



Unravelling Evolutionary Links: The Symbiotic Gut Microbiota of Ruminants and Cetacean Family.

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Abstract : The gut microbiome, an intricate ecosystem of diverse microorganisms residing within the digestive systems of animals, holds profound implications for evolutionary biology and ecosystem dynamics. This review paper explores the symbiotic relationships between ruminants and their gut microbiomes, shedding light on their evolutionary implications and ecological significance. Ruminants, such as cows and sheep, have co-evolved with their gut microbes to efficiently digest tough plant material, facilitated by microbial fermentation in specialized stomach chambers. Comparative analysis with cetaceans, the marine mammals including whales, reveals intriguing parallels in digestive adaptations and microbial functionalities despite vastly different diets and habitats. Insights from ruminant microbiomes offer valuable perspectives on cetacean evolution, suggesting convergent evolutionary pressures in developing digestive structures and microbial communities. Moreover, the ecological and functional significance of these symbiotic relationships extends beyond individual species to shape ecosystem dynamics, nutrient cycling, and climate change. Future research directions include elucidating the genetic basis of microbial communities, exploring the impact of diet on microbiome composition, and investigating microbiome manipulation for improving animal health and ecosystem resilience. Overall, this review highlights the intricate interplay between animals, their gut microbiomes, and evolutionary processes, emphasizing the importance of microbial symbiosis in shaping the diversity and functioning of terrestrial and marine ecosystems.

Keywords: Evolution, Ruminants, Gut Microflora, Rumen Microbiota, Co-existence

INTRODUCTION

The gut microbiome, a universe of diverse microbes residing within our digestive system, holds fascinating clues to our evolutionary past and future. Studying this intricate ecosystem from an evolutionary perspective unveils several intriguing insights such as Host and microbes co-existence, shaping each other's evolution (Shapira Michael, 2016).

Ruminants, like cows, sheep, and goats, thrive on a diet of plant material that humans and other animals struggle to digest. This unique ability stems from a symbiotic relationship with the diverse community of microorganisms residing in their gastrointestinal tract (GIT), collectively known as the gut microbiome (Cholewińska, Paulina et al., 2020). Research has revealed the critical importance of these microbes in various aspects of ruminant health and well-being.

Both ruminants and cetaceans belong to the larger clade Cetartiodactyla, originating from a common ancestor millions of years ago. This shared ancestry implies their gut microbiomes might share some ancestral features. It points towards faster evolution rates in the gut microbiomes of this clade compared to other mammalian lineages (Nishida et al., 2018). Interestingly, baleen whales (like blue whales) exhibit a unique gut microbiome with similarities to both carnivores and herbivores. They show some functional capacity and taxonomic features similar to the herbivorous terrestrial mammals, likely due to their reliance on fermenting chitin from krill in their diet (Sanders et al., 2015).

While a direct link between the current gut microbiomes of cetaceans and the evolution of ruminants doesn't exist, their shared ancestry, convergent evolution of digestive features, and unique microbial communities offer intriguing starting points for further research into the complex interplay between gut microbes and mammalian evolution. (Zhang et al, 2016)

1. Symbiotic Gut Microbiomes in Ruminants:

Ruminant animals, like cows, sheep, and goats, possess a unique digestive system that relies heavily on their gut microbiome. This complex ecosystem of microbes plays a vital role in breaking down tough plant material and extracting essential nutrients (Alipour et al., 2018). Bacteria are the most abundant residents of the ruminant gut, particularly in the rumen (first stomach). Research suggests over 200 bacterial species can be present, with Firmicutes and Bacteroidetes being the dominant phyla (Matthews et al., 2018) (Welch et al., 2022). These bacteria specialize in breaking down complex carbohydrates like cellulose and hemicellulose into simpler molecules. While less abundant than bacteria, archaea play a crucial role in methane production (Forcina et al., 2022) highlights their contribution to this greenhouse gas emission, which is a significant environmental concern associated with ruminant agriculture. Protozoa are single-celled organisms that contribute to nutrient cycling within the gut. They consume bacteria, further breaking them down and releasing nutrients usable by the ruminant (Forcina et al., 2022). Fungi, though less prevalent, also contribute to digestion by aiding in the breakdown of complex plant fibers, complementing the role of bacteria (Welch et al., 2022). The ruminant digestive system is a marvel of nature, allowing these animals to thrive on a diet of tough plant material. This feat is achieved through a remarkable example of symbiosis – a close and mutually beneficial relationship between the ruminant and its gut microbiome. The ruminant provides the microbes with a warm, moist environment rich in carbohydrates, while the microbes, in turn, break down these complex plant fibers into simpler molecules that the ruminant can absorb. This process, known as microbial fermentation, is essential for ruminant digestion (Monteiro et al., 2022). A study by (Forcina et al., 2022) emphasizes the role of volatile fatty acids (VFAs) produced by the microbes as the primary energy source for the ruminant.

