STRUCTURE AND FUNCTION IN THE CATARRHINE STOMACH,
WITH PARTICULAR REFERENCE TO THE FAMILY COLOBIDAE.

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the degree of Master of Arts in Biological Anthropology
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DECLARATION

Except where otherwise indicated, this thesis is my own work.

Judith M. Caton

J.M. CATON
SEPTEMBER 1990.
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ABSTRACT

A review of the literature on the gastric morphology of the family Colobidae, indicated that a plurilocular stomach is characteristic of all species, and is an adaptation to diets that contain considerable amounts of plant structural compounds, like cellulose. Parts of the colobid stomach act as fermentation chambers, as they house populations of cellulolytic bacteria. The volatile fatty acids produced and the bacterial cells themselves are an important source of metabolites for these monkeys.

The general plan of the stomach in most colobid species, including Presbytis femoralis, is tripartite, and the system of nomenclature used in these descriptions is based on the work of Kuhn (1964) and Langer (1988). The oesophagus opens into a greatly expanded saccus gastricus, which is the main fermentation chamber. This, in turn, opens into the narrow, elongate tubus gastricus, which has two functional regions. The cranial two-thirds are part of the fermentation area, while the caudal third is involved in gastric digestion, like that in other mammals. This last region is continuous with the pars pylorica, which appears to be similar in structure to that in the stomachs of other catarrhines. The longitudinal muscle layer of the walls of the saccus and the tubus is concentrated into two flat bands, the taeniae, which run along the two curvatures. These structures play an important role in the mixing of gastric contents. The sulcus ventriculi follows the inner surface of the lesser curvature. When the muscle in the lips bordering the sulcus contract, it closes to form a duct-like structure that can carry liquids and easily digested food directly from the oesophageal orifice to the caudal part of the tubus. The major variation to this basic plan among the Colobidae is the presence of a fourth chamber, the praesaccus. This is a diverticulum of the saccus gastricus, and is probably a food storage area.

The gastric mucosa in the colobids contains the three principal gland types common to mammalian stomachs, namely cardiac, oxyntic and pyloric, and they can be easily distinguished even in the mucosa of poorly preserved specimens, like that of Presbytis femoralis. The distributions of these glands are different from those in the stomach of catarrhines, such as Papio cynocephalus, which have unilocular stomachs. Cardiac glands, which line the saccus and the cranial part of the tubus, are the principal gland type of the gastric mucosa of Presbytis femoralis and other colobids, and they may be involved in pH regulation of the contents of the fermentation chambers. The oxyntic glands are restricted in their distribution to the mucosa of the caudal part of the tubus, unlike the situation in other catarrhines, in which they are the main gland type. The pyloric glands appear to be similar in general form and function in this whole group of Old World primates. The mucosa of the praesaccus contains cardiac glands in Procolobus and Rhinopithecus, but in Nasalis larvatus and Pygathrix nemaeus it is reported to be lined with a stratified squamous epithelium. Confirmation of these reports may help in understanding more about the phylogeny of the Colobidae.
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Introduction

The stomach in mammals and other vertebrates is the most dilated portion of the alimentary canal, being formed from a muscular expansion of the foregut (Romer 1956). It is located between the end of the oesophagus and the beginning of the small intestine, in the anterior part of the abdominal cavity. Its main functions are the storage and physical breakdown of recently ingested food, and its secretions are responsible for the initial stages of protein digestion.

This thesis presents the results of a study of gastric anatomy in Old World monkeys, in particular those with “complex” stomachs, the members of the family Colobidae. This is one of the major features that can be used to separate them from the members of the other family, the Cercopithecidae, which have “simple” stomachs. Complex and simple are relative terms that are used to describe anatomical differences; in reality all stomachs are complex organs, both anatomically and physiologically. As relatively little has been written about the anatomy of the complex stomach of these monkeys (Figure 1.2), the main aim of this study was to review all the relevant literature and to add to the general pool of knowledge on colobid stomachs by describing that from a Sumatran leaf-monkey, *Presbytis femoralis*. It was hoped it would also throw more light on the phylogenetic relationships within the Colobidae, as this is a complex problem, that is worthy of further consideration (Napier 1985, Groves 1989). Despite its poor state of preservation, the histology of the mucosa of this specimen was studied, as even less had been written about this aspect of the anatomy (Appendix 1). This section of the work was expanded to include observations on the histology of the gastric mucosa of the yellow baboon, *Papio cynocephalus*, a cercopithecid. This was a “perfect” specimen with the mucosa intact, and it provided a unique opportunity to describe the structure and to make comparisons with the histology of the gastric mucosa in other catarrhines, particularly the colobids.

The major emphasis throughout has been on the stomachs of the Colobidae, with particular attention to the relationship between structure and function in these organs. This study was confined to the stomach, rather than the whole gastro-intestinal tract, as it was in a better state of preservation than the rest in the only specimen that was available. These observations and the review of the literature emphasized both the homogeneity of the morphology of the stomach in different colobid genera and the lack of knowledge about these monkeys; they are still “the forgotten leaf-eaters” (Groves 1970). This preliminary reading also emphasized the confusion about the taxonomy of these monkeys (Table 1.2). Information obtained about differences in gastric morphology raised more questions about colobid phylogeny than it answered, and thus it became an indicator of possible lines of research for the future.
The descriptive content of this thesis is divided into two parts, the content of each of them being dictated by the different aspects of anatomy considered, and by the availability of suitable material. This last constraint is a particular problem in Australia, because of its isolation and the excellent health of the monkeys in the various zoos throughout the country.

Part 1. Structure and function in the stomachs of the members of the family Colobidae.

This section, dealing with gross anatomy, starts with a review of the literature, then the anatomy of the stomach in general is discussed. This introductory section provided a basis both for describing the anatomy of the stomach of *Presbytis femoralis* and the comparison with those of other colobids.

Part 2. The histology of the gastric mucosa in members of the section Catarrhini.

The specimens of the stomachs of *Presbytis femoralis* and *Papio cynocephalus* provided an opportunity to describe the structure of the mucosa and to make intraspecific comparisons between them and other catarrhines. This part is sub-divided into:

1. a description of the histology of the gastric mucosa of *Papio cynocephalus*.
2. a description of the gastric mucosa in *Presbytis femoralis*. Useful information was obtained about its general structure and the pattern of degeneration in the various glandular regions.

These two species, *Papio cynocephalus* and *Presbytis femoralis*, represent the two sides of the dichotomy that is evident within the Old World monkeys. The leaf-monkeys of the family Colobidae, like *Presbytis femoralis*, tend to be more arboreal and more folivorous than the members of the other family, Cercopithecidae. *Papio cynocephalus* belongs to this family, and baboons, like many of the others, tend to be more terrestrial and more omnivorous in their diets, which consist predominantly of plant reproductive parts and any animal food that is available. These animals are thus adapted to the demands of different ecological niches and this is reflected in their total morphology.

To separate these groups at the family level immediately raises a taxonomic problem that has yet to be resolved. This is discussed briefly in Part 1. The taxonomy of the family Colobidae is itself a "minefield" and there is a considerable amount of disagreement about it. It is important to know exactly which species of monkeys are being described when considering the anatomical differences that might be used in deciphering and understanding phylogenetic relationships; a
clearly defined taxonomic scheme is essential to avoid this type of confusion. The scheme used was that proposed by Groves in 1989, as it is the most recent and takes into account unpublished data (e.g. Weitzel 1983) and recently translated information such as that on *Rhinopithecus spp.* (e.g. Peng et al. 1983) and it is a continuation of Groves' own work on this problem. Similarly, with the anatomical descriptions a clear system of nomenclature avoids confusion, making descriptions of morphology easier to understand and compare. Kuhn (1964) provided such a system for his descriptions, which has been used by many authors in subsequent years. Some minor modifications to Kuhn's system were needed and the reasons for these are discussed in Chapter 3. Providing well-defined schemes like these ensure that other researchers know exactly what animals are being discussed and the anatomical features are being described. Thus it is easier for others to repeat the work and evaluate the findings.

Each species of mammal, through the course of its evolution, becomes adapted to life in a particular niche in its environment. Andrewartha (1966) considered that the environment of a particular species was everything that influenced its chance to survive and multiply. He saw the environment as a complex set of factors, which could be divided into four major components: weather, food, other animals and a place in which to live. These were not static, for they would interact with each other, and a particular species, itself, would be in equilibrium with them. It is this interaction through adaptation that measures the success of a species, and it is ultimately measured as reproductive success (Andrewartha 1966). As environments are never static, flexibility in adaptation is necessary if a species is to survive. The more conservative it becomes, the narrower is its range of options and this may lead to a decline, especially if it has to compete with a more adaptable species in the same habitat. This would seem to have been the case with the colobids; for from comparisons of the numbers of their species with the number of cercopithecid species, especially in Africa, it would appear that the more specialized colobids have, on the whole, been at a disadvantage.

Diet, food and digestive physiology together form one aspect of the adaptation of these monkeys to arboreal niches in tropical rainforest environments. Within the body of any mammal the structure and function of an organ, or a system of organs, are interdependent and reflect adaptation to a given environmental situation. The whole body of the animal is adapted, not just specific and isolated parts. Adaptation is a process; it, too, is never static and is an on-going part of evolutionary change, even if that change ultimately leads to extinction. It is most convenient to study the morphology of an animal by dissecting it into its component parts after death. It thus becomes frozen in time and the structures described are in fact artefacts; nevertheless such studies do lead to greater understanding of the relationship between structure
and function, or adaptation to a particular niche.

The gastro-intestinal tract in mammals provides a good example of this interplay between structure and function. Most members of the family Colobidae are arboreal folivores found, mainly, in evergreen tropical rainforests in Africa and Asia (Table 2.2), and they consume large amounts of plant structural polysaccharides which mammals are incapable of digesting. The colobids have adapted to this problem in a number of ways -

1. through the development of gastric diverticula, which house populations of cellulolytic bacteria.
2. through the provision of a stable environment that encourages bacterial growth.
3. by the use of short-chain fatty acids as a primary energy source.

Complex stomachs are not the only modifications to an arboreal lifestyle that are seen in these monkeys. Their limb proportions are those of climbers and leapers (Fleagle 1988) and their behaviour is characterized by long rest periods between feeding bouts, which aids in the fermentation process (Rose 1978), and group size may also be dictated by the availability of food sources. Even the loss or reduction of the hallux that is characteristic of the group is probably a similar adaptation as it is seen in other arboreal primates.

Just looking at a particular feature in one group of animals, like the Colobidae, cannot be done in isolation, as they and the Cercopithecidae must have shared a common ancestry. Thus comparison of the structure of a particular organ or organ system will ultimately lead to a greater understanding of the evolutionary relationships between all of these monkeys. Differences are seen to be the results of adaptations to other niches which require distinct anatomical and physiological responses.

Paradoxically, the study of anatomy is not solely a description of the structure of a dead animal, as has so often been the case, but it is part of the study of living animals and how they are adapted to their particular environmental niches. In this regard it has widespread applications in many fields of biology.
PART ONE

STRUCTURE AND FUNCTION IN THE STOMACHS OF THE MEMBERS OF THE FAMILY COLOBIDAE

A number of authors have commented on the paucity of descriptions of the stomachs of the primates (and in particular of Old World monkeys) from which to base a systematic analysis of the anatomy and function of the stomach. The discovery of the stomach of the Cercopithecus aethiops (Wright 1929 and 1930) and of the stomach of the Macaca mulatta (Wright 1935) led to an increase in knowledge of the stomachs of the monkeys. The stomachs of other species have also been examined, including those of the orang utan (Wright 1935), the chimpanzee (Wright 1935), the gorilla (Wright 1935), and the mandrill (Wright 1935). However, the stomachs of the Old World monkeys have been the subject of much less attention, and the stomachs of the New World monkeys have received even less attention.

The stomachs of the Old World monkeys have been studied in detail, and their anatomy and function have been described in detail. The stomachs of the New World monkeys have been studied less, and their anatomy and function have been described less. The stomachs of the African monkeys have been studied more, and their anatomy and function have been described more. The stomachs of the Asian monkeys have been studied less, and their anatomy and function have been described less. The stomachs of the American monkeys have been studied more, and their anatomy and function have been described more.

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Chapter 1.

A review of the literature on the gastric anatomy in the family Colobidae

A number of authors have commented on the paucity of descriptions of the anatomy of the stomach in this family of Old World monkeys; from Polack who wrote in 1908 that "very little has been written about the stomach of the Semnopithecæ" (page 104), to Langer who wrote, 80 years later, that "the number of detailed descriptions of the digestive tracts of the different species of the Colobidae is not large" (1988: 281). Groves (1989) recognized 35 colobid species, and descriptions of gastric morphology are available for 20 (57 percent of the total number) of them (Table 1.1 and Figure 1.1A). There are detailed descriptions for 15 (43 percent of total number, or 18 percent of descriptions) of these - Table 1.1 and Figure 1.1B. A large number of these studies have been of the more accessible species, like the sacred langur (*Semnopithecus entellus* from India and Sri Lanka - Plate 1.1), or of the more exotic, like the proboscis monkey (*Nasalis larvatus* of Borneo - Plate 1.2) and the douc (*Pygathrix nemaæus* from Indochina - Plate 1.3) - Table 1.1. The availability of specimens also appears to be linked to the spread of European exploration and colonization in Africa and Asia, for example the British in India (Pocock 1928) and Africa (Murie 1865, Hill 1952), the French in Indochina (Duvernoy 1834), and the Germans in Africa (Polack 1908, perhaps Kuhn 1964). It was also closely linked to the establishment of large zoological gardens in London (Owen 1833-41, Sonntag 1924) and Paris (Duvernoy 1834). These collections of living animals were an important source of material as many colobids are notoriously difficult to maintain in captivity (Hill 1964) and the mortality rate among such animals was high. Zoo specimens are still important, for Hollihn (1971) studied the stomachs of animals that had lived and died in various German zoos.

Owen referred to Otto, whose description of a colobid stomach was published in 1825, as "the first observer of this peculiar structure among the monkeys" (1833: 74). Two later authors, Martin (1837) and Hill (1958), cited a description of the stomach of the proboscis monkey by Wurmb published in 1787, which would take precedence. Otto's paper was the type description of a monkey he named *Cercopithecus (?) leucopyrumns*, which can easily be identified from the drawing of the animal as the Sri Lankan species, *Trachypithecus vetulus*. Otto described its sacculated stomach, comparing it with that of ruminants, and noting its similarity to the stomachs of *Nasalis larvatus* and *Pygathrix nemaæus*, which he had also examined. He emphasized that this was a major feature uniting these species in a group, and separating them from other Old World monkeys, which have simple stomachs.
Since this beginning there have been some 30 further accounts of the form of the stomach in various colobid species (Appendix 1), and these can be divided into three broad groupings:

1. those papers in which the authors were primarily concerned with the anatomy of the stomach in colobids,
2. descriptions of gastric morphology that were part of a study of the anatomy of the whole animal,
3. studies comparing the stomachs of colobids with those of other members of the infra-order Catarrhini, which includes cercopithecids, apes and humans, as well as the colobids (Groves 1989).

While there is considerable overlap between these categories, as most authors draw some comparisons with other species, both colobid and non-colobid, they provide a useful means of organizing the available data.

Group 1 - Papers in which the authors were primarily concerned with the anatomy of the stomach in colobids.

This is the largest of the three groups, and it begins with Owen's studies (1833, 1834, 1835 and 1841) of animals that died in the menagerie of the Zoological Society of London. In the first paper (1833) Owen described the stomachs of the Indian langur, *Semnopithecus entellus*, and what he called the "croo monkey" from Sumatra, *Semnopithecus fascicularis*. Confusion has arisen about the actual identification of this animal. Owen, in 1835, said that it was the same as *Semnopithecus comata*. Desmarest published the original description of this species, which he thought came from Sumatra, but he was in error as his specimen had come from Java (Napier 1985). Hill (1954) thought this specimen was most probably *Trachypithecus cristatus*; but he had some reservations about this, as there might have been a slight chance that it could have been a specimen of *Presbytis melalophos*. These were brief descriptions which Owen expanded in the paper of 1835. He noted in each of these reports that the food of these monkeys was "strictly vegetable" (1835: 69), and that they differed from other Old World monkeys in their lack of cheek pouches, and in the possession of complex, sacculated stomachs. Owen compared the structure of their stomachs to those of other herbivorous mammals, including ruminants and kangaroos. The report of 1834 was a short one on the stomach of *Semnopithecus maura (= Trachypithecus auratus* - Hill 1954), the black Javan species (Plate 2.3). It was found to have a structure similar to those previously described.

Mr. Owen's impression that this remarkable modification of the stomach is a genetic peculiarity receives confirmation from its occurrence in the first previously unexamined species which has been dissected within the Society's reach since the publication of his remarks. (Proceedings of the Zoological Society of London, Jan. 28, 1834 - W. Yarrell, Esq. in the Chair)
Finally, in 1841, Owen published an account of his dissection of the stomach of *Colobus ursinus* (= *Colobus polykomos* - Napier 1985), and wrote that it "presents the same complicated structure as in the Semnopithecini" (page 84). This specimen was very young, so its stomach was somewhat smaller than those in the other species he had studied.

At the same time that Owen was working in England, Duverney (1834) published a description of the anatomy of the stomachs of a number of Asian colobids, including *Nasalis larvatus*, *Pygathrix nemaeus* and a foetal specimen he described as "the red-capped langur from the Malabar Coast", probably *Trachypithecus johnii* (Plate 1.4), which is dark brown with a red-brown head (the only other langur in this part of India is the lighter, grey *Semnopithecus entellus* - Plate 1.1). Duverney was fulsome in his praise of the work of both Otto and Owen, and his findings coincided with theirs. He also pointed out that these similarities in gastric anatomy united this group of monkeys.

In 1845 Hombron and Jacquinot described in some detail the gastric anatomy of *Nasalis larvatus*, which was like that of the other "Semnopitheques". The stomach was very large and could be divided into 2 major regions -

1. the upper or cranial one, which consists of three parts - a cul-de-sac, a paunch, and a tubular region.
2. a lower or caudal region, pyriform in shape, which opens into the duodenum.

These authors also noted the presence of a well-developed sulcus ventriculi on the inner surface of the lesser curvature, underneath the "superior tendinous ribbon". On the basis of the histology of the mucosa in these two regions Hombron and Jacquinot considered that in *Nasalis larvatus* the first region was a fermentation chamber and that digestion occurred in the second. They felt that this conclusion was supported by the nature of the dentition and the form of the temporo-maxillary articulation in these animals, for it was like that in other mammalian herbivores. Martin (1837), in a much shorter paper, also described the anatomy of the stomach of the proboscis monkey, which he called *Simia nasalis*. He also concluded, on the basis of the form of the stomach and a number of other characters, that *N. larvatus* was very similar to the rest of the "Semnopithecini". The specimen that Martin dissected was in poor condition as it had been preserved in brine.

The stomach of the douc, *Pygathrix nemaeus*, was studied by Pilliet and Boulart (1898), who reported that it was like those of other colobids in general form, being a major character that separated them from "other simians". Their description included both gross anatomy and histology, and they related structure to function, noting like others before them, the similarities...
between the stomachs of these monkeys and those of kangaroos and ruminants. Pilliet and Boulart thought that the stomach of *P. nemaeus* was intermediate between the simple stomach of humans and the complex four-chambered stomach of ruminants.

Berenberg-Gossler's paper (1911) gave some details of the histology of the stomach in an easily recognised species, *Semnopithecus schistaceus*, now *S. entellus schistaceus* the Himalayan subspecies of *S. entellus* (Napier 1985). He was unable to describe the structure of the mucosa in the first part of the stomach, as the langur had died during the night, and this part of the wall had been destroyed before it could be preserved. This is a common problem with the stomachs of colobids (Kuhn 1964). The tissues in the lower, or caudal parts, of the stomach were unaffected. In the second part Berenberg-Gossler discussed the development of the stomach in foetuses of *Semnopithecus maura* (= *Trachypithecus auratus*), *Nasalis larvatus*, and *Semnopithecus mitratus* (= *Presbytis melalophos* - Napier 1985, Groves 1989). He remarked upon the similarities between the stomachs of these colobids and those of human children and chimpanzees, as had Keith and Wood Jones in 1901. This work, with Hill's paper in 1954, are the two major ones on the ontogeny of the stomach in the Colobidae.

Hill studied the developing stomachs of a number of embryos and foetuses of *Semnopithecus priam* (= *S. entellus priam* - Napier 1985), *Kasi senex nestor* (= *Trachypithecus vetulus nestor* - Napier 1985, Groves 1989), *Colobus badius preussi* (= *Procolobus preussi* - Groves 1989) and *Presbytis femoralis*. In the introduction to this paper Hill gave a valuable review of the literature on the anatomy of colobid stomach to that date.

Kuhn's study, published in 1964, is one of the most detailed and important works on colobid gastric anatomy and physiology. His descriptions were of three African species, *Procolobus verus*, *Procolobus badius* and *Colobus polykomos*, as well as *Presbytis cristatus pyrrhus* (= *Trachypithecus auratus* - Weitzel and Groves 1985), from Indonesia. In this work he used a clear system for naming the various parts of the stomach, which has subsequently been adopted by many other authors. The first part of Kuhn's paper was concerned with the morphology of the stomach, and he found that the major difference between these genera was the presence of a fourth chamber, the praesaccus, in *Procolobus*. Kuhn looked at the histology of the stomach wall in the second part, and finally he discussed the physiology of gastric digestion in these animals. This was the first study of the role played by symbiotic bacteria in the metabolism of cellulose in the foreparts of the colobid stomach. Kuhn's paper has been widely read and has been quoted or used by a number of authors writing on a diversity of topics - Hladik (1978) on colobid ecology, Bauchop (1978) on the physiology of gastric digestion, Chivers and Hladik
Hollihn (1971) was mainly concerned with diet and parasitic diseases of colobids kept in zoos in Germany. His brief discussion of stomach anatomy in these monkeys was largely based on Kuhn (1964). He noted, almost in passing, that there were differences in the structure of the mucosa of the praesaccus in *Nasalis larvatus* and *Pygathrix nemaeus*, when compared with that of *Procolobus*. This fact was also mentioned by Kuhn (1964) when he compared his findings with those of Pilliet and Boulart (1998).

Peng, Ye and Zhang were the principal co-authors of a series of three papers published in 1983 (Peng et al.), 1985 (Ye et al.) and 1988 (Zhang et al.) on the Chinese species of *Rhinopithecus*. The 1983 paper was the most detailed, and was the first published account of the gastric morphology and physiology in this subgenus. Peng et al. is an important work, which is not often cited as it is written in Chinese; an English translation was made available to me, so that the information it contained could be included in this thesis. The other papers are shorter and summaries of their contents are given in English. The one of 1985 was a review of the chief characteristics of the gastro-intestinal tract in *Rhinopithecus*. The 1988 paper was on the histology of the gastro-oesophageal junction.

Suzuki et al. (1985) published a very short description of the histology of the mucosa of the stomach of *Presbytis francoisi* (= *Trachypithecus francoisi* - Groves 1989). Some of the descriptive terminology used by these authors was confusing, and the paper's brevity makes comparisons difficult. This is the only description of the morphology of the stomach in this threatened colobid species from Vietnam and southern China.

The final study in this group is that of Langer (1988), who devoted a chapter in his book, *The Mammalian Herbivore Stomach*, to the Colobidae. Langer began with a discussion of colobid ecology and phylogeny. He described the stomachs in a number of species (Table 1.2), most of which were foetuses or very young animals obtained from museum collections. In his descriptions Langer made extensive comparisons with the work of other authors. His descriptions were detailed and well-illustrated, making this an important work on the comparative anatomy of the colobid stomach.
Group 2 - Detailed descriptions of gastric morphology included in studies of the anatomy of the whole animal.

There are three works in this category and all of them have been important sources for comparative studies since they were written. The first is that of Polack (1908), who studied the anatomy of *Colobus ursinus* (= *C. polykomos*), *Semnopithecus leucopyrhnus* (= *Trachypithecus vetulus*) and *Semnopithecus entellus*. Her study of the stomach began with a description of its position in relation to the other abdominal organs, and then she described its morphology. Included in this were Polack's rather unique findings on the arrangement of the longitudinal fibres of the muscularis externa, which form flat bands or taeniae that run along the two curvatures. Polack compared her observations with those of Owen (1833) and Duvernoy (1834).

Ayer's monograph on the anatomy of *Semnopithecus entellus*, published in 1948, was an important milestone in the study of the stomach of these animals, and is still one of the most frequently quoted works on the topic. His chapter on the anatomy of the stomach begins with a short review of the literature, and then describes the various regions of the stomach and the detail of the musculature of the wall. Ayer compared his findings with those of Owen (1833 and 1835), Keith and Wood Jones (1901), Polack (1908) and Duckworth (1915).

Hill's account of the anatomy of *Procolobus verus* appeared in 1952. In his description of the stomach he noted the presence of a fourth chamber, which he called the dorsal diverticulum of the fundus; otherwise the plan of the stomach was the similar to that seen in the other members of the family Colobidae. Hill found that the form of the gastro-oesophageal junction differed from species to species and he suggested that this could be a useful diagnostic characteristic.

Group 3 - Studies comparing the stomachs of colobids with those of other members of the infra-order Catarrhini.

Murie published a paper in 1865, in which he described the anatomy of the stomachs of *Presbytes albigena* and *Colobus guereza*. He doubted that the specimen identified as *Presbytes albigena* was a member of this genus, for the stomach was simple; this monkey had originally come from Gabon in western Africa, whereas *Presbytes*, Murie noted, was from Asian. Murie's use of generic names for Asian colobids was confusing, as he started with "Presbytis albigena", changed to "Presbytes abigena" and then referred to "Semnopithecus (Presbytes)". He showed, through detailed comparisons of the anatomy of *Semnopithecus, Colobus* and the African cercopithecid, *Cercocebus*, that his specimen was probably a member of the latter genus. The specimen of *Colobus guereza* was shot during a trip along the White Nile and was dissected in the field. Murie suggested that that the form of the stomach in this species was indicative of a close
relationship to the Asian colobids, especially as they were also linked by dental characters. Hill (1954) referred to this monkey as *Colobus abyssinicus*, which is a synonym for *C. guereza* (Napier 1985).

Salmon's paper of 1893 presents a problem. It is a description of the histology of the gastric mucosa in two species of Old World monkeys, which he called *Inuus cynomologus* (= *Macaca fascicularis*, the crab-eating macaque of Southeast Asia - Ellerman and Morrison-Scott 1951) and *Cercopithecus fuliginosus*. Burki (1958), on the basis of the presence of a blind sac in Salmon's description of the stomach, believed that this latter specimen was *Colobus fuliginosus* (= *Procolobus badius temminckii* - Napier 1985). This identification must be treated with caution as the terminology that Salmon employed to describe the various parts of the stomach is confusing, and it might well refer to a well-developed fundic area in a unilocular stomach. This is a common feature in the stomachs of many of the Papioninae (Hill 1966). Groves (1990 - personal communication) believes that *Cercopithecus fuliginosus* is a synonym for the sooty mangabey, *Cercocebus atys*; if, however, Burki's identification is correct, this would be the first detailed description of the histology of the tunica mucosa in a colobid stomach.

Keith and Wood Jones (1901) compared the morphology of the human stomach with that of colobids. In particular they were interested in the developing stomach of human foetuses of 3-4 months gestational age, which they found to have marked similarities with adult colobid stomachs. They then went on to describe the stomachs of the Semnopithecidae (= Asian members of the family Colobidae) and other primates. As the result of this study -

> the authors concluded ... from the evidence of development and comparative anatomy, the stomach of Primates (excluding the Lemuroidea) is probably tripartite in nature, consisting of a fundus, a body and a pyloric part. (190: XXXVII)

This is an interesting and thought-provoking paper, but in it Keith and Wood Jones failed to identify the the species of colobid they studied. They called it "*Semnopithecus*, an ape found in the East, from India to Borneo" (1901:XXXVI). Ayer (1948) considered, probably on the basis of their illustration of the stomach, that they had described the Indian langur, *Semnopithecus entellus*, but a number of other Asian colobids also have tripartite stomachs, like *Presbytis femoralis*, which is described later in this thesis. Thus Keith and Wood Jones' description could apply to any of these.

A brief description of the stomach of *Nasalis larvatus* was provided by Duckworth (1915), in his general comparative study of primate morphology. In this species the stomach was "enormously sacculated" like those in the other Asian and African members of the family.
Sonntag (1921), in a study of the tongues and salivary glands of Old World monkeys, mentioned the unusual form of the stomach in the purple-faced langur, *Presbytis cephalopterus* (= *Trachypithecus vetulus* - Napier 1985) from Sri Lanka. He felt that this was an adaptation to a diet, thought to consist almost entirely of leaves, and that the first chamber of the stomach replaced the cheek-pouches of the cercopithecids. Sonntag also felt that insalivation of the ingesta was completed in this chamber. Pocock (1928) included a very brief description of the "capacious, sacculated stomach" of this same species, which he called *Pithecus senex vetulus*, in his comparison of the differences between langurs and macaques.

There was a considerable gap in time between these comparative studies and the next group which were all published in *Primatologia* (Band 3 Teil 1) in 1958. Burki reviewed the histology of the oesophagus, stomach and intestines in a number of primate species, including colobids (Table 1.2). He wrote that the colobids showed extreme specialization of the tripartite plan of the stomach, which was common to all primates. Burki found that the fine structure of the stomach wall was basically the same in all of the species he studied, with variations largely confined to the mucosa, especially in the cardiac blind sac. He made comparisons with the findings of other authors, including Pilliet and Boulart (1894), Berenberg-Gossler (1911) and Hill (1952).

Hill's contribution to this volume was a general review of primate gastric anatomy. In it he wrote that -

> The Old World subfamily Colobinae differs widely from all other primates in the extremely large size and complexity of their stomachs. (1958: 153)

Starck in his chapter described the "topography" of the abdominal organs of *Colobus polykomos abyssinicus* (= *C. guereza* - Napier 1985). These organs showed many specializations that Starck considered to be due to the shape and size of the stomach. His description was brief, but gave a clear over-all picture of the abdominal cavity.

The final paper included in the third group was that of Chivers and Hladik (1980). In it they examined the relationship between the surface area of the gut and diet in primates, and then made comparisons with the dimensions of the gut in members of other mammalian orders with similar dietary patterns. Nine colobid species were included in this study (Table 1.2), which provided a bridge between ecological, morphological and physiological studies.

Through these writings there has been a slow increase in the knowledge of the unique anatomy of the stomach in this group of Old World monkeys, which are still largely "forgotten", as Groves...
described them in 1970 (Figure 1.2). A brief summary of the all of these descriptions of the stomach morphology is provided in Appendix 1. With this knowledge has come a greater understanding of the relationship between structure and function, or of adaptations for dealing with a diet that has a high cellulose content. Two other points emerged from this survey of the literature. Firstly, there is a need to discuss the taxonomy of the group in the light of current ideas, to ensure that there is conformity in naming the species that have been studied. The confusion that can arise is illustrated by the data presented in Table 1.2, which compares the species names used by the authors of the papers discussed in this review with those currently used by Groves (1989). Secondly it is necessary to define a system of nomenclature for use in descriptions and discussions of stomach morphology in this group of monkeys; a point made by Langer in 1988.
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Figure 1.1
Comparisons of the numbers of descriptions of stomach anatomy in the family Colobidae

A. The number of descriptions of colobid stomach by species. These represent 57% of the known species.

B. The number of detailed descriptions of the stomachs of these species. These represent 43% of the known species and 18% of the total number of descriptions.
FIGURE 1.2
The chronological sequence of papers on colobid gastric anatomy.

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PLATE 1.1 Semnopithecus entellus

A group of female sacred langurs resting on a pathway in the Mandore Gardens (Jodhpur). These langurs are fed regularly by the local people and are not disturbed by the presence of humans. The neonate that can be seen clutching the fur of the female in the foreground was about an hour old.
PLATE 1.2 Nasalis larvatus
Male and female proboscis monkeys, showing the characteristic form of the nose in each of the sexes.
(photo from a post card)

PLATE 1.4 Trachypithecus johnii
This Nilgiri langur, originally from southwestern India, was photographed in the Delhi Zoo.
(Photo: C.P. Groves)
PLATE 1.3 *Pygathrix (Pygathrix) nemaeus*

The douc is one of the colobids from the rainforests of Vietnam and Laos.

(Photo: Kavanagh 1983)
Chapter 2

A review of the taxonomy of the leaf-eating monkeys of the family Colobidae

The taxonomic scheme followed in this thesis is based on that proposed by Groves in 1989 (Figure 2.1). The leaf-eaters are one of two groups of Old World monkeys, which belong to the superfamily Cercopithecoida Gray, 1821 of the order Primates Linnaeus, 1758. They are separated from each other on the basis of specializations in cranial and alimentary morphology (Szalay and Delson 1979, Napier 1985, Strasser and Delson 1987, Groves 1989). Both Luckett (1976) and Groves (1989) have stressed that taxonomic divisions within the Primates must be largely dependent upon the characters shown by extant forms, a point that is particularly relevant to this study. Stomach morphology, and in particular the histological structure of the mucosa, appears to be a relatively conservative character in mammals (Ito 1965), including the primates (Burki, 1958). Thus differences in stomach morphology could be an important way of distinguishing between the two groups of cercopithecoids, and also between some of the genera in the leaf-eating group.

Groves (1989) gave familial status to each of these groups of Old World monkeys (Figure 2.2A). These are -

**Cercopithecidae** Gray, 1821 - this family contains the baboons, guenons, mangabeys and their relatives from Africa, as well as the Asian macaques. They have simple (unilocular) stomachs and cheek pouches for the storage and insalivation of food. Cercopithecids are frequently described as generalist omnivores (Kavanagh 1983, Groves 1989).

**Colobidae** Blyth, 1875 - this group tends to be more arboreal than the cercopithecids and their diet is more folivorous. The members of this family are the colobus monkeys of Africa and the large variety of Asian leaf-eaters, langurs and odd-nosed monkeys. They have no cheek pouches, and storage and insalivation of food occurs in the first chamber of their complex (plurilocular) stomachs. The first regions of the stomach house bacteria, which are responsible for the breakdown of cellulose from plant material, releasing organic compounds that are used as metabolites by these monkeys (Kuhn 1964, Bauchop and Martucci 1968, Peng et al. 1983).

This approach to the classification of the Old World monkeys was also used by Hill (1936, 1954, 1966) and Langer (1988), but it is not the usual one adopted by most authors.

The two groups are usually given subfamilial status, **Cercopithecinae** Gray, 1821 and **Colobinae** Blyth, 1875, within one family **Cercopithecidae** Gray, 1821 (Delson 1973 and 1976, Szalay and Delson 1979, Brandon-Jones 1984, Napier 1985, Strasser and Delson...
1987) - Figure 2.2B. Schultz (1970) drew attention to the uniformity of the cercopithecoid post-cranial skeleton, emphasizing that the homogeneity within the superfamily was greater than that within any other similar grouping of Primates. Schultz's observations thus identify the source of the problems involved in trying to separate the Old World monkeys. Napier concluded that this lack of differences reinforced "...Simpson's decision (1945) to separate the leaf-eaters from the omnivorous Old World monkeys at the subfamily rather than the family level" (1985: Introduction). This view was also accepted by Delson (1973). On the other hand Groves (1989), after some 20 years consideration of this question wrote "... the clarity of the divisions within the superfamily render it profitable to recognise two full families, Cercopithecidae and Colobidae." (page 132).

