## Contributions of Microbes in Vertebrate Gastrointestinal Tract to Production and Conservation of Nutrients

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Stevens, C. Edward, and Ian D. Hume. Contributions of Microbes in Vertebrate Gastrointestinal Tract to Production and Conservation of Nutrients. *Physiol. Rev.* 78: 393–427, 1998.—The vertebrate gastrointestinal tract is populated by bacteria and, in some species, protozoa and fungi that can convert dietary and endogenous substrates into absorbable nutrients. Because of a neutral pH and longer digesta retention time, the largest bacterial populations are found in the hindgut or large intestine of mammals, birds, reptiles, and adult amphibians and in the foregut of a few mammals and at least one species of bird. Bacteria ferment carbohydrates into short-chain fatty acids (SCFA), convert dietary and endogenous nitrogenous compounds into ammonia and microbial protein, and synthesize B vitamins. Absorption of SCFA provides energy for the gut epithelial cells and plays an important role in the absorption of Na and water. Ammonia absorption aids in the conservation of nitrogen and water. A larger gut capacity and longer digesta retention time provide herbivores with additional SCFA for maintenance energy and foregut-fermenting and coprophagous hindgut-fermenting species with access to microbially synthesized protein and B vitamins. Protozoa and fungi also contribute nutrients to the host. This review discusses the contributions of gut microorganisms common to all vertebrates, the numerous digestive strategies that allow herbivores to maximize these contributions, and the effects of low-fiber diets and discontinuous feeding schedules on these microbial digestive processes.
I. INTRODUCTION

One of the most prevalent and interesting characteristics of the digestive system is the symbiotic relationship between an animal and the microorganisms that inhabit its digestive tract. The gastrointestinal tract of vertebrates becomes colonized with bacteria shortly after birth or hatching. This includes transient microorganisms and the autochthonous bacteria, which develop into relatively stable populations that are characteristic of the species (76). The number and species of microorganisms in a given gut segment are affected by the pH and retention time of digesta. This review emphasizes the ubiquitous role that gut microbes play in the provision and conservation of nutrients and their role in expanding the nutritional niches available to herbivores. The nutritional contributions of gut microbes are dependent on the diet, habitat, and anatomy of the digestive system and the pH and retention time of digesta. Therefore, we begin with a discussion of the variations in diet, habitat, and the structure and function of the digestive system that are related to the microbial production of nutrients. This is followed by a description of the gut microbes and their contributions to nutritional requirements. Section IX discusses some of the major dysfunctions in microbial digestive processes that can result from improper diets and feeding practices.

II. VARIATIONS IN DIET, HABITAT, AND GENERAL CHARACTERISTICS OF THE DIGESTIVE SYSTEM

The vertebrates are believed to have evolved ~500 million years ago and presently consist of ~45,000 species, which can be divided into 8 classes of fish, amphibians, reptiles, birds, and mammals. These animals show a wide range of variation in habitat, diet, and the structural characteristics of their digestive system. Because of species variations, comparisons of the digestive tract are best described under the general headings of headgut (mouthparts and pharynx), foregut (esophagus and stomach), and the midgut and hindgut, which are the small and large intestine in many species.

A. Fish

Almost one-half of the vertebrate species belong to four classes of fish: the Cephalaspidomorphi, Myxini, Chondrichthyes, and Ostechthyes. The first two classes contain the lowest craniate vertebrates, the cyclostomes (lampreys and hagfish). The Chondrichthyes contains fish with a cartilaginous skeleton (chimeras, sharks, skates, and rays). Ostechthyes (teleosts or bony fish) can be subdivided into four subclasses: Crossopterygii (lobe-finned fish), Dipneusti (lung fish), Brachiopterygii (gar, sturgeon, paddlefish, and bowfin), and Actinopterygii. The Actinopterygii, which contains 38 orders, includes a large number of present-day fish and a majority of the North American freshwater species.

The fish include macrophagous and microphagous carnivores, omnivores, and herbivores, which may feed on living or dead material. Some can vary their diet from fish in the summer to plankton in the winter, even utilizing bacteria and algae as food (22). The anatomy of the fish digestive system has been reviewed by Harder (117, 118)
The esophagus of fish is generally short, and the stomach is absent in cyclostomes and some advanced groups. When present, the stomach is either straight, U-shaped, or Y-shaped with a blind sac on its greater curvature. It is lined with regions of proper gastric mucosa, which secretes HCl, pepsinogen, and mucus, and pyloric mucosa, which secretes HCO₃ and mucus. The midgut can vary from one that is short and straight to a longer structure with spirals and loops. In some species with a small or absent stomach and short intestine, folds of the midgut extend varying distances into the lumen to form a spiral valve, which increases its surface area and delays digesta passage. In many species that have a stomach, the surface area and digesta retention time of the cranial midgut are increased by the presence of anywhere from 1 to 1,000 pyloric ceca. The hindgut of most fish is short and difficult to distinguish from the midgut. However, the intestine is divided into two distinct segments, separated by a valve or sphincter, in a few species.

The exocrine pancreatic tissue is present in primitive ceca along the midgut of cyclostomes and some species in the more advanced classes of fish. However, the pancreas is a compact organ in sharks, skates, rays, many teleosts, and all other vertebrates. The liver is a compact organ in all vertebrates, and biliary secretions are stored in a gallbladder in most vertebrates, but a gallbladder is absent in some species of fish and mammals.

Herbivores are relatively rare among fish and confined to teleosts. Most herbivores are of intermediate body size. Horn (130) classified the digestive tracts of herbivorous marine fish into four types, based on adaptations designed to degrade cell walls of algae and/or bacteria by acid lysis, mechanical trituration, or microbial fermentation (Fig. 1). The first type, which includes surgeon fish, has no mechanisms for the trituration of food and a thin-walled stomach, but a relatively long intestine. The second type, which includes the mullets, features a thick-walled, gizzardlike segment of stomach and an intestine of variable length. The third type, which includes the marine parrotfish and freshwater grass carp, has pharyngeal teeth that grind food to a small particle size but no stomach and a relatively short intestine. The fourth type, seen in the sea chubs, has a long intestine that includes a distinct hindgut.

B. Amphibians

All ectothermic tetrapods (amphibians and reptiles) are found within 45° of the equator, and their greatest diversity is seen within 20° (90). Amphibians presently contain ~4,000 species belonging to three orders: the Gymnophiona (wormlike burrowing amphibians), Caudata (salamanders, newts, and congo eels), and Salientia (frogs and toads). Most species begin life as free-living aquatic larvae, which metamorphose into terrestrial adults. Larval amphibians may be carnivores, omnivores, or herbivores (218). Some have a large mouth and can engulf their entire prey of crustaceans, mosquito larva,
or worms. Others have complex, microphagous, filtering mechanisms for ingestion of bacteria, zooplankton, or phytoplankton, which can be aided by the removal of encrusted material with horny teeth in anurans (frog and toad) tadpoles. Most larval anurans lack a stomach or gastric pouch. The gastric region usually forms a thickened sheath, which produces mucus, a proteolytic cathepsin, and a low pH. Pepsin has been rarely reported. The intestine is relatively long, with no distinct separation into a midgut and hindgut.

Adult amphibians are carnivores with weak dentition that serves for the grasping of food while it is being swallowed. Metamorphose of anurians is accompanied by profound changes in diet, feeding practices, and the structure and function of the gastrointestinal tract (133, 218). This includes the appearance of a stomach lined with areas of proper and pyloric glandular mucosa, joined by an additional area of cardiac glandular mucosa in some species. The intestine is shortened, with removal and regeneration of intestinal epithelium and the appearance of a distinct hindgut (Fig. 2).

C. Reptiles

Class Reptilia presently consists of ~6,250 species in three orders: Crocodilia, Testudinata, and Squamata. The Crocodilia includes crocodiles, alligators, caimans, and gavials. The Testudinata, or chelonians, can be subdivided into turtles (marine), terrapins (freshwater), and tortoises (terrestrial) but are often referred to collectively as turtles. The Squamata consist of snakes, lizards, worm lizards, and the tuatara, a primitive New Zealand reptile.

The anatomy of the reptilian digestive system has been reviewed by Parsons and Cameron (201), Luppaa (171), and Bjorndal (26). The mouth parts of most reptiles are used for grasping, cutting, and tearing their food. This is accomplished with a beak in the chelonians and teeth in other reptiles. A few species have teeth that can crush their food, but the scissorlike action of the reptilian jaw prevents the grinding of food into small particles (196). The salivary glands of reptiles, birds, and mammals secrete mucus and fluid that aid in the deglutition of food, and digestive enzymes in some species. The stomach of reptiles tends to be tubular, but it is larger and more outpocketed in crocodilians. The pylorus of alligators is muscular and separated from the remainder of the stomach by a constriction. Gastroliths (stones, gravel, or sand) have been reported in crocodilians, chelonians, and lizards. These were found in 100% of the stomachs of Crocodylus niloticus over 2 m in length (65), where they may provide ballast or serve the same triturative function as the gizzard in birds. Like the adult amphibians, the mucosal surface of the stomach is divided into regions of proper gastric, pyloric, and, sometimes, cardiac glandular mucosa.

The gastrointestinal tracts of a carnivorous, an omnivorous, and two herbivorous reptiles are illustrated in Figure 2. Most reptiles are carnivores or omnivores, and many subsist on insects during their early or entire life. Herbivores are limited to ~50 species of lizards (211), 40 species of tortoise (183), and a few turtles. The midgut tends to be longest in carnivores and shortest in herbivores. The opposite is true for the length of the hindgut, with the exception is the herbivorous Florida red-bellied turtle (Pseudemys nelsoni), which has an extremely long

FIG. 2. Gastrointestinal tracts of an adult amphibian and a carnivorous caiman, an omnivorous turtle, and herbivorous tortoise and lizard. Note cecum, larger volume, and greater relative length of hindgut in reptilian herbivores as well as baffles provided by projecting tissue in cecum and proximal colon of iguana. [From Stevens and Hume (252). Reprinted with permission of Cambridge University Press.]
small intestine that contained 68% of the gut contents (27). The hindgut includes a cecum in most herbivores. The cecum and proximal colon of herbivorous lizards in the families Iguanidae, Agamidae, and Scincidae are compartmentalized by mucosal folds (Fig. 2), which slow digesta passage and increase absorptive surface area.

Reptilian herbivores include terrestrial, freshwater and marine species, and a few lizards and tortoises that have adapted to desert environments. Herbivores appear to be limited in both their minimum and maximum body size. Juveniles of herbivorous species of lizard are carnivores or omnivores, and the adults weighed more than 300 g (211). An increase in body mass was associated with an increase in the relative gut capacity of herbivorous iguanas (263) and fiber digestibility in the herbivorous green turtle (Chelonia mydas) (25). The largest herbivores are the arboreal common iguanas (Iguana iguana), which weigh up to 13 kg (157), and tortoises (Testudo elephantus and Testudo gigantea), which weigh up to 250 kg with a high proportion of their body weight comprised of carapace (183).

The relative paucity of reptilian herbivores has been attributed to a poor masticatory apparatus, ectothermy, and the limitations of a small body size on the gut capacity of most species. However, this is difficult to explain in light of the striking success of herbivorous dinosaurs, which were the dominant terrestrial vertebrates during the Jurassic and Cretaceous periods and included both the largest species and others with a wide range of body size (64). The presence of smooth stones with their fossil remains suggest that some species may have used a gizzard to reduce plant material to a small particle size (17). However, Norman and Weishampel (191) concluded that the ornithopods, a large and diverse group of late Mesozoic dinosaurs, had a masticatory apparatus that approached the efficiency of mammals.

Dinosaurs also may have differed from present-day reptiles in their ability to maintain a stable body temperature. Farlow (89) concluded that a low mass-specific metabolic rate would reduce the total energy requirements and rate of digesta passage in large dinosaurs, and fermentation could provide heat for thermoregulation. The possibility that dinosaurs were endotherms also has been raised, based on their success in number of species and distribution long after the first appearance of mammals and comparisons of the structure and oxygen isotope composition of dinosaur bones with those of present-day reptiles, birds, and mammals (17, 21, 44, 223).

D. Birds

Birds are endotherms that differ from other vertebrates in their cover of feathers and (with the exception of bats) modifications for flight, which include the absence of teeth, decreased weight of the jaw skeleton and muscles, acquisition of a gizzard as the organ for trituration, and limitations in gut capacity. Storer (256) listed the ~8,600 species of existing birds under 28 orders. They include carnivores, piscivores, insectivores, carrion eaters, and species that feed principally on fruit, seeds, pollen, nectar, leaves, or roots. Many of the common species are found in the orders Galliformes (cocklike) and Passiformes (sparrowlike).

