Morphology and enzymatic activity of the small intestinal mucosa of Iberian pigs as compared with a lean pig strain

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Morphology and enzymatic activity of the small intestinal mucosa of Iberian pigs as compared with a lean pig strain[1]

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ABSTRACT: Castrated male Iberian (n = 12) and Landrace × Large White (n = 12) pigs were used to study histological structure and enzymatic activity in the small intestine at 3 points of the productive cycle (BW = 15, 50, and 115 kg). Both strains were fed the same cereal-based diets (DE = 2,799 kcal·kg^{-1}, and CP = 15%) throughout the entire experimental period. Differences ($P < 0.05$) in histometrical variables (villus height, width and surface, crypt depth, villus height/crypt depth relationship, mucosal thickness, muscular layer thickness, and number of goblet cells) were found among samples of small intestinal sections (duodenum, jejunum, and ileum) at the 3 productive stages studied. Also, differences ($P < 0.05$) in histometrical variables of small intestinal samples were found between Iberian and lean pigs at all productive stages, although these differences tended to disappear with age. Differences ($P < 0.05$) in enzymatic activities (lactase, sucrase, maltase, isomaltase, aminopeptidase, and alkaline phosphatase) of small intestinal samples were found between the different intestinal sections at all productive stages studied. Although differences ($P < 0.05$) in enzymatic activities of small intestinal samples were found between Iberian and lean pigs at all productive stages, values tended to equalize with pig age. We concluded that differences previously found in dietary nutritional utilization between Iberian and lean strains are likely not due to differences in intestinal absorption or hydrolytic capacity.

Key words: enzymatic activity, histological structure, Iberian pig, lean pig strain, small intestine

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INTRODUCTION

Extensive pig production systems in Europe are at present tending to increase at the expense of those based on intensive procedures (Nieto et al., 2002b). The reasons for this trend are mainly related to the surplus pig meat production and growing public concern about animal welfare and soil pollution problems. This has resulted in encouragement of the production of native pig breeds, such as the Iberian pig, which are well adapted to local feed resources and provide high quality products (Aparicio Macarro, 1992; Rey and López-Bote, 2001). As a consequence, increased interest is being devoted to this breed in Spain at present, and several reports on its nutritional requirements and feed utilization recently have been published (Lachica and Aguilera, 2000; Morales et al., 2002a,b; Nieto et al., 2002a; Rubio, 2005; Rubio et al., 2005).

Both N retention and fecal N digestibility have been reported to be less in Iberian than in modern pig breeds (Morales et al., 2002a,b; Rivera-Ferre et al., 2005, 2006). On the other hand, intestinal digestive efficiency is determined by its capacity to hydrolyze feed or feed components and absorb nutrients, which ultimately depends on histological structure and activity of digestive enzymes. Therefore, the starting hypothesis of the present work was that the observed differences in digestive utilization of nutrients between Iberian and lean pigs are due to differences in intestinal structure or function between the 2 breeds. No previous work has been reported, to our knowledge, comparing intestinal morphology and enzymatic activity of Iberian with modern pig strains. Accordingly, the present work was designed to compare intestinal histological and enzymatic activity variables of the Iberian with a lean (Landrace × Large White) pig breed at 3 different productive stages (BW = 15, 50, and 115 kg).

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MATERIALS AND METHODS

The experimental protocol was reviewed and approved by the Institutional Animal Care and Use Committee of the Spanish Council for Scientific Research (Madrid, Spain), and the animals were cared for in accordance with the Spanish Ministry of Agriculture guidelines.

Animals, Diets, and Feeding Regimen

Male castrated piglets (BW 10 ± 0.5 kg) from the Iberian (n = 12) or lean (Landrace × Large White, n = 12) breeds were purchased from Sanchez Romero Carvajal S.A. (Huelva, Spain) or Granja El Arenal (Córdoba, Spain), respectively. They were housed individually in 4-m^2 pens in a temperature-controlled (20 ± 1°C) room. Feed was the same for pigs of both strains; it was given at approximately twice their calculated energy maintenance needs (ME_m = 458 kJ per kg of $BW^{0.75}$; NRC, 1998) and offered in 2 meals (at 0900 and 1800 h, respectively) of equal quantities. Animals were fed a cereal-based diet [composition (%) as-fed basis: barley meal, 84.9, defatted soy, 11.1, vitamins plus minerals mix, 3.3, supplemented AA, 0.7], which contained DE = 2,799 kcal·kg^{-1}, and CP = 15%. Water was always freely available from low-pressure drinking nipples.

