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# Avian Gastrointestinal Anatomy and Physiology

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A bird's gastrointestinal (GI) tract morphology, digestive strategy, and metabolic capability have been intimately intertwined during evolution to match the nutrient content and physical attributes of foods available in its natural habitat. The most commonly kept companion species are granivorous with a tendency toward omnivory. The beak, oral cavity, and tongue of granivorous birds have anatomic adaptations for shelling seeds, including ridges in the tomia of their beak for slicing the hull and a dexterous tongue for manipulating the seed and disposing the hull. Granivorous species possess a sizeable crop or an expandable esophageal pouch for storing food so that large meals can be consumed. Their proventriculus is somewhat small, and their gizzard is large, muscular, and possesses a thick cuticle relative to carnivores or frugivores. A vestigial ceca and short rectum provide little area for use of symbiotic bacteria to aid in the digestion of the fibrous components of food.

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**Key words:** Digestion, companion birds, gastrointestinal tract.

More than 9,000 species of birds (more than twice as many as mammals) fill many of the possible niches within the earth's food web. A bird's gastrointestinal (GI) tract morphology, digestive strategy, and metabolic capability have been intimately intertwined during evolution to match the nutrient content and physical attributes of foods available in its natural habitat. When compared across species, the GI tract is the most anatomically diverse organ system. However, distantly related species consuming similar food items often display morphological convergence because of similar nutritional and ecological selection pressures.<sup>1,2</sup> The most commonly kept companion species are granivorous with a tendency toward omnivory (Table 1), and

their GI tracts appear to be morphologically more similar to chickens and turkeys than to birds with very different dietary patterns, such as carnivorous or herbivorous species. This permits us to use the well-studied chicken as a point of reference when examining the GI tracts of companion avian species.

The GI tract of a bird provides an environment for the physical and chemical reduction in the size and molecular complexity of food and then absorbs the end products of digestion, which are needed in widely differing quantities. A young chick requires a diet with more than 15% protein, but only 0.0000003% of vitamin B<sub>12</sub>. The anatomy and digestive functions of the GI tract are designed to accommodate this wide range of quantitative needs. The GI tract has sufficient morphological plasticity to accommodate changes in nutritional needs during the life cycle and to adapt to changing physical and nutritional characteristics of the diet.<sup>3,4</sup>

## Anatomy and Physiology of the Digestive System

The avian digestive tract is a continuous tube that opens at either end (beak and vent) to the outside world and consists of a mouth, esophagus, crop, proventriculus, ventriculus or gizzard, intestine, ceca, rectum, and cloaca (Fig 1). As food progresses through these organs, a specific sequence of digestive events occurs, including grinding, acidifying, hydrolyzing, emulsifying, and transporting of the end products.

The distinctive anatomy and physiology of the avian GI tract reflects the constraints of flight, in that most of the tract's weight is centralized within the body cavity to optimize aerial maneuverability. The avian GI tract has a larger number of organs, which have greater interorgan cooperation than their mammalian counterparts. The precise anatomic plan of the digestive tract of companion birds varies somewhat, depending on their typical diet.

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**Table 1.** Eating Habits of Some Species of Captively Propagated Birds

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Mostly granivorous species
Gouldian Finch
Zebra Finch
Canary
Budgerigar
Cockatiel
Domestic Pigeons
Omnivorous, but tending to be granivorous
Conures
Rosella
Sulfur-crested Cockatoo
African Grey Parrot
Amazon Parrot
Macaw
Chicken
Omnivorous, but tending to be frugivorous
Toucan
Mynah
Barbets
Omnivores, but tending to be nectarivorous and frugivorous
Lorikeets
Lories

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### Beak, Tongue, and Oral Cavity

The beak, tongue, and oral cavity function in grasping, testing, mechanical processing, and lubricating food and propelling the food to the esophagus. Their specific morphology reflects the physical requirements of obtaining and processing food items. The granivorous tendency of most companion birds is evident in their short stout beaks with pronounced ridges designed for cracking seeds and dexterous tongue for manipulating the seed when shelling it.