Structural characteristics of the avian digestive system are described by Ziswiler and Farner (287) and Duke (77). Mouth parts show wide diversification with the diet. This is particularly true for the bill, which can serve for cutting, tearing, crushing, filter-feeding, or other purposes. However, as with other nonmammalian vertebrates, the jaws are not constructed for efficient trituration or grinding of food. Figure 3 shows the gastrointestinal tracts of a carnivorous, an omnivorous, and four herbivorous species. The functions attributed to the stomach of other vertebrates are carried out by a crop (storage), proventriculus (pepsinogen and HCl secretion), and gizzard (trituration). The proventriculus is lined with proper gastric and pyloric glandular mucosa. The relative size of these organs tends to vary with the diet. Granivores and herbivores generally have a larger crop and a larger, more muscular gizzard.

Most birds have a relatively short midgut and a hindgut that consists of a short, straight colon and, often, paired ceca. Poppema (210) measured the relative lengths of intestinal segments in 644 specimens representing 24 orders, 51 families, 124 genera, and 166 species of birds. She found that ceca were absent or poorly developed in all species belonging to 13 of these orders. This included small passerine species and most of the larger species that feed on fruit, nectar, carrion, or small vertebrates. The most developed ceca and highest ratio of cecal length to total intestinal length were found in granivores and species whose diet contained high levels of plant fiber or chitin.

Most herbivores belong to the orders Galliformes and Rheiformes. Galliformes are predominantly ground birds that tend to fly only short distances. Suborder Opisthocomi contains only one species, the hoatzin (189), a 750-g South American folivore that is unique among birds in its use of an enlarged crop and distal esophagus (Fig. 3) for microbial fermentation (112). Suborder Galli contains a number of herbivorous grouse and two species of herbivorous partridge with a distensible crop, well-developed gizzard, and relatively large ceca (190).

Grouse consist of 11 genera and 18 species that weigh between 350 and 6,500 g. Prairie chicken inhabit North American steppes and semideserts, and hazel grouse, which include the ruffed grouse (Fig. 3), are inhabitants of mixed forests and semideserts of North America and Eurasia. Forest grouse include capercaillie, black grouse,
spruce grouse, and ptarmigan. Capercaille and spruce grouse can consume large amounts of conifer needles, and the ceca of spruce grouse doubled in length during the winter (202). Ptarmigans are distributed the furthest north of all land birds, in the tundra of North America, Greenland, and Eurasia, where they feed on twigs and buds during winter months. Most partridges are omnivores, but snow partridge and snow cocks are herbivores found in mountains up to 5,000 m above sea level (215).

Rheiformes (ratites) are flightless birds that include the herbivorous rheas, emus, ostriches, and recently extinct moas (234). Rheas, which inhabit the South American steppes and high plains, weigh up to 25 kg and use enormous ceca as the principal site for microbial fermentation. Emus, Australian birds that reach weights of 55 kg, have relatively short ceca and a short colon and long midgut (Fig. 3), which contained 37% of the gut contents and serves as the principal site of microbial fermentation (124). The largest living birds are the ostriches, which weigh up to 150 kg. Their principal site for microbial fermentation is their colon, which is much longer than that of other birds (Fig. 3). Although the moas of New Zealand are extinct, the presence of grass and twigs in the crop and feces of giant moas, which reached weights of 250 kg, indicate that they were herbivores as well.

E. Mammals

Mammals, which also are endothermic, consist of ~4,150 species. Mammals can be subdivided into two subclasses, Prototheria (echidnas and platypus) and Theria (marsupial and placental mammals), and can be further subdivided into 20 orders. One of the major advances in the evolution of mammals was the development of an extremely efficient masticatory apparatus (67). Although a few species have either lost their teeth or adapted them for other purposes, the teeth of most mammals include incisors for cutting, canines or fang teeth for grasping and tearing, and premolars and molars with uneven occluding surfaces. The latter are used for crushing. The lateral movements of the lower jaw seen in most mammals or the anterior-posterior movements seen in rodents and elephants provide a grinding action as well. Eisenberg (82) divided mammals into 16 categories of dietary specialization, and Langer and Chivers (165) discussed other dietary classifications. However, Table 1 lists the mammalian orders divided more simply into three categories based on the principal diet(s) of inclusive species.

The earliest mammals are believed to have been small carnivores, and 13 of the 20 orders contain species that feed principally on invertebrates or other vertebrates. The gastrointestinal tract of most carnivores is relatively short and simple (Fig. 4). The stomach is generally a unilateral dilatation of the digestive tract. The only exceptions to this are seen in the cetaceans (dolphins, porpoises, and whales), which have a large multicompartamental stomach (Fig. 4) that is believed to be conserved from herbivorous ancestors (182), and vampire bats, which have a convoluted stomach that is approximately twice the length of their body. A distinct hindgut is absent in some Insectivora, Carnivora, cetaceans, bats, and marsupials, and it lacks a valvular separation from the midgut in some of these species. Where present, the hindgut is relatively...
### TABLE 1. Mammalian orders and diets of inclusive species

<table>
<thead>
<tr>
<th>Order</th>
<th>Species</th>
<th>Diet</th>
<th>Animal and plant or plant concentrates</th>
<th>Plant fiber</th>
</tr>
</thead>
<tbody>
<tr>
<td>Monotremata</td>
<td>Echidna and platypus</td>
<td>✓</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pholidota</td>
<td>Anteaters</td>
<td>✓</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tubulidentata</td>
<td>Aardvarks</td>
<td>✓</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cetacea</td>
<td>Whales, dolphins, and porpoises</td>
<td>✓</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Macroscelidea</td>
<td>Elephant shrews</td>
<td>✓</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Insectivora</td>
<td>Moles, shrews, tenrecs, and hedgehogs</td>
<td>✓</td>
<td>✓</td>
<td></td>
</tr>
<tr>
<td>Scandentia</td>
<td>Tree shrews</td>
<td>✓</td>
<td>✓</td>
<td></td>
</tr>
<tr>
<td>Chiroptera</td>
<td>Bats</td>
<td>✓</td>
<td>✓</td>
<td></td>
</tr>
<tr>
<td>Carnivora</td>
<td>Dogs, cats, bears, panda, etc.</td>
<td>✓</td>
<td>✓</td>
<td></td>
</tr>
<tr>
<td>Marsupialia</td>
<td>Kangaroos, possums, koalas, etc.</td>
<td>✓</td>
<td>✓</td>
<td></td>
</tr>
<tr>
<td>Edentata</td>
<td>Anteaters, armadillos, and sloths</td>
<td>✓</td>
<td>✓</td>
<td></td>
</tr>
<tr>
<td>Rodentia</td>
<td>Rats, hamsters, squirrels, etc.</td>
<td>✓</td>
<td>✓</td>
<td></td>
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<tr>
<td>Primates</td>
<td>Lemurs, monkeys, apes, and humans</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Dermoptera</td>
<td>Colugos</td>
<td>✓</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Artiodactyla</td>
<td>Pigs, hippos, camelids, and ruminants</td>
<td>✓</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lagomorpha</td>
<td>Rabbits, hares, and pika</td>
<td>✓</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Perissodactyla</td>
<td>Horses, rhinos, and tapirs</td>
<td>✓</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Proboscidea</td>
<td>Elephants</td>
<td>✓</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sirenia</td>
<td>Manatees and dugongs</td>
<td>✓</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hyracoidea</td>
<td>Conies</td>
<td>✓</td>
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[Modified from Stevens (248).]

short and seldom haustrated, but it includes a cecum in some species.

Ten orders include omnivores, which feed on both plants and animals or on plant concentrates such as seeds, fruit, nectar, pollen, or roots, usually in addition to invertebrates. Some examples of omnivorous mammals are illustrated in Figure 5. With the exception of some rodents and frugivorous and nectivorous bats, their stomach is simple. The intestine varies in both its total length as a function of body length and the relative length of the midgut and hindgut. Bears have an extremely long intestine, with a short and indistinct hindgut, but the opossum intestine is almost equally divided between a midgut (small intestine) and hindgut (large intestine). Digesta re-

![Gastrointestinal tracts of mammalian carnivores.](http://physrev.physiology.org/Downloaded from http://physrev.physiology.org)
FIG. 5. Gastrointestinal tracts of mammalian omnivores. With exception of some rodents, such as rat, omnivores have simple stomachs. Their intestine is generally longer than that of carnivores, but midgut-to-hindgut ratio varies greatly. Bears and pandas have a very long midgut and a short and indistinct hindgut, whereas opossum's hindgut constitutes one-half of intestinal length. A cecum may be absent or present; it is well-developed in rats, in common with other rodents. Cecum and varying length of colon are haustrated in domesticated pigs, many herbivorous monkeys, apes, and humans. Illustration of rat gastrointestinal tract demonstrates effects of feeding time on relative size of stomach and cecum. Specimen on left was collected 4 h after feeding, and that on right was collected immediately after feeding; animals were fed at 12-h intervals. [Pig from Argenzio and Southworth (12). Human from Wrong et al. (282). Rat from Stevens (247). Copyright 1977 by Cornell University. Used by permission of the publisher, Cornell University Press. Armadillo from Stevens (248). Opossum and bear from Stevens and Hume (252). Reprinted with permission of Cambridge University Press.]

A large number of herbivores ranging from 6-g voles to large aquatic beavers and 40-kg capybara (101). They inhabit all types of environment, including the desert species of gerbils and jirds and Arctic lemmings. Landry (164) attributed much of their success to a flexible masticatory apparatus. Anterior movement of the mandible allows the occlusion of incisors outside of their mouth, enabling seizure of prey, clipping of stems and leaves, or removal of bark from shrubs and trees. Posterior movement occludes the molars for the grinding of food material.

The lagomorphs consist of 11 genera of hares and rabbits and one genus of pika that weigh from 400 to 2,000 g (5). They are widely distributed throughout the world, including species that inhabit deserts, arctic tundra, and altitudes up to 6,000 m. The small marsupial cecum fermenters are members of three families of arboreal herbivores: Phascolarctidae (koala), Phalangeridae (cucuses and brushtail possums), and Pseudochieridae (greater gliders and ringtail possums) (137). Hyraxes presently consist of one family and three genera that range from 2,500 to 3,500 g in body weight (216). Tree hyrax are principally arboreal folivores, but rock hyrax inhabits forests, steppes, and mountainous plains up to 3,700 m, and the Sahara hyrax in the mountains of Nigeria can survive practically without drinking water. Nonhuman primates also have a cecum, which is quite well developed in some lemurs and monkeys, but only a few of these species are predominantly herbivores (41).
FIG. 6. Gastrointestinal tracts of small hindgut-fermenting mammalian herbivores. Note domination of hindgut by an extremely well-developed cecum that is characteristic of herbivorous rodents, lagomorphs, small marsupial herbivores, and hyrax. Unlike other vertebrates, hyrax have both a well-developed cecum and a pair of colonic appendages. Stomach is also expanded and partly compartmentalized in hyrax and some rodents. (Rabbit from Stevens (247). Copyright 1977 by Cornell University. Used by permission of the publisher, Cornell University Press. Rock hyrax from Clemens (50). Copyright J. Nutr., American Institute of Nutrition. Koala from Harrop and Hume (121). Guinea pig and hamster from Stevens and Hume (252). Reprinted with permission of Cambridge University Press.)

An enlarged colon is the principal site for microbial fermentation in many of the larger herbivorous mammals, such as the perissodactyls, elephants, wombats, sirenians (manatees and dugongs), orangutans, and gorillas (Fig. 7). Perissodactyls include the equids and white rhinos, which graze on grasses and forbs, and the tapirs and black rhinos, which are browsers (271). Some equids, such as the African and Asiatic asses, inhabit semiarid and arid environments. Elephants are found in the forests and steppes of Asia and Africa, where they graze on grasses and browse on shrubs and small trees and the bark of large trees (4).

Gorillas and orangutans are chiefly folivores (91). Wombats consist of two genera and three species of mar-
FIG. 8. Gastrointestinal tracts of foregut-fermenting mammalian herbivores. Note extremely large stomach of these animals, which is either haustrated as a result of longitudinal bands of muscle, as seen in kangaroo and colobus monkey, or compartmentalized, as seen in sloth, sheep, and llama. Hindgut is less developed in most of these species, but its continued importance for recovery of electrolytes and water is demonstrated by extremely long colon of camels. [Kangaroo and sheep from Stevens (247). Copyright 1977 by Cornell University. Used by permission from the publisher, Cornell University Press. Sloth from Stevens (248). Colobus monkey from Stevens (249). Llama from Stevens and Hume (252). Reprinted with permission of Cambridge University Press.]

supial grazers that weigh up to 50 kg and inhabit the forests and semiarid regions of Australia (113). Haustrations extend over the cecum and the entire length of the colon of these species, and the colon is additionally divided into permanent compartments in the perissodactyls and elephants. Manatees inhabit rivers, river mouths, and freshwater lakes, feeding on marine algae, seaweed, and freshwater plants, but dugongs inhabit coastal seas and feed principally on four species of large algae (163).