Delson (1973) divided the Colobinae into two subtribes, Colobina Blyth,1875 for the African genera, and Presbytina Gray,1825 for the Asian (Figure 2.2C). The characters used to separate these subtribes are described by Delson (1973) and Strasser and Delson (1987). They included the geographical isolation of the African and Asian genera, as well as morphological features in this list. Szalay and Delson (1979) commented that "the phyletic geometry" of the Colobinae was more confusing than that of the Cercopithecinae, and that Delson's proposal for two subtribes had not been widely accepted, despite the fact that Hill (1936) had previously suggested that the Asian and African genera should be separated. Groves (1989) expressed doubts about the validity of the subtribe Presbytina, as its members appear to lack derived features and are united only by a set of primitive retentions.

Groves (1989) also divided the Colobidae into two subgroups, but his were quite different from Delson's. He considered that Nasalis larvatus, the proboscis monkey from Borneo, and its close relative Nasalis concolor, the simakobu from the Mentawai Islands, were distinctive enough to form a separate subfamily, Nasalinae Groves, 1989. This division was based on a number of differences, including cranial morphology, karyotype, molar enamel thickness, and the colour of the neonate pelage. Groves concluded that -

The evidence is therefore fairly good that Nasalis is the sister group of the other colobids and should be placed in the subfamily Nasalinae, apart from the other genera, Colobinae. (1989: 148)

All of these proposals for the rankings of the subdivisions of Old World monkeys, and the leaf-eaters in particular, emphasize that any of the decisions reached are very much a question of personal interpretation of the data in the light of a range of morphological, palaeontological and ecological factors, and the need for further research into the problem. The number of genera and species that have been included in the family Colobidae have undergone significant changes
throughout the years. This is illustrated by the information in Tables 1.2 and 2.1, and also by Napier (1985), who in her review of the taxonomy of the family provides a list of the synonyms that have been applied to these animals.

The African colobids are united by three major characters -

1. extreme pollical reduction (Napier 1985),
2. the loss of the facet between the cuboid and the cuneiform (Strasser and Delson 1987),
3. the loss of the insertion of m. flexor fibularis into the hallux (Strasser and Delson 1987).

African colobid fossil history dates back 16-14 million years to the middle of the Miocene (Andrews 1985), and it is generally held that there are two extant genera, Colobus and the more primitive Procolobus (Table 2.1). Napier (1985) and Strasser and Delson (1987) give details of the characters that are used to separate them, including differences in the morphology of the stomach (three chambers in Colobus and four in Procolobus). There is not total agreement on the number of African genera, for Fleagle (1988) divides them into three Colobus, Procolobus and Piliocolobus, while Strasser and Delson (1987) go to the other extreme with one genus Colobus divided into three subgenera (Table 2.1).

The genus Colobus Illiger, 1811 contains all of the black and white species from Sub-Saharan Africa (Table 2.2). There were four species, C. polykomos, C. satanas, C. angolensis and C. guereza (Plate 2.1), to which a fifth, C. vellerosus, has been added by Oates and Trocco (1983). C. vellerosus can be separated from the neighbouring C. polykomos on the basis of its call, which is similar to that of C. guereza, and they also have similar pelage colour patterns.

For Groves (1989) the olive colobus (Procolobus) and the red colobus (Piliocolobus) monkeys are subgenera of the genus Procolobus Rochebrune, 1866-67. He had previously placed the red colobus monkey in the genus Colobus (Thorington and Groves 1970). Napier (1985) has continued to follow Thorington and Groves, although she gives an outline of characters that support Groves' present stance. Fleagle (1988) separated them into two full genera (Table 2.1). The taxonomic status of the olive colobus, Procolobus (Procolobus) verus Van Beneden, 1838 has not been questioned in the literature, as it is quite distinctive, being the most primitive member of the whole family (Groves 1989). Groves considered that there were four species of red colobus monkeys included in the subgenus Piliocolobus - P. (Piliocolobus) pennantii, P. (Piliocolobus) rufomitratus, P. (Piliocolobus) badius and P. (Piliocolobus) preussi; there is, however, some confusion about this number as Napier (1985) illustrated. She cited two extreme points of view - the more traditional one of one species.
Colobus (Piliocolobus)badius, with fourteen subspecies (Rahm 1970), compared with Dandelot's (1971) view of eight species of red colobus monkeys. Napier, herself, recognized only two species C. (Piliocolobus)badius and C. (Piliocolobus)kirkii, with the remainder of Groves' species being considered by her to be subspecies of C. (Piliocolobus)badius.

The Asian Colobidae form a much less homogeneous group than the African genera. They can be divided into two groups, firstly the leaf-monkeys and the langurs and, secondly, the odd-nosed monkeys. The two groups differ from each other in a number of features, including cranial morphology, limb proportions and the form of the stomach. It has four chambers in all of the genera of odd-nosed monkeys that have been studied, and three in the langurs and leaf-monkeys. The knowledge of the evolutionary history of this group is not as detailed as that of the African colobids (Hooijer 1962, Szalay and Delson 1979, Groves 1989). There are far more extant colobid species in this region than there are in Africa.

The traditional approach to the taxonomy of the leaf-monkeys and langurs has been to include them in a single genus. At first this was Simia Linnaeus, 1758, but as it contained all of the Old World monkeys, it was split up and then dropped altogether. Those species with complex stomachs were assigned to the genus Semnopithecus Desmarest, 1822. Later, Pocock (1928) placed them all in the genus Pithecus Cuvier and E. Geoffroy, 1795 and this was also used by Chasen in 1940. Pithecus was suppressed in Opinion 114 of the International Committee of Zoological Nomenclature (Ellerman and Morrison-Scott 1951), as the type specimen Simia veter, described by Linnaeus, was not an Asian colobid. If all of these monkeys are to be included in one genus it would have to be Presbytis Eschscholtz, 1821, as it predates Semnopithecus by a year. This approach is still in use and has been widely accepted by a number of authors (Table 2.1), as well as in the earlier works of Ellerman and Morrison-Scott (1951), and Napier and Napier (1967). Pocock (1928) divided these monkeys into three subgroups on the basis of the colour of the pelage of the neonate. These were -

1. the Pithecus entellus group, with black neonates (Plate 2.2).
2. the Pithecus cristatus group, with orange neonates (Plate 2.3).
3. the Pithecus melalophos group, with white neonate which have a darker cruciger pattern down the back and across the shoulders (Plate 2.4).

In 1936 Hill gave each of these groups generic status and divided the entellus group into two, adding a fourth genus. His genera were -

1. Presbytis Eschscholtz, 1821 for the melalophos group
   (white neonates with the cruciger pattern).
2. *Trachypithecus* Reichenbach, 1862 for the *cristatus* group (orange neonates).

3. *Semnopithecus* Desmarest, 1822 for the *entellus* group, with black neonates. Hill recognized several species in this genus, which is now confined to one *S. entellus* (Napier 1985).


Since then various authors have used different combinations of these genera. Hooijer (1962) and Medway (1970) recognised two genera in Southeast Asia, *Presbytis* and *Trachypithecus*, as they believed that these were based on clear differences in morphology and neonate colour. Brandon-Jones (1984) also recognized two genera, but these were *Presbytis* for the *melalophos* group and *Semnopithecus* for the remainder. Roomwal and Mohnot (1971) and Fleagle (1988), with Napier (1985), are among those who have retained *Presbytis* as the generic name for all Asian colobids, with the exception of the odd-nosed species. The generic names used in five recent publications are compared in Table 2.1. Groves' decision, in 1989, to allocate these colobids to three separate genera - *Presbytis*, *Trachypithecus* and *Semnopithecus* - was based on the differences in neonate colour and cranial morphology.

The genus *Presbytis, sensu stricto*, is confined to the *melalophos* group (Groves 1989) and is considered to be monophyletic (Pocock 1934, Hill 1939, Hooijer 1962, Thorington and Groves 1970, Groves 1989). It contains eight species (Figure 2.1), that are restricted in distribution to Malaysia and Western Indonesia (Table 2.2). The members of this genus are characterized by their exceptionally thick dental enamel, short faces, a lack of supra-orbital ridges and a larynx that is reduced in size (Groves 1989). *P. femoralis* (the species studied in this thesis), long regarded as a subspecies of *P. melalophos* (Napier 1985), was given full specific status by Wilson and Wilson (1976) on the basis of differences in their calls. *P. melalophos* was found to be restricted to Sumatra, while *P. femoralis* (Plate 2.4) was more widespread, being found in peninsular Malaysia, Sumatra and Borneo (Groves 1989). The species of *Presbytis* from Java (as well as Borneo and Sumatra) was previously known as *P. aygula*. A change had to be made when it was found the name *Simia aygula* Linnaeus, 1758 was based on a description of a macaque (Napier and Groves 1983); the correct name for this species is *Presbytis comata* (Desmarest, 1821). Apart from these changes, there is general agreement about the other members of this genus.
Groves (1989) included the *cristatus* group, with the langurs that Hill (1936) ascribed to the genus *Kasi*, in the genus *Trachypithecus*. There are nine species in this genus (Figure 2.1), which are widespread in their distribution. *T. vetulus* (Plate 2.4) and *T. johnii* (Plate 1.4) form an isolated group in Sri Lanka and southwestern India, while the others extend from Bhutan through Burma, Indochina, southern China to Malaysia and Indonesia (Table 2.2). They are set apart from *Presbytis* by cranial and dental features and neonate colour (Napier 1985). Hill (1936) proposed that both *T. vetulus* and *T. johnii* should be included in the genus *Kasi*, which was closely related to both *Trachypithecus* and *Semnopithecus*. This genus was restricted in its distribution to the southern-most tip of the Indian Subcontinent, where it was sympatric with *Semnopithecus entellus*. He also reported that grey neonates were common to both Indian species of *Trachypithecus*. This has been substantiated by Rudran (1979) for *T. vetulus*, but there is some confusion in the literature about *T. johnii*. Oates (1982) reported that the neonates in the brown morph of *T. johnii* had reddish-brown fur, and Roonwal and Mohnot (1977) also described them as being reddish-brown and black. It would seem that the neonate colour in *T. johnii* could be a darker variation of the more brightly coloured eastern (non-Indian) members of the genus, or even midway between that of *S. entellus* and *Trachypithecus* in general. These two species are considered to be the most primitive members of the genus (Brandon-Jones 1984, Groves 1989) and it would seem that more data are needed to clarify their relationship to the other members of the genus. Pocock (1928) and Weitzel (1983) considered *Kasi* to be a subgenus of *Trachypithecus*.

*Semnopithecus entellus*, the sacred langur of India, is the only member of this genus (Napier 1985 and Groves 1989). It has been divided into 15 (Napier 1985) or 16 subspecies (Roonwal and Mohnot 1973), which separate into southern and northern groups. *Semnopithecus* is closely related to *Trachypithecus*. They differ from each other in aspects of cranial morphology and neonate colour (Napier 1985, Groves 1989).

The odd-nosed monkeys (excluding the members of the genus *Nasalis*) of the subfamily Colobinae are separated from the other genera by features of cranial and facial anatomy (Napier 1985, Groves 1989), their four-chambered stomachs (Holihn 1971, Peng et al. 1983) and by differences in limb proportions (Fleagle 1988). They are restricted in their distribution to Indochina, and southern China (Table 2.2), and are usually included in the genus *Pygathrix* E. Geoffroy, 1812 (Table 2.1) with two subgenera *Pygathrix* and *Rhinopithecus* (Groves 1989). In *P. (Pygathrix) nemaeus* Linnaeus, 1771, the only member of the first subgenus, the distinguishing flaps on the upper borders of the nostrils lie flat, while in the second subgenus *Rhinopithecus* they stand erect (Napier 1985). Four species - *avunculus*, *roxellana* (Plate
2.5), *brelichi* and *bieti* - are included in this subgenus by Brandon-Jones (1984) and Groves (1989). These authors also considered that *avunculus* is the sister species of the group containing the other three from southern China. Recent work (Peng et al. 1983) has substantiated the presence of three species of snub-nosed monkeys in China, rather than two, and they also give them full generic status. Napier (1985) and Fleagle (1988) consider *bieti* to be a subspecies of *roxellana*. *P. (Rhinopithecus) avunculus* comes from the tropical forests of Vietnam, and was placed by Pocock (1934) in a separate genus *Presbytis* on the basis of minor differences in the bones of the hand. Groves (1970) noted its close relationship to *P. (Rhinopithecus) brelichi*, and placed it in the same subgenus.

The Nasalinae are considered by everyone, with the exception of Groves (1989), to be members of the odd-nosed group of Asian colobids. Groves (1970 and 1989) believed that this subfamily contained one genus *Nasalis* E. Geoffroy, 1812, with two species *Nasalis larvatus* van Wurmb, 1781 and *N. concolor* (Miller, 1903). Prior to 1970 *N. concolor* was the only member of the genus *Simias*, but Groves thought that it had enough in common with *N. larvatus* to include it in the same genus. There is a creamy-fawn morph of *N. concolor* that is very like *N. larvatus*, and there are also similarities in hair-banding patterns, cranial morphology and limb proportions (Groves 1989). The nose of the adult *N. concolor* is very like that of the juvenile *N. larvatus*, a fact that Groves also considered to be important. Napier (1985) expressed uncertainty about this inclusion, mainly because of the extreme specialization of the nose in adult males of *N. larvatus* and she retained the genus *Simias*, as did Fleagle (1988) - Table 2.1.

The taxonomy of the whole family is set out in Figure 2.1, and for clarity and consistency this scheme is adhered to throughout this study of stomach anatomy. It is possible for confusion to arise very easily, if a taxonomic basis is not established in this way, using the most recent information available. There are a number of examples that can be used to illustrate this point. The most recent is Langer (1988), who considered that he had two specimens of one species, *Colobus abyssinicus uellensis* and *C. abyssinicus cottoni*. These are in fact two different species: *C. guereza occidentalis* (= *C. abyssinicus uellensis*), which has a wide distribution from eastern Nigeria, the Cameroon to Zaire, and *C. angolensis cottoni* (= *C. abyssinicus cottoni*), which is restricted to north-eastern Zaire (Napier 1985). They are separated from each other by the Zaire River and Napier (1985) noted that they could be distinguished on the basis of pelage differences. Langer (1988) dissected mostly foetal and very young juvenile specimens and this can present problems when comparing them with adults, for the coat colour changes with increasing age, as does the form of the stomach (Hill 1954, Kuhn 1964). On the positive side, these findings of Langer's do confirm that there are generic similarities in stomach morphology
among the Colobidae. Salmon (1893) provides another example of this confusion, for it is difficult to be sure, from the information provided, that *Cercopithecus fuliginosus* is a colobid at all.
### Taxonomy of the Colobidae (extant species only)

**Order Primates Linnaeus, 1758**
- **Infra-order Catarrhini E. Geoffroy, 1812**
- **Superfamily Cercopithecioidea Gray, 1821**
- **Family Colobidae Blyth, 1875**
- **Subfamily Colobinae Gray, 1812**

#### Genus *Colobus* Illiger, 1811
- *Colobus polykomos* (Zimmerman, 1780)
- *Colobus velilerosus* (L. Geoffroy, 1830)
- *Colobus angolensis* Sclater, 1860
- *Colobus guereza* Ruppell, 1835
- *Colobus satanas* Waterhouse, 1838

#### Genus *Procolobus* Rochebrune, 1866-7
- **Subgenus *Procolobus* (Rochebrune, 1866-7)**
  - *Procolobus (Procolobus) verus* Van Benedin, 1838
- **Subgenus *Piliocolobus* (Rochebrune, 1866-7)**
  - *Procolobus (Piliocolobus) badius* (Kerr, 1792)
  - *Procolobus (Piliocolobus) pennantii* (Waterhouse, 1838)
  - *Procolobus (Piliocolobus) rufoventratus* (Peters, 1879)
  - *Procolobus (Piliocolobus) preussi* (Matschie, 1900)

#### Genus *Presbytis* Eschscholtz, 1821
- *Presbytis melalophos* (Raffles, 1821)
- *Presbytis comata* (Desmarest, 1822)
- *Presbytis frontata* (Müller, 1838)
- *Presbytis hosei* (Thomas, 1889)
- *Presbytis potenziani* (Bonaparte, 1856)
- *Presbytis rubicunda* (Müller, 1838)
- *Presbytis thomasi* (Collett, 1839)
- *Presbytis femoralis* (Martin, 1838)

#### Genus *Trachypithecus* Reichenbach, 1862
- *Trachypithecus auratus* (E. Geoffroy, 1812)
- *Trachypithecus cristatus* (Raffles, 1821)
- *Trachypithecus francoisi* (Poursargues, 1898)
- *Trachypithecus geei* Gee, 1956
- *Trachypithecus obscurus* (Reid, 1837)
- *Trachypithecus phayrei* (Blyth, 1847)
- *Trachypithecus pileatus* (Blyth, 1843)
- *Trachypithecus johnii* (Fischer, 1829)
- *Trachypithecus vetulus* (Erxleben, 1777)

#### Genus *Semnopithecus* Desmarest, 1822
- *Semnopithecus entellus* (Dufresne, 1797)

#### Genus *Pygathrix* E. Geoffroy, 1812
- **Subgenus *Pygathrix* E. Geoffroy, 1812**
  - *Pygathrix (Pygathrix) nemaeus* (Linnaeus, 1771)
- **Subgenus *Rhinopithecus* (Milne Edwards, 1872)**
  - *Pygathrix (Rhinopithecus) avunculus* (Dollman, 1912)
  - *Pygathrix (Rhinopithecus) roxellana* (Milne Edwards, 1870)
  - *Pygathrix (Rhinopithecus) brelichi* (Thomas, 1903)
  - *Pygathrix (Rhinopithecus) bieti* (Milne Edwards, 1897)

