



Fig. 4.5. Mucosal surface of the stomach from a pouch young *M. giganteus* (approximate age, 10-12 weeks). Note well developed gastric sulcus as compared to that in the adult (Fig. 4.4, p 45). The gastric sulcus does not traverse the full length of the tubiform forestomach.

Within the sacciform forestomach of M. eugenii there is an almost equal distribution of squamous and cardiac epithelia (Fig. 4.4.b). In M. giganteus, squamous epithelium lines all of the sacciform forestomach wall except for an isolated, raised area of thick cardiac glandular epithelium (Fig. 4.3.b) which is confined to the parietal blind sac and the immediate surrounding area (Fig. 4.4.b). The sacciform forestomach wall of T. thetis, on the other hand, is lined entirely by squamous epithelium (Fig. 4.4.b).

The tubiform forestomach wall, of all three species, is lined mainly by rugose cardiac glandular epithelium. Squamous epithelium is found only on the floor and the lips of the gastric sulcus in the tubiform forestomach of M. eugenii, and on the floor of the gastric sulcus of M. giganteus. In T. thetis, squamous epithelium is found only at the cranial border of the tubiform forestomach as an extension of the sacciform forestomach epithelium.

The fundic and pyloric glandular epithelia are restricted to the hindstomach and are homologous to those found in simple stomached animals (Langer, Dellow and Hume, in press).

4.3.2 Stomach structure of M. robustus robustus, T. billarderi and T. stigmatica

Photographs of the stomach and of the stomach mucosal lining of adult specimens of M. robustus robustus and T. billarderi are presented in Fig. 4.6 and Fig. 4.7, respectively.

The gross structure of the stomach of M. robustus robustus is similar to that of M. eugenii. The gastric sulcus is wide and extends almost half the length of the tubiform forestomach, both lips are well developed. Squamous epithelium lies in close approximation to the cardia and extends as a wide band in association with the cardia, it is not cornified.



(a), External features, Sacciform forestomach

much smaller than in *M. thotig* (Fig. 4.1, p 38)

Fig. 4.6. The stomach of *M. robustus robustus*.

(a), External features. Note similarities to *M. eugenii* (Fig. 4.1, p 38). Note extensive

(b), Washed mucosal surface. In this species the gastric sulcus is wide and traverses from the cardia to midway along the tubiform forestomach.



Fig.4.7. The stomach of *T. billarderi*.

(a), External features. Sacciform forestomach is much smaller than in *T. thetis* (Fig. 4.1, p 38) or in *T. stigmatica* and there is no predominant dorsal pouch.

(b), Washed mucosal surface. Note extensive distribution of cornified squamous epithelium (similar to *T. stigmatica*), and presence of a gastric sulcus.

The gross structure of the stomach of T. billarderi also resembles that of M. eugenii. Unlike that of T. thetis the sacciform forestomach pouches are smaller, there is no large dorsal pouch and there is no obvious constriction at the sacciform-tubiform forestomach junction. The sacciform forestomach of T. billarderi is relatively much smaller than that of T. thetis.

In T. billarderi, a gastric sulcus is present and although the lips are well developed, the sulcus is narrow and more closely resembles that of M. giganteus than M. eugenii. Squamous epithelium lines all of the sacciform forestomach and 60% of the tubiform forestomach. The gastric sulcus extends to the caudal border of the squamous epithelium.

The structure of the stomach of T. stigmatica (not represented here) on the other hand, closely resembles that of T. thetis. The relative size and morphology of the sacciform forestomach is similar in both species, and there is no gastric sulcus. However, like T. billarderi, the squamous epithelium in T. stigmatica extends into the tubiform forestomach and glandular epithelium is restricted to the caudal region.

The squamous epithelium in all three Thylogale spp. is cornified.

4.3.3 Stomach structure of Me. rufa, W. bicolor, M. rufogriseus and M. parma

Photographs of the stomach, and of the stomach mucosal lining, of mature specimens of Me. rufa, W. bicolor, M. rufogriseus and M. parma are presented in the Appendix.

The two blind sacs in the sacciform forestomach vary in shape and size among all four species, as does the degree of haustration of the tubiform forestomach wall. Definition of the haustrations are more evident in this specimen of W. bicolor, but the appearance of haustrations

of the forestomach wall in recently killed animals can be deceptive. Post-death contractions and relaxation of the stomach wall, and production of gas in the stomach markedly alter the appearance of the haustrations.

All four species possess a gastric sulcus. In Me. rufa and M. parma the sulcus extends almost the full length of the tubiform forestomach but the left lip of the sulcus in these two species is poorly defined.

