THE COMPARATIVE ANATOMY

OF THE

OESOPHAGUS

by

MYINT THEIN

A THESIS

PRESENTED FOR THE DEGREE OF

MASTER OF SCIENCE

OF

THE UNIVERSITY OF ST. ANDREWS

DECLARATION

I hereby declare that the following Thesis is based on the results of original work carried out by me; the Thesis is my own composition and has not previously been presented for a Higher Degree.

The research was carried out in the Department of Anatomy, St. Salvator's College, Bute Medical Buildings, University of St. Andrews.

Myint Thein

CERTIFICATE

I certify that Myint Thein has spent six terms at research work in the Department of Anatomy under my direction, that he has fulfilled the conditions of Ordinance No. 51 (St. Andrews) and that he is qualified to submit the accompanying thesis in application for the degree of M. Sc.

Professor of Anatomy,
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May 1964

CAREER

I graduated M.B., B.S. in March 1955 from the University of Rangoon, Burma. After completing residential hospital training for one year in Rangoon General Hospital, I worked as a Civil Assistant Surgeon for five years in Mandalay General Hospital and as a Demonstrator in the Department of Anatomy, University of Mandalay for one and a half years.

In October 1962, I commenced the research on 'The Comparative Anatomy of the Oesophagus' under the supervision of Professor R. Walmsley and have completed the work which forms the subject of the Thesis.

Myint Thein

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INTRODUCTION

INTRODUCTION

My main reason for undertaking the work incorporated in this thesis is that I wished to gain experience in undertaking a problem involving histological techniques and photography and also to learn something about the methods used in obtaining references to recent literature on an anatomical subject. The oesophagus is a part of the digestive system which presents many interesting comparative problems, both naked-eye and microscopic, and it is for that reason that it was chosen. I had no previous experience in the preparation and staining of tissues for microscopic examination and I have gained considerable experience in the routine staining methods such as haematoxylin and eosin, van Gieson and elastic tissue stains; and the glandular tissues of the oesophagus have allowed me to become familiar with the use of special staining methods such as the periodic acid-Schiff technique and the mucicarmine method for mucus.

It was known to me that there is variation in oesophageal structure throughout the vertebrates and I felt that these methods of preparation could be used to determine the pattern in the various species. I was particularly interested in the variation in nature of the lining epithelium and in the comparative study of the type of muscle to be found in the oesophageal wall in the different species examined. The number of animals examined has, of necessity, been small but I have personally processed the tissues, cut the sections (many of them serially) and carried out the various staining procedures.

MATERIAL AND METHODS

MATERIAL AND METHODS

The material used for the present investigation consists of four trout (Salmo trutta), one whiting (Gadus merlangus), one cod (Gadus morrhua), one ling (Molva vulgaris) to represent fish (Pisces); six frogs (Ran temporaris temporaria) are taken to represent amphibia; twelve lizards (Lacerta muralis) are representatives of reptilia; three pigeons (Columba) represent the birds (Aves); three rabbits (Oryctolagus), one guinea pig (Cavia), one rat (Mus norvigicus albinus), and pig (Sus) embryos at 6 mm., 10 mm., 15 mm. and 35 mm. stages were the mammals examined.

In addition to these, specimens of oesophagus of dog (Canis) cat (Felis), pig (Sus) and one human specimen of gastro-oesophageal junction were obtained in fixative for use in the present work.

The specimen of gastro-eosophageal junction was from a five year old child and except for the pig embryos, all the animals used were adult.

The above mentioned animals were selected for this research because they are easily obtained.

All the animals used except the frogs and lizards were killed by coal gas. Frogs and lizards were found to be quite resistant to coal gas and they were killed with chloroform.

The oesophagus was exposed and examined in situ in the first instance. Its gross features and general relations in the body were noted briefly. The length of the oesophagus was measured in those animals in which the external line of demarcation between the oesophagus and the stomach is evident, the cranial end of the oesophagus being taken as the level corresponding to the lower border of the cricoid cartilage. In the case of the trout in which no external demarcation was present it was measured directly on the section prepared for histological examination. The oesophagus was then dissected out together with a portion of stomach caudally, and put straight away into the fixative. Special care has been taken to ensure rapid fixation and the tissues were handled gently to avoid damage to the epithelium as far as possible.

The lumen of the oesophagus was cut open before fixation (except for the lizards) in those instances where longitudinal sections were to be examined. In the case of the lizards, the lumen of the oesophagus is so narrow that its being opened causes epithelial damage which is unavoidable. The tissue from the lizard was therefore fixed, processed and embedded intact and then cut longitudinally.

The fixative used for the pig embryos was Bouin's solution and 10% formal saline for the lizard. Formal corrosive (9 parts of 40% formalin and 1 part of mercuric chloride) was used for the remaining tissue.

After dehydration by passing the tissue through the series of graduated concentration of alcohol, and clearing in two changes of chloroform the tissue was embedded in paraffin. In the case of lizard oesophagus, a double embedding method was used (after the usual dehydration, the tissue was passed through two changes, each of 1% celloidin in methyl benzoate and benzene and embedding was done in paraffin.).

The paraffin sections were cut 8 microns thick except for the pig embryos which were cut 10 microns thick. Serial sections of the embryos were prepared. Every section in 6 mm., 10 mm. and 15 mm. embryo was mounted: and every fourth section was mounted in the 35 mm. embryo. In mounting the pig embryo sections, a small piece of gelatin sheet dissolved in water tinged with potassium dichromate was used to prevent the sections from coming off the slides during staining. (This difficulty was experienced without the application of this procedure).

Staining methods used were Ehrlich's haematoxylin and eosin, van Gieson's stain, picro-Mallory, orcein for the elastic tissue, Southgate's mucicarmine, periodic acid-Schiff technique (Everson Pearse, 1961), Fontana stain for argentaffin cells (Culling, 1963), Lendrum's phloxine-tartrazine stain (Culling, 1963), Hollande's chlorcarmine stain (Duckworth, 1952) and Heidenhain's Azan stain.

Photomicrographs of the sections were taken at different magnifications. Drawings were made to illustrate the variation in the gross form of the oesophagus in different vertebrate groups.

OBSERVATIONS

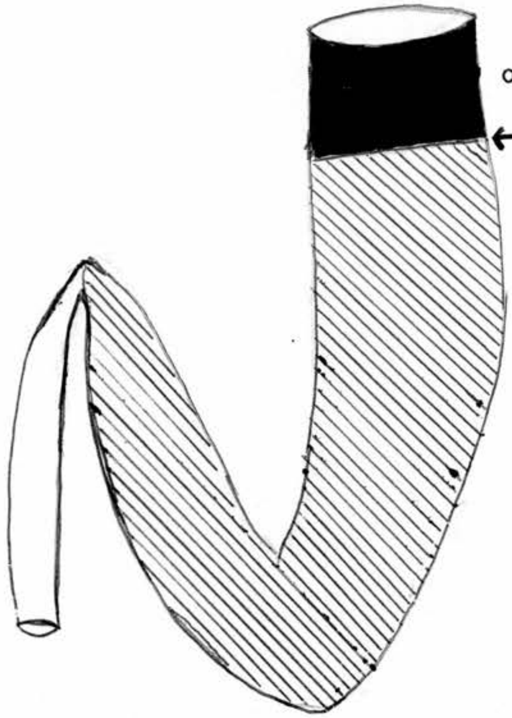

Fig.A. Drawing of the oesophagus & stomach of trout (fish) from ventral aspect.

Note the absence of external indication of the junction between the oesophagus & the stomach. The two together forming 'U' shaped tube. The oesophagus is very short.

OBSERVATIONS

THE OESOPHAGUS OF PISCES

Macroscopic appearance

The oesophagus of the trout (Salmo trutta) is a muscular tube extending from the pharynx to the stomach. The pharynx, as it is the customary pattern in fish, is perforated by a number of branchial clefts. These branchial clefts are specialised as 'water lungs' and so allow fish to be so ideally adapted to their aquatic life. A short distance caudal to the perforation of the last branchial cleft the pharynx merges with the oesophagus.

The oesophagus passes caudally for about 1 cm. to merge imperceptibly into the stomach. It is therefore a relatively short and poorly demarcated segment of the digestive tract and it has a diameter which is almost as great as the empty stomach. There is no external indication of the junction between the oesophagus and the stomach and they are therefore regarded together as forming a single entity; together they have the form of the letter "U", extending caudally from the pharynx. The cranial limb of the "U" consists of the oesophagus together with the cardiac portion of the stomach. The caudal limb of the "U" curves dorsally to its junction with the intestine and is formed by the remaining portion of the stomach which is demarcated from the intestine by the pyloric constriction (Fig. A).

The oesophagus is invested externally by the visceral layer of peritoneum except for its cranial extremity. The investing peritoneum on each side of the oesophagus is connected both dorsally and ventrally by suspensory or 'peritoneal mesenteries' to the middorsal and midventral walls of the coelomic cavity. The peritoneum of the mesenteries is in turn continuous with the parietal layer of peritoneum which lines the inner surface of the body wall. The greater part of the ventral aspect of the oesophagus is related to the relatively large liver which is a feature of all teleosts.

The mucosal lining of the oesophagus is folded in a very complex manner. In its caudal part longitudinal folds are very prominent and are continuous with corresponding folds in the stomach.

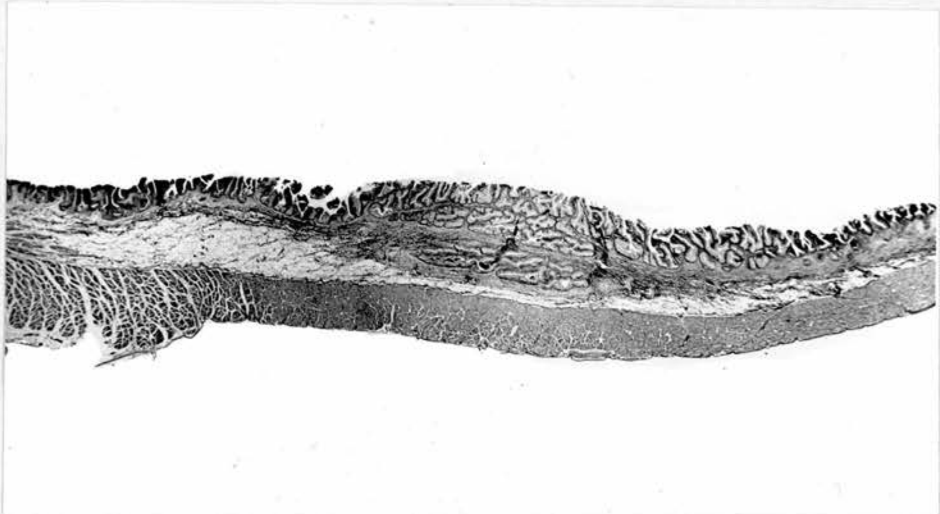

Fig.1. L.S. through the whole length of trout oesophagus. Note that complicated folds in the mucous membrane give an appearance which simulates the appearance of glands. H & E. X 12

Fig.2. L.S. Lining epithelium of trout oesophagus. Note foamy cytoplasm and basal nuclei of mucus-secreting tall columnal cells and the appearance of the interrupted layer of surface squamous cells. H & E. X 1000

Microscopic appearance

Histologically, the wall of the oesophagus of the trout consists of three distinct coats, in addition to the covering lamina of visceral peritoneum already referred to. These three coats of the wall of the oesophagus of trout are from within outwards (Fig.1):-

1) Tunica mucosa
2) Tunica submucosa, and
3) Tunica muscularis.

1) The tunica mucosa is formed by simple columnar (Fig.3) or in some parts by pseudostratified columnar epithelium without cilia (Fig.2). The columnar cells have well defined cell boundaries and their cytoplasm has a foamy appearance in sections stained with haematoxylin and eosin (Fig.2). Though they are PAS positive, yet they give only faint red reaction with mucicarmine. The nuclei of the columnar cells lie in the basal part of the cells.

In addition to these epithelial cells there are squamous cells on the luminal surface of the tall columnar cells (Figs.2 & 3). These surface squamous cells do not form a continuous layer. They have oval nuclei and scanty eosinophilic cytoplasm. They give a negative reaction with both PAS and mucicarmine and are neither phloxinophilic nor do they give a reaction with Fontana staining method for argentaffin cells.

In addition to the surface squamous cells other cells lie interposed among the columnar epithelial cells. These are few in

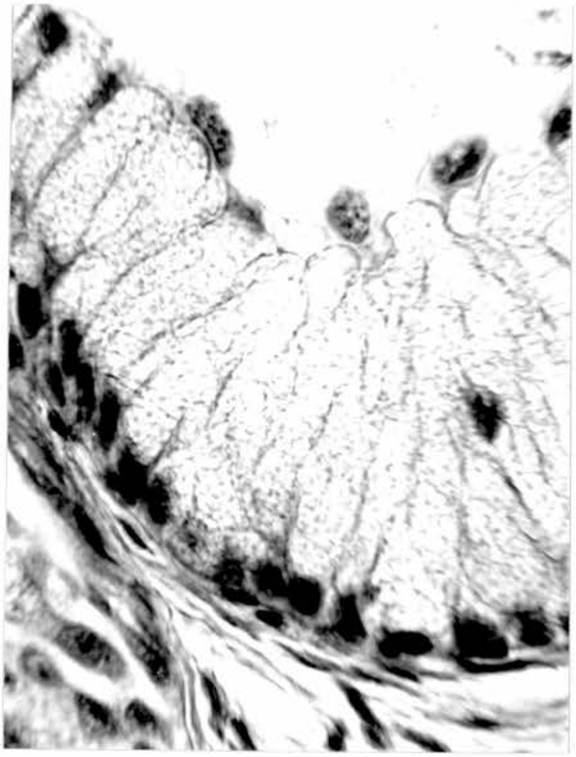

Fig.3. Lining epithelium of trout oesophagus. Note solitary nucleus lying in the middle of the thickness of the epithelium and surface squamous cells with scanty cytoplasm. H & E. X 1000

Fig.4. T.S. Middle third of trout oesophagus. Note complexity of mucosal folds. H & E. X 60

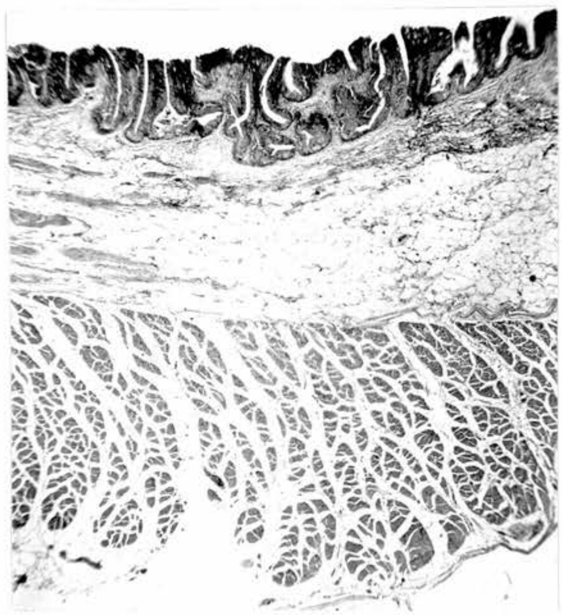

Fig.5. L.S. Pharyngeal end of trout oesophagus. Note the additional inner longitudinal layer of striated muscle fibres in the pharynx. H & E. X 30

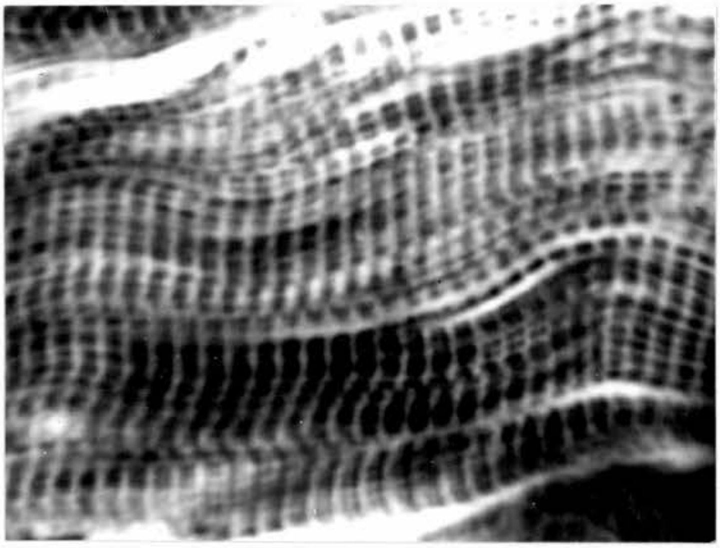

Fig.6. Striated muscle fibres of tunica muscularis of trout oesophagus. Chlorcarmine stain X 1600

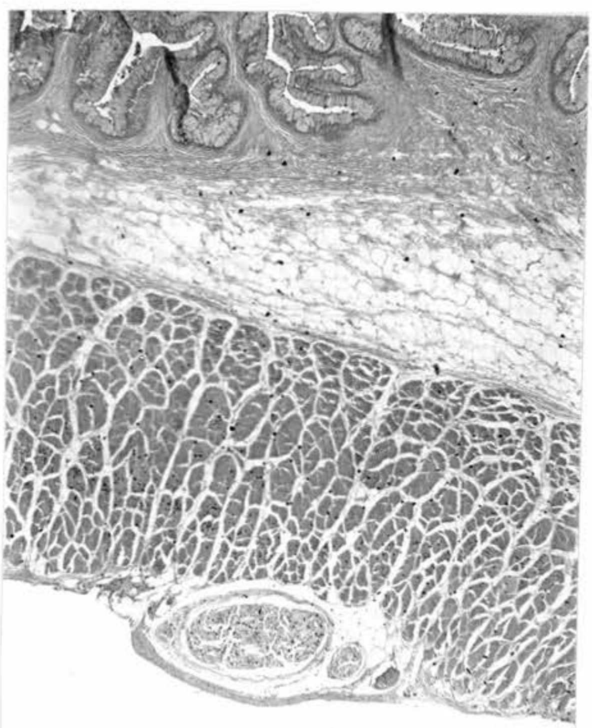

Fig.7. L.S. Oesophagus of trout. A bundle of nerve fibres is seen between the outer layer of connective tissue and the inner single layer of circularly arranged striated muscle fibres. Fat is seen in the outer part of the submucosa. H & E. X 40

number and their nuclei may be seen in the middle of the thickness of the epithelium (Fig.3).