Euthanization and Sampling

The time required to grow between BW of 15 and 50 kg was 52 ± 7 and 71 ± 3 d for lean and Iberian pigs, respectively; between BW of 15 and 115 kg the time was 120 ± 9 and 161 ± 13 d for lean and Iberian pigs, respectively. Four animals from each group (Iberian or Landrace × Large White) were euthanized by electric stunning as they reached 15, 50, or 115 kg of BW, immediately exsanguinated, and the abdomen opened from sternum to pubis. The entire small intestine was quickly removed and freed from the mesentery. The segment from the pyloric anthrum to 100 cm caudal to the pyloric anthrum was considered the duodenal region; the segment extending from the cecum to 100 cm cranial to the cecum was considered the ileum; and the segment between duodenum and ileum was considered the jejunal region. At the same locations, a sample of 2 cm from the middle section was removed for histological analysis. Samples for enzyme analysis (5 to 6 cm in length) were taken in duplicate caudally at the same places. Mucosa was scrapped off the underlying muscular layers, put into Eppendorf tubes (Labortecnic S.A.L., Granada, Spain), and kept at −80°C until analysis.

Histological Analysis

After 24 h in 10% neutral buffered formaldehyde (Sigma, Alcobendas, Spain), the tissue samples were carefully cleaned of remaining digesta with deionized water and then transferred to a fresh solution of 10% neutral buffered formaldehyde. Subsequently, the samples were dehydrated and embedded in paraffin wax. Three slides were prepared from each sample, and each slide contained a minimum of 2 sections cut at 4 μm, at least 50 μm apart. The slides were stained with hematoxylin and eosin. All measures were made with a light microscope at 4 and 40× magnification. Measurements were made by using the image analysis system (Cell[A] Imagen Software, Olympus, Hamburg, Germany) with a monitor. Fifteen well-oriented villi and crypts were selected on each slide to determine villus height and width as well as crypt depth. The villus height was determined as the distance from the tip to the bottom of the villi, and the crypt depth as the distance between the mouth of the crypt and its base. Villus surface area was calculated as 3.1416 × villus width × villus height. Mucosal thickness was determined as the distance between mucosal epithelium and the muscular layer and the muscularis as the inner circular and outer longitudinal layers of smooth-muscle cells. The crypt density was determined by counting the number of crypts included in a defined area of the same size for each sample calculated with a marked zone. The number of goblet cells was calculated as percentage of these cells in 2 representative fields at 40× counting goblet and epithelial cells.

Enzyme Activity Analysis

Mucosal samples were homogenized in EDTA-saline phosphate buffer (pH 7.4) by means of a Wiggen Hauser D-500 homogenizer and analyzed in triplicate. Protein was determined by a BCA (bicinchoninic acid) Protein Assay kit (Thermo, Rockford, IL). The activities of lactase (E.C. 3.2.1.23), sucrase (E.C. 3.2.1.48), maltase (E.C. 3.2.1.20), and isomaltase (E.C. 3.2.1.10) were assayed as in Dahlqvist (1968) using a glucose kit (Megazyme, Wicklow, Ireland) to determine the amount of liberated glucose. Intestinal alkaline phosphatase (E.C. 3.1.3.1) activity was determined according to Goldstein et al. (1971), and aminopeptidase (E.C. 3.4.11.2) activity according to Maroux et al. (1973), using L-alanine-4-nitroanilide (Sigma, Steinheim, Germany) as substrate. Enzyme activities were expressed as units per milligram of protein. One unit was defined as the amount of enzyme that hydrolyzed 1 μmol of substrate per minute.

