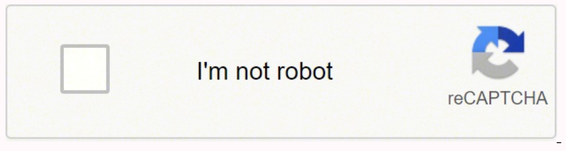

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Digestion in non ruminant animals pdf download pc windows 7 full

Digestive system of ruminants and non ruminants. Digestive system of non ruminants.

1995. Revue de Zoologie et de Botanique Africaine 16:373-419. Clauss, M.; Hume, I. Ecology Letters 12:538-549. Methane yield phenotypes linked to differential gene expression in the sheep rumen microbiome. Instead, the proportions of different fibre types (hemicellulose, cellulose, lignin) were demonstrated to differ between grass and browse forages, as well as the fermentation behaviour of these forages (Hummel et al., 2006Hummel, J.; Südekum, K.-H.; Streich, W. In: Physiological aspects of digestion and metabolism in ruminants. In terms of anatomy, these included drastic differences in salivary gland size (Hofmann et al., 2008Hofmann, R. Modelling equid/ruminant competition in the fossil record. Proceedings of the Royal Society B 279:3339-3346. M. and Janis, C. taurus), muskoxen (Ovibos moschatus) and moose (Alces alces). Physical characteristics of reticuloruminal contents of cattle in relation to forage type and time after feeding. K. The intake-retention time relationship can be modulated by gut capacity (Clauss et al., 2007Clauss, M.; Streich, W. Given the evidence from wild ruminants that not only retention time in general, but the difference between fluid and particle retention in the rumen is a species-specific and hence genetic/heritable characteristic, selective breeding for this measure would theoretically be feasible, if appropriate proxies could be found to evaluate phenotypes. Biological Reviews 86:733-758. R.; Croom, W. R. Australian Journal of Agricultural Research 40:1065-1074.; Smuts et al., 1995Smuts, M.; Meissner, H. and Müller, D. Journal of Zoology 257:13-26. Proceedings of the New Zealand Society of Animal Production 57:19-21. E. This may be linked to a less efficient morphophysiological design of their sorting mechanism (Dittmann et al., 2014Dittmann, M. Dimensions of the intestine, diet and faecal water loss in some African antelope. Pérez, W.; König, H. p.179-200. PLoS One 9:e112035.) in ruminants, one could consider breeding domestic ruminants for wider muzzles to enhance their foraging efficiency, if muzzle width was identified as a constraint. and Ehrhardt, D. Oecologia 131:343-349. A.; Moser, D.; Galeffi, C.; Schwarm, A.; Kreuzer, M. G.; Beever, D. True rumination only evolved twice, in the camelids and the true ruminants. European Journal of Wildlife Research 52:88-98.; Dittmann et al., 2015aDittmann, M. 1989. Differences in fecal particle size between free-ranging and captive individuals of two browser species. B. Journal of Zoology 281:12-25.; Meier et al., 2016Meier, A. Mechanisms of thermoregulation and water balance in desert ungulates. Rumination and its significance. 2000. Because the production of these proteins becomes the limiting step in saliva release, they have large salivary glands; yet, they do not achieve great amounts of saliva output. Gegenbaurs Morphologisches Jahrbuch 119:633-695.), it was the seminal, comparative works of Hofmann (1973Hofmann, R. Functional Ecology 2:15-22.; Janis and Ehrhardt, 1988Janis, C. Animal Feed Science and Technology 144:196-211.) and in vivo experiments with domestic ruminants (Harrison et al., 1975Harrison, D. Clauss, M.; Hummel, J. Ruminants have evolved particular adaptations to solve this dilemma. Facilitation versus competition in grazing herbivore assemblages. Effects of a salivary stimulant, slaframine, on ruminal fermentation, bacterial protein synthesis and digestion in frequently fed steers. Australian Journal of Agricultural Research 40:1065-1074. Stoichiometry of carbohydrate fermentation and microbial growth efficiency in a continous culture of mixed rumen bacteria. Acta Veterinaria Scandinavica 86(Suppl.):196-203.; Woodall and Skinner, 1993Woodall, P. 2017. Oecologia 157:377-385.; Heywood, 2010Heywood, J. 2010a. European Journal of Applied Microbiology and Biotechnology 7:111-120.). European Journal of Wildlife Research 52:88-98. The omasum has been interpreted as the organ that reabsorbs this fluid and hence facilitates an efficient sorting mechanism and a great fluid throughput linked to high feed intake (Clauss and Rössner, 2014Clauss, M. On the relationship between hypsodonty and feeding ecology in ungulate mammals, and its utility in palaeoecology. A reevaluation of an old debate and a new hypothesis. 2014. Genome Research 24:1517-1525.) of the microbiome itself. Comparative Biochemistry and Physiology A 152:504-512. World Review of Nutrition and Dietetics 9:251-273. Mammalian Biology 78:142-152.). Journal of Animal Science 71:1634-1640. 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). Animal 4:979-992. This fluid could represent a burden on the enzyme-secreting function of the abomasum and small intestine (that would have to compensate for the dilution effect with increased secretion rates). Explanatory approach IIIa: maximizing stratification? Solute and particle retention in a small grazing antelope, the blackbuck (Antilope cervicapra). 2003. The evolution of phylogenetic differences in the efficiency of digestion in ruminants. Oecologia 157:377-385. Rogers, J. 2008a. Particle retention in the forestomach of a browsing ruminant, the roe deer (Capreolus capreolus). Differential passage of fluids and different-sized particles in fistulated oxen (Bos primigenius f. Arsenault, R. Recherches anatomiques sur l'okapi (Okapia johnstoni). Comparative Biochemistry and Physiology A 182:22-26.). Vendl, C.; Munn, A.; Leggett, K. Journal of Arid Environments 107:41-48. It has been suggested that domestic ruminants could be selected for increased digestive efficiency, based on phenotypic characteristics of the way digesta moves through their digestive tract (Hegarty, 2004Hegarty, R. Although merycism (i.e., regurgitation and re-mastication) and the presence of comparatively fine digesta particles have been reported in non-ruminant foregut fermenters such as kangaroos (Schwarm et al., 2013Schwarm, A.; Ortmann, S.; Fritz, J.; Rietschel, W.; Flach, E. R.; Rosenstock, S. Selective breeding for digesta washing? and Derscheid, J. O.; Karachi, M. Mendoza, M.; Janis, C. Animal 7:316-321. Springer, Heidelberg.). and Purvis, A. and Shipley, L. L'estomac. p.47-88. Comparative Biochemistry and Physiology A 149:142-149.; Müller et al., 2011Müller, D. considered the major difference between grass and browse to be the general fibre concentration, with lower values in browse. 