THE LARGE INTESTINE

ITS ROLE IN MAMMALIAN NUTRITION AND HOMEOSTASIS

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The Large Intestine: Its Role in Mammalian Nutrition and Homeostasis

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Preface

The research worker developing an interest in the large intestine finds that the organ has been relatively neglected in comparison with most other parts of the alimentary tract. He is faced with further difficulty in that scientific contributions have been widely scattered in the literature, appearing in journals of physiology, clinical medicine, nutrition, pharmacology, microbiology, zoology and veterinary science, often with few cross-references. As a result the existing body of knowledge may seem much smaller than is actually the case.

As clinicians with an interest in the physiology and pathophysiology of the large intestine we have become very conscious of the need for an up-to-date guide to knowledge on this subject. Several years ago we set out to write a review on the topic, which has grown to the present book. The work is intended primarily for the young investigator, whether physiologist or clinician, who requires background information for his own research, and for this purpose we include an index and a large bibliography.

We have confined ourselves to nutritional and homeostatic aspects of the large intestine, leaving aside the questions of innervation and motility, though we recognize the influence of these subjects on our chosen topics. We have also given scant attention to several currently popular aspects of bowel function – for example the immunology of the large intestine, the colon as a generator of carcinogens, and the putative value of vegetable fibre in preventing human disease – except where these can be shown to involve nutritional or homeostatic aspects of bowel function.

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1 Comparative anatomy and physiology

1.1 SPECIES DIFFERENCES

Throughout mammals the large intestine is clearly demarcated from the more proximal small intestine, from which, except in a few carnivorous species, it is separated by a definite valve. A cloaca (the terminal chamber into which the alimentary, urinary and genital tracts all open) is present in amphibians, reptiles and birds, but only a very few mammals (e.g. monotremes).

The large intestine itself has traditionally been divided into three parts – the more proximal blind caecum, the colon, and the more distal rectum. These subdivisions are to some extent artificial. Some mammals have no caecum, and in many others there is no sharp demarcation, either functionally or anatomically, between caecum and colon; for example, in horse and rabbit the proximal colon is a bulky organ containing semi-fluid faeces, of similar structure to the caecum (Figures 6 and 7) whereas the distal colon is a much narrower viscus occupied by segmented solid faeces. In most mammals the anatomical demarcation between colon and rectum is even less definite (Figures 2–4), being chiefly characterized by a sharp caudal change in direction. In man there are no sharp demarcations between caecum, colon and rectum, and workers primarily concerned with man have often used the term 'colon' loosely to refer to the large intestine as a whole.

Within mammals the large intestine shows extreme variations in form, from a short and simple tube without a caecal appendage, to a voluminous structure which may occupy up to three-quarters of the volume of the abdominal cavity (Mitchell, 1916; Anderson and Jones, 1967; McBee, 1970; Dorst, 1973). To obtain some idea of its relative size in different animals its volume or the weight of its contents may be expressed as a proportion of that of the whole alimentary tract, or of total body weight. The first detailed study of this kind was published from Paris by Colin almost a hundred years ago, and is summarized in Table 1. Colin (1886) distinguished between the caecum and the rest of the large intestine in most of the species he studied; his figures show well the enormous development of the large intestine in herbivores, especially in nonruminants in which the caecum is particularly large. Table 2 shows data from more recent sources expressing the weight of the contents of the large intestine as a percentage of total body weight.

Table 1. Absolute and relative capacities (mean values) of segments of alimentary tract from different mammals. From Colin (1886)

	Volume (litres) (*Proportion of total volume* (%))			
	Stomach, including rumen, etc.	*Small intestine*	*Caecum*	*Colon and rectum*
Dog	4.3 (62)	1.62 (23)	0.09 (1.3)	0.91 (13)
Cat	0.34 (70)	0.11 (15)	0.12 (16)	
Pig	8.0 (29)	9.2 (34)	1.6 (5.6)	8.7 (32)
Ox	252 (71)	66 (19)	9.9 (2.8)	28 (7.9)
Sheep and goat	29.6 (67)	9.0 (20)	1.0 (2.3)	4.6 (10.4)
Dromedary	245 (81)	40 (13)	3.4 (1.1)	15 (4.8)
Horse	18 (8.5)	64 (30)	34 (16)	96 (45)
Donkey	10 (9.7)	24 (23)	21 (20)	50 (47)

Table 2. Weight of contents of large intestine as percentage of total weight. Some values refer to caecum alone. Mean values are given for each source