Statistical Analyses

Individual pigs were considered the experimental unit. The morphological measures and the enzyme activities of the small intestine were analyzed by 2-way repeated measures ANOVA using the GLM procedure (SAS Inst. Inc., Cary, NC), according to the following model:

$$Y_{ijk} = \mu + \alpha_i + \beta_{ij} + \omega_k + (\alpha\omega)_{ik} + \varepsilon_{ijk},$$

where μ is the mean, α_i is the effect of genotype (Iberian, Landrace × Large White), β_{ij} is the subject effect, ω_k is the segment effect (duodenum, jejunum, or ileum), $(\alpha\omega)_{ik}$ is the interaction effect between genotype and segment, and ε_{ijk} represents the error term. Means were compared using the LSD test at $P < 0.05$ level of significance.

RESULTS

Histological Structure

Differences ($P < 0.05$) in histometrical variables of small intestinal samples were found between Iberian and lean pigs at the 3 productive stages studied (BW 15, 50, and 115 kg). In 15-kg pigs (Table 1), villus height, villus surface, mucosal thickness, and muscular layer thickness were greater ($P < 0.05$) for Iberian pigs. There was no difference ($P > 0.10$) in crypt depth, villus height/crypt depth relationship, villus width, or number of goblet cells. In 50-kg pigs (Table 2), villus height, together with villus height/crypt depth relationship, crypt depth, and muscular layer thickness, were greater ($P < 0.05$) for lean pigs. There was no difference in villus surface, mucosal thickness, or number of goblet cells ($P > 0.10$), although there was a tendency ($P = 0.082$) for greater values in villus width for Iberian pigs. No difference ($P > 0.10$) was found in small intestinal morphology between lean and Iberian pigs at 115 kg, except for muscular layer thickness and number of goblet cells, which were greater ($P < 0.05$) for lean pigs (Table 3). Mucosal thickness tended to be greater ($P = 0.076$) in lean than in Iberian pigs.

When intestinal sections were compared, differences ($P < 0.05$) in histometrical variables were found between duodenal, jejunal, and ileal samples at the 3 productive stages studied (Tables 1, 2, and 3). In 15-kg pigs (Table 1), duodenal and jejunal villus height and crypt depth and mucosal thickness were greater ($P < 0.01$) than ileal values. Mucosal thickness was not different between jejunum and ileum values, but duodenal values were greater ($P < 0.01$) than ileal values. Conversely, ileal villus width and muscular layer thickness were greater ($P < 0.05$) than duodenal values. Jejunal villus width was not different from duodenal or ileal values. There was no difference ($P > 0.10$) in villus surface and number of goblet cells. Villus height/crypt depth relationship tended ($P = 0.097$) to be greater in duodenal samples. In 50-kg pigs (Table 2), duodenal and jejunal crypt depth and mucosal thickness were greater ($P < 0.05$) than ileal, whereas ileal villus height/crypt depth relationship and muscular layer thickness were greater ($P < 0.001$) than duodenal or jejunal values. There was no difference ($P > 0.10$) in villus height, width or surface, or in the number of goblet cells. In 115-kg pigs (Table 3), duodenal crypt depth was greater ($P < 0.05$) than jejunal and ileal values, whereas jejunal and ileal villus height/crypt depth relationship was greater ($P < 0.05$) than duodenal values. Duodenal and jejunal

Table 1. Small intestinal morphology of Iberian and lean (Landrace × Large White) pigs at 15 kg of BW[1]

	Genotype[2]		Intestinal section					*P*-value[3]		
Item	Lean[4]	Iberian	Duodenum	Jejunum	Ileum	SEM	Genotype	Intestinal section	G × IS
Villus height, μm	323[A]	365[B]	381[a]	353[a]	297[b]	7	0.015	<0.001	<0.001
Crypt depth, μm	292	309	312[a]	324[a]	266[b]	9	0.356	0.005	0.012
Villus height/crypt depth	1.11	1.20	1.24	1.10	1.14	0.04	0.316	0.097	0.250
Villus width, μm	124	133	114[a]	127[ab]	142[b]	5	0.389	0.004	0.269
Villus surface area, μm^2	125,111[A]	152,107[B]	138,162	143,202	134,462	5,368	0.027	0.597	0.001
Mucosal thickness, μm	596[A]	671[B]	682[a]	631[ab]	588[b]	14	0.021	0.003	0.002
Muscular layer thickness, μm	262[A]	317[B]	223[a]	180[b]	466[c]	6	<0.001	<0.001	0.199
No. of goblet cells/100 cells	15.0	16.7	20.3	15.5	11.8	2.0	0.686	0.209	0.465

