STUDIES ON MARSUPIAL NUTRITION

I. RUMINANT-LIKE DIGESTION IN A HERBIVOROUS MARSUPIAL (SETONIX BRACHYURUS QUOY & GAIMARD)

By R. J. Moir*, M. Somers*, and H. Waring†

[*Manuscript received November* 22, 1955]

Summary

Some anatomical, digestive, and metabolic features of *Setonix brachyurus* Quoy & Gaimard, the Rottnest Island wallaby or "quokka", have been investigated. *Setonix* is a small macropod marsupial weighing 2–5 kg.

The complex stomach is large, sacculated, and has an oesophageal groove by-passing the sacculated region. Except in the oesophageal groove area, which has a stratified squamous epithelium, as in the ruminant, there is a columnar epithelium with tubular glands. The stomach contents amount to one-fifteenth of the body weight, and are six times greater than the contents of the caecum and upper colon.

The bacterial population of the stomach consists of some 15 morphological types, most forms being comparable with those in the rumen of sheep. Microbial attack on both cellulose and starch were observed.

Carbohydrates are fermented by these bacteria with the formation of volatile fatty acids (V.F.A.). The level of fatty acid varies according to feeding conditions from 2–14 m-moles per 100 ml "rumen" fluid. The pH varied in relation to these changes from 8·0–4·6. The gas of the stomach has a very high CO_2 content. Fermentation also occurs in the non-sacculated caecum and upper colon to a lesser extent.

Blood sugar determinations on five males indicate that the sugar level (15·8–78·9 mg per cent.) is more variable than in ruminants but of the same order. It is low compared with non-ruminants. V.F.A. was shown to be absorbed into the portal system, and some removed in the liver and by the tissues. At very low blood sugar levels (below 20 mg per cent.) the "body" appears to contribute sugar to the blood.

These findings, which are discussed and considered as an example of convergent evolution, show conclusively the ruminant-like digestion in the wallaby.

I. Introduction

A number of features converge to suggest that the digestion and the metabolism of carbohydrates in macropod marsupials is of a similar pattern to that found in ruminants (Moir *et al.* 1954).

There are a number of unpublished reports of cud chewing in kangaroos. However, Wood Jones (1923) reports that "no marsupial chews the cud, as do ruminants among the *Monodelphia*; but kangaroos and wallabies, as well as bandicoots, and probably some other forms have a curious habit of regurgitating their food. The animal, after a meal, makes a vigorous heaving movement of its chest and abdomen, and the stomach contents, which are forced up into the mouth, appear to be re-swallowed without any further chewing." Observations confirm this regurgita-

* Institute of Agriculture, University of Western Australia.

† Department of Zoology, University of Western Australia.

tion which sometimes leads to ejection of a food bolus. We have also frequently observed chewing in kangaroos, usually in a lying posture, sometimes several hours after feeding. It therefore seems probable, but not proven, that they chew the cud or "ruminate".

The large size and sacculated condition of the wallaby stomach, together with the small flask-like caecum (Clark 1948), suggest that a pre-gastric bacterial fermentation of ingesta predominates, as in the ruminant, rather than the caecal fermentation of other herbivores. Figure 1 shows the general anatomy of the stomach region.

