MASTER CLASS

ANATOMY AND PHYSIOLOGY OF THE REPTILIAN GASTROINTESTINAL TRACT

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ABSTRACT: This overview covers the anatomy and physiology of the gastrointestinal system of reptiles. I include the alimentary canal, pharynx, oral cavity and digestive glands. Where possible, similarities and contrasts among taxa are provided. I cover the literature for chelonians, squamates (lizards and snakes), crocodilians, and where possible, tuataras. I do not cover amphisbaenians; limited descriptions are available elsewhere (Mader, 2006; Parsons and Cameron, 1977). The literature describing the gastrointestinal system is voluminous but quite uneven in breadth and depth; that variation is reflected in this text.

KEY WORDS: gastrointestinal tract, GI system, anatomy, physiology

INTRODUCTION

The gastrointestinal (GI) system starts with the oral cavity and extends to the cloacal orifice. It includes the oral glands liver, pancreas and their ducts. Overall, the reptilian GI system is relatively simple and bears gross resemblance to a mammalian system. In general, herbivorous and omnivorous animals have longer intestinal tracts than carnivores. All reptiles have orals glands, a tongue, esophagus, stomach, liver with multiple lobes, pancreas, small intestine, large intestine, and cloaca. GI anatomy and physiology are relevant to understanding pathology including, but are not limited to: anorexia, calcium regulation, stomatitis, vomiting/regurgitation, diarrhea, constipation and prolapse. Comprehensive discussions on GI anatomy, physiology and diagnostics are available (Divers, 2000; Jacobson, 2007; Kardong, 2011; Lawson, 1979; Mader, 2006; Romer and Parsons, 1986).

Normal Anatomy and Function

Oral Cavity and Pharynx

In most species, and particularly snakes, the mouth has two major roles: catch or apprehend the food and transport it to the esophagus. The mouth also serves in aggression (display and biting) and sometimes display. The anterior-most parts of the GI and respiratory systems form the oral cavity; The oral cavity, includes the buccal cavity (mouth, tongue, and cheeks), the jaws and teeth, palate, and the choanae (Kardong, 2011; Lawson, 1979). The mouth is bordered by the

lips and includes the tongue, teeth, palate and oral glands (sometimes termed salivary glands). The oral cavity ends at the pharynx where it joins the esophagus.

Most reptiles lack a secondary palate. When present, it is best developed in species that lack cranial kinesis (movement of the snout relative to the braincase). Some aquatic turtles and crocodilians have the best-developed separation of air and food passages. Lizards, snakes, most chelonians, and tuataras lack even a partial secondary palate

The lining the oral cavity is regionally differentiated and includes squamous and columnar epithelium, ciliated epithelium and goblet cells (unicellular mucous glands) (Luppa, 1977). Taste buds are scattered in the oral epithelium. Salivary glands, per se, are usually absent (Kardong, 2011; Parsons and Cameron, 1977; Stevens and Hume, 2004). Oral glands are described by location as lingual, sublingual, palatal, and labial. The tongue typically has many mucous secreting glands opening on the lingual and sublingual surfaces. Species with fleshy tongues tend to have more mucous glands (Jacobson, 2007; Kardong, 2011; Luppa, 1977). The mucoid "saliva" that is produced has little or no digestive significance; its major role is lubricatory. The mouth may receive secretions from other derived oral glands. In nonvenomous snakes, the Duvernoy's gland, located deep to the posterior upper lip releases secretions that appear to lubricate food and may play other roles. In venomous snakes the Duvernoy's gland is modified as a venom gland. The venom glands of helodermid lizards are modified mandibular glands located deep to the skin of the lower jaw (Beck, 2005). Oral glands are found in all terrestrial reptiles but many are lost or very reduced in aquatic species (Diaz-Figueroa, 2006). The notable exceptions are the sea snakes and crocodilians (Kardong, 2011).

The tongues of reptiles are as varied as the species. The form of the tongue can range from exceptionally protrusible (for example, chameleons), to the flat nonprotrusible tongues of freshwater emydid turtles (*Trachemys* spp.), and crocodilians. The forked tongues of snakes and monitor lizards (for example, teids and varanids) are protrusible and transport scent molecules from the air or substrate to the vomeronasal organ in roof of the mouth, but play little or no role in food transport (Kardong, 2011; Schwenk, 2000). Taxa that have fleshy tongues, such as in geckos, iguanids, tuataras and some tortoises may use the tongue in prey capture, lingual feeding, food manipulation in the mouth, taste, and in display.