[A,B, a–c]Means with different superscripts in each row within genotype (uppercase) or within intestinal section (lowercase) were different ($P < 0.05$).
[1]Four pigs of each genotype were used. Values are the means of 15 observations per intestinal section and per pig.
[2]The average BW of the pigs were 16.5 ± 1.3 kg and 15.5 ± 0.7 kg for lean and Iberian strains, respectively.
[3]Effects of genotype (G; Landrace × Large White, Iberian), intestinal section (IS; duodenum, jejunum, ileum), or genotype × intestinal section (G × IS).
[4]Landrace × Large White.

Table 2. Small intestinal morphology of Iberian and lean (Landrace × Large White) pigs at 50 kg of BW[1]

Item	Genotype[2]		Intestinal section			SEM	*P*-value[3]		
	Lean[4]	Iberian	Duodenum	Jejunum	Ileum		G	IS	G × IS
Villus height, μm	355[A]	299[B]	341	314	327	5	<0.001	0.352	0.554
Crypt depth, μm	345[A]	320[B]	374[a]	352[a]	270[a]	6	0.046	<0.001	<0.001
Villus height/crypt depth	1.07[A]	0.97[B]	0.92[a]	0.92[a]	1.22[b]	0.02	0.033	<0.001	0.003
Villus width, μm	125	137	135	128	131	3	0.082	0.662	0.011
Villus surface area, μm^2	139,461	130,230	145,381	126,203	132,953	4,430	0.263	0.159	0.124
Mucosal thickness, μm	697	657	707[a]	687[a]	636[b]	13	0.157	0.026	<0.001
Muscular layer thickness, μm	509[A]	451[B]	420[a]	383[a]	652[b]	7	0.004	0.001	0.451
No. of goblet cells/100 cells	22.0	22.0	19.5	27.0	19.5	2.2	0.900	0.415	0.982

[A,B, a,b]Means with different superscripts in each row within genotype (uppercase) or within intestinal section (lowercase) were different ($P < 0.05$).
[1]Four pigs of each genotype were used. Values are the means of 15 observations per intestinal section and per pig.
[2]The average BW of the pigs were 47.8 ± 1.8 kg and 48.8 ± 2.0 kg for lean and Iberian strains, respectively.
[3]Effects of genotype (G; Landrace × Large White, Iberian), intestinal section (IS; duodenum, jejunum, ileum), or genotype × intestinal section (G × IS).
[4]Landrace × Large White.

muscular layer thickness were greater ($P < 0.05$) than ileal values. Ileal number of goblet cells was greater ($P < 0.05$) than jejunal, whereas duodenal values were not different from jejunal or ileal. There was no difference ($P > 0.10$) in villus height, width or surface, or in mucosal thickness.

Enzymatic Activity

Differences ($P < 0.05$) in the enzymatic activities of small intestinal samples were found between Iberian and lean pigs at 15 and 50 kg (Tables 4 and 5), but much less at 115 kg (Table 6). In 15-kg piglets (Table 4), activities of lactase, sucrase, and alkaline phosphatase were greater ($P < 0.05$) for lean than for Iberian piglets. There was no difference ($P > 0.10$) in mucosal protein content or in maltase and aminopeptidase activities; isomaltase activity tended ($P = 0.064$) to be greater in lean pigs. In 50-kg pigs (Table 5), mucosal protein was less ($P < 0.05$) for Iberian pigs, whereas activities of sucrase, maltase, and isomaltase were less ($P < 0.05$) for lean than for Iberian pigs. Lactase activity tended to be greater for Iberian pigs ($P = 0.055$). There was no difference in aminopeptidase and alkaline phosphatase activities ($P > 0.10$). There was no difference ($P > 0.10$) in the activity of any of the enzymes tested at 115 kg (Table 6) between animals of the Iberian and lean pig strains except for isomaltase activity, which was greater ($P < 0.05$) for lean pigs. Also, maltase activity tended ($P = 0.074$) to be greater in lean than in Iberian pigs.