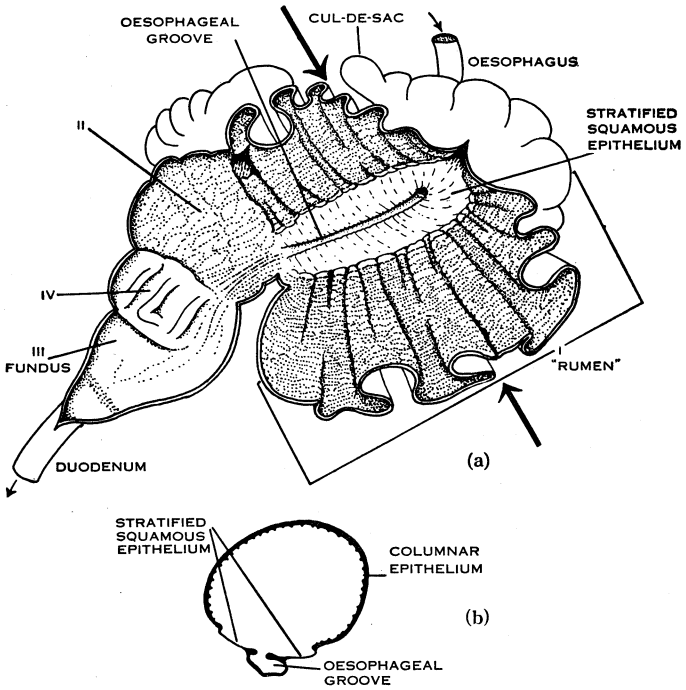

Fig. 1.—(*a*) General anatomy of the stomach of *Setonix*. (*b*) Transverse section of the stomach of *Setonix* at the arrows indicated in (*a*) showing the location of the oesophageal groove, stratified squamous epithelium, and columnar epithelium.

The fore-stomach, the putative rumen (region I), is sacculated and reflects above the oesophageal entrance to a cul-de-sac. A well-defined oesophageal groove runs from the oesophagus to the non-sacculated area (region II).

Unlike the rumen of sheep where the whole of the rumen, reticulum, and omasum has a stratified squamous epithelium, the epithelium of most of the stomach of the wallaby is columnar and possesses well-developed tubular glands. The only area of stratified squamous epithelium is the area about the oesophageal groove. Region III in Figure 1 is highly acidic and analagous to the abomasum of the ruminant. The functions of regions II and IV are not known. A more detailed account of the histology and anatomy of the alimentary tract will be published separately.

In ruminants, the fermentation of carbohydrates in the rumen restricts the glucose available for absorption. The low blood sugar level found in sheep, which can be lowered still further by insulin without overt ill-effect (Reid 1951), is already known to be paralleled in the wallaby (Buttle, Kirk, and Waring 1952).

A ruminant-type digestion with its unique exploitation of the synthetic and fermentative abilities of bacteria in the foregut, where the products of these activities are accessible to absorption, could explain the well-known ability of kangaroos and wallabies to survive on poor grazing.

Together, these considerations were considered sufficient to merit an exploratory investigation.

The possible parallel in the digestion and metabolism of carbohydrate between *Setonix* and ruminants was investigated on the following bases: (*a*) confirmation of bacterial fermentation in, and recovery of volatile fatty acids (V.F.A.) from, the stomach; and (*b*) recovery of V.F.A. from the blood with appropriate arterio-venous differences, coupled with low blood sugar levels.

II. Methods

The procedure adopted was to take the required blood samples, then examine gut contents for bacterial populations, fatty acids, pH, and weight of contents.

To obtain data from a variety of alimentary conditions, animals (*Setonix brachyurus* Quoy & Gaimard) were subjected to one of the following three sampling regimens:

Sampling was done at 10 a.m. and food was withdrawn either (1) 22 hr before sampling, or (2) 12 hr before sampling, or (3) about 6 p.m. and replaced at midnight. This latter treatment ensured a full stomach at sampling time, as the animals are night feeders. In all cases food consisted of commercial sheep nuts (mainly linseed and wheat products) and oaten chaff. Water was freely available at all times.

(*a*) *Alimentary Tract*

Samples for microscopical examination of gut contents were preserved by taking 10-g portions in 10 ml of 10 per cent. formalin. For this purpose samples from sites I and II (Fig. 1) were pooled, and samples from the caecum and the upper third of the colon were also pooled. The pH of fresh samples from these various sites was obtained by packing the contents about the electrodes of a Cambridge pH meter and allowing 2 min to equilibrate. V.F.A. were estimated in fluids expressed from fresh stomach or intestinal samples, which were distilled at constant volume in a Markham still as described by Elsden (1945) for rumen material. Results are expressed as m-moles acetic acid per 100 ml "rumen" fluid.

Ten-ml samples of gas were taken from two animals and passed through 10 per cent. KOH to determine the approximate CO_2 content. The residual volume was measured at constant pressure.