Relative distribution of the squamous and cardiac glandular epithelia in the forestomach of all four species is similar, and closely parallels that of M. eugenii and M. robustus robustus. The squamous epithelium in the forestomach of W. bicolor is cornified, as it is in the Thylogale spp.

4.3.4 The large intestine

The topographical features of the large intestine of M. giganteus are pictured in Fig. 4.2.a. The caecum-proximal colon of T. thetis, illustrated in Fig. 4.2.b, is of similar structure to that of M. eugenii.

In all three species the large intestine is essentially a simple and relatively undifferentiated tube of maximum diameter in the caecum-proximal colon region. It is considerably shorter than the small intestine (see Table 4.1, Section 4.3.5) but contains more digesta. There is no dilatation of the caudal segments of the colon, nor of the rectum, to allow accumulation of faecal pellets prior to defaecation as is found in the sheep.

The caecum is relatively short in both M. eugenii and T. thetis (10 cm and 12 cm, respectively, Table 4.1) and approximately half the length of the combined caecum-proximal colon region (20 cm in M. eugenii, 22 cm in T. thetis). In these two species, the diameter of the caecum-proximal colon reaches a maximum immediately caudad

to the ileo-caecal junction. The caecum of M. giganteus is considerably longer (30 cm) than the proximal colon (total length of caecum-proximal colon, 47 cm).

Two taeniae are readily distinguishable on the external wall of the caecum-proximal colon of M. giganteus. The parietal taenia extends from near the pole of the caecum to the caudal end of the proximal colon. The medial caecal taenia extends from near the pole of the caecum to the cranial end of the proximal colon. A third (or secondary medial) taenia, which essentially replaces the caecal medial taenia, begins close to the ileo-caecal junction, runs close to and parallel to the end of the caecal medial taenia for 2-5 cm, and continues to the end of the proximal colon. The caecum-proximal colon taeniae result in the formation of haustrations, which are more obvious on the proximal colon where the taeniae are broader, but in comparison to the stomach these haustrations are poorly defined.

Taeniae are present on the wall of the caecum-proximal colon of other species of macropodines, including T. thetis and M. eugenii, but they are not as obvious as those seen in M. giganteus.

The caecum of the other two larger macropodine species, Me. rufa and M. robustus robustus, is of similar length to that of M. giganteus. In the wallabies W. bicolor, M. rufogriseus and M. parma, the caecum is relatively short and of similar structure to that of T. thetis and M. eugenii.

4.3.5 Physical dimensions of the digestive tract

The means (+ s.e.) of the body weights, dry matter intakes of chopped lucerne hay (expressed as $\text{g/kgW}^{0.75}/\text{d}$), and the relative capacities and dimensions of the digestive tracts of four animals from each of the three species (M. eugenii, T. thetis and M. giganteus) are presented in

Table 4.1. The term capacity herein refers to the total wet weight of digesta contents contained in a defined region of the gut at the time of slaughter. For comparative purposes, the capacities of regions of the gut are expressed as a percentage of body weight, and as a percentage of either total gut contents or total stomach contents.

The capacity of the stomach, as a percentage of body weight, was 6.4% in M. eugenii, 7.6% in T. thetis and 10.0% in M. giganteus. As a percentage of total gut capacity, the stomach was the largest region (75.6% in M. eugenii, 75.5% in T. thetis and 80.4% in M. giganteus).

As a percentage of total stomach capacity, the hindstomach was the smallest of the three regions in all three species; 14.6% in M. eugenii, 9.7% in T. thetis and 7.3% in M. giganteus. In M. eugenii and M. giganteus, the tubiform forestomach contained relatively more digesta (55.7% and 69.9%, respectively) than the sacciform forestomach (29.7% and 22.8%, respectively). However, in T. thetis the sacciform forestomach was considerably larger (50.7%) than the tubiform forestomach (39.7%).

The total length of the large intestine, including the caecum (100 cm in M. eugenii, 90 cm in T. thetis, 165 cm in M. giganteus), was considerably shorter than the small intestine (271 cm in M. eugenii, 254 cm in T. thetis, 407 cm in M. giganteus). However, as a percentage of total gut contents, the large intestine contained more digesta (15.2% in M. eugenii, 16.5% in T. thetis, 10.7% in M. giganteus) than the small intestine (9.3% in M. eugenii, 8.1% in T. thetis, 9.0% in M. giganteus).