As the muscularis mucosae is absent (Fig.1) in the oesophagus of the trout, the lamina propria is continuous with the submucosa. The inner part of submucosa will be referred to as subepithelial tissue.

The mucous membrane is folded in an extremely complex manner and the folds extend both transversely (Fig.1) and also in the longitudinal direction; the longitudinal folds are particularly prominent (Fig.4). In microscopic sections the folds of the mucosa are cut across and give the appearance of mucous glands (Fig.1). It was considered, however, that there are no true glands in the subepithelial layer of the trout oesophagus.

2) <u>The tunica submucosa</u> is composed of a loose areolar connective tissue. The inner part of the submucosa is composed of collagen fibres (subepithelial tissue). The outer part of the submucosa consists largely of adipose tissue (Fig.5). Elastic tissue is present throughout this layer and is particularly well developed in its outer part.

There are no glands in the submucosa.

3) <u>The tunica muscularis</u>. In the <u>pharynx</u>, there are two layers of striated muscle. The muscle fibres are arranged in an outer circular and an inner longitudinal layer (Fig.1). The inner longitudinal layer lies in the plane of the adipose tissue of the tunica submucosa of the oesophagus (Fig.5).

The tunica muscularis of the <u>oesophagus</u> on the other hand, is formed by a thick <u>single layer</u> of circularly arranged striated muscle fibres but there is no evidence whatsoever of <u>smooth</u> muscle fibres (Fig.6). The striated muscle extends down for a short distance into the stomach where it is replaced by smooth muscle fibres which are also arranged in a circular manner. At about the level of change from striated to smooth muscle a thin outer longitudinal layer of smooth muscle fibres is added to the stomach.

There are bundles of nerve fibres and ganglion cells (Fig.7) in the oesophagus between the collagenous fibres of its peritoneal covering and the circular muscle coat. It is postulated that these are homologous with Auerbach's plexus and that their position superficial to the circular muscle coat is due to the fact that the longitudinal muscle layer is not developed in the oesophagus of the trout.

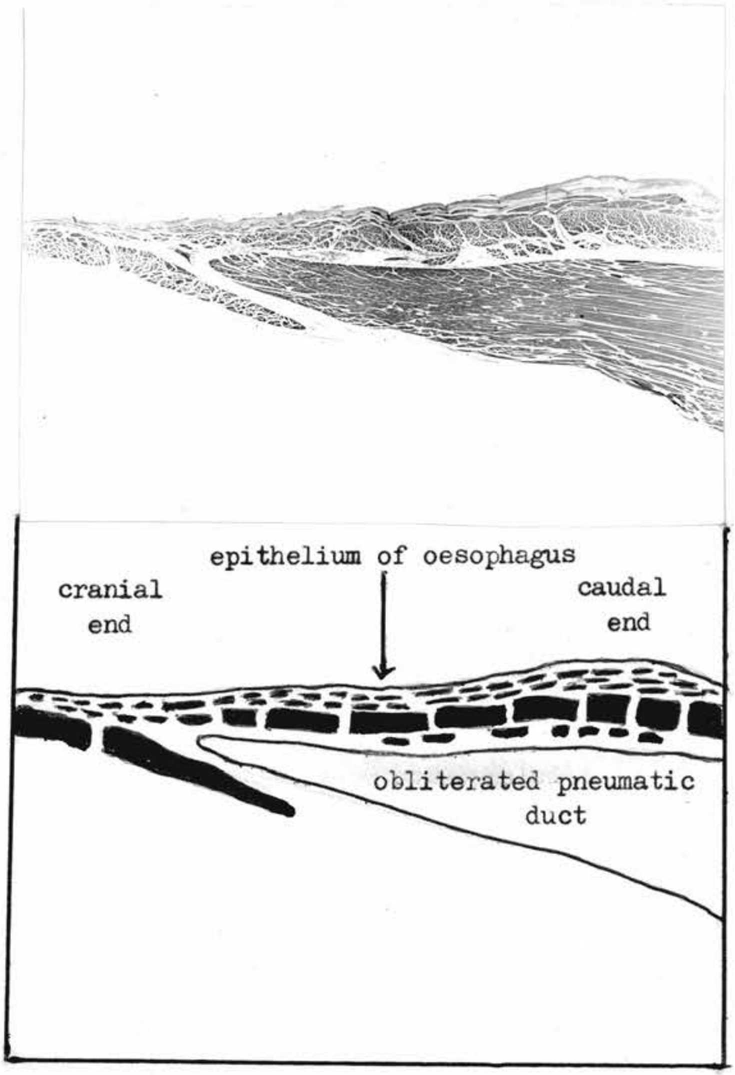

Fig.8. L.S. Region of junction of obliterated pneumatic duct with oesophagus in the Whiting. There is marked thickening of the muscular coat of oesophagus (solid black) in this region. H & E. X 30

SWIM-BLADDER

Macroscopic appearance

Almost all bony fishes with the exception of a few species possess a swim-bladder which is connected to the alimentary tract, either to the pharynx, the oesophagus or to the stomach, by means of a single or by a pair of pneumatic ducts. These ducts may not remain patent into adult life.

In the trout, neither the pneumatic ducts nor any other ducts open into the oesophagus.

In the whiting (Gadus merlangus), the pneumatic ducts are paired and are connected to the commencement of the oesophagus just caudal to the last gill cleft of the pharynx; but, they are obliterated and found to be a pair of solid cords running between the dorsal aspect of the oesophagus and the ventral aspect of the cranial part of the swim-bladder on either side of the midline.

Microscopic appearance

The connecting cords between the oesophagus and the swim-bladder of the whiting are entirely composed of longitudinally placed striated muscle fibres. There is no lumen inside the muscular cords (Fig.8).

At the point of junction of the connecting muscular cords with the oesophagus there is thickening of both the inner longitudinal and the outer circular layer of muscle of the oesophageal wall (Fig.8).

Macroscopic appearance in cod and ling

In cod (Gadus morrhua) the oesophagus is connected to the swim-bladder by a pair of muscular cords on either side of the midline. This arrangement is similar to that in the whiting.

In ling (Molva vulgaris), the connecting muscular cords are attached to the oesophagus at one end and, at the other end, they are attached not directly to the swim-bladder, but to that part of the vertebral column on either side of the midline, adjacent to the dorsal aspect of the cranial portion of the swim-bladder.

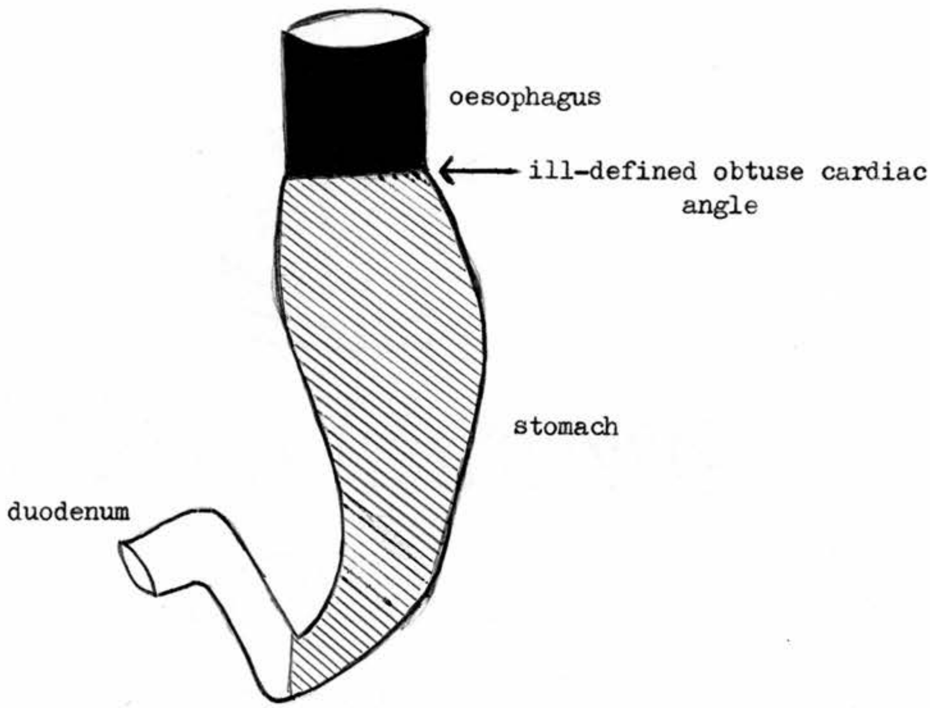

Fig.B. <u>Drawing of the oesophagus & stomach of frog (amphibia) from ventral aspect.</u>

Note the ill-defined cardiac angle & slight dilatation of stomach.

THE OESOPHAGUS OF AMPHIBIA

Macroscopic appearance

The oesophagus of the frog (Rana temporaria) is a muscular tube extending from the pharynx to the stomach. The pharynx is confined to the region of the head. The branchial clefts disappear completely from the pharyngeal wall after the tadpole stage as the gills are no longer required as the animal changes its habitat from water to land. The gills are duly replaced by a pair of lungs. As a result of these changes, the pharynx becomes restricted within the confines of the head and decreases in length. Correspondingly, the oesophagus gains somewhat in length as compared with the fish.

The oesophagus of the frog forms a short (about 1 cm.), wide muscular tube interposed between the pharynx and the stomach.

The stomach has the appearance of a fusiform dilatation bulging to the left of the midline. The fundus of the stomach is still absent but, there forms a definite obtuse cardiac angle between the terminal end of the oesophagus and the fusiform dilatation of the stomach, on the left of the midline (Fig. B).

The oesophagus is connected with the surrounding structures by means of a layer of loose areolar connective tissue.

There are prominent longitudinal folds on the luminal surface of the oesophageal wall which are continuous with those of the pharynx.

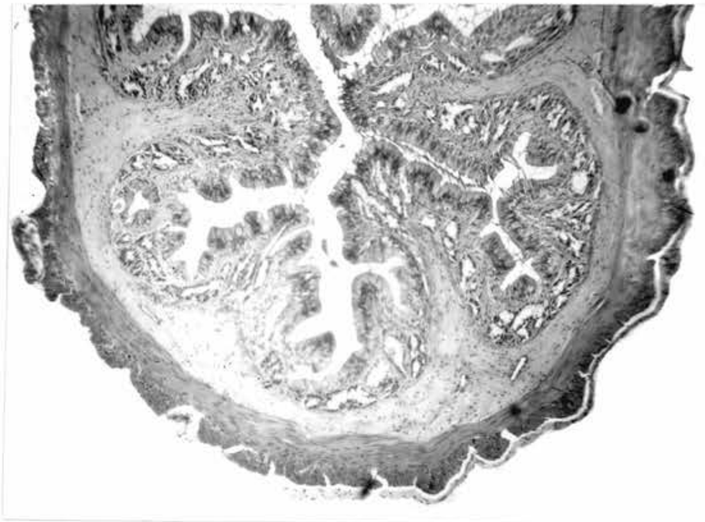

Fig.9. T.S. Caudal part of the frog oesophagus. Note smooth inner circular and outer longitudinal layers of the external muscle coat. Glands lie only in lamina propria. H & E. X 60

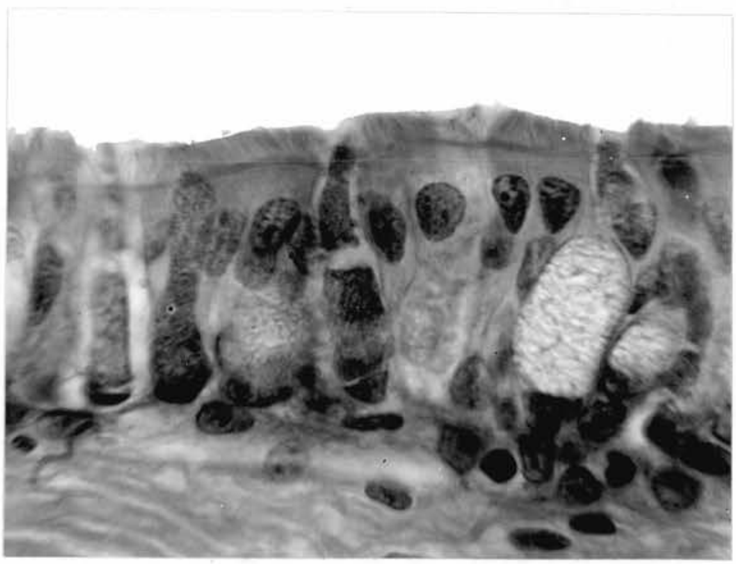

Fig.10. Ciliated pseudostratified columnar epithelium with goblet cells lining frog oesophagus. Note some goblet cells stained dark blue, some very lightly. Discharging goblet cell is seen in the middle of the field. H & E. X 1000

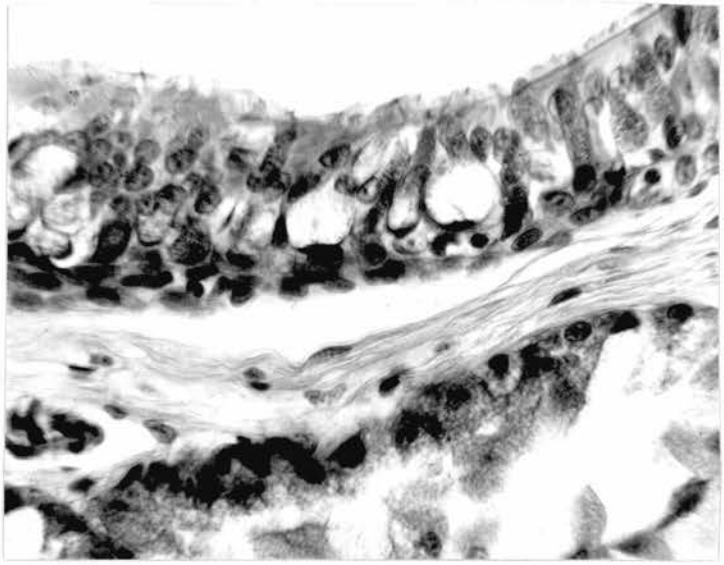

Fig.11. L.S. Lining epithelium of frog oesophagus
Note the flattened nuclei at the base of goblet cells.
H & E. X 440

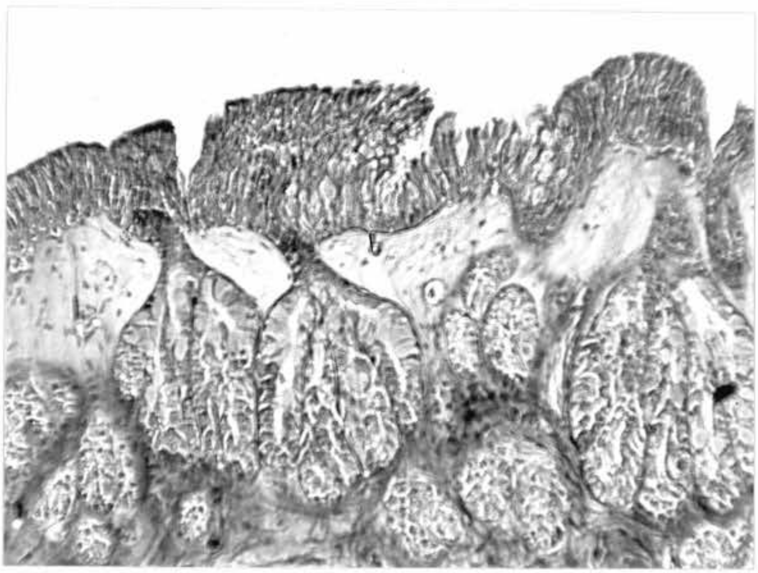

Fig. 12 Glands of the frog oesophagus. Note simple branched mucoserous glands opening on the surface of the epithelium. Heidenhain's Azan stain. X 120

Fig.13. Frog oesophagus. Mass of oesophageal glands. Note some serous some mucous and some mixed secretory units. H & E. X 190

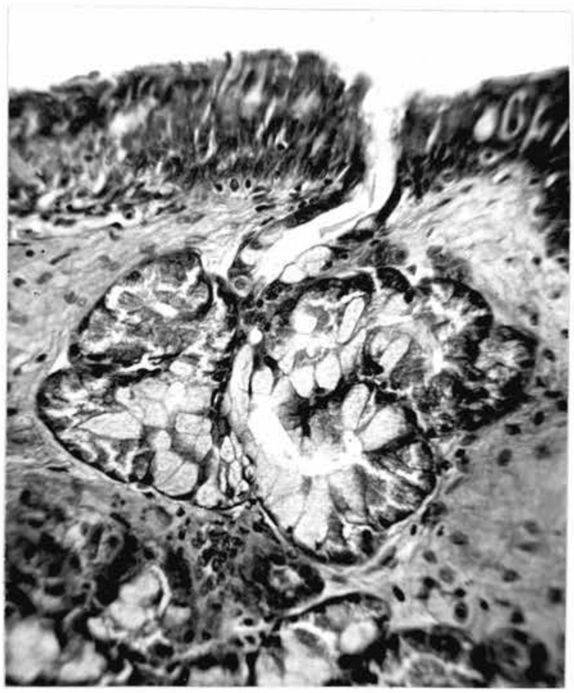

Fig.14. Simple branched mucoserous gland of the frog oesophagus. Note mucous and serous cells lining the duct. H & E. X 275

Microscopic appearance

Histologically, the oesophagus of the frog is composed of three coats surrounded by a layer of loose areolar connective tissue of tunica adventitia. These three coats are from within outwards (Fig. 9):-

1) tunica mucosa which consists of -

(a) lining epithelium

(b) lamina propria, and

(c) muscularis mucosae.

