Part I

Introduction

1

Gut form and function: variations and terminology

DAVID J. CHIVERS and PETER LANGER

The aim in this volume is to present a synthesis of a wide range of data pertinent to the digestive system in mammals, focussing on three areas, food, form and function. There are introductions to each of these three sections and a final discussion encompassing all aspects but working from the viewpoints of the three groups of contributors. The essence of this volume is that it brings together very different lines of research, and that an integrating process is initiated to develop a broader understanding of the digestive system.

In this preliminary section we set the scene and discuss general, often problematic, issues and then Langer (Ch. 2) presents an evolutionary perspective. This is followed by introductions to modelling gut function by Martinez del Rio, Cork and Karasov (Ch. 3) and optimum gut structure for specified diets by McNeill Alexander (Ch. 4).

As we focus on the details of diets and digestive systems (structure and function), we need to think about the nature of the niches to which they are adapted: in particular, as to how broad or narrow these may be or how variable in the short (days) or long term (seasons, years). To what extent is form and function accounted for by preferred food and body size? To what extent are they moulded by critical events ('bottlenecks' in food availability). We need to think about them against an evolutionary background of increasing environmental diversity over the last 50 million years in relation to the dramatic radiation of angiosperm (flowering) plants. It is the increasingly dynamic nature of environments that encourages more dietary plasticity, varied adaptations and niche breadth – polytrophism or omnivory – but these may be discouraged by anatomical and/or physiological constraints of the digestive system.

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Gut form and function

Gastro-intestinal tracts show dramatic variation from those adapted for pro-cessing animal matter (very nutritious and easy to digest) mainly in the small intestine, with small stomachs and large intestines, to those dominated by stomach and/or caecum and colon for the processing of plant cell walls (very common food but very difficult to digest) by fermentation. Here, then, is the contrast between specialist **faunivores** and **folivores**, with an intermediate morphology shown by **frugivores** (with a larger small intestine if sup-plementing the fruit staple with animal matter, or larger fermenting chambers if leaves are the main supplement). This dietary spectrum corresponds closely with body size and even more so with biomass density. This is because ani-mal matter is scarce compared with plant material.

 Herbivory (or **florivory**) – the consumption of plant material – needs to be sub-divided into **frugivory** and **folivory**, with numerous sub-divisions of each (see Ch. 5). Folivory ranges from the more selective 'browsers', through to the less selective bulk-feeders, 'grazers'. Chitin, the skeleton of invert-ebrates, can be digested in those mammals that have the enzyme chitinase. Its digestion requires at least a comparable dentition to folivores (although much smaller) to similarly maximise the surface area available for digestion.

 The concept of **omnivory** is weakened by the anatomical and physiological difficulties of digesting significant quantities of animal matter *and* fruit *and* leaves. The supposed evolutionary pathway shown by mammals radiating from their insectivorous ancestor is reflected by evolving anatomy and physi-ology. As mammals increased in size (over about 1 kg for primates), so they were able to add plant material (mainly the more digestible fruit) to their insectivorous diet. Increasing body size allowed even more voluminous guts that allowed the fermentation of plant cell walls, giving nutritional access to foliage. Adaptations for digesting seed coats (by fermentation) is perhaps the link between fruit- and leaf-eating diets (Bodmer, 1989). Therefore, animal matter is swamped in a large gut, and foliage cannot be digested in a small gut. A compromise is not really feasible, although some rodents (dormice), pigs and opportunistic primates (macaques, baboons and chimpanzees) may be true omnivores. Humans are only omnivorous thanks to food processing and cookery; their guts have the dimensions of a (faunivore) carnivore but the taeniae, haustra and semi-lunar folds are characteristic of folivores. Among the so-called omnivores, most eat either mainly fruit and animal mat-ter (if smaller) or fruit and foliage (if larger) but not all three.

