Narrative 1: Browsers and grazers

I entered the literature debate (between Prof. R. Hofmann on the one side claiming ‘browsers are different from grazers’, and several research groups on the other claiming body size is the main reason for observed differences) on whether ruminants (and, to some extent, mammals in general) that feed on browse or grass show clear-cut morphophysiological differences ‘from the side’. I came from the point of view of zoo husbandry literature. That literature suggested that browsers are much more difficult to maintain in captivity than grazers (my MSc and Dr.med.vet. theses were on the nutrition of zoo giraffe and moose, respectively – two strict browsers). This biased me to suspect a functional difference. Exploring that literature opened the realm of herbivore digestive physiology and of scientific literature in general for me. My first own experiment – a passage study in giraffe (the largest ruminant, and a browser, so inadvertently a test case for the two opposing views)

Clauss et al. (**1998**) Passage rate of fluid and particle phase in captive giraffe (*Giraffa camelopardalis*). ***Adv Ethol*** 33:98 (abstract)

found retention times much shorter than expected based body mass, and hence supported the ‘Hofmann side’, and – what a coincidence – I found my first employment at the institute directed by Prof. Hofmann.

Rather than on statistical aspects (as was the main issue at the time), I focussed on functional aspects of the current hypotheses, detected an overlooked contradiction in the classic Hofmann theory (that postulated that those ruminants that produce more saliva have smaller omasa – although a major function of the omasum is to re-absorb fluid coming from the rumen), and developed a new functional theory

Clauss et al. (**2003**) Ruminant diversification as an adaptation to the physicomechanical characteristics of forage. A reevaluation of an old debate and a new hypothesis. ***Oikos*** 102:253-262.

Work testing the hypotheses originating from this concept was partially funded by a grant from the German Wildlife Foundation 2003

In parallel, I was lucky in being granted access to unpublished data by Prof. Hofmann after his retirement in 2000, which allowed, for the first time, large-scale testing of functional morphological hypotheses and their further development, e.g.

Hofmann, ..., **Clauss** (**2008**) Convergent evolution in feeding types: Salivary gland mass differences in wild ruminant species. ***J Morphol*** 269:240-257,

Clauss, Hofmann et al. (**2009**) The intraruminal papillation gradient in wild ruminants of different feeding types: implications for rumen physiology. ***J Morphol*** 270:929-942.

Our work led to the invitation to contribute to a now classic book on the browser-grazer topic

Clauss et al. (**2008**) The morphophysiological adaptations of browsing and grazing mammals. In: Gordon IJ, Prins HHT (eds) *The ecology of browsing and grazing*. Springer, Heidelberg, pp 47-88.

and its applied aspects led to the invitation to contribute to a textbook on zoo animal medicine

Clauss & Dierenfeld (**2008**) The nutrition of browsers. In: Fowler ME, Miller RE (eds) *Zoo and wild animal medicine. Current therapy Vol. 6*. Saunders Elsevier, St. Louis, pp. 444-454

We also generated own experimental data in a growing body of passage experiments but also field measurements in free-ranging ruminants, e.g.

Clauss et al. (**2009**) Physical characteristics of rumen contents in four large ruminants of different feeding type, the addax (*Addax nasomaculatus*), bison (*Bison bison*), red deer (*Cervus elaphus*) and moose (*Alces alces*). ***Comp Biochem Physiol A*** 152:398-406.

These works led to the invitation as plenary speaker at the International Symposium on Ruminant Physiology, Clermont-Ferrand, France, 2009

and the review publication associated with that invitation is – for my field – comparatively well-cited,

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

Subsequently, we tested our hypothesis experimentally in fistulated nondomestic ruminants

as part of my first SNSF project 3100A0-115958/1

Lechner, ..., **Clauss** (**2010**) Differential passage of fluids and different-sized particles in fistulated oxen (*Bos primigenius* f. *taurus*), muskoxen (*Ovibos moschatus*), reindeer (*Rangifer tarandus*) and moose (*Alces alces*): rumen particle size discrimination is independent from contents stratification. ***Comp Biochem Physiol A*** 155:211-222,

and discarded it, to focus on a different concept that explains the observed characteristics.

The works on ruminants led to the invitation as plenary speaker at the International Conference on Ruminant Phylogeny, Munich, Germany, 2013

with the associated review publication

Clauss (**2014**) Soft tissue characteristics for the reconstruction of ruminant phylogeny. ***Zitteliana B*** 32: 1-14.

Our work led to the invitation to contribute to a book on wild cattle

Clauss & Hofmann (**2014**) The digestive system of ruminants, and peculiarities of (wild) cattle. In: Melletti M, Burton J (eds) *Ecology, evolution and behaviour of wild cattle: implications for conservation*. Cambridge University Press, Cambridge, pp 57-62

The reputation in this area led to the invitation as plenary speaker at the 1st International Meeting of Advances in Animal Science, Jaboticabal, Brazil, 2016

and the associated review is the currently best summary of the fate of the 'Hofmann hypothesis', which is linked to the adaptive value of a high fluid throughput through the rumen (see 'digesta separation mechanism' narrative)

Clauss, Hummel (2017) Physiological adaptations of ruminants and their potential relevance for production systems. Rev Bras Zootec 46: 606-613.

The measurement catalogues that we amassed over the years makes ruminants a fascinating example how links between anatomy and physiology can be traced, with a very comprehensive example including the anatomy of the omasum – a particular part of the ruminant forestomach

Ehrlich, ..., Hofmann, ..., **Clauss** (**2019**) Comparative omasum anatomy in ruminants: relationships with natural diet, digestive physiology, and general considerations on allometric investigations. ***J Morphol*** 280:259-277.

that also allowed the development of an evolutionary narrative that explains a pattern in the fossil record where tragulids – ruminants without an omasum – were replaced over evolutionary time by omasum-bearing taxa

Clauss & Rössner (**2014**) Old world ruminant morphophysiology, life history, and fossil record: exploring key innovations of a diversification sequence. ***Annales Zoologici Fennici*** 51: 80-94.

My continuous engagement in this field led to the second invitation to contribute to a second edition of the book on the browser-grazer topic

Codron, Hofmann, **Clauss** (**2019**) Morphological and physiological adaptations for browsing and grazing. In: Gordon IJ, Prins HHT (eds) *The ecology of browsing and grazing II*. Springer, Berlin, Germany, pp 81-125.

More recently, we found that the eland antelope is an ideal model ruminant (compared to the more difficult-to-maintain moose, roe deer or giraffe) to study the difference between cattle (with a high fluid throughput) and 'moose-type' ruminants (with a low fluid throughput) in more detail:

Hejcmanová, ..., **Clauss** (**2020**) Digesta passage in common eland (*Taurotragus oryx*) on a monocot or a dicot diet. Comparative Biochemistry and Physiology A 246:110720

For the future, apart from continuously expanding the comparative database with more ruminant species as well as husbandry surveys on peculiar herbivore species, further experiments on contrasting effects of browse and grass on ingestive and digestive functions of ruminants are planned.