

Flavor Improvement in Pork from Barrows and Gilts via Inhibition of Intestinal Skatole Formation with Resistant Potato Starch

DOROTHEA LÖSEL,[†] MARKUS LACORN,[†] DIRK BÜTTNER,[‡] AND ROLF CLAUS^{*,†}

Institut für Tierhaltung und Tierzucht, Universität Hohenheim, 70599 Stuttgart, Germany, and Landesanstalt für Schweinezucht Forchheim, 76287 Rheinstetten, Germany

Skatole originates from microbial processing of tryptophan in the large intestine of pigs and accumulates in adipose tissue. Formation may be inhibited by the anti-apoptotic function of butyrate formed out of raw potato starch. Two groups of pigs (each consisting of gilts and barrows) were fed from 30 to 110 kg live weight either a conventional diet (controls; $n = 35$) or an isocaloric diet containing 300 g of raw potato starch/kg of body weight (RS; $n = 34$). Skatole concentrations were measured in colon content, blood, and adipose tissue. Odor of cooked meat samples was evaluated by a test panel. RS reduced concentrations in colon content and blood plasma ($P < 0.001$). Back fat concentrations were decreased significantly from 25 to 1.40 ng/g (barrows; $P < 0.001$) and from 40 to 9 ng/g (gilts; $P < 0.001$). Odor rating (scale of 1–5 from very unpleasant to very pleasant) was 3.07 for low skatole concentrations and 2.66 for both medium and high skatole concentrations ($P < 0.05$).

KEYWORDS: Skatole; barrows; gilts; potato starch; odor improvement

INTRODUCTION

Traditionally, meat consumption is not primarily influenced by nutritional considerations. Rather, the organoleptic quality and thus the enjoyment of eating is the main determinant. Organoleptic quality in large part depends on the flavor. Meaty flavor which is present in raw meat is essentially the same for all species (1), so flavor volatiles which are formed by heat-induced reactions between free amino acids and monosaccharides during cooking are relevant for the eating quality (2). In addition, fat soluble substances may modify the overall flavor in a positive direction, but they may also be responsible for less pleasant odors such as species-specific compounds, e.g., branched-chain fatty acids in goat and sheep (3). Additionally, sex-specific compounds such as androstenone in the pig and feed-derived substances can be stored in adipose tissue and interfere with sensorial quality (4).

One such substance is 3-methylindole (skatole). It plays a specific role because it is formed in the gastrointestinal tract of both ruminants and monogastric species. Skatole is a fecal-like smelling substance and has an extremely low odor threshold value so that it is perceived at a level of 0.5 ng/L of air by the human nose (5). This substance is formed by microorganisms

and is measurable in various matrices. Trace amounts formed by yeast were assumed to contribute to the complex aroma of wine (6).

In the pig, skatole is formed in the colon out of tryptophan. This amino acid is first converted to indoleacetic acid by many microbes. The further metabolization to skatole is performed by only a few specialized bacteria. The most important one is *Lactobacillus* sp. strain 11201, but *Clostridium scatologenes* probably contributes to skatole formation (7). This substance is absorbed in the colon. Its storage in adipose tissue is explained by its lipophilic properties but may be modified by hepatic enzymes which metabolize skatole to varying degrees (8). Inhibition of its intestinal formation is a promising approach to reducing off odor from pigs. Supplementation of rations with free L-tryptophan did not influence skatole formation (e.g., ref 9). Therefore, tryptophan out of shedded mucosa cells from the distal small intestine and the colon is the substrate (10, 11). As a consequence, high-energy rations which increase the rate of mucosa cell proliferation and counteract apoptosis led to higher levels of skatole formation in the colon and thus also to higher concentrations in feces, peripheral blood plasma, and adipose tissue (12). Feeding of resistant potato starch leads to butyrate formation in the colon which is a potent inhibitor of apoptosis in the colon in vivo (13) and leads to a dramatic drop in skatole concentrations in barrows (10). Such an effect was later confirmed for boars (14). In addition, in a field trial with barrows and gilts, it was possible to inhibit skatole formation by feeding resistant potato starch and thus to reduce odor emission to the environment (15).

* To whom correspondence should be addressed: FG Tierhaltung und Leistungsphysiologie, Institut für Tierhaltung und Tierzucht, Universität Hohenheim, Garbenstr. 17, 70599 Stuttgart, Germany. Telephone: 0049/711/459-2455. Fax: 0049/711/459-2498. E-mail: thsekret@uni-hohenheim.de.

