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The Morphology of the Gastrointestinal Tract and Food Transit Time in the Fruit Bats *Pteropus alecto* and *P. poliocephalus* (Megachiroptera)

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Abstract

The gastrointestinal tract of *Pteropus alecto* and *P. poliocephalus* was investigated by dissection and by light and electron microscopy. Food transit time was recorded for a variety of cultivated fruits and roentgenograms were obtained from animals fed with barium-labelled food. Minimum food transit time varied from 12 to 34 min for cultivated fruits but this was extended to 44 min by the addition of barium. There was little variation between the gastrointestinal tracts of the two species. The stomach has an elongated terminal part, and expanded cardiac and fundic regions which display a relatively thick gastric mucosa and abundant parietal cells. These features probably ensure exposure of ingested material to a substantial flow of HCl, perhaps counterbalancing a short exposure to digestive fluids. A caecum and appendix are absent. Well developed villi of the small intestine feature absorptive cells with relatively large microvilli ($\leqslant 5{\cdot}7$ μm tall), which are probably associated with a rapid rate of absorption. The intestinal mucosa displays many more goblet cells in *P. poliocephalus* than in *P. alecto*. The large intestine is short and features prominent longitudinal folds; however, the mucosa undergoes a gradual transition, with number and size of villi decreasing in the distal part of the intestine. Although a distinct rectum cannot be distinguished, the colonic mucosa is restricted to a short segment, slightly shorter in *P. poliocephalus* than in *P. alecto* (5–7% and 8–10% of intestinal length respectively).

This study highlights several anatomical features of the gastrointestinal tract, which probably allow fruit bats to rapidly process large quantities of food. The advantage of this to a flying mammal is a reduction in bulk carried in the digestive tract, enabling it to reduce the energy expenditure associated with foraging flights.

Introduction

The passage of food through the gastrointestinal tract in at least seven old-world species of Megachiroptera (Keegan 1975; Okon 1977; Wolton *et al.* 1982) and in the Australian species *Pteropus alecto* and *P. poliocephalus* (Tedman and Hall 1982), has been shown to be remarkably rapid (15–100 min). However, very little is known of the mechanism which permits these bats to process food so rapidly.

The gross and/or light microscopic morphology of either the stomach or the entire alimentary canal has been reported for numerous species of Microchiroptera (e.g. Schultz 1965; Rouk and Glass 1970; Forman 1972, 1973; Kamiya and Pirlot 1975; Madkour 1977), but less attention has been paid to the digestive tract of the Megachiroptera (e.g. Schultz 1965, 1970; Halstead and Segun 1975; Kamiya and Pirlot 1975; Madkour 1977; Okon 1977; Bhide 1980; Madkour *et al.* 1982). Manley and Williams (1979) briefly commented on some adaptations in the gastrointestinal tract of *P. poliocephalus* in relation to a frugivorous diet. However, there is no detailed published information on the digestive tract of any of the Australian Chiroptera.

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The nocturnal activity of fruit bats or flying foxes (*Pteropus* spp.) around feeding trees in eastern and northern Australia is legendary. Fruit bats are important nocturnal pollinators and dispersal agents for fruit seeds in eastern and northern Australian forests (Ratcliffe 1931*a*), but very little is known about their feeding ecology.

The present study is an attempt to determine the relationships between the morphology of the gastrointestinal tract and food transit times in two Australian fruit bats, *Pteropus alecto* and *P. poliocephalus*.

Materials and Methods

For food passage times, one wild-caught adult female *P. alecto* and one *P. poliocephalus* were maintained in captivity for several months on a diet of fruit such as pawpaws, apples, grapes, bananas, pears and mangoes. During this period body weight remained constant. Intestinal transport times were determined by feeding these bats a variety of fruits and observing continuously until the first faecal pellets were produced. Since individual fruits are easily identified in fresh faecal pellets, different fruits were fed to the bats on consecutive evenings to ensure that the faecal pellets did not contain fruit from a previous meal which had been retained by the gastrointestinal tract.

Food passage and transit times were confirmed by means of food which had been thoroughly mixed with 25% by weight of barium sulphate (Vectron Medic X-ray Accessories, Brisbane) and 5% glucose. On two occasions one specimen of *P. alecto* was fasted for 24 h and then fed approximately 100 g of this mixture. Roentgenograms were taken at intervals of 5–10 min for 1 h.

Three adult specimens of *P. alecto* and four of *P. poliocephalus*, with mean body weights respectively of 540 g and 692 g, were collected from a colony in mangrove trees on the South Pine River, 22 km north of Brisbane.

All animals were killed by intraperitoneal injection of pentobarbital sodium, and the entire alimentary canal was immediately dissected out. The different regions were measured, and samples were cut out and fixed in either 10% phosphate-buffered formalin or 3% cacodylate-buffered glutaraldehyde.

Formalin-fixed tissues were embedded in paraffin, cut at 8 μm, and stained with haematoxylin and eosin. Glutaraldehyde-fixed tissues were embedded in epon; thin sections were stained with uranyl acetate and finally with lead citrate, and examined with either a Zeiss EM10 or Jeol 100S transmission electron microscope.

The measurements of the gastric glands, gastric pits and intestinal glands were made with an eyepiece micrometer. Microvilli were measured on prints at a final magnification of ×5600.

Table 1. Food transit times for the gastrointestinal tract of *P. alecto* and *P. poliocephalus*

Food	*P. alecto* time (min)		*P. poliocephalus* time (min)	
	Range	*N*	Range	*N*
Pawpaw	22–28	4	18–31	9
Pear	–	–	27–32	2
Pear + apple	26–34	2	–	–
Mango	12–30	5	24–30	3
Barium + pawpaw	30	1	–	–
Chalk + pawpaw	35	1	–	–
Barium + honey	44	1	–	–

Results

Food Passage Rates

The mean minimum transit times for the gastrointestinal tract of both species were similar (12–34 min) for a variety of fruits (Table 1).

Barium mixtures entered the small intestine within 10 min of feeding, and faecal pellet formation began approximately 25 min later. The first pellets were defaecated 44 min after feeding (Table 1; Fig. 1). The stomach was empty at 21 min after feeding.

Gross Morphology

In both species the oesophagus is a long (102–145 mm) narrow (2 mm) tube positioned ventral and slightly to the right of the thoracic vertebral bodies. On passing through the diaphragm the oesophagus bends to the left to pass into the cardiac vestibule of the stomach (Fig. 2).

Although most of the stomach is covered by the left lobe of the liver, the greater curvature, to which the spleen is attached by peritoneum, protrudes caudal to the liver.

