DIGESTIVE PHYSIOLOGY

- *See Kidder and Manners (1978), Maynard et al. (1979), Davenport (1982), Moran (1982), Swenoen and Reece (1993), Kellesm and Church (1998), Yen (2001) in Lewis & Southern (2001), Jurgens (2002), and others for details/additional information.*

INTRODUCTION

1. **Classification of Various Digestive Systems?**

   A. Variations among the GI tracts of the common domestic animals are related to the type of diets they consume & utilize.
   B. Generally, animals are classified into groups based on their type of diet . . . with many subgroups:

      1) Herbivores - Animals that consume primarily plant materials.
      2) Carnivores - Animals that eat other animals.
      3) Omnivores - Animals that eat a combination of plant and animal matter.

   C. Classifying animals based on their digestive physiology?

      1) Nonruminant animals

         a) Pigs - Nonruminant animals that are omnivorous, thus consume both plant and animal matter.
         b) Poultry - Nonruminants that are omnivorous, and they have a complex foregut (three sections that replaces the normal stomach) and a relatively simple intestinal tract.
         c) Dogs and cats - Nonruminant animals that are carnivorous.
         d) Horses and mules - Nonruminant animals, but they are herbivorous and have a rather large and complex large intestine.
         e) Rabbits - A nonruminant animal that is a herbivore with a complex large intestine.

      2) Ruminant animals

         a) Capable to consume and digest plant materials and classified as herbivores.
         b) Include cattle, sheep, goats, deer, elk, and many other wild species.

2. **Similarities & Differences Between Pigs & Poultry**

   A. Similarities?

      1) Are nonruminants, thus less "meaningful" symbiotic relationships with microorganisms along the gastrointestinal system vs ruminants.

2) Need amino acids, not protein *per se*.
3) Have a limited ability to utilize fibrous components of the diet.
4) Diets consist predominantly of grains and soybean meal in the modern production system, ∴ more susceptible to mineral and(or) vitamin deficiencies.
5) Are raised in confinement facilities in the modern production system.
6) Are relatively fast growing & efficient in conversion of feed to body tissues.

B. Differences

1) Pigs are delivered in the "litter," and chicks are hatched from the "egg" - "Chicks" embryonate away from its dam, ∴ eggs must contain all essential nutrients before being laid/incubation!
2) Pigs have hair, and chicks have feathers - "Chicks" - Feathers make up a relatively larger proportion of body weight, ∴ influencing the requirement for certain amino acids.
3) Pigs have an immature digestive system at birth, whereas chicks have a full complement of digestive enzymes at hatching - "Chicks" can utilize corn and soybean meal diets efficiently from day one, whereas baby pigs must depend on milk or milk-based diets!
4) Chicks have higher metabolic rate, respiration rate and heart rate. (May want to read : "Schmidt-Nielsen, K. 1970. Energy metabolism, boy size, and problems of scaling. Fed. Proc. 29:1524-1532.")
5) Laying hens mobilize large amounts of Ca, and are susceptible to leg problems. (Also true for lactating sows!)
6) Chicks have a different digestive tract and digestive process:

   a) No teeth.
   b) Have a crop and gizzard, and no true stomach for storage or enzyme secretion.
   c) Have two ceca which contribute little to digestion.
   d) Have a very fast rate of digesta passage.
   e) Absorb fatty acids via portal system - Lymphatic system is poorly developed.
   f) Excrete N as "uric acid" - Influences the requirement for certain amino acids, and dietary metabolizable energy values.

3. **How About Horses and Ruminant Species?**

A. Horses?

1) Classified as one of the nonruminant species based on the anatomy of the digestive tract.
2) But, more specifically, the horse is a "hind gut fermenter," thus may have some advantages of both nonruminant and ruminant species in terms of satisfying the protein/amino acid and vitamin needs, an also the utilization of fiber.
3) Horses & digestive system?

a) Horses may have evolved as a continuous grazer and better equipped to utilize small frequent meals rather than large meals of readily fermentable concentrates.
b) Their digestive system can be easily overwhelmed, and develop various problems such as excessive gas production, colic, stomach rupture, laminitis, etc.

4) Feed to maintain hindgut function:

a) Maximize the contribution of forage - Ensure adequate fiber intake.
b) More frequent, smaller meals - Regularity of feeding might be crucial.
c) Reduce carbohydrate overload of the cecum - Manage the feeding program to promote gut homeostasis.

B. Ruminant species?

1) Ruminants, so named because they ruminate (chew the cud).
2) There are major modifications of the GI tract relating to the stomach area, which is divided into four compartments - a nonsecretory forestomach and a secretory stomach compartment.
3) A few species (such as the camel & related species), the stomach has only three compartments, thus classified as pseudoruminants.
4) In herbivores, 20% or more of the diet may consist of substances that can be digested only by the action of microorganisms.
5) Ingested feed is subjected to very extensive pregastric microbial fermentation:

a) Most of the ingesta (60 to 75%) are fermented by microbes before being exposed to the gastric and intestinal digestive processes.
b) Thus, very different system vs a typical nonruminant animal.

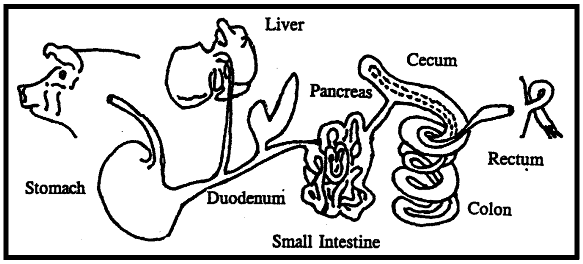
6) The symbiotic relationship between microorganisms and host is developed to the highest degree in ruminants simply because the rumen provides the favorable environment.

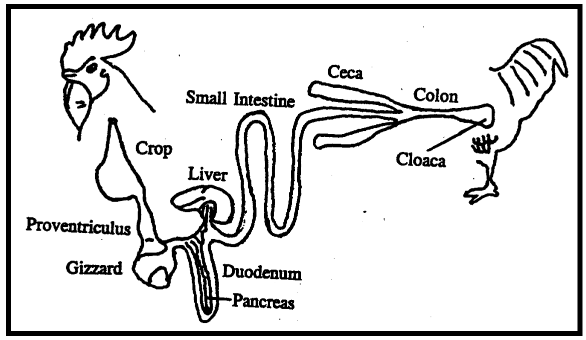
FROM FEED DETECTION TO ESOPHAGUS

1. Food/Feed for Our Animals?

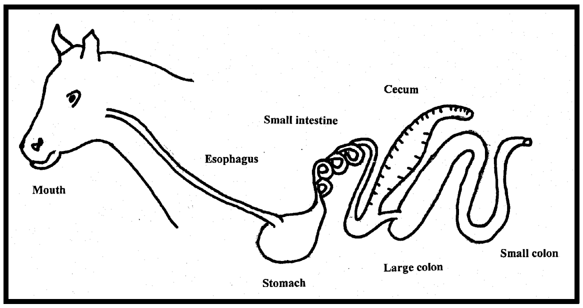
"*We feed our horses hay and oats, with grass for cows and sheep and goats.*
Chickens look for grain to eat, while ducks find worms, and dogs get meat.
Cats have meat and milk and fish.
To each, its own peculiar dish. Some are fussy, others not,
but pigs, of course, will eat a lot.
(Kidder & Manners, 1978)

