Changes from birth to maturity in the pattern of distribution of lactase and sucrase activity in the mucosa of the small intestine of pigs

By M. J. MANNERS and J. A. STEVENS*

Department of Animal Husbandry, School of Veterinary Science, University of Bristol

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1. Measurements were made of changes in lactase and sucrase activity of homogenates of small intestine mucosa of sixty-one pigs varying in age from newborn to mature animals.

2. From each pig, samples for enzyme determination were taken from six sites along the small intestine. These sites were at 5, 20, 40, 60, 80 and 95 % of the length of the small intestine, measured from the pylorus.

3. Lactase activity was present at high levels in the newborn pig, the maximum being found at the 20 % site. Between birth and 8 weeks of age there was a fall in the amount of activity in the mucosa of the small intestine. In older pigs the levels of mucosal lactase activity were not greatly different from those found in 8-week-old pigs, although the distribution along the small intestine tended to change with advancing age.

4. Sucrase activity was found only once in thirty-six samples from the small intestine of six newborn pigs, but was present in all six pigs sampled at 1 week of age. Levels of activity continued to rise until maturity. Maximum activity was found at the 20 or 40 % site in the younger pigs (1–8 weeks of age). In the older pigs, high activity was found at a wider range of sites, the peak of activity generally being at the 40 and 60 % sites.

The hydrolytic activities of the intestinal mucosa towards sucrose and lactose have been studied intensively. The hydrolytic activity towards sucrose is due to one of the α-D-glucoside glucohydrolases (α-glucosidase, *EC* 3.2.1.20) which Dahlqvist (1962) called 'maltase Ib'. The hydrolytic activity of small intestine mucosa towards lactose is due to two types of enzyme (Asp, Dahlqvist & Koldovský, 1969). One of these, with β-galactosidase (*EC* 3.2.1.23) and β-glucosidase (*EC* 3.2.1.21) activity, is attached to the brush border and is a true digestive enzyme with a pH optimum of 5·5–6·0. Within the mucosal cell, and readily released into solution on disruption of the cell, there are one or more soluble or acid β-galactosidases with an optimum pH around 3·5. Most measurements of mucosal 'β-galactosidase' or 'lactase' are the sum of the activities of these two enzymes.

For some years it has been known that, during the early postnatal development of the pig, there are drastic and complementary changes in the levels of lactase and sucrase activity in the mucosa of the small intestine. In the newborn pig, lactase activity is higher than in the adult, whereas the α-glucosidases are absent, or present at low levels (Dahlqvist, 1961*b*). Lactase activity falls during the first 2 months of life, but the activity of other disaccharidases rises (Bailey, Kitts & Wood, 1956; Walker, 1959*b*; Hartman, Hays, Baker, Neagle & Catron, 1961). At birth, sucrase activity has generally been found to be absent from the mucosa of the small intestine or present at very

* Present address: The Meat Research Institute, Langford, Bristol BS18 7DY.

low levels, but activity rises rapidly with age (Bailey *et al.* 1956; Walker, 1959*b*; Hartman *et al.* 1961).

Before this study, little detail was known of the patterns of distribution of mucosal lactase and sucrase activity along the length of the small intestine in young pigs, although Bailey *et al.* (1956) and Hartman *et al.* (1961) had presented results for proximal, medial and distal thirds of the small intestine in their studies. A few detailed studies had been made by earlier authors of the distribution of disaccharidases along the mucosa of the small intestine of older pigs but the results were from either one pig in each study (Dahlqvist, 1961*a*; Walker, 1959*b*) or two pigs (Kojecký & Matlocha, 1964). Thus, there was little opportunity to assess variability between pigs in mucosal enzyme distribution. Indeed, one of the reasons for the present study was the discrepancy between the findings of Dahlqvist (1961*b*) and those of Kojecký & Matlocha (1964) with regard to the site of maximum sucrase activity in the small intestine of the adult pig. The former author found maximum activity in the middle third of the small intestine and the amounts in the terminal ileum were also high. Kojecký & Matlocha, on the other hand, found sucrase activity to be confined to the proximal two-thirds of the small intestine. In an 8-week-old pig, Walker (1959*b*) found a distribution of sucrase activity which agreed more with that found by Dahlqvist (1961*a*) than with that found by Kojecký & Matlocha. The values reported by Walker (1959*b*), Dahlqvist (1961*a*) and Kojecký & Matlocha (1964) were in general agreement that maximum lactase activity was to be found in the proximal part of the small intestine, with negligible amounts in the distal part.

In the present study, the distribution of lactase and sucrase activity along the mucosa of the small intestine was studied at six evenly spaced sites in each of sixty-one pigs. Young pigs of known breeding and age were studied over the period from birth to 4 weeks of age. Values for older pigs were obtained from animals of various, mainly commercial, origins.

