SOME MORPHOLOGICAL ASPECTS OF THE RESPIRATORY SYSTEM OF THE COMMON WATERSNAKE, *NATRIX SIPEDON*

Thesis for the Degree of M. A.

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Aaldert Mennega

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SOME MORPHOLOGICAL ASPECTS OF THE RESPIRATORY SYSTEM OF THE COMMON WATERSNAKE, NATRIX SIPEDON

by

Aaldert Mennega

AN ABSTRACT

Submitted to the College of Science and Arts of Michigan State University of Agriculture and Applied Science in partial fulfillment of the requirements for the degree of

MASTER OF ARTS

Department of Zoology

1960

Approved by M. M. Hensley

Aaldert Mennega

ABSTRACT

The anatomy of the respiratory system of the common water-snake, Natrix Sipedon was investigated. It was found to have a functional right lung, which is separated into an anterior alveolar part and a posterior mechanical part.

The trachea contains the tracheal lung, which, though functional, is developed only slightly. The pulmonary bronchus is the contimuation of the trachea into the lung tissue and extends to the mechanical part of the lung.

The rudimentary left lung is found at the extreme end of the trachea. It has alveoli and a narrow communication with the trachea.

The pulmonary artery lies on the ventral right side of the lung, giving off large branches to the left and small branches to the right. The pulmonary vein emerges from the lung tissue at the anterior tip of the lung and empties into the left atrium.

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Grateful thanks also to [illegible], Director of the Museum, and Mr. [illegible], Department of [illegible], for serving as committee members and [illegible] this thesis.

Acknowledgment is made to Dr. [illegible] for his advice in regard to the [illegible] of this work.

This is also [illegible] Department, [illegible] detailed [illegible].

Appreciation is [illegible], [illegible] to my wife, [illegible], who [illegible] and [illegible].

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INTRODUCTION

Throughout the ages snakes have been known, by primitive people as well as by the civilized. Snakes have appeared in the folklore of many tribes and nations, and have given rise to superstitions in many instances. Presumably it is through ignorance that fear of snakes is so widespread and deeply rooted in people. Even in scientific literature there is a striking paucity of information on the anatomy of this group of animals. Being made aware of the gap in the knowledge of this subject, the author attempted to investigate some general aspects of snake anatomy, with the interest drawn especially to the respiratory system.

Preserved specimens of the water snake, Natrix sipedon, were readily available, and since the species is representative of the Serpentes, it was selected for this study. Although studies on fresh specimens are certainly more ideal, yet the use of preserved specimens was considered more practical for our purpose.

The distribution of N. *sipedon* ranges from southerly Canada to Florida and westward to the Mississippi (Ditmars, 1941). It is closely confined to the neighborhood of water and can thus be found in many swamps, marshes, streams and lake borders (Allee and Schmidt, 1951). Its food consists mainly of fish (Oliver, 1955).

The primary objectives of the problem were: (a) to survey and compile pertinent literature dealing with the morphology of the respiratory system in snakes; (b) to make a series of illustrations showing the respiratory anatomy and the location of the major organs, in N. *sipedon*; and (c) to correlate these data with available studies of other species.

It is hoped that this study will provide a basis for future work with dissections of fresh specimens and histological analysis of the various internal structures.

The distribution of A. gigas [illegible] Carolina to Florida and westward to the [illegible] (Rathbun, 1941). It is closely confined to the neighborhood of water as [illegible] thus is found [illegible] borders [illegible]. The food consists mainly of fish (Oliver, 1956).

The primary objectives of the present work are: (a) to survey and [illegible] the [illegible] morphology of the respiratory system [illegible] (b) to give a series of illustrations showing the body [illegible] and the location of the major organs, i.e. [illegible] and (c) to correlate [illegible].

It is hoped that this study will provide a basis for future work [illegible] dissections [illegible] analysis of the various internal structures.

METHODS AND MATERIALS

The animals utilized had been fixed in formalin and later transferred to an alcohol solution to facilitate handling. The snakes were a mixed lot of sexually mature males and females of varying ages and sizes, selected at random from a large number of individuals. Approximately ten specimens were dissected and examined internally. Normal dissecting techniques were employed to expose, measure, and analyze the various organs. A handlens was used for those structures which could not be readily observed. Measurements were made with a millimeter rule. A statistical analysis of the organs and locations was made on twenty specimens, ten each of male and female individuals.

THE RELATIONS OF THE RESPIRATORY SYSTEM TO OTHER ORGANS

Figures 1-7 show the relative position of the respiratory system with respect to the associated major organs in *Natrix sipedon*.

The nasal passages may easily be determined between the external and internal nares. The trachea starts at the glottis and extends posteriorly dorsal to the tongue sheath (Fig. 2). With the esophagus to its left, the trachea continues until it passes the heart on the left side. At the level of the apex of the heart the trachea joins the anterior end of the lung in the vicinity of the 30th ventral scute. At the junction of the trachea and the lung proper, the rudimentary left lung may be found (Fig. 5). The functional part of the right lung continues past the anterior tip of the liver, to about the 43rd ventral scute. The mechanical part of the right lung lies dorsal to the liver (Fig. 7), and extends caudad beyond the liver.

For the computation of tables I and II, ten male and ten female specimens were examined and measured. The females attained the greatest overall length, while the males showed a greater number of ventral scutes from snout to vent. The males ranged in size from 54.0 to 82.0 cm., with an average of 67.9 cm. Their ventral scutes numbered from 182 to 219, averaging 208.2. The females measured from 51.0 to 94.0 cm., with an average of

Graph I. Graph showing comparative position of the ventral scute at which some organs start in males and females. The mean of the starting scute is indicated by the horizontal mark; the range by the vertical line.