A keratin sheath (rhamphotheca) growing from the upper and lower mandible forms the beak. The keratin is continually lost by wear and replaced by new growth. The location and rate of growth and wear influence the exact shape of the beak, and subtle changes may occur as food types change. The tomia, or outer edges, are somewhat sharp to facilitate cutting seed coats. Several structural attributes of the beak, jaws, and skull provide unique functional characteristics that are important in obtaining food. The attachment of the lower beak to the skull is somewhat loose, permitting a large gape. A bird's gape places the upper limit on the size of food item that can be consumed and is particularly large in frugivorous species (eg, toucans). A second structural adaptation found in parrots is the articulation of the upper mandible in the cranium at the

naso-frontal hinge, permitting an increased gape of the beak and providing flexion that absorbs some of the shock associated with pecking and seed cracking.<sup>5,6</sup>

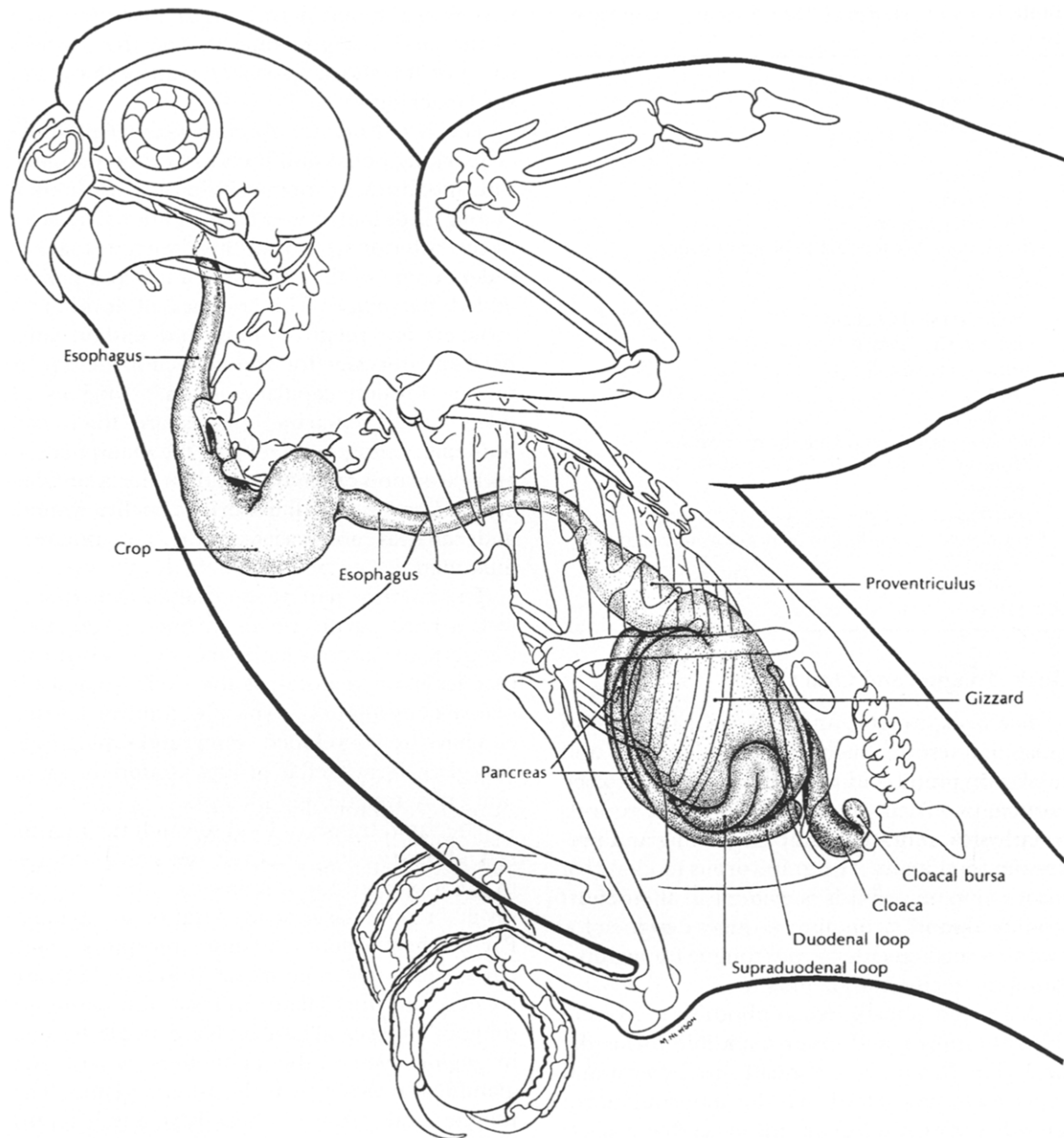
The hyoid apparatus, consisting of multiple articulating bones and their associated musculature, mobilizes the tongue. Psittacidae are unique among birds in that they have additional muscles in the anterior regions of their tongues that are independent of the hyoid apparatus and permit added flexibility.<sup>7</sup> The tongues of lorries and lorikeets are relatively long and end in fine, hairlike processes for the collection of sap or nectar through capillary action.<sup>8</sup> Tongues of many other psittacine species are thick and muscular, acting as fingers for the manipulation and extraction of seeds from their husks or from cones. The tongues of passerines, such as finches and canaries, are narrow, short, and not very muscular.

