1 THE RESPIRATORY SYSTEM AND THE MECHANISM OF RESPIRATION IN LISSEMYS, TRIONYX, GEOMYDA AND TESTUDO

2 A COMPARATIVE STUDY OF THE MORPHOLOGY OF THE REPTILIAN LUNG

THE RESPIRATORY SYSTEM AND THE MECHANISM OF RESPIRATION IN LISSEMYS, TRIONYX, GEOMYDA AND TESTUDO

The organs of respiration in the Chelonia are the lungs and in the freshwater forms the skin is also considered to be respiratory (Root,1949). Lissemys as in other Trionychidae, possesses a prominent snout which helps the animal to keep the external nares above the water. The opening of the glottis is a vertical slit guarded by a pair of lip-like muscular structures one on either side of the opening. Ventrally the glottis is supported by the main body of the hyoid to which the muscles of the glottis are attached. The glottis leads into a long trachea whose wall is supported by cartilaginous rings. More or less at the level of the base of the neck the trachea bifurcates into two bronchi, the left one of which is longer than the right one. The bronchi too possess complete cartilaginous rings. Each bronchus goes to the lung of its respective side and traverses through the substance of the lung for a considerable distance.

The respiratory mechanism in the Chelonia has received considerable attention from zoologists because of the physiological problems involved as a result of the unique skeletal adaptations that have taken place in these animals. The rigid shell has made all free movements of the body wall impossible and consequently the respiratory movements characteristic of other amniote groups are absent. The structural modifications in the Chelonia naturally have created an intriguing situation for zoologists, since the mechanism of respiration in them can not be explained on the same lines as for the other reptiles.

Malpighi, Cuvier, Agassiz (1857) and even some of the recent authors like Noble and Noble (1940) and Walters (1949) have suggested that the throat movements as in the frogs are the effective part of the respiratory mechanism. Mitchell and Morehouse (1863) have laid great emphasis on the part played by the musculature of the glottis in respiration but much attention had not been paid to their work by later investigators. Wolf (1933) proposed that the movements of the neck and the limbs indirectly served the purpose of the body-wall movements necessary for primary pulmonary action. Ludicke (1936) studied the role of throat movements and observed that aquatic forms like Emys orbicularis, swallow air but terrestrial ones like Testudo gracea do not do so on account of their inability to secure an airtight closure of the mouth.

McCutcheon (1943) conducted some intersting experiments to study the respiratory mechanism of turtles and brought forth certain significant findings. He observed that the contraction of the anterior and posterior flank cavity muscles, the serratus magnus and the oblique abdominis causes increase in the volume of the body cavity. The decrease in pressure caused there, forces the lungs to expand, and air from outside rushes into the lungs, bringing about inspiration. On the other hand when the diaphragmaticus and the transverse abdominis contract, pressure is exerted on the lungs resulting in expiration. He refers to the posterior flank cavity muscle, the oblique abdominis as the more important agent in the inspiratory mechanism. He is also of the opinion that the throat movements can not pump air into the lungs, because the force created thereby is insufficient to open the glottis. Moreover, he points out that evidence is available to show that the throat movements are associated with olfaction. This is also supported by Root (1949).

While examining the anatomical features involved in the respiration of the pond turtle (Lissemys punctata), it was found that (in addition to the muscles mentioned by McCutcheon) a muscular membrane covering the lungs occurs (inner muscle sheath, Fig. 47,64). It was surmised that this enveloping muscle case must have a significant role in respiration in this species. Structurally it was found to be composed of striated muscle fibres. The fibres of this muscle arise from a small elliptical tract on the dorsum from the second to fifth thoracic ribs. The exact limits of their origin are indicated in the Fig. 47,64. After leaving their place of origin they converge ventrally not only enveloping, but also fusing with the lung, leaving only its bronchus exposed.

Another striated muscle (outer muscle sheath, Fig. 47,64) occurring outside the one mentioned above, covers the lungs as well as most of the visceral organs for about two thirds of the body cavity in its anterior region. This muscle arises from a border tract on the dorsum beginning from the first thoracic rib and ending with the seventh. Its exact position of origin is also shown in the Fig. 64 . It should be mentioned that though this muscle is in its origin composed entire~~s~~ly of fibres, as it converges towards the ventral side, the fibres thin out till a more or less membranous structure results.

The following experiment was conducted to find out the working of both these muscles. The turtle was pithed first and then the thoracic plastron was removed carefully. The nerves going to the inner muscle sheath covering the lungs were noted and one of them was then stimulated by an induced electric current. By make and break arrangement the stimuli were given and in response the muscle contracted. But when the current was stopped by breaking it, the muscle relaxed. As the electric stimuli were given to the inner muscle sheath, the outer muscle sheath which surrounds most of the viscera also responded. This suggests that during expiration both these muscle sheaths contract and compress the lung tissue which pushes the pulmonary air out. When these muscles relax, the pressure in the lung falls and air enters the lung, and thus inspiration is caused.