EXPERIMENTAL

Animals

Sixty-one pigs were used. Three litters of Large White ♂ × Wessex (British Saddleback) ♀ pigs from the University herd, all sired by the same boar, provided thirty pigs. From each litter, pairs of pigs were killed weekly from birth to 4 weeks of age for mucosal enzyme assay. The six newborn pigs were taken from their dams and killed for sampling before they had suckled. In litter 1, all pigs were reared on the sow. Half of each of litters 2 and 3 were weaned from the sow at 2 d of age and reared artificially, the remainder of each litter being reared by their dams. Thus, at 1, 2, 3 and 4 weeks of age the pigs from litters 2 and 3 were litter-mate pairs, one suckled by its dam and the other reared artificially. The artificially reared pigs were fed twice daily on the diet shown in Table 1, and kept in individual cages in a controlled environment. At each feed the amount of food offered (g) was $0{\cdot}24W^{0{\cdot}75}$ (where W = weight of pig in g); pigs were weighed every 2 or 3 d and feed intakes were adjusted according to this. On successive days between weighings, the amount of feed was increased by 5%/d. The diet was mixed into a gruel with an equal weight of warm water. Drinking-water was

Table 1. *Composition (g/100 g) of the diet given to the artificially reared pigs*

Low-temperature spray-dried skim milk	15·0
Casein	30·8
Glucose	40·9
Sucrose	5·0
Maize oil (mixed into the dry diet)	5·0
Mineral supplement*	3·2
Vitamin supplement†	0·2

* Supplied (per 100 g diet): 1·823 g $CaHPO_4$, 907 mg $Ca_3(PO_4)_2$, 210 mg magnesium lactate, 57·2 mg KCl, 38·1 mg NaCl, 110·2 mg $FeSO_4.7H_2O$, 11·2 mg ZnO, 2·06 mg $CuSO_4.5H_2O$, 1·83 mg $MnSO_4.4H_2O$, 437 μg KI.

† Supplied (per 100 g diet): 108·3 mg choline chloride, 2·04 mg nicotinic acid, 897 μg calcium pantothenate, 203 μg α-tocopheryl acetate, 190 μg pyridoxine hydrochloride, 128 μg thiamin hydrochloride, 84 μg riboflavin, 9·3 μg menaphthone, 509 μg biotin, 1·7 μg cyanocobalamin, 265 i.u. vitamin A, 66 i.u. cholecalciferol.

supplied, in addition, in a separate compartment of the feeding trough. Sow-reared pigs were killed approximately 1 h after being taken from the sow. Sow-reared pigs were housed indoors in concrete-floored pens with infrared-heated creep areas. Intramuscular injections of iron-dextran (Imposil 200, Fisons Pharmaceuticals Ltd, Loughborough; 200 mg Fe/dose) were given at 2 d of age. No creep feed was given. Bedding was limited to wood shavings. On the day of slaughter, artificially reared pigs were fed 2·5 h before being killed.

The remaining thirty-one pigs were of varying origins; details are given in Table 2. For the purpose of presentation of results, the animals were divided into five age groups, as follows: four 8-week-old pigs, four 17- to 19-week-old pigs, seven 22- to 27-week-old pigs, twelve 27- to 31-week-old young boars and four adult pigs (1 year 7 months to 6 years 3 months).

Sampling

Pigs less than 8 weeks old were killed by intracardiac injection of a solution of sodium pentabarbitone (194 mg/ml), followed by immediate bleeding out, and the small intestine was dissected from the carcass with minimal delay. All larger pigs were killed by electrical stunning followed by bleeding and removal of the gastro-intestinal tract, from which the small intestine was dissected. When possible, the gastro-intestinal tract was removed immediately after death and the small intestine was dissected from the rest of the gut and sampled in a cold room at 4°. Many of the larger pigs were killed at commercial abattoirs and delays of up to 1 h occurred between death and the removal of samples. Tests comparing the enzyme activities of mucosa from freshly killed pigs (within 5–10 min of slaughter) with those of mucosa from adjacent sites in the intestine of the same pigs after the intestine had been left for a further 50 min at room temperature showed close agreement between the two sets of values.

Samples for enzyme assay were taken from six intestinal sites at 5, 20, 40, 60, 80 and 95% of the length of the small intestine, measured from the pylorus. Assay samples were 10^{-2} m lengths of intestine, opened, gently rinsed twice in chilled (4°) 0·9% (w/v) saline, and then stored separately in chilled saline. Mucosal samples were taken by

blotting a piece of intestine to remove surface moisture and debris and gently scraping off some mucosa with a small spatula. A sample (100 mg) was weighed quickly and rinsed into a Griffiths' tube homogenizer for disintegration. In the latter part of the experiment the sample was rinsed into a wide test-tube and homogenized with an ultrasonic probe (Soniprobe 1130A; Dawe Instruments, London). Homogenates were normally in the ratio of 1:100 tissue:water concentration and, after preparation, were stored in tubes packed around with ice.

Analysis of samples

Lactase and sucrase were assayed by a technique based on the method of Dahlqvist (1964). Portions of 0·2 ml mucosal homogenate were incubated with 0·1 ml pH 6·0 phosphate buffer and 0·2 ml 0·1 M-disaccharide solution at 37° for 20 min. Hydrolysis was terminated by immersing the tubes in boiling water for 2 min. Glucose produced during incubation was then determined by adding 10 ml tris-glucose oxidase reagent (Dahlqvist, 1964), incubating the tubes for 1·25 h at 37°, and measuring the extinction of the coloured complex formed in a spectrophotometer at 436 nm. Two tests and a blank were run for each sample and the results were compared with standard measurements on 0–2·0 mmol-glucose solutions. Results were expressed as μmol disaccharide hydrolysed per g wet mucosa per min. The use of lactose as substrate and the relatively high pH will have minimized the contribution of the 'soluble' β-galactosidases in the lactase assay. The mucosal enzyme assay was found to give closely repeatable results in tests done by two different persons, each scraping mucosa and homogenizing samples from adjacent areas along the intestine.

