

<Review>

닭의 대장을 돼지의 대장이나 소의 제 1위 (Rumen)와 비교 연구

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Comparison of the Chicken Large Intestine to the Large Intestine of Pigs and the Rumen of Cows

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ABSTRACT The large intestine of the chicken differs both anatomically and physiologically from the pig's large intestine and the rumen of the cow. The chicken's large intestine is less developed than the pig's large intestine or the cow's rumen. This paper summarizes these differences. The chicken's large intestine contains a microbiological population similar to that found in the rumen. The chicken's caeca especially contains a large number of microorganisms, but this population varies according to age, feed, maturity, antibiotic use and etc.. Protein is an essential nutrient for the formation of intestinal microvilli. A study showed that the length of the small intestine was 63 % of the total gastrointestinal tract (GIT) length, while caecum was 8.1 %, and the colon and rectum were 4.6 %. The establishment of the microbial population of the small intestine occurs earlier than that of the caeca, but the identity of approximately 90 % of microbial population of the chicken GIT is unknown. Recent studies have shown that energy, volatile fatty acid (VFA) and electrolytes that are found in the large intestine may be absorbed to a certain degree. The chicken small intestine is the primary location for digestion with a variety of enzymes being secreted here. Much research is being conducted into the digestion of sucrose thermal oligosaccharide caramel (STOP), fructooligosaccharides (FOS), mannanoligosaccharide (MOS), galactooligosaccharides (GOS) and isomalto-oligosaccharides (IMO) in the chicken caeca and large intestine. Excessive fibre content in the feed has detrimental effects, but proper fibre supplementation to chicken diets can improve the length and capacity of the small intestine.

(Key words: caeca, microvilli, total gastrointestinal tract, volatile fatty acid, sucrose thermal oligosaccharide caramel, fructooligosaccharides, mannanoligosaccharide, galactooligosaccharides, isomaltooligosaccharides)

Introduction

Significant anatomical and functional differences exist between the large intestine of the chicken compared to the large intestine of the pig and the rumen of cattle. Unlike pigs or ruminants, the chicken has a very short colon, and caeca have until recently been thought to have little functional significance. Microbial digestion of fiber occurs in the caeca of the chicken, but it is of little benefit to the host animals (Moran, 1982).

Microbial activity is found through the whole gastrointestinal tract (GIT) of the chicken and this activity affects enzymatic secretion and digestion (Noy and Sklan, 1997). However, 90 % of this microbial activity is still unknown (Lan et al., 2002).

Non-digestible oligosaccharides are currently being studied for their effect on rate of feed passage, dietary energy absorption, and overall health (Coon et al., 1990).

The nitrogen excreted in chicken faeces is relatively higher than other animal species, and this nitrogen is metabolized by bacteria in the litter to ammonia, which is responsible for air pollution. Reducing the nitrogen content in feed will reduce the ammonia produced from chicken manure. Air pollution will be reduced as well through proper litter and manure management programs. The following discussion is a summary of research on the comparison of the chicken large intestine to the swine large intestine and cattle rumen. It will focus on the nutrient reactions in chicken large intestine.

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Anatomy and Physiology of the Pig Large Intestine Compared to Cow Rumen

The space found within the gastrointestinal tract (GIT) is an occluded part of the animal's environment. There are three functional regions found in the pig's digestive tract: the stomach, small intestine and large intestine. All digestion that takes place in the large intestine is microbial (Bryant, 1974). Leser et al. (2000) reported that when swine were experimentally infected with *Brachyspira hyodysenteriae*, the organism causing swine dysentery, many of the T-RFs fluctuated, which suggested that the microbial community was destabilized. These scientists were comparing bacterial communities in the large intestine of swine using terminal restriction fragment length polymorphism (T-RFLP) analysis targeting the 16S ribosomal DNA. The *Bifidobacterium* spp. population found in fecal samples from suckling piglets has also been investigated (Mikkelsen et al., 2003), with results showing that the population of bifidobacteria in the feces of suckling pig is numerically low, and a phylogenetic analysis of the 16S rRNA gene from bifidobacterial isolates suggested that a new bifidobacterium species had possibly been isolated. Beerens, raffinose-*Bifidobacterium* (RB), and modified Wilkins-Chalgren (MW) agar media did not selectively grow bifidobacteria from the fecal samples. Microbial fermentation uses as a substrate the material that escapes hydrolysis and absorption of passes through the small intestine. The low oxygen tension and absence of readily fermentable substrates in the large intestine limit microflora to scavenging residues that escape enzyme digestion in the small intestine. These microorganisms release volatile fatty acids (VFA), amines and ammonia from the nitrogenous compounds found in this residue (Colin, 1886). Swine have similar microflora in their large intestine as that found in the rumen (Salanitro et al., 1977), but there are quantitative differences between the dependence of microbial growth upon ammonia concentration. This indicates that there is some regulation of microbial activity by the availability of nitrogenous compounds in the rumen and large intestine (Baylay, 1978).