A large compartmentalized or haustrated stomach is the principal site for microbial fermentation in the remainder of the large herbivores (Fig. 8). This includes most artiodactyls, and the sloths, macropod marsupials (kangaroos, wallabies and rat-kangaroos), and colobus and langur monkeys. The artiodactyls can be divided into the suborders Ruminantia (bovids, sheep, goats, giraffe, antelope, and deer), Tylopoda (new and old world camels), and Suiformes (hippos, peccaries, Malayan pig deer, and pigs). All but a few species of pigs are herbivores with an enlarged, compartmentalized stomach. The stomach of Ruminantia is divided into a large multicompartmental forestomach (reticulum, rumen, and omasum) and a secretory compartment (abomasum) that is similar to the entire stomach of most other vertebrates.

The rumen and reticulum serve as the major fermentation organ, and the omasum serves principally for the transfer of digesta from the reticulum into the abomasum. Hofmann (129) classified Ruminantia into bulk and roughage eaters that were relatively nonselective in their browsing or grazing, concentrate selectors that browsed on the more nutritious succulent portion of plants, and an intermediate group that varied their feeding habits according to the availability of food. Bulk and roughage eaters, such as cattle and sheep, had the most well-developed forestomach and smallest cecum. Concentrate selectors, such as the dik dik, had a comparatively small reticulumen and omasum and larger cecum. Development of the forestomach and cecum of the intermediate group fell between these two.

The forestomach of other herbivorous artiodactyls and sloths also is divided into permanent compartments, but the forestomach of macropod marsupials and colobid and langur monkeys is sacculated by haustra, like those seen in the cecum and colon of many mammals (Fig. 8). Sloths are small (4–9 kg) arboreal inhabitants of the forests of Central and South America that feed on leaves, young shoots, blossoms, and fruit. Macropod marsupial are represented by the small (1–3 kg) Potoridae (rat-kangaroos) and the Macropodidae (kangaroos and wallabies), which vary in size from 1-kg hare-wallabies to 70-kg kangaroos and are distributed in a wide range of habitats including arid environments (114). Most of the forestomach of rat-kangaroos consists of a cranial sac that serves for the immediate storage of ingesta (141), but the forestomach of kangaroos and wallabies consists principally of an enlarged, haustraed tube (Fig. 8) that resembles the colon of colon-fermenting herbivores. The small and many of the intermediate-sized macropod marsupials are browsers, but the larger species tend to be grazers.

The Colibidae consist of four genera of langur, snub-nosed, and proboscis monkeys in southeast Asia and one genera of African colobus monkeys with large sacculated
forests or swamps, but the largest langur, Presbytis entellus schistaceus, inhabits conifer and rhododendron forests of the Himalayas at elevations up to 4,000 m, which can be deeply covered with snow.

Many occupy tropical rain forests or swamps, but the largest langur, Presbytis entellus schistaceus, inhabits conifer and rhododendron forests of the Himalayas at elevations up to 4,000 m, which can be deeply covered with snow.

Digestion of food and passage of digesta require the secretion of large amounts of fluid and electrolytes by the salivary glands, stomach, pancreas, biliary system, and intestine. These are released intermittently into the digestive tract of carnivores and omnivores in association with feeding, but the more continuous feeding and greater microbial fermentation capacity of herbivores requires a more continuous secretion of larger volumes of fluid.

Gut contents represent a small percentage of the body water of most carnivores and only ~4% of the body water of humans, but the gastrointestinal tract of sheep contains 29% of its total body water, with much of this in the forestomach. Table 2 lists the daily secretions of fluid by various components of the digestive system of humans, sheep, and ponies. The digestive system (without the large intestine) of human subjects secreted 7 l/100 kg body mass, which is equivalent to ~35% of the extracellular fluid volume. However, daily secretions into the digestive tract of sheep and ponies were equivalent to >220% of their extracellular fluid volume. This was largely the result of salivary and gastric secretions in the sheep and salivary, pancreatic, and large intestinal secretions in the pony. Ninety-eight percent of this fluid was reabsorbed by the gastrointestinal tract of each of these species. Much of this is reabsorbed by the midgut or small intestine of most species, but the hindgut plays a critical role in terrestrial vertebrates and, particularly, hindgut-fermenting herbivores.

The reticulorumen also serves as a reservoir for water in some desert species. Black bedouin goats can survive 3 days without water, losing 40% of their body weight, and regain their weight rapidly by drinking (239). Slow release of digesta from the forestomach aids in the conservation of water during deprivation and prevents overhydration after drinking.

### III. DIGESTA PASSAGE AND RETENTION TIME

The time that digesta are retained in a given segment of the gastrointestinal tract can also determine the number and type of indigenous bacteria and the degree of microbial fermentation. Techniques for the use of markers to measure the kinetics of passage for fluid and particulate digesta have been reviewed by Clemens (52), Faichney (86), Warner (275), and Van Soest (269). The gastrointestinal transit time of food or a digesta marker is defined as the interval between its administration as a pulse dose into the stomach and its first appearance in the feces. A much more useful measure is the mean retention time (MRT), which is the average time that a marker remains in the gut.

The rates of food intake and digesta passage in ectothermic vertebrates are highly dependent on the ambient temperature. The temperature sensitivity of a biological function can be expressed by its Q10 value, which is the amount of change over a temperature span of 10°C. Information compiled by Fange and Grove (88) showed a Q10 value of 2.6 for the effect of body temperature on digesta transit time in a group of fish, and Q10 values varied between 2.7 and 3.8 in snakes and lizards (242, 272). Although reduction in body temperature reduced the rates of food intake and increased digesta retention time in desert iguanas, it had no effect on gross energy digestibility in animals that were force-fed in amounts based on the field metabolic rate calculated for each temperature (286). Therefore, the increase in digesta retention time at lower body temperatures appeared to compensate for reduction in the rates of microbial fermentation and absorption of end products.

Horn (130) summarized information on the rate of passage of food particles through the digestive tract of principally freshwater fish. The total gut-emptying time for carnivores ranged from 10 to 158 h, but the time for most herbivores was <10 h. Even an omnivorous hemi-ramphid, which feeds on seagrass during the day and crustaceans at night, passed seagrass through the gut at about twice the rate of crustaceans. Longer transit times have been recorded in a few marine herbivores (222). One of the most studied herbivorous fish is the grass carp, a freshwater species that can consume its weight in vegetation each day and reduce plant material to 3-mm3 particles with its pharyngeal teeth. However, it lacks a stomach and pyloric ceca and has an intestine only two to three times its body length. An increase in water temperature from 10 to 27°C increased its feeding activity (257) and reduced food transit time from 18 to 8 h (22, 125).

### TABLE 2. Daily secretion and absorption of fluid by the gastrointestinal tract of humans, sheep, and ponies

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Human l/100 kg body wt</th>
<th>Sheep l/100 kg body wt</th>
<th>Pony l/100 kg body wt</th>
</tr>
</thead>
<tbody>
<tr>
<td>Salivary secretion</td>
<td>1.0</td>
<td>17</td>
<td>12</td>
</tr>
<tr>
<td>Gastric secretion</td>
<td>2.0</td>
<td>16</td>
<td></td>
</tr>
<tr>
<td>Pancreatic secretion</td>
<td>2.0</td>
<td>0.6–1.1</td>
<td>10–12</td>
</tr>
<tr>
<td>Biliary secretion</td>
<td>1.0</td>
<td>1.1–4.0</td>
<td>4</td>
</tr>
<tr>
<td>Small intestinal secretion</td>
<td>1.0</td>
<td>8.6</td>
<td>12</td>
</tr>
<tr>
<td>Ileal-cecal-colonic flow</td>
<td>1.5</td>
<td>7.5</td>
<td></td>
</tr>
<tr>
<td>Large intestinal secretion</td>
<td>0.1</td>
<td>0.7</td>
<td>0.9</td>
</tr>
</tbody>
</table>

Values for humans are from Powell (212). Results for sheep are mean values for secretions of salivary glands (73, 153), abomasum (126), pancreas (176, 260), bile (120), and ileal-cecal flow (154). Estimates of salivary, pancreatic, and biliary secretions of the pony are from Alexander and Hickson (2); those for ileocecal flow, large intestinal secretion, and fecal excretion are from Argenzio et al. (9).
FIG. 9. Evolution of nephron and hindgut in relation to habitat. Nephrons of fish, reptile, and bird kidneys are limited in their ability to concentrate urine. However, urine is excreted into cloaca of adult amphibians, reptiles, and birds and refluxed along with digesta for recovery of electrolytes and water by hindgut of some reptiles and most birds. Microbial digestion of uric acid also aids in conservation of nitrogen. In most mammals, digestive and urinary tracts exit body separately. Recovery of urinary electrolytes and water is aided by kidney’s loop of Henle, and nitrogen conservation is aided by microbial digestion of urea. [From Stevens (247). Copyright 1977 by Cornell University. Used by permission from the publisher, Cornell University Press.]

Hindgut retention of digesta appears to have evolved in response to the need of terrestrial vertebrates to conserve electrolytes and water secreted into the upper digestive tract and excreted by the kidneys. The hindgut of adult amphibians, reptiles, and birds exits, along with the urinary tract, into a cloaca (Fig. 9). Retention and resorption of electrolytes and water by some reptiles and most birds is aided by a pacemaker in the cloacal region that generates antiperistaltic waves of contraction that reflux digesta and urine the length of the hindgut. One exception is the ostrich, which does not reflux digesta and urine from its cloaca (78). The urinary and digestive tracts of most mammals develop separate exits before birth, and the colon is generally longer, with its pacemaker located in a more proximal segment. Retention of digesta in the hindgut also results in larger populations of indigenous bacteria.

The MRT values for digesta markers in a carnivorous, omnivorous, and two herbivorous reptiles are shown in Table 3. Particles were retained longer than fluid by the gastrointestinal tract of all of these species, and both were retained longest by the herbivores. Birds have a much shorter digesta retention time than reptiles (Table 4). Particulate markers are retained longer than fluid in most birds due principally to their retention in the gizzard, but fluid is selectively retained by the ceca of some species.

Björnham and Sperber (31) found that after ileal contents passed through the colon of geese, turkeys, and guinea fowl, they were mixed with urine in the cloaca and fluid, and fine digesta particles were refluxed along the colon wall and forced through the narrow openings into the ceca. Leopold (166) stated that the feces of gallinaceous birds contained two types of digesta, and one of these had the composition of cecal contents. Administration of digesta markers to the Alaskan rock ptarmigan resulted in prolonged excretion of the particles and a rapid periodic excretion of fluid markers at intervals of ~8.5 h, with an average discharge of ~50% of the cecal contents (106).

### Table 3. Mean transit time for digesta markers through the gastrointestinal tract of reptiles

<table>
<thead>
<tr>
<th>Species</th>
<th>Fluid marker</th>
<th>Particulate markers, mm</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>2 × 2</td>
</tr>
<tr>
<td><em>Caiman crocodilus</em></td>
<td>41</td>
<td>162</td>
</tr>
<tr>
<td><em>Chrysemys picta belli</em></td>
<td>35</td>
<td>56</td>
</tr>
<tr>
<td><em>Geochelone carbonaria</em></td>
<td>&lt;48</td>
<td>270</td>
</tr>
<tr>
<td><em>Iguana iguana</em></td>
<td>&lt;48</td>
<td>207</td>
</tr>
</tbody>
</table>

Mean values from 4 specimens of each species except *C. crocodilus* (3 specimens). Liquid marker was polyethylene glycol or BaSO₄. Particulate markers were segments of polyethylene tubing. [From Guard (115).]
### Table 4. Mean retention time for fluid and particulate digesta markers in the gastrointestinal tract of birds and mammals