RESULTS

The results for the Large White × Wessex piglets studied between birth and 4 weeks of age are presented individually in Figs 1 and 2 to allow an assessment to be made of the variability between pigs in the levels of the enzymes studied. Figs 3 and 4 show mean levels of lactase and sucrase activity found in the mucosa of the small intestine of the older pigs, the variability at a given site being shown as a vertical line indicating the standard error above and below the mean. Table 2 shows, for each pig studied, mean levels for the two enzymes averaged over the whole intestine, together with peak levels recorded and the site of occurrence of the latter.

Lactase activity

From Fig. 1 it will be seen that there was great variation from one pig to another. In the newborn pigs, lactase activity was high, with a peak at the 20% site in five of the six pigs. In the remaining animal, peak activity was found at the 5% site. From the peak, activity fell in a proximal to distal direction to its lowest level at the 95% site. Between birth and 1 week of age there was a considerable fall in lactase activity in the proximal half of the small intestine, particularly at the 5 and 20% sites. From 1–4 weeks of age some pigs showed a peak of activity for lactase at the 20, 40 or 60% site, but in others two peaks of activity were shown (at the 20 and the 60 or 80% sites).

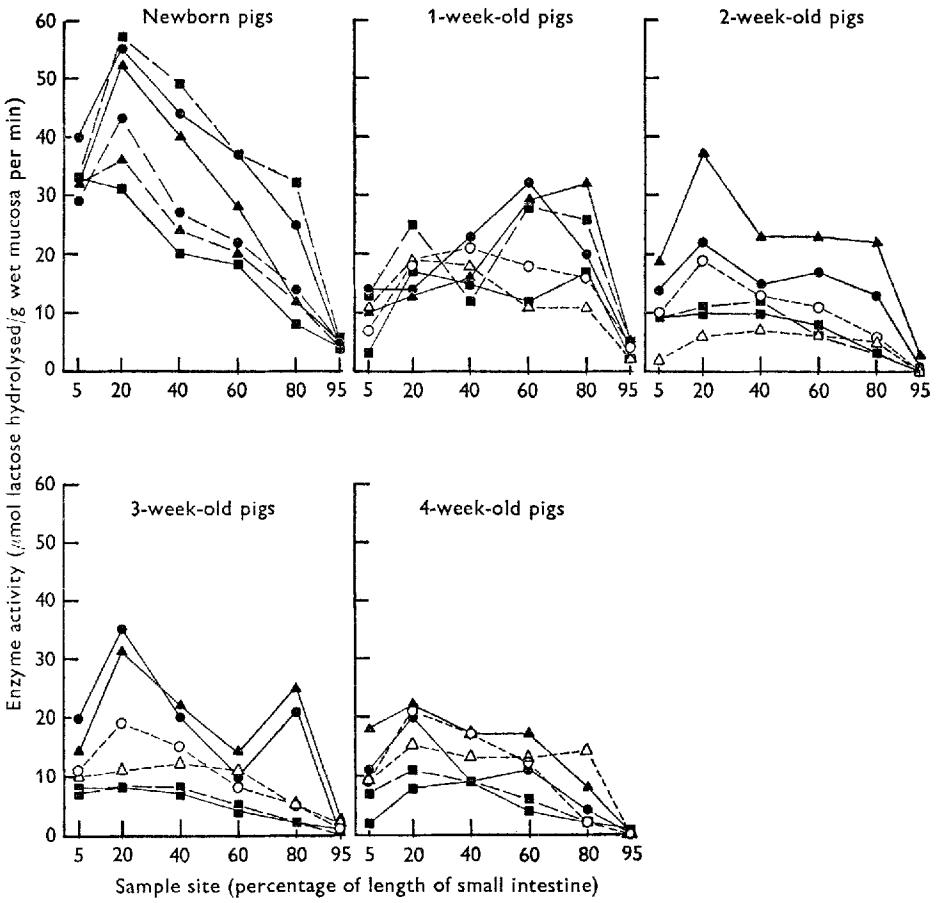

Fig. 1. Lactase activity in the mucosa at six standardized sites along the small intestine of individual members of pairs of pigs from three litters of Large White × Wessex pigs killed at weekly intervals from birth to 4 weeks of age. Litter 1, sow-reared, ■——■, ■— —■. Litter 2, sow-reared, ▲——▲, ▲— —▲; artificially reared, △ – – – △. Litter 3, sow-reared, ●——●, ●— —●; artificially-reared, ○ – – – ○.

Because of the variation from one animal to another it was difficult to discern any definite trend in the levels found over this period.

It appeared that by 4 weeks of age a more regular pattern of activity tended to be established. There was no indication of any difference in lactase levels between artificially reared and sow-reared pigs in the small number of animals studied.

In the older pigs (8 weeks of age to adult) the area of the small intestine showing lactase activity contracted with advancing age (Fig. 3), although mean levels of lactase activity averaged over all six sites in the small intestine fell only marginally after 8 weeks of age. The peak of activity was generally at the 20% site (Table 2), but activity in the distal part of the small intestine was much reduced in the older pigs and was negligible at the 80 and 95% sites from 8 weeks of age onwards. After about 20 weeks of age activity at the 60% site dwindled.