Teeth: Lizards, snakes, crocodilians and tuataras have teeth. The role of the teeth is to capture, grasp, and/or cut food items. Very little mastication, if any, occurs and hence food is swallowed whole or as large particles. Teeth may be all one type (homodont) or vary in form (heterodont) and are either attached to bony ridges of the jaw (pleurodont) or in sockets (thecodont). Teeth are replaced through out life in many species of lizards and all snakes; however some species with pleurodont teeth, such as chameleons and tuataras, do not replace teeth. Tuataras and many snakes have two rows of teeth on the upper jaw (Newman, 1877; Romer and Parsons, 1986; Schaffner, 1998). Chelonians lack teeth and instead rely on the keratinous rhamphothecae to grasp or cut food (Kardong, 2011; Romer and Parsons, 1986; Wyneken, 2001).

Species that feed in water utilize a fundamentally different mechanism to apprehend food than terrestrial feeders. The mouth is opened as the hyoid apparatus is depressed creating a negative pressure into which the food is drawn along with the water. The water to be expelled must also exit through the mouth and or choanae while the food item is retained. In contrast, terrestrial feeders apprehend food with the tongue or teeth then manipulate the bolus of food to the esophagus via movements of the tongue, hyoid apparatus, jaws, and sometimes gravity (Cleuren and DeVree, 2000; Greene, 2000; Kardong, 2011; Schaffner, 1998).

Esophagus

The esophagus is the supply passage from the mouth; it extends from the caudal pharynx to the stomach and is positioned eccentrically dorsal to the trachea. The esophagus of most reptiles has a ciliated epithelium with goblet cells that may be numerous caudally. Taxa vary in the extent of their esophageal glands; they are seen frequently in chelonians. When present, the esophageal glands often secrete water or viscous mucous (Luppa, 1977).

The relaxed esophagus has several longitudinal folds that allow for great distensibility to accommodate large food items. In some reptiles, particularly chelonians, the base of the esophagus contains secretory cells that are presumed to be lubrigatory. The esophagus also contains aggregated lymph tissue that extends into the epithelium. In snakes, the esophagus is very thin-walled, with little or no muscle. It is quite muscular in lizards, turtles, and crocodilians. In marine turtles, well-developed keratinized papillae line the esophageal wall. The esophagus is muscular and contacts after transporting food and seawater into the esophagus. The saltwater is forcefully expelled while the papillae trap and macerate food (Parsons and Cameron, 1977; Skoczylas, 1978).

Stomach

The stomach is responsible storage of food during digestion. Both mechanical and chemical digestion occurs. In species that swallow their prey whole (most snakes and some lizards), gastric secretions are small in volume so a thin coating of low pH liquid surrounds the prey (pH ~ 2.5-3.5) that favors pepsin activity. In species that swallow their prey in portions, the gastric secretions and stomach content together are close to the optimum pH for pepsin action (2.2-2.5) [21]. The stomach in all reptiles is located on the left side of the body and attaches to the left lung (when present) by a gastropulmonary ligament. In snakes, the stomach is short and fusiform; its junction with the esophagus is found approximately 55% caudal of the snout and at three quarters of the liver's length. The stomach extends to about 65% of the total length body length and ends in a muscular sphincter, the pylorus, at the pyloroduodenal junction. In most lizards and chelonians the stomach is c-shaped with a clear cardiac portion but the similarities to mammalian stomach morphology differ across taxa (Diaz-Figueroa and Mitchell, 2006; Kardong, 2011; Skoczylas, 1978; Stevens and Hume, 2004).

The terms cardiac, fundus, and pyloric regions are used as for convenience, but do not represent homologous parts. Functionally, its glandular regions may best describe the reptilian stomach.

The cardiac region is located at the transition from the esophagus and has a glandular mucosa. The glandular stomach secretes mucous and hydrochloric acid (Kardong, 2011; Parsons and Cameron, 1977; Skoczylas, 1978). The middle portion of the stomach, analogous to the fundus has several types of epithelial glands, often is smooth-walled in lizards and chelonians, but textured with rugae, folds, and a spongy mucosa in most snakes and some skinks (Luppa, 1977). The pyloric end of the stomach has longitudinal ridges and is rich in mucous glands (Parsons and Cameron, 1977).

The stomach of crocodilians grossly has two parts. The cardiac region is externally similar to the esophagus; internally it is unlike the esophagus as it has few folds and leads into and becomes is continuous with the fundic portion that has many folds and rugae. These two portions are primarily responsible for chemical digestion. The stomach has a smaller, distinct, muscular pyloric portion with thick folds. The pyloric region likely provides mechanical digestion and is sometimes termed a gizzard because of its similarity to that structure in birds (Diaz-Figueroa and Mitchell, 2006; Kardong, 2011; Romer and Parsons, 1986; Skoczylas, 1978). It connects distally to the duodenum at the muscular pylorus.

Gastroliths, in the form of stones or gravel, are frequently found in the stomachs of crocodilians, chelonians and some lizards and likely aid mechanical digestion (Kardong, 2011; Stevens and Hume, 2004).