On examination of the structure of the lung, it is found that the alveoli are comparatively large and the inter-alveolar spaces filled with smooth muscle fibres which are grouped in large bundles (Fig. 69). This enormous amount of smooth muscle in the lung of this animal is a remarkable feature, since in other amniotes though smooth muscle, is present, its extent is limited. It is surmised that the lung is pressed to contraction as a result of the combined action of the outer striated muscle sheath, the inner enveloping muscle as well as the smooth muscle of the lung tissue. This is an unusual arrangement not met with elsewhere.

The outer enveloping muscle which covers most of the visceral organs including the lungs, can be homologised to the *diaphragmaticus* plus the *transverse abdominis* though the boundries of these two muscles are not demarcated as in *Emys europea* (Owen, 1866) or as in *Malaclemys centrata* (McCutcheon, 1943). The homology of the inner muscle sheath, however, remains doubtful. From its position it is reasonable to assume that it represents the *intercostal* muscles. Here in this case instead of having the original pattern of origin and insertion ~~and origin~~, the fibres seem to have lost their insertion and migrated inwards to closely envelop the lungs. This supposed homology receives confirmation from the fact that the corresponding nerves to the intercostal muscles in other reptiles, birds and mammals, innervate this muscle. Thus it became evident that the inner and the outer muscle sheaths enabled the lungs to function as a pair of bellows. On studying the histology of the lung in the two other subspecies of *Lissemys punctata*, namely *Lissemys punctata typica* and *Lissemys punctata scutata* and another chelonian *Geomyda trijuga* it was found that the inner muscle sheath of the lung was present in these forms also (Figs47,49,64). These findings encouraged me to believe that such a muscle sheath might be universally present in the chelonians (George and Shah, 1955). But on studying the structure of the lung of an aquatic form Trionyx, a terrestrial one Testudo and a marine one Eretmochelys it was found that the inner muscle sheath was absent in all these three chelonians.

The inner muscle sheath in Lissemys and Geomyda arises from a small elliptical tract on the carapace at the level of the second to the fifth ribs near the vertebral column. In Lissemys this muscle sheath envelopes the lung completely but in Geomyda the sheath is partly fleshy and partly membranous, being fleshy medially, anteriorly and antero-laterally, while the remaining portion membranous. In Testudo, Trionyx and Eretmochelys, however, there is no fleshy muscular envelope over the lungs but there is a thin membranous covering instead. Such a condition appears to be a secondary modification of the muscular sheath as found in Lissemys with that of Geomyda presenting an intermediate stage of transition between Lissemys on one hand and Trionyx, Testudo and Eretmochelys on the other.

These observations have thrown some light on the evolution of the chelonian lung. The presence of the inner muscle sheath on the lung in Lissemys is a primitive condition which must have given the early chelonians, in whom the fused body shell posed a respiratory problem, their survival value. The question as to why such a muscle sheath which was an asset to the early chelonians gradually disappeared in evolution is quite a relevant one. So the Lissemydinae are to be regarded as a primitive group. Support for this belief is also available from the studies on the plastron (Williams and McDowell, 1952).

It has already been pointed out in the chapter dealing with the musculature of the trunk, that the probable cause for the loss of this muscle sheath on the lung of the higher Chelonia and the degeneration of the <u>diaphragmaticus</u> in the terrestrial forms like Testudo could be the evolution of larger lungs on which the muscle bag is more of a hindrance to their full expansion; and in the mean while the acquisition of a better physiological equipment for fixing a greater amount of oxygen store in the body for slow and gradual utilization. On estimating the haemoglobin content of the blood of these chelonians it is found as is to be expected that, it is least in Lissemys, highest in Trionyx and Eretmochelys. (Vide chapter 5 Composition of blood).

Regarding the mechanism of respiration the following conclusions may be arrived at.

1. Respiration in the Chelonia in general is effected by the action of the flank cavity muscles (McCutcheon, 1943) and probably by the movements of the neck and the limbs too (Wolf, 1933).

2. In a primitive chelonian like Lissemys with smaller lungs and lesser oxyphoric capacity of the blood, the inner muscle sheath on the lung should be acting as a pair of bellows in effecting expiration and inspiration. The movements of the flank cavity muscles and the neck and limbs should also be helpful in the process.

3. Among the higher forms like Trionyx and Eretmochelys

in which there is no muscle sheath on the lung, the lungs are considerably larger and their blood possess higher oxyphoric capacity. Amongst them, the less active form like Testudo, the oxyphoric capacity is considerably less than the more active ones like Trionyx and Eretmochelys. In this connection it may be mentioned that the inner muscle sheath on the lung in Geomyda is ill-developed and not complete and the animal being more terrestrial than aquatic and as much less active as Testudo, has the oxyphoric capacity of blood same as that of Testudo.