Fibrous diets are normally fed to horses and cattle; these are normally digested in the large intestine of the horse which is its major part of the digestive tract while this diet is digested primarily in the rumen of the cow, with little material that can be fermented passing into the hindgut (Rerat, 1978). The digesta

passes into the large intestine before being voided in the feces, and the only changes that occur in the digesta here are due to microbial fermentation. In healthy animals, the microflora of the large intestine only receives the ingesta that has escaped digestion in the stomach and small intestine. Potentially useful compounds formed by the microorganisms are of no value to the host animal unless they can be absorbed before the digesta is voided.

The inhibitory effect of fermented feed on the bacterial population of the gastrointestinal tract has been studied *in vivo* with pigs (van Winsen et al., 2001). Results demonstrated a significant positive correlation between pH and *lactobacilli* in the stomach contents of pigs fed dry feed as well as in the stomach contents of pigs fed fermented feed. The bacterial ecology of the gastrointestinal tract was influenced by fermented feed and the levels of *Enterobacteriaceae* were reduced in the different parts of the gastrointestinal tract. Hojberg et al. (2003) reported fermented liquid feed (FLF) fed to pigs had a great impact on the indigenous microbiota, as measured by bacterial numbers, short-chain fatty acid concentration, and substrate utilization. However, completely different mechanisms may be involved in the proximal and the distal parts of the gastrointestinal tract. In cows fed rations without antibiotics, cellulose digestion in the rumen was higher ($P < 0.01$) at 24, 30, 48 and 72 h; fungi had almost disappeared by 24 h, while bacterial concentration increased over 100-fold in 24 h and then decreased gradually up to 72 h. In cows fed rations with added antibiotics, fungal concentrations increased 4-fold by 30 h and up to 42-fold at 72 h; bacterial concentrations were markedly reduced by 24 h and remained low through 72 h (Dehority and Tirabasso, 2000). Streptococci isolated from rumen sources were tested for the production of antibacterial compounds using a deferred-antagonism plating assay (Whitford et al., 2001). The characteristics of the isolated antibacterial peptide were very similar to those described for class II bacteriocins of gram-positive bacteria. Mackie et al. (2003) investigated the ecology of the uncultured rumen bacterium *Oscillospira* spp.. They suggested *Oscillospira* species were commonly present in various rumen ecosystems with the level, and most likely the morphological form, dependent on diet. The highest counts were associated with the feeding of fresh forage diets to cattle and sheep. Grauke et al. (2002) studied sheep and cattle experimentally

inoculated with *E. coli*. They reported that the colon is the site for *E. coli* O157:H7 persistence and proliferation in mature ruminant animals.

The VFA transport across isolated gastric and large intestinal mucosa has been examined (Argenzio and Southworth, 1974). All four types of gastric mucosa (cardiac mucosa, stratified squamous, proper gastric and pyloric mucosa) absorbed and transported VFA at substantial rates. Mucosa of pig caecum and colon transported VFA at much greater rates than gastric mucosa and greater rates than previously determined in equine large intestinal mucosa or even bovine rumen epithelium (Argenzio and Southworth, 1974). A possible energy contribution by acetic, propionic and butyric acids in the pig was calculated to be between 184 and 330 kcal daily or 15 and 28% of the maintenance energy requirement (Friend et al., 1964; Imoto and Namioka, 1978). Farrell and Johnson (1970) reported that pigs on a 26%-cellulose diet had larger amounts of digesta in the caecum, and lower caecal retention times, than pigs on the 8%-cellulose diet. They said that measurements of production rates of VFAs in the pig caecum indicated that only 2.7% 1.9% of the apparent digestible energy of the 26% - and 8%-cellulose diets respectively came from the acids, and it was concluded that the caecum played only a small role in the breakdown of feed substances.

Properties of fibre believed to be important in nutrition include solubility and water holding capacity (Bjorck et al., 1984), particle size (Khalon et al., 1986) and fermentability (Cummings et al., 1978; Ehle et al., 1982). Starch is a molecule made up of alpha-linked chains of glucose that are stored by plants in crystalline granules. There is a great variation in the rates of fermentation and digestion, depending on the processing, storage method, and plant source of the starch. When starch ferments, lactic acid may form (Englyst and Cummings, 1985). Corn and wheat starches are well digested in the small intestine, whereas raw potato starch granules accumulate in the caecum where they are attacked by bacteria (Baker et al., 1950). Konstantinov et al. (2004) studied the responses of ileal and colonic bacterial communities of weaning piglets to four fermentable carbohydrates (inulin, lactulose, wheat starch, and sugar beet pulp) added to their diets. Their results indicate that fermentable carbohydrate addition supports the growth of specific lactobacilli in the ilea and colons of weaning piglets. The

digestion of starch in the small intestine is 15 to 40 times higher than in the large intestine, the latter being only little concerned with cereal digestion (Holmes et al., 1973). Numerous compounds (ranging from 30 to more than 200) have been identified from the anaerobic degradation of livestock manures (Hartung and Phillips, 1994; Hobbs et al., 1995). Mikkelsen et al. (2004) investigated the effect of feed grinding (fine and coarse) and feed processing (pelleted and nonpelleted) on physicochemical properties, microbial populations, and survival of *Salmonella enterica* serovar. *typhimurium* DT12 in the GIT of pigs. It was concluded that feeding a coarsely ground meal feed to pigs changes the physicochemical and microbial properties of content in the stomach, resulting in a decreased survival of *Salmonella* during passage through the stomach. The stomach acts as a barrier in this way preventing harmful bacteria from entering and proliferating in the lower part of the gastrointestinal tract.