The symbiotic relationship between ruminants and their gut microbiome goes beyond simply aiding digestion. Nutrient Synthesis: The microbes act as tiny factories, synthesizing essential nutrients like microbial protein and B vitamins, which the ruminant absorbs to supplement its diet (Welch et al., 2022). Immune System Modulation: A balanced gut microbiome can help regulate the ruminant's immune system and protect it from pathogens (Welch et al., 2022). The ruminant benefits from the breakdown of complex carbohydrates, nutrient synthesis, and immune system support provided by the microbes. In turn, the microbes have a constant food source and a favorable environment for growth and reproduction within the ruminant's gut. This mutually beneficial relationship exemplifies a successful case of symbiosis.

2. Evolutionary Implications in Ruminants:

The ruminant's ancestors lacked the enzymes needed to digest tough plant material. Research suggests this evolutionary pressure led to the development of a complex digestive system, including a multi-chambered stomach to house microbes capable of breaking down these complex carbohydrates (Hofmann, 1989), (Henderson et al., 2015). Over time, a symbiotic relationship between the ruminant and its gut microbes likely emerged.

The ruminant gut provides a stable environment with a constant food source for microbes. In turn, microbes break down plant fibers, providing the ruminant with essential nutrients it cannot obtain on its own. This symbiotic relationship offered a selective advantage to both parties, promoting their survival and reproduction (Clemmons et al., 2019), (Clauss et al., 2010).

Research by (Matthews et al., 2018) suggests that both the ruminant and its gut microbiome have undergone co-evolutionary adaptations. The ruminant's digestive system provides a selective environment for microbes that excel at breaking down plant fibers. Conversely, the gut microbes have likely evolved adaptations to thrive within the ruminant's gut.

The composition of the gut microbiome is not static. A study by (Newbold & Ramos-Morales, 2020) highlights that factors like diet can influence the types of microbes present. Over generations, ruminant populations consuming different diets may have harbored distinct gut microbial communities, reflecting adaptation to specific food sources.

The gut microbiome composition is not uniform across all ruminant species. A study by (Henderson et al., 2015) emphasizes that diet plays a significant role in shaping the types of microbes present. Over generations, ruminant populations consuming different diets may have harbored distinct gut microbial communities reflecting adaptation to specific ecological niches. For instance, some microbes might be better suited for processing grass-rich diets, while others excel at breaking down browse (leaves and twigs). This microbiome diversity likely mirrored the diversification of ruminant species into grazers, browsers, and mixed feeders.

Recent research is exploring the genetic basis of this co-evolution. Studies like (Auffret et al., 2020) suggest that the ruminant host genome might harbor specific genes that influence the composition and functionality of the gut microbiome. Conversely, the gut microbes themselves might possess genes that allow them to better adapt to their ruminant host. Unveiling these genetic signatures can provide deeper insights into the intricate co-evolutionary dance between ruminants and their microbial partners.

3. Comparative Analysis with Cetaceans:

The study of ruminant gut microbiomes, with their complex communities and co-evolutionary relationship with their hosts, can offer valuable insights into cetacean evolution. While these groups have distinct diets and gut microbial compositions, there are intriguing parallels that shed light on the evolutionary journey of whales. Let's delve into how ruminant microbiomes inform our understanding of cetacean evolution. While ruminants and cetaceans occupy vastly different ecological niches, with one grazing on land and the other filtering the oceans, the study of their gut microbiomes reveals a fascinating evolutionary connection.

3.1 Convergent Evolution and the Multi-Chambered Stomach:

Ruminant Adaptation: Ruminants possess a complex digestive system, including the rumen, which houses microbes capable of breaking down tough plant fibers like cellulose (de Tarso, 2016). This adaptation allows them to extract energy from a diet otherwise inaccessible to most mammals.