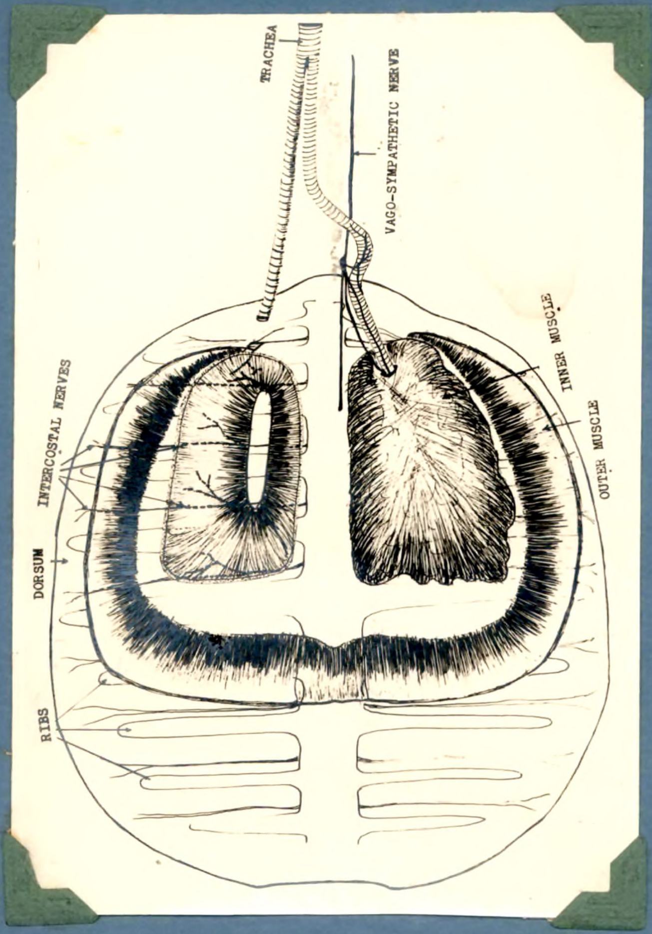

TRACHEA
VAGO-SYMPATHETIC NERVE
INNER MUSCLE
OUTER MUSCLE
INTERCOSTAL NERVES
DORSUM
RIBS

FIG. 64

A COMPARATIVE STUDY OF THE MORPHOLOGY OF THE REPTILIAN LUNG

The structure of the lung varies widely in the Reptilia. The lizards show a primitive type of lung somewhat more complicated in structure than that of amphibian. The main difference between the amphibian lung and that of a lizard is that the latter has considerably more alveolar chambers as a result of the primary alveoli becoming more expanded and secondarily folded. The inner surface of the lacertilian lung shows the same kind of honey-comb-like structure which is visible in the amphibian lung as a consequence of the connective tissue forming a net-work around the alveolar spaces. The network also contains smooth muscle fibres. The alveolar chambers are lined by a thin epithelial lining. The epithelial cells possess a large nucleus. The wall of the lung consists of a frame-work of connective tissue in which the blood vessels and the smooth muscle fibres are embedded. On the outer side of the lung wall there is a thin layer of connective tissue.

Generally in lizards the anterior three-fourths of the lung is more alveolar and better supplied with blood than the remaining hind portion of the lung which is less alveolar and poorly supplied with blood. The posterior one-fourth of the lung is made up of a saccular chamber. In certain lizards like Varanus the posterior saccular portion is restricted and the lung is divided into a number of chambers. This is certainly a specialised condition. The trachea in reptiles in its anterior part possesses complete cartilaginous rings, while posteriorly the rings are incomplete. The bronchi also have incomplete rings. The bronchus enters the respective lung at its anterior medial surface and does not extend into the lung tissue.

The lung of Urodeles is long and compatible with the length of the trunk is provided with a saccular posterior region. In Anura the saccular portion is wanting. In Sphenodon the lung is similar to that of the Anura in the absence of a posterior sac-like extension, but the alveolar structure is more complicated with more folds and cavities. ~~In~~ The Pythonidae and Boidae are the only exceptions among snakes in which both the right and left lungs are present. In others the left is either reduced to a vestigeal one, or completely lost. The right lung which is persistant in these has become more elongated. In its histological structure the lung of snakes is similar to that of lizards. The saccular portion of the lung, however, in snakes is extensive and in some reaches the posterior region of the trunk (George and Varde,1941). The blood supply to this saccular region is very much less than in the anterior alveolar portion. The trachea possesses complete cartilaginous rings in its anterior portion but the greater part of it possesses incomplete cartilaginous rings. The gap between the free ends of the incomplete tracheal rings is filled up by a thin membranous connective tissue. In some snakes some portion of the trachea develops alveolar chambers and gives rise to the tracheal lung (George and Varde, 1941).

Apart from the tracheal lung developed in the Vipers, Echis, Lycodon and in Typhlops, the variations in lung structure could be grouped into four categories.

Category 1: In this category can be included the primitive snakes like Pythons, Natrix and the Sea snakes. In Natrix (Figs 65,79) the trachea has incomplete cartilaginous rings for most of its length. The bronchus is short and all around it the alveolar tissue is developed. The saccular portion is not so extensive and does not reach the posterior limit of the visceral cavity as it happens in other snakes viz., Ptyas, Vipera and Echis.

Category 2: In the second category be included Typhlops. Typhlops (figs 68,79) possesses comparatively a short trachea with a short tracheal lung. The tracheal lung continues as the bronchial lung without any line of demarcation. The posterior saccular part of the lung is very short. The posterior part of the lung is also poorly supplied with blood. The trachea is provided throughout its length with complete rings of cartilage. The lung of Typhlops shows, however, absence of deep septa arising from the lung wall and dividing the lung into a number of chambers. This condition appear to be a degeneration.

The systematic position of Typhlops remains unsettled, since recently Mcdowell and Bogart (1954) has included it in the Anguimorpha, a branch of the Lacertilia, and not in Ophidia.