(*b*) *Blood*

Since the wallaby has no large superficial blood vessels, sampling involved dissection. At first concussion was used, and later anaesthesia with and without

artificial insufflation. In the initial experiments using concussion, excitement hyperglycaemia was clearly involved. Blood drawn by rapid heart puncture was therefore used as a reference. Five ml of blood can be obtained in this way within 45 sec of first handling the animal. After intraperitoneal injection of "Veterinary Nembutal" (Abbott), the blood sugar values did not differ significantly from those of the heart puncture sample until 45 min after injection.

The procedure finally used was: injection of "Nembutal" (80–100 mg/kg) intraperitoneally into unexcited caged animals, rapid incision of the abdomen, injection of freshly dissolved heparin (10 mg) into the inferior vena cava (I.V.C.), dissection of the neck to expose the carotid artery, and, finally, withdrawal of 6 ml of blood from each site. Each sample as withdrawn was run into a bottle with oxalate (10 mg $K_2C_2O_4$). The limiting factor in speedy bleeding was the slow withdrawal from the veins and this necessitated the heparin treatment. All procedures were timed, and Table I shows a typical schedule.

TABLE 1

TYPICAL SCHEDULE* OF PROCEDURE FOLLOWED IN OBTAINING BLOOD SAMPLES

Animal weighed, anaesthetized with "Nembutal" (100 mg/kg)

Step No.	Procedure	Time (min)
1	Animal injected with "Nembutal"	0
2	Abdomen opened and heparin injected into inferior vena cava	8·45
3	Blood drawn from caudal inferior vena cava	11·15
4	Blood drawn from carotid artery	12·14
5	Blood drawn from hepatic vein	13·55
6	Blood drawn from portal vein	15·23
7	Chest opened and blood drawn from superior vena cava	16·45

* This schedule taken from records of July 24, 1953 for animal No. 23, weight 3·4 kg.

Before withdrawal of blood from the superior vena cava (S.V.C.) a clip was placed on the venous entrance to the heart. Although desirable, it was found impossible to clamp the hepatic vein (H.V.) near its entrance to the I.V.C. without delay and trauma, as this vein is very short. The H.V. samples may, therefore, have been diluted with some blood from the I.V.C.

Blood V.F.A. was determined by the method of Scarisbrick (1952), but using plasma instead of whole blood, since it was found that the red cells caused excessive difficulty and variability. V.F.A. values are expressed as mg acetic acid per 100 ml plasma. The identity of the V.F.A. was not determined. Blood glucose was estimated by the method of Somogyi (1937) using well-mixed whole blood.

III. EXPERIMENTAL RESULTS

(*a*) *Alimentary Canal*

(i) *Weights of Ingesta.*—The weights of the stomach contents of 13 animals ranged from 80 to 485 g moist material. The mean weight was 207·5 g, whilst the

mean weight of the animals was 3·16 kg. As some of these animals were not in a fully-fed condition this value for the weight of stomach contents must be considered conservative. It nevertheless represents approximately one-fifteenth of the total body weight.

On the other hand, the pooled contents from the caecum and the upper third of the colon, where water absorption had not influenced the consistency of the ingesta, averaged only 35 g, or one-ninetieth of the total body weight, and the fundus (region III, Fig. 1) contained only 15–20 g.

TABLE 2

pH AND VOLATILE FATTY ACID (V.F.A.) LEVELS OF INGESTA IN THE ALIMENTARY TRACT

Figures in parentheses are number of determinations

Sampling Regimen		Fore-stomach (rumen)		Post-stomach (fundus)		Caecum plus Upper Third of Colon	
		pH	V.F.A. (m-moles/ 100 ml "rumen" fluid)	pH	V.F.A. (m-moles/ 100 ml "rumen" fluid)	pH	V.F.A. (m-moles/ 100 ml "rumen" fluid)
1 (fasted 22 hr +)	Mean	7·58 (6)	2·25 (6)	2·38 (6)	0·32 (2)	7·00 (2)	3·9 (2)
	Range	7·05–7·95	1·8–2·6	1·76–5·42	0·31–0·33	7·00	3·4–4·4
2 (fasted 12 hr +)	Mean	7·12 (9)	3·57 (9)	2·75 (8)	0·52 (5)	6·8 (5)	6·9 (4)
	Range	5·75–8·00	2·1–6·5	2·00–6·30	0·35–0·75	6·0–7·35	4·4–9·6
3 (fully fed)	Mean	5·67 (6)	10·51 (6)	2·40 (6)	1·06 (2)	6·6 (2)	5·5 (2)
	Range	4·60–6·85	5·5–14·7	1·86–3·06	0·79–1·33	6·48–6·70	5·3–5·6

