Studies on gastric digestion of protein and carbohydrate, gastric secretion and exocrine pancreatic secretion in the growing pig

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1. Six pigs, initially of 35 kg mean live weight, were each fitted with a re-entrant cannula. This was formed on either side of a short pouch of duodenum into which the pancreatic duct opened and which contained a simple cannula linked to the centre of the re-entrant cannula.

2. Each pig received two diets: diet A was based on wheat starch, sucrose and casein, while diet B was based on barley and soya-bean meal. The diets were given in equal amounts at 12 h intervals.

3. Digesta and pancreatic juice were collected continuously during three 12 h periods for each pig on each diet.

4. Mean duodenal output: dietary intake values for diets A and B respectively were: digesta 1·80, 2·86; dry matter 1·05, 1·03; nitrogen 1·05, 1·06; trichloroacetic acid (TCA)-soluble N 7·69, 9·10; glucose 0·97, 0·89. For diet A the proportion of TCA-soluble N in total N rose from 13 to 50% during 12 h, while it was approximately 50% throughout 12 h for diet B.

5. Mean total pepsin (*EC* 3.4.23.1) activities (units/24 h) were 760449 (diet A) and 1466571 (diet B).

6. Salivary and gastric secretions were calculated to be approximately 4 and 8 kg/24 h for diets A and B respectively.

7. Mean flows in pancreatic juice (g/24 h) for diets A and B respectively were: juice 1204, 2182; protein 10·94, 12·10; N 1·98, 2·14; ash 9·46, 17·31; sodium 3·88, 6·91; potassium 0·23, 0·54; calcium 0·031, 0·046; phosphorus 0·024, 0·026.

8. Mean total enzyme activities (units $\times 10^{-3}$/24 h) for diets A and B respectively were: trypsin (*EC* 3.4.21.4) 138, 114; chymotrypsin (*EC* 3.4.21.1) 84, 84; carboxypeptidase A (*EC* 3.4.2.1) 5, 4; carboxypeptidase B (*EC* 3.4.2.2) 15, 17; amylase (*EC* 3.2.1.1) 1061, 981.

9. It was calculated that the minimum amount of endogenous N from saliva and gastric secretion was 0·3–0·6 g in 24 h. This assumes no absorption of N occurred anterior to the duodenal cannula.

It is generally thought that the major roles of the stomach in growing pigs are to provide a reservoir of diet for controlled release to the small intestine and to initiate protein and carbohydrate digestion. However, detailed information about its role in digestion remains scarce.

Braude *et al.* (1970) found that only 18% of the nitrogen in the gastric contents of 28-d-old piglets killed 1 h after receiving a milk-based diet was soluble, and only 32% of the soluble N was soluble in trichloroacetic acid (TCA). In older pigs given a cereal-based diet, Horszczaruk (1971) found that 80% of the N in the stomach was in the form of true protein 2·5–3 h after feeding. In a study in which 40-kg pigs were given barley-weatings and soya-bean-meal diets (A. G. Low, unpublished results), an average of 20% of the N in gastric digesta 1–4 h after feeding was TCA-soluble.

In pigs of about 40 kg live weight fitted with re-entrant cannulas in the duodenum 300–800 mm from the pylorus, Zebrowska (1973) found that during 24-h periods 35–50% of the N was in short peptide or free amino acid form (i.e. equivalent to TCA-soluble N); the exact amount differed according to the type of diet given. In a similar study, Low (1979) found that 35–47% of the N was TCA-soluble. In both cases the cannulas were placed posterior to the pancreatic duct, so that the extensive proteolysis indicated by the large amounts of TCA-soluble N could have been the result of gastric acid and peptic hydrolysis,

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as well as hydrolysis by the pancreatic proteases. However, although it was not possible to cool all the digesta sufficiently rapidly during collections to stop pancreatic enzyme activity completely, the amount of digestion may have been small; O. Simon (personal communication) found that digesta from pigs (with cannulas anterior to the pancreatic duct) collected either surrounded by ice, or directly into TCA, contained similar amounts of TCA-soluble N.

