

**Morphology of the Respiratory System  
and Its Musculature in Different Snake Genera  
(Part II) *Charina bottae***

By

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With 6 Figures and 1 Table

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**Larynx and Associated Structures<sup>1</sup>**

**Larynx (Fig. 12)**

Three major supportive elements may be identified in the larynx of *Charina bottae*, a pair of arytenoid cartilages and a single V-shaped cricoid cartilage. In union with the cricoid are several anterior remnants of tracheal rings.

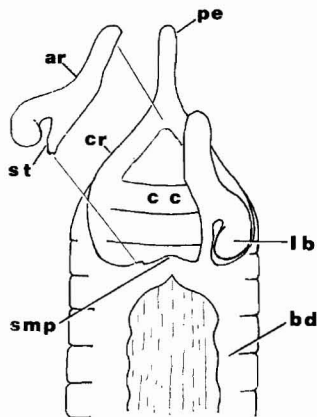
Positioned dorsally on the larynx, each arytenoid bears a lateral flange which attaches to the middle of each cartilage by means of a narrow stalk. The flange is bulbular in shape and provides an area of attachment for various slips of the intrinsic laryngeal musculature. Embedded in muscle and connective tissue, each arytenoid cartilage lies lengthwise in the opening to the trachea and hence defines the edges of the slit-like glottis. The slender caudal tip of the arytenoid attaches to the posterior margin of the larynx, formed by the cricoid and associated cartilage elements.

The anterior convergence of the sides of the V-shaped cricoid cartilage bears a forward directed process, the processus epiglotticus. In *Crotalus viridis* and *Elaphe obsoleta* the processus epiglotticus is a short prominence on the apex of the cricoid, whereas in *Charina bottae* it is an elongate dorso-ventrally flattened bar which serves as an area of attachment for intrinsic laryngeal muscles and also supports the anterior connective tissue lips of the glottis.

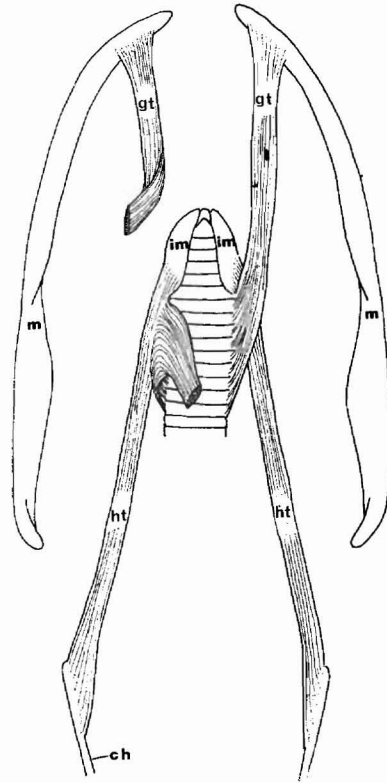
The sides of the cricoid extend caudally, diverging from one another to form the lateral edges of the larynx. Three cartilaginous elements, derived from ventral sections

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<sup>1</sup> For Introduction, Materials and Methods, Synonymy and Abbreviations see part I in this Journal vol. **117** (1972) page 285.



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Fig. 12. *Charina bottae*. Dorsal view of larynx and first part of glottal tube with left arytenoid (ar) displaced from its union with the larynx

Fig. 13. *Charina bottae*. Ventral view of lower jaws with superficial musculature removed to expose extrinsic laryngeal musculature; right *M. genio-trachealis* (gt) deflected

of anterior tracheal supportive rings, join the two sides of the cricoid and constitute the rounded ventral floor of the larynx. A V-shaped cartilage arch, which joins the two posterior tips of the cricoid, bears on its mid-dorsal rim a forward directed prominence, the superior median process. This process and its V-shaped cartilage arch provide a surface from which arises the intrinsic muscle, *sphinctor laryngis*.