Cetacean Parallel: Interestingly, some cetacean lineages, like sperm whales, also possess a multi-chambered stomach (Erwin et al., 2017). While not functioning identically to the ruminant rumen, this convergence suggests a similar evolutionary pressure to create a suitable environment for gut microbes to aid in digestion.

Microbiome Link: The presence of a multi-chambered stomach in both groups hints at the potential role of gut microbes in driving the evolution of this digestive adaptation. Studying the symbiotic relationship between ruminants and their gut microbes can offer insights into the potential role of similar microbial communities in the development of the multi-chambered stomach in some cetaceans (Olsen et al., 1994).

3.2 Microbial Assistance and Dietary Shifts:

Ruminant Microbiome Function: Ruminant gut microbes play a crucial role in their herbivorous lifestyle. These microbes break down complex carbohydrates and synthesize essential nutrients the ruminant cannot obtain on its own (Shapira, 2016)

Cetacean Microbiome and Baleen Whales: Baleen whales transitioned from filter-feeding on small crustaceans to consuming larger prey with complex carbohydrates in their chitinous exoskeletons. Research suggests their gut microbiome harbors microbes capable of fermenting these carbohydrates (Sanders et al., 2015).

Evolutionary Bridge: Understanding how ruminant gut microbes aid in complex carbohydrate breakdown can provide insights into the potential role of similar microbial communities in facilitating the dietary shift observed in baleen whale evolution. The presence of these microbes in baleen whales suggests a possible convergence in gut microbial functionality despite the vast dietary differences between ruminants and cetaceans (Wang et al., 2022).

4. Ecological and Functional Significance:

4.1 Ruminants: Shaping Grasslands and Nutrient Cycling

Digestive Powerhouse: Ruminant gut microbes enable them to thrive on a diet of tough plant material like grasses. Microbial fermentation unlocks the energy trapped within these plants, allowing ruminants to graze in nutrient-limited ecosystems like grasslands (Jami & Mizrahi, 2012).

Nutrient Cycling: Through digestion and waste excretion, ruminants contribute to nutrient cycling by returning essential elements like nitrogen and phosphorus back to the soil, promoting plant growth (Steinfeld & Wassenaar, 2007).

Methane Emissions and Climate Change: While beneficial, ruminant gut microbes also produce methane, a potent greenhouse gas. Research by (Tseten et al., 2022) highlights the ecological impact of methane emissions from ruminant agriculture on climate change.

4.2 Cetaceans: Top Predators and Ocean Health

Efficient Energy Extraction: Cetacean gut microbes assist in breaking down prey and extracting nutrients, allowing these marine mammals to efficiently utilize resources within the food web (Sanders et al., 2015b).

Top Predator Regulation: As top predators, cetaceans can influence prey populations and maintain the balance of marine ecosystems (Hazen et al., 2019). A healthy gut microbiome, by promoting efficient digestion and nutrient absorption, can contribute to a cetacean's overall health and predatory effectiveness.

Nutrient Transfer: Whales, particularly large baleen whales, can migrate long distances. Research by (Ratnarajah et al., 2016) suggests that their waste products, enriched with nutrients from gut microbes, can fertilize ocean surfaces, promoting phytoplankton growth and supporting marine food webs at a global scale.

4.3 Symbiosis and Ecosystem Resilience:

Disease Resistance: A balanced gut microbiome can strengthen the immune system of both ruminants and cetaceans, making them more resistant to pathogens (Romano et al., 2002). This can contribute to the overall health and resilience of populations within their respective ecosystems.

Adaptability and Niche Expansion: The gut microbiome can influence an animal's ability to adapt to changing environments and potentially new food sources (Khalil et al., 2022). This can be crucial for populations facing ecological pressures like climate change or habitat loss.

5. Future Directions and Challenges:

Understanding the role of the gut microbiome in ruminant evolution can inform future research efforts. Genetic basis of microbial communities: How the genetic makeup of gut microbes influences their functionality and adaptation within different ruminant hosts (Li et al., 2011).

Impact of the microbiome on ruminant phenotypes: How the gut microbiome influences traits like digestive efficiency, feed utilization, and even disease resistance in ruminants (Auffret et al., 2017).