Differences ($P < 0.05$) in enzymatic activities of small intestinal samples were found between the different sections at the 3 productive stages studied (Tables 4, 5, and 6). In 15-kg pigs (Table 4), duodenal or jejunal mucosal protein were greater ($P < 0.05$) than ileal, and jejunal lactase, sucrase, maltase, and isomaltase activities were greater ($P < 0.01$) than duodenal or ileal activities. Jejunal and ileal aminopeptidase and alkaline phosphatase activities were greater ($P < 0.05$) than duodenal. In 50-kg pigs (Table 5), jejunal protein content of mucosa was greater ($P < 0.05$) than duodenal or ileal content. Ileal lactase activity was less ($P < 0.001$) than duodenal or jejunal activities. Sucrase activity was greater ($P < 0.001$) for jejunal and ileal than duodenal samples. Ileal maltase, isomaltase, and aminopeptidase were greater ($P < 0.001$) than duodenal. Jejunal alkaline phosphatase activity was greater ($P < 0.001$) than duodenal and ileal activities. In 115-kg pigs (Table 6), duodenal protein content was greater ($P < 0.001$) than jejunal or ileal. Duodenal and jejunal lactase activities were greater ($P < 0.001$) than ileal, whereas ileal aminopeptidase activity was greater ($P < 0.001$) than duodenal or jejunal activity. Jejunal alkaline phosphatase activity was greater ($P < 0.001$) than duodenal or ileal activity. Jejunal and ileal sucrase activities were greater ($P < 0.001$) than duodenal activity, and ileal isomaltase was greater ($P < 0.05$) than duodenal. There was no difference ($P > 0.10$) in maltase activity among intestinal segments.

Table 3. Small intestinal morphology of Iberian and lean (Landrace × Large White) pigs at 115 kg of BW[1]

Item	Genotype[2]		Intestinal section			SEM	*P*-value[3]		
	Lean[4]	Iberian	Duodenum	Jejunum	Ileum		G	IS	G × IS
Villus height, μm	297	288	294	289	296	4	0.226	0.695	<0.001
Crypt depth, μm	253	234	263[a]	227[b]	240[a]	6	0.151	0.034	<0.001
Villus height/crypt depth	1.21	1.27	1.13[a]	1.32[b]	1.27	0.04	0.481	0.030	0.014
Villus width, μm	135	140	137	141	135	3	0.420	0.569	0.031
Villus surface area, μm^2	126,737	127,479	126,468	128,081	126,775	3,390	0.962	0.969	0.001
Mucosal thickness, μm	561	535	561	544	539	6	0.076	0.457	<0.001
Muscular layer thickness, μm	567[A]	488[B]	503[a]	501[a]	577[b]	5	<0.001	0.003	<0.001
No. of goblet cells/100 cells	20.2[A]	11.8[B]	15.7[ab]	11.5[a]	20.8[b]	1.2	0.015	0.048	0.212

[A,B, a,b]Means with different superscripts in each row within genotype (uppercase) or within intestinal section (lowercase) were different ($P < 0.05$).
[1]Four pigs of each genotype were used. Values are the means of 15 observations per intestinal section and per pig.
[2]The average BW of the pigs were 114.7 ± 2.0 kg and 113.7 ± 2.0 kg for lean and Iberian strains, respectively.
[3]Effects of genotype (G; Landrace × Large White, Iberian), intestinal section (IS; duodenum, jejunum, ileum), or genotype × intestinal section (G × IS).
[4]Landrace × Large White.