4.3.6 Radiological observations

The macropodine stomach in situ is wound spirally in a clockwise direction as viewed from the left side of the animal (Fig. 4.8). The sacciform forestomach and the

Table 4.1. The relative capacities and dimensions of regions of the digestive tract of three macropodine species, *M. eugenii*, *T. thetis* and *M. giganteus*, fed chopped lucerne hay ad libitum. All gut content weights and relative capacities refer to the wet weight of digesta contents. Values are the means (\pm s.e.) of four animals of each species.

| | <u><i>M. eugenii</i></u> | <u><i>T. thetis</i></u> | <u><i>M. giganteus</i></u> |
|--|--------------------------|-------------------------|----------------------------|
| Body weight (kg) | 4.45 \pm 0.26 | 5.85 \pm 1.03 | 19.05 \pm 0.74 |
| Dry matter intake (g/W ^{0.75} /d) | 33 \pm 5 | 58 \pm 4 | 57 \pm 5 |
| Total stomach contents (g) | 279 \pm 23 | 448 \pm 86 | 1924 \pm 198 |
| <u>Total stomach contents</u> Body weight (%) | 6.4 \pm 0.7 | 7.6 \pm 0.6 | 10.0 \pm 0.7 |
| Relative capacities: | | | |
| <u>Forestomach contents</u> Stomach contents (%) | 29.7 \pm 2.7 | 50.7 \pm 3.0 | 22.8 \pm 1.9 |
| <u>Midstomach contents</u> Stomach contents (%) | 55.7 \pm 3.6 | 39.7 \pm 2.9 | 69.9 \pm 2.0 |
| <u>Hindstomach contents</u> Stomach contents (%) | 14.6 \pm 1.0 | 9.7 \pm 0.7 | 7.3 \pm 1.3 |
| <u>Total stomach contents</u> Total gut contents (%) | 75.6 \pm 3.6 | 75.5 \pm 2.5 | 80.4 \pm 1.2 |
| <u>Small intestine contents</u> Total gut contents (%) | 9.3 \pm 1.2 | 8.1 \pm 1.4 | 9.0 \pm 1.1 |
| <u>Large intestine contents</u> Total gut contents (%) | 15.2 \pm 2.4 | 16.5 \pm 1.2 | 10.7 \pm 0.2 |
| Lengths: | | | |
| Small intestine (cm) | 271 \pm 14 | 254 \pm 23 | 407 \pm 28 |
| Caecum (cm) | 10 \pm 1 | 12 \pm 1 | 30 \pm 2 |
| Caecum-proximal colon (cm) | 20 \pm 3 | 22 \pm 2 | 47 \pm 2 |
| Total large intestine (cm) (incl. caecum-proximal colon) | 100 \pm 3 | 90 \pm 11 | 165 \pm 17 |

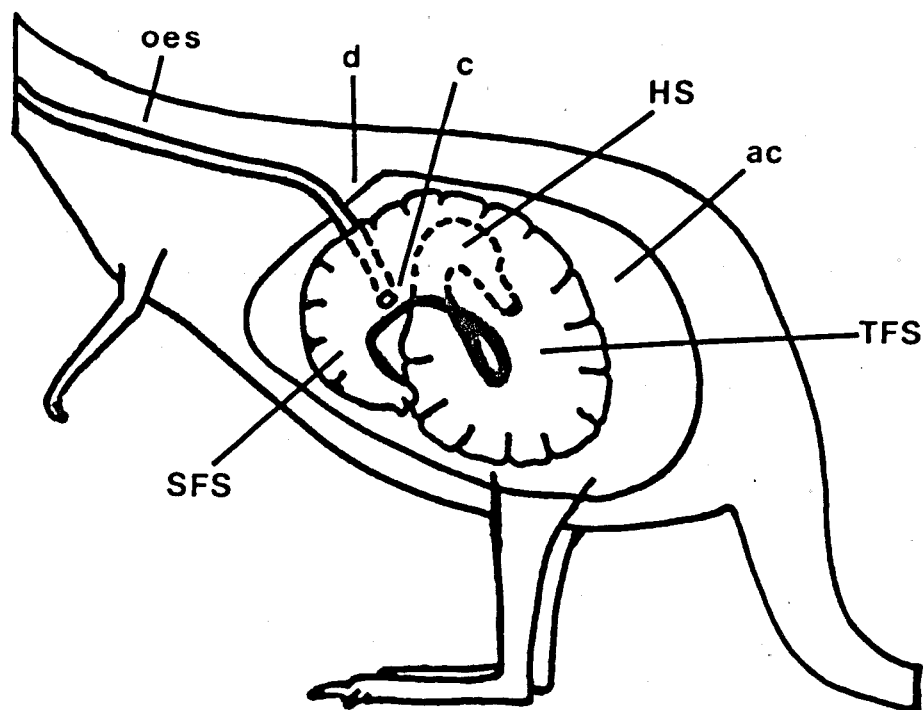


Fig. 4.8. Left lateral (diagrammatic) view of the stomach of *M. giganteus* in situ.