Functional traits of gut microbes: Identifying specific genes or metabolic pathways in gut microbes that are crucial for efficient fiber degradation and nutrient provision to the ruminant host (Yoshiaki et al., 2021).

Impact of Diet on Microbiome: Exploring how specific dietary components shape the gut microbiome in both ruminants and cetaceans.

Microbiome Manipulation: Investigating the potential for manipulating the gut microbiome to improve digestion, nutrient utilization, and overall health in both groups.

Fossil Analysis and Microbiome Reconstruction: Exploring the possibility of reconstructing gut microbiomes from fossilized gut contents of ancient cetaceans to understand how their microbial communities evolved alongside dietary changes (Fordyce, 2018).

Comparative Microbiome Studies: Conducting detailed comparisons of gut microbiomes in various cetacean species with different diets to identify potential links between microbial composition and dietary adaptations.

Conclusion

Our exploration underscores the intricate relationship between ruminants, cetaceans, and their gut microbiomes, highlighting the pivotal role of microbial symbiosis in shaping their evolutionary trajectories. Beyond facilitating digestion, these symbiotic partnerships contribute to the broader ecological functioning of terrestrial and marine ecosystems. The co-evolutionary dynamics observed between hosts and their gut microbes emphasize the adaptability of microbial communities to diverse dietary niches, reflecting an ongoing dialogue between organisms and their environments.

Moreover, the parallels in gut functionalities and digestive structures between ruminants and cetaceans hint at shared evolutionary pressures driving the development of specialized digestive adaptations. This suggests a fascinating avenue for future research into the evolutionary origins of complex digestive systems and the role of microbial communities therein.

Furthermore, the ecological implications of these symbiotic relationships extend to nutrient cycling, predator-prey dynamics, and climate change mitigation. Understanding the interplay between gut microbiomes and ecosystem processes is crucial for conservation efforts and sustainable management of both terrestrial and marine environments.

In sum, the symbiotic interplay between animals and their gut microbiomes not only shapes individual fitness and ecological roles but also provides valuable insights into broader evolutionary patterns and ecosystem dynamics.

References

- [1] Alessandri, G., Rizzo, S. M., Ossiprandi, M. C., van Sinderen, D., & Ventura, M. (2022). Creating an atlas to visualize the biodiversity of the mammalian gut microbiota. *Current Opinion in Biotechnology*, 73, 28–33. <https://doi.org/10.1016/j.copbio.2021.06.028>
- [2] Alipour, M. J., Jalanka, J., Pessa-Morikawa, T., Kokkonen, T., Satokari, R., Hynönen, U., Iivanainen, A., & Niku, M. (2018). The composition of the perinatal intestinal microbiota in cattle. *Scientific Reports*, 8(1). <https://doi.org/10.1038/s41598-018-28733-y>
- [3] Amato, K. R., G. Sanders, J., Song, S. J., Nute, M., Metcalf, J. L., Thompson, L. R., Morton, J. T., Amir, A., J. McKenzie, V., Humphrey, G., Gogul, G., Gaffney, J., L. Baden, A., A.O. Britton, G., P. Cuozzo, F., Di Fiore, A., J. Dominy, N., L. Goldberg, T., Gomez, A., & Kowalewski, M. M. (2018). Evolutionary trends in host physiology outweigh dietary niche in structuring primate gut microbiomes. *The ISME Journal*, 13(3), 576–587. <https://doi.org/10.1038/s41396-018-0175-0>
- [4] Arshad, M. A., Hassan, F., Rehman, M. S., Huws, S. A., Cheng, Y., & Din, A. U. (2021). Gut microbiome colonization and development in neonatal ruminants: Strategies, prospects, and opportunities. *Animal Nutrition*, 7(3), 883–895. <https://doi.org/10.1016/j.aninu.2021.03.004>
- [5] Auffret, M. D., Dewhurst, R. J., Duthie, C.-A., Rooke, J. A., John Wallace, R., Freeman, T. C., Stewart, R., Watson, M., & Roehe, R. (2017). The rumen microbiome as a reservoir of antimicrobial resistance and pathogenicity genes is directly affected by diet in beef cattle. *Microbiome*, 5(1). <https://doi.org/10.1186/s40168-017-0378-z>
- [6] Auffret, M. D., Stewart, R. D., Dewhurst, R. J., Duthie, C.-A., Watson, M., & Roehe, R. (2020). Identification of Microbial Genetic Capacities and Potential Mechanisms Within the Rumen Microbiome Explaining Differences in Beef Cattle Feed Efficiency. *Frontiers in Microbiology*, 11. <https://doi.org/10.3389/fmicb.2020.01229>
- [7] Bai, S., Zhang, P., Zhang, C., Du, J., Du, X., Zhu, C., Liu, J., Xie, P., & Li, S. (2021). *Comparative Study of the Gut Microbiota Among Four Different Marine Mammals in an Aquarium*. 12. <https://doi.org/10.3389/fmicb.2021.769012>
- [8] Chen, L., Qiu, Q., Jiang, Y., Wang, K., Lin, Z., Li, Z., Bibi, F., Yang, Y., Wang, J., Nie, W., Su, W., Liu, G., Li, Q., Fu, W., Pan, X., Liu, C., Yang, J., Zhang, C., Yin, Y., & Wang, Y. (2019). Large-scale ruminant genome sequencing provides insights into their evolution and distinct traits. *Science*, 364(6446), eaav6202. <https://doi.org/10.1126/science.aav6202>