 The basic gut design persists clearly, as reflected by development, basic position, innervation and blood supply (Fig. 1.1), despite dramatic diversifi-
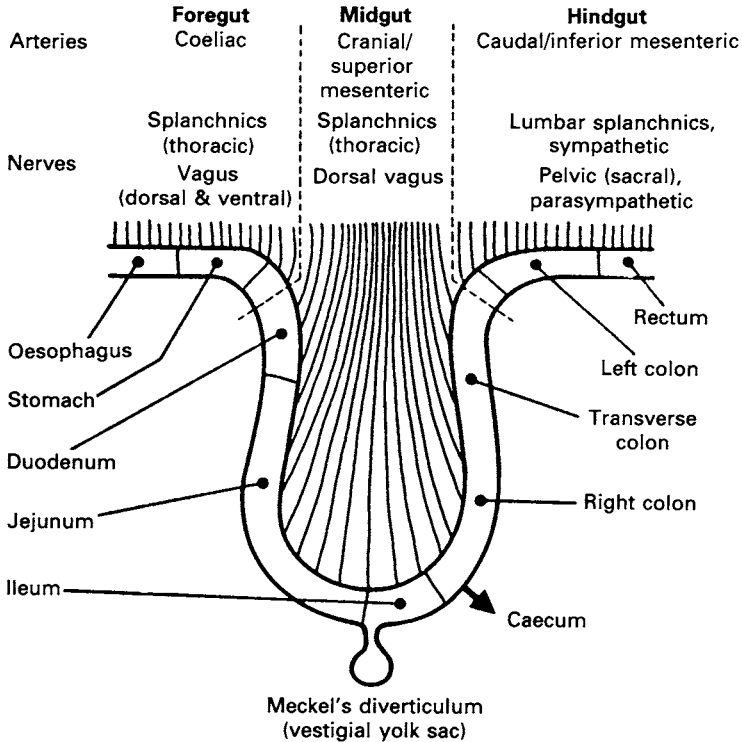
Fig. 1.1. The basic design of the gastro-intestinal tract showing the blood supply and innervation.

cation among different dietary types. Thus, the **stomach** and start of the **duodenum** (as far as the entrance of the bile duct) develop from the first relatively-fixed part of the **foregut** in the abdomen, crossing from left to right, and are innervated by the **dorsal** *and* **ventral vagus** (Xth cranial) nerves (parasympathetic) and the **splanchnic nerves** (sympathetic). They are supplied with blood by branches of the **coeliac artery** and blood is drained into the **hepatic portal vein** by gastro-splenic and gastro-duodenal veins. The **left (descending) colon** and **rectum** are relatively unvarying in all mammals, with little digestive function, and run caudally to the anus; this **hindgut** is innervated by **sacral (pelvic) nerves** (parasympathetic) and **lumbar splanchnic nerves** (sympathetic) and is supplied with blood by the **caudal mesenteric artery**, draining into the vein of the same name. Therefore, ana- tomically speaking, *hindgut* cannot be equated with large intestine as is so commonly done.