DISCUSSION

The values here obtained for histometrical and enzymatic activity variables were in the same range as those previously reported for pigs (Hedemann et al., 2006a,b). Differences in structure and enzymatic activity of the small intestine were determined among intestinal sections (duodenum, jejunum, ileum) and between Iberian and lean (Landrace × Large White) pig strains at the 3 different productive stages studied (BW = 15, 50, and 115 kg). Concerning gut morphology, differences in histometrical variables (villus height, width and surface, crypt depth, villus height/crypt depth relationship, mucosal thickness, muscular layer thickness, and number of goblet cells) of small intestinal samples were found among samples of small intestinal sections (duodenum, jejunum, ileum). Except for muscular layer thickness, values in duodenum and jejunum were greater than in ileum. This is in agreement with data previously reported in pigs from the Danish Landrace × Yorkshire strain (Hedemann et al., 2006b) and occurred in both Iberian and lean pigs in the present investigation. Therefore, these mucosal morphological characteristics of the small intestine seem to be rather constant for pigs. However, as described above, we used the same diet for the whole growth period to avoid including more factors of variation. It has been reported that variations in the amounts of dietary protein may affect mucosal structure and composition (Guay et al., 2006). Therefore, an interesting point to address in the future would be to compare variations in intestinal structure, enzymatic activity, and composition in pigs of both breeds fed diets of different composition.

No previous work has, to our knowledge, been reported comparing intestinal morphology of Iberian with a lean pig strain. Histometrical values were greater for 15-kg Iberian pigs, whereas the opposite occurred at 50 kg of BW. These differences tended to disappear with age and at 115 kg of BW, the only differences between Iberian and lean pigs were in muscular layer thickness and number of goblet cells. The villus height/crypt depth ratio has been reported as a useful criterion to estimate nutrient digestion and absorption capacity of the small intestine (Montagne et al., 2003), and maximal digestion and absorption occurred when this ratio increased (Pluske et al., 1996). This ratio was not different between Iberian and lean pigs at any stage tested. Also, villus surface was greater for Iberian pigs only at 15 kg of BW.

Concerning enzymatic activity, jejunal values were usually greater than duodenal or ileal values, which is in agreement with previous work (Hedemann et al., 2006a,b). As in the case of histometrical variables, no previous work has been reported comparing intestinal enzymatic activity of Iberian with a lean pig strain. Values were smaller for Iberian pigs at 15 kg of BW, but the situation reversed in animals of 50 kg, and there was no difference at 115 kg. Therefore, the hydrolytic capacity of the small intestinal mucosa of Iberian pigs

Table 4. Enzymatic activity in the small intestinal mucosa of Iberian and lean (Landrace × Large White) pigs at 15 kg of BW[1]

	Genotype		Intestinal section				*P*-value[2]		
Item	Lean[3]	Iberian	Duodenum	Jejunum	Ileum	SEM	G	IS	G × IS
Mucosal protein, mg/g of mucosa	80.2	78.8	83.7[a]	80.8[a]	74.0[b]	1.4	0.611	0.003	0.077
Lactase, U/mg of protein	28.5[A]	20.7[B]	32.1[a]	39.1[b]	2.7[c]	1.6	0.034	<0.001	0.033
Sucrase, U/mg of protein	45.0[A]	30.8[B]	26.6[a]	55.9[b]	31.1[a]	2.8	0.031	<0.001	0.008
Maltase, U/mg of protein	248	244	260[a]	303[b]	174[c]	15	0.900	0.001	0.136
Isomaltase, U/mg of protein	40.0	31.7	31.3[a]	45.0[b]	31.3[a]	2.0	0.064	<0.001	0.501
Aminopeptidase, U/mg of protein	129.0	123.3	87.6[a]	142.6[b]	148.3[b]	3.2	0.393	<0.001	0.001
Alkaline phosphatase, U/mg of protein	6.6[A]	4.3[B]	4.3[a]	6.2[b]	5.9[b]	0.3	<0.001	<0.001	0.079

[A,B, a–c]Means with different superscripts in each row within genotype (uppercase) or within intestinal section (lowercase) were different ($P < 0.05$).

[1]Four pigs of each genotype were used. Values are the means of 2 samples per intestinal section per pig analyzed in triplicate.

