Oesophagus This is a distensible muscular tube connecting pharynx with stomach (Fig. 5.25). In a few vertebrates the oesophagus is lined with fingerlike papillae but more often the lining has longitudinal folds or is smooth. Peristalsis begins at the oesophagus. The endodermal lining of the oesophagus is frequently stratified epithelium which contains mucous glands whose secretion help lubricate the ingested food. The upper area of the

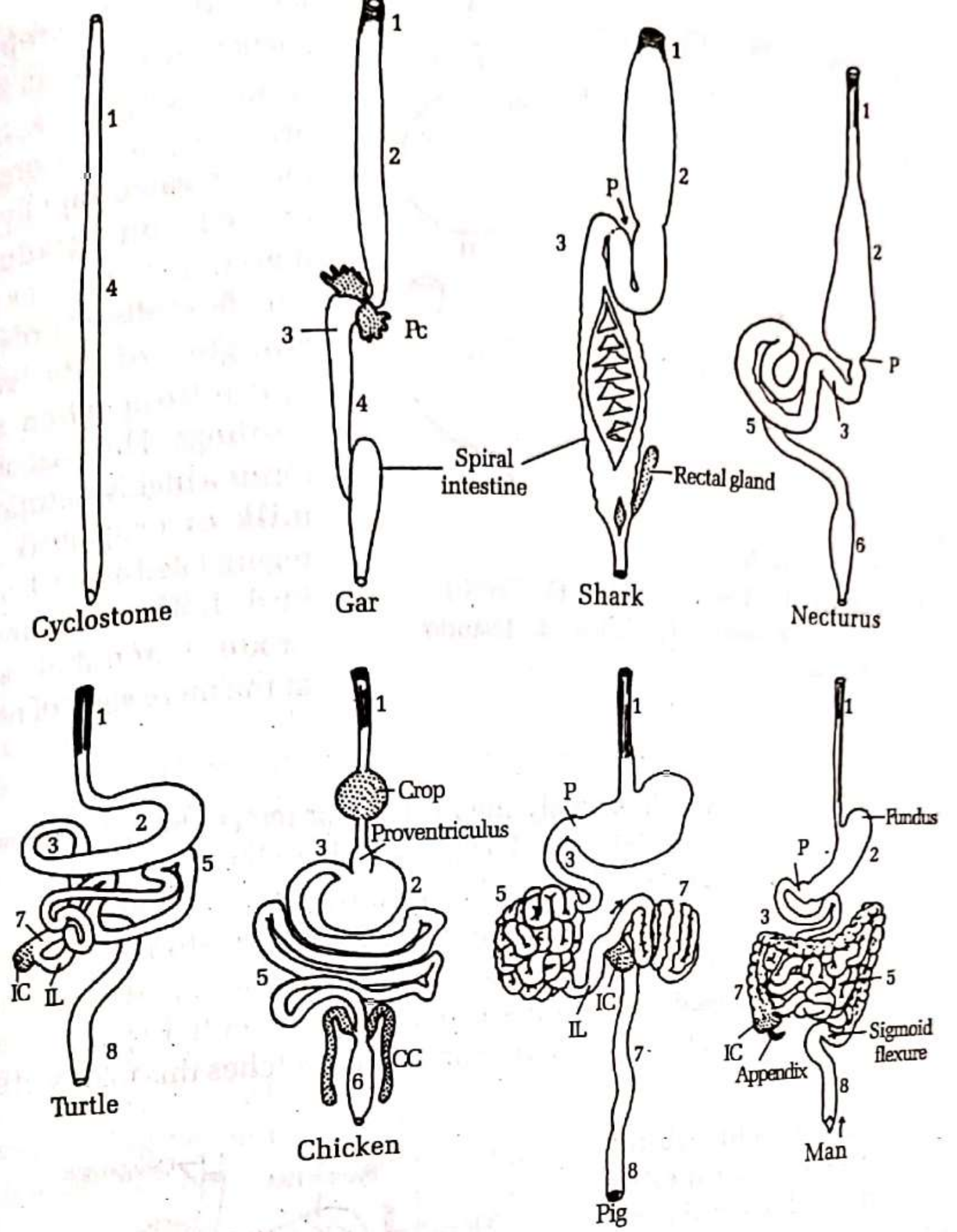

Figure 5.25
Alimentary canal of a few craniates after pharynx showing different modifications

1. Oesophagus
2. Stomach
3. Duodenum
4. Intestine
5. Small intestine
6. Large intestine
7. Colon
8. Rectum

CC Paired caeca of bird
IC Ileocolic caecum
IL Ileum
P Pyloric sphincter
PC Pyloric caeca

oesophagus is wrapped by stratified musculature and its lower by smooth musculature except in ruminants whose entire oesophagus is walled by striated musculature. Ruminants, therefore, have more control over their oesophagus than do most vertebrates and can regurgitate their food—the cud which is rechewed.