2) tunica submucosa, and

3) tunica muscularis externa.

1) The tunica mucosa (Figs. 10 & 11).

(a) The lining epithelium of the oesophageal mucous membrane of the frog consists of pseudostratified or, in some places, stratified columnar epithelium, bearing cilia. There are numerous goblet cells interposed among the columnar cells.

Invagination of the epithelial cells lining the mucous membrane of the oesophagus gives rise to simple branched tubular mucoserous glands situated in the lamina propria and submucosa. These glands form a very conspicuous feature in a section of the wall of the oesophagus (Figs. 12 & 13); the mucous cells are also seen in the ducts (Fig. 14). The secretory units of the glands are formed by both mucous and serous cells. Some secretory units are composed entirely of mucous cells and some are purely serous and other secretory units are mixed. No serous demilunes are seen (Figs. 13 & 14).

Fig.15. Gastro-oesophageal junction of frog is marked with arrow. Oesophagus lies to right of arrow. H & E. X 60

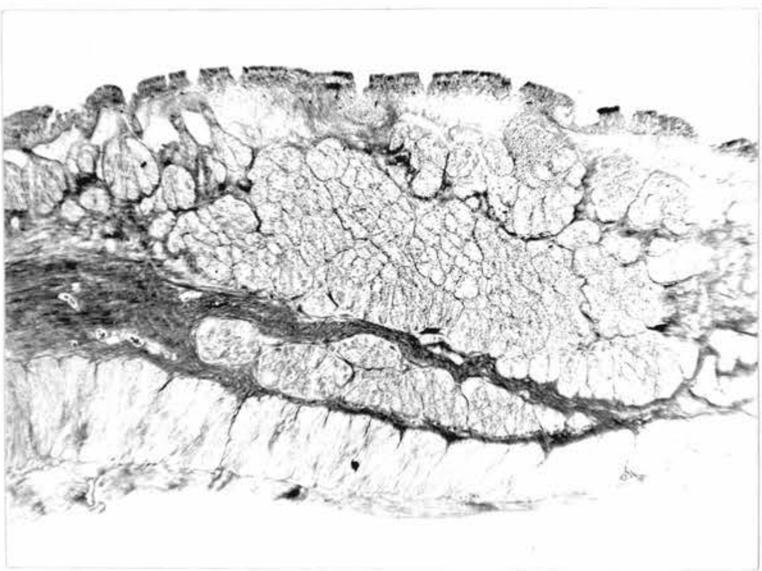

Fig.16. L.S. Oesophagus of the frog. Note the mass of glands occupying both lamina propria and submucosa. Heindenhain's Azan stain. X 30

The mucus in the goblet cells of the surface epithelium and the mucus in the mucous cells of the glands show a different staining reaction. The goblet cells are stained red by mucicarmine but, the mucous cells of the glands are not stained by mucicarmine. Staining of mucus in some goblet cells with haematoxylin and eosin is dark blue and in others it appears clear with this staining method (Fig.10). It is found, however, that goblet cell mucus and the mucus in the mucous cells of the glands both give positive PAS reaction. The mucous and the serous secretory units are easily distinguished with Azan staining. The mucous cells stain pale blue and the serous cells contain red granules.

(b) The lamina propria is formed by a thin layer of loose areolar connective tissue just underneath the lining epithelium (Fig.12), the deeper part being invaded by the secretory units of the glands.

(c) The muscularis mucosae of the stomach is arranged in an inner circular and an outer longitudinal layer. The longitudinal layer is continued into the lower end of the oesophagus but, the circular layer does not extend above the cardia (Fig.15). The oesophageal glands extend out from the lamina propria to occupy the submucosa thus spreading through the muscularis mucosae to reach the external muscle coat (Fig.16). For this reason the muscularis mucosae is fragmented throughout its course with the exception of the region just above the cardia. In this region glands are found only in the lamina propria (Figs.9 & 15).

2) The tunica submucosa is occupied by the oesophageal glands of which description has already been made.

3) The tunica muscularis externa (Figs.9 & 16) is composed of two layers of smooth muscle fibres. The inner layer is better developed and is formed by circularly arranged muscle fibres whereas the outer is longitudinal.

There are bundles of nerve fibres between the two layers of muscularis externa.

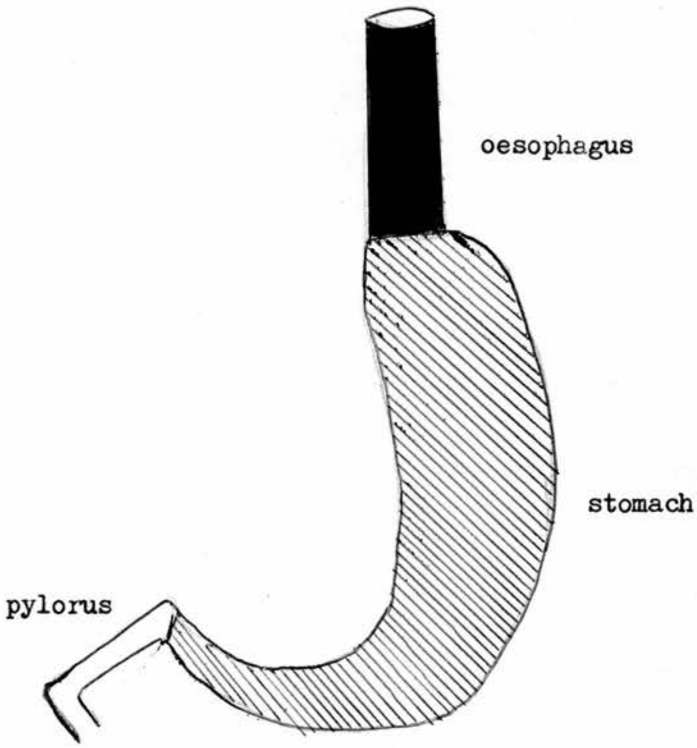

Fig.C. Drawing of the oesophagus & stomach of lizard (reptile) from ventral aspect.

The cardiac angle is better marked than in amphibia but the fundus of the stomach is is relatively insignificant.

THE OESOPHAGUS OF REPTILIA

Macroscopic appearance

The oesophagus of the wall lizard (*Lacerta muralis*) is a thin walled muscular tube. It is about 1.5 cm. in length.

In the lizard, the pharynx is located within the confines of the head as in amphibia: but, the neck has been differentiated and as a result the oesophagus has become correspondingly increased in length. The stomach of the lizard is markedly dilated and for that reason is readily distinguishable from the oesophagus on naked eye examination (Fig. C). The fundus of the stomach is not significant but, there forms a well marked cardiac angle between it and the oesophagus.

The longitudinal folds of the mucous membrane of the oesophagus are prominent and are easily visible to the naked eye.

The oesophagus is surrounded by a layer of loose areolar connective tissue which connects it with the neighbouring structures.

Fig.17. T.S. Caudal part of lizard oesophagus. Note the mucosal folds each with a core of submucosa. Glands are absent. H & E. X 80

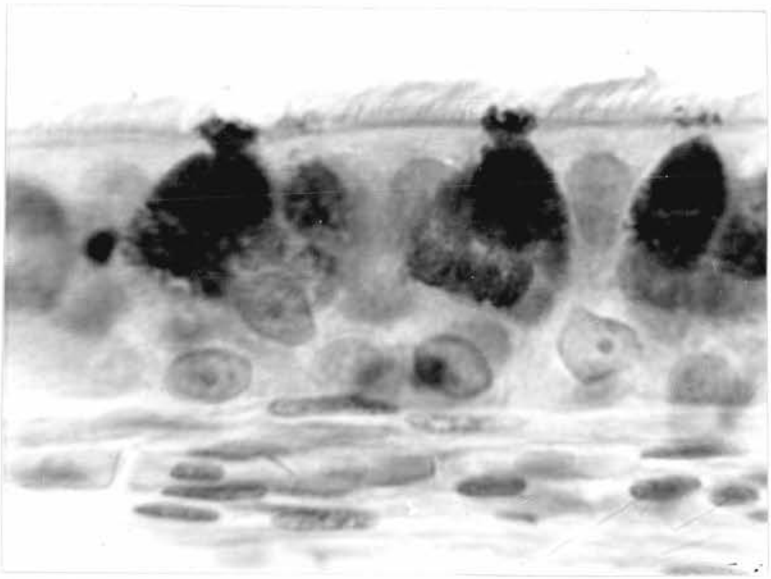

Fig.18. L.S. Oesophagus of lizard. Ciliated pseudo-stratified epithelium interspersed with goblet cells discharging mucus among cilia at the surface.
H & E. X 1600

Microscopic appearance

Histologically, the wall of the oesophagus of the wall lizard is comparatively thin (Fig.17) and consists of three coats connected with the surrounding structures by a layer of loose connective tissue which is designated the tunica adventitia. These three coats are from within outwards:-

1) Tunica mucosa which again is formed by:-

(a) lining epithelium

(b) lamina propria, and

(c) muscularis mucosae.

2) Tunica submucosa, and

3) Tunica muscularis externa.

1) The tunica mucosa (Figs.18 & 19)

(a) The lining epithelium is formed by ciliated pseudostratified columnar epithelium. There are numerous goblet cells; in some places many cells are seen lying in a continuous row (Figs.18 & 19) among the ciliated columnar cells. The ciliated cells disappear immediately above the level of disappearance of gastric glands i.e. just above the cardia (Fig.20). The goblet cells are more numerous in the caudal part of the oesophagus. They are PAS positive and stained red with mucicarmine.

(b) The lamina propria forms a very thin layer of connective tissue underlying the lining epithelial cells. There are no glands in the lamina propria (Figs.17 & 19).

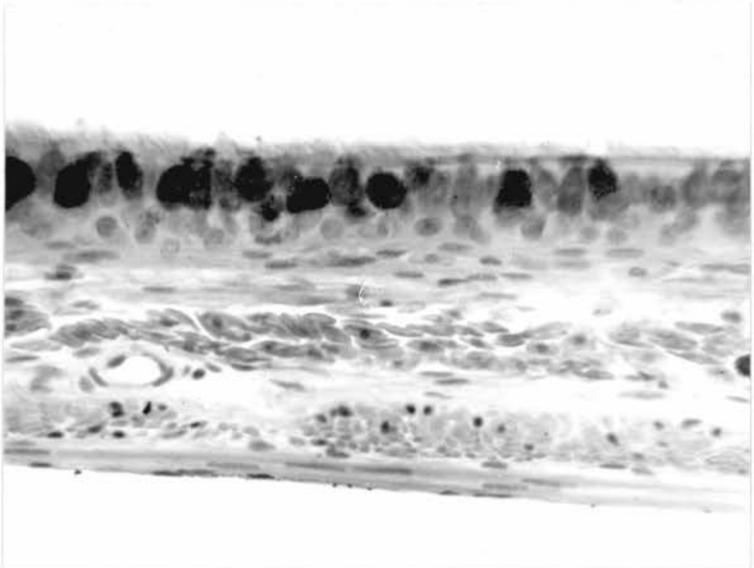

Fig.19. Oesophagus of lizard. Note continuous row of several goblet cells distended with dark stained mucus. Inner circular and outer longitudinal layers of smooth muscle fibres of external muscle coat are seen.

H & E. X 450

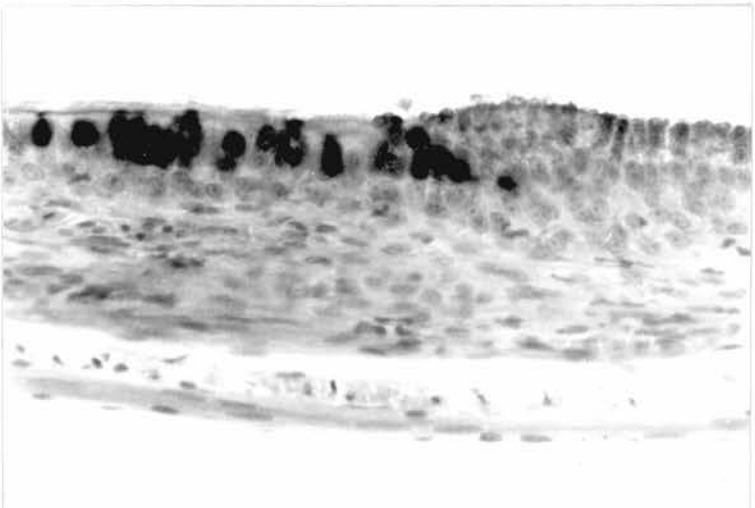

Fig.20. L.S. Caudal end of the lizard oesophagus. Note the disappearance of cilia at this level.

H & E. X 400

(c) The muscularis mucosae (Fig.19) consists of small bundles of longitudinally placed smooth muscle fibres which lie very close to the deep surface of the epithelium, since the lamina propria is so sparse.

2) The tunica submucosa (Fig.17 & 19) consists of loose areolar connective tissue which forms the cores of the prominent longitudinal folds.

3) The muscularis externa (Fig.19) is composed of two layers of smooth muscle fibres. The inner layer is better developed than the outer and the muscle fibres are circular in arrangement, whereas the outer layer of muscle fibres is longitudinal. There is no evidence of any thickening of the muscular coat in the region of the cardia.

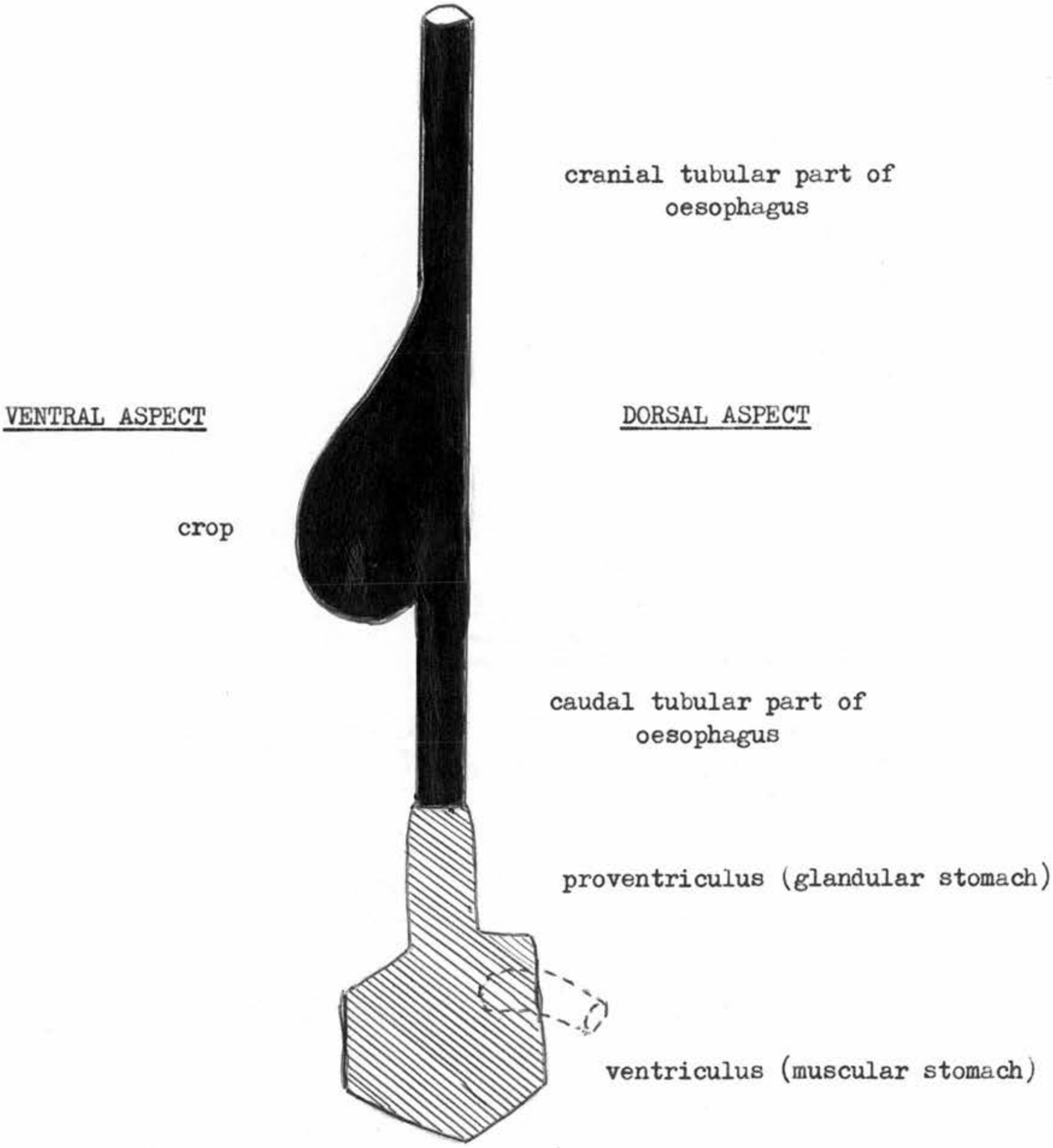

Fig.D. Drawing of the oesophagus & stomach of pigeon (Aves) from lateral aspect.

Note the cranial tubular part, crop (ventral diverticulum) & caudal tubular part.

THE OESOPHAGUS OF AVES

Macroscopic appearance

The oesophagus of the pigeon is a continuation from the pharynx and terminates at the proventriculus or glandular portion of the stomach. The pharynx is confined within the head. The stomach of the pigeon has two parts, namely, the proventriculus or glandular stomach and the gizzard or muscular stomach (i.e. the true stomach).

In the pigeon owing to the growth in length of the neck, the oesophagus becomes very much elongated, measuring about 10 - 12 cm. in length. A peculiar feature in the oesophagus of the pigeon is that it is not of uniform calibre throughout its length, as is usual with the other animals. In fact, the cranial portion of the oesophagus extends for a short distance before it dilates on its ventral aspect into a thin walled sac. This diverticulum is called the crop (ingluvies) (Fig. D). The tubular portion caudal to the crop ends by passing through delicate membranous partition which divides the pleuroperitoneal cavity into the cranial pleural cavity and the caudal peritoneal cavity. Having passed through this partition the oesophagus joins the proventriculus.