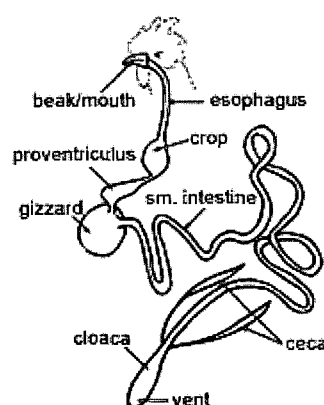
Sutton et al. (1999) indicated that primary odour-causing compounds in pig evolve from excess degradable proteins and lack of specific fermentable carbohydrates during microbial fermentation. The volatile compounds have been placed into the general groups of volatile amines, sulfides, disulfides, organic acids, phenols, alcohols, carbonyls, nitrogen heterocycles, esters, fixed gases and mercaptans (Miner, 1975). A precise adjustment of dietary protein and amino acid supply to the specific requirements of the pig (Henry et al., 1979) at the different physiological stages is the first approach to reduce nutritional N losses. Manure production in livestock animal is a major problem because of its nitrogen (N) and phosphorus (P) content, in relation to environment: gaseous ammonia emission causing in pollution and the leaching of nitrates and eutrophication of P after spreading manure leading to water pollution (Lee and Coulter, 1990). An adhesion-promoting protein involved in the binding of *Lactobacillus fermentum* strain 104R to the small intestinal mucus of piglets and to partially purified gastric mucin has been isolated and characterized (Rojas et al., 2002). The purified protein could be digested with protein trypsin. Alignment of amino acids of the adhering peptides showed poor homology. This protein represents an important molecule for probiotics. Under the title of "The influence of diet crude protein level on odour and ammonia emissions from finishing pig houses", Hayes et al. (2004) reported that the odour emi-

ssion rate per livestock unit (500 kg) for the 130, 160, 190 and 222 g kg⁻¹ crude protein diets were 77.6, 80.0, 115.8 and 102.9 OU_ES⁻¹LU⁻¹ (OU_ES⁻¹ = Odor emission rate, OU_E = Odor equivalent, LU = Livestock Unit) respectively ($P \leq 0.01$). The ammonia emission rates per animal for the 130, 160, 190 and 220 g kg⁻¹ crude protein diets were 3.11, 3.89, 5.89 and 8.27 g d⁻¹ animal⁻¹, respectively ($P \leq 0.01$).

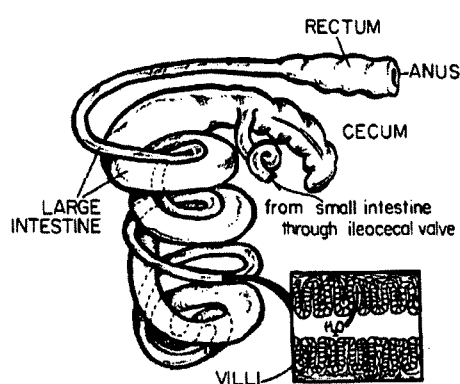
Physiology and Anatomy of the Chicken Large Intestine

There are large differences between species both from an anatomical point of view (Simic and Ilic, 1976) and in terms of rate of passage of digesta (Hecker and Grovum, 1975). Thus, the large intestine is relatively less developed in the chicken, a species having a rapid passage of digesta and it is more voluminous in mammals. The pig with its functional large intestine is better able to utilize fibrous cereal milling by-products as an energy resource than poultry (Elsden et al., 1946). Chicken and swine have major anatomical differences (Fig. 1). Chickens have two large caeca and a short colon, branching from the ileocolonic junction (Clark, 1978), while swine have one short caecum and a long colon.

Considerable attention has been directed to the physiology of the caeca of the chicken. Browne (1922) regarded the caeca as playing as unimportant part in digestion; in his opinion, they were mainly for absorptive purposes. Caecotomy has almost no effect on cellulose digestibility; however, such a conclusion cannot be generalized on account of the low cellulose contents of the diets used (Loyd et al., 1958). Chicken caeca do not contribute significantly to the digestion of dietary fibre (Nakahiro et al., 1974; Nahm, 1984). And there is almost no absorption of nutrients in the hindgut of the chicken, so researchers now measure the material in the posterior ileum (Silversides and Bedford, 1999). Feed compounders play an important role in the modulation of gut microflora and consequently in prevention of gastrointestinal disorders in broiler chickens (Apajalahti et al., 2001). Feed withdrawal does not always effectively evacuate the contents of the caeca and the caeca of broilers subjected to feed withdrawal can remain a source of foodborne bacterial pathogens (Hinton et al., 2000).



Chicken Gastrointestinal Tract (Vent = Anus)



Pig Intestinal Tract

Fig. 1. The colon of the chicken is below the cecum and above the rectum. The cloaca is a common chamber to the digestive, urinary and reproductive passages, which opens externally at the vent (Card and Nesheim, 1972).