The oesophagus has a good deal of elastic tissue, enabling it to stretch enough to accommodate large pieces of food. Some tetrapods such as snakes and fish can swallow pieces of food larger than their own diameter. In most birds the posterior part of the oesophagus forms a

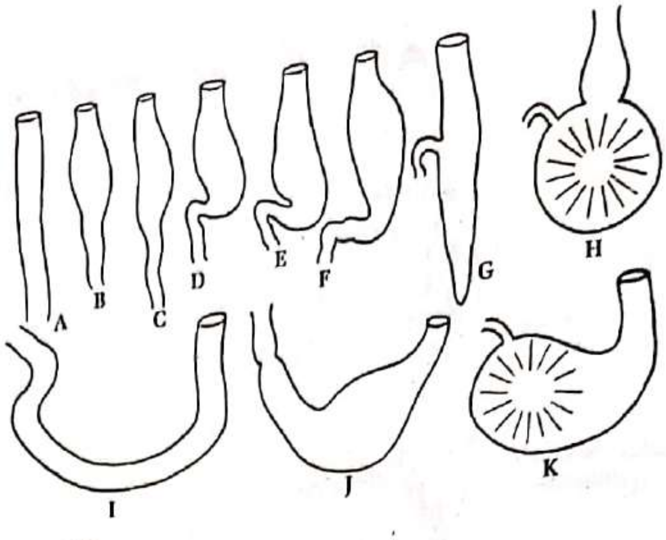

Figure 5.26
Shapes of vertebrate stomach
A. Belone B. proteus C. Tropidonotus D. Gobius
E. Shark F. phoca G. polypterus H. Fulica I. Testudo
J. Land tortoise K. owl

sac, called the **crop** which is particularly large in seed eaters (Fig. 5.26). The crop acts primarily as a storage depot; food is eaten rapidly and then passed on gradually for digestion. In pigeons (Fig. 5.29) and few other birds the crop sloughs of its squamous epithelium when there are nestlings. This cast off material forms a highly nutritious **pigeon milk** or crop milk which is regurgitated and fed to the young bird. Both males and females produce crop milk, apparently at the mere sight of nestlings.

Stomach

The portion of the stomach which is solely meant for storage is close to the oesophagus, and is called the cardiac stomach (Fig. 5.27). Here the diameter of the alimentary canal is increased-a great deal in vertebrates that eat discontinuously and much less or not all in those fish whose easily digested diet is continuously consumed. Storage also occurs in the remainder at part of the stomach. In most stomach: bands of muscular tissue in the external layer cause folds, called **rugae**, these folds provide the potential space for additional distension. When the stomach is filled, internal pressure stretches this folds and obliterates the rugae.

A large stomach contributes significantly to a more mobile lifestyle. For many terrestrial animals it is advantageous to eat rapidly and then hide from potential predators while digestion occurs. For predators it allow the animal to stock up while the kill is still fresh.

Digestion

The breaking up of food by mechanical digestion provides a greater surface area on which digestive enzymes can work. The wall of stomach is more muscular than those of other parts of the alimentary canal. There are often encircling oblique bands of muscle, which by powerful rhythmical contractions churn and break down the