Species	*Weight of large bowel contents* % / *Weight of whole animal*	*Reference*
Man	0.43	Wrong, unpublished*
Wallaby	1.1	Moir *et al.*, 1956
Sheep	1.4	Elsden *et al.*, 1946
Ox	1.6	Elsden *et al.*, 1946
Rat	1.6	Elsden *et al.*, 1946
	2.2 (caecum)	Hoover and Clarke, 1972
Beaver	3.7	Hoover and Clarke, 1972
Porcupine	4.4 (caecum)	Johnson and McBee, 1967
Pig	4.8	Elsden *et al.*, 1946
Vole	4.8	Elsden *et al.*, 1946
Rabbit	4.9 (caecum)	McBee, 1970
	7.8 (caecum)	Hoover, and Clarke, 1972
Hyrax	8.5 (including midgut sacculation, Figure 8)	Leon, 1980
Dugong	10	Murray *et al.*, 1977
Elephant	10	Benedict, 1936
	13	Hungate *et al.*, 1959
Horse	13.1	Elsden *et al.*, 1946

* The figure for man is the mean (range 0.16–0.76 %) obtained from necropsy measurements of four adult London males who died suddenly and unexpectedly of cardiovascular disease. A larger figure would probably have been obtained from rural Africans, eating a high residue diet, in whom daily faecal weights may average more than four times as much as in British adults consuming a refined Western style diet (Burkitt *et al.*, 1972).

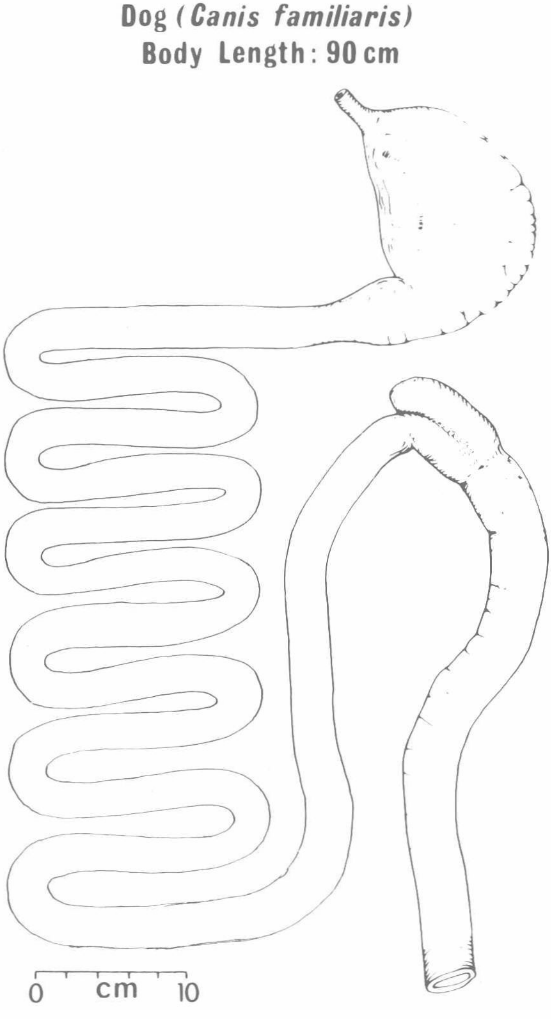

Figure 1 Gastrointestinal tract of the dog. From Stevens (1977). This Figure and Figures 2 and 4–7 are reprinted from Melvin J. Swenson (ed.), *Dukes' Physiology of Domestic Animals*. Copyright © 1970, 1977 by Cornell University, and used by permission of the publisher, Cornell University Press

Anatomical development of the large intestine in different species is closely related to their food, and in particular to the need of herbivorous mammals to provide, at some site in the alimentary tract, a fermentation chamber in which the complex structural polysaccharides of plants can be hydrolysed by bacteria (Moir, 1964). Physiological species differences are most marked in the metabolism of non-mineral nutrients, particularly carbohydrates, vitamins and nitrogen compounds; in comparison the handling of fluid and electrolytes

Rat *(Rattus norvegicus)*
Body Length: 17 cm

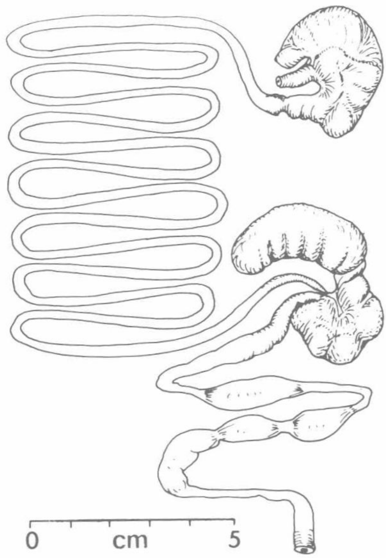

Figure 2 Gastrointestinal tract of the brown rat. From Stevens (1977)

in the large intestine differs little between different animals. In terms of feeding habits and alimentary development the following subdivisions of mammals can be made:

(a) Carnivorous and insectivorous mammals

This group includes Cetacea and Insectivora, most Carnivora, and many Chiroptera (bats) and marsupials, in which the large intestine is short and the caecum absent or very simple. An example from the dog is shown in Figure 1. The organ appears to be unimportant as a fermentation chamber in this group of mammals, except perhaps in the breakdown of chitin and chitosans by cetaceous and insectivorous animals.