<table>
<thead>
<tr>
<th>Species</th>
<th>Body Mass, kg</th>
<th>Diet</th>
<th>Mean Retention Time, h</th>
<th>Reference No.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Fluid</td>
<td>Particles</td>
<td>Particles/fluid</td>
</tr>
<tr>
<td><strong>Birds</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rock ptarmigan</td>
<td>0.46</td>
<td>Game bird food</td>
<td>9.9</td>
<td>1.9</td>
</tr>
<tr>
<td>Sooty albatross</td>
<td>2.5</td>
<td>Fish</td>
<td>6.3</td>
<td>15</td>
</tr>
<tr>
<td>Rockhopper penguin</td>
<td>2.5</td>
<td>Fish</td>
<td>3.8</td>
<td>17</td>
</tr>
<tr>
<td>Emu</td>
<td>38</td>
<td>Ground grain and straw</td>
<td>3.9</td>
<td>4.7</td>
</tr>
<tr>
<td><strong>Mammals</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cecum fermenters</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Elephant shrew</td>
<td>0.05</td>
<td>Cereal</td>
<td>3.2</td>
<td>3.4</td>
</tr>
<tr>
<td>Vole</td>
<td>0.06</td>
<td>Pelleted</td>
<td>15</td>
<td>14</td>
</tr>
<tr>
<td>Degu</td>
<td>0.18</td>
<td>Pelleted</td>
<td>20</td>
<td>16</td>
</tr>
<tr>
<td>Rat</td>
<td>0.2</td>
<td>Pelleted</td>
<td>20</td>
<td>22</td>
</tr>
<tr>
<td>Guinea pig</td>
<td>0.6</td>
<td>Pelleted, Alfalfa meal</td>
<td>13</td>
<td>13</td>
</tr>
<tr>
<td>Ringtail possum</td>
<td>0.6</td>
<td>Eucalyptus leaves</td>
<td>63</td>
<td>57</td>
</tr>
<tr>
<td>Greater glider</td>
<td>1.1</td>
<td>Eucalyptus leaves</td>
<td>50</td>
<td>23</td>
</tr>
<tr>
<td>Rabbit</td>
<td>2.1</td>
<td>Pelleted</td>
<td>39</td>
<td>27</td>
</tr>
<tr>
<td>Brushtail possum</td>
<td>2.5</td>
<td>Eucalyptus leaves</td>
<td>51</td>
<td>46</td>
</tr>
<tr>
<td>Nutria</td>
<td>4.4</td>
<td>Pelleted</td>
<td>44</td>
<td>44</td>
</tr>
<tr>
<td>Koala</td>
<td>6.6</td>
<td>Eucalyptus leaves</td>
<td>200</td>
<td>140</td>
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<tr>
<td>Colon fermenters</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Common wombat</td>
<td>29</td>
<td>Pelleted low fiber</td>
<td>50</td>
<td>75</td>
</tr>
<tr>
<td></td>
<td>29</td>
<td>Pelleted high fiber</td>
<td>36</td>
<td>62</td>
</tr>
<tr>
<td>Orangutan</td>
<td>45</td>
<td>Pelleted</td>
<td>71</td>
<td>74</td>
</tr>
<tr>
<td>Gorilla</td>
<td>51</td>
<td>Pelleted</td>
<td>45</td>
<td>57</td>
</tr>
<tr>
<td>Pony</td>
<td>170</td>
<td>Pelleted</td>
<td>67</td>
<td>94</td>
</tr>
<tr>
<td>Pig</td>
<td>176</td>
<td>Hay/grain</td>
<td>39</td>
<td>48</td>
</tr>
<tr>
<td>Horse</td>
<td>210</td>
<td>Hay</td>
<td>20</td>
<td>25</td>
</tr>
<tr>
<td>Forestomach fermenters</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Potoroo</td>
<td>1.0</td>
<td>Pelleted</td>
<td>20</td>
<td>20</td>
</tr>
<tr>
<td>R. hare-wallaby</td>
<td>1.2</td>
<td>Pelleted</td>
<td>23</td>
<td>38</td>
</tr>
<tr>
<td>Sloth</td>
<td>2.4</td>
<td>Cecropia</td>
<td>151</td>
<td>147</td>
</tr>
<tr>
<td>R. rat-kangaroo</td>
<td>3.0</td>
<td>Pelleted</td>
<td>31</td>
<td>34</td>
</tr>
<tr>
<td>E. gray kangaroo</td>
<td>20.8</td>
<td>Hay</td>
<td>14</td>
<td>30</td>
</tr>
<tr>
<td>Hill kangaroo</td>
<td>21.3</td>
<td>Pelleted</td>
<td>19</td>
<td>30</td>
</tr>
<tr>
<td>Goat</td>
<td>34.1</td>
<td>Pelleted</td>
<td>35</td>
<td>39</td>
</tr>
<tr>
<td>Sheep</td>
<td>49.5</td>
<td>Pelleted</td>
<td>35</td>
<td>50</td>
</tr>
<tr>
<td>Llama</td>
<td>135</td>
<td>Hay</td>
<td>36</td>
<td>56</td>
</tr>
<tr>
<td>Ox</td>
<td>220</td>
<td>Hay</td>
<td>20</td>
<td>55</td>
</tr>
</tbody>
</table>

Albatross, penguin, and elephant shrew are carnivores, and rat and pig are omnivores. All other birds and mammals are herbivores. Note that fluid was retained as long or longer than particles by most small cecum- and forestomach-fermenting herbivores, and conversion from a more readily fermentable ground, pelleted diet to alfalfa hay increased fluid retention time in guinea pig. However, colon-fermenting mammals retained particles longer than fluid and addition of fiber or conversion from pelleted to hay diets decreased fluid and particle retention times in wombat and equids. Larger forestomach fermenters also retained particles longer than fluid, and longest particle retention times were seen in ruminants on a hay diet. [Modified from Stevens and Hume (252).]

This would account for the much longer retention of fluid than particles in their gastrointestinal tract (Table 4).

Particles were retained longer than fluid by the stomach of the dog, pig, and rabbit and the large intestine of the dog and pig (Fig. 10). However, fluid was retained by the cecum of the rabbit with a more rapid elimination of particles in the feces. Fluid and fine particles are selectively retained by the cecum of most small mammalian herbivores <10 kg in body weight. Parra (200) found that the relative volume of gut contents in small mammalian herbivores decreased with a decrease in the body mass of the species. This, plus a higher mass-specific metabolic rate, limits the extent to which small animals can delay digesta passage. Selective retention of fluid and small particles concentrates fermentative effort on the more readily digestible fraction and minimizes the gut-filling effect of larger particles. Because of this process, small herbivores are able to utilize plant material of lower protein and higher fiber content than would be predicted on the basis of body size alone.

Coprophagy, the ingestion of feces, offers another avenue for the recovery of nutrients produced by gut microbes. Ingestion of maternal feces serves as a source of nutrients and bacteria for neonates in a number of spe-
C. EDWARD STEVENS AND IAN D. HUME

FIG. 10. Percentage of digesta fluid and particulate markers (±SE) recovered from gastrointestinal tract of dog, pig, and rabbit at various times after administration. Dogs were fed a meat diet; pigs were fed a pelleted, low-concentrate, high-fiber diet; and rabbits were fed a commercially prepared, pelleted rabbit diet. Animals were fed at 12-h intervals for at least 2 wk before study. Digesta markers were administered orally at time of feeding. Fluid markers consisted of polyethylene glycol or 51Cr-EDTA. Plastic markers consisted of polyethylene tubing with an outside diameter of 2 mm, cut into lengths of 2 mm. Animals were killed in groups of 3 at times designated after the meal, and sections of gut were immediately separated by ligatures for recovery of markers. Solid bars, fluid marker; open bars, particulate marker. S, stomach; SI, small intestine; Ce, cecum; C, colon; PC, proximal colon; TC, terminal colon; Fe, feces. [Dog from Banta et al. (19). Pig from Clemens et al. (57). Copyright J. Nutr., American Institute of Nutrition. Rabbit from Pickard and Stevens (207).]

cies, and coprophagy has been observed during periods of nutritional deficiency in domestic cats (179) and horses (236). However, coprophagy is a regular practice in many small herbivorous mammals. Diurnal coprophagy has been reported in rabbits, hares, pika, rats, beavers, ground squirrels, lemmings, guinea pigs, chinchillas, capybara, nutria, ringtail possums, and a folivorous lemur, Lepilemur mustelinus leucopus (252).

Ingestion of feces can only benefit an animal if they contain more nutrients than the food they displace. This is overcome in many small mammalian herbivores by cecotrophy, the selective ingestion of highly nutritious feces that are derived from cecal contents (131). Domesticated rabbits excrete dry fecal pellets during the day and soft, moist pellets at night. Dry pellets are the result of a colonic separation mechanism (CSM), which allows the more rapid passage of larger particles into the feces. Interruption of this process results in the formation of cecal contents into soft pellets and their passage through the colon. The nutritional significance of cecotrophy was reviewed by Hörnicke and Björnhag (131) and Björnhag (30). The soft feces of rabbits contain high levels of SCFA, microbial protein, B vitamins, Na, K, and water. They provided up to 30% of the nitrogen intake, and much of this was microbial protein with a high content of essential amino acids. Their content of B vitamins can exceed the animal’s needs. The nitrogen content of cecotrophs greatly exceeded that of the diet and normal feces of Scandinavian lemmings, nutria, guinea pigs and chinchillas, and Norwegian and kangaroo rats. Chilcott and Hume (43) estimated that cecotrophs provided the ringtail possum with 58% of its daily intake of digestible energy and 81% of its daily intake of nitrogen.
Björnhag (30) reviewed studies of the CSM in the rabbit and other species. The cecal contents of rabbits are passed periodically into the proximal colon, where fluid and small particles are collected along the walls of the haustra and returned to the cecum by antiperistaltic contractions (28). Larger particles, such as those derived from the thicker and more lignified cell walls of seed hulls, bark, and wood, are moved aborally with cecal digesta outflow. Finely ground diets result in no separation of fluid and particles, or differences in the composition of cecotrophs and other feces. However, the degree of separation increases with an increase in dietary fiber. The ringtail possum, greater glider, and koala appear to have CSMs similar to that of the rabbit. Lemmings and voles have a CSM that selectively returns bacteria to the cecum, compensating for a cecal digesta retention time too brief for their maintenance by replication alone. The CSMs of guinea pigs, chinchilla, and nutria are similar to, but less efficient than, that of lemmings and voles. Colonic separation mechanisms appear to be absent in the brushtail possum and rock hyrax. Although fluid is selectively retained by the equine cecum, this is followed by selective retention of particles and then fluid by the subsequent ventral and dorsal compartments of the colon.

Table 4 lists the MRTs for fluid and particulate digesta markers in the gastrointestinal tract of cecum-fermenting herbivores in relation to the body size of the species. Retention time of fluid was shortest in animals on finely ground, more readily fermentable, pelleted diets and longest in those fed eucalyptus foliage, with no consistent correlation between retention time and body size. Fluid was retained as long or longer than particles by most of these species. Cecotrophy exacerbates this difference in MRTs due to the higher water content of cecotrophs in comparison with other feces. Therefore, the total gastrointestinal tract MRTs in cecotrophic species is the net result of slower gastric release of particles, slower cecal release of fluid, and the recycling of digesta through the tract.

Conversion of guinea pigs from a pelleted to an alfalfa meal diet increased the MRT of both fluid and particles (Table 4). Choshniak and Yahav (45) measured the MRT for particles in voles and fat jirds fed alfalfa hay versus less digestible Panicum (rhodes grass). Voles fed Rhodes grass showed a marked reduction in fiber digestibility with no change in the MRTs for particles from those observed on either the alfalfa hay or the pelleted diet shown in Table 4. However, conversion from alfalfa hay to Rhodes grass almost doubled the particle MRT in jirds, with no reduction in fiber digestibility. Analysis of the excretion curves indicated that this was due solely to differences in cecal retention time, suggesting that cecal retention time of particles was dependent on the selectivity of the CSM and digestibility of the diet. Rapid fermentation can produce osmotically active end products faster than they are absorbed, with a net diffusion of water into the gut until osmotic equilibrium is reached (9, 47). Thus, except for periods of cecotroph passage, available evidence suggests that the rate at which fluid and small particles leave the cecum is governed by the rate of cecal fermentation and degree of fluid distension. This would explain the longer retention time in guinea pigs fed alfalfa meal, fat jirds fed rhodes grass, and the marsupials on eucalyptus foliage.

Unlike cecum fermenters, the colon-fermenting herbivores (wombats, pigs, equids, orangutans, and gorillas) retained particulate digesta as long or longer than fluid, and the retention time of both was reduced with the addition of more fiber to the diet of wombats and the conversion of equids from a pelleted to a hay diet (Table 4). Domesticated donkeys of desert tribesman in the Middle East showed a longer MRT for particles (37 h) and greater digestive efficiency than horses on alfalfa hay, and the donkeys increased their intake on less digestible wheat straw with no change in particle MRT (143). This suggests that colonic retention time is more dependent on the physical characteristics of the fiber than its rate of fermentation. Colon fermenters also showed no relationship between MRTs and body size (Table 4). Foose (99) found that although the MRT for dye-marked hay tended to increase with an increase in the body size of perissodactyls (tapirs < equids < rhinos), the MRT for elephants fell between that of equids and rhinos, and the MRT of rhinos was less than that of smaller, foregut-fermenting bovids and camels.

The retention time of fluid by forestomach fermenters also appears to be related more to gastric morphology than body size (Table 4). Mean retention times for fluid and particles were extremely and equally long in the sloth, with 65% of this time spent in their multicompartmental forestomach (94). Retention times for fluid and particles also were similar in the potoroo and rufus rat-kangaroos, whose forestomachs have large sacciform segments. However, particles were retained longer than fluid by the rufus hare-wallaby and larger kangaroos, which have longer segments of tubiform stomach, and by the llama, sheep, goat, and ox. The longest retention times for particles were seen in ruminants on a hay diet. Kangaroos maintained their rate of food intake with an increase in dietary fiber (102, 104), but an increase in the fiber content reduces intake of forage by ruminants, because of extended retention of large particles by the reticulorumen. Because of the ventral location of the reticulo-omasal orifice and a filter formed by projecting leafs of omosal tissue, particulate digesta are retained by the reticulorumen of cattle until they are reduced to a size and specific gravity that allows their release (158, 253).