(ii) *Microscopical Examination of Stomach Contents.*—Microscopical examination of "rumen" contents showed a dense bacterial population strikingly similar to that of the sheep's rumen under similar conditions. This population consisted mainly of Gram-negative rods and cocci, with a few spiral forms. Gram-positive rods were also present and these dominated the population where the pH was below 5·5.

There were fewer forms of bacteria observed than for the sheep. Approximately 15 types were discernable compared with over 30 for the sheep (Moir and Masson 1952). Ciliates were not detected in any sample examined, either from the stomach, caecum, or colon. It is possible that this may have been the result of the diet, which may also explain the absence of many of the other striking components of the sheep's ruminal flora.

Cellulose and starch were both attacked by some of these organisms. The extent of cellulose digestion was not determined.

(iii) *Metabolic Data.*—The data in Table 2 demonstrate unequivocally that fermentation with the production of steam-volatile fatty acids occurs in the "rumen".

The level of fatty acid was clearly related to the time after feeding, varying from 2·25 m-moles per 100 ml "rumen" fluid in fasted animals, to 10·5 m-moles per 100 ml "rumen" fluid in those recently fed. The pH conditions bear a very close relationship to the level of acid (Fig. 2). The very low pH observed in some cases was probably related to lactic acid production. The upper pH level of the fasted animal (pH 8·0) was somewhat higher than that generally found in the rumen of sheep. The pH of the saliva was of the order of 8·5.

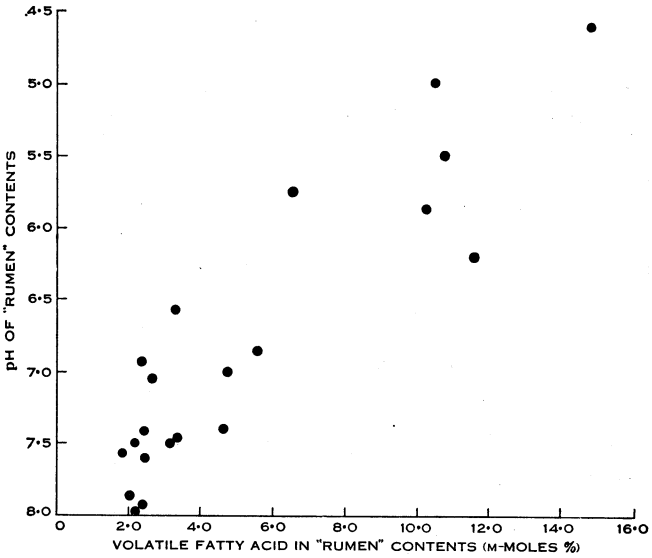

Fig. 2.—Relationship between volatile fatty acid levels and pH in the "rumen" of *Setonix*.

The very low level of V.F.A. in the fundus (0·32–1·06 m-moles per cent.) strongly suggests that the fermentation products were absorbed directly from the stomach as in the ruminant. Data from a single experiment support this, as the V.F.A. level was lower in region II (7·3 m-moles) than in region I (10·7 m-moles).

Large volumes of gas were not always found in the stomach, except during active fermentation, when the organ was usually distended. Gas samples taken from two fully-fed animals contained 60 and 75 per cent., respectively, of carbon dioxide. The nature of the residual gasses was not investigated.

Fermentation also occurs in the caecum and colon where both the pH and V.F.A. levels were found to be more constant (Table 2). The data indicate that a significant amount of V.F.A. was released in this region. Further, it appears that fermentation here was stimulated within a few hours of feeding, rose until at least 12 hr after feeding, then declined within 24 hr.