#### Subfamily Nasalinae Groves, 1989
- **Genus *Nasalis* E. Geoffroy, 1812**
  - *Nasalis larvatus* (Wurmb, 1784)
  - *Nasalis concolor* (Miller, 1903)
FIGURE 2.2
SUBDIVISIONS OF THE SUPERFAMILY CERCOPITHECOIDEA, WITH PARTICULAR REFERENCE TO THE LEAF-EATING GROUP OF OLD WORLD MONKEYS.


```
  COLOBINAE
   /\NASALINAE
   \/<CERCOPITHECIDAE
       \/
       CERCOPITHECOIDEA
       <
       CERCOPITHECIDAE
       /
       CERCOPITHECOIDEA


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  COLOBINAE
   /\CERCOPITHECINAE
   \/<CERCOPITHECIDAE
       \/
       CERCOPITHECOIDEA

C. AFTER DELSON (1973).

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```
  COLOBINAE
   /\PRESBYTINA
   \/<CERCOPITHECINAE
       \/
       CERCOPITHECOIDEA

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TABLE 2.1
A comparison of the colobid generic names used by authors of recent publications with those used by Groves (1989) and in this thesis.

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<td><strong>Southern China on border with Vietnam; high conifer forests</strong></td>
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<td><strong>Mentawai Islands; rain- and mangrove - forests</strong></td>
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PLATE 2.1 *Colobus guereza*
This photograph shows the spectacular pelage and the characteristic facial profile of these colobids. These animals, in the Melbourne Zoo, were resting and grooming in the early afternoon.
PLATE 2.2A Infant coloration in Asian colobids: *Semnopithecus entellus* (*entellus* group)
A group of females with black neonates in the Mandore Gardens, Jodhpur.

PLATE 2.2B Infant coloration in Asian colobids: *Trachypithecus auratus* (*cristatus* group)
This female is one of a colony in the Melbourne Zoo. The orange pelage of the infant she is holding is typical of the members of this genus. In this infant the head and shoulders are just beginning to darken.
PLATE 2.2C. Infant coloration in Asian colobids: *Presbytis melalophos* (*melalophos* group)

The neonate shows the characteristic pattern for this genus, which is white overall with the darker cruciger pattern on the back, head and shoulders.

(Photo: from the cover of *Zeitschrift des Kolner Zoo* Vol 1.20, 1979)
PLATE 2.4a *Presbytis femoralis*
The grey form of the banded leaf-monkey from the Malay Peninsula.
(Photo: Kavanagh 1983)

PLATE 2.3b *Presbytis femoralis*
A juvenile of the dark form from Sumatra.
(Photo: C.P. Groves)
PLATE 2.4 *Trachypithecus vetulus*
This pair of purple-faced langurs have been in the Adelaide Zoo (South Australia) for a number of years.

PLATE 2.5 *Rhinopithecus roxellana*
Male and female golden snub-nosed from China.
(Photo: postcard from Singapore Zoo)
Chapter 3

Nomenclature for use in descriptions of Colobid gastric anatomy

The general need for standardization of anatomical nomenclature has been discussed for many years (Grossman 1958); Habel (1965), in a review of the nomenclature used for describing the ruminant stomach based on recommendations from the International Committee on Veterinary Nomenclature (ICVAN), wrote that -

... revision is necessary ... when it is discovered that the same structures have received different names in different species, or in different countries, or when new anatomical studies demonstrate that the old system of nomenclature is no longer consistent with the facts. (1965: 15)

Such trends can be seen in the literature on the colobid stomach (Table 3.1), and this quotation emphasises two important points, which are applicable to the present situation. Firstly, the need to arrive at some consistent standard of nomenclature and, secondly, the need to maintain the awareness that "no system of scientific nomenclature can be considered complete and permanent as long as research is in the field continues" (ICVAN 1973:XII).

The second edition of the *Nomina Anatomica Veterinaria* by ICVAN was published in 1973. In the Introduction the Committee provided a set of guidelines which they had followed in its preparation. In brief summary, these were -

1. Where possible an anatomical concept should be designated by a single term, so that such terms are easy to remember and have instructional and descriptive value, i.e. they should be as short and as simple as possible.

2. Anatomists are free to translate the terms from Latin into their own language.

3. Structures that are closely related should have similar names, and differentiating adjectives should in general be opposites.

4. Terms derived from proper names should not be included.

This standardized nomenclature was primarily for use in describing the anatomy of domestic animals; Richardson (1980), however, created a precedent for its wider application when he used this system in his description of the stomach of the Tammar wallaby, *Macropus eugenii*. Details of the nomenclature are given in Figure 3.1 and will provide the basis for descriptions in this thesis. There are slight differences, as the regions of the stomach in colobids are not the same as those in ruminants (Langer 1988).

Following the example of Keith and Wood Jones (1901) and Napier and Napier (1967), it can be argued that the basic plan of the stomach of most primates is tripartite, and this reaches its extreme development in the complex stomachs of the Colobidae. Langer (1988) calls this type of
stomach plurilocular, when compared with the other type of primate stomach, which is unilocular as it has only "a simple chamber" (Langer 1988). He defines a plurilocular stomach as one "in which the lumen is subdivided by folds into two or more chambers" (page 31). In the colobid stomach, with the possible exception of the fourth chamber or praesaccus, the regions are not separated by marked folds like the different compartments in the stomachs of ruminants and some other herbivores (Langer 1988). Separation is achieved through narrowing of the lumen and by distance. The more literal meaning of "pluri-locular", as many spaces or chambers is probably better for the colobid stomach.

In the colobids the oesophagus opens into a large sacculated region, the saccus gastricus of Hill (1958) and Kuhn (1964) (Figure 3.2A), which acts as a storage region for recently ingested food and as a fermentation chamber, where symbiotic bacteria break down cellulose into volatile fatty acids and other organic compounds that are important in the metabolism of these monkeys (Bauchop 1978a, Kuhn 1964, Peng et al. 1983). The saccus gastricus opens into the middle intestiniform or tubular portion, called by Kuhn (1964) and Langer (1988) the tubus gastricus (Figure 3.2). Fermentation continues in the cranial two-thirds of this region and normal gastric digestion occurs in the caudal third. In this last region the glandular structure of the mucosa changes from mucus-secreting cardiac glands to enzyme-secreting oxyntic glands (Kuhn 1964). These regions are shown diagrammatically in Figure 3.3A. The pronounced sacculations, or haustra, in the walls of these two regions are formed by two taeniae, which run along the greater and lesser curvatures (Figure 3.2C). The canalis gastricus of Ayer (1948), Hill (1952) and Kuhn (1964) is found on the inner surface of the stomach wall, immediately beneath the taenia of the lesser curvature. When closed this canal forms a hollow tube for the transport of liquids, that by-passes the fermentation areas and empties directly into the the caudal part of the tubus gastricus (Kuhn 1964). The tubus gastricus opens directly into the pars pylorica (Kuhn 1964, Langer 1988), which is separated from the duodenum by the pyloric sphincter (Figure 3.2C). The pars pylorica is smooth-walled as muscle fibres from the taeniae fan out to form a continuous layer (Langer 1988). In three genera, Pygathrix (Pilliet and Boulart 1898, Hollihn 1971, Peng et al. 1983), Nasalis (Berengberg-Gossler 1911, Duckworth 1915, Hollihn 1971) and Procolobus (Hill 1952, Kuhn 1964, Langer 1988), a fourth chamber has been described. This is a diverticulum from the first chamber, the praesaccus of Kuhn (1964); it lies dorsal to the saccus gastricus (Figure 3.2B). This system of nomenclature was first used in full by Kuhn (1964), and partially by Hill (1952), in their important works on the anatomy of the colobid stomach.

One change needs to be made to the scheme, and that is the renaming of the canalis gastricus. In
the *Nomina Anatomica Veterinaria* (ICVAN 1973) it was noted that a "canal" in anatomical terminology is a tubular duct. The term *sulcus ventriculi*, or gastric groove, is more appropriate for the "canalis gastricus" (ICVAN 1973). In ruminants the original term used for the sulcus was "Magenrinne" or stomach groove (ICVAN 1973). Polack (1908) used this term in her descriptions of colobid stomachs. In other papers on colobids it was called the "Magenstrasse" or stomach street (Table 3.1), which emphasizes that it was a groove rather than a tubular structure. For the above reason *sulcus ventriculi* should be used in preference to *canalis gastricus*, following Langer's example (1988). Figure 3.1 summarizes the nomenclature that ICVAN (1973) recommended for use when describing the anatomy and histology of the stomach, plus giving the specialized terms that are needed for the colobid stomach.

A number of other terms have been used for the parts of the colobid stomach (Table 3.1) and some of these have led to confusion, which appears to have arisen from the use of -

1. **the same terms that are used for the ruminant stomach**

   These include the rumen or paunch (Pilliet and Boulart 1898) and oesophageal groove (Berenberg-Gossler 1911). The colobid stomach, while fulfilling a similar physiological function to the ruminant stomach, is quite unlike it anatomically and histologically (Langer 1988). For example the first parts of the colobid stomach and the *sulcus ventriculi* are lined with a mucus-secreting glandular epithelium, which is quite distinct from the stratified squamous epithelium lining the first parts and the *sulcus ventriculi* of the ruminant stomach (Langer 1988). The term oesophageal groove for the sulcus of ruminants was used to describe its function and as it was lined with stratified squamous epithelium it was thought to have been derived from the oesophagus during development. This is not so and "there is no morphological justification for its use" in either group of animals (ICVAN 1973).

2. **the fundus**

   Keith and Wood Jones (1901), Ayer (1948) and Peng et al. (1983) called the first chamber of the stomach the fundus. In the human stomach the fundus has been defined as "that part of the stomach which is to the left of a line prolonging the abdominal part of the oesophagus" (Keith and Wood Jones 1901: XXXIV) - Figure 3.3A. If this definition is applied to the colobid stomach, the saccus gastricus would be divided into two in a way that would be functionally inappropriate. Romer (1956) defines the fundus as "the expanded middle part of the stomach, between the cardiac region at the proximal end near the heart
and oesophagus, and the distal pyloric region that opens into the duodenum". Romer also noted that "the fundus region of the stomach is characterized by the presence of numerous tubular glands in which are produced digestive enzymes" (1956: 371-372). For the colobid stomach this would refer to the distal part of the tubus gastricus (Figure 3.3). It would be less confusing if this term was dropped.

3. the forestomach (Berenberg-Gossler 1911, Bauchop 1978B)

Langer (1988) in the introduction to his discussion of gut specializations in mammalian herbivores said that the Colobidae had "a well-developed forestomach system" (page 14) where breakdown of cellulose by symbiotic bacteria occurred. The term forestomach is generally applied to all those regions where this fermentation occurs (Romer 1956, Warner and Flatt 1965, Langer 1988) and not to one particular chamber (Berenberg-Gossler 1911). A similar inconsistency arises when colobids are described as "foregut fermenters" (Parra 1978, Bergman 1990). This term is inappropriate as fermentation takes place in the stomach not the foregut, which consists of all parts of the gastro-intestinal tract anterior to the pylorus (Romer 1956). To overcome this problem the gastric fermentation could be used.

4. terms that refer to the saccus gastricus as a blind sac or cardiac pouch

There are a number of variations using very similar terminology (Table 3.1) and these do not give a clear indication of the form of the saccus gastricus, which is a well-defined region (Kuhn 1964, Langer 1988). In other cases the term is applied to the praesaccus (Hill 1952). A number of other monkeys with unilocular stomachs have well-developed fundal regions (Hill 1958) and these have been referred to as "blind sacs" (Burki 1958). The difficulties that can arise in this way have been discussed in relation to Salmon (1893).

The system of nomenclature that was used by Kuhn (1964) in his descriptions of colobid gastric anatomy, with the modification noted above, fulfills the ICVAN criteria and takes into account the unique form of this organ. These terms which are emphasised in bold type in Table 3.1 have been used by many other authors over the years (e.g. Bauchop and Martucci 1968, Hollihn 1971, Chivers and Hladik 1980, Groves 1989), and this has led to clarity in making comparisons with other species, as well as providing a basis for making accurate anatomical descriptions, as Langer (1988) has shown.
Some clarification is also needed for the names of the three types of glands that are found in different areas of the tunica mucosa of the stomach. The mucus-secreting *cardiac glands* are found in the region surrounding the opening of the oesophagus into the stomach in most primates (Grossman 1958, Burki 1958, Ito 1967). The *pyloric glands* are also mucus-secreting and are found in the mucosa of the pars pylorica (Grossman 1958, Ito 1967). The names of these glands describe their distribution and emphasize the slight differences in structure between them, so there is no ambiguity if they are retained (Grossman 1958). It is different with the enzyme- and hydrochloric acid-secreting glands, which have been given a variety of names, including gastric glands, chief glands, principal gastric glands and fundic glands (Grossman 1958, Ito 1967, ICVAN 1973). These terms have been mainly applied to the glands in simple mammalian stomachs, where they are the main glands of the mucosa of the fundus and body (Ham and Leeson 1961, Garven 1965, Kelly et al. 1984) which is the largest part of the stomach (Figure 3.3A).

The situation is different in colobid stomachs, as the largest area of the mucosa is that lining the saccus and the cranial two-thirds of the tubus (Figure 3.3B), and it contains cardiac-type glands (Kuhn 1964, Langer 1988, and this study), i.e. they could be described as the "principal gastric glands" in these monkeys, and are found lining the area that Langer (1988) considered to be equivalent to the fundus. The enzyme-producing glands are restricted in distribution to the mucosa of the caudal third of the tubus gastricus. For these reasons it was decided to adopt the suggestion made by Grossman (1958), that these glands be called *oxyntic* (acid-producing) *glands*. This name was first used by Langley in 1881 to avoid similar ambiguities, and the practice was followed by Ito (1967) in his important study of the mammalian gastric mucosa. The term gastric gland is also confusing and should be avoided, as it could be used as a collective name that would include all the types of glands in the stomach. These terms - cardiac, oxyntic and pyloric - will be used throughout this thesis in all descriptions of the histology of the gastric mucosa.
FIGURE 3.1
Anatomical and histological nomenclature of the mammalian stomach

A. comparison of anatomical position in humans and quadrupeds [after Habel 1965 and International Committee on Veterinary Anatomical Nomenclature (ICVAN) 1973]

<table>
<thead>
<tr>
<th>human nomenclature</th>
<th>veterinary nomenclature</th>
</tr>
</thead>
<tbody>
<tr>
<td>anterior</td>
<td>ventral</td>
</tr>
<tr>
<td>posterior</td>
<td>dorsal</td>
</tr>
<tr>
<td>superior</td>
<td>cranial</td>
</tr>
<tr>
<td>inferior</td>
<td>caudal</td>
</tr>
<tr>
<td>vertical plane</td>
<td>median or sagittal plane</td>
</tr>
<tr>
<td>horizontal plane</td>
<td>transverse plane</td>
</tr>
<tr>
<td>frontal plane</td>
<td>dorsal plane</td>
</tr>
</tbody>
</table>

B. systematic nomenclature for various regions and structures seen in the stomach (after Habel 1965 and ICVAN 1973)

<table>
<thead>
<tr>
<th>Latin</th>
<th>English</th>
</tr>
</thead>
<tbody>
<tr>
<td>ventriculus (gaster)</td>
<td>stomach</td>
</tr>
<tr>
<td>facies parietalis</td>
<td>parietal surface</td>
</tr>
<tr>
<td>facies visceralis</td>
<td>visceral surface</td>
</tr>
<tr>
<td>curvatura ventriculi major</td>
<td>greater curvature of the stomach</td>
</tr>
<tr>
<td>curvatura ventriculi minor</td>
<td>lesser curvature of the stomach</td>
</tr>
<tr>
<td>incisura angularis</td>
<td>angular notch</td>
</tr>
<tr>
<td>pars cardiaca</td>
<td>cardiac part</td>
</tr>
<tr>
<td>ostium cardiacum</td>
<td>cardiac opening</td>
</tr>
<tr>
<td>fundus ventriculi</td>
<td>fundus of the stomach</td>
</tr>
<tr>
<td>incisura cardiaca</td>
<td>cardiac notch</td>
</tr>
<tr>
<td>corpus ventriculi</td>
<td>body of the stomach</td>
</tr>
<tr>
<td>sulcus ventriculi</td>
<td>gastric groove</td>
</tr>
<tr>
<td>pars pylorica</td>
<td>pyloric part</td>
</tr>
<tr>
<td>antrum pyloricum</td>
<td>pyloric antrum</td>
</tr>
<tr>
<td>canalis pyloricum</td>
<td>pyloric canal</td>
</tr>
<tr>
<td>pylorus</td>
<td>pylorus</td>
</tr>
<tr>
<td>ostium pyloricum</td>
<td>pyloric opening</td>
</tr>
</tbody>
</table>

C. systematic nomenclature for the various regions of the colobid stomach (after Kuhn 1964, ICVAN 1973)

<table>
<thead>
<tr>
<th>Latin</th>
<th>English</th>
</tr>
</thead>
<tbody>
<tr>
<td>praesaccus</td>
<td></td>
</tr>
<tr>
<td>saccus gastricus</td>
<td></td>
</tr>
<tr>
<td>tubus gastricus</td>
<td></td>
</tr>
<tr>
<td>pars pylorica</td>
<td></td>
</tr>
<tr>
<td>pyloric antrum</td>
<td></td>
</tr>
<tr>
<td>pyloric canal</td>
<td></td>
</tr>
<tr>
<td>taenia curvaturae minoris</td>
<td></td>
</tr>
<tr>
<td>taenia curvaturae majoris</td>
<td></td>
</tr>
</tbody>
</table>

Continued...
D. histological nomenclature for the structures in the stomach wall (Habel 1985, ICVAN 1973 - English equivalents in parentheses)

- tunica serosa (serous coat)
- tela subserosa (subserosa)
- tunica muscularis (muscular coat)
  - stratum longitudinale (longitudinal layer)
  - stratum circulare (circular layer)
  - m. sphincter pylori (pyloric sphincter)
- fibrae oblique externae (external oblique fibres)
- fibrae oblique internae (internal oblique fibres)
- tunica mucosa (mucous membrane)
- tela submucosa (submucosa)
- pars glandularis (glandular part)
- plica gastricae (gastric folds)
- lamina muscularis mucosae (muscularis mucosae)
- areae gastricae
- faveolae gastricae (pits of gastric glands)
- glandulae cardiaceae (cardiac glands)
- glandulae gastricae (gastric glands)
- glandulae pyloricae (pyloric glands)
- noduli lymphatici gastrici (gastric lymph nodules)

Habel (1965) included the following, which would be applicable to colobid stomachs:

- epithelium
  - simple columnar
  - stratified squamous
- basement membrane
- lamina propria mucosae (lamina propria)

E. modifications to the histological nomenclature for the glands in the stomach wall (after Grossman 1958, Ito 1967 and Kelly et al. 1984)

- cardiac glands
  - mucus-secreting cells, entero-endocrine cells
- oxyntic glands
  - neck, isthmus, base
  - mucus neck cells, parietal cells, zymogenic cells, entero-endocrine cells
- pyloric glands
  - mucus-secreting cells, entero-endocrine cells
A. VENTRAL ASPECT OF THE TRIPARTITE COLOBID STOMACH.

OESOPHAGUS

DIAPHRAGM

SACCUS GASTRICUS

TUBUS GASTRICUS

PARS PYLORICA

DUODENUM

B. LATERAL ASPECT OF THE QUADRIPATITE COLOBID STOMACH.

OESOPHAGUS

SACCUS GASTRICUS

TUBUS GASTRICUS

DUODENUM

PARS PYLORICA

C. THE EXTENDED TRIPARTITE STOMACH.

OESOPHAGUS

SACCUS GASTRICUS

HAUSTRA FORMED BY THE GATHERING OF THE WALL BETWEEN THE TWO TAENIAE

TUBUS GASTRICUS

TAENIA OF THE GREATER CURVATURE

DUODENUM

TAENIA OF THE LESSER CURVATURE WHICH MARKS THE POSITION OF THE UNDERLYING SULCUS VENTRICULI

PYLORIC ANTRUM

PYLORIC CANAL

PARS PYLORICA

FIGURE 3.2
DIAGRAMS OF COLOBID STOMACHS SHOWING THE MAJOR ANATOMICAL FEATURES.
FIGURE 3.3
COMPARISON OF THE TWO FORMS OF CATARRHINE STOMACH, SHOWING THE MAJOR GLANDULAR REGIONS OF THE MUCOSA.

A. IN A UNILOCULAR STOMACH.

B. IN A PLURILOCULAR STOMACH.
TABLE 3.1
A checklist of the names used by various authors for the major anatomical features of the colobid stomach. The names in bold type show how Kuhn's (1964) terminology has been adopted in recent years; apart from the sulcus ventriculi, which is after ICVAN 1973

<table>
<thead>
<tr>
<th>Author</th>
<th>Major Anatomical Feature</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>diverticulum of the cranial portion</td>
</tr>
<tr>
<td>Otto (1825)</td>
<td>blind part of the stomach</td>
</tr>
<tr>
<td>Owen (1833 - 1841)</td>
<td>cardiac blind pouch</td>
</tr>
<tr>
<td>Duvernoy (1834)</td>
<td>cardiac blind sac - upper lobe</td>
</tr>
<tr>
<td>Martin (1837)</td>
<td>upper cardiac pouch</td>
</tr>
<tr>
<td>Hombron and Jacquinot (1845)</td>
<td>cul-de-sac of paunch</td>
</tr>
<tr>
<td>Pillet and Boulart (1898)</td>
<td>first diverticulum or rumen</td>
</tr>
<tr>
<td>Keith and Wood Jones (1901)</td>
<td>first stomach (fundus)</td>
</tr>
<tr>
<td>Polack (1908)</td>
<td>cardia (sac-shaped)</td>
</tr>
</tbody>
</table>

continued...
<table>
<thead>
<tr>
<th>Berenberg-Gossler (1911)</th>
<th>diverticulum of the forestomach</th>
<th>forestomach</th>
<th>middle or digestive part</th>
<th>pylorus</th>
<th>oesophageal groove</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ayer (1948)</td>
<td></td>
<td>fundus</td>
<td>body</td>
<td>pyloric part - antrum and canal</td>
<td>gastric canal</td>
</tr>
<tr>
<td>Hill (1952)</td>
<td>conical dorsal diverticulum</td>
<td>fundus, cardiac region or cardiac sac</td>
<td>middle intestiniform portion</td>
<td>pyloric segment</td>
<td>canalis gasticus or Magenstrasse</td>
</tr>
<tr>
<td>Hill (1958)</td>
<td>blind or fundal sac</td>
<td>saccus gasticus</td>
<td>tubus gasticus</td>
<td>pyloric segment</td>
<td>canalis gasticus</td>
</tr>
<tr>
<td>Kuhn (1964)</td>
<td>praesaccus</td>
<td>saccus gasticus</td>
<td>tubus gasticus</td>
<td>pars pylorica</td>
<td>canalis gasticus</td>
</tr>
<tr>
<td>Hollihn (1971)</td>
<td>praesaccus</td>
<td>saccus gastricus</td>
<td>tubus gasticus</td>
<td>pars pylorica</td>
<td>canalis gasticus</td>
</tr>
<tr>
<td>Peng et al. (1983)</td>
<td>fundus 1</td>
<td>fundus 2</td>
<td>body</td>
<td>pyloric part - antrum and canal</td>
<td>stomach tube</td>
</tr>
<tr>
<td>Suzuki et al. (1985)</td>
<td>saccus</td>
<td>tubus gasticus</td>
<td>pars pylorica</td>
<td>gastric groove</td>
<td>gastric sulcus or sulcus ventriculi</td>
</tr>
<tr>
<td>Langer (1988)</td>
<td>praesaccus</td>
<td>saccus gastricus</td>
<td>tubus gasticus</td>
<td>pars pylorica</td>
<td>sulcus ventriculi</td>
</tr>
<tr>
<td>This Thesis</td>
<td>praesaccus</td>
<td>saccus gastricus</td>
<td>tubus gasticus</td>
<td>pars pylorica</td>
<td>sulcus ventriculi</td>
</tr>
</tbody>
</table>
Chapter 4
The morphology of the stomach in the family Colobidae

In the organs of the body of all mammals structure and function are closely related. The function will dictate the appearance of a particular organ and the relative proportions of the tissues from which they are composed, and vice versa. This is illustrated by the gastro-intestinal tract and its component parts, in particular the stomach, in which morphology is related to the nature of the diet (Chivers and Hladik 1980, Langer 1988) - Table 4.1. The colobids consume large quantities of leaves and other plant parts that contain a high percentage of cellulose and other structural compounds. This presents a problem, for no mammal is known to produce the enzymes necessary for the hydrolysis of these macromolecules (Moir 1968, Langer 1988). The only organisms that do so are certain bacteria and a few species of ciliate protozoans. Relationships have evolved between herbivorous mammals and these cellulolytic micro-organisms, which have become symbionts in their gastro-intestinal tracts, leading to obvious advantages for both (Bauchop 1978A, Bergman 1990). These herbivores in the course of their evolution have developed special compartments in their guts for housing the micro-organisms. The chambers provide the optimum conditions for environmental growth and act as a reservoir for food. In them the micro-organisms are separated from other regions where they would be destroyed by the normal digestive processes. Kuhn (1964) found this destruction of bacteria occurred in Procolobus verus and Procolobus badius, for he saw only bacterial detritus in the chyme taken from the middle region of the tubus, where it would be more acidic due to the presence of secretions from the oxyntic glands. There are two types of these compartments in the mammalian gastro-intestinal tracts -

1. diverticula are found just below the oesophageal opening, above a restricted oxyntic gland area. Such stomachs, called plurilocular by Langer (1988), are seen in a wide variety of herbivorous mammals including ruminants, colobids and macropod marsupials.

2. a well-developed diverticulum or caecum is found at the junction of the ileum and the colon. The caecum is outside the range of secretion and activity of the enzymes of the small intestine. This arrangement is not as efficient as the "stomach method", as valuable nutrients are lost because they cannot be absorbed in the colon. Some of the smaller herbivores overcome this problem by practicing caecotrophy. Only one primate, Lepilemur leucopus, is thought to do this (Hladik 1978), although many of them, including a number of Old World monkeys, have enlarged caeca (Chivers and Hladik 1980).

The gastro-intestinal tract of mammals is a long tube with four layers of tissue in its walls (Figure 4.1), which enable it to perform the many functions associated with the process of
beginning at the lumen or inner surface, the four layers are -

1. **tunica mucosa**, which consists of the epithelial layer with the underlying lamina propria and muscularis mucosae,
2. **tela submucosa** of dense connective tissue,
3. **tunica muscularis** of at least two layers of smooth or visceral muscle fibres,
4. **tunica serosa** of connective tissue covered by the simple squamous epithelium of the peritoneum.

Various areas of the tract have different functions which have led to modifications to this basic structure, especially in the tunica mucosa and the tunica muscularis. Such modifications are particularly evident in the structure of the stomach which is a specialized region between the end of the oesophagus and the beginning of the duodenum (Romer 1956).

The general functions of the stomach are as follows -

1. **motor functions**
   - i. storage of large quantities of food until it can be accommodated further down the tract.
   - ii. mixing of the food with gastric secretions until it forms a semiliquid mass, the chyme. Mixing movements also aid digestion, ensuring that the food particles and enzymes are mixed together.
   - iii. slow emptying of the chyme into the duodenum, at a rate suitable for subsequent digestion and absorption.

2. **secretory functions**
   - i. the cells of the surface epithelium secrete mucus which covers and protects the mucosa.
   - ii. tubular glands in the various regions of the mucosa secrete mucus, hydrochloric acid (HCl) and the enzymes, predominantly the protease pepsin, that is involved in the initial stages of the digestion of the food.
   - iii. endocrine cells in the bases of the glands secrete hormones which stimulate the activities of other parts of the gut.

With the colobid stomach there are additional functions that are associated with their relationship with cellulolytic bacteria, for, despite Hladik's assertion to the contrary (1978), colobid stomachs do not house any ciliates (Kuhn 1964, Bauchop 1978A, Peng et al. 1983).

These additional functions include -

- i. storage and mixing the food with the bacteria.
- ii. physical breakdown of the food into particles that are small enough for the release of
molecules for the bacteria to ferment (Bergman 1990).

iii. provision and maintenance of the correct environment for bacterial growth, metabolism and reproduction.

iv. absorption of the volatile fatty acids (VFA), which are the main products of bacterial metabolism, from the contents of the fermentation chamber. Colobids use these compounds as metabolites (Bauchop 1978A). It seems to me that the removal of these organic acids could have an additional benefit, for absorption of the VFA as they are produced could help to prevent a drop in pH, which would inhibit the fermentation process.

All of these functions are reflected in the structure of the stomach, particularly in the glands of the mucosa and in the arrangement of the smooth muscle layers (Table 4.2 and Figure 4.2). In all mammalian stomachs there are three layers in the tunica muscularis, instead of the two found in other regions of the gut, which emphasizes the importance of its churning function in the physical breakdown of the food. It is common among herbivores with plurilocular stomachs to have a groove, the sulcus ventriculi, connecting the oesophagus to the digestive area (Langer 1988). When the muscular lips of the sulcus close they form a passageway that by-passes the fermentation chambers, taking liquids and easily digested food straight to the enzyme-secreting area. The basic plan of the colobid stomach is tripartite (Keith and Wood Jones 1901, Berenberg-Gossler 1911, Hill 1952), as shown in Figure 4.3B, with a fourth chamber found in three genera (Figure 4.3C).

In the next part of this chapter, the literature describing the stomachs of colobids will be reviewed in detail, as it provides a basis for a better understanding of gastric physiology in the Colobidae (Kuhn 1964, Peng et al. 1983), and of their successful adaptation to life as arboreal folivores of tropical evergreen rainforests. Illustrations from the works of other authors have been used extensively in this chapter to emphasize the points that they made about the anatomical features they were describing. The reason for doing so was based on the concept that developed during this study, that anatomy is a visual science and verbal descriptions with few illustrations lead to ambiguity and confusion. It does not seem that these organs and their component parts can be adequately described without illustrations, and as it was not possible to obtain any more specimens, despite exhaustive searches, this seemed the only way to overcome this problem.
### TABLE 4.1
The relationship between structure and function in the colobid stomach

<table>
<thead>
<tr>
<th>Function</th>
<th>Anatomical Feature Involved</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>storage</strong> of large quantities of food</td>
<td>elastic sacculated walls that expand to provide additional space</td>
</tr>
<tr>
<td>mixing the food with gastric secretions and bacteria; these movements also help with the physical breakdown of the food</td>
<td>external muscle layers and the intermural plexuses</td>
</tr>
<tr>
<td>slowing down the passage of food so that the bacteria have time to work</td>
<td>haustra formed by the longitudinal muscle of the taenia</td>
</tr>
<tr>
<td>movement of food from the oesophageal opening to the pyloric sphincter</td>
<td>external muscle layers and the intermural plexuses</td>
</tr>
<tr>
<td>emptying of the food into the duodenum at a rate suitable for subsequent digestion and absorption</td>
<td>pyloric sphincter</td>
</tr>
<tr>
<td>physical separation of the fermentation chamber from the area where digestion takes place</td>
<td>division of the stomach into a saccus gastricus (and praesaccus) where the bulk of fermentation occurs; the tubus gastricus acts as an intermediate zone - the cephalic two-thirds for fermentation, the caudal third for digestion</td>
</tr>
<tr>
<td>secretion of protective mucus</td>
<td>surface epithelial cells that line the entire lumen; secretions from cardiac and pyloric glands, and mucous neck cells in oxyntic glands</td>
</tr>
<tr>
<td>secretion of enzymes and hydrochloric acid</td>
<td>zymogen and parietal cells in the oxyntic glands</td>
</tr>
<tr>
<td>secretion of hormones which stimulate the secretory and muscular activities of the various regions of the gut</td>
<td>entero-endocrine cells in the bases of the glands, mainly in the pyloric and oxyntic areas; blood in the capillary networks of the wall carrying them to their various target cells</td>
</tr>
<tr>
<td>provision and maintenance of the correct environment for bacterial metabolism, growth and reproduction</td>
<td>secretion of an alkaline mucus by cardiac glands lining the fermentation chamber; removal of short chain fatty acids via capillary networks in the lamina propria</td>
</tr>
</tbody>
</table>
FIGURE 4.1
THE GENERAL STRUCTURE OF THE WALL IN THE MAMMALIAN GASTRO-INTESTINAL TRACT.
FIGURE 4.2A
The basic plan of the colobid stomach related to its function.

<table>
<thead>
<tr>
<th>Oesophagus</th>
<th>Passageway</th>
</tr>
</thead>
<tbody>
<tr>
<td>Praesaccus (if present)</td>
<td>Storage and some fermentation</td>
</tr>
<tr>
<td>Saccus Gastricus</td>
<td>Fermentation and absorption</td>
</tr>
<tr>
<td>Tubus Gastricus</td>
<td>Fermentation</td>
</tr>
<tr>
<td>Cephalic two-thirds</td>
<td>Digestion</td>
</tr>
<tr>
<td>Caudal third</td>
<td></td>
</tr>
<tr>
<td>Pars Pylorica</td>
<td>Passageway</td>
</tr>
<tr>
<td>Duodenum</td>
<td>Digestion</td>
</tr>
</tbody>
</table>

FIGURE 4.2B
Processing of food in the colobid stomach.
FIGURE 4.3
THE BASIC FORMS OF THE STOMACH IN THE MEMBERS OF THE FAMILY COLOBIDAE.

A. THE TRIPARTITE STOMACH.

B. THE QUADRIPARTITE STOMACH.
Section 1. The external morphology of the colobid stomach

1. the position of the stomach in the abdominal cavity
   In adult colobids the stomach is immediately obvious when the abdominal cavity is opened, as it occupies at least half of this area (Polack 1908, Duckworth 1915, Starck 1958, Kuhn 1964, Langer 1988) - Figures 4.4A (Starck 1958) and 4.8 (Duckworth 1915). The saccus gastricus fills the entire cranial part of the cavity, running the full length of the diaphragm, displacing the liver caudally and to the right of the midline (Figure 4.5D - Kuhn 1964). There is a pars affixa attaching the cardiac region of the saccus gastricus to the centrum tendineum of the diaphragm (Figure 4.6 - Langer 1988). The tubus gastricus leaves to the left of the saccus (Figure 4.5D - Kuhn 1964), and then turns slightly dorsally and caudally, before passing over the ventral lower margin of the saccus to the right abdominal wall (Figure 4.4A - Starck 1958). Here the tubus turns dorsally and makes an acute turn to the left at its junction with the pars pylorica. In this region the stomach is S-shaped and the lumen takes a spiral course (Ayer 1948). In Procolobus verus the praesaccus lies dorsal to the saccus gastricus and is in contact with the diaphragm and the left abdominal wall (Langer 1988). The full development of the stomach and the displacement of the liver starts when young colobids begin to ingest solid food (Figure 4.5E and F - Kuhn 1964). Similar changes are seen in the stomachs of young ruminants, when they too begin to eat solid food (Warner and Flatt 1965). The greater omentum is attached to the greater curvature of the stomach and it hangs below the tubus, covering the loops of the intestine (Figure 4.4 - Starck 1958, Figure 4.6 - Langer 1988). The saccus and the tubus are attached to each other by a continuation of the lesser omentum (Starck 1958).

2. the saccus gastricus
   The saccus gastricus, which commences to the left of the oesophagus, is the principal fermentation and storage chamber (Kuhn 1964). It is the largest region of the stomach, holding two-thirds of its total volume (Langer 1988). In the species without a praesaccus, the saccus is spheroidal in form (Hill 19058) and fills the entire space beneath the diaphragm (Figure 4.4 - Starck 1958, Figure 4.5D - Kuhn 1964). In Procolobus verus the saccus is more elongate, and Hill (1952) described it as forming the ventral limb of a U, with the praesaccus forming the dorsal one (Figure 4.7 - Langer 1988). The walls of this first chamber are deeply sacculated, with the haustra being more pronounced on the ventral surface (Ayer 1948, Hill 1952, Kuhn 1964). The haustra and the intervening semilunar folds begin at what Ayer calls the fibromuscular condensations, that are found
dorsal and ventral to the opening of the oesophagus or cardiac orifice and are best seen on
the inner surface (Figure 4.13 - Ayer 1948). The size and number of the semilunar folds
appears to be variable and dependent upon the state of the organ at death (Langer 1988).
Some of these folds are quite deep and this appears to have caused some confusion about the
number of compartments in the stomach. Duverney (1834) described two parts to the
"blind sac" in *Semnopithecus entellus*, which were separated by an intermediate band.
Other authors, in particular Ayer (1948) and Owen (1835), in their detailed descriptions
of the stomach in these species, do not mention such a structure, so it must be presumed
that Duverney was describing an unusually pronounced semilunar fold. Even Langer
(1988) seems to have been caught in this way, for he is undecided whether his specimen of
*Presbytis melalophos* had a praesaccus or not. In the text he says not, but in Table 42 (page
286) he said that it had a praesaccus.

On the left and ventrally the saccus narrows at its junction with the tubus gastricus
(Figure 4.8 - Duckworth 1915, Figure 4.14 - Ayer 1948, Figure 4.5D - Kuhn 1964,
Figure 4.7 - Langer 1988). In *Semnopithecus entellus* Owen (1835) described a
constriction separating these two parts of the stomach and noted that a ring of circular
muscle fibres marked this area. This arrangement of muscle fibres was not mentioned by
any of the other authors, although Hill (1952) and Kuhn (1964) both observed that the
saccus constricted strongly to the right, dorsal and lateral at its junction with the tubus,
forming a distinct upper cavity. The cardiac orifice is located immediately above the
junction of the saccus and the tubus (Figure 4.7 - Langer 1988).

3. the praesaccus

The praesaccus is a diverticulum from the saccus gastricus (Figure 4.7 - Langer 1988),
that terminates either as a "blind conical extremity" in *Procolobus* (Hill 1952) and
It is hardly visible when the abdominal cavity is opened, as it is covered by the more
voluminous saccus (Hill 1952, Kuhn 1964). The walls are thicker than those of the
saccus and are not haustrated according to Kuhn (1964), but there is no general agreement
on this point, as Hill (1952) described it as sacculated in *Procolobus verus*, but less so
than the saccus. The cardiac orifice opens at the apex of the notch separating these two
regions (Hill 1952). The praesaccus seems to function as a preliminary storage area, for
in freshly killed specimens of *Procolobus verus* it contained finely chewed leaf material,
with little fluid (Kuhn 1964).
4. the taeniae of the colobid stomach

These longitudinal bands of smooth muscle fibres from the tunica muscularis are a characteristic feature of the walls of the saccus and tubus and are found opposite each other on the lesser and greater curvatures of the stomach. The taenia curvaturae majoris begins on the left wall of the saccus, at a short distance from the cardiac orifice, running ventrally across the margin of the saccus and then dorsally onto the tubus (Langer 1988). The taenia curvaturae minoris begins at the cardiac orifice and, after a short course over the wall of the saccus, passes to the wall of the tubus. It is much shorter than the taenia of the greater curvature (Owen 1835, Polack 1908, Ayer 1948, Hill 1952). At the junction of the tubus and the pars pylorica the taeniae disappear as the longitudinal fibres fan out forming a complete coat around the last segment of the stomach (Hill 1952, Langer 1988). As the taeniae are elastic and shorter in length than the rest of the stomach wall, so that it becomes pleated or gathered between them, forming the haustra and giving the stomach its colon-like appearance. This is especially noticeable in the tubus gastricus (Hill 1952 and 1958). The haustra develop slowly and increase with age in foetal specimens (Langer 1988). This fact, with the the changing form and position of the stomach in very young colobids (Kuhn 1964), emphasizes some of the difficulties that can arise when dissecting and describing such specimens, as Langer was forced to do; he made the point, however, that the characteristic form of the stomach was evident very early in foetal life, so that differences in gross anatomy between them and adults of the same species may have been relatively minor. Polack (1908), in her description of the stomach of Colobus polykomos, noted the presence of three taeniae - taenia curvaturae majoris, taenia curvaturae minoris and taenia tertia. The last of these ran parallel to the taenia curvaturae minoris along the greater curvature (Figure 4.9 (1) - Polack 1908). In the stomach of Semnopithecus entellus she described a taenia quarta, also on the lesser curvature and parallel to the other two - Figure 4.9 (2). From Polack’s diagrams it would appear that she was describing the ridges that border the sulcus ventriculi (Langer 1988). The taeniae and the haustra that they produce are important in mixing the contents of the saccus and the tubus and in physically breaking it up to form the semiliquid chyme (Kuhn 1964, Langer 1988). These structures also play an important part in slowing the rate of passage of the chyme through these areas.

5. the tubus gastricus

The tubus gastricus, as its name implies, is narrow, elongated and has well-developed haustra formed by the taeniae along the two curvatures (Owen 1835, Duckworth 1915, Kuhn 1964, Langer 1988). The sacculations, which are more marked on the ventral wall
than the dorsal (Ayer 1948), gradually diminish caudally along the tube, disappearing near the junction with the pars pylorica. The tubus commences just to the right of the cardiac orifice and then runs transversely across the middle of the abdominal cavity, making a sharp turn dorsally at the junction with the pars pylorica, near the medial aspect of the liver (Hill 1952, Figure 4.4A - Starck 1958, Figure 4.5D - Kuhn 1964). This region of the stomach is functionally and histologically divided into two sections. The cranial two-thirds are a continuation of the fermentation chamber and have the same mucosal structure as the saccus, while the caudal third is lined with the glands that secrete digestive enzymes and hydrochloric acid (Kuhn 1964, Peng et al. 1983).

6. the pars pylorica

The pars pylorica is separated from the tubus gastricus by a weakly developed circular fold (Hill 1952, Langer 1988). It lies under the transverse colon and disappears under the right caudal margin of the liver (Figure 4.5D - Kuhn 1964). The wall is much thicker than that in other areas as it is completely surrounded by two thick muscle coats, which give the pyloric antrum a smooth external appearance (Figure 4.14 - Ayer 1948). In the terminal part, the pyloric canal, the lumen is constricted by the pyloric sphincter. Its position is marked by a groove on the exterior of the stomach. In the human stomach the sphincter controls the emptying of chyme into the duodenum and the muscles of the antrum wall act as a mill mixing the contents together (Guyton 1976). As these areas have similar structures in these two species of primate, it is reasonable to assume that they perform similar functions. The pyloro-duodenal junction is almost on the medial plane in the abdomen and is hidden behind the tubus gastricus (Hill 1952).