Category 3: Ptyas mucosus (Figs 66,79) :- In this the trachea at its beginning possesses complete cartilaginous rings but later the rings become incomplete and the gap between the free ends of these rings is filled up by a thin membranous connective tissue. The trachea just anterior to the heart bifurcates into two bronchi, the left and the right ones. The former is very small and narrow to which the left vestigeal lung is attached, while the latter is wider and it opens into the right lung. The bronchus is also provided with cartilaginous half-hoops, similar to those in the trachea. On the mid-ventral side of the bronchial lung there is a thin membranous tract of connective tissue which replaces in that region the cartilaginous rings of the bronchus. The bronchial lung posteriorly merges with the saccular reservoir portion of the lung. About four-fifths of the lung is made up of the membranous saccular reservoir, which extends almost up to the posterior end of the visceral cavity. It has been described by Varde (1951) that in *Ptyas mucosus* the bronchial lung posteriorly extends into a short reservoir, but this is an incorrect observation, as the reservoir in this snake extends almost up to the posterior end of the visceral cavity as in Distira.

The nature of the lung in the cobra, *Naija tripudians* (Fig 65) is similar to that in Ptyas , but the saccular reservoir part of the lung is not so extensive.

In the Lycodon (figs 66,79) the structure of the lung is almost similar to that of Ptyas and Naija, with the difference that the saccular part is not extensive as in Ptyas and also that anterior to the heart, the trachea has a little portion of alveolar development forming a short tracheal lung.

(figs 67,79)

Category 4: *Vipera russelli*:- In this animal the lung consists of three parts, the tracheal lung, the bronchial lung and the membranous reservoir. The trachea as usual in the beginning possesses complete cartilaginous rings, but later the rings become incomplete. A considerable part of trachea in front of the heart has developed alveolar chambers giving rise to the tracheal lung. This tracheal lung merges with the bronchial lung which possesses a great number of alveolar chambers and these two portions together constitute the effective respiratory tissue of the lung. Throughout the length of the bronchial lung, the bronchus is present on the mid-ventral part of the lung as a strip with the half-hoops still persisting. In this portion of the lung in Ptyas and Naja the bronchus is represented by the thin membranous strip running in the mid-ventral line. ~~The~~ The saccular portion of the lung is in continuation of the bronchial lung and extends almosts up to the hind end of the visceral cavity as seen in *Ptyas mucosus*. *Echis carinata* (fig 67) shows almost similar structure and also the extension of the lung as seen in *Vipera russelli*.

The chelonian lung is more modified than those of the lizards and snakes. They are more spongy in texture and occupy a considerable part of the dorsal region of the body cavity. The trachea in Chelonia is quite long and bifurcates almost at the base of the neck resulting in two bronchi, of which the left one in some is longer than the right one. Sometimes the trachea is shorter than the bronchus. The bronchus extends into the tissue of the lung for a considerable distance dividing into branches on its way. Ultimately each branch terminates in a large chamber which divides into numerous alveolar air spaces. The bronchi, like trachea possess complete cartilaginous rings, unlike in lizards and most snakes. The microscopical structure of the chelonian lung shows that the alveoli are comparatively large in comparision with those of the lizards and snakes and the inter-alveolar space is filled up with a large amount of smooth muscle fibres which are grouped in large bundles.

As mentioned in connection with the muscular system, in Lissemys there is an envelope of striated muscle sheath over the pleural membrane. This muscle sheath has been homologised with the intercostal muscles which have shifted their position. In Geomyda the muscle sheath is incomplete, in some portion ~~and~~ occupied only by a thin membrane. In Testudo, Trionyx and Eretmochelys the lungs are covered with only a thin layer of membrane which resembles ~~that being~~ the non-muscular part of the muscle sheath over the lung in Geomyda.

In crocodiles the structure of the lung is more or less like that of chelonians. As in the chelonian lung the branches of the bronchi terminate in chambers each of which is divided into a number of alveoli. But the alveoli are more numerous and smaller and consequently the lung is more spongy. Since the respiratory surface is considerably increased it is more efficient as a pulmonary organ. The smaller bronchi like those of chelonian lung are supported by cartilaginous elements in their wall. The histological structure of the alveoli in the crocodilian lung is similar to that of the chelonian.

Discussion:

The structure of the lung in the reptilian orders Lacertilia, Ophidia, Chelonia and Crocodilia shows ~~a~~ considerable variations. It means that in the radiation of the reptiles the lung has undergone considerable variation.

Among the orders of reptiles, the lacertilian lung as found in Calotes is a simple type with a short bronchus which leads into a central pulmonary chamber which through its lateral chambers gives rise to the lung tissue. There is a small posterior saccular chamber.

The chelonian lung appears relatively large in size. It has essentially the same structure as that of the lizard but is more elaborated with little or no saccular portion of the lung. Each lateral chamber leading from the central space is split up into numerous alveoli. The alveoli are larger in size commensurate with the larger size of the lung.

The great peculiarity of the ophidian lung is its long posterior saccular chamber. It is an obvious adaptation to store up a large amount of air. It also serves to inflate the body to stiffen it in taking short leaps when greatly terrified.

