SOME REMARKS ON THE PULMONARY ARTERY IN SNAKES WITH TWO LUNGS

by

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With 9 plates and 1 text-figure

The respiratory organs of snakes show a great diversity according to genera and species. In the Boidae (two genera excepted; cf. Brongersma, 1951 *a* and 1951 *b*), and in *Xenopeltis unicolor* (Reinw.) both lungs are well developed, although the left is shorter than the right (Butler, 1895). The difference in length between the right and the left lung is not the same in all genera and species, but it also shows individual variations within the species. In the Anilidae the left lung has undergone further reduction than in the Boidae; in *Cylindrophis rufus* (Laur.) the left lung is still rather well developed, its length is 12% of that of the right lung; in *Anilius scytale* (L.) the left lung is rudimentary, its length being only 3.5% of that of the right lung; in *Anomochilus weberi* (Lidth) the left lung has disappeared completely (Brongersma & Helle, 1951). Among the Colubridae, Elapidae, and Viperidae a rudimentary left lung is present in some species, while it has disappeared in others. A rudimentary left lung is present in the following species examined by me: *Elaphe radiata* (Schleg.) and *Elaphe flavolineata* (Schleg.) (Colubridae), *Bungarus candidus* (L.) and *Bungarus fasciatus* (Schn.) (Elapidae), *Crotalus durissus* L. and *Trimeresurus wagleri* (Boie). The diagram in fig. 1 shows the relative length of the left lung in a number of species of Boidae, Anilidae, and in *Xenopeltis unicolor* (Reinw.). It must be remembered that these diagrams are based on measurements taken from preserved specimens; therefore, the values found are only approximately correct.

Differences according to genera and species also exist in the structure of the lungs, e.g., with regard to the area of the internal wall that is alveolar, and the development of a smooth-walled anangious air-sac at the caudal end of the lung.

Several authors (e. g., Wolf, 1933) have referred to these differences in the lungs, but it is remarkable that hardly any attention has been paid to the ramifications of the pulmonary artery. These ramifications show peculiarities in which snakes with two lungs differ from other Amniotes with two lungs.

In Amniotes that have two well developed lungs the usual situation with regard to the pulmonary artery is as follows. The pulmonary artery arises from the ventricle as a single pulmonary trunk, which divides into two branches: the ramus dexter or right pulmonary artery that goes to the right lung, and the ramus sinister or left pulmonary artery that passes to the left lung. With regard to these two rami two points must be stressed: 1. The