SFS = sacciform forestomach,
 TFS = tubiform forestomach,
 HS = hindstomach.

ac = abdominal cavity, c = cardia, d = diaphragm,
 oes = oesophagus.

cranial limb of the tubiform forestomach lie on the left lateral side of the abdomen. The tubiform forestomach extends ventro-caudally from the left dorso-lateral side, then turns and crosses the floor of the abdomen to the right side, and passes dorso-cranially to the hindstomach. The hindstomach lies on the right dorso-lateral side of the abdomen and the pylorus extends ventro-caudally to the duodenum.

The sacciform forestomach is flexed ventrad to the tubiform forestomach. It is maintained in this position in situ by both a layer of connective tissue connecting the parietal surfaces of the sacciform forestomach and the cranial region of the tubiform forestomach, and by a short gastrophrenic ligament on the medial side of the sacciform forestomach - tubiform forestomach junction. This produces a transverse fold in the forestomach wall which protrudes into the stomach lumen. This ventral fold was prominent in anatomical preparations fixed in situ (Langer, Dellow and Hume, in press), but in the stomach specimens in Fig. 4.1.b, the omentum and the mesenteric attachments have been dissected away and the fold is not obvious.

In M. eugenii the cardia is caudal to this ventral fold and opens into the cranial region of the tubiform forestomach. However, in T. thetis and in M. giganteus the cardia lies on, or ventro-cranial to, the fold and opens into the sacciform forestomach.

a) Dispersion of contrast medium in the stomach

A comparison of the initial dispersion and subsequent distribution of radiographic contrast medium (page 35) in the stomachs of M. eugenii, T. thetis and M. giganteus is diagrammatically depicted in Fig. 4.9.

Initial dispersion in the sacciform forestomach is pictured in M. giganteus (Fig. 4.10.a), M. eugenii (Fig. 4.10.b,c) and in T. thetis (Fig. 4.11.a).

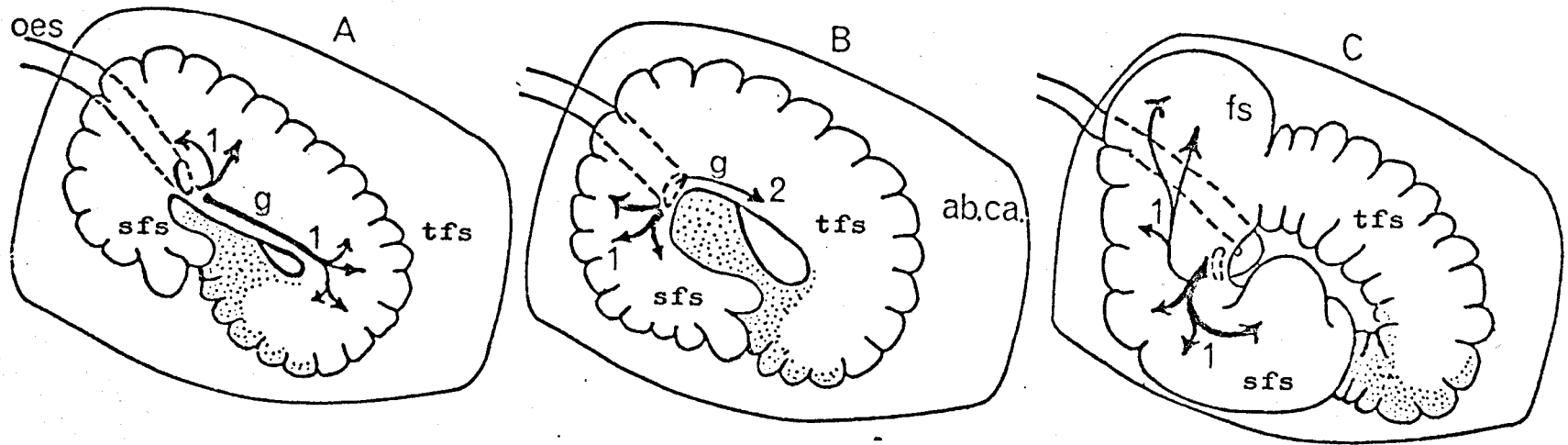


Fig. 4.9. Dispersion of contrast medium in the macropodine stomach. A = M. eugenii, B = M. giganteus, C = T. thetis. Arrows represent initial dispersion of contrast medium within 20 min of swallowing (1 = major pathways; in B, 2 = a smaller secondary dispersion). Stippled areas represent residual marked digesta present 24 h later.

Diagrams were compiled from single radiographs and videotape data with the animals viewed from the left side.

(ab. ca. = abdominal cavity, g = region of gastric sulcus, sfs = sacciform forestomach, tfs = tubiform forestomach, oes = oesophagus).

Subsequent distribution of contrast medium in the forestomach of T. thetis is pictured in Fig. 4.11.b,c.