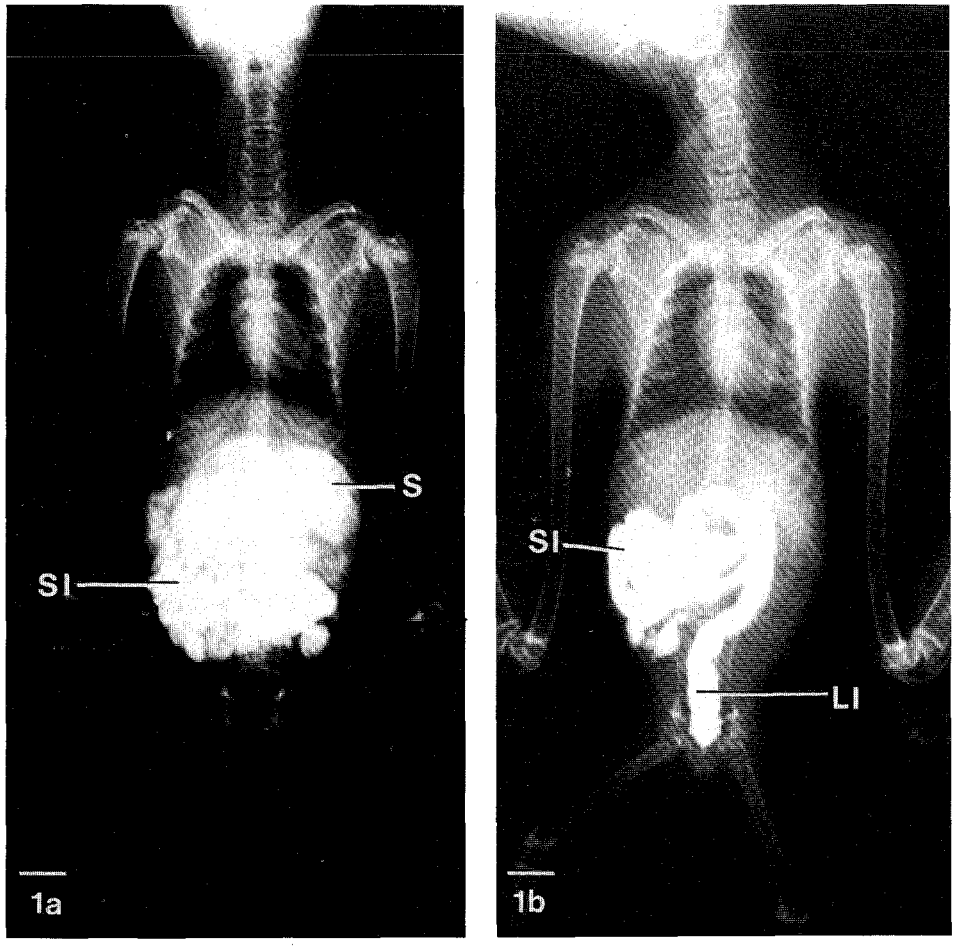


Fig. 1. Roentgenograms of *P. alecto* 10 min (*a*) and 32 min (*b*) following a barium sulphate meal. *LI*, large intestine; *S*, stomach; *SI*, small intestine. Note that in (*b*) food has left the stomach and faecal pellets are forming in the large intestine. Scale bar, 1 cm.

Although the stomach varies greatly in length, in *P. poliocephalus* it is much longer than in *P. alecto*. The length variation appears to be independent of body weight (Table 2). In both species there are well developed fundic and cardiac regions which are closely held together by peritoneum. The fundic caecum is much longer than the cardiac vestibule in *P. poliocephalus*, but is of similar length or shorter in *P. alecto*. The main body of the stomach is shaped like a long cone extending into a very long terminal portion, which is folded under the left lateral and right medial lobes of the liver. The pyloric sphincter is marked by a slight constriction and a narrow band which encircles the tube (Fig. 3).

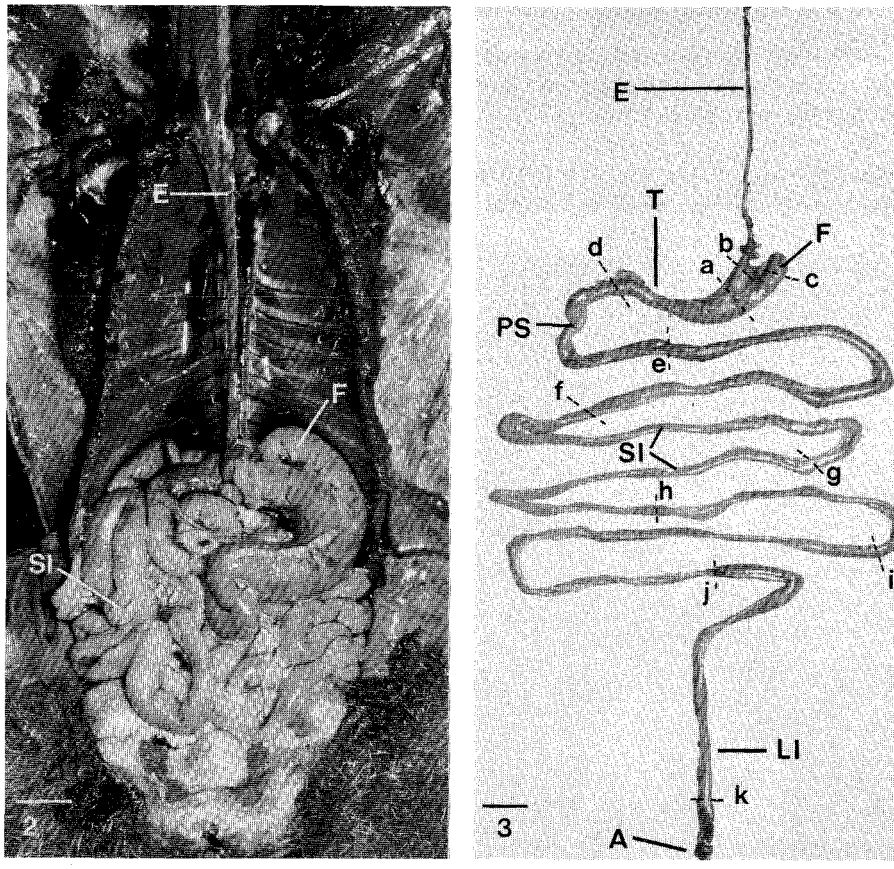


Fig. 2. Ventral view of *P. poliocephalus* showing the gastrointestinal tract *in situ*. The contents of the thoracic cavity, the diaphragm and the liver have been removed. *E*, oesophagus; *F*, fundus of stomach; *SI*, small intestine. Scale bar, 1 cm.