In all the snakes studied except the Typhlops the posterior part of the trachea possesses incomplete rings of cartilage and this is continued in the bronchus for varying lengths. In the first category, snakes, the alveolar development is all round the bronchus as in lizards. So also in Typhlops. In the third category snakes, the mid-ventral part of the lung which lies against the ventral scales, is devoid of alveolar lining. In the fourth category also this condition persists, but the mid-ventral part of the lung here is occupied by the bronchus with incomplete cartilaginous rings. This non-development of lung tissue and the bronchus at the region where the lung lies against the shields on the ventral side, which come in contact with the ground appears to be a variation with the ground habit. In Pythons and also in the water snakes it is absent.

It was interesting to note that when a vibrating tunning fork is brought near these ground snakes resonance is produced within in the air column of the lungs. This suggests that the saccular part of the lung enables the ground snakes to detect vibrations and that is a device to enable the animal that has lost its external ears to collect vibrations of sound from the ground.

The corocodilian lung is even more specialised than that of the chelonian inasmuch as there are more numerous alveoli in each lateral chamber. Due to the greater subdivisions of the pulmonary surface, the alveoli are much smaller.

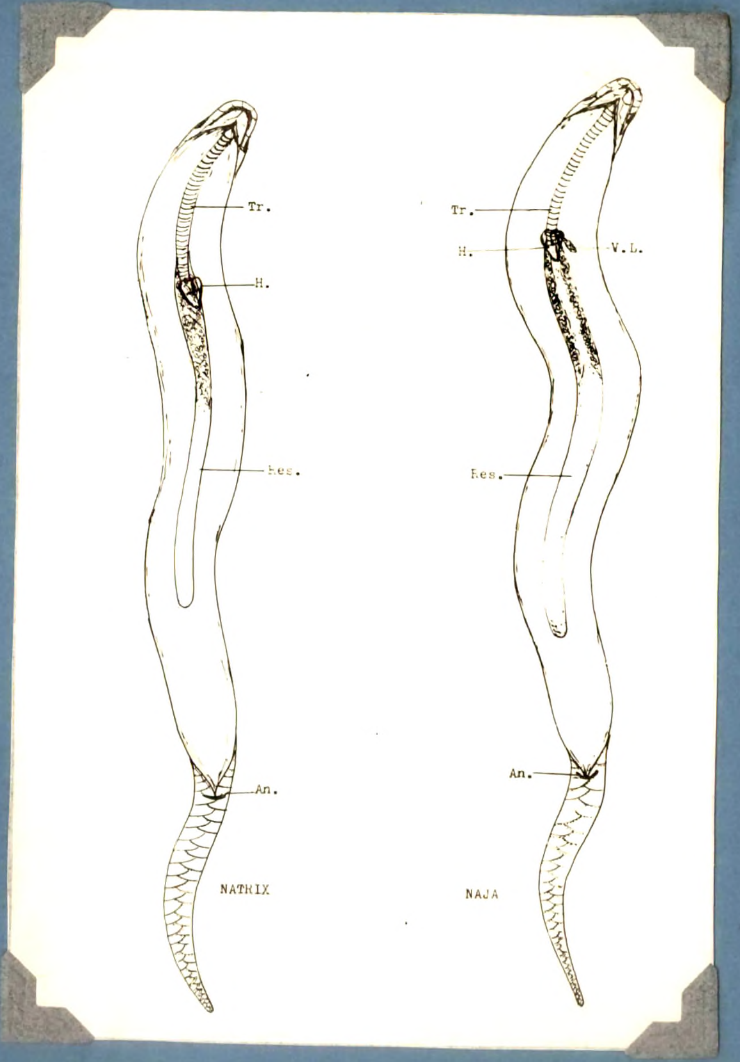

Tr.
H.
Res.
An.
NATRIX
Tr.
H.
V.L.
Res.
An.
NAJA

FIG. 65

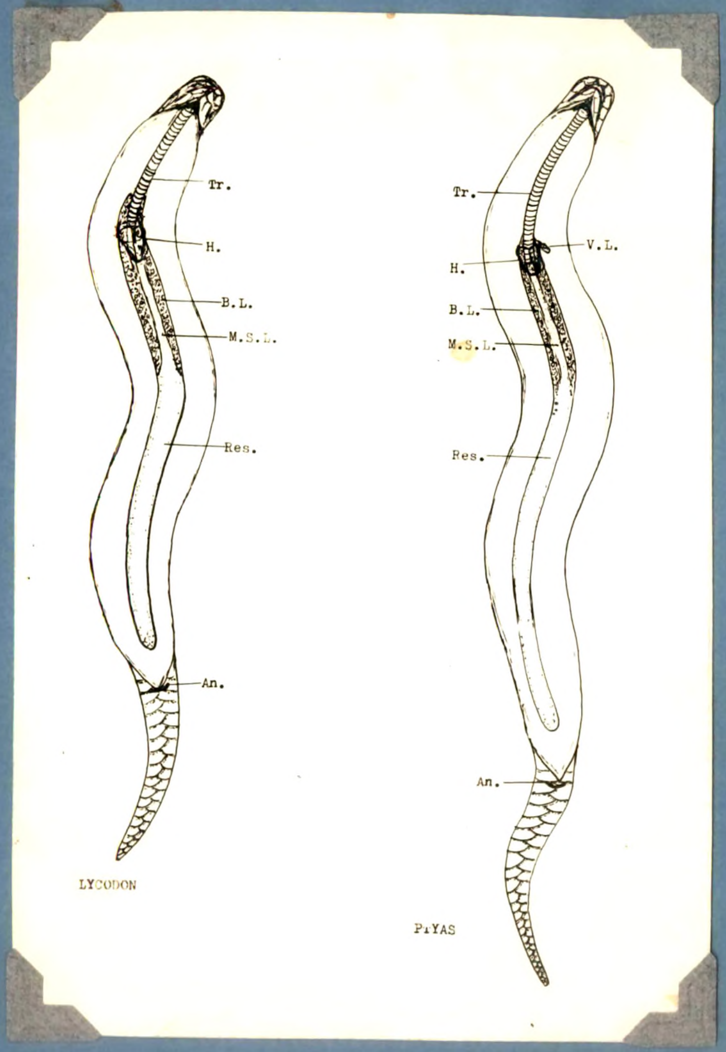
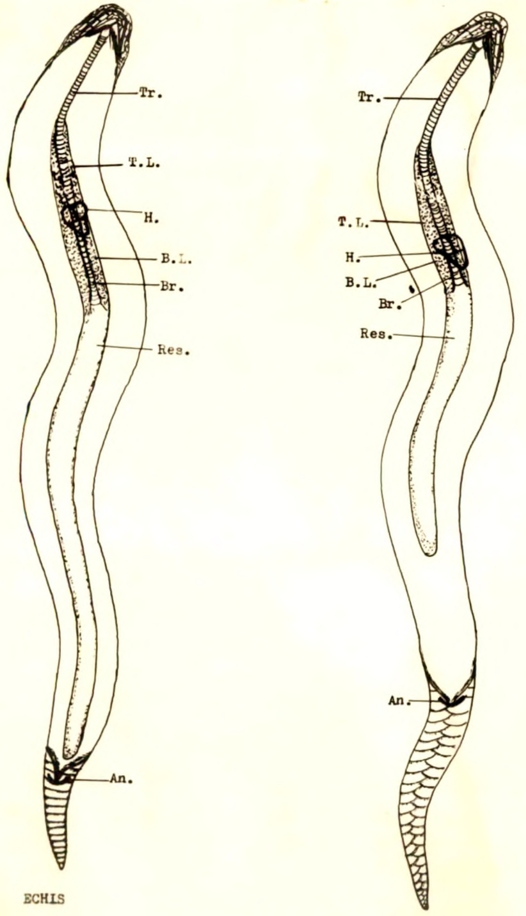