The types of microbes found in the large intestine of the chicken are very similar to those found in the rumen. Microbial populations also vary according age, diets, maturity, antibiotics, etc. (Hofacre, 2005; Tellez, 2005). The caeca provide a habitat for numerous micro-organisms (Barnes et al., 1972) and various species of protozoa and helminthes (Cromptons and Nesheim, 1976). *Lactobacillus crispatus* and *Clostridium lactofermentans*, both isolated from the caeca of chicken, grown together in an *in vitro* model system are able to ferment lactose to acetate and propionate (Van Der Wielen et al., 2002). Under *in vivo* conditions applied in this study a mixture of *L. crispatus* and *C. lactofermentans* with dietary lactose was able to increase lactate concentrations but was unable to increase concentrates of ace-

tate and propionate in the caeca of broiler chick caeca. Also caecal functions attributed to the avian caeca include water absorption, carbohydrate digestion, protein digestion and vitamin synthesis and/or absorption (McNab, 1973). These functions are performed almost entirely by the microbial population of the caecum, which is reported to resemble ruminant populations in size and complexity (Savage, 1986).

Knarreborg et al. (2002) studied the effect of dietary fat source (soy oil or a mixture of lard and tallow) and dietary supplementation with antibiotics (a combination of avilamycin at 10 mg kg of feed⁻¹ and salinomycin at 40 mg kg of feed⁻¹) on the bacterial community in the ileum of broiler chickens at different ages (7, 14, 21, and 35 days). Bacterial enumeration results showed that the composition of the microflora was age dependent and influenced by dietary fat source and antibiotic supplementation. *Lactobacilli* and *C. perfringens* were the bacterial groups most strongly affected by the dietary treatments. Different strains (clonal variants of the alpha-toxin gene) of *C. perfringens* type A were detected in response to age, dietary fat source, and dietary supplementation with antibiotics. The microbiota of the intestinal tract of chickens plays an important role in inhibiting the establishment of intestinal pathogens (Zhu et al., 2002). These scientists reported that sequences most closely related to those of the other bacteria were generally 97 % or less identical to those in the data bases and therefore might be from currently unknown species. Random cloning indicated that certain phylogenetic subgroups were common to all birds analyzed and provided evidence for qualitative and quantitative differences among the caecal microbiota of individual birds reared under very similar conditions. *In vitro* adherence of *Lactobacillus* strains to cell and tissue types along the chicken alimentary tract and to ileal mucus were determined (Edelman et al., 2002). However, no adherence to the apical surfaces of undifferentiated enterocytes, the mucus-producing goblet cells, or the ileal mucus was detected.

A study (Van Leeuwen et al., 2004) of the morphological response of the villi of the small intestinal mucosal surface to a stimulation of microbial activity in the digesta after addition of highly methylated pectin to the soybean meal (SBM) diet was conducted. By day 21 the birds fed the pectin diet had decreased weight gain and higher feed conversion. The mucosal surface was affected by the pectin through decreasing the area

with the zigzag pattern and increasing the area with convoluted, mainly ridge-shaped villi. *Salmonella typhimurium* infection increased the detrimental effects of pectin on performance and mucosal morphology.

The relative volume of the large intestine (caecum, colon and rectum) in the pig was 38% of the entire GIT with 29% in stomach and 33% in small intestine (Colin, 1886). The length of caecum as well as rectum and colon in chicks was 5 cm and 4 cm at 20 days after hatching, and 18 cm and 11 cm at 1.5 years after hatching, while the length of duodenum as well as ileum and jejunum was 12 cm and 49 cm at 20 days after hatching, and 20 cm and 120 cm at 1.5 years after hatching (Swenson, 1977). Nahm (1984) reported that the levels of gut dimensions were 76.5 cm in proximal small intestine, 51.5 cm in distal small intestine, 16.2 cm in caecum and 7.0 cm in colon and rectum after 6 weeks of hatching. The large intestine (colon and rectum) of the chicken was 4.6 %, caecum is 8.1 %, while small intestine in chicken is 63.2 % (Jurgens, 1974).

The microbial community is distributed along the entire GIT of broiler chickens and the major region for anaerobic bacteria is the caecum (Barnes et al., 1980). Previously unknown species of bacteria represent 90 % of the bacteria in the chicken GIT (Lan et al., 2002). Earlier culture-base studies found that host factors such as age influence the composition of the caecal microbiota (Mead and Adams, 1975). Occasionally it was found that strains of anaerobic bacteria isolated from the predominant flora of 4- to 14-d-old birds could not be grown when tested by the conventional method. During the 14-d period, approximately 100 % of the organisms isolated on anaerobic plates utilized uric acid up to the third day but the incidence subsequently declined and in one case represented only 4 % of the total flora. In contrast, the microbial population of the caecum is established at a later age than the small intestine. The establishment of microbial communities in the caecum requires 6~7 weeks (Coloe et al., 1984). The caecum is colonized by a large variety of facultative and strictly anaerobic organisms. Isolates have included fecal *Streptococci*, *Chlostridia*, *Enterobacteria*, *Pediococci* and occasionally *Pseudomonas aeruginosa*. After one day of feeding, there is much variability in the numbers of lactobacilli in the caeca, but by the third day of feeding, there are large numbers of bacteria found throughout the alimentary tract. A large number of these species are transient,

but after 40 days the flora stabilizes, consisting predominantly of fecal *Streptococci*, *Escherichia coli*, *Bacteroids* spp., and *Lactobacillus* spp. (Coloe et al., 1984). Although the intestinal mucosa which strain was structurally developed at hatch, there was much change in structure with age, especially over the first 7 days post hatch (Lji et al., 2001). The rate of development was most rapid in the jejunum but the other regions are also important, on account of villus height or relative length of the region.