Fig. 3. Gastrointestinal tract of *P. poliocephalus* displayed to show oesophagus (*E*), fundus of stomach (*F*), terminal part of stomach (*T*), pyloric sphincter (*PS*), small intestine (*SI*), large intestine (*LI*) and anus (*A*). Sections *a–k* are also indicated. Scale bar, 1 cm.

Table 2. Lengths of parts of the gastrointestinal tract, and body measurements of *P. alecto* and *P. poliocephalus*

Measurement	*P. alecto*		*P. poliocephalus*	
	Mean	Range	Mean	Range
Length (mm)				
Stomach	145	142, 147	173	140–190
Cardiac vestibule	26	23, 29	28	21–34
Fundic caecum	21	19, 23	39	28–46
Intestine	1630	1560, 1700	1690	1290–2030
Forearm	166	162, 169	162	159–167
Intestine: body length ratio	6·6	6·2, 7·0	6·2	5·0–7·2
Total body weight (g)	540	520, 560	692	510–915
Number of specimens	2		4	

Internally the stomach in both species is lined by longitudinal rugae which vary in appearance in different individuals and along the length of the stomach. The fundic caecum is compartmentalized by diagonal and transverse rugae which branch from the longitudinal rugae near the proximal part of this region of the stomach. The rugae in the main part of the stomach are widely separated with few side branches. Nearer the pylorus the rugae are reduced in height, and are much more numerous than in the rest of the stomach. At the distal end of the pyloric sphincter the rugae are replaced by a mat of villi.

Macroscopically there is no external surface delimitation of small and large intestine, and there is no caecum nor appendix.

Intestinal length varies greatly in both *Pteropus* species, with no obvious correlation with body weight or forearm length. The ratio of intestinal length to body length varies from 5·0 to 7·2 (Table 2).

Microscopic Morphology

The microscopic appearance of the gastrointestinal tract is, with a few exceptions, identical in the two species.

The oesophagus is lined with a thick layer of stratified squamous epithelium. The lamina propria and muscularis mucosae are indistinct but the submucosa is extensive. The muscularis externa is prominent and contains myenteric (Auerbach's) plexuses.

At the gastro-oesophageal junction the appearance of the tissue changes abruptly, so that both layers of the muscularis externa are enlarged and form a sphincter. There is a small area at the entrance to the stomach which is entirely lined with mucous cells.

In the body of the stomach (Fig. 3, *a*) the surface epithelium is lined by mucous cells. The gastric pits are shallow (4–6 cells deep) and lined by mucous neck cells. Parietal (oxyntic) cells are prominent and line 80–90% of the gastric glands, which are 210–350 μm deep (Fig. 4).

In two of the three *P. poliocephalus* specimens examined, the parietal cells feature an extensive system of intracellular canaliculi lined by closely packed microvilli, numerous globular mitochondria and no secretory granules (Fig. 10). A few profiles of rough endoplasmic reticulum (RER) and scattered tubulovesicular elements are present. Parietal cells of tissues from one specimen of *P. poliocephalus* and two specimens of *P. alecto* displayed poorly developed intracellular canaliculi and microvilli, but were packed with tubulovesicular structures and globular mitochondria (Fig. 11). The RER was not prominent.

Large homogeneous, electron-opaque granules, abundant tubular RER and a few scattered mitochondria tightly packed the zymogen cells of both species (Fig. 12). Occasional enteroendocrine cells displaying small, numerous, very dense-staining, membrane-bound granules are scattered singly throughout the gastric glands. These cells have inconspicuous RER and few mitochondria.

The cardiac region of the stomach (Fig. 3, *b*) contains shallow gastric pits lined by mucous neck cells. In the gastric glands (265–390 μm deep) parietal cells are prominent in the mid-part; zymogen cells occupy the basal 20–40% of the glands in *P. poliocephalus* and up to 55% in *P. alecto*. Enteroendocrine cells are also present.

The fundic region (Fig. 3, *c*) resembles the cardiac region except that the glands are deeper (305–425 μm) in *P. alecto* and the zymogen cells occupy a larger proportion of the glands in both species (Fig. 5).

The height of the gastric glands is reduced in the extended terminal part of the stomach (180–275 μm) (Fig. 3, *d*). This area represents a wide transitional zone between gastric and pyloric mucosa. Gastric pits are a few cells deeper than in the body of the stomach, so there are more mucous neck cells present. Parietal cells line the gastric glands almost entirely, and there are only a few scattered zymogen cells at the base of each gland. Enteroendocrine cells are scattered throughout the glands, being located on the basement membrane. In the pyloric region there are Brunner's glands in the submucosa.

The gastroduodenal junction is marked by a prominent sphincter caused by an enlargement of the muscularis externa.