Tr.
H.
B.L.
M.S.L.
Res.
An.
LYCODON
Tr.
V.L.
H.
B.L.
M.S.L.
Res.
An.
PTYAS

FIG. 66



ECHIS VIPERA

FIG. 67

TYPHLOPS

FIG. 68

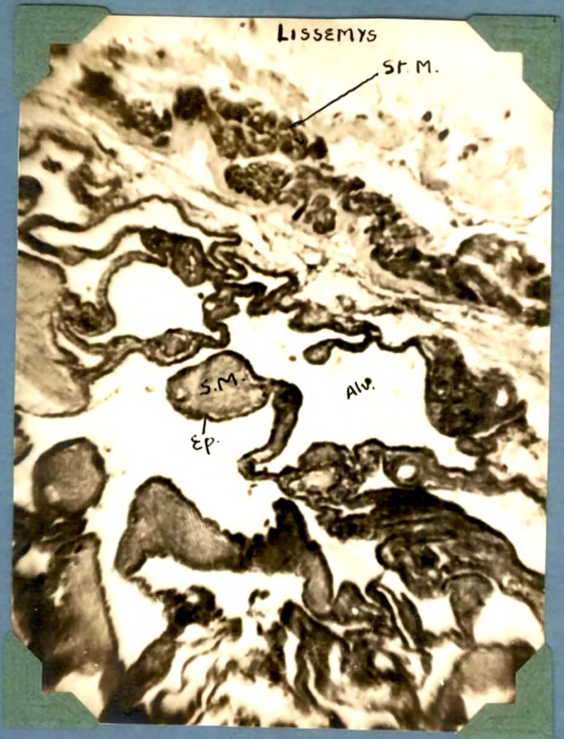


FIG. 69

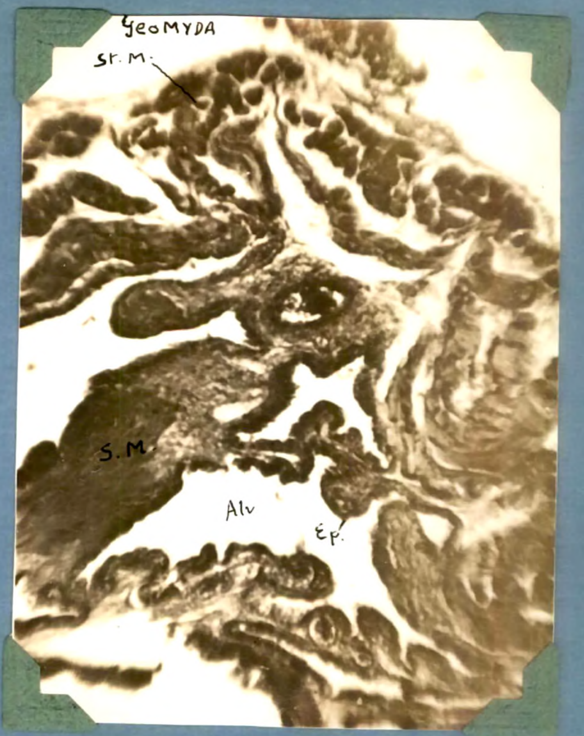


FIG 70

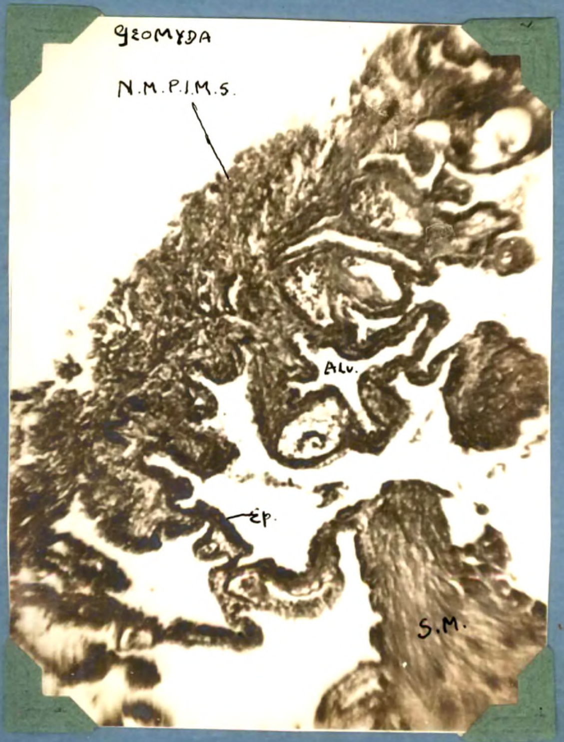


FIG. 71