[2]Effects of genotype (G; Landrace × Large White, Iberian), intestinal section (IS; duodenum, jejunum, ileum), or genotype × intestinal section (G × IS).

[3]Landrace × Large White.

is comparable with that of lean strains when the whole life span of these animals is considered. However, due to their potential practical implications, it is probably important to take into account the differences in enzymatic activity found at 15 kg of BW, particularly those concerning lactase activity. It is generally known that problems associated with intestinal disorders at different production stages are among those of greatest economic impact for the current pig production industry, and this holds true not only for lean but also for Iberian pig production systems, where costs derived from gastrointestinal disorders sometimes exceed market prices (Sánchez Romero Carvajal Jabugo S.A., Huelva, Spain, personal communication). On the other hand, it is common practice in nutrition of piglets up to 20 to 25 kg of BW to include whey as a source of highly available protein and energy (NRC, 1998). Sugar content of dried milk whey in Spain is typically about 60 to 70% (high lactose) or 39 to 45% (low lactose), most of it lactose (FEDNA, 1994). Much research exists regarding the benefits of lactose on growth performance of weanling pigs (O'Doherty et al., 2004; Pierce et al., 2006; Cromwell et al., 2008). Greater lactose inclusion rates in piglet diets have been related with improved feed intakes and growth rates, but also with improved health status and intestinal environment due to a prebiotic effect on the microbiota composition because lactose has been shown to act as a specific substrate for *Lactobacillus* spp. (Wells et al., 2005; Pierce et al., 2006). Therefore, a decreased lactase activity in young Iberian piglets might not represent a disadvantage but a somewhat beneficial situation due to greater amounts of lactose available for lactic acid bacteria fermentation. More research would be needed to establish the potential beneficial effects of greater lactose in Iberian piglet nutrition.

Previous studies with growing Iberian pigs (Nieto et al., 2002a,b) demonstrated their small genetic potential for lean tissue deposition when compared with conventional breeds such as Landrace. Surprisingly, muscle fractional protein synthesis was greater in Iberian than in Landrace growing gilts (Rivera-Ferre et al., 2005), although muscles were between 20 to 32% smaller in the former. The reasons that limit protein deposition

Table 5. Enzymatic activity in the small intestinal mucosa of Iberian and lean (Landrace × Large White) pigs at 50 kg of BW[1]

	Genotype		Intestinal section				*P*-value[2]		
Item	Lean[3]	Iberian	Duodenum	Jejunum	Ileum	SEM	G	IS	G × IS
Mucosal protein, mg/g of mucosa	62.8[A]	49.7[B]	51.6[a]	67.6[b]	49.5[a]	2.0	0.006	0.001	0.134
Lactase, U/mg of protein	16.6	23.6	29.2[a]	26.6[a]	4.4[b]	1.6	0.055	0.001	0.140
Sucrase, U/mg of protein	35.6[A]	68.8[B]	23.6[a]	60.9[b]	72.0[b]	3.6	0.001	<0.001	0.175
Maltase, U/mg of protein	159[A]	264[B]	146[a]	162[a]	323[b]	23	0.037	<0.001	0.024
Isomaltase, U/mg of protein	50.0[A]	70.7[B]	48[a]	61[ab]	86[b]	4	0.023	<0.001	0.611
Aminopeptidase, U/mg of protein	59.8	65.3	42.1[a]	59.6[ab]	85.8[b]	3.5	0.442	<0.001	0.227
Alkaline phosphatase, U/mg of protein	145	175	141[a]	235[b]	104[a]	16	0.358	<0.001	0.095

[A,B, a,b]Means with different superscripts in each row within genotype (uppercase) or within intestinal section (lowercase) were different ($P < 0.05$).

[1]Four pigs of each genotype were used. Values are the means of 2 samples per intestinal section per pig analyzed in triplicate.

[2]Effects of genotype (G; Landrace × Large White, Iberian), intestinal section (IS; duodenum, jejunum, ileum), or genotype × intestinal section (G × IS).

[3]Landrace × Large White.