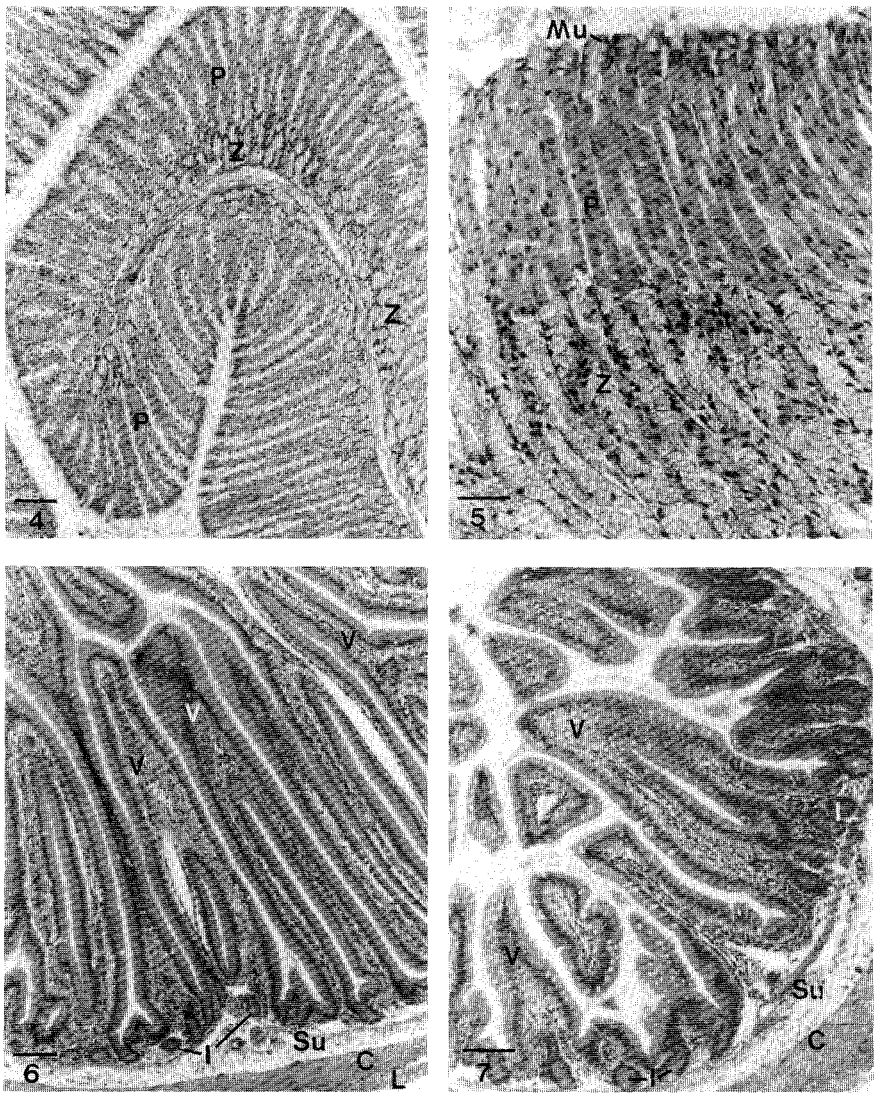


Fig. 4. Body of stomach (Fig. 3, section *a*) of *P. poliocephalus*. Scale bar, 100 μm.
Fig. 5. Fundus of stomach (Fig. 3, section *c*) of *P. alecto*. Scale bar, 50 μm.
Fig. 6. Small intestine (Fig. 3, section *f*) of *P. alecto*. Scale bar, 100 μm.
Fig. 7. Small intestine (Fig. 3, section *h*) of *P. alecto*. Scale bar, 100 μm.
C, circular muscle layer; *I*, intestinal glands; *L*, longitudinal muscle layer; *Mu*, mucous cells; *P*, parietal cells; *Su*, submucosa; *V*, villi; *Z*, zymogen cells. All stained with haematoxylin and eosin.

In the duodenum (Fig. 3, *e*) the surface epithelium forms numerous villi, which are prominent and long (up to 1·8 mm) in comparison to the short intestinal glands (crypts; 50–160 μm) (Fig. 6). Columnar epithelial (absorptive) cells display numerous elongate mitochondria, and sparse tubular RER. Densely packed, very long microvilli (up to 5·7 μm) project into the lumen (Fig. 13).

A small number of goblet (mucous) cells, featuring sparse mitochondria and RER plus abundant mucous droplets accumulated apically, are visible. Scattered enteroendocrine cells characterized by numerous, membrane-bound, electron-dense granules, few mitochondria and inconspicuous RER are also present (Fig. 13).

Intestinal glands display columnar epithelial cells similar to those lining the villi, except that the microvilli are much shorter (up to 1·4 μm) (Fig. 14). Goblet cells and enteroendocrine cells are visible. A few scattered paneth cells are found lining the bases of the glands.

Central lacteals occupy all villi. The muscularis mucosa is thicker than in the stomach and two layers can be seen. There are small lymphatic nodules in the lamina propria. Brunner's glands are abundant in the submucosa of the proximal portion of the duodenum. The muscularis externa is thin, caused by a reduction of the inner circular layer.