At present there is no direct evidence that amino acids are absorbed by the stomach. It has usually been found that rather more N and amino acids are present in the duodenum of pigs than are eaten, as a result of endogenous secretions. This indirect evidence has supported the view that amino acids are not absorbed in the stomach.

Information on carbohydrate digestion in the stomach is also scarce. Kvasnitskii (1951) found that half the starch given to pigs of unspecified weight was digested to oligo-, di- or monosaccharides in the stomach and that 20% of the glucose derived from starch had disappeared anterior to a re-entrant cannula in the duodenum; similar results were obtained in 40-kg pigs given a variety of diets by Sambrook (1979). In both studies the cannulas were located posterior to the pancreatic duct so some pancreatic amylase (*EC* 3.2.1.1) activity had probably contributed to the results. These results contrast with those of Holmes *et al.* (1974) who found that 41–53% of the starch in maize-based diets was digested to glucose and absorbed proximal to the pancreatic duct in pigs with re-entrant cannulas.

Measurements of the flow of digesta through the proximal duodenum of pigs show a very large dilution of the diet by endogenous secretions (Low *et al.* 1978). However, the contribution of the stomach secretions has only been estimated indirectly by Tkachev (1973) by extrapolation based on the relative areas of the mucosal surfaces of gastric pouches and whole stomachs.

Although it is clear that endogenous sources of N are an important component of digesta in the duodenum, the quantitative contributions of the individual secretions are not entirely clear. Measurements are available of the amounts of N in the bile (Sambrook, 1981) and pancreatic juice (Corring *et al.* 1972; Partridge *et al.* 1982). Although estimates of the amounts of trypsin (*EC* 3.4.21.4), chymotrypsin (*EC* 3.4.21.1) and amylase are available (Corring *et al.* 1972), the amounts of pepsin (*EC* 3.4.23.1) and carboxypeptidases A (*EC* 3.4.2.1) and B (*EC* 3.4.2.2) respectively have only recently been measured (Low, 1982; Partridge *et al.* 1982).

The mineral content of pancreatic juice secreted by pigs has received minimal attention hitherto except in studies by Partridge *et al.* (1982).

The aims of the present study were: (*a*) to prepare pigs with cannulas arranged so that digesta could be collected from the duodenum before it was mixed with pancreatic juice, and to collect these fluids separately; (*b*) measurement of the time-course of protein and carbohydrate digestion in the stomach; (*c*) estimation of the amount of endogenous N secretion by the salivary glands and stomach; (*d*) measurement of the amount of pepsin secreted; (*e*) measurement of any N and glucose absorption apparently occurring in the stomach; (*f*) estimation of the volume of gastric secretion; (*g*) measurement of the volume and composition of pancreatic juice.

A brief report on this work has already been published (Zebrowska *et al.* 1981).

EXPERIMENTAL METHODS

Animals and surgery

Six castrated male Large White × Norwegian Landrace pigs, initially of approximately 35 kg, were used. They were each fitted with a re-entrant cannula in the duodenum. This was formed on either side of a pouch of duodenum about 30 mm long, into which the pancreatic duct opened. The re-entrant cannula was made from two T-piece PVC cannulas

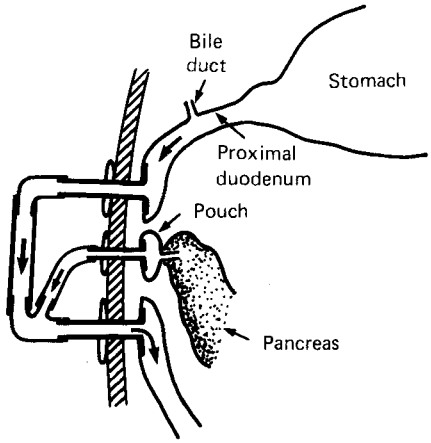

Fig. 1. Duodenal re-entrant cannula and pancreatic pouch preparation.