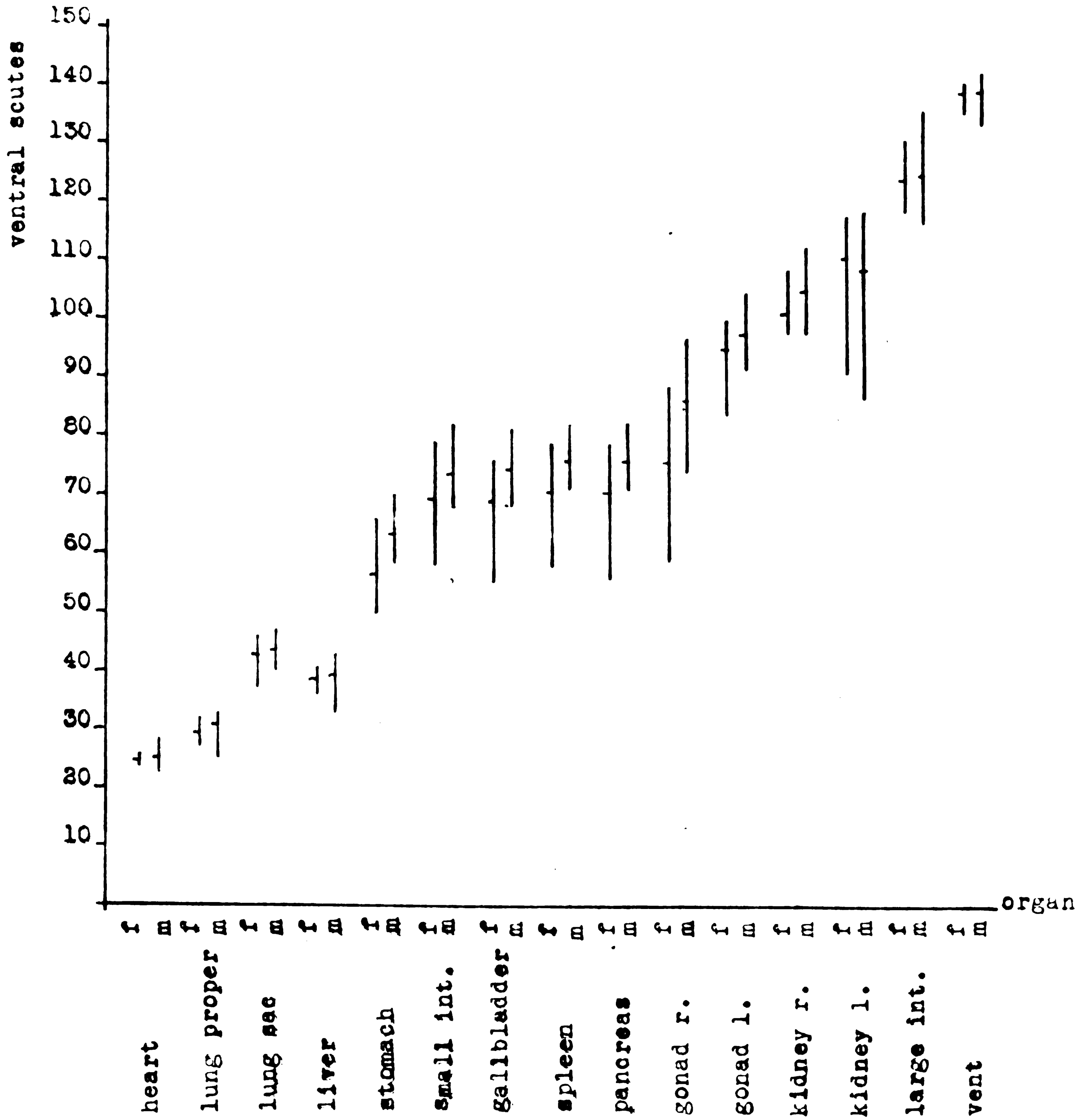

TABLE I

Measurements and calculations of the organs of the ten male snakes

organs	starting scale mean	starting scale range	dimension in cm mean	dimension in cm range length	dimension in cm range width
tail	139.6	134-143	16.6	12.0-22.0	
heart	25.7	23-29	2.0x0.9	1.5-2.6	0.7-1.0
lung proper	30.7	25-33	5.3x0.8	2.5-8.0	0.4-1.2
lung sac	43.7	40-47	-------	--------	-------
trachea	-----	------	11.0x0.3	9.5-13.0	0.2-0.3
liver	39.5	33-43	11.4x0.9	9.0-15.0	0.6-1.2
stomach	63.1	58-70	4.0x0.8	2.5-5.0	0.5-1.1
pancreas	76.0	71-82	1.2x0.5	0.8-1.7	0.3-0.7
gallbladder	74.2	68-81	1.1x0.8	0.6-1.5	0.6-0.8
spleen	75.8	71-82	0.3x0.3	0.2-0.3	0.2-0.3
gonad, r.	86.3	74-97	3.5x0.7	2.0-6.0	0.1-1.2
gonad, l.	98.0	92-105	3.0x0.7	1.5-4.8	0.3-1.0
kidney, r.	105.7	98-113	6.0x0.5	4.0-7.5	0.3-0.7
kidney, l.	109.3	87-119	5.6x0.5	3.8-6.8	0.3-0.6
adrenal, r.	93.4	86-97	1.1x0.1	0.5-1.7	0.1-0.2
adrenal, l.	102.6	96-109	0.8x0.1	0.3-1.6	0.1-0.2
small int.	73.9	68-82	55.0x0.2	43.0-66.0	0.2-0.3
large int.	125.1	117-136	4.2x0.4	3.0-5.5	0.4-0.5
thyroid body	24.5	20-28	0.3x0.1	0.1-0.5	0.1-0.3
tongue sheath	-----	-------	6.0x0.1	5.0-7.0	0.1-0.2

[illegible]	[illegible]	[illegible]	[illegible]	[illegible] Length	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	
heart	22.7	[illegible]	[illegible]	[illegible]	[illegible]
lung proper	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
lung sac	[illegible]	[illegible]	———	———	———
trachea	———	———	[illegible]	[illegible]	[illegible]
liver	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
stomach	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
pancreas	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
gallbladder	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
gonad, r.	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
gonad, l.	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
kidney, r.	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
kidney, l.	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
adrenal, r.	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
adrenal, l.	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
small int.	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
large int.	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
thyroid body	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	———	———	[illegible]	[illegible]	[illegible]

TABLE II

Measurements and calculations of the organs of the ten female snakes.

	starting scale		dimension in cm		
organs	mean	range	mean	range length	width
tail	139.1	136-141	15.3	11.5-21.0	
heart	24.7	24-26	2.0x1.0	1.5-2.5	0.6-1.3
lung proper	29.3	27-32	4.3x0.8	3.0-7.0	0.4-1.1
lung sac	42.3	37-46	-------	-------	-------
trachea	-----	------	10.4x0.3	9.5-12.5	0.2-0.4
liver	38.6	36-41	10.2x1.0	7.5-13.5	0.7-1.3
stomach	56.4	50-66	5.2x0.9	3.5-9.0	0.5-1.3
pancreas	70.7	56-79	1.4x0.6	0.7-2.3	0.4-1.0
gallbladder	68.9	55-76	1.3x0.8	1.0-1.8	0.4-1.2
spleen	70.9	58-79	0.3x0.3	0.2-0.3	0.2-0.3
gonad, r.	75.9	59-89	5.1x0.3	1.5-12.0	0.2-0.4
gonad, l.	95.1	84-100	3.8x0.3	1.3-11.5	0.2-0.5
kidney, r.	101.6	98-109	5.4x0.4	3.8-7.5	0.3-0.6
kidney, l.	111.0	91-118	4.6x0.5	3.0-6.5	0.3-0.6
adrenal, r.	88.3	79-92	1.4x0.1	0.8-3.0	0.1-0.2
adrenal, l.	100.7	93-103	1.2x0.1	0.5-2.7	0.1-0.2
small int.	69.7	58-79	60.2x0.3	42.0-81.0	0.2-0.4
large int.	124.1	119-131	4.9x0.5	3.5-6.5	0.3-1.0
thyroid body	23.3	22-25	0.3x0.2	0.1-0.5	0.1-0.3
tongue sheath	-----	-------	5.6x0.1	4.5-7.5	0.1-0.2

68.0 cm. They had from 179 to 207 ventral scutes, averaging 201.4.

From this we can see that the organs, when located by the number of the ventral scute at which the organ starts, were found to be more caudad in the males than in the females (Graph I). This is substantiated by the figures obtained by Bragdon (1953).

The heart starts at about the 25th scute and the lung begins at approximately the 30th. The size of the functional part of the right lung differed greatly, ranging in length from 2.5 cm. to 8.0 cm. in males and from 3.0 cm. to 7.0 cm. in females. The mechanical part of the lung slightly exceeded the alveolar part in length; no definite measurements could be obtained. The width of the lung in the males was from 0.4 cm. to 1.2 cm., while in the females it ranged from 0.4 cm. to 1.1 cm. The trachea measured from 9.5 cm. to 13.0 cm. in males and from 9.5 cm. to 12.5 cm. in females.