The anterior part of the oral cavity is roofed with a hard palate, which in finches, canaries, budgerigars, and cockatiels contains two ridges that facilitate removal of the shell from seeds before consumption. Typically, granivorous species have well-developed compound tubular salivary glands scattered in groups around the lower oral cavity, tongue, and pharynx.

The rapid transit of food through the mouth, lack of mastication, relatively low saliva addition to the food, and low numbers of taste receptors result in poor taste acuity relative to humans. Parrots have about 350 taste receptors, compared with 9,000 in humans.<sup>9</sup> Most taste buds are located on the palate and on the posterior tongue. The palatal taste buds are usually located in regions where the epithelium is soft and glandular, typically near the salivary glands. The tongue, oral cavity, and beak have a rich supply of touch receptors that augment the bird's relatively poor gustatory capacity with a strong tactile sense.

### Esophagus and Crop

The esophagus extends down the neck into the thoracic cavity and terminates in the proventriculus. In the budgerigar, the esophagus is dorsal to the trachea in the anterior regions of the neck and then runs along the right side.<sup>10</sup> Peristaltic contraction of inner circular and outer longitudinal muscles in the tunica muscularis propels food posteriorly through the esophagus.



**Figure 1.** The digestive tract of a Budgerigar. (Reprinted with permission.<sup>10</sup>)

To aid in swallowing large food items, the esophagus is expandable as a result of a series of longitudinal folds. This accordion-like arrangement is enriched with mucous glands to provide lubrication. The epithelial lining is thick and cornified for protection against mechanical damage as a result of swallowing food items whole. In many species, the esophagus widens into a crop just before entering the thoracic cavity. In the budgerigar, the inlet to the crop is on the right

side of the neck, and this organ extends transversely to the left side. The presence of large folds of mucosa allows considerable expansion and shrinkage, depending on the amount of contents. Immediately cranial to the thoracic inlet, the crop narrows to reform an esophageal tube and passes between the coracoid bones to the right of the syrinx and dorsal to the heart.<sup>10</sup> Some granivorous species (eg, Cardueline Finches) do not have a true crop, but they

usually have a very expandable esophageal pouch that can store food items.