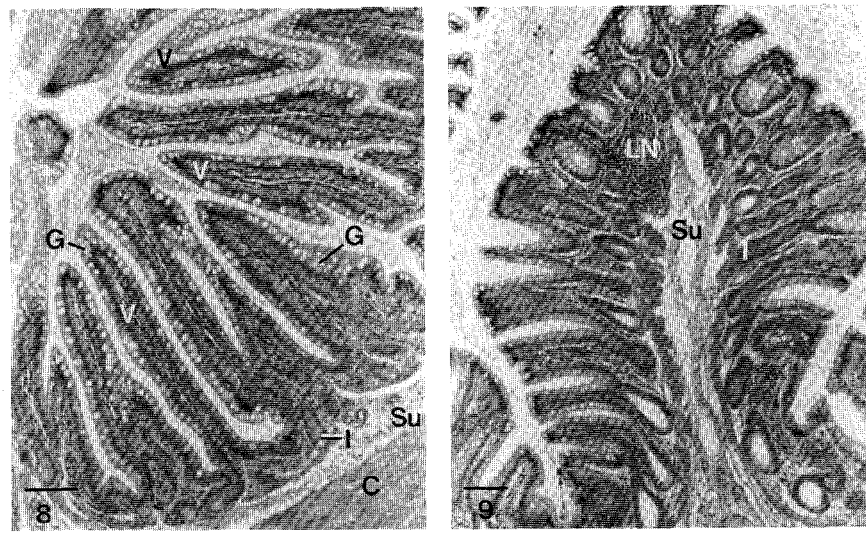


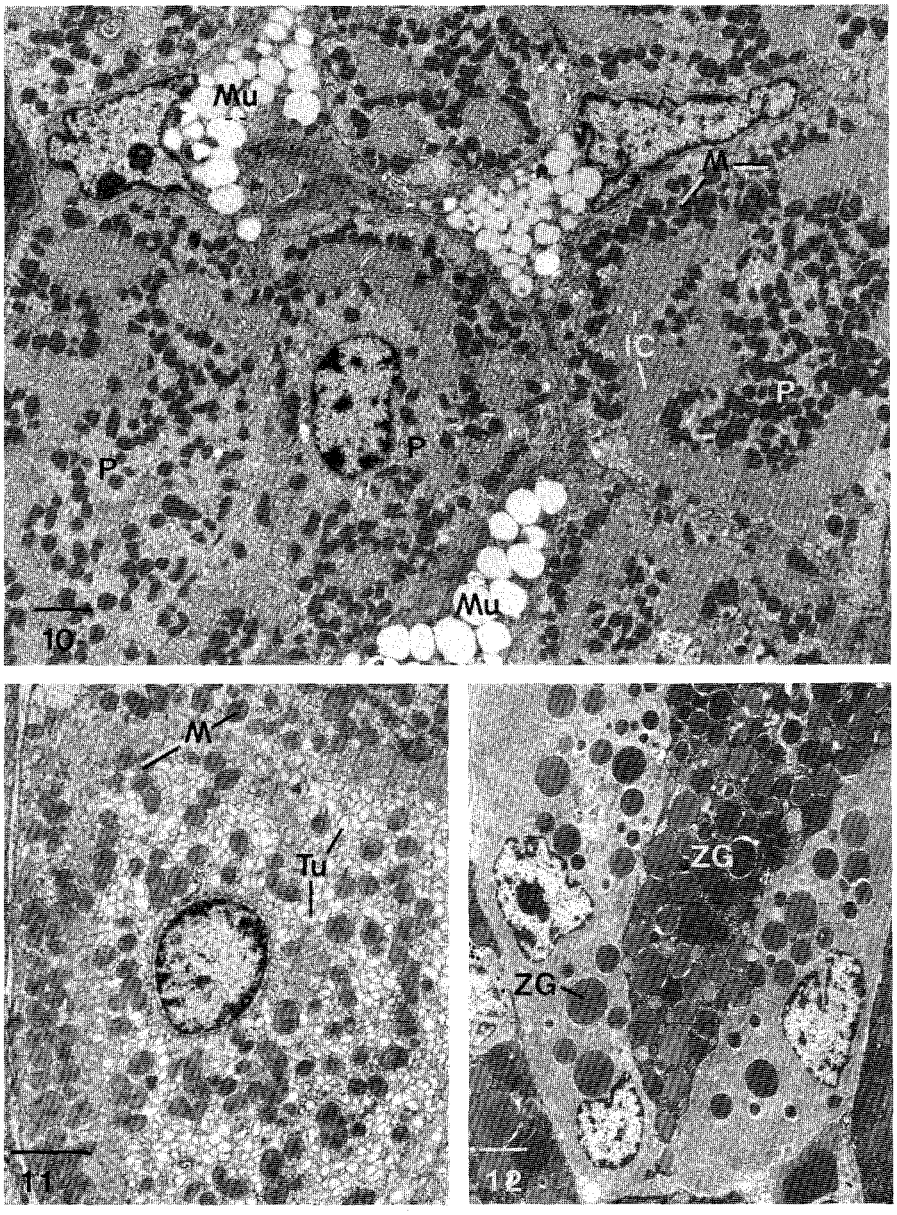
Fig. 8. Small intestine (Fig. 3, section *h*) of *P. poliocephalus*.
Fig. 9. Large intestine (Fig. 3, section *j*) of *P. poliocephalus*.
C, circular muscle layer; *G*, goblet cells; *I*, intestinal glands; *LN*, lymphoid nodule; *Su*, submucosa; *V*, villi. Haematoxylin and eosin. Scale bars, 100 μm.

The proximal to mid-part of the intestine (Fig. 3, *f*, *g*) resembles the duodenum but features increased numbers of goblet cells, and no paneth cells or Brunner's glands. Enteroendocrine cells are present, villi are still long, and intestinal glands are relatively short (50–150 μm). The inner circular layer of the muscularis externa is thicker than in the proximal duodenum.

Distally, the intestinal epithelium gradually undergoes several changes (Fig. 3, *h*, *i*). Villi are present, although their height decreases and they are more widely spaced and therefore reduced in number. Plicae circulares are present and a small amount of lymphatic tissue is found in the lamina propria. The muscularis mucosa becomes thicker. The muscularis externa, especially the circular layer, continues to increase in thickness. Intestinal glands become more sparsely distributed and goblet cells increase in number. Throughout the intestine, *P. poliocephalus* has far more goblet cells than *P. alecto* (more than six times as many in some parts; Figs 7, 8), except for the distal end where comparable numbers are present. Intestinal absorptive cells lining the villi retain numerous well developed microvilli (Fig. 15).

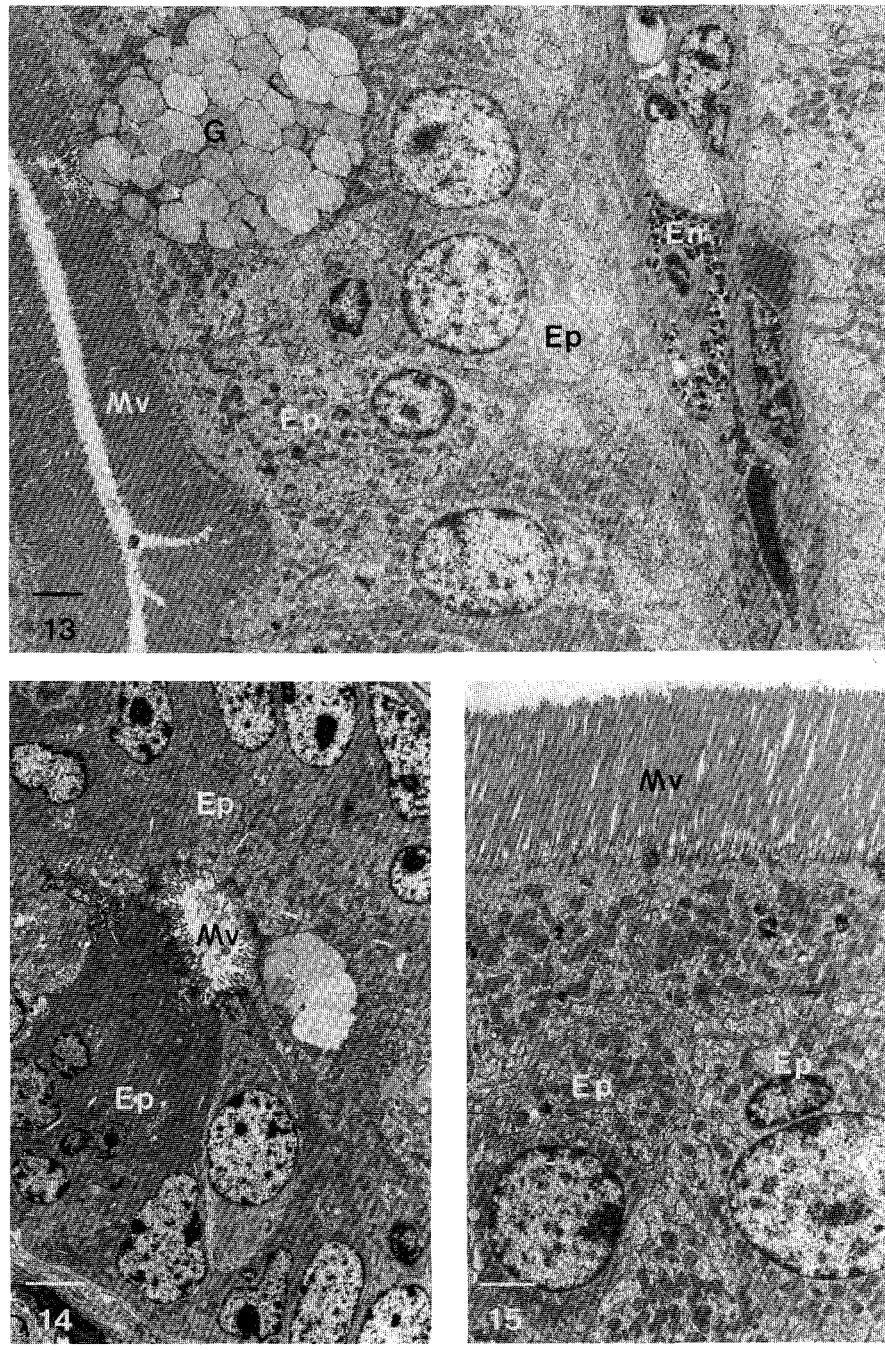
Further distally (Fig. 3, *j*, *k*) the intestine becomes colonic in appearance. However, a

distinct rectum cannot be distinguished. Villi disappear in some areas and elsewhere they are replaced by blunt, shortened processes which clump together (Fig. 9). Longitudinal folds