26.0 cm. They ranged from 172 to 297 ventral scutes, averaging 291.4.

From this we can see that the [illegible], that formed by the number of the ventral scutes to which the [illegible], were found to be more [illegible] in the males than in the females (Graph 2). This is substantiated by the figures obtained by Bragdon (1953).

The heart starts at about the 15th [illegible] body, began at approximately the 30th. The size of the intestinal tract of the right lung differed greatly, ranging in length from 4.5 cm. to 8.0 cm. in males and from 2.6 cm. to 7.0 cm. in females. The medial part of the lung usually exceeded the [illegible] part in length, so that [illegible] could be obtained. The width of the lung in the males was from 0.4 cm. to 1.4 cm., while in the females it ranged from 0.4 cm. to 1.1 cm. The trachea measured from 5.5 cm. to 15.0 cm. in males and from 9.5 cm. to 11.5 cm. in females.

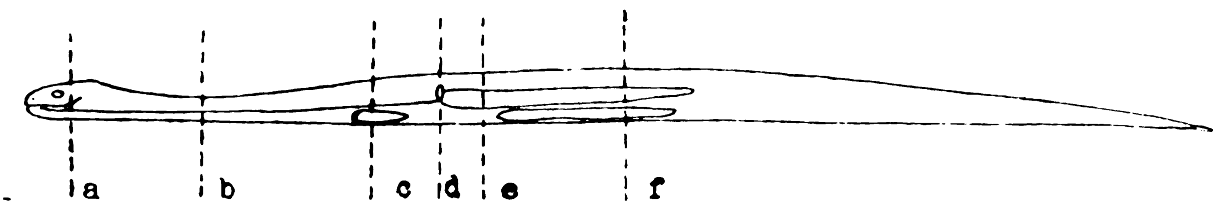

Fig. 1. Diagram for cross-sections.