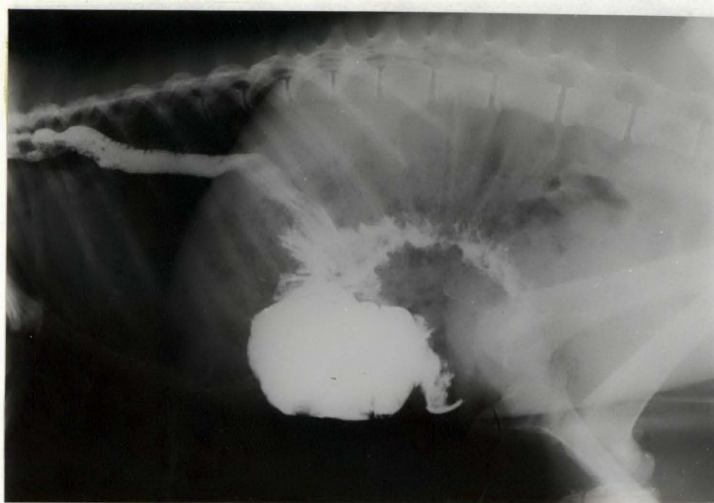
Contrast medium entering the stomach through the cardia in M. eugenii was directed either cranial and dorsal and mixed with the digesta in the sacciform forestomach and opposite the cardia, or it was directed caudally along the lesser curvature of the cranial limb of the tubiform forestomach (Fig.4.9.a, Fig. 4.10.b,c). In the latter situation the contrast medium appeared to be directed along the floor and the immediate region of the gastric sulcus and mixed with digesta in the cranial and central regions of the tubiform forestomach.

In M. giganteus (Fig. 4.9.b, Fig. 4.10.a) the major portion of the contrast medium was directed initially into the sacciform forestomach, although some was directed along the lesser curvature of the cranial region of the tubiform forestomach close to the gastric sulcus.

In T. thetis (Fig. 4.9.c, Fig. 4.11.a,b) all of the contrast medium was directed into the sacciform forestomach. The majority of this moved ventrally and into the parietal and ventral blind sacs, while the remainder outlined and mixed with digesta in the dorsal pouch.

After a period of one hour, the contrast medium in the stomach of M. eugenii was well mixed with the digesta in the sacciform forestomach and in the cranial and central regions of the tubiform forestomach. In M. giganteus, after this period of time, contrast medium was well mixed with the digesta of the sacciform forestomach and the cranial region of the tubiform forestomach only. Up to 60 min elapsed before any contrast medium was detected in the tubiform forestomach of T. thetis; prior to this the contrast medium was distributed throughout the sacciform forestomach contents.

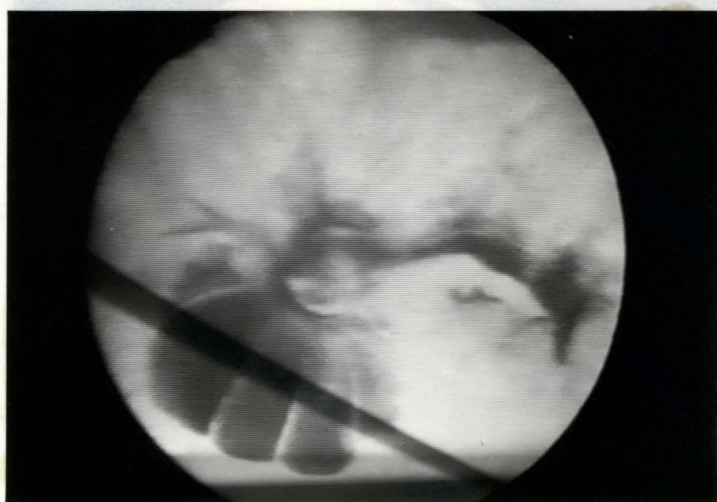
Subsequent observations showed that in all three species, the marked digesta was transported gradually along



(a)



(b)

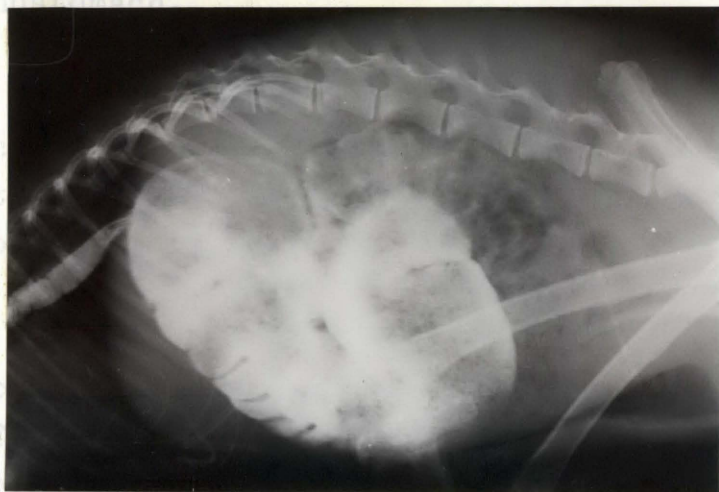


(c)

