Narrative 4: Nonruminant foregut fermenters

Traditionally, animals with a forestomach such as hippos, sloths, peccaries, kangaroos, colobine monkeys and camelids had been termed 'ruminant-like'. In series of digestion studies that started with the doctoral thesis of Angela Schwarm

sponsored by grant OR 86/1-1 of the German Research Foundation (PI Sylvia Ortmann) in 2005 and a matching NaFöG grant of the Free University of Berlin

using particle markers of different size, e.g.

Schwarm, ..., **Clauss** (**2009**) More efficient mastication allows increasing intake without compromising digestibility or necessitating a larger gut: comparative feeding trials in banteng (*Bos javanicus*) and pygmy hippopotamus (*Hexaprotodon liberiensis*). ***Comp Biochem Physiol A*** 152:504-512,

and physical investigations on digestive tract contents, e.g.

Schwarm, ..., **Clauss** (**2013**) No distinct stratification of ingesta particles and no distinct moisture gradient in the forestomach of nonruminants: the wallaby, peccary, hippopotamus, and sloth. ***Mamm Biol*** 78:412-421,

we demonstrated that particle sorting for rumination and the subsequent extreme chewing efficiency achieved by ruminating foregut fermenters sets them functionally apart from nonruminant foregut fermenters with distinct ecophysiological consequences:

Clauss et al. (**2010**) Evolutionary adaptations of ruminants and their potential relevance for modern production systems. ***Animal*** 4:979-992.

Clauss et al. (**2023**) Teeth and the gastrointestinal tract in mammals: when 1 + 1 = 3. ***Phil Trans R Soc B*** 378:20220544

In particular, we argued that rumination is not – as typically conceptualized in the literature on domestic animals – a constraint on food intake; on the contrary, it facilitates to combine foregut fermentation with high food intake levels.

This theory led to the involvement into data evaluation of first reports of 'rumination' behaviour in a primate species that apparently supported the concept that rumination is not a constraint for food intake, but facilitates higher food intakes:

Matsuda, ..., **Clauss** et al. (**2011**) Regurgitation and remastication in the foregut-fermenting proboscis monkey (*Nasalis larvatus*). ***Biol Lett*** 7:786-789.

with an ensuing long-standing research collaboration on foregut-fermenting primates with Ikki Matsuda; as well as involvement in work on macropods, with another long-standing cooperation with Adam Munn, e.g.,

Munn, ..., **Clauss** (**2012**) Retention of different-sized particles and derived gut fill estimate in tammar wallabies (*Macropus eugenii*): Physiological and methodological considerations. ***Comp Biochem Physiol A*** 161: 243-249

also using the macropod digestive tract as a model for multiple-phasic growth

Munn, ..., **Clauss** (**2022**) Scaling at different ontogenetic stages: gastrointestinal tract contents of a marsupial foregut fermenter, the western grey kangaroo *Macropus fuliginosus melanops*. ***Comp Biochem Physiol A*** 264: 111100

The fact that 'rumination', or 'merycism', occurs in various species that do not have apparent adaptations for digesta sorting keeps fascinating me, but so far, attempts to find patterns in the use of 'merycism' have not been successful:

Vendl, ..., **Clauss** (**2017**) Merycism in western grey (*Macropus fuliginosus*) and red kangaroos (*Macropus rufus*). ***Mamm Biol*** 86:21-26

Work on camelids corroborated the existing view of convergent evolution in camelids and taxonomic ruminants (as both groups ruminate, and have a separation mechanism in their forestomach), due to the difference in morphology but the similarity in function:

Pérez , ..., **Clauss** (**2016**) Macroanatomical aspects of the gastrointestinal tract of the alpaca (Vicugna pacos) and dromedary (Camelus dromedarius). ***Vertebr Z***ool 66:419-425

Dittmann, ..., **Clauss** (**2015**) Digesta retention patterns of solutes and different-sized particles in camelids compared with ruminants and other foregut fermenters. ***J Comp Physiol B*** 185:559-573,

Dittmann, ..., **Clauss M** (**2017**) Ingestive mastication in horses resembles rumination but not ingestive mastication in cattle and camels. ***J Exp Zool A*** 327: 98-109

Idalan, ..., **Clauss** (**2019**) Physical characteristics of gastrointestinal content of llama (*Lama glama*). ***J Anim Physiol Anim Nutr*** 103:1015-1022.

As reviewed in our global eutherian evaluation

Langer, **Clauss** (**2018**) Morphological adaptation of the eutherian gastrointestinal tract to diet. ***Vertebr Zool*** 68: 237-252

the functions of the forestomach in cetaceans and muroid rodents remain to be described. For the muroid forestomach, we presented a very comprehensive catalogue of anatomy and demonstrated that quantitative anatomical data that could be derived from existing drawings does not correlate with any relevant biological species characteristic that we had access to

Steiner, **Clauss** et al. (**2022**) No news from old drawings? Stomach anatomy in muroid rodents in relation to body size and ecology. ***J Morphol*** 283: 1200-1209

Work on nonruminant foregut fermenters continues through collaborations on colobine monkeys and muroid rodents.