

## EVOLUTION OF THE MACROPODIDAE DIGESTIVE SYSTEM

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Before speculating on the evolution of the Macropodidae digestive system, it is necessary to review some ideas on the evolution of the digestive system of other cellulose-digesters (or fibrivores), principally the ungulates (hoofed mammals). There are two main groups of extant ungulates, the Perissodactyla and the Artiodactyla (the cloven-hoofed mammals). The two groups are distinguished by a basic difference in foot morphology, which indicates that they arose independently from a basal "proto-ungulate" stock, in the early Tertiary. The perissodactyls surviving today are the horses (Equidae), rhinos and tapirs, but digestive physiology has been studied to any extent only in the horse. The artiodactyls include pigs (Suidae), hippos (Hippopotamidae), camels (Camelidae) and ruminants (Ruminantia) such as sheep, cattle, deer and antelope. The Ruminantia have been most extensively studied.

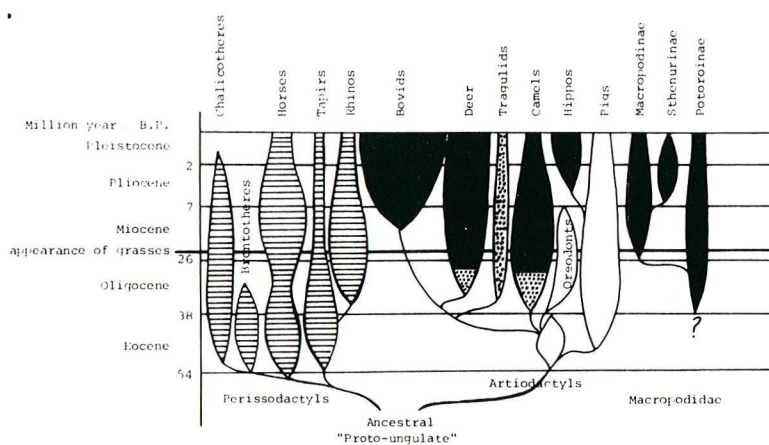
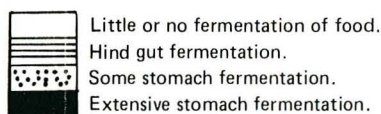


Fig. 1: Simplified diagram of ungulate and Macropodidae evolution during the Tertiary. Width of column indicates approximate compromise between species diversity and density. Adapted from Janis 1976.



### Stomach versus hindgut fermentation:

Radiation of the Equidae preceded that of the Ruminantia (Fig. 1), but it appears that the appearance of ruminating artiodactyls in the Oligocene coincided with a reduction in diversity of the Equidae. Several theories have been advanced to account for this (Janis 1976). However, both the Equidae and the Ruminantia expanded in the Miocene following the appearance of grasses in the flora fossil record. Thus it has been surmised that both groups expanded to utilize the new food resource. In order to utilize grasses, herbivores have to rely on symbiotic bacteria within their gut to hydrolyse the B 1-4 glycosidic bonds of cellulose, since no mammal has developed a cellulase. The success of the Equidae undoubtedly was due to the development of the hindgut (the caecum and proximal colon) into a large fermentation chamber. In contrast, the success of the Ruminantia was due to the development of the cardiac region of the stomach into the rumen and reticulum to form a pre-gastric fermentation organ.

Moir (1965) has argued that the apparent dominance of the artiodactyls over the perissodactyls in the post-Oligocene period indicates that the stomach fermentation of the Ruminantia is more efficient than the hindgut fermentation of the Equidae. The literature contains numerous reports of lower fibre digestibility in horses than in ruminants (e.g., Olsson 1969). The primary reason for this difference is the

faster rate of passage of food residues through the alimentary tract of the horse; coarse particles are retained longer in the rumen-reticulum than in the equine caecum-proximal colon, allowing more complete microbial digestion of the cellulose. Since the maintenance energy requirements of ruminants and horses are similar on a metabolic body weight basis, the lower digestibility in horses means that in order to meet their energy requirements horses need to eat more dry matter than do ruminants fed the same diet. The literature also supports this idea (e.g., Haenlein *et al.* 1966).

The reason for the longer retention times of coarse feed particles in the rumen-reticulum is the time required for them to be broken down to a certain size by rumination and fermentation before they can pass out of the reticulum into the omasum. On high fibre diets the intake of dry matter by ruminants is often depressed because of a slow rate of particle breakdown in the rumen, and therefore a decrease in the rate of passage and an increase in rumen fill; the end result is that the animal may not be able to satisfy its energy requirements (McClymont 1968).