[†] Universität Hohenheim.

[‡] Landesanstalt für Schweinezucht Forchheim.

Table 1. Composition of the Experimental Diets and the Resulting Energy, Crude Protein, and Crude Fiber Contents on an As-Fed Basis^a

component	30–60 kg		60–85 kg		85 kg to slaughter	
	controls	RS	controls	RS	controls	RS
barley	391.7	57.5	409	74.6	500	128
maize	—	197.3	—	204	—	100
potato starch	—	300	—	300	—	300
wheat	385	—	405	39	377	129.8
wheat bran	—	120	—	110	—	100
soy bean	—	160	—	130	—	110
(extracted) ^b						
soy bean	160	—	123	—	80	—
(extracted) ^c						
rape seed oil	—	25	—	20	—	20
potato protein	—	17.5	—	10	—	—
wheat gluten	—	50	—	40	—	40
wheat flour	30	38	30	38	10	38
DL-methionine	3	1.7	—	1.4	—	1.2
L-lysine-HCl	3	3	3	3	3	3
minerals and vitamins	30	30	30	30	30	30
metabolizable energy (MJ/kg)	12.95	12.74	12.91	12.68	12.78	12.62
crude protein (g/kg)	172.2	176.8	158.1	158.2	139.7	146.5
crude fiber (g/kg)	34.0	33.6	34.1	32.3	35.7	32.2

^a The composition changed with an increase in live weight in three stages (RS, resistant starch group). ^b At 440 g/kg of crude protein. ^c At 490 g/kg of crude protein.

Skatole concentrations in fat of castrated male (barrows) and female pigs (gilts) were found to be in a similar range (70–160 and 60–160 ng/g, respectively) (16). Because concentrations as low as 26 ng/g of fat are easily detected by the human nose, it can be assumed that skatole content decreases the sensorial quality of pig meat in general (17).

Therefore, the aim of this field study was to inhibit skatole formation in gilts and barrows via diet and to validate its consequences for the sensorial quality of meat.

MATERIALS AND METHODS

Animals. The experiment was conducted at the experimental station for pig breeding of the state of Baden-Württemberg at Forchheim, Germany (Landesanstalt für Schweinezücht Forchheim).

A total of 80 crossbred pigs [Pietrain × (Large White × German Landrace)] with an average weight of 29.2 ± 0.13 kg (range of 26–31 kg) were included in the experiment. The pigs were allocated to two feeding groups. Each group was composed of 20 barrows and 20 gilts. The controls were fed with conventional diets, and the other group received isocaloric diets which had been supplemented with resistant potato starch to increase the rate of butyrate formation in the colon (RS group). Barrows and gilts were slaughtered at a weight of 105 and 115 kg, respectively. All pigs were housed in the same stable under equal conditions in groups of ten. The pens (2.90 m × 2.90 m) had semislatted floors.

Due to health problems which were not related to the diets, three individuals had to be removed from the controls until the end of the fattening period and five from the RS group.

Feeding. The composition of the diet for the RS group was based on an earlier pilot study which demonstrated that 300 g of raw potato starch/kg of feed led to a sufficient effect on skatole formation (18). The controls were fed a conventional diet based on grain and soy. The diets were formulated for three fattening stages. Stage 1 covered the weight between 30 and 60 kg, stage 2 from 60 to 85 kg, and stage 3 from 85 kg to slaughter. The detailed composition of the different diets is documented in **Table 1** as well as the calculated energy and protein

contents. Potato starch was obtained from Emsland-Stärke GmbH (Emlichheim, Germany).

Feed was supplied twice daily under a semi ad libitum regimen, so the mean uptake per pig increased from 1.6 kg in the beginning to 3.1 kg at the end of the fattening period. Water was available ad libitum. No antibiotics were applied during the fattening period.

Sample Collection. The animals were not fed for 19 h before slaughter. On the day of slaughter, the pigs were transported to the local slaughterhouse (500 m away). Blood samples were collected into heparinized vials at exsanguination, and the plasma was stored at –20 °C until it was assayed. An aliquot from gut content was obtained from the distal part of the colon because it is known that skatole production is maximal in this compartment (19, 20).

Cutlets including bones, fat, and skin were taken from the 13th to the 14th rib from each animal. They were removed immediately after slaughter, cooled overnight at 4 °C, and then vacuum-packed and frozen at –20 °C. The storage time did not exceed 3 months. Three different anatomical positions of fat were sampled (subcutaneous fat from the cutlet, flare fat, and ventral fat) and also stored at –20 °C.