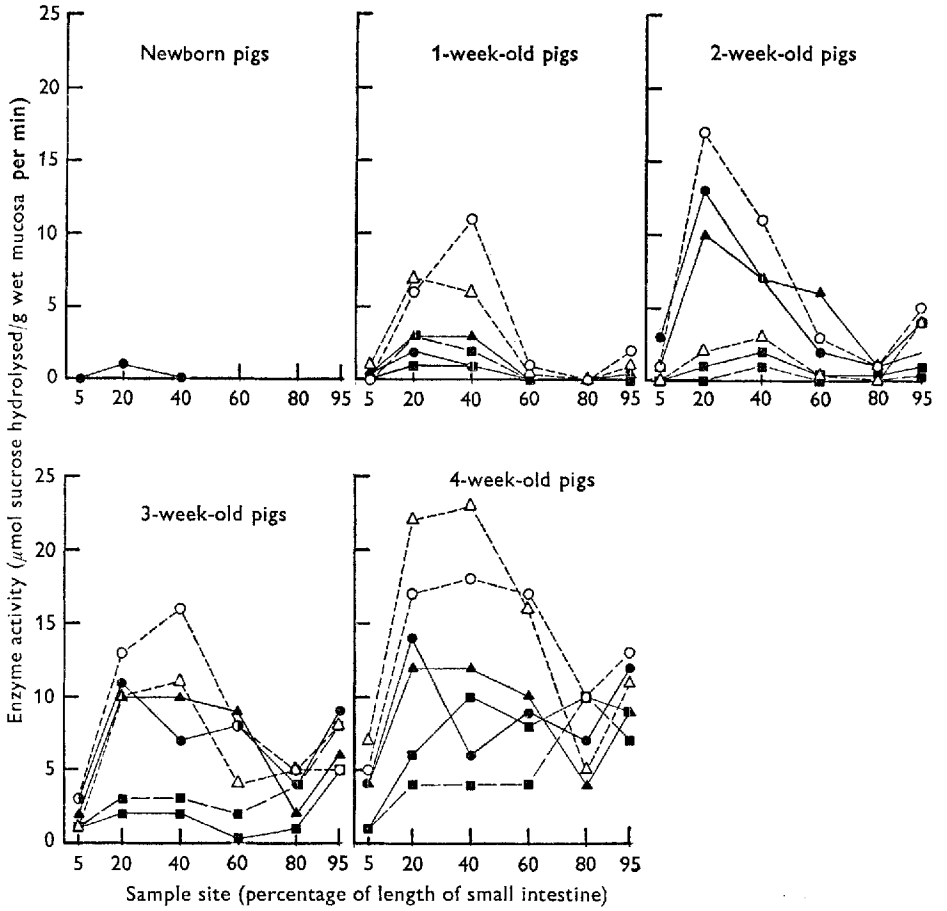

Fig. 2. Sucrase activity in the mucosa at six standardized sites along the small intestine of individual members of pairs of pigs from three litters of Large White × Wessex pigs killed at weekly intervals from birth to 4 weeks of age. Litter 1, sow-reared, ■——■, ■— —■. Litter 2, sow-reared, ▲——▲, ▲— —▲; artificially-reared, △ – – – △. Litter 3, sow-reared, ●——●, ●— —●; artificially-reared, ○ – – – ○.

Sucrase activity

Sucrase levels in the young pigs (Fig. 2) were very variable from pig to pig, apart from the virtual lack of activity shown by the newborn pigs. The production of this enzyme developed more rapidly in some pigs than in others (note the lower levels found in litter 1 throughout the period studied). In seven out of the eight comparisons between litter-mate pairs, peak sucrase levels in pigs being reared artificially on diets containing sucrose were higher than those of their sow-reared controls. However, in the remaining comparison, sucrase levels were very much higher in the sow-reared control pig (a 2-week-old pig in litter 2) than in its litter-mate being fed on a diet containing sucrose. In a high proportion of the animals studied between 1 and 4 weeks of age and the level of sucrase activity was higher at the 95% site than at the 80% site.

Despite the variability shown, there was a trend towards extension of sucrase

Table 2. *Mean levels and peak levels of lactase and sucrase activity found in individual pigs killed to provide the results summarized in Figs 3 and 4. Details of sex, age and breed or cross-breed are also given*

					Enzyme activity (μmol disaccharide hydrolysed/g wet mucosa per min)			
		Animals			Lactase		Sucrase	
Age-group	Sex	Age (weeks)	Hot carcass weight (kg)	Breed or cross-breed*	Mean activity at the six sites	Peak activity and site†	Mean activity at the six sites	Peak activity and site†
8 weeks	♀	8	—	LW × W	3	7(b)	5	9(c)
	♀	8	—	LW × W	5	13(b)	4	8(c)
	♀	8	—	LW × W	2	5(b)	8	16(c)
	♂	8	—	LW × W	1	3(b)	4	7(d)
17–19 weeks	♂	17	—	LW	1	3(b)	8	17(e)
	♀	17+	—	Piétrain	4	8(b)	10	18(c)
	♂	18	—	LW × W	2	7(b)	10	16(d)
	♂	18+	—	Piétrain	2	4(c)	11	17(d)
22–27 weeks	♂	22	49	LW	2	5(b)	8	15(d)
	♀	24	47	LW	2	6(b)	17	27(d)
	♀	—	48	Landrace	3	7(b)	13	20(e)
	♂	24	49	LW	1	4(b)	14	21(c)
	♂	25	39	LW	1	3(b)	11	23(d)
	♀	26	51	LW	2	4(b)	8	11(d)
	♂	—	52	Piétrain	3	8(b)	10	18(e)
27–31 weeks (young boars)	♂	27	—	LW	3	10(a)	14	22(c)
	♂	27	—	LW	2	6(a)	22	31(c)
	♂	28	—	Landrace	4	13(b)	23	30(c)
	♂	28	—	Landrace	2	6(b)	15	25(c)
	♂	28	—	Landrace	1	3(c)	18	32(d)
	♂	28	—	Landrace	2	6(a)	17	26(c)
	♂	28	—	LW	4	11(b)	17	29(d)
	♂	28	—	LW	2	7(b)	17	30(d)
	♂	30	—	LW	2	8(b)	18	23(c)
	♂	30	—	LW	2	5(a)	17	27(c)
	♂	31	—	LW	2	6(b)	18	25(c)
	♂	31	—	LW	2	5(b)	17	26(c)
Adult sows	♀	1 year 7 months		Wessex	2	5(b)	18	25(d)
	♀	2 years 5 months		Wessex	2	6(a)	18	31(b)
	♀	4 years 8 months		Wessex	1	2(b)	9	13(b)
	♀	6 years 3 months		Wessex	3	9(a)	42	57(d)