Bedouin goats and donkeys digested wheat straw with equal efficiency (35, 143). However, the goats did so by reducing their intake of food and water on the wheat straw diet, and a reduction in the drinking frequency of...
goats resulted in a further decrease in food intake and an increase in the MRT of particles in the rumen (35, 36). Comparisons of grazing zebra and wildebeest of the Serengeti plains of Africa showed that the zebra could subsist on a lower quality forage than could the wildebeest if provided with access to sufficient water (197).

Ruminants can also differ in their relative dependence on forestomach versus hindgut fermentation. The principal large herbivores inhabiting arctic tundra are moose, caribou, reindeer, and muskoxen. Moose, which are concentrate selectors with a relatively small reticulo-rumen and omasum, are confined to the lower Arctic zones, where they adjust to winter conditions by an increase in rumination and digesta retention time (220). Caribou and reindeer are intermediate feeders, and the significantly larger cecum of high-Arctic subspecies of reindeer during winter months suggested that they relied more heavily on cecum fermentation (246). Muskoxen have both the large reticulorumen and omasum of nonselective grazers and large cecal size of concentrate selectors. Postruminal digestibilities of 53–64% indicated that their cecum played a more important role during summer months (245). However, an increase in both the MRT for particulate digesta and the digestibility of organic matter indicated a greater dependence on forestomach fermentation during winter months (1).

IV. CHARACTERISTICS AND DISTRIBUTION OF INDIGENOUS GUT MICROBES

A. Ruminant Forestomach

Much of our understanding of gut microbiology derives from early studies of the ruminant forestomach. During the first weeks after birth, the forestomach becomes colonized with *Escherichia coli aerogenes* and streptococci, which are joined by lactobacilli in the suckling animal (79). Weaning is followed by development of the extremely complex microbiota that are characteristic of adult animals (3, 142, 277). Culture counts give estimates of $10^{10}$ to $10^{11}$ of predominantly anaerobic bacteria per gram of fluid in rumen contents. Microscopic counts, which include organisms that are dead or require specific culture media, give higher numbers. Table 5 lists the principal bacterial species found in the rumen of sheep and cattle and their fermentative properties. Their interactions are discussed by Van Soest (269), but they collectively ferment carbohydrate into SCFA, utilize protein and other nitrogenous compounds for synthesis of microbial protein, synthesize B vitamins, hydrolyze lipids, and hydrogenate fatty acids.

Although protozoa are much less numerous ($10^4$ to $10^5/g$), they can occupy an equal volume of forestomach contents. The predominant species are anaerobic ciliates, which are capable of fermenting carbohydrates, storing starch, digesting protein, hydrogenating fatty acids, and regulating the numbers of bacteria (100, 128, 192, 213). They contribute relatively little to carbohydrate fermentation but store starch and produce protein for subsequent digestion during passage through the abomasum and midgut. Uptake of starch and sugars by protozoa also has a stabilizing effect in ruminants fed high-grain diets (267), where rapid bacterial production of SCFA and lactic acid can result in ulceration of the forestomach, and systemic acidosis and dehydration (74). Defaunation of the rumen impaired the absorption of calcium, magnesium, and phosphorus and changed the peptide patterns of duodenal digesta. Thus the protozoa play an integral role in digestion in ruminants. In addition to the bacteria and protozoa, anaerobic fungi can be found at concentrations of $10^3$ to $10^5$ zoospores/g fluid digesta in animals on high-fiber diets (97). They contain relatively high concentrations of protein with an amino acid composition similar to that of alfalfa (98) and may be an important source of nutrients for ruminants on low-quality diets.

B. Foregut of Other Species

Bacterial counts similar to those of the ruminant forestomach have been demonstrated in the forestomach of other artiodactyls (camels, llamas, hippos, peccaries), cetaceans (gray, bowhead, and minke whales), macropod marsupials, sloths, colobus and langur monkeys, and the crop and distal esophagus of the hoatzin (252). The forestomach of minke whales included organisms that can digest the chitinous exoskeleton of krill (177, 178). Bacteria were accompanied by $10^4$ to $10^6$ protozoa/g digesta in the forestomach of camels, hippos, the hoatzin, and some macropod marsupials, but protozoa appeared to be absent from the forestomach of sloths and the colobus and langur monkeys. Colonies of fungal sporangia, like those of the rumen, were found in the forestomach of four species of kangaroos and wallabies (71). Where measured, bacterial counts in the secretory compartment of animals with a forestomach and the simple stomach of other vertebrates tend to be much lower than those of the forestomach. Mean concentrations of $10^6$ to $10^7$/ml of predominantly aerobic bacteria have been reported in the gastric juice of fasting humans (217).

C. Midgut

The numbers of bacteria in the mammalian midgut are generally much lower than those in the rumen. Savage (235) reported that the human small intestine contained $10^4$ to $10^5$ viable, predominantly anaerobic organisms per gram of digesta. Rambaud (217) also reported counts of $10^5$ bacteria/ml in the small intestinal contents of two-
TABLE 5. Fermentative properties of rumenal bacteria

<table>
<thead>
<tr>
<th>Species</th>
<th>Function</th>
<th>Products</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bacteroides succinogenes</td>
<td>C, A</td>
<td>F, A, S</td>
</tr>
<tr>
<td>Ruminococcus albus</td>
<td>C, X</td>
<td>F, A, E, H, C</td>
</tr>
<tr>
<td>R. flavocaci</td>
<td>C, X</td>
<td>F, A, S, H</td>
</tr>
<tr>
<td>Butyrivibrio fibrisolvens</td>
<td>C, X, PR</td>
<td>F, A, L, B, E, H, C</td>
</tr>
<tr>
<td>Clostridium lochheadii</td>
<td>C, PR</td>
<td>F, A, B, E, H, C</td>
</tr>
<tr>
<td>Streptococcus bovis</td>
<td>A, S, SS, PR</td>
<td>L, A, F</td>
</tr>
<tr>
<td>B. amylophilus</td>
<td>A, PR</td>
<td>F, A, S</td>
</tr>
<tr>
<td>B. ruminicola</td>
<td>A, X, P, PR</td>
<td>F, A, P, S</td>
</tr>
<tr>
<td>Succinibacter amylolytic</td>
<td>A, D</td>
<td>A, S</td>
</tr>
<tr>
<td>Selenomonas ruminantium</td>
<td>A, SS, GU, LU, PR</td>
<td>A, L, P, H, C</td>
</tr>
<tr>
<td>Lachnospira multipartus</td>
<td>P, PR, A</td>
<td>F, A, L, E, H, C</td>
</tr>
<tr>
<td>Succinivibrio dextrinosolvens</td>
<td>P, D</td>
<td>F, A, L, S</td>
</tr>
<tr>
<td>Methanobrevibacter ruminantium</td>
<td>M, HU</td>
<td>M</td>
</tr>
<tr>
<td>Methanosarcina barkeri</td>
<td>M, HU</td>
<td>MC</td>
</tr>
<tr>
<td>Spirochete species</td>
<td>P, SS</td>
<td>F, A, L, S, E</td>
</tr>
<tr>
<td>Megaplasma ebdenii</td>
<td>SS, LU</td>
<td>A, P, B, V, CP, H, C</td>
</tr>
<tr>
<td>Lactobacillus sp.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anaerovibrio lipolytica</td>
<td>L, GU</td>
<td>A, P, S</td>
</tr>
<tr>
<td>Eubacterium ruminantium</td>
<td>SS</td>
<td>F, A, B, C</td>
</tr>
</tbody>
</table>

C, cellulolytic; X, xylanolytic; A, amylolytic; D, dextrinolytic; P, pectinolytic; PR, proteolytic; L, lipolytic; M, methanogenic; GU, glycerol utilizing; LU, lactate utilizing; SS, major soluble sugar fermenter; HU, hydrogen utilizing; F, formate; A, acetate; E, ethanol; P, propionate; L, lactate; B, butyrate; S, succinate; V, valerate; CP, caproate; H, hydrogen; C, carbon dioxide; M, methane. [From Allison (3).]

Of the human subjects. These were predominantly aerobes, but the number increased to 10^9/ml, with the appearance of enterobacteria and strict anaerobes in the ileum of one-third of the subjects. Mackie and Wilkins (175) found that the counts of anaerobic bacteria in grass-fed horses ranged from 10^6/g in the duodenum to 10^9/g in the ileum. The high percentage of proteolytic organisms, particularly in the duodenum of these animals, raised the question of whether they digest or compete with endogenous enzymes.

Although there is little information available on bacterial counts in the midgut of birds, reptiles, or amphibians, aerobes and facultative anaerobes in concentrations of 10^4 to 10^8/g digesta were found in the midgut of a variety of teleosts (132, 167, 265). The number of anaerobes in the intestine of rainbow trout was insignificant, but Trust et al. (264) found 10^7 to 10^8 anaerobes/g in the intestine of the grass carp and 10^9/g in the goldfish intestine. In a review of the bacteria of fishes, Cahill (39) concluded that large populations of facultative and obligate anaerobes were present in the gut of many species.

Chitinolytic bacteria in counts of 10^7 to 10^12/g reported in the intestine of a number of marine fish (68, 109) may aid in digestion of chitin in the exoskeleton of insects, crustaceans, and other invertebrates in their diet. Substantial numbers (10^4 to 10^7/ml contents) of extremely large (600 × 80 μm) bacteria were found consistently in the intestinal contents of herbivorous surgeonfish in the Red Sea (93) and on the Great Barrier Reef (62). They were identified as gram-positive cocci related to the Clostridium (6). A study in brown surgeon fish showed that they reduced the amylase, protease, and lipase activity of host enzymes but may contribute to the digestion of lipid (209). Protozoa, in counts of 10^9 to 10^12/g digesta, were also reported in the midgut of the herbivorous herring cale (58).

D. Hindgut

Bacterial counts of 10^7 to 10^12/g have been reported in the hindgut of mammals (humans, vervet and samango monkeys, naked mole rats, capybara), birds (chickens), reptiles (green sea turtles, green iguanas), leopard frogs (252), and the sea chub Kyphosus cornelii (59). Substantial numbers of protozoa also were found in the hindgut of horses, rhinos, elephants, naked mole rats, capybara, green iguanas, and sea chubs. The bacterial species inhabiting the large intestine that have been described for a number of mammals are generally similar to those found in the rumen (3, 278). At least 400 species, representing 40 genera, were isolated from human feces (92, 235). Most were bacteroides (up to 30% of the anaerobes), bifidobacteria (up to 25%), eubacteria, clostridia, and a variety of gram-positive cocci belonging to the genera Ruminococcus, Peptococcus, Peptostreptoccocus, and Streptococcus (173). However, bacterial populations associated with the epithelial surface and lumen contents of the hindgut can differ from one another and from those in the feces. They also can vary between segments of the hindgut. Methanogenic bacteria appear to preferentially colonize the distal colon of humans that are CH₄ excretors (208). The epithelial surface of the cecum and proximal colon of the koala is populated with large numbers of bacteria...
capable of degrading tannin-protein complexes in their normal diet of eucalyptus foliage (195).

Gossling et al. (111) examined the effects of hibernation on the hindgut bacteria of the leopard frog. They found counts of $10^{10}$/g wet wt of the intestinal contents and $10^7$/g wet wt of the mucosal scrapings of frogs before, during, and after hibernation at 4°C. Hibernation reduced the total bacterial count of the hindgut and, in some cases, the variety of bacteria present, but subcultures of isolates showed that the bacteria continued to grow at temperatures near freezing.

V. FERMENTATION OF CARBOHYDRATES

A. Ruminant Forestomach

Although the metabolic characteristics of individual species of bacteria vary, the end result of their combined fermentation activities is shown in Figure 11. Rumen microorganisms ferment sugars, starches, cellulose, hemicelluloses, and pectins into SCFA, CO$_2$, CH$_4$, and H$_2$. Their extracellular enzymes digest polysaccharides into monosaccharides, which are converted by intracellular enzymes to pyruvate, as in the body cells of vertebrates.

However, rather than entering a Krebs cycle for aerobic metabolism to CO$_2$ and H$_2$O, pyruvate is reduced anaerobically to short-chain organic acids, principally acetate, propionate, and butyrate plus CO$_2$, H$_2$, CH$_4$, and H$_2$O. These organic acids were called volatile fatty acids (VFA) in the earlier literature, due to their ready separation from other components of digesta by steam distillation, but they are now referred to as SCFA. Although fermentation of starch produces 20% less energy than its conversion to glucose by endogenous enzymes, microbial fermentation of structural carbohydrates is a tremendous advantage to animals on a high-fiber diet.

The total concentration of SCFA in the forestomach of sheep and cattle varies between 60 and 120 mM, depending on diet and time after feeding (206). The rate of SCFA production depends on the substrate: soluble carbohydrate (starches and sugars) $> \text{pectin} > \text{cellulose}$.
H₂ in the rumen, except for the first few days of a fasting period. Nitrogen and O₂ are added from swallowed air, and N₂ can diffuse into the rumen from the blood as well. Oxygen is rapidly reduced by rumen microorganisms, and some of the CO₂ is directly absorbed into the blood, but much of the CO₂ and most of the CH₄ produced in the rumen is removed by eructation. Kleiber (159) found that an adult cow on a diet of 5 kg hay lost 191 liters of CH₄ through eructation and flatulence, which was equivalent to a 10% loss of their daily digestible energy intake.