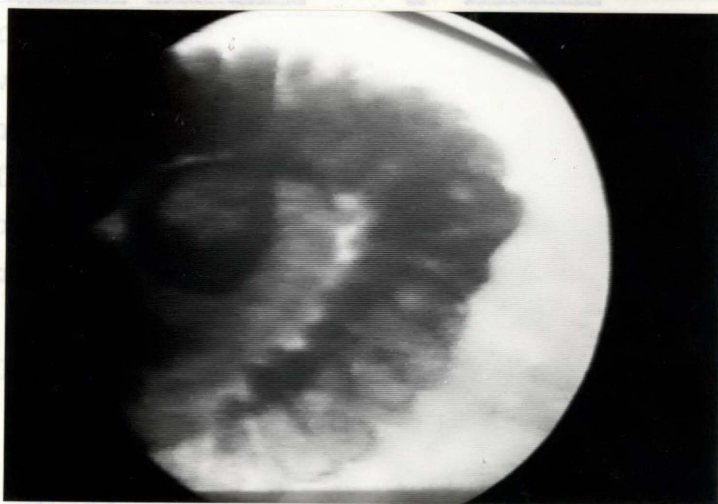
Fig. 4.10. Radiographic views of the initial dispersion of contrast medium in the stomach of (a), M. giganteus; (b), (c), M. eugenii. In (a) and (b) contrast medium was directed mainly into the sacciform forestomach. In (c) a second swallowing of contrast medium was directed along the region of the gastric sulcus to the central tubiform forestomach (see Fig. 9, p 58).



(a)



(b)



(c)

Fig. 4.11. Radiographic views of dispersion of contrast medium in the forestomach of T. thetis. (a) Initial dispersion, (b) at 90 min, whole of the sacciform forestomach is outlined. (Note contrast medium in the oesophagus in (a) and (b)). (c), T. thetis viewed from a dorso-lateral plane 6 h after infusion; medial blind sac is central, most of the tubiform forestomach is outlined with marked digesta.

the tubiform forestomach (Fig. 4.11.c). After eight hours, little of the contrast medium remained in the sacciform forestomach, the whole of the tubiform forestomach had been outlined, and marked digesta was observed in the hindstomach.

Food ingested after 6 h was not mixed with previously administered contrast medium. At 24 h, any contrast medium remaining in the stomach was confined almost entirely to the hindstomach.

When contrast medium was injected slowly into the hindstomach of M. eugenii and of T. thetis, it mixed with the digesta and outlined this region of the stomach only. Transfer of marked digesta to the duodenum was relatively rapid.

The pattern of initial dispersion of contrast medium in the sacciform forestomach, and the tubiform forestomach of both M. robustus robustus and W. bicolor was similar to that observed in M. eugenii. Both of these species possess a well developed gastric sulcus (Fig. 4.6 and Appendix Fig. 2) and contrast medium was directed initially into either the sacciform forestomach, or along the lesser curvature of the tubiform forestomach in close association with the gastric sulcus.

b) Dispersion of contrast medium in the large intestine

Some 24 h after oral infusion, digesta in the large intestine of all three species was thoroughly marked with the contrast medium. Contractions of the caecum-proximal colon wall appeared to result in mixing of digesta throughout this region, but once the digesta entered the distal colon pellet formation was initiated. Faecal pellets transported along the colon were not effectively accumulated in the rectum. Rather, defaecation appeared to include evacuation of both the few pellets in the rectum and pellets from the distal colon.

c) Contractions of the stomach wall

Local mixing of digesta contents and transport of the

marked digesta along the stomach was observed at short intervals with the image intensifier. Contractions of the haustrations of the greater curvature wall were of two predominant forms (Fig. 4.12).

Localised contractions involved the contraction of each haustration and associated semilunar folds (Fig. 4.12.a). These contractions occurred over a 4 to 6 second cycle and were independent but associated with sequential contractions of two or more adjoining haustrations.

The second form of contraction was seen as a stronger sequential wave of contraction that traversed a short distance along the greater curvature wall (Fig. 4.12.b). Each of these latter contractions appeared to be a caudal displacement of a semilunar fold along the stomach wall, associated with a relaxation of the successive caudal fold and reforming of another fold cranial to the wave of contraction. Clearly, the semilunar folds associated with the haustrations are not permanent structures.