FIGURE 4.4 (from Starck 1958)
The abdominal cavity of *Colobus guereza.*

A. The organs in the cavity.

B. With the small intestine removed to show the caecum, colon and mesenteries.
FIGURE 4.5 (from Kuhn 1964)
The stomachs of *Colobus polykomos* and *Procolobus badius*.

A. Saccus gastricus of *Colobus polykomos*.  
B. Tubus gastricus of *Colobus polykomos*.  
C. Pars pylorica of *Colobus polykomos*.  
D. The abdominal organs of *Colobus polykomos*.  
E. The abdominal organs of an embryo of *Procolobus badius*.  
F. The abdominal organs of a juvenile *Procolobus badius*.  

*Oesophagus*  
*Magenstrasse*  
*Tubus gastricus*  
*Magenstrasse*  
*Gebiet der Hauptdrüsen*  
*Pars pylorica*  
*Saccus gastricus*  
*Omentum minus*  
*Leber*  
*Duodenum*  
*Gallenblase*  
*colon*  
*Saccus gastricus*  
*Tubus gastricus*  
*Pars pylorica*
FIGURE 4.6 (from Langer 1988)

Dorsal aspect of the stomach, the greater omentum, and the diaphragm in three species of Colobidae.

a  
Nasalis larvatus

b  
Presbytis (Trachypithecus) cristatus

c  
Colobus verus

diaphragm
lig. gastrophrenicum
saccus gastr.
praesaccus
omentum majus
spleen
kidney
adrenal

1 cm

1 cm

1 cm
Viscera of a Nasalis monkey (Cercopithecidae): the extraordinarily modified form of the stomach and the consequent displacement of the liver to the right are to be noticed. These features are found throughout the genus Semnopithecus, which includes many species of monkeys found in Asia.
1. stomach; 2. liver; 3. pancreas; 4. spleen; 5. duodenum; 6. caecum.
Section 2. The internal morphology of the colobid stomach

Hill (1958) believed that internally the stomachs of the Colobidae were characterized by four features:

1. The extension of the oesophageal mucosa to a varying extent beyond the cardiac orifice, forming the cardiac shield.
2. The presence of two muscular folds extending from the right of the cardia along the lesser curvature to the tubus gastricus. Between them they form a groove, the sulcus ventriculi.
3. Semilunar folds or septa which are produced by the pleating of the wall between the taeniae of the two curvatures.
4. An abrupt change in the appearance of the mucosa and the folding, as well as the narrowing of the lumen in the pars pylorica, which is due to the change in the thickness of the tunica muscularis.

The presence of these features has been verified by other authors, with the possible exception of the cardiac shield.

Hill placed great emphasis on the importance of the form of the cardiac shield in the different genera, describing them in detail (Figure 4.10 - Hill 1952). In Procolobus verus the cardiac shield was clearly distinguishable from the thinner mucosa of the saccus by its "firm, horny texture, opaque white appearance and rolled margin" (Hill 1952:151). This region was more extensive dorsal to the cardiac orifice, with a small ventral rim and it was slightly wider on the right and left sides of the orifice (Figure 4.10A - Hill 1952). The shield was given a trifoliate appearance by notches on the right and left margins. Hill found similar extensions of the oesophageal mucosa in Colobus guereza and in the Asian genera Semnopithecus, Trachypithecus and Presbytis. In Presbytis (probably P. melalophos) the edges of the cardiac shield were "undermined", so that it could be raised as a flap. Kuhn (1964) described a similar cardiac shield in Procolobus badius. The light-coloured field of oesophageal mucosa extended dorsally around the orifice and it had scalloped edges. These are seen clearly in Figure 4.11, which is from his paper. Kuhn found that there was a long extension of the right side of the field into the saccus gastricus where it overlay the entrance to the gastric sulcus and that the edges of the field were free in the praesaccus. He noted that the form of this area was individually very variable and that this variability was not consistent between species. The glandular mucosa of the stomach wall is rapidly destroyed after death in colobids, while that of the oesophagus is more resistant (Plate 8.32 and Kuhn 1964). Thus the form of the cardiac shield and its detachment might be due to post mortem changes in the two different types of mucosa. This would account for the individual variation observed by Kuhn (1964). Peng et al. (1983) described this area in
Rhinopithecus as being like a begonia leaf in shape and they said it was clearly visible with the naked eye. It stretched dorsally to the dorsal or left lip of the sulcus ventriculi (Peng et al. 1983, Figure 4.12 - Ye et al. 1983). They also described two fibromuscular condensations, like those in Semnopithecus entellus (Ayer 1948), that were found on the right and left sides of the cardiac shield (Figure 4.12 - Ye et al. 1983). It was from these areas that the ridges bordering the sulcus ventriculi arise.

Ayer (1948) gave a detailed description of this region in the stomach of Semnopithecus entellus and he noted that there was a clear line of demarcation between the paler oesophageal epithelium and that of the saccus gastricus. This region was oval in shape, with the cardiac orifice in the ventral part of the field, which was more extensive dorsally (Figure 4.13 - Ayer 1948). The surface was finely wrinkled and there was a prominent dorsal fold which projected into the lumen and partially divided the orifice into two grooves. The left groove led into the saccus gastricus and the right into the sulcus ventriculi, which then passed to the right between the "right horns" of the fibromuscular condensations, dorsal and ventral to the cardiac orifice (Figure 4.13 - Ayer 1948). From here well-developed muscular folds marked the course of the sulcus along the lesser curvature (Figures 4.13, 4.14 and 4.15 - Ayer 1948). Langer did not mention the presence of a cardiac shield in any of the species he studied. This might be a reflection of their young age, or that the structures described by Hill, Kuhn and Peng et al. were the result of degenerative changes in the two different types of mucosa in this region.

The sulcus ventriculi is a characteristic feature of the stomach of all colobids (Hombron and Jacquinot 1845, Polack 1908, Hill 1958, Kuhn 1964, Peng et al. 1983, Langer 1988). It is thought to form a direct passageway between the oesophagus and the lower part of the tubus, probably for the transport of liquids and semiliquid, easily digested food to the oxyntic gland region (Kuhn 1964). Kuhn also suggested that it might be involved in the transport of the gaseous by-products of fermentation to the exterior. In all colobids the sulcus starts to the right of the cardiac orifice and is defined by well-developed fibromuscular ridges or lips throughout its length (Polack 1908, Hill 1958, Kuhn 1964, Langer 1988). There are slight differences in the form of the sulcus in those genera without a praesaccus when compared with those that have one. In those without, the cardia is surrounded by a U-shaped loop, with the fold forming the left branch of the U passing ventrally from the cardiac orifice to the tubus gastricus (Figure 4.16 - Langer 1988). The right ridge comes from the cardia, passes under the left ridge and then continues along the lesser curvature of the tubus, running parallel to the left ridge, so that they form the borders of the sulcus (Figure 4.5A and B - Kuhn 1964, Figure 4.16B - Langer 1988). In the stomach of Procolobus verus, which has a praesaccus, the path of the left ridge is more
complicated than that of the right. It passes straight to the lesser curvature of the tubus, and there is continuity between it and the fold that separates the praesaccus from the saccus gastricus (Figure 4.17 - Langer 1988). This arrangement was not seen in the stomach of *Nasalis larvatus* (Figure 4.18 - Langer 1988), and it is to be wondered if the very young age of the specimen he dissected might have been a contributing factor, as his specimen of *Procolobus verus* was almost adult. The left ridge forms the ventral-most part of the opening between the saccus and the tubus and the sulcus runs perpendicular to this fold, along the lesser curvature of the tubus (Langer 1988). The two ridges or lips bordering the sulcus ventriculi flatten out towards the caudal end of the tubus, at the sharp bend where it turns left, just before the junction with the pars pylorica (Figure 4.9 - Ayer 1948, Figure 4.5B - Langer 1988). The structure of the sulcus was essentially the same in *Rhinopithecus*, except that the dorsal or left lip was lower than the ventral or right one (Figure 4.14 - Ye et al. 1983).

The other permanent folds or ridges that are visible on the interior of the stomach are those separating the various regions from each other. Langer (1988) described a well-defined fold between the saccus and the praesaccus in *Procolobus verus* (Figure 4.17), and a similar structure was seen in the stomach of *Procolobus badius* (Figure 4.13 - Kuhn 1964). Kuhn described two ridges bordering this junction, that stood out in the lumen. They were better defined caudally than cranially. He noted that the opening between the saccus and the praesaccus was smaller in *P._verus* than in *P._badius* and that these folds were similar in structure in both species. There appear to be similar folds in the stomachs of the *Rhinopithecus* species (Figure 4.19 - Ye et al. 1983). There is also a junction fold between the saccus and the tubus, which Hill (1952) felt could form a partial sphincter for separating the two regions. A well-defined fold separates the pars pylorica and the tubus gastricus (Figure 4.5C - Kuhn 1964, Langer 1988).

Internally the wall of the pars pylorica is quite different in appearance from that of the rest of the stomach. The walls are thicker and longitudinal folds lead to a narrowing of the lumen (Owen 1835, Ayer 1948 - Figure 4.9, Kuhn 1964). Kuhn (1964) found that there was a constant fold, which appeared on the first third of the cranio-dorsal side of the pyloric antrum. At the pylorus the powerful sphincter further reduced the size of the lumen (Owen 1835, Hill 1952, Kuhn 1964, Langer 1988).
FIGURE 4.9 (from Polack 1908)
Cross sections of the pars pylorica in *Colobus polykomos* (1) and *Semnopithecus entellus* (2), showing the positions of the taeniae.
*T.c.min.* - taenia curvaturae minoris; *T.c.ma.* - taenia curvaturae majoris; *T.tert.* - taenia tercia; *T.qu.* - taenia quarta.

FIGURE 4.10 (from Hill 1952)
View of the internal appearance of the cardio-oesophageal junction and neighbouring parts of the gastric mucosa in
*A. Procolobus verus; B. Procolobus badius badius; C. Semnopithecus entellus priam.*
FIGURE 4.11 (from Kuhn 1964)
The opening into the saccus gastricus and praesaccus in Procolobus badius

FIGURE 4.12 (from Peng et al. 1983)
The cardio-oesophageal junction in Rhinopithecus.
1. cardiac orifice; 2. right lip of the sulcus ventriculi; 3. left lip of the
sulcus ventriculi; 4. haustra; 5. saccus gastricus; 6. praesaccus; 7.
semilunar fold; 8. right fibromuscular condensation; 9 and 10. left
fibromuscular condensation.
FIGURE 4.13 (from Ayer 1948)
The region of the cardiac orifice in an opened stomach of *Semnopithecus entellus*.
1. folds of the mucous membrane of the fundus; 2. demarcation between the epithelium of the oesophagus and stomach; 3. folds in the cardiac orifice; 4. the prominent dorsal fold; 5. posterior fibromuscular condensation; 6. posterior lip of gastric canal; 7. anterior lip of gastric canal; 8. continuation of 2 in the floor of the gastric canal; 9. anterior fibromuscular condensation.

FIGURE 4.14 (from Ayer 1948)
The stomach of *Semnopithecus entellus* opened along the greater curvature.
1. oesophagus; 2. cardiac orifice; 3. fundus; 4. proximal part of body; 5. posterior lip of gastric canal; 6. distal part of the body; 7. pyloric antrum; 8. longitudinal fold in the pyloric canal; 9. pyloric canal; 10. anterior lip of gastric canal.
FIGURE 4.15 (from Ayer 1948)
Views of the interior of the fundus of the stomach of *Semnopithecus entellus*, after it had been inflated and dried. An oblique sagittal section divided it into a left part containing part of the fundus (upper figure) and a right part containing the rest of the stomach.

1. posterior saccule of the fundus; 2. the extreme left saccule of the fundus; 3. greater omentum attached to the greater curvature; 4. oesophagus; 5. gastric canal; 6. aperture between fundus and body; 7. body; 8. pyloric part; 9. line of attachment of greater omentum.
A. Right aspect of the opened stomach of a juvenile Colobus abyssinicus

- ligamentum hepatoduodenodenale
- liver (schematic)
- pars pylorica
- omentum minus
- ligamentum hepatogastricum
- taeniae curvatarum majoris
- plicae semilunares
- saccus gastricus
- right lip of sulcus ventriculi
- left lip of sulcus ventriculi
- tubus gastricus

B. Left aspect of the stomach in a juvenile Colobus abyssinicus

- squamous epithelium
- cardia
- plica semilunaris
- saccus gastricus
- tubus gastricus
- spleen

Figure 4.16 (from Langer 1988)
A. Right aspect of the opened stomach of a juvenile Colobus. The liver has been pushed dorsally and its visceral facies (represented schematically) can be seen. The curved white arrow into the saccus gastricus.
B. The left aspect of the same organ. The saccus gastricus is opened and the red arrow points into the gastric tube.
O: oesophagus; D: duodenum.
Figure 4.17 (from Langer 1988)
Left view into the opened saccus gastricus of an adult Procolobus varus. The black arrows indicate the oesophagus and the cardia, the white arrow points into the extensive praesaccus. O: oesophagus.
Figure 4.18 (from Langer 1988)
Right aspect of a stomach of a foetal *Nasalis larvatus*. The ventricular groove can be seen in the proximal part of the opened gastric tube. The lips of the groove can be followed to the sharp bend of the tube (between the two asterisks). The white arrow points into the saccus gastricus. The taeniae cannot be clearly distinguished in this specimen. O: oesophagus; D: duodenum.

**Figure 4.19 (from Ye et al. 1983)**
The interior of the stomach of *Rhinopithecus*.
1. cardiac shield; 2. right lip of sulcus ventriculi; 3. left lip of sulcus ventriculi; 4. haustra; 5. saccus gastricus (fundus I); 6. praesaccus (fundus II); 7. oesophagus; 8. sulcus ventriculi; 9. duodenum; 10. pyloric canal; 11. longitudinal folds in pyloric canal; 12. pyloric antrum; 13. oxyntic gland area.
Section 3. The external musculature of the wall of the colobid stomach

The arrangement of the layers of smooth muscle fibres in the tunica muscularis is very characteristic and underlies many of the morphological features described, as well as the functional differences between regions. Primate stomachs have three layers of fibres in the tunica muscularis and traditionally these have been defined, on the basis of the direction of the fibres, as the outer longitudinal layer (on the serosa side), the middle circular layer, and the innermost oblique layer - Figure 4.1 (Birmingham 1900, Ham and Leeson 1961, Garven 1965). As these layers are modified in the colobid stomach, Langer (1988) divided them into two groups -

1. the superficial layer

The outermost layer of longitudinal fibres is contracted into the two taeniae that follow the greater and lesser curvatures (Figure 4.20 - Langer 1988). These disappear at the junction of the tubus and pars pylorica, where the fibres fan out and completely encircle the caudal part of the stomach (Figure 4.20 - Langer 1988). Langer found that there were slight differences between species in the form of the taeniae. They were "rich in connective tissue and muscle" in Procolobus verus and Colobus guereza. In Colobus angolensis he found that the taenia curvaturae majoris was expanded where the gastrolienal ligament attached to the stomach wall. Langer felt that this was equivalent to a similar expansion in the same taenia in the stomach of Semnopithecus entellus described by Ayer in 1948 (Figure 4.21).

Peng et al. (1983) noted that in Rhinopithecus the taenia curvaturae majoris was wider and not as strong as that of the lesser curvature.

2. the deep layers

There are two deep layers, one of circularly arranged fibres and the other of oblique. The cardiac orifice is surrounded on the left by a loop of circular muscle fibres (Figure 4.21 - Ayer 1948, Figures 4.20 and 4.22 - Langer 1988), the arms of which extend along the lesser curvature, forming the right and left ridges that border the sulcus ventriculi. The floor of this groove is formed by circular muscle fibres (Figure 4.23 - Polack 1908). In the tubus gastricus the circular muscle fibres run from the lesser curvature to the greater (Ayer 1948) and they completely surround the wall of the pars pylorica, which has only two layers in the tunica muscularis, like the duodenum (Figure 4.20 - Langer 1988). Langer described the circular muscle layer in the saccus as being "incompletely differentiated" (Figure 4.20). The overall distribution of oblique fibres is somewhat different, and on this basis Langer divided the stomach into the corpus ventriculi, which
consisted of the caudal part of the saccus and the tubus, and the fornix, the cranial part of the saccus (Figure 4.20 - Langer 1988). In the corpus ventriculi the oblique fibres joined those of the ridges bordering the sulcus, while in the fornix they did not. The praesaccus, if present, is found in the fornalical region (Langer 1988).

Langer's findings confirm those of Ayer (1948) with *Semnopithecus entellus* and Peng et al. (1983) described a similar feature in the musculature of the stomach of *Rhinopithecus*. There was one difference in this subgenus, however, and that was that the oblique fibres were found only in the ridges bordering the sulcus ventriculi. Kuhn (1964) wrote that the longitudinal bundles forming these ridges constituted a fourth layer, overlying the others on the lumen side. Although both Ayer (1948) and Peng et al. (1983) noted that the two fibromuscular condensations on the dorsal and ventral sides of the cardiac orifice were formed from circular muscle fibres, neither Kuhn (1964) nor Langer (1988) mentioned them. No details, apart from the lack of taeniae, were given about the musculature of the praesaccus (Kuhn 1964, Peng et al. 1983, Langer 1988).

The arrangement of the muscle fibres in the layers of the tunica muscularis of the various areas of the colobid stomach is closely correlated with their functions. The sacculated walls of the of the saccus and the tubus allow considerable expansion and thus the storage of large quantities of food. The concentration of longitudinal fibres into the taeniae and the resultant pleating of the walls between them has two effects on the function of the saccus and the tubus that can be deduced by looking at similar structures in the human colon, which is also haustrated by taeniae (Guyton 1976), and by comparisons with the data from herbivores with similar stomachs (Langer 1988).

It is thus probable that slow, ring-like waves of contraction pass along the stomach from the cardia to the end of the tubus. These would involve the combined contraction of both circular and longitudinal fibres and between them the unstimulated portions would bulge out into haustra (Guyton 1976, Langer 1988). These kneading movements would result in the gradual breakdown of the ingested food and the mixing of the contents with bacteria. In addition the chyme would be brought into contact with the mucosa so that absorption of metabolites could occur more readily and secretions from the cardiac glands could be mixed with the chyme. Both of these things could play an important part in maintaining the pH at the required level, for most of the products of bacterial fermentation are organic acids (Bauchop 1978A). That the secretion from the cardiac glands in this area is involved in pH regulation is purely conjecture based on the work of Ohwaki et al. (1974), as nothing is
known of the chemical composition of their secretions or about the method of pH regulation in the saccus. The passage of food through this haustrated area would be slow, as in the colon (Guyton 1976), which would allow sufficient time for the bacteria to break down the cellulose in the food consumed. This slow rate of digestion of the food in the stomach can be correlated with feeding behaviour and daily activity patterns in colobids. They have two feeding peaks, one in the early part of the morning and the other late in the afternoon. Rose (1978) observed this in *Colobus guereza* and he noted that their life styles were characterized by energy conservation, i.e. they move less during the day and had concentrated bouts of feeding with the major part of the day spent resting. This is in marked contrast to cercopithecids, like baboons, which spend a much greater amount of their day in feeding and ranging activities (Rose 1978). Rose felt that this was related to their ruminant-like physiology, with the rapid accumulation of food that could be fermented over a longer period of time, and to "digestive-efficiency", rather than low energy returns. Similar patterns of behaviour have been noted in other colobid species (Ripley 1970, Struhsaker and Oates 1975). Colobids appear to be rather more lethargic than cercopithecids living in the same forest areas (Rose 1978). In the pars pylorica the arrangement of muscle layers is similar to that in the human stomach which suggests that peristaltic waves that originate in this region mix the food with digestive enzymes and are also responsible for the opening of the pyloric sphincter (Guyton 1976), which releases small amounts of chyme into the duodenum.
Semischematic illustration of the muscle layers of the gastric wall in *Colobus*. The longitudinal fibres in the superficial layer of the saccus and the tubus gastricus can only be found in two taeniae. The longitudinal fibres are represented without signature. The oblique fibres of the corpus are irregularly stippled, the oblique fibres of the fornix are hatched. Circular fibres are marked by waves. O: oesophagus; D: duodenum.

**FIGURE 4.21** (from Ayer 1948)

*Semnopithecus entellus*: the upper, middle and lower figures represent the oblique, circular and longitudinal musculature of the stomach, respectively, as seen when consecutively by a dissection beginning from the interior.

1. cardiac orifice; 2. oblique fibres on lips of gastric canal and forming a loop round the cardiac orifice; 3. anterior fibromuscular condensation; 4. posterior fibromuscular condensation (circular fibres start from these and radiate on to the wall of the fundus); 5. the apex of the fundus where the circular fibres are deficient; 6. longitudinal musculature of the lesser curvature; 7. longitudinal musculature of the fundus; 8. longitudinal musculature of the greater curvature.

**FIGURE 4.22** (from Langer 1988)

View into the open saccus gastricus of an adult *Procolobus verus*, showing the musculature architecture. The white arrows point to the praessaccus.
Section 4. The blood supply to the colobid stomach

The arterial supply to the stomach was described by Ayer (1948), Kuhn (1964) and Langer (1988). In *Colobus guereza* the coeliac artery branches directly from the abdominal aorta after it has crossed the diaphragm (Figure 4.24 - Langer 1988). After a short course it branches into -

1. the common hepatic artery, which does not appear to be involved in the gastric circulation (Langer 1988).

2. the splenic artery, or A. lienalis (Langer 1988), which passes to the hilus of the spleen, where it gives off small branches and then runs along the greater curvature of the saccus gastricus as the left gastro-epiploic artery (Figure 4.24 - Langer 1988).

3. the arteria sacci gastrici, which has three branches -
   
   i. the proventricular artery, running cranially in the sulcus between the saccus and the tubus, passing the oesophagus to the right and then bending to the left on the dorsal margin of the saccus.

   ii. the left gastric artery, which passes for a short distance over the right dorsal part of the saccus and the runs along the lesser curvature to the tubus where it anastomoses with the right gastric artery.

   iii. the right gastric artery sends out branches to the pancreas as well as to the greater curvature of the tubus and pars pylorica.

Kuhn (1964) described the arterial circulation to the stomachs of *Procolobus verus* and *Procolobus badius*. It was essentially the same as that in *C. guereza*, except that the aboral gastric parts were supplied by branches from the superior mesenteric artery. Langer (1988) was not able to verify this in his specimen of *C. guereza*, which suggests that it might reflect a difference between the two genera. Ayer (1948) described an arterial supply to the stomach of *Semnopithecus entellus* from the superior mesenteric artery. One of its branches, the gastroduodenal artery, has two colic branches which pass along the greater curvature of the stomach (Figures 4.25 and 4.26 - Ayer 1948). In *Rhinopithecus* the circulation to the stomach appears to be similar to that in *C. guereza*, but the account by Ye et al. (1983) is not as detailed as the others. The left gastric artery is the largest branch of the coeliac artery, which appears to be correlated with the large size of the stomach and the need for a greater blood supply if absorption of metabolites is taking place in this organ.
FIGURE 4.23 (from Polack 1908)
The sulcus ventriculi in the stomach of *Colobus polykomos*. 
*Pyl.* - pylorus; *L.* - lips bordering the sulcus; *Rl.* - floor of the sulcus; *Ca.* - cardia.

![Diagram of the stomach of *Colobus polykomos*](image)

Aorta -------  A. coeliaca
A. coeliaca -------  A. lienalis
A. hepatica communis
ductus choledochus

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FIGURE 4.24 (from Langer 1988)
Arterial supply of the stomach of a juvenile *Colobus abyssinicus*. The two stippled rings in this right aspect represent the remaining parts of the diaphragm and the hiatus aoticus and the hiatus oesophageus. *O*: oesophagus; *D*: duodenum.

![Diagram of arterial supply to the stomach](image)

A. aortica
da d.d...
Semnopithecus entellus: The coeliac axis. The lower border of the stomach is thrown up.

D. duodenum; P. pancreas; S. stomach; Sp. spleen; 1. coeliac axis; 2, 2': hepatic arteries; 3. splenic artery; 4. left gastric; 5. gastroduodenal (branch of the superior mesenteric); 6. terminal part of left gastric; 7. terminal part of right gastric.

Semnopithecus entellus: blood supply of the pylorus and duodenum.
1. right gastroepiploic; 2. pancreatoduodenal; 3. right gastric; 4. pancreas; 5. duodenum; 6. stomach.
Section 5. The mesenteries

The attachments of the two mesogastria are in the regions of the greater and lesser curvatures of the stomach in the Colobidae, which is essentially the same as in primates with unilocular stomachs (Langer 1988). The lesser omentum, formed from the ventral mesogastrium, is attached to the taenia of the lesser curvature (Kuhn 1964, Langer 1988 - Figure 4.27). It begins near the pars affixa between the diaphragm and the saccus gastricus (Figure 4.16A - Langer 1988), where it forms the hepato-gastric ligament, then it passes a short distance over the saccus to reach the tubus gastricus. The lesser omentum extends along the whole length of the tubus and the pars pylorica (Figure 4.26 - Langer 1988).

The attachment of the greater omentum, which is formed from the dorsal mesogastrium, also begins at the pars affixa, but to the left of the oesophagus (Figure 4.27 - Langer 1988). From there it follows the taenia over the saccus and the tubus to reach the pars pylorica (Figure 4.27 - Langer 1988). In those species with a praesaccus, the greater omentum either passes caudally over it, as in *Procolobus verus* (Figure 4.7 - Langer 1988), or it passes between the praesaccus and the dorsal part of the saccus, as in *Nasalis larvatus* (Figure 4.29 - Langer 1988). On the dorsal border of the praesaccus the greater omentum is fused to the diaphragm (Kuhn 1964). Langer (1988) also noted that the bursa omentalis is extensive in volume (Figure 4.29) and its inferior recess covers the whole of the tubus and the intestines (Figures 4.6 and 4.28). There is a well-defined gastrocolic ligament between the pars pylorica and the transverse colon (Kuhn 1964, Langer 1988) and this is the only region where there is fusion of the mesenteries (Kuhn 1964).
FIGURE 4.27 (from Langer 1988)
Semischematic illustration of the dorsal and ventral mesogastrium in "Colobus abyssinicus". The two mesogastria are drawn as small bands. O: oesophagus; D: duodenum.

FIGURE 4.28 (from Langer 1988)
Left view into the saccus gastricus of Presbytis cristatus (a) and Nasalis larvatus (b). Both animals are foetal. The arrow in (a) and the lower arrow in (b) point into the tubus gastricus; the upper arrow in (b) points into the praeasaccus, which cannot be discerned from externally in Nasalis larvatus. The greater omentum has been resected to a small band in both species, and only the ligamentum gastrolienale is represented; it is interrupted by the fenestration of the saccus gastricus.
Left and ventral aspect of the stomach and other abdominal organs in a foetal *Trachypithecus cristatus*. The spleen has been pushed slightly upwards and the inferior recess of the bursa omentalis has been resected. Only the stump of the greater omentum remains. The red arrows point into the bursa omentalis.
Discussion

The following general conclusions can be drawn from these descriptions of the anatomy of the stomach in many species of colobids the following general conclusions can be drawn -

1. the plurilocular stomach that is characteristic of the family Colobidae is an adaptation to a diet that contains considerable quantities of plant structural compounds, like cellulose.

2. as mammals do not produce the enzymes that are capable of hydrolysing these substances, some herbivores and folivores, including the colobids, have evolved a symbiotic relationship with species of cellulolytic bacteria. In the colobids these populations of micro-organisms are housed in what are functionally fermentation chambers, located before the oxyntic gland area of the stomach. The optimum environment for bacterial activity is probably maintained through absorption of the acidic fermentation products, constant mixing of the contents of the chamber and perhaps by glandular secretions which help maintain the pH at the required level.

3. the colobids are able to utilize the end-products of bacterial fermentation of cellulose as an energy source. These are predominantly volatile fatty acids (Kuhn 1964, Bauchop and Martucci 1968, Peng et al. 1983).

4. the major anatomical difference between colobid stomachs is the presence or absence of a praesaccus. This appears to be a storage area (Kuhn 1964) and it would seem to be characteristic of three genera, Procolobus, Pygathrix and Nasalis, appearing at an early age in foetal development (Berenberg-Gossler 1911, Hill 1954, Langer 1988). There are slight differences between the in the gross anatomy of this region, but there may be major differences in the histology of the mucosa (Pilliet and Boulart 1898, Langer 1988). The remainder of the genera all have a three-chambered stomach and this could be described as the common pattern for the Colobidae; on this basis they can thus be divided into two broad groups (Figure 10.1A).

The basic plan of the stomach is similar throughout the members of the family Colobidae and this has two important implications -

1. it is a conservative character, with little or no variation between species of the same genus, from a phylogenetic point of view and thus is an important feature in separating the two families of Old World monkeys. Ito (1967) emphasised this point with regard to mammals in general and primates would not be an exception.

2. similarities in structure mean similarities in function, thus the family as a whole is adapted to coping with a diet in indigestible (for a mammal) plant structural compounds, most of which are complex polysaccharides like cellulose. These are found in leaves,
stems, seeds and bark, and to a lesser extent in fruit and flower parts. Apart from the Indian langur, which is semiterrestrial, the colobids are arboreal and most live in evergreen tropical rainforests (Table 2.2).
Chapter 5

The anatomy of the stomach of *Presbytis femoralis*: a reconstruction of a damaged specimen.

The stomach described in this chapter came from a young female pale-thighed leaf-monkey, which was one of a pair brought to Australia from Sumatra in 1986, and kept at the Bulen Primate Research Foundation in Perth, Western Australia (Carati 1986). The leaf-monkey was reported to have died of acute renal failure, and an autopsy was performed following her death (Carati 1986). The male remains healthy and is living in a faunal park on the outer suburbs of Perth.

The stomach and intestines were removed from the abdominal cavity during this examination and preserved in formalin. They were later placed in plastic bags with cotton-wool that had been soaked in formalin for transport, with the cadaver, to the Australian National University. As some dehydration had taken place during the three years it was stored in the Department of Prehistory and Anthropology, it was necessary to rehydrate it before beginning the study. This was done in an aqueous solution of 10 percent ethanol, which was gradually increased to 50 percent over a two-week period. Ethanol was used in preference to formalin, as it was decided that blocks of tissue would later be taken from the various regions of the stomach for the preparation of sections for histological examination. During the autopsy the stomach had been cut in two, through the middle part of the tubus gastricus (Plate 5.1), and partially opened by a slit along the dorsal surface of the saccus gastricus (Plate 5.6). This was an advantage as it was possible to see features, like the attachment of the greater omentum (Plate 5.2) and the internal folding (Plate 5.6), more clearly. By comparing this stomach with the descriptions of those of other colobids (Chapter 4) it was possible to "reconstruct" the anatomy and thus to describe the form of the stomach in *Presbytis femoralis*. This study had to be limited to the anatomy of the stomach, as the intestines were in much worse condition. Exhaustive enquiries were made both in Australia and overseas about the possibility of obtaining more colobid material, but these were not successful.

The stomach was quite small, as can be seen in Plate 5.3, which has portion of a human hand in the left corner for comparison, and also from the scale in Plate 5.4, which shows the saccus and part of the tubus. This section was the largest part of the stomach (Plate 5.1). The average length of the head and body (HBL) in this species is 40.6-58.4 cm, and they weigh 5.9-7.5 kg and are therefore, not large animals (Brandon-Jones 1984). This female was 3-4 years old and thus may not have reached full adult size (Brandon-Jones, 1984), but this seemed unlikely as
the headless cadaver measured 40 cm from the base of the neck to the base of the tail. Chivers and Hadlik (1980) noted that considerable contraction occurred when the guts of freshly-killed animals were placed in 10 percent formal saline. Given the history of this particular specimen, it is likely that considerable shrinkage had occurred, and that, in life, the stomach was somewhat larger. In their paper Chivers and Hladik had a photograph of the stomach of a freshly killed specimen of *Trachypithecus obscurus*, which is reproduced in Appendix 2. This species is sympatric with *P. femoralis* and is of a similar size (HBL 40.6-70 cm, weight 5-8.6 kg - Brandon-Jones 1984). In this photograph of the stomach of *T. obscurus* an indication of size is given by the accompanying scale, and it seems possible that the size of the stomach in *P. femoralis* may have been similar. This is a very tentative conclusion as many unknown variables, like age, sex, species differences and the state of preservation, will be involved. In the stomach of this specimen of *P. femoralis* the three major regions are evident and show the same general features as other colobids with similar gastric morphology. There was no praesaccus present in the stomach of this specimen, contrary to the observation made by Weitzel and Groves (1988). They appear to have described a region near the beginning of the tubus as a small praesaccus. This was due to the way the stomach had been opened, with the cranial part of the tubus intact. From the inside it looked like a small diverticulum. Careful restructuring and positioning of the specimen, with the aid of photographs of the stomachs of other species (Chivers and Hladik 1980), resulted in a reassessment of the observation made by Weitzel and Groves. For comparative purposes the description of its morphology will follow the same general outline used in Chapter 4.

Section 1. The external morphology of the stomach in *Presbytis femoralis*.

Nothing is known about the position of the stomach in the abdomen of this animal, but given the consistency of the reports on this in other colobid species, and the fact that these monkeys had long been weaned (i.e. had adult digestive systems, Kuhn 1964), it is safe to assume that the saccus gastricus filled the entire space underneath the diaphragm (Starck 1958, Kuhn 1964). The upper part of this chamber was still attached to portion of the diaphragm by a pars affixa around the gastro-oesophageal junction (Plate 5.2). There were a number of lymph nodes in this region, near the beginning of the lesser curvature (Plate 5.4). It was also assumed, for the above reasons, that the junction between the saccus and the tubus gastricus was positioned to the left of the abdominal cavity, as in *Colobus polykomos* (Starck 1958 - Figure 4.4). The tubus gastricus would then have passed to the right abdominal wall, where it would have turned dorsally and bent sharply at the pars pylorica, forming a sigmoid curve (Kuhn 1964, Langer 1988). The greater omentum was attached to the the wall along the greater curvature (Plate
5.2. The division between the tubus and the pars pylorica was evident externally, because of the smooth wall of the pyloric region (Plate 5.1). Figure 5.1 is a reconstruction of the entire stomach made from the specimen, with the aid of illustrations from Starck (1958) and Chivers and Hladik (1980).

1. The saccus gastricus

The saccus gastricus would have had its origin to the left of the oesophagus, as Kuhn (1964) described, and it appeared to have been the spheroidal shape that Hill (1958) said was characteristic of the Asian colobids (Plate 5.4). It was the largest single chamber of this stomach. The wall in this part of the stomach was very thin and the sacculation of the wall was very conspicuous, giving the saccus the appearance of an old-fashioned ice pack (Plate 5.4). The whole region seemed to resemble the same part of the stomach in *Semnopithecus entellus*, Figure 4.14 (Ayer 1948), more than it did that in *T. obscurus* (Chivers and Hladik 1980 - Appendix 2); although, the lack of fine pleating in Chivers and Hladik's specimen was due to its distention by the water, after the death of this animal. The haustra and the folds that separate them radiated out from the left of the cardiac orifice. To the right they were formed by the constricting bands of the taeniae of the two curvatures (Plate 5.3) and they began to align at right-angles to the longitudinal axis of the stomach (Plate 5.4). Towards the junction with the tubus, the saccus narrowed rapidly, and this was the only feature that marked the junction on both the internal and external surfaces (Plate 5.5). Presumably the cardiac orifice was immediately above this region, as it is in other colobids (Langer 1988). The oesophagus had a total diameter of 0.5 cm and its wall was thick and muscular (Plate 5.5). Oblique fibres in the muscularis externa could be seen clearly on the outer surface of the saccus (Plate 5.5).

2. The tubus gastricus

The colon-like appearance of the stomach was most noticeable in the narrower and more elongate tubus gastricus (cf. *Procolobus verus* - Hill 1952, 1958). There was no distinguishing anatomical feature observed indicating a junction region between the tubus and the saccus in the stomach of *P. femoralis*, and this region had been left intact (Plate 5.4). The walls were sacculated, with the folds at right angles to the longitudinal axis of the stomach (Plate 5.4), and there appeared to be little difference in degree of sacculation between the dorsal and ventral walls, or between the saccus and the tubus. Macroscopically the whole wall of the tubus looked very like that of the saccus.
3. the taeniae of the two curvatures of the stomach

Both of these taeniae, which were responsible for the pleating or folding of the walls of the saccus and the tubus, were clearly visible on the external surface of the stomach. The length of the taenia of the greater curvature was slightly more than twice that of the lesser curvature, which was much "tighter". Similar differences in the length of the two taeniae were noted by other authors (Owen, 1835, Duvernoy, 1834, Polack, 1908, Hill, 1952, Ayer, 1948). This fact was also noted by Peng et al. (1983) in their description of the stomach of *Rhinopithecus spp.* The longitudinal arrangement of the fasciculi of the smooth muscle fibres that formed these taeniae could be seen with the naked eye on their external surfaces. The taenia curvaturae majoris started just below and to the left of the cardiac orifice (cf. *Colobus guereza* Figure 5.2 - Langer 1988). At its beginning the fasciculi were spread out in a delta shape that had its broad base directed towards the oesophagus. As they merged together the band became more clearly defined, as can be seen in Plate 5.3. The haustra overhung and covered the full extent of the taenia along the greater curvature (Plate 5.4). The taenia curvaturae minoris started from the opposite side of the gastro-oesophageal junction to the taenia curvaturae minoris, and passed for only a short distance over the wall of the saccus, with the longer part running along the tubus (Plate 5.5). Both of the taeniae ended just before the junction between the tubus gastricus and the pars pylorica, in the region where the character of the wall changed.

4. the pars pylorica

The commencement of the pars pylorica was marked by this change in the appearance of the wall (Plate 5.1), which became uniformly thick and smooth as it lacked taeniae. There was a constriction at the pyloro-duodenal junction, which indicated the position of the pyloric sphincter.

5. the mesenteries

The greater omentum was a delicate membrane, attached to the dorsal margin of the taenia of the greater curvature (Plate 5.3). It extended from the pars affixa on the left of the oesophagus around the entire length of this curvature to the pars pylorica. The lesser omentum had been cut close to its attachment to the taenia curvaturae minoris, but it could be seen that it also extended from the pars affixa, but to the right of the oesophagus, then along the lesser curvature to the pars pylorus. On the external surface of the lesser curvature, just below the cardio-oesophageal junction, there were a number of encapsulated lymph nodes within the membrane of the lesser omentum (Plate 5.4).
Section 2. The internal morphology of the stomach of *Presbytis femoralis*

Hill (1958) described four features that he considered to be characteristic of the internal anatomy of colobid stomachs. These were:
1. the extension of the oesophageal mucosa around the cardiac orifice into a structure he called the cardiac shield.
2. the presence of a sulcus ventriculi.