of 10 mm internal diameter and the pouch was fitted with a T-piece cannula, made from silicone rubber, of 3 mm internal diameter. The latter cannula was linked externally to the re-entrant cannula as shown in Fig. 1. The general surgical method was as described by Aliev (1974). Anaesthesia was maintained with diethyl ether. The pigs were allowed to recover in pens during 14 d after surgery and were then allocated to one or other of the experimental diets A or B.

Housing

The pigs were kept individually in pens for the first 4 d of feeding with each experimental diet and were then transferred to metabolism cages for the following 3 d of digesta and pancreatic juice collection.

Diets and feeding

Details of diets are shown in Table 1. Diets A and B were given to all pigs in a randomized order. The diets were chosen to be of contrasting composition, but of a similar N content. Diet A was a semi-purified diet of the type used in many previous studies on digestion in pigs, while diet B was a typical European practical pig diet. The diets were given to the pigs daily at 08.00 and 20.00 hours in equal portions, at a level of 40 g/kg live weight/d. The diets were mixed with water (1:2·5, w/v) immediately before feeding.

Digesta collection procedures

Digesta and pancreatic juice were collected continuously for three consecutive 12 h periods, into beakers surrounded by ice. When 150–200 g digesta had been collected, it was weighed, sampled, warmed to approximately 40° and returned to the pig.

Pancreatic juice was collected every hour and sampled; it was then mixed with digesta before being poured slowly back into the duodenum. Digesta samples were pooled for the following periods: 08.00–09.00, 09.00–11.00, 11.00–15.00, 15.00–20.00 hours. The collection, sampling and return method was manual throughout. The digesta were frozen before analysis; the pancreatic juice was kept at 2° until the enzyme assays were complete, when it was frozen.

Analytical methods

Dry matter (DM). This was measured by heating the samples overnight at 60°, followed by 4 h at 105°.

Table 1. *Composition of diets (g/kg diet)*

	Diet	
	A	B
Casein	190	—
Wheat starch	607	—
Sucrose	100	—
Cellulose	50	—
Soya-bean oil	20	—
Sodium chloride	3	3
Calcium carbonate	10	10
Mineral–vitamin mix	20	10
Barley meal	—	867
Soya-bean meal	—	110

N. This was estimated by the Kjeldahl method. Digesta samples were analysed both for their total N content and for the N soluble in TCA (final concentration 100 g TCA/kg digesta). After precipitation with TCA overnight, samples were centrifuged at 1500 ***g*** for 15 min before analysis.

Pepsin. The activity in the supernatant fraction of digesta (obtained by centrifugation for 10 min at 1500 ***g***) was estimated by measurement of the rate of release of tyrosine from casein (Light, soluble; BDH Ltd, Poole, Dorset) at pH 2·0 and 37° (Anson, 1938). One unit is defined as an absorbance increase of 0·001 at 280 nm/min, due to release of TCA-soluble hydrolysis products.

Trypsin. This was estimated by measuring the rate of hydrolysis of α-N-toluene-*p*-sulphonyl L-arginine methyl ester hydrochloride (Hummel, 1959) at pH 8·1.

Chymotrypsin. This was estimated by measuring the rate of hydrolysis of N-benzoyl L-tyrosine ethyl ester (Hummel, 1959) at pH 7·8.

Carboxypeptidase A. This was estimated by measuring the rate of hydrolysis of hippuryl-L-phenylalanine (Folk & Schirmer, 1963) at pH 7·5.

Carboxypeptidase B. This was estimated by measuring the rate of hydrolysis of hippuryl-L-arginine (Folk *et al.* 1960) at pH 7·65.

