Narrative 2: Digestive morphophysiology and adaptations to ecological niches

At the beginning of my scientific career, I was involved in a large number of digestibility studies in (mainly large) nondomestic herbivores.

This work was partly supported by a research grant from the International Rhino Foundation (2000-2004)

e.g., **Clauss** et al. (**2001**) The comparative use of four marker systems for the estimation of digestibility, and low food intake, in a group of captive giraffe (*Giraffa camelopardalis*). ***Zoo Biol*** 20: 315-329
Clauss et al. (**2003**) Studies on feed digestibilities in captive Asian elephants (*Elephas maximus*). ***J Anim Physiol Anim Nutr*** 87: 160-173
Clauss et al. (**2004**) Intake, ingesta retention, particle size distribution and digestibility in the *hippopotamidae*. ***Comp Biochem Physiol A*** 139: 449-459
Clauss et al. (**2005**) Studies on digestive physiology and feed digestibilities in captive Indian rhinoceros (*Rhinoceros unicornis*). ***J Anim Physiol Anim Nutr*** 89: 229-237

By intuition rather than education, I considered the fossil record as an important part of evolution's possible solutions, and hence collaboration with palaeontologist Gertrud Rössner essential when formulating a 'rule of constraint'

Clauss, ..., Rössner, et al. (**2003**) The maximum attainable body size of herbivorous mammals: morphophysiological constraints on foregut, and adaptations of hindgut fermenters. ***Oecologia*** 136: 14-27

Based on the reputation gained by that work, I was able, together with Jürgen Hummel, to participate in the 8-year-long DFG Research Unit on the Biology of Sauropod Dinosaurs (Grants CL 182/3-1, CL 182/3-2, CL 182/5-1, CL 182/6-1, CL 182/7-1; publications listed below and in their respective topics)
Involvement with this Research Unit led to my most-cited publication

Sander, ..., **Clauss**, et al. (**2011**) Biology of the sauropod dinosaurs: the evolution of gigantism. ***Biological Reviews*** 86: 117-155

and an invited review to Science

Sander & **Clauss** (**2008**) Sauropod gigantism. ***Science*** 322: 200-201

But most importantly, the interaction with scientists from many other disciplines in that Research Unit broadened my horizon in terms of topics I was interested in enormously. Most specifically, it allowed me to free myself from a discipline-promoting view (as in 'digestive physiology is the most important explanatory factor') to a holistic biological view of evolution. This is best exemplified in our review

Clauss et al. (**2013**) Herbivory and body size: allometries of diet quality and gastrointestinal physiology, and implications for herbivore ecology and dinosaur gigantism. ***PloS One*** 8: e68714

in which we explain why digestive physiology is most likely not a constraint in terms of body size evolution.

The comparative approach to digestion, where many different species are studied (necessarily mostly in individual projects) led to

invited plenary lecture on *Comparative fibre digestion* at the Conference of the European Society of Veterinary and Comparative Nutrition, Zaragoza, Spain, 2011

In the narration that links form and function, we typically describe how a certain morphology and physiology of the digestive tract is suited to digest a certain type of food. I started out with this concept in mind, and have used this narrative in my own teaching.
Over time, I began to view, due to the data sets I worked with, different species less as a bunch of organisms each equipped with its own, perfect adaptation, but

- on the one hand, as organisms subject to quite common conditions, for example with respect to protein and fat digestibility within carnivores, and across mammals

  Clauss et al. (**2010**) Carnivorous mammals: nutrient digestibility and energy evaluation. ***Zoo Biol*** 29: 687–704
  Richard, ..., **Clauss** (**2017**) Little differences in digestive efficiency for protein and fat in mammals of different trophic guilds and digestive strategies: data constraints or fundamental functional similarity? ***J Anim Physiol Anim Nutr*** 101(Suppl.1): 127-141

- on the other hand, as a large variety of forms that can all fulfil similar functions, as evident in the lack of, or limited degree of, correlation of quantifiers of gastrointestinal morphology and diet

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

My expertise in vertebrate digestive physiology led to participation in SNSF Sinergia project CRSII5_189970/1

Duque-Correa, ..., **Clauss** (**2021**) Mammalian intestinal allometry, phylogeny, trophic level and climate. ***Proc R Soc B*** 288: 20202888
Hoppe, ..., **Clauss** et al. (**2021**) Less need for differentiation? Intestinal length of reptiles as compared to mammals. ***PLoS One*** 16: e0253182

These observations also match records of untypical feeding behaviour, which represent a challenge to our common, 'rule-based' biological understanding

Clauss et al. (**2016**) Carcass consumption by domestic rabbits (*Oryctolagus cuniculus*). ***Eur J Wildl Res*** 62: 143-145

The expertise in digestion studies led to various involvement in ecological and isotope-related projects (see below).

I hosted Daryl Codron as an International Incoming Marie Curie Fellow 2009-2011 for a project on stable isotope physiology -

a collaboration that spawned one of my most permanent and fruitful collaborations with common publications still ongoing, e.g. a ground-breaking theoretical achievement that combines the theories of competition and niche neutrality

Codron, ..., **Clauss** et al. (**2023**) Competition drives the evolution of emergent neutrality in the dietary niches of mammalian herbivores. ***Quaternary International*** 650: 28-39

For example, our work on faecal nitrogen (= protein) as an indicator of digestive processes

Schwarm, ..., **Clauss** (**2009**) No easy solution for the fractionation of faecal nitrogen in captive wild herbivores: results of a pilot study. ***J Anim Physiol Anim Nutr*** 93: 596-605

led to an

invited plenary lecture on *Nitrogen fractionation in faeces* (University of Bonn Symposium for the 75th birthday of Prof. Dr. Dr. h.c. Pfeffer 2014)

or a study in which we demonstrated that faecal nitrogen is related to diet digestibility and not diet protein content in a carefully designed study

Gálvez-Cerón, ..., **Clauss**, Serrano (**2015**) Gastrointestinal nematodes and dietary fibre: two aspects to take into account when FN is used for wildlife nutrition monitoring. ***Ecol Ind*** 52:161-169

In terms of comparative digestive adaptations, the shunting of calcium away from the digestive towards the urinary tract in hindgut fermenters was something I was taught as a species peculiarity in rabbits and horses. Unwilling to believe in such a peculiarity, we amassed evidence that this is a common physiological feature of hindgut-fermenting herbivores and suggested that the ultimate reason lies in the prevention of calcium-phosphorus-complexes that render phosphorus unavailable for gut bacteria

Clauss, Hummel (**2008**) Getting it out of the (digestive) system: hindgut fermenters and calcium. ***Proc Comp Nutr Soc*** 7: 30-36

Hagen, ..., **Clauss** (**2015**) Organic matter and macromineral digestibility in domestic rabbits (*Oryctolagus cuniculus*) as compared to other hindgut fermenters. ***J Anim Physiol Anim Nutr*** 99: 1197-1209

In *in vitro* studies, we could demonstrate an increase in the active absorption of calcium in rabbits at increasing dietary calcium levels – a finding that would have to be considered paradoxical if calcium was to be obtained for the organism, but that makes sense if the removal of calcium from the gut is the major aim

Liesegang, ..., **Clauss** (**2024**) Rabbits increase caecal calcium absorption at increasing dietary calcium levels. ***J Anim Physiol Anim Nutr*** (online).

We are exploring options to further confirm this hypothesis.