1991. This is probably due to an increased microbial flow to the lower digestive tract. and Hatt, J.-M. Journal of Zoology 270:346-358. This seeming contradiction could be resolved if the focus is no longer placed on adaptations to properties of the respective forages (grass or browse). As the forestomach is followed by auto-enzymatic digestion, this allows a continuous, increased harvest of microbes from the forestomach. 1975. Fritz, S. Pérez-Barbería, F. R., 2014. 2007. particles, (i.e., a "washing" or "flushing" of the forestomach contents; Müller et al., 2011Müller, D. Comparative Biochemistry and Physiology A 149:142-149. F. However, many other differences between grazers and browsers cannot be logically linked to fibre characteristics. Other components of observed differences that had also been originally linked to the feeding type differences, such as the length of intestinal sections (Hofmann, 1989Hofmann, R. Moss, A. Reproduction Nutrition Development 31:335-359.), for which a high moisture content is an important prerogative (Clauss et al., 2009bClauss, M.; Fritz, J.; Bayer, D.; Nygren, K.; Hammer, S.; Hatt, J.-M.; Südekum, K.-H. and Köhler, M. Odadi, W. and Prins, H. Australian Journal of Experimental Agriculture 44:459-467.). Species diversity of browsing and grazing ungulates: consequences for the structure and abundance of secondary production. However, among the cattle-type ruminants, there is no clear association between the degree by which their characteristics are expressed and the percentage of grass in their natural diet (Codron and Clauss, 2010Codron, D. and Becker, K. These both evolved a density-dependent sorting mechanism based on physical separation of the digesta by the process of flotation and sedimentation, ensuring that the process of rumination is applied to large particles. Canadian Journal of Zoology 88:1129-1138. Most ruminants share the characteristic of "digesta washing": fluid moves through their digestive tract faster than particles, thus effectively washing very fine particles, such as bacteria, out of the digesta plug. and Hardin, R. p.455-482. Journal of Morphology 277:351-362.) or behavioural foraging strategies (Searle and Shipley, 2008Searle, K. Riginos, C.; Porensky, L. Data from Isaacson et al. Cambridge University Press, Cambridge UK. Zoological Journal of the Linnean Society 92:267-284. Physical characteristics of rumen contents in two small ruminants of different feeding type, the mouflon (Ovis ammon musimon) and the roe deer (Capreolus capreolus). D.; Arambel, M. and Walters, J. Oikos 102:253-262. T. In taxonomic ruminants, the particle sorting mechanism is based on a flotation-sedimentation mechanism in the reticulum (Sutherland, 1988Sutherland, T. In other words, the most extreme grazers are not necessarily the most extreme cattle-type ruminants. Cattle-type ruminants are characterised by a high throughput of a non-viscous fluid (produced by small salivary glands) and corresponding well-stratified rumen contents and an intraruminal papillae gradient, higher reticular crests, and larger omasa (to absorb the higher amount of fluid passing through the reticulorumen; cattle-type) (Clauss et al., 2010bClauss, M.; Hume, I. Fermentation substrate and dilution rate interact to affect microbial growth and efficiency. In: The ecology of browsing and grazing mammals. Schwarm, A.; Ortmann, S.; Fritz, J.; Rietschel, W.; Flach, E. Hummel, J.; Fritz, J.; Kienzle, E.; Medici, E. Oikos 118:1623-1632. While there appears to be no functional difference in the forestomach particle sorting mechanism between these two functional ruminant groups (Dittmann et al., 2015bDittmann, M. Tropical pasture hay utilization with slaframine and cottonseed meal: ruminal characteristics and digesta passage in wethers. and Martin, P. A report of a successful breeding program to reduce bloat susceptibility (Morris et al., 1997Morris, C. p.1-20. and Illius, A. Comparative Biochemistry and Physiology A 164:129-140.), a major determinant of digestibility. British Journal of Nutrition 111:578-585.). Comparative Biochemistry and Physiology A 154:376-382.). Effect of mineral salts, carbachol, and pilocarpine on nutrient digestibility and ruminal characteristics in cattle. A.; Gordon, I. and Pérez-Espés, B. Journal of Morphology 269:240-257.), intraruminal papillae distribution (Clauss et al., 2009cClauss, M.; Hofmann, R. Codron, D. Schwarm, A.; Ortmann, S.; Wolf, C.; Streich, W. Gegenbaurs Morphologisches Jahrbuch 119:633-695. p.43-58. Oecologia 78:443-457.), were probably best explained by concepts completely unrelated to feeding types (Woodall and Skinner, 1993Woodall, P. American Journal of Physiology 271:R157-R179. The relationship of food intake and ingesta passage predicts feeding ecology in two different megaherbivore groups. J.; Südekum, K.-H. Other characteristics, such as those related to dental anatomy and durability, could be interesting in respect to intentions to prolong domestic ruminant lifespan. and Hofmann, R. E.; Haynes, F.; Barnett, M. Publication in this collectionJuly 2017 Received19 Dec 2016 Accepted25 Mar 2017 Given the variety of muzzle width (Gordon and Illius, 1988Gordon, I. Digesta washing, microbial harvest, microbial metabolism A variety of in vitro assays (Isaacson et al., 1975Isaacson, H. Garrod, A. Journal of Animal Physiology and Animal Nutrition 101:61-69.). 