Characterizing developmental changes in plasma and tissue skatole concentrations in the prepubescent intact male pig\textsuperscript{1}

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ABSTRACT: The accumulation of skatole in boars to concentrations resulting in carcass taint has been associated with elevated concentrations of steroid hormones in plasma. Studying boar taint in vivo has been challenging because steroid hormones are highly variable between individual boars. However, a peak in steroid hormones occurs between 2 and 4 wk postpartum; therefore, skatole production was investigated in the prepubescent pig. Plasma concentrations of estrone sulphate, dehydroepiandrosterone sulphate, and testosterone peaked between 2 and 4 wk postpartum in intact male pigs, whereas plasma concentrations of these steroid hormones remained low or undetectable in gilts and barrows. However, plasma skatole concentration peaked in all 3 groups of animals between 2 and 3 wk postweaning. The effects of weaning time, intestinal cell turnover, and diet on tissue skatole concentrations were then investigated. Intact male piglets were weaned at 14, 21, 28, or 35 d of age. Plasma skatole concentrations were measured weekly for a period of 63 d and peaked at 17 ± 1, 14 ± 1, 13 ± 1, and 10 ± 2 d postweaning, respectively. Intestinal cell turnover, as evaluated by villous height: crypt depth ratio, was not correlated with skatole concentrations in cecal contents, suggesting that cellular debris did not constitute a gross source of tryptophan for hindgut fermentation. The inclusion of 10% chicory inulin to piglet diets suppressed the postweaning increase in plasma skatole. Cecal skatole concentrations were also 3.3-fold lower in inulin-supplemented piglets compared with controls. The rise in plasma skatole in the prepubescent intact male pig was not associated with increased steroidogenesis but is likely due to the postweaning adaptation of the intestinal flora to an abrupt dietary change.

Key words: boar taint, nonstarch polysaccharide, pig, prepubescent, steroid hormone, weaning

INTRODUCTION

Three-methylindole (skatole) is produced by the microbial degradation of tryptophan in the hindgut of pigs (Yokoyama and Carlson, 1979) and is a major component of the fecal-like odor and bitter taste known as boar taint (Bonneau et al., 2000). Male pigs destined for meat are castrated. However, this practice increases production costs and reduces carcass advantages such as lean meat yield and feed efficiency (Babol and Squires, 1995).

A relationship between steroid hormones and boar taint due to skatole has long been acknowledged; however, it has yet to be fully elucidated. Increased plasma skatole concentrations reported by Babol et al. (2004) coincided with puberty, a time during which plasma steroid hormones also increase (Tan and Raeside, 1980; Ford, 1983). The onset of puberty, and therefore the ensuing rise in steroidogenesis, is highly variable between individual boars and is influenced by factors such as nutritional status (Brown, 1994), stress, social rank (DeJonge et al., 1996), and breed (Babol et al., 2004). Due to the wide time span over which puberty occurs, studying boar taint during pubertal development is impractical.

Zamaratskaia et al. (2004) reported elevated plasma skatole between 8 and 10 wk of age and then again after 22 wk of age in boars. The latter rise in plasma skatole coincided with puberty and was correlated (\(P < 0.05\)) with increased concentrations of steroid hormones; however, the former rise in plasma skatole was not characterized. Between 2 and 4 wk postnataally, plasma steroid hormone concentrations in male piglets are comparable with concentrations in mature boars (Schwarzenberger et al., 1993). The prepubescent hormonal wave occurs within a narrow window of time, potentially offering a predictable timeframe during

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which to characterize skatole production in pigs. The objective of this work was to characterize the developmental changes in plasma and tissue skatole concentrations in the prepubescent intact male pig.

MATERIALS AND METHODS

Animals and Sampling

All experiments were done in accordance with and approved by the University of Guelph Animal Care and Use Committee regulations.

Yorkshire pigs used in the following experiments were obtained from the Arkell Swine Research Station at the University of Guelph. After weaning, animals in Exp. 1 and 2 were fed the control diet shown in Table 1 ad libitum. For the duration of the experiments, blood samples (5 mL) were collected from the orbital sinus once weekly (Exp. 1 and 2) or twice weekly (Exp. 3). Samples were collected between 0800 and 0900 to minimize the potential effect of diurnal variations in plasma hormone and skatole concentrations. Samples were centrifuged (1,100 × g) at 4°C to collect plasma and stored at −20°C until analyses were performed.