- [9] Chi, X., Gao, H., Wu, G., Qin, W., Song, P., Wang, L., Chen, J., Cai, Z., & Zhang, T. (2019). Comparison of gut microbiota diversity between wild and captive bharals (*Pseudois nayaur*). *BMC Veterinary Research*, 15(1). <https://doi.org/10.1186/s12917-019-1993-7>
- [10] Cholewińska, P., Czyż, K., Nowakowski, P., & Wyrostek, A. (2020). The microbiome of the digestive system of ruminants – a review. *Animal Health Research Reviews*, 21(1), 3–14. <https://doi.org/10.1017/S1466252319000069>
- [11] Clauss, M., Hume, I. D., & Hummel, J. (2010). Evolutionary adaptations of ruminants and their potential relevance for modern production systems. *Animal*, 4(7), 979–992. <https://doi.org/10.1017/s1751731110000388>
- [12] Clayton, J. B., Gomez, A., Amato, K., Knights, D., Travis, D. A., Blekhman, R., Knight, R., Leigh, S., Stumpf, R., Wolf, T., Glander, K. E., Cabana, F., & Johnson, T. J. (2018). The gut microbiome of nonhuman primates: Lessons in ecology and evolution. *American Journal of Primatology*, 80(6), e22867. <https://doi.org/10.1002/ajp.22867>
- [13] Clemmons, B. A., Martino, C., Schneider, L. G., Lefler, J., Embree, M. M., & Myer, P. R. (2019). Temporal Stability of the Ruminant Bacterial Communities in Beef Steers. *Scientific Reports*, 9(1). <https://doi.org/10.1038/s41598-019-45995-2>
- [14] de Tarso, S. G. da S. (2016). Ruminants as Part of the Global Food System: How Evolutionary Adaptations and Diversity of the Digestive System Brought them to the Future. *Journal of Dairy, Veterinary & Animal Research*, 3(5). <https://doi.org/10.15406/jdvar.2016.03.00094>
- [15] Development and physiology of the rumen and the lower gut: Targets for improving gut health. (2016). *Journal of Dairy Science*, 99(6), 4955–4966. <https://doi.org/10.3168/jds.2015-10351>
- [16] Dill-McFarland, K. A., Breaker, J. D., & Suen, G. (2017). Microbial succession in the gastrointestinal tract of dairy cows from 2 weeks to first lactation. *Scientific Reports*, 7(1). <https://doi.org/10.1038/srep40864>
- [17] Erwin, P. M., Rhodes, R. G., Kiser, K. B., Keenan-Bateman, T. F., McLellan, W. A., & Pabst, D. A. (2017). High diversity and unique composition of gut microbiomes in pygmy (*Kogia breviceps*) and dwarf (*K. sima*) sperm whales. *Scientific Reports*, 7(1). <https://doi.org/10.1038/s41598-017-07425-z>
- [18] Forcina, G., Pérez-Pardal, L., Carvalheira, J., & Beja-Pereira, A. (2022a). Gut Microbiome Studies in Livestock: Achievements, Challenges, and Perspectives. *Animals*, 12(23), 3375. <https://doi.org/10.3390/ani12233375>
- [19] Forcina, G., Pérez-Pardal, L., Carvalheira, J., & Beja-Pereira, A. (2022b). Gut Microbiome Studies in Livestock: Achievements, Challenges, and Perspectives. *Animals*, 12(23), 3375. <https://doi.org/10.3390/ani12233375>