* LW = Large White; W = Wessex (now British Saddleback).

† % of length of small intestine, measured from the pylorus: a = 5%; b = 20%; c = 40%; d = 60% and e = 80%.

activity in a proximal to distal direction along the small intestine with advancing age from an initial locus at the 20 and 40% sites in the week-old pigs to a more general presence of this enzyme at 4 weeks of age. In the older pigs studied, this extension continued (Fig. 4, Table 2), so that by 17–19 weeks of age an adult pattern appeared to have been established with a broad peak of activity at the 40, 60 and 80% sites, i.e. further along the gut than the peak in 1–4-week old pigs. The extension of the locus of sucrase activity with advancing age was a notable contrast to the contraction of the area of lactase activity which was observed as the pigs grew older. In the older pigs

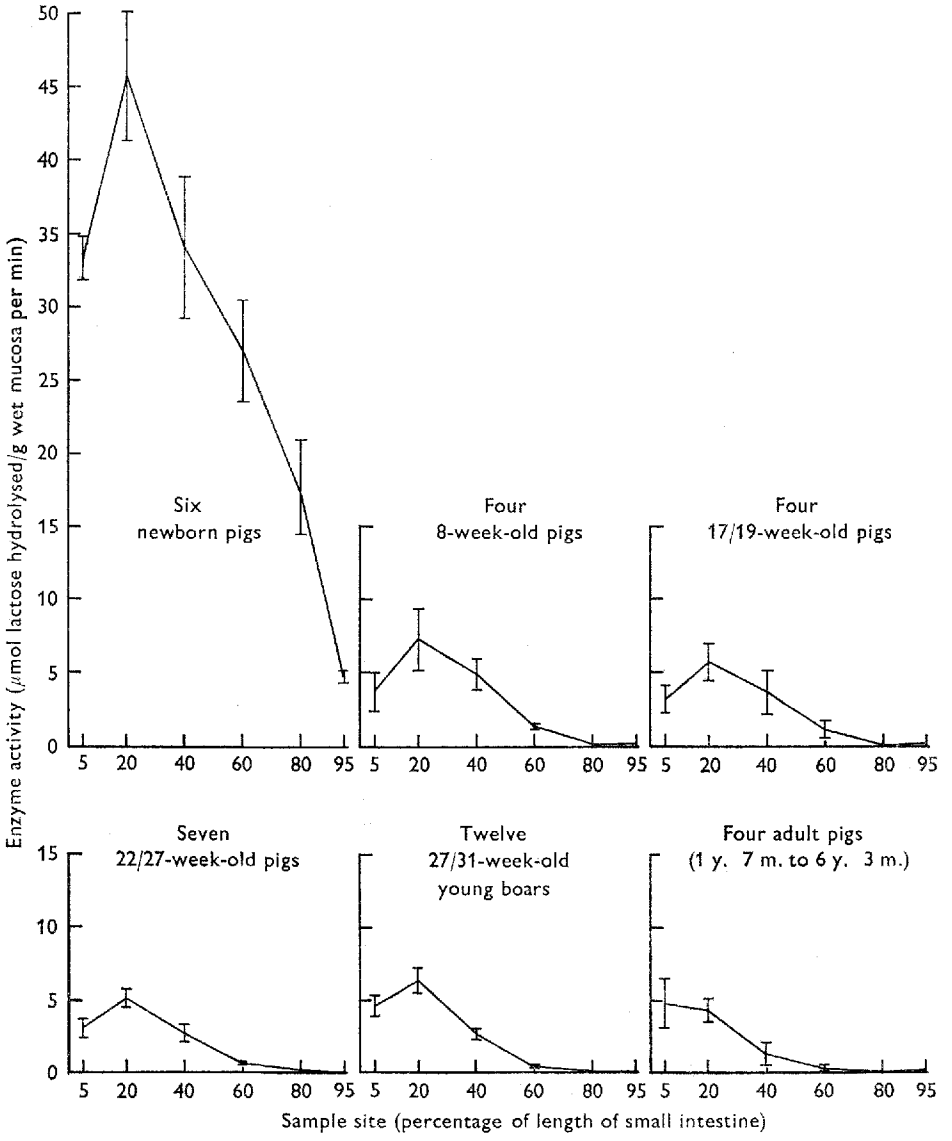

Fig. 3. Lactase activity at six standardized sites along the small intestine of pigs killed between birth and maturity. The vertical bars represent the standard errors of the mean.

studied, in any given age group, variability in the levels of sucrase found at a given site along the intestine was not excessive except that very great differences were found between one animal and another in the sucrase activity in the mucosa of the four adult animals. The site of peak activity in these animals also varied considerably.