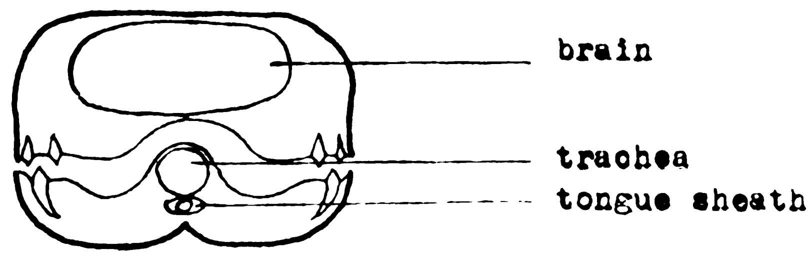

Fig. 2. Cross-section through head, in plane "a"
Scale 2:1

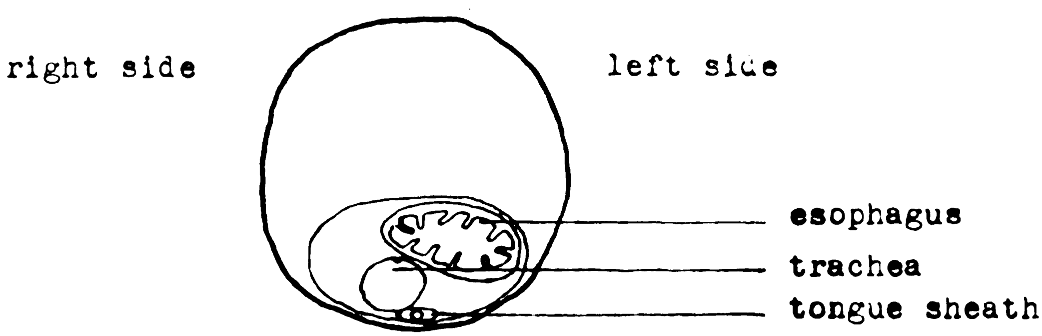

Fig. 3. Cross-section through neck, in plane (b). Scale 2:1

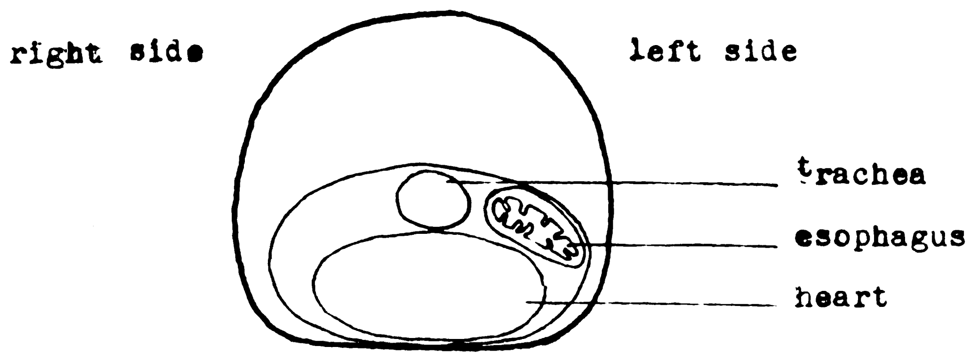

Fig. 4. Cross-section through heart, in plane (c). Scale 2:1

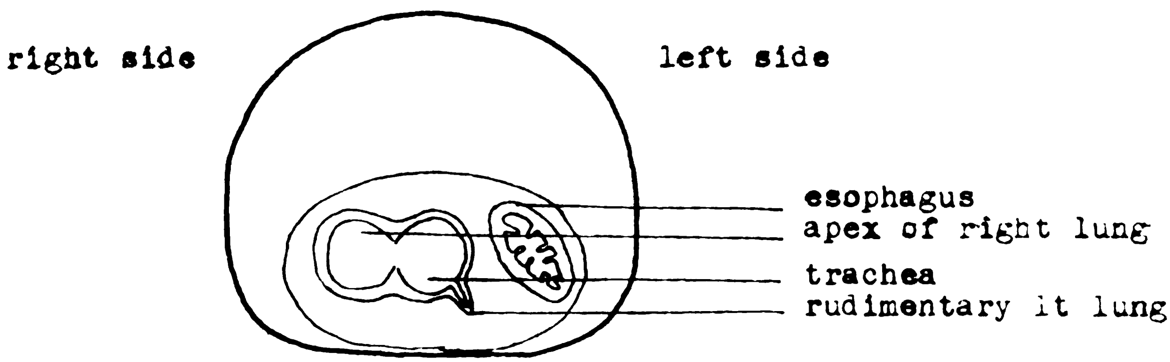

Fig. 5. Cross-section through rudimentary left lung in plane (d). Scale 2:1

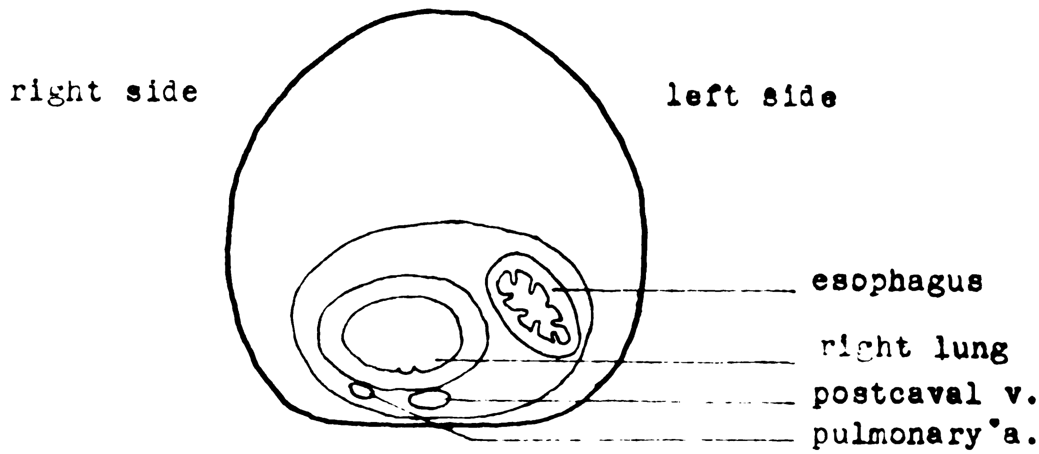

Fig. 6. Cross-section through the functional part of the lung, in plane (e). Scale 2:1

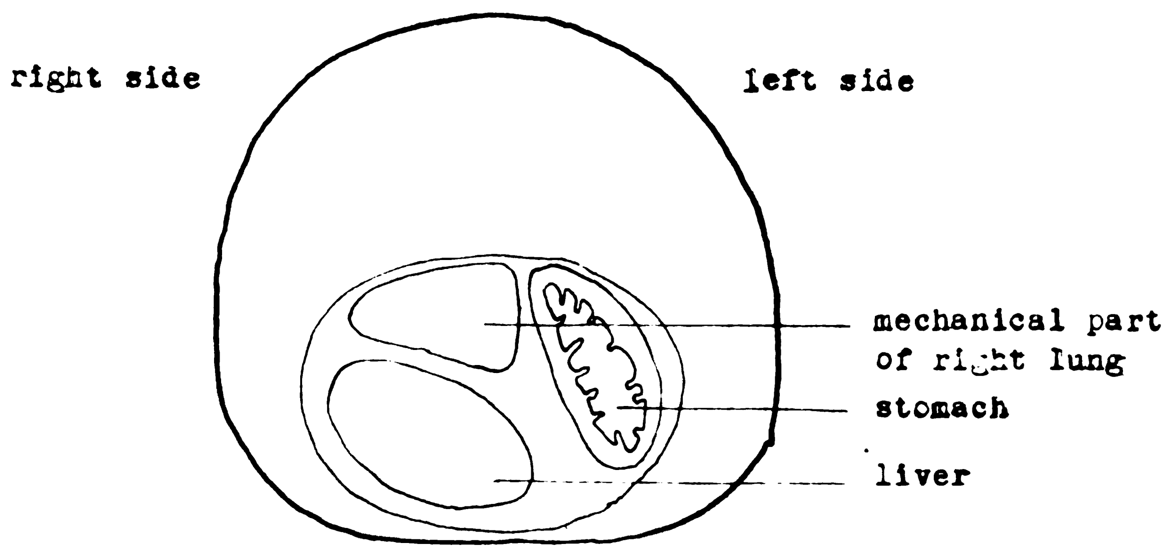

Fig. 7. Cross-section through mechanical part of right lung and liver, in plane (f). Scale 2:1

THE NASAL PASSAGES

The external nares in most snakes are found close to the tip of the snout, well in front of the eye. They are small openings which afford the entrance of air when the mouth is in its usual, *i.e.*, closed, position. In *N. sipedon* these openings are approximately one mm. in diameter, and can be found in the position indicated in Fig. 8. It is generally assumed that the external nares of the landsnakes require no special mechanism to close off the air passages from the environment. However, in those snakes which spend much, or all, of their time in the water, this is stated to be different. Katharinar (1899), in his studies, found that all of the latter species have a special mechanism, which keeps the external nares closed constantly, and requires muscular effort only when the nares are to be opened for respiratory purposes. During breathing the blood supply to the cavernous tissue, which normally closes off the nares, is shut off by the surrounding smooth muscles. The cavernous tissue thus collapses, and the air is free to enter the nasal cavity. Cavernous tissue is not present in *N. sipedon*, so far as could be determined from the preserved specimens used in this study.

The nasal cavity is divided into a vestibule and

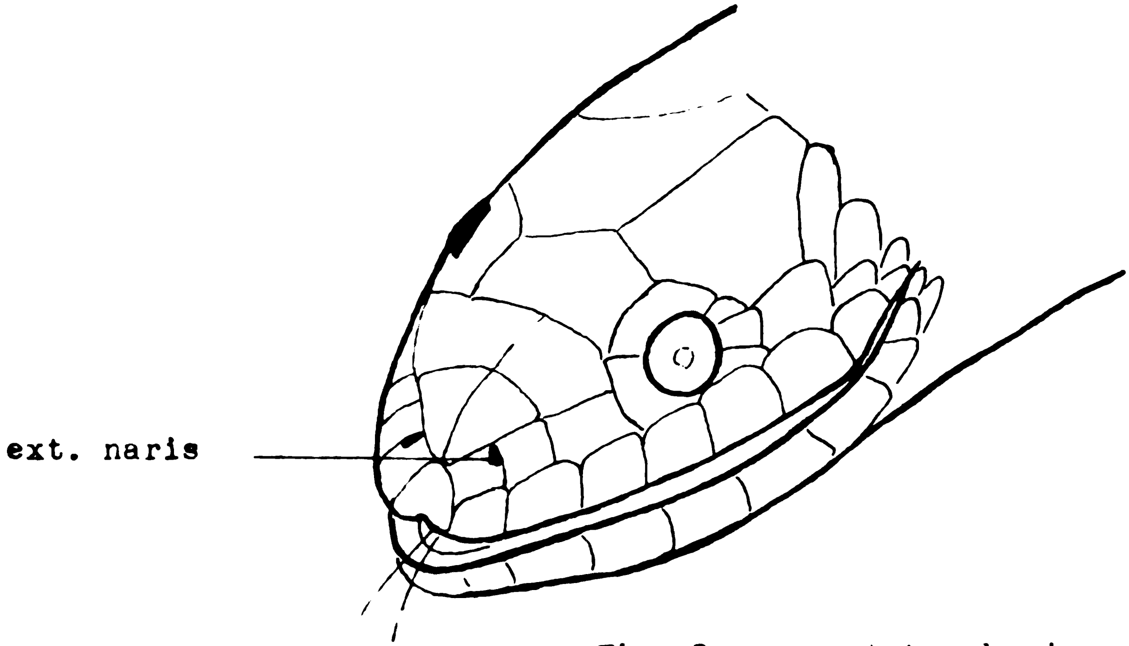

Fig. 8. Dorsolateral view of head of *Natrix sipedon*.