There are numerous longitudinal folds in the mucous membrane of the tubular portions of the oesophagus but, in the crop these longitudinal folds diverge to flatten out and disappear ventrally. On the dorsal aspect these folds converge to form larger folds as the crop continues into the caudal tubular oesophagus. Surrounding the oesophagus in both the tubular portions and in the crop there is a layer of loose connective tissue connecting it with the neighbouring structures and constituting an adventitial coat.

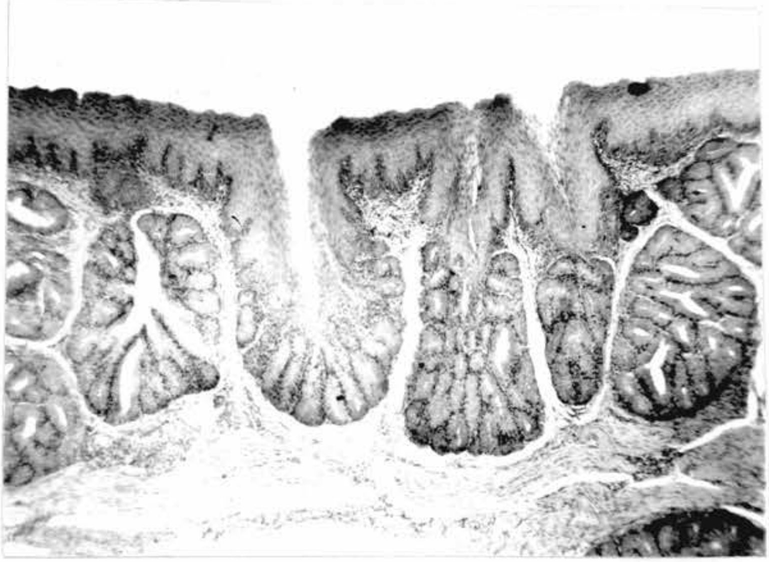

Fig. 25. L.S. Oesophageal glands of pigeon with ducts. Note the tubules of the glandular mass towards the left of the field opening into a central cavity.
Mucicarmine. X 80

Fig.26. Oesophageal glands of pigeon. Note that some glands appear to lie within the epithelium.
Mucicarmine. X 120

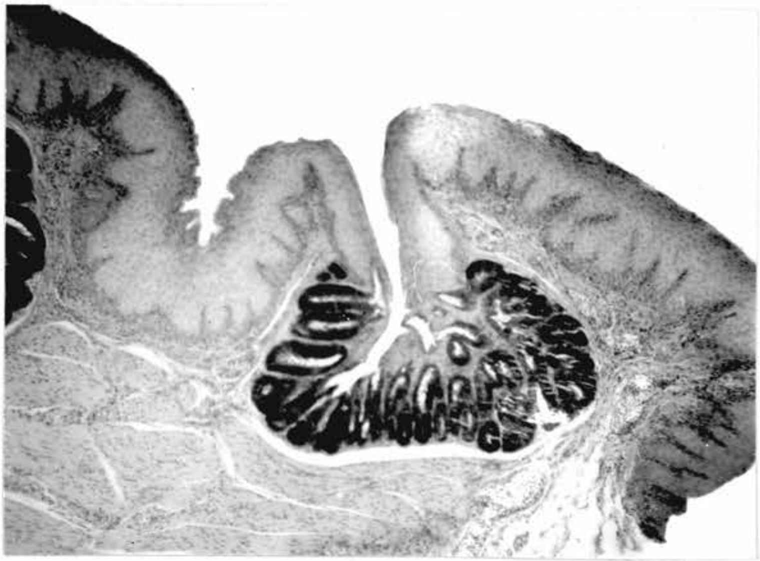

Fig. 23. L.S. Epithelial lining and glands of oesophagus of pigeon. Note the simple branched tubular mucous glands. Mucicarmine. X 80

Fig. 24. L.S. Epithelial lining and oesophageal glands of pigeon. Note the duct lined by stratified squamous epithelium.
Mucicarmine. X 110

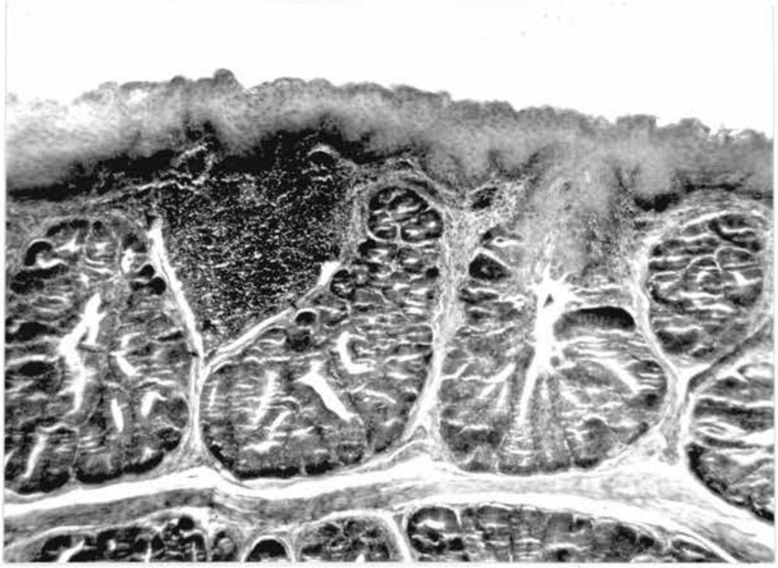

Fig.21. L.S. Non-cornified stratified squamous epithelium lining and mucous glands of the pigeon oesophagus. Note the mass of lymphatic tissue between the glands. H & E. X 90

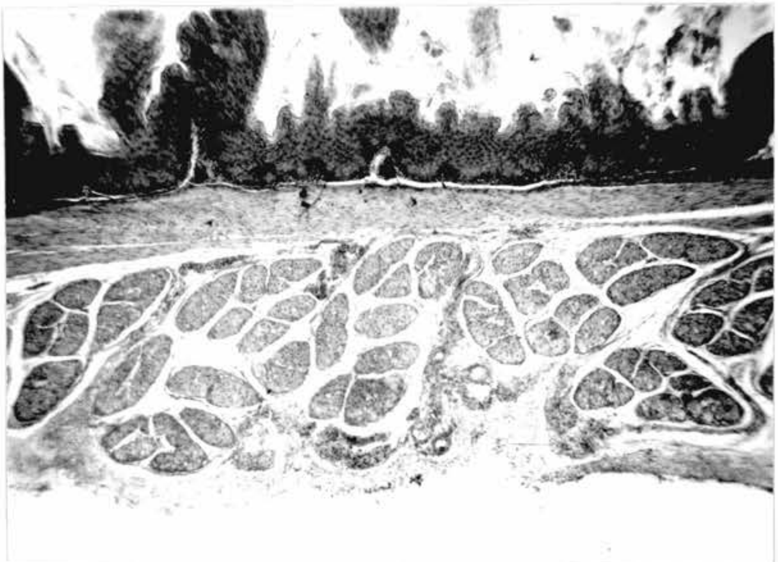

Fig.22. L.S. Cranial tubular portion of pigeon oesophagus. Note the epithelial papillae. Inner longitudinal and outer circular arrangement of external muscle coat is seen. No glands are present at this level. Note nerve bundles between the outer circular muscle layer and the tunica adventitia. H & E. X 60

Microscopic appearance

Histologically, the oesophagus of the pigeon is composed of three layers in both tubular portions as well as in the crop which are surrounded by a layer of loose connective tissue called the tunica adventitia. These three layers are from within outwards (Fig.22):-

1) Tunica mucosa

2) Tunica submucosa, and

3) Tunica muscularis.

1) The tunica mucosa (Figs.21 & 23) of both tubular portion and the crop is lined by a thick layer of non-cornified stratified squamous epithelium. The nuclei of the surface layers of flattened cells are darkly stained and flattened. There are small papillae projecting from the epithelium into the lumen of the oesophagus (Fig.22). There is no muscularis mucosae so that lamina propria and submucosa are continuous.

2) The tunica submucosa contains many glands in the caudal tubular part of the oesophagus. There are no glands in the crop nor in the cranial tubular part. The glands in the caudal tubular part are simple branched tubular and are purely mucus-secreting, staining red with mucicarmine and giving a positive PAS reaction. The tubules may be arranged in a spherical manner with a central cavity which is continuous with a duct lined by stratified squamous epithelium (Fig.23). In some instances the glands appear to lie within the epithelium (Figs.25 & 26).

Masses of lymphatic tissue are seen in the subepithelial tissue (Fig.21).

In the cranial tubular portion, that is where glands are absent, the submucosa is extremely thin (Fig.22).

3) The tunica muscularis externa consists of two layers (Fig.22). The muscle fibres of the inner layer are orientated longitudinally and those of the outer are circular in arrangement. The outer circular layer is better developed than the inner longitudinal layer and both layers are of smooth muscle. The arrangement of tunica muscularis is the same in both tubular and the crop portions of the oesophagus of the pigeon, but it is comparatively thin in the region of the crop.

There are bundles of nerve fibres between the outer circular muscle layer and the tunica adventitia (Fig.22).

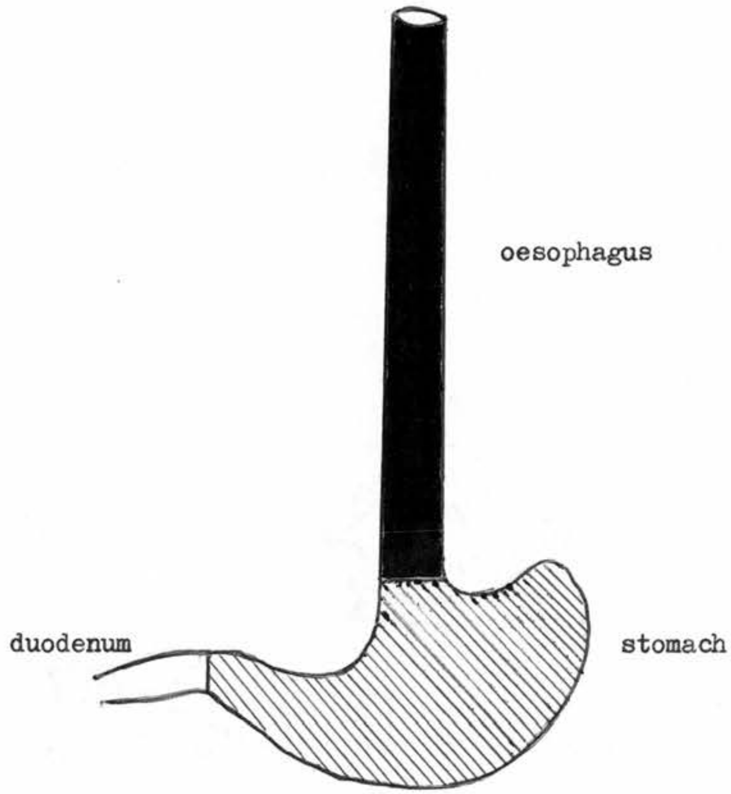

Fig.E. <u>Drawing of the oesophagus & stomach of rabbit (mammal) from ventral aspect.</u>

Note the elongated uniformly tubular form of the oesophagus & the well developed fundus of the stomach which is lying in a transverse plane.

THE OESOPHAGUS OF MAMMALIA

Macroscopic appearance

The oesophagus of the rabbit is an elongated muscular tube interposed between the pharynx and the stomach. The elongation of the oesophagus is due to growth of the neck and the caudal descent of the abdominal viscera. It is uniformly tubular and has a length of about 10 - 12 cm. in the adult.

The distinction between the oesophagus and the stomach is easily made on naked eye examination. The stomach lies almost transversely in the abdominal cavity, being more or less at right angles to the oesophagus. Therefore, there is a definite cardiac angle between the oesophagus and the stomach (Fig. E).

The mucous membrane of the oesophagus is thrown into a number of longitudinal folds and there is a particularly well marked fold of mucous membrane at the cardiac orifice (Fig. 27).

Microscopic appearance

Histologically, the oesophagus of the rabbit is composed of a mucosal layer and a thick muscular coat with an intermediate layer of connective tissue. It is connected with the surrounding structures by means of connective tissue layer of tunica adventitia. The different coats of the oesophageal wall of the rabbit are from within outwards (Fig.27):-

1) Tunica mucosa, which is composed of:-

(a) lining epithelium,

(b) lamina propria, and

(c) muscularis mucosae.

2) Tunica submucosa, and

3) Tunica muscularis externa.

1) The tunica mucosa (Fig.28).

(a) The lining epithelium is formed by a thick layer of stratified squamous epithelium. It is not cornified except for an area of the mucosa (described below) immediately above the cardia where a few layers of squames are seen with no associated nuclei (Fig.30). Throughout the remainder of the oesophagus the surface cells have pyknotic nuclei.

At the caudal end of the oesophagus the lining epithelium becomes very much thickened and at the junction of the oesophagus with the stomach, it forms a prominent fold with a core of fanned out muscularis mucosae within it (Fig.27).

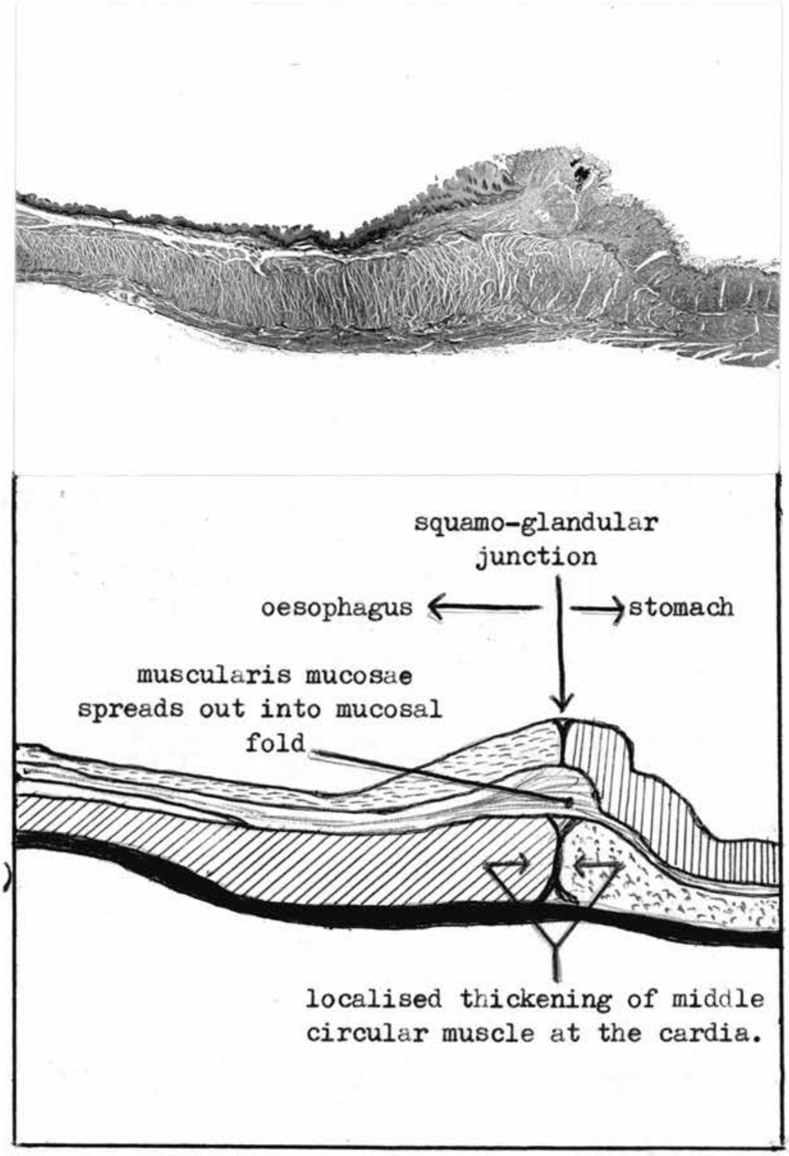

Fig.27. L.S. Caudal part of the rabbit oesophagus & cardio-oesophageal junction. Note the abrupt change in epithelium. Inner longitudinal muscle layer of oesophagus ends cranial to the cardia. H & E. X 10.

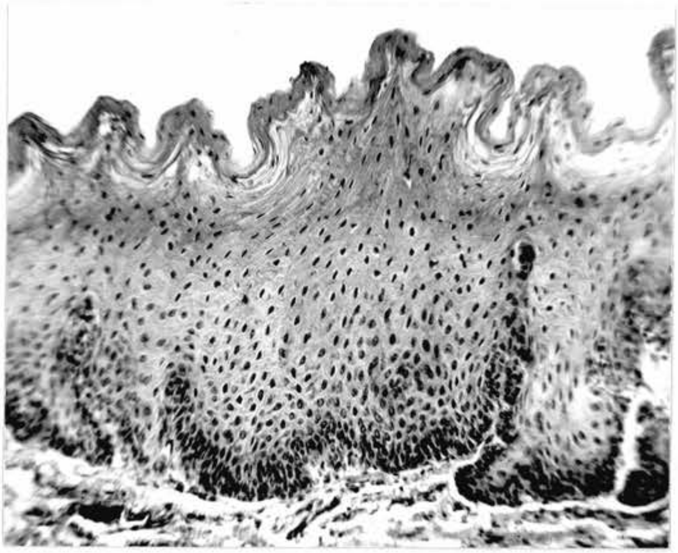

Fig.28. L.S. Non-cornified stratified squamous lining epithelium of the rabbit oesophagus. Note the high papillae of lamina propria. H & E. X 140.

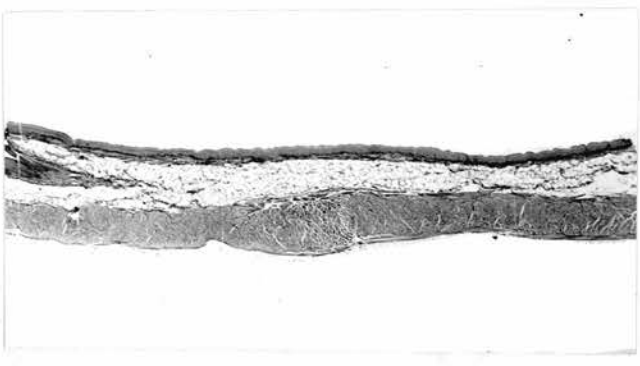

Fig.29. L.S. Cranial part of the rabbit oesophagus. Note fat in the submucosa. H & E. X 12.