Table 1. Composition of weanling pig diets for Experiment 3, as-fed basis

<table>
<thead>
<tr>
<th>Ingredient, %</th>
<th>Control</th>
<th>Fishmeal</th>
<th>Fishmeal + inulin</th>
</tr>
</thead>
<tbody>
<tr>
<td>Corn</td>
<td>29.17</td>
<td>22.05</td>
<td>22.10</td>
</tr>
<tr>
<td>Barley</td>
<td>4.00</td>
<td>4.00</td>
<td>4.00</td>
</tr>
<tr>
<td>Wheat</td>
<td>20.00</td>
<td>20.00</td>
<td>20.00</td>
</tr>
<tr>
<td>Soybean meal</td>
<td>29.00</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Fish meal</td>
<td>5.00</td>
<td>29.00</td>
<td>29.00</td>
</tr>
<tr>
<td>Whey</td>
<td>8.00</td>
<td>22.00</td>
<td>22.00</td>
</tr>
<tr>
<td>Chicory inulin extract</td>
<td>—</td>
<td>—</td>
<td>10.00</td>
</tr>
<tr>
<td>Fat</td>
<td>2.00</td>
<td>1.10</td>
<td>2.20</td>
</tr>
<tr>
<td>Lysine-HCl (79%)</td>
<td>0.08</td>
<td>—</td>
<td>0.09</td>
</tr>
<tr>
<td>Dicalcium phosphate</td>
<td>1.10</td>
<td>1.10</td>
<td>1.40</td>
</tr>
<tr>
<td>Limestone (CaCO₃)</td>
<td>0.90</td>
<td>—</td>
<td>1.20</td>
</tr>
<tr>
<td>Iodized salt</td>
<td>0.30</td>
<td>0.30</td>
<td>0.30</td>
</tr>
<tr>
<td>Calciumin premix¹</td>
<td>0.25</td>
<td>0.25</td>
<td>0.50</td>
</tr>
<tr>
<td>Vitamin premix²</td>
<td>0.25</td>
<td>0.10</td>
<td>0.20</td>
</tr>
<tr>
<td>Lincomycin 44³</td>
<td>0.10</td>
<td>0.10</td>
<td>0.20</td>
</tr>
<tr>
<td>Calculated nutritive value</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DE, kcal/g</td>
<td>3.46</td>
<td>3.50</td>
<td>3.40</td>
</tr>
<tr>
<td>CP, %</td>
<td>22.18</td>
<td>25.46</td>
<td>22.93</td>
</tr>
<tr>
<td>Ca, %</td>
<td>1.02</td>
<td>1.94</td>
<td>0.92</td>
</tr>
<tr>
<td>Ca from bulky ingredients, %</td>
<td>0.43</td>
<td>1.69</td>
<td>0.15</td>
</tr>
<tr>
<td>Total P, %</td>
<td>0.77</td>
<td>1.39</td>
<td>0.69</td>
</tr>
<tr>
<td>Ca:total P ratio</td>
<td>1.33</td>
<td>1.39</td>
<td>1.34</td>
</tr>
</tbody>
</table>

¹Supplied by Quali-Tech Foods Inc., Tiverton, Ontario.
²Supplied per kilogram of complete diet: 10,000 IU of vitamin A, 1,000 IU of vitamin D₃, 40 IU of vitamin E, 25 mg of vitamin B₁₂, 2.5 mg of menadione, 500 mg of choline, 15 mg of pantothenic acid, 5 mg of riboflavin, 2 mg of folic acid, 25 mg of niacin, 1.5 mg of thiamin, 1.5 mg of pyridoxine, and 200 µg of biotin.
³Supplied per kilogram of complete diet: 15 mg of Cu, 100 mg of Zn, 100 mg of Fe, 20 mg of Mn, 0.3 mg of I, and 0.3 mg of Se.
⁴Lincomycin hydrochloride premix, Pfizer Animal Health, Kirkland, Quebec.

Experiment 1: Relationships Between Plasma Steroid Hormone and Plasma Skatole Concentrations in Prepubescent Pigs

Twenty-eight intact male pigs from 6 litters, 20 gilts from 5 litters, and 22 barrows from 6 litters were weaned at 21 d of age, and blood samples were collected weekly beginning at 1 wk of age for a period of 63 d. Plasma samples were analyzed for skatole, dehydroepiandrosterone sulfate (DHEAS), estrone sulfate (E₁S), and testosterone (T) concentrations.

