cities of the Maya, 50,000 at Tikal alone (*20*), were supported. Finally, the use of an intensive and sophisticated system of agriculture, one requiring considerable management, may also explain at least part of the vulnerability to the systemic collapse that the Maya suffered about A.D. 900.

We recognize that this work is preliminary. The radar imagery represents a large-scale perspective on ancient land use that has not been available before, but it also presents us with problems of full validation. The immense area covered means that it will be sometime before adequate ground checks can be made of all the potential canal areas. To date there has been some excavation of raised fields in Belize and in the Candelaria zone (*3*, *6*). Only excavation can produce more precise estimates of the total areas of raised field growing surfaces used in any given period. Excavated data are also needed on the populations in the raised field zones, as well as detailed information on water and land management techniques. Excavation at hamlets associated with raised field zones will throw light on matters such as stone technology, food crops, and developmental trajectories of the canal systems.

Finally, the new information may allow more effective land use planning by the modern governments of Guatemala, Belize, and Mexico. These nations are using the Maya lowlands, and their people are moving into the zones in great numbers in both planned and unplanned agricultural colonies. Radar technology and archeology may combine to provide at least some of the data needed about intensive agriculture in these tropical forest areas.

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Fermentation in the Rumen and Human Large Intestine

Meyer J. Wolin

A portion of the intestinal tract of mammals is a chamber where a large microbial community ferments components of the host's diet. In many mammals the fermentation occurs in a complex stomach. Ruminants (for example, cows, sheep, and deer) are the most familiar of these animals. Nonruminants, including those that chew their cud, that is, ruminate (for example, camels and llamas) and those that do not ruminate (for example, colobine monkeys and kangaroos) also have complex stomachs that are microbial fermentation chambers. Mammals with simple stomachs that do not support pregastric fermentation include herbivores (for example, horses and rabbits), carnivores (cats and dogs), and omnivores (humans and rats). Whether mammals have a complex or a simple stomach, they usually have a fermentation chamber in the large intestine.

The microbial ecosystem of the complex stomach (rumen) of domesticated ruminants is the most clearly understood intestinal fermentation system (*1–3*). Ruminants rely on digestion of food by microorganisms for essential macro- and micronutrients. Because these animals are excellent sources of milk, meat, wool, and leather, there is a significant amount of contemporary research on ways to manipulate the rumen community, for example, by adding antibiotics or other chemicals to feeds in order to increase the animals' economic value. The intestinal microbial ecosystems of other animals with complex stomachs have not been studied in as great detail, but there has been a recent surge of interest in the large intestine ecosystem of humans. There is increasing recognition that interrelations between diet and the characteristics of the microbial community are significant for human health.

I review here the general features of the rumen ecosystem and indicate how (and why) manipulations of the microbial community are being carried out. I also compare the features of the rumen and large intestine ecosystems and indicate how fermentation may influence human health.

Fermentation in the Rumen

The forestomach of ruminants is a self-contained factory where fermentation of the animal's food forms products essential to the animal (Fig. 1). Ingested polymers in grasses, hay, corn, and silage, for example, are comminuted by masti-

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cation in the oral cavity and swallowed. The polymers are then fermented in the rumen to short-chain volatile fatty acids (VFA)—principally acetate, propionate, and butyrate—and the gases methane and carbon dioxide. Energy from the fermentation and nutrients derived from the animal's food are used to form the large mass of bacteria and protozoa that sustain the fermentation. The VFA are transported from the rumen into the blood and used as the major source of carbon and energy for metabolic activities. Both CH_4 and CO_2 are removed from the rumen by belching.

An important feature of the system is that microorganisms are the primary digesting elements. Cellulose is not digested by enzymes of the ruminant but is fermented by the microbial community. Other constituents of feed, that is, hemicelluloses, starch, soluble carbohydrates, proteins, and lipids, are subject to microbial decomposition whether or not the animal has intestinal digestive enzymes that attack these compounds.