It is the mobile **midgut** loop that is so readily lengthened, proximally in

faunivores and distally in folivores. It herniates through the umbilicus early
in development and is later withdrawn into the peritoneal cavity by an anti-
clockwise rotation (viewed from ventrally) at the base of the loop, with the
proximal end preceding the distal end so that the **caeco-colic junction** comes
to lie ventral to the duodenum (Fig. 1.2). The midgut is supplied by the
cranial mesenteric artery and **vein** and is innervated by the **dorsal vagus**
and **splanchnic nerves**. The duodenum, crossing from right to left, gives
way to coils of **jejunum**, with the **small intestine** terminating as the **ileum**
on the right. The **large intestine** starts with the **caecum** (with an appendix
sometimes, where lymphatic tissue may be concentrated distally) which
branches blindly off the large intestine. It continues with the **right
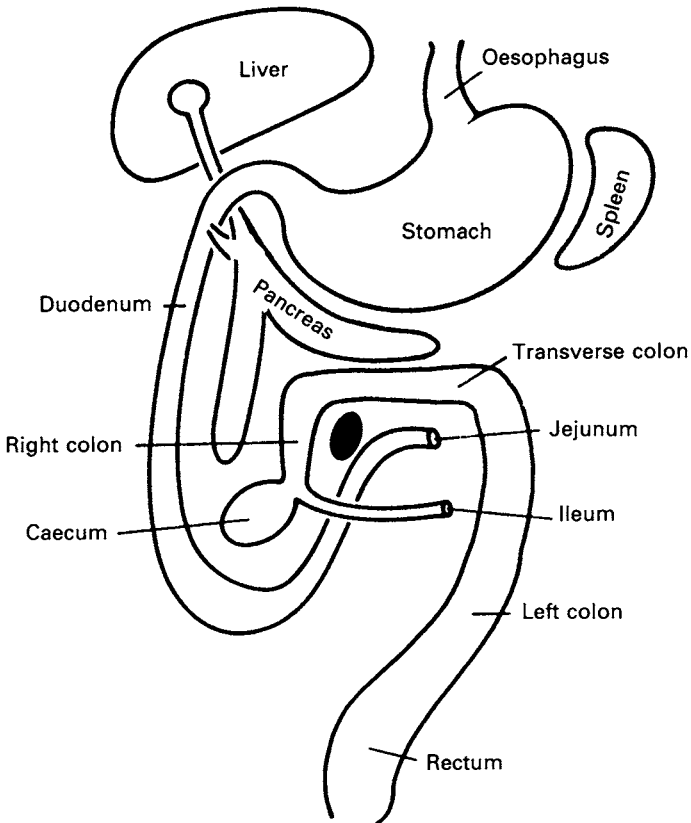(ascending) colon**, which can expand dramatically, and very variably in

Fig. 1.2. Basic layout of the mamalian gut (ventral view) with the stomach crossing
from left to right, duodenum on the right and the colon crossing from right to left.

mammals, into a fermenting chamber (instead of or as well as the caecum) in many folivores; this in turn gives way to the usually short **transverse colon**, near the stomach. Thus, we have the contrasting strategies for fermenting plant cell walls of **caeco-colic fermentation** (or caecal or colic), often called hindgut or post-gastric fermentation, and of **foregut fermentation**, often called pre-gastric or forestomach fermentation. The latter occurs in the keratinised (except in Camelidae and Macropodidae) enlarged first part of the stomach, before the true glandular part of the stomach that contains the gastric (cardial, fundic and pyloric) glands.

Terminology

We have already defined numerous terms. It remains to clarify others and give the synonyms that appear in this volume. The parts of the gut nearest to the head are proximal, cranial or oral, those nearer the tail are distal, caudal or aboral.

    Stomachs are enlarged parts of the otherwise tubular gut; they are simple, one-chambered (uni-locular) or compound, multi-chambered (pluri-locular). The entrance is the **cardia**, the exit is the **pylorus**, with the body (or **fundus**) in between. Since it is now clear that they always develop from the simple gastric spindle, it is not correct to talk about monogastric or polygastric mammals – no mammal has more than one stomach! The confusion was generated by the contrast in ruminants between keratinised (like the oesophagus) and glandular parts of the stomach, implying that they might have had different origins.

    Such enlargements of the stomach may be sac-like (sacculation, sacciform), diverticulated (diverticulum), or tube-like (tubiform). Enlargements in the large intestine, in particular, where the cylindrical shape is maintained, are sacculations when they are separated from each other by circular folds, or **plicae circulares**. These folds may occur in the small and large intestines. When longitudinal muscular bands, or **taeniae**, are differentiated in the outer layer of the muscular wall which 'anchor' so-called **semi-lunar folds** or **plicae semilunares**, the widened lumina between these folds are called **haustra** (singular haustrum). The two main regions of the large intestine, the colon and the caecum, can be haustrated. Only in the colobid monkeys, kangaroos and rat kangaroos are parts of the forestomach haustrated.