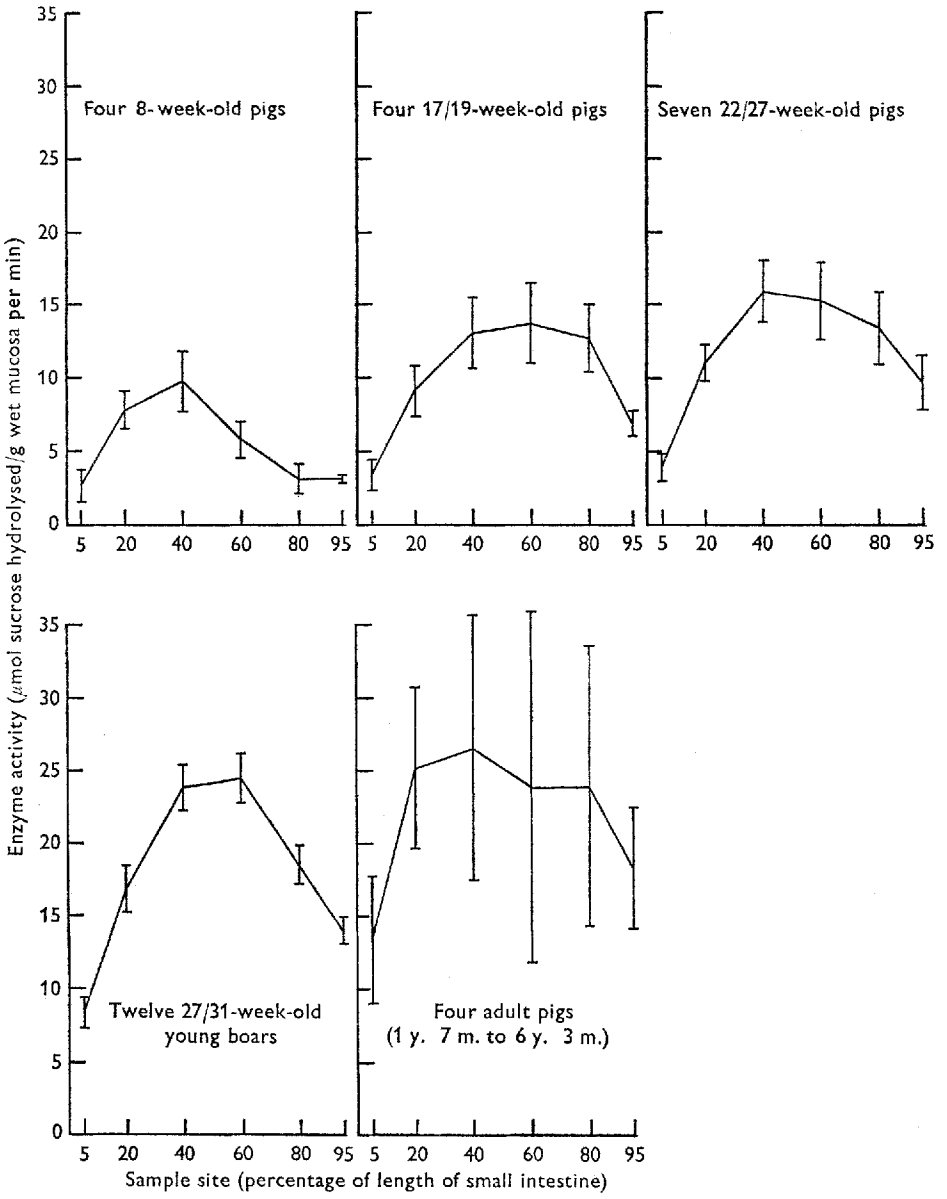

Fig. 4. Sucrase activity at six standardized sites along the small intestine of pigs killed between 8 weeks of age and maturity. The vertical bars represent the standard errors of the mean.

DISCUSSION

This study differs from those of earlier workers in various respects. Firstly, with young pigs, enzyme activity was measured at a larger number of sites in the small intestine, and the activity of the mucosa, rather than that of the intestinal tissue, was studied. Since the former is the active tissue, the present results are, perhaps, more precise. Secondly, with older pigs a fairly large sample of animals was used and, again,

Table 3. *Number and type of pigs used in the experiments of earlier workers and in the present experiment, together with details of subdivision of the intestine, preparation of homogenates and pH at which enzyme activity was measured*

No. and type of animals studied and age or weight when killed	Subdivision of the small intestine for study	Details of preparation where homogenates were made from whole intestinal tissue	pH at which the enzyme activity was measured: Lactase	pH at which the enzyme activity was measured: Sucrase
	Bailey *et al.* (1956)			
Sow-reared pigs (not creep-fed, but with access to dams' feed); 4 newborn, 4 at 7 d, 4 at 14 d, 4 at 21 d, 3 at 35–36 d and 2 at 49–51 d of age.	Wet intestinal tissue (mucosa plus intestinal wall) Samples taken from 3 sections of equal length—proximal, medial and distal thirds	Intestines washed out with cold water, at the time of slaughter, frozen, subsequently thawed and divided into three sections; each section was comminuted and then ground up with quartz sand, after which the material was diluted with water and allowed to autolyse for 24 h	5·5	4·5
	De Groot & Hoogendoorn (1957)			
28 pigs killed at intervals from birth to 33 months of age; pigs < 8 weeks old were artificially reared on diets based on skim milk and lard: older pigs were from abattoirs (~ their ages were estimated)	Results given as 'per g of intestinal wall', '...only that part adjacent to the stomach was used for assay purposes.' From the larger animals a part of the duodenum was used	Contents of the intestine were brushed away with a piece of cotton wool; the tissue was then homogenized with water	5·0	Not measured
	Walker (1959*b*)			
Sow-reared pigs (not creep-fed) (*a*) 40 pigs killed at regular intervals between 1 and 37 d of age (*b*) One 8-week-old pig killed for study of distribution of enzyme activity along the small intestine	Wet intestinal tissue (mucosa plus intestinal wall) (*a*) from a sample of the whole small intestine (*b*) from duodenum and proximal, medial and distal thirds of the rest of the small intestine	After squeezing out contents (Walker, 1959*a*), the samples of intestine were chopped up and then ground with sand and phosphate buffer (pH 8·5); the intestinal enzymes were extracted for 20 h at room temperature before testing the extract for enzyme activity	6·0	6·5
	Dahlqvist (1961*a*)			
One adult pig	Mucosa from duodenum and at 1, 6, 9·5 and < 16 m from pylorus. (Small intestine length = 16 m)	—	6·0	6·5