Table 6. Enzymatic activity in the small intestinal mucosa of Iberian and lean (Landrace × Large White) pigs at 115 kg of BW[1]

	Genotype		Intestinal section				*P*-value[2]		
Item	Lean[3]	Iberian	Duodenum	Jejunum	Ileum	SEM	G	IS	G × IS
Mucosal protein, mg/g of mucosa	64.4	66.5	84.7[a]	58.3[b]	52.5[b]	2.8	0.267	<0.001	0.008
Lactase, U/mg of protein	7.2	6.5	8.3[a]	10.5[a]	2.6[b]	0.9	0.126	<0.001	0.005
Sucrase, U/mg of protein	37.2	31.5	22.0[a]	43.4[b]	39.2	2.6	0.398	<0.001	<0.001
Maltase, U/mg of protein	208.1	165.2	210.8	186.7	166.1	12.4	0.074	0.268	<0.001
Isomaltase, U/mg of protein	47.2[A]	24.2[B]	27.3[a]	30.3[ab]	48.7[b]	4.4	0.030	0.014	0.021
Aminopeptidase, U/mg of protein	69.1	72.4	45.1[a]	60.9[a]	106.1	3.2	0.612	<0.001	0.043
Alkaline phosphatase, U/mg of protein	100.0	132.4	73.4[a]	172.3[b]	93.2[a]	10.1	0.159	<0.001	0.003

[A,B, a,b]Means with different superscripts in each row within genotype (uppercase) or within intestinal section (lowercase) were different ($P < 0.05$).

[1]Four pigs of each genotype were used. Values are the means of 2 samples per intestinal section per pig analyzed in triplicate.

[2]Effects of genotype (G; Landrace × Large White, Iberian), intestinal section (IS; duodenum, jejunum, ileum), or genotype × intestinal section (G × IS).

[3]Landrace × Large White.

in Iberian pigs remain unknown, but differences in hormonal status are likely to contribute to the unequal protein accretion capacities and growth rates observed between Iberian and modern porcine breeds (Fernández-Fígares et al., 2007). Both N retention and fecal N digestibility have been reported to be less in Iberian than in Landrace pigs (Morales et al., 2002a,b; Rivera-Ferre et al., 2005, 2006). However, recent work by our group [R. Barea, R. Nieto, and J. F. Aguilera, Dpto. de Fisiología y Bioquímica de la Nutrición Animal (IFNA, Estación Experimental del Zaidín, CSIC), Granada, Spain, unpublished data] has shown that although N digestibility was greater for lean pigs at 30 kg of BW, the same was not true for N, DM, and energy digestibilities at 80 kg of BW, which were greater for Iberian than for lean pigs. This is probably because, although histological structure (absorptive capacity) and enzymatic activity (hydrolytic activity) are similar for both pig strains between 50 and 115 kg of BW, intestinal relative size is greater for Iberian pigs (R. Barea, Estación Experimental del Zaidín, Granada, Spain, personal communication), which would result in a greater final digestive capacity. Nevertheless, as already mentioned, N retention and balance were greater for lean pigs at all productive stages studied (Nieto et al., 2002a; Rivera-Ferre et al., 2005, 2006). Because histological structure and enzymatic activity of the mucosa were found to be different between Iberian and lean pigs, particularly at 15 kg of BW, but tended to decrease or disappear between 50 and 115 kg of BW; differences found in N and energy utilization between Iberian and lean strains are likely to be related to other factors such as metabolic differences including hormonal status (Fernández-Fígares et al., 2007) and not to decreased absorptive or hydrolytic capacity.

In summary, differences in small intestinal morphology and in enzymatic activity of the mucosa were found between Iberian and Landrace pigs at all productive stages, although values tended to equalize as pigs aged. The decreased lactase activity in intestinal mucosa of Iberian piglets here determined up to 50 kg of BW might not represent a disadvantage but a somewhat beneficial situation due to greater amounts of lactose available for lactic acid bacteria fermentation. Differences in histometrical variables and in enzymatic activity were also found among samples of small intestinal sections (duodenum, jejunum, and ileum) of both strains at the 3 productive stages studied. We conclude that differences found in nutritional utilization between Iberian and lean strains are likely not due to less absorptive or hydrolytic capacity.

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