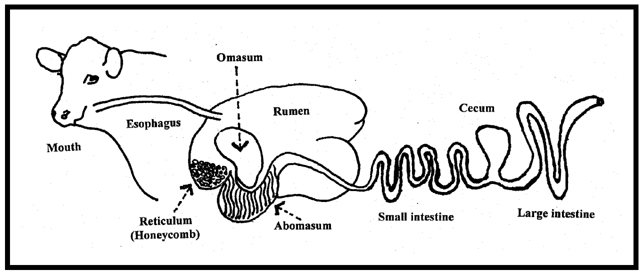
2. **Pig's & Fowl's Gastrointestinal System** [Redrawn from Moran (1982)]





3. **Horse's & Cattle's Gastrointestinal System** [Redrawn from Jurgens (2002)]





4. **Sight & Smell**

A. Normally, all domestic species use their eye to some degree in finding food, thus it must be considered as one of the initial steps/aspects of nutrition.
B. Smell & taste have a great effect on the palatability and consumption of feedstuffs:

1) Much remains to be learned about the interaction of the chemical sense in determining food intake & their practical applications.
2) Goats - Enjoy a wide variety of plants that are distasteful to others because they do not have taste receptors that correspond to bitter taste sensations in humans.
3) Cattle prefer Bermuda grass to many other kinds of forage, but may eat poisonous weeds that they usually ignore when forage is scarce, indicating they can distinguish feedstuffs, perhaps based on smell and(or) taste.

C. Some proposed models on food preference in ruminants [Pisani, J. M. (Accessed 2005). http://canis.tamu.edu/wfscCourses/Concepts/FoodPref.html]:

1) Euphagia - Animals would have preprogrammed capacity to recognize nutrients and toxins through the smell and taste?!
2) Hedyphagia - Animals harvest nutritive food because they are pleasant to smell, taste and touch. Contrarily, animals avoid toxical foods because they smell and taste bad.

3) Body morphology and size:

   a) Morphological adaptations of ruminants constrain the range of foods they can eat.
   b) Mouth size, mobility of lips, form of teeth & development of multichamber stomach determine that some are grassers (e.g., cattle, sheep, bison), browsers (e.g., giraffe, deer, some antelopes), or mixed (e.g., goat, some antelopes).
   c) Smaller animals - Should select foods with high digestibility because of their higher metabolic rate vs larger animals.

4) Learning through foraging consequences - Based on positive or negative "postingestive feedback" as determinant of food preferences, which involve possibly taste receptors (olfactory) and viscera receptors.

D. Pigs and poultry:

1) Fowl and pig retinae have both rod and cone cells, thus they can see "color" - It is thought that primates, birds, reptiles, amphibians and fish perceive color much better than domestic mammals such as pigs.
2) Birds have poor sense of smell, thus they depend mostly on acute eye sight in seeking food, whereas pigs are completely opposite!
3) Poultry:

   a) Eyes occupy a larger proportion of head in fowl than in pigs, and also domestic fowl's eyes are located laterally on the head (vs frontal in pigs), thus a much greater panoramic view or larger retinal image for birds vs pigs.
   b) Have a greater No. of visual cells communicating to the brain (vs pigs).
   c) Have a poorly developed sense of smell.
   ☞ Their sense of smell may be oriented toward other purposes, i.e., other than feed detection and(or) evaluation such as ascertaining "orientation & direction."

4). Pigs:

   a) Eyes are recessed and shielded, and also their eyes are located more frontally (i.e., about 70° visual axis) than other non-carnivorous animals, thus a lower visual capacity compared to birds. (Probably, the result of an evolutionary protective mechanism arising from extensive burrowing in the search of food?)
   b) Overall, pigs are well equipped with olfactory apparatus, and the sense of smell is used extensively in seeking/evaluating feeds. (Also, important in detection of sex steroids, identification of individuals, etc.)

5. **Mouth**

A. Prehension:

1) Refers to seizing and conveying of food to the mouth.
2) Vary among different animals, but the lips, teeth, and tongue are the principal prgans of this function.
3) The dog & cat often use their forelimbs to hold food, but it is passed into the mouth largely by the movement of the head and jaw.

B. The relative importance of the mouth and its components (teeth, tongue, cheek, and salivary glands) varies with species.
C. In most species, the functions of the mouth would be to bring in feed, mechanically brea it up, and mix it with saliva, which act as a lubricant to facilitate swallowing.
D. Pigs:

1) Snout for rooting & digging for food, lips for prehension, and cheeks to aid mastication and mixing.
2) Teeth? Incisors for biting, grazing, etc., molars for chewing to divide food into fine particles, thus increasing the surface area, and to mix with saliva for swallowing. Also, have canine teeth, which is long and sharp in the male.

E. Poultry:

1) No teeth and swallow their food whole.
2) Comprised largely of "hard" tissues, i.e., very little oral manipulation of food.
3) Thus, having a difficulty in consuming larger or smaller particles because:

   a) Cannot divide if too large, and
   b) Reduce the efficiency (i.e., need the additional work, which ↑ the energy expenditure) if too fine.

F. Horses:

1) Prehensive agents include teeth, upper lips, and tongue, but the sensitive, mobile lips during feeding from a manger.
2) During the grazing, the lips are drawn back to allow the incisor teeth to severe the grass at its base - Use both vertical & lateral movements of the jaws to shred fibrous plant materials.
3) Upper jaw is wider than lower jaw, thus mastication on only one side of the mouth at a time.

G. Ruminant species - Cattle & sheep:

1) No upper incisors & only an upper dental pad and lower incisors, which act in conjunction with lips and tongue for prehension of feedstuffs.

2) The lips have only limited movement, thus the tongue is the main perhensive organ.
3) The tongue is long, rough, & mobile - Can be readily curved through herbage, which is drawn between incisor teeth & dental pad & severed by movement of the head.
4) Because of the shape and spacing of the molar teeth, can chew only on one side of the jaw at the time - Lateral jaw movements can help shredding tough plant fibers.

H. Dogs and cats:

1) Carnivores, such as dogs and cats, often swallow large chunks of meat with little mastication.
2) The teeth are adapted to the tearing of muscle and bone, while the pointed molars are adapted for the crushing bones and also mastication of food to a limited extent.
3) Convey fluids to the mouth by means of the tongue - The free mobile end of which forms a ladle.

6. **Taste**

A. Total No. of taste buds in the mouth: [Kare & Ficken, 1963. In: Y. Zotterman (Ed.) Olfaction and Taste]

Animal	Number
Chicken	24
Pigeon	37
Japanese quail	62
Duck	200
Parrot	350
Kitten	473
Bat	800
Pig	15,000
Rabbit	17,000
Calf	25,000
Human	*9,000*

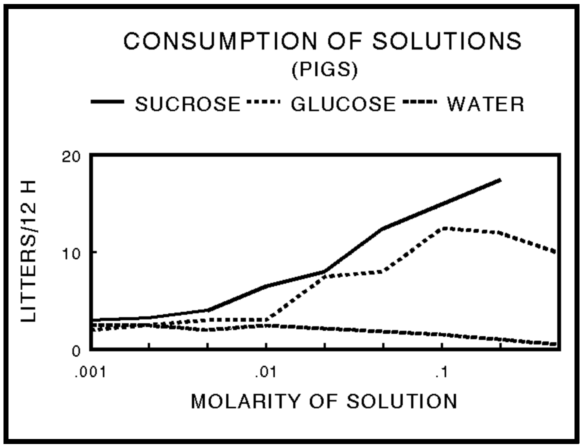
1) Taste buds - A group of cells that are approximately 20 x 90 µm in size.
2) Taste buds are located throughout the oral cavity, particularly on tongue in pigs, whereas they are restricted to or located on the back of the mouth in birds.
☛ Taste apparatus is present in fowl, but not extensive as in swine!