    Histologically, the gastro-intestinal tract has (a) an inner epithelial layer of **tunica mucosa**, with a thin layer of muscle, the **lamina muscularis mucosa**; (b) a connective tissue layer of **tela sub-mucosa** containing vessels and nerves; (c) an inner circular and outer longitudinal layer of **smooth mus-**

cle (with an additional third – oblique – layer in the body of the stomach); (d) an outer connective tissue coat – **tunica serosa** – overlaid by (e) **visceral peritoneum** or, in retroperitoneal organs, by an **adventitia**. The tunica mucosa is of endodermal origin, the rest is derived from mesoderm.

An important parameter in understanding the relation between structure and function in the digestive system is the amount of time that digesta spends in the system. Terms commonly used are transit time, retention time, mean retention time, residence time, passage time, passage rate and turnover time (Martinez del Rio *et al*, Ch. 3). **Transit time** has been used for every possible measurement of **retention time**! It is usually used for the time of first appearance; transit time will only equal **mean retention time** if there is no mixing (otherwise it will underestimate mean retention time). **Residence time** refers to time spent in various gut compartments; **gut clearance time** refers to time to completely evacuate the gut under a starvation regime.

The digestive processes are modelled in terms of **plug flow** (PFR), a **piston** or **tubular reactor** and a **continuous stirred tank reactor** (CSTR); there are also **batch-stirred reactors** (BSR). Digestion may be **catalytic** or **auto-catalytic, alloenzymatic** or **autoenzymatic**. Observations may be made **post-prandially** (after a meal) or **post-injectionally**.

This, then, provides the mainly structural background to the initial discussion of evolutionary and functional issues (Part I) and the detailed discussion of food (Part II), form (Part III) and function (Part IV). We aim to integrate very different lines of research to promote a better understanding of the digestive system in mammals.

Reference

Bodmer, I. (1989). Frugivory in Amazon ungulates. Ph.D. thesis, University of Cambridge.

2

Food and digestion of Cenozoic mammals in Europe

PETER LANGER

Fossil European mammalian species belonging to orders that have survived to the present day can – most probably – be allocated to the same *type of digestion* as their extant close relatives. The general habitus can be determined from fossil remains; the habitus – as well as the dentition – represents adaptations to a certain mode of life and a certain type of digestion that is similar to conditions in a closely-related species from the Recent (Holocene). Of course, the type of digestion in an extinct taxon can only be considered as highly probable, and not as absolutely certain.

It is also probable that the *type of food* is similar in extinct and recent species of the same order and/or family. For example, it is plausible that a perissodactyl ingested plant material and was certainly not zoophagous. Also, it was most probably a caecum-colon fermenter, as are its present-day relatives, and did not ferment the ingested plant material in a forestomach. The above-mentioned assumptions accepted, it is possible to classify mammals from the Cenozoic era (fossil mammals) according to the food they ate and according to their type of digestion – as long as they belong to orders that still survive today!

The following questions will be covered in the present study:

1. What were the steps – and when were these steps undertaken – to widen the range of *food* that could be used by European fossil mammals?
2. When did major steps in the differentiation of new types of *digestion* take place?
3. What can be said about the combinations between types of food and types of digestion in European mammalian orders and families?
4. Which answers to the previous questions present insights into the relationships between body weight, class of food and type of digestion during mammalian evolution in Europe?

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Materials and methods

Extinct species, as well as their families and orders, are listed by Savage and Russell (1983). From textbooks of paleontology (Romer, 1966; Carroll, 1988) the approximate body size of a species can be obtained by comparing fossil species with well-known recent ones (Flindt, 1985). 'We cannot measure body mass directly for fossil species and must derive estimates from skeletal remains that are usually fragmentary and incomplete' (Damuth and Mac-Fadden, 1990, p. 3). Difficulties in the determination of body size from fossil material were emphasized by Heinrich (1991): changes in *proportions* of body parts have to be identified to avoid confusion with changes in body *size*. Although it is not possible to obtain direct biological measurements for members of an extinct fauna, the variables of skeletal elements 'have Gaussian distribution, and thus averages are biologically valid species parameters' (Martin, 1990, p. 63).