Determination of Skatole Levels. Skatole levels in blood plasma were determined as described previously (19). In brief, a diethyl ether extract of plasma was evaporated after addition of the HPLC eluent and chromatographed by reversed-phase HPLC with fluorescence detection (excitation at 275 nm and emission at 352 nm). The chromatographic conditions were as follows: column, 125 mm × 4 mm Lichrospher (particle size of 5 µm; Bischoff, Leonberg, Germany); eluent, 0.02 M acetic acid, acetonitrile, and 2-propanol (50:30:15, v:v:v); flow rate, 1.2 mL/min. For quantification, multilevel calibration using the internal standard 2-methylindole was performed. The lower limit of detection was 0.06 ng/mL of plasma.

Skatole levels in adipose tissue were determined as described previously (21). Melted fat was dissolved in *n*-hexane and extracted with acetonitrile and water (3:1, v:v). The extract was chromatographed using the same conditions that were described for the determination of skatole levels in plasma. The lower limit of detection was 0.8 ng/g of fat (determined by spiking a blank with increasing amounts of skatole until the signal-to-noise ratio is above 3).

Skatole levels in gut content were also determined by reversed-phase HPLC (22). Samples were extracted with methanol and purified on adsorber resin Amberlite XAD-7 (Merck, Darmstadt, Germany). Skatole concentrations were referenced to the dry matter (DM) of the extracted matrix. The chromatographic conditions were the same as those described above. The wavelength for UV detection was 280 nm. The lower limit of detection was 0.4 µg/g of DM (for calculation, see determination of skatole levels in adipose tissue).

Sensory Evaluation. All potential panelists were tested at the same time. Sensory evaluations were performed in a room which contained six single booths and additional tables, so each person had his/her own table.

Selection of Panelists. First, we tested with an aptitude test whether the panelists had a sufficient olfactory sensitivity to distinguish skatole levels within a narrow range of concentrations. Test solutions were prepared from distilled water and sunflower oil (5:1, v:v; total volume of 25 mL) and mixed thoroughly on a Vortex mixer. Then skatole from a standard solution was added to produce concentrations of 0.1 (high) and 0.05 µg/mL (low). No skatole was added to the blank. These concentrations were chosen according to detection thresholds reported to vary between 0.026 and 0.1 µg/g in fat (17, 23). Sets of three encoded samples were presented in a triangular test. Two of the samples were identical, and one was different. Each set contained either the high or low concentration of the spiked samples. The two identical samples could be blanks or spiked samples.

Immediately before the test, the glass vials containing the test solutions were heated to 50 °C in a water bath and then mixed on a Vortex mixer. Each panelist had to evaluate one triangle with a high concentration of skatole and one with a low concentration. On their test record they had to mark the differing sample.

Persons who were not able to detect skatole within the range of detection thresholds as mentioned above (17, 23) were excluded from the subsequent evaluation of the meat samples. Ten of 12 possible panelists met the requirement to distinguish 0.1 µg/mL from a blank

Table 2. Fattening Performance in Barrows and Gilts (mean \pm standard error of the mean)^a Fed Isocalorically with either a Conventional Diet (controls) or a Diet with Resistant Starch (RS)

	barrows		gilts	
	controls	RS	controls	RS
daily weight gain (g/day)	832 \pm 80.4	813 \pm 71.7	743 \pm 65.7	776 \pm 63.9
slaughter weight (kg)	85.9 \pm 3.7	84.0 \pm 4.2	93.0 \pm 4.6a	90.3 \pm 4.9b
back fat thickness (cm)	1.5 \pm 0.3	1.5 \pm 0.3	1.3 \pm 0.3a	1.1 \pm 0.3c
lean meat percentage (%)	56.7 \pm 2.2	58.0 \pm 1.2	59.9 \pm 2.1	60.6 \pm 2.2
pH value (45 min post mortem)	5.9 \pm 0.2	6.0 \pm 0.3	6.1 \pm 0.2	6.2 \pm 0.2

^a Lowercase letters indicate differences within a row (a vs b, $P \leq 0.05$; a vs c, $P \leq 0.01$).

and participated in the meat evaluation. Eight persons even could differentiate the samples from the low-concentration triangle (0.05 $\mu\text{g}/\text{mL}$). Therefore, the results described below are not representative for the consumer reaction, because we excluded some possible consumers.