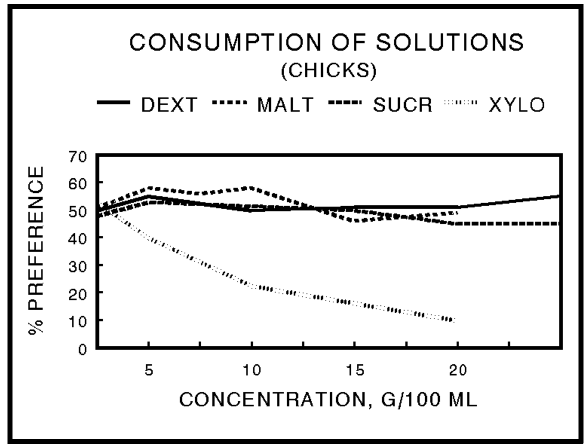
B. Consumption of various solutions by pigs (Kennedy & Baldwin, 1972. Anim. Behav. 20:706; See Figure on the left) and chicks (Kare & Medway, 1959. Poult. Sci. 38:1119; See figure on the right):

C. The Bottom Line?

1) Taste preferences exist in swine! But addition of sugar/flavors in the diet has been resulted in very inconsistent responses or minimal effects on performance.
2) A sense of taste also exists in poultry:

(1) But, may be associated more with "aversion" rather than "preference."
(2) Ingredients with different taste had minimal beneficial or adverse effects on poultry.
☛ May respond to flavor changes more when water is a medium rather than feed because of the absence of a fluid saliva & mastication in birds.





7. **Salivary Glands**

A. Pigs:

1) Saliva contains water, mucus, bicarbonates, & ptyalin (or salivary α-amylase), and moistens feed, lubricates esophagus, initiates starch digestion, and other functions.
2) Types? a) Serous - Contains water, electrolytes & α-amylase, b) Mucus - Contains mucoproteins/glycoproteins, and c) Mixed.
3) Glands (three pairs are responsible for most secretions):

a) Parotid - Largest, triangular in shape & located at the apex ventral to the ear, and secrete fluid devoid of mucin.
b) Submaxillary or submandible - Found ventral to the parotid & just behind mandibles, and secrete mucin-containing saliva (mixed).
c) Sublingual - Closely associated with the tongue & found below the floor of mouth, and secrete mucin-containing saliva (mucous).

4) Type of diets & saliva flow rate: (Cromwell. Pers. Comm.)

Feed	mL/1st 5 min
Corn	55
Potatoes	27
Milk	0

a) Secretion rate is affected by the DM content of diets.
b) ≈ 1-2 liters/d on a conventional dry diet.
c) Saliva flow is stimulated mostly by the presence of food in the mouth.

B. Poultry - Minimum in the quantity, and glands composed entirely of mucus cells, thus secrete only thick mucus type saliva. Probably, saliva is nothing more than just lubricating "food bolus" in poultry!?

C. Horses - Contains no enzyme, and secretion is stimulated by "scratching" of feed on mucus membrane of inner cheeks. May secrete up to 10 gal/day?

D. Ruminants:

1) Production is relatively continuous, but greater when eating & ruminating - Can reach 12 gal/day in cattle & 2 gal or more in sheep.
2) Contains no enzymes, but has an additional importance, i.e., provides N, P, Na for rumen microbes.
3) Also, highly buffered (particularly rich in HCO_3 & PO_4), which aid in maintaining an appropriate pH in the rumen.

E. Dogs & cats:

1) Saliva of carnivores contains no enzyme.
2) Unlike horses, the salivary reflex in dogs (& humans) can be conditioned by the sight of food!?
3) Salivary secretion has the special function of evaporative cooling - The parotid gland of the dog under intense parasympathetic stimulation is capable of secreting at 10 times the rate (per g of gland) in humans, thus, as effective as evaporation of sweat in humans?

7. **Esophagus**

A. Food passes from the mouth to the stomach or forestomach via the esophagus:

1) Made up of four layers - a) an outer connective tissue, b) a layer of muscle, c) submucosa, and d) mucosa.
2) Dogs, cattle, and sheep - The muscular layer consists of only striated muscle fibers.
3) Pigs, horses, and humans - The portion adjacent to the stomach is composed of smooth muscle.
4) Esophagus is normally closed at the pharyngoesophageal junction by the upper esophageal sphincter (an intrinsic or functional sphincter at this region in all, even though some may not have anatomically defined sphincter).

B. The central nervous system controls the contractions:

1) "Peristaltic action" (wave of contractions) moves food (as a form of "bolus") to the stomach in nonruminant animals.
2) e.g. - In the dog, it takes about five seconds for food to move from the mouth to the stomach.
3) The bolus can be moved in both directions in the ruminants, and the process is called "rumination."

4) In contrast to most species, horses seldom vomit:

   a) Reasons? Perhaps, they have only one-way peristaltic movement, or because of the marked tonus of the lower esophageal sphincter!?
   b) Only domestic species in which acute gastric dilatation can occur to the point of rupture of the stomach wall!

B. Poultry:

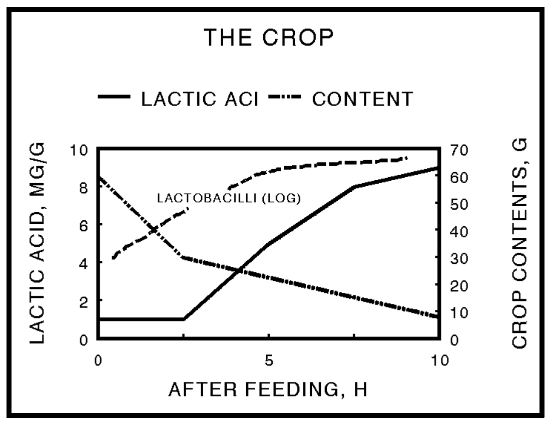
1) Relatively similar to that of the pig but most birds (except insect-eating and some waterfowl) have the "crop," and their esophagus is longer in terms of body dimension.
2) The crop in general:

   a) Is an esophageal "outpocketing."
   b) Mucus glands in the upper esophagus lubricate & move "bolus" to the crop.
   c) The crop is filled & emptied by peristaltic movements.
   d) A main function of the crop? - Probably serving as a food storage site.

3) But, there are some microbial & digestive activities in the crop:

   a) Hydrolysis of starch.
   b) Lactobacilli & lactic acid production: [Jayne-Williams and Fuller, 1971. In: D.J. Bell & B.M. Freeman (Ed.) Physiology & Biochemistry of the Domestic Fowl]

      ▹ Organic acids (. . . mostly lactic & acetic acids) account for ≤ 3% of maintenance needs!



4) The importance of crop?

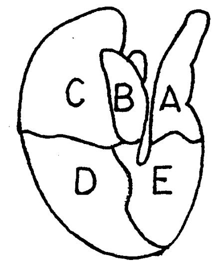
   a) Maintaining the microbial balance (e.g., inhibition of *E. coli*).
   b) But, not essential for "well-being" or maximal performance of the bird unless feed is restricted severely, i.e., the crop provides more flexibility to the animal!

STOMACH

1. **Functions of the Stomach in Nonruminant Species**

A. Mixing and storage of the ingested food.
B. Initiation of protein and fat digestion.

- Its most important function is storage of food and the controlled release of its contents into the duodenum.