In addition to VFA, the vitamins and protein synthesized by microbial growth are extremely important to the host. Microbial synthesis satisfies the animal's requirements for B vitamins. A good portion (40 to 60 percent) of food protein is digested and used by the microorganisms, which in turn serve as a source of protein to the animal. If the feed protein is better suited to the animal's requirements than the microbial protein, the result is a loss in quality. In contrast, poor quality food proteins are upgraded by conversion to microbial protein. Urea, a nonprotein source of nitrogen, enters the rumen in saliva and by diffusion from the blood and is also used as a feed additive. It is decomposed to ammonia and CO_2 by microorganisms in the rumen, and the NH_3 is incorporated into microbial protein that is used by the animal.

Summary. Fermentation of food by the microbial community of the rumen is essential for the maintenance and growth of ruminants. The microbial ecosystem and its interaction with the host are described, along with recent attempts to manipulate the composition and activity of the microbial community by adding antibiotics and other chemicals to ruminant diets. A similar microbial community and fermentation occur in the large intestine or cecum of most nonruminant animals including the large intestine of humans. The microbial ecosystems of the rumen and human large intestine are compared.

The rumen environment is a product of microbial and host contributions. The large volumes of gases and vast numbers of microorganisms create a highly anaerobic environment. The temperature of the rumen depends on that of the animal, and *p*H is controlled by the large amounts of bicarbonate and phosphate entering the rumen in saliva. Muscle contractions of the rumen mix the contents of the system, and regurgitation and chewing the cud assist in the mixing and grinding of rumen contents.

Typical amounts of rumen microorganisms and major products are shown in Fig. 1 and Table 1. A 500-kilogram bovine has about 70 liters of rumen contents; a 35-kg ovine has about 5 liters. Estimates of the fermentation products formed daily by rumen microorganisms are shown in Table 2. Most of the VFA are absorbed from the rumen and enter the bloodstream. The contents are pumped out of the rumen by the omasum, where water and solutes are transported into the blood, and into the abomasum, which is physiologically similar to a true stomach. The digesta then enter a small intestine and large intestine digestive system like that of animals with simple stomachs. Microorganisms and undigested nutrients are digested by typical mammalian intestinal enzymes and secretions.

Approximately 60 liters of saliva and 40 liters of water enter the rumen of a 500-kg nonlactating bovine each day. Turnover times for the liquid portion of the rumen vary from 4 to 30 hours. The turnover of solids is generally slower, ranging from 10 to 55 hours. Factors that influence turnover times include the level of food intake, the cell wall content, and the particle size of the diet (*4*). Turnover times set important constraints on microbial activity, since the products of this activity are determined by the balance between rates of microbial processes and rates of passage of rumen contents. Rates of passage can also influence the composition of the community. Populations whose generation times are longer than the turnover time would wash out of the system.

In addition to interactions between the microbial community and the animal, many interactions between different microbial populations are essential for maintaining the community and its activity. The 17 species of nonsporing, anaerobic bacteria and six genera of protozoa that tend to dominate the rumen interact