- [20] Fordyce, R. E. (2018). Cetacean Evolution. *Encyclopedia of Marine Mammals*, 180–185. <https://doi.org/10.1016/b978-0-12-804327-1.00088-1>
- [21] Gatesy, J., Geisler, J. H., Chang, J., Buell, C., Berta, A., Meredith, R. W., Springer, M. S., & McGowen, M. R. (2013). A phylogenetic blueprint for a modern whale. *Molecular Phylogenetics and Evolution*, 66(2), 479–506. <https://doi.org/10.1016/j.ympev.2012.10.012>
- [22] Gaulke, C. A., Arnold, H. K., Humphreys, I. R., Kembel, S. W., O'Dwyer, J. P., & Sharpton, T. J. (2018). Ecophylogenetics Clarifies the Evolutionary Association between Mammals and Their Gut Microbiota. *MBio*, 9(5). <https://doi.org/10.1128/mbio.01348-18>
- [23] Guo, C. Y., Ji, S. K., Yan, H., Wang, Y. J., Liu, J. J., Cao, Z. J., Yang, H. J., Zhang, W. J., & Li, S. L. (2020). Dynamic change of the gastrointestinal bacterial ecology in cows from birth to adulthood. *MicrobiologyOpen*, 9(11). <https://doi.org/10.1002/mbo3.1119>
- [24] Hassan, F., Arshad, M. A., Ebeid, H. M., Rehman, M. S., Khan, M. S., Shahid, S., & Yang, C. (2020). Phytogetic Additives Can Modulate Rumen Microbiome to Mediate Fermentation Kinetics and Methanogenesis Through Exploiting Diet–Microbe Interaction. *Frontiers in Veterinary Science*, 7. <https://doi.org/10.3389/fvets.2020.575801>
- [25] Hazen, E. L., Abrahms, B., Brodie, S., Carroll, G., Jacox, M. G., Savoca, M. S., Scales, K. L., Sydeman, W. J., & Bograd, S. J. (2019). Marine top predators as climate and ecosystem sentinels. *Frontiers in Ecology and the Environment*, 17(10), 565–574. <https://doi.org/10.1002/fee.2125>
- [26] Henderson, G., Cox, F., Ganesh, S., Jonker, A., Young, W., & Janssen, P. H. (2015). Rumen microbial community composition varies with diet and host, but a core microbiome is found across a wide geographical range. *Scientific Reports*, 5(1). <https://doi.org/10.1038/srep14567>
- [27] Hofmann, R. R. (1989). Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. *Oecologia*, 78(4), 443–457. <https://doi.org/10.1007/bf00378733>
- [28] Jami, E., & Mizrahi, I. (2012). Composition and Similarity of Bovine Rumen Microbiota across Individual Animals. *PLoS ONE*, 7(3), e33306. <https://doi.org/10.1371/journal.pone.0033306>
- [29] Khalil, A., Batool, A., & Arif, S. (2022). Healthy Cattle Microbiome and Dysbiosis in Diseased Phenotypes. *Ruminants*, 2(1), 134–156. <https://doi.org/10.3390/ruminants2010009>
- [30] Li, R. W., Connor, E. E., Li, C., Baldwin VI, R. L., & Sparks, M. E. (2011). Characterization of the rumen microbiota of pre-ruminant calves using metagenomic tools. *Environmental Microbiology*, 14(1), 129–139. <https://doi.org/10.1111/j.1462-2920.2011.02543.x>
- [31] Malmuthuge, N., & Guan, L. L. (2016). Gut microbiome and omics: a new definition to ruminant production and health. *Animal Frontiers*, 6(2), 8–12. <https://doi.org/10.2527/af.2016-0017>