Preparation of Meat Samples. Cutlets from 24 animals (12 control and 12 RS) were chosen randomly for sensory evaluation without knowing their concentrations of skatole. In four sessions (two sessions per week), a balanced number of samples from both treatments were presented in a random arrangement. Frozen cutlets were thawed overnight at 4 °C; bones and fat were removed, and the remaining tissue was cut into 18 mm slices. The meat slices were then wrapped in two layers of aluminum foil and heated at 200 °C in an oven for 15 min so that the internal temperature of the meat was 70 °C. The juice from each meat slice was poured into a separate jar which was sealed. The meat slices were then cut into equal cuboids (2 cm \times 2 cm) and put into sealed plastic jars.

The kitchen and the sensory evaluation room were separated so that the evaluation was unaffected by the smell from the kitchen. Cooking was performed in 5 min intervals, and the samples were presented consecutively to the panelists. Under normal eating conditions, meat and juice odor contribute to the overall impression. Because the volume of the meat juice was too small to give an aliquot to each panelist, the jar with the juice was passed from panelist to panelist within 5 min, whereas each panelist received his own meat sample. The panelists evaluated samples for odor of meat juice and meat according to a 5-point scale covering the range from "very unpleasant" to "very pleasant". The scores for the individual samples were then combined. White bread and still mineral water were served to the panelists for neutralization between the samples.

Statistical Analysis. Daily weight gain, slaughter weight, back fat thickness, lean meat percentage, and pH value (45 min post mortem) in musculus longissimus dorsi were determined according to German progeny testing standards and analyzed by two-way ANOVA followed by Duncan's post-hoc test which is routinely used to evaluate data in the progeny test station. All other statistical evaluations were performed using the Statistical Package for the Social Sciences (SPSS version 12.0, SPSS Inc., Chicago, IL). Residuals were tested for normal distribution and for homogeneity of variances. Details of the statistical evaluation of the different parameters are outlined below.

Skatole. Since feeding of RS led to very low values or even to values below the detection limit, data for skatole concentrations did not meet the assumptions of normal distribution and homogeneity of variances required for linear models, even after mathematical transformation. Therefore, nonparametric statistics were applied. Data are given as medians and ranges. As the animals within one feeding group and gender were kept in two pens with 10 places each, the Mann–Whitney test (Exact test) was used to determine differences between the two pens for each parameter (colon content, plasma, flare fat, ventral fat, and back fat). Because only one of 28 cases showed a significant difference between two pens, it was decided that the effect of pens was negligible. Medians between groups and genders were tested for differences with the Kruskal–Wallis test for independent samples followed by the Mann–Whitney U-test (Exact test). Differences between the three adipose tissues within one group were evaluated with the Friedman test followed by the Wilcoxon test (Exact test).

Sensorial Quality. The ratings for meat juice and meat were summarized and termed overall odor.

Table 3. Skatole Concentrations in Colon Content and Blood Plasma (median and range)^a in Barrows and Gilts Fed Isocalorically with either a Conventional Diet (controls) or a Diet with Resistant Starch (RS)

		barrows		gilts	
		colon content ($\mu\text{g}/\text{g}$)	blood plasma (ng/mL)	colon content ($\mu\text{g}/\text{g}$)	blood plasma (ng/mL)
controls	median	39.8a	0.77a	58.9a	1.15a
	range	8.0–103.8	0.46–1.35	17.2–113.4	0.3–2.51
RS	median	nd ^b	0.42b	0.8b	0.36b
	range	nd to 6.74	0.22–1.28	nd to 32.4	0.23–1.05

^a Lowercase letters indicate differences within a column ($P < 0.001$). ^b Not detected ($\leq 0.4 \mu\text{g}/\text{g}$).

The 24 meat samples were divided into three classes ($n = 8$ for each) of skatole concentrations (low, 0–2.87 ng/g; medium, 3.52–28.7 ng/g; high, 29.9–78.5 ng/g). In the "low" class, there were eight animals from the RS group. The "medium" class consisted of five control animals and three RS animals, and the "high" group contained seven control animals and one RS animal. Skatole concentrations between classes were tested for differences with the Kruskal–Wallis test for independent samples followed by the Mann–Whitney U-test (Exact test). The ratings for overall odor were tested for differences using the following Mixed Model:

$$y_{ijkl} = \mu + \alpha_i + \beta_j + \gamma_k + (\beta\gamma)_{jk} + f_l + g_{ij} + h_{ik} + m_{ijk} + e_{ijkl}$$

where y_{ijkl} is the mean rating of overall odor, μ is the general effect, α_i is the main effect of the i th class, β_j is the main effect of the j th panelist, γ_k is the main effect of k th day of sensorial evaluation, $(\beta\gamma)_{jk}$ is the interaction of the j th panelist on the k th day, f_l is the effect of the l th animal, g_{ij} is the interaction of the i th class and j th panelist, h_{ik} is the interaction of the i th class and k th day, m_{ijk} is the interaction among the i th class, j th panelist, and k th day, and e_{ijkl} is the residual error.