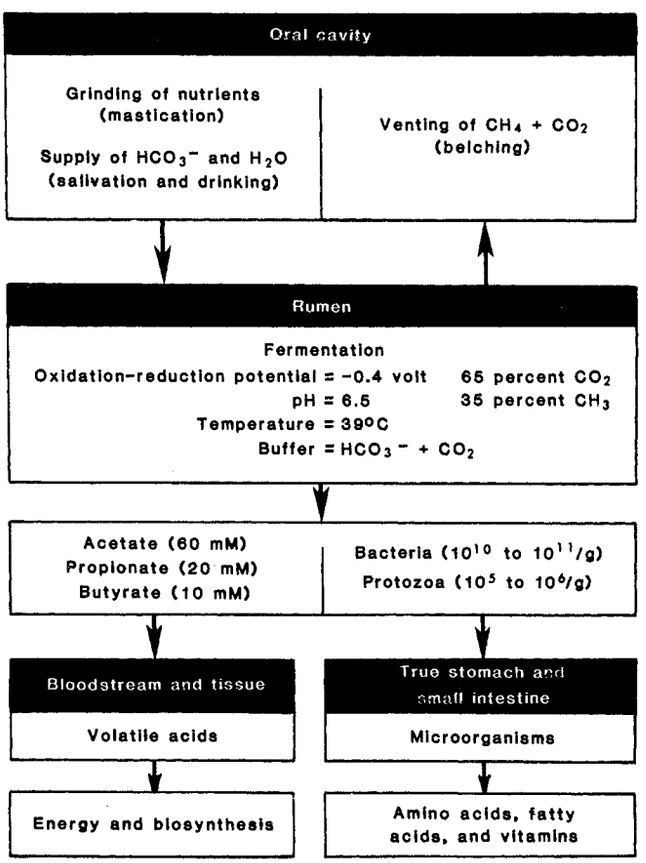

Fig. 1. Schematic representation of the ruminant as a factory for conversion of food to animal products. [From Wolin (*3*)]

Table 1. Dry weight (measured in grams) of bacteria and protozoa and microbial protein in the rumen. [From Wolin (*3*), courtesy of Plenum Publishing Corporation]

Microorganism	Ruminant	
	Bovine	Ovine
Protozoa		
Cells	315	22.5
Cell protein	172	12.3
Bacteria		
Cells	399	28.5
Cell protein	217	15.5

nutritionally. Some synthesize and excrete vitamins that others require for growth. Protein is hydrolyzed and fermented to organic acids and NH_3 by some, and the NH_3 is used by almost all of the bacteria as their major source of nitrogen. Protozoa eat bacteria as their source of protein.

Some interactions determine the overall course of the fermentation (Fig. 2). Most of the fermentation results from the breakdown of carbohydrate polymers. Populations that produce small molecular weight products from these large molecular weight substrates feed not only themselves but also the populations that cannot degrade the polymers.

A very important interaction involves the fermentation of carbohydrates to produce hydrogen, which is required by CH_4-producing species. These methanogens obtain energy for growth by using the H_2 to reduce CO_2 to CH_4. For this reason, although H_2 is an important intermediate product of fermentation by many of the major carbohydrate-fermenting species, it never accumulates in the rumen. Succinate, another important product of the fermentations of several significant species, never accumulates in the rumen because certain species rapidly decarboxylate it to propionate and CO_2.

The rapid use of H_2 by methanogens affects H_2 production by carbohydrate-fermenting populations (*5*). Some H_2-evolving biochemical reactions are not inhibited by H_2, but others are. Removal of H_2 permits the latter reactions to proceed. Inhibition is due to reversal of H_2-producing reactions whose equilibrium constants favor utilization rather than production of H_2. The most important of these is the production of H_2 from reduced pyridine nucleotides [reduced nicotinamide adenine dinucleotide (NADH) and nicotinamide adenine dinucleotide phosphate (NADPH)]. Continual reduction and oxidation of pyridine nucleotides is a key process in any fermentation, and reoxidation is normally accomplished by reduction of a fermentation intermediate to a fermentation product. Pathways for formation of fermentation products such as lactate, ethanol, propionate, succinate, and butyrate involve the reoxidation of NADH or NADPH. Reduction of protons to H_2 by NADH or NADPH can prevent the formation of these compounds, and their precursors can then be used to form more oxidized products. Some important rumen bacteria that produce ethanol, lactate, succinate, or propionate produce less of these products and more acetate and CO_2 when they are cocultured with H_2-using bacteria such as methanogens.

Table 2. Daily production of volatile fatty acids in the rumen. [From Wolin (*3*), courtesy of Plenum Publishing Corporation]

Volatile acid	Ruminant	
	Bovine	Ovine
Acetic		
Moles per rumen	62	4.4
Kilograms per rumen	3.7	0.26
Propionic		
Moles per rumen	15	1.1
Kilograms per rumen	1.1	0.08
Butyric		
Moles per rumen	7	0.5
Kilograms per rumen	0.6	0.04

Modification of Rumen Fermentation

The relation between the formation of VFA and CH_4 has stimulated the investigation of methods to decrease CH_4 production and simultaneously to increase the production of VFA. The production of CH_4 and its loss through belching represents a loss of about 10 percent of the energy intake of ruminants. Retention of the energy in the form of VFA would represent a more economical use of feed. Specific inhibitors of methanogenesis, for example, higher unsaturated fatty acids and chloroform, have caused the desired fermentation shifts in experiments both in vitro and in vivo (*6*). They have not been useful for husbandry because of undesirable side effects or ineffectiveness in improving animal performance.