Experiment 2: Effect of Weaning on Plasma Skatole Concentrations in Pigs

Forty-five intact male pigs from 12 litters were utilized for this experiment. Piglets from a litter were weaned at the same time and assigned randomly to each treatment. Treatment groups consisted of 4 weaning times: 14, 21, 28, and 35 d. After weaning, piglets were moved to raised pens to avoid feces and urine accumulation in the pens, and the control diet (Table 1) was fed ad libitum. Blood samples were collected weekly beginning at 1 wk of age for a period of 63 d and subsequently analyzed for plasma concentrations of skatole, DHEAS, E₁S, and T.

Experiment 3: Effect of Feed Composition and Small Intestinal Morphology on Concentration of skatole in Cecum, Plasma, and Backfat

Forty-seven intact males were weaned at 28 d of age and assigned randomly to 1 of 3 diets: control, fishmeal, and fishmeal supplemented with 10% chicory inulin extract (Table 1). These dietary treatments were designed to assess the effects of dietary protein and chickory inulin (Rideout et al., 2004) on small intestinal morphology and also on skatole concentrations in cecal contents, plasma, and fat. Pigs were housed in 9 pens, and 3 pens were assigned to each diet. Blood samples were collected twice a week for a period of 4 wk after weaning, whereas BW and feed consumption per pen were collected daily.

At 14 d postweaning, 2 pigs from each pen were slaughtered by electrical stunning followed by exsanguination to collect ileal, jejunal, and duodenal segments from the small intestine, as well as cecal contents, plasma, and backfat. Sections of approximately 10 cm of ileum, jejunum, and duodenum were rinsed twice with 50 mL of 0.1% phenylmethylsulfonyl fluoride solution, and each section was suspended individually in 10 cm of ileum, jejunum, and duodenum were rinsed twice with 50 mL of 0.1% phenylmethylsulfonyl fluoride solution, and each section was suspended individually in 10% phosphate-buffered formalin. Sections were further processed and stained with haematoxylin and eosin as described previously (Junqueira et al., 1995). Villous height and crypt depth were measured utilizing the Openlab 2.2.5 alias software (Improvision Ltd., Coventry, UK). Cecal contents were snap-frozen in liquid nitrogen at the time of collection and stored at −70°C until analysis for concentrations of skatole.
Biochemical Analyses

Concentrations of skatole in plasma and cecal contents were determined by a HPLC method modified from those of Claus et al. (1993) and Dehnhard et al. (1993). Briefly, skatole was first extracted from 0.5 mL of plasma with 2 mL of diethylether, and the ether fraction was mixed with 1 mL of 40% acetonitrile. The ether was evaporated after the samples were placed in a water bath at 47°C, and 200 μL of the extract were analyzed for skatole concentration by HPLC. To determine the skatole concentration in cecal contents, a 1-g sample of cecal content was extracted twice with 4 mL of methanol. Suspensions were vortexed for 30 s and then centrifuged at 2,000 × g for 20 min at 4°C before 100 μL were directly injected into the HPLC. A Spectra Physics HPLC system (Spectra-Physics, San Jose, CA) was used with a guard column attachment and equipped with a Spectra 100 UV-Vis Detector set at 250 nm and a C18 reverse phase column (ODS-3, 5 μm, 250 × 4.6 mm, Supelco, Oakville, Ontario, Canada). The retention time for skatole was 7.1 min. The mobile phase consisted of 2 solvents: 1) 50% of 0.01 M potassium hydrogen, pH 3.9, and 50% of acetonitrile; and 2) 100% acetonitrile with the following gradient profile: decrease from 100% A to 100% B from 0 min to 6 min, followed by 100% B from 6 to 13 min and then 100% A from 14 min to 20 min. The flow rate was 1.2 mL/min.

Plasma samples from Exp. 2 and 3 were analyzed by RIA for the measurement of DHEAS, E1S (Schwarzenberger et al., 1993), and T (Raeside and Middleton, 1979). The sensitivity of the assays averaged 0.15 ng/mL, the intraassay CV averaged 5.5%, and the interassay CV averaged 6.7%.

Statistical Analyses

A quadratic regression of plasma concentrations of skatole on age was fitted for each pig, and a Student’s t-test was performed on the linear and quadratic coefficients to determine the presence of a peak in plasma concentrations of skatole in Exp. 1 through 3.