3. the semilunar folds and haustra of the walls of the saccus and the tubus.
4. the abrupt change in general appearance and folding of the gastric wall at the junction between the tubus and the pars pylorica.

Some variation in these features was noted in *P. femoralis* when compared with the descriptions of different species by other authors (Hill 1952, Kuhn 1964, Peng et al. 1983, Langer 1988).

1. the gastro-oesophageal junction

In this specimen there was no clear-cut cardiac shield as described by Hill (1952) for a number of species, Kuhn (1964) for *Procolobus badius*, or Peng et al. (1983) for *Rhinopithecus spp.*, and the margin between the oesophageal-type mucosa and that of the saccus could not be seen with the naked eye in this specimen (Plate 5.8).

2. the sulcus ventriculi

The mucosa of the oesophagus just above the cardiac orifice had a number of longitudinal folds. Two of these were more prominent than the others and eventually broadened to form the lips of the sulcus ventriculi (Figure 5.3). These lips, which ran parallel to each other for most of their length, were not equal in size or development. The dorsal one was smaller and not as well-developed as the ventral, being little more than a ridge for most of its length (Figures 5.3 and 5.4A). The ventral lip was flap-like (Figure 5.4) and had a very broad external surface (Figure 5.3). This flap covered the greater part of the floor of the sulcus, but did not reach to the dorsal ridge when the muscle was in its core relaxed and the sulcus was patent (Figure 5.4B). If the muscle fibres in the lips of the sulcus were contracted, a tube with a relatively large lumen would have been formed (Figure 5.4C). Lymph nodules were closely packed in the mucosa of the first two-thirds of the length of the sulcus and were clearly visible to the naked eye (Plate 5.8). The lips of the sulcus ended in the caudal part of the tubus (Plate 5.7) and here the space between them narrowed. The ventral lip was still more prominent than the dorsal, which became more pleat-like in this end-region. Peng et al. (1983) noted a similar difference between the
two lips bordering the sulcus in the three *Rhinopithecus* species. The floor of the sulcus was formed by the taenia curvaturae minoris.

3. the semilunar folds and haustra

These were well-developed in the first parts of the stomach of *P. femoralis* and were produced by the tighter tension of the taeniae gathering the thinner parts of the wall between them (Plate 5.6). With the exception of the well-developed pyloric sphincter (Plate 5.7), no other permanent folds, such as described by Kuhn (1964), Ye et al. (1985) and Langer (1988), were observed in the junction areas between the various regions of this stomach.

4. the tubo-pyloric junction

The junction between the tubus gastricus and the pars pylorica was marked by a distinctive change in the direction of the mucosal folding (Plate 5.7). In the tubus the folds were at right-angles to the long axis of the stomach, but in the pars pylorica they were parallel to it and fewer in number (Plate 5.7). In the pyloric canal these folds were organised into two groups and the surfaces of the wall between them were relatively smooth. There were three major folds in the group running along the lesser curvature and five in the group along the greater curvature. These folds were more pronounced than those in the smaller group. The lumen of the pylorus narrowed rapidly in the region of the sphincter and the separation of the pyloric mucosa was marked by the latter's rust-red colour (Plate 5.7).

As the stomach had been removed from the abdominal cavity and cut in two, as well as being separated from the intestines, it was not possible to determine the path of the blood supply to this organ. On the other hand parts of the lymphatic system were very obvious, and Carati (1986) in his post mortem report (Appendix 3) mentioned the appearance of the lymph nodes in the pyloric region. The lymph nodes that were clustered along the lesser curvature, between the end of the oesophagus and the beginning of the tubus, varied between 0.5-1.0 cm in diameter (Plate 5.4). This appears to be similar to the situation in other primates, for in *Homo sapiens* lymph nodes are to be found in the same region of the lesser curvature, as well as towards the pyloric end of the greater curvature (Pick and Howden 1901, Pansky and House 1975). None were seen in this area in *P. femoralis*, as it seems likely that they were removed during the autopsy. Carati reported that these nodes were enlarged (Appendix 3). In addition numerous lymph nodules were found in the mucosa of the entire fermentation area and were most obvious in the region of the sulcus ventriculi (Plate 5.8). Kuhn (1964) also noted the presence of nodules in this area of the stomach.
PLATE 5.1
The two sections of the stomach of *Presbytis femoralis*. The larger section, on the left, consists of the saccus gastricus (SG) and most of the cranial part of the tubus gastricus (TG). The oesophagus (O) is clearly visible and below it are two lymph nodes (arrow). Portion of the greater omentum (lower arrow) is still attached to the taenia of the greater curvature. The smaller section, on the right, consists of the caudal part of the tubus (TG) and the duodenum (D). The contrast between the thin, sacculated wall of the saccus and the thicker wall of the pars pylorica (arrow) can be seen in this photograph.
(Photo: C. P. Groves)
The saccus gastricus and the tubus gastricus of the stomach of *Presbytis femoralis*. The junction between the oesophagus (O) and the saccus gastricus (SG) can be seen in the cardiac region of the stomach, where some of the diaphragm (arrow) is still attached at the pars afixa. The way in which the saccus was opened left the taenia curvaturae majoris intact. The greater omentum (GO) is attached to the dorsal border of the taenia.
The beginning of the taenia curvaturae majoris on the exterior wall of the saccus gastricus has a delta shape. Its edges are shown by two arrows. The thin membrane of the greater omentum (GO) is attached to the dorsal border of the taenia, which becomes narrower and more clearly defined as it passes towards the tubus gastricus. The oesophagus (O) and the diaphragm (uppermost arrow) are visible in the upper part of the photograph.
PLATE 5.4
A group of lymph nodes (arrow) can be seen below the pars affixa of the diaphragm, at the beginning of the lesser curvature. When the cut edges of the saccus wall were placed together, it could be seen that this part of the stomach was spheroidal in shape, like the stomachs of other Asian colobids. The rapid narrowing of the lumen (arrow), forming the separation between the saccus gastricus (SG) and the tubus gastricus (TG), is evident, as is the change in direction of the folds and haustra. These radiate out from the cardia in the saccus, and are at right angles to the long axis of the stomach in the tubus. The haustra conceal the taenia curvaturae majoris when the stomach is positioned in this manner.
PLATE 5.5
The narrowing of the lumen (arrows) between the saccus gastricus (SG) and the tubus (TG) gastricus is also clear in this photograph. The cluster of lymph nodes (LN) can be seen underneath the diaphragm. The thoracic portion of the oesophagus (O) is thick-walled and narrow; remnants of connective from the mediastinum (arrow) surrounding it. A very small portion of the lesser omentum (LO) is evident on the lower part of the tubus.
PLATE 5.6
The interior of the saccus gastricus in the stomach of *Presbytis femoralis*. The haustra (lower arrows) and the semilunar folds separating them are pronounced. The position of the taenia curvaturae majoris is marked by the pleating of the mucosa above it. The sulcus ventriculi can just be seen on the inner surface of the lesser curvature (upper arrow).
PLATE 5.7
The internal appearance of the wall of the caudal part of the tubus gastricus, the pars pylorica and the duodenum in *Presbytis femoralis*. There is a gradual change in the pattern of the folding of the wall in this region of the stomach. In the tubus (TG) the folds are at right angles to the long axis. Their direction gradually changes in the pyloric antrum (PA) and they become parallel to this axis and fewer in number in the pyloric canal (PC). In the canal the folds are concentrated into two groups and the wall between them is smooth. The pyloric sphincter is well-developed (arrows), marking the junction with the duodenum (D). The arrow on the right shows the ending of the ventral lip of the gastric sulcus, running parallel to the lesser curvature. The rust-red colour of the duodenal mucosa is in marked contrast to the paler colour of the mucosa of the stomach.
(Photo: B. Dowhy)
PLATE 5.8
This photograph of the cardiac region of the stomach of *Presbytis femoralis* shows the opening of the oesophagus and the beginning of the sulcus ventriculi (upper arrow). It is the region where the cardiac shield should be found, but there is no evidence of such a structure or a macroscopically clear demarcation between the extension of the oesophageal mucosa and that of the saccus. The only sign of any possible junction is shown by the arrow marked J, where there is a line on the left of the cardiac orifice. The size differences in the lips bordering the sulcus is evident, with the ventral one (V) being more prominent than the dorsal (D). The numerous lymph nodules in the mucosa (lower arrows) are a prominent feature, and give the surface a bubbly appearance. They are more tightly packed in the first part of the sulcus than in any other part of the wall.
FIGURE 5.1
A RECONSTRUCTION OF THE STOMACH OF *PRESBYTIS FEMORALIS.*
FIGURE 5.2 (from Langer 1988)
Right (A) and left (B) aspects of a stretched out stomach of a juvenile "Colobus abyssinicus". O: oesophagus; D: duodenum.
FIGURE 5.3
THE BEGINNING OF THE SULCUS VENTRICULI IN THE STOMACH OF
PRESBYTIS FEMORALIS.

A.

B.

C.

FIGURE 5.4
CROSS SECTIONS OF THE SULCUS VENTRICULI IN THE STOMACH OF
PRESBYTIS FEMORALIS.
Chapter 6
Comparison of the anatomy of the stomach of *Presbytis femoralis* with that of other colobids

It would appear that both internally and externally the form of the stomach in *Presbytis femoralis* was very similar to that of other three-chambered colobid stomachs (Ayer 1948, Kuhn 1964, Langer 1988), with similarities in function most likely. The main differences between the stomachs of other species and that of *P. femoralis* appeared to be in features of internal morphology. These included:

1. the unequal development of the lips forming the border of the sulcus ventriculi.

   This may not be unique to the stomach of *P. femoralis*, for Langer (1988) seemed to depict a similar inequality in the lips of the sulcus in his illustration of the interior of the stomach of *Colobus guereza* (Figure 4.16). He did not mention this difference in the text and this feature was not mentioned by other authors, for example Polack (1908), Ayer (1948), Hill (1952), Kuhn (1964), and Peng et al. (1983), all of whom wrote major works on colobid gastric anatomy. The origins of the sulcus lips from two prominent longitudinal folds in the oesophageal mucosa appears to be a common feature in these monkeys, as it was described by Hill (1952) in *Procolobus verus* and by Owen (1835) and Ayer (1948) in *Semnopithecus entellus*. In *Presbytis femoralis* the course of the sulcus appeared to follow a more direct and simpler path beneath the taenia curvatae minoris than in *Colobus* (Langer 1988), as no U-shaped loop was seen encircling the cardia, with its branches forming the lips of the sulcus and there were also no other folds joining either lip (Langer 1988). At its beginning the sulcus ventriculi appeared to be very similar to that in *S. entellus*, although the fibromuscular condensations described by Ayer (1948) could not be identified. These differences can be seen when Figures 4.13 and 5.3 are compared.

2. the lack of a cardiac shield and any clear macroscopic demarcation between the mucosa of the oesophagus and the saccus gastricus.

   This was a major difference between the present specimen and those colobid stomachs described by Hill (1952) and Kuhn (1964). Hill described very clearly defined shield areas in both African and Asian species (Figure 4.10) and he noted that in the shield of the stomach of *Presbytis melalophos* "the edges were undermined, enabling it to be raised as a
flap" (Hill 1952:152). Nothing like this was observed in this specimen of *P. femoralis*, as can be seen from Plate 5.8, which is of the shield area. Kuhn's descriptions of the cardiac shield in *Colobus polykomos* (Figure 4.5A) and *Procobus badius* (Figure 4.11) are similar to Hill's. Kuhn noted that the edges of the shield were "scalloped" in both, and that in *Procobus badius* the edges of the shield were free in the praesaccus. Peng et al. (1983) described a cardiac shield in *Rhinopithecus*. Apart from noting that there was a clear line of demarcation between the two types of mucosa in this region, Ayer (1948), Suzuki et al. (1985) and Langer (1988) did not mention the presence of any shield-like structures. There are two possible explanations for these differing observations. Firstly, that the cardiac shields, which were individually variable in form (Kuhn 1964), could have been an artefact produced by differential post mortem degeneration in the two types of mucosa, as decay was found to be much greater in the mucosa of the saccus than in the stratified squamous epithelium of the oesophageal part of the junction (Plate 8.32). This could have resulted in the undermining of the more resistant area, leaving it as a flap with scalloped edges. On the other hand, as this specimen had been left for some time after death before the stomach was preserved, the shield itself might have been destroyed, leaving what looks like a very small remnant (Plate 5.8). The lack of a clearly defined junction between the two types of mucosa in *P. femoralis* was surprising, as it was a conspicuous feature in other species, including the closely related *Presbytis melalophos* (Ayer 1948, Hill 1952, Kuhn 1964, Peng et al. 1983 and Langer 1988). Hill said that the extension of the oesophageal mucosa was firm, with a "horny texture" and white in colour. It is also possible that this lack of obvious demarcation may have been due to the fact that this stomach had been kept in preservatives for a number of years, giving the wall a uniformly yellow-grey appearance (Plate 5.7). It would seem that the only way to resolve this problem would be to dissect carefully a preserved specimen.

3. the lack of a permanent internal junctional folds between various regions in the stomach of *Presbytis femoralis*.

The lack of a permanent fold between the saccus and the tubus is in accord with the findings of Hill (1952) and Kuhn (1964) for a number of different colobid species. This area in all of them, as well as in *P. femoralis*, was marked by a rapid narrowing of the lumen (Plate 5.4). Kuhn (1964) described a permanent fold separating the tubus and the pars pylorica in *Colobus polykomos*, and Langer (1988) also saw one in *C. guereza*, as Hill (1952) did in the stomach of *Procobus verus*. They all described this fold as being weakly developed. Plate 5.7 shows this area in the stomach of *P. femoralis* and no such fold is evident. This junction was marked by changes in the thickness of the wall, the absence of
taeniae on the external surface and the change in direction of the mucosal folds (Plate 5.7).

4. the presence of a well-developed lymphatic system associated with the first parts of the stomach in *Presbytis femoralis*.

This may have been related to the presence of a large population of potentially harmful bacteria living in the fermentation chamber, rather than a pathological condition (Carati 1986). Any physical damage to the delicate mucosa lining the lumen would provide a portal of entry for these micro-organisms. The nature of the diet in these monkeys, with a high percentage of tougher plant parts, would increase the risk of such an occurrence. The numerous lymph nodules in the tunica mucosa in this area would form the first line of defence against bacterial invasion, backed-up by the filtration mechanisms of the externally-placed lymph nodes.

This theory of mine receives indirect support from a report by Loomis and White (1986) on the cause of death of a female guereza (*Colobus guereza*) in a zoo in North Carolina, USA. She had a heavy, and apparently long-standing infection, of the nematode *Trichuris sp.* in the saccus gastricus. The activity of these worms, which obtain their nourishment by penetrating the epithelial cells of the mucosa, had resulted in the formation of numerous necrotic nodules over the entire mucosal surface. Some of these had worms protruding from them. Surface mucous cell hyperplasia was evident and the whole of the lumen was lined with a fibrinocatarrhal mat, which contained many gram-positive bacteria. The guereza died of septicaemia, which Loomis and White felt was due to bacteria gaining entry to the circulation via the necrotic areas of the saccus mucosa. In this case the amount of damage to the mucosa was so great that the lymphatic system was unable to cope with the invading micro-organisms. The three other guerezas also had trichurid infections and were treated for them as was the female, but evidently they were not as great and these animals survived (Loomis and White 1986). Ruch (1959) also mentioned that monkeys with trichurid infections were likely to die of secondary infections. Kuhn (1964) noted the presence of similar lymph nodules in the mucosa of the saccus gastricus of *Trachypithecus auratus* and it was the same in *Rhinopithecus* (Peng et al. 1983).

In the stomach of *P. femoralis* it was observed that the lymph nodules were most numerous and closely packed around the cardiac orifice and along the first part of the sulcus ventriculi (Plate 5.4), which suggests that there was a greater risk here from drier, recently swallowed food pieces. In the human stomach recently swallowed food does not drop from the opening of the oesophagus into the chamber of the stomach, but follows a path
down the lesser curvature (Shanks and Kurley 1969, Netter 1971, Guyton 1976, personal observation). The presence of these lymph nodules suggests that the food may follow a similar path in *P. femoralis*. It would be of considerable interest to see if there are similar arrangements of the gastric lymphatic system in other colobids, especially in those with a praesaccus where storage of recently ingested food takes place (Kuhn 1964, Holllhn 1971).

The information available about the portion of the lymphatic system draining the stomachs of colobids was confined to descriptions of nodules in the tunica mucosa and submucosa. It seems to me that the development of the lymphatic system in this organ would be a natural outcome of maintaining a population of potentially harmful bacteria within the abdominal cavity close to many vital organs, especially via the circulation. The rapid regeneration of the epithelial cells in the mucosa (Stevens and Leblond 1953, Ham and Leeson 1961) suggests that damage to the mucosa is frequent in most mammals. Thus colobids with their rough food and their bacteria would need added protection.

Despite its poor preservation, this specimen of the stomach of *Presbytis femoralis* provided useful information about gastric morphology in a species that had not, as far as is known, had these features described by any other author. It would seem that there are many similarities between this stomach and those of other colobid species, and that the differences observed appeared to be relatively minor. Some caution is necessary, however, when reaching conclusions about this stomach, and in making comparisons with other colobid species, because of the past history of this specimen.
PART TWO

THE HISTOLOGY OF THE GASTRIC MUCOSA IN THE MEMBERS OF THE SECTION CATARRHINI.
ABBREVIATIONS USED WITH THE PLATES IN CHAPTERS 7 AND 8.

\[ \begin{align*}
P & : \text{PITS} \\
P & : \text{GLANDS} \\
LP & : \text{LAMINA PROPRIA} \\
LN & : \text{LYMPH NODULE} \\
GC & : \text{GERMINAL CENTRE} \\
MM & : \text{MUSCULARIS MUCOSAE} \\
CL & : \text{CIRCULAR LAYER OF SMOOTH MUSCLE FIBRES IN THE MUSCULARIS MUCOSAE} \\
LL & : \text{LONGITUDINAL LAYER OF SMOOTH MUSCLE FIBRES IN THE MUSCULARIS MUCOSAE} \\
SM & : \text{SUBMUCOSA} \\
TM & : \text{TUNICA MUSCULARIS} \\
SP & : \text{SURFACE EPITHELIUM AND PITS} \\
MR & : \text{MIDDLE REGION OF THE OXYNTIC GLANDS} \\
BA & : \text{BASAL REGION OF THE OXYNTIC GLANDS} \\
IS & : \text{ISTHMUS OF THE OXYNTIC GLANDS} \\
NE & : \text{NECK OF THE OXYNTIC GLANDS} \\
SSE & : \text{STRATIFIED SQUAMOUS EPITHELIUM} \\
VI & : \text{VILLI OF THE DUODENAL MUCOSA} \\
CR & : \text{INTESTINAL CRYPTS} \\
SE & : \text{SEROSA} \\
\end{align*} \]

S ARROW : SMALL ARROW \\
M ARROW : MEDIUM ARROW \\
L ARROW : LARGE ARROW \\

HE : SECTION STAINED WITH HAEMATOXYLIN AND EOSIN \\
PAS : SECTION STAINED WITH PERIODIC ACID SCHIFF-REAGENT, COUNTER STAINED WITH HAEMATOXYLIN
The yellow baboon, *Papio cynocephalus* (Plate 7.1), is found in the semi-arid savannah and bushland of central Africa, extending from south-east Kenya to south-west Angola (Groves 1989). This species is a member of the subfamily Papioninae, of the second family of Old World monkeys, the Cercopithecidae (Groves 1989). These yellow baboons are terrestrial and range widely while feeding, taking advantage of whatever plant, invertebrate and vertebrate foods are available (Kavanagh 1983).

Section 1. A general description of the anatomy of the stomach in baboons

Several accounts of the anatomy of baboon stomachs were available from the literature, and the general description that follows is based primarily on these sources, as the specimen was handled as little as possible to avoid damaging the mucosa. No major inconsistencies were observed between them and the stomach of *Papio cynocephalus* used in this study.

When the abdominal cavity of the baboon is opened the most conspicuous organ is the liver, which occupies the cranial portion of the cavity (Figure 7.1-Swindler and Wood 1973). The stomach is just visible underneath its caudal margin. Its axis is almost horizontal and it can be divided into fundic, body and pyloric regions. The fundus lies under the left cupola of the diaphragm, to the left of the oesophagus. The pyloric limb is upturned and directed to the right, slightly dorsally (Hill 1970, Swindler and Wood 1973). When empty this organ is bent back sharply on itself in the region of the incisura angularis, a notch that can be seen clearly on the lesser curvature (Hill 1970). This is a considerable contrast to the colobids, in which the liver is displaced and the stomach is the major feature of the abdominal cavity.

The body and fundus merge imperceptibly (Hill 1970) and the sulcus intermedius on the the external surface of the greater curvature marks the junction of the body and the pars pylorica. Internally there is a well-defined annular thickening in this region, which Hill (1970) considered to be a sphincter-like mechanism associated with hypertrophy of the tunica muscularis in the pylorus, for it did not disappear like the rugae when the stomach was full. The site of the pyloric sphincter is marked by an external annular sulcus (Hill 1970, Swindler and Wood 1973). This annular structure is most clearly defined internally (Hill 1970). The wall of the pars pylorica is thicker than that of the rest of the stomach and it retains its tubular shape when empty, unlike the cranial regions where the dorsal and ventral walls are in apposition if
the stomach is empty (Hill 1970). The internal surface is folded and along the lesser curvature there are two parallel, longitudinal ridges, running from the cardia to the incisura angularis, which form the borders of a smooth-walled groove (Hill 1970). This was evident in my specimen, and the presence of such a groove is a feature of other non-colobid primate stomachs (Jefferson 1915, Siwek 1979). In the region of the greater curvature the mucosal folds or rugae form a reticular pattern.

The lesser omentum is well-developed and passes from the lesser curvature of the stomach to the liver (Swindler and Wood 1973). On the lesser curvature its attachment extends from the cardio-oesophageal junction to the pyloro-duodenal junction. The greater omentum is attached to the full extent of the greater curvature, being very large and apron-like in *Papio* (Figure 7.1 - Swindler and Wood 1973). Hill described the stomach in the genus *Papio* as being of the "usual cercopithecid type" (1970: 134), that is unilocular (Langer 1988) or simple, with the major gland type being oxyntic.
FIGURE 7.1 (from Swindler and Wood 1973)
The abdominal organs of *Papio* sp., *in situ*. The liver and intestines are more conspicuous than the stomach in these monkeys.
PLATE 7.1 *Papio cynocephalus*
Adult male yellow baboons from the troop in Adelaide Zoo.
Section 2. A review of the main elements of the gastric mucosa in the Catarrhini

The section Catarrhini of the order Primates includes the superfamilies Cercopithecoidea and Hominioidea (Groves 1989). Within this group of Old World primates a considerable amount of information is available about the histology of the gastric mucosa in humans (e.g. Garven 1965, Kelly et al. 1984, Whitehead 1985) and in the rhesus monkey, Macaca mulatta (Burki 1958), but little is known about most of the other species, especially the Colobidae. The gastric mucosa is very difficult to preserve, as the chemicals released by the glands and those already in the chyme quickly destroy it after death (Bensley 1902, Whitehead 1985). During the course of this study an extremely well-preserved stomach of an adult male yellow baboon, Papio cynocephalus, became available and this provided an ideal opportunity to make comparisons with the data available for other catarrhines, including Presbytis femoralis, a Sumatran leaf-monkey.

The tunica mucosa lines the lumen of the entire gastro-intestinal tract (Figure 4.1), and its structure, with its function, varies from region to region. In the stomachs of catarrhines the mucosa has the following characteristics (Figure 7.1) -
1. a continuous layer of mucus-secreting surface epithelium lining the lumen,
2. gastric pits or foveolae opening on to the surface of the mucosa,
3. tubular glands opening into the bases of the pits: functionally the most important part of the mucosa,
4. the connective tissue of the lamina propria surrounding the glands and supporting the epithelium,
5. the muscularis mucosae, a relatively thin layer of smooth muscle fibres, forming the junction with the submucosa.

ICOVAN (1973) includes the tela submucosa in the tunica mucosa (Figure 3.1), but in this thesis, following the example of Ham and Leeson (1961) and Garven (1965), it is not regarded as part of this layer. Functionally, the submucosa acts as a supporting and connecting zone (Figure 4.1), which plays little direct part in the digestive role of the stomach. For this reason it was not included in the tunica mucosa.

The structure of the surface epithelium, the lamina propria and the muscularis mucosae are relatively constant throughout the entire gastric mucosa, but the nature of the glands varies in different areas. There are three main types -
1. the cardiac glands
These are mucus-secreting glands, and in most catarrhines are confined to a narrow region around the cardiac orifice (Burki 1958); in the colobid stomach, however, they are the
main gland type found in the mucosa (Kuhn 1964).

2. **the oxyntic glands**
   These glands contain the cells which secrete HCl and the proteolytic enzyme, pepsin, which is responsible for most gastric digestion. In catarrhines with unilocular stomachs they are the major gland type.

3. **the pyloric glands**
   The pyloric glands also secrete mucus and are found in the mucosa of the pyloric antrum and canal.

These tissues are found in the mucosae of all catarrhine stomachs and their relative distributions appear to reflect difference in diet and the functions of the two types of stomach.
FIGURE 7.2
THE GENERAL STRUCTURE OF THE GASTRIC MUCOSA IN MAMMALS
Section 3. The histology of the mucosa in the stomach of *Papio cynocephalus*

The stomach used in this study came from an adult male yellow baboon from the troop in the Adelaide Zoo (South Australia) - Plate 7.1. It had been the dominant male for a number of years and died as the result of injuries received in a fight with a younger male. The stomach was removed by the Veterinary Surgeon at the Zoo immediately after death, opened along the greater curvature and then placed in 10 percent neutral buffered formal saline. It was flown to Canberra, where two weeks later I removed small blocks of tissue from the region of the gastro-oesophageal junction, the body and the pyloro-duodenal junction. The material was processed for me by the staff of the Histology Unit of the John Curtin School of Medical Research at the ANU, as there were no facilities available for me to personally prepare sections in the Department of Prehistory and Anthropology. The blocks were embedded in paraffin wax for the cutting of two sets of 5 micron thick sections. One of these sets was stained with haematoxylin and eosin (HE), and the other was stained with Periodic Acid-Schiff reagent, counter stained with haematoxylin (PAS). Kodak Technical Pan film was used for all of the black and white photographs in Chapters 7 and 8, and Ektachrome Tungsten film (EPY 404) was used for the colour photographs. All were taken with an automatic camera attached to a Leitz Diaplan Scientific microscope. To ensure consistent magnification in all of the prints made from the negatives, photographs of a stage micrometer were taken at the magnifications used for examining the sections. These were used as standards for the printing.

1. the surface epithelium and gastric pits (foveolae gastricae)

The surface epithelium of the stomach consists of a single layer of mucus-secreting columnar cells (Burki 1958, Garven 1965, Ito 1967, Kelly et al. 1984, Whitehead 1985) - Plate 7.2, which were easily distinguished by their position and the mucin which filled the supra-nuclear cytoplasm (Plate 7.2). The ovoid nuclei, surrounded by a narrow rim of cytoplasm, were found in the bases of these cells (Plate 7.3). A clear thecal area may separate the basal region of the cell from the apical mucin (Ito 1967), but this was not evident in these sections. The pits are invaginations of the surface epithelium and are lined with surface mucous cells (Plate 7.3). These cells became shorter and more cuboidal towards the bases of the pits (Plate 7.2) and their nuclei were more spherical. Burki (1958) noted that in *Macaca mulatta*, another papionine, there were regional variations in the heights of the surface cells, which were highest in the cardiac and pyloric areas. This also was the case in *Papio cynocephalus*, with those in the cardiac area being noticeably taller (Plates 7.2, 7.3 and 7.4).

The mucin in these cells does not stain in HE preparations (Plate 7.3), but it stains deeply
with PAS (Plate 7.5). The amount of mucin in these cells is very variable, with those on
the surface and the upper parts of the pits containing more than the cells in the bases of
the pits (Ito 1967). In this animal there were regional difference in mucus content of
these cells, in contrast to the appearance described by Ito (Plates 7.2, 7.3 and 7.4). Ito
also found that feeding stimulated a marked reduction in the cellular mucin content in some
mammals. It is not known if feeding has a similar effect in primates. The mucin in the
surface cells of the human stomach has a faintly granular appearance (Whitehead 1985),
as it did in this specimen (Plate 7.5).

The mucus produced by the surface cells in the human stomach is a mixture of water,
electrolytes and mucopolysaccharides (Guyton 1976). It is viscous and has adherent
properties which enable it to form a protective coating, up to 1mm thick, over the entire
lumen. This prevents damage occurring to the underlying cells from the action of enzymes
and hydrochloric acid (HCl), as well as preventing abrasion by food particles (Guyton
1976, Kelly et al. 1984). These mucopolysaccharides have amphoteric properties, which
enable them to buffer small amounts of acids and bases. In addition the mucus contains
bicarbonate ions, which also help to buffer acids (Guyton 1976).

2. the cardiac glands

These glands are found in an area immediately surrounding the cardiac orifice. The extent
of this area varies among different species of catarrhines, being 10 -20mm wide in
humans, 30mm in chimpanzees and only 2mm in Papio hamadryas (Bensley 1902, Burki
1958). The pits in this region are relatively shorter than in the pyloric area (Plates
7.2, 7.3 and 7.4) and occupy about half the total mucosal thickness (Whitehead 1985)
and they are lined with surface mucous cells (Plate 7.3). Near the junction with the
oesophagus some of the pits are wider and more duct-like, with a number of tubular glands
opening into them (Garven 1965). A number of these are well-developed in this
specimen of Papio cynocephalus (Plate 7.12). The branching of the cardiac glands
gradually diminishes as the distance from the oesophagus increases in both Homo sapiens
(Bensley 1902) and Papio cynocephalus. Lymph nodules are common in this area and the
thickness of the mucosa is dependent on their presence (Plates 7.6). The transitional zone
between the cardiac and oxyntic gland areas is not clear cut and zymogen and parietal cells
gradually replace the bases of the glands (Ito 1967, Kelly et al. 1984).

Histologically the mucus-secreting cells of the cardiac glands are reported to be very like
those of the pyloric glands and the mucous neck cells of the oxyntic glands (Ito 1967) -
Plates 7.9 and 7.20. Their apical regions are filled with mucin granules, which are not as
tightly packed as those in the surface mucus cells (Plates 7.7, 7.8 and 7.9), giving the cytoplasm a darker, more granular appearance (Plates 7.10 and 7.11). These granules or droplets stain with PAS (Plate 7.8), but are unstained with HE (Plate 7.10). The nuclei are found in the bases of the secretory cells and their shape varies from circular to flattened ovoid, with the long axis parallel to the base of the cell (Plate 7.10). The nuclear shape is probably related to the amount of secretion contained in the supra-nuclear or apical cytoplasm.

Argentaffin or entero-endocrine cells are found in the bases of the cardiac glands. In HE sections they appear as small cells with clear cytoplasm and a centrally placed nucleus (Plate 7.13). They do not reach the lumen of the glands and seem to be squashed between the basement membrane of the glands (unstained with HE) and the bases of the secretory cells. Their original name, argentaffin, described the ability of the contents of their secretory granules to reduce the silver salts that were used to stain them (Ham and Leeson 1961, Garven 1965). Entero-endocrine is considered by Kelly et al. (1984) to be a better name, as it refers to their function and their widespread distribution throughout the digestive tract. Entero-endocrine cells secrete a number of hormone-like substances into the capillaries of the lamina propria. These include gastrin (which helps regulate the secretion of HCl by the oxyntic glands and the emptying of the stomach), secretin and histamine, which also stimulates gastric secretion (Ham and Leeson 1961, Guyton 1976). Entero-endocrine cells are stimulated to secrete by food distending the stomach and by chemicals in the food, in particular partially digested proteins (Guyton 1976).

The mucus secreted by the cardiac glands is less viscous than that from the surface mucous cells (Guyton 1976, Kelly et al. 1984). It helps to protect the stomach wall against the corrosive chemicals produced by the oxyntic glands (Guyton 1976).

3. the oxyntic glands

Oxyntic glands are simple, tubular and very closely packed together (Plate 7.14). In the human stomach they are long and take up three-quarters of the thickness of the mucosa (Whitehead 1985) as they do in the baboon (Plate 7.14). In humans there may be 3 - 7 glands opening into the same pit (Ito 1967). It is probable that the situation is the same in the baboon, although this was not directly obvious. Three regions are visible in this area of the mucosa (Plate 7.14) - the surface epithelium and pit region next to the lumen, a middle section where the cells have pale cytoplasm and a basal region where the cells have darker cytoplasm. These correspond to the distribution of the different cell types within
this area of the mucosa. The individual oxyntic glands are divided into the following areas (Stevens and Leblond 1953) -

The isthmus, which is the junction region immediately beneath the opening of the gland into the pit. This region is lined with surface mucous cells and some parietal cells. In the isthmus the surface mucous cells do not contain as much mucin as they do in the upper parts of the membrane (Ham and Leeson 1961) - Plate 7.18.

The neck is the middle part of the gland where the mucous neck cells and parietal cells are abundant. With the isthmus area it forms the pale middle region of the mucosa seen in HE-stained sections (Plate 7.14).

The base of the gland containing the more darkly staining zymogen cells (Plate 6.14), with some parietal cells and a few entero-endocrine cells. The bases are often curved and cut in cross-section as the glands are longer than the depth of the mucosa (Garven 1965) - Plates 7.14 and 7.17.

Oxyntic glands are made up of four distinct types of secretory cell which enable them to perform their functions -

i. zymogen cells
These are large, enzyme-secreting cells (Plate 7.15), that are pyramidal in shape, with their broad bases resting against the basement membrane (Ito 1967). Their cytoplasm is basophilic (Plate 7.15) and there are numerous zymogen granules, which contain pepsin, in the apical part of the cytoplasm (Plate 7.15). These are unstained with HE which gives this area of the cytoplasm a pale, granular appearance (Plates 7.15 and 7.16). The nuclei of the zymogen cells are spherical and are located towards their bases, where they are surrounded by a layer of denser basophilic cytoplasm (Plate 7.15), which gives the basal region its characteristic appearance (Plates 7.16 and 7.17). Occasionally zymogen cells with two or more nuclei may be seen.

ii. parietal cells
These cells secrete HCl and are characteristic of the stomachs of the whole of the order Mammalia (Ito 1967). They are most numerous in the isthmus and oxyntic glands (Plates 7.19 and 7.14), and some are also found in the bases of the glands (Plate 7.15). They are the largest of the glandular cells and are more rounded in shape, with abundant acidophilic cytoplasm (Plates 7.15 and 7.16). Parietal cell nuclei are spherical and are found in the centre of the cytoplasm. Usually there is only one nucleus per cell, but there may be more (Kelly et al. 1984).
iii. mucous neck cells

These cells are common in the neck regions of the glands, with occasional ones being found in the bases (Ito 1967). They are hard to distinguish in HE sections, but are easily recognized with PAS (Plates 7.20 and 7.21). The mucin droplets are scattered throughout the cytoplasm which is more basophilic than that of the surface cells. Mucous neck cells are relatively small and cuboidal and they tend to be deformed by the larger parietal cells. Their nuclei are large, with prominent nucleoli (Kelly et al. 1984) and are located towards the bases of the cells. Cytologically mucous neck cells are said to be very similar to the mucus-secreting cells of the cardiac and pyloric glands (Ito 1967).

iv. entero-endocrine cells

The entero-endocrine cells are usually found wedged underneath the zymogen cells in the bases of the glands (Plate 7.16). They are more numerous here than in the cardiac glands and have the same structure in all areas of the gastric mucosa.

The principal function of this region of the mucosa is the secretion of the proteolytic enzyme pepsin, which is produced by the zymogen cells. It is stored in the cytoplasm as the inactive form pepsinogen, which is activated extracellulary by contact with HCl from the parietal cells and previously formed pepsin (Guyton 1976). Pepsin is active only in acid media with a pH range of 2.0 - 5.0 (Guyton 1976). The mucus secreted by the mucous neck cells is resistant to the action of these substances. Small amounts of gastric lipase and amylase are also secreted by the oxyntic glands, but they appear to play a very minor role in gastric digestion. In primates the intrinsic factor that facilitates the absorption of vitamin B12 later in the intestines is produced by the parietal cells (Ito 1967).
4. the pyloric glands

The area occupied by the pyloric glands is about one fifth of the total area of the stomach mucosa (Ito 1967) and there is a poorly defined transitional zone between it and the oxyntic gland area. In this transitional zone the glands contain various combinations of the cells of the two gland types, until those of the oxyntic glands are entirely replaced by pyloric gland cells (Kelly et al. 1984, Whitehead 1985). The pits into which the glands open occupy half the thickness of the mucosa (Burki 1958, Ito 1967). They are deeper here than elsewhere in the stomach (Kelly et al. 1984) - Plate 7.3, compared with Plates 7.2 and 7.4. These glands are strongly branched in *Papio hamadryas* and other cercopithecids (Burki 1958) - Plate 7.24. This branching seems to be reduced near the pyloro-duodenal junction (Plates 7.3 and 7.23). In *Homo sapiens* they may be coiled towards their bases (Whitehead 1985) and some coiling occurs in *Papio cynocephalus* (Plate 7.3). Several pyloric glands may empty into the same pit (Whitehead 1985). The lamina propria is more obvious in this area, as the pyloric glands are not as tightly-packed as the oxyntic glands (Plates 7.3 and 7.14).

The cuboidal gland cells are arranged around a wide lumen (Plate 7.24). They have taller, more ovoid nuclei than the cardiac or mucous neck cells and they lie parallel to the long axis of the cell (Plate 7.24). In the basal regions of the glands the cells are tightly packed with mucin granules, that are PAS-positive (Plates 7.25, 7.26 and 7.4). This mucus protects the surface from enzyme activity (Guyton 1976). Entero-endocrine cells are reported to be most numerous in this area of the mucosa in the human stomach (Whitehead 1985), but did not appear to be so with *Papio cynocephalus* (Plate 7.24, compared with Plates 7.19 and 7.16).

5. the lamina propria

The lamina propria is the connective tissue of the tunica mucosa, which is found between the surface epithelium and the muscularis mucosae, filling the spaces in between the glands. It has essentially the same structure throughout the gastric mucosa, being made up of the following elements -

i. a fine network or mesh of collagen and reticular fibres (Plates 7.27 and 7.3), with some elastic fibres which are more concentrated near the muscularis mucosae (Burki 1958). With HE it is difficult to distinguish between the different types of fibre (Ham and Leeson 1961). The whole of the epithelial surfaces, both columnar and glandular, are supported by a basement membrane, that also is not stained with HE (Garven 1965). The function of all of these fibres is to provide a flexible support for the
whole tunica mucosa and to anchor it to the underlying tissues.

ii. within the fibre network there are large numbers of cells of varying types, including fibroblasts, macrophages, smooth muscle fibres, lymphocytes, plasma cells and small numbers of white blood cells (Ham and Leeson 1961) - Plate 7.27. The numbers of these "wandering cells" is variable and may depend upon conditions in the lumen of the stomach, for example there are marked increases in the numbers of eosinophils with nematode infections (Chapter 8, Section 2).