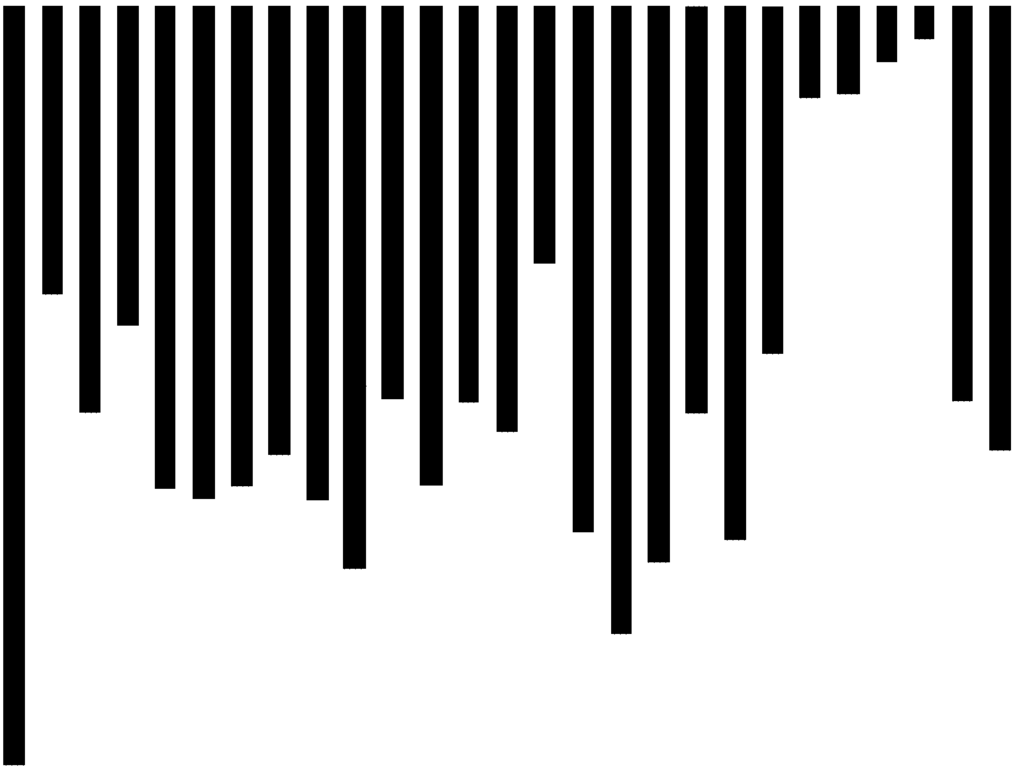

Fig. 1. Diagrams showing the relative length of the left lung as compared to that of the right lung. *a*, length of right lung as standard length; *b, Botrochilus boa* (Schleg.); *c, Liasis amethistinus amethistinus* (Schn.); *d, Liasis mackloti mackloti* Dum. & Bibr.; *e, Python molurus molurus* (L.); *f, Python molurus bivittatus* Kuhl; *g, Python curtus brongersmai* Stull; *h, Python regius* (Shaw); *i, Python sebae* (Gmel.); *j, Chondropython viridis* (Schleg.); *k, l, Morelia argus* (L.); *m, Calabaria reinhardtii* (Schleg.); *n, Epicrates cenchria cenchria* (L.); *o, Enygrus bibroni bibroni* Hombr. & Jacq.; *p, q, Eunectes scytale* (L.), foetuses; r, *Eunectes scytale* (L.), ♀; *s, Constrictor constrictor constrictor* (L.), juv.; *t, Constrictor constrictor occidentalis* (Phil.); *u, Eryx jaculus jaculus* (L.); *v, Cylindrophis rufus* (Laur.); *w, Cylindrophis isolepis* Blgr.; *x, Cylindrophis boulengeri* Roux; *y, Anilius scytale* (L.); *z, Xenopeltis unicolor* (Reinw.), ♂; *z', Xenopeltis unicolor* (Reinw.), ♀.

ramifications of the right pulmonary artery remain within the right lung, just as those of the left pulmonary artery are confined to the left lung. 2. Except for their origin from a common trunk, the right and left pulmonary arteries have no connexion whatsoever with one another.

Snakes with two lungs differ from other Amniotes in the first point. In the Boidae, Anilidae, Xenopeltidae, Colubridae, and Elapidae, that have two lungs, one or more branches of the right pulmonary artery send ramifications to the left lung, even in those species in which the left pulmonary artery is present. Moreover, in a number of Boidae, in the Anilidae, and in *Xenopeltis unicolor* (Reinw.) anastomoses exist between the system of the right pulmonary artery and that of the left pulmonary artery.

The fact that branches of the right pulmonary artery pass to the left lung has been mentioned already by Meckel (1831, p. 259). This author states that in snakes with two lungs (species not mentioned) the left pulmonary artery is restricted to the anterior half of the left lung; the right pulmonary artery first gives off a branch that supplies only the ventral surface of the right lung, while farther posteriorly branches cross to the mesial surface of the left lung, along which they run caudad, giving off ramifications to that wall. As will be shown in the descriptions of the specimens examined by me, the situation often is much more complicated than that described by Meckel.

Jacquart (1855, Pl. 9 fig. 1) figured one branch that crosses from the right to the left lung; this branch is mentioned in the explanation of the plate (l.c., p. 355; nos. 71, 73), but no mention is made of it in the text of his paper. The specimen dissected by Jacquart was a "python molure"; from this name one would suppose it to have been a specimen of *Python molurus* (L.), but according to Beddard (1906, p. 27) the specimen belongs to *Python sebae* (Gmel.). The branches of the right pulmonary artery that pass to the left lung are not mentioned by Hoffmann (1885-1886) in his survey of ophidian anatomy, nor are they mentioned in recent treatises on comparative anatomy.

As far as I am aware, anastomoses between the right and left pulmonary arteries have not been mentioned in literature. I believe, however, that such an anastomosis has been indicated in *Constrictor constrictor* (L.) by Jacquart (1864, Pl. XII: *Boa constrictor*) in a paper on the pneumo-gastric nerve.