#### Glottal Tube (Fig. 12, 15)

The glottal tube is a unit of mutually fused elements of the trachea and larynx. It is composed specifically of the cricoid, the supporting arch of the superior median process, and twelve tracheal rings or their derivatives. The first three tracheal derivatives support the floor of the larynx and cross-connect the two sides of the cricoid. The next successive series of nine C-shaped rings fuse at their tips to form two linking bridges of hyaline cartilage along each dorso-lateral side of the trachea. To these

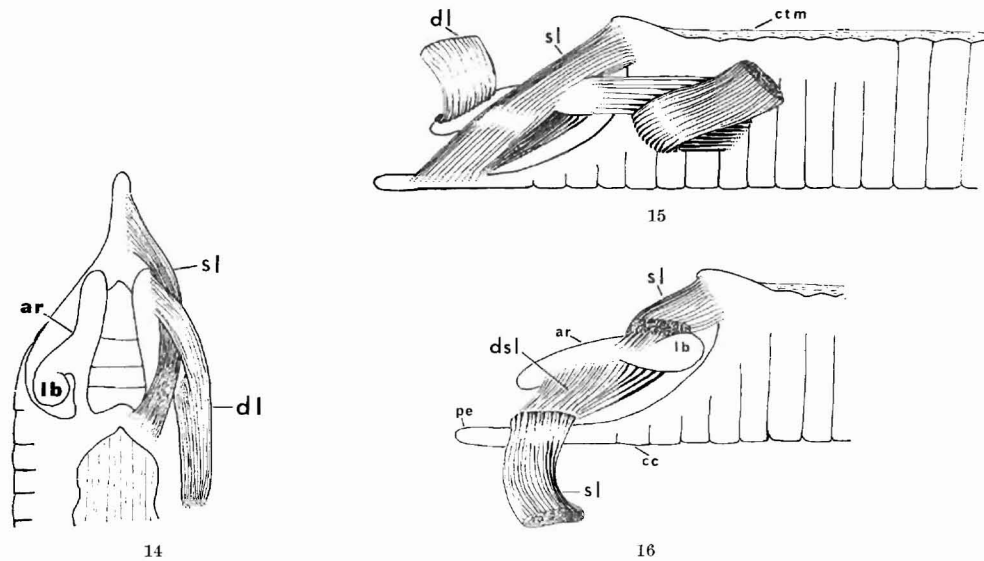


Fig. 14. *Charina bottae*. Dorsal view of intrinsic laryngeal musculature with muscles of left side removed to show arytenoid cartilage (ar) and its lateral bulbular flange (lb)

Fig. 15. *Charina bottae*. Lateral view of intrinsic laryngeal musculature; *M. dilatator laryngis* (dl) has been cut and deflected to expose *M. sphinctor laryngis* (sl)

Fig. 16. *Charina bottae*. Lateral view of *M. sphinctor laryngis* (sl) with some of superficial fibers peeled down to expose deep fibers of *sphinctor laryngis* (dsl); *M. dilatator laryngis* has been completely removed

bridges are joined the two respective posterior tips of the ericoid and the supporting arch of the superior median process.

#### Extrinsic Musculature

##### *M. genio-trachealis* (gt)

(Fig. 13)

As in the other two species examined, the *genio-trachealis* takes origin along the ventral inside margin of the mandible where the anterior tip of the dentary curves mesad to the symphyseal joint. The *genio-trachealis* courses caudally as a flattened ribbon of muscle, passes ventral to *hyo-trachealis*, and inserts on the lateral surface of the seventh through the fifteenth tracheal cartilages.

##### *M. hyo-trachealis* (ht)

(Fig. 13)

Of smaller girth than *genio-trachealis*, *hyo-trachealis* takes origin from the hyoid and surrounding connective tissue. Its direction is forward and mesad across the ventral floor of the buccal cavity. It inserts in the fascia of the intrinsic laryngeal musculature on the lateral side of the larynx, immediately anterior to the point of insertion of *genio-trachealis*.

*M. protractor laryngeus* (pl)

This muscle – present in *Crotalus viridis* and *Elaphe obsoleta* – is absent in *Charina*. KARLSTROM (1952), first to report the presence of this muscle in certain colubrid snake species, also stated that it was not present in a specimen of *Charina bottae* which he examined.

## Intrinsic Musculature

*M. sphinctor laryngis* (sl)

(Fig. 14, 15, 16)

This muscle is composed of superficial and deep fibers. Both arise from the dorsal surface of the superior median process and its supporting arch and extend forward over the narrow stalk of the lateral flange of the arytenoid cartilage. The deep fibers of *sphinctor laryngis* insert on the anterior and posterior margins of the stalk of this bulbular flange. The superficial fibers do not insert here, but continue forward, descending into the ventral position below the anterior tip of the arytenoid cartilage, and attach along the lateral sides of the processus epiglotticus. Deep fibers of *sphinctor laryngis* also develop ventrally beneath the arytenoid and run to the cricoid cartilage. These deep fibers form a thin slip of muscle which takes origin from the processus epiglotticus and cricoid cartilage, and inserts along the anterior lower edge of the arytenoid and its lateral flange.