In the horse, however, there is no structure comparable to the omasum and the reticulo-omasal orifice in the digestive tract, either in the stomach or the hindgut, to impede the movement of coarse particles (Argenzio *et al.* 1974). As a result the intake of high fibre diets by horses is not necessarily depressed. Darlington and Hershberger (1968) reported that horses maintained their intake of *Phleum pratense* (timothy) and *Dactylis glomerata* (orchardgrass) as the grasses matured. Similarly, Hoover and Heitmann (1970) found that increases in dietary fibre level had no effect on food intake of rabbits, which have a similar hindgut fermentation. Fibre digestibility may fall as a result of increased lignification of the grass, but the supply of total digestible nutrients to the animal may decline proportionally much less than in ruminants. It follows then, that so long as food availability is not limiting, horses may be at an advantage over ruminants when grazing poor quality (high fibre) diets. Indeed, it has been demonstrated (Bell 1970) that zebra consistently select more stem (the highest fibre component) of grasses than do the ruminant wildebeest and topi grazing in association with the zebra.

#### Caecum versus colon fermentation:

It is usually assumed that most of the fibre digestion in non-ruminant herbivores occurs in the caecum rather than the proximal colon. This is no doubt true in many species in which there is little development of the proximal colon as a fermentation organ compared with the caecum (e.g., *Schoinobates volans*, the greater glider). However, in grazing nonruminant herbivores there is always significant development of the proximal colon, but there may not be very much enlargement of the caecum (e.g., *Vombatus ursinus*, the common wombat). Even in grazing nonruminant herbivores in which caecal development is considerable, there are suggestions that the proximal colon rather than the caecum is the main site of fibre digestion. For instance, Pickard and Stevens (1972) found that most of the large digesta particles did not accumulate in the rabbit caecum at all. Furthermore, removal of the rabbit caecum by Herndon and Hove (1955) did not result in any significant reduction in growth rate. Thus it could be that the role of the proximal colon in fibre digestion has been underestimated. Unfortunately there are no data available on the extent of fibre digestion in the wombat which must rely entirely on microbial fermentation in the proximal colon in order to utilize grasses.

The proximal colon in the horse and other colon fermenters, is a wide, tubular, often sacculated organ, characterised by longitudinal muscle bands, taenia. It is delineated from the caecum by the ileocaecal valve, and from the distal colon by a reduction in diameter and by an increase in dry matter content of the digesta, often accompanied by pellet formation. Movement of digesta is predominantly caudal, but retrograde movement of digesta has also been shown to occur in the colon of the rabbit (Pickard and Stevens 1972), and of the sheep (MacRae *et al.* 1973). Argenzio *et al.*, (1974) found no evidence for retrograde movement in the equine colon, but nevertheless retention time of digesta in the colon was at least as long as in the ruminant forestomach, thus allowing substantial digestion of fibre to occur.

#### Evolution of the Macropodidae stomach:

According to Bartholomai (1972), the family Macropodidae was represented in the Oligocene by the sub-family Potoroinae (rat-kangaroos), including a species of the extant genus *Bettongia*. The living Potoroinae are all small in size, and their dietary habits range from omnivory (e.g., *Hypsipryminodon moschatus*) to herbivory. All the herbivorous Potoroinae are browsers, and most Potoroinae species have a distribution restricted to moist forest or tussock grassland adjacent to forest. The distribution of many Macropodinae is much more extensive.

The Macropodidae stomach can be conveniently divided into three regions, the forestomach (the region adjacent to, and the cul-de-sac oral to, the point of entry of the oesophagus), the midstomach (the main tubular body of the organ), and the hindstomach (the gastric pouch and the adjacent region terminating at the pylorus) (Fig. 2). However, these regions are not as distinctly separate anatomically as are the compartments of the ruminant stomach.