My attention was drawn to these anastomoses when I noticed that the Indian ink injected into the right pulmonary artery of a specimen of *Python reticulatus* (Schn.) also filled the caudal part of the left pulmonary artery. The present study was undertaken to check whether branches passing from the right pulmonary artery to the left lung and anastomoses between the right and left pulmonary arteries are of common occurrence in snakes that possess two lungs. To this purpose I examined 79 specimens belonging to 35 species and subspecies of Boidae (representing 16 genera out of the 21 that have two lungs), 6 specimens belonging to 5 species of Anilidae (representing the 2 genera with two lungs), and 4 specimens of *Xenopeltis unicolor* (Reinw.) (the only species of the Xenopeltidae). The study was extended to include some species of the Colubridae, Elapidae, and Viperidae, in all of which the left lung is rudimentary. The species and subspecies examined by me are enumerated in the list given on pp. 7-8.

For comparison I examined three species of lizards with a snake-like body, viz., *Anguis fragilis* L. (Anguidae), *Monopeltis capensis* Smith and *Trogonophis wiegmanni* Kaup (Amphisbaenidae). In these lizards the ramifications of the right and left pulmonary arteries are confined to the right and left lungs respectively.

Before passing to the descriptions some attention must be paid to the position of the lungs, the heart, and the liver.

Snakes never have long external bronchi. Of many species it may be said that the trachea at its caudal end opens into the two lungs without discernable external bronchi being formed. Hence the lungs are placed close to one another. Just caudad of the point where the trachea opens into the lungs, the mesial walls of the lungs are firmly united. Somewhat more posteriorly the mesial walls are still in contact; here they are connected to each other by loose connective tissue. In the region of the liver the lungs are separated from one another by the dorsal mesentery of the liver. As the anteriormost hepatic artery and the anteriormost affluent branch of the portal vein reach the liver somewhat caudad of the latter's anterior tip, the region of contact between the lungs may extend caudad just beyond the anterior end of the liver. Roughly speaking it may be said that the lungs are in contact over a distance that extends from the apex of the heart to the cranial tip of the liver. In this region branches of the right pulmonary artery send ramifications to the left lung. The interval between the heart and the liver is extremely small in some species, while it is large in others. Moreover, the length of the interval is subject to individual variation, and it may also change with age. It might be supposed that the number of branches that send ramifications to the left lung will be higher in species with a large interval than in those with a small interval. However, this is not always the case. There are species with a large interval, but which show only a few branches that cross to the left lung. Every species shows a more or less characteristical pattern, which may be subject to rather wide variations.

In most species the right lung is not only longer than the left, but it also has a greater diameter. In these species the right lung may extend dorsally of the left lung. In the descriptions the whole area over which the walls of the two lungs are in contact with one another has been considered to be the mesial wall.

Craniad of the orifices of the trachea (or of the bronchi) each lung shows an anterior lobe that extends forwards along the sides of the trachea.

The majority of the snakes examined by me were spirit specimens from the collections of the Rijksmuseum van Natuurlijke Historie, Leiden. I am indebted to Prof. H. Engel for permission to examine some specimens in the Zoologisch Museum, Amsterdam. Of great value to my studies were some Boid snakes that were sent to me by the Zoological Gardens "Blij-Dorp", Rotterdam; to Mr. F. Siewertsz van Reesema, director, and to Ir. F. J. Appelman of these zoological gardens I am greatly indebted for providing me with these fresh specimens.

Not all species were examined in equal detail. In some the course of the ramifications was traced to ascertain which parts of the left lung received their blood supply from the right pulmonary artery. In a number of cases I had to restrict my examination to observations on the presence or absence of an anastomosis. This may explain why the account of many species and subspecies is only very brief.

Diagrammatic drawings were made to show the position of the branches that cross to the left lung, i.e., that send ramifications to the left lung. Most of these drawings show the ventral side of the lungs; the course of the branches is shown up to the point where the branch itself curves dorsad between the lungs. Besides the branches that cross to the left lung there are others that remain confined to the right lung; these latter have not always been indicated, nor do the drawings show branches that arise on the lateral side of the right pulmonary artery. Only in a few instances have the branches of the left pulmonary artery been indicated, but it may be emphasized that I never found branches of the left pulmonary artery to cross to the right lung.

List of the species and subspecies examined.