4.4 Discussion

Among the three species examined in detail, M. eugenii, T. thetis and M. giganteus, there are distinct differences in both the gross structure and dimensions of the stomach, and in the distribution of the forestomach mucosal epithelia. Initial dispersion and distribution of contrast medium in the forestomach also differed among all three species, and this can be related to the position of the cardia, and the degree of development, or absence, of a gastric sulcus.

4.4.1 Stomach structure of the Macropodinae

The gross structure of the stomach of M. eugenii appears to be the most representative of other species of the Macropodinae. Anatomical examination of the stomachs from M. robustus robustus, W. bicolor, M. rufogriseus, M. parma and Me. rufa also revealed many similarities to M. eugenii (as does the description for S. brachyurus by

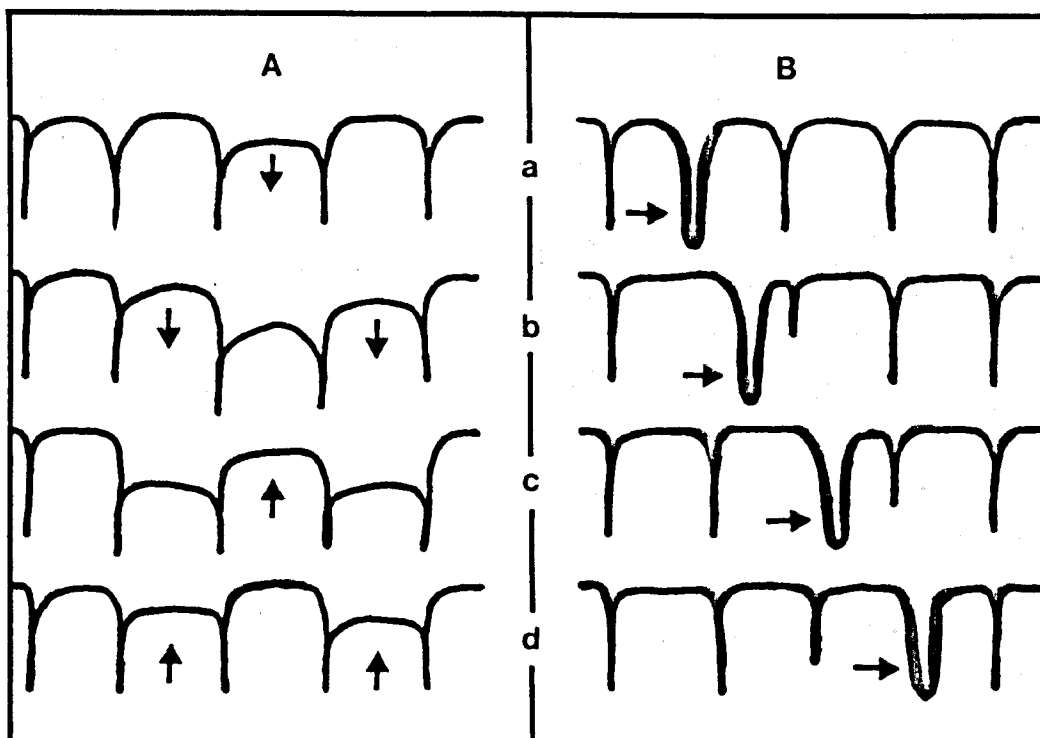


Fig. 4.12. Schematic presentation of the two major types of contraction of the macropodine forestomach wall.

A = localised contractions; each haustration contracts independently but in association with adjoining haustrations.

B = propulsive contractions; a wave of stronger contraction moves caudally along the greater curvature of the forestomach wall. These contractions result in the displacement and reformation of the semilunar folds in association with the haustrations.

The contractions were observed with the use of an image intensifier.

a,b,c,d, represent 3 second intervals.

Moir, Somers and Waring, 1956). In these species the cardia opens into the cranial region of the tubiform forestomach and is associated with a well defined gastric sulcus. The relative length and width of the sulcus, and the degree of development of the lips varied, but in none of the specimens examined was the sulcus as poorly developed as that seen in adult specimens of M. giganteus. Preserved specimens representing other genera, Onychogalea, Largorchestes and Dendrolagus were also examined and found to have a prominent gastric sulcus. In some specimens of M. giganteus, the isolated area of glandular epithelium associated with the parietal blind sac (first noted by Owen, 1868) is connected by a narrow isthmus of similar tissue traversing the greater curvature wall of the forestomach to link with the cardiac glandular epithelium of the tubiform forestomach (Schäfer and Williams, 1876). Both forms of this epithelial distribution have been observed in specimens of M. giganteus from Victoria (D.L. Obendorf, pers comm). Thus it appears some minor differences in epithelial distribution may occur among separate populations of the same species.

