J. Dairy Sci. 99:1–12
http://dx.doi.org/10.3168/jds.2015-10351

Development and physiology of the rumen and the lower gut: Targets for improving gut health[1]

Michael A. Steele,*[2] Greg B. Penner,† Frédérique Chaucheyras-Durand,‡ and Le Luo Guan*
*Department of Agricultural, Food and Nutritional Science, University of Alberta, Edmonton, Canada, T6G 2P5
†Department of Animal and Poultry Science, University of Saskatchewan, Saskatoon, Canada, S7N 5A2
‡Lallemand Animal Nutrition, Blagnac, France, 63122

ABSTRACT

The gastrointestinal epithelium of the dairy cow and calf faces the challenge of protecting the host from the contents of the luminal milieu while controlling the absorption and metabolism of nutrients. Adaptations of the gastrointestinal tract play an important role in animal energetics as the portal-drained viscera accounts for 20% of the total oxygen consumption of the ruminant. The mechanisms that govern growth and barrier function of the gastrointestinal epithelium have received particular attention over the past decade, especially with advancements in molecular-based techniques, such as microarrays and next-generation DNA sequencing. The rumen has been the focal point of dairy cow and calf nutritional physiology research, whereas the lower gut has received less attention. Three key areas that require discovery-based and applied research include (1) early-life intestinal gut barrier function and growth; (2) how the weaning transition affects function of the rumen and intestine; and (3) gastrointestinal adaptations during the transition to high-energy diets in early lactation. In dairy nutrition, nutrients are seen not only as metabolic substrates, but also as signals that can alter gastrointestinal growth and barrier function. Nutrients have been shown to affect epithelial cell gene expression directly and, in concert with insulin-like growth factor, growth hormone, and glucagon-like peptide 2, play a pivotal role in gut tissue growth. The latest research suggests that ruminal and intestinal barrier function is compromised during the preweaning phase, at weaning, and in early lactation. Gastrointestinal barrier function is influenced by the presence of metabolites, such as butyrate, the resident microbiota, and the microbes provided in feed. In the first studies that investigated barrier function in cows and calves, it was determined that the expression of genes encoding tight junction proteins, such as claudins, occludins, and desmosomal cadherins, are affected by age and diet. Recent evidence suggests that the upper and lower gut can communicate, but the exact mechanisms of gastrointestinal cross-talk in ruminants have not been studied in detail. A deeper understanding of how diet and microbiota can affect growth and barrier function of the intestinal tract may facilitate the development of specific management regimens that could effectively influence gut function.
Key words: rumen, lower gut, gut function

INTRODUCTION

The primary roles of the gastrointestinal epithelium (**GE**) are to protect the host from the mixture of microorganisms, toxins, and chemicals in the lumen and to prevent unregulated movement of these compounds into the lymphatic or portal circulation (Gäbel et al., 2002). The GE continuously senses the luminal composition to protect against threats to its integrity and enhance nutrient absorption (Furness et al., 2013). In addition to protecting the host, the GE controls nutrient absorption, metabolism, and delivery of nutrients to other body tissues. The gastrointestinal tract (**GIT**) plays a significant role in animal energetics as it utilizes 20% of the oxygen in the whole animal and accounts for 30% of metabolic and protein synthesis activities of the cow (Cant et al., 1996). Thus, although adaptations to the gut are local, they can influence the entire dairy cow or calf system.

Study of the ruminal epithelium has expanded over the last 5 yr, with particular attention being paid to the modulation of ruminal function in response to increasing rapidly fermentable carbohydrates (Penner et al., 2011; Steele et al., 2011a,b) and butyrate supplementation (Górka et al., 2011; Baldwin et al., 2012; Kowalski et al., 2015). However, the mechanisms controlling GE

Received September 5, 2015.
Accepted January 15, 2016.
[1]Presented as part of the ADSA Production Division Symposium: The Rumen and Beyond—Nutritional Physiology of the Modern Dairy Cow at the ADSA-ASAS Joint Annual Meeting, Orlando, Florida, July 2015.
[2]Corresponding author: masteele@ualberta.ca

responses, especially in the lower gut, during dietary adaptation are poorly understood. Moreover, microbes and digesta metabolites and their effects on the function and expression of genes of the lower gut are not well characterized, thus generating the need for further research. The ability to modulate gut epithelial function using nutrients and feeding schemes is of relevance and interest to the dairy industry as it will improve dairy cow and calf health and performance.