Figs 10–12. Electronmicrographs of mucosa of stomach: *10*, fundus, *P. poliocephalus*; *11*, body of stomach, *P. alecto*, showing a parietal cell; *12*, body of stomach, *P. poliocephalus*, showing zymogen cells. *IC*, intracellular canaliculus packed with microvilli; *M*, mitochondria; *Mu*, mucous cells; *P*, parietal cells; *Tu*, tubulovesicles; *ZG*, zymogen granules. Scale bars, 2·5 μm.

involving mucosal and submucosal layers are well developed. The muscularis mucosa is thicker, as is the muscularis externa. There are no taeniae coli and lymphatic nodules are pronounced. The numbers of goblet cells remain high.



Figs 13–15. Electronmicrographs of intestinal mucosa: *13, P. poliocephalus* (Fig. 3, section *e*) (scale bar, 2·5 μm); *14, P. alecto*, showing an intestinal gland (Fig. 3, section *e*) (scale bar, 3·5 μm); *15, P. poliocephalus* (Fig. 3, section *h*) (scale bar, 2 μm). *En*, enteroendocrine cell; *Ep*, columnar epithelial cells; *G*, goblet cells; *Mv*, microvilli.

The transition of intestinal mucosa from small intestine is gradual and occurs closer to the anus in *P. poliocephalus* than in *P. alecto*. The large intestine represents 5–7% and 8–10% of the total intestinal length in *P. poliocephalus* and *P. alecto* respectively.

Discussion

Hall and Richards (1979) list native hardwood blossoms as the principal food of fruit bats in eastern Australia. Ratcliffe (1931*b*) found that large numbers of cultivated fruits were also eaten, particularly during periods of poor flowering of native hardwoods. All types of fruit used in the feeding trials are listed by Ratcliffe (1931*b*) as being eaten by fruit bats. However, the percentage of the total diet contributed by fruit (particularly cultivated varieties) in the wild is unknown.

Several reports have described a rapid digestive process in the fruit bat *Eidolon helvum* (Okon 1977), and Keegan (1975) reported intestinal transit times of 18–100 min (mean 46; SD ± 24) for the Egyptian fruit bat *Rousettus aegyptiacus*. Wolton *et al.* (1982) recorded mean food transit times, for bats fed bananas labelled with coloured food dyes, of 20–69 min for six species of Megachiroptera from Liberia. Food transit times increased with the size of the animal, except for *Rousettus aegyptiacus*. The fast passage of food through the gastrointestinal tract of *P. alecto* and *P. poliocephalus* (12–34 min, mean 26·5; SD ± 4·7; present study) is spectacular for such a large animal. The body weights of these *Pteropus* species are from four to five times that of *Rousettus*.

Food passage times for active free-flying *Pteropus* may be even shorter than those recorded for the captive animals used in the present study. Buchler (1975) found that the food passage times for insectivorous *Myotis lucifugus* (Microchiroptera) decreased as the postfeeding activity level of caged animals increased, and suggested that active, free-flying individuals might digest their food more rapidly than active caged animals.

Roentgenograms verify the rapid transit of food through the stomach. In *P. alecto* barium-impregnated fruit enters the small intestine within 10 min of feeding, and is emptied from the stomach within a further 11 min.

Comparisons of food passage rates within the Chiroptera are difficult, because of the paucity of data. Passage times reported for caged *Myotis lucifugus* (insectivorous) vary from 35 to 170 min, depending on the postfeeding level of activity (Buchler 1975). Active animals digest their food more rapidly. Luckens *et al.* (1971) reported an average passage time of 122 min for barium–food mixtures in *Eptesicus fuscus*, with a minimum of 90 min at room temperature. In this insectivorous species food enters the duodenum by 15 min after feeding (not greatly different from the barium mixtures in *P. alecto*) but the passage through the intestine is much more prolonged than in the frugivorous *Pteropus* (present study) and *Artibeus jamaicensis* (Morrison 1980). The piscivorous bat, *Noctilio noctula*, reportedly has a transit time of 28 min (Cranbrook 1965). This is much shorter than times for insectivorous bats, but is a single record only and it is impossible to say whether it is typical for the species. An ingested blood–barium mixture begins to leave the stomach of *Desmodus rotundus* after 30 min (Mitchell and Tigner 1970).

Only a few reports detail the microscopic appearance of the entire alimentary canal of megachiropterans, for example Schultz (1965, 1970), Okon (1977), and Madkour *et al.* (1982). The present study of *P. alecto* and *P. poliocephalus*, is, we believe, the first published account to include electron microscopic observations of the entire digestive tract.

The elongated terminal part, and expanded cardiac and fundic regions, of the stomach of *P. alecto* and *P. poliocephalus* are features characteristic of other frugivorous species of Chiroptera (Kamiya and Pirlot 1975; Okon 1977; Bhide 1980), and may be adaptations for accumulating large quantities of bulky food material (Forman 1972). However, *Pteropus* sp. spit out most of the fibrous material when masticating food, swallowing mainly juice and fleshy particles (Radcliffe 1931*b*). The extremely well developed cardiac vestibule and fundic caecum increase the surface area to which ingested material is exposed during the gastric phase of digestion (Forman 1972).

The sphincter-like development of muscularis externa at the gastro-oesophageal junction in the two *Pteropus* species studied resembles that found in the fruit bats *Eidolon helvum* (Okon 1977) and *P. g. giganteus* (Bhide 1980). No such development is present in the Indian fruit bat *Rousettus leschenaulti* (Bhide 1980). Such a sphincter could be important in providing a strong resistance to back pressure toward the oesophageal opening from liquid food material contained within the stomach, especially since fruit bats hang upside-down except when defaecating.

The gastric mucosa and gastric glands of *P. alecto* and *P. poliocephalus* are similar in depth to those of the fruit bat *R. leschenaulti* (Bhide 1980), the omnivorous *Phylostomus* sp. (Forman 1972), and several carnivorous Microchiroptera (Forman 1973), but deeper than in many species such as the fruit bats *E. helvum* (Okon 1977), *Pteropus intermedius*, *Penthetor lucasi* and *Eonycteris spelaea* (Kamiya and Pirlot 1975), and frugivorous Microchiroptera (Rouk and Glass 1970; Forman 1973). However, the gastric mucosa is thicker in several insectivorous Microchiroptera examined by Forman (1972) and Kamiya and Pirlot (1975).