### **Stomach**

The stomach consists of the proventriculus (glandular stomach) and the gizzard (muscular stomach), which is sometimes called the ventriculus. The proventriculus is the site at which digestion is initiated. Its epithelium contains glands of two principal types: the tubular glands that secrete mucous and the gastric glands that secrete hydrochloric acid (HCl) and pepsin. These compound glands compose most of the thickness of the proventricular wall. In granivorous species, the proventriculus is elongated and relatively small in diameter relative to the gizzard.<sup>11</sup>

The function of the gizzard is to mechanically massage and grind food to reduce its size and increase its surface area. It also serves as a location for the action of HCl and pepsin added to the food during passage through the proventriculus. The gizzard of species that feed on foods that are soft and easily digested (eg, lories, mynahs, and toucans) is a relatively round organ similar in thickness and muscularity to the proventriculus. In granivores, the gizzard is a larger and more muscular organ than in frugivores and nectarivores and is typically larger in size than the proventriculus.

The gizzard consists of two pairs of smooth muscles arranged in distinct bands that both originate and terminate on a circular tendon. The asymmetrical arrangement of these four muscles provides mixing and grinding actions during contraction. High myoglobin concentrations give these muscles their distinctive red coloration. The interior lining of the gizzard contains numerous deep tubular glands that produce a protein-rich secretion that hardens into rod-like projections.<sup>12</sup> These rods trap desquamated epithelial cells and form the cuticle lining of the lumen. The cuticle acts as a grinding surface and protects the underlying mucosa from digestion by the acid and pepsin that was secreted by the proventriculus. The rods ( $\approx 20$   $\mu\text{m}$  in diameter) act to increase the abrasiveness of the cuticle. Grit may also lodge in the gizzard to add a more coarse abrasive action.<sup>13</sup> Grit is particularly important for species that do not remove the shell from seeds before swallowing (eg, doves, pheasants, and quail).

The thickness and physical properties of the cuticle are highly correlated with food consumed, being especially thick in granivores, but thin and soft in frugivores and nectarivores. It is thickest and toughest directly under the thick muscles, which provide much of the grinding within the gizzard. The cuticle lining wears down steadily and undergoes continual renewal. It is often green, brown, or yellow in color because of the reflux of bile pigments from the small intestine. A pyloric fold separates the gizzard from the small intestine and regulates the passage of food between these organs.

The size of the gizzard can change with diet, and in most wild species, the gizzard size follows a seasonal rhythm. For example, facultative granivores-frugivores have a large, muscular, and grit-filled gizzard with a hard cuticle in the winter when they eat mostly seeds; but in the summer, when the birds eat mostly soft fruits, the gizzard weighs half as much and has a softened cuticle with little grit.<sup>14</sup>

### **Intestines**

The form and function of the small intestine is less variable than the more anterior digestive organs, probably because the diverse physical nature of different foods is reduced to a relatively uniform and fluid chyme. The duodenal loop of the intestine encircles the pancreas and receives the pancreatic and hepatic ducts. The jejunum and ileum are not clearly demarcated in birds.

The epithelium of the intestine contains villi and intestinal crypts.<sup>15</sup> Epithelial cells of the villi have about  $10^5$  microvilli per square millimeter on their apical surface, increasing the absorbing surface area 15-fold. The villi contain a rich capillary bed, which picks up the absorbed nutrients and transfers them to the portal blood vessels. Goblet cells located in the intestinal epithelium secrete copious mucous that functions to protect the intestinal epithelium from digestive enzymes and abrasion by the digesta. The mucous is particularly thick along the anterior duodenum, where it protects the villi from excessive acidity of the digesta leaving the gizzard. The intestine is surrounded by two muscle layers, the inner circular and outer longitudinal, which are responsible for mixing the digesta and propelling it through the tract.