One unit of activity of trypsin, chymotrypsin, carboxypeptidase A and carboxypeptidase B is defined as the activity which results in the hydrolysis of one μmol substrate/min at 25°.

Amylase. This was estimated by measuring the rate of hydrolysis of soluble starch (Bernfield, 1951). One unit is defined as the activity which liberates 1 μmol reducing groups (calculated as maltose)/min at 25°.

Glucose. This was measured in digesta and in its supernatant fraction by the methods described by Sambrook (1979).

Minerals. Samples of digesta and pancreatic juice were weighed into quartz crucibles, dried at 105° and ashed at 480°. The residues were dissolved in hydrochloric acid, transferred to volumetric flasks and made up to volume. The phosphorus content was measured spectrophotometrically using molybdovanadate as the colour-forming agent. The other minerals were measured by atomic absorption spectrometry.

RESULTS

The results are presented as the mean values for 24-h periods (except Table 2) of measurement in pigs receiving 1500 g diet and 3750 ml water/d. Two pigs which received

Table 2. *The mean digesta (g/h), dry matter (DM), total nitrogen, trichloroacetic acid (TCA)-soluble N and glucose flow during 12 h periods through the proximal duodenum of six 40 kg pigs with re-entrant cannulas*

Time of day (hours) ...	08.00–09.00		09.00–11.00		11.00–15.00		15.00–20.00	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
			Diet A*					
Digesta (g/h)	960	230·7	411	164·9	427	123·0	247	31·5
DM (% of intake)	76	18·4	16	7·6	16	2·6	6	1·6
Total N (% of intake)	76	21·0	16	6·6	16	3·2	8	3·4
TCA-soluble N (% of intake)	10	5·0	4	0·2	6	2·0	4	0·8
Glucose (% of intake)	72	20·0	14	5·6	16	2·0	6	2·0
% of N in TCA-soluble form	13	—	25	—	38	—	50	—
			Diet B*					
Digesta (g/h)	1143	367·3	876	96·0	618	114·1	428	83·5
DM (% of intake)	36	10·6	24	13·6	18	17·4	10	1·8
Total N (% of intake)	28	7·0	24	2·0	22	3·6	12	1·6
TCA-soluble N (% of intake)	14	2·0	12	1·2	10	1·4	6	0·6
Glucose (% of intake)	34	9·2	22	3·0	16	3·4	8	1·0
% of N in TCA-soluble form	50	—	50	—	45	—	50	—

* For details of diets, see Table 1.

Table 3. *The mean duodenal output: dietary intake values for digesta, dry matter (DM), total nitrogen, trichloroacetic acid (TCA)-soluble N and total glucose in 24 h for six 40 kg pigs with re-entrant cannulas*

	Diet†		Difference (B – A) (5 df)	
	A	B	Mean	SE
Digesta	1·80	2·86	1·06**	0·174
DM	1·05	1·03	−0·02	0·036
Total N	1·05	1·06	−0·01	0·021
TCA-soluble N	7·69	9·10	1·41	0·595
Total glucose	0·97	0·89	−0·08	0·032

** $P < 0·01$.
† For details of diets, see Table 1.

1300 g diet/d for part of the test are included, with the results multiplied by 15/13 before statistical analysis. Thus it has been assumed that the responses measured are related to intake and live weight in a linear manner.

In Table 3 the results are expressed as output from the duodenal cannula as a ratio of the intake of the nutrient in the diet. In the case of digesta, the intake is the sum of diet and water consumed.

The mean hourly flow rates of digesta and its content of DM, N, TCA-soluble N and glucose are shown in Table 2. A greater proportion of the total flow in 12 h for all components occurred in the first hour after feeding for diet A than for diet B. The proportion of N in TCA-soluble form increased from 13 to 50% as time passed for diet A, while it remained approximately 50% for diet B throughout the 12-h period.