Skatole concentrations in Exp. 1 through 3 were evaluated using a repeated measures analysis to provide information on time trends (Kuehl, 2000). Peak plasma skatole concentrations and the number of days to reach the peak plasma skatole concentration were evaluated using a completely randomized design: \( Y_{ij} = \mu + \tau_i + \rho_j + \varepsilon_{ij} \), where \( Y \) is the response variable, with \( i \) corresponding to pig and \( j \) to day; \( \mu \) is the general mean; \( \tau_i \) is treatment (sex) effect; \( \rho_j \) is the random (litter) effect; and \( \varepsilon_{ij} \) is the normally distributed experimental error.

For Exp. 2, the relationship between day of weaning and the timing of the peak plasma skatole concentration was evaluated by linear regression, where the day of weaning was the independent variable and the day of the peak plasma skatole concentration was the dependent variable. The analysis was also performed with the addition of day of hormone (E1S, DHEAS, or T) peak as a covariate.

For Exp. 3, ADG and ADFI for individual pens were analyzed using the 2-slope, broken-line model to determine the point in time where the slope of ADG and ADFI changed (Robbins, 1986). The pattern of plasma concentrations of skatole was established using all the animals. Analyses of cecal skatole concentrations, fat, and intestinal segments were performed with the pigs slaughtered at 14 d postweaning. Concentrations of skatole in plasma, fat, and cecal contents, as well as villous heights and crypt depths for ileal, jejunal, and duodenal samples, were analyzed by GLM as a completely randomized design: \( Y_{ij} = \mu + \tau_i + \rho_j + \varepsilon_{ij} \), where \( Y_{ij} \) is the response variable, \( \mu \) is the general mean, \( \tau_i \) is treatment (diet) effect, \( \rho_j \) is the random (litter) effect, and \( \varepsilon_{ij} \) is the normally distributed experimental error. Linear contrasts were used to evaluate dietary treatment effects on concentrations of skatole in plasma, fat, and cecal contents. In addition, Pearson’s correlation coefficients were determined within diets to evaluate the relationship between the ileal, jejunal, and duodenal villous height to crypt depth ratios and skatole concentrations in cecal contents. All statistical procedures were performed using SAS (version 8.1, SAS Inst. Inc., Cary, NC).

RESULTS

Experiment 1

Linear and quadratic coefficients obtained from the regression of plasma skatole on age at sampling were not different (linear \( P = 0.82 \); quadratic \( P = 0.37 \)) among intact males, gilts, and barrows, indicating that there were no differences in the plasma concentrations of skatole among these groups (Figure 1). Mean concentrations of plasma skatole did not differ (\( P = 0.99 \)) between the sexes and ranged from 9.0 to 11.2 ng/mL and occurred between 14 and 21 d postweaning (Table 2). Plasma concentrations (Figure 2) of E1S (A), DHEAS (B), and T (C) were greatest in intact males between 14 and 28 d of age, whereas plasma steroid concentrations remained low in gilts and barrows throughout the 63-d sampling period.

Experiment 2

Concentrations of plasma skatole concentrations for intact males weaned at 14, 21, 28, and 35 d of age are shown in Figure 3. Plasma skatole concentrations for intact males weaned at 14 d of age peaked at 17 ± 1 d postweaning. Time to the appearance of the skatole peak decreased (\( P < 0.05 \)) to 14 ± 1 d postweaning when animals were weaned at 21 d of age. Time to appearance of the skatole peak continued to decrease (\( P < 0.05 \)) to 13 ± 1 and 10 ± 2 d postweaning when animals were weaned at 28 and 35 d of age, respectively. These differences in days postweaning coincide with 31, 35, 41 and
Figure 1. Plasma skatole concentrations of intact males (solid black; n = 28), gilts (solid white; n = 20), and barrows (diagonal stripes; n = 22) weaned at 21 d of age (weaning indicated by the arrow). Values are means ± SEM. Mean plasma skatole concentrations did not differ (P = 0.99) among boars, gilts, and barrows.