GÖPPERT (1899) identifies a muscle lying dorsal to the arytenoid cartilage, *M. laryngis dorsalis*, and a muscle mass occupying a position below the arytenoid cartilage, *M. laryngis ventralis*. Collectively, these muscles are comparable to the total muscle described above as *M. sphinctor laryngis*.

*M. dilatator laryngis* (dl)

(Fig. 14, 15)

The lateral side of the anterior trachea is covered by a wide sheet of parallel muscle fibers, *dilatator laryngis*. The first fibers of this sheet take origin on the seventh tracheal cartilage, immediately forward from the anterior points of insertion of the extrinsic muscle, *genio-trachealis*. Additional fibers contribute to *dilatator laryngis* as it continues cranial toward the larynx. Its dorsal fibers insert on the expanded lateral flange of the arytenoid along the ventral and posterior surfaces. The ventral fibers of *dilatator laryngis* progress dorsally over the anterior end of *sphinctor laryngis* to insert on the anterior half of the arytenoid cartilage.

## Trachea

The tracheal wall is supported by incomplete, U-shaped cartilaginous rings. The open edges of the tracheal wall form a continuous slit along the length of the trachea. The open edges are joined across the space of this slit by a connective tissue membrane. Shortly past the angle of the jaws this connective tissue membrane moves from a mid-dorsal to a lateral position on the right side of the trachea. At the posterior tip of the ventricle, the trachea widens slightly and three of its supportive rings

mutually join through interconnecting cartilaginous bridges. Caudal to this widening, the trachea bifurcates to provide a pair of bronchi for the passage of respired air.

The left lateral bronchus resulting from this bifurcation is very short, and is composed of three complete tracheal rings. This bronchus penetrates the respiratory tissue of the left lung and terminates immediately, thus serving as a conduit between the lumen of the lung and the trachea.

The second bronchus resulting from the bifurcation of the trachea penetrates the pulmonary tissue of the right lung. This bronchus does not terminate but proceeds caudally (21 cartilaginous rings) becoming progressively more embedded within the lung tissue. The cartilaginous supports of the bronchus flatten to form a "trough" which passes along the lumen within the respiratory tissue of the right lung.

#### Lungs (Fig. 17)

As implied in the discussion of the trachea, *Charina* possesses two rather well developed lungs. However, the two are not of comparable size or vascularization. The left lung is about one-third the length of the more extensive right lung. The difference in size between the two lungs is reflected in the pulmonary arteries supplying them. Each lung is separately supplied by a pulmonary artery, the right pulmonary artery measures about twice the calibre of the left.

The anterior half of each lung is heavily vascularized, feeling spongy to the touch. This vascularization diminishes as the more posterior regions of the lung are reached. As in *Crotalus* and *Elaphe*, the honey-comb texture lining the lumen of each lung is formed by a network of smooth muscles. This network becomes less evident near the caudal portion of right and left lungs, so that the saccular terminal end of each respective lung is characterized by a predominance of fibrous connective tissue impregnated with a weakly discernable honey-comb network. Hence, the lungs of *Charina* exhibit