The mean duodenal digesta: dietary intake values for digesta, DM, N, TCA-soluble N and glucose are shown in Table 3. They indicate that the endogenous additions (mainly of water)

Table 4. *Comparison of intake (g) and duodenal flow (g) of dry matter (DM), total nitrogen, trichloroacetic acid (TCA)-soluble N and total glucose in 24 h for six 40 kg pigs with re-entrant cannulas*

	Diet†	Intake (I)	Duodenal digesta (D)	Difference (D − I) (5 df)	
				Mean	SE
DM	A	1350·0	1418·2	68·2*	21·31
	B	1324·0	1359·2	35·2	40·59
Total N	A	49·6	52·0	2·4	1·30
	B	38·3	40·5	2·2*	0·68
TCA-soluble N	A	1·6	12·2	10·6***	0·83
	B	2·1	19·2	17·1***	0·65
Total glucose	A	817·0	789·6	−27·4	14·46
	B	767·4	680·8	−86·6*	27·98

* $P < 0{\cdot}05$, *** $P < 0{\cdot}001$.
† For details of diets, see Table 1.

Table 5. *Mean pepsin activity (units/24 h)† and free glucose (g) in digesta collected from six 40 kg pigs with re-entrant cannulas in the proximal duodenum*

	Diet‡		Difference (B − A)	
	A	B	Mean	SE
Pepsin	760449	1466571	706122**	119981·6
Free glucose	53·3	14·2	−39·1**	8·94

** $P < 0{\cdot}01$.
† For definition of units, see p. 404.
‡ For details of diets, see Table 1.

to the digesta were much larger for diet B than for diet A. When the amounts of DM, N, TCA-soluble N and glucose flow through the duodenum were compared with the amounts ingested, as shown in Table 4, there was evidence of net secretion of DM and N, and net absorption of glucose. A much larger proportion of the N was TCA-soluble in the digesta than in the diets.

The amounts of pepsin and free glucose in duodenal digesta are shown in Table 5. Twice as much pepsin was apparently secreted in response to diet B than to diet A. Free glucose represented 6·8 and 2·1% of the total glucose flow through the duodenum for diets A and B respectively.

The volumes of pancreatic juice and many of its major constituents secreted by the pigs are shown in Table 6. The only significant differences in the amounts of secretion between the diets were for the volume of the juice and the amounts of sodium, potassium, calcium and ash, all of which were higher for diet B than for diet A.

DISCUSSION

Digesta flow pattern during 12-h periods

The pattern of flow of digesta and of its constituents through the re-entrant cannulas was generally similar to that found in studies in which re-entrant cannulas have been placed posterior to the pancreatic duct in the duodenum of growing pigs. For example, very similar

Table 6. *Mean output of pancreatic juice and some of its mineral and enzymic components† in six 40 kg pigs in 24 h*

	Diet‡		Difference (B−A) (5 df)	
	A	B	Mean	SE
Pancreatic juice (g)	1204	2182	978***	178·0
Protein (g)	10·94	12·10	1·16	1·412
Total N (g)	1·98	2·14	1·64	1·494
Ash (g)	9·46	17·31	7·85**	1·690
Sodium (mg)	3876	6906	3030**	633·9
Potassium (mg)	228	543	315**	66·0
Calcium (mg)	31·2	45·7	14·5*	3·66
Phosphorus (mg)	24·4	25·8	1·4	3·49
Trypsin (*EC* 3.4.21.4):				
Units × 10^{-3}	138·3	113·5	24·8	22·65
Specific activity	13·4	10·9	−2·5	3·41
Chymotrypsin (*EC* 3.4.21.1):				
Units × 10^{-3}	83·7	84·0	0·3	7·34
Specific activity	9·7	9·3	−0·4	1·65
Carboxypeptidase A (*EC* 3.4.2.1):				
Units × 10^{-3}	4·9	4·2	−0·7	0·38
Specific activity	0·6	0·5	−0·2	0·12
Carboxypeptidase B (*EC* 3.4.2.2):				
Units × 10^{-3}	15·2	16·7	1·5	1·22
Specific activity	1·5	1·6	0·1	0·20
Amylase (*EC* 3.4.23.1):				
Units × 10^{-3}	1060·7	981·2	−79·4	13·94
Specific activity	89·7	81·7	−8·0	6·88