Plasma skatole concentrations did not change in the piglets fed the fishmeal + inulin diet during the postweaning sampling period. At 14 d postweaning, skatole concentrations in cecal contents (P = 0.27), plasma (P = 0.09), and fat (P = 0.41) were not different between the pigs fed the control and fishmeal diets; however, pigs fed the fishmeal + inulin diet had lower concentrations (P < 0.05) of skatole in cecal contents, plasma, and fat (Figure 6). There were no correlations within diets between skatole concentrations in cecal contents and plasma concentrations of T, DHEAS, or E1S at 14 d postweaning. There was no difference in ADG (Phase 1, P = 0.06; Phase 2, P = 0.26) or ADFI (Phase 1, P = 0.63; Phase 2, P = 0.92) across the 3 dietary treatments (Table 3). All dietary treatments had increased ADG (P < 0.05) and ADFI (P < 0.05) during phase II compared with phase I. The crossover points for ADG and ADFI did not differ across diets.

There were no differences in villous height from ileum, jejunum, and duodenum sections in animals on the different dietary treatments (Figure 7A). However, pigs fed the fishmeal diet had shorter (P < 0.05) crypt depths in the ileal and duodenal sections, whereas there were no differences in crypt depth among dietary treatments in the jejunal sections (Figure 7B). Intestinal (ileal, jejunal, and duodenal) villous height to crypt depth ratios and concentrations of skatole in cecal contents were not correlated in the control diet (P = 0.16, 0.54, and 0.89, respectively), fishmeal diet (P = 0.17, 0.12, and 0.15, respectively) and fishmeal + inulin diet (P = 0.12, 0.83, and 0.42, respectively).

Experiment 3

Plasma concentrations of skatole for the intact male pigs fed the control, fishmeal, or fishmeal + inulin diets and weaned at 28 d of age are shown in Figure 5. A rise in plasma skatole was observed in piglets fed the fishmeal and control diets, whereas plasma skatole concentrations did not change in the piglets fed the fishmeal + inulin diet during the postweaning sampling period. At 14 d postweaning, skatole concentrations in cecal contents (P = 0.27), plasma (P = 0.09), and fat (P = 0.41) were not different between the pigs fed the control and fishmeal diets; however, pigs fed the fishmeal + inulin diet had lower concentrations (P < 0.05) of skatole in cecal contents, plasma, and fat (Figure 6). There were no correlations within diets between skatole concentrations in cecal contents and plasma concentrations of T, DHEAS, or E1S at 14 d postweaning. There was no difference in ADG (Phase 1, P = 0.06; Phase 2, P = 0.26) or ADFI (Phase 1, P = 0.63; Phase 2, P = 0.92) across the 3 dietary treatments (Table 3). All dietary treatments had increased ADG (P < 0.05) and ADFI (P < 0.05) during phase II compared with phase I. The crossover points for ADG and ADFI did not differ across diets.

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Table 2. Peaks and ranges of plasma concentrations of skatole in intact males, gilts, and barrows weaned at 21 d of age1

<table>
<thead>
<tr>
<th>Plasma skatole, ng/mL</th>
<th>Intact males (n = 28)</th>
<th>Gilts (n = 20)</th>
<th>Barrows (n = 22)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Peak</td>
<td>11.1 ± 3.4</td>
<td>11.2 ± 3.7</td>
<td>9.0 ± 3.8</td>
</tr>
<tr>
<td>Range</td>
<td>4.9 to 32.2</td>
<td>3.8 to 32.3</td>
<td>3.7 to 36.1</td>
</tr>
</tbody>
</table>

1Means ± SEM.
Figure 2. Plasma dehydroepiandrosterone sulfate (DHEAS, panel A), estrone sulfate (E₁S, panel B), and testosterone (T, panel C) concentrations of intact males (solid black; n = 28), gilts (solid white; n = 20), and barrows (diagonal stripes n = 22) weaned at 21 d of age. Values are means ± SEM. For panels A, B, and C, hormone concentrations were greater for boars compared with gilts and barrows at each day (P < 0.05). Differences (P < 0.05) over time in plasma DHEAS (A), E₁S (B), and T (C) concentrations for intact males are identified by different letters.
**DISCUSSION**

A greater accumulation of skatole in backfat and feces has been shown in boars compared with gilts and barrows, likely due to the anabolic status of the male (Bejerholm and Barton-Gade, 1992; Poltársky et al., 1998). Boars are known to secrete large amounts of many steroids, including estrogens, compared with males of other species (Claus and Hoffmann, 1980; Ford, 1983).