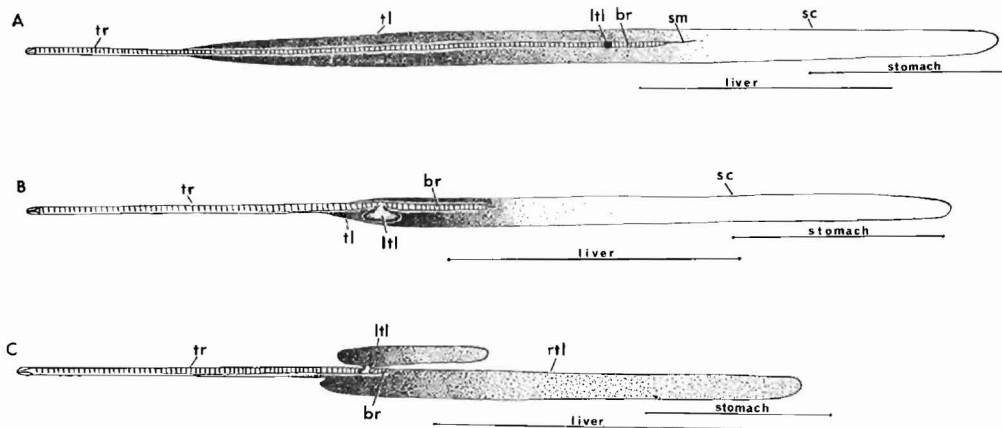


Fig. 17. Diagrammatic representation of lungs and tracheae of *Crotalus viridis* (A), *Elaphe obsoleta* (B), and *Charina bottae* (C); the lengths and positions of the stomachs and livers are indicated; distribution and concentration of vascular tissue is represented by stippling; the proportions of the three lungs are drawn as if the three species were of equal snout-to-vent length

a gradient of texture, reflecting a progressive change in the extent of vascularization. Proceeding from anterior to posterior, the spongy and vascularized tissue diminishes in prominence so that toward their caudal terminations the lungs tend to be saccular and very poorly supplied with blood vessels.

Both lungs have extensions of respiratory tissue which reach a short distance forward from the tracheal bifurcation. In the left lung this forward extension is a diverticulum projecting cranial for a distance of about 8 mm along the left lateral side of the trachea.

In the right lung, however, the forward extension of pulmonary tissue arises not from a diverticulum, but develops as a short (6 mm) investment of the tracheal membrane with spongy vascularized tissue. Because this short expanse of respiratory tissue forms in the tracheal membrane, it is considered to be an incipient tracheal lung.

#### Vascularization

A pair of aortic arches originate individually on the base of the ventricle, course forward between the atria, and turn caudally to join near the posterior region of the heart. Unlike *Crotalus viridis* and *Elaphe obsoleta*, *Charina bottae* possesses two carotid arteries which supply the anterior portion of the snake, including the trachea and its connective tissue membrane. The two carotids branch from the right aortic arch as it bends posteriad around the anterior tip of the right atrium. Further along its course the right aortic arch sends off a forward projecting vertebral artery.

The common jugular, precava, and postcava collectively contribute to the sinus venosus situated on the right atrium.

The pulmonary artery arises as a single trunk from the base of the ventricle, dorsal to the two systemic arches. It soon bifurcates sending one branch to each lung. The branch to the right lung curves posterior and dorsad to come into immediate contact with the surface of the lung. It proceeds along the ventral surface of the lung sending lateral branches first to the tracheal lung, then distributes to the remainder of the right lung's respiratory tissue. One lateral branch of the right pulmonary artery even runs over the tracheal bifurcation to supply the left lung. The left pulmonary artery likewise turns caudad and dorsad to immediately come into contact with respiratory tissue. It supplies lateral branches first to the pulmonary diverticulum, then continues posteriorly along the ventral surface of the left lung to supply the remaining respiratory tissue.

The single pulmonary vein begins in the posterior region of the right lung. It runs forward along the ventral surface of the lung medial to the pulmonary artery, receiving venous tributaries emerging from the respiratory tissue. As the pulmonary vein reaches an anterior level in the vicinity of the tracheal bifurcation, it receives three or four prominent veins which drain the left lung. The pulmonary vein then curves ventrally away from the surface of the lung and enters the left atrium.

## Discussion

Before drawing comparisons among the three species, a word is in order about variety of lung morphologies within their respective taxonomic families. Table 1, compiled from my own dissections and literature reports, summarizes information on the lungs of boid, colubrid, and viperid snakes. BRONGERSMA (1951a) stated that "all but two genera of the Boidae have two well developed lungs" – *Tropidophis* and *Trachyboa*. More recently *Ungaliophis* has been reported to have a vestigial left lung