(*b*) *Blood*

A desirable summary of results would correlate V.F.A. titres in the alimentary canal with conditions in the bloodstream. This was not possible because, while our

various methods of killing and drawing blood could not have introduced great differences into the conditions obtaining in the alimentary canal, hyperglycaemia intervened during the earlier experiments. For the blood samples, therefore, it seemed better to record only the figures for the final five animals for which all desirable precautions, indicated by previous experiments, were incorporated. The earlier results obtained are merely commented on where they indicate significant trends. Table 3 shows the V.F.A. and glucose titres collected under final conditions from five male animals.

TABLE 3

BLOOD PICTURE OF FIVE MALE SETONIX ANAESTHETIZED WITH "NEMBUTAL"

Sampling Regimen	Animal	Glucose or V.F.A. Levels (mg %)	Aorta	Inferior Vena Cava	Superior Vena Cava	Portal Vein	Hepatic Vein
1 (fasted 22 hr +)	A	Glucose	17·8	29·6	—	31·6	29·6
		V.F.A.	6·00	4·80	—	9·42	4·80
	B	Glucose	15·8	17·8	—	23·7	29·6
		V.F.A.	7·94	5·14	—	9·71	9·65
2 (fasted 12 hr +)	C	Glucose	25·6	21·7	33·5	43·4	45·36
		V.F.A.	5·94	5·94	2·17	4·68	8·97
3 (fully fed)	D	Glucose	45·4	29·6	45·4	84·8	76·9
		V.F.A.	11·36	4·51	5·25	34·89	22·04
	E	Glucose	78·9	39·4	65·1	63·1	96·6
		V.F.A.	7·02	2·34	1·83	17·8	14·51

The portal vein (P.V.) of animals on sampling regimen 3 carry a high V.F.A. and glucose content compared with the systemic circulation, but low glucose compared with non-ruminant herbivores. After passage through the liver (i.e. in the H.V.) the blood titre of V.F.A. has dropped. The glucose may have dropped or been elevated. One possible explanation for the consistent fall in V.F.A. concentration could be the conversion of some V.F.A. components to glucose. There is no direct evidence for this as the composition of the V.F.A. was not determined. Comparison of the concentrations in arterial and venous blood show that both glucose and V.F.A. were removed by the tissues. Whereas the "body" and the "head" reduced the concentration of V.F.A., equally, the "head" removed much less glucose.

Animals on regimen 1 showed a similar ratio of V.F.A. and glucose values in the various trunks except that comparison of I.V.C. and aorta levels on their face value imply that the body in these circumstances was contributing glucose to the blood.

The figures from the animal on regimen 2 were consistent with the liver contributing glucose to the blood. The "body", as in fasted animals, was taking very little V.F.A., and unlike those on regimen 1, was not contributing glucose to the

blood. V.F.A. utilization appeared to vary directly with the level in the blood as indeed did the glucose utilization (Fig. 3).

Clearly, the measured blood sugar level was very dependent on feeding conditions in these experiments. Whether this applies to field conditions or other dietary regimens is not yet known.

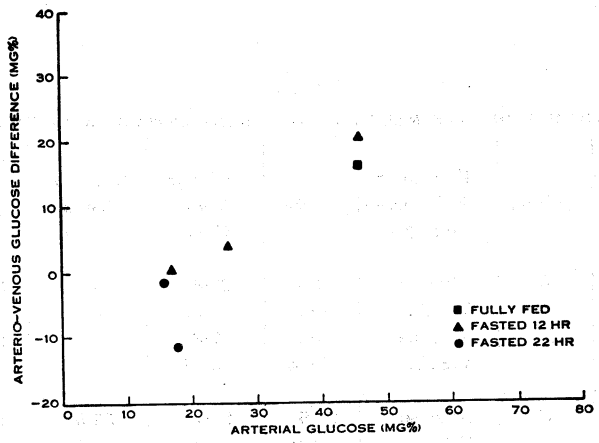

Fig. 3.—Relationship of blood glucose level to arterio-venous glucose difference in *Setonix*.