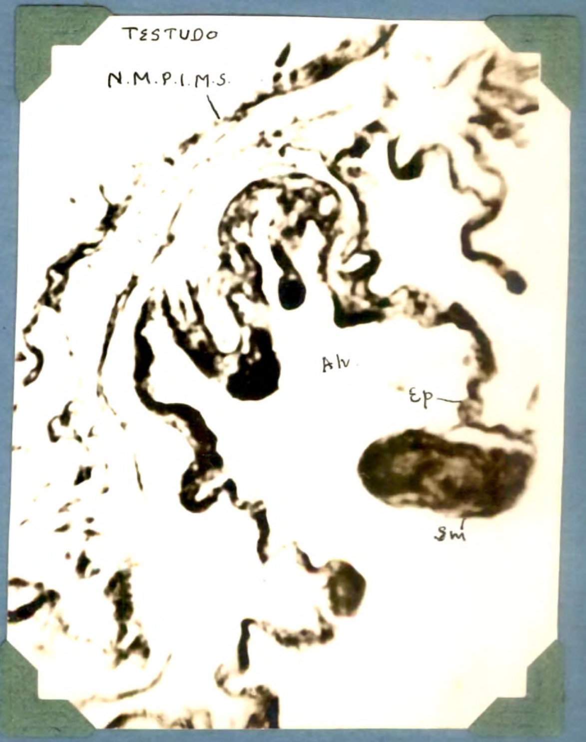


FIG. 72

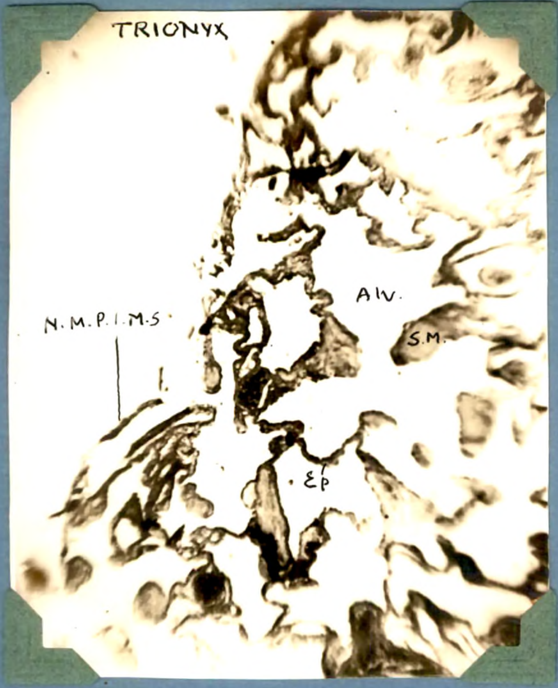


FIG. 73

FIG. 74

FIG. 75

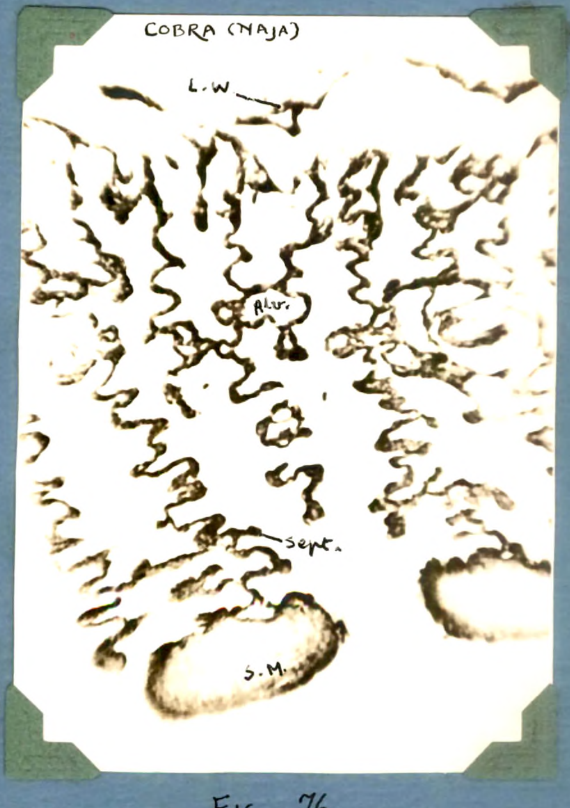


FIG. 76

FIG. 77

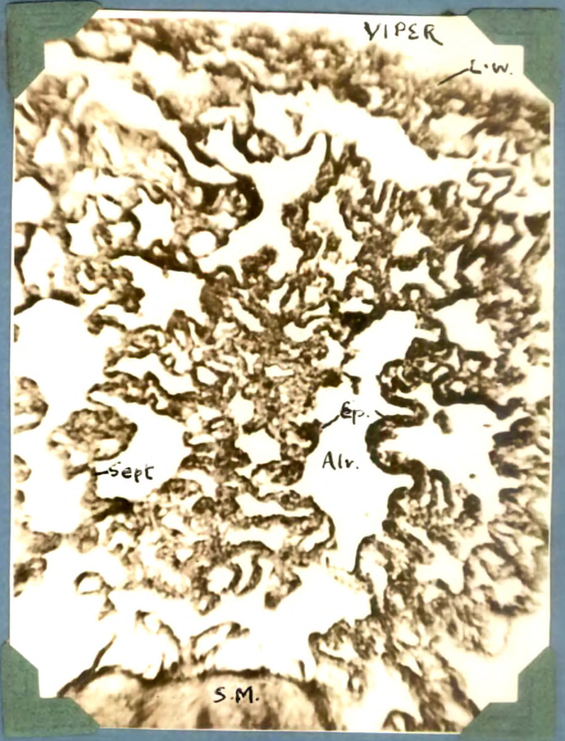


FIG. 78

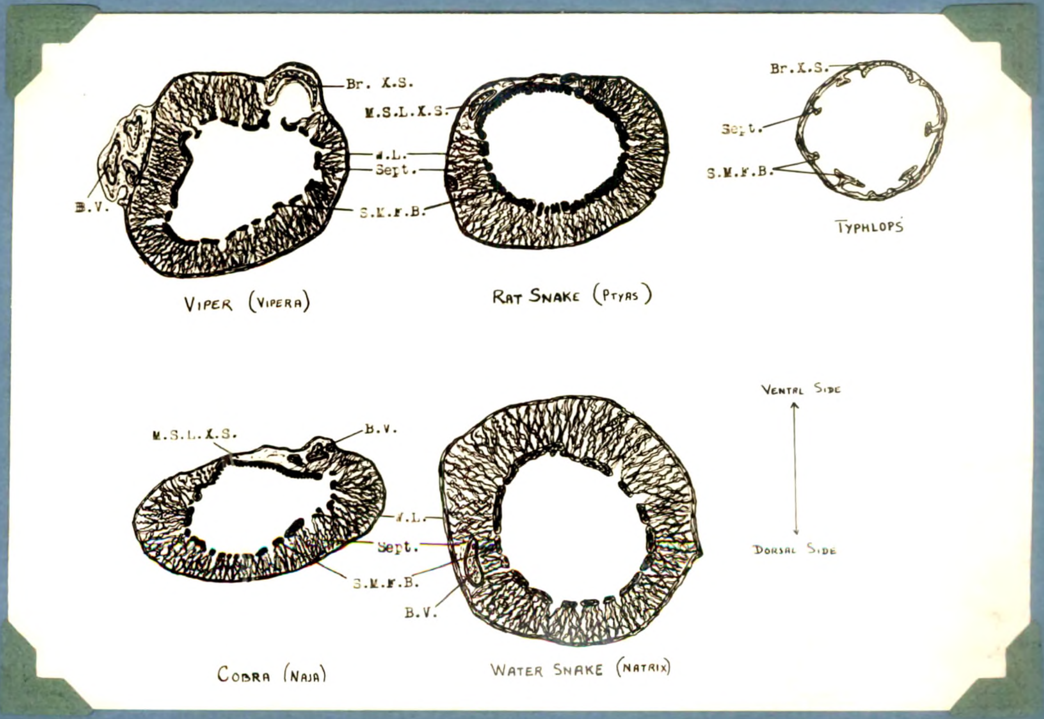


FIG. 79