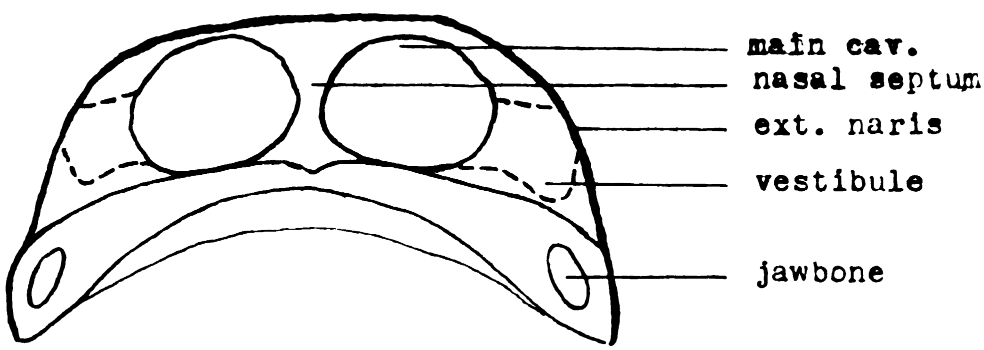

Fig. 9. Posterior view of transverse section through tip of nose, immediately behind the external naris.

main cavity. Generally the vestibule in snakes is poorly developed, except in the case of the marine snakes (Kathariner, 1899; Matthes, 1934; VanderKlauw, 1952). The vestibule in N. sipedon is poorly developed, measuring no more than 1x1 mm. It is not clearly separated from the main cavity (Fig. 9). A concha is present on the lateral wall of the nasal cavity (Weichert, 1953; Romer, 1956), and extends from the vestibule to almost the end of the nasal cavity (Fig. 10). It measures approximately 4x1 mm. Its function is to increase the available sensory surface (Weichert, 1953). The nasal cavity has the functions of olfaction and of air passage. The two nasal cavities are separated by the nasal septum (Kellicott, 1898). The nasal cavities open into the oral cavity by means of the internal nares. These openings are in close relation to the opening of the trachea so that a good connection of the air passages is established when the mouth is closed.

THE TRACHEA AND THE TRACHEAL LUNG

An open-mouth view of N. sipedon (Fig. 10) shows the trachea as a raised area on the floor of the mouth from opposite the internal nares to the opening of the esophagus. The trachea is covered on the outside with oral mucosa. At its anterior end the glottis may be seen immediately posterior and dorsal to the opening of the tongue sheath. As mentioned above, the glottis is in direct relation to the internal nares, and thus the larynx is found far rostrally (Vander Klauw, 1952): ca. 1.0 cm. from the tip of the snout. Kathariner (1899) observes that the glottis prevents food or water from entering the trachea during the act of swallowing. While the prey is in the mouth, the trachea is compressed (George and Varde, 1941). In Heterodon it is at the same time protracted by the genio-trachealis muscle (Kellicot, 1898), to allow adequate breathing. The opening of the glottis is flanked by the arytenoid cartilages, to which are attached the muscles which dilate the glottis. The cricoid cartilage is elongated and fused with several tracheal rings in most species (Romer, 1956).

Natrix sipedon has no epiglottis, although, in other species, a slightly developed lip or valve at the lower part of the glottis is reported as being present (Hopley, 1884). Only in the bullsnake (Pituophis) is the epiglottis found as a

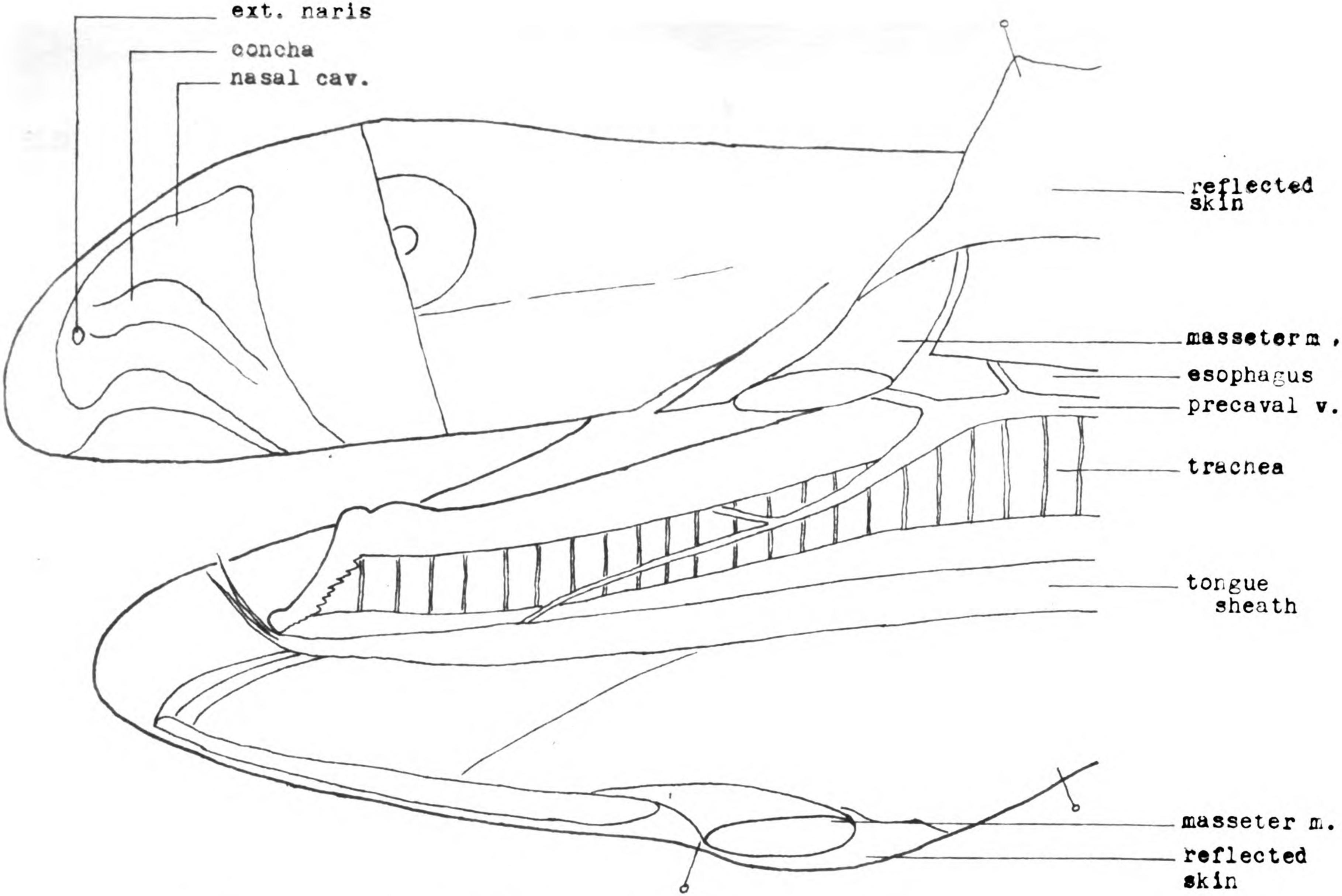

Fig. 10. Side view of head with air passages laid open.

definite structure (White, 1884; Hopley, 1884). It not only aids in closing the glottis, but also accounts for the "hiss" of the bull snake. The hissing of other snakes is caused by the rapid passage of air through the partly closed glottis (Bolk, 1939).

Among snakes the tracheal rings vary in number, size and structure. Generally the rings are complete at the anterior end of the trachea (Thompson, 1913; Bronn, 1890; Bolk, 1939), but after a short distance the sides of the rings fail to meet dorsally, thus leaving an opening, which is filled in with soft, fibrous tissue, or sometimes with a musclebundle (Beddard, 1903 and 1906-a; Bronn, 1890). In N. sipedon the tracheal rings are incomplete from glottis to lung, and the gap is closed by fibrous tissue.