(b) Omnivorous mammals

No natural order is exclusively omnivorous, but this group contains the majority of primates, including man, and some rodents (e.g. old-world rats and mice, squirrels, marmots), carnivora (e.g. bears, racoon) and marsupials. There is no foregut fermentation chamber, and these animals rely on their large intestine for the digestion of plant fibre. The organ is well developed, usually with a caecum, but not to the extent seen in group 4 below. Examples shown are the rat (Figure 2) and man (Figure 3).

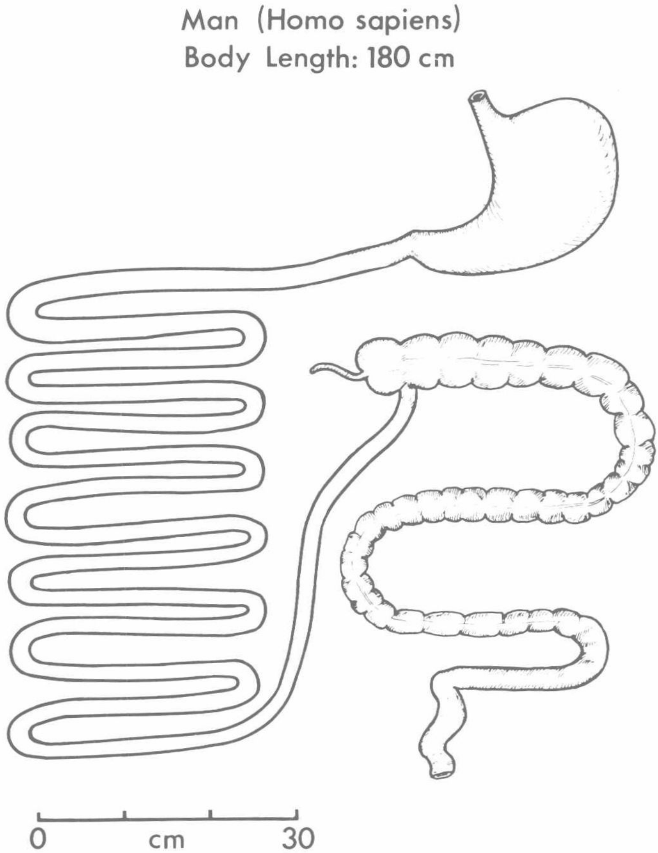

Figure 3 Gastrointestinal tract of man

(c) Herbivorous mammals with a foregut fermentation chamber (Bauchop, 1977)

This group includes all ruminants, both four-chambered (cattle, sheep, goats, antelopes, giraffes) and three-chambered (camels, llama). Some nonruminating members of the Artiodactyla (peccary, hippopotamus) should probably be included, for their stomachs are often subdivided into two or more chambers, and gastric fermentation has been demonstrated in several of them (Moir, 1968; Thurston *et al.*, 1968) though its contribution to the nutrition of the host remains uncertain. Gastric fermentation of plant fibre is a feature also of diprotodont marsupials (Moir *et al.*, 1956; Moir, 1968; Hume, 1977), the foliage-eating sloth (Jennings, 1965) and the Colobos monkey (Kuhn, 1964; Bauchop and Martucci, 1968). The two-chambered stomach of the aquatic Sirenia (dugong and manatee) suggests that they also make use of foregut fermentation (Bertram and Bertram, 1968), though Moir (1968) has pointed out that the high unsaturated content of their depot fat implies that this plays only a minor role in their nutrition. In general, the large intestine of these species is like that of omnivores and more complex than that of carnivorous mammals, but is very variable in its development, probably in inverse relation to the importance of foregut fermentation; usually a caecum is present (ruminants), but there may be none (e.g. hippopotamus). Examples are shown in Figure 4 (sheep) and Figure 5 (kangaroo).