B. Digestive Tract of Other Species

Because of the low levels of SCFA in food and blood, and their rapid absorption from the digestive tract, their presence is an index of microbial fermentation. This applies, to a lesser extent, to lactic acid as well. Microbial fermentation, similar to that reported in the ruminant foregut, has been demonstrated to varying degrees along the gastrointestinal tract of all classes of vertebrate.

1. Foregut

Short-chain fatty acid concentrations ranging from 55 to 220 mM have been reported in the forestomach of other artiodactyls (camels, llamas, hippos, and peccaries), macropod marsupials (kangaroos and wallabies), edentates (sloths), primates (colobus and langur monkeys), rodents (hamsters), cetaceans (bowhead, Minke, and small, toothed whales), and hyrax and in the crop and distal esophagus of the hoatzin (252). Where measured, the proportions of acetate, propionate, and butyrate were generally similar to those in the ruminant forestomach. However, Ruhsamen et al. (226) found that acetate was the predominant SCFA (87–98%) in the hyrax stomach, and this was accompanied by relatively high levels of lactic acid. Lower levels of SCFA (5–45 mM) were found in the simple stomachs of the raccoon, dog, pig, bush baby, vervet monkey, and pony (Fig. 13), as well as the baboon and Sykes monkey (54) and elephant (53). As in the hyrax, this was accompanied by substantial concentrations of lactic acid in the stomachs of the dog, pig, and pony. Although the quantity of SCFA was of little nutritional significance, their presence indicates microbial fermentation in the stomach of most mammals.

The forestomach of marsupials contained CO₂, H₂, and CH₄, with higher levels of H₂ and lower levels of CH₄ than that of ruminants (71, 85, 155). The more rapid transit of digesta through the macropod forestomach may inhibit the establishment of slow-growing methanogenic bacteria (137). Alternatively, H₂ and CO₂ may be utilized for the production of acetate, rather than CH₄, as demonstrated in the hindgut of termites and several mammalian herbivores (174). The principal gases in the forestomach of the langur monkey were CO₂ and CH₄ (23). Kuhn (162)
reported similar findings for the colobus monkey, but Ohwaki et al. (193) found no \( \text{CH}_4 \) in the stomach of these animals.

2. **Midgut**

Measurable concentrations of SCFA have been reported in the midgut of all species of vertebrates that have been studied, with the highest concentrations generally in the distal segments (252). Low levels were reported in the small intestine of dogs, raccoons, and ponies, and higher concentrations (30–45 mM) were found in the terminal midgut of the pig, bush baby, and vervet monkey (Fig. 13) as well as grass-fed horses (175). Short-chain fatty acid concentrations equivalent to those of the rumen were found in the midgut of the Florida red-bellied turtle (27) and the emu (124). Although this might be attributed to reflux of digesta from the hindgut, they would include substantial concentrations of bacteria, which would presumably compete with endogenous enzymes for both substrates and existence.

There appear to have been no studies of SCFA or cellulase activity in the intestine of larval amphibians. However, SCFA concentrations of 7–37 mM were found in the midgut of carnivorous rainbow trout, omnivorous common carp, and herbivorous grass carp and tilapia (252). Low SCFA concentrations, coupled with limited gut capacity and rapid digesta transit, suggest that grass carp obtain most of their nutrients by rapid passage of digesta rather than microbial fermentation. Clements and Choat (60) reported SCFA concentrations that ranged between 6 and 47 mM in the intestine of 31 species of tropical marine fish, with the highest levels found in species that fed on microalgae. Acetate was the predominant fatty acid in all of these species. Cellulose digestion has been reported in the gut of carp (238), freshwater catfish, and 16 species of marine detritus feeders (255). Cellulolytic activity was absent in some algae-feeding fish, but Clements et al. (61) pointed out that algae contain polysaccharides other than cellulose, principally laminarin.

3. **Hindgut**

A series of comparative studies demonstrated high concentrations of SCFA in the hindgut of mammalian carnivores, omnivores, and herbivores over a 12-h period between meals (Fig. 13). Concentrations varied among segments of hindgut and species, but acetate-to-propionate-to-butyrate ratios were similar to those of the rumen forestomach, and addition of fiber to the diet had a similar effect on the acetate-to-propionate ratio in the pig. The total concentrations of SCFA in the hindgut of these animals were relatively unaffected by changes in diet or by time after feeding. However, the addition of fiber to the diet increased the total volume (and SCFA content) of hindgut contents. Compartmental analysis of the hindgut of the pig, raccoon, and vervet monkey showed marked, cyclic changes in the rates of SCFA production with time after feeding (Fig. 14). Therefore, the relatively constant levels of SCFA in hindgut contents were maintained by their absorption and compensatory secretion and absorption of water.

Subsequent studies have demonstrated the ubiquitous presence of SCFA in the hindgut contents of all classes of vertebrates (252). Short-chain fatty acid concentrations ranging from 65 to 235 mM have been reported in the hindgut of Carnivora (dogs and raccoons), marsupials (brush-tail possum and wombats), primates (humans, baboons, bush babies, and vervet, Sykes and samango monkeys), lagomorphs (rabbits), rodents (Norwegian and naked mole rats, hamsters, guinea pigs, and porcupines), artiodactyls (pigs), perissodactyls (horses), sirenians (dugongs), elephants, and hyrax. Similar concentrations were found in birds (gosee and partrigian) and reptiles (green sea turtle and gopher tortoise). Lower concentrations of SCFA (15–63 mM) were reported in the hindgut of the capybara, some marsupials (greater glider and koala), some reptiles (caiman, green iguana, and tortoises), and the sea chub. The lower levels of SCFA found in the hindgut of the marsupial folivores were attributed to the tannins in their diet of eucalyptus foliage. Although there
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Acetogenesis may compete with methanogenesis at relatively high pH values (>10^4 atm) and at a pH of 6.5 or less (107), but more quantitative information is needed.

The substrates for SCFA production in the mammalian hindgut are shown in Figure 15A. Dietary starches and endogenous carbohydrates serve as the principal substrates in carnivores and omnivores. Significant quantities of dietary starch were shown to reach the large intestine of rats, mice, hamsters, guinea pigs, rabbits, pigs, cattle, sheep, ponies, and humans (252). The amount of starch that escaped digestion in the small intestine depended on the dietary source, and it was reduced by either boiling or grinding. Endogenous carbohydrates appear to be the principal substrates for SCFA production in the human hindgut (81). Mucus, which is 80% polysaccharide, may be a major substrate (270), judged by the large quantities of mucus that accumulate in the cecum of germ-free rats and guinea pigs (110). Carbohydrates and the carbon skeletons of amino acids in epithelial cells that are sloughed into the intestine can serve as additional substrates. However, dietary cellulose, hemicelluloses, and pectin are major substrates in the hindgut of herbivores. Microbial fermentation accounted for 63–73% of the neutral detergent fiber digested in the hindgut of ponies (127) and 12% of the cellulose digested in the gastrointestinal tract of sheep (108).

C. Absorption of Short-Chain Fatty Acids

1. Mechanisms of absorption

Studies of SCFA absorption are complicated by their presence as both undissociated acids and anions and their metabolism by gut epithelium. Because of their low pK (4.75–4.81), the undissociated forms constitute only 1–6% of the total SCFA in the normal range of digesta pH and <1% at the pH of blood. However, cell membranes tend to be permeable to the passive diffusion of lipid-soluble undissociated organic acids down their concentration gradient, and the degree of lipid solubility increases by a factor of ~2.8 with each additional CH_2 group (acetate < propionate < butyrate). Absorption as anions would require either carrier-mediated transport across the epithelial cell membranes or passive diffusion down their electrochemical gradient. Measurements of concentration gradients across the epithelial cells are further complicated by the lower pH of epithelial cell contents and the fact that the three fatty acids are metabolized to varying degrees by epithelial cells in the course of transport.

In vitro and in vivo studies reviewed by Engelhardt (83) and Stevens and Hume (252) showed that SCFA were absorbed in a similar manner from the ruminant forestomach and the large intestine of pigs, ponies, humans, dogs, and guinea pigs. The rate of absorption increased in the hindgut of the green turtle (25). Acetogenesis may compete with methanogenesis at relatively high pH values (>10^4 atm) and at a pH of 6.5 or less (107), but more quantitative information is needed.

The substrates for SCFA production in the mammalian hindgut are shown in Figure 15A. Dietary starches and endogenous carbohydrates serve as the principal substrates in carnivores and omnivores. Significant quantities of dietary starch were shown to reach the large intestine of rats, mice, hamsters, guinea pigs, rabbits, pigs, cattle, sheep, ponies, and humans (252). The amount of starch that escaped digestion in the small intestine depended on the dietary source, and it was reduced by either boiling or grinding. Endogenous carbohydrates appear to be the principal substrates for SCFA production in the human hindgut (81). Mucus, which is 80% polysaccharide, may be a major substrate (270), judged by the large quantities of mucus that accumulate in the cecum of germ-free rats and guinea pigs (110). Carbohydrates and the carbon skeletons of amino acids in epithelial cells that are sloughed into the intestine can serve as additional substrates. However, dietary cellulose, hemicelluloses, and pectin are major substrates in the hindgut of herbivores. Microbial fermentation accounted for 63–73% of the neutral detergent fiber digested in the hindgut of ponies (127) and 12% of the cellulose digested in the gastrointestinal tract of sheep (108).

FIG. 14. Volume, net transmucosal exchange of water, and net appearance and disappearance of volatile fatty acids (VFA), protein, and urea plus ammonia nitrogen in pony large intestine as a function of time. All values, other than volume, are corrected for exchange between segments resulting from digesta flow. [Adapted from Argenzio (7) and Wootton and Argenzio (280).]
FIG. 15. Bacterial metabolism of nitrogen and fermentation of carbohydrates in hindgut of mammals. A: bacterial fermentation of dietary and endogenous carbohydrates to short-chain fatty acids (SCFA), which are largely absorbed before defecation. B: resident bacteria also convert protein and other nitrogen-containing compounds into ammonia and bacterial protein. [Modified from Stevens and Hume (252) and Wrong and Vince (283).]

with either an increase in chain length or a reduction in the pH of gut contents. However, the correlation with chain length could be partially attributed to the effects of metabolism (butyrate >> propionate > acetate) on the concentration gradients between lumen and cell contents, and the pH effects were less than those predicted for an increase in the concentration of undissociated acids.

In vitro studies indicated that the transport of undissociated SCFA is influenced by the pH of both the contents of the epithelial cells and a microlayer at their lumen surface. In vivo perfusion studies showed that SCFA absorption was accompanied by a decrease in Pco2 and an increase in the HCO3 levels of luminal contents and linked partially to the absorption of Na. These results led to the conclusion that absorption of undissociated SCFA from the lumen is aided by protons that are generated from intraluminal hydration of CO2 and secreted into the lumen by Na/H exchange.

Passive diffusion of SCFA anions between epithelial cells was ruled out by the finding that SCFA transport was unaffected by the application of a transepithelial electrical potential gradient, and a net secretion of small amounts of SCFA in the absence of an electrochemical gradient appeared to similarly rule out absorption of anions by active transport. However, studies of membrane vesicles prepared from epithelial cells of the tilapia midgut, rat distal colon, and human proximal colon provided evidence for carrier-mediated transport of SCFA, in exchange for HCO3 across the apical membranes, and for either HCO3 or Cl across basolateral membranes.

Figure 16 combines the models that have been proposed for transport of SCFA across rumen and hindgut epithelia. The concentration gradients for passive diffusion of undissociated acids across the lumen-facing membrane could be influenced by the donation of H ions produced by the hydration of the large quantities of CO2 produced by fermentation and secreted into the lumen in exchange for Na. It also would be influenced by the pH maintained in a microlayer at the luminal surface of the cells and that of cell contents. The relationship between SCFA and Na absorption could be attributed to intracellular metabolism of SCFA, resulting in the generation and subsequent secretion of H ions in exchange for Na, and secretion of HCO3 in exchange for SCFA. Absorption of SCFA anions by membrane carriers would become saturated at higher concentrations of SCFA in the lumen. It was estimated that carrier-mediated transport would account for only 40% of the acetate absorbed by the tilapia intestine from solutions containing 15 mmol acetate/l (261) and a small percentage of the acetate absorbed at concentrations normally present in the hindgut of the prairie vole (138).