1992. (1975)Isaacson, H. 1980. and Pfeffer, E. Comparative Biochemistry and Physiology A 160:207-220.; Hummel et al., 2015Hummel, J.; Hammer, S.; Hammer, C.; Ruf, J.; Lechenne, M. C.; Janssen, P. 1994. and McEwan, J. Particle separation in the forestomach of sheep. The concept suggests that moose-type ruminants have adopted a strategy of defending themselves against secondary plant compounds by salivary tannin-binding proteins, which render the saliva comparatively viscous. Archer, D. This shift might occur because of an effect similar to the "partitioning factor" of feeds, that is, the degree by which they trigger energy transfer into microbial growth or into short-chain fatty acid and hence also CH_4 production (Blümmel et al., 1997Blümmel, M.; Steingass, H. Comparative Biochemistry and Physiology A 179:182-191. Many of the resulting hypotheses were later corroborated by statistical evaluations (Pérez-Barbería et al., 2004Pérez-Barbería, F. Müller, D. and Reese, S. Matsuda, I.; Tuuga, A.; Hashimoto, C.; Bernard, H.; Yamagiwa, J.; Fritz, J.; Tsubokawa, K.; Yayota, M.; Murai, T.; Iwata, Y. 1997. Oikos 118:1623-1632.), which allows them to increase intake (as compared with non-ruminant foregut fermenters) without compromising digestibility (Schwarm et al., 2009Schwarm, A.; Ortmann, S.; Wolf, C.; Streich, W. Comparative Biochemistry and Physiology A 154:376-382. K.; Mathison, G. Oecologia 131:343-349.). At the same time, it should result in a metabolic state of the microbiome more tuned towards biomass production and less towards methanogenesis. Ecology Letters 12:538-549.). 2016. W.; Fritz, J.; Steuer, P.; Schwarm, A.; Kreuzer, M. Oecologia 157:377-385.; Meier et al., 2016Meier, A. J. 2012. 2009a. Convergent evolution in feeding types: salivary gland mass differences in wild ruminant species. The effect of size and density on the mean retention time of particles in the reticulorumen of cattle (Bos primigenius f. and Deswysen, A. Comparative Biochemistry and Physiology A 152:398-406.). Explanatory approach IIIb: optimizing microbial harvest Since then, our explanatory focus for the observed differences in fluid throughput and stratification has been on an optimization of digesta washing and hence harvest of microbes from the forestomach. Biological Reviews 87:965-990. African wild ungulates compete with or facilitate cattle depending on season. For example, although reticulorumen volume is not a direct selection criterion, a particularly voluminous reticulorumen most likely results as an effect of breeding for phenotypes with a high intake capacity for a high milk yield. Faecal particle size: digestive physiology meets herbivore diversity. Clauss, M.; Streich, W. Oecologia 78:443-457.; Kay, 1989Kay, R. Regurgitation and remastication in the foregut-fermenting proboscis monkey (Nasalis larvatus). R.; Hinds, F. Hummel, J.; Steuer, P.; Südekum, K.-H.; Hammer, S.; Hammer, C.; Streich, W. Comparative Biochemistry and Physiology A 155:211-222. Phylogenetic constraints on digesta separation: variation in fluid throughput in the digestive tract in mammalian herbivores. Journal of Animal Science 67:827-834. Academic Press, San Diego CA. Hume, I. Oikos 97:313-318. A.; Bininda-Emonds, O. E.; Evans, J. The macroscopic anatomy of the omasum of free-ranging moose (Alces alces) and muskoxen (Ovibos moschatus) and a comparison of the omasal laminal surface area in 34 ruminant species. Fondevila, M. E.; Jerbi, H. Comparative Biochemistry and Physiology A 164:129-140. Acta Veterinaria Scandinavica 86(Suppl.):196-203. H.; Chen, F.; Visel, A.; Wang, Z.; Attwood, G. and Osbourn, D. Journal of Dairy Science 70:284-289.; Froetschel et al., 1989Froetschel, M. R.; Fickel, J.; Streich, W. A.; Cullen, N. The impact of hexose partitioning on methane production in vitro. Shi, W.; Moon, C. A first hypothesis developed to explain these patterns was based on the finding that rumen contents of a browser did not seem to stratify in vivo as previously reported for grazers (Clauss et al., 2001Clauss, M.; Lechner-Doll, M.; Behrend, A.; Lason, K.; Lang, D. Invited Review • •   copy Marcus Clauss Jürgen Hummel About the authors Herbivores face the dilemma that the level of feed intake is negatively related to factors that determine digestive efficiency, such as thoroughness of ingesta comminution by chewing, and retention of digesta in the digestive tract. Rumination of different-sized particles in muskoxen (Ovibos moschatus) and moose (Alces alces) on grass and browse diets, and implications for rumination in different ruminant feeding types. Comparative chewing efficiency in mammalian herbivores. Wildlife Society Bulletin 34:570-581. Mammalian Biology 86:21-26.) and proboscic monkeys (Nasalis larvatus) (Matsuda et al., 2011Matsuda, I.; Murai, T.; Clauss, M.; Yamada, T.; Tuuga, A.; Bernard, H. Oecologia 174:1127-1137.), true rumination linked to a sorting mechanism and with a physiologically fixed motor sequence (Gordon, 1968Gordon, J. Clauss, M.; Hofmann, R. and has been elaborated since (Clauss et al., 2010bClauss, M.; Hume, I. Journal of Dairy Science 62:1599-1605. Explanatory approach I: fibre content of forages In the initial concept, Hofmann (1989)Hofmann, R. M.; Young, E. Comparative Biochemistry and Physiology A 160:207-220. Springer, Berlin Heidelberg.). L.; Kimuyu, D.; Keesing, F.; Wilkerson, M. W.; Krausman, P. American Journal of Physiology 271:R157-R179.; Cain et al., 2006Cain, J. Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. 2005. C.; Davis, C. British Journal of Nutrition 105:634-644.; Lauper et al., 2013Lauper, M.; Lechner, I.; Barboza, P.; Collins, W.; Hummel, J.; Codron, D. With this great fluid throughput, the ruminant forestomach displays a similar characteristic to most other foregut fermenters (with the exception of primates): a relatively faster movement of fluid vs. Higher masseter mass in grazing than in browsing ruminants. Clauss, M.; Fritz, J.; Bayer, D.; Nygren, K.; Hammer, S.; Hatt, J.-M.; Südekum, K.-H. and Belyea, R. Functional anatomy of bovid upper molar occlusal surfaces with respect to diet. Mammalian Biology 78:142-152. and Streich, W. A.; Marks, B. Journal of Dairy Science 58:1645-1659. Form and function of the selenodont molar in southern African ruminants in relation to their feeding habits. T., eds. New Zealand Journal of Agricultural Research 23:33-41.) and decreased ruminal fluid passage rates (Okine et al., 1989Okine, E. British Journal of Nutrition 105:634-644. 