We have glucose values from another four fasted animals which were killed by concussion and blood drawn rapidly from the aorta, I.V.C., and P.V. These animals were part of an initial experiment performed in the belief that we could draw the blood samples before stress symptoms set in. In this we were wrong, but the fact that stress had supervened (as evidenced by raised blood sugar) makes the conditions worthy of note. The averages of recorded figures are: P.V.—49·5, aorta—66·7, and I.V.C.—53·6 mg per cent. Here, with the blood sugar augmented presumably from the liver (comparison of I.V.C. and P.V. showed that it was not from the gut), aortic blood sugar was higher than in the I.V.C. so there is no evidence of the body generally supplying sugar to the circulation.

In sampling regimen 2 there was information from five animals killed by concussion. There was no uniformity in sugar values so averaging of results would be meaningless. Where the aortic blood sugar was above 30 mg per cent., sugar was taken up by the tissues and the P.V. values obtained later showed a considerable increase in sugar due to stress. With the two animals where the aortic sugar was about 20 mg per cent. this same increase was not shown in the P.V., and the I.V.C. blood value was higher than the aortic, as was noted in the starved animals under "Nembutal" treatment. These figures, again, appear to imply that, where liver carbohydrate reserves are low, stress brings about release of muscle carbohydrate into the circulation.

IV. Discussion

In this exploratory investigation of digestion in *Setonix* many unexplained observations are recorded. However, a clear general picture emerges.

As in ruminants there is a capacious stomach region in which food is fermented by a dense bacterial population. The average ratio of stomach contents to large intestinal contents in *Setonix* is approximately 6:1. This is essentially the same as for ruminants, and the reverse of that in non-ruminant herbivores (Dukes 1947). The ratio of stomach content to body weight of 1:15 is, however, considerably less than for the larger true ruminants for which it is nearer 1:5 to 1:10 according to size (Elsden *et al.* 1946).

The stomach is not as clearly defined into four separate regions as in the ruminant, but has a well-defined oesophageal groove which by-passes the main fermentative region. Other points of difference are the columnar epithelium, and slightly higher fasting pH of the contents.

In ruminants, the rumen is buffered by bicarbonate, phosphate, and V.F.A. (Turner and Hodgetts 1955). A considerable quantity of both bicarbonate and phosphate is introduced into the rumen by the continuous and copious salivary flow (McDougall 1948). It is not known whether similar systems operate in the wallaby. *Setonix* does, however, exhibit copious salivary secretion under ether anaesthesia, and at high temperatures. It also has a strongly alkaline saliva.

Carbohydrates are fermented to V.F.A. by a bacterial population, apparently similar in composition and density to that of the sheep. The level of fatty acids is similar to that in ruminants (Elsden 1946). Their absorption is clearly indicated by the low level in the fundus (cf. Phillipson and McAnally 1942). The V.F.A. are absorbed into the P.V. directly from the upper stomach and probably also from the caecum (cf. Barcroft *et al.* 1944). The absence of information about the separate blood volume contribution of P.V. and hepatic artery to the total outflow from the liver in the H.V. makes it impossible to decide whether the disparity of V.F.A. values recorded is due to dilution or removal of V.F.A. by the liver. The difference in V.F.A. levels in these vessels is so great, however, that taken with the known events in the sheep, based on separate estimation of acetic and propionic acids, it seems likely that some fatty acid is being removed during vascular flow through the liver. Concurrently some glucose is absorbed from the alimentary canal, but both the intestinal and blood titres are low compared with those found in non-ruminant animals. There is clear evidence that both V.F.A. and glucose are utilized by the tissues, and, from the insulin experiments performed in another context (Buttle *et al.* 1952), it is known that only minimal quantities of blood glucose are essential for existence. The range of sugar levels (15·8–78·9 mg per cent.) is greater than that given for sheep by Reid (1950*a*), namely 18–57 mg per cent. A more marked hyperglycaemia after feeding occurred in these experiments. The V.F.A. levels and uptakes are essentially the same as in sheep (Reid 1950*b*) but the interplay between sugar and V.F.A. is not apparent from the limited data available. Exploratory dissection of other grazing macropods, e.g. *Bettongia*, *Protemnodon* ("tammar"), and *Macropus* (large kangaroos), shows similar alimentary anatomy. Stomach contents of a large kangaroo yielded a similar

microbial population. It appears probable, therefore, that the general pattern of digestive physiology is similar in all macropods.