(b) The lamina propria is a very thin layer of connective tissue. There are high papillae of lamina propria protruding into the epithelium (Fig.28). These papillae lie at various angles and in some places there apical parts are seen as islands of lamina propria surrounded by epithelial cells (Fig.30). No glands are found in the lamina propria in any part of the oesophagus.

(c) The muscularis mucosae consists of longitudinally orientated smooth muscle fibres. It is thin and fragmented in the cranial part but, it is better developed towards the caudal end of the oesophagus. It is particularly well marked at the cardia spreading out towards the junction of the oesophageal and gastric mucosae. Distal to this level, it becomes thinner again and is continuous with the muscularis mucosae of the stomach (Fig.27).

2) <u>The tunica submucosa</u>. In the upper part of this layer there is much fat (Fig.29), but in the caudal part the fat disappears as the submucosa becomes thinner and the inner longitudinal layer of tunica muscularis externa becomes thickened (see below) (Figs.29 & 27).

No glands are seen in the tunica submucosa of the oesophagus in any part of its length.

3) <u>The tunica muscularis externa</u> is composed of three distinct layers of muscle fibres (Fig.27). They is an inner longitudinal, a middle circular and an outer longitudinal layer. The circular layer is the best developed of the three layers. The muscle fibres of all three layers are striated throughout the entire length of the oesophagus.

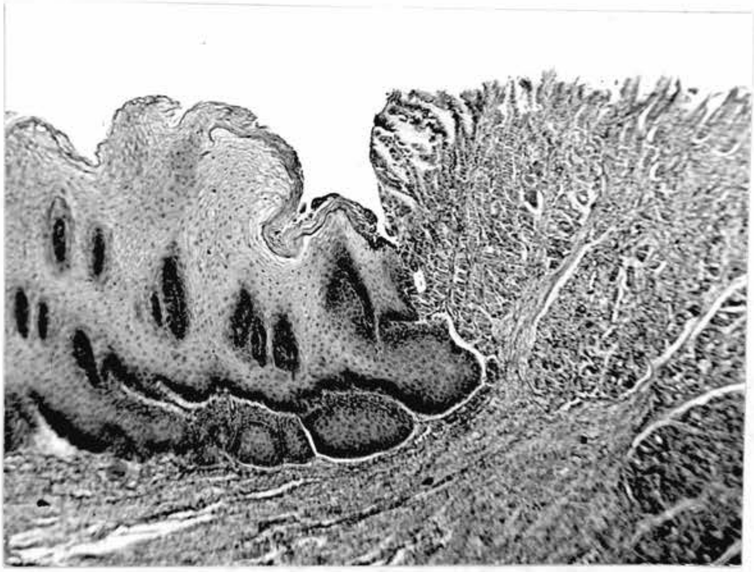

Fig.30. L.S. Lining epithelium at the cardia of rabbit oesophagus. Note thickened epithelium (c.f. fig.29), the few squames on the surface and change of stratified epithelium into simple columnar at the cardia. H & E. X 55.

The inner longitudinal layer gradually thickens from the cranial end towards the middle of the oesophagus; but, it disappears abruptly at the caudal end of the oesophagus, a short distance above the cardia (Fig.27). It is at the level of disappearance of this inner longitudinal muscle that there appears the thickening of the muscularis mucosae in the cardiac region mentioned above.

The middle circular muscle layer becomes gradually thicker towards the cardia where it forms the cranial part of a localised mass of muscle fibres surrounding the cardia. This thickened muscle band consists in its cranial part of striated muscle and in its caudal part of smooth muscle with a very limited intermixed zone in the middle. The caudal smooth portion of thickened muscle band soon becomes thinner and is continuous with the inner smooth circular muscle layer of the stomach (Fig.27).

The outer longitudinal layer of oesophageal muscle is thin and is continuous with the outer longitudinal muscle layer of the stomach where it becomes smooth muscle.

There are bundles of nerve fibres between the middle circular and the outer longitudinal muscle layers.

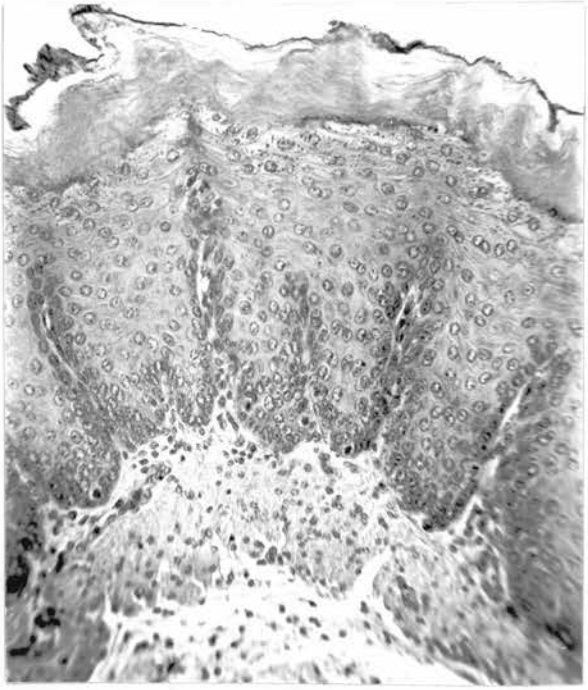

Fig.31. T.S. Lining epithelium of guinea pig oesophagus. Note highly cornified stratified squamous epithelium with stratum granulosum. High papillae of lamina propria are seen. H & E. X 200.

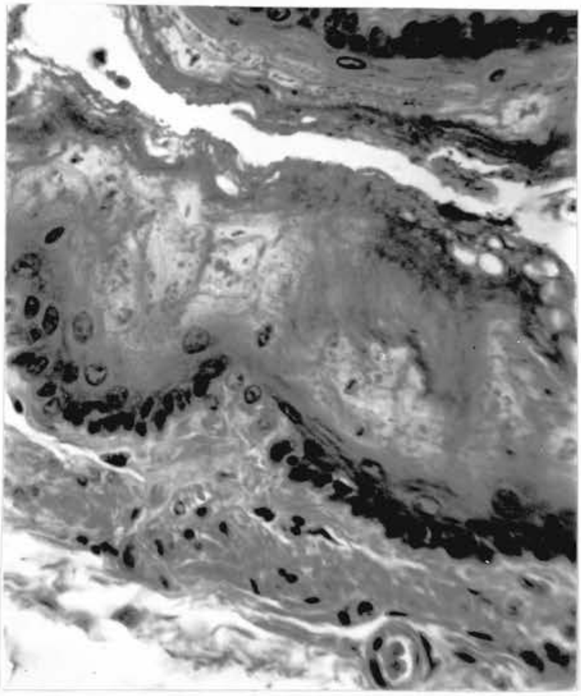

Fig.32. T.S. Lining epithelium of rat oesophagus. Note highly cornified stratified squamous epithelium with stratum granulosum. H & E. X 200.

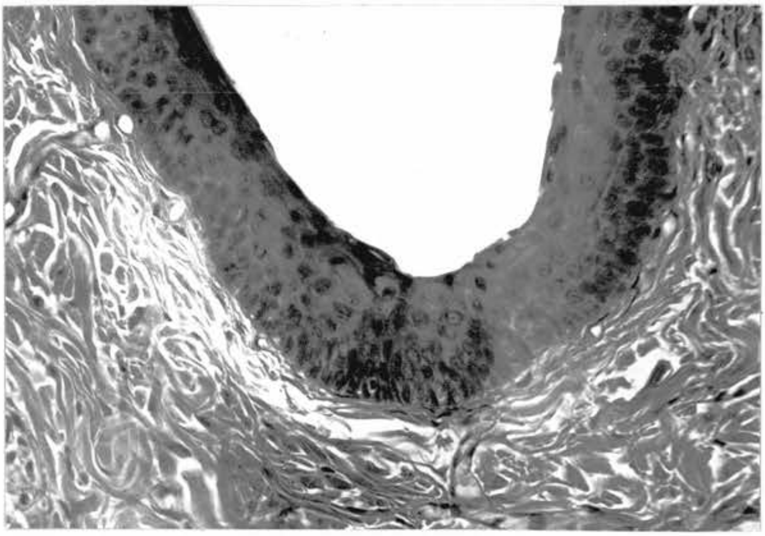

Fig.33. T.S. Lining epithelium of dog oesophagus. Note non-cornified stratified squamous epithelium. H & E. X 300.

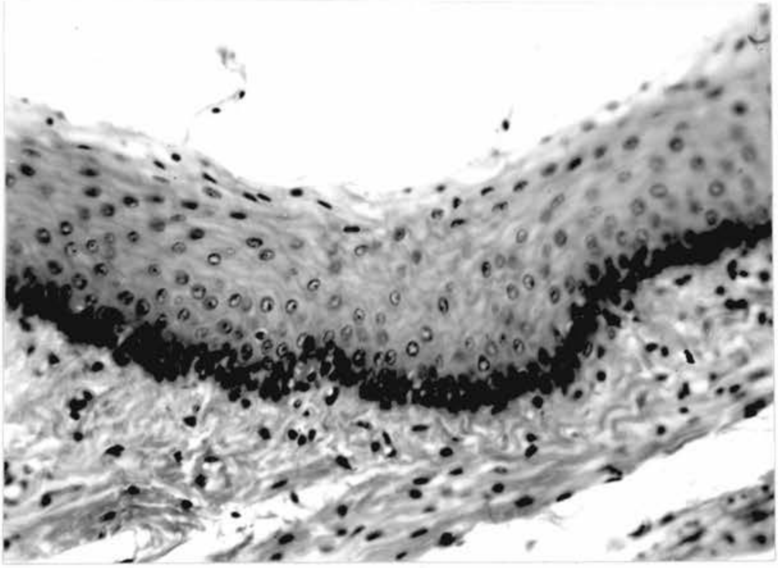

Fig.34. L.S. Non-cornified stratified squamous epithelium lining of the cat oesophagus. Note few squamous cells with pyknotic nuclei flaking off from the surface. H & E. X 280.

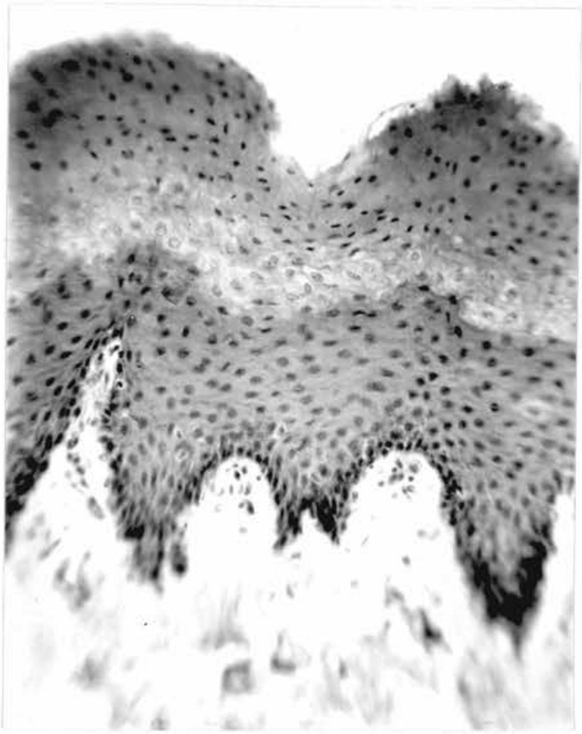

Fig.35. Non-cornified stratified squamous epithelium lining of the pig oesophagus. Note that the nuclei of surface cells are pyknotic but there is no stratum corneum. H & E. X 200.

Fig.38. T.S. Mucous glands and their ducts opening to the surface in the caudal part of the dog oesophagus. Note well developed muscularis mucosae at this level. H & E. X 60.

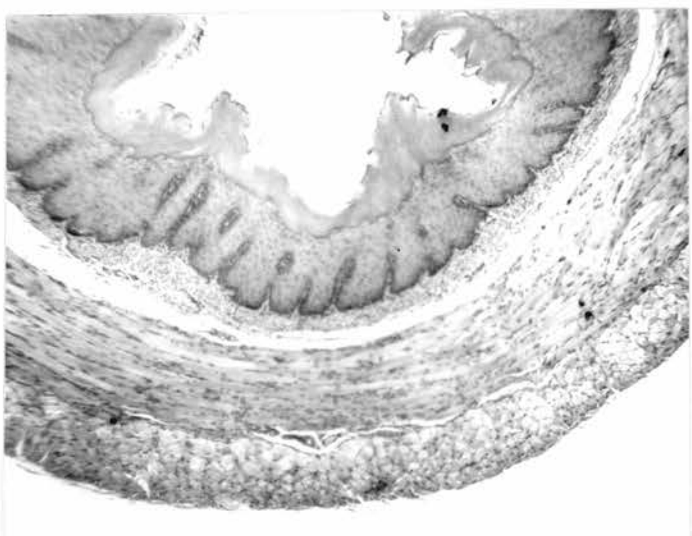

Fig.39. T.S. Oesophagus of guinea pig. Note inner circular and outer longitudinal muscle layers and absence of glands. H & E. X 60.

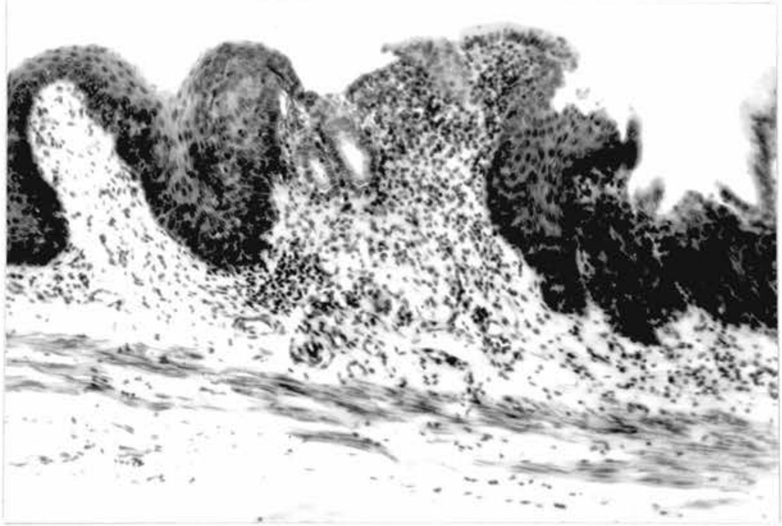

Fig.36. L.S. Oesophagus of the cat just above the cardia. Note glands in the lamina propria and aggregation of lymphatic tissue around the glands. The epithelium overlying the glands is simple columnar in contrast to the stratified squamous epithelium throughout the rest of the oesophagus. Gastric epithelium is seen on the extreme right of the photograph. Muscularis mucosae is well developed at cardiac region. H & E. X 140.

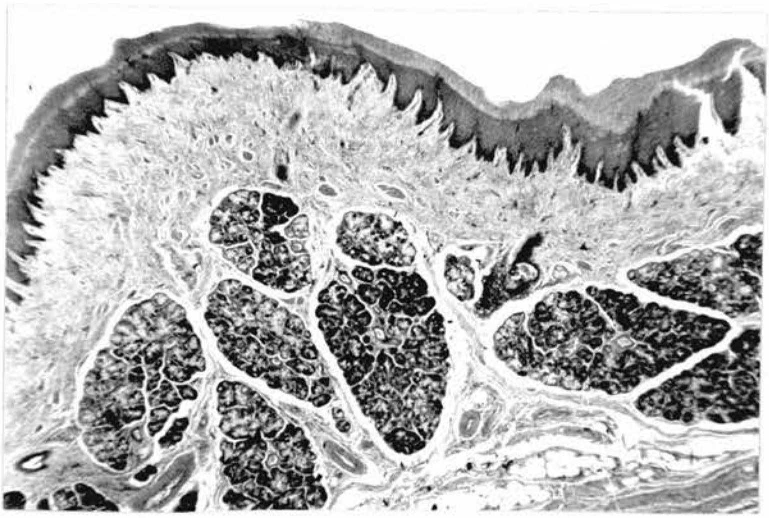

Fig.37. T.S. Cranial part of the pig oesophagus. Note the presence of glands in the submucosa. Few and scattered bundles of muscularis mucosae are seen. H & E. X 40.

<u>Microscopic appearance</u> of the oesophagus of other mammals examined (guinea-pig, rat, dog, cat and pig).

The general histological make-up of the oesophagus of all other mammals examined (guinea-pig, rat, dog, cat and pig) is the same as that of the rabbit. Variation of this general pattern will now be mentioned, the five species being considered together.

1) <u>The tunica mucosa</u>. (a) The lining epithelium of all five mammals (guinea-pig, rat, dog, cat and pig) examined is formed by stratified squamous epithelium varying only in thickness (Figs. 31, 32, 33, 34 and 35). In the guinea-pig and the rat the stratified squamous epithelium is highly cornified (Figs. 31 & 32) and in the dog, cat and the pig it is not cornified (Figs. 33, 34 & 35). The epithelium is thicker in the pig (Fig. 35) than in the dog and the cat (Figs. 33 & 34).