For the present study, five classes of animals based on differing mean body weights were compiled. In the following diagrams the weight groups will be identified by their numbers (1 through 5), thus sub-dividing the continuous mammalian weight range between the pygmy white-toothed shrew (*Suncus etruscus*) weighing 2 g and the African elephant (*Loxodonta africana*) weighing 6 t into just five steps. The following **groups of weight** were differentiated:

1 (W1). Minute mammals: weight below 5 kg
2 (W2). Small mammals: weight between 5 and 50 kg
3 (W3). Medium-heavy mammals: weight between 50 and 500 kg
4 (W4). Heavy mammals: weight between 500 and 5000 kg
5 (W5). Very heavy mammals: weight above 5000 kg.

In a further endeavour to differentiate fossil species, the dietary categories of mammals were attributed to the species listed by Savage and Russell (1983) according to the actuo-zoological approach. To avoid the misleading impression of over-exactness, four food or **dietary classes** were determined here, considering and modifying data from Eisenberg (1981) and Langer (1991).

1 (F1). **Zoophages** (faunivores): piscivores and squid-eaters, crustacivores, carnivores (eating vertebrates), sanguinivores, planktonivores, myrmecophages and insectivores
2 (F2). **Polyphages** (omnivores): species that eat foods of animal *and* of plant origin

3 (F3). **Phytophages** (florivores): nectarivores, gumivores, frugivores, granivores, herbivores and browsers

4 (F4). **Poëphages** (grazers, graminivores): the grazers.

Graminivores is based on the Greek name for grass (Werner, 1961); plant taxonomists apply the name Poaceae as well as the Latin Gramineae for the grass family (Jones and Luchsinger, 1987).

The different **strategies of digestion**, as they can be found in mammals, were also grouped into four main types, following Langer (1988) and Langer and Snipes (1991).

1 (D1). Autoenzymatic digestion: digestion with the mammal's own set of digestive enzymes

2 (D2). Alloenzymatic digestion in the caecum-colon complex or large intestine: fermention is performed by microbes

3 (D3). Alloenzymatic digestion in the forestomach without rumination: again microbes perform the fermentation of the food

4 (D4). Alloenzymatic digestion in the forestomach plus repeated chewing of the cud (rumination): microbial fermentation.

The differentiation of groups of body weight, food classes and types of digestion was made for fossil European mammalian species listed by Savage and Russell (1983) for 13 geological units, of varying ages given in million years before the Present (Ma BP): five for the European Eocene (Sparnacian, approximately 54; Cuisian, 48; Lutetian, 46; Rubiacian, 44; Headonian, 38), three for the Oligocene (Early Oli, 35; Middle Oli, 30; Late Oli, 24) and five for the Miocene (Agenian, 22; Orleanian, 18; Astaracian, 14; Vallesian, 11; Turolian, 8). Because of Quaternary extinctions and extirpations under the influence of man during the Pleistocene era (Barnosky, 1991), especially of forms with higher body weights (Edwards, 1967; Caughley and Krebs, 1983; Caughley, 1987), only the Tertiary will be dealt with in this paper.

Three-dimensional diagrams were drawn to help to clarify the interrelationships (Figs. 2.1 and 2.2). The first type (*a*) compares dietary category or food class, group of body weight and the number of species that show the respective combination of both criteria. In the second type of diagram (*b*) the connection between the type of digestion, the weight group and the number of species is given. Finally, the third type of diagram (*c*) illustrates dietary category or food class, type of digestion and the number of species with the respective combination.

Setting the diagrams in chronological order, it was possible to obtain a visual impression as to how European mammals during the Tertiary era occupied niches that were characterised by different classes of food and types of