RESULTS

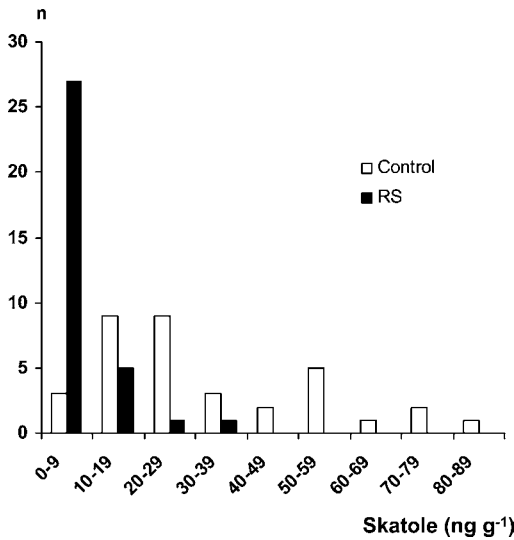
The data for the production traits and carcass characteristics are given in **Table 2** separately for barrows and gilts because they are known to differ in their growth traits. Within the group of barrows, the type of feeding had no significant effect on any of the parameters, thus additionally confirming that the diets were equivalent in their energy and protein supply. In gilts, only a minor difference occurred in the slaughter weight and consequently also in the corresponding back fat thickness.

The consequences of the two rations for skatole concentrations in colon content and blood plasma are shown in **Table 3** again separately for barrows and gilts. The concentrations in colon content of barrows decreased from a median of nearly 40 $\mu\text{g}/\text{g}$ to a level which was below the detection limit of the method ($P < 0.001$). Mean skatole concentrations in the colon of control gilts were higher than those of control barrows, but the difference was not significant. They decreased to 0.8 $\mu\text{g}/\text{g}$ due to RS feeding. The median in the RS gilts was significantly

Table 4. Skatole Concentrations (nanograms per gram) in Different Adipose Tissues (flare fat, ventral fat, and back fat) in Barrows and Gilts Fed Isocalorically with either a Conventional Diet (controls) or a Diet with Resistant Starch (RS)^a

		barrows			gilts		
		flare	ventral	back	flare	ventral	back
controls	median	45.2a	29.6b	25.0c	53.8x	32.9y	39.9z
	range	9.3–94.4	7.23–64.0	6.23–51.8	19.1–139.1	11.3–125.8	9.4–84.0
RS	median	4.16a	1.10ab	1.43b	11.8xy	10.4y	9.06x
	range	nd ^b to 17.0	nd to 15.5	nd to 7.66	nd to 52.8	1.83–48.2	nd to 39.5

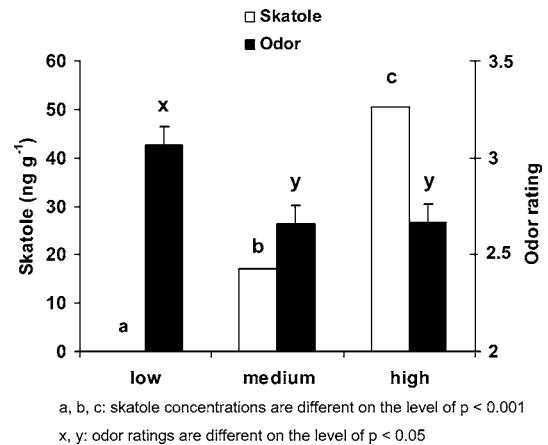
^a Median values from barrows (a, b, and c) or gilts (x, y, and z) within a row lacking a common letter differ significantly ($P < 0.05$). ^b Not detected (≤ 0.8 ng/g).