The proportions of mucous neck cells, parietal cells and zymogen cells vary in different parts of the stomach and in different species of bats. Parietal cells are well developed and occupy a larger proportion of the gastric glands than zymogen cells in *P. alecto* and *P. poliocephalus* (present study) and *R. leschenaulti* (Bhide 1980), but are relatively less developed in *E. helvum* (Okon 1977). However, Kamiya and Pirlot (1975) found much variation in the percentage of each cell type in *P. intermedius*, *Pen. lucasi* and *Eon. spelaea*, plus several species of Microchiroptera. These authors concluded subjectively that, although parietal cells decreased in numbers towards the pylorus, the zymogen cells decreased faster in the pteropids. A similar trend is found in *P. alecto* and *P. poliocephalus*. Forman (1972) concluded from a study of 13 species of Microchiroptera that there are no clearcut patterns in terms of abundance of zymogen or parietal cells in relation to foods consumed. Rather, he suggested that perhaps the abundance of parietal cells and even other cell types of the gastric mucosa is related to the rate of food passage in some species.

In *P. alecto* and *P. poliocephalus* the depth of parietal cells is quite large, exceeding that found in many Microchiroptera including several insectivorous species (Rouk and Glass 1970; Forman 1972, 1973; Kamiya and Pirlot 1975). Hence a substantial flow of hydrochloric acid produced by abundant parietal cells might counterbalance a short exposure to digestive fluids.

In these two species, rapid digestion of large quantities of ingested material is further ensured by the extension of gastric mucosa through the enlarged cardiac vestibule to the entrance of the oesophagus, thus increasing the surface area of contact with food material. This is characteristic of other megachiropteran species (Kamiya and Pirlot 1975; Okon 1977; Bhide 1980) as well as frugivorous Microchiroptera (Forman 1972).

The elongated terminal part of the stomach of *P. alecto* and *P. poliocephalus* resembles that in the three pteropid species examined by Kamiya and Pirlot (1975) and in *R. leschenaulti* (Bhide 1980), where the transitional mucosal epithelium features decreasing numbers of parietal and zymogen cells towards the pyloric region. However, in frugivorous Microchiroptera this terminal portion is lined by an extensive pyloric mucosa featuring abundant mucous secretion, and a very narrow transitional zone (Forman 1972).

Like *E. helvum* (Okon 1977) and *R. leschenaulti* (Bhide 1980), *P. alecto* and *P. poliocephalus* have abundant Brunner's glands in the pyloric and duodenal regions. If these glands protect the duodenum from acid-pepsin chyme from the stomach (Bloom and Fawcett 1975), then their presence in the pyloric and duodenal regions in these bats might play an important role in neutralizing the secretions from abundant parietal cells in the gastric glands of these species. Most fruit-eating Microchiroptera lack Brunner's glands (Forman 1973).

The extensive development of tubulovesicles in parietal cells from the *P. alecto* and *P. poliocephalus* specimens resembles structures characteristic of gastric epithelium during

resting phases or inhibition of acid secretion in a variety of species (see Sedar 1962; Vial and Orrego 1963; Rubin *et al.* 1968; Ito and Schofield 1974).

Stimulation of acid secretion is interpreted by many authors to be followed by the fusion of tubulovesicles with the plasmalemma as they release their contents into the canaliculi and lumina (Helander and Hirschowitz 1972; Leeson 1973). This is believed to produce an increase in canalicular and apical cell membrane surface area, including enhanced development of microvilli. The number of tubulovesicles subsequently decrease. Alternatively this process may involve dissolution of tubulovesicular membrane and reconstruction of microvillous and canalicular membrane (Ito and Schofield 1974). Parietal cells from two of the three *P. poliocephalus* specimens therefore resemble cells that have been stimulated to release acid.

For each fruit bat studied, the parietal cells were uniform in appearance, either typically acid-secreting or non-acid-secreting. With available data it is not possible to account for this difference in the gastric mucosa in the two species of pteropids. Both species are thought to have similar feeding habits, often flying considerable distances at night in search of flowering native trees and shrubs, as well as utilizing a wide range of cultivated fruits (Ratcliffe 1931*b*; Nelson 1965*a*. These bats return to roosting camps to spend the daylight hours grooming, fighting and sleeping (Nelson 1965*b*). Individuals of both species were collected from roosting camps during daylight hours and kept in cages, without food, for 2–3 h before being killed. Neither species therefore should have been feeding or have shown evidence of stimulation of acid secretion at the time of death. In addition, the gastrointestinal tracts of all individuals examined were empty. Further work is in progress to attempt to clarify this apparent anomaly.

In an electron-microscopic study of the stomach of the insectivorous little brown bat *Myotis l. lucifugus*, Ito and Winchester (1963) described parietal cells with well developed intracellular canaliculi and few tubulovesicles. However, individuals were killed during hibernation or after arousal and so presumably would have been fasting before death, so it is difficult to understand why the cells showed evidence of having been stimulated for acid secretion.

Zymogen cells from *Pteropus* (present study) featured secretory granules which resembled those described for other mammals and for the three genera of carnivorous phyllostomatid bats reported by Phillips and Studholme (1982). However, the pale, granular secretory product of the chief cells reported by Phillips and Studholme (1982) for three genera of frugivorous phyllostomatids resembled mucous cells from *Pteropus* gastric mucosa rather than zymogen cells.

The duodenum in *P. alecto* and *P. poliocephalus* is identifiable by the presence of Brunner's glands in the submucosa. Distally there is a gradual change in the mucosa with an increase in goblet cells and a decrease in the height of the villi from the jejunum to the anus. These changes would undoubtedly facilitate the rapid movement of food through the lower parts of the gastrointestinal tract.

External morphology does not allow small and large intestine to be distinguished in practically all species of Chiroptera for which data are available, including *P. alecto* and *P. poliocephalus*. The absence of a caecum and an appendix is claimed to be a feature of the gastrointestinal tract of the Chiroptera (Dobson 1878; Okon 1977). This may not apply to all species; for example, Owen (1868) reported a caecum about ¼ in. long in the microchiropterans *Rhinopoma hardwickii* and *Megaderma spasma*. Dobson (1878) found a small 'caecum-like appendage' in *M. spasma*, but was unable to locate an opening into the intestine. Dobson (1878) thought that the rapid passage of food in frugivorous Chiroptera was due to the uniform diameter of the intestine and the absence of either a caecum or valves in the intestine. However, this is not the only determinant of food passage rate and certainly cannot alone account for the rapid food transit time in these bats. Food type as well as stomach and intestinal morphology are likely to influence food transit times (Stevens 1980).