2. **Swine**

A. Serving as a reservoir for food, but some digestion in the stomach:
B. The pig's stomach - See the figure [Redrawn from Pekas (1991) in Miller et al. (1991)]

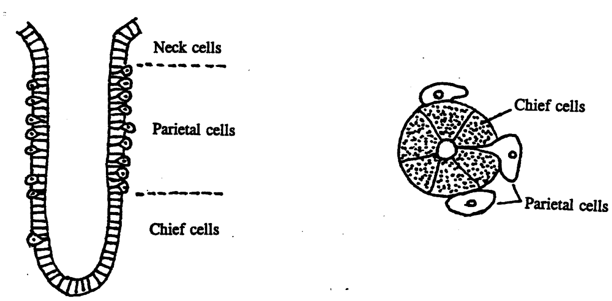
C. Esophageal:

1) An extension of the esophagus into the stomach.
2) Glandless area, thus no secretion.
3) Subject to "ulceration" - Processing (e.g., fine grinding, pelleting, etc.) or diets that tends to make stomach contents more fluid can cause "ulcer" in pigs!

D. Cardiac:

1) Located adjacent to the esophageal area, and occupies about ⅓ to ½ of the stomach area in the pig.
2) Secretes mucus, which can protect stomach linings from HCl.

E. Fundic or gastric:



1) The major secretory portion of the stomach.
2) Three types of cells:

a) Neck cells are responsible for secretion of mucus.
b) Oxyntic (parietal) cells are responsible for secretion of HCl & exchange of Na^+ with H^+. ("HCl" denatures protein, activates pepsin (from pepsinogen), provides optimal pH for pepsin, etc.)
c) Chief cells are responsible for secretion of enzymes [pepsinogen & rennin (acts on casein to form a curd)], electrolytes (Na, K, Cl) and water.

F. Pyloric:

1) The last region before entry into the SI.

2) Responsible for secretion of a hormone, gastrin - Gastrin is responsible for secretion of acid, water, electrolytes, enzymes, etc.

G. Control of gastric secretion:

1) Cephalic phase:

a) Food perception by senses can lead to "vagal stimulation" of glands.
b) Plays significant part in the initiation of eating after fasting.
☛ Make small contributions in swine & poultry because their gastric lumens are seldom empty between meals!

2) Gastric phase:

a) A combination of distension and chemical sensors.
b) Distension of the stomach can activate neural receptors.
c) Chemical stimulations involve pH and(or) digesta sensitive cells.

3) Intestinal phase:

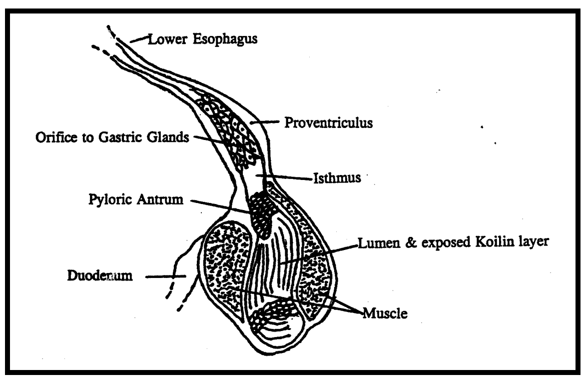
a) The response to digesta in the duodenum, which is mediated by hormonal and neural mechanisms.
b) Hormones in this phase include gastric inhibitory polypeptides (GIP), cholecystokinin, etc.
c) Neural mechanisms would be expected, but have not been clearly demonstrated.

☛ "Gastrin" is probably the focal point of controlling gastric secretions!

3. **Poultry**

A. Use the crop for storage, and proventriculus and gizzard for gastric digestion:

1) Proventriculus provides HCl and pepsinogen.
2) Gizzard is a site for grinding & gastric digestion.



B. Proventriculus-gizzard complex - Redrawn from Hill, 1971. In: D.J. Bell & B.M. Freeman (Ed.) Physiology & Biochemistry of the Domestic Fowl.

1) Proventriculus:

a) An ovoid structure found between the lower esophagus and gizzard.
b) Two types of cells for secretion:

(1) "Oxynticopeptic" cells are structurally intermediate between chief and oxyntic cells of mammals, and are responsible for secretion of pepsinogen and HCl.
(2) The second type is similar to the neck cells of mammals, and those cells are responsible for secretion of mucus.

c) Little is known about the control of gastric secretion, but mechanisms similar to those of mammals may exist.

2) Gizzard (ventriculus or "muscular stomach"):

a) It combines the activity of grinding and proteolysis.
b) Has a massive musculature and extremely durable luminal lining.
c) The luminal lining is synthesized continually as it's worn away by constant abrasions.
☞ However, the response to the addition of "grits" in diets, thus in the gizzard, has been very inconsistent in terms of performance!

4. **Horses**

A. Compared to others, have a small stomach - ≈ 10% of volume: [Capacities (L) of Digestive Tract (Argenzio, 1993. In: Swenson & Reece (Ed.) Dukes' Phisiology of Domestic Animals. 11th Ed. Comstock Publishing Assoc., Ithaca]

Item	Horse	Pig	Dog
Stomach	17.96 (8.5%)	8.00 (29.2%)	4.33 (62.3%)
Small Intestine	63.82	9.20	1.62
Cecum	33.54	1.55	0.09
L. colon	81.28	8.70 (Colon + rectum)	0.91 (Colon + rectum)
S. colon & Rectum	14.77		
Total	211.34	27.45	6.95

B. Does not have as extensive muscular movement activity as other species, and ingesta tends to arrange itself in layers - A reason for being prone to greater digestive disorders?
C. A flow rate - Relatively fast.

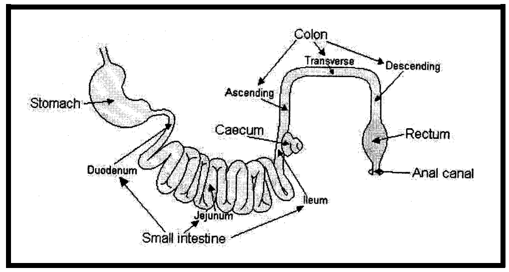
1) A large meal passes more quickly vs feed eaten continuously in small amounts.
2) Passing of majority of ingesta to the small intestine within 12 h following a meal?

D. When the stomach remains empty, the excess gas produced can cause rupture of the stomach. Thus, "continuous consumption" would be optimum?

5. **Ruminant Species** - Please see Section 3 ("Rumen Microbiology and Fermentation").

6. **Dogs and Cats**

A. Dog's digestive tract in general - Perhaps, typical of "carnivores!?"



1) See the figure - Available at: http://137.222.110.150/calnet/vetAB5/page2.htm:
2) Anatomy of digestive tract: [Currie, W. B. 1988. Structure and Function of Domestic Animals. Butterworth, Boston]

a) The dog's stomach seems to be typical of "carnivores."
b) The most striking feature is the apparent simplicity of the gut in general:

(1) The small intestine is short and has a wide luminal diameter.
(2) Cecum is poorly developed, and colon is unremarkable - Seems like elongated rectum!
(3) In view of the fecal mass passed by dogs, the anatomical structure of the lower gut is quite consistent with its simple reservoir function.

B. The dog's stomach:

1) A sac-like structure designed to store large volumes of food and begin the digestive process.
2) In the interior surface, a series of folds called gastric folds, which help grind and digest food.
3) The inner stomach lining secretes acids and enzymes to break food down as the initial step in the digestive process.
4) Once eaten, most food leaves the stomach within 12 hr.

