage that determine the functional density gradient of its particles are warranted. The stratified rumen contents of grazing ruminants are reflected by a higher dry matter content in the dorsal region and a higher fluid content in the ventral region (Hauffe & von Engelhardt, 1975), and by larger particles in the floating fraction (Sutherland, 1988). The general principle of a voluminous gastrointestinal compartment with stratifying particles of ingesta is that if the outflow is ventral, then small particles will leave earlier than large ones (as in ruminants), and if the outflow is dorsal, then large particles should leave earlier than small ones (a theoretical assumption), simply due to the difference in likelihood of particles of different sizes being near the outflow when it opens.
It is reasonable to suspect that a stratification of gastrointestinal contents occurs in animals other than ruminants, for example in sections of the large hindgut of forage-fed equids. Reports of impactions in the caecal head in horses that had been fed chopped grass indicates that these longer particles float on top of the other caecal contents and form a “fibrous raft” just as grass particles do in the rumen of a cow. Regarding the colonic separation mechanism in horses, Björnhag et al. (1984) state that it will only function if “the contents of the right dorsal colon separate easily into a fluid and a more solid portion” – the functional density gradient proposed here could be one solution for this problem.

An obvious, yet important characteristic of the separation of particles due to a density gradient is that it only functions along a gravity gradient. Lighter, larger particles will only gather in the dorsal region is higher than the ventral region. The relevance of this simple truth is reflected by the one resting and sleeping posture all ruminating animals invariably share: They do not lie on their side, but rest in sternal recumbency (Balch, 1955), thus ensuring that the relative positions of the in- and outflow orifices of their forestomach remain unchanged. In this respect, it is interesting to note that horses also hardly ever change their relative position to the gravity gradient – when resting, these animals either remain standing with a patellar tendon locked, or they also remain in sternal recumbency when sleeping, lateral recumbency being the exception (Littlejohn & Munro, 1972).

The hypothesis that a potential functional density gradient of ingested forage could play a role in animals other than ruminants would gain further credibility if similar observations in another animal group could be cited. I suggest that sloths
(Bradypodidae and Megalonychidae) could present such a case, and I propose a new interpretation of observations made on the forestomach contents of sloths. In terms of the positioning of body parts relative to the gravity gradient, the sloth is an obvious deviator from the common mammal pattern, moving in its well-known “upside-down” position (Goffart, 1971). However, this position, although considered to pose very little energy demands on the animals due to their characteristic limb anatomy (Mendel, 1985), is not the one these animals adopt for the major part of the day.

Goffart (1971) comments that “it has been wrongly stated that these arboreal animals spend most of their time hanging from the boughs. This is untrue for both species.” Sloths spend most of their time resting in a perched-sitting position, mostly squatting in a tree fork, or sometimes embracing a small trunk (Goffart, 1971). It is in this resting posture that the fundus of the sloth’s complex forestomach is closer to the ground, and the connecting pouch and the entrance to the prepyloric stomach (Klinckowström, 1895; Goffart, 1971; Langer, 1988) are farther from the ground. It has been reported that the prepyloric stomach and the connecting pouch contain larger particles than the other forestomach compartments (Britton, 1941; Langer, 1988), and that the proportion of large particles increases from the fundus to the connecting pouch and the prepyloric stomach (Foley et al., 1995; c.f. Fig. 2). Additionally, the contents of the prepyloric stomach have been found to be drier than those of other compartments (Böker, 1932; Britton, 1941; Denis et al. 1967), and again an increase in dry matter content from fundus to connecting pouch and prepyloric stomach was demonstrated (Foley et al., 1995). Therefore I hypothesize that the interplay of the sloth’s resting position, its forestomach anatomy, and a density gradient in its gut contents enable these animals to achieve, with a forestomach, a digestive strategy that
other arboreal folivores achieve with a hindgut fermentation chamber: the selective passage of larger and the selective retention of smaller particles (Cork & Foley, 1991).

Sloths have very long ingesta passage rates (Honigmann, 1936; Montgomery & Sunquist, 1978; Foley et al., 1995). A potential differential passage of large and fine particles from the forestomach would have to be confirmed by experimental studies. Foley et al. (1995) did use both solid and particle markers in their study and found no difference in their excretion kinetics, but admitted that their particle markers were representative of very fine particles only. Montgomery & Sunquist (1978) observed extremely long retention times for comparatively large glass beads, but the high density of these particles probably prevents the results from representing actual ingesta movements. In general, ingesta passage studies in sloths are complicated due to the long defecation interval in these animals (e.g. Montgomery & Sunquist, 1978), which necessitates either the sacrifice of several animals dosed at different time intervals (Foley et al., 1995) or the use of forestomach fistulas (Montgomery & Sunquist, 1978), for the determination of differential passage rates from the forestomach. Montgomery & Sunquist (1978) determined the dry matter digestibility of large forage particles in the forestomach of fistulated free-ranging sloths. They measured a low digestion rate, which can be explained by the slow rate of fermentation documented by Foley et al. (1995), which in turn might, among other factors, be due to the sloths’ low metabolic rates (McNab, 1978) and accordingly low body temperatures (Goffart, 1971). Montgomery & Sunquist (1978) explicitly mention that sloths could be in danger of “starving with a full stomach because of low rates of food flow and because only a small portion of the food in the gut could be digested.” In theory, these animals, therefore, would benefit from a comparatively fast
excretion of larger, harder-to-digest particles, and retention of smaller, easier-to-digest particles.

Whether a stratification of forestomach contents in the sloth are part of a digestive adaptation mechanism, or are an insignificant side-effect of the sloth resting posture, remains an open question. It is interesting, however, that Goffart (1971) states that of the two existing sloth genera, *Choloepus* also rests or sleeps occasionally in the suspended hanging position. While *Bradypus* is strictly folivorous (Chiarello, 1998) and therefore theoretically more dependent on a particular particle separation mechanism, *Choloepus* includes a proportion of fruits, flowers and buds in its diet (Meritt, 1985). Such material that is more readily fermentable might give these species the freedom to vary their resting postures. Regrettably, quantitative data on the choice of resting postures in sloths is missing. Whereas browse material does not seem to induce a forestomach stratification in ruminants (Hofmann, 1973; Clauss et al., 2001), potential differences in forestomach motility and saliva characteristics might allow such a stratification to occur more distinctively in sloths.

Finally, I conclude that a detailed analysis of the positions of in- and outflow openings in the digestive tract of mammalian herbivores with respect to the gravity gradient, and to resting postures, could provide additional insight to the physiological mechanisms that allow mammals to be herbivorous.
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References


Fig. 1. Ruminant forestomach (rumen and reticulum, left lateral view) with ingesta stratification. Modified from Grau (1955). The arrow indicates the gravity gradient in both standing and resting position.
Fig. 2. Sloth forestomach (dorsal view) with ingesta stratification. Modified from Klinckowström (1895); nomenclature according to Langer (1988); particle sizes indicated according to Langer (1988) and Foley et al. (1995). The arrow indicates the gravity gradient in the sitting resting position.