Six group-specific 16S rRNA-targeted oligonucleotide probes were used in one study to investigate the composition of the microbiota in caecal contents and mucus from broiler chickens (Zhu and Jergert, 2003). In the caecal contents from 1-wk-old chicks, all six probes gave signals, and in samples from 6-wk-old birds approximately 3, 9, 6, 32, 22, and 8% of the bacteria detectable with the universal probe hybridized with the probes Enter 1432, Lacto 722, Bif 164, Clept 1240, Erec 492, and Bacto 1080, respectively. At 6 weeks of age, the six probes detected the phylogenetic groups in similar proportions in the microbiota of caecal contents and caecal mucus.

In the 108 h post hatch, a rapid transition takes place from total jejunal epithelial cell proliferation and immature crypts to a defined proliferative zone in the crypts, having constant division and migration (Uni et al., 2000). Sklan and Noy (2003) determined absorption, secretion of digestive enzymes and intestinal morphology in poult from hatching to 19 d. According to their study, in the posthatch poult intestinal surface area is not a limiting factor for growth, which was correlated with digestive secretions, fat and protein uptake. Another study showed that more increased intestinal growth (weight and length) and maturation (villus length) allowed ducks to achieve an additional 143 g of bodyweight gain during the critical hatch through 7 days of growth (Applegate et al., 2005). At 5 weeks posthatch the absolute mass of the small intestine in domesticated ducks declined by 38% (Watkins et al., 2004). They reported that there is no obvious explanation for this decline because the masses of other digestive organs, daily feed intake and body mass continued to rise.

Recently studies have shown that energy, VFA and electrolytes such as sodium have been produced by microorganisms found in the chicken's large intestine. Some of these nutrients may be absorbed from the large intestine and affect the nutrient

balance of the chicken (Tellez, 2005). Gel-Garber et al. (2003) reported that the Na^+ - K^+ -ATP use, localized in the basolateral membrane of enterocyte, contributes significantly to nutrient transport in the small intestine by transferring K^+ ions into- and Na^+ out of the cell. Within the enterocyte, homeostasis is maintained by active exclusion of Na from the cell by Na^+ , K^+ -adenosine triphosphatase (ATPase) or the sodium pump.

VFA are known to inhibit growth of species of the family *Enterobacteriaceae* *in vitro*. However, it is unknown whether these VFAs affect bacterial populations in the caeca of chicken (van der Wielen et al., 2000). Their study showed that members of the *Enterobacteriaceae* and enterococci are present in large numbers in 3-day old broilers and start to decrease when broilers grow older. Lactobacilli are present in large numbers as well in 3-day-old broilers, but they remain stable during the growth of broilers. Acetate, butyrate, and propionate increase from levels that cannot be detected in 1-day-old broilers to high concentrations in 15-day-old broilers, after which they stabilize. Growth rates and maximal optical density decreased when these strains were cultured in the presence of increasing VFA concentrations. This study concluded that VFAs are responsible for the reduction in members of *Enterobacteriaceae* in the caeca of broiler chickens during growth. Lactic acid and short-chained fatty acid (SCFA) are the primary products of the fermentative part of microbial activity. Re-absorption of water is stimulated by the microbial populations in the caeca (Mead, 1989). Kubena et al. (2001) indicated that caecal concentration of VFA can be affected by toxins, such as high concentrations of T-2 toxin, and that resistance to *Salmonella* colonization may be reduced. Further research is necessary to determine the biological significance of these changes.

The final stages of digestion in the chicken are accomplished by brush border enzymes in the small intestine, which is primary site of chicken digestion. The size, morphology, and mucosal enzyme activity of small intestines in poult were determined from hatch to 12 d of age (Uni et al., 1999). Mucin glycoproteins are important in the regular function of the epithelium of the gastrointestinal tract. Changes in mucin dynamics affects the absorptive and protective functions of the small intestine (Uni et al., 2003). Mass and length increased at different rates in the duodenum, jejunum, and ileum and mass increased more than length. Intestinal weight increased more

rapidly than other body organs, reaching a peak at about day 6, and then decreased. Villous height and area increased several fold in the jejunum and duodenum and less in the ileum over this same period.