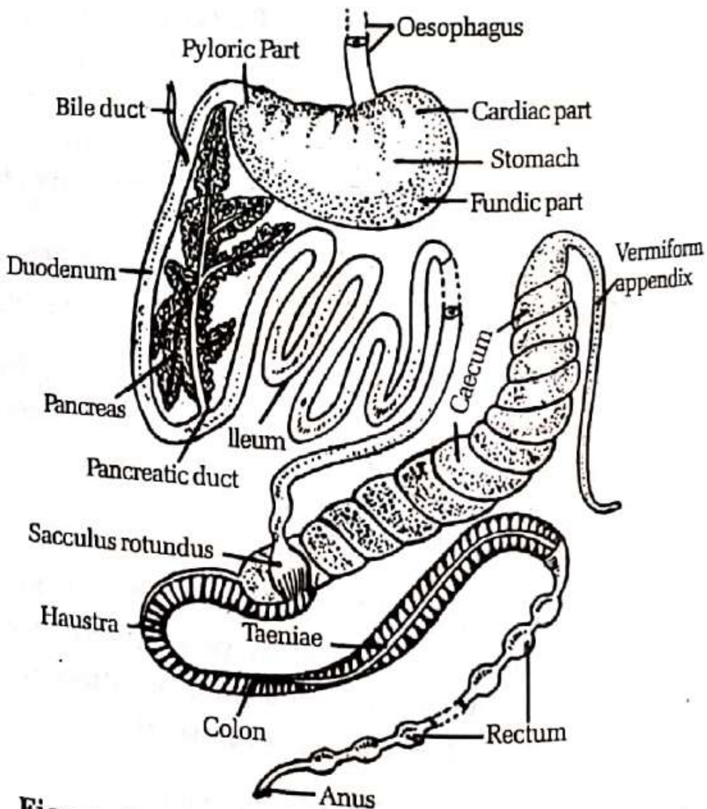

Figure 5.27
Rabbit, alimentary canal with associated glands

food. This mechanical action plus the effect of the gastric juice reduces the food to a semiliquid state.

Now chemical digestion follows immediately. Protein digestion begins in the stomach with secretions from gastric glands in the central (fundic) region (Fig. 5.27, 5.28). In mammals gastric glands have two secretory cell types (i) Chief cells secrete proteolytic enzymes collectively called pepsin. (ii) Parietal cells secrete hydrochloric acid.

In nonmammals gastric glands have only one secretory cell type which evidently secrete both hydrochloric acid and pepsin.

Mucus glands are present throughout the alimentary canal, and are particularly prominent and usually multicellular in pyloric region of the stomach. Their secretion lubricate the food and protect the delicate epithelium of stomach from mechanical damage or chemical digestion by its own enzymes.

Stomach has acquired specializations to meet diversity of diet. In the mucosa are many depressions, called gastric pits, lined with columnar epithelium (Fig. 5.28). In both cardiac and fundic region of stomach, tubular fundic glands lie within the lamina propria and contain secretory cells, called **body** cells, which evidently secrete both pepsin and hydrochloric acid. In the pyloric region instead of fundic glands there are mucus secreting pyloric glands also opening into the base of the gastric pits. The stomach is present in **protochordates** and is simple, and the stomach is poorly delineated in cyclostomes. The boundary between the oesophagus and stomach is indefinite or lacking in vertebrates below birds. The stomach is straight when it first develop in-embryo and may remain so throughout life in lower vertebrates. More often, flexure* develop producing a J shaped or U-shaped stomach (Fig. 5.26). As a result, the stomach may exhibit a concave border (lesser curvature) and a convex border (greater curvature). The stomach also undergoes torsion in higher forms so that it may finally lie across the long axis of the trunk. As flexion and torsion gets pronounced during development of mammalian stomachs; the dorsal mesentery of the stomach (mesogaster) becomes twisted and finally get suspended from the greater curvature. The part of the dorsal mesentery attached to the greater curvature is then called the **greater omentum**. The stomach of some vertebrates, especially of fish, exhibit one or more blind pouches, or caeca. The stomach of some marine teleosts is lined with a horny membrane that may exhibit some spiny projections.

Amphibians and reptiles: The stomach of amphibians and most reptiles, when examine grossly are relatively simple dilations of the alimentary canal. On detailed microscopic examination they can be divided into regions by types of gland present. In crocodilians stomach the smooth musculature is thickened and extremely powerful, it functions analogously to the avian **gizzard**, violently and efficiently macerating food.

Birds: The avian stomach is differentiated into two sections:

i) The glandular portion—**proventriculus** and

ii) Mastigatory portion—**gizzard**

Food is stored in the crop located at the distal end of the oesophagus and is periodically released in the stomach at the junction between gizzard and proventriculus

* In mammals, e.g. mouse a constriction in the middle part of the stomach mark off a cardic chamber from a pyloric chamber. In Man the stomach bear resemblance to this condition found in mice and is called "hour glass" stomach.