Screening for compounds that produce improved animal performance is difficult. Costs of direct testing in ruminants are immense. Experimental designs are expected to include test and control groups of large animals, the use of various doses of the additive, and concerns about both animal and human toxicity. Screening in the laboratory to detect promising compounds typically involves the removal of rumen contents from a fistulated animal and incubation with feed substrates with and without a test compound. If the compound causes an increase in VFA production, or a decrease in CH_4, or both, consideration is given to using it in feeding trials.

The ionophore antibiotic monensin showed promise in laboratory screens and feeding trials and now is heavily used as a feed supplement for beef cattle. Monensin increases the production of propionate and decreases the production of CH_4 in the rumen (*7*). The proportion of propionate in the VFA of the rumen increases. Animals fed monensin also show greater efficiency of feed utilization: they eat less food than control animals but gain weight at the same rate (*8*). It is not clear how monensin causes this increased efficiency of feed utilization. It is likely that more energy is available from the same amount of feed when more propionate and less CH_4 are produced.

Of the three major VFA's in the rumen, only propionate is gluconeogenic, that is, the animal produces the glucose its tissues require by converting propionate to glucose in the liver. Modification of ruminants' diets to include relatively more starch than carbohydrates from plant cell walls also increases the propor-

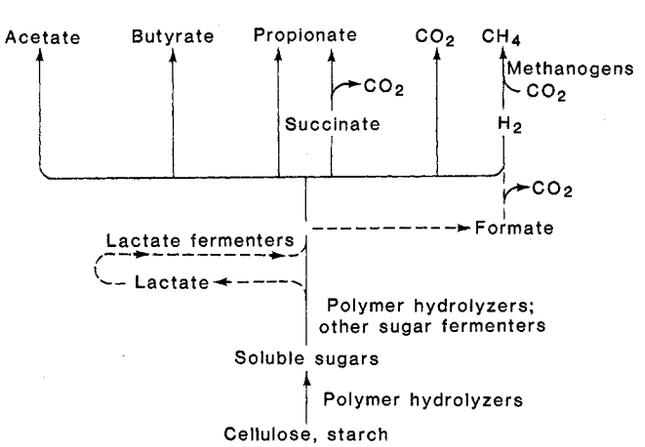

Fig. 2. Intermediates and products of the rumen fermentation of plant polysaccharides. The dashed line represents minor pathways. [From Wolin (*3*)]

tion of propionate in the rumen, increases the synthesis of animal protein, and decreases the formation of milk fat (*9*). Monensin or other treatments that increase propionate production are thus of no benefit to dairy farmers, who receive more money for milk as its fat content increases.

We have shown that monensin and another ionophore antibiotic, lasalocid, inhibit those bacterial species in the rumen that are of major importance in producing acetate, butyrate, and H_2, the precursor of CH_4 (*10*). The species that produce propionate and most of the succinate (a precursor of propionate) and little H_2 are either insensitive to the antibiotics or easily develop resistance to them. The inhibited populations are Gram-positive bacteria; the resistant populations are Gram-negative. Gram-positive bacteria in general are more sensitive to ionophore antibiotics than are Gram-negative species. Our studies suggest that monensin changes the fermentation pattern in the rumen by selecting for populations that produce more propionate and less H_2; the decrease in H_2 causes a decrease in the formation of CH_4.

Another interesting strategy for altering fermentation depends essentially on an alteration of the system's turnover time. This is accomplished by feeding the ruminant salts, such as $NaHCO_3$ or NaCl. Increased ion concentrations in the rumen result in greater water consumption because of the need to maintain an osmotic balance with blood plasma. The increase in water intake causes greater water flow from the rumen. This more rapid turnover is accompanied by increased production of acetate and butyrate and decreased production of propionate and CH_4 (*11*). The buffering action of anions such as HCO_3^- may also contribute to the shifts in fermentation. The specific microbiological changes that cause the alteration are not clear (*12*).