2. Contribution to energy requirements

The SCFA make a major contribution to the nutrition of forestomach and hindgut epithelial cells. Substantial

FIG. 16. Hypothesis for mechanisms of short-chain fatty acid transport across rumen and hindgut epithelium. [Modifications and combination of models from Stevens et al. (250) and Titus and Ahearn (202).]
amounts are metabolized by rumen epithelium, with part of the acetate and most of the butyrate converted to ketone bodies (254). Short-chain fatty acid metabolism also provides a majority of the energy required by hindgut epithelium (224, 232). Henning and Hird (123) found that butyrate was metabolized to CO$_2$ and ketone bodies by ileal, cecal, and colonic mucosa of the rabbit. Ketogenesis was low in the ileum and distal colon but high in the cecum and proximal colon. Colonic epithelial cells metabolized smaller quantities of propionate and acetate, and butyrate appeared to provide their major source of energy (49).

The SCFA also contribute to the general maintenance energy requirements, which can be calculated as twice the basal metabolic rate or assumed to be equivalent to the ad libitum intake of digestible energy by captive, non-producing adult animals. Studies of SCFA production or absorption in various segments of the digestive tract of a variety of species were reviewed by Stevens and Hume (252). Although the diets and procedures varied among these studies, they offer some useful comparisons. Among ruminants bulk and roughage feeders, SCFA absorbed from the forestomach accounted for $\geq$60% of the maintenance energy requirement of cattle and wildebeest and 29–79% of the energy required for maintenance of sheep. Absorption from the smaller forestomach of concentrate selectors such as deer, moose, and duikers provided a lesser contribution (18–40%) to their maintenance energy. Short-chain fatty acids absorbed from the forestomach of red-necked wallabies could account for 21–42% of their maintenance energy requirements. The high concentrations of SCFA and large volumes of digesta in the forestomach of camels, hippos, sloths, and colobus and langur monkeys suggest that they provide a significant fraction of their maintenance energy, as well.

The low levels of SCFA in the midgut of most species indicate relatively little absorption. However, it was estimated that SCFA absorption from the ileum and colon accounted for 11% of the maintenance energy of the emu, and the total intestinal (largely midgut) absorption of SCFA accounted for all of the daily energy requirement of the Florida red-bellied turtle. Although the SCFA levels in the midgut of fish suggest that they are a relatively unimportant source of nutrients, the energy requirements of ectotherms are at least an order of magnitude lower than those of endotherms. Therefore, their contributions to the nutrition of herbivorous fish await measurements of their rates of production and absorption.

Hindgut absorption of SCFA accounted for only 2% of the maintenance energy of dogs and 6–9% of the maintenance energy of humans, but it could account for 10–31% of the maintenance energy required by pigs. Hindgut absorption could account for 16% of maintenance energy of the brushtail possum, and the contributions of cecal absorption alone to the maintenance energy were equivalent to 8–9% in ptarmigan and greater gliders, 15% in green turtles, and 30–38% in green iguana and rabbits. Absorption from the cecum and proximal colon accounted for only 9% of the koala’s maintenance energy, but 17% of that required by guinea pigs and 46% of the energy required for the maintenance of ponies. Absorption from the cecum and colonic appendages also generated 31–35% of the energy required for maintenance of the Cape hyrax, and colonic absorption of SCFA could account for 33% of the maintenance energy of wombats. The relatively low contributions of SCFA to the maintenance energy of the marsupials may be attributed to their diet of eucalyptus foliage, and the contribution to ptarmigan may be increased with the greater consumption of plant fiber and cecal size during winter months (105).

3. Contributions to the absorption of Na and water

The principal cation and anions in the ruminant forestomach and throughout the length of the hindgut of most species are Na and SCFA. Both Na and SCFA are rapidly absorbed from these segments of the gut, and Na absorption is partially coupled to the absorption of SCFA. However, they remain as the predominant cation and anions because of the simultaneous absorption of water. Perfusion studies of the rumen and the colon of a wide range of mammals indicated that most of the water was removed from these solutions as a result of SCFA and Na absorption (252).

VI. PRODUCTION OF MICROBIAL PROTEIN AND RECYCLING OF NITROGEN

A. Ruminant Forestomach

When provided with adequate amounts of dietary nitrogen, the microbial protein synthesized in the forestomach makes ruminants independent of the form in which it is provided. This is because most forms of dietary nitrogen are degraded by ruminal bacteria to ammonia, which is the principal form of nitrogen used for microbial protein synthesis. Dietary protein is degraded by the microbes to peptides, amino acids, and ammonia, but 50–80% of the nitrogen incorporated into microbial protein comes from ammonia, with most of the remainder coming from peptides. Most rumen bacteria have transport systems for a range of peptides and ammonia but not for free amino acids.

The amount of microbial protein produced in the rumen is closely related to the rate of SCFA production. About 9–10 g microbial protein are synthesized per mole of ATP produced in the fermentation (69). Only 10% of the substrate energy is released as ATP, with most of the remainder appearing as SCFA. The SCFA are too highly
reduced to be available to the microbes; they are instead absorbed and oxidized in the aerobic environment of the host animal’s tissues. Anaerobiosis sets the limit to the amount of amino acids that can be supplied by the rumen microbes to the animal. This is sufficient for maintenance and slow growth, but for higher levels of production of meat or milk, the diet must include protein that escapes degradation in the rumen for digestion in the small intestine. Only 10–20% of the protein of fresh forage escapes ruminal degradation, but the proportion escaping can be increased by treating the forage with heat or with chemicals such as formic acid or formaldehyde.

The nitrogen required for microbial protein synthesis is also of endogenous origin. This includes urea, a waste product of protein metabolism in the mammalian liver. Much of the urea is normally excreted via the kidneys, but in ruminants, loss of urea nitrogen is reduced by recycling through the forestomach. This is achieved by release of urea into the saliva and by the diffusion of urea down a steep concentration gradient from blood across the rumen wall, which is maintained by the ureolytic activity of bacteria attached to the ruminal epithelium (80, 134). Therefore, much of the waste from nitrogen metabolism joins the rumen ammonia pool, and a portion is incorporated into microbial protein, then absorbed as amino acids after its digestion in the small intestine. Excess ammonia is absorbed and converted to nonessential amino acids and urea by the liver.

On low-protein diets, nitrogen recycling can contribute the greater part of the protein flowing out of the ruminant forestomach. Urea recycling also reduces the amount of water required for the renal excretion of urea. Conversely, a restriction of water intake reduces urea excretion and increases the rate of urea-nitrogen recycling through the forestomach (103, 170, 185, 203, 204, 268).

### B. Foregut of Other Species

Urea-nitrogen recycling has been also reported in the forestomach of camelds, kangaroos, and wallabies. Camels fed low-protein dry desert grass recycled 95% of the urea synthesized by their liver (185). Wallabies on a low-protein diet recycled 84% of their endogenous urea (156). Dellow and Hume (70) followed the fate of several dietary components along the tubular stomach of kangaroos (Fig. 17). Soluble carbohydrate disappeared shortly after its entrance from the esophagus, indicating rapid fermentation to SCFA. In contrast, the disappearance of fiber indicated a continuous, but slower, fermentation of ~60% of the digestible fiber by the time it reached the distal end of the forestomach. However, the protein levels increased to 115% of intake in the proximal forestomach, because of the incorporation of endogenous nitrogen, mainly from urea, into microbial protein. The subsequent decline in protein concentration along the foregut was the net result of the continued cycling of urea nitrogen into microbial protein and the degradation of dietary and microbial protein by proteolytic bacteria.

### C. Hindgut

Urea is released into all segments of the mammalian intestine, but nitrogen recycling is most effective in the hindgut, where a steep transepithelial concentration gradient is maintained by large numbers of ureolytic bacteria at the lumen surface. Figure 15B shows the major substrates degraded for the production of ammonia and synthesis of microbial protein in the hindgut of mammals. These include endogenous nitrogen contained in urea, creatinine, digestive enzymes, mucus, and sloughed cells as well as nitrogen contained in dietary residues (281). Most of the amino acids appear to be derived from mucin and amino acids that are least efficiently absorbed from the small intestine. High concentrations of urea found in the colon of germ-free rats (168), the experimentally cleansed colon of humans (282), and the perfused colon of sheep and goats (84) indicate that most of the urea entering the hindgut is hydrolyzed to ammonia by bacteria attached to its epithelial surface. Most of the ammonia is

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**FIG. 17.** Pattern of digestion and absorption of organic matter (a), acid-detergent fiber (b), crude protein (c), and total soluble sugars (d) along stomach of eastern gray kangaroos fed chopped alfalfa hay ad libitum. Sites of sampling were sacciform forestomach (SFS), tubiform forestomach (TFS), and hindstomach (HS). [From Dellow and Hume (70).]
either incorporated into microbial protein or absorbed and recycled to the liver for synthesis of nonessential amino acids or urea.

Urea nitrogen was extensively recycled through the hindgut of the rabbit (219), pony (214), rock hyrax (140), greater glider and brush-tail possum (95), and donkey (144). Nitrogen balance was maintained in rabbits on a low-protein diet by infusion of urea into the cecum (233), and utilization of urea by the hyrax hindgut increased with either a reduction in dietary protein or restriction of water (140), in a manner similar to that of the ruminant forestomach. The recycling of urea nitrogen improved the utilization of dietary energy by maintaining higher numbers of bacterial populations in the hindgut of the rock hyrax, greater gliders, and donkeys. Conversion of fat jirds, donkeys, and bedouin goats from alfalfa or lucerne hay to Rhodes grass or wheat straw increased the recycling of urea from 53 to 89%, 16 to 75%, and 40 to 69%, respectively, with no loss in body weight (37, 144, 284). Black bears recycled 20% of their endogenous urea through their digestive tract during hibernation, when they do not drink, eat, or defecate (116). Recycling of urea also was demonstrated in the gut of sharks (160) and the gulf toadfish (274).

Uric acid, the principal waste product of protein metabolism in reptiles and birds, does not readily diffuse across the gut epithelium. However, uric acid was converted to ammonia and microbial protein after the reflux of urine from the cloaca to the ceca of chickens (181) and ptarmigan (184) and increased with a reduction in dietary protein (30). Birds conserve water by urinary excretion of nitrogenous wastes and electrolytes in osmotically inactive uric acid-urate complexes into the cloaca and reabsorption of urinary and digesta electrolytes by the hindgut. Boykin and Braun (32) found that the ureteral urine of chickens contained 4.7 nmol uric acid and 4.2 g protein/l. Because uric acid has an aqueous solubility of only 0.4 mM, they suggested that the protein served as a coating to maintain uric acid in small spheres (0.5–15 µm in diameter) and prevent its precipitation as large, damaging crystals during passage through the urinary tract. Microbial degradation of uric acid to ammonia, with subsequent absorption of ammonia from the cecum, could play an important role in the nitrogen economy of birds (33).

D. Absorption of Ammonia and Amino Acids Produced by Microbes

Ammonia, like SCFA, is present in undissociated (NH₃) and ionized (NH₄⁺) forms. However, with a pK of ~9, it is present principally as NH₄⁺ ions at the normal pH of rumen and hindgut contents. As with SCFA, ammonia was assumed to be absorbed as the more lipid-soluble NH₃. However, the pH and concentration of ammonia at the lumen surface, where much of the microbial hydrolysis of urea occurs, is unknown. Furthermore, there is some evidence for carrier-mediated exchange of NH₄⁺ and Na ions by the rat ileum (161) and the rectal pad of locusts (205).

Microbial degradation of endogenous and microbial protein in the hindgut by proteolytic bacteria also produces amino acids. Carrier-mediated absorption of amino acids has been demonstrated in the ceca of birds and the colon of chickens on a high-Na diet (241). However, only passive diffusion of amino acids has been shown in the hindgut of adult tortoises (16), rats (24), prairie voles (138), and other mammals, and undigested microbial protein is voided in the feces and lost in the absence of coprophagy.

VII. PRODUCTION AND ABSORPTION OF VITAMINS

Gut microbial cells also synthesize B vitamins, a complex of 10 separate water-soluble compounds. Ruminants do not require a dietary source of B vitamins because they are synthesized by the microbes in their forestomach and subsequently absorbed from the small intestine. Microbial synthesis of vitamin B₁₂ requires Co, and the low efficiency of Co incorporation into microbial vitamin B₁₂ (3%) accounts for its relatively high requirement in ruminants compared with nonforegut fermenters, which require preformed vitamin B₁₂ (269). The same is assumed to be true for other foregut-fermenting herbivores. The B-complex vitamins appear to be absorbed mainly from the small intestine by carrier-mediated, Na-dependent transport mechanisms (149, 225).

B vitamins also are synthesized by hindgut bacteria, but the extent to which they are absorbed from the hindgut is unclear. Wrong et al. (282) concluded that there was good evidence that nicotinic acid, riboflavin, pantothenic acid, thiamin, biotin, pyridoxine, folic acid, and vitamin B₁₂ are synthesized by microbes in the human colon, and all but the first three were absorbed to some degree. Kasper (150) demonstrated that thiamin was absorbed from the rat cecum, and Sorrell et al. (244) found that pantothenic acid, pyridoxine, and vitamin B₁₂ were absorbed equally well after their oral versus large intestinal administration to humans. In contrast, limited uptake from the hindgut is suggested by several studies that showed that rats fed a diet lacking riboflavin, pantothenic acid, biotin, pyridoxine, folic acid, or vitamin B₁₂ showed severe deficiencies unless they were allowed to ingest their feces.