**Figure 1.** Frequency of skatole concentrations (nanograms per gram) in back fat from 35 controls and 34 RS pigs.

higher than in RS barrows ($P < 0.05$), as well as the range of concentrations. Concentrations of skatole in blood plasma were also reduced by RS ($P < 0.001$) in both barrows and gilts. Gilts from the control group had skatole concentrations in plasma higher than those of barrows of the same feeding regimen ($P < 0.01$). As suggested already by the RS-dependent decrease in skatole concentration in colon content and blood plasma, the concentrations in adipose tissue were also decreased by RS (Table 4).

The three fat compartments differed significantly from each other in the controls of both barrows and gilts ($P < 0.05$). Flare fat always had the highest values. The differences between ventral and back fat were less pronounced; however, in the barrows, ventral fat concentrations were higher than those in back fat, whereas in gilts, the order of concentrations was reversed. Compared to the controls, the RS-dependent decrease in skatole concentrations in all three fat compartments is obvious and statistically highly significant ($P < 0.001$). It is also obvious that the absolute decrease is much more pronounced in barrows than in gilts. As a consequence, values remaining after RS feeding in gilts were ~8-fold higher (ventral and back fat) or 3-fold higher (flare fat) than in barrows, although the sex-dependent differences were much lower in the controls.

The effects of feeding are further analyzed in Figure 1 which gives the frequency of occurrence of skatole in back fat without differentiation between the sexes. Most of the RS animals (79%) were in the lowest category, and only 6% exceeded 19 ng/g. Controls, in contrast, covered a broad range of concentrations, and 66% exceeded 19 ng/g. Data of sensorial evaluation are shown in Figure 2. The retrospective grouping of the skatole concentrations into three equal groups (each represented by eight samples) led to median values for the low (nondetectable



a, b, c: skatole concentrations are different on the level of $p < 0.001$
x, y: odor ratings are different on the level of $p < 0.05$

Figure 2. Odor rating of musculus longissimus dorsi (mean \pm standard error of the mean) and skatole concentrations (nanograms per gram, medians) in corresponding back fat. Grouping into low, medium, and high skatole concentrations in the fat ($n = 8$ each) was performed after sensory evaluation. Groups of skatole concentrations differ significantly ($P < 0.001$). The median in the low skatole group was zero.

values), medium (17.2 ng/g), and high group (50.4 ng/g). All eight samples in the lowest group originated from the RS group; the medium group contained only three RS samples, and the high group included one RS sample. The concentrations of the three groups all differed significantly ($P < 0.001$). The odor rating shows that panelists clearly distinguished between the group with low skatole concentrations and the other groups with much higher skatole concentrations in back fat ($P < 0.05$). An odor rating of 3 on our scale of 1–5 represents a neutral rating, and the value of 3.07 for the group with the lowest concentrations thus fulfills expectations of normal pig meat odor; the other two groups with increased concentrations clearly fell into an unpleasant rating (odor rating of 2.66 for both groups).

DISCUSSION

This study shows that it is possible to reduce the level of skatole formation in the large intestine and correspondingly tissue concentrations in barrows and gilts by feeding the animals resistant potato starch. It could also be shown that the reduction in tissue levels led to an improvement in sensorial quality.

In the controls, the mean value and the range of tissue concentrations were in an order which was determined earlier for pig genotypes in Germany (24). In other studies, higher concentrations were also reported (25, 26), but whether the genotype or production system was the reason was not investigated.

In this study, gilts revealed generally higher concentrations than barrows. Skatole formation depends on both environmental factors, including feeding, and the influence of endogenous anabolic hormones. Insulin-like growth factor 1 (IGF-1) seems

to be linked to skatole formation because it was shown to be influenced by the supply of digestible starch (11) and leads to higher skatole concentrations in the tissue (12). In addition, IGF-1 is stimulated by estradiol, so the rate of skatole formation is increased in the follicular phase of cyclic sows (27). Because gilts start ovarian function and estradiol formation around 180 days and could be used for first insemination at a weight of ~120 kg (28), the higher skatole concentrations are most likely attributable to pubertal development within the fattening period.

Differences in tissue concentrations between barrows and gilts also had an influence on the effectiveness in decreasing skatole concentrations with resistant starch, so remaining concentrations were higher in gilts. It is likely that an increased supply of resistant starch would have led to a steeper decrease in the level of skatole in gilts, but 30% of resistant starch in the diet was chosen because it is an acceptable compromise between costs and effectiveness as shown previously (18). The addition of resistant starch in the study presented here was performed over the whole fattening period to successfully reduce odor emission to the environment (15). For improving carcass quality alone, it might be possible to shorten the application time to only a few days before slaughter because the rate of intestinal formation was rapidly reduced after the change of diet (10).