In many snakes the dorsal tracheal soft tissue is continuous with the lung tissue, and actually carries on respiratory function (Beddard, 1906-b). This "tracheal lung", as it is called, exhibits considerable variation in the different snakes (Beddard, 1906-b). Varde (1951) showed that in Echis carinata, Hydrophis cyanocinctus, and others "the trachea gives off laterally a series of tiny tracheal branches, which after repeated sub-branching form the tracheoles that terminate in alveoli, giving rise to the lung tissue called 'the tracheal lung', in contradistinction to the bronchial lung." The function of this structure seems quite obvious if we keep in mind the snake's difficulty in breathing while swallowing its food. When actlike structure (White, [illegible]; [illegible]). [illegible], with in closing the glottis, and accounts for the "blades" of the bill shape. The blades [illegible] or other are closed by the [illegible] passage of air through the partly closed glottis ([illegible], [illegible]).

Among snakes the tracheal rings vary in number, size and structure. Generally the rings are [illegible] of the trachea (Thompson, [illegible]; [illegible], [illegible]; [illegible], [illegible]), but after a short distance the ends of the rings fail to meet dorsally, thus leaving an opening, which is filled in with soft, fibrous tissue, or sometimes with a membrane ([illegible], [illegible] and [illegible]; [illegible], [illegible]). In [illegible] the tracheal rings are incomplete from glottis to lung, and the gap is closed by fibrous tissue.

In many snakes the dorsal tracheal soft tissue is [illegible] with the lung tissue, and probably carries on respiratory function ([illegible], [illegible]). This "tracheal lung", as [illegible], exhibits considerable variation [illegible] ([illegible], [illegible]). Verte ([illegible]) showed that [illegible], [illegible], [illegible], and others "the trachea [illegible] of [illegible] bronchi, which after [illegible] the bronchioles [illegible] terminate in alveoli, [illegible] 'tracheal lung', [illegible] lung." The function of this [illegible] the snake's difficulty [illegible] breathing [illegible] food. [illegible] the air in the lung proper is not available, due to the closing off of the air passages by a large-size prey, the tracheal lung may be prevailed upon for a sufficient supply of oxygen (George and Barde, 1941). However, in some cases, as in the Black snake, no tracheal lung is present (Attwood, 1916). In other species, such as Causus rhombeatus, a viper, the tracheal lung may carry on the respiratory function completely (Beddard, 1960-a). The respiratory tissue may start at the glottis, or any point posterior to it; sometimes this tissue is even to be found as a wide band, exceeding the width of the trachea (Thompson, 1914-b).

A tracheal lung is present in most snakes as stated early by Cope (Beddard, 1906-a), and since then affirmed by several other investigators (Bolk, 1939); Beddard, 1906-b; Rothley, 1930).

The structure of the tracheal lung is similar to that of the bronchial lung (Varde, 1951; Vander Klauw, 1952; Beddard, 1906-b; Rothley, 1930); the latter will be discussed later.

A special condition exists where the trachea is perforated by large foramina which lead to air-chambers which are divided into compartments by stout connective tissue. Only three species, Ophiophagus bungarus, Pseudoxenodon chinensis and Coluber oxycephalus, are known to possess these special airchambers (Thompson, 1914-b; Beddard, 1903).

[illegible] of the air passages [illegible] -the species, and [illegible] provided that [illegible] origin (Negus and [illegible], 1949). However, [illegible] as [illegible] Ramsay, [illegible] Lang is present [illegible]). In other species, such as Gyrinus Kushakewitsch, a vapor, [illegible] branched lung may carry on the respiratory function [illegible]. The respiratory [illegible] may start as the glottis, or any [illegible] as we [illegible] to be found as a wide band, [illegible] of the branches ([illegible], 1933-b).

A branched lung is present [illegible] as [illegible] (Kessler, [illegible]), and [illegible] by several other investigators ([illegible]; [illegible], [illegible]; [illegible], [illegible]).

The structure of the branched lung is similar to that of the non-branched lung ([illegible], 1952; Vander Adams, 1953; [illegible], [illegible]; [illegible], [illegible]), the latter will be discussed later.

A special condition exists where the [illegible] is [illegible] by large formations which [illegible] sac-chambers which are divided into compartments by [illegible] connective tissue [illegible], [illegible] and [illegible], are known to possess these special [illegible] (Thompson, 1933-b; [illegible], 1950).

In N. *sipedon* the tracheal lung may be found on the dorsal inner surface of the trachea. It starts at the glottis as a barely perceptible line which gradually widens into a 2 mm. wide band, and continues to the thoracic lung (Fig. 11). Shallow alveoli are present in the posterior two-thirds of this band, along with longitudinal folds of fibrous tissue.

In many species the trachea does not end abruptly at the beginning of the thoracic lung, but usually penetrates into the lung tissue a certain length before its distinction is lost (Attwood, 1916; Beddard, 1906-a). The condition in N. *sipedon* will be discussed in greater detail below, in connection with the intrapulmonary bronchus.

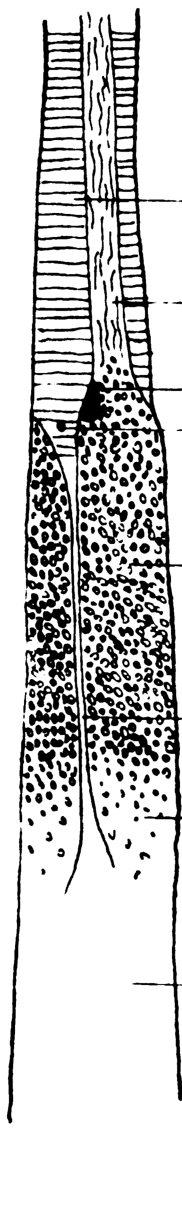

Fig.11. Trachea and lung cut open to show the tracheal lung and intrapulmonary bronchus. Scale 2:1

THE LUNG PROPER AND THE RUDIMENTARY LUNG

In snakes the anterior tip of the lung usually is found in the vicinity of the heart (Brongersma, 1951-a), as is the case with _N. sipedon_ (Fig. 12). The length of the lungs varies greatly; in some cases, _e.g._, _Distira cyanocincta_, they may even reach all the way to the cloaca (George and Varde, 1941; Thompson, 1914-b). In _N. sipedon_ the lungs grow posteriorly to approximately the end of the liver.

In any reptilian lung we may expect to find a clear separation into mechanical and respiratory parts (Wolf, 1933; Bolk, 1939). The respiratory part is that part which is alveolar and carries on the function of gas-exchange. The mechanical part is the posterior portion which is smooth and appears as a mere membranous sac. The respiratory part is usually found in the anterior one-third of the lung (Wolf, 1933), although both extremes may be found: some snakes, _e.g._, _Cylindrophis maculatus_ and _Cerberus rhynchops_, have the lung lined throughout with pulmonary tissue (Thompson, 1914-a), while others are lined with pulmonary tissue very scantily, _e.g._, _Causus rhombeatus_ (Thompson, 1914-b).