Table 1  
Gross Lung Morphology

Species	× – Indicates presence of feature				Source
	Two well-developed lungs	Vestigial left lung	One lung	Extensive tracheal lung	
<b>BOIDAE</b>					
<i>Eryx conicus</i>	×				Dissection
<i>Eryx johni</i>	×				Dissection
<i>Charina bottae</i>	×				Dissection
<i>Boa constrictor</i>	×				Dissection
<i>Python regius</i>	×				Cope, 1898
<i>Python molurus</i>	×				Cope, 1898
<i>Morelia argus</i>	×				Butler, 1895 Cope, 1898 Butler, 1895 Brongersma, 1951 b
<i>Epicrates cenchria</i>	×				Cope, 1898 Butler, 1895
<i>Candoia carinata</i>	×				Butler, 1895 Brongersma, 1951 b
<i>Python curtus</i>	×				Brongersma, 1951 b
<i>Python sebae</i>	×				Brongersma, 1951 b
<i>Acrantophis madagascariensis</i>	×				Brongersma, 1951 b
<i>Eryx jaculus</i>	×				Brongersma, 1951 b
<i>Liasis amethystinus</i>	×				Brongersma, 1951 b
<i>Liasis mackloti</i>	×				Brongersma, 1951 b
<i>Corallus carinus</i>	×				Brongersma, 1951 b
<i>Corallus enhydris</i>	×				Brongersma, 1951 b
<i>Candoia asper</i>	×				Brongersma, 1951 b
<i>Python reticulatus</i>	×				Butler, 1895
<i>Tropidophis melanurus</i>			×	×	Brongersma, 1951 b
<i>Trachyboa gularis</i>			×	×	Brongersma, 1951 b
<i>Ungaliophis panamensis</i>		×		×	Butner, 1963
<b>COLUBRIDAE</b>					
<i>Thamnophis sirtalis</i>		×		very short	Dissection
<i>Natrix sipedon</i>		×		very short	Dissection
<i>Dryophis nasuta</i>		×			Dissection

Species	× – Indicates presence of feature				Source
	Two well-developed lungs	Vestigial left lung	One lung	Extensive tracheal lung	
<i>Hypsiglena torquata</i>			×	×	Dissection
<i>Natrix rhombifera</i>		×		very short	Dissection
<i>Rhinocheilus lecontei</i>			×		Dissection
<i>Masticophis flagellum</i>		×			Dissection
<i>Lampropeltis getulus</i>			×		Dissection
<i>Lampropeltis calligaster</i>			×		Dissection
<i>Tantilla nigriceps</i>			×	×	Dissection
<i>Elaphe obsoleta</i>		×		very short	Dissection
<i>Coluber constrictor</i>		×		very short	Dissection
<i>Arizona elegans</i>			×		Dissection
<i>Heterodon platyrhinus</i>		×		short	Dissection
<i>Chemophora coccinea</i>		×			Dissection
<i>Pituophis melanuleucus</i>			×	very short	Dissection
<i>Elaphe radiata</i>		×			Brongersma, 1951 b
<i>Natrix taxispilota</i>		×			Karlstrom, 1952
<i>Dendrophis pictus</i>		×			Butler, 1895
<i>Natrix natrix</i>		×			Butler, 1895
<i>Coluber longissimus</i>		×			Butler, 1895
<b>VIPERIDAE</b>					
<i>Crotalus cerastes</i>			×	×	Dissection
<i>Crotalus viridis</i>			×	×	Dissection
<i>Crotalus horridus</i>		×		×	Dissection: Butler, 1895
<i>Bothrops pictus</i>		×		×	Cope, 1898
<i>Bothrops enythrurus</i>		×		×	Cope, 1898
<i>Agkistrodon contortrix</i>		×		×	Cope, 1898
<i>Bothrops lanceolatus</i>			×	×	Cope, 1898
<i>Agkistrodon piscivorus</i>			×	×	Cope, 1898
<i>Sistrurus catenatus</i>			×	×	Cope, 1898
<i>Crotalus adamteus</i>			×	×	Cope, 1898 Butler, 1895 Klauber, 1956
<i>Crotalus durissus</i>		usually		×	Brongersma, 1951 b Butler, 1895 Klauber, 1956
<i>Trimeresurus wagleri</i>		×		×	Brongersma, 1951 b
<i>Crotalus basiliscus</i>		×		×	Klauber, 1956
<i>Crotalus molossus</i>		×		×	Klauber, 1956
<i>Crotalus enyo</i>			usually	×	Klauber, 1956
<i>Crotalus exsul</i>			usually	×	Klauber, 1956
<i>Vipera berus</i>			×	×	Butler, 1895
<i>Vipera aspis</i>			×	×	Butler, 1895
<i>Crotalus lepidus</i>			usually	×	Klauber, 1956
<i>Crotalus intermedius</i>			×	×	Klauber, 1956



and prominent tracheal lung (BUTNER 1963). Typically, however, the left lung in boids, though smaller than the right, is prominent and well invested with vascular tissue. A very short stretch of vascular tissue may extend along the trachea, but the extensive tracheal lung common to some other families is not a characteristic feature of the boid lung.