In addition, the half-life is similarly short in blood plasma (29) and tissue (30). Minor differences in half-life in adipose tissue depending on the anatomical location may reflect the allometric development (31) and presumably explain the differences in skatole concentrations (18).

Differences in the odor rating were significant between the group of low concentrations, which was only represented by RS pigs and the other groups. The rating of the medium and high concentration group was not significantly different. As discussed above, higher skatole concentrations were found in other studies so that a further differentiation depending on the concentrations can be expected.

ACKNOWLEDGMENT

We appreciate the help of the staff of the Landesanstalt für Schweinezucht Forchheim (Baden-Württemberg, Germany), specifically valuable suggestions from Dr. Alfred Oster and Harald Friedrich. We also thank Prof. Dr. Hans-Peter Piepho for his statistical advice and the staff of the Fachgebiet Tierhaltung und Leistungsphysiologie for participation in the sensory evaluation.

LITERATURE CITED

- Gray, J. I.; Pearson, A. M.; Monahan, F. J. Flavor and aroma problems and their measurement in meat, poultry and fish products. *Adv. Meat Res.* **1994**, *9*, 250–288.
- Shankaranarayana, M. L.; Raghavan, B.; Abraham, K. O.; Natarajan, C. P. Sulphur compounds in flavours. *Dev. Food Sci.* **1982**, *3A*, 169–282.
- Ha, J. K.; Lindsay, R. C. Distribution of volatile branched-chain fatty acids in perinephric fats of various red meat species. *Lebensm.-Wiss. -Technol.* **1990**, *23*, 433–440.
- Melton, S. L. Effects of feeds on flavor of red meat: A review. *J. Anim. Sci.* **1990**, *68*, 4421–4435.
- Zahn, J. A.; DiSpirito, A. A.; Do, Y. S.; Brooks, B. E.; Cooper, E. E.; Hatfield, J. L. Correlation of human olfactory responses to airborne concentrations of malodorous volatile organic compounds emitted from swine effluent. *J. Environ. Qual.* **2001**, *30*, 624–634.
- Mattivi, F.; Vrhovsek, U.; Versini, G. Determination of indol-3-acetic acid, tryptophan and other indoles in must and wine by high-performance liquid chromatography with fluorescence detection. *J. Chromatogr., A* **1999**, *855*, 227–235.
- Mikkelsen, L. L.; Jensen, B. B. Growth and skatole (3-methylindole) production by *Clostridium scatologenes* grown in batch and continuous cultures. *Soc. Appl. Bacteriol. Symp. Ser.* **1996**, *81*, XVIII.
- Squires, E. J.; Lundström, K. Relationship between cytochrome P4502E1 in liver and levels of skatole and its metabolites in intact male pigs. *J. Anim. Sci.* **1997**, *75*, 2506–2511.
- Bernal-Barragan, H. Physiologische und nutritive Einflüsse auf die Bildung von Skatol (3-Methylindol) im Dickdarm von Schweinen. Ph.D. Thesis, Universität Hohenheim, Stuttgart, Germany, 1992.
- Claus, R.; Lösel, D.; Lacorn, M.; Mentschel, J.; Schenkel, H. Effects of butyrate on apoptosis in the pig colon and its consequences for skatole formation and tissue accumulation. *J. Anim. Sci.* **2003**, *81*, 239–248.
- Raab, S.; Leiser, R.; Kemmer, H.; Claus, R. Effects of energy and purines in the diet on the proliferation, differentiation and apoptosis in the small intestine of the pig. *J. Metab.* **1998**, *47*, 1105–1111.
- Claus, R.; Raab, S.; Röckle, S. Skatole concentrations in blood plasma of pigs as influenced by the effect of dietary factors on gut mucosa proliferation. *J. Anim. Sci. Anim. Nutr.* **1996**, *76*, 170–179.
- Mentschel, J.; Claus, R. Increased butyrate formation in the pig colon by feeding raw potato starch leads to a reduction of colonocyte apoptosis and a shift to the stem cell compartment. *Metabolism* **2003**, *52*, 1400–1405.
- Zamaratskaia, G.; Babol, J.; Andersson, H. K.; Andersson, K.; Lundström, K. Effect of live weight and dietary supplement of raw potato starch on the levels of skatole, androstenone, testosterone and oestrone sulphate in entire male pigs. *Livest. Prod. Sci.* **2005**, *93*, 235–243.
- Willig, S.; Lösel, D.; Claus, R. Effects of resistant potato starch on odor emission from feces in swine production units. *J. Agric. Food Chem.* **2005**, *53*, 1173–1178.
- Babol, J.; Squires, E. J.; Gullet, E. A. Investigation of factors responsible for boar taint. *Food Res. Int.* **1996**, *28*, 573–581.
- Annor-Frempong, I. E.; Nute, G. R.; Whittington, F. W.; Wood, J. D. The problem of taint in pork: 1. Detection thresholds and odor profiles of androstenone and skatole in a model system. *Meat Sci.* **1997**, *46*, 45–55.
- Lösel, D.; Claus, R. Dose-dependent effects of resistant potato starch in the diet on intestinal skatole formation and adipose tissue accumulation in the pig. *J. Vet. Med., Ser. A* **2005**, *52*, 209–212.
- Claus, R.; Dehnhard, M.; Herzog, A.; Bernal-Barragan, H.; Giménez, T. Parallel measurements of indole and skatole (3-methylindole) in feces and blood plasma of pigs by HPLC. *Livest. Prod. Sci.* **1993**, *34*, 115–126.
- Jensen, M. T.; Cox, R. P.; Jensen, B. B. Microbial production of skatole in the hindgut of pigs given different diets and its relation to skatole deposition in back fat. *Anim. Sci.* **1995**, *61*, 293–304.
- Dehnhard, M.; Claus, R.; Hillenbrand, M.; Herzog, A. High-performance liquid chromatographic method for the determination of 3-methylindole (skatole) and indole in adipose tissue of pigs. *J. Chromatogr.* **1993**, *616*, 205–209.
- Dehnhard, M.; Bernal-Barragan, H.; Claus, R. Rapid and accurate high-performance liquid chromatographic method for the determination of 3-methylindole (skatole) in feces of various species. *J. Chromatogr.* **1991**, *566*, 101–107.
- Garcia-Regueiro, J. A.; Diaz, I. Evaluation of the contribution of skatole, indole, androstenone, and androstenols to boar taint in back fat of pigs by HPLC and capillary gas chromatography (CGC). *Meat Sci.* **1989**, *25*, 307–316.