(b) The lamina propria is composed of a thin layer of collagen fibres through which the ducts of the oesophageal glands pass to open on the surface of the mucous membrane in the dog and the pig (Figs. 38, 41 & 44). In the guinea-pig the high narrow papillae of the lamina propria usually seen in the oesophagus are particularly well marked (Fig. 31). In the cat some glands are found in the lamina propria immediately above the cardia. These glands are few in number and are found only in this region and do not extend throughout the whole circumference. It is to be noted that in the region of these glands the stratified squamous epithelium of the oesophagus is replaced by a simple columnar epithelium. The

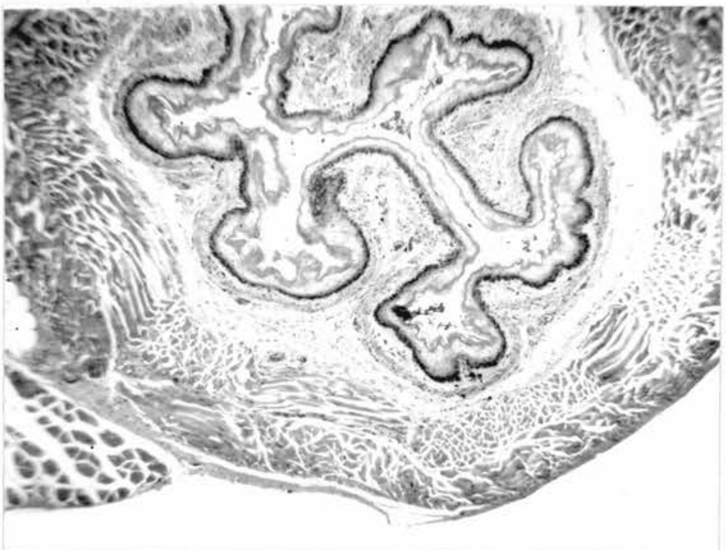

Fig.40. T.S. Oesophagus of rat. Note the spiral arrangement of external muscle coat and absence of glands. H & E. X 60.

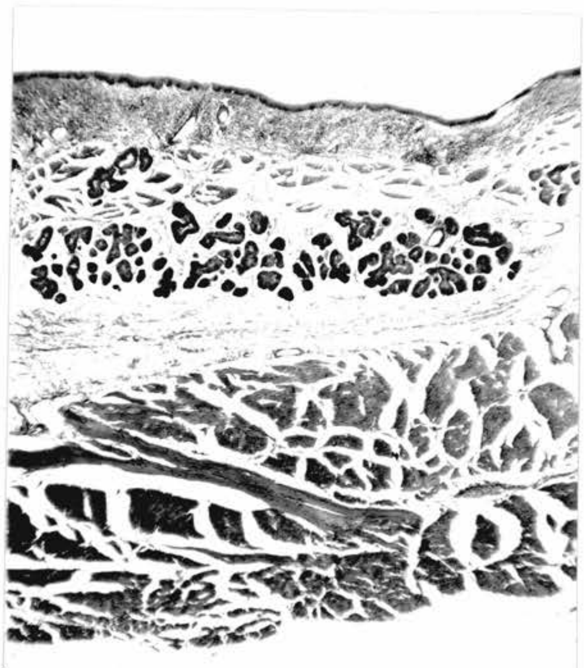

Fig.41. T.S. Oesophagus of dog. Note the presence of glands in the submucosa and muscle fibres communicating between the two muscle layers. H & E. X 30.

glands are surrounded by a collection of lymphocytes in the lamina propria (Fig.36).

(c) The muscularis mucosae is formed by the bundles of smooth muscle fibres arranged longitudinally. They are few and scattered in the upper part of the oesophagus in all five species particularly in the pig (Fig.37) but, well developed in the caudal part of the oesophagus (compare Figs.37 and 45).

2) The tunica submucosa. There are numerous oesophageal glands throughout the whole length of the oesophagus in the dog (Fig.41), only in the cranial part in the pig (Fig.44), in the submucosa. There are no oesophageal glands in the guinea-pig and the rat throughout the whole length of the oesophagus (Figs.39 and 40).

3) The tunica muscularis externa is formed entirely by striated muscle fibres in the guinea-pig, rat and dog differing only in thickness and the arrangement of the muscle layers. The arrangement in these three animals will be considered together and then the cat and the pig will be considered separately.

In the guinea-pig, an inner circular and an outer longitudinal layer can be clearly defined (Fig.39). In the rat and the dog, two layers can again be defined but in each instance the muscle fibres have an irregular arrangement (Figs.40 & 41). Some muscle fibres appear to take an oblique or spiral course and muscle fibres may pass from one layer into the other.

In the cat also, the external muscle coat consists of two layers.

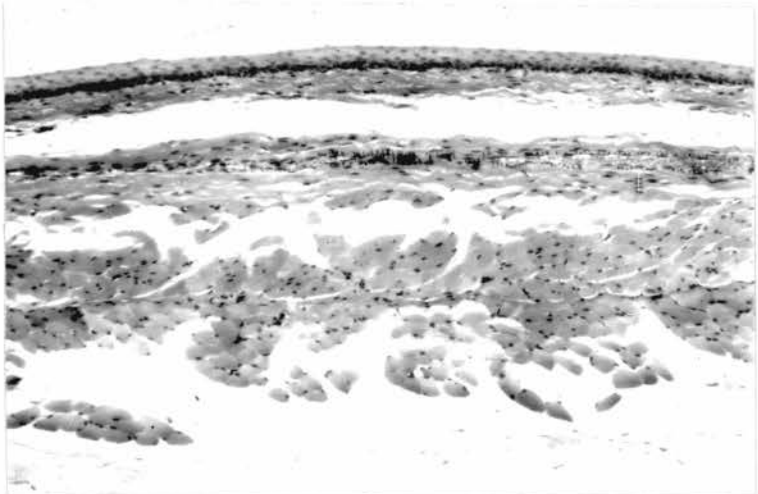

Fig.42. L.S. Cranial part of the cat oesophagus. Note striated inner irregularly arranged and outer circular layers of external muscle coat. H & E. X 90.

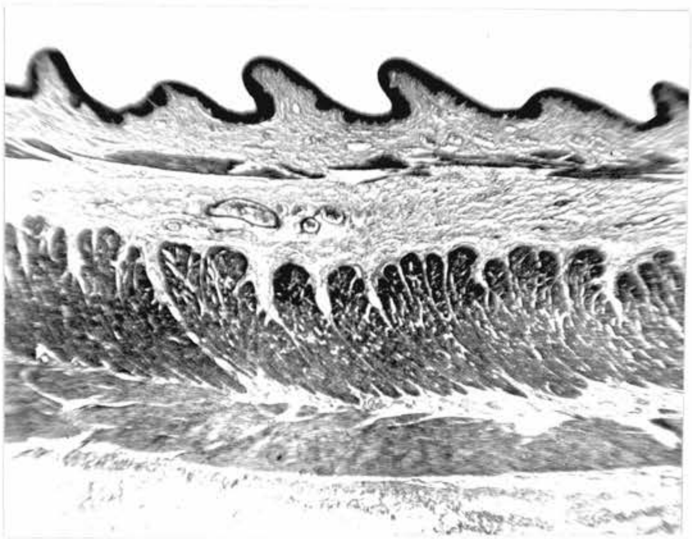

Fig.43. L.S. Caudal part of the cat oesophagus. Note smooth inner circular and outer longitudinal external muscle layers. Well developed muscularis mucosae is present at this level. H & E. X 25.

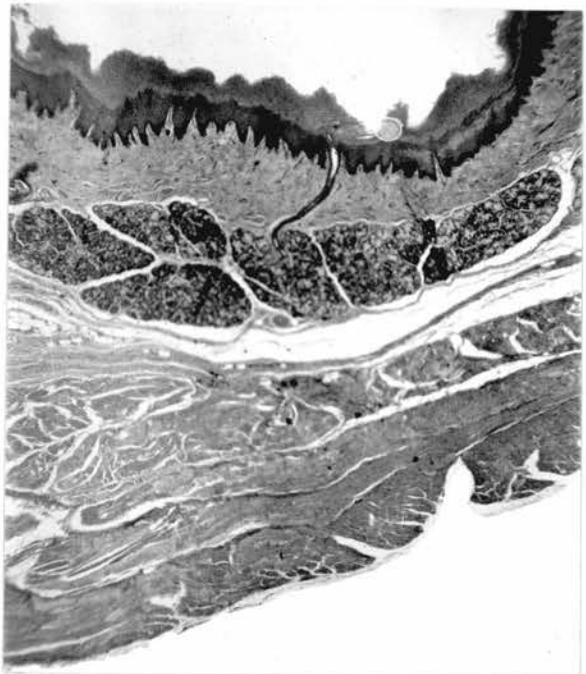

Fig.44. T.S. Cranial part of pig oesophagus. Note the glands in the submucosa. H & E. X 25.

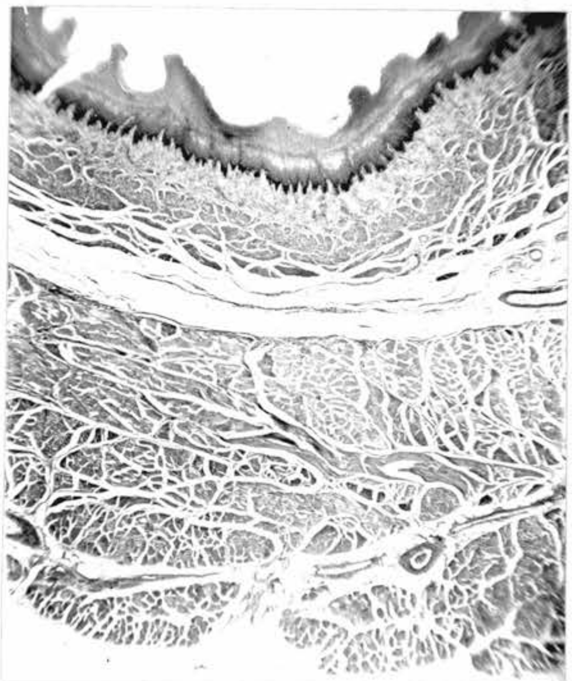

Fig.45. T.S. Caudal part of the pig oesophagus. Note well developed muscularis mucosae at this level (c.f. fig.37), absence of glands (c.f. fig.44) and irregular arrangement of external muscle layers. H & E. X 25.

In the cranial part of the oesophagus both layers are striated (Fig. 42). The inner layer is formed by obliquely arranged muscle fibres and the outer layer consists of circularly arranged muscle fibres (Fig. 42). In the caudal part the striated muscle fibres are gradually replaced by smooth muscle. The replacement by the smooth muscle in the outer muscle layer occurs at a slightly more caudal level than it does in the inner layer. In the caudal third of the oesophagus the arrangement of muscle is much more regular. There is an inner circular and an outer longitudinal layer. Both layers consist entirely of smooth muscle (Fig. 43).

In the pig the external muscle coat is well developed. Its pattern is the most irregular of all the mammals examined (Fig. 45). This muscle coat could not readily be divided into layers. Most of the muscle fibres appear to run in a longitudinal direction but, a few oblique or spiral fibres are seen mixed among the longitudinal ones. At the caudal end a few smooth muscle fibres are seen scattered among the striated muscle, but striated muscle predominates.

Fig.46. T.S. Cranial part of human oesophagus. The muscularis mucosae consists of small scattered bundles of smooth muscle. Mucous glands are seen in the submucosa but no glands are present in the lamina propria.
Prof. Lendrum's Haematoxylin-Phloxin method. X 35.

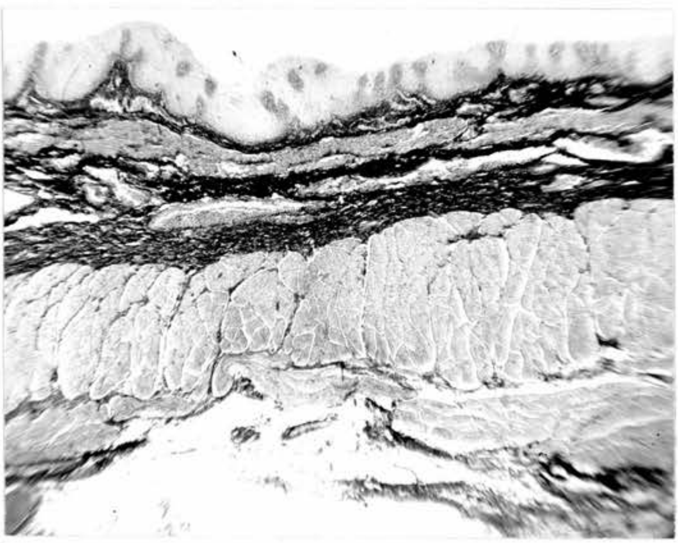

Fig.47. L.S. Caudal end of human oesophagus (five year old child). The muscularis mucosae is a well defined longitudinal bundle of smooth muscle at this level. Note inner circular and outer longitudinal layers of smooth muscle (c.f. fig.46). van Gieson. X 20.

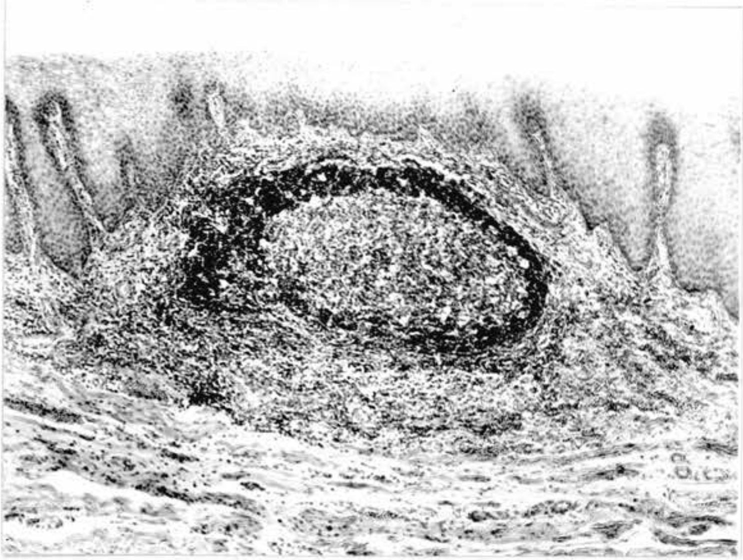

Fig.48. L.S. Human oesophagus, (five year old child).
Note lymphatic nodule with germinal centre in lamina propria.
H & E. X 60.

HUMAN OESOPHAGUS

Microscopic appearance

In the specimen of human oesophagus examined the mucous membrane is lined by stratified squamous non-cornified epithelium. The muscularis mucosae is poorly developed in the cranial part (Fig. 46) and well developed in the caudal part (Fig. 47).

Some lymphatic nodules are seen in the lamina propria (Fig. 48).

Oesophageal glands are found in the submucosa but not in the lamina propria (Fig. 46) in this specimen.

The external muscle coat consists of an inner circular and an outer longitudinal layer (Fig. 47). The cranial third of the external muscle coat is formed by striated muscle; in the middle third there is a mixture of striated and smooth muscle and the caudal third is composed of smooth muscle in both layers.

No evidence of thickening of the circular muscle layer nor is a mucosal fold seen in the specimen which is under consideration.

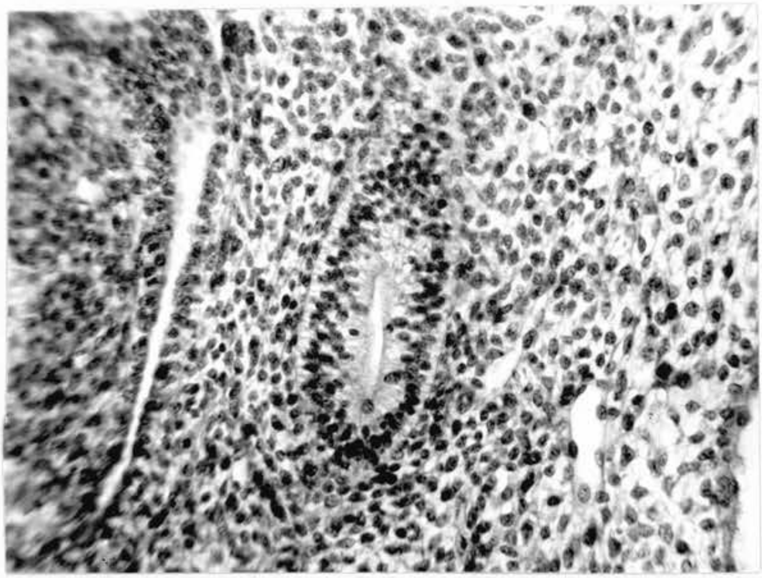

Fig.49. T.S. Oesophagus of the pig embryo at 6mm. stage. Note two to three layers of epithelium with mitotic figures in some of the luminal cells. Undifferentiated mesenchymal cells surround the epithelial tube.

H & E. X 260.

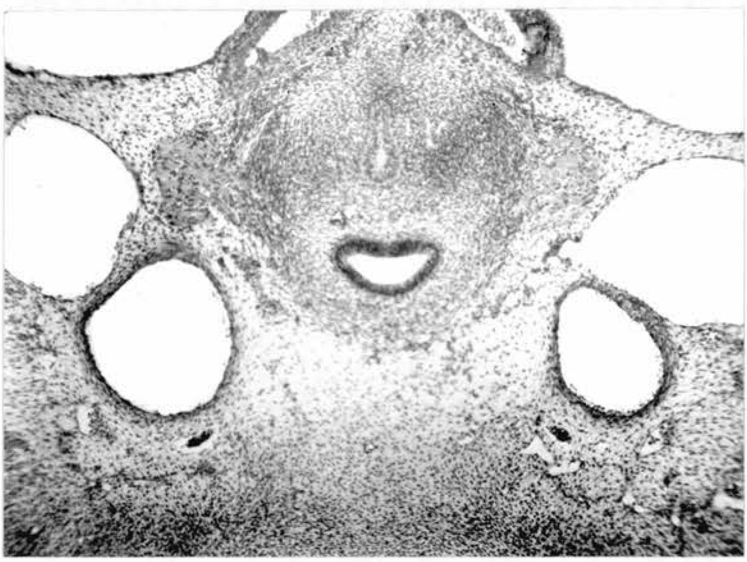

Fig.50. T.S. Oesophagus of the pig embryo at 10 mm. stage. Note the crescent shape of the oesophagus and the condensation of the surrounding mesenchymal cells.

H & E. X 60.