1988. 2006b. and Fritz, H. Clauss, M.; Kaiser, T. Wiedmeier, R. Okine, E. II. Cornell University Press, Ithaca, NY.; Baumont and Deswysen, 1991Baumont, R. and Rubin, E. Journal of Zoology 281:1-11. Canadian Journal of Zoology 88:1129-1138.). Gordon, I. and Clark, J. Zoological Journal of the Linnean Society 92:267-284.; Tennant and MacLeod, 2014Tennant, J. N. Lauper, M.; Lechner, I.; Barboza, P.; Collins, W.; Hummel, J.; Codron, D. A. and Owens, F. Reproduction Nutrition Development 40:211-212.). and Geertsema, H. and Owen-Smith, N. Digesta retention patterns of solutes and different-sized particles in camelids compared with ruminants and other foregut fermenters. Journal of Morphology 269:240-257. Journal of Animal Science 73:206-210. Macroanatomical aspects of the gastrointestinal tract of the alpaca (Vicugna pacos) and dromedary (Camelus dromedarius). Convergence of macroscopic tongue anatomy in ruminants and scaling relationships with body mass or tongue length. Isaacson, H. Kay, R. In contrast to domestic pigs, camelids, or horses, they belong to a family (Bovidae) that comprises an enormous extant variety of more than 100 species (Fritz et al., 2009bFritz, S. 1993. Bird, A. Correlation of the relative muzzle width and relative incisor width with dietary preferences in ungulates. Oecologia 78:443-457. Woodall, P. Journal of Arid Environments 107:41-48.). New Zealand Journal of Agricultural Research 23:33-41. The major challenge in these studies was not the statistical evaluation, but the development of an explanatory concept of biological validity. Concepts of digestive efficiency. Heywood, J. Clauss, M.; Lechner-Doll, M. Hofmann, R. R.; Hummel, J.; Adamczewski, J.; Nygren, K.; Pitra, C.; Streich, W. Searle, K. p.43-73. This increased chewing efficiency is not achieved by a particular dental design, but by a density-depending sorting mechanism in the forestomach, which separates the small particles from the large ones that are then regurgitated to be masticated again (i.e., rumination) (Lechner-Doll et al., 1991Lechner-Doll, M.; Kaske, M. 2009c. When this theory was tested experimentally, however, results indicated that the particle retention and sorting mechanism did not differ fundamentally between a moose-type and a cattle-type species, even though differences in rumen content stratification, rumen fluid viscosity, and the relative rumen fluid throughput could be demonstrated (Lechner et al., 2010Lechner, I.; Barboza, P.; Collins, W.; Fritz, J.; Günther, D.; Hattendorf, B.; Hummel, J.; Südekum, K.-H. Based on those early observations, a theory was developed that linked the throughput of great amounts of a low-viscosity fluid in cattle-type ruminants to adaptations whose ultimate objective was considered to be the enhancement of the natural tendency of grass forage to stratify in the rumen, thus facilitating a more efficient selective particle retention, size reduction via rumination, and hence digestibility (Clauss et al., 2003Clauss, M.; Lechner-Doll, M. 1968. Dittmann, M. C.; Bryant, M. Zoology 112:195-205. Acta Theriologica 46:103-107. M.; Fickel, J.; Streich, W. Such moose-type ruminants are typically browsers. In the analyses of the adaptive values of these characteristics, we recently introduced the terms "moose-type" and "cattle-type" ruminants. MC thanks Izabelle Auxiliadora Molina de Almeida Teixeira for the invitation to contribute to the 1st International Meeting of Advances in Animal Science in Jaboticabal, São Paulo, Brazil, in June 2016. Rather, we think that it is more promising to put the focus on an optimization of microbial harvest, which may be beneficial on any kind of forage. The intraruminal papillation gradient in wild ruminants of different feeding types: implications for rumen physiology. Mammalian Biology 78:412-421. Low-methane yield sheep have smaller rumens and shorter rumen retention time. and Rössner, G. The dissociation of the fluid and particle phase in the forestomach as a physiological characteristic of large grazing ruminants: an evaluation of available, comparable ruminant passage data. H.; Codron, D.; Meloro, C.; Munn, A.; Schwarm, A.; Hummel, J. Annales Zoologici Fennici 51:80-94.). Explanatory approach III: a cohesive set of observations Evident relationships between plant properties and the oral and dental processing apparatus notwithstanding, the observed differences between species in the anatomy and physiology of the forestomach and related structures still begged for a coherent explanation. R.; Streich, W. Manipulation of rumen fermentation in sheep by increasing the rate of flow of water from the rumen. Adaptation of the ruminant digestive tract to diet. Reproductive seasonality in captive wild ruminants: implications for biogeographical adaptation, photoperiodic control, and life history. Acta Theriologica 46:103-107.) and that, in captivity, browsing ruminants had larger faecal particles (i.e. a lesser particle size reduction efficiency) than grazing ruminants (Clauss et al., 2002Clauss, M.; Lechner-Doll, M. Comparative Biochemistry and Physiology A 160:207-220.). S. Increasing the degree of digesta washing even more should increase microbial harvest from the forestomach and reduce the susceptibility to acidosis. African Journal of Ecology 30:181-185. In: Aspects of digestive physiology in ruminants. S.; Hickey, S. Some characteristics of that catalogue have most likely been selected indirectly during the process of breeding for phenotypes of high production value. 2013. Science 333:1753-1755.; Riginos et al., 2012Riginos, C.; Porensky, L. Vertebrate Zoology 66:419-425.); however, conclusive physiological studies are lacking. Ruminant species cover a large variety of ecological niches and hence display a large variety of morphophysiological adaptations (Hofmann, 1989Hofmann, R. Journal of Dairy Science 58:1645-1659.; Hummel et al., 2015Hummel, J.; Hammer, S.; Hammer, C.; Ruf, J.; Lechenne, M. Goopy, J. Clauss, M. G. 2002. No distinct stratification of ingesta particles and no distinct moisture gradient in the forestomach of nonruminants: the wallaby, peccary, hippopotamus, and sloth. Vergleichend-anatomische Untersuchungen am Magen der Artiodactyla. A method for investigating salivation in cattle using pilocarpine as a sialagogue. Hummel, J.; Südekum, K.