- (24) Herzog, A.; Herbert, E.; Dehnhard, M.; Claus, R. Vergleichende Messungen von Androstenon und Skatol in verschiedenen Geweben. *Mitteilungsblatt der Bundesanstalt für Fleischforschung Kulmbach* **1993**, *32*, 116–124.
- (25) Bonneau, M.; Le Denmat, M.; Vaudelet, J. C.; Veloso Nunes, J. R.; Mortensen, A. B.; Mortensen, H. P. Contributions of fat androstenone and skatole to boar taint: I. Sensory attributes of fat and pork meat. *Livest. Prod. Sci.* **1992**, *32*, 63–80.
- (26) Hansen, L. L.; Larsen, A. E.; Jensen, B. B.; Hansen-Møller, J.; Barton-Gade, P. Influence of stocking rate and faeces deposition in the pen at different temperatures on skatole concentration (boar taint) in subcutaneous fat. *Anim. Prod.* **1994**, *59*, 99–110.
- (27) Claus, R.; Bernal-Barragan, H.; Dehnhard, M. Effect of gonadal hormones in mature cyclic sows on food intake and skatole concentrations in faeces. *J. Anim. Physiol. Anim. Nutr.* **1991**, *66*, 61–68.
- (28) Mezger, K. Die Pubertät der Jungsauen und ihre Beeinflussung durch Licht. Ph.D. Thesis, Universität Hohenheim, Stuttgart, Germany, 1994.
- (29) Agergaard, N.; Laue, A. Absorption from the gastrointestinal tract and liver turnover of skatole. *Colloq.-Inst. Natl. Rech. Agron.* **1993**, *60*, 107–111.
- (30) Claus, R.; Weiler, U.; Herzog, A. Physiological aspects of androstenone and skatole formation in the boar: A review with experimental data. *Meat Sci.* **1994**, *38*, 289–305.
- (31) Kouba, M.; Bonneau, M.; Noblet, J. Relative development of subcutaneous, intermuscular, and kidney fat in growing pigs with different body compositions. *J. Anim. Sci.* **1999**, *77*, 622–629.

Received for review March 22, 2006. Revised manuscript received June 13, 2006. Accepted June 18, 2006. We thank the MLR (Ministerium für Ernährung und Ländlichen Raum Baden-Württemberg) for financial support.

JF0608017