Since the microscopic appearance of the intestine is fairly uniform in all bats, morphological features such as intestinal length and diameter, mucosal folding, types of villi and thickness of muscle layers might be important in determining digestive rates. Very few data of this type are available for chiropterans.

Frugivorous Chiroptera possess longer intestines relative to body length than species favouring other diets (see Robin 1881; Eisentraut 1950; Madkour 1977). This trend is maximized in the megachiropteran fruit bats, where the intestine may be up to nine times the body length (Okon 1977). It is difficult to determine the significance of such a long intestine, considering the rapid digestive process in the frugivores. In these bats the intestine may provide increased surface area for absorption of nutrients, thus maximizing the exposure of the predominantly fluid digesta to the intestinal absorptive cells in order to balance the short exposure due to the rapid passage of food.

Although available data are limited, there appears to be no consistent correlation between intestinal length and food transit times in fruit bats. For example, the intestines in *Pteropus* species (present study) are far longer than in *R. aegyptiacus* (Madkour 1977) and yet the food transit times are either similar or far shorter in *Pteropus* (see Keegan 1975; Wolton *et al.* 1982). Whereas in other species of Megachiroptera food transit times increase with increasing body weight (presumably increasing intestinal length; Wolton *et al.* 1982), the type of fruit and proportion of fibrous tissue consumed might influence these times, with the more fluid digesta being assimilated more rapidly.

One feature of the small intestine of fruit bats that is probably related to the ability of these bats to rapidly process their food, concerns the rate of fluid absorption. Keegan (1975, 1977) reported that in *R. aegyptiacus* fluid absorption and rate of assimilation of both glucose and fructose are much higher than in the rat.

The gross structure of the small intestine of *R. aegyptiacus* is not modified sufficiently to account for the rapid glucose absorption recorded in this species by Keegan and Modinger (1979). These authors found that the bat's microvilli were over three times longer than the rat's, and that the microvillus structure increases the mucosal surface area of the intestinal cells by a factor of 57 in the bat compared with 18 in the rat. The assimilatory surface of the small intestine of the bat is three times greater than that in the rat, and hence was thought to account in part for the rapid rate of absorption of monosaccharides, provided that the plasma membrane was a limiting factor in determining the rate of absorption. Microvilli of intestinal absorptive cells are larger in *P. alecto* and *P. poliocephalus* than in *R. aegyptiacus*. Likewise the microvilli may play an important role in rapid absorption which must accompany the rapid rate of food passage in pteropids.

All the bats used in the present study were killed shortly after capture, at least 12–18 h after their normal feeding time. Consequently the gastrointestinal tracts were empty. Further work is in progress to determine the influence of feeding on the intestinal mucosal surface area, since there are indications that villus height and microvillus length vary in response to feeding and fasting (see Stevenson *et al.* 1979; Misch *et al.* 1980).

In the *Pteropus* species studied, the large intestine can be distinguished by the appearance of well developed longitudinal folds. However, there is a gradual change in the histological appearance of the mucosa towards the distal end of the intestine. The transition from small intestine, marked by a noticeable decrease in the number and size of villi, is closer to the anus in *P. poliocephalus* than *P. alecto*.

Even though the data on chiropteran intestines are limited, there are some inconsistencies in the recognition of the large intestine and its subdivision into colon and rectum (see Robin 1881; Mitchell 1916; Forman 1974; Barry 1976; Okon 1977).

In 29 species of Microchiroptera, Robin (1881) recognized a short large intestine (less than 25 mm) consisting of a straight rectal portion only, whereas in the Megachiroptera the large intestine is slightly longer and convoluted in its proximal part. The transition from small to large intestine (characterized by parallel, longitudinal folds and reduced or absent villi) is abrupt in some species and more gradual in others.

The large intestine of the *Pteropus* species studied resembles that described for *Harpyionycteris whiteheadi* (Schultz 1970), except that the transition from small intestine mucosa is more abrupt in *H. whiteheadi* and the large intestine is far longer in *P. alecto*.

The colon normally secretes mucus and absorbs water from the digesta before they are passed out as faeces. However, Ogunbiyi and Okon (1976) found high activity of maltase and trypsin in the colon of *E. helvum*, suggesting further digestion of food and absorption of its products. In a subsequent study, Okon and Ogunbiyi (1979) demonstrated the presence of pepsin and amylase throughout the colon. In the same species, Okon (1977) considered that the well developed colon had an important absorptive function and a less important role in mucus secretion. It is not possible to compare the relative importance of the absorptive and mucus-secreting roles of the distal part of the intestine in *P. alecto* and *P. poliocephalus* with those of the colon of *E. helvum*, because Okon's descriptions are purely qualitative. However, mucus secretion appears to be important in the two *Pteropus* species, since the goblet cells in the distal intestine of these species are numerous. Furthermore, the goblet cells are more numerous throughout the intestine in *P. poliocephalus* than in *P. alecto*, except for the distal end where numbers of goblet cells are comparable. Further studies involving enzyme distribution, carbohydrate absorption and perhaps other techniques will be required before a possible role of food digestion and absorption for the distal part of the intestine of *P. alecto* and *P. poliocephalus* can be ascertained. In addition, more data on dietary components of these species are required to help determine the significance of differences in relative lengths of large intestine and numbers of goblet cells.

Rapid food passage has many advantages for fruit bats. The ability to consume, digest and excrete food in a short time would obviate the necessity to fly from one feeding site to another with the weight burden of a full gastrointestinal tract. This would mean that while flying the animal is more energy efficient, more manoeuvreable, faster, and more able to evade predators.

Quick passage rate would also mean that pollen and fruit seeds would not be carried any great distance. Faeces in the camp where the fruit bats were captured did contain a large percentage of pollen grains but there was little evidence of bulk food items such as seeds. The ground under most fruit bat camps visited by the authors, however, was not conducive for seed germination. Nevertheless, many fruit bats are believed to be important agents in the spread of plants, through contributing to seed dispersal (Wolton *et al.* 1982).

Fruit bats possess an ability to extract nutrients, particularly short-chain sugars, in a short time (Keegan 1975, 1977). Fruits such as mango and pawpaw are consumed as part of the normal diet of *P. alecto* and *P. poliocephalus*. However, if pollen and nectar are the principal sources of nutrition for these bats, as stated by Ratcliffe (1931*b*), Nelson (1965*a*) and Hall and Richards (1979), the digestive process of these bats requires further investigation to determine the extent to which the processing of pollen and nectar differs from that of various fruits.

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