In addition to finding ways to change fermentation, nutritionists have been interested in providing ruminants with proteins and amino acids that do not require processing into microbial protein. Wool production is limited by the amount of sulfur amino acids in microbial protein. An analog of methionine, the methyl ester of 2-hydroxy-4-methylthiobutyric acid, escapes microbial decomposition in the rumen, is absorbed into the blood, and causes increases in plasma cystine and methionine. Feeding the ester to sheep significantly increases wool production (*13*). Other methods used to protect protein from digestion in the rumen include treatment with heat or formaldehyde. Formaldehyde-treated feeds tested experimentally in sheep increased wool production. Despite extensive evidence that microbial protein synthesis limits the production of meat and milk, there has been no demonstrated effect of a protected protein or any other compound on the synthesis of meat or milk.

Supplying potentially useful feed additives to pasture-fed animals such as sheep is difficult, in contrast to the factory-like operations in most feedlots used for the finishing of beef cattle. This difference, as well as the importance of beef in the United States, has led to an emphasis on the development of additives that benefit the production of beef, rather than milk and wool. Diets used in feedlots are high in starch and protein. However, it is important to increase the efficiency of use of the world's vast resources of highly cellulosic pasture crops which ruminants effectively convert to meat, milk, leather, and wool.

The empirical screening of potentially useful compounds would be more effective if pure cultures of the major species of the rumen microbial ecosystem were tested individually for their response to tests to predict in vivo effects. Since many of the species have been isolated and characterized and their roles in the overall fermentation are reasonably well understood, such screening with pure cultures is certainly feasible.

Reasonable facsimiles of this ecosystem, including most of the major populations, can be initiated with rumen contents and maintained on ruminant diets in semicontinuous culture in the laboratory (*14*). One advantage of these cultures is that the community and its activities can be subjected to the selective pressures of alterations in diet, for example, hay versus grain. With the screening procedures now used, the effect of an agent on the fermentation of rumen contents taken directly from an animal may reflect only its effect on the particular community developed in response to that animal's diet.

A problem with attempts to manipulate the rumen microbial community is insufficient understanding of the factors that determine the quantitative relations between populations of the community and their contributions to ecosystem activity. If there were some way to place pure cultures of all of the major species of rumen bacteria and protozoa in a laboratory culture vessel, feed them ruminant feeds, and make them carry out a rumen fermentation, the contributions of each population to the growth and activities of the community might be determined. Rational approaches, including modern techniques of genetic engineering, could then be taken to manipulate populations to achieve particular ends. For example, populations might be introduced and maintained that hydrolyze cellulose faster, produce more propionate, or even produce amino acids that could be used by the animal. Acetate could also be produced instead of methane by substitution of species that use H_2 to reduce CO_2 to acetate (*15*). This approach, however, would be a striking departure in microbiological research, which has historically involved manipulation of pure cultures of single species of bacteria and protozoa, rather than manipulation of ecosystems constructed with pure cultures.

Fermentation in the Large Intestine

The digestion of dietary components by microbes in the large intestine is not essential for digestion in humans. Enzymic digestion in the oral cavity, stomach, and small intestine removes most dietary constituents (*16*). However, the fibrous constituents of the human diet, which come mainly from plant cell wall material, are not digested by mammalian enzymes. Cellulose, hemicelluloses, and pectins of vegetables and fruits are thus available for microbial fermentation in the large intestine (*17*). Polysaccharides of mucins produced by the host and in meat are not digested by the host and are also available for microbial fermentation (*18*). Some small molecular weight carbohydrates—including stachyose in beans, raffinose in cottonseed meal, and the artificial sugar lactulose—are also not attacked by mammalian enzymes but are degraded by the microbial community of the large intestine. Furthermore, some humans have genetic deficiencies that prevent them from hydrolyzing milk sugar, lactose, in the small intestine. Native lactose cannot be absorbed and thus becomes available for fermentation in the large intestine.