Boidae Pythoninae	Number of specimens	Group (cf. p. 9)
Bothrochilus boa (Schleg.)	1	I
Liasis amethistinus amethistinus (Schn.)	3	III
Liasis amethistinus kinghorni Stull	1	III
Liasis fuscus albertisii Ptrs. & Doria	1	III
Liasis mackloti mackloti Dum. & Bibr.	3	III

	Number of specimens	Group (cf. p. 9)
Liasis olivaceus papuanus Ptrs. & Doria	1	III
Python curtus brongersmai Stull	3	I
Python curtus curtus Schleg.	1	II
Python molurus bivittatus Kuhl	2	II
Python molurus molurus (L.)	4	II (I?)
Python regius (Shaw)	3	I
Python reticulatus (Schn.)	4	III
Python sebae (Gmel.)	2	II
Python timoriensis (Ptrs.)	1	I
Chondropython viridis (Schleg.)	2	III
Morelia argus (L.)	7	III
Calabaria reinhardtii (Schleg.)	2	IV
Boinae		
Epicrates cenchria cenchria (L.)	2	III
Epicrates inornatus inornatus (Reinh.)	2	III
Epicrates striatus striatus Fisch.	1	I
Boa canina L.	2	III (I?)
Boa enydris enydris L.	3	III and I
Sanzinia madagascariensis (Dum. & Bibr.)	2	I
Enygrus asper schmidti Stull	2	III
Enygrus bibroni bibroni Hombr. & Jacq.	2	III
Enygrus carinatus (Schn.)	3	I
Eunectes scytale (L.)	5	III
Constrictor constrictor constrictor (L.)	5	III (II?)
Constrictor constrictor imperator (Daud.)	1	III
Constrictor constrictor occidentalis (Phil.)	1	III
Acrantophis madagascariensis (Dum. & Bibr.)	1	II
Eryx jaculus jaculus (L.)	2	II (I?)
Eryx johnii johnii (Russ.)	1	I
Charina bottae bottae (Blainv.)	2	I
Lichanura roseofusca roseofusca Cope	1	I
Xenopeltidae		
Xenopeltis unicolor (Reinw.)	4	
Anilidae		
Cylindrophis rufus (Laur.)	1	
Cylindrophis boulengeri Roux	1	
Cylindrophis maculatus (L.)	1	
Cylindrophis isolepis Blgr.	1	
Anilius scytale (L.)	2	
Colubridae		
Elaphe radiata (Schleg.)	2	
Elaphe flavolineata (Schleg.)	2	
Elapidae		
Bungarus candidus (L.)	1	
Bungarus fasciatus Shaw	1	
Viperidae		
Crotalinae		
Trimeresurus wagleri (Boie)	1	
Crotalus durissus L.	1	

BOIDAE

In all Boidae with two lungs the left lung receives ramifications of the right pulmonary artery, but the situation is not the same in all species. For the sake of convenience the descriptions of the species and subspecies have been divided into four groups, which have been indicated by the roman numerals I to IV in the list on pp. 7-8.

Group I contains a small number of species and subspecies in which no connexion between the ramifications of the right and left pulmonary arteries was found. It is possible that the examination of better preserved specimens will show that these forms must be referred to one of the other groups.

In group II, I have placed the species and subspecies in which a branch of the right pulmonary artery is connected to, or unites with one of the left pulmonary.

Group III contains the forms in which a branch of the right pulmonary artery forms a direct connexion with the left pulmonary. The distinction between groups II and III is more or less arbitrary; some forms might be placed in group II as well as in group III. In some instances an anastomosis was found in some specimens, while it is apparently absent in other specimens of the same species. I have indicated these species in the list on pp. 7-8 by two numerals.

Group IV consists of a single species (*Calabaria reinhardtii* (Schleg.)); the left pulmonary artery is present only as a mere basal rudiment. The right pulmonary artery has taken over the function of transporting blood to the left lung.

The groups I to III do not constitute taxonomic units, for the species of a single genus (e.g., *Python*) and even specimens of a single species (e.g., *Boa enydris* L.) may be referred to different groups.

To avoid too many repetitions in the descriptions some general remarks may be made about the branches of the right pulmonary artery. Branches arise from this artery on its lateral, dorsal, and mesial sides. The dorsal branches are very narrow; they enter immediately into the wall of the lung. The lateral branches ramify in the lateral wall of the lung; with a few exceptions these lateral branches have not been indicated in the diagrams. Some of the mesial branches ramify in the ventral and mesial walls of the right lung only; these branches generally are narrow, and in specimens that have not been injected they easily escape notice. When these branches have been indicated in the diagrams, only their basal part is drawn. Other mesial branches send ramifications to the left lung. In some instances the branch itself crosses to the left lung to ramify in the latter's ventral wall. More often the branch bifurcates into a ventral and a dorsal ramus. The ventral ramus passes to the ventral surface of the left lung, and there it ramifies. The dorsal ramus passes between the lungs; in its course it gives off small arteries to the mesial walls of both lungs, on reaching the dorsal surface of the lungs the ramus bifurcates, sending one artery to the dorsal surface of the right lung, and one artery to the dorsal surface of the left lung. Although in these cases only a ramus (and not the mesial branch itself) crosses to the left lung, I have mentioned these branches as crossing, instead of stating in every description that the branch sends a ramus to the left lung. In many species and subspecies one of the crossing branches unites with the left pulmonary artery and thus an anastomosis is formed. The branches that cross to the left lung generally pass dorsad of the pulmonary vein; only in a few instances a branch was found to cross ventrad of the vein.