The ceca of psittacines and passerines are

vestigial in that they are not readily observable by the naked eye. The ceca are visible histologically as a nodule of lymphatic tissue within the intestinal wall at the junction of the small intestine and the rectum. Many familiar avian species, such as ducks, chickens, and ratites, have very large ceca, which aid in the digestion of vegetation and in water balance.<sup>16,17</sup>

The rectum extends between the ileocecal junction and the cloaca. A frequently used synonym for the avian rectum is "colon." It is very short and small in diameter compared with the large intestine of mammals (except in the ostrich), and thus is not appropriately referred to as a "large intestine." Histologically, the rectum is similar to the small intestine, except that the villi are shorter and richer in lymphoid follicles.

### Cloaca

The cloaca is the terminal chamber into which the digestive tract and the urogenital ducts empty and has a much larger diameter than the rectum. The rectum enters midventrally into the coprodeum region of the cloaca, which serves as a storage area for urine and feces. A mucosal fold separates the coprodeum from the urodeum, which receives the ureters and the oviduct, or the deferent ducts in males. Upon defecation, this fold can be everted through the vent, permitting the expulsion of feces without passing through and contaminating the urodeum and proctodeum. This fold closes during egg laying by the female and ejaculation by the male to prevent fecal contamination of the egg or semen, respectively. The proctodeum forms the posterior region of the cloaca and receives the opening of the bursa of Fabricius.

The vent is a transverse slit that has lips on both the dorsal and ventral sides. The proctodeum and the vent are surrounded by voluntary muscles that form a sphincter that provides the bird some control over the timing of its defecation. During defecation, the dorsal and ventral lips are partly everted, forming a circular orifice for passage of the feces and urine.

### Accessory Organs

The liver, gall bladder, and pancreas are important accessory organs of the digestive system. The liver has two lobes of nearly equal size. Its primary digestive role is the production of

bile acids and bile salts. Bile acids and salts, phospholipids, and cholesterol are secreted into the bile canaliculi and collected by the bile ducts. A gall bladder is present in some species, but is absent in others (eg, many psittacines, such as budgerigars).

The pancreas lies within a loop of the duodenum. The digestive enzymes produced in the tubulo-ascinar glands of the pancreas are collected into ducts. In budgerigars, the three pancreatic lobes are each drained by a separate duct, two of which enter on the inner surface of the distal duodenal loop next to the bile duct and one that enters on the opposite side of the duodenum.<sup>10</sup> Avian pancreatic juice contains enzymes similar to those of mammals, including amylase, lipases, trypsin, chymotrypsin, carboxypeptidases A, B, and C, deoxyribonucleases, ribonucleases, and elastases.<sup>18</sup> The pancreas also produces bicarbonate, which buffers the intestinal pH.

## Digestion of Food

The assimilation of nutrients present in food requires mechanical and enzymatic digestion in the lumen of the GI tract and absorption through the intestinal epithelium. Digesta moves in the general direction of mouth to vent, but in many species of birds that have been studied, this posterior flow is interrupted by refluxes in the opposite direction. Retrograde movement of digesta occurs between (1) the proventriculus and the gizzard, (2) the small intestine and the gizzard, (3) the rectum and the small intestine, and (4) the cloaca and the rectum. The reflux of digesta between the proventriculus and gizzard is thought to be necessary to optimize the action of enzymatic and mechanical digestion, whereas the reflux from cloaca to rectum is necessary because of the need to resorb protein, salts, and water present in the urine.<sup>3,19</sup>

Most species of birds kept in captivity rely almost exclusively on the action of enzymes coded for by genes within their own genome (autoenzymatic digestion). These enzymes are produced in the proventriculus, small intestine, pancreas, and possibly, other organs of the tract. Alloenzymatic digestion caused by enzymes of microbial origin seems to be of little importance in most companion birds. This is illustrated by the small size of the rectum and the vestigial

form of the ceca in Passeriformes and Piciformes, and the almost complete absence of ceca in Psittaciformes.<sup>16</sup> Unfortunately, most physiological and metabolic details of digestive processes of companion birds are based on knowledge generated with poultry, and these inferences generally await confirmation by investigative research.