-H.; Streich, W. and Young, T. and Oddy, V. 2009d. This short review is concerned with this latter option. Froetschel, M. Lechner, I.; Barboza, P.; Collins, W.; Fritz, J.; Günther, D.; Hattendorf, B.; Hummel, J.; Südekum, K.-H. The focus we place herein on digestive physiology is, at the moment, a subjective one. Journal of Zoology 281:26-38.), or omasum size (Clauss et al., 2006aClauss, M.; Hofmann, R. J.; Croom, W. In: Ecology, evolution and behaviour of wild cattle: implications for conservation. Clauss, M.; Lechner-Doll, M.; Behrend, A.; Lason, K.; Lang, D. 2006a. Comparative Biochemistry and Physiology A 152:398-406.; Hummel et al., 2009Hummel, J.; Südekum, K.-H.; Bayer, D.; Ortmann, S.; Hatt, J.-M.; Streich, W. J.; Elston, D. Oikos 116:209-216.) and the retention time-digestibility relationship can be modulated by particle size reduction (i.e., chewing efficiency; Clauss et al., 2009dClauss, M.; Nunn, C.; Fritz, J. (2008b)Hummel, J.; Steuer, P.; Südekum, K.-H.; Hammer, S.; Hammer, C.; Streich, W. and Turner, J. Journal of Dairy Science 62:1599-1605.), or by pharmacologically enhancing saliva production (Wiedmeier et al., 1987aWiedmeier, R. Journal of Dairy Science 70:284-289. However, empirical data on the fibre concentration in rumen contents in specimens of different feeding types did not support this hypothesis (Woodall, 1992Woodall, P. and Kawashima, R., eds. Comparative Biochemistry and Physiology A 182:22-26. Gordon, J. P.; Lang, S.; Zimmermann, W.; Streich, W. Comparative Biochemistry and Physiology A 179:182-191.). J.; Fickel, J.; Hummel, J. Journal of Zoology 281:12-25. D.; Leahy, S. Journal of Comparative Physiology B 185:559-573.; Pérez et al., 2016Pérez, W.; König, H. Oikos 97:313-318.; Odadi et al., 2011Odadi, W. Zerbe, P.; Clauss, M.; Codron, D.; Bingaman Lackey, L.; Rensch, E.; Streich, W. Effect of orally administered pilocarpine on ruminal characteristics and nutrient digestibility in cattle. Basic ruminant digestive physiology Herbivore digestive physiology can be conceptualized as the dilemma to maximize feed intake while also maximizing diet quality and diet digestibility (Hume, 2005Hume, I. 1987b. Science Publishers, Enfield NH.). J.; Hummel, J. Animal 4:979-992.). Genotype differences and their impact on digestive tract function of ruminants: a review. Animal 7:316-321.). Carefully designed experiments are warranted to test the effect of differentially increasing rumen fluid throughput, by infusion of artificial saliva via fistula (Rogers et al., 1979Rogers, J. For example, given the variety of dental traits (Archer and Sanson, 2002Archer, D. and Hummel, J. British Journal of Nutrition 77:911-921. Clauss, M.; Lechner, I.; Barboza, P.; Collins, W.; Tervoort, T.; Südekum, K.-H.; Codron, D. The sorting mechanism automatically leads to the outflow of the fluid from the reticulum together with small particles. Oikos 102:253-262.; Clauss et al., 2010aClauss, M.; Hofmann, R. T.; Hummel, J.; Hammer, S.; Arif, A.; Hebel, C.; Müller, D. and Palmqvist, P. Jordana, X.; Marín-Moratalla, N.; DeMiguel, D.; Kaiser, T. and Wang, T., eds. 1973. Clauss, M.; Nunn, C.; Fritz, J. Hummel, J.; Hammer, S.; Hammer, C.; Ruf, J.; Lechenne, M. and von Engelhardt, W. Untersuchungen am Magen der Tylopoda und Ruminantia. R.; Schmuck, U.; Meloro, C.; Clauss, M. Explanatory approach II: various characteristics of forages and different niche characteristics Various differences between forages might be linked to differences characterising the anatomy and physiology of browsers and grazers. Journal of Animal Science 67:827-834.; Bird et al., 1993Bird, A. 1999. Journal of Dairy Science 70:592-600.; Wiedmeier et al., 1987bWiedmeier, R. The comparative feeding bahaviour of large browsing and grazing herbivores. Pastoralism 2:1-22.), but not always (Prins and Fritz, 2008Prins, H. K.; Abdulrazak, S. An evaluation of a rapid method for estimating digestibility. Figure 1 In vitro experiment on the effect on increasing dilution rate (i.e., fluid throughput) on measures of microbial activity – volatile fatty acids (VFA), methane (CH_4), carbon dioxide (CO_2), and cell numbers. PLoS One 9:e112035. Snout shape in extant ruminants. Journal of Agricultural Science, Cambridge 85:93-101. In terms of physiology, these related mainly to distinct differences in the relative retention times of fluids and particles in the reticulorumen (Hummel et al., 2005Hummel, J.; Clauss, M.; Zimmermann, W.; Johanson, K.; Norgaard, C. Zoology 112:195-205.; Clauss et al., 2009bClauss, M.; Fritz, J.; Bayer, D.; Nygren, K.; Hammer, S.; Hatt, J.-M.; Südekum, K.-H. Proceedings of the Royal Society B 279:3339-3346.) in ruminants, one could consider breeding domestic ruminants for more complex and higher-crowned teeth, if there was evidence that the production potential of domestic ruminants was constrained by the durability of their teeth. Zoo Biology 27:70-77. Journal of Comparative Physiology B 185:559-573.), a major difference between them is the generally lower metabolism and lower feed intake in camelids (Dittmann et al., 2014Dittmann, M. Thompson, B. Tennant, J. Journal of Animal Physiology and Animal Nutrition 93:209-220.; Clauss et al., 2017Clauss, M.; Fritz, J.; Tschuor, A.; Braun, U.; Hummel, J. Notes on the visceral anatomy and osteology of the ruminants, with a suggestion regarding a method of expressing the relations of species by means of formulae. Zoo Biology 27:70-77.; Clauss et al., 2009aClauss, M.; Fritz, J.; Bayer, D.; Hummel, J.; Streich, W. Proceedings of the Royal Society B 271:1081-1090.; Clauss et al., 2008aClauss, M.; Hofmann, R. W. Oikos 116:209-216. Digesta retention in gazelles in comparison to other ruminants: Evidence for taxon-specific rumen fluid throughput to adjust digesta washing to the natural diet. T.; Hummel, J.; Runge, U.; Galeffi, C.; Kreuzer, M. M.; Gordon, G. This in turn links to hypotheses of grazers requiring longer digesta retention times and hence a larger rumen (Clauss et al., 2003Clauss, M.; Lechner-Doll, M. Oikos 102:253-262.; Clauss et al., 2008bClauss, M.; Kaiser, T. Structure and concentrating ability of the mammalian kidney: correlations with habitat. A.; Amos, H. Fritz, J.; Hummel, J.; Kienzle, E.; Arnold, C.; Nunn, C. Additionally, the metabolic state of the ruminal microflora is most likely tuned to faster growth rates probably fuelled by a higher digestive capacity of the microbes, with the majority of microbial cells in the growth and reproductive stages (Isaacson et al., 1975Isaacson, H. Langer, P. The ruminant stomach. Comparative Biochemistry and Physiology A 152:504-512.; Clauss et al., 2015Clauss, M.; Steuer, P.; Erlinghagen-Lückerath, K.; Kaandorp, J.; Fritz, J.; Südekum, K.