* $P < 0·05$, ** $P < 0·01$, *** $P < 0·001$.
† For definition of units, see p. 404.
‡ For details of diets see Table 1.

diets were used by Braude *et al.* (1976) who found a higher flow rate in the first 1–2 h after feeding for a semi-purified diet than for one based on cereals, but subsequently the flow rate was higher for the latter diet. A similar contrast has been found for other types of semi-purified and cereal-based diets by Zebrowska (1973). The flows of DM, ash, N and glucose were similar to those described for diets like A and B by Low *et al.* (1978), Low (1979) and Sambrook (1979).

The high proportion of TCA-soluble N in total N found in this study is of interest, because the amount of gastric digestion of the casein in diet A was apparently less than that of the barley and soya-bean proteins in diet B in the first 3 h after feeding. In part this difference may have been due to the short contact-time for diet A, the N content of which left the stomach nearly three times faster in the first hour after feeding. On the other hand, it may be that casein is more resistant to gastric hydrolysis than barley and soya-bean proteins. Similar high levels of N in short-peptide and free amino acid form were found in pigs, with cannulas distal to the pancreatic duct, given a wide variety of diets by Zebrowska (1973) and Low (1979); our present results imply that this extensive digestion occurred in the stomach rather than after action by the pancreatic proteases and peptidases.

Approximately half the N leaving the stomach after the pigs received diet B was TCA-soluble, whereas Horszczaruk (1971) and A. G. Low (unpublished results) found that only 20% of the N in gastric digesta was TCA-soluble. This implies that the digesta leaving the stomach had a higher TCA-soluble N content than the gastric contents as a whole.

Total flow in 24-h periods

The different amounts of digesta collected during 24-h periods for diets A and B correspond with differences found by Zebrowska (1973) and Braude *et al.* (1976) for similar diets. Although the total amounts collected were lower in the present study than those found previously, this was due in part at least to the absence of pancreatic juice.

After subtracting an estimated value for DM content of bile (since the cannulas were placed distal to the bile duct) using values from Sambrook (1981), it can be calculated that there was very little net secretion of DM from the saliva, stomach or proximal duodenum. Similarly, using values for the N content of bile (Sambrook, 1981) one can calculate that net secretion of 0·3–0·6 g N occurred from other sources in 24 h. These results may thus imply that some absorption of DM and possibly also of N, occurred anterior to the cannula site; this is accounted for in part by the observed apparent absorption of glucose. The apparent absorption of glucose found in this study compares well with that reported by Sambrook (1979), who used diets similar to A and B, but it is substantially less than that found by Holmes *et al.* (1974) who used maize-based diets. The reason for this difference is not clear. It is possible that bacteria may ferment glucose in the stomach, but no quantitative values are available for this.

Endogenous N secretion

The amounts of N secreted individually by the salivary glands and the gastric mucosa of growing pigs have not been measured. On the other hand, the ability of the gastric mucosa to absorb nutrients appears to be very limited, since neither amino acids nor glucose appear to be actively transported by this tissue (A. G. Low, unpublished results); in addition, the concentrations there are not appropriate for passive diffusion of these compounds. Since most, if not all, of the apparent endogenous N secretion can be accounted for by the pepsin measured in the duodenal digesta, it seems likely that the amounts secreted were balanced by some disappearance of amino acids proximal to the duodenal cannula.

Pepsin

There do not appear to be any published values for pepsin output from the stomach with which those of the present study can be directly compared. The mean values are lower than those of Low (1982) but the latter were measured using haemoglobin as a substrate. The results do indicate that the potential hydrolytic capacity of the pepsin secreted is very high, even when measured in the duodenum: the total amounts actually secreted may be higher, because autodigestion could occur in the stomach.