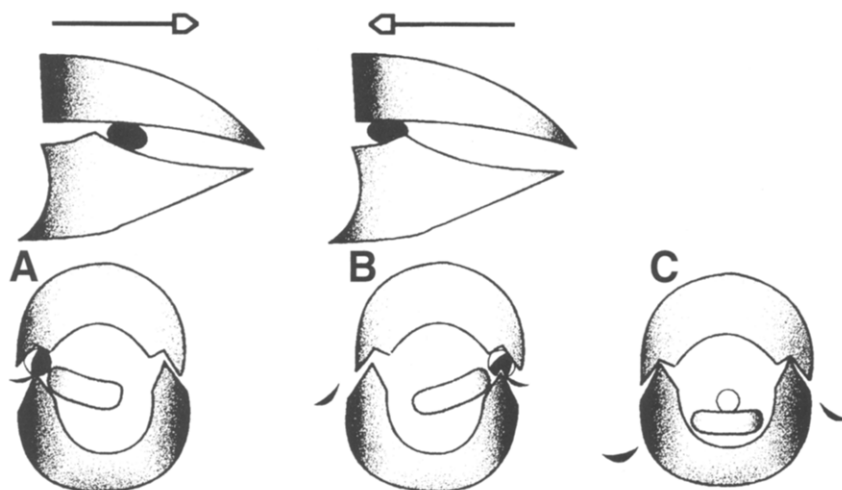
### Prehension and Swallowing

The beak is used for grasping of food items and often functions, together with the tongue, in processing food by sorting, hulling, tearing, or crushing. Salivary flow is triggered by the anticipation of food consumption and by the physical distention of the oral cavity. Saliva and mucous secreted within the esophagus lubricate the food when it is swallowed.<sup>20</sup> Swallowing usually occurs quickly after procurement of food. The tactile stimulation of the tongue by food causes a series of rapid posterior tongue movements that push the food to the pharynx. The esophagus moves forward to receive the food and propels it downward by a constriction of muscles behind the bolus of food and dilation of muscles ahead. This peristaltic action delivers the food bolus to the proventriculus or to the crop if the proventriculus is full. Because of low level of enzymes, minimal mechanical action, and short time be-

fore swallowing, little breakdown of food occurs in the mouth.<sup>21</sup>

Water consumption requires similar coordination of the tongue, laryngeal mound, and esophagus as swallowing food and may be aided by elevation of the head. Many species of psittacines also propel water backward into their esophagus by lapping motions of their tongue.

The techniques that birds use to process seeds are dependent on the characteristics of the seed. Dicotyledonous seeds (eg, legumes, sunflowers, and many woody trees and shrubs) are cut, whereas a crushing action is used to remove the coat from monocotyledonous seeds (eg, grains). Finches in the families Fringillidae and Estrildidae have two lateral grooves in their upper palate that are wide and deep at the posterior end of the palate and shallow and narrow near the beak tip.<sup>11,22</sup> Large seeds are positioned by the action of the tongue into the broad region of the proximal ridge, and smaller seeds are cradled in the narrower ridge toward the tip. Once wedged in place, the shell is cut by rapid anterior-posterior movements of the sharp-edged lower beak (Fig 2). The tongue is used to repeatedly turn the seed until weak spots are found in the shell and also to transfer the seed to the other side of the beak so the opposite side of the seed



**Figure 2.** Shell of an oval-shaped seed is removed by a finch by wedging it into the grooves of its beak and cutting it with anterior-posterior movements of the mandibles (lateral views shown in the two top illustrations; cross-sectional views shown in bottom three illustrations). (A) The tongue is used to position the seed in one side of the beak, and part of the shell is removed. (B) The seed is transferred to the other side of the beak where the rest of the shell is removed. (C) The deshelled seed (light color) can then be swallowed. (Reprinted with permission.<sup>3</sup>)

can be cut next. This process is repeated until the seed is opened and the shell is removed by the tongue and discarded. Birds that frequently feed on monocotyledonous seeds (buntings, cardinals, tanagers, weavers and various other Emberizidae, Estrildidae, and Ploceidae) position them against enlarged buttress-like ridges in the hard palate and crush them with an upward thrust of the lower mandible. In contrast, round seeds are placed into the lateral groove of the palate and crushed by the lower mandible. In both cases, the tongue is used to separate the seed from the crushed shell. Birds, such as large parrots (macaws, cockatoos), that feed on very hard seeds can develop tremendous pressure with their enlarged jaw muscles.