INTESTINAL SYSTEM

- Regardless of the species, most of digestion and absorption of nutrients take place in the small intestine!

1. **Swine**

◦ *Articles by Pekas [1991. In: Miller, Ullrey & Lewis (Ed.)] and Yen [2001. In: Lewis & Southern (Ed.)] contain excellent diagrams of the swine intestinal system.*

A. Swine intestinal system in general:

1) The SI in a fully grown pig:

   a) ≈ 18 m long, and the body length to SI length ratio is ≈ 1:14. (Ratios for other species - horse = 1:12, cattle = 1:20, sheep/goat = 1:27, dog = 1:6 & cat = 1:4.)
   b) ≈ 90% as jejunum & remaining 10% divided equally between duodenum & ileum.

2) The LI (a fully grown pig) - ≈ 5 m long & first 7-8% being cecum.

B. Duodenum:

1) Primarily a mixing site for digesta:

   a) Responsible for secretion of viscous & alkaline substances, which protect the intestinal wall from "acidic" gastric contents.
   b) “Bile” (stored in the gall bladder) from liver contains 97% water, 0.7% salts, 0.2% pigments, 0.06% cholesterol & others.
   c) Pancreatic secretions:

      (1) Alkaline substances are rich in bicarbonate, and buffer "acidic" contents from the stomach.
      (2) Digestive enzymes include lipase, amylase, trypsin, chymotrypsin, carboxypeptidases, etc.
      (3) Controlled by two hormones - (a) “Secretin” stimulates bicarbonate & water flow, and (b) “CCK-PZ” stimulates enzyme flow.

2) The volume of secretions in a 40-kg pig:

   a) Bile, 2 L/day & pancreatic fluids, 5 L/day, thus total fluids of 10 L/day.
   b) The flow from the stomach is ≈ 3 L/day, plus passage of ≈ 2 kg of feed & 5 L of water/day!

C. Jejunum & ileum:

1) “Villi” cover the SI, which increase the surface area:

   a) Longest in the jejunum, and the length decreases progressively.
   b) Very active area with rapid turnover of cells - ≈ 20-30 million cells sloughed off/min.

2) Brush boarder enzymes are located at the brush boarder of the intestinal villi:

   a) Enzymes include aminopeptidase, dipeptidase, sucrase, maltase, lactase, phosphatase, polynucleotidase, lecithinase, etc.

b) Enzymes are integral parts of the membrane at the brush boarder, i.e., not secreted, but "shed" into the lumen.

☛ The jejunum digests & absorbs the majority of nutrients!

D. Cecum and colon:

1) The site to retrieve nutrients remained in digesta before excretion - primary nutrients recovered are water & electrolytes.
2) Fairly high in the microbial population:

a) "VFA" produced by microbes:

(1) Can be absorbed, and may be an important source of energy.
(2) May contribute as much as 30% of maintenance energy for older animals vs. only 2-3% for young animals (some differences among species!).

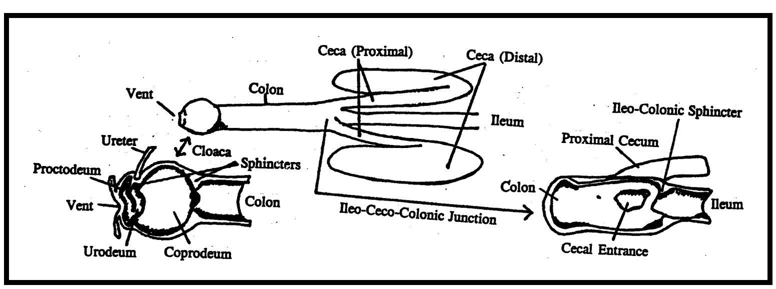
b) Microbial vitamin K & B-vitamins? - Questions on the absorption, but obtaining vitamins via coprophagy may be important in some situations?
c) Synthesis of amino acids:

(1) When lysine is infused into the cecum, "N" appears as urea in the urine or excreted in the feces, indicating that AA synthesized are used by other microbes or metabolized by the intestinal wall.
(2) Thus, may have no or little value to the pig.

E. Apparent digestion coefficients: (Keys & Debarthe, 1974. J. Anim. Sci. 39:57)

Item	Site	Wheat	Corn	Barley
DM	Duodenum	3.9	4.1	2.5
	Ileum	68.5	66.6	63.6
	Rectum	81.7	80.7	81.0
Energy	Duodenum	4.5	-7.3	-5.9
	Ileum	69.6	65.8	62.2
	Rectum	82.9	78.4	80.2
Protein	Duodenum	42.3	20.1	25.9
	Ileum	74.5	74.6	66.7
	Rectum	84.1	81.7	78.7

2. **Poultry**



A. Small intestine:

1) ≈ 125 cm long & occupies ≈ 50% of the total GI tract in adult chickens.
2) Relatively short, but ↑ absorptive effectiveness by using "back & forth" peristalsis.

3) In general, similar to swine in anatomy and functions.

B. Large intestine - See the figure (Redrawn from Moran, 1982).

1) Have a short colon and two long ceca (vs a short cecum & long colon in swine).
2) Ceca - Only fluids, solutes and fine particulate matters enter the ceca:

a) The VFA production site, but make a small contribution to the overall needs.
b) Vitamins can be synthesized, but their availabilities are low.

3) Colon - Probably acts more to convey ileal and cecal digesta rather than active fermentation & absorption.

☛ Both the ceca & colon are capable of absorbing water, electrolytes, glucose & amino acids.

C. Cloaca - Combines functions of both rectum & bladder into one, and mechanisms are present to conserve water & NaCl (processes require energy) if the situation demands.

3. **Horses** [http://www.ianr.unl.edu/pubs/horse/g1350.htm]

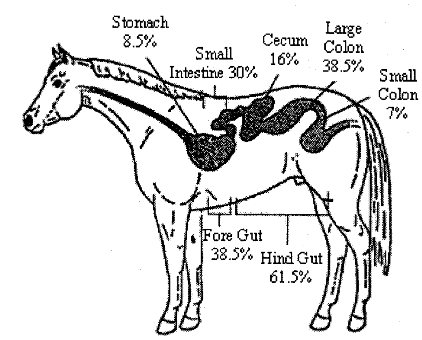


Figure 1. Digestive system of the horse.

A. Small Intestine:

1) About 30% of the volume of the total digestive tract, and the main site of both digestion & absorption.
2) Horses do not have a "gallbladder," thus a direct secretion of bile into duodenum.
3) Flow rate - Affected by the size of meal (↑ with larger meals), physical form (e.g., ↑ with pelleted diets & liquids), etc.
4) Within 2 - 4 h, undigested & unabsorbed ingesta to the cecum & colon - Easy to overwhelm the digestive capacity of the stomach and small intestine because of the limited capacity/volume.
5) Designed to digest carbohydrates & proteins in grains in the upper gut, thus important to feed small amounts, 2-4 times each day for safer, more efficient digestion.

B. Large intestine or cecum and colon:

1) Together, about 50% (over 60%?) of the volume of the total digestive tract.
2) Sites for microbial digestion/fermentation:

a) Contain an active flora of bacteria similar to the microbial population in the ruminants.

b) Bacterial breakdown of cellulose and other carbohydrates to produce VFA (acetic, propionic, butyric), and bacterial synthesis of B vitamins and protein.
c) Some absorption of VFA from cecum, but microbial protein/amino acids - ???