- [32] Matthews, C., Crispie, F., Lewis, E., Reid, M., O'Toole, P. W., & Cotter, P. D. (2018). The rumen microbiome: a crucial consideration when optimising milk and meat production and nitrogen utilisation efficiency. *Gut Microbes*, *10*(2), 115–132. <https://doi.org/10.1080/19490976.2018.1505176>
- [33] Moeller, A. H., & Sanders, J. G. (2020). Roles of the gut microbiota in the adaptive evolution of mammalian species. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1808), 20190597. <https://doi.org/10.1098/rstb.2019.0597>
- [34] Monteiro, H. F., Zhou, Z., Gomes, M. S., Peixoto, P. M., Bonsaglia, E. C. R., Canisso, I. F., Weimer, B. C., & Lima, F. S. (2022). Rumen and lower gut microbiomes relationship with feed efficiency and production traits throughout the lactation of Holstein dairy cows. *Scientific Reports*, *12*(1). <https://doi.org/10.1038/s41598-022-08761-5>
- [35] Newbold, C. J., & Ramos-Morales, E. (2020). Review: Ruminant microbiome and microbial metabolome: effects of diet and ruminant host. *Animal*, *14*(S1), s78–s86. <https://doi.org/10.1017/s1751731119003252>
- [36] Nishida, A. H., & Ochman, H. (2018). Rates of gut microbiome divergence in mammals. *Molecular Ecology*, *27*(8), 1884–1897. <https://doi.org/10.1111/mec.14473>
- [37] O'Donnell, M. M., Harris, H. M. B., Ross, R. P., & O'Toole, P. W. (2017). Core fecal microbiota of domesticated herbivorous ruminant, hindgut fermenters, and monogastric animals. *MicrobiologyOpen*, *6*(5), e00509. <https://doi.org/10.1002/mbo3.509>
- [38] Olsen, M. A., Nordøy, E. S., Blix, A. S., & Mathiesen, S. D. (1994). Functional anatomy of the gastrointestinal system of Northeastern Atlantic minke whales (*Balaenoptera acutorostrata*). *Journal of Zoology*, *234*(1), 55–74. <https://doi.org/10.1111/j.1469-7998.1994.tb06056.x>
- [39] Ratnarajah, L., Melbourne-Thomas, J., Marzloff, M. P., Lannuzel, D., Meiners, K. M., Chever, F., Nicol, S., & Bowie, A. R. (2016). A preliminary model of iron fertilisation by baleen whales and Antarctic krill in the Southern Ocean: Sensitivity of primary productivity estimates to parameter uncertainty. *Ecological Modelling*, *320*, 203–212. <https://doi.org/10.1016/j.ecolmodel.2015.10.007>
- [40] Sanders, J. G., Beichman, A. C., Roman, J., Scott, J. J., Emerson, D., McCarthy, J. J., & Girguis, P. R. (2015a). Baleen whales host a unique gut microbiome with similarities to both carnivores and herbivores. *Nature Communications*, *6*(1). <https://doi.org/10.1038/ncomms9285>
- [41] Sanders, J. G., Beichman, A. C., Roman, J., Scott, J. J., Emerson, D., McCarthy, J. J., & Girguis, P. R. (2015b). Baleen whales host a unique gut microbiome with similarities to both carnivores and herbivores. *Nature Communications*, *6*(1). <https://doi.org/10.1038/ncomms9285>
- [42] Scheelings, T. F., Moore, R. J., Van, T. T. H., Klaassen, M., & Reina, R. D. (2020). Microbial symbiosis and coevolution of an entire clade of ancient vertebrates: the gut microbiota of sea turtles and its relationship to their phylogenetic history. *Animal Microbiome*, *2*(1). <https://doi.org/10.1186/s42523-020-00034-8>
- [43] Shapira, M. (2016a). Gut Microbiotas and Host Evolution: Scaling Up Symbiosis. *Trends in Ecology & Evolution*, *31*(7), 539–549. <https://doi.org/10.1016/j.tree.2016.03.006>
- [44] Shapira, M. (2016b). Gut Microbiotas and Host Evolution: Scaling Up Symbiosis. *Trends in Ecology & Evolution*, *31*(7), 539–549. <https://doi.org/10.1016/j.tree.2016.03.006>
- [45] Sharpton, T. J. (2018). Role of the Gut Microbiome in Vertebrate Evolution. *MSystems*, *3*(2), e00174-17. <https://doi.org/10.1128/msystems.00174-17>
- [46] Steinfeld, H., & Wassenaar, T. (2007). The Role of Livestock Production in Carbon and Nitrogen Cycles. *Annual Review of Environment and Resources*, *32*(1), 271–294. <https://doi.org/10.1146/annurev.energy.32.041806.143508>
- [47] Theis, K. R., Dheilly, N. M., Klassen, J. L., Brucker, R. M., Baines, J. F., Bosch, T. C. G., Cryan, J. F., Gilbert, S. F., Goodnight, C. J., Lloyd, E. A., Sapp, J., Vandenkoornhuyse, P., Zilber-Rosenberg, I., Rosenberg, E., & Bordenstein, S. R. (2016). Getting the Hologenome Concept Right: an Eco-Evolutionary Framework for Hosts and Their Microbiomes. *MSystems*, *1*(2). <https://doi.org/10.1128/msystems.00028-16>
- [48] Tseten, T., Sanjorjo, R. A., Kwon, M., & Kim, S.-W. (2022). Strategies to Mitigate Enteric Methane Emissions from Ruminant Animals. *Journal of Microbiology and Biotechnology*, *32*(3), 269–277. <https://doi.org/10.4014/jmb.2202.02019>
- [49] Wang, X., Wu, X., Shang, Y., Mei, X., Zhou, S., Wei, Q., Sun, G., Dong, Y., & Zhang, H. (2022). Convergent evolution of the gut microbiome in marine carnivores. *Ecology and Evolution*, *12*(10). <https://doi.org/10.1002/ece3.9373>
- [50] Wang, Y., & McAllister, T. A. (2002). Rumen Microbes, Enzymes and Feed Digestion-A Review. *Asian-Australasian Journal of Animal Sciences*, *15*(11), 1659–1676. <https://doi.org/10.5713/ajas.2002.1659>
- [51] Welch, C. B., Ryman, V. E., Pringle, T. D., & Lourenco, J. M. (2022a). Utilizing the Gastrointestinal Microbiota to Modulate Cattle Health through the Microbiome-Gut-Organ Axes. *Microorganisms*, *10*(7), 1391. <https://doi.org/10.3390/microorganisms10071391>
- [52] Welch, C. B., Ryman, V. E., Pringle, T. D., & Lourenco, J. M. (2022b). Utilizing the Gastrointestinal Microbiota to Modulate Cattle Health through the Microbiome-Gut-Organ Axes. *Microorganisms*, *10*(7), 1391. <https://doi.org/10.3390/microorganisms10071391>