Its inner surface appears spongy and alveolar (Varde, 1951), and _e.g._, in _Tropidonotus natrix_, may contain a complicated

[illegible]

In [illegible] of the heart ([illegible]), [illegible]

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the way to the cloaca ([illegible]), [illegible].

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the posterior portion [illegible] smooth [illegible] were [illegible]

[illegible]

[illegible]

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[illegible], e.g., [illegible] ([illegible]).

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[illegible], e.g., [illegible]

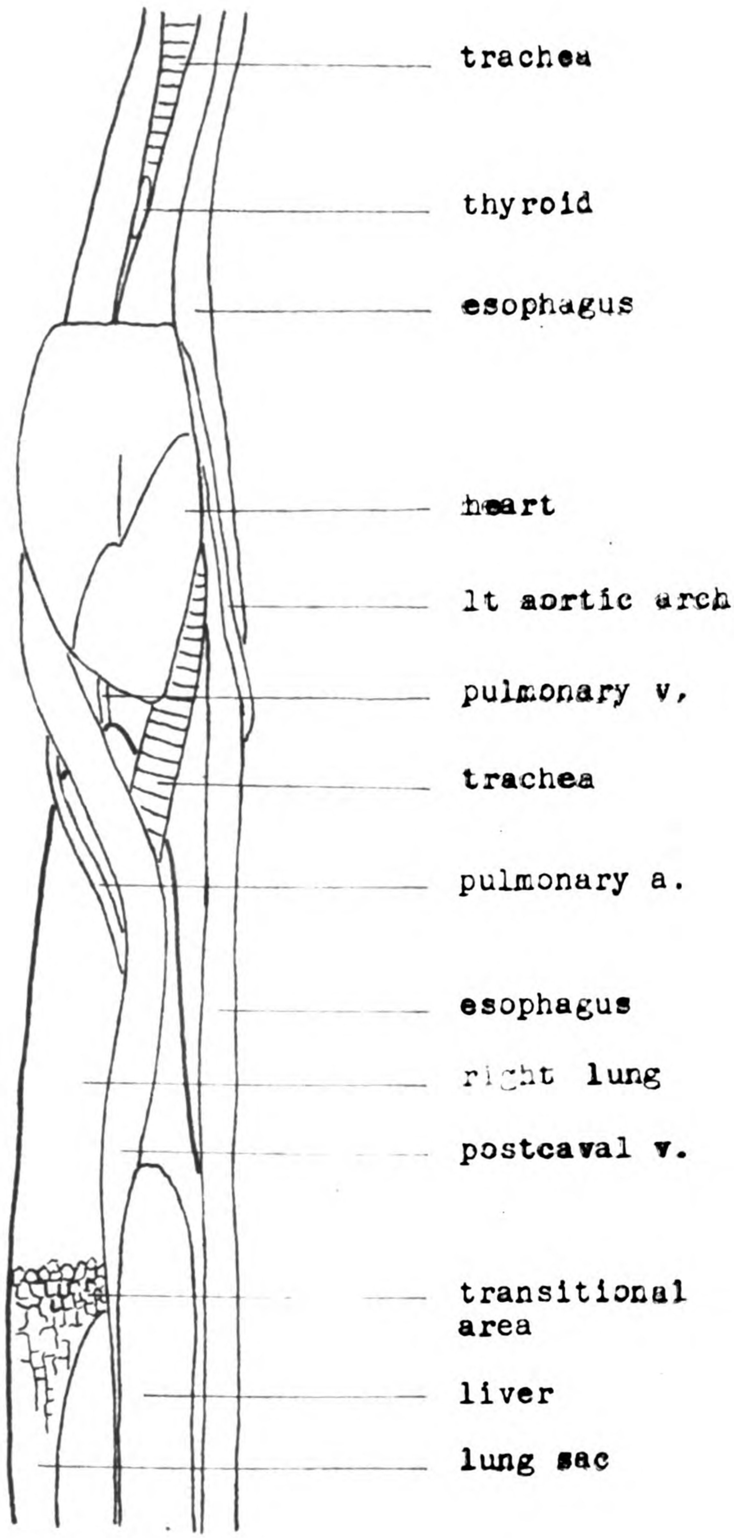

Fig.12. Ventral view of respiratory organs in relation to heart and liver. Scale 2:1

system of niches and crypts, which gives it a toadstool effect (Schmallhausen, 1905). These compartments are separated by partitions which grow perpendicular to the lung-wall to form, more or less, a honeycomb structure (Rothley, 1930). No lobes are found in the snake lung (Graeper, 1929). The development of alveoli in snake lungs shows great variety and ranges from primitive to complex (Varde, 1949). In N. sipedon the alveoli are polygonal in shape, varying from quadrangles to hexagons. They are from 0.5 to 2 mm. deep, depending on the size of the snake and the location in the lung. Particularly at the transition to the mechanical lung they tend to become shallow. There are approximately 250 to 300 alveoli per square cm. of surface area of lung tissue.

As mentioned above, in most snakes the trachea does not end immediately upon meeting the lung, but usually enters the lung a short way. In N. sipedon, however, the trachea ends as soon as it reaches the lung tissue. Ventrally, however, there is a narrow groove (Fig. 11), approximately one mm. wide, which is referred to as the intrapulmonary bronchus or intrapulmonary streak. This structure may be expected in all reptiles (Wolf, 1933), and has been found repeatedly in snakes (Bronn, 1890; Thompson, 1914-a and 1914-b), where it continues to the end of the alveolar tissue,

fans out and is lost in the membrane of the mechanical portion of the lung. This groove has longitudinal folds, and a few shallow alveoli. It seems to have the function of directing part of the air more directly to the posterior part of the lung (Wolf, 1933).

Because the trachea does not meet the lung at its most anterior part, an apex is formed anterior to the junction of these two organs (Thompson, 1913 and 1914-a; Attwood, 1916). Its inner surface is identical to that of the main part of the lung, and its communication with the latter is ample (Fig. 11 and 12). In some cases, e.g., Cylindrophis rufus, only a narrow tube connects the two (Thompson, 1914-a).

In N. sipedon (Fig. 12), as well as in other snakes, the transition from the alveolar to the mechanical part of the lung may be found at about the beginning of the liver (Graeper, 1929). The mechanical portion of the lung has no alveoli and appears as a smooth membrane, continuing along the liver at a uniform diameter, but narrowing down in the end. In some cases the mechanical portion gradually merges into the connective tissues of the body (Attwood, 1916). In some of the Viperidae the thoracic lung has been found to be completely devoid of alveoli (Beddard, 1906-b),

and the respiratory function is assumed entirely by the tracheal lung. In those specimens of N. sipedon where the posterior end of the mechanical part of the lung could be approximately determined, it was found to be almost an inch caudal to the posterior end of the liver. Thus the mechanical part exceeds the alveolar part in length.

Although the mechanical part of the lung is denied any function by some (Bolk, 1939), yet its usefulness as an air reservoir cannot be denied (Varde, 1951; Wolf, 1933; Graeper, 1929). This is supported by an experiment with a viper, Vipera berus, which showed that the stored air was sufficient for survival for 29 hours at 7.5 degrees centigrade, while at 29.5 degrees this air lasted for 1.5 hours (Suomalainen, 1939). This store of air is useful during feeding time, or for time spent under water. For marine species the buoyancy, which the mechanical lung affords, may also be significant.