3) With large amounts of concentrates, rapid fermentation & production of excessive gas or lactic acid, causing colic or laminitis.
4) Flow rate - Relatively slow . . . may be several days after eating?
5) The diameter of different segments of the large colon varies & arrangement includes several flexures where the colon turns back onto itself, susceptible to digestive upsets when nutrient flow is abnormal. (Fewer problems with hay & pasture though!)

4. **Ruminant Species**

- Although there might be some differences, many aspects of the ruminant gastrointestinal structures and functions other than rumen seem to be similar to those described for pigs.

5. **Digs and Cats**

A. See "Digestive Tract in General" described briefly in the section for stomach.
B. Small intestine:

1) A tube-like structure & the longest portion of the intestinal tract - About two and a half times the animal's total body length.
2) In the dog - Duodenum (connected to the gall bladder & pancreas by the duct) is bout 10" long in a 40-lb dog, jejunum (covered with villi & the main absorption site) is the longest, and the shortest part is the ileum.

C. Large intestine:

1) In the dog - Basically connects the small intestine to the anus.
2) About 16" in length in a 40-lb dog.
3) Distinct parts: Cecum - a small, finger-like projection near the junction with the SI - function unknown), and colon - longest & terminates just inside the anus to the final portion of the LI, rectum. The terms "colon" & "large intestine" are commonly used interchangeably
4) The primary function is to absorb water from the digesta/ingesta & the other function being to store fecal matter.

LIVER AND PANCREAS

1. **Liver**

A. About 3 and 1.75% of body weight for the fowl and swine, respectively.

B. Vital to digestion & assimilation of absorbed nutrients:

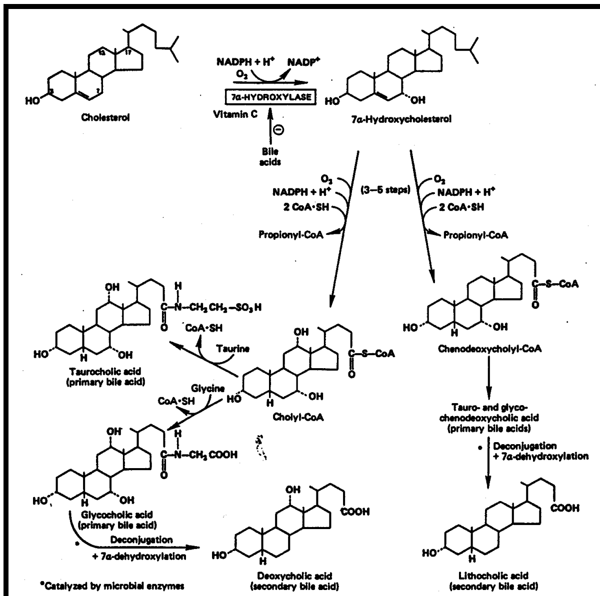


Figure 41–2. Biosynthesis and degradation of bile acids.

1) Bile for emulsification of dietary fat - See "Biosynthesis & degradation of bile acids" by Martin et al. (1983).
2) Makes metabolic modifications - Majority absorbed nutrients pass through the liver.
3) Mostly associated with the maintenance metabolism in adult animals (i.e., in those not involved in reproduction!).

C. Lobes - Two in the fowl and several lobes in the swine, but fundamentally similar in shape, location of gall bladder and major vessels.

D. Vascularization:

1) Pigs receive blood from the portal vein (nutrients) & hepatic artery (O_2), and blood exits through the hepatic vein and lymphatic system.
2) Similar in the fowl, but a contribution of lymphatic system is small (vs swine) simply because it is poorly developed in birds.

E. Bile & digestion/absorption of lipids:

1) Formed by the hepatocyte - All bile acids are steroidal compounds synthesized from cholesterol in the liver:

   a) Composition - Water, bile acids, mucin, pigments, cholesterol, esterified & free fatty acids and inorganic salts.
   b) Cholic & chenodeoxycholic acids are 1° acids, but pigs produce little cholic & hyocholic acid takes place as the 1° trihydroxy unit.
   c) To reduce their toxicity, all bile acids are conjugated with taurine in fowl & either taurine or glycine in pigs.
   d) Secondary bile acids - Arise from microbial fermentation when 1° acids are within the intestine . . . after absorption, can be reused by the live for bile synthesis.
   e) Bile pigments - Metabolic end products of heme catabolism & give the bile its characteristic color . . . biliverdin, bilirubin . . .

2). Secreted from the live directly into the duodenum or via gallbladder (stores bile, which is little more concentrated vs hepatic bile).

3) Control of bile movement - "More" via intramural plexus coordination (e.g., gastric digesta/lipids & neural receptors) than the hormone, cholecystokinin (CCK)?
4) Enterohepatic circulation - ≈ 99% of the primary and secondary bile acids are absorbed in the ileum and return to the liver via hepatic portal vein.
5) Daily bile acid use by the animal - Far exceeds its capacity for synthesis:

   a) An enterohepatic recirculation to cope with the demand.
   b) Control of the total pool of bile to meet the needs.

5) Functions of bile:

   a) Emulsification - The bile salts have considerable ability to lower surface tension, ∴ capable of emulsifying fats (micelle formation).
   b) Neutralization of acid - The bile is a reservoir of alkali.
   c) Excretion of cholesterol, and also many drugs, toxins, bile pigments, inorganic substances (e.g., Cu, Zn & Hg), etc.

2. **Pancreas**

A. Three major functions:

   1) Supplying enzymes to the SI for starch, protein & fat digestion.
   2) Secretion of water, bicarbonate & others into the duodenum area.
   3) Supplying hormones to manipulate nutrient metabolism on a moment-to-moment basis.

B. Gross appearance & anatomy:

   1) Swine - a) Pinkish-red in color, b) difficult to discern because of connective tissues, adipose tissues, etc., and c) ductules permeate the gland & give rises to one duct, which supply zymogens to the duodenum area.
   2) Fowl - a) Grey-white in color, b) visually apparent, c) have three separate lobes with ductules, and d) all ducts meet on a common papilla with two bile ducts at the duodenal-jejunal junction.

C. Exocrine tissues & endocrine islets:

   1) Acinar tissues dominate pancreatic tissues:

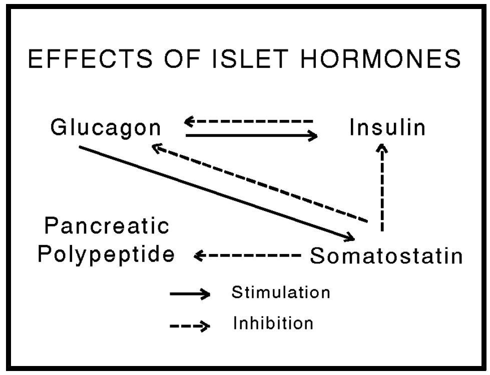
      a) Acinar cells are responsible for secretion of enzymes or zymogens.
      b) Centroacinar & duct cells are responsible for secretion of water, electrolytes, etc.

   2) Islets of Langerhans - Distributed throughout the pancreas:

a) Four types of cells - A-cells, glucagon; B-cells, insulin; D-cells - somatostatin, and F-cells, pancreatic polypeptide.
b) A-, B- & D-cells are found in every islets in pigs, whereas A-/D- or B-/D-cell composite in birds.