iii. blood and lymph capillaries are numerous, but hard to distinguish as their thin walls collapse during the preparation of sections. The blood supply to the mucosa comes from the arterial plexus in the submucosa (Plates 7.28 and 7.30). Small arteries pass through the muscularis mucosae to supply these rich capillary beds (Ito 1967). The capillaries drain into small veins, which ultimately drain into the submucosal venous plexus (Plate 7.29). These vessels run together with fine, unmyelinated nerves in neuro-vascular bundles. The nerve fibres, which come from autonomic plexuses in the submucosa, are difficult to see in routine sections.

iv. lymph nodules are a characteristic feature of the gastric lamina propria and large ones are found in both the cardiac (Plate 7.6) and pyloric regions (Plate 7.23). They have diffuse borders and lymphocytes invade the nearby regions of the mesh (Plates 7.12B and 7.29). It is thought that they protect the underlying tissues from microbial invasion if the surface epithelium is broken (Ham and Leeson 1961). This is achieved by filtering any micro-organisms from the interstitial fluid and destroying them by phagocytosis and/or the production of antibodies. These areas have a characteristic dark, speckled appearance in sections (Plate 7.6) that is due to the basophilic nuclei of the lymphocytes, which are closely packed as they have little cytoplasm (Plate 7.29). The larger nodules may have paler germinal centres (Plate 7.29), where the production of lymphocytes and plasma cells occurs (Ham and Leeson 1961). Lymph nodules may be entirely confined to the lamina propria (Plate 7.29B), or may break through the the muscularis mucosae into the submucosa (Plate 7.6).

The lamina propria is most obvious in the cardiac (Plate 7.6) and pyloric (Plate 7.22) areas, as the glands are further apart. In the oxyntic area they are so tightly packed that it is reduced to fine strands of fibres between the secretory units (Plates 7.19 and 7.31).

6. the muscularis mucosae

This layer of smooth muscle fibres, with some elastic fibres, forms the junction between the mucosa and the submucosa (Plate 7.11). It is 0.05 - 0.001mm thick in adult humans (Klein 1870) and 0.016 - 0.047mm in Papio cynocephalus (Table 8.2). The fibres are
which is most likely to be glycogen in animal tissues (Ham and Leeson 1961). This seemed to be an unusual finding, until I remembered some lecture notes that I wrote in 1980, while teaching reproductive anatomy and physiology to midwifery students at a local hospital; unfortunately only the notes remain, not the sources. The human vagina is lined by a similar nonkeratinized stratified squamous epithelium that produces glycogen. This glycogen is metabolized by Doderlein's bacillus, a lactogenic bacteria (Garven 1965). This creates an acidic environment that protects the body from invasion by pathogenic bacteria, which could enter via the lumen of the uterus and oviducts. Most pathogens require a pH of 6-7, which is the pH of blood and tissue fluids. It would seem that a similar situation might occur in the oesophagus, for the presence of a stratified squamous epithelium suggests that added physical protection is needed for the underlying tissues. Garven (1965) also mentions that lymphocytes invade the vaginal epithelium; they are also found in the oesophageal epithelium (Plate 7.36).

Non-keratinized, stratified squamous epithelia are found on wet surfaces that are subjected to considerable wear and tear (Ham and Leeson 1961). This is the prime function of the oesophageal mucosa and it is kept moist by secretions from glands in the submucosa. The continual division of cells in the basal layer ensures that damaged cells are replaced rapidly (Ham and Leeson 1961). No submucosal glands were seen in the junction area in *Papio cynocephalus*, and Klein (1870) noted that this was generally the case. In *Homo sapiens* some of the cardiac glands may extend under the oesophageal mucosa (Kelly et al. 1984), but this was not observed either, the junction being very clear cut (Plate 7.39).

8. the pyloro-duodenal junction

There is also an abrupt change in the form of the mucosa (Burki 1958, Garven 1965, Kelly et al. 1984), but it is not as dramatic as in the cardio-oesophageal junction. There is a narrow transitional zone (Plates 7.23 and 7.42) in which the glands shorten and become more crypt-like (Klein 1870), and acini of mucus-secreting glands are found in the submucosa (Plate 7.45). Goblet cells appear in the surface epithelium (Plates 7.40 and 7.42) and in the walls of the pits, and the apical cytoplasm of the tall columnar cells is no longer packed with mucin granules (Plate 7.42). Eventually well-defined villi are present (Plates 7.43 and 7.44). Lymph nodules are present both in the lamina propria and the submucosa, so that the muscularis mucosae is not as clear is in other areas (Plate 7.23). In this region there is a rapid increase in the thickness of the mucosa from the pylorus to the duodenum.
arranged in -

i. a circular layer, against the lamina propria, that is very thin (Plates 7.11B) and often difficult to distinguish (Plates 7.15 and 7.32).

ii. a thicker longitudinal layer on the submucosal side (Plate 7.11B). Strands of smooth muscle fibres pass up from the muscularis mucosae into the lamina propria between the glands (Plates 7.13B and 7.33), eventually becoming attached to the basement membrane underneath the surface epithelial cells (Garven 1965). The gastric muscularis mucosae is continuous with that of the oesophagus and the duodenum (Ito 1967). It forms a complete layer that is broken at intervals by lymph nodules (Plate 7.6) and neuro-vascular bundles (Plate 7.32).

Contraction and relaxation of the fibres in the muscularis mucosae will change the depth and folding of the mucosa, which helps to to increase the surface area in contact with the chyme (Guyton 1976). It also seems that such movements would assist in the emptying of the secretions from the gastric glands, especially contractions of the fibres attached to the basement membrane. This was a personal observation, as no mention was made of this function in the literature. Guyton noted that the contractions of the muscularis mucosae were stimulated by impulses from the inter-mural plexuses and the sympathetic nervous system. Such contractions will also aid in moving the contents of the stomach away from the wall, thus preventing physical damage to the mucosa (Burki 1958).

7. the gastro-oesophageal junction

There is an abrupt change in the mucosa at the junction between the oesophagus and the cardiac region of the stomach (Ham and Leeson 1961, Garven 1965, Kelly et al. 1984) - Plate 7.14. The surface epithelium of the oesophagus is a non-keratinized stratified squamous one (Plates 7.35 and 7.37A) and the lamina propria is fine mesh (Plate 7.35) that extends into the papillae that attach the epithelium to the membrane (Plate 7.36). The basal cells are closely-packed and columnar in shape (Plate 7.36B), as in Homo sapiens (Ham and Leeson 1961). As these cells are pushed towards the surface they become polyhedral and then squamous in shape (Plate 7.36). There appear to be two layers in this epithelium (Plate 7.35) -

i. an inner layer in which the cells are more compact, their nuclei are paler and more open and their cytoplasm is denser.

ii. the surface layer is more "ragged", the nuclei of the cells are darker and cytoplasmic breakdown is occurring. This is probably the normal appearance of this epithelium, which may function as an outer protective layer. The pink colour of the cells in this area (Plate 7.38) when stained with PAS indicates the presence of polysaccharides,
The preservation of the entire mucosal layer was excellent in this stomach, making it very easy to make comparisons with information about the mucosa in other catarrhines. The histology of the gastric mucosa in *Papio cynocephalus* is essentially the same as that of the human stomach (Ham and Leeson 1961, Garven 1965, Kelly et al. 1984, Whitehead 1985) and in other cercopithecids (Burki 1958), as well as other mammals with unilocular stomachs (Ito 1967). The major histological difference between all of them is the extent of the various glandular areas (Bensley 1902, Burki 1958, Ito 1967), which may be related to differences in their diets.
HISTOLOGY OF THE MUCOSA IN THE STOMACH OF *PAPIO CYNOCEPHALUS*: THE PLATES
1. THE SURFACE EPITHELIMUM AND GASTRIC PITS

PLATE 7.2
Surface epithelium and pits from the oxyntic gland area.
The epithelium lining the lumen of the stomach consists of a single layer of closely-packed columnar cells. The apical regions of their cytoplasm are filled with mucin that does not stain with HE (S arrows). The elongate nuclei are found in the bases of the cells. The cells in the bases of the pits are more cuboidal in shape (L arrow).
HE (x250)

PLATE 7.3
Surface epithelium and pits from the cardiac gland area.
The surface of the mucosa is covered with a layer of mucus. The height of the surface mucous cells is greater in this region, and they are not as tightly packed in the pits, so that the bases of the cells are wider and the nuclei more ovoid (L arrow). The pits in this region of the mucosa are deeper than in the oxyntic gland area. More lamina propria is evident and the fibre mesh is packed with lymphocytes. Some fibroblast nuclei can be distinguished (S arrow to right) and entero-endocrine cells can be seen in the bases of the pits (S arrow to left).
HE (x250)
PLATE 7.4
Surface epithelium and pits from the pyloric gland area.
The pits, which are invaginations of the surface epithelium, are deeper in this region. The lamina propria, which supports these structures, is not as cellular as that in the cardiac area, but it still contains many lymphocytes. A number of entero-endocrine cells can be seen near the bases of the pits. They are small clear cells with centrally placed nuclei, found underneath the mucus-secreting cells (S arrows). The surface mucous cells are tightly packed. HE (x100)

PLATE 7.5
Surface epithelium from the pyloric area.
The mucin in the epithelial cells is stained a deep magenta. It is confined to the supra-nuclear cytoplasm, and the individual droplets give it a granular appearance. This distribution and intense staining of the mucin is characteristic of these epithelial cells in the gastric mucosa. Small clear entero-endocrine cells are present in the upper parts of the glands. The lamina propria is fibrous and there are few lymphocytes present; oval fibroblast nuclei can be seen. HE (x250) PAS
PLATE 7.6
The mucosa of the cardiac region.

A. The mucosa is thinner where there are no lymph nodules present. The pits occupy about half the mucosal thickness, and many are large and duct-like (S arrow). The fibre mesh of the lamina propria contains numerous lymphocytes, and the muscularis mucosae is thick. The submucosa contains clumps of fat cells (L arrow) and above them is a group of blood vessels.
HE (x100)

B. A large lymph nodule extends from the mucosa into the submucosa in this section. Strands of smooth muscle fibres can be seen in the nodule (S arrow). The glands have been pushed aside by the lymphoid tissue, and are not as closely packed. A large lymph vessel borders the nodule in the submucosa (lower L arrow). A duct-like pit, filled with mucus (upper L arrow), is evident on the lumen surface.
HE (x100)
C. Detail of the lymph nodule in Pl. 7.6A; the lymph nodule occupies a large volume of the lamina propria in this region. The muscularis mucosae is diffuse and reduced to strands running through the nodule. Endothelial cells (arrows) in the wall of the lymph vessel can be seen, and it contains a few lymphocytes. No germinal centre is evident in this nodule.

HE (x250)
PLATE 7.7
The mucosa of the cardia, showing the presence of mucopolysaccharides in the various secretory cells. The surface mucous cells contain more mucin than the gland cells. The pits have large diameters in this region of the mucosa, and the glands are closer together where no lymph nodules are present. The muscularis mucosae is thick, and clumps of fat cells can be seen in the submucosa.
PAS (x100)

PLATE 7.8
Surface mucous cells in the cardia. These cells are not as densely stained as those in other areas, for they appeared to contain less mucin. The surface of the mucosa is covered by a layer of mucus, and many of the surface cells were depleted of their mucin (L arrow), suggesting that there might have been differences in secretory activity between this and other areas of the mucosa. Entero-endocrine cells can be seen in the upper parts of the glands (S arrow). The fibre network of the lamina propria is clear in this section.
PAS (x250)
A. The cardiac glands have relatively wide lumina and may be branched (S arrow). The cells in the upper of the glands contain mucin scattered throughout their cytoplasm, while only scattered cells in the bases contain this substance. These cells are columnar, with basophilic cytoplasm and spherical nuclei. Their staining reaction with PAS seems to be different from that of the pyloric gland cells (Pl. 7.25). Strands of smooth muscle fibres from the muscularis mucosae pass up into the lamina propria (L arrow). PAS (x250)

B. The mucin granules in the cells of the cardiac glands are not as tightly packed as those in the mucus-secreting cells of other gastric glands, suggesting differences in either secretory activity or function. The lamina propria contains a variety of cell types. Entero-endocrine cells are common in the glands (S arrow). PAS (x250)
PLATE 7.10
Detail of the surface of the cardia.
The surface mucous cells vary in height from columnar to cuboidal in the bases of the pits. The apical cytoplasm in the gland cells is granular in appearance, which suggests that their mucin droplets are not as tightly packed as those in the surface cells. The nuclei of the gland cells are ovoid or flattened along their bases.
HE (x400)

PLATE 7.11
Detail of the bases of the cardiac glands.
The granular, more basophilic appearance of the cytoplasm of the gland cells is evident, and the two layers of the muscularis mucosae can be seen. A bundle of smooth muscle fibres passes from the circular layer into the connective tissue of the lamina propria.
HE (x250)
PLATE 7.12
Detail of the large duct at the
gastro-oesophageal junction

A. Many pits open into this large duct-like structure. Coiled cardiac glands open into their bases (arrows). The lamina propria contains large numbers of lymphocytes, and the two layers of the muscularis mucosae are clearly defined.
HE (x100)

B. The same structure stained with PAS shows that its lumen is filled with mucus, that spills out on to the epithelial surface. Some of the secretory units of the cardiac glands appear to be underneath the muscularis mucosae of the oesophageal mucosa (arrows). They could be mistaken for submucosal glands. A large lymph nodule, with a paler germinal centre, can be seen in the lamina propria and submucosa.
PAS (x100)
The pit and gland cells of the cardiac area of the mucosa

A. The differences in the staining reactions, due to the distribution and abundance of secretory granules can be seen in this section. The cells in the bases of the pits are more cuboidal in shape than those on the surface. More entero-endocrine cells are present in this region of the glands (arrow), than in the bases. The glands are coiled, and the layers of the muscularis mucosae are clear.
HE (x250)

B. Smooth muscle fibres can be seen entering the lamina propria (S arrows). Some entero-endocrine cells are evident in the bases of the glands, but they are not as numerous as in the upper regions of the mucosa. The position of a capillary in the lamina propria is shown by the L arrow. The differences between gland cells and surface cells is distinct.
HE (x400)
PLATE 7.14
The oxyntic glands of the gastric mucosa.
The three areas of the mucosa in this region are easily distinguished, and this appearance is due to differences in cell types in each. The glands are much longer and more tightly packed than those in other parts of the mucosa. Their bases are coiled and bent against the muscularis mucosae.
HE (x100)
The bases of the oxyntic glands. The principal cell type in the bases of these glands is the enzyme-secreting zymogen cell (L arrows). These cells have spherical basal nuclei, that are surrounded by basophilic cytoplasm. Their supranuclear region contain pepsinogen granules, which give this region of the cytoplasm its paler appearance. Acid-secreting parietal cells are also found in the bases of the glands (S arrows). They are the largest of the gland cells, with centrally placed nuclei and paler acidophilic cytoplasm.

HE (x400)
PLATE 7.16

Bases of the oxytic glands.
The coiling of the bases of the glands, and the reduction of the lamina propria are evident. There are numerous parietal cells, at the junction with the isthmus area is shown. Entero-endocrine cells are also numerous (arrow).

HE (x400)
A. Pit and neck regions.

The pits of these glands are shallow, and are lined with surface mucus cells. Parietal cells predominate in the neck region (5 arrow). Mucous neck cells can be recognized by their deformed nuclei. Their mucin does not stain with HE.

B. Neck and isthmus regions.

The large parietal cells predominate in this region. Mucous neck cells are scattered between them. The pale cytoplasm of the parietal cells gives this region its characteristic appearance.

C. Basal region.

Here the zymogen cells are the most numerous cell type. They have dark basophilic cytoplasm. The glands are bent against the muscularis mucosae, which is thin in the oxyntic area.
PLATE 7.18
Surface epithelium and pits in the oxyntic gland area.
The surface mucous cells contain more mucin than the mucous neck cells. Remnants of mucus from these cells are found on the surface and in the pits. Cells in various stages of activity can be seen, like those without mucin (arrow). The lamina propria is sparse, but there is more in this area than between the glands. PAS (x250)

PLATE 7.19
The middle section of the oxyntic gland area.
There are more mucous neck cells in the region immediately beneath the pits. These cells tend to be squashed between the parietal cells (S arrows) and the entire cytoplasm is filled with mucin, unlike that in the surface mucous cells. The glands are tightly packed and there is little lamina propria evident. The path of a capillary near the bases of the glands is marked by a regular row of mast cell nuclei (L arrows). PAS (x250)
PLATE 7.20
The oxyntic glands of the gastric mucosa.
The differences in the staining properties and the distribution of mucus-secreting cells can be seen in this plate. The muscularis mucosae is thin compared to that in other areas. The clear areas between the glands mark the position of blood vessels in the lamina propria, and contain muscle fibres from the muscularis mucosae (arrow).
PAS (x100)
PLATE 7.21
Detail of the secretory cells in the oxyntic glands.

A. The mucous neck cells (arrows) are said to be similar to the mucus-secreting cells of the cardiac and pyloric glands. They are smaller and contain mucin granules throughout their cytoplasm. They are squashed between the larger parietal cells, giving them a variety of shapes. The parietal cells are large and pale, with centrally placed nuclei.
PAS (x250)

B. In this photograph of the basal regions of these glands a small amount of lamina propria can be seen. It contains lymphocytes (L arrow) and some smooth muscle cells. Parietal cells are found in the gland bases (S arrows), and the lower one has two nuclei.
PAS (x250)
4. THE PYLORIC GLANDS

The pyloric glands. The mucosa in the pyloric area was folded. The pits are deeper than in other areas, and the muscularis mucosae is relatively thick. It is broken at intervals by blood vessels entering the lamina propria (L arrow). The glands are branched and some coiling is evident (S arrows). HE (x100)
The transition zone between the pyloric and duodenal mucosae. The pyloric glands are not as branched in this area, and the epithelium changes from the typical stomach type (S arrow on right), to that of the intestine with individual goblet cells (S arrow to left). The glands underneath the gastric epithelium also contain goblet cells (L arrow). A lymph nodule and abundant lymphocytes are found in the lamina propria. Submucosal glands are present (M arrow). HE (x250)
A. The cytoplasm of the secretory cells is filled with mucin, giving it a granular appearance and flattening the nuclei against their bases (S arrow). Entero-endocrine cells are more numerous in the upper parts of the glands (upper L arrow), than in the bases. The glands are branched (lower L arrow), and the two layers are visible in the muscularis mucosae. HE (x250)

B. At this magnification the cytoplasm of both surface mucous cells (L arrow) and gland cells has a granular appearance, due to the presence of mucin droplets. Entero-endocrine cells are present in the bases of the glands (M arrow), and lymphocytes are common in the lamina propria. A capillary lined with endothelial cells runs towards the pit area (S arrows). HE (x400)
PLATE 7.25
Distribution of mucopolysaccharides in the pyloric mucosa.
Both the gland cells and the surface epithelium stained deeply. The surface cells contain more mucin, giving their cytoplasm a more homogenous appearance.
PAS (x100)

PLATE 7.26
Detail of the mucosa in the pyloric region.
The mucin in the gland cells is distributed throughout the cytoplasm, pushing their nuclei into the bases (S arrow). Cells in the region between the bases of the glands and the pits are columnar and contain little mucin (L arrow). The lamina propria is fibrous and contains the usual cell types.
PAS (x250)
5. THE LAMINA PROPRIA

PLATE 7.27
The lamina propria of the cardiac mucosa.
Lymphocytes are the predominant cell type in this section of the mucosa, and make it difficult to distinguish any of the others. Smooth muscle fibres from the muscularis mucosae enter the lamina propria (arrows) and pass upwards to the surface epithelium.
HE (x250)

PLATE 7.28
Blood vessels in the lamina propria of the oxyntic region.
The smaller arrows indicate the position of a vein that drains blood away from the capillary beds of the lamina propria. Capillaries are difficult to distinguish as their walls collapse during preparation of the sections. These veins will eventually drain into the submucosal plexus. Strands of muscle fibres pass upwards from the muscularis mucosae (L arrow).
HE (x250)
PLATE 7.29
Lymph nodules In the lamina propria.
A. Lymphocytes are small cells that produce antibodies. Their nuclei are densely stained and are surrounded by a small rim of cytoplasm, that is unstained with HE. Nodules, like this one from the cardiac mucosa, are composed almost entirely of lymphocytes, but occasionally other types, like reticulo-endothelial cells can be seen in them (L arrow). They are phagocytes which are fixed to the connective tissue fibres that form the basis of the nodule. A small lymph vessel run underneath the muscularis mucosae (S arrows).
HE (x256)

This is part of a larger lymph nodule with a paler germinal centre, where the nuclei of reticulo-endothelial cells can be seen (L arrow). The nuclei of the lymphocytes are smaller and denser (M arrow).
HE (x400)
PLATE 7.30
Vessels of the submucosal plexus. Arteries with muscular walls (S arrow) run with the thinner-walled veins (L arrow) in the connective tissue of the submucosa. They are filled with blood cells and plasma. Nerves usually accompany the vessels, but they are difficult to see in sections stained with HE.
HE (x100)

PLATE 7.31
Lamina propria in the oxyntic area. The oxyntic glands are tightly packed, so that they support each other and there is little lamina propria between them. The need for protection against micro-organisms is not as great in this area, as they would be destroyed by the glandular secretions.
HE (x250)
6. THE MUSCULARIS MUCOSAE

Plate 7.32
The muscularis mucosae in the oxyntic area of the mucosa. The muscularis mucosae is thinnest in this region, and it consists mainly of longitudinal fibres. Blood vessels run through the muscularis mucosae to enter the lamina propria (arrows). HE (x250)

Plate 7.33
Detail of the muscularis mucosae in the oxyntic area. Only longitudinally arranged fibres are evident (S arrows). There is a small blood vessel immediately above the muscularis mucosae (L arrow). HE (x400)
PLATE 7.34
The stratified squamous epithelium of the gastro-oesophageal junction. This is a continuation of the oesophageal mucosa, and it consists of two regions; a basal one where the living cells are being pushed towards the surface by the division of cells in the deepest layers, and an outer protective one where the cells are flattened, dying and constantly being shed. HE (x250)

PLATE 7.35
The junction between cardiac and oesophageal mucosae. The junction between these two types of epithelia is abrupt, with no transition zone. There are more lymphocytes in the lamina propria underneath the cardiac glands, and the cytoplasm of a number can be seen (arrow). Lymphocytes are also present inside the stratified squamous epithelium (arrow). HE (x400)
PLATE 7.36
The lamina propria underneath the stratified squamous epithelium.
The papillae that attach the epithelium to the lamina propria are long and tapering. The lamina propria is fibrous and contains few lymphocytes. A number of these cells are found within the stratified squamous epithelium (S arrows). No submucosal glands were present in the junction.
HE (x250)
all of the regions within the stratified squamous epithelium.

A. The cells in the upper region, near the lumen surface, are desquamating. Their appearance suggests that they contain some keratin.

HE (x400)

basal cells of this epithelium are flat in shape and tightly packed. As they are pushed upwards by the division of the basal cells, they become polyhedral, and then flatten.

of cells that have recently divided are seen (L arrow) and changes in the occur as the cells age. columnar cells

erythrocytes are found within the lumen (S arrow).
PLATE 7.38
Stratified squamous epithelium of the gastro-oesophageal junction.
The upper layers of the epithelium are stained pink with PAS, indicating the presence of a polysaccharide like glycogen. This may have a protective function. Cellular debris and some mucus from nearby cardiac glands can be seen on the lumen surface (S arrow). There is a small lymph nodule in the submucosa (L arrow). PAS (x250)

PLATE 7.39
The gastric side of the junction.
There was a large duct-like structure in this area, with many pits opening into it. The lumen contained large quantities of mucus that was being liberated on to the lumen surface. Such structures would help to increase the amount of secretory tissue in the mucosa. PAS (x100)
Gastric pits in the transition area. The surface epithelium changes from the gastric type to the intestinal type, with mucus-secreting goblet cells (S arrow). These can be seen discharging their secretions into the pits. The lamina propria contains numerous lymphocytes, and a small capillary can be seen (L arrow). HE (x400)

The submucosal glands on the duodenal side of the junction. These mucus-secreting glands are a characteristic feature of the duodenum. The acini are arranged in lobules separated from each other by septa of connective tissue. Blood vessels to the lobules run in the septa (arrow). The apical cytoplasm of the gland cells is granular, indicating the presence of mucin droplets. The nuclei are flattened against the bases of the cells by their accumulating secretions. HE (x400)
PLATE 7.42
The pyloro-duodenal junction.
The change from the pyloric to duodenal mucosa is abrupt (arrow), and the characteristic cell differences show more clearly with PAS. Folding of the mucosa is evident from the arrangement of the gastric pits in the lower part of the photograph.
PAS (x100)
PLATE 7.43
VIII of the duodenal mucosa.

A. Villi mark the beginning of the small intestine, and the finger-like extensions of the mucosa increase the surface area to aid in the absorption of nutrients. The connective tissue cores of the villi contain numerous lymphocytes and capillaries. Mucus on the surface of the epithelium is secreted by the submucosal glands and the goblet cells.
HE (x250)

B. The surface epithelium consists of tall, columnar cells, with goblet cells scattered among them (S arrows). These cells are in various stages of secretory activity. The free surfaces of the columnar cells have striated borders (M arrow). These are due to the presence of microvilli, which increase the surface area for absorption. A number of lymphocytes have invaded the epithelial layer.
HE (x400)
A. The distribution of the mucus-secreting cells is quite different from the gastric mucosa. The goblet cells are scattered throughout the epithelium and are fewer in number. The submucosal glands produce substantial amounts of protective mucus.

PAS (x250)

B. Mucin in the goblet cells is not as tightly packed as in the surface mucous cells of the stomach. The striated borders of the epithelial cells is clearer as mucus will have been trapped between the microvilli.

PAS (x400)
The lower part of the duodenal mucosa.

A. The crypts, which are found between the villi, are pit-like in form and extend to the muscularis mucosae. They contain goblet cells. Acini of the submucosal glands lie under the muscularis mucosae. HE (x400)

B. The acini of the submucosal glands are clustered into lobules. The cells are packed with mucin, that flattens their nuclei. Entero-endocrine cells are found in the walls of the crypts (arrow). PAS (x250)
Chapter 8
The histology of the mucosa of the stomachs of the members of the family Colobidae

Only ten of the papers on colobid stomachs have included histological data in their anatomical descriptions; the first of these descriptions was in Duvernay’s paper on *Semnopithecus entellus* in 1834. The studies of Kuhn (1964) and Peng et al. (1983) are the most detailed, and in the major emphasis was placed on this aspect of the anatomy. Studies of the histology of the stomach in these monkeys are hampered by the rapid degeneration of the mucosa that occurs after death (Berenberg-Gossler 1911, Kuhn 1964). This is a normal occurrence with mammalian stomachs (Bensley 1902, Whitehead 1985), but it appears to be more rapid in colobids because of the presence of the bacteria in the fermentation chambers. It is likely that fermentation would continue after death, until the rising organic acid concentrations limit bacterial activity (Bauchop 1978A). This chapter begins with a detailed review of the literature on the histology of the gastric mucosa in colobids, which is followed by observations on the form of the mucosa in *Presbytis femoralis*.

Section 1. The histology of the mucosa in the stomachs of the Colobidae

The three main types of gastric gland are found in the mucosa of the colobid stomach, but their distribution is somewhat different from that in the rest of the Catarrhini. This is related to the general morphology of these plurilocular stomachs and their functioning as fermentation chambers (Figure 3.3). The distribution of the various glands corresponds poorly to the anatomical divisions of the stomach (Table 8.1).

1. the surface epithelium and the gastric pits
   
   In colobids, like other catarrhines, the surface of the lumen is lined by a single layer of mucus-secreting columnar epithelium (Burki 1958, Kuhn 1964, Peng et al. 1983, Suzuki et al. 1985). Peng et al. (1983) described the "bubbly" appearance of the supra-nuclear cytoplasm with HE, which was due to the presence of unstained mucin droplets, which stained with PAS. Kuhn (1964) noted that the mucus produced by these cells covered the entire inner surface of the stomach, and he was able to remove it from the mucosa in freshly-killed specimens. This suggests that it was viscous and gel-like in consistency like that in other catarrhines. The pits are invaginations of the surface epithelium and are lined with surface mucous cells (Kuhn 1964).
2. the mucosa of the praesaccus

In the stomachs of *Nasalis larvatus* (Homborn and Jacquinot 1845, Hollihn 1971, Langer 1988) and *Pygathrix nemaeus* (Pilliet and Boulart 1898, Hollihn 1971) the praesaccus was lined with a nonglandular stratified squamous epithelium. This means that this mucosa was quite different from that reported to line the praesaccus in *Rhinopithecus* (Peng et al. 1983) and *Procolobus* (Kuhn 1964). In these the mucosa in this chamber was of the cardiac type. Stratified squamous and cardiac epithelia are quite distinct and there is little chance of confusing them in sections (Plate 7.34), even in poorly preserved material (Plate 8.32). Further material, particularly from the Asian genera, is needed to verify these descriptions.

3. the cardiac glands

The cardiac glands are the principal gland type in the colobid gastric mucosa, as they line the saccus and the caudal two-thirds of the tubus gastricus (Pilliet and Boulart 1898, Kuhn 1964, Peng et al. 1983, Suzuki et al. 1985). In *Trachypithecus francoisi* the average depth of the cardiac mucosa was 0.4 - 0.6mm, and the length of the glands was 0.1 - 0.2mm (Suzuki et al. 1985), which means that the pits were quite deep in this area. The tubular glands open into the bottom of the pits and there was little coiling or branching of the secretory units (Kuhn 1964, Suzuki et al. 1985). In *Trachypithecus auratus* most of the glands reach to the muscularis mucosae, and may bend so that their ends ran parallel to it (Kuhn 1964). The gland cells were columnar with round to oval nuclei in their bases. The cytoplasm had the typical "bubbly" appearance that was due to the presence of mucin (Peng et al. 1983). They stained with PAS (Kuhn 1964, Peng et al. 1983), although Kuhn mentioned that the staining reaction was not as pronounced as in the surface mucous cells. He also found there was a zone of fine granules in the cytoplasm between the nucleus and the apical mucin, that stained with Best's carmine. These had also been seen in the stomachs of other cercopithecoids (Kuhn 1964). Best's carmine stains glycogen (Garven 1965), which suggests that these cells may store this polysaccharide for the production of the mucopolysaccharides that they secrete in the mucus. Occasional parietal cells are seen in these in the cardiac glands (Kuhn 1964).

4. the oxyntic glands

The region containing the oxyntic glands is found in the caudal third of the tubus gastricus (Kuhn 1964, Peng et al. 1983, Suzuki et al. 1985) and they cover a relatively smaller area than in the rest of the catarrhines (Burki 1958). The oxyntic glands are tightly packed together, with their average depth in the mucosa of *Trachypithecus francoisi* being 0.48mm (total mucosal depth 0.5mm) - Suzuki et al. 1985. The secretory units reach to
the muscularis mucosae and three zones could be recognized - the pit region, a middle section with numerous parietal and mucous neck cells, and a basal section with zymogen cells (Kuhn 1964, Peng et al. 1983), like those in the same glandular area of *Papio cynocephalus*. The apical cytoplasm of the mucous neck cells and those in the isthmus of the glands was PAS-positive and it was tightly packed with mucin droplets (Kuhn 1964). In *Trachypithecus francoisi*, as in other species, the glands were straight and there was little coiling of the secretory units (Suzuki et al. 1985).

5. the pyloric glands

The transition between the oxyntic and the pyloric gland areas occurred at the level of the cranio-dorsal fold in the pylorus (Kuhn 1964). Here the pits were deeper and the glands are branched; the mucosal thickness in *Trachypithecus francoisi* was 0.4mm and the length of the glands was 0.15mm (Suzuki et al. 1985). The cells stained in the same way with PAS and Best's carmine as those in the cardiac region (Kuhn 1964). They were tall and columnar in shape with light-coloured "bubbly" cytoplasm when stained with HE (Peng et al. 1985).

6. the lamina propria

In the saccus of *Trachypithecus auratus* Kuhn (1964) reported that the lamina propria was a delicate fibre mesh filled with phagocytes and eosinophils. Lymph nodules were common in this region, but there were fewer in the lamina propria in other regions of the stomach (Kuhn 1964, Peng et al. 1983). Burki (1958) said that there were none in the oxyntic gland area, while Kuhn said that the numbers were reduced. The lamina propria contains abundant blood vessels and nerve fibres (Peng et al. 1983). It is sparse in the oxyntic gland region, where the glands are tightly packed, and the mesh contained fewer "wandering" cells (Burki 1958).

7. the muscularis mucosae

The muscularis mucosae formed a complete layer in most regions and none of the glands penetrated it, but lymph nodules did pass through it into the submucosa (Kuhn 1964). Peng et al. (1983) noted that in *Rhinopithecus* that the muscularis mucosae was thicker in the cardiac gland regions than elsewhere. The muscularis mucosae in the stomach was continuous with that of the oesophagus (Peng et al. 1983).

8. the cardiac shield

The epithelium covering the cardiac shield is non-keratinized stratified squamous (Duvernoy 1834, Kuhn 1964, Peng et al. 1983), and its border with the saccus
epithelium is sharp (Kuhn 1964, Zhang et al. 1988). In *Trachypithecus auratus* Kuhn noted the presence of submucosal glands; Zhang et al. (1988) said that there were none in *Rhinopithecus*. These authors also differed from Kuhn, who wrote that in *T. auratus* the lamina propria was broken. In the Chinese snub-nosed monkeys it was not, and was quite broad. The tubular cardiac glands in this region were short and branched and their cells were PAS-positive (Zhang et al. 1988). The stratified squamous epithelium of the shield did not suffer as much from post mortem degeneration as the neighbouring cardiac mucosa, according to Kuhn (1964).

9. the sulcus ventriculi

This groove, which runs along the inner surface of the lesser curvature of the stomach, is lined with cardiac-type mucosa, like the areas that it passes through (Kuhn 1964).

These descriptions cover a range of species (Appendix 1) and, although the amount of information they contain is small, it is clear that histologically the structure of the glands in the mucosa of colobid stomachs is essentially the same as those in other catarrhines. The major histological difference between them is the extent of the cardiac gland area, which is perhaps an adaptation to a more folivorous diet in these monkeys and to the requirements of providing a suitable environment for holding a population of cellulolytic bacteria in the gut. It appears that the secretions from these glands might be involved in the maintenance of the correct pH for bacterial metabolism (Kay et al. 1976). The mucus, as it is thin and watery, would also contribute fluid to assist in liquifying the chyme. This is also a necessary requirement for bacterial fermentation, which is extracellular (Bergman 1990).

The major difference in stomach morphology between members of the family Colobidae is the presence or absence of a praesaccus. Within those genera with a praesaccus there was the unexpected finding, from the literature, that this chamber is lined with a nonglandular epithelium in *Nasalis larvatus* and *Pygathrix nemaeus*. This raises some interesting questions about the phylogenetic relationships within the Colobidae. The stratified squamous epithelium would provide mechanical protection in this storage area, but why it is found in some and not in others is obscure; it may perhaps be related to differences in diet. *Nasalis larvatus* is a folivore/frugivore, with the main components of its diet being leaves (52 percent) and fruit, including seeds (40 percent) - Yeager (1989). This is similar to the diet of *Colobus satanas*, which consumes 58 percent seeds and 37 percent leaves (McKay 1978), but does not have a praesaccus. *Procolobus badius*, another species with a praesaccus, eats 73 percent leaves, with the remainder being predominantly fruit and flower parts (Struhsaker 1978). The diets of the Chinese species probably include bamboo, and in the winter when little else is available the
needles and bark of pines (Li et al. 1982, Poirier 1983). All of these are harsh and woody (Table 2.2). In these monkeys the praesaccus is lined with cardiac glands. At this stage, from the data available, the adaptive significance of this mucosal difference is not really clear and might be related to other dietary factors, like levels of secondary compounds in the main food sources or the need for increased gastric storage of food.

Kuhn (1964) recorded the presence of whipworms (Trichuris sp.) in the stomachs of all of his specimens of Procolobus (in the praesaccus and saccus) and in the one specimen of Trachypithecus auratus (in the saccus) that he studied. It is possible from his descriptions of the histology of the mucosa that these monkeys showed pathological changes related to the presence of these worms. Trichuris is a nematode parasite of humans and other primates (Manson-Bahr 1966) and it is not uncommon in colobids, both in captivity and in the wild (Kuhn 1964, Manson-Bahr 1966, Hollihn 1971, Palmieri et al. 1980, Loomis and Wright 1986). The adult worms are found in the lower parts of the colon in most of other primates (Wakelin and Lee 1987), but in colobids they are found in the first chambers of the stomach. Loomis and Wright (1986) thought that this area would provide an ideal environment for the worms, with its neutral pH, and the slow rate of passage of food through the stomach might also be important. The larval stages develop within the tissues of the lamina propria, while the adults are found attached to the surface of the mucosa by their long, tapering oesophageal regions which are inserted into tunnels within the epithelial cells (Wakelin and Lee 1986). The presence of Trichuris in a number of primates is associated with weight loss, moderate eosinophilia (Levine 1968, Wakelin and Lee 1987), increased mucus production, defective absorption (Wakelin and Lee 1987) and pronounced general inflammation of the mucosa with tissue oedema (Klein et al. 1970). Loomis and Wright described the permanent tissue damage that was the result of a long-term trichurid infection in Colobus guereza.

Kuhn mentioned some unusual findings in his description of the histology of the mucosa in these infected monkeys. They included the following:

1. In Procolobus verus and Procolobus badius the form of the epithelial lining of the praesaccus, saccus and upper part of the tubus was described by Kuhn (1964) as stratified columnar. This type of epithelium is extremely rare and in humans is found lining the ducts of few glands and a small portion of the male urethra (Ham and Leeson 1961, Garven 1965), so it seems unlikely that it would be found anywhere in the normal gastro-intestinal tract. There are two possible explanations for Kuhn's observation:
   i. In Figure 6 of Kuhn's paper (Plate 8.1) it appears that there could be two layers of epithelial cells. This is due to the presence in them of a clearly defined thecal area
separating the basal parts with the nuclei from the apical areas that are filled with mucin. This gives the appearance of two layers of cells.

ii. if there were more than two layers of cells this might have been due to hyperplasia of the epithelium due to the activity of the nematodes. Loomis and Wright (1986) reported that this occurred in their specimen of *Colobus guereza*, but they did not describe the actual appearance of the cells.