In T. thetis the cardia opens into a capacious sacciform forestomach that possesses a distinctive dorsal pouch, and there is no gastric sulcus. These features were also observed in T. stigmatica. Distinctive to all three Thylogale spp is the extensive distribution of cornified squamous epithelium, but the gross morphology of the stomach of T. billarderi is surprisingly different from that of the other two species. Brown (1964) also noted the presence of a gastric sulcus in specimens of Thylogale spp, apparently T. billarderi. The stomach structure of T. billarderi more closely resembles that of Dorcopsis luctuosa as described by Schäfer and Williams (1876).

a) The forestomach epithelia

The relative distributions of squamous and cardiac glandular epithelia lining the forestomach vary markedly

among some species of macropodines. Whether any differences in function exist between the epithelial types in terms of aiding efficient microbial digestion is unknown. Rüksamen and Engelhardt (1978) demonstrated that the rate of absorption of VFA through the cardiac glandular epithelia of the llama (Lama guanicoe) stomach was faster than through the squamous epithelium of the ovine stomach. However, there is little reason to surmise that VFA are not adequately absorbed through the squamous epithelium of the macropodine forestomach.

4.4.2 Proportions of the digestive tract

The data on relative capacities and dimensions of the digestive tract of the three species were obtained from adult animals maintained under similar conditions and fed chopped lucerne hay ad libitum, at 6 h intervals, up until the time of slaughter. Such measurements should provide more meaningful data for comparative purposes than measurements made on animals fed at infrequent intervals or starved for a significant period prior to slaughter.

Among the three species, the distribution of digesta in the forestomach clearly varies, but in all three the forestomach is by far the largest region of the digestive tract. The forestomach capacity may not be as large as that of ruminants; in sheep fed the same diet at hourly intervals, the mean capacity of the ruminoreticulum was 14.2% of body weight (Hume, 1977a).

The small and the large intestine are much shorter than those of ruminants (Nickel, Schummer and Seiferle, 1973) although, as discussed by these authors, it is difficult to obtain an accurate measure of the length of the small intestine in particular. Estimates can only be strictly comparable if made under similar conditions.

4.4.3 Mixing and flow of digesta within the stomach

The use of a contrast medium, such as barium sulphate, in the present experiments cannot be considered as a quantitative measure of digesta flow. However, it does allow interpretation of the initial dispersion of material entering the stomach, outlines the position in situ of regions of the digestive tract in the live animal, and provides an indication of the adequacy of mixing of digesta contents in the stomach and the mode of subsequent flow.

Initial dispersion of the contrast medium in the forestomach was distinctly different among the three species, and can be related to differences in stomach structure and to the position of the cardia. In M. eugenii, M. robustus robustus and W. bicolor some of the contrast medium was initially distributed along the zone of the gastric sulcus and mixed with digesta in the cranial and central regions of the tubiform forestomach. The sulcus does not traverse the full length of the tubiform forestomach in these species and there was no evidence of rapid transfer of contrast medium directly to the hindstomach.

Subsequent dispersion of the contrast medium along the tubiform forestomach was similar in all species and several hours elapsed before any was observed in the hindstomach. Injection of the contrast medium directly into the hindstomach resulted in the outlining of the hindstomach alone and relatively rapid transfer of the material through the pylorus into the duodenum. There was no evidence of retrograde flow of digesta from the hindstomach to the tubiform forestomach.

The localised contractions and progressive contractions of the haustrations resulted in mixing of the contrast medium with the digesta and, as far as could be judged with this technique, regional mixing of the digesta appeared to be very effective. One hour after oral infusion the

contrast medium was thoroughly mixed with digesta in the cranial regions of the stomach in all species, but on no occasion was the contrast medium seen to mix entirely with the digesta throughout the entire forestomach.

Subsequent observations up to eight hours, in all three species, showed repeatedly that the large bolus of marked digesta moved progressively along the tubiform forestomach. There appeared to be no retrograde flow of digesta, since food ingested at this time was not marked by contrast medium.

The dispersion pattern of contrast medium in the ruminoreticulum of sheep is quite different (Waghorn and Reid, 1977). These workers observed that the contrast medium defined spiralling dispersion patterns in a lateral plane, over periods up to 90 minutes, with subsequent dispersion of the contrast medium throughout the ruminoreticulum. Further, 5-10 minutes after oral infusion, some of the contrast medium was detected in the omasum.

4.5 Conclusion

Species-specific differences in gross structure of the stomach and distribution of the forestomach epithelial lining are likely to occur among all macropodines. Of the species examined, the most distinctive variations were represented by M. eugenii, T. thetis and M. giganteus. Whether these differences constitute any causal and significant variations in efficiency of microbial digestion and activity is not known and will be examined in the following chapters.