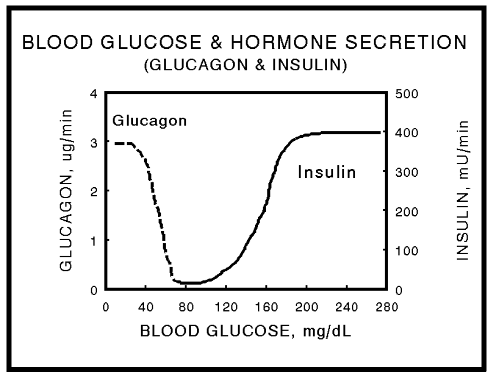
D. Islet hormones:

1) The islets may function as secretory units in the regulation of nutrient homeostasis.
2) Effects of islet hormones: (Redrawn from Ganong, 1983)



3) Somatostatin:

a) Responsible for coordinating “GI tract activities” & regulate the rate of energy (& other nutrients) entry into the animal - responsible for a short term regulation?
b) But, also seems to be involved in a long term homeostasis through instructions from the brain.



3) Insulin - Has glycogenic, antigluconeogenic, antilipolytic, and antiketotic activities. i.e., insulin is a hormone of “energy storage!”
4) Glucagon - Has glycogenolytic, gluconeogenic, lipolytic, and ketogenic activities, i.e., glucagon is a hormone of “energy release!”
5) Control of insulin & glucagon secretions:

a) Many factors affect insulin & glucagon secretions, but the principal factor seems to be plasma glucose.
b) Blood glucose and insulin/glucagon secretions - Redrawn from Ganong (1983).
c) Insulin-glucagon molar ratios (I/G): (Ganong, 1983)

Condition	Hepatic glucose storage (S) or production (P)[a]	I/G
Glucose availability:		
Large CH_2O meal	4+ (S)	70
IV glucose	2+ (S)	25
Small meal	1+ (S)	7
Glucose need:		
Overnight fast	1+ (P)	2.3
Low-CH_2O diet	2+ (P)	1.8
Starvation	4+ (P)	.4

[a]1+ to 4+ indicate relative magnitude.

(1) Need energy - Lower I/G ratios & favor glycogen breakdown & gluconeogenesis.
(2) Energy need is low - Higher I/G ratios & favor deposition of glycogen, protein & fat.

6) Insulin & glucagon for swine & fowl - Both species have a comparable set of enzymes:

a) Insulin:

(1) Swine - Insulin removes circulating glucose rapidly for hepatic & adipose tissue fatty acid synthesis, i.e., stimulation of pyruvate dehydrogenase & acetyl CoA carboxylase.
(2) Fowl - Not responsive to hypoglycemic action of insulin. (Fatty acid synthesis is largely restricted in the liver!)

b) Glucagon:

(1) Swine - Glucagon affects lipolysis of hepatic stores, but has minimal effect on adipocytes.
(2) Fowl - Glucagon can elicit strong lipolytic response.

☛ These differences can lead to "obesity" in pigs, and "rapid" release of fatty acids in birds (possibly to cope with daily stress of life?)!

7) Pancreatic polypeptide:

a) Function or significance has not been completely elucidated.
b) Isolated first in chickens - It decreased hepatic glycogen without changing plasma glucose, and also decreased plasma glycerol & free fatty acids.
c) Inhibits pancreatic secretions & relaxes gallbladder.

GASTROINTESTINAL HORMONES

- Secretion and motility in the GI tract are regulated by a combination of nervous & hormonal stimuli.

1. **Polypeptide Hormones in Genral**

A. Produced by mucosa of various parts of the tract.
B. Either act locally or released into the circulation.
C. Many are structurally similar, and exhibit "overlapping" activities:

2. **Gastrointestinal Polypeptide Hormones**: (Martin et al., 1983)

Established hormones:

Gastrin

AA residues	17
MW	2100
Homologue	CCK-PZ
Location	G cells of antrum & duodenum, brain
Stimulus	Gastric distention & protein in the stomach
Actions	Stimulates acid & pepsin secretion, gastric mucosal growth & possibly lower esophageal sphincter

Cholecystokinin (Pancreozymin) or CCK-PZ

AA residues	33
MW	3883
Homologue	Gastrin
Location	Mucosa of entire small intestine, brain, islets, etc
Stimulus	Fat, protein & their digestion products
Actions	Stimulates gallbladder contraction, pancreatic enzyme secretion, pancreatic growth, and inhibits gastric emptying

Secretin

AA residues	27
MW	3056
Homologue	Glucagon
Location	Mucosa of duodenum & jejunum
Stimulus	Low pH in the duodenum (threshold pH, 4.5)
Actions	Stimulates pancreatic & biliary HCO_3^- secretion, and augments action of CCK-PZ on pancreatic enzyme secretion

Other hormones:

Gastric inhibitory polypeptide (GIP)

AA residues	43
MW	5105
Homologue	Secretin, glucagon
Location	Mucosa of duodenum & jejunum, brain
Stimulus	Glucose or fat in the duodenum
Actions	Stimulates release of insulin from pancreas, inhibits gastric H^+ secretion & astric motility, and antilipolytic

Vasoactive intestinal polypeptide (VIP)

AA residues	28
MW	3100
Homologue	Secretin
Location	Mucosa of entire small intestine
Stimulus	?
Actions	Inhibits gastric H^+ and pepsin secretion, stimulates pancreatic HCO_3^- secretion & secretion from intestinal mucosa, and inhibits gastric & gallbladder motility

Motilin

AA residues	22
MW	2700
Homologue	?
Location	Mucosa of duodenum & jejunum
Stimulus	Alkaline pH (8.2)
Actions	Stimulates gastric motility

Enterogastrone

AA residues	?
MW	?
Homologue	?
Location	Mucosa of small intestine
Stimulus	Fat in the intestine
Actions	Inhibits gastric H^+ secretion

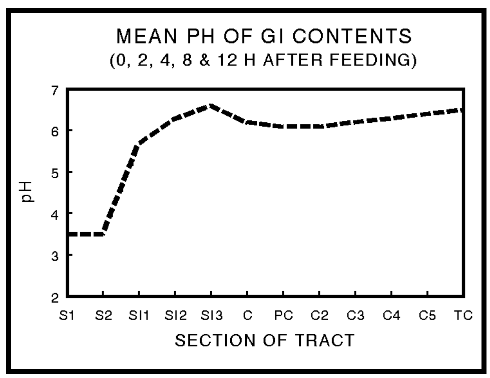
Entero-oxyntin

AA residues	?
MW	?

Homologue	?
Location	Mucosa of small intestine
Stimulus	Protein in the intestine
Actions	Stimulates gastric H^+ secretion
Enteroglucagon	
AA residues	?
MW	3500-7000
Homologue	Glucagon
Location	Mucosa of small intestine
Stimulus	Glucose or fat in the intestine
Actions	Glycogenolysis
Chymodenin	
AA residues	43
MW	4900
Homologue	?
Location	Mucosa of small intestine
Stimulus	Fat in the intestine
Actions	Specific stimulation of chymotrypsin secretion by the pancreas
Bulbogastrone	
AA residues	?
MW	?
Homologue	?
Location	Duodenal bulb
Stimulus	Acid in the duodenal bulb
Actions	Inhibits gastric H^+ secretion

THE pH AND DIGESTIVE PROCESS

- Digestive secretions & type of reactions change as ingesta or digesta moving through the GI tracts in the digestion process.



1. **Mean pH of Gastrointestinal Contents** - Redrawn from Clemens et al. (1975. J. Nutr. 105:759.)