It is well known that in the non-ruminants usually studied, there is an alimentary hyperglycaemia after feeding, with a heavy load of sugar carried to the liver where glycogen is deposited. This glycogen serves as a carbohydrate reservoir from which, by interplay of hormones, notably insulin and adrenalin, the blood sugar is kept within the narrow limits required by the central nervous system. In the ruminant and in *Setonix*, which are able to survive on low blood sugar levels and can utilize V.F.A. as a metabolic fuel, a different pattern exists. The extent to which other mammals are able to use V.F.A., particularly in hypoglycaemia, is unknown. In some animals (e.g. man, dog, and pig) carbohydrate metabolism is dominant, and in others (e.g. sheep and wallaby) V.F.A. metabolism is dominant, whilst other herbivores (e.g. horse, rabbit, and guinea pig) are intermediate between these two types, or variable, according to the structure of the alimentary canal, or the level of fermentation in the large intestines. It is profitless to discuss this further until much more data from a range of animal species are available but it is appropriate to consider briefly (*a*) the merits of the ruminant-type digestion in colonizing geographic areas not capable of supporting mammals lacking pre-gastric digestive apparatus, and (*b*) the reasons for believing that the similar digestive physiology exhibited by sheep and *Setonix* is a clear-cut example of convergent evolution.

With regard to (*a*) three related features of ruminal-type digestion are of particular significance. These are cellulose utilization, nitrogen metabolism, and vitamin synthesis. Fermentation of cellulose in herbivores normally occurs to a limited extent in the caecum and colon. Digestion is not as efficient in these as in the rumen, largely because the rate of passage is too rapid to permit efficient bacterial action. In the horse, food is eliminated in 24–27 hr (Alexander 1946), whereas in the cow 80 per cent. is eliminated in 70–90 hr and the remainder in 7–10 days (Balch 1950). In the ruminant, removal of cellulose and growth of bacteria *precede* normal alimentary digestion and absorption. This enables the products of fermentative breakdown by bacteria, along with the products of bacterial synthesis and food nutrients enclosed within the plant cell walls, to become readily available for absorption.

These facts show clearly that pre-gastric bacterial digestion confers important benefits upon the animal. Energy from poor fibrous foods is more efficiently garnered and the available energy is yielded over a longer period of time so that the animal is more resistant to periods of starvation; the uptake of nitrogen and other nutrients is enhanced; and considerable synthesis of vitamins and essential amino acids can take place. Although the gross value of ruminant digestion is apparent, a study of its minutiae as a basis for understanding ecology has been largely neglected. Raven and Gregery (1946) have discussed the radiation of macropods in relation to habitat. This investigation, based on museum and field studies, shows the adaptive branching in relation to forest, thicket, and grassland. This now could profitably be supplemented by a comparative study of digestive physiology of various macropods and their ecologically equivalent eutherian ruminants. Already it is known that there is a broad similarity between the sheep and the wallaby.

At one time the mammals were considered monophyletic because it seemed unlikely that monotremes, marsupials, and Eutheria would have developed the mammalian features independently. This monophyletic origin is not supported by recent authors. With some variation in detail there is considerable agreement that there has been separate derivation from therapsid reptiles. According to Olson (1944) "it would appear that more than one line of therapsids, probably three to five, crossed the mammalian threshold and that the common ancestry of mammals lies well below the level of the first mammals, probably somewhere below the level of the upper Permian." To Olson the monotremes "appear to have little to do with other groups of mammals and must have had a history long independent." Simpson (1950) also favours a very early origin of monotremes and his view that they are really highly modified therapsid reptiles is epitomized in his description of them as "mammals by definition rather than ancestry." Watson (1953) expresses the opinion that monotremes could readily be derived, with small modifications, from tritylodont reptiles. Evidence from cytology (Matthey 1949) and pharmacology (Feakes *et al.* 1950) is consistent with monotremes having closer affinities with present day reptiles than with other mammals. Olson and Simpson agree in deriving marsupials and placentals from Pantotheria (Jurassic mammals) with a divergence between these two sometime during the Cretaceous.