Activities of mucosal enzymes also increased at different rates in the different intestinal segments and sucrase, maltase, and α -glutamyltransferase activities per gram of intestine peaked at 2 to 5 day posthatch before decreasing. The secretion of pancreatic enzymes per gram of feed intake did not change significantly with age (Noy and Sklan, 1997). In contrast, there have been reports of increases in mucosal disaccharidases and alkaline phosphatase activity in hatching chicks, with the peak activity of disaccharidases reported at 2 days of age (Uni et al., 1998). Villous size and area initially rapidly increases in the 1 to 2 day old posthatch chicks, but the rate of growth then declines and reaches a plateau 5 to 10 days after hatch (Uni et al., 1995, 1996). Compared with germ-free chicks, conventional chicks have an increased proteolytic activity and a decreased amylase activity (Philips and Fuller, 1983). Net duodenal secretion of amylase, trypsin, and lipase was lower at 4 days and increased 100-, 50-, and 20- fold, respectively, by 21 days. Enzyme activity decreased in the small intestine and this change was greater with age (Noy and Sklan, 1995). During the first 21 days in poults, amylase and trypsin concentrations in the pancreas increase considerably (Krogdahl and Sell, 1989), and starch digestion has been found to not be limiting in young chicks (Moran, 1982). The concentrations of pancreatic lipase increased less posthatch and may be limiting in some diets (Krogdahl and Sell, 1989). Fat digestion has been shown to increase during the initial weeks after hatching (Carew et al., 1972; Krogdahl and Sell, 1989). Supplemental bile salts have been shown to enhance fat digestion in 7-day-old chicks (Polin and Hussein, 1982). The activity of digestive enzymes can be affected by the GIT bacteria. This effect is related to bacterial metabolic end products and their influence on gut mucosal morphology and intestinal cell proliferation in the chicken (Palmer and Rolls, 1983). A critical review of this process has been described by Lan et al. (2005).

Nutrient Utilization in the Chicken Large Intestine

The amount of energy derived from diets may be influenced

by the rate of food passage (RFP) through the digestive tract (Kass et al., 1980) since this affects the length of time during which ingesta is exposed to the digestive enzymes and to the absorptive surfaces. RFP has been shown to be modified by several management and environmental factors such as temperature (Wilson et al., 1980), age (Hillerman et al., 1953), genetic background (Cherry and Siegel, 1978), excitement (Henry et al., 1979), amount of feed intake (Wilson et al., 1980), pelleting of the ration (Seerley et al., 1962) and fibrous diets (Hertz and Bar, 1966; Svihus et al., 2002). Mateos and Sell (1981) observed that supplemental fat decreased the RFP of semipurified, laying-hen diets containing either sucrose or starch. Mateos et al. (1982) reported that transit time, measured as percentage of marker recovered in excreta 10 hr after feeding, was faster for the control than for the fat-supplemented diets. There was a tendency for faster feed passage with additions of coarsely ground oat hulls, but no effect with supplemental finely ground oat hulls was found (Hetland and Svihus, 2001). Slower rate of passage improves nutrient absorption by increased time of contact with absorptive cells and increases digestibility of dietary fiber by allowing more time for microbial fermentation (Washburn, 1991).

The most current successful methods to slow RFP have included non-digestible oligosaccharides, especially those containing fructose, xylose, galactose, glucose and mannose (Gibson and Roberfroid, 1993; Gibson, 1998). One surprising finding has been that sucrose thermal oligosaccharide caramel (STOP) has been shown to increase the populations of bifidobacteria in poultry studies (Orban et al., 1993, 1995a,b), but microbial populations in the pig were not significantly altered by STCP or antibiotics as seen in the average daily gain (ADG), AD feed intake (ADFI), feed efficiency, or cereal microbial populations (Orban et al., 1997). Scientists (Orban et al., 1993, 1995a,b) have found that STOP poultry enhances performance and increases caecal populations of bacteria.

Kubena et al. (2005) indicated that fructooligosaccharides (FOS) addition helps to improve chicken growth and activity of colonic bacteria resulting in improved host health. Their study showed that two levels of FOS (0.375 % and 0.75 %) added to a 90 % alfalfa + 10 % layer ration reduced invasion of organs by *Salmonella enteritidis* after a 9 day molt, and total VFA and lactic acid contents in the GIT were higher as well.

They indicated that it may be possible to feed a lower quantity of FOS and still retain the benefits of a higher dosage. Another study (Loddi et al., 2005) showed that broiler performance reduction due to *Salmonella* infections could be overcome by adding 0.5~1.0 kg mannanoligosaccharide (MOS) per ton of feed. The reduction in broiler growth performance due to a sub-clinical *Salmonella* infection could be overcome by adding MOS or MOS in combination with organic acid to the diet. It has been reported that oligosaccharides and polysaccharides are specifically utilizable by bifidobacteria (Yazawa et al., 1978).