A variety of pulmonary structures and arrangements exist in colubrids. The tracheal lung may be a prominent expanse of respiratory tissue, weakly developed, or absent completely. The left lung is either present as a diminutive rudimentary lung or lost entirely. A lung sac is usually present and a pulmonary diverticulum may be present or absent. No single species could be expected to show this variety of lung conditions. In this paper, specific attention is given to the respiratory system of *Elaphe obsoleta quadrivittata* because its lung is anatomically intermediate between the lungs of boids and viperids.

An extensive tracheal lung and a long avascular lung sac characterize viperid snakes. The left lung is always lost completely or reduced to a rudimentary lung. *Crotalus viridis oreganus* is seen to display a greater degree of lung modification than can be found in either *Charina*<sup>1</sup> or *Elaphe*<sup>2</sup>. Consequently, it is a convenient species by which to show the marked degree of possible lung modifications.

On the basis of gross lung morphology, the three species described in this paper represent three distinct pulmonary types. A comparison of these three structural types discloses several anatomical differences. First, the predominance of the left lung varies among the three species. In *Crotalus*, the left lung is represented by a very diminutive cap of cartilage. Various authors (COPE 1894, BEDDARD 1906, THOMPSON 1914, VARDE 1951, BELLAIRS and UNDERWOOD 1951) have remarked that in certain viperid snakes there are in fact no remnants of the left lung. In *Elaphe*, the left lung is present as a small vascularized sac on the predominant right lung (see Fig. 17 B). The left lung of *Charina* constitutes a well developed vascular lung about one-third the length of the right lung.

Most extant lizards possess two lungs of almost equal length and vascularization; thus the lizard ancestor(s) from which snakes evolved, most likely, possessed a pair of well-developed lungs. But all three species of snakes described here show some degree of lung inequality.

KLAUBER (1956) speculated that the attenuated shape of the ophidian body was a factor favoring decrease in size of the left lung. In legless lizards (COPE 1894) and amphisbaenids (BUTLER 1895) one lung, in the attenuated bodies of these reptiles, is shorter than the other. Such instances of parallelism tend to support KLAUBER's proposal. Furthermore, BERGMAN (1950) found that other paired visceral organs (kidneys, gonads) also show inequality in width and length. However, the hypothesis

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<sup>1</sup> Throughout the discussion and summary sections, the species *Charina bottae*, *Elaphe obsoleta quadrivittata*, and *Crotalus viridis oreganus* are referred to simply as *Charina*, *Elaphe*, and *Crotalus* respectively.

<sup>2</sup> Some of the older scientific names have been changed to conform to most recently accepted taxonomic nomenclature.

posed by KLAUBER is at best too general, for it does not suggest what specific factors, mechanical or otherwise, are involved in the alteration of lung structure.

BUTLER (1895) suggested that a correlation exists between asymmetry of the stomach and asymmetry of other organs, and that the "first cause of inequality" of the lungs may have been the displacement of the stomach to the left. Stomach displacement may, perhaps, be the first cause of lung inequality, but what is the subsequent cause of lung reduction in say *Elaphe* or *Crotalus*? No satisfying answer, supported by experimental work, exists for this question.

Factors discussed above may be important in the evolution of the situation in viperids, or alternatively the Viperidae may have evolved from ancestors possessing a reduced left lung and a well developed right lung which efficiently served the animal's metabolic requirements. A respiratory system so suited to the attenuated body form may have been under no selective pressure to revert to a paired lung condition. Regardless of how one views changes in lung inequality, the basic factors favoring reduction of one lung are incompletely understood, because no hypothesis accounts for the extreme degree to which selection has acted to reduce one lung.

A second anatomical difference among the three structural types is the loss of the left pulmonary artery. BRONGERSMA (1951 b) noted that in the Boidae there was an increasing tendency for the right pulmonary to assume responsibility for the transport of blood to the left lung. In *Elaphe*, the left pulmonary artery has been lost and the vascular supply to the diminutive left lung is provided by the remaining (right) pulmonary artery.