2. the appearance of the surface mucous cells is constant throughout the Mammalia (Ito 1967), but the cells from the saccus shown in Plate 8.1 appear to be broader than those in a parasite free animal, like *Papio cynocephalus* (Plate 7.2). They also contain less mucin which suggests they were more active, i.e. secreting more mucous. This is a common occurrence in *Trichuris* infections (Wakelin and Lee 1987).

3. evidence for an inflammatory response in the mucosa is seen in the wide capillaries and the presence of eosinophils and macrophages (Plate 8.1 - Figure 6, Kuhn 1964). The absence of lymphocytes is also marked when compared with sections of the mucosa from the same area in *Presbytis femoralis* (Plate 8.11). The lamina-propria is also less fibrous in appearance, but this may have been due to the staining method used.

4. Kuhn noted that the surface of the mucosa was covered by a thick layer of mucus that could be peeled away in the freshly-killed specimens, and this layer can be seen readily in Figure 8.1(5). This may have been due to the presence of the nematodes as Loomis and Wright (1986) mentioned that the mucosa in their specimen was covered by a thick fibro-catarhal mat.

Such changes in the mucosa of the fermentation area could have serious repercussions for colobids, apart from the bacterial invasion of the underlying tissues and the risk of septicaemia (Loomis and Wright 1986). The volatile fatty acids produced by bacterial fermentation of cellulose are absorbed from this part of the stomach. The mucosa plays an important role in this process (Bergman 1990) and any changes to this layer caused by the nematodes could have had serious effects on the metabolism in these animals, such as the weight-loss recorded by Loomis and Wright (1986). If the rate of volatile fatty acid removal from the the gastric contents is lowered the fermentation rate could be inhibited by the pH dropping below 5 - 7, which is optimal range for fermentation. Falling pH levels are known to inhibit fermentation (Kay et al. 1976).

Kuhn's specimens of *Procolobus verus* and *Procolobus badius* came from the wild, and the
leaf-monkey (*Trachypithecus auratus*) was purchased from an animal dealer. From the observations of other authors (Ruch 1959, Manson-Bahr 1966, Palmieri et al. 1980, Loomis and Wright 1986), it would appear that this nematode parasite is common in both wild and captive colobids, in Africa and Asia. If this is the case, then the infections in wild animals would not necessarily be as severe, as they will have built up immunity to the nematodes (Wakelin and Lee 1987). In humans severe *Trichuris* infections are common in children, but rare in adults for this reason. The situation could be different in captive animals, which are subjected to stresses of many kinds, including changes in habitat and diet, as well as crowding. Such stress may affect their immune systems, rendering them more susceptible to infectious diseases and heavier parasite loads. Both these examples of severe *Trichuris* infections were captive animals: *Trachypithecus auratus* (Kuhn 1964) and *Colobus guereza* (Loomis and Wright 1986). Such a finding might have useful implication for the captive management of these monkeys.
Figure 0.1 (from Kuhn 1964)

1. Surface epithelium of the saccus gastricus of *Trachypithecus auratus*. GABE (X225)

2. Mucosa of the pars pylorica in *Trachypithecus auratus*. PAS (x70)

3. *Cebus badius badius*

4. *Cebus apella*

5. Mucosa of the saccus gastricus of *Trachypithecus auratus*. GABE (x70)

6. Mucosa of the caudal part of the tubus gastricus in *Trachypithecus auratus*. PAS (x25)

7. Mucosa of the tubus gastricus of *Trachypithecus auratus*. GABE (x20)
The surface epithelium and lamina propria of *Trachypthecus auratus*. (from Kuhn 1964 - detail of Figure 8.1, part 6)

The surface mucus cells contain relatively small amounts of mucin, and there seems to be a thecal area between the mucin and the nucleus (S arrow). Eosinophils are scattered throughout the lamina propria (M arrows), and a large capillary is evident (L arrow), suggesting oedema.

Glutacondialdehyde and 2-thio-barbituraure (x180)
Section 2. The histology of the gastric mucosa in a poorly preserved specimen of *Presbytis femoralis*.

This leaf-monkey was autopsied on the day after it had died and the stomach was removed and opened. During the autopsy a small block of tissue was removed from the wall of the saccus for preparation for histological examination. The stomach was preserved in formalin and then placed in a plastic bag with formalin-impregnated cotton wool for transport to Canberra, and it was stored in this bag for two years. At the beginning of this study it was necessary to rehydrate it and this was done in a graded series of ethanol, with the concentration being gradually increased from 10 to 50 percent. Ethanol was used in preference to formalin because it is part of the routine paraffin wax embedding procedure used in the preparation of sections for light microscopy. Five micron sections were cut from the blocks taken from the various areas in the stomach and were stained with HE and PAS-haematoxylin in the same way as those from the baboon stomach. The storage and subsequent dehydration of the specimen did not appear to have any further effect on the mucosa. Comparison of a section made from tissue removed from the saccus during the autopsy with one made in 1989 showed no differences in the structure of the mucosa, suggesting that there was no further damage in the intervening period.

1. the surface epithelium and gastric pits

Nothing remained of the surface layer of the gastric mucosa in any part of the stomach and the only remnants of the pits were seen in a section from the pars pylorica, where some of the mucosa had been protected by one of the longitudinal folds (Plate 8.3). The cells were more obvious in PAS stained sections (Plate 8.3), than those stained with HE (Plate 8.4). The surface mucous cells lining these pits were columnar in shape, with basal nuclei, and the apical cytoplasm was filled with with granules that stained strongly with PAS (Plate 8.5).

2. the tunica mucosa of the saccus gastricus

The wall of the saccus was thin (Plate 8.6) and all of the layers that made up the wall are clearly visible. The damage to the mucosa was variable, being greatest on the exposed surfaces where it was as thin as 0.094mm. Where it was protected by folding it was more than double that thickness (0.23mm) - Table 8.2 and Plate 8.2. Remains of the glands could be seen and they appeared to be fewer in number, with more lamina propria between them, than in other areas (Plates 8.7, 8.4 and 8.20). These remnants can be seen in Plates 8.2, 8.9 and 8.10. Some of these glands appear to have been coiled as a number of their bases have been cut in cross-section (Plate 8.12) and branched (Plate 8.11). The cardiac gland cells were columnar (Plates 8.10 and 8.11), with basal nuclei and dark,
granular cytoplasm (Plate 8.11). The cytoplasm in the apical regions of the cells seemed to have degenerated first, before that of the basal regions (Plate 8.10). The cytoplasm is weakly PAS-positive (Plate 8.13), suggesting that these glands were mucus-secreting like those in other catarrhines. The fibre network of the lamina propria could be seen between the remnants of the glands, and the nuclei of the cells in the connective tissue were clearly visible (Plate 8.12). They appeared to be small, dark and rounded like those of lymphocytes, but this might be due to degeneration as it was difficult to distinguish those of any of the other types (Plate 8.10). Large lymph nodules were evident in the mucosa (Plate 8.14) and they contained tightly packed nuclei. Some of the larger ones may have had germinal centres (Plate 8.14), but these were not easily seen. The borders of the nodules were diffuse, and lymphocytes spread out into the neighbouring connective tissue as can be seen in Plate 8.2, where the lymph nodule is on the left of the photograph. The thickness of the mucosa in this area is increased considerably where lymph nodules are present, reaching a height of 3mm (Table 8.2). The muscularis mucosae is well developed in the wall of the saccus gastricus (Plates 8.6 and 8.7) having an average width of 0.48mm (Table 8.2). It consisted of a thin inner circular layer and a thick longitudinal layer next to the submucosa (Plate 8.8). The cytoplasm of the smooth muscle cells in these sections does not look normal when compared with *Papio cynocephalus*, suggesting that some post mortem degeneration had taken place (Plates 8.8 and 7.13).

3. the tunica mucosa of the tubus gastricus

i. in the cranial part of the tubus

The mucosa in this area was very thin, varying from 0.094 to 0.30mm where lymph nodules were present (Table 8.2). It contained cardiac glands that were mucus-secreting, as they were weakly PAS-positive (Plate 8.18), but little remained of the glands themselves (Plate 8.16). The secretory cells were columnar and their circular nuclei were found in their basal regions. The apical cytoplasm contained mucin (Plate 8.17), and the cytoplasm of these cells was very similar in appearance to that of the cells of the cardiac glands of the saccus (Plates 8.17 and 8.12). As the bases of the glands seen in this region were cut in cross-section, it suggested that they were coiled or bent against the muscularis mucosae. The lamina propria was evident between the glands and it had a similar appearance to that in the saccus. Numerous lymph nodules were present in both the lamina propria (Plate 8.16) and in the submucosa (Plate 8.15). The muscularis mucosae could be seen clearly (Plates 8.15 and 8.16), but it was not as thick as that of the saccus, having a average thickness of 0.025mm (Table 8.2), and the inner circular layer of fibres was hardly visible (Plate 8.19). The only differences observed between the mucosa in the saccus and that
in this part of the tubus was the greater thinness of muscularis mucosae in the latter.

ii. in the caudal part of the tubus

The mucosa in this area contained the oxyntic glands, and the degeneration of the whole of the layer was not as marked as in the saccus or the cranial part of the tubus (Plate 8.20). It had an average thickness of 0.30mm (Table 8.2), which was greater than in the other areas (Plate 9.1). A remnant of the pit region was seen where it had been protected by a fold in the mucosa, and the cells contained mucin that was PAS-positive (Plate 8.25). The cellular degeneration was more pronounced in the oxyntic glands, especially the basal cells, as they had lost most individual detail, and it was difficult to distinguish the individual cell types (Plates 8.22, 8.23 and 8.24) with either HE or PAS staining. The mucus neck cells had lost most of their mucin and a large part of their apical cytoplasm (Plate 8.22), leaving a wider lumen. The glands had become detached from their basement membranes, and the lack of fibrous connective tissue between them was evident. The muscularis mucosae was thin in this region (0.03mm) and was more normal in appearance (Plates 8.23 and 8.24).

4. the mucosa of the pars pylorica

The mucosa in this region was better preserved than in any of the others, especially where protected by overlying folds (Plate 8.3) and it had an average thickness of 0.17mm (Table 8.2). The pyloric glands were closely packed together and branching and coiling was evident (Plate 8.26). The secretory units were made up of tall cells with spherical, open-faced nuclei found in their bases. The cytoplasm of these cells was dark and granular in appearance (Plate 8.28). Small, clear entero-endocrine cells were numerous and were found between the gland cells and the basement membrane (Plate 8.27). In Plate 8.27 several glands can be seen opening into the base of a single pit. The pits were lined with surface mucous cells that stained brightly in PAS-stained sections (Plate 8.3). The cytoplasm in the apical regions of the gland cells contained mucin that was also PAS-positive, but the reaction was not as great as that in the surface cells (Plate 8.5). As the glands were closely packed the amount of lamina propria around them was reduced and it was not heavily infiltrated with lymphocytes (Plates 8.3 and 8.27) and there were few lymph nodules evident. The muscularis mucosae increased in thickness to 0.052mm in the pyloric region (Table 8.2) and the circular and longitudinal layers were almost equal in thickness (Plate 8.28).

5. the mucosa of the sulcus ventriculi

The mucosa of the sulcus ventriculi contained cardiac glands like those in the saccus and the
The amount of decay observed was variable and depended upon the protection given by the ventral lip of the sulcus (Plate 8.30). On the upper side of this lip, where it was exposed to the lumen, the average thickness of the mucosa was 0.075mm, while underneath it was 0.175mm. Numerous lymph nodules were present in sections from this area and the lamina propria was heavily infiltrated with lymphocytes (Plate 8.29). Some of them penetrated through the muscularis mucosae into the submucosa (Plate 8.30). The muscularis mucosae had an average thickness of 0.44mm and it is frequently broken by the lymph nodules (Plate 8.29).

6. the mucosa of the gastro-oesophageal junction

The junction between the stratified squamous epithelium of the oesophagus and the glandular mucosa of the saccus was abrupt, as sections of this area show (Plate 8.31). The stratified squamous epithelium did not appear to be keratinized (Plate 8.32). While it was more resistant than the glandular epithelium, some of the outer layer appeared to have been lost as the lumen surface was very straight. This epithelium was attached to the underlying lamina propria by narrow papillae (Plates 8.32 and 8.33). The basal layer of cells in this membrane had small, dark nuclei and were columnar in shape (Plate 8.37A). The cells gradually became more polyhedral and their nuclei more open-faced as they were pushed into the upper layers. In the outer most layers the cells were flattened (Plates 8.32 and 8.33). Some PAS-positive material was seen in the middle region of portion of this epithelium (Plate 8.34), and from the appearance of the cells it seemed likely that it had been depleted when compared with Papio cynocephalus, perhaps as a result of the degeneration process (Plates 8.34 and 7.38). The lamina propria throughout the junction area was made up of a delicate fibre mesh, heavily infiltrated with lymphocytes and there were numerous lymph nodules, some of which extended into the submucosa. The cardiac glands in the junction were similar in structure to those in the rest of the saccus and the cytoplasm of the gland cells was weakly PAS-positive (Plate 8.31B). In one section it looked as if there were submucosal glands present underneath the stratified squamous epithelium (Plates 8.34 and 8.36), but there was some doubt about this as it seemed that secretory units from neighbouring cardiac glands extended underneath the non-glandular epithelium (Plates 8.34 and 8.36) giving the appearance of submucosal glands. The muscularis mucosae was broken up in this region (Plate 8.31), making verification of this particular finding difficult.
Discussion: comparison of the histology of the gastric mucosa in *Presbytis femoralis* with that in other colobids.

There appears to be no difference in the structure of the gastric mucosa in *Presbytis femoralis*, when compared with those from other colobids with three-chambered stomachs, or even those with four chambers, if the praesaccus is excluded. This is not entirely unexpected, as the structure of the gastric mucosa in mammals, as a group, is relatively conservative (Romer 1956, Ito 1967). The variations observed, which are in the relative amounts of the three gland types, are largely adaptations to different types of diet (Romer 1956, Chivers and Hladik 1980, Langer 1988). There do not seem to be any differences in the structure of the glands or in their secretory cells (Kuhn 1964, Ito 1967, Peng et al. 1983, Suzuki et al. 1985, this Thesis).

There were three points of difference between *Presbytis femoralis* and some of the other descriptions of colobid gastric mucosa. Kuhn (1964) described the presence of submucosal glands in the cardiac shield of *Trachypithecus auratus*. At first they appeared to be present in *P. femoralis* as well, but further examination of the sections of the cardio-oesophageal junction suggested that the cardiac glands extended under the stratified squamous epithelium (Plate 8.34). There were no submucosal glands in *Rhinopithecus* (Zhang et al. 1988). The second difference was in the mucous neck cells of the oxyntic glands. The supranuclear regions of these cells were tightly packed with mucin granules in both *Trachypithecus auratus* (Kuhn 1964) and *Rhinopithecus* (Peng et al. 1983), but this was so in *P. temoralis* (Plate 8.25B). From the appearance of these cells, this was probably due to post mortem degeneration and not a normal reflection of the state of the mucosa. Thirdly, Kuhn mentioned the presence of large numbers of eosinophils and phagocytes in the lamina propria of the saccus of *T. auratus*. This may have been due to the presence of parasitic nematodes in this region, for large numbers of these cells are not reported to be normal components of the mucosa (Berenberg-Gossler 1911, Peng et al. 1983).

The differences observed do not seem to be significant, despite the degeneration of the mucosa in *P. femoralis*. These findings support those obtained from the study of the gross anatomy of the stomach, which emphasized the constant overall morphological pattern among colobids with three-chambered stomachs. Given this fact, it would seem that the presence of the praesaccus in some genera might be phylogenetically significant.
The pattern of degeneration in the gastric mucosa of *Presbytis femoralis*

The histological structure of the gastric mucosa in mammals is relatively conservative (Ito 1967) and among primates the major differences appear to be in the extent of the wall covered by oxyntic and cardiac glands (Burki 1958, Ito 1967, Langer 1988), with the area containing the pyloric glands being relatively constant. To estimate the relative amounts of tissue lost from the mucosa in *Presbytis femoralis* comparisons were made with the thickness of the three glandular areas in the baboon stomach, which had suffered no post mortem degeneration. In these sections the thickness of the mucosa was measured from the lumen surface to the lower margin of the muscularis mucosae next to the submucosa (Diagram with Table 8.2). To obtain these estimates it had to be assumed that there was no difference in general thickness in these areas between the species, but this may not be the case in life. If this assumption is correct, the relative losses in *P. femoralis* would be as follows -

- 53 percent in the cardiac gland area (average for the saccus and tubus),
- 14 percent in the oxyntic gland area (caudal end of the tubus),
- 50 percent in the pyloric region.

Suzuki et al. (1985) measured the mucosal thickness of these mucosal areas in the stomach of *Trachypithecus francoisi* and these were also used to estimate the relative loss of mucosa in *P. femoralis*, as they were the only other measurements for a colobid species available. If these figures of Suzuki et al. are accurate, the relative loss in *P. femoralis* would be -

- 66 percent in the cardiac gland area,
- 45 percent in the oxyntic gland area,
- 57 percent in the pyloric gland area.

These estimates must be treated with some caution as Suzuki et al. did not define the reference points they used when taking these measurements. It is evident, nevertheless, that something has happened to the mucosa in *P. femoralis*, and the same general pattern of decay is evident in both sets of data, being greatest in the cardiac gland area and least in the oxyntic, with the loss of the pyloric mucosa being intermediate between these two (Plate 9.1). The amount of mucosal degeneration appears to be dependent on two factors -

1. the presence of mucosal folds, where the overlying tissues protect the mucosa underneath the fold.
2. the “environment” of a particular glandular region, for example the presence of bacteria in the fermentation chambers appears to have had more effect on the degeneration of the whole mucosa than the enzymes and HCl of the oxyntic glands. This results in a different pattern of degeneration in each of the three glandular areas.
From the appearance of the surface of the mucosa it seems that the process of post mortem degeneration starts with an exfoliation of the most of the surface of the mucosa, including the upper parts of the gastric pits (Plates 8.21B and 8.27). Support for this observation came from sections taken from two Tammar wallaby (Macropus eugenii) stomachs (Plates 8.36). These animals are very similar in gastric morphology and physiology to the colobids (Langer 1988), and a brief study of the mucosa of their stomachs was made to see if changes like those in P. femoralis could be observed. Samples of tissue were taken at 15-minute intervals for one hour after death in these animals and by the end this time the exfoliation of the surface layer was observed (Plate 8.36).

The changes observed in the different regions of the mucosa in P. femoralis were as follows:

1. In the cardiac gland area of the saccus gastricus and the tubus there were never any remnants of the surface mucous evident in the sections and the glands that were left were fewer in number. The general columnar shape of the secretory cells was evident (Plate 8.10) and the degeneration within the glands followed what appeared a constant pattern:
   i. the apical cytoplasm of the cells (next to the lumen of the gland) started to break down first (Plate 8.11), and this was followed by the basal areas which contained the nuclei of the secretory cells (Plate 8.10). During this process the individual cells separated from each other (Plate 8.10).
   ii. when all of the cells had disappeared the position of the gland could be be seen as a gap in the lamina propria (Plate 8.9).
   iii. the cells in the lamina propria appeared to have been protected to a greater degree, probably by the fibre networks and the amorphous intercellular substance that form the basis of this type of connective tissue (Plate 8.10).

The decay process worked down in layers through the mucosa, with the upper tissues protecting for a time those beneath them. This could be seen in the upper layer of the muscularis mucosae where the appearance of the smooth muscle cells was more altered on the lumen side of the layer (Plate 8.11). There was less change in these cells if they were protected by an overlying lymph nodule (Plate 8.14). In many areas, where the mucosa was not protected by overlying folds there was very little of it left (Plate 8.15) and this was particularly noticeable on the outer surface of the ventral lip of the sulcus ventriculi (Plate 8.29). These changes were common to the whole of the cardiac gland area (Plate 8.7 - saccus gastricus, Plate 8.15- tubus gastricus).

2. The relative loss of mucosa in the oxyntic gland area was smaller than in the other regions, but the degeneration of the cytoplasm of the secretory cells was more marked (Plates 8.22
and 8.23), for not much cellular detail remained. The cytoplasm of these cells appeared to be more broken up and it was difficult to distinguish both the outlines of individual cells and the different cell types themselves. Shrinkage of the glandular cells away from the basement membranes was evident, and this served to emphasize the lack of fibrous connective tissue in the lamina propria in this region (Plate 8.21). The nuclear area in these cells also remained intact for longer than the apical regions. Little change was observed in the smooth muscle cells of the muscularis mucosae, which was much thinner in this region (Plate 8.23). Remnants of pits were seen, especially were the mucosa had been protected by overlying folds (Plate 8.3).

3. In the pyloric area much more glandular structure was evident than in the other two, and there appeared to be very little breakdown of gland cells (Plate 8.26), even on the exposed surfaces (Plate 8.27). Branching of the glands was clear (Plate 8.26) and there appeared to be very little damage to the muscularis mucosae. More of the lower pit area survived and they too were evident in some sections where they were not protected by folds (Plate 8.29). The cellular structure of the lamina propria was clear.

The pattern of post mortem degeneration was quite distinct in each of these three mucosal areas and could be related to the function that each performed in the living animal. In the regions lined with cardiac glands, where the decay was greatest, bacteria fermented cellulose and other complex carbohydrates. Here the decay appeared to progress in layers through the mucosa from the lumen surface downwards, with the outer layers protecting those beneath them. This progression suggests some kind of chemical involvement, perhaps from bacterial metabolism. The cardiac glands secrete mucus, which would not be particularly damaging as it is designed to protect the surface cells, a fact that is born out by the appearance of the pyloric glands, which are thought to have a similar function to the pyloric cells (Ito 1967). In the pyloric region the most obvious feature of the degeneration process was the loss of the surface layer. The changes in the oxyntic glands were quite different. Individual cell detail had been lost, suggesting autolysis by the proteolytic enzyme, pepsin, and by HCl manufactured and secreted by the cells in these glands. The appearance of the mucous neck cells and the wide lumina of the glands suggests that small amounts of these substances were released. More of the mucosa remained, including the bases of the pits lined with surface mucous cells. The decay observed seemed to be a self-destruction rather than an external process like that in the saccus and the tubus, where it would have been increased because of the presence of the bacteria. Loss of the surface layer down to the bases of the pits appeared to be the first and most dramatic change that occurred in all regions and this, no doubt, was due to the potentially damaging substances that are always found
in the chyme, in addition to the hungry bacteria in the fermentation chambers.

<table>
<thead>
<tr>
<th>Region</th>
<th>Part of the Stomach</th>
<th>Main Salivary Gland Type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stomach chamber</td>
<td>gastric parasites</td>
<td>stomach-producing glands</td>
</tr>
<tr>
<td>Enzyme-producing area</td>
<td>duodenal part of the pars</td>
<td>exocrine glands</td>
</tr>
<tr>
<td>Pancreas</td>
<td>para-acinar</td>
<td>exocrine-producing glands</td>
</tr>
<tr>
<td>Intestine</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
### Distribution of the main gland types of the mucosa in the colobid stomach.

<table>
<thead>
<tr>
<th>Functional Region</th>
<th>Part of the Stomach</th>
<th>Mucosal Gland Type</th>
</tr>
</thead>
<tbody>
<tr>
<td>fermentation chamber</td>
<td>saccus gastricus and cranial two-thirds of the tubus gastricus</td>
<td>mucus-secreting cardiac glands</td>
</tr>
<tr>
<td>enzyme-producing area</td>
<td>caudal part of the saccus gastricus</td>
<td>oxyntic glands</td>
</tr>
<tr>
<td>mixing and chyme releasing area</td>
<td>pars pylorica</td>
<td>mucus-secreting pyloric glands</td>
</tr>
</tbody>
</table>
TABLE 8.2  
A comparison of mucosal thickness in various regions of catarrhine stomachs.

A. *Papio cynocephalus*  

<table>
<thead>
<tr>
<th>Mucosal Type</th>
<th>Mucosal Thickness (mm)</th>
<th>Thickness of the Muscularis Mucosae (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Total  Variation</td>
<td>Total  Variation</td>
</tr>
<tr>
<td>cardiac</td>
<td>0.36  0.31-0.39</td>
<td>0.042  0.031-0.056</td>
</tr>
<tr>
<td>oxyntic</td>
<td>0.35  0.31-0.39</td>
<td>0.016  0.013-0.019</td>
</tr>
<tr>
<td>pyloric</td>
<td>0.34  0.27-0.41</td>
<td>0.047  0.038-0.056</td>
</tr>
<tr>
<td>oesophageal</td>
<td>0.42</td>
<td>. . . . .</td>
</tr>
</tbody>
</table>

B. *Presbytis femoralis*  

<table>
<thead>
<tr>
<th>Mucosal Type</th>
<th>Mucosal Thickness (mm)</th>
<th>Thickness of the Muscularis Mucosae (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Total  Variation</td>
<td>Total  Variation</td>
</tr>
<tr>
<td>cardiac</td>
<td>0.17  . . . . .</td>
<td>0.048  . . . . .</td>
</tr>
<tr>
<td>saccus</td>
<td>0.20  0.11-0.27</td>
<td>0.046  0.038-0.063</td>
</tr>
<tr>
<td>tubus</td>
<td>0.14  0.094-0.30</td>
<td>0.025  0.019-0.031</td>
</tr>
<tr>
<td>oxyntic</td>
<td>0.30  0.30-0.31</td>
<td>0.016  0.013-0.019</td>
</tr>
<tr>
<td>pyloric</td>
<td>0.17  0.12-0.22</td>
<td>0.052  0.038-0.069</td>
</tr>
<tr>
<td>oesophageal</td>
<td>0.29  . . . . .</td>
<td>0.028  0.025-0.031</td>
</tr>
</tbody>
</table>

C. *Trachypithecus francoisi*  
(from Suzuki et al. 1985)  

<table>
<thead>
<tr>
<th>Mucosal Type</th>
<th>Mucosal Thickness (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>cardiac</td>
<td>0.4 - 0.6</td>
</tr>
<tr>
<td>oxyntic</td>
<td>0.55</td>
</tr>
<tr>
<td>pyloric</td>
<td>0.4</td>
</tr>
</tbody>
</table>
HISTOLOGY OF THE GASTRIC MUCOSA IN *PRESBYTIS FEMORALIS*:
THE PLATES
1. THE SURFACE EPITHELium

PLATE 8.2
The mucosa of the saccus gastricus.

A. The layers forming the wall of the saccus are clearly defined. The pits and the surface epithelium have been lost, and only a few remnants of glands remain. The muscularis mucosae is thick and broken by a lymph nodule. Blood vessels from the submucosa run towards the lamina propria (arrow).
HE (x100)

B. The amount of degeneration in the mucosa varied considerably, and was greatest on exposed surfaces like this one. Few cardiac gland cells remain, but the spaces they filled in the lamina propria can be seen (arrow). The fibre network is filled with lymphocytes.
HE (x100)
PLATE 8.3
Remnants of the pits in the pyloric mucosa.
Some bases of pits remain in the pyloric area, where they were covered by a large mucosal fold. This is best seen in PAS stained sections. The surface mucous cells contain tightly packed mucin granules, like those in the baboon mucosa. The muscularis mucosae is thick in this area.
PAS (x100)

PLATE 8.4
Surface mucous cells in the pars pylorica.
These are more difficult to recognize with HE staining (arrow), as the mucin is unstained. Blood vessels of the submucosal plexus can be seen in the submucosa.
HE (x250)
PLATE 8.5
Remnants of the pits in the gastric mucosa.

A. The pits are lined with columnar cells, that contain densely stained mucin in their apical regions (arrow). Below these pits the secretory units of the pyloric glands can be seen, lined with mucus-secreting cells. They contain entero-endocrine (arrow) and parietal cells. Fibroblasts are the most common cell type in the lamina propria.

B. Smaller remnants of the bases of the pits were visible in the oxyntic gland area. The cells appeared to contain less mucin and to be shorter, but this may have been due to post mortem damage by secretions from the glands.

PAS (x250)
PLATE 8.6
Entire wall of the saccus gastricus. A photograph shows the various layers of tissue that make up the wall of the saccus. (X100)

PLATE 8.7
The wall of the saccus gastricus. Remnants of cardiac glands can be seen in the lamina propria and the smooth appearance of the lumen surface is characteristic of this area. Large blood vessels are conspicuous in the submucosa. HE (x100)
The muscularis mucosae in the wall of the saccus gastricus. The two layers of smooth muscle cells are distinct. The inner one consists of circularly arranged fibres, and the outer layer, next to the submucosa, is of longitudinally arranged fibres. Some cytoplasmic damage is evident in these cells. HE (x400)
PLATE 8.9
Remnants of cardiac glands in the wall of the saccus gastricus.

A. Most of the gland cells have disappeared, leaving scattered remnants (arrows) in the spaces that were occupied by the whole gland. These spaces show that the cardiac glands were branched. The two layers of the muscularis mucosae are clear. HE (x250)

B. Less of the mucosa remains on unprotected surfaces. The gland cells appear to have been columnar in shape, with their nuclei in the basal regions. The cytoplasm of the smooth muscle cells in the circular layer of the muscularis mucosae has an open appearance due to post mortem damage. The connective tissue fibres in the submucosa are thick in this area. HE (x250)
PLATE 8.12
Cardiac glands in the saccus mucosa.
The secretory units of the glands are cut in cross section, suggesting that they were coiled and bent against the muscularis mucosae. The muscularis mucosae is starting to disintergrate and fasciculi of smooth muscle cells are starting to pull away from each other.
HE (x250)

PLATE 8.13
Cardiac glands in the mucosa of the saccus.
The secretory cells of the glands still contain mucopolysaccharides in their cytoplasm. This is mainly in their apical regions, and it does not appear to be found in all of the cells (arrow).
PAS (x250)
PLATE 8.14
The lymphatic system in the wall of the stomach.

A. This large lymph nodule filled the lamina propria, and appears to have had a large germinal centre. Nuclei of reticulo-endothelial cells can be seen (arrow). There are remnants of cardiac glands on either side of the nodule, and a prominent artery runs through the submucosa.
HE (x250)

B. A large lymph vessel (arrow), filled with lymphocytes, runs near blood vessels in the submucosa of the tubus gastricus. The fibre network of the submucosa is not as cellular as that of the lamina propria, and only scattered fibroblast nuclei are evident among the collagen fibres.
HE (x100)
3. THE MUCOSA OF THE TUBUS GASTRICUS
(1) THE CRANIAL PART OF THE TUBUS

PLATE 8.15
The mucosa in the cranial portion of the tubus gastricus.

A. The lamina propria and glands are reduced to a thin surface layer, that is predominantly fibrous. The lymph nodule is in the submucosa, beneath the relatively thin muscularis mucosae.
HE (x100)

B. Little remains of the surface of the mucosa. The cytoplasm of the smooth muscle cells in the muscularis mucosae is starting to decay, and the lymph nodule is more open in appearance. Reticulo-endothelial cells (arrow) can be seen among the lymphocytes.
HE (x250)
PLATE 8.17
Detail of the cardiac glands in the mucosa of the tubus gastricus.
This photograph shows the detail of the structure of the glands in Pl. 8.16. The secretory cells are columnar, with granular cytoplasm and spherical nuclei. They are surrounded by the lymphoid tissue of the nodule. Nuclei of reticulo-endothelial cells can be seen among the lymphocytes (arrow).
HE (x400)

PLATE 8.16
Remnant of a lymph nodule in the mucosa of the tubus gastricus.
This photograph shows the extent of the loss of the mucosa in this area, as most of this large lymph nodule has been lost. The cell detail in the glands underneath the nodule suggests that they were protected by it.
HE (x100)
Remnants of cardiac glands in the mucosa of the tubus.

**A.** The gland cells stained with PAS (arrow) indicating the presence of mucopolysaccharide. The muscularis mucosae is thick, and there are numerous blood vessels in the submucosa. PAS (x100)

**B.** Cellular breakdown is advanced in the cardiac gland cells. It appears that they contain mucin throughout the cytoplasm, and they have large, spherical, open-faced nuclei. PAS (x250)
PLATE 8.19
Cardiac glands in the mucosa of the tubus gastricus.
The fibre mesh of the lamina propria has broken down, and it appears to be thinner than in other areas. Remnants of glands are in an advanced state of decay, but the cytoplasm of the cells still contains PAS-positive material. The muscularis mucosae consists mainly of longitudinal fibres, with a few circularly arranged ones (arrow) cut in cross section.
PAS (x250)
Oxyntic glands in the mucosa of the tubus gastricus. The mucosa in this region was thicker, and the overall degeneration was not as marked as in the cardiac gland areas. Remnants of surface epithelium can be seen underneath the fold. The muscularis mucosae is much thinner in this region. PAS (x100)
PLATE 8.21
Oxyntic glands in the mucosa of the caudal part of the tubus.

A. The surface of the mucosa has a clean-cut edge, unlike that in the saccus and cranial part of the tubus, which suggests that the pattern of decay is different in these areas. The glands are tightly packed and branched (arrow). HE (x100)

B. The characteristic appearance of the mucosal surface is evident, as is the arrangement of the oxyntic glands, which are branched (S arrow). Entero-endocrine cells (L arrow) can be seen in these glands. The differences in the staining of the various gland cells is not as obvious in this specimen, as it is in Papio cynocephalus. HE (x100)
PLATE 8.22
The upper regions of the oxyntic glands.
Most of the isthmus region has gone, and only palietal cells can be distinguished (arrows). In the upper parts of the basal regions of the glands, they appear to be better-preserved than the zymogen cells. HE (x250)

PLATE 8.23
The bases of the oxyntic glands.
The nuclei of the zymogen cells are intact, but lack detail. The cytoplasm of the individual cells merges together, unlike that in the other mucosal areas, and the whole mass is breaking up. The glands have separated from each other, and it can be seen that there is little lamina propria between them (arrows). HE (x250)
Post mortem degeneration changes in oxyntic glands.
There has been a loss of structural detail in the basal cells, and only isolated parietal cells are seen (S arrow). In the paler isthmus region of the glands the apical cytoplasm of the cells has been lost, so that they are cuboidal in shape and the lumen of the glands has become larger (M arrow), when compared with those in the baboon. The lamina propria is sparse, and entero-endocrine cells are present in the glands (L arrow).
HE (x250)
A. Surface mucous cells in the remnants of the pits contain densely stained mucin. They are not as tall as those in the pyloric mucosa, and do not contain as much mucin. Isolated mucous neck cells, containing little mucus, are evident (arrows). PAS (x250)

B. The cellular breakdown in the basophilic zymogen cells is marked (M arrow). The mucous neck cells have only a rim of mucin on their lumen surfaces, suggesting that there has been considerable cytoplasmic loss from these cells (S arrow). Fine strands of lamina propria are evident between the tubular secretory units. PAS (x160)
THE MUCOSA OF THE PARS PYLORICA

B. It is possible to differentiate between the columnar surface mucous cells (L arrow) and the more cuboidal gland cells, with their flattened nuclei. Parietal cells are also found in the glands (S arrow), as well as entero-endocrine cells. The lamina propria is not very cellular and contains relatively few lymphocytes. Most of the nuclei are those of fibroblasts. Strands of smooth muscle fibres pass up from the muscularis mucosae.

HE (x250)

PLATE 8.26
The mucosa of the pars pylorica.

A. The pyloric glands are short and branched (L arrow) and a considerable amount of cell detail is visible. The muscularis mucosae is thick, and the two layers of muscle fibres are evident. Blood vessels penetrate it at regular intervals (S arrow). The appearance of the lumen surface is like that in the oxyntic gland area.

HE (x100)
PLATE 8.27
The glands of the mucosa of the pars pylorica.
Remnants of the long pits remain (L arrow), and the branched tubular glands are short. The cytoplasm of the gland cells is more densely stained than that of the surface mucous cells. Parietal cells (M arrow) and entero-endocrine cells (S arrow) are common in the walls of the glands. The two layers of the muscularis mucosae are clear.
HE (x250)
PLATE 8.28
The muscularis mucosae of the pars pylorica.
The muscularis mucosae is thick and the two layers of muscle cells can be readily distinguished.
HE (x250)
5. THE MUCOSA OF THE SULCUS VENTRICULI

PLATE 8.29
The mucosa of the sulcus ventriculii.

A. The mucosa is of the cardiac type and contains numerous lymph nodules, supporting the macroscopic findings. This section was taken from underneath the ventral lip of the sulcus, where it was protected by the overlying tissues. Numerous remnants of cardiac glands remain. The muscularis mucosae is thick, but broken by a lymph nodule extending into the submucosa (arrows). HE (x100)

B. The mucosa on the outer surface of the ventral lip shows more post mortem degeneration, and is much thinner. The muscularis mucosae is thick and broken by a lymph nodule (L arrow). Blood vessels are seen in the lamina propria (S arrow). HE (x100)
C. The extent to which lymph nodules break through the muscularis mucosae is clearly shown in this photograph of the sulcus mucosa.

HE (x250)
PLATE 8.30
A lymph nodule in the lamina propria of the sulcus ventriculi.
The muscularis mucosae is broken up by the lymphoid tissue. Portions of two small lymph vessels can be seen (arrows).
HE (x100)
A. The junction between the oesophageal and cardiac epithelia is abrupt, with no transition zone. The stratified squamous epithelium shows much less damage than the mucosa of the saccus, where most glands have disappeared. The muscularis mucosae is thick, but broken up. The lamina propria contains numerous lymphocytes.
HE (x100)

B. Few secretory units of cardiac glands remain, and there are a number of large cystic structures (L arrows). Glands like this are not uncommon in normal cardiac mucosa (Whitehead 1985). The cardiac glands extend under the stratified squamous epithelium (S arrow), and their cytoplasm contains PAS-positive material.
PAS (x100)
The stratified squamous epithelium of the junction.

This has the characteristic structure of such epithelia, with columnar basal cells gradually becoming polyhedral and then flattened as they are pushed towards the surface. The lamina propria contains numerous lymphocytes, and the muscularis mucosae is diffuse.

HE (x500)
PLATE 8.33
Longitudinal section of the papillae of the stratified squamous epithelium.

The stratified squamous epithelium is attached to the lamina propria by long, narrow papillae of connective tissue, which appear circular when cut in this direction (L arrow). Some of the epithelial cells contain keratohyaline granules in their cytoplasm (S arrow). Lymphocytes are found in the epithelium (M arrow).

HE (x260)

PLATE 8.34
The stratified squamous epithelium of the gastro-oesophageal junction.

The outer cells of the stratified squamous epithelium contain clumps of material that stains with PAS. When compared with the same region in Papio cynocephalus, it would appear that some of the surface has been lost, for the papillae are closer to the lumen (L arrow). Cardiac glands extend under this epithelium (S arrow).

PAS (x100)
The lamina propria of the gastro-oesophageal junction.

A. A lymph nodule with a small germinal centre has broken through the muscularis mucosae. Strands of smooth muscle are found around the cardiac glands (arrow), giving them the appearance of submucosal glands. HE (x160)

B. Detail of the same area shows the terminal portions of the glands, and the smooth muscle fibres close to the basal cells of the stratified squamous epithelium (arrow). The fibre network of the lamina propria is filled with lymphocytes. HE (x250)
The early stages of post mortem degeneration in the gastric mucosa of the Tammar wallaby, *Macropus eugeni*.

**A. 45 minutes after death.**
Cellular debris has broken away from the surface of the mucosa in the oxyntic area (arrow), leaving a clean edge.
WALLABY 2; HE (x100)

**B. 50 minutes after death.**
Large amounts of the mucosal surface are breaking away (arrows). The degree of degeneration is variable in this region.
WALABY 1; HE (x100)
Section 4. The unusual appearance of the duodenal mucosa in *Presbytis femoralis*