Babol et al. (1999) found that plasma E1S concentrations were correlated with backfat skatole concentrations; however, mechanisms by which steroid hormones might influence skatole in the boar have yet to be elucidated. Our results show that in the prepubescent pig, circulating concentrations of E1S, T, and DHEAS are not associated with plasma concentrations of skatole. Intact males showed increased steroidogenesis between 2 and 4 wk of age; however, plasma concentrations of skatole were similar among sexes. Additionally, plasma concentrations of E1S, T, and DHEAS for intact male piglets weaned at 14, 21, 28, or 35 d of age did not differ, which is in agreement with previous reports (Schwarzenberger et al., 1993; Sinclair et al., 2001).
Figure 5. Plasma skatole concentrations of intact male pigs fed a control (diagonal stripes), fishmeal (solid white), or fishmeal + inulin (solid black) diet. Values are means ± SEM. a,bColumns with a different letter at a particular time postweaning differ (P < 0.05).

however, the pattern of skatole concentrations in plasma shifted relative to the day of weaning.

Time elapsed between weaning and the occurrence of the peak in skatole concentrations in plasma decreased progressively as weaning was delayed. Mathew et al. (1996) suggested that a longer period of exposure to creep feed in pigs weaned at an older age could allow the enteric microflora to adapt to the dietary change more gradually. This group also proposed that bacterial populations are less stable in pigs weaned at an earlier age due to a more extended period of postweaning feed refusal compared with pigs weaned at an older age. In pigs weaned at 14, 21, or 28 d of age, Leibbrandt et al. (1975) observed that feed intake recovery after the postweaning lag was more rapid in pigs weaned at an older age. Therefore, it is likely that the increase in plasma skatole occurs closer to the day of weaning in pigs weaned at an older age because of the combined effects of a microbial flora that is better adapted to ferment the diet and a greater feed consumption.

Lower concentrations of skatole in cecal contents, plasma, and fat were found in pigs fed the fishmeal + inulin diet compared with the pigs fed the control and fishmeal diets. Because of the minimal amount of hydrolysis of complex polysaccharides in the small intestine (Slominski, 1994), the majority will be available for bacterial fermentation in the hindgut. Addition of carbohydrates of low ileal digestibility to pig rations, and specifically the addition of chicory inulin extract (Rideout et al., 2004), has been shown to reduce skatole concentrations in plasma and feces (Hawe et al., 1992; Claus et al., 2003). Jensen et al. (1995) found that both protein-rich and carbohydrate-rich substrates resulted in high microbial activity in the cecum, suggesting that the activity of proteolytic bacteria could be decreased due to competition with carbohydrate-fermenting bacteria. This is likely what occurred in the weanling pigs fed the inulin-supplemented diet in the current experiments; however, the evaluation of microbial populations and their activity would be required to confirm the effect of dietary substrates on intestinal microbes and the formation of skatole in the weanling pig.

Experiments reported here suggest that the rise in skatole concentrations observed in prepubescent pigs is related to weaning and possibly to changes in the intestinal microflora during this time. Although tryptophan is the substrate for skatole formation, it has been suggested that the fermentative environment and its predisposition to favor anaerobic bacterial growth is of greater relative importance in the production of skatole than the amounts of tryptophan ingested (Yost, 1989). Swords et al. (1993) found that members of the gram-negative genus Bacteroides replace gram-positive anaerobes at weaning. Bacteroides are involved in the first decarboxylation step in the production of skatole from L-tryptophan (Deslandes et al., 2001). Katouli et al. (1997) found that the fermentative capacity of the intestinal flora decreased immediately postweaning in piglets, after which it gradually increased for 1 wk postweaning. Analysis of the fecal microflora of piglets (Katouli et al., 1997) shows that there are shifts in microbial populations from weaning to 3 wk postweaning but that populations appear to stabilize at 5 to 6 wk postweaning. The timing of the rise and subsequent

Figure 6. Mean concentrations of skatole in cecal contents, plasma, and fat of intact male pigs weaned at 14 d and fed a control (diagonal stripes), fishmeal (solid white), or fishmeal + inulin (solid black) diet during the experimental period. Values are means ± SEM of 6 pigs/group. a,bMeans within tissue with a different letter differ (P < 0.05).
Table 3. Growth performance and feed intake of pigs fed a control, fishmeal, or fishmeal + inulin diet