The Pythons and Boas are known to have two lungs (George and Varde, 1941; Beddard, 1906-b), although the left one is invariably reduced in size. All other snakes have only one functional lung, i.e., the right one, while the left lung is [illegible] ached, it was found to be [illegible] part of length.

Although [illegible] part of the [illegible] by some (Wolk, 1939), yet the conditions [illegible] re [illegible] cannot be [illegible] 1939; Wolk, 1939; [illegible] 1937). This is supported by an [illegible] Bakke, who showed that the [illegible] survival for [illegible] hours at 7.5 degrees centigrade, while at 27.5 degrees it is [illegible] for 1.4 hours (centigrade, 1937). [illegible] is usual during [illegible] for the spore [illegible] species the [illegible] may also be significant.

The [illegible] have been [illegible] and Vardy, 1941; Haddard, 1950 [illegible] invariably reduced [illegible] fructi[illegible] i.e., [illegible] either completely absent or rudimentary (Attwood, 1916; Beddard, 1906-b; Varde, 1951; Bronn, 1890; Thompson, 1914-a; Cope, 1894; Butler, 1895; George and Varde, 1941). In those cases where the lung is rudimentary it lies perpendicular to the right lung (Bolk, 1939). The water-snake, N. sipedon, does have a rudimentary left lung (Fig. 13), measuring only 2 to 4 mm. in length. Although for practical purposes it is considered non-functional, in some snakes, including N. sipedon, the rudimentary lung does have alveoli and is highly vascular (Schmalhausen, 1905; Beddard, 1906-b). Its opening may be found as a tiny hole at the very end of the trachea. The growth of the left lung may be minimal, yet no regression occurs during development (Flint, 1906; Baumann, 1902). Although in the early studies there existed a difference of opinion as to whether the single lung of a snake was the right one or the left, Butler (1895) has found sufficient evidence to state clearly that the larger, or only lung, is the homologue of the right lung of other vertebrates.

THE RIBS

Reptiles have motile ribs to promote their breathing (Romer, 1956). In snakes the ribs are used not only for inhalation and exhalation of air, but also for the inner ventilation of the inhaled air between successive breaths. The pairs of ribs move independently of each other (Wolf, 1933; Bolk, 1939). It is considered to be beyond the scope of this work to determine precisely the contribution of the ribs to respiration.

THE BLOOD SUPPLY

Arterial

Since the bloodvascular system plays an essential part in the exchange of gases, it seems advisable to note briefly the main parts of the pulmonary circulation. The pulmonary artery leaves the right side of the ventricle dorsally and runs cranied to the anterior end of the heart. It turns at the right atrium and then runs posteriorly to enter upon the right side of the ventral surface of the lung and extends nearly to the end of this organ (Ray, 1934; Attwood, 1916; O'Donoghue, 1912; Kellicott, 1898). Usually the branches given off to the left side are larger than those given off to the right side. This was proven to be the case also in N. sipedon (Fig. 13). In many cases the tracheal lung may be supplied by a branch from the pulmonary artery (Brongersma, 1951-a and 1951-b; Beddard, 1906-a; Thompson, 1914-b). The posterior part of the lung may sometimes be supplied directly by branches from the dorsal aorta (Brongersma, 1952-b).

Venous

The pulmonary vein is found medial to the pulmonary artery (Fig. 13). It is imbedded ventrally in the lung tissue, and receives branches throughout the length of the lung. It then courses forward and upward to enter the heart on the posterior dorsal side of the left atrium (O'Donoghue, 1912; Ray, 1936; Attwood, 1916).

[illegible]

[illegible]

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the crests of gonad, it seems [illegible] to some [illegible]

ranch of the [illegible] artery [illegible]

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[illegible], 1941; [illegible], 1943. [illegible] the [illegible]

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many cases the stomach [illegible] may be supplied by a branch from the

pulmonary artery ([illegible], 1951-a and [illegible]; [illegible], [illegible];

[illegible], [illegible]). The posterior part of the lung may [illegible]

supplied directly by branches from the dorsal aorta ([illegible],

[illegible]).

[illegible]

The pulmonary vein is [illegible] to the pulmonary artery

(Fig. [illegible]). It [illegible] the lung [illegible], and [illegible]

[illegible] throughout the length of the lung. It [illegible]

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[illegible] ([illegible], 1915; [illegible], 1924; [illegible], 1 [illegible]).

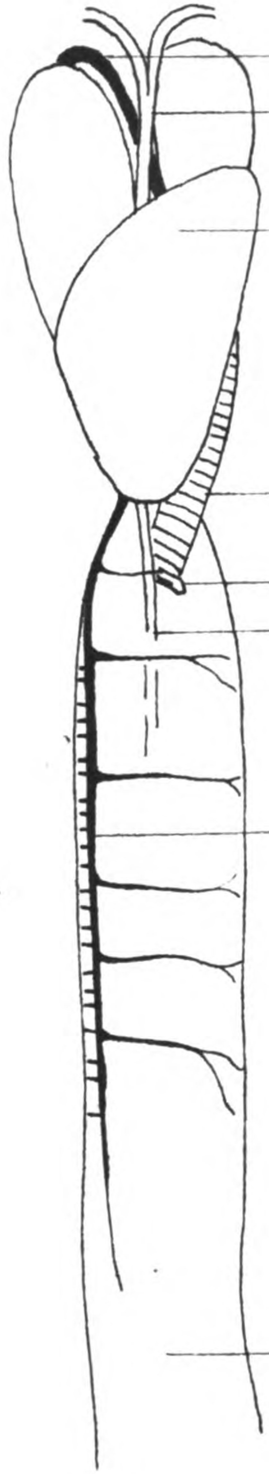

Fig. 13. Ventral view of heart and lungs, including blood vessels. Scale 2:1

SUMMARY

Natrix sipedon was considered a suitable species for studies of the respiratory anatomy of the snake. Preserved specimens were used.

The lung starts at about the 30th ventral scute. The respiratory part extends to about the 43rd ventral scute. The mechanical part continues a short distance beyond the caudal end of the liver.

The organs in the male snake lie more caudad than in the female.

The external and internal nares are easily identified. The vestibule is poorly developed. The concha is present, enlarging the surface area of the nasal cavity.

The trachea starts at the glottis, opposite the internal nares. The tracheal rings are incomplete from the glottis to the lung. A tracheal lung is present, but not greatly developed.

The developed right lung is separated into an alveolar and a mechanical part. An intrapulmonary bronchus is present. A free apex is formed at the anterior end of the lung. The left lung is rudimentary, but has alveoli and communicates with the posterior end of the trachea.

The ribs are movable in pairs, independently of each other. This enhances the inner ventilation.

The pulmonary artery lies on the ventral right side of the lung; its branches to the left side of the lung are larger than those to the right. The pulmonary vein is imbedded in the lung tissue until it emerges at the trachea. It empties into the posterior dorsal side of the left atrium.

Wherever N. sipedon could be compared with other species of snakes the results of this study indicated that the respiratory system of N. sipedon is representative of the Serpentes. In those instances where a structure was shown to be different from that in a certain other species, it usually proved to be the species in question, rather than N. sipedon, which showed the peculiarity.

No specific adaptations or distinctive structures could be found in the respiratory anatomy of N. sipedon to single it out as being better or less well adapted to its environment or to its mode of life.

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