-H. Meier, A. Journal of Agricultural Science, Cambridge 85:93-101.; Wiedmeier et al., 1987bWiedmeier, R. Journal of Dairy Science 58:1645-1659.; Van Nevel and Demeyer, 1979Van Nevel, C. P.; Donaldson, A.; Hegarty, R.; Vercoe, P. and Codron, D. and MacLeod, N. and Cronje, P. Note the decrease in methane and the increase in microbial biomass (cell numbers). Clauss, M.; Steuer, P.; Erlinghagen-Lückerath, K.; Kaandorp, J.; Fritz, J.; Südekum, K.-H. Science 333:1753-1755. Relations between passage rates of rumen fluid and particulate matter and foam production in rumen contents of cattle fed on different diets ad lib. In: Physiological and ecological adaptations to feeding in vertebrates. East African Literature Bureau, Nairobi.; 1988; 1989) and, to a less well-known extent, of Kay (1989)Kay, R. taurus), muskoxen (Ovibos moschatus), reindeer (Rangifer tarandus) and moose (Alces alces): rumen particle size discrimination is independent from contents stratification. Tsuda, T.; Sasaki, Y. The exceptional reduction of ingesta particle size that functional ruminants achieve is the hallmark of ruminant digestive physiology (Fritz et al., 2009aFritz, J.; Hummel, J.; Kienzle, E.; Arnold, C.; Nunn, C. Journal of Animal Science 71:1634-1640.) support the concept that an increased fluid throughput through the rumen, in other words, an increase in the relative passage of fluid (as compared with particles) or an enhanced "digesta washing", increases the microbial yield from the rumen system (Figure 1). Comparative Biochemistry and Physiology A 140:436-444.; Clauss et al., 2006bClauss, M.; Hummel, J. Genetic studies of bloat susceptibility in cattle. British Journal of Nutrition 111:578-585. Comparative Biochemistry and Physiology A 140:436-444. Journal of Dairy Science 58:1645-1659.; Meng et al., 1999Meng, Q.; Kerley, M. Journal of Zoology 258:223-246.; Damuth and Janis, 2011Damuth, J. J.; Hatt, J.-M. C.; Dellow, D. and Skinner, J. This idea was first proposed by Hummel et al. 2009b. Morris, C. Damuth, J. Dobson, A. Journal of Zoology 270:346-358.). It has been claimed that an important effect of such a "digesta washing" is the efficient harvest of microbes from the forestomach (Hummel et al., 2008bHummel, J.; Steuer, P.; Südekum, K.-H.; Hammer, S.; Hammer, C.; Streich, W. Harrison, D. Pastoralism 2:1-22. 2008b. We propose that the characteristic of pronounced digesta washing and the associated microbial harvest and change of the microbial metabolism could represent a target for selective breeding that could further improve the efficiency of domestic ruminants. Among these properties of forages might be their growth form, their spatial arrangement, the heterogeneity of their harvestable units, their physical resistance to mastication, and their content of phytoliths and secondary plant compounds (reviewed in Clauss et al., 2008bClauss, M.; Kaiser, T. In ruminants of the tribe Bovini, the omasum has reached the largest size and this group has a particularly great forestomach fluid throughput. Springer, Heidelberg. Cain, J. Fluid and particle retention in the digestive tract of the addax antelope (Addax nasomaculatus) – adaptations of a grazing desert ruminant. Old world ruminant morphophysiology, life history, and fossil record: exploring key innovations of a diversification sequence. Conclusions The diversity of ruminant species can be considered a catalogue of genetically fixed, morphophysiological characteristics that could, in theory, be exploited in domestic species by selective breeding. I. V.; O'Sullivan, B. Characterising an artiodactyl family inhabiting arid habitats by its metabolism: low metabolism and maintenance requirements in camelids. Mélange et propulsion du contenu du réticulo-rumen. The effect of selection for fleece weight upon urea metabolism and digestive function in Romney sheep. 1996. Lower amounts of saliva in combination with a high saliva viscosity reduce the tendency of rumen contents to stratify. Lessons on the relationship between livestock husbandry and biodiversity from the Kenya Long-term Exclosure Experiment (KLEE). Evidently, any characteristic could be chosen as a target for selective breeding. This difference in species diversity between bovids on the one hand, and suids, camelids, or equids on the other hand, has been interpreted as a result of a displacement of previously more speciose large herbivore groups by ruminants (Janis et al., 1994Janis, C. 1979. 2015. J.; Lamb, R. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. Journal of Zoology 258:223-246. 2015a. Hummel, J.; Südekum, K.-H.; Bayer, D.; Ortmann, S.; Hatt, J.-M.; Streich, W. Neuville, H. Functional Ecology 20:989-1002. Morphophysiological evolutionary adaptations of the ruminant digestive system. Academic Press, San Diego CA.). P.; Jones, W. 2015b. The digestive system of ruminants, and peculiarities of (wild) cattle. Rumen physiology constrains diet niche: linking digestive physiology and food selection across wild ruminant species. On the one hand, certain production systems, in particular more extensive systems, sometimes might benefit from employing this existing variety of ruminant species to increase the overall efficiency of resource use (Arsenault and Owen-Smith, 2002Arsenault, R. Cornell University Press, Ithaca, NY. IV. Proceedings of the Royal Society B 271:1081-1090. 