The third morphological feature of notable comparison concerns the relative length of the lungs. In Figure 17, the three lungs are drawn as if they were measured from specimens of equal snout-to-vent length. The right lung does not extend as far posteriorly in *Charina* as in the other two species. The left lung, small in *Elaphe* and absent in *Crotalus*, is of less assistance in external respiration than in the boid, *Charina*. The relatively long right lungs of *Elaphe* and *Crotalus* possibly represent a compensation for the reduced left lungs.

Finally, a comparison of the three structural types reveals one other notable difference – the position of the respiratory tissue. In *Charina*, the respiratory tissue is located posterior to the heart and is distributed in a diminishing degree through the caudal regions of the tubular lung. In *Elaphe*, the respiratory tissue does not extend to the posterior end of the lung as in *Charina*, but is concentrated immediately dorsal to and behind the heart. In *Crotalus*, this area has developed forward of the heart to form the extensive tracheal lung of the neck and thorax.

Several workers have attempted to account for this craniad migration of respiratory tissue. THOMPSON (1913) suggested that venom production required a large liver which "crowded" the pulmonary tissue that would then "seek the direction of least resistance which is [forward] along the tracheal membrane" (pp. 414–415). This explanation does not, however, account for the anterior location of respiratory tissue in such non-venomous species as *Elaphe obsoleta*, *Heterodon platyrhinus*, (BUTLER 1895), and *Coluber corais* (= *Drymarchon corais*), (BEDDARD 1906).

COPE (1894) proposed that the presence of large food items may exert pressure on the lung and hence an anterior position of respiratory tissue would be favored. The passage of food along the esophagus does press against respiratory lung tissue; however, the time taken by most snakes to swallow prey is a matter of minutes, whereas the retention of prey in the stomach may last for several days. It thus seems more likely that the position of the stomach has a greater effect on placement of respiratory tissue than does swallowing. In *Charina*, the stomach impinges on only the most posterior portion of the right lung; in *Elaphe* and *Crotalus* the stomach, situated caudally, overlaps none of the spongy tissue of the right lung. In *Crotalus*, the tracheal lung extends well forward to the throat almost to the floor of the mouth. But, in *Elaphe* the vascular pulmonary tissue ventures only a brief distance forward as a short tracheal lung. Overlapping and interference with the stomach may establish the posterior boundary for the respiratory tissue, however, COPE's hypothesis does not explain why the tracheal lung of *Elaphe* is only a short extension anterad while the tracheal lung of *Crotalus* extends forward nearly to the floor of the pharynx. Nor does it account for the variety of conditions in Colubridae where the tracheal lung may be extensive (e. g. *Hypsiglena torquata*), mildly developed (e. g. *Natrix sipedon*), or absent (e. g. *Masticophis flagellum*).

#### Summary

The detailed gross morphology of the respiratory system and associated muscles for three species of snakes (*Charina bottae*, *Elaphe obsoleta quadrivittata*, *Crotalus viridis oreganus*) is examined. For each species the larynx, intrinsic and extrinsic musculature, trachea, and particulars of lung modification and structure are described and discussed.

Found in *Charina*, *Elaphe*, and *Crotalus* are three distinct lung morphologies. To facilitate comparison, these three lung types can be arranged into an anatomical series running from *Charina* to *Elaphe* to *Crotalus*. Within this anatomical series, several changes in lung proportions and vascularization occur:

1. The left lung tends to be reduced in size. In *Charina*, it is about  $\frac{1}{3}$  the length of the right lung. In *Elaphe*, it is much smaller and in *Crotalus* almost completely absent save for a small vestigial cap of cartilage and connective tissue.
2. Accompanying reduction of the left lung is the loss of the left pulmonary artery. It is present in *Charina*, but absent in both *Elaphe* and *Crotalus*.
3. Attendant with the reduction of the left lung is the lengthening of the right lung. The right lungs of both *Elaphe* and *Crotalus* are long perhaps to compensate for the reduction in tidal volume resulting from reduction and loss of the left lung.
4. Another notable difference in the lung morphologies of these three species is the position and concentration of vascular tissue. In *Charina*, the pulmonary tissue begins in the vicinity of the heart and distributes posteriorly in a progressively decreasing amount along the lung. In *Elaphe*, the respiratory tissue concentrates in that part of the lung near the heart whereas in *Crotalus* most of the respiratory tissue

extends forward from the heart as the tracheal lung. Thus, in this anatomical series, the spongy respiratory tissue tends toward a more forward position along the lung.

Several hypotheses are discussed which attempt to account for these various conditions.

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