SOME OBSERVATIONS ON THE DEVELOPMENT OF THE PIG OESOPHAGUS

(Pig embryos of 6 mm., 10 mm., 15 mm. & 35 mm. stages)

In a pig embryo of 6 mm. stage the oesophagus can be made out quite definitely. It has already separated from the trachea: the communication between the two persists only at the upper end. On cross section it appears laterally flattened with its lumen as a dorsoventral slit thoughout its whole length.

At the later stages, the oesophagus is crescentic in shape (Fig. 50) at the cranial end, with the concavity of crescent towards the trachea. It gradually becomes oval and then rounded caudally. The lumen appears as a dorsoventral slit only at its caudal end.

In the 6 mm. stage, the wall of the oesophagus consists merely of two or three layers of epithelial cells: the luminal cells are tall columnar with pale cytoplasm. Numerous mitotic figures are seen among them (Fig. 49). At the later stages the epithelium is thicker: it is four to six layers thick in the 35 mm. embryo (Fig. 52). At this stage the luminal surface has an irregular appearance due to the presence of small protrusions at the apices of the surface columnar cells into the lumen (Fig. 52). The cytoplasm of these surface cells is vacuolated. In none of the stages examined are cilia found in the epithelium. The deep surface of the epithelium is regular and is bounded by a well defined basement membrane (Fig. 51).

At the 6 mm. stage the mesenchymal cells around the epithelial tube are arranged at random (Fig. 49). At the 10 mm. stage these

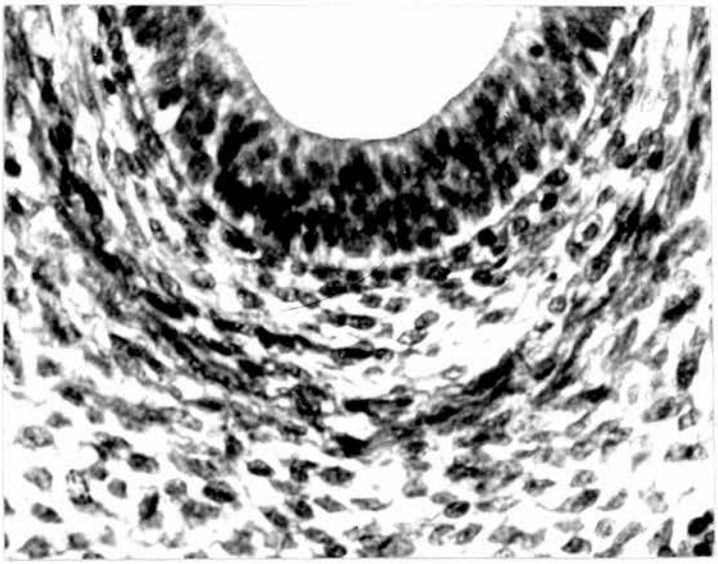

Fig.51. T.S. Oesophagus of the pig embryo at 15 mm. stage. Note increase in thickness of epithelium. (Denser and more compact cells at some distance from the embryonic mucosa are arranged in a circumferential manner.)

H & E. X 550.

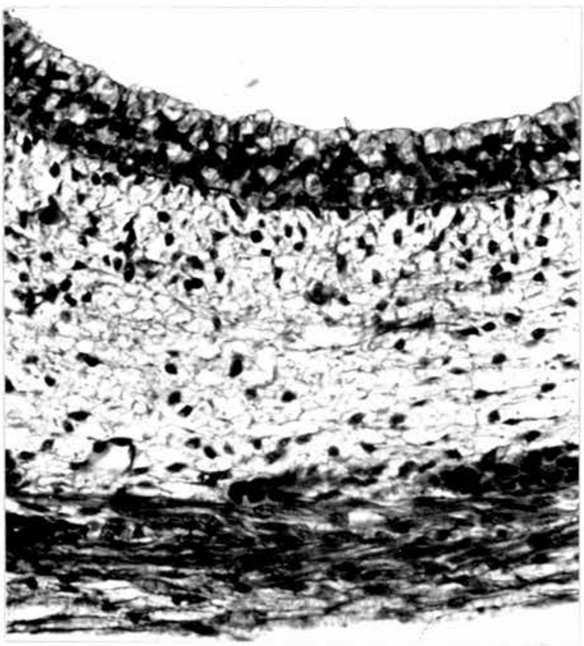

Fig.52. T.S. Oesophagus of the pig embryo at 35 mm. stage. Note cellular submucosa and differentiation of external muscle layer. H & E. X 360.

cells are condensed around the trachea and the oesophagus (Fig. 50). At the 15 mm. stage among the condensed mass of surrounding mesenchymal cells, those at some distance from the embryonic mucosa are seen to have a chiefly circumferential orientation (Fig. 51). This may be said to represent the anlage of the tunica muscularis. At the 35 mm. stage the thick cellular submucosa and the compactly arranged external muscle coat are readily identifiable. (Fig. 52). No glands are found to have developed in any of the stages examined.

DISCUSSION

DISCUSSION

The structure of the wall of the oesophagus of vertebrates undoubtedly reflects the mode of their life and the nature of the food on which they live. Thus, there is considerable diversity in structure of the oesophagus in the different animals studied although the general plan of its constitution remains the same in so far as it forms a canal for the transport of food from the mouth and pharynx to the stomach.

The structural make-up of the oesophagus in each species is independently evolved according to its own inherent pattern of growth. The general form, particularly the length of the oesophagus as well as the detailed histological pattern changes as evolution advances from the lower to higher forms. These changes depend upon the new demands made by the animals for their survival in the differing environments as they move from water to land and as they come to exist under varied conditions on land.

It has been considered advantageous to discuss and compare first the gross general form of the oesophagus in the different vertebrates examined and then to consider the histological appearances in each case.

DISCUSSION

Macroscopic appearance of Oesophagus

Pisces

In all species of fish the oesophagus appears as a very short simple muscular tube interposed in the case of most of these species between the pharynx and the stomach and, in the case of a few, between the pharynx and the intestine. The oesophagus in fish is not only remarkably short compared with that of the higher vertebrates but, also it lies freely in the coelomic cavity covered by peritoneum except for its most cranial part where it is connected to the surrounding structures by a layer of connective tissue without any peritoneal covering.

In a number of jawed fishes as well as some lung fishes and certain teleosts the oesophagus consists merely of a simple tube interconnected between the pharynx and the intestine, although in higher species of fish the stomach is recognisable. In all other lung fishes, elasmobranchs and most ray-finned forms a stomach is present in the foregut leaving a short ill-defined area cranial to it and this cranial portion is considered to represent the oesophagus (Romer, 1962).

In fish, in general, there is no means of distinguishing externally between the oesophagus and the stomach as the former merges imperceptibly into the latter. This contrasts very markedly with the arrangement encountered in higher vertebrates. It is in the land vertebrates that the oesophagus first becomes prominent.

In addition to the prominent longitudinal folds of the mucous membrane there are mumerous small irregular papillae in the oesophagus of fish which are not usually seen in the higher vertebrates.

In all the three Ganoidei, Acipenser (Sturgeon), Amia (Bowfin) and Lepidosteus (Garpike) the oesophagus is said to be comparatively very short. There is no external indication between it and the stomach and there are numerous papillae of the mucous membrane of the oesophagus (Macallum, 1886).

The absence of an external indication of the junction of oesophagus and stomach and the presence of complexly folded mucous membrane of the oesophagus of plaice were observed by Dawes (1929). Similar features were observed in king salmon (Greene, 1912), sea bass and sea robin (Blake, 1930 & 1936) and minnow (Rogick, 1931).

<u>Amphibia</u>

As the name itself suggests, the amphibia have a double mode of life. The attempt at invasion of land by amphibia has not been completely successful as they are chained to water for reproductive purposes. Modification has to be made in many organs of the amphibia to suit their new mode of life on land and in this the oesophagus is no exception although the changes in this part of the digestive tract are not very striking.

With the reduction in relative length of the pharynx resulting from the disappearance of the gill clefts, there is a relative increase in the length of the oesophagus of amphibia in comparison with that of fish. Not only is there a comparative increase in the length of the oesophagus but also in the case of the majority of amphibia (Anura and Urodela) <u>the stomach</u> is noticeably dilated and a cardiac angle for the first time appears, albeit an ill-defined one, during the process of evolution; but, in Proteus, there is no gastric enlargement (Gegenbaur, 1878) so that its appearance is quite similar to that of the fish oesophagus to which reference has already been made.

Among the Anura the dilated stomach of Bufo is easily distinguishable on naked eye examination from the oesophagus and lies transversely in the abdominal cavity (Gegenbaur, 1878). The mucous membrane of the oesophagus of amphibia unlike that of fish, has no papillae though there are prominent longitudinal folds throughout the whole length of the oesophagus.

Reptilia

The reptiles are distinguished from the lower vertebrates already described on account of their mode of reproduction involving the evolution and development of amniote eggs. Consequently, they are no longer chained to water for reproduction as in the case of amphibia and thus completely succeed in the invasion of land during the process of evolution.

The oesophagus of reptiles becomes relatively much longer than in the lower vertebrates (though not as elongated as in the case of higher vertebrates) due to the differentiation of the neck region and the general caudal descent of the viscera. The oesophagus of reptiles is demarcated externally from the wider stomach. The cardiac angle is better marked than that of amphibia but the fundus of the stomach is not yet well differentiated. As in the case of the amphibia there are prominent longitudinal folds in the mucous membrane of reptilian oesophagus, but no papillae such as are found in fish. The longitudinal folds in the reptilian oesophagus are to be associated with the enormous distensibility of the oesophagus found in those reptiles who have the ability of swallowing very large objects.

In some reptiles such as Chelonian the stomach is not only wider than the oesophagus but also it lies transversely (Wiedersheim & Parker, 1907).

According to Gegenbaur (1878), in Ophidii and Saurii among the reptiles, the foregut is of a lower form in that the oesophagus and stomach have not differentiated from each other. The oesophagus is more sharply separated from the stomach in the Chelonii and Crocodilini (Gegenbaur, 1878).

The snake oesophagus is characterised by extreme elongation and by great distensibility conforming with the shape of the body and the habit of swallowing large objects (Quiring, 1950).

Aves

Birds are adapted for aerial life and several parts of their body structure are greatly modified in accordance with the demands of flight and their bipedal locomotion on land. They are aptly termed 'glorified reptiles' (Romer, 1962).

The oesophagus of birds is relatively very much elongated as compared with that of fish, amphibia and reptiles, owing to the remarkable development of the neck and the general caudal descent of the viscera.

A unique modification seen in many birds is that the tubular oesophagus extends for a short distance and then dilates on its ventral aspect into a thin walled sac to form a diverticulum called the crop. Gegenbaur (1878) considered that the crop is used mainly for storage of food in which it is softened by means of moisture to facilitate proper digestion in the stomach.

It is considered that such modification to form a dilated sac in the oesophagus of birds is primarily useful in permitting them to secure an abundance of food in a short period, thus lessening the time during which they are in danger from enemies. This enables birds to compete with other animals for a limited amount of food (Weichert, 1958).

Another peculiar adaptation in the pigeon is that certain areas in the wall of the crop are modified to produce 'crop milk'. The 'crop milk' is regurgitated during the breeding period in both male and female to feed the young. According to Kendall (1947) the production of the milky secretion used in feeding the young is associated with increased thickness of the epithelial membrane and fatty accumulation in the cells which are shed into the lumen where they disintegrate. An additional source of the 'crop milk' may be from the mucous oesophageal glands. Caudal to the crop the oesophagus becomes tubular again and this part can be readily distinguished from the thick walled glandular stomach.

Except in the crop, the oesophagus of birds has longitudinal folds of mucous membrane like those in the amphibian and reptilian oesophagus but there are no papillae of the mucous membrane such as are found in the fish oesophagus.

Mammalia

Mammals have attained the highest stage of evolution. The oesophagus is an elongated tubular structure in comparison with that of lower vertebrates. The length of the oesophagus, of course, varies in different species of mammal very considerably according to the size of the animal and the degree of differentiation of the neck region. The giraffe, for example, has the most elongated neck among the mammals and therefore has a very long oesophagus. In man the oesophagus is about 25 cm. in length in the adult.

It is only in mammals that the fundus of the stomach is fully developed and a well marked cardiac angle is formed which allows the oesophagus to be distinctly demarcated externally from the transversely lying stomach. The cardiac incisura has generally been accepted as one of the factors responsible for the prevention of regurgitation of gastric contents into the lower of the oesophagus.

In ruminants there is the peculiar modification of the formation of four pouches in the foregut adapted to the habit of rumination. There has been a difference of opinion as to which of the four pouches belongs to the oesophagus. Gegenbaur (1878) was of the opinion that the oesophagus shared in the formation of first two pouches. Other workers thought that the first three out of the four divisions were actually modified regions of the oesophagus principally because they are lined by stratified squamous epithelium. Embryological studies indicate, however, that those who hold either of these views are in error and that these pouches are in fact modified regions of the true stomach (Weichert, 1958).

DISCUSSION - Continued

Microscopic appearance of Oesophagus

The various layers of the oesophageal wall will be discussed in sequence from within out.

Mucous membrane

When consideration is made of the composition of the mucous membrane of the oesophagus of different species of fish, diversity is seen in the detailed structure depending in part upon the character of food on which they live and the difference in their habits. Greene (1912) observed that the mucous membrane of the oesophagus of King salmon was formed by a single layer of mucus-secreting cells. These cells are not ciliated and are supported by one or two layers of small unmodified cells which gradually disappear as they are traced caudally. This appearance is similar to the findings in the trout. No reference is made by Greene to the interrupted layer of surface squamous cells which I have described in the trout.

In Sea robin, Sea bass and Minnow the mucous membrane is found to be lined with stratified epithelium. The surface layer of columnar cells is either modified into mucus-secreting cells as in Sea robin (Blake, 1936) and Minnow (Rogick, 1931) or provided with numerous goblet cells among the columnar cells as in Sea bass (Blake, 1930). However, in all these three species of fish the epithelium was said by these workers to be non-ciliated.

On the other hand, Dawes (1929) reported that in plaice the oesophageal epithelium is mainly simple columnar with goblet cells and evidence of stratification is seen in only a few parts.

Warren Andrew (1958) stated that in the fish oesophagus the epithelium is stratified and that there is a discontinuous layer of surface squamous cells: this I have confirmed in the case of the trout.

I have concluded that the epithelial lining in fish is variable and that the most striking feature of the trout oesophageal epithelium is the presence of the interrupted layer of surface squamous cells.

Glands are generally lacking from the oesophagus of fish. Macallum (1886), however, reported the presence of some glands in the oesophagus of one species of Ganoides. It is quite usual to find in sections that the complicated folds of the mucosa may give an appearance which simulates that of glands. A similar observation has been made in King salmon (Greene, 1912), in Sea robin and Sea bass (Blake, 1936 & 1930), in Minnow (Rogick, 1931) and in plaice (Dawes, 1929). Though glands are generally lacking in almost all species of fish the lining epithelium of the oesophagus is provided with a great number of mucus-producing cells either in the form of the lining epithelium cells specially modified for that purpose; in some instances the modification takes the form of goblet cells.

In the present series ciliated epithelium is found only in the frog and lizard and these ciliated cells are associated with goblet cells. The epithelium is pseudostratified columnar in the lizard and mainly pseudostratified but in parts stratified columnar in the frog. Warren Andrew (1958) reported that in the Anura (amphibia) the oesophageal epithelium is ciliated in Rana esculenta, Rana arvalis, Rana agilis, Bufo iridis, Hyla arborea, Bombinator igreus and Bufo pachypus and not ciliated only in Bufo vulgaris. The author states that the reptilian oesophagus usually has ciliated epithelium but that an exception is Chelonidi where a stratified squamous cornified epithelium without cilia is found. The function of these cilia in the oesophagus is to sweep small food particles towards the stomach (Weichert, 1958).

In addition to the goblet cell secretion produced by the surface cells there is a secretion from simple branched tubular mucoserous glands in the lamina propria and submucosa of the oesophagus of the frog though the staining reaction of the mucus secreting cells of the glands differs from that of mucus in the goblet cells. According to Weichert (1958) the secretory cells of the oesophagus of the frog contain propepsin (unlike the secretory cells of the oesophagus of fish which do not contain any digestive enzymes) but it is inactive until it is acted upon by hydrochloric acid in the stomach when propepsin is converted into pepsin. According to Warren Andrew (1958) oesophageal glands are also present in other amphibia such as Bufo and Proteus particularly in the lower part of the oesophagus but are absent in Salamander, Scredon and Pipa. This writer does not say whether or not serous cells are present.

The presence of both mucous and serous cells in the oesophagus of the frog seems to indicate that their function might be more than merely the mechanical one of providing lubrication.

Oesophageal glands are absent from the oesophagus of the lizard but glands of a purely mucous nature are usually present in the upper portion of the oesophagus of the tortoise (Testudo graeca) (Warren Andrew, 1958).

A striking advance made by birds over the other vertebrates during evolution is that the mucous membrane in the oesophagus of birds is lined by stratified squamous epithelium. Though the stratified squamous epithelium lining of the oesophagus of the pigeon (examined in this series) is non-cornified, it is, however, cornified in the dove and duck as it is in certain mammals such as guinea pig and rat which live on a diet of a coarse nature. Among the mammals it is non-cornified in the dog, cat and the pig. It is of interest that the epithelium in the region just cranial to the cardia in the cat oesophagus is in places simple columnar rather than stratified squamous. This simple columnar epithelium which resembles gastric epithelium is found in the region where a few glands are present in the lamina propria of the oesophagus (see below). In the rabbit, stratified squamous epithelium lining the mucous membrane of the oesophagus is non-cornified except for an area over the mucosal fold at the cardia where it is cornified but only to a slight degree. This localised cornification may be associated with the suggested role played by the mucosal fold in the closing mechanism at the cardia. This variation in cornification is due to the difference in the physical character of the food on which the different animals live.

Warren Andrew (1958) stated that in the guinea pig and mouse there is a cornified epithelium and a well developed stratum granulosum such as is seen in the epidermis. He stated that the epithelium is thicker and generally shows more cornification in those mammals which live on a diet of coarse vegetable material than in insectivorous and carnivorous mammals.