Fossil evidence indicates that, of the "warm blooded" stocks that emerged from the therapsid reptiles, two survive to the present. These two—Prototheria (monotremes) and Theria (marsupials and Eutheria) have only a tenuous and remote relationship to each other but they possess many characters indicating convergent evolution. The marsupials and Eutheria, though having a distant common ancestral group (Pantotheria) have been separate since the Cretaceous; Eutheria are not derived phylogenetically from Marsupialia. It can be concluded therefore that adaptive modifications, e.g. the ruminant-type digestion found in these groups, have been independently and convergently arrived at and do not reflect phylogenetic relationships. Whilst not in any way invalidating this general conclusion, it would clearly be valuable to know, in the present context, whether marsupials, other than grazing macropods, have alimentary canals similar to those described here for *Setonix*. Dissection of koalas, Australian opossums, and bandicoots offers no support for this possibility, nor does Johnstone's (1898) description of a greater range.

V. Acknowledgments

We wish to thank Mr. G. G. Sharman for assistance and Dr. E. P. Hodgkin for drawing Figure 1. The investigation was financed in part by grants from the Nuffield Foundation, Commonwealth Bank, and University of W.A. Research Committee.

VI. References

Alexander, F. (1946).—*J. Comp. Path.* **56**: 266.

Balch, C. C. (1950).—*Brit. J. Nutrit.* **4**: 361.

Barcroft, J., McAnally, R. A., and Phillipson, A. T. (1944).—*J. Exp. Biol.* **20**: 120.

Buttle, J. M., Kirk, R. L., and Waring, H. (1952).—*J. Endocrinol.* **8**: 281.

Clark, J. R. (1948).—*J. R. Soc. W. Aust.* **33**: 59.

DUKES, H. H. (1947).—"The Physiology of Domestic Animals." 6th Ed. (Comstock Publ. Co.: New York.)

ELSDEN, S. R. (1946).—*J. Exp. Biol.* **22**: 51.

ELSDEN, S. R., HITCHCOCK, M. W. S., MARSHALL, R. A., and PHILLIPSON, A. T. (1946).—*J. Exp. Biol.* **22**: 191.

FEAKES, M. J., HODGKIN, E. P., STRAHAN, R., and WARING, H. (1950).—*J. Exp. Biol.* **27**: 50.

JOHNSTONE, J. (1898).—*J. Linn. Soc. (Zool.)* **27**: 1.

MCDOUGALL, E. I. (1948).—*Biochem. J.* **43**: 99.

MATTHEY, R. (1949).—"Les Chromosomes des Vertebres." (F. Rouge: Lausanne.)

MOIR, R. J., and MASSON, M. J. (1952).—*J. Path. Bact.* **64**: 343.

MOIR, R. J., SOMERS, M., SHARMAN, G., and WARING, H. (1954).—*Nature* **173**: 269.

OLSON, E. C. (1944).—*Spec. Pap. Geol. Soc. Amer.* **55**: 1.

PHILLIPSON, A. T., and MCANALLY, R. A. (1942).—*J. Exp. Biol.* **19**: 199.

RAVEN, H. C., and GREGERY, W. K. (1946).—*Amer. Mus. Novit.* **1309**: 1.

REID, R. L. (1950*a*).—*Aust. J. Agric. Res.* **1**: 182.

REID, R. L. (1950*b*).—*Aust. J. Agric. Res.* **1**: 338.

REID, R. L. (1951).—*Aust. J. Agric. Res.* **2**: 132.

SCARISBRICK, R. (1952).—*Biochem. J.* **50**: xxxiv.

SIMPSON, G. G. (1950).—"Meaning of Evolution." (Yale Univ. Press: New Haven.)

SOMOGYI, M. (1937).—*J. Biol. Chem.* **117**: 771.

TURNER, A. W., and HODGETTS, V. ELIZABETH (1955).—*Aust. J. Agric. Res.* **6**: 125.

WATSON, D. M. S. (1953).—*Evolution* **7**: 159.

WOOD JONES, F. (1923).—"The Mammals of Southern Australia." Pt. I. p. 59. (Govt. Printer: Adelaide.)