Gastric secretion

Direct quantitative measurements of gastric secretion in pigs are lacking at present because of the difficulty of obtaining pure gastric juice from the whole stomach. Tkachev (1973) extrapolated the secretion from gastric pouches, on the basis of the relative areas of the pouch and the whole stomach mucosal surfaces, to estimate that the amount of gastric juice secreted was 6 l/kg diet eaten per d in 35–40 kg pigs. On this basis the pigs in the present study would be expected to secrete 9 l gastric juice in 24 h. After subtracting the volume of bile secreted in response to diets very similar to diets A and B (Sambrook, 1981) we estimate that approximately 4 and 8 l gastric juice were secreted in 24 h by the pigs receiving diets A and B respectively. This estimate is also based on the assumption that the volume of saliva secreted is minimal (Corring, 1980). A similar proportional difference in gastric secretion was found by Kvasnitskii (1951) when milk-based and cereal-based diets were given to pigs which were 2 months old and prepared with gastric pouches. The reasons for

the large difference in gastric secretion remain obscure but there is evidence that gastric secretion in man is higher after eating unrefined than after eating refined carbohydrate, i.e. additional dietary fibre may increase gastric secretion. This is consistent with the differences in fibre content between diets A and B in the present study.

Pancreatic secretion

Most of the measurements made on pancreatic secretion are similar to those reported by Partridge *et al.* (1982). In the latter study similar diets were used except that the cereal diet (similar to diet B) contained 200 g fine wheat offal/kg and the purified diet contained maize starch rather than wheat starch. These differences, which include the type of dietary fibre, might account for the differences between the two studies in the volume of juice and amount of amylase secreted: various types of fibre have been found to influence the output of pancreatic juice and amylase in acute studies with rats (Sommer & Kasper, 1980).

The amount of protein secreted in the pancreatic juice was higher than those found by Corring *et al.* (1972) and Partridge *et al.* (1982) after taking live weight and diet intake differences into account. This may be because of the protein content of the mucosal cells shed into the duodenal pouch, into which the pancreatic duct opened.

The amounts of ash secreted in the pancreatic juice may be compared with the amounts passing the duodenum distal to the opening of the pancreatic duct; these were 25 and 43 g higher than the amounts eaten of diets similar to diets A and B respectively in this study (Low *et al.* 1978). It thus seems that about 40% of the endogenous minerals found in the duodenum are secreted by the pancreas.

The differences in the amounts of Na and K secreted between the two diets correspond with the differences in juice volume; their concentration in the juice is similar. This is consistent with the values of Hickson (1970) who used anaesthetized pigs and who found that the concentration of Na and K in the juice did not change when the flow rate was increased by secretin or by vagal stimulation. Partridge *et al.* (1982) found similar concentrations of Na and K in pigs given diets similar to those used in this study.

The amounts of Ca and P secreted by the pancreas were very low compared with those found to be passing the duodenum in a previous study; indeed, net absorption of both minerals occurred proximal to the duodenal cannula (Partridge, 1978).

The pancreatic enzyme activities measured here were in a similar range to those of Partridge *et al.* (1982) in pancreatic juice, and to those found in duodenal digesta (Low, 1982). A characteristic feature of all these studies is the very high level of within-study variation. However, because different surgical and sampling methods but identical assay methods were used in the different studies, it seems that this variation is of biological origin rather than an artefact. The total production of pancreatic enzymes appears to exceed the amounts theoretically required for hydrolysis of the diet under optimal conditions by as much as 100-fold. In spite of this apparent over-production, there are reports of adaptation of pancreatic enzyme secretion to diets containing different amounts of protein (Corring *et al.* 1972) and to diets with or without trypsin inhibitors (Schneeman, 1982). This enigma provides an interesting challenge for future research.

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