Most of the constituents of meats are digested by mammalian enzymes. It is not known if significant amounts of the constituents of meats ever reach the large intestine. There is a source of digestible animal nutrients, however, in the sloughed-off intestinal epithelium of the small and large intestines (*19*). Urea is a source of nitrogen for microbial biosynthesis in the large intestine (*20*). Urea is produced by host breakdown of nitrogenous compounds and enters the intestine from the blood. Microorganisms hydrolyze the urea to NH_3 and

CO_2, and the NH_3 is used for biosynthesis. Other significant inputs into the large intestine originate from the host or host metabolism. Salts in the fluid of the small intestine move into the large intestine from the ileum. Salts are transported in and out of the large intestine from and to the bloodstream. The ion composition of the human fermentation system is probably similar to that of the rumen, being high in Na^+ and HCO_3^-. One significant difference between the rumen and the large intestine is that, in the latter, the contents are exposed to metabolic products in bile, including primary and secondary bile acids, cholesterol, and bile pigments.

The hydraulic conditions that influence the large intestine system are uncertain. One possibility is that most microbial growth and activity occur in a liquid suspension soon after fluid from the small intestine enters the large intestine (*21*). According to another model, there is a plug-flow system, in which significant growth of microorganisms occurs after the water is removed from large intestine contents in the process of formation of feces. Perhaps both kinds of growth systems coexist.

Products of the large intestine fermentation are similar to those of the rumen. Acetate, propionate, and butyrate are formed along with CH_4, H_2, and CO_2. The fermentation is sustained by a large community of bacteria. Viable bacteria in feces number approximately 1×10^{11} per gram of wet weight. About 120 g of feces, wet weight, are produced daily by adults on high-meat, low-fiber diets (*22*). Thus the total daily production of excreted bacteria is about 1.2×10^{13} cells, which is equivalent to about 16.0 g dry weight (*23*).

There is no certainty that the only major products of fermentation in the large intestine are VFA, CH_4, H_2, and CO_2. In about 33 percent of the population CH_4 is a major product (*22*). Although simultaneous measurements of H_2 and CH_4 production are rare, in one study both were produced in the same individual (*24*). Non-CH_4-producing systems also produce H_2 (*25*). Rates of production of the other products have not been measured, but it is possible to estimate the daily production by making four broad assumptions: (i) VFA, CH_4, and CO_2 are the only products; (ii) all products are formed from $C_6H_{10}O_5$, the major monomeric unit of cellulose; (iii) fermentation of 1 mole of hexose generates 4 moles of adenosine triphosphate (ATP), and each mole of ATP provides energy for synthesis of 10.5 g dry weight of cells; (iv) VFA's are produced in the same proportions as are found in feces.

Table 3. Growth and fermentation of human fecal bacteria.

Substrate and products	Per gram (wet)	Per 120 g (wet)
Bacteria	1×10^{11} cells	1.2×13^{13} cells
Bacterial mass (dry weight)	133 mg	16 g
ATP required*	12.9 mmole	1551 mmole
Hexose required†	3.08 mmole	369 mmole
Acetate formed	4.26 mmole	511 mmole
Propionate formed	0.98 mmole	117 mmole
Butyrate formed	0.46 mmole	55 mmole
Methane formed	2.10 mmole	252 mmole
Carbon dioxide formed	3.08 mmole	369 mmole

*One mole of ATP is required for 10.5 g of cells, dry weight. †Four moles of ATP are formed per mole of hexose.

From these assumptions it is possible to calculate an equation for the assumed fermentation, based on fecal VFA concentrations determined by Zijlstra *et al.* (*26*):

$$34.5\ C_6H_{10}O_5 \rightarrow 48 \text{ acetic acid} + 11 \text{ propionic acid} + 5 \text{ butyric acid} + 23.75\ CH_4 + 34.25\ CO_2 + 9.5\ H_2O$$

The daily amount of hexose required by the community can be calculated from the amount of ATP required for synthesis of biomass. Then the amount of products can be calculated from the equation.

The calculations (Table 3) indicate that far more VFA are produced than can be accounted for in excreted feces. A reasonable conclusion is that most VFA enter the bloodstream and are metabolized by the host. Similar conclusions were inferred from measurements of inputs and outputs of cellulosic and hemicellulosic materials and outputs of VFA (*27*). VFA are absorbed across the colonic wall, accompanied by absorption of blood HCO_3^- into the colon (*28*). Pigs and rabbits absorb and utilize VFA produced by bacteria in the large intestine (*29*). In the rabbit VFA production can supply up to 30 to 40 percent of its energy requirement (*30*).