While not directly related to the histology of the stomach, sections of the duodenal mucosa were studied to determine the cause of its unusual rust-red colour (Plate 5.7). In the sections stained with HE clumps of golden material were seen to be scattered in the lamina propria (Plate 8.37). Macroscopically the colour of the mucosa suggested the presence of iron; to test if this was so further sections were treated with Perle stain. The results were positive, as this material stained deep blue (Plate 8.38). Probably the iron had been contained in the cytoplasm of macrophages (Guyton 1976), but this could not be verified as the preservation of the mucosa was so poor that most of the villi had disappeared. The amount of degeneration that had taken place can be gauged by comparing it with the duodenal mucosa in *Papio cynocephalus* (Plate 7.41) The colour of the mucosa was intense (Plate 5.7), which suggests that prior to death it must have contained considerably more iron, and this could have been a contributing factor, or even the actual cause of death.

Acute iron poisoning, when it occurs in humans, is usually fatal and presents the following pattern of symptoms (Committee on Medical and Biological Effects of Environmental Pollutants - CMBEEP 1978) -

*First phase* - characterized by vomiting, lethargy, diarrhoea, pallor, tachycardia and increased respiration.

*Improvement phase* - the symptoms largely disappear and the individual appears to be recovering.

*Final phase* - this is marked by a return of symptoms, which include fever, peritonitis, shock, coma, convulsions and eventually death.

The symptoms observed by Carati in the female (1986 - Appendix 2) commenced four weeks after the leaf-monkeys arrived in Australia: they were as follows -

1. the animal became lethargic and developed diarrhoea.
2. during the next two weeks her condition fluctuated and there appeared to be some improvement.
3. then she was found severely dehydrated and in shock one morning, dying two hours later.

Carati reported that she died of acute renal failure (Appendix 3) and that there was evidence of colitis of unknown cause, and that the lymph nodes in the pyloric region were expanded, all of which suggest inflammation. There is considerable overlap between these two lists of symptoms, which lends support to the hypothesis that the monkey's death was caused by acute iron poisoning.
These leaf-monkeys had undergone considerable dietary change in their transfer from Sumatra to Australia, and a number of factors could have contributed to the female’s condition. Iron absorption occurs in the duodenum (Guyton 1976) and increased uptake can occur in the following ways -

1. through decreased motility of the gut (Guyton 1976);
2. through increased acidity of the duodenal contents, which could result from increased gastric acid secretion, or increased amounts of ascorbic acid in the diet (CMBEEP 1978);
3. through increased amounts of iron in the diet (CMBEEP 1978). It was mentioned that lettuce and soya beans are two dietary items that can have this effect (CMBEEP 1978).
4. iron absorption will increase if the body reserves are low (Guyton 1976).

One or a combination of any of these factors could have been operating in these monkeys during their adjustment period and thus could have caused a severe dietary imbalance that resulted in the death of the female. The male also exhibited some of these symptoms, but they were much less severe and may have been a reflection of differences in individual tolerance to excess iron. Such individual differences in tolerance to iron have been observed in humans (CMBEEP 1978). Such an imbalance would not be an unusual occurrence as colobids are notoriously difficult to maintain in captivity because of their specialized digestive physiology (Hill 1964, Hollihn 1971).

There was one other possible explanation for this appearance of the duodenal mucosa, and that was the presence of hookworms. Carati (1986) noted the presence of the ova from this nematode parasite in the faeces of these animals. Hookworms attach themselves to the mucosa of the wall of the small intestine and cause haemorrhages in the lamina propria. This results in macrophages ingesting and breaking down red blood cells so that iron-containing compounds accumulate in their cytoplasm (Manson-Bahr 1966). As the iron was confined to the duodenal mucosa, it seems unlikely to have resulted from hookworm activity, for they are found in their greatest numbers in the jejunum, or the middle region of the small intestine (Manson-Bahr 1966). The mucosa in these areas was normal in colour, and it was only the duodenum that was different.
Iron in the duodenal mucosa of *Presbytis femorallis.*

**A.** The red colour of the duodenal mucosa was due to the iron deposits that can be seen in the lamina propria. In the sections the iron was yellow and was found mainly in the remnants of the villi.

HE (x100)

**B.** The iron-containing compound appears to be in discrete granules in the lamina propria. This is probably because it was ingested by phagocytes.

HE (x400)
PLATE 8.38
Iron in the duodenal mucosa of *Presbytis femoralis*.

A. Perle stain turns blue in the presence of iron. Most of the iron was located in the lamina propria of the villi.
PERLE (x100)

B. Detail of the iron deposits in the duodenal mucosa. This must reflect a fraction of the total that was present when the animal was alive, for most of the villi have disappeared.
PERLE (x 400)
Chapter 9  
Comparison of the histology of the gastric mucosa in catarrhines

In the Catarrhini, whether baboons, humans or colobids, the gastric mucosa has the same components, namely the mucus-secreting surface epithelium, three types of gastric glands, the lamina propria and the muscularis mucosae (Romer 1956, Burki 1958, Ito 1967). The major difference in the mucosa of the plurilocular stomachs of colobids and the unilocular stomachs of the rest of the catarrhines is the extent of the glandular areas (Burki 1958, Ito 1967).

In the unilocular stomachs of the Cercopithecidae and the Hominoidea the cardiac gland area is reduced in size, to a ring surrounding the cardiac orifice (Burki 1958, Ito 1967), and the oxyntic glands which line the fundus and body are the principal gland type. Cardiac glands are the most abundant of the mucosal glands in colobid stomachs for they are found lining the saccus gastricus and the cranial two-thirds of the tubus (Kuhn 1964). In these stomachs the area of the mucosa containing the oxyntic glands is reduced in size and is confined to the caudal third of the tubus (Burki 1958, Kuhn 1964, Peng et al. 1983). In both types of stomach the pyloric gland area appears to be relatively constant in size. In the human stomach it accounts for 13.8 percent of the total surface area (Landboe-Christensen 1944) and it appears to be the same in the other catarrhines, although no figures could be found. This suggests that it might be more conservative in structure than the other areas. These differences may reflect major differences in the functions of the stomachs in these two groups of primates, and may be associated with adaptation to different diets.

Those catarrhines with unilocular stomachs, the Cercopithecidae and the Hominoidea (apes and humans), are basically frugivores, but most of them supplement the fruit with any other plant and animal food that is available (Chivers and Hladik 1980, Kavanagh 1983); although there are some exceptions, like the gorillas, which eat little or no fruit. The bulk of such diets consist of readily digestible sugars and proteins (Chivers and Hladik 1980). The principal functions of the stomach in these animals are -

1. the storage of food, during which it is physically broken down into the semi-liquid chyme.
2. the preliminary digestion of proteins by pepsin from the oxyntic glands. Movements of the muscle layers in the walls mix the enzymes and the chyme.

The pyloric area in the human stomach is important in this mixing process and in the controlled release of the chyme into the duodenum (Netter 1971, Guyton 1976). Hormones from the entero-endocrine cells in these glands stimulate and help to coordinate the muscular and
secretory activities of other parts of the gastro-intestinal tract, as well as maintaining secretory activity in the stomach. It is also likely that secretions from the pyloric glands might help in raising the pH of the chyme as it passes into the duodenum, for excess acidity will block the activity of the enzymes that are released and working in this area (Guyton 1976).

Colobid stomachs are adapted to dealing with a diet of plant material that contains large quantities of long chain structural carbohydrates. These include cellulose, hemicelluloses and pectins (Bergman 1990). No mammal is capable of producing the enzymes necessary for hydrolysing these compounds (Moir 1968) and some herbivores, like the colobids, have overcome the problem by evolving symbiotic relationships with cellulolytic bacteria, that are held in special chambers in the stomach. The hydrolysis of these complex carbohydrates occurs in anaerobic conditions and results in the release of short-chain fatty acids that play an important part in the energy metabolism of these monkeys (Kuhn 1964, Bauchop and Martucci 1968, Bergman 1990). To maintain such a population of bacteria necessitates the maintenance of constant set of environmental conditions that will favour bacterial metabolism, growth and reproduction (Bergman 1990). By drawing together information on bacterial metabolic requirements, based largely on personal general knowledge, and details of colobid gastric physiology from the literature, it seemed to me that the following environmental factors would be important -

1. provision of a constant supply of food
   Kuhn (1964) mentioned that he found that the stomachs in the colobids he studied were never empty, no matter at what time of the day they were collected. The food is chewed into small pieces before it is swallowed and then further broken down by the movements of the wall releasing molecules for the bacteria to ferment. Lack of food in the stomach could possibly result in severe depletion of bacteria, or they might damage the mucosa in the absence of any other substrate.

2. lowered oxygen tensions
   Fermentation is an anaerobic process, requiring lowered oxygen tensions (Bergman 1990). To produce this state is probably not difficult in the large well-filled stomachs of the Colobidae.

3. maintenance of a constant temperature
   This is important for bacterial metabolism, but again this would not be a problem for primates that are capable of maintaining their body temperatures at relatively constant values through both physiological and behavioural mechanisms. The optimum temperature for bacterial metabolism will be the normal body temperatures of these animals.
4. a slow rate of passage of food through the stomach

This is important as it gives the bacteria time to ferment the complex carbohydrates and the monkeys time to absorb the metabolites they produce. It would also ensure that the population of bacteria is always maintained and that large numbers of them are not destroyed at any one time as the chyme is moved through the oxyntic gland area (Langer 1988). This is achieved by the taeniae and the haustra, which also play an important role in mixing the contents of the fermentation areas (Guyton 1976, Langer 1988). Mixing ensures that the bacteria are supplied with the substrates they need; it aids in the absorption by bringing the chyme into contact with the mucosal surface, and ensures that the glandular secretions are mixed into the chyme.

5. maintenance of the optimum pH for bacterial activity

These bacteria need an environmental pH of 5 - 7 (Kuhn 1964), which would present a problem in most mammalian stomachs in which the contents are highly acidic, with a pH of 1 to 2. In colobid stomachs the problem has been overcome in two ways -

i. the physical separation of the area where the bulk of fermentation takes place. In colobids this seems to have been accompanied by a reduction in the size of the oxyntic gland area. The role played these glands in proteolysis is not as important as that of the pancreatic enzymes (Guyton 1976), so a reduction of the oxyntic gland area in favour of more cardiac glands would not affect the nutrition of these monkeys to any great extent. Support for this hypothesis comes indirectly from the work of Chivers and Hladik (1980), who showed that the surface area in colobid small intestines was larger, on the average, than those in cercopithecids.

ii. by the possible buffering action of the cardiac glands, as Ohwaki et al. (1974) suggested. Colobids also have large salivary glands compared to other cercopithecoids (Sonntag 1921, Hill 1958). As saliva is known to buffer the stomach contents in ruminants (Blair-West et al. 1965), it may play a similar role in colobids; there is, however, a major difference between these two groups of mammals, which is that is that colobids are not known to ruminate (Owen 1835). This would mean that the buffering action of their saliva would be limited, and it would seem that some other secretory mechanism is operating, perhaps from the cardiac glands.

6. moisture

Moisture or water is important for initial break down of the large molecules by the
bacteria which occurs extracellularly (Bergman 1990) and it is also important for the absorption of the volatile fatty acids they produce (Bergman 1990). The necessary moisture will be provided by the secretions from the mucosal glands.

There is a complex interplay of many factors involved in maintaining such a relationship with a group of cellulolytic bacteria, and this appears to be the predominant function of the colobid stomach.

It would seem that the cardiac mucosa plays a vital role in maintaining this environment, and there are a number of factors supporting the hypothesis that it is not merely mucus-secreting -

1. The reduction of the cardiac gland area in mammals in which gastric fermentation is not an important contributor to the overall metabolism. This situation is seen in most catarrhine stomachs, where it is reduced to a very small and unimportant area around the cardiac orifice (Ito 1967).

2. Many authors stress that the secretory cells of both cardiac and pyloric glands are similar and their main function is the secretion of mucus that plays a protective role (Ito 1967, Guyton 1976, Kelly et al. 1984). The cardiac gland cells are not as densely stained with PAS as those in the pyloric area. This was obvious in sections from the stomach of *Presbytis femoralis* (Plates 8.13 and 8.5), and was also noted by Kuhn (1964) in *Trachypithecus auratus* and Suzuki et al. (1985) in *Trachypithecus francoisi*. Interestingly this difference was also evident in these glands in *Papio cynocephalus* (Plates 7.7 and 7.26). This suggests that there may be differences in the composition, and thus the functions, of their secretions. More detailed histochemical testing of freshly killed material is needed to verify this observation.

3. The mucus secreted by these glands is less viscous than that produced by the surface mucous cells (Guyton 1976, Kelly et al. 1984), which suggests a difference in composition and thus in function.

To these can be added the observation that the muscularis mucosae is thick in this region in colobids (Table 8.2, Kuhn 1964, Peng et al. 1983). According to Guyton (1976) the contraction of the muscularis mucosae would increase the surface area in contact with the chyme, which would aid in the absorption of volatile fatty acids, which would help to lower the pH. On the basis of personal observation it would seem that the contraction of the muscularis mucosae would also help in emptying the secretions from these glands into the chyme. If these
glands are involved with this function, it would also help in maintaining the pH at optimum levels. Hormones produced by the entero-endocrine cells stimulate the motility of the stomach (Guyton 1976), and these cells are abundant in the pyloric glands (Plate 8.28). It would appear that there is considerable evidence to indicate that these glands could be playing an important part in pH regulation in these areas of the colobid stomach.

The other histological feature that was important was the difference in the epithelial lining of the praesaccus in Procolobus, Pygathrix, Rhinopithecus and Nasalis. In Pygathrix nemaeus this region was reported to be lined with a nonglandular stratified squamous epithelium (Pilliet and Boulart 1898, Hollihn 1971), as was also the case with the praesaccus of Nasalis larvatus (Hombron and Jacquinot 1845, Hollihn 1971). The function of this type of epithelium is primarily a protective one (Ham and Leeson 1961). In Procolobus (Kuhn 1964) and Rhinopithecus (Peng et al. 1983) the praesaccus is lined with a mucosa containing cardiac glands. This would seem to be a very real difference as it is impossible to confuse the two types, even in poorly preserved material (Plate 8.31). Kuhn suggested that the praesaccus in Procolobus badius was a storage organ as it contained finely-chewed leaf pieces with little fluid. He also noted that "typical" direction of the mouth of the oesophagus was towards the praesaccus, so that food entered it first.

These differences in structure of the mucosa of the suggest that there might be differences in the functions of these areas, which seems unlikely. It seems more reasonable to assume that they reflect adaptations to different diets. For example the nonglandular epithelium would provide greater protection against harsher plant material than the more delicate cardiac epithelium. As the examples in Chapter 8 (Discussion) show, there are many unanswered questions remaining.
Comparison of the three glandular areas of the gastric mucosa in *Papio cynocephalus* and *Presbytis femoralis*. These photographs emphasise the differences in the preservation of these two specimens, and show that it is possible to learn much about the structure of the gastric mucosa in poorly preserved specimens. It helps to have a specimen, like *Papio cynocephalus*, for use as a control. The differences in the pattern of degeneration in each of the glandular areas of the stomach may have been due to differences in glandular secretions, and to the presence of bacteria in the fermentation chambers. PAS (x100)
A. The cardiac region of the gastric mucosa.

The amount of mucosal loss in this region of the mucosa has been extensive in *Presbytis femoralis*, leaving only a few of the bases of the glands, and the tissues in the wall are breaking away from each other.
B. The oxyntic gland region of the gastric mucosa.

The loss of cell detail and the changes in the general structure of the glands in the oxyntic area of the mucosa in *Presbytis femoralis* becomes apparent when these two sections are compared. The pattern of degeneration appears to be different from that in the cardiac area, where there was erosion of the surface, leaving some cell detail in the glands.
C. The pyloric gland region of the gastric mucosa.
This area shows the least damage in *Presbytis femorals*, with much cell detail evident. The staining reaction of the gland cells is not as intense as in *Papio cynocephalus*, but it still gives an indication of their staining reaction and the presence of mucopolysaccharides in the cytoplasm.
Chapter 10

Functional gastric anatomy and some implications for understanding the phylogeny of the family Colobidae

The stomach of *Presbytis femoralis* is very like that of other colobids with three chambers. The differences observed were relatively minor, emphasizing the common morphological pattern in these organs. The study of the histology of the mucosa in this specimen showed that, despite its poor state of preservation, it was like that of other colobids and that they all differed from *Papio cynocephalus* in the extent of the cardiac mucosa and perhaps in the relative thickness of the muscularis mucosae in this region. The basic structure of the gastric glands appeared to be similar in all of the catarrhines. A considerable amount of information was obtained about the structure of the mucosa in *Presbytis femoralis*, which was surprising as a number of authors had cautioned against using such material (Berenberg-Gossler 1911, Kuhn 1964). This was encouraging as it means that material that might have been rejected because of its state of decay can be used, but always cautiously, to provide more knowledge about these monkeys. This is an important finding as many colobid species are rare or endangered.

The study of the findings of other authors provided the foundations for describing the anatomy of the stomach in *Presbytis femoralis*, and it resulted in a review of the morphological differences observed in the various members of the family that had been studied over the years. The stomachs of mammals reflect adaptations to diets in particular ecological niches and can be considered to be phylogenetically conservative (Romer 1956, Ito 1967, Langer 1988). As they are complex organs, both structurally and functionally, whether plurilocular or unilocular, they must be indicators of a long evolutionary history. For this reason it is likely that major differences in stomach structure would provide a clear indication of taxonomic separation, especially if there are other characters to support this, as appears to be the case with the Old World monkeys. The Cercopithecidae have unilocular stomachs in which proteolysis is the major digestive function, while the Colobidae have plurilocular stomachs, in which bacterial fermentation of complex polysaccharides is of prime importance. As the members of each of these groups share other common derived characters (Napier 1985, Strasser and Delson 1987, Groves 1989), many of which are related to their differing lifestyles, it would seem that the two groups are quite distinct, which might provide support for the hypothesis that there are two families of Old World monkeys (Groves 1989).

There were other findings that came from this study of the literature on the colobid stomach,
some of them quite unexpected, which raised questions about the traditional approach to the taxonomy of the members of this family, and the affinities between genera in particular. At the present state of our knowledge, the morphology of the colobid stomach appears to be constant in the different genera, with only very minor variations between the species within them (Langer 1988, Chapters 4 and 5 of this thesis). This can be widened, as there are only very minor differences in the morphology in the three-chambered stomachs, but those genera with four-chambered stomachs are not as homogeneous. Common adaptations seen in a group of animals at levels above the species suggest they are long-standing and successful, from an evolutionary point of view, and have enabled these animals to widen their dietary options through their symbiotic relationships with cellulolytic bacteria (Langer 1988).

Patterns of stomach morphology, which must be based on generalizations as information is not available for all species within the family Colobidae (Table 1.1), result in two major groupings of genera (Table 10.1A) -

1. **those without a praesaccus** - *Colobus, Presbytis, Semnopithecus* and *Trachypithecus*.

   This group contains the bulk of the extant species, most of which are Asian.

2. **those with a praesaccus** - *Procolobus, Pygathrix* and *Nasalis*.

   Again there are more Asian species than African.

The smaller numbers of African species may possibly be due to two factors -

1. a reduction in the rainforest habitat in Africa due to climatic changes that began in the Pleistocene.

2. increased ecological competition from the cercopithecids, which were more adaptable than the colobids. This is supported by the fact that the colobids are more restricted in their distributions, although they are often abundant where they do occur, and are known to be dependent on a relatively restricted range of plant foods (Rose 1978, Struhsaker 1978). There are far more cercopithecids species in Africa than Asia.

It would seem that the two African genera are closely related to each other, despite the stomach differences, as they share a number of derived characters (Strasser and Delson 1987, Groves 1989). *Procolobus spp.* are considered to be the most primitive members of the family and the two subgenera are united by a set of characters (Groves 1989). Stomach structure is an important character separating the African genera, but at this stage it is not known which form is the primitive and which the derived condition. This difference suggests that there are differences in diet and the limited information available tends to supports this observation. For example, *Procolobus badius*, which Groves considers to be *P. pennantii tephrosceles* (personal communication), is sympatric with *Colobus guereza* in the Kibale Forest of Uganda, and there are
differences in their diets. These may only be apparent at certain times of the year, for the diets of colobids are influenced by seasonal variations in fruiting and leaf-flush patterns in the species of food trees (Clutton-Brock 1977). Oates (1977) used indices to compare the dietary diversity throughout the year in these two species of colobid. The dietary index of *C. guereza* varied from 1.21 - 2.14 (average 1.67) for a twelve-month period, from February 1971 to January 1972 (Oates 1977). The diet of *P. pennanti* was more diverse as averaged 2.51, varying between 1.97 and 3.05 during an eighteen-month period, November 1970 to March 1972 (Oates 1977). Ecological separation also occurs, for *P. pennanti* is more likely to be found in areas of mature forest, while *C. guereza* tends to inhabit secondary forest areas (Struhsaker 1978). The information available for making comparisons between colobid species with three and four chambered stomachs is very limited, and at this stage it is difficult to discern any definite patterns. On the basis of the characters that unite them, it would seem valid to separate the African genera from the Asian, as Hill (1936) and Strasser and Delson (1987) suggested, but probably as a subfamily, in which case Colobinae, Gray 1812 would be the most appropriate name.

The relationships between the Asian genera appear to be much more complex. Those genera with three-chambered stomachs (*Presbytis, Semnopithecus* and *Trachypithecus*) are closely related and share a number of features in common (Napier 1985, Groves 1989), which suggests that they might form a monophyletic group. The other two genera have a praesaccus, but there are histological differences:

1. in the Chinese species of *Rhinopithecus* the praesaccus is lined with cardiac glands, like those of the saccus gastricus (Peng et al. 1983).
2. the praesaccus in *Pygathrix nemaeus* and in *Nasalis larvatus* is reported to be lined with a nonglandular stratified squamous epithelium (Hombron and Jacquinot 1845, Pilliet and Boulart 1898, Hollihn 1971).

Structurally these two types of epithelia are quite distinct and it is very unlikely that they would be confused. Peng et al. (1983) considered that the Chinese species of snub-nosed monkeys should be given full generic status and this would be in accord with their stomach morphology. Nothing is known about stomach morphology in the fourth species, *Pygathrix (Rhinopithecus) avunculus*. *Nasalis larvatus* and *Pygathrix nemaeus* are united in this anatomical feature, which is unique among catarrhines and primates in general (Burki 1958). Groves' proposal (1989) that *N. larvatus* should be included in a separate subfamily, Nasalinae, would be given added support if this finding could be verified; but if the praesaccus of *P. nemaeus* is also lined with stratified squamous epithelium, then its relationship to *Rhinopithecus* should be questioned, and
there would seem be grounds for placing it instead with *N. larvatus*. As well as being structurally distinct, these types of epithelia are also very different functionally. Stratified squamous epithelia provide mechanical protection against physical damage, while the cardiac type of mucosa produces secretions which would have some protective function, but largely against chemicals. To have such differences in structure and function suggests that there are major dietary differences as well. That so little is known about these animals makes it difficult to understand the significance of these findings. It leaves unresolved questions about the evolution of the praesaccus and the possibility of convergent evolution in these genera. These facts also raise queries about the subgroups of Asian colobids, for it is unlikely that they monophyletic. It is possible that there are 2 - 3 subfamilies, depending upon the derived characters that they share.

What started as a simple project, to study the anatomy of the stomach of *Presbytis femoralis*, was not so simple after all, and has had much wider implications for research into the phylogenetic relationships within the family Colobidae, by looking at their total adaptations to life as arboreal folivores.
FIGURE 10.1
GROUPS WITHIN THE FAMILY COLOBIDAE, THAT CAN BE SEPARATED FROM EACH OTHER ON THE BASIS OF DIFFERENCES IN THE MORPHOLOGY OF THE STOMACH.

A. WITHIN THE FAMILY AS A WHOLE

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<table>
<thead>
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<td>Presbytis</td>
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<td>Colobus</td>
<td>Procolobus</td>
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B. WITHIN THE AFRICAN GENERA

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C. WITHIN THE ASIAN GENERA

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D. WITHIN THE ASIAN GENERA THAT HAVE A PRAESACCUS

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<td>Pygathrix</td>
</tr>
<tr>
<td></td>
<td>Nasalis</td>
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ASIAN COLOBIDAE
References


Martin, W.C.L. (1837). Notes on the anatomy of the proboscis monkey (*Simia nasalis*). *Proceedings of the Zoological Society of London* 1837.70-3


APPENDIX 1
A summary of the contents of the descriptions of stomach anatomy in colobid genera and species.

<table>
<thead>
<tr>
<th>Genus</th>
<th>Species</th>
<th>Author</th>
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<td>Hollihn (1971)</td>
<td>brief description based on Kuhn's descriptions</td>
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<td>Chivers and Hladik (1980)</td>
<td>form of the gut in relation to diet; based on measurements of surface areas</td>
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<td>geureza</td>
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<td>Murie (1865)</td>
<td>anatomy of a freshly killed specimen compared with S. entellus</td>
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<td></td>
<td></td>
<td>Polack (1908)</td>
<td>brief comparisons with S. entellus and C. polykomos noting similar form of the stomachs</td>
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<td></td>
<td></td>
<td>Hill (1952)</td>
<td>stomach more like those of Asian colobids than Procolobus verus</td>
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<td></td>
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<td>Kuhn (1964)</td>
<td>noted presence of nematodes in the stomach</td>
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<td>Hollihn (1971)</td>
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<td>form of the stomach very like that in S. entellus</td>
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<td>Procolobus</td>
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<td>detailed description of the stomach and comparisons with other colobid species, especially the gastro-oesophageal junction</td>
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<td>(Procolobus)</td>
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<td>description based on Hill (1952), part of a comparison of primate stomachs in general</td>
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<td>Burki (1958)</td>
<td>description based on Hill (1952) - very brief</td>
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<td>Kuhn (1964)</td>
<td>comparisons with P. badius; physiology of gastric digestion; nematodes found in the first part of stomach</td>
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<td>Langer (1988)</td>
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<tr>
<th>Species</th>
<th>Form of Stomach</th>
<th>Authors and Dates</th>
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<tr>
<td>Procolobus badius</td>
<td>First detailed description of histology of colobid stomach, if identification correct</td>
<td>Salmon (1893)</td>
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<td>Form of stomach similar to that of P. verus; form of the gastro-oesophageal junction described</td>
<td>Hill (1952)</td>
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<td>Mentions that this is the species described by Salmon (1893)</td>
<td>Burki (1958)</td>
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<td>Detailed description of the stomach; discusses physiology and the role of bacteria; nematodes present in the stomach</td>
<td>Kuhn (1964)</td>
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<td>Semnopithecus entellus</td>
<td>Brief description of the form of the stomach</td>
<td>Owen (1833)</td>
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<td>Detailed description of the above specimen</td>
<td>Owen (1835)</td>
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<td>Detailed description of the anatomy; comparisons with other Asian colobids</td>
<td>Duvernoy (1834)</td>
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<td></td>
<td>Comparison with C. polykomos; unusual arrangement of the taeniae not seen by other authors</td>
<td>Polack (1908)</td>
</tr>
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<td></td>
<td>Histological study of the mucosa limited by post mortem degeneration; detailed description of the anatomy, especially the external muscle</td>
<td>Berenberg-Gossler (1911)</td>
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<td>The most detailed description of the langur stomach; comparisons made with other colobids</td>
<td>Ayer (1948)</td>
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<td>Brief comparison with the stomachs of other colobids, especially the gastro-oesophageal junction</td>
<td>Hill (1952)</td>
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<td>Commented on Polack's description of the taeniae; part of a general comparison of primate stomachs</td>
<td>Hill (1958)</td>
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<td>Discussion of Berenberg-Gossler's findings for a comparison with stomachs of other colobids</td>
<td>Burki (1958)</td>
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<td>Form of the gut in relation to diet; based on measurements of surface areas</td>
<td>Chivers and Hladik (1980)</td>
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<td>Used the descriptions of other authors to make comparisons with the colobid stomachs he studied</td>
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<td>Trachypithecus vetulus</td>
<td>Detailed description of the anatomy of the stomach</td>
<td>Otto (1825)</td>
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<td>Comparison with stomach of C. polykomos</td>
<td>Polack (1908)</td>
</tr>
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<td>Brief comparison with S. entellus, noted that the stomachs were very similar in form</td>
<td>Berenberg-Gossler (1911)</td>
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<td>Mentions function of stomach in storage and insalivation of ingested food</td>
<td>Sonntag (1921)</td>
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<td>Very brief comparison with the simple stomach of macaques</td>
<td>Pocock (1928)</td>
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<td><em>Auratus</em></td>
<td>Owen (1834)</td>
<td>Brief description of a common character in this group of monkeys.</td>
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<td><em>Obscurus</em></td>
<td>Hill (1952)</td>
<td>Form of the gastro-oesophageal junction compared with other species.</td>
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<td>Chivers and Hladik (1980)</td>
<td>Form of the gut in relation to diet; based on measurements of surface areas.</td>
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<td><em>Cristatus</em></td>
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<td>Form of the gut in relation to diet; based on measurements of surface areas.</td>
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<td><em>Francoisi</em></td>
<td>Suzuki et al. (1985)</td>
<td>Brief description of the anatomy and histology of the stomach.</td>
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<td><em>Presbytis</em></td>
<td>Hill (1952)</td>
<td>Form of the gastro-oesophageal junction compared with other colobids.</td>
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<td>Chivers and Hladik (1980)</td>
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<td>Owen (1833)</td>
<td>Brief comparison with <em>S. entellus</em></td>
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<td>Owen (1835)</td>
<td>More detailed description and comparison of the above animals.</td>
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<td><em>Rubicunda</em></td>
<td>Chivers and Hladik (1980)</td>
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<td><em>Pygathrix</em> (Pygathrix)</td>
<td>Otto (1825)</td>
<td>Brief note on its complex form.</td>
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<td>Duvernoy (1834)</td>
<td>Brief description comparing it with <em>S. entellus</em>.</td>
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<td>Pilliet and Boulart (1898)</td>
<td>Detailed description of the anatomy of the stomach; some detail of the histology of the mucosa.</td>
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<td>Burki (1958)</td>
<td>Pilliet and Boulart's description discussed for comparison with the histological structure of the stomach in <em>S. entellus</em>.</td>
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<td>Hollihn (1971)</td>
<td>Brief description of the anatomy for comparison with other colobids.</td>
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<td><em>Pygathrix</em> (Rhinopithecus)</td>
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<td>Peng et al. (1983)</td>
<td>Details of anatomy, histology of the mucosa and physiology of the stomach.</td>
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<tr>
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<td><strong>Nasalis larvatus</strong></td>
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<td>very brief description for comparison with <em>T. vetulus</em></td>
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<td>Duverney (1834)</td>
<td>mentions that it has a complex form</td>
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<td>Martin (1837)</td>
<td>description of the anatomy of the stomach</td>
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<td>Hombron and Jacquinot (1893)</td>
<td>description of the anatomy and the histology of the mucosa</td>
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<td>Polack (1908)</td>
<td>very brief description of the position of the stomach in the abdomen</td>
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<td>Duckworth (1915)</td>
<td>brief description comparing it with those of other “Semnopithecii”</td>
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<td>Burkl (1958)</td>
<td>thought that there was no detail of the histology available, only studies of gross anatomy</td>
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<td>brief description of the anatomy and mentions the form of the mucosa</td>
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<td>form of the gut in relation to diet; based on measurements of surface area</td>
</tr>
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<td>Langer (1988)</td>
<td>anatomy in a foetal specimen</td>
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APPENDIX 2
The gastro-intestinal tract of the dusky leaf monkey, *Presbytis obscura*.

Upper right, the disposition of the tract within the abdominal cavity. Upper left, the stomach (partially distended with water) displayed to show the large sac, the gastric tube (on the right), and the pylorus (lower left). Below, the complete abdominal part of the tract, with a different aspect of the stomach on the left, and the coils of small intestine, caecum (directed downwards), and colon leading around to the rectum, successively on the right.

(Photograph: D.J. Chivers, from Chivers and Hladik 1980)
APPENDIX 3

The autopsy report on the specimen of *Presbytis femorallis* used in this study.

Notes on Leaf Monkey Husbandry

As mentioned in the last Bulletin (AP 1(1):11), two young leaf monkeys (*Presbytis femorallis* ssp.) recently arrived in Perth from Sumatra. These animals had spent the previous 3 years as companions to Terry and Pam Turner, and were offered to the Bullen Primate Research Foundation for reproductive, behavioural and husbandry research. The offer was viewed with some trepidation, as these animals have a reputation for being difficult to keep in captivity. However, given the rarity of the animals, the fact that their only other fate was destruction and the excellent husbandry record of the Turners, it was decided to overcome bureaucracy and give them a new home.

To satisfy quarantine conditions, they have been housed in the same cage at the Bullen Primate Research Foundation's holding facilities at the Queen Elizabeth II Medical Centre. During this time, the Turners monitored their well-being daily, providing their diet and exercise. Some four weeks after arriving, the female became lethargic and developed diarrhoea, which was conservatively treated with subtle diet changes and 1-2 ml Kapectate (Upjohn Pty. Ltd.) daily for a week. Examination of faecal material microscopically and by culture had previously demonstrated ova of hookworm, but no pathogens were detected. The condition fluctuated over the ensuing two weeks, and appeared to be resolving when we found her severely dehydrated and in shock early one morning. Attempts to rehydrate her intravenously failed, and she died two hours later. Blood analysis showed evidence of acute renal failure. An autopsy was performed the following day. Her gut was full of food, although her stomach was bloated above the pyloric region. In this region, there were expanded lymph nodes, and subsequent histology confirmed mesenteric lymphadenosis. Below this region the small bowel was largely empty and of narrow diameter. The large bowel and colon were full of reasonably solid material. All other body regions were clear. Histological sections of the heart, lung, kidney, pancreas and adrenals showed these organs to be in good condition. Sections of the colon showed evidence of colitis, with an inflamed lining and cystic formations within its crypts. No organisms which could be responsible were detected. There was no sign of TB in any sections. This animal had been tested for human, atypical and avian strains of TB in the month prior to its demise, and all tests were negative.

This animal evidently died from renal failure and dehydration, secondary to colitis, the cause of which is unknown. A notable aspect to the incident was the rapidity with which the animal succumbed and became dehydrated. On the day previous to its demise, it was considerably improved in demeanour and body condition, and the animal appeared on the road to recovery. Its male companion is currently in good health, despite having fairly loose stools. Extensive testing of faecal material has failed to demonstrate any pathogens or parasites.

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