(d) Herbivorous mammals without a foregut fermentation chamber
This group comprises the majority of rodents (including guinea-pig, hamster, and the wood pulp-consuming beaver and porcupine), the Perissodactyla (horse, zebra, ass, tapir, rhinoceros), elephants, lagomorphs (rabbits and hares), Dermoptera (flying lemurs), several higher apes, and a few marsupials and bears. In these mammals the large intestine shows its greatest develop-

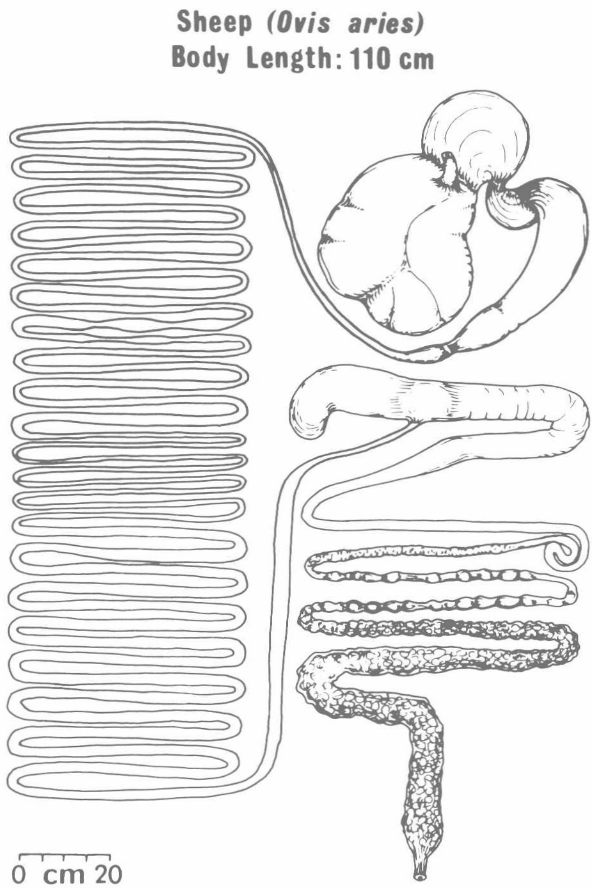

Figure 4 Gastrointestinal tract of the sheep. From Stevens (1977)

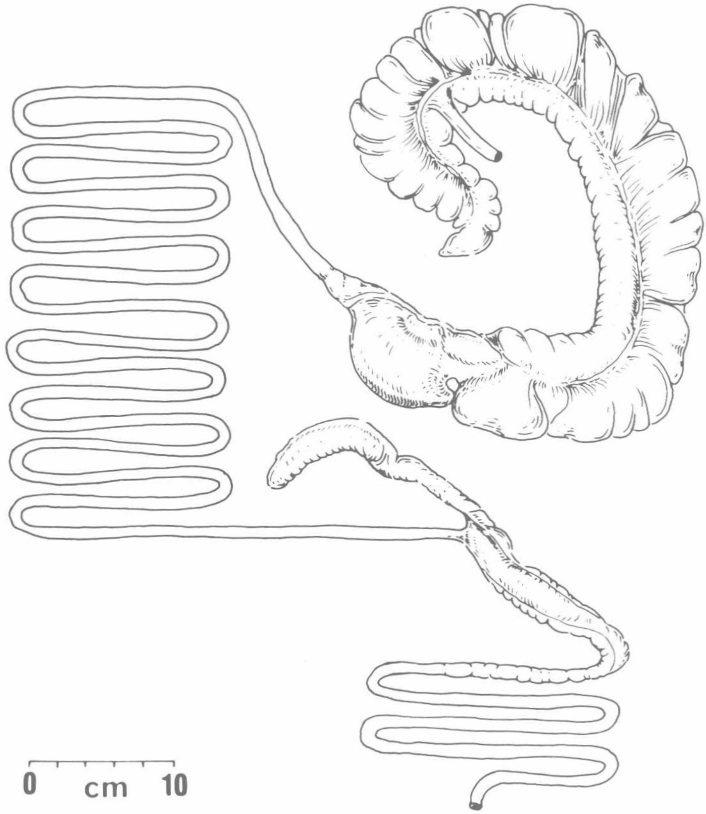

Figure 5 Gastrointestinal tract of the kangaroo. From Stevens (1977)

ment (Tables 1 and 2). The caecum is large, often much larger than the remaining large intestine, and may be divided by septa or a spiral valve. Examples are shown in Figure 6 (pony) and Figure 7 (rabbit). Bizarre developments, apparently unique, include gravel derived from soil in the koala caecum (Bollinger, 1962), and caecal villi in the pika (Lagomys) (McBee, 1970). Coprophagy, discussed below, is a feature of many animals in this group.

The ingenuities of gastrointestinal evolution are such that not all mammals can be easily fitted into the above classification. Gastric fermentation with production of organic acid has been shown to occur after a meal in the single-chambered stomach of the horse, pig and macaque monkey (Friend *et al.*, 1963; Argenzio *et al.*, 1974b; Argenzio and Southworth, 1975; Clemens *et al.*, 1975; Takasaka, 1978), though this is not nutritionally of much importance as