Seed preferences of a species are determined by beak morphology, gape, and jaw muscle strength, not by body size.<sup>6,22-24</sup> Further, seed hardness is more important in limiting seed utilization than seed size.

### Food Storage

At the beginning of a meal, the food bolus passes directly into the proventriculus. As the meal continues, the proventriculus and the gizzard fill to capacity, and subsequent food boluses are diverted into the crop (Fig 3), if present, or remain in the distensible esophagus.<sup>25</sup> Within the crop, food softens as a result of hydration by saliva added to food during swallowing, mucus secreted into the crop, and water consumed after a meal. Glucose in the food or released by amylase can be absorbed from the crop. More significant digestion may occur because of the presence of enzymes in the food itself or from microbial action in the warm moist environment of the crop.<sup>11,26</sup> Emptying of the crop or esophagus plays an important role in regulating the rate of passage of digesta through the entire tract.

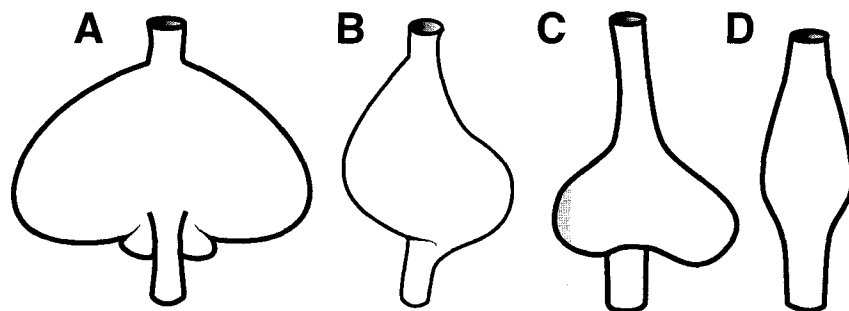
The crop provides a temporary storage area

that permits a bird to rapidly forage for large amounts of food and then fly off to digest the meal in safe cover. A crop also permits "tanking up" in the evening, so that food can be slowly released to supply nutrients during the nighttime.<sup>27,28</sup> In small species (eg, hummingbirds), the filling of a large crop by extensive foraging at dusk fuels their high metabolic rate for several hours into the night. In larger species, food stored during evening feeding supplies the majority of the nocturnal energy needs.

The crop and the esophagus play an important role in nourishing the young by permitting the storage and softening of food, which is later regurgitated into the beak of the nestlings. The nutritional and immunologic contribution of the hen to the regurgitated food is not known for most species, but is important in pigeons.<sup>29</sup>

### Proventriculus and Gizzard

Passage of food through the proventriculus occurs quickly and coats food particles with acid and pepsin.<sup>30</sup> Control of gastric secretions and emptying is coordinated by vagal input and the actions of the hormones gastrin, pancreatic polypeptide, cholecystokinin, and secretin. Food can move rapidly through the proventriculus and enter into the gizzard with little progression of enzymatic digestion. Contractions within the gizzard act in concert with grit to crush the food and grind the edges of the resulting particles together. Studies in a variety of species have shown a complex cycle of proventricular, gizzard, and duodenal contractions that propels the food in alternate directions between these three organs.<sup>31-34</sup> Food is ground in the gizzard, followed by reflux of larger food particles back into the proventriculus for addition of fresh pepsin and HCl. This refluxing provides additional time for the hydrolysis of protein, continues the breakup of large lipid globules, and homogenizes the