- [53] Youngblut, N. D., Reischer, G. H., Walters, W., Schuster, N., Walzer, C., Stalder, G., Ley, R. E., & Farnleitner, A. H. (2019). Host diet and evolutionary history explain different aspects of gut microbiome diversity among vertebrate clades. *Nature Communications*, 10(1), 2200. <https://doi.org/10.1038/s41467-019-10191-3>
- [54] Zhang, Z., Xu, D., Wang, L., Hao, J., Wang, J., Zhou, X., Wang, W., Qiu, Q., Huang, X., Zhou, J., Long, R., Zhao, F., & Shi, P. (2016). Convergent Evolution of Rumen Microbiomes in High-Altitude Mammals. *Current Biology*, 26(14), 1873–1879. <https://doi.org/10.1016/j.cub.2016.05.012>
- [55] Romano, T. A., Olschowka, J. A., Felten, S. Y., Quaranta, V., Ridgway, S. H., & Felten, D. L. (2002). Immune response, stress, and environment: Implications for cetaceans. *Cell and Molecular Biology of Marine Mammals; CJ Pfeiffer, ed. Krieger Publishing Co., Inc.*
- [56] Yoshiaki Sato, Hiroaki Takebe, Kento Tominaga, Kazato Oishi, Hajime Kumagai, Takashi Yoshida, Hiroyuki Hirooka. (2021). Taxonomic and functional characterization of the rumen microbiome of Japanese Black cattle revealed by 16S rRNA gene amplicon and metagenome shotgun sequencing. *FEMS Microbiology Ecology*, Volume 97, Issue 12, December, fiab152. <https://doi.org/10.1093/femsec/fiab152>