2001. Enhancing the forestomach fluid throughput by selective breeding could represent a promising way to further advance the productivity of the ruminant digestive tract. The morphophysiological adaptations of browsing and grazing mammals. Journal of Zoology 281:1-11.; Kaiser et al., 2010Kaiser, T. Lechner-Doll, M.; Kaske, M. This was exemplified by Clauss and Hofmann (2014)Clauss, M. Convergence in the macroscopic anatomy of the reticulum in wild ruminant species of different feeding types and a new resulting hypothesis on reticular function. Gurnsey, M. The level of feed intake is typically negatively related with digesta mean retention time (Müller et al., 2013Müller, D. Journal of Zoology 281:12-25.) and hypsodonty (Mendoza et al., 2002Mendoza, M.; Janis, C. Moose-type species are characterised by a low throughput of relatively viscous fluid (produced by large salivary glands) and a corresponding lack of stratification of rumen contents and intraruminal papillae gradient, low reticular crests, and small omasa. and Marcinkowski, D. Journal of Dairy Science 70:592-600. Such a shift in microbial metabolism (Shi et al., 2014Shi, W.; Moon, C. Journal of Zoology 281:26-38. Variation in ruminal digesta retention time is currently considered the most likely explanation for the inherited differences in methane emissions (Pinares-Patiño et al., 2013Pinares-Patiño, C. G.; MacLean, S.; Molano, G.; Sandoval, E.; Kjestrup, H.; Harland, R.; Hunt, C.; Pickering, N. 2010. C.; Kang, D.; Froula, J.; Kittelmann, S.; Fan, C.; Deutsch, S.; Gagic, D.; Seedorf, H.; Kelly, W. Retention time of digesta in the rumen: its repeatability and relationship with wool production of Merino rams. Historical Biology 8:15-29. Fluid and particle retention in captive okapi (Okapia johnstoni). M.; Gordon, I. Journal of Arid Environments 107:41-48.; Dittmann et al., 2015bDittmann, M. Comparative ruminant digestive morphophysiology Although morphological differences of the digestive tract between ruminant species had been known for a long time (Garrod, 1877Garrod, A. Journal of Morphology 277:351-362. and Dobson, M. Biology Letters 7:786-789.; Matsuda et al., 2014Matsuda, I.; Tuuga, A.; Hashimoto, C.; Bernard, H.; Yamagiwa, J.; Fritz, J.; Tsubokawa, K.; Yayota, M.; Murai, T.; Iwata, Y. Comparative Biochemistry and Physiology A 185:58-68. and Clauss, M. and Newbold, C. East African Literature Bureau, Nairobi. Journal of Comparative Physiology B 185:559-573. Reproduction Nutrition Development 31:335-359. Baumont, R. Comparative Biochemistry and Physiology A 185:58-68.). Evidence of correlated evolution of hypsodonty and exceptional longevity in endemic insular mammals. 1929. Australian Journal of Experimental Agriculture 44:459-467. Journal of Animal Physiology and Animal Nutrition 93:209-220. (2015)Hummel, J.; Hammer, S.; Hammer, C.; Ruf, J.; Lechenne, M. Smuts, M.; Meissner, H. We note that both findings have been corrected since (Hummel et al., 2008aHummel, J.; Fritz, J.; Kienzle, E.; Medici, E. Historical Biology 8:15-29.). In particular, our approach focuses on digestive physiology. British Journal of Nutrition 77:911-921.; Moss and Newbold, 2000Moss, A. A.; Dodds, K. Hegarty, R. The hallmark of ruminant digestive anatomy is the omasum, in which the fluid required for both digesta washing and the reticular separation mechanism is re-absorbed. Mammalian Biology 78:412-421.; Vendl et al., 2017Vendl, C.; Munn, A.; Leggett, K. J.; Atua, R.; Sang, C.; Soni, P.; Li, D.; Pinares-Patiño, C. Corresponding adaptations of ruminants include those related to oral and dental processing (Archer and Sanson, 2002Archer, D. Genome Research 24:1517-1525. S.; McEwan, J. Journal of Zoology 281:26-38.). Ruminant diversification as an adaptation to the physicomechanical characteristics of forage. A new in vitro system to study the effect of liquid phase turnover and pH on microbial fermentation of concentrate diets for ruminants. Hummel et al. Pinares-Patiño, C. Starck, J. We chose this terminology to avoid circular reasoning when comparing the botanical composition of the diet ("browser-grazer diet") with the adaptations of the species ("browser-grazer anatomy/physiology"). Clauss, M.; Fritz, J.; Bayer, D.; Hummel, J.; Streich, W. Alteration of rumen fermentation in steers by increasing rumen fluid dilution rate with mineral salts. Blümmel, M.; Steingass, H. Efficiency of energy utilization by mixed rumen bacteria in continuous culture. African Journal of Ecology 30:181-185.). Janis, C. O.; Sensenig, R. and Barry, T. Functional Ecology 20:989-1002.). J., eds. Hummel, J.; Clauss, M.; Zimmermann, W.; Johanson, K.; Norgaard, C. Enamel ridge alignment in upper molars of ruminants in relation to their natural diet. Characterizing complex craniodental patterns related to feeding behaviour in ungulates: a multivariate approach. 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). Animal 4:979-992.; Müller et al., 2011Müller, D. 2011. T.; Runge, U.; Ortmann, S.; Lang, R. Heritability estimates of methane emissions from sheep. Sutherland, T. Prins, H. 2010b. 2008. Biology Letters 7:786-789. Assessing the Jarman-Bell Principle: scaling of intake, digestibility, retention time and gut fill with body mass in mammalian herbivores. M.; Hagler, W. Journal of Zoology 257:13-26.; Heywood, 2010Heywood, J. 2006. Reproduction Nutrition Development 40:211-212. Journal of Zoology 229:457-471.; Beuchat, 1996Beuchat, C. Meng, Q.; Kerley, M. D. World Review of Nutrition and Dietetics 9:251-273.) only evolved twice, in the camelids and the taxonomic ruminants. H. Forage fermentation patterns and their implications for herbivore ingesta retention times. This new concept considers the different cattle-type ruminants as different stages in an evolution towards optimized microbial harvest from the forestomach. Wildlife Society Bulletin 34:570-581.; Zerbe et al., 2012Zerbe, P.; Clauss, M.; Codron, D.; Bingaman Lackey, L.; Rensch, E.; Streich, W. and Reid, C. and Sanson, G. British Journal of Nutrition 61:387-395.). Proceedings