The stomach's surface mucosa can be very dynamic in shape and thickness (Starck and Beese, 2002; Stevens and Hume, 2004). In episodic feeders, such as many snakes and some crocodilians, the lining of the stomach may be pale and folded during periods of fasting. After feeding, the mucosa of the stomach and intestines become pink, the epithelial cells elongate, thickening the mucosa and increasing area for absorption. When full the stomach's muscular wall can be stretched thin (Parsons and Cameron, 1977).

Liver

The liver is the largest visceral organ in reptiles. Its shape is variable and generally conforms to the shape of the coelomic cavity. It usually consists of two lobes. The right lobe is the often larger and attaches to the right lung via hepatopulmonary ligament and to the duodenum via the hepatoduodenal ligament. In chelonians the liver attaches to the transverse septum via the coronary ligament medially and the left lobe attached to the stomachs' dorsomedial surface by the gastrohepatic ligament. In snakes the liver lies lateral to the right lung in contact or is retrocoelomic (Kardong, 2011; Lawson, 1979; Schaffner, 1998). The liver is caudal to the heart and mostly cranial to the stomach. Across lizard taxa, the liver varies in shape. In some species, it is located primarily on the right side. Iguanine lizards have a liver that can span the coelomic width; some have a well-developed middle lobe. There is an elongated "tail" from the right lobe that extends caudally and encases part of the postcava.

The liver of the tuatara has thin left and right lobes and a larger dorsomedial lobe. The liver is reported to have ligamentous attachment to the pelvis (Newman, 1877).

The crocodilian liver is large; the right lobe tends to be larger than the left. The liver is lies cranial and ventral to the posthepatic septum (= pseudodiaphram), which separates the pleural cardiac and hepatic cavities from the mover caudal visceral coelom (Kardong, 2011; Romer and Parsons, 1986). Movement of the liver and visceral mass cranially participate in lung compression during exhalation (termed the hepatic piston) (Claessens, 2009).

The liver receives several large vessels. The hepatic portal vein drains into liver near the left and, if present, the middle lobe. Blood from the gastroesophageal vein enters the liver dorsally as do the parietohepatic veins from the vertebral veins. The hepatic artery Absorbed nutrients liver are thought to reach the liver primarily via the portal vein where as the hepatic artery is thought to supply the liver with O_2 (Schaffner, 1998). Blood leaves the liver via the hepatic veins, which are short in chelonians and in most snakes and some varanids there is a single long hepatic vein.

The liver's main functions are glucose supply, fat metabolism, fat storage, protein metabolism, filtration and exocrine products. Carbohydrate metabolism leads to glucose formation in hepatocytes as glycogen or via pyruvate or lactate. Under anaerobic conditions the liver can produce lactate. Fats entering the liver from the gut are bound proteins and converted to phospholipids and cholesterols, which function structurally and in the formation of bile salts. Bile aids in digestion and absorption. It also is mechanism for excretion of cholesterols and the breakdown of hemoglobin (Skoczylas, 1978).

Hepatocytes form bile, which is released as an exocrine product via the bile ducts to the gallbladder and duodenum (Kardong, 2011). Bile acids of reptiles are similar among all reptilian taxa differing primarily in their side chains and hydroxylation, which have implications for lipid absorption and bile flow (Hagey cited in Stevens and Hume, 2004). Bile is transported to the gall bladder and duodenum via bile ducts formed by coalescing bile ductules (Kardong, 2011; Skoczylas, 1978).

Bile traveling to the duodenum is transported by the common bile duct, which is lined by cuboidal epithelium and goblets cells (Luppa, 1977). Bile is transported to and from the gallbladder via the short cystic duct. The gallbladder located in the right lobe of the liver in chelonians and lizards. It is caudal to the liver in snakes (Diaz-Figueroa and Mitchell, 2006; Divers, 2000; Jacobson, 2007).

Liver plays a major role in hibernation.   It functions in blood sugar regulation and protein metabolism.   Deliver forms sermon of human forms clotting factors, fibrinogen, prothombrin. Vitellogenins, responsible for yolk formation, are formed by the liver (Skoczylas, 1978).

Filtration is accomplished by the organization of the liver's structure. Sheets of hepatocytes surround blood sinusoids and filter and detoxify substances in blood. The sinusoids are lined by endothelial cells, melanomacrophages, and stellate (Ito) cells. The melanomacrophages are thought to play a role if scavenging free-radicles in lower vertebrates (Henniger and Beresford cited in Skoczylas, 1978). The density of melanomacrophages varies with taxa, across individuals, and with nutritional state. Animals that have not eaten for prolonged periods have

intensely pigmented livers.   The stellate cells store fat as a vitamin A compounds. They may also lose their vitamin A and become active during injury converting to myofibroblasts, which produce collagen (Skoczylas, 1978).