<table>
<thead>
<tr>
<th>Variable</th>
<th>Control</th>
<th>Fishmeal</th>
<th>Fishmeal + inulin</th>
<th>Across-diet comparison (P value)</th>
</tr>
</thead>
<tbody>
<tr>
<td>ADG phase I, g/d</td>
<td>164 ± 69a</td>
<td>153 ± 58a</td>
<td>141 ± 33a</td>
<td>0.06</td>
</tr>
<tr>
<td>ADG phase II, g/d</td>
<td>493 ± 40b</td>
<td>542 ± 11b</td>
<td>491 ± 65b</td>
<td>0.27</td>
</tr>
<tr>
<td>Crossover point ADG, d</td>
<td>40.4</td>
<td>35.8</td>
<td>34.4</td>
<td></td>
</tr>
<tr>
<td>ADFI, phase I, g/pig</td>
<td>284.1 ± 35.5a</td>
<td>250.7 ± 30.4a</td>
<td>310.5 ± 25.9a</td>
<td>0.63</td>
</tr>
<tr>
<td>ADFI, phase II, g/pig</td>
<td>1,028.0 ± 60.3b</td>
<td>923.6 ± 55.2b</td>
<td>1,095.4 ± 15.1b</td>
<td>0.92</td>
</tr>
<tr>
<td>Crossover point ADFI, g/pig</td>
<td>41.2</td>
<td>37.5</td>
<td>38.4</td>
<td></td>
</tr>
</tbody>
</table>

a,bPhase I and phase II means within a diet appearing with a different superscript differ (P < 0.05).
1Data are means ± SE of 3 replicates.
2The phase I and phase II values for ADG and ADFI are the slopes obtained from the 2-slope broken line analysis, calculated before and after the crossover point, respectively.

fall of plasma skatole observed throughout the series of experiments reported here coincides with the changes in microbial populations observed by Katouli et al. (1997), suggesting that the changes in plasma skatole after weaning can, in part, be attributed to the post-weaning dynamics of the intestinal flora.

Claus et al. (1996) suggested that cell debris from the intestinal mucosa could serve as a source of tryptophan for skatole formation. At weaning, the gut of the piglet undergoes morphological as well as functional changes to adapt to a plant-based diet (Nabuurs, 1995; Boudry et al., 2002). There is a reduction in villous height, resulting from the sloughing off of cells, which in turn induces cell production from the crypt, increasing crypt depth (Pluske et al., 1996). The villous height:depth ratios observed here in Exp. 3 are similar to those observed by Hampson (1986), who found that the villous height:depth ratio remains stable from 5 d to 5 wk postweaning. Tang et al. (1999) reported a decrease in villous height:depth ratio in piglets at 3 d postweaning, but no difference was observed thereafter. These previous studies suggest that there is increased cell turnover on the day after weaning as the intestine adapts to the dietary change, but that within approximately 1 wk the rate of new cell production from the crypt and older cell sloughing from the villous apex has stabilized. In the present work, no negative correlations between the villous height:depth ratio (from the ileum, jejunum, and duodenum) and cecal skatole concentrations were observed during the period of peak plasma skatole, indicating that increased cellular turnover in the small intestine did not contribute increased substrates for skatole formation in the pig at 14 d postweaning. We observed shorter crypt depths (P < 0.05) in the ileal and duodenal sections of the fishmeal group. The fishmeal diet contained no soybean meal or inulin, whereas the inulin and control diets contained 10.0% and 29.0% inulin or soybean meal, respectively. Dunsford et al. (1989) reported greater crypt depths (P < 0.05) in pigs fed soybean-based diets compared with pigs fed protein from hydrolyzed casein. Dréau et al. (1994) found that exposure to soybean meal stimulated a localized immune response in the crypt area. It is possible that the deeper crypts observed in the weanling pigs fed a soybean-based diet were due to inflammation resulting from the antigenic-
ity of the soy protein. However, immunological assays were not performed in this series of experiments; thus, the cause for the differences in crypt depths observed between dietary treatments remains unclear.

This series of studies confirms the occurrence of a prepubescent rise in skatole concentration in pigs. The prepubescent pig accumulates skatole in the ranges previously reported in mature boars. However, the prepubescent period of the pig does offer a relatively predictable timeframe during which a rise in plasma skatole is observed. Therefore, the prepubescent pig could potentially be developed as an in vivo model for evaluating skatole metabolism but may not be useful as a model for studying boar taint in market-weight boars.

LITERATURE CITED