Table 3 (*cont.*)

No. and type of animals studied and age or weight when killed	Subdivision of the small intestine for study	Details of preparation where homogenates were made from whole intestinal tissue	pH at which the enzyme activity was measured	
			Lactase	Sucrase
	Hartman *et al.* (1961)			
16 litters of pigs used, each randomly allocated to one of two treatments, either suckled for the 8-week period, or weaned at 1 week and self-fed on dry rations which contained sucrose up to the end of the 5th week of life 16 newborn and 16/week thereafter (144 pigs in all). From the 1st week of life two randomly selected pigs were killed from each litter every other week	As for Bailey *et al.* (1956) (see above)	Intestinal contents were expressed and collected for separate assay of enzyme activity. Authors did not state whether or not the intestine was washed to remove residues of contents before freezing. The frozen tissue was chopped into small pieces and samples were homogenized with water; subsequently, the homogenate was held at room temperature for 3–6 h with agitation before enzyme assay	No details given	
	Kojecký & Matlocha (1964)			
Two pigs (80–100 kg)	Mucosa, every 0·75 m along the small intestine	—	Not buffered	
	The present experiment			
30 pigs from 3 litters from which pairs were killed weekly from birth to 4 weeks of age. In one litter all pigs were sow-reared. In the other two litters, half of the pigs were weaned at 2 d of age and in these litters litter-mate pairs, one suckled by its dam and the other reared artificially, were killed at 1, 2, 3 and 4 weeks of age. 31 pigs of varying ages from 8 weeks of age to maturity (see Table 2)	Samples of mucosa were taken from 6 intestinal sites at 5, 20, 40, 60, 80 and 95 % of the length of the small intestine, measured from the pylorus. The intestine was opened, rinsed twice in chilled 0·9 % saline, and stored separately in chilled saline	—	6·0	6·0

a sufficiently large number of sites within the small intestine were studied to get a picture of the distribution of the two enzymes. In comparing results obtained by earlier workers with those of the present experiment, it is desirable to have a clear understanding of the procedures followed in the different studies; these are summarized in Table 3.

Of the earlier workers, De Groot & Hoogendoorn (1957) used sufficient pigs to demonstrate the fall in lactase activity with age from birth to maturity, but they only made limited studies of the distribution of lactase along the small intestine. Earlier reports of the precise distribution of lactase and sucrase along the small intestine in older pigs were confined to studies of single animals (Dahlqvist, 1961*a*; Walker, 1959*b*) or a pair of animals (Kojecký & Matlocha, 1964). From the present results it would seem that mucosal sucrase activity is distributed throughout the length of the small intestine in older pigs, in contrast to the findings of Kojecký & Matlocha (1964) that this enzyme was confined to the proximal two-thirds of the small intestine mucosa. Breed differences may be responsible for the discrepancies between our findings and those of Kojecký & Matlocha. However, several breeds were used in the present experiments, and in all pigs of 3 weeks of age and over, sucrase activity was found to be distributed throughout the length of the small intestine.

Comparison of our results with those of the earlier workers who studied age-changes and differences between sites in both lactase and sucrase activities in the small intestine of the pig shows that there is a much greater similarity between the trends that we observed and those found by Walker (1959*b*) than between our results and those of either Bailey *et al.* (1956) or Hartman *et al.* (1961). In assessing variations in enzyme activity related to intestinal site the latter two groups of workers both divided the small intestine into three equal sections and estimated enzyme activities of these sections separately. Using homogenates consisting of such a large length of intestine, rather than our procedure of using a sample of mucosa from a standardized site, is likely to have tended to obscure any differences in enzyme activity related to mucosal site.

The procedure used by Bailey *et al.* (1956) could be criticized because of the likely effect of the initial washing with water in causing rupture of the delicate mucosal cells and possible loss (or transfer along the gut) of enzyme activity. De Groot & Hoogendoorn (1957) found that, when pig intestine was washed with water, part of the lactase was taken up by the rinsing water. A similar effect might be expected with sucrase and other mucosal enzymes. Bailey *et al.* recognized that the pH used for sucrase assay had been inappropriate and likely to have given results which were about one-third of the levels of activity at the optimum pH (6·5; Dahlqvist, 1960) for this enzyme.