The liver is a metabolically demanding organ, similar in energetic costs to the kidneys but slightly less than the heart. The liver's function is temperature dependent and scales linearly so that liver function declines sharply with temperature declines (Schaffner, 1998).

Pancreas

The pancreas is both and endocrine and exocrine organ located along the duodenum. Pancreatic cells produce two major kinds of exocrine products: alkaline fluid and enzymes (proteolytic enzymes, amylases, and lipases).   These products enter the duodenum via the pancreatic duct that opens into the ampulla of Vater (Kardong, 2011; Romer and Parsons, 1986). The pancreatic duct joins the common duct in colubrid snakes. In some igunanine lizards the common bile duct enters the ampulla of Vater directly; others have paired bile ducts that both enter the duodenum separately from the pancreatic duct. Pancreatic islet cells produce insulin and glucagon which both regulate blood glucose (Diaz-Figueroa and Mitchell, 2006; Jacobson, 2007; Kardong, 2011; Stevens and Hume, 2004).

Intestines

The intestines function in digestion and absorption. The length of the intestine along with elaborations of the mucosa increase surface area. As digesta passes through the intestines, the mucosa adds secretions, absorbs nutrients, absorbs water, and ions. The combined actions of longitudinal and circumferential muscle effectively move digesta and expose surface area for absorption.

The small intestine may be either straight or be composed of short transverse loops. In snakes, the intestine may have many largely longitudinal folds that allow for expansion and high surface area during digestion. Organ size is dynamic and responsive. In garter snakes (*Thamnophis sirtalis parietalis*) that were fed frequently, liver and intestine size was large while snakes fed less frequently showed a marked up- and down regulation of organ size (Starck and Beese, 2002). The small intestine in the lizard and turtle has many loops and convolutions, while that of snakes is relatively simple with alternating bends. The small intestine of carnivores tends to be the longest and that of herbivores the shortest (Stevens and Hume, 2004).   The small intestine of the tuatara is short as is the colon (Newman, 1877).

The small intestine ends in an ileocecal valve or sphincter. Many reptiles have a well-developed caecum. A caecum is present in most lizards and chelonians, but absent in most snakes, except for pythons. Crocodilians appear the lack a caecum (Kardong, 2011). The caecum and proximal large intestine tends to be larger in herbivorous and omnivorous species than in carnivores. In some herbivorous lizards, including members of the Agamidae, Scincidae, and Iguanidae, this

region is partially compartmentalized. In *Iguana iguana*, the cecum and proximal colon has folds that may function as valves (Jacobson, 2007; Mader, 2006; Parsons and Cameron, 1977).

The large intestine is usually pink in color however it may be darkly pigmented (in many chameleons and some turtles). It tends to have a much larger capacity in herbivorous species than in carnivores and omnivores (summarized in Bjorndal, 1997). Large intestine length is longest in herbivores and shortest in carnivores (Stevens and Hume, 2004).

The digestive efficiency of reptile intestines is much lower than that of mammals, largely because mammals have much greater surface area and to some extent because reptile digestive efficiency is linked to basking or other post feeding thermal regulatory behavior (Harlow et al., 1976; Skoczylas, 1978; Stevens and Hume, 2004). Digestion in some herbivorous species is aided by fermentation and in some species by the activity of some nematodes. Fermentation is commonly in the large intestine; however, Bjorndal (1997) documented fermentation in the small intestine one species of freshwater turtle *Pseudemys nelsoni.*

The large intestine functions in reclaiming water, absorbing calcium ions, and degrading complex carbohydrates. Urea and/or uric acid transfer into the intestine by retrograde movement of urine into the intestine in reptiles. In some herbivorous chelonians and lizards microbial fermentation occurs in the large intestine (Bjorndal, 1977). Intestinal microbes in the reptile colon appear to degrade urea and uric acid. While nitrogen assimilation levels are much lower in reptiles than in birds and mammals, nitrogen reclaimed in the colon is co-opted for amino acid synthesis (Skoczylas, 1978).

The food transit times through reptilian GI systems are variable and are usually measured in days to weeks. In addition to thermoregulatory behavior, several mechanisms influence transit times and digestive efficiency. For example, in species that ferment digesta in the hind gut, antiperistalsis may increase transit time and allow functional flexibility how different foods are transported through the gut (Bjorndal, 1997).

Cloaca

The large intestine terminates at the anus that opens into the cloaca. The cloaca is a short, large-bore tube. As in birds, the reptilian cloaca is formed of three contiguous chambers or regions that are described based upon the body's products they receive. Their morphologic distinctness from one another may from vary across taxa. The feces are discharged into the most craniad chamber, the coprodeum. The urodeum receives the urogenital ducts. The largest chamber is the posterior proctodeum acts as a general collecting area for digestive and excretory wastes (Kardong, 2011; Romer and Parsons, 1986). Often these regions are in close proximity to one another.

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