(Fig. 5.25/5.29 A, B). The gizzard, a unique modification for flight, is found only in birds, although the thickened stomach walls of crocodiles which function similarly are interesting in this regard since crocodiles descended with birds from a common ancestor. The avian gizzard has extremely thick powerful muscular walls and a glandular mucosa that produces a very hard, keratin like protein called koilin. The koilin is analogous to teeth, when the gizzard muscles contract the food is crushed. The gizzard is another means of accomplishing mechanical digestion (essential for an animal with a high metabolic rate). If instead of a gizzard birds had a mammalian type masticatory apparatus with teeth muscles and skeletal supports, the weight of the head would create disastrous aerodynamic problems. The extent of muscular development in the gizzard depends on both heredity and diet. For instance, if herring gulls are fed their usual soft fish diet their gizzard remain thin walled and relatively inconspicuous. If they are forced to eat grain, however, the gizzard walls soon proliferate and strengthen.

Mammals: Like birds, mammals have a high metabolic rate and require an efficient digestive system. There is no need for a masticatory apparatus in the stomach since mammalian heterodont teeth provide grinding surface in the oral cavity. The stomach however, must act as a large storage reservoir, and in most mammals, the cardiac portion is distensible. In small insectivorous mammals, such as the *grasshopper mouse* the cardiac portion is lined with keratinized, stratified squamous epithelium, which protects the stomach from damage by the chitinous exoskeleton of insects. The gastric glands, instead of opening through numerous gastric pits are all funnelled into one short duct. Since this duct is the only place where they contact the lumen, the opportunity for damage to the glands is greatly minimized.

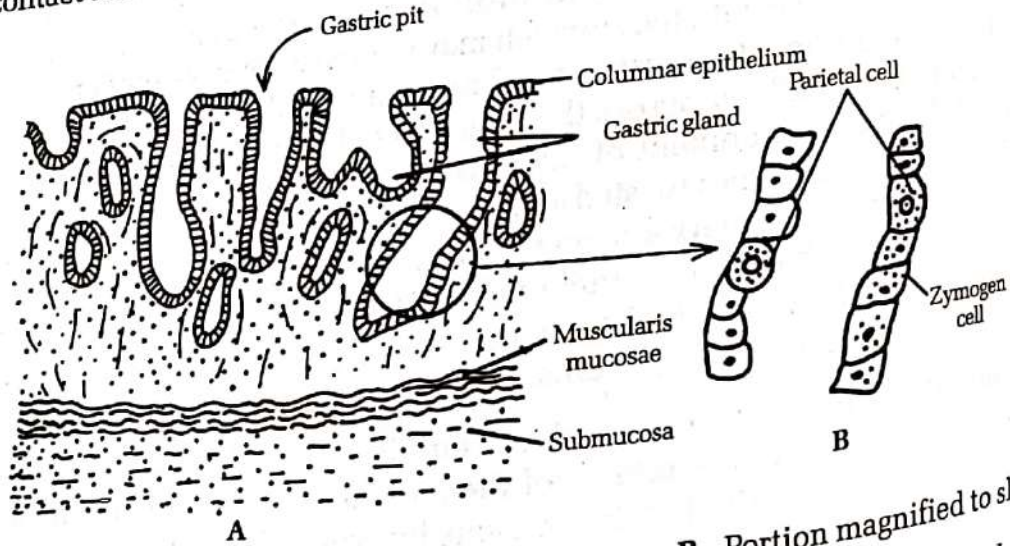

Figure 5.28
A. Histology of alimentary canal showing secretory cell types **B.** Portion magnified to show cells

Ruminant stomach The most bizarre vertebrate stomach, however, is surely that of the ruminant *Artiodactyl*, a four chambered structure with a capacity of up to 60 gallons (Fig. 5.30A, B, C). The first and largest part of this stomach into which the food enters is the **rumen**, its simple epithelial wall is filled with symbiotic bacteria which can digest plant cellulose. The next part is **reticulum**, the mucosal lining of this chamber usually also contains symbiotic bacteria. This lining is folded in such a way which produces geometric configuration similar to honey comb.