The data in Table 6, extracted from National Research Council reports on nutritional requirements (187, 189), also suggest limited B vitamin uptake from the hindgut of several small hindgut fermenters. The degree to which the mouse, guinea pig, and rabbit require a dietary...
source of these vitamins was inversely proportional to the degree that they recycle microbially synthesized B vitamins to their stomach and small intestine. Thus rabbits, which are cecotrophic, appeared to be independent of a dietary source of all but three B vitamins. However, guinea pigs, which are coprophagic but not cecotrophic, require 7 of the 10 B vitamins in their diet. Laboratory mice ingest little of their feces and require all of the B vitamins in their diet.

VIII. MICROBIAL DETOXIFICATION

Plants have evolved a wide range of compounds (plant secondary metabolites, PSM) as protection against being eaten by animals, with the coevolution of detoxification mechanisms in either the tissues (principally the liver) of herbivores (46) or in the microbes inhabiting their gut. Foregut fermenters can often detoxify or reduce the toxicity of protected plants, although biotransformation in the gut can enhance the toxicity of some PSMs as well (180). Microbial adaptation to PSM often involves the induction of specific enzymes in a consortium of microbes and the growth of subpopulations. Microbial adaptation may also involve the selection of mutants with altered enzyme specificities or novel metabolic activities (180). Detoxification of PSM may have played an important role in defining the niche occupied by some foregut-fermenting herbivores.

IX. DISEASES ASSOCIATED WITH MICROBIAL FERMENTATION

Oral administration of broad-spectrum antibiotics can destroy indigenous microorganisms, and prolonged sequestration of digesta in any segment of the gastrointestinal tract, due to torsion, volvulus, herniation, or postsurgical adhesions, can result in their replacement with pathogenic organisms. However, a number of diseases can be attributed to inappropriate diets or feeding schedules.

Engorgement of grain, fruit, or other foods containing high levels of rapidly fermentable carbohydrate or rapid conversion to a high-grain diet can result in a fulminating production of SCFA and depression of the pH in the rumen of cattle, with an increase in lactobacilli and production of lactic acid (Fig. 12, A and B). High levels of SCFA and lactic acid result in hypertonic rumen digesta and systemic dehydration, and rapid absorption of these organic acids can produce rumen atony, ulceration of the forestomach epithelium, and systemic acidosis (74). High-concentrate diets also produce bloat or tympani, because of the rapid production and entrapment of fermentative gasses (75), with intraruminal pressures that can result in cardiovascular collapse and death. They can also produce distension and displacement of the abomasum (258). Increased concentrations of SCFA may also account for the abomasal ulcers found in calves and adult cattle fed high-concentrate diets. The high incidence of ulcers in the stratified squamous epithelium of the stomach of pigs subjected to intensive husbandry practices may be similarly attributed to the high levels of SCFA and low pH in this region (8).

Any condition that leads to malabsorption of carbohydrates in the midgut can result in diarrhea due to their hindgut fermentation to SCFA and lactic acid at rates too rapid for efficient absorption. This includes the ingestion of lactose-containing milk or milk products by neonates or adults with an inherent lactase deficiency, or infectious diseases that interrupt the normal processes of carbohydrate digestion and absorption. Neonates are particularly susceptible. Transmissible gastroenteritis (TGE) is characterized by atrophy of the villi in the small intestine, profuse diarrhea, and 100% mortality in pigs infected the first week after birth, but only a 2% mortality rate in pigs that are infected at three or more weeks in age. Argenzio et al. (11) found that TGE produced a marked increase in the volume of fluid secreted into the small intestine and a twofold increase in the amount of fluid presented to the hindgut. Three-day-old pigs were unable to ferment carbohydrate and absorb the excess fluid, but the more highly developed hindgut of older pigs converted most of the unabsorbed carbohydrate to SCFA, resulting in a sixfold increase in the absorption of water.

High levels of dietary starch also resulted in high concentrations of SCFA and lactic acid, a reduction in pH, and atony in the cecum of cattle (258) and horses (47). The cecal contents of horses showed a 25-fold increase in lactate concentration and a one-unit reduction in pH, which remained low for 5–6 h after feeding even after prolonged adaptation to the diet. At a pH of 5.5 or less, colonic epithelium can be severely damaged or destroyed.
by either SCFA or lactic acid (10). Therefore, rapid produc-
tion of these organic acids and gas could account for the
high incidence of large intestinal torsion, impaction, and
colic in horses fed high-concentrate diets.

Secretion and absorption by the equine hindgut is also influenced by the feeding schedule. Horses that would normally spend 12–16 h of the day grazing are often given one or two meals of a pelleted ration for convenience in feeding. The large intestine of ponies fed a pelleted hay-grain diet at 12-h intervals showed marked cyclic changes in volume (Fig. 14). This was most marked in the ventral colon, which underwent a fivefold increase in volume during the first 8 h after feeding. Clarke et al. (48) found that the plasma volume of ponies fed at 12-h intervals dropped 15% within 1 h after feeding, followed by a return to normal values within 2 h and a subsequent, smaller reduction 6 h after feeding. They attributed the initial reduction to salivary and pancreatic secretions and the second reduction to the hindgut response to increased microbial fermentation. The reduction in plasma volume was associated with increased plasma levels of renin and aldosterone. Release of renin from the kidney promotes the release of angiotensin. Angiotensin reduces urinary excretion and stimulates both thirst and the release of aldosterone, which stimulates Na and water absorption by the kidney and hindgut. Renin and aldosterone concentrations returned to prefeeding levels by 12 h after the meal. Ponies fed at 2-h intervals showed neither the cyclic changes in large intestinal and plasma volume nor the increase in renin or aldosterone levels.

Early studies of Burkitt (38) showing a relationship between low-fiber, high-protein, high-fat diets and the higher incidence of colorectal cancer and other diseases of the human large intestine in affluent Western civilizations have been confirmed by numerous epidemiological and case-control studies (147). However, the reasons are unclear. Insoluble fiber (cellulose, lignin, and some hemicellulose) can reduce digesta retention time and increase the volume of digesta in the large intestine. Soluble forms of dietary fiber (pectins, gums, and hemicellulose) can form gels that may sequester potential carcinogens, and all forms but lignin can be fermented to SCFA (269). Although wheat bran and cellulose had a protective effect against colonic cancer, more rapidly fermentable carbohydrates (corn bran, pectin, carrageenan, agar, and metamu-
cul) enhanced the development of chemically induced tumors in laboratory animals (172). Lack of enhancement in germ-free animals suggested that the end products of fermentation were the causative agents, but SCFA, particularly butyrate, also play an important role in the maintenance and repair of large intestinal epithelium (285).

Colonic cancer also has been attributed to the toxic effect of high levels of ammonia produced by microbial catabolism of protein. Administration of ammonium acetate increased the incidence of chemically induced col-

X. CONCLUSIONS

Bacteria colonize the gastrointestinal tract of all vertebrates. The longer retention time and relatively neutral pH of digesta in the hindgut of most terrestrial vertebrates and the foregut of a few of these species result in large numbers and greater diversification. These bacteria are accompanied by colonies of protozoa in the foregut or hindgut of some herbivores and by colonies of fungi in the forestomach of a few of these species. The bacteria produce SCFA by fermentation of carbohydrates, convert nitrogenous compounds into ammonia and microbial protein, and synthesize B vitamins. Protozoa can store starch and synthesize protein and appear to aid in the absorption of magnesium and phosphorus. Fungi can also synthesize protein useful to their host.

Hindgut bacteria produce substantial levels of SCFA by microbial fermentation of dietary starches that escape digestion in the upper digestive tract and the endogenous carbohydrates contained in mucus and sloughed epithelial cells. They also produce ammonia and microbial protein from digestion of amino acids that escape absorption in the midgut, and from urea (or uric acid), digestive enzymes, mucus, and sloughed cells released into the gut. Absorption of SCFA provides energy for the hindgut epithelium and makes a minor contribution to the maintenance energy of carnivores and most omnivores. It also plays a critical role in hindgut absorption of Na and water. Absorption of ammonia serves to recycle urea- or uric acid-nitrogen, conserving both nitrogen and water. Some of the microbial protein is digested by proteolytic bacteria, but, with the exception of birds, it appears that the hindgut lacks the ability to actively absorb amino acids. Hindgut absorption of B vitamins also appears to be limited. Therefore, the nutritional contributions of microbial protein and B vitamins synthesized by hindgut microbes are restricted in animals that do not practice coprophagy.
The greater gut capacity and digesta retention time of most herbivores allow the additional fermentation of structural carbohydrates of plant cell walls and increases the amount of nitrogen that can be recycled for hepatic synthesis of nonessential amino acids. Use of the midgut as the principal site of microbial fermentation in most herbivorous fish, larval amphibians, and one herbivorous species of turtle and bird would seem to provide a conflict between microbes and endogenous digestive enzymes. However, the cecum or colon serves as the principal site for microbial fermentation in most herbivorous reptiles, birds, and mammals, and the foregut is the principal site in one species of bird and a number of mammals. Increased production and absorption of SCFA provides a substantial amount of the maintenance energy required by these animals. Hindgut fermenters can recover nutrients from food digested by endogenous enzymes before its less efficient fermentation by bacteria. Coprophagic hindgut fermenters and foregut fermenters can utilize their midgut for digestion of microbial protein and absorption of amino acids and absorption of the B vitamins synthesized by bacteria.

Most small herbivorous birds and mammals compensate for a limited gut capacity and higher rate of metabolism by selective retention of fluid and small particles in their cecum and more rapid excretion of larger digesta particles. Some species can adapt to a reduction in the digestibility of dietary fiber by increasing the cecal retention time of fluid, bacteria, and, to varying degrees, the smaller digesta particles. Selective retention of fluid, and the ingestion of water-rich feces by cecotrophic species, also aids in the conservation of water. The ability of cecum fermenters to recover soluble nutrients in their upper digestive tract gives them an advantage over small forestomach fermenters. Their ability to increase cecal retention time on high-fiber diets and the recovery of microbial protein and B vitamins by cecotropic species also give them an advantage over small colon fermenters. This could account for the absence of colon fermenters and rarity of forestomach fermenters among small avian and mammalian herbivores. However, increased cecal retention time limits their ability to increase food intake and recover soluble nutrients on poorly digestible high-fiber diets.

Greater gut capacities and lower mass-specific energy requirements allow larger herbivores to adapt to less digestible diets by either increasing digesta passage, food intake, and soluble nutrient recovery, as seen in colon fermenters, or increasing digesta retention and fermentation time in a forestomach. Some colon fermenters can adapt as well or better than forestomach fermenters to low-quality forage. However, prolonged retention of plant particles in the forestomach increases the extent of fiber fermentation and favors the destruction of some plant toxins. Foregut-fermenting herbivores also have the advantage of utilizing both their midgut and hindgut for recovery of the large secretions of fluid and electrolytes required for microbial fermentation. This ability to adapt to conditions where forage, water, or both are sparse accounts for the fact that ruminants are the only large herbivores found at high altitudes and in arctic or extremely arid climates.

The absence of herbivores among adult amphibians and low percentage of herbivorous fish and reptiles have been attributed to an inefficient masticatory apparatus, limited gut capacity, and the effect of low ambient temperatures on food intake, digesta transit, and microbial fermentation in ectotherms. However, limitations in gut capacity would not explain the rarity of large herbivorous fish and reptiles, and reductions in body temperature result in compensatory reductions in the rate of digesta passage and requirements for nutrients. Therefore, the rarity of herbivorous fish and reptiles may be due to additional factors related to ectothermy. The restrictions of flight on the capacity and distribution of gut contents has also limited the number of herbivorous birds to a few species that are either flightless or limited in their flight.

The extreme success of mammalian herbivores can be attributed to endothermy, an efficient masticatory apparatus and an expansion in gut capacity. The parallel success of herbivorous dinosaurs suggests that they were endotherms with an efficient masticatory apparatus and similar suite of digestive strategies, according to their body size, habitat, and the quality and availability of forage and water.

Many of the gastrointestinal diseases of domesticated and captive herbivores can be attributed to inappropriate diets and/or feeding schedules. The digestive tract of most herbivores is constructed for almost continuous feeding on a diet high in plant fiber and relatively low in protein, starches, and sugars. Therefore, major problems can arise from the intermittent feeding or diets that contains low levels of fiber and high levels of rapidly fermentable starch or sugar. The hindgut of omnivores with a well-developed large intestine also appears to require a minimal amount of plant fiber for normal function, as evidenced by the higher incidence of cancer and other diseases in the colon of humans on low-fiber diets. The protective effects of dietary fiber may be attributed to a more rapid rate of digesta passage, to a greater volume dilution of hindgut digesta, or to differences in the quantity or composition of the bacterial populations.

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CONTRIBUTIONS OF GUT MICROBES TO VERTEBRATES

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