Fermentation of galactooligosaccharides (GOS) results in production of flatulent gases (i.e., carbon dioxide, hydrogen, methane) which increase feed RFP and reduce nutrient digestibility (Coon et al., 1990). Water soluble and viscous beta-glucan, as well as arabinoxylan found in cereal grains interfere with nutrient digestion and the sticky droppings they produce may cause some health problems. The nutritive components of animal feed are often encapsulated by a cell wall and their utilization is prevented (Theander et al., 1989). Different levels of dietary mannan-oligosaccharide (MOS) administered for 16 wk to commercial male turkeys were evaluated for their effect on performance and on microbial activity in the GIT (Zdunczyk et al., 2005). The concentration of short-chain fatty acids in the caeca decreased with increasing amounts of MOS in a diet, especially acetate concentrations. Dietary MOS did not significantly affect the caecal populations of *Bifidobacterium* and *Lactobacillus*. The study showed that the population of caecal *Escherichia coli* was decreased, especially by the medium or high experimental treatment levels. Dose effects of dietary isomalto-oligosaccharides (IMO) on broiler growth performance and characteristics of the intestinal microflora were compared (Zhang et al., 2003). IMO supplementation did not affect the facultative microflora of the crop and caecum. However, the thymus index was increased significantly in chicks consuming diets containing 0.3 % IMO.

Different types of digestive organs, size of each digestive organ, level of intake, production, particle size and many other factors affect the carbohydrate requirement (Van Soest, 1994; Hall, 1997). Fibre is not a nutritionally, chemically, or physically uniform material. The energy content of cereal grains is generally related inversely to the fibre content since many of the fiber components, non-starch polysaccharides (NSP), may

not be digestible and available to the bird (Goodman et al., 1993). NSP complex could be summarized water-insoluble NSP and lignin and water-soluble NSP (Carre, 1991). Digestion of water-insoluble NSP is nearly zero in poultry (Carre, 1990), while birds are able to digest a major part of water-soluble NSP (Carre, 1991). In chicken, the contribution of energy derived from the formation of VFA has been reported as very small relative to the total need (Moran, 1982). Therefore, higher dietary fibre at the expense of starch and simple sugar has negative implications for the net energy value of the feed. Proper feeding of fibre in the chicken ration helps improve nutrient utilization and prevent cannibalism. Excess fibre in the chicken rations may, however, have negative effects on feed efficiency and body composition (Esmail, 1997). Sklan et al. (2003) reported that total small intestinal length and surface area were increased by high dietary crude fibre intake between 11 and 14 wks of age in the turkey. Crude fibre can be utilized to a certain extent by turkeys and concentrations of 60 g fibre/kg in the diet did not result in decreased performance after 6 wks of age.

The effects of a drug-free feeding program on broiler performance and intestinal morphology showed that feeding birds without growth promoters resulted in higher mortality and decreased growth performance, and the combination of Bio-Mos and All-Lac XCL helped to reduce negative effects (Sun et al., 2005). Engberg et al. (2004) carried out a study to investigate these effects of different forms of wheat (airtight silo stored whole wheat, conventionally stored whole wheat, and ground wheat included in pellets) and dietary xylanase addition on production and gastrointestinal characteristics of broiler chickens. Whole wheat feeding improved feed conversion ratio, reduced water consumption, increased the relative weight of the pancreas and gizzard and the dry matter concentration of gizzard content, reduced the pH in the gizzard contents, increased ileal viscosity and reduces the ileal and caecal numbers of *Clostridium perfringens*. The addition of xylase reduced ileal viscosity in birds receiving whole wheat and increased chymotrypsin and lipase activities. Taylor and Jones (2004) reported similar findings which showed evidence of a complex interaction between higher viscosity and pH being involved in differences in ileal relative mass was found through significant relationships being produced by enzyme use on the wheat diet alone. Vitamin C decreased *in vivo* viscosity by 20 % but did not affect perfor-

mance. Both enzyme forms gave similar improvements in performance in the absence of copper sulphate (Marron et al., 2001).

Wu et al. (2004) reported that another effect of whole wheat supplementation was an improvement in performance when whole wheat was included post-pelleting. It was postulated that this improvement was due to increased gizzard size and improved AME. This hypothesis does not explain improvements in performance when whole wheat is supplemented pre-pelleting and suggests the involvement of other factors. A complete pelleted feed was compared with free choice feeding of whole wheat and a pelleted protein concentrate, given from 7 to 29 days of age in broiler chickens (Gabriel et al., 2003). This study indicated that whole grain feeding increases the chemical (pepsin in proventriculus) and physical (gizzard muscle) function of the upper GIT but decreases the digestive capacity of the intestine. The lower digestive enzyme activities in the intestine may be detrimental in when there is mucosal deterioration caused by intestinal disease.

According to investigations using microflora from chicken caeca (Guo et al., 2003), two medicinal mushrooms (*Lentinus edodes*; *Tremella fuciformis*), and materials (*Astragalus membranaceus*), particularly their polysaccharide extracts, show promise in altering microbial activities and composition in chicken caeca. Plasma concentrations of Na, glucose, triglycerides, and phospholipids were not influenced by feed deprivation; however, nonesterified fatty acid concentrations were enhanced in feed-deprived poult, indicating a greater use of fatty acids for energy. Maneewan and Yamauchi (2004) demonstrated that protein is the most important nutrient needed for the recovery of intestinal villi after feed withdrawal.