of the Zoological Society of London:2-18. This framework suggested convergences between feeding types (browser, intermediate feeder, grazer). Biological Reviews 87:965-990.). Evidence for a tradeoff between retention time and chewing efficiency in large mammalian herbivores. Evolutionary adaptations of ruminants and their potential relevance for modern production systems. Ruminants can actually be bred to differ in the mean retention time of digesta (Thompson et al., 1989Thompson, B. J.; Fickel, J. demonstrated with an example calculation that because of the digesta washing effect, cattle-type ruminants could have a 10% higher microbial efficiency, quantified as the amount of microbial nitrogen produced in the rumen per unit of fermented organic matter. The relationship between in vitro gas production, in vitro microbial biomass yield and N incorporation and its implications for the prediction of voluntary feed intake of roughages. Springer, Berlin Heidelberg. Incisor arcade structure and diet selection in ruminants. Science Publishers, Enfield NH. S.; Ludden, P. On the other hand, one could consider the variety of existing ruminant morphophysiologies as a pool from which one might choose certain traits as targets for selective breeding in domestic ruminant breeding programs (Clauss et al., 2010bClauss, M.; Hume, I. Journal of Animal Science 73:206-210.; Goopy et al., 2014Goopy, J. Comparative Biochemistry and Physiology A 152:398-406. European Journal of Applied Microbiology and Biotechnology 7:111-120. Mammalian Biology 86:21-26. Functional Ecology 2:15-22. Journal of Morphology 277:351-362.). M.; Veblen, K. Matsuda, I.; Murai, T.; Clauss, M.; Yamada, T.; Tuuga, A.; Bernard, H. Differences in this sorting mechanism might facilitate a faster digesta processing in true ruminants as compared with camelids. C. P. Van Nevel, C. In: The ecology of browsing and grazing. Journal of Zoology 229:457-471. p.117-148. cattle; digesta washing; foregut fermenter; microbial harvest; microbiome Domestic ruminants are special. Vertebrate Zoology 66:419-425. J.; Bailey, J. Journal of Morphology 270:929-942. Journal of Zoology 257:13-26.; Clauss et al., 2008aClauss, M.; Hofmann, R. Journal of Animal Physiology and Animal Nutrition 101:61-69. Comparative Biochemistry and Physiology A 155:211-222.; Clauss et al., 2011Clauss, M.; Lechner, I.; Barboza, P.; Collins, W.; Tervoort, T.; Südekum, K.-H.; Codron, D. and Hagler, W. 2004. E.; Odadi, W. Merycism in western grey (Macropus fuliginosus) and red kangaroos (Macropus rufus). However, in many cases, correlations of investigated characteristics with the percentage of grass in the natural diet included substantial scatter, though being significant. 2009. L. Beuchat, C. Revue de Zoologie et de Botanique Africaine 16:373-419.; Langer, 1973Langer, P. Journal of Animal Science 77:206-214. Animal Feed Science and Technology 144:196-211. Factors affecting the mean retention time of particles in the forestomach of ruminants and camelids. Relations between passage rates of rumen fluid and particulate matter and foam production in rumen contents of cattle fed on different diets ad lib British Journal of Nutrition 61:387-395. A higher fluid throughput due to a higher saliva production should also be protective against acidosis. and Higashi, S. Clauss, M.; Fritz, J.; Tschuor, A.; Braun, U.; Hummel, J. Faecal particle size in free-ranging primates supports 'rumination' strategy in the proboscis monkey (Nasalis larvatus). and Demeyer, D. Journal of Morphology 270:929-942.), height of the reticular crests (Clauss et al., 2010aClauss, M.; Hofmann, R. Journal of Animal Science 77:206-214.; Fondevila and Pérez-Espés, 2008Fondevila, M. Biological Reviews 86:733-758.; Jordana et al., 2012Jordana, X.; Marín-Moratalla, N.; DeMiguel, D.; Kaiser, T. Melletti, M.; Burton, J., eds. Oecologia 174:1127-1137. Journal of Animal Science 71:1634-1640.), not only on measures of digestive efficiency, pH, and microbial and methane yield, but also on the metabolic state (Shi et al., 2014Shi, W.; Moon, C. Oecologia 78:443-457.. Faecal particle size distribution in captive wild ruminants: an approach to the browser/grazer dichotomy from the other end. Dry matter and digesta particle size gradients along the goat digestive tract on grass and browse diets. Annales Zoologici Fennici 51:80-94. J.; Schwarm, A.; Ortmann, S. Therefore, they lead to a homogenous intraruminal papillae formation pattern, make lower reticular crests understandable (to avoid complete emptying during reticular contractions that would cause a slow refilling of the reticulum because of the small amount of viscous saliva available), and do not require considerable omasal tissue for re-absorption (Clauss et al., 2010bClauss, M.; Hume, I. Proceedings of the Zoological Society of London:2-18.; Neuville and Derscheid, 1929Neuville, H. Comparative Biochemistry and Physiology A 160:207-220.; Dittmann et al., 2015aDittmann, M. 1987a. Acta Veterinaria Scandinavica 86(Suppl.):196-203., that placed these differences in a comprehensive ecological framework. Journal of Dairy Science 58:1645-1659.. Kaiser, T. 1877. Frothy bloat in cattle is associated with decreased saliva production (Gurnsey et al., 1980Gurnsey, M. Journal of Zoology 229:457-471.). For example, there is no logical concept why a high-fibre diet should be linked to small salivary glands or why a low-fibre diet should be linked to a more voluminous large intestine, as proposed in Hofmann (1989)Hofmann, R. listing a series of species from the taxonomic group of cattle, which have the most prominent cattle-type characteristics, yet consume higher amounts of browse (i.e., more "intermediate-type" diets) than strict grazers. Proceedings of the New Zealand Society of Animal Production 57:19-21.) therefore suggests that increased saliva flows can be achieved. p.57-62. H.; Caton, J.; Codron, D.; Schwarm, A.; Lentle, R.; Streich, W. E.; Thomson, D. Genome Research 24:1517-1525.) might also lead to a decrease in methane yield (Isaacson et al., 1975Isaacson, H.

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