Narrative 10: Chewing and particle size reduction

Chewing efficiency is a crucial part of herbivore digestive physiology. I was introduced to the principle of sieve analysis when assessing a larger set of zoo samples on my own

Clauss et al. (**2002**) Faecal particle size distribution in captive wild ruminants: An approach to the grazer/browser-dichotomy from the other end. ***Oecologia*** 131: 343-349

Originating from this, were the first introduce chewing efficiency as a concept in a broad comparative context, with a large original dataset

Fritz, ..., **Clauss** (**2009**) Comparative chewing efficiency in mammalian herbivores. ***Oikos*** 118:1623-1632
Fritz, ..., **Clauss** (**2010**) To chew or not to chew: faecal particle size in herbivorous reptiles and mammals. ***J Exp Zool A*** 313: 579-586
Fritz, ..., **Clauss** (**2011**) Gizzard vs. teeth, it's a tie: food-processing efficiency in herbivorous birds and mammals and implications for dinosaur feeding strategies. ***Paleobiol*** 37: 577-586

For her dissertation, Julia Fritz was awarded the "**Award of the H. Wilhelm Schaumann Stiftung**" for an excellent dissertation thesis in the field of animal nutrition in 2008.

setting an analytical standard

Fritz, ..., **Clauss** (**2012**) Condensing results of wet sieving analyses into a single data: a comparison of methods for particle size description. ***J Anim Physiol Anim Nutr*** 96:783-797

For the contribution "Condensing results of wet sieving analyses into a single data: a comparison of methods for particle size description", Julia Fritz was awarded the "**Helmut-Meyer-Award 2011**" of the European Society of Veterinary and Comparative Nutrition (ESVCN).

Using these data, we could show that the tradeoff between chewing efficiency and digesta retention (because larger particles need more time for digestion) is reflected in the digestive physiology of nonruminant herbivores

Clauss et al. (**2009**) Evidence for a tradeoff between retention time and chewing efficiency in large mammalian herbivores. ***Comp Biochem Physiol A*** 154: 376-382

We corroborated our results in a second large-scale original dataset, also again showing that functional ruminants (i.e., ruminants and camelids) are peculiar in terms of their chewing efficiency

Clauss et al. (**2015**) Faecal particle size: digestive physiology meets herbivore diversity. ***Comp Biochem Physiol A*** 179:182-191,

Our standardized approach has since been used repeatedly, and led to collaborations with primatologists, e.g.

Weary, Wrangham, **Clauss** (**2017**) Applying wet sieving fecal particle size measurement to frugivores: a case study of the Eastern chimpanzee (*Pan troglodytes schweinfurthii*). ***Am J Phys Anthropol*** 163: 510-518

but also with researchers dealing with other species, e.g.

Naumova, ..., **Clauss** , Degen (**2021**) Particle size distribution along the digestive tract of fat sand rats (*Psammomys obesus*) fed four chenopods. ***J Comp Physiol B*** 191: 831-841

We demonstrated differences in chewing behaviour between equids and ruminants, e.g. first in a pilot study using conventional counting

Janis, ..., **Clauss M** (**2010**) Comparative ingestive mastication in domestic horses and cattle: a pilot investigation. ***J Anim Physiol Anim Nutr*** 94: e402-e409,

and later in a comparative study with chewing halters

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

Our work on chewing behaviour led to invited plenary talks at the 6th European Equine Health & Nutrition Congress, Gent 2013 ('*Digestive physiology and feeding behaviour of equids – a comparative approach*'), the 5th Meeting on Dysphagia in Zurich 2014 ('*Merycism and rumination – a comparative view of an evolutionary adaptation and a behavioural disorder*') and at the German Veterinary Congress, Leipzig 2018 ('*Chewing and dental biology of equids compared to other herbivores*').

The finding that ruminants apparently delay heavy-duty chewing until after digesta is washed and regurgitated found support from a series of studies showing that abrasives are washed off from digesta at those locations from which material is recruited for regurgitation in the forestomach of ruminants and camemlids, e.g.

Hatt, ..., **Clauss** (**2019**) The rumen washes off abrasives before heavy-duty chewing in ruminants. ***Mamm Biol*** 97:104-111.
Valerio, ..., **Clauss** (**2022**) The ruminant sorting mechanism protects teeth from abrasives. ***PNAS*** 119: e2212447119

The 2022 PNAS paper received its own praising commentary in the same journal: *Sanson GD (2023) Reassessing assumptions about the evolution of herbivore teeth. PNAS 120: e2219060120*

Two studies aimed at other hypotheses generated evidence for the relevance of the number of teeth and the corresponding size of occlusal surface available for chewing, showing a decrease in chewing intensity in cattle – putatively linked to the molar eruption sequence

Grandl, ..., **Clauss** (**2018**) Kinetics of solutes and particles of different size in the digestive tract of cattle of 0.5 to 10 years of age, and relationships with methane production. ***J Anim Physiol Anim Nutr*** 102: 639-651,

and in the never-described effect of the peculiar dental physiology of elephants that led to comparatively high level of media attention (https://www.3sat.de/wissen/nano/nano-vom-15-juni-2016-100.html)

Schiffmann, ..., **Clauss** (**2019**) Elephant body mass cyclicity suggests effect of molar progression on chewing efficiency. ***Mamm Biol*** 96:81-86.

In ruminants, the resting posture is linked to the sorting mechanism in the forestomach, forcing adult ruminants to mainly rest in sternal recumbency. We performed a pilot study on a shift in the main resting posture during ontogeny in calves

Pucora & **Clauss** (**2018**) Change in resting position in dairy calves during the first weeks of life. ***Can J Anim Sci*** 98: 386-389,

and across a large variety of mammalian herbivore species

Pucora, ..., **Clauss** (**2019**) Resting postures in terrestrial mammalian herbivores. ***J Mammal*** 100: 552-563.

We showed that chewing intensity does not substantially vary with food intake in rabbits and goats

Findeisen, ..., **Clauss** (**2021**) Increasing food intake in domestic goats (*Capra hircus*): measured effects on chewing intensity are probably driven by escape of few, large particles from the forestomach. ***Comp Biochem Physiol A*** 257: 110972,

Findeisen, ..., **Clauss** (**2021**) Increasing food intake affects digesta retention, digestibility and gut fill but not chewing efficiency in domestic rabbits (*Oryctolagus cuniculus*). ***J Exp Zool A*** 335: 614-622.

and demonstrated adaptations of the anterior dentition (incisors and canines) across mammals to facilitate the translational chewing stroke

Avedik, ..., **Clauss** (**2023**) Avoiding the lockdown: morphological facilitation of transversal chewing movements in mammals. ***J Morphol*** 284: e21554

While we pursue the documentation of chewing characteristics in individual taxa

Hohl, ..., **Clauss** (**2020**) Chewing, dental morphology and wear in tapirs (*Tapirus* spp.) and a comparison of free-ranging and captive specimens. ***PLoS One*** 15: e0234826

we also demonstrated intra-individual differences in chewing behaviour in cattle

Zhang, ..., **Clauss** (**2023**) Individual differences in digesta retention and their relation to chewing in cattle – a pilot investigation. ***J Anim Physiol Anim Nutr*** 107: 394-406

and in doing so, were, to my knowledge, the first to stress the relevance of knowing the dental status of animals (in particular, cattle) when recording their chewing behaviour for physiological studies.

We are currently exploring ways to link dental status, individual chewing patterns and digestive performance in domestic ruminants.