COMPARATIVE STRUCTURE OF EPITHELIA

The contents of the gastrointestinal lumen are separated from the lymphatic and portal circulation by 2 distinct epithelia: the stratified squamous epithelium (**SSE**) found in the reticulo-rumen and omasum (Figure 1A; Figure 2) and the columnar epithelium (**CE**) of the abomasum, small intestine, cecum, and large intestine, otherwise known as the lower gut (Figure 1B; Figure 2). In the reticulo-rumen and omasum, the SSE epithelial surface area is increased by papillae that protrude from the ruminal epithelium to increase absorption of short-chain fatty acids (**SCFA**) and minerals (Lavker and Matoltsy, 1970) and secretion of bicarbonate into the lumen (Aschenbach et al., 2011). The reticulo-ruminal and omasal SSE is composed of 4 distinct strata with multiple functions (Figure 1A). The stratum basale is the first cell layer adjacent to the basal lamina and to the stratum spinosum. The cells of the both the stratum basale and spinosum contain mitochondria that contribute to the metabolic properties of the ruminal SSE, including the metabolism of SCFA to ketones (Baldwin et al., 2004b). Adjacent to the stratum spinosum is the stratum granulosum, which is characterized by tight junctions (occludins, claudins), adherin junctions, and desmosomes, which add mechanical strength to the epithelium (Graham and Simmons, 2005). The stratum corneum is in direct contact with the ruminal and omasal contents and consists of dead cornified keratinocytes (Steele et al., 2011b). The corneum acts as protective barrier between the rumen contents and the lower living strata and is eventually sloughed into the rumen milieu (Graham and Simmons, 2005). Epimural microbes colonize the surface of the corneum but do not penetrate to the stratum granulosum (Steele et al., 2011b). The exact mechanisms controlling how cells differentiate and migrate through the highly metabolic regions of the basale and spinosum to the protective

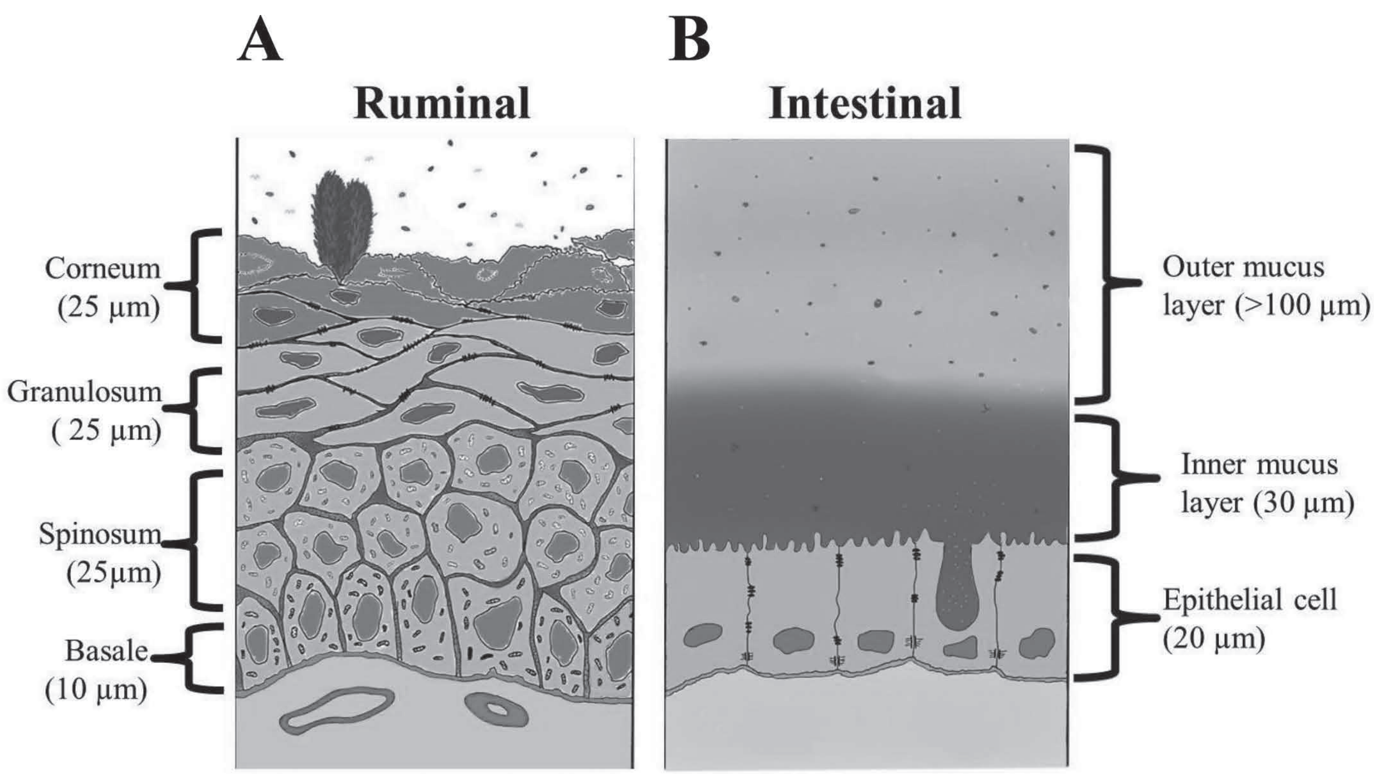

Figure 1. The large contrast of the ruminal and intestinal epithelia. (A) Stratified squamous epithelium of the rumen, and (B) columnar epithelium of the lower gut. Color version available online.