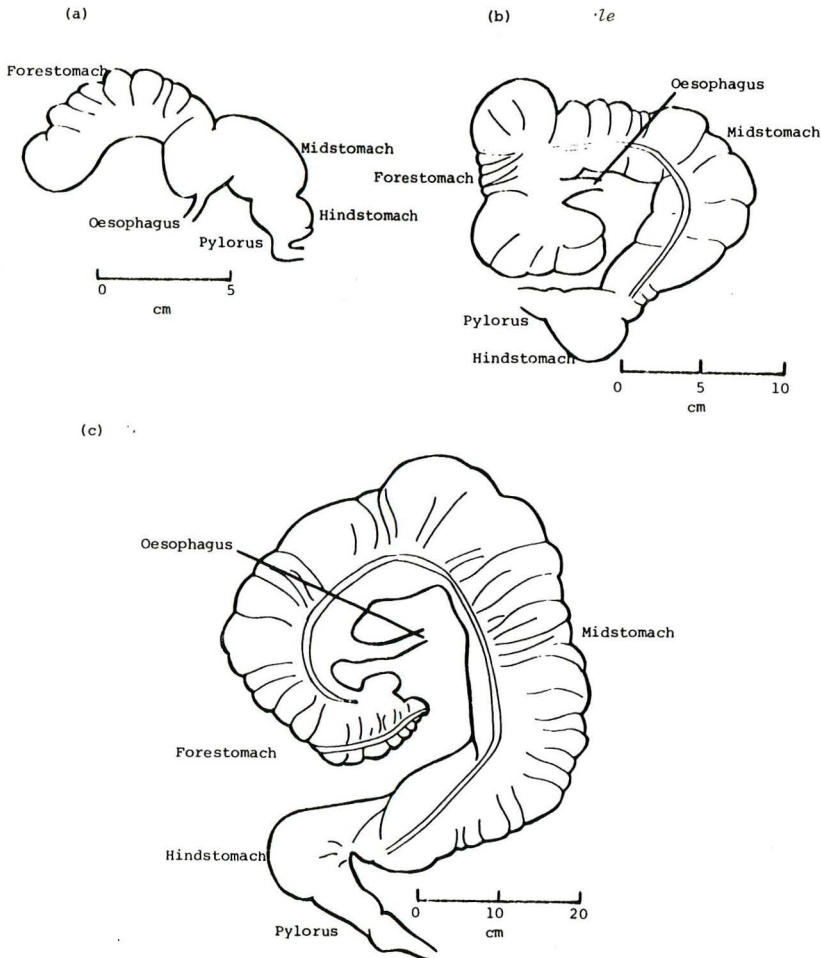


Fig. 2: The stomachs of (a) *Bettongia* sp (Subfamily Potoroinae), (b) *Thylogale thetis* (Subfamily Macropodidae), and (c) *Macropus giganteus* (Subfamily Macropodinae).

The digestive system of the Potoroinae is characterised by a very large forestomach, little development of the midstomach with only limited sacculations (Fig. 2a), and the absence of a ventricular groove along the lesser curvature of the midstomach. In *Aepyprymnus rufescens* (the rufous rat-kangaroo) the midstomach is entirely absent. The Potoroinae hindgut exhibits a well developed, though simple, caecum and proximal colon.

The large forestomach, at first appearance, resembles the rumenreticulum in that it is a cul-de-sac and would be expected to be an important site of fibre digestion. However, the fibre content of the diet of Potoroinae would not be expected to be very high. An alternative explanation may be that the forestomach evolved in part as a storage organ. Predator evasion by the small Potoroinae depends on extensive use of forest cover, with brief excursions to feeding areas which are usually more exposed than the refuge areas. The success of this strategy would depend on active feeding over short periods of time, and on a storage area for ingested feed.

According to Bartholomai (1972) the subfamily Macropodinae was almost certainly distinct from the Potoroinae by the end of the Oligocene, and before the appearance of grasses. On this basis it might be expected that early members of the Macropodinae would exhibit some features characteristic of the Potoroinae. The stomach of the extant genus *Thylogale* resembles the Potoroinae stomach in several ways: the forestomach is very large, and it has no ventricular groove running along the inner curvature of the short midstomach (Fig. 2b). The dentition of *Thylogale* is that of a browser (Sansón 1976). For these reasons *Thylogale* is regarded here as a primitive Macropodinae.

The hypothesis developed here is that the grazing Macropodinae evolved to utilize the large areas of grassland in inland Australia by the development of a stomach more like the colon of the equine large intestine than a rumen. The grazing Macropodinae stomach, contrary to what may be expected, features a comparatively reduced forestomach capacity, and instead a great development of the midstomach (Fig. 2c). The midstomach is long, tubular, and sacculated, and has prominent taenia, all characteristics of the equine proximal colon. There is also a ventricular groove along the lesser curvature of most species of grazing Macropodinae, especially *Macropus* spp., but it is ill-defined in *Petrogale*. The generally greater size of the grazing Macropodinae would also give them an advantage on high fibre diets; larger fibrivores have a greater gut capacity relative to their energy requirements, and hence are able to accommodate a bulkier diet and to afford a longer total passage time (Hungate *et al.* 1959).