It has been estimated that VFA produced in the large intestine could provide appreciable metabolizable energy for humans whose diets regularly contain large amounts of plant fiber (*28*). VFA also inhibit the growth of several bacterial pathogens that cause intestinal infections (*31*). Butyrate is a potent effector of cellular differentiation in various tissue culture systems at concentrations that are at or below those present in feces (*32*), but the possibility that butyrate can influence host cell differentiation in the large intestine has not yet been considered.

Most of the H_2 and CH_4 produced in the large bowel are absorbed by the blood, removed from the blood in the lungs, and exhaled (*24, 25*) and a portion of these gases is excreted in flatus. Overproduction of these gases, particularly H_2, can cause serious discomfort and is generally associated with rapid fermentation of small molecular weight compounds, such as stachyose, that escape monogastric digestion. Since fermentation provides the energy and carbon for sustaining the microbial community, it supports the production of all other microbial products including transformed bile pigments, secondary bile acids, and extracellular enzymes. Certain indigenous large intestine bacteria cause infections after gaining entry to other body tissues, and the activities of the microbial community have been implicated or suggested to be associated with specific disorders of the intestinal tract (*33*).

Microorganisms of the Rumen and Large Intestine

The communities of the rumen and large intestine are dominated by microorganisms that are extremely sensitive to oxygen (*34*). In addition to bacteria, the rumen contains many protozoa, mainly ciliates. Recent studies indicate that anaerobic phycomycetes may be populous in the rumen of animals fed high-roughage diets (*35*). The molds are firmly attached to plant fiber and may be important in the digestion of lignocellulose. Protozoa are not present in the normal human intestine.

There are distinct differences in the spectra of bacterial genera and species found in the two ecosystems. At least one genus, *Bacteroides*, is important in both, but the species in the two environments differ. Members of the so-called coliform group, particularly *Escherichia coli*, are not in high concentration in either ecosystem, although their proportions are higher in the large intestine (0.1 to 1.0 percent of the total viable count) than in the rumen (10^{-5} to 10^{-6} percent). Methanogenic bacteria are always present in high concentration in the normal rumen, whereas the sporadic CH_4 pro-

duction in humans indicates that high concentrations of methanogens are sporadic. In addition to the microbial population in the lumen, specific types of bacteria are firmly attached to and even embedded in epithelial cells of the rumen and large intestine (*36*).

Interactions between species in the large intestine are probably similar to those in the rumen, but they have not been investigated. Since protozoa are not normally present and methanogens are not always present, interactions involving these organisms are relevant to the human large intestine only when CH_4 is produced. Human intestinal *Bacteroides* produce succinate and propionate from carbohydrate (*37*), and formation of propionate requires vitamin B_{12}. In contrast, rumen *Bacteroides* produce only succinate, whether or not vitamin B_{12} is present, and a non-*Bacteroides* species is required to decarboxylate succinate to propionate (*37*). Other similarities and differences between the systems probably will become apparent as more is learned about the large intestine ecosystem.

Future Research

The rumen system is reasonably well understood. New information about its microorganisms, their activities and host physiology will no doubt continue to be uncovered and will improve our understanding of how the system operates. However, sufficient information is available to allow the investigation of rational approaches for manipulating the microbial community to achieve more effective production of milk, meat, and fiber. Suggested approaches have been discussed in this article.

The characteristics of the large intestine ecosystem are more poorly understood than those of the rumen. Comparison of the two systems is useful for identifying similarities and differences between the systems, and more precise information about the rumen provides a basis for speculating about features of the large intestine that are difficult to investigate. The recent interest in the interrelations between diet, large intestine microbial activities, and disease, particularly colon cancer (*38*), has emphasized the need for more exact information about the operation of the ecosystem of the large intestine. The information about the rumen and approaches used to study its microbial ecosystem may provide useful new ideas for investigating the factors that influence the composition of the large intestine microbial community, its activities, and its interaction with the host.

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