Food is frequently regurgitated from both rumen and reticulum (Fig. 5.30B, C) to the oral cavity, there it is resalivated, rechewed and reswallowed to pass once again through the rumen and reticulum, for further cellulose digestion by the symbiotic bacteria. During this

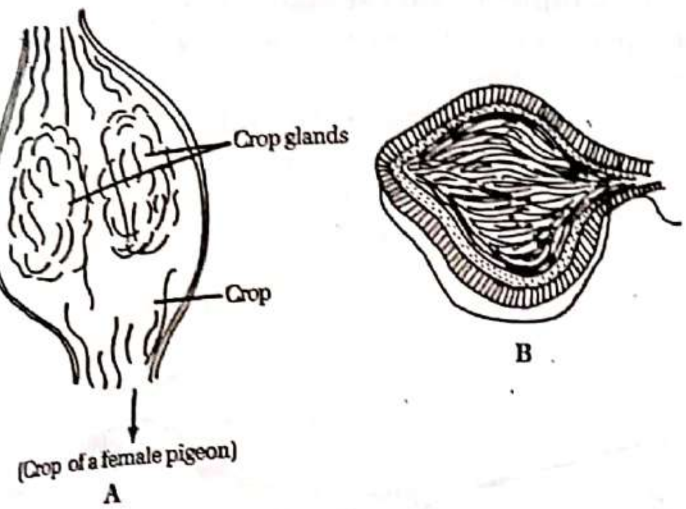

Figure 5.29 A, B
A. Crop gland of pigeon B. Gizzard (dissected) of a grain eating bird

process much of the water and sugar present in food are reabsorbed through the walls of the rumen and reticulum into the circulatory system. From the reticulum the food is passed to the **omasum**, a heavy muscular structure with longitudinal muscle folds. The walls of **omasum** subject the food to mechanical churning, the purpose of which is unclear. Surgical experimentation, has shown that cows suffer no ill effect if the omasum is removed. The fourth chamber is the glandular **abomasum**, and it is the site of initial digestion of protein.

At the junction of stomach and intestine the circular smooth muscles are greatly thickened, forming the pyloric sphincter. When the sphincter contracts it completely closes the alimentary canal; thus it controls the rate at which food passes from stomach to intestine. The pyloric sphincter itself is controlled by the autonomic nervous system and by endocrines.

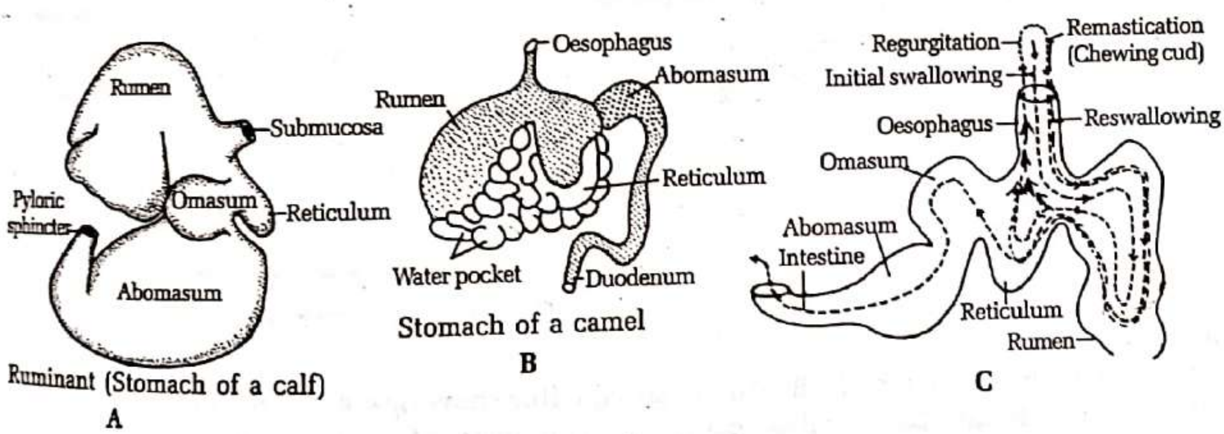

Figure 5.30 A, B, C
Diagram of Ruminant stomach A. Stomach of calf B. Stomach of camel C. Functional relationship. Dotted lines show initial swallowing and swallowing after chewing cud.