Glands

The oesophageal glands in birds are always purely mucous in character unlike those of the frog which are mixed. In the swallow they appear to lie within the stratified squamous epithelium, only a small proportion protruding into the connective tissue (Warren Andrew, 1958). A similar feature has been observed with respect to the oesophageal glands of the pigeon during the present investigation. The oesophageal glands of mammals lie mainly in the submucosa whereas in the frog the oesophageal glands are found to be occupying both the lamina propria and the submucosa. In the dog the oesophageal glands are seen entirely in the submucosa throughout the whole length of the oesophagus, even extending for a short distance into the stomach. However, according to Warren Andrew the ducts of these glands return to empty into the lumen of the oesophagus. In the pig, the oesophageal glands are present only in the cranial part of the oesophagus and entirely lacking in the caudal part. In the rabbit oesophageal glands are totally absent throughout the whole length of the oesophagus as in the guinea pig and rat. The observations in the present work agree with the findings of Elias (1944), Mosher & McGregor (1928) in the dog and the pig and with the findings of Goetsch (1910) in the guinea pig, the rat, the dog, the pig and the rabbit. According to Goetsch (1910) the absence of oesophageal glands in the rabbit was, however, denied by Graff and Vogt and Yung. Reports have been made by Velichko (1939) and Carlier (1892) that the oesophageal glands are absent in the six species of wild rodents and in the hedgehog which they examined respectively.

Elias (1944) claimed that oesophageal glands are present only in the cranial end of the cat oesophagus which differs from the findings of Goetsch (1910) that the glands were entirely absent in the oesophagus of the cat. In the present series only a few glands are seen and these lie in the lamina propria just above the cardia. No submucosal glands were, however, present in the specimens examined.

In the dog and pig though Goetsch (1910) claimed to have observed serous demilunes in the oesophageal glands no such demilunes are seen in the oesophagus of the dog and pig used in this present work.

Muscularis mucosae

Among the lower vertebrates, in the case of the trout the muscularis mucosae is entirely absent from the oesophagus. Its definite absence has been noted in some other fish such as King salmon (Greene, 1912) and Minnow (Rogick, 1931). In the Sea bass and Sea robin its presence was reported by Blake (1930 & 1936), but this author is in some doubt about this observation.

Among the reptiles it is lacking in the turtle (Warren Andrew, 1958) but present in many other reptiles where it is poorly developed in the cranial part and better developed towards the caudal end.

In many birds the muscularis mucosae is lacking. It is absent from the pigeon in the present investigation, but it is present in the fowl (Warren Andrew, 1958). In those birds in which muscularis mucosae is lacking, the layer which should correspond to the muscularis mucosae is represented by the inner longitudinal layer of the external muscle coat with a circular muscle layer external to it. Thus, the arrangement of the external muscle coat becomes inner longitudinal and the outer circular in pigeon and some other birds (the reverse arrangement to that usually seen in other animals).

Ivey and Edger (1952) observed that in the pigeon the longitudinal layer of the muscularis externa was either poorly developed or absent and the submucosa was reduced greatly during the last quarter of incubation. They postulated for this reason that the muscularis mucosae was part of the muscularis externa and therefore the oesophagus of the pigeon was described as having no <u>muscularis mucosae</u> but having an inner longitudinal and an outer circular layer of the <u>external muscle coat</u>. However, the true homology of these layers remain open to discussion.

Goetsch (1910) stated that in the pig oesophagus the muscularis mucosae is <u>entirely absent</u> in the cranial part of the oesophagus in the region where glands are so numerous. My finding of small scattered bundles of muscularis mucosae in this cranial part is therefore in disagreement with the finding of Goetsch. My finding of a well developed muscularis mucosae in the caudal part of the pig oesophagus in which region there is an absence of glands is, however, in agreement with the findings of Goetsch with respect to this region.

In mammals the muscularis mucosae is always present at least in some part of the oesophagus. In the guinea pig, rat, dog, cat and rabbit it is poorly developed in the cranial part and better developed towards the caudal end. The muscularis mucosae was present in the oesophagus of six species of wild rodents examined by Velichko (1939) varying only in its degree of development. Its presence was also noted in the hedgehog by Carlier (1892-93).

External muscle layer

Diversity in the number of layers, the arrangement and nature of muscle fibres (striated or smooth) is seen not only when comparison is made of different groups of vertebrates but also among the various species within the same group. This variation is particularly noticeable in the different mammalian species.

In the trout, only a single layer of striated muscle is seen. A similar observation was made by Greene (1912) in King salmon, Blake (1930) in Sea bass and Botha (1958) in the Dog fish. An external longitudinal striated layer is added to the inner circular layer in Sea robin (Blake, 1936), in the Minnow (Rogick, 1931) and in Plaice (Dawes,(1929). In these fishes the external muscle coat of the entire oesophagus consists of striated muscle fibres. In the trout it is seen extending well into the stomach.

In amphibia and reptiles there are better developed inner circular and an outer thinner longitudinal layer.

In birds though both layers of the external muscle coat consist of smooth muscle fibres as in amphibia and reptiles, the arrangement of the layers is the reverse of that in amphibia and reptiles, there being, in birds, an inner longitudinal and an outer circular layer. According to Warren Andrew, there are few birds which have a muscularis mucosae, but in these few species the external muscle coat is arranged as in reptiles and amphibia (inner circular and outer longitudinal) rather than in the usual avian pattern (inner longitudinal and outer circular).

In mammals, there are always striated muscle fibres at least in the cranial part of the oesophagus. In the guinea pig, rat, dog, pig and rabbit the external muscle coat is composed of striated muscle throughout almost the whole extent.

Among mammals, the muscle fibres are arranged into two different layers in the guinea pig, rat, dog and cat but of these only the guinea pig shows a regularly arranged inner circular and outer longitudinal layers. In the rat and dog there are moreover, irregular oblique muscle fibres intercommunicating between the two layers. In the pig an even more irregular manner of arrangement of the muscle fibres is seen though Warren Andrew stated that four layers could be made out in this animal. He described in the pig an inner and an outer longitudinal layer and two middle layers with a circular arrangement. These four layers have not been identified, however, in the present investigation. In the cat, again two layers are found but, only at the caudal end is the arrangement regular, there being an inner circular and an outer longitudinal layer; and in this part it consists entirely of smooth muscle fibres. In the cranial end of the cat oesophagus an irregular inner and an outer circular muscle layer is present and the fibres are striated. In this respect the cat oesophagus resembles the human oesophagus. My observations regarding the musculature of the oesophagus of the cat entirely agree with the findings of Goodall (1905) except in the manner of the orientation of the fibres as he considered the outer layer to be obliquely longitudinal and the inner, circular. The arrangement of muscle layers in some groups of mammals described by Warren Andrew (1958) is of three layers in carnivorous, ungulates and ruminants. In other mammals including man there are only two layers and they are regularly arranged as an inner circular and an outer longitudinal layer.

In the six species of wild rodents examined by Velichko (1939) it is found that there is an inner circular and an outer longitudinal muscle layer and that both layers are of striated muscle. In hedgehog, two obliquely arranged striated muscle layers are observed in the oesophagus (Carlier, 1892).

According to Arey and Tremaine (1933) early observations were made by Ficinus and Valentin and the striated muscle of the oesophagus of Man extends caudally as far as the cardiac orifice though Valentin later identified smooth muscle in the caudal part of the human oesophagus. However, Gillette (quoted by Arey and Tremaine), Coakley and Hartridge & Haybes attributed the origin of the striated muscle in the caudal part of the human oesophagus described by Ficinus and Valentin to be from the diaphram. On the other hand, Klein and Schaffer claimed to have seen smooth muscle at the cranial end of the human oesophagus.

In the series of 74 specimens of human oesophagus examined by Arey and Tremaine (1933) only in one specimen was the continuation of striated muscle on to the stomach wall found. However, it is now generally accepted that in the human oesophagus there is striated muscle in the cranial third and smooth muscle in the caudal third with a mixture of the two types in the intermediate third (Maximow, 1962).

Region of the cardia

According to Young (1962) there is a sphincter at the junction of the oesophagus and the stomach of the trout to prevent entry of the respiratory stream of water into the stomach but this author does not say whether this sphincter is one that is recognisable anatomically. I must categorically state that I have no evidence whatsoever of a thickening in the muscular coat of the specimens of trout oesophagus that have been examined in the present work. It is postulated, however, that the short oesophageal tube of the trout oesophagus with its powerful thick single layer of muscular coat acts as a sphincter and thus prevents the entry of the respiratory stream of water into the stomach.

Among the vertebrates examined in this investigation a localised thickening of the circular muscle layer has been seen in the rabbit oesophagus only and it consists of both striated and smooth muscle fibres. This anatomical sphincter has also been described by Botha (1958 & 1962). This author, in addition, described a prominent mucosal fold which may play a part in the closing mechanism at the cardia. The localised cornification of the stratified squamous epithelium over this mucosal fold just cranial to the cardia may be due to the probable role played by it in closure of the cardiac orifice because, if it does have a valvular action, it will be subject to more 'wear and tear' than the remaining part of the lining epithelium.

Discussion has been made by Botha (1958) in his paper regarding the functional role of the mucosal fold at the cardia. Such a mucosal fold in the human oesophagus was demonstrated by Creamer (1955). This fold was not present in the single specimen of the cardia of human oesophagus examined by me. Neither was there evidence of thickening of the external muscle coat in this specimen of human oesophagus.

Botha (1958) found thickening of inner circular muscle layer at the cardia in the bat and in the rabbit. In the case of the bat this thickened muscle is entirely smooth but in the rabbit the thickening is composed of both striated and smooth muscle. The finding in the rabbit agrees with my present observation.

DISCUSSION - Continued

Development of the Oesophagus

Of the different layers of oesophageal wall, the lining epithelium and its glandular outgrowths are derived from endoderm and the remaining layers from surrounding mesoderm.

In the 2.5 mm. human embryo, no definite oesophagus can be made out. Botha (1959) described that it was represented merely by a constricted part between the pharynx and the more dilated caudal portion of the foregut. In the series of human embryos examined by Johns (1952), three layers of stratified columnar cells were observed lining the oesophagus at this stage. The primitive oesophagus is not yet separated from the trachea even in the 4 mm. human embryo (Keibel & Mall, 1912) and it is greatly flattened laterally, the lumen having the appearance of dorso-ventral cleft, lined by 1 - 2 rows of epithelium, the luminal row of which has numerous mitotic figures.

At the 5 mm. stage (4 weeks) the oesophagus is about 1 mm. in length (Frazer, 1940) and has several layers of epithelium cells in its wall. Keibel & Mall (1912) quoted Forssner in saying that the epithelial tube has 3 - 4 layers of cells at the 7.5 mm. stage. It is smaller in size than that of younger embryos and laterally flattened only at the caudal end but rounded in the remaining part. Mitotic figures are present at the luminal border as in the younger embryos.

According to Ivey & Edger (1952) a report has been made by Lille that the oesophagus appears as a constricted portion caudal to the pharynx on the third day of incubation in bird embryos.

In the series of pig embryos examined, Flint (1907) described the oesophagus as a tube with a flattened rhomboidal appearance in cross section, passing caudally from the last gill pouch and narrowing gradually until its lumen forms an asymmetrical sagitally placed fissure, lined by 1 - 2 layers of low columnar cells. A longitudinal furrow indicates the line of separation between the trachea and the oesophagus and appears at the 4.5 mm. stage. The separation has been inaugurated at about the 5 mm. stage and communication between the oesophagus and the trachea exists only at the upper end at the 6 mm. stage where it is lined by a double layer of cells, the inner of which is distinctly columnar in shape.

In the series of pig embryos examined in this present work, the oesophagus is laterally flattened with its lumen in the form of a dorsoventral slit lined by 2 - 3 layers of cells; those of the luminal layer are tall columnar with numerous mitotic figures and there is no appreciable differentiation in the surrounding mesenchymal cells.

In John's(1952) series of human embryos, the oesophagus is lined by three layers of cells with those at the basal row columnar in 7 mm., 9mm. & 11.5 mm. stages. Vacuolisation begins in the 13 mm. stage and the vacuoles appear larger in the 16 mm.stage, the epithelium being the same as in younger embryos. Similar vacuolisation was reported in the 16 mm. stage by Frazer (1940) and in the 20 mm. stage by Johns (1952) and in the 12 mm. stage by Botha (1959). Vacuolisation was also reported in the rat and rabbit by Johnson (1910), and according to Botha (1959) by Forssner in the hedgehog. The significance of this vacuolisation of the epithelial cells is not clear.

The mesoderm surrounding the endodermal tube differentiated into connective tissue and muscle of which the circular muscle layer is formed in the 12 mm. (6 week) stage, as observed by Botha (1959). The longitudinal muscle layer differentiates at a later stage. The muscularis mucosae is well differentiated in an embryo at 10 weeks (Botha, 1959).

In Flint's (1907) series of pig embryos in the 13 mm. stage, the thickness of the epithelium increases to 4 - 5 layers with a distinct basement membrane. The surrounding mesenchymal cells become condensed and there are denser masses of cells arranged circumferentially away from the embryonic epithelium. A similar observation is made in the present series of pig embryos in the 15 mm. stage. This seems to represent the anlage of external muscle coat of the oesophagus. In the 10 mm. stage no further differentiation than the condensation of the surrounding mesenchyme is observed.

In the 34 mm., 40 mm & 41 mm. human embryos the epithelium becomes thicker generally at least 4 layers thick (Johns, 1952).

Flint (1907) reported that in the 30 mm. stage of the pig embryo there is a decrease in the definiteness of the columnar character of the cells next to the lumen and the contours were no longer sharp. He has observed the infolding of mucosa at this stage, giving its lumen the appearance of a Greek cross. The submucosa becomes increased in size and the external muscle layer is more sharply differentiated and may be readily divided into inner circular and outer longitudinal layers with some interlacing between the two.

In the 35 mm. stage of the pig embryo in the present series, the luminal border of the epithelial cells is found irregular with some protrusion into the lumen at some places. The external muscle coat has also differentiated into two layers at least in some parts of the circumference of its wall with some fibres intercommunicating between the two layers; the inner circular and the outer longitudinal arrangement can hardly be made out in some parts. No folding of the mucosa is seen.

According to Johns (1952) ciliated cells in the epithelium of the embryonic oesophagus of Man was noted by Neumann Jahrmacker. He reported his findings of ciliated epithelium in the 40 mm. human embryo and then that these cells were replaced by stratified squamous epithelium in the 130 mm. stage. Johnson (1910) found ciliated cells at the 55 mm. stage right up till the time of birth. In the series of human embryos examined by Botha ciliated cells were observed in the 41 mm. stage. Willis (1962) reported extensive persistence of ciliated epithelium in the oesophagus until late in foetal life, as did Healey (1920); Rector & Connerley (1941) fouhd ciliated epithelium in a new born infant and Raeburn (1951) in the case of a 35 years old woman.

Ivey and Edger (1952) considered that the development of ciliated epithelium in the oesophagus of turkey was similar to that in man and the development in the chick also followed the same pattern.

The ciliated cells were not seen by Flint (1907) in his series of pig embryos. No ciliated cells are observed in all four stages of pig embryos examined in this present work.

According to Keibel and Mall (1912) the earliest evidence of gland formation is seen in the 78 mm. human embryo. Johns (1910) reported the appearance of superficial glands in the 78 mm. stage and deep glands in the 240 mm. stage. Johns (1952) also reported his finding of superficial oesophageal glands in the 130 mm. stage of the human embryo, in his series.

Flint (1907) observed the first appearance of oesophageal glands in his series of pig embryos in the 210 mm. stage. He recognised muscularis mucosae in the 75 mm. stage. In the human embryo, muscularis mucosae does not appear till the 78 mm. stage (Keibel and Mall, 1912).

In the series of pig embryos at the four stages examined in this present work, neither the muscularis mucosae nor oesophageal glands are observed.

GENERAL CONCLUSIONS

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On the basis of the observations made by other workers on various species of vertebrates and as a result of my own observations on the present series of vertebrates, it is postulated that the following are the general principal characteristics of the gross and microscopic appearance of each group of vertebrates.

1) In fish, the characteristic features are

(a) the short course with no external means of distinction between the oesophagus and the stomach and the complexly folded mucosa of oesophagus.

(b) the presence of numerous mucus secreting cells in the lining epithelium which consists of more than one layer of cells. In the case of the trout a noticeable feature is the presence of an interrupted layer of squamous cells on the luminal aspect of the epithelium.

(c) the absence of oesophageal glands.

(d) the external muscle layer consisting of striated muscle fibres.

2) In amphibia, the main features are

(a) the short and wide course with an ill-defined cardiac angle which demarcates the oesophagus from the stomach.

(b) the ciliated columnar epithelium with goblet cells lining the mucous membrane.

(c) the presence of oesophageal glands.

(d) the external muscle layer composed entirely of smooth muscle fibres.

3) In reptiles, the chief characteristics are

(a) the comparatively elongated form with better developed cardiac angle and insignificant fundus of the stomach.

(b) The ciliated columnar epithelium with numerous goblet cells lining the mucous membrane.

(c) the absence of oesophageal glands.

(d) The external muscle layer entirely formed by smooth muscle fibres.

4) In birds the main features are

(a) the elongated tubular form with a ventral diverticulum in the intermediate third of its length.

(b) the mucous membrane lined by stratified squamous epithelium.

(c) the presence of oesophageal glands.

(d) the external muscle layer formed by smooth muscle fibres.

5) In mammals the characteristic features are

(a) the well elongated tubular form with well marked cardiac angle and fully developed fundus of the stomach.

(b) stratified squamous epithelium lining of the mucous membrane.

(c) the presence of striated muscle at least in its cranial part.

SUMMARY

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A comparative study of the oesophagus has been carried out on animals representing each group of the vertebrates.

Variation in type of epithelium, nature and extent of secretory cells in the oesophageal wall, and in the type and arrangement of muscle has been described.

These findings have been discussed and compared with those of previously published accounts.

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