In contrast with our findings, Hartman *et al.* (1961) reported appreciable sucrase activity in intestinal homogenates from newborn pigs. They found little evidence of adaptation to a dry diet containing sucrose. As in the present experiment, Walker (1959*b*) found no sucrase activity in the intestine of very young pigs, but found an almost linear rise to 3 weeks of age followed by fairly constant activity up to 5 weeks of age when the experiment ended. In the present experiment sucrase activity was found

to rise steadily from birth to about 30 weeks of age; the mean levels of sucrase in four adult pigs were similar to those in the 30-week-old pigs but, as mentioned earlier, the values for the adult pigs were very variable.

In the present experiment, lactase levels fell rapidly from birth to 2 weeks of age and then continued to fall at a slower rate until 8 weeks of age; beyond 8 weeks of age there was little change in the mean level of this enzyme. With regard to the distribution of lactase activity in the mucosa of the small intestine of pigs, the results of the present experiment show a rise from the 5% point to a point 20% of the way along the small intestine, and a fall from the 20% point, in a distal direction (if one ignores the complex situation between 1 and 4 weeks of age). It would seem likely that insufficient samples were taken by most earlier workers to distinguish the true state of affairs. A serious criticism of the present experiment is that no sample of duodenal mucosa was taken and therefore the level of either lactase or sucrase activity in the duodenum of the pigs is not known.

Because of the lack of sucrase in the intestinal mucosa of newborn pigs and the slow rate of development of production of this enzyme, there is a great danger of death among pigs fed from a very early age on diets rich in sucrose. This situation was originally reported by Johnson (1949) and was confirmed by Becker, Ullrey & Terrill (1954). Recent work by Aherne, Hays, Ewan & Speer (1969) showed that deaths did not occur among pigs weaned at 6–7 d of age on to diets containing 56·6% sucrose, whereas deaths were frequent if pigs were weaned on to such diets of 2–4 d of age. Studies at Bristol (Kidder, Manners, McCrea & Osborne, 1968) have shown that sucrose, when present at as little as 15% of the diet, is not always well hydrolysed, even at 3 weeks of age, although when present at a lower level (5%) it was hydrolysed fairly efficiently by 2 weeks of age. Thus, though it may be possible to rear piglets on diets with a very high content of sucrose, such diets are likely to be inefficiently used in the 1st fortnight of life owing to insufficiency of sucrase. A further point of interest in comparing the results of the present study with those of Kidder *et al.* (1968) is that, in the latter experiments, it was found that sucrose which escaped hydrolysis in the first half of the small intestine tended to remain unhydrolysed as it passed through the remainder of this organ, especially in the younger pigs studied. Our present finding that, in 1- and 2-week-old pigs, sucrase activity is largely confined to the mucosa of the proximal half of the small intestine explains the earlier results.

The limited findings from the present study suggest that between 3 and 4 weeks of age there may be a rapid development in sucrase production which might make a 4-week-old pig much less susceptible than a 3-week-old pig to any detrimental effects of a high-sucrose diet. Kidder *et al.* (1968) found variability in the disappearance of sucrose from the lumen of the small intestine of pigs in different experiments. In one experiment, using a diet containing 19% sucrose, this sugar was completely hydrolysed by 3 weeks of age, in contrast to only partial hydrolysis at earlier ages. In another experiment by the same authors, using a lower proportion of sucrose in the diet (15%), although there was steady improvement in the efficiency of hydrolysis between 1 and 3 weeks of age, there was still a substantial quantity of unhydrolysed sucrose in the distal half of the small intestine at the 3rd week of life. Such anomalous results

appear to be explained by the great differences between individual pigs and between litters in mucosal sucrase activities revealed by the present study.

Intolerance to dietary lactose might well have been shown by certain of the older pigs studied in the present experiment. Though the mean levels of lactase activity in groups of pigs of similar ages fell only marginally with advancing age after the 8th week of life, in certain isolated individuals in each age-group the mucosal lactase levels throughout the small intestine were so low as to indicate likely intolerance to diets containing large amounts of whey. It seems reasonable to suggest that, in selection programmes for pigs, the level of intestinal lactase might well be taken into account in circumstances where whey products are widely used in the feeding of fattening pigs.

Feeding trials have shown that lactose is a very suitable carbohydrate for inclusion in diets for very young pigs being reared artificially (Becker *et al.* 1954). In diets for 9- and for 16-week old pigs, however, Becker & Terrill (1954) showed that 50% lactose in the diet suppressed growth and caused diarrhoea, whereas a diet containing 25% lactose was satisfactory for the 16-week-old pigs. A suppression of growth by lower levels of dietary lactose was shown by Shearer & Dunkin (1968*a*), who replaced wheat starch by lactose at increasing levels (15, 30 and 45%) in diets for pigs of 23 kg (50 lb) live weight and found a trend towards slower growth and poorer economy of food conversion as the lactose level of the diet rose. Animals showed unwillingness to eat the diet containing 45% lactose. The incidence of diarrhoea rose progressively with increasing levels of lactose over the first 4 weeks of the experiment but subsequently there was a marked reduction in the incidence of diarrhoea. At slaughter, the pigs that had received lactose in the diet showed caecal enlargement and concomitant development of the colon and rectum (Shearer & Dunkin, 1968*b*). This finding was taken to indicate that enlargement of the caecum had been stimulated by the presence of unhydrolysed lactose in the intestinal contents passing into the organ and it was postulated that the reduction in diarrhoea which was observed as the experiment progressed was likely to have been due to an increase in the production of lactase by organisms in the caecum. In further studies of identical diets by Shearer & Dunkin (1969), no lactose was detected in faeces of pigs under any circumstances. This confirmed the suggestion that lactose escaping digestion in the small intestine was hydrolysed in the lower regions of the gut.

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