No damaged epithelial cells were observed in the chicken GIT due to consumption of acidified drinking water (Chaveerach et al., 2004). Acidified drinking water could play a crucial role in a biosecurity strategy for preventing *Campylobacter* spread via drinking water in broiler flocks. No significant differences were observed for numbers of *Salmonella* caecal culture-positive chicks or in the numbers of *Samonella typhimurium* in the caecal contents the dietary content of tannic acid was changed (Kubena et al., 2001). Further research is necessary to determine the biological significance of these changes. King et al. (2000) demonstrated that nutrient utilization in the

White Peking duck was lower in the group fed the high tannin sorghum cultivar than from the low-tannin sorghum cultivar. Their results also suggested that the anti-nutritive effects of tannins in foodstuffs are due partly to their inhibitory effect on intestinal brush border bound amino acid transporter proteins.

Batal and Parsons (2002) compared the growth rates of chicks fed a crystalline amino acid (AA) diet to a corn-soybean meal diet. The reduced growth of chicks fed a crystalline AA diet is due partially to slower growth and development of the gastrointestinal tract. The level of crude protein, protein source, and AA content of diets affect the growth of *C. perfringens* in the lower intestinal tract of the broiler chicken and might be a predisposing factor to out breaks of clinical necrotic enteritis (Drew et al., 2004).

Ascites occurs through an imbalance between available oxygen and the oxygen demand of the broiler. Solis de los Santos et al. (2005) hypothesized that promoting neonatal gut development with a prebiotic, such as *Aspergillus* meal (prebiotic-AM), would enhance gut efficiency, decrease the oxygen demand of the gut, and reduce ascites incidence. The simulated high altitude decreased gut development, but pre-biotic-treated birds reared in hypoxic conditions gut development that was similar to control birds reared at local altitude. Their study suggested that a feed ration supplemented with pre-biotic-AM reduced the effect of hypoxia on broiler gut development and incidence of ascites.

Caecal ligation and caecectomy in chicken have been studied, but their effects are a little different. The effect of caecal ligation (Son and Nahm, 1996) was an increase in feed intake, and water intake and excretion were increased significantly. The caecectomy tended to increase nitrogen balance and nitrogen utilization, but uric acid content (mg/kg body weight/day) decreased significantly (Son et al., 1996). It has been reported that caecal ligation and caecectomy improved nitrogen utilization and decreased urinary uric acid excretion in chicken (Karasawa et al., 1997).

Conclusion and Future Research

Anatomically and functionally the chicken's large intestine is very different from the cow's rumen or the pig's large intestine.

The chicken's large intestine is less developed than that of other animals and it also has a rapid rate of passage. The caeca of the chicken does not contribute significantly to the host animal with respect to fibre digestion (Moran, 1982). The function of the caeca includes water absorption, carbohydrate digestion, protein digestion and vitamin synthesis and/or absorption. These functions are performed almost entirely by the microbial population of the caecum (Coon et al., 1990). The primary site of digestion is the small intestine, with various enzymes being secreted here (Noy and Sklan, 1997).

Further research is needed in:

- 1) Complete identification of the microbial population in the GIT and large intestine (including the caecum)
- 2) Complete investigation into this starch digestion process in the chicken GIT and large intestine
- 3) Study on the role of NPS, STOP, FOS, MOS, GOS and IMO in the chicken large intestine
- 4) Complete study on the effects of caecal-ligation and caecotomy in the chicken

적 요

닭의 대장은 해부학적, 생리학적으로 돼지의 대장이나 소의 rumen과 다르다. 닭의 대장은 소의 rumen이나 돼지의 대장에 비교하여 잘 발달되어 있지 않다. 그러나 닭의 대장속에 있는 미생물군은 rumen 속의 것과 비슷하다. 특히 닭의 맹장속에는 많은 미생물이 있으며 이 미생물군은 나이, 사료, 성숙도의 정도, 항생제 사용 유무 등에 따라서 다양하게 나타난다. 단백질은 장내의 미생물 형성에 중요한 영양소이다. 닭에서 소장의 길이는 전장 길이의 65%를 차지하며 닭의 맹장은 8.1 % 그리고 직장과 공장은 4.6 %를 차지한다. 소장 내에 분포하는 미생물 군은 현재까지 약 10%가 구명된 상태로서 나머지 90%에 대한 정보는 전무하다. 최근의 연구에 따르면 에너지, 저급지방산 (VFA)과 그리고 전해물질이 대장에서 약간씩 흡수되는 것으로 알려져 있다. 닭의 소장은 각종 효소등이 분비되어 소화가 일어나는 중추적인 역할을 하는 것으로 알려져 있다. 앞으로도 많은 연구가 과당류 즉 sucrose thermal oligosaccharide caramel (STOP), fructooligosaccharides (FOS), mannanoligosaccharide (MOS), galactooligosaccharide (GOS) 그리고 isomaltoligosaccharides (IMO)등이 맹장과 대장내에서 어떻게 소화가 일어나는지에 관해서 집

중되어야 한다. 과량의 섬유질 함량은 닭의 소화에 치명적일 수 있지만 적당량을 사료에 혼합하여 급여하면 소장의 길이와 함량을 증가시킬 수 있는 효과가 있다.

(색인어 : 맹장, 미생물군, 총 소화관, 저급 지방산, STO, FOS, MOS, GOS, IMO)

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