It is argued further than the development of the colon-like midstomach by some members of the Macropodinae enabled them to utilize high fibre grass, not by retaining it longer in the forestomach to improve unit digestive efficiency, but by moving it through the stomach, at the expense of high unit digestive efficiency, thereby maintaining their food intake and digestible nutrient supply at a higher level than would otherwise be possible.

There are few data to support this hypothesis. However, the often reported finding that mature Macropodidae eat no more of a high fibre diet than do sheep does not destroy the argument. This is because the maintenance energy requirement of the Macropodidae is at least 20% below that of the sheep (Hume 1974). Only if the total energy requirement of the Macropodidae was greater than that of the ruminant would a higher digestible energy intake be expected. Only one experiment has been reported which compares intake of a high fibre diet between mature ruminants and growing Macropodidae, when the total energy requirement of the Macropodidae may be expected to be substantially higher than maintenance. The results of this experiment (Foot and Romberg 1965) (Table 1) support the hypothesis developed in this paper. The young red kangaroos (*Megaleia rufa*) consumed less of the high quality chopped lucerne hay diet than did the mature Corriedale wethers. However, on the poor quality chopped oaten straw diet, although dry matter intake by both herbivores declined, intake by the red kangaroos was 40% greater than by the sheep. Apparent digestibility was lower in the red kangaroos on both diets, but the intake of apparently digestible dry matter on the oaten straw diet was greater. Thus it appears from this study that the red kangaroo is able to better maintain its intake of a high fibre diet than is the sheep. Similar studies with browsing Macropodinae and with Potoroinae would be necessary to further test this idea.

Table 1. Intake and digestion by three young red kangaroo and three mature sheep.

	RED KANGAROO	SHEEP	RED KANGAROO AS % OF SHEEP
BODY WEIGHT (kg)	11.4	38.8	
DRY MATTER INTAKE (g/kg W <sup>0.75</sup> /d)			
Lucerne hay	58.1	71.7	81.0
Oaten straw	36.0	38.8	92.8
DIGESTIBLE DRY MATTER INTAKE (g/kg W <sup>0.75</sup> /d)			
Lucerne hay	31.4	45.1	69.6
Oaten straw	14.5	11.4	127.1

From: Foot and Romberg (1965).

## Conclusion

Notwithstanding the paucity of supporting data, the above hypothesis of the evolution of the Macropodidae digestive system is consistent with existing schemes for the evolution of the Macropodidae (Bartholomai 1972), with the development of other digestive systems among the ungulates, and with the appearance of grasses in the early Miocene and their subsequent radiation since that time as world climates became progressively more arid. The idea that the grazing Macropodinae are derived from the browsing Macropodinae, which in turn are derived from the Potoroinae, is consistent with the conclusions of Sanson (1976).

Rather less can be said about the phylogeny of the Macropodinae on the basis of digestive tract morphology than can be concluded from skeletal and dental characteristics. The development of a ventricular groove in the midstomach appears to be a recent phenomenon. It is assumed that the function of the groove in the pouch young is the same as in the suckling ruminant, (Black and Sharkey 1970); — to provide a means for the milk to pass as directly as possible to the hindstomach, the site of peptic digestion, and to avoid fermentation in the fore- and midstomach regions. Its function in the adult Macropodidae is not clear, although it can be inferred from the cineradiographic studies of Dellow (1978) that the groove directs the flow of the more fluid digesta along the lesser curvature of the midstomach.

The fact that in adult *Petrogale* the ventricular groove is ill-defined could be used to suggest that this genus is intermediate between the more primitive browsing and the more recently derived grazing Macropodinae. Sanson (1978) also reached this tentative conclusion from his studies on the dentition of the Macropodidae.

Fig. 1 is adapted from Janis (1976). Included with her representation of ungulate evolution during the Tertiary is a proposed scheme for the Macropodidae. In this scheme the Potoroinae evolved from some primitive marsupial stock long before the first appearance of grasses. The Macropodinae first appeared in the fossil record in the Oligocene (Bartholomai 1972), before the first appearance of grasses, and radiated during the Miocene after the development of the grasses. The idea that the more ancestral Macropodinae were browsers, and the more recently derived Macropodinae were grazers, is consistent with this scheme. The other Macropodidae subfamily, the Sthenurinae, now extinct, is thought to have separated from the Macropodinae in the late Miocene (Bartholomai 1972), and to have disappeared at the end of the Pleistocene. The Sthenurinae were all browsers as judged by their dentition, but the form of their digestive system is a matter for speculation, as also is the reason for their extinction (Merriam 1968).

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