**Figure 3.** The crop of a (A) pigeon; (B) budgerigar; and (C) Cockatoo. In some species, a true crop is absent, but some food may be stored in an expandable esophagus (eg, Canary, shown in [D]).

food. When high lipid meals are consumed, lipid is retained in the anterior region of the tract and digested more slowly than protein and carbohydrate components of the meal.<sup>30</sup>

### Small Intestine

The small intestine is the primary site for enzymatic digestion and absorption of nutrients. Release of pancreatic and intestinal secretions is stimulated by duodenal distention, HCl, vagal stimulation, secretin, vasoactive intestinal peptide, and cholecystokinin.<sup>31,35</sup> Differential release of these regulatory factors matches the amount of individual digestive enzymes released to the type and amount of substrate in the digesta. Most protein, starches, and nucleic acids present in the food are hydrolyzed within the lumen of the small intestine by pancreatic enzymes giving smaller oligomers. These are further hydrolyzed at the enterocyte brush border to constitutive molecules (eg, monosaccharides, free amino acids, and nucleotides) that are absorbed. The presence of an intestinal lactase has not been shown in those birds tested,<sup>36,37</sup> and feeding significant amounts of lactose-containing foods is usually not advised.

### Rectum

In the rectum, electrolytes, water, and some nutrients (simple sugars, amino acids) remaining in the digesta are absorbed. Companion birds in the Passeriforme, Piciforme, and Psittaciforme families lack extensive areas for microbial attack of dietary fiber, so plant cell wall components are not digested. These undigested food components, together with bacteria, urine, and endogenous losses, collect in the rectum and cloaca and may be stored there for short periods of time. Endogenous losses include epithelial cells, digestive enzymes, mucous, and bile pigments, which give the feces their greenish hue.

During defecation, there is an intense peristaltic contraction beginning in the anterior rectum that propels the fecal material through the entire rectum and cloaca in a few seconds. Uric acid can be observed as white crystals, usually on the surface of the feces.

### Ontogeny of Digestive Capacity

All florivorous and omnivorous birds undergo dramatic changes in their diet as they develop.

The embryo develops on a diet of lipid and protein (yolk and albumen), but essentially no carbohydrate. After hatching, granivorous birds are fed a diet that is high in carbohydrate and low in protein and fat. They must quickly make the appropriate digestive and enzymatic adaptations to facilitate this abrupt switch. Our understanding of the posthatch digestive and metabolic changes of altricial birds has yet to be investigated in detail, but has been described in chickens.<sup>38</sup>

There are important temporal differences between precocial and the altricial birds in the development and maturation of their digestive systems into a completely functional organ system.<sup>39-42</sup> The allometric growth rate of the embryonic digestive tract is faster than that of the rest of the body, so that at hatching, it is relatively large and functionally developed. This gives the young altricial chick the capacity to receive and efficiently digest the large quantities of food supplied by its parents and permits very rapid postnatal growth. For example, in the budgerigar, the absorptive area of the intestines relative to body weight is maximal at hatching and decreases later as growth slows.

The gizzard is relatively small and weak after hatching and increases in strength and resistance to abrasion as the chick begins to consume food. This developmental pattern constrains the size and hardness of foods that many young chicks can consume. The parents of altricial chicks may contribute to the digestion of food by softening it with saliva and sometimes by enzymatic action before regurgitation.

Birds hatch from the egg with a completely sterile digestive tract. Altricial chicks are fed by their parents, and the food material is contaminated with a robust population of microflora from the parents' anterior digestive tract. Spontaneous sucking movements of the vent (cloacal drinking) facilitate the uptake of microflora from the nest environment for colonization of the posterior digestive tract. Some of the microflora ingested by the chick will not find the conditions suitable and are either killed by digestive secretions, eliminated by the immune system (eg, IgA), or are unable to attach to the epithelium and are defecated. The remaining microflora proliferate and compete for space and nutritional resources. This process continues until the "normal" flora develops.



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