2. **Significance of pH in the GI Tract**

   A. Low pH in the stomach prevents multiplication of ingested bacteria (except lactobacilli).
   B. Digestive enzymes have a fairly narrow range of optimum pH, ∴ decrease the rate of hydrolysis or activity at either side of the peak.

3. **Summary of the Digestive Process**: (Martin et al., 1983)

Enzyme	Activation & optimum pH	Substrate	End products or action
Salivary gland of mouth - Secrete saliva in reflex response to presence of food in mouth.			
Salivary amylase	Cl ion needed; pH 6.6-6.8	Starch; Glycogen	Maltose + 1:6 Glucosides + Maltotriose
Stomach glands - Chief cells & parietal cells secrete gastric juice in response to reflex stimulation & chemical action of gastrin.			

Pepsin A (fundas) & B (pylorus)	Pepsinogen conv. to active pepsin by HCl; pH 1-2	Protein	Proteoses; Peptones
Rennin	Ca needed for activity; pH 4	Casein of milk	Coagulates milk

Pancreas - Presence of "acid-chyme" from the stomach activates duodenum to produce secretin, which stimulates flow of pancreatic juice & CCK-PZ, which stimulates production of enzymes.

Trypsin	Trypsinogen conv. to active trypsin by enterokinase at pH 5.2-6; auto-catalytic at pH 7.9	Protein; Proteoses; Peptones	Polypeptides; Dipeptides
Chymotrypsin	Chymotrypsinogen conv. to active form by trypsin; pH 8	Protein; Proteoses; Peptones	Same as trypsin; more coagulating power for milk
Carboxypeptidase	Procarboxypeptidase to active form by trypsin	Polypeptides at the free carboxyl end	Lower peptides; Free amino acids
Pancreaticamylase	pH 7.1	Starch; Glycogen	Maltose + 1:6 glucosides + Maltotriose
Lipase	Activated by salts, phospholipids, colipase; pH 8.0	1° triacyl-glycerols	FA, Mono- & Diacylglycerols, Glycerol
Ribonuclease		Ribonucleic acid	Nucleotides
Deoxyribonuclease		Deoxyribonu-cleic acids	Nucleotides
Cholesteryl ester hydrolase	Activated by bile salts	Cholesterol esters	Free cholesterol + FA
Phospho lipase A_2		Phospholipids	FA, lysophospholipids

Liver & gallbladder - CCK, and also possibly gastrin & secretin, stimulates the gallbladder & secretion of bile by the liver.

(Bile salts &alkali)		Fats - also neutralize acid chyme	FA, Bile salt conjugates & Emulsified micelles

Small intestine - Secretions of Brunner's glands of the duodenum and glands of Lieberkuhn.

Aminopeptidase		Polypeptides at the free amino end	Lower peptides; Free amino acids
Dipeptidase		Dipeptides	Amino acids
Sucrase	pH 5.0-7.0	Sucrose	Fructose; Glucose
Maltase	pH 5.8-6.2	Maltose	Glucose
Lactase	pH 5.4-6.0	Lactose	Glucose; Galactose
Trehalase		Trehalose	Glucose
Phosphatase	pH 8.6	Organic phosphates	Free Phosphate
Isomaltase		1:6 glucosides	Glucose
Polynucleotidase		Nucleic acid	Nucleotides
Nucleosidases		Purine or pyrimidine nucleosides	Purine or Pyrimidine bases; Pentose phosphate

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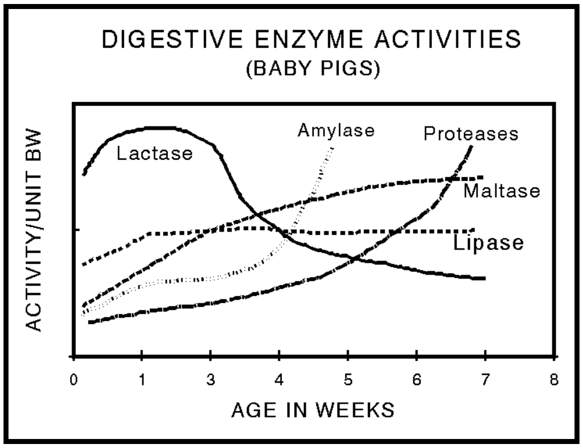
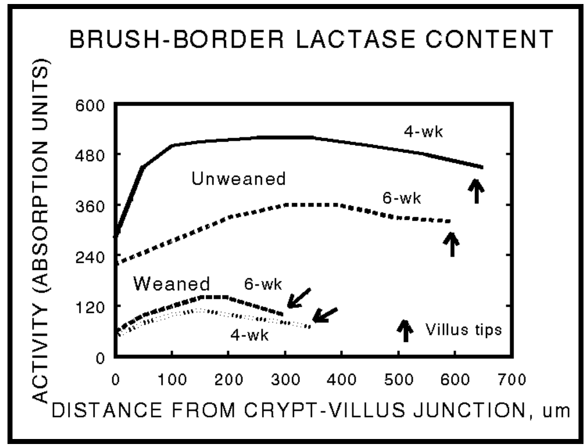
DIGESTIVE ENZYME ACTIVITIES IN PIGS

1. **Digestive Enzyme Activities -** [Adapted & redrawn from PIC Publ. 11(1). The figure on the left]

2. **The Brush-Border Lactase Content in Weaned & Unweaned Piglets** (Adapted & redrawn from Miller et al., 1986. J. Agric. Sci. Cambridge 107:579. The figure on the right)





3. **Age and Digestive Specimen on Protease & Amylase Activities in Pigs** (Shields et al., 1980. J. Anim. Sci. 50:257)

Age, wk:	0	2	4	6	8	10
Amylase activity[a]						
Total	15	52	98	208	540	1222
Pancreas	5	10	48	164	317	939
Intestinal contents	1	20	21	15	158	207
Intestinal mucosa	9	22	29	29	65	76
Protease activity[b]						
Total	6	12	49	84	166	338
Pancreas	5	9	38	57	77	169
Intestinal contents	1	3	11	27	89	169

[a]Grams of starch hydrolyzed per minute.
[b]Milligram tyrosine equivalents produced per minute.

4. **The Bottom Line?** - "*Pigs have an immature digestive system at birth!*"

   A. Enzyme profile - Geared toward digesting milk sugar & fat during the first 4 to 5 weeks.
   B. Enzymes necessary for starch & plant protein digestion are increasing, but still not adequate.
   C. Thus, to alleviate potential problems, complex diets must be fed to young pigs! (Complex diets - Diets containing many special ingredients that are highly palatable & digestible such as milk products (dried skim milk, dried whey), fish products, lipids, sugar, rolled oat groat, etc.)
   D. Birds, on the other hand, have a full complement of digestive enzymes from day one, thus can utilize a simple, corn-soybean meal-based diet from day one!

FOOD FOR THOUGHT!

1. Superalimentation?

Effects of superalimentation on performance of pigs[a]: (Pekas, 1985. Growth 49:19)

	Control	Super Alimentation	Response (% of C)	*P*-value
Body weight, kg				
Day 1	48.3	45.2	-	NS
Day 8	56.4	56.1	-	NS
Day 31	77.3	85.5	+ 10.5	.05
23-d period				
DM, kg	70.9	93.1	+ 31.3	.025
Gain, kg	21.0	29.3	+ 40.0	.005
Gain:feed	.30	.32	+ 7.3	NS

[a]Superalimentation - Started on day 8 at 120% of control intake.