In many of the specimens I counted the number of branches that cross to the left lung. Sometimes it was difficult to be certain about the number of these branches, as I examined specimens that had been preserved in alcohol for a considerable time; therefore, it may be that some branches have been overlooked. To obtain better results fresh material, suitable for injections, should be studied.

The left pulmonary artery gives off a series of rather strong branches on its lateral side. Much smaller branches may arise on the mesial side of the left pulmonary. These branches are very distinct in the region of the anterior lobe of the left lung; more posteriorly they seem to be absent in some of the specimens examined by me. Never did I find a branch of the left pulmonary to send ramifications to the right lung.

The pulmonary vein arises from the uniting of small veins at the caudal end of the respiratory area of both lungs. Thus, in each lung a longitudinal vein is formed that goes anteriorly along the mesio-ventral side of the lung. At about the level of the last arterial branch that crosses to the left lung, the right and left pulmonary veins unite into a single vessel. This common pulmonary vein goes anteriorly to the heart, ventrad of the line of contact between the two lungs; sometimes it is more or less embedded between the mesial walls of the lungs. The common pulmonary vein receives affluent branches on its right and left sides from the ventral and lateral walls of the lungs. The veins that come from the lateral walls pass between the pulmonary arteries and the lungs. Moreover, the common pulmonary vein receives affluent branches on its dorsal side; these branches return blood from the dorsal surface of the lungs. The veins of the dorsal wall of the right lung unite with the corresponding veins of the left lung, and thus a series of veins is formed that pass ventrad between the lungs to empty into the common pulmonary vein. The veins of the anterior lobes of the right and left lung go posteriorly and they empty into the common pulmonary vein at the level of the caudal end of the trachea.

1. Species and subspecies without an anastomosis.

Bothrochilus boa (Schleg.)

A single specimen has been examined. Three branches of the right pulmonary artery cross to the left lung. There is no anastomosis. The third branch passes dorsad between the lungs; at the dorsal surface it bifurcates: one ramus passing posteriorly along the dorso-mesial surface of the right lung, the other ramus runs posteriorly along the dorso-mesial surface of the left lung.

Python regius (Shaw) (Pl. I fig. *b*)

Three specimens have been examined and in none of these an anastomosis was found. Pl. I fig. *b* shows the situation such as it was found in a female of which the length of head and body was 1004 mm. Three branches of the right pulmonary artery cross to the left lung. The third branch (3) goes posteriorly along the mesial surface of the left lung. On reaching the left lung this branch sends ramifications to the ventral surface of this lung; other ramifications return to the mesial surface of the right lung. Rami of all three branches pass dorsad between the lungs, and they ramify in the dorsal wall of both lungs.

Python curtus brongersmai Stull

No anastomosis was found in the three specimens examined by me. The examination of better preserved material is necessary, as one specimen of *Python curtus curtus* Schleg. showed a connexion between a branch of the right pulmonary artery and one of the left pulmonary. The number of branches that cross to the left lung seems to be smaller than in *Python curtus curtus*; in two specimens of *Python curtus brongersmai* I could trace four of such branches only. In one of these specimens a ramus of the third branch goes to the ventral surface of the left lung, passing ventrad of the pulmonary vein.

Enygrus carinatus (Schn.) (Pl. VII figs. *a, b*)

The pulmonary artery in this species is remarkable in several respects. In all other species of Boidae that have been examined, the common pulmonary trunk bifurcates at the anterior level of the auricles, and the two branches do not only curve to the right and to the left respectively, but they also curve dorsad. In the specimens of *Enygrus carinatus* the common pulmonary trunk itself curves dorsad before bifurcating (Pl. VII fig. *a*: CP).

The following description is based on a single specimen.

On the ventral side of the lungs two branches of the right pulmonary artery cross to the left lung. The first of these (Pl. VII fig *a*: 1) arises on the lateral side of the artery; almost immediately after its origin it bifurcates. One ramus (V) crosses to the left lung; it passes dorsad of the right pulmonary artery; the other ramus (DA) curves around the lateral side of the right lung to the latter's dorsal surface. The ramus (V) that remains on the ventral side sends collaterals both to the right and to the left lung. The dorsal ramus (DA) ramifies in the dorsal surface of the right lung (Pl. VII fig. *b*). The ramifications of this dorsal ramus freely anastomose with one another, and they are also connected with collaterals (Pl. VII fig. *b*: RD) of the right pulmonary artery that curve around the mesial and lateral surfaces of the right lung. A similar arterial network is to be found in *Enygrus asper schmidti* Stull (cf. p. 26) and in *Enygrus bibroni bibroni* Hombr. & Jac. (cf. p. 27). The ramus (DA) also sends an artery (Pl. VII fig. *b*: B) to the dorsal surface of the left lung.

The second branch (Pl. VII fig. *a*: 2) of the right pulmonary artery that crosses to the left lung goes posteriorly along the ventral surface of that lung, parallel to the left pulmonary artery. No connexions between this branch and the left pulmonary were found.

A third strong branch (Pl. VII fig. *a*: 3) of the right pulmonary artery reaches the mesial surface of the right lung, but as far as could be ascertained, no collaterals are given off to the left lung.

Two further specimens have been examined to search for a possible anastomosis, but none was found.

More suitable material should be examined to verify whether there are really no connexions between the systems of the right and left pulmonary arteries.

Python timoriensis (Ptrs.)

In the single specimen examined no trace of a connexion between the systems of the right and left pulmonary arteries was found.

Epicrates striatus striatus Fisch.

No anastomosis was found.

Sanzinia madagascariensis (Dum. & Bibr.)

A branch of the right pulmonary artery crosses to the left lung; it turns posteriorly and it pursues its caudad course along the mesial surface of the left lung, parallel to the left pulmonary artery. No connexion between this branch and the left pulmonary artery was found.

Eryx johnii johnii (Russ.)

In the single specimen examined four branches of the right pulmonary artery cross to the left lung. The fourth branch on reaching the left lung turns posteriorly; it continues its course caudad, parallel to the left pulmonary artery. No connexion between the systems of the right and left pulmonary arteries was found.

Lichanura roseofusca roseofusca Cope

A single specimen was examined; the soft parts were not too well preserved, and I can only state that the right pulmonary artery sends branches to the left lung; an anastomosis was not found.

Charina bottae bottae (Blainv.) (Pl. I fig. *e*)

Two specimens have been examined. They show only one branch that crosses to the left lung. This branch (Pl. I fig. *e*: 1) sends a small artery (VL) to the ventral surface of the left lung; the further ramifications of this branch go to the dorsal surface of the right (DR) and left (DL) lungs No connexion with the left pulmonary artery was found.

To this group also belong specimens of *Python molurus molurus* (L.), *Boa canina* L., *Boa enydris enydris* L., and *Eryx jaculus jaculus* (L.). As other specimens of these forms show connexions between the systems of the right and left pulmonary arteries they are dealt with in the second and third groups.

II. Species and subspecies in which an anastomosis exists between the branches of the right and left pulmonary artery.

Python curtus curtus Schleg. (Pl. II fig. *c*)

The only specimen examined shows six branches of the right pulmonary artery that cross to the left lung.

The first of these branches (Pl. II fig. *c*: 1) arises close to the anterior tip of the right lung; it goes obliquely posteriorly across the ventral surface of the right lung till it reaches the point where the trachea ends, and where the mesial walls of the two lungs come into contact. From this point the branch runs caudad; gradually it moves dorsad, and thus it pursues its course between the mesial walls of the lungs. Just in front of its caudad curve the branch gives off a small artery to the anterior lobe of the left lung; this artery bifurcates, and one ramus (LV) ramifies in the ventral wall of the left lung, while the other ramus (LD) passes between the trachea and the lung to the latter's dorsal surface. From the main branch arises a narrow artery (B) that goes caudad along the adjoining mesial borders of the lungs; this artery ramifies (VR, VL) in the ventral walls of the two lungs. In its further caudad course the branch gives off arteries (M) to the mesial walls and to the mesio-dorsal surface (MD) of the lungs. One of these arteries (C) curves ventrad and joins another branch (2) of the right pulmonary artery. This latter branch (2) ramifies in the ventral wall of the right lung; one of its rami could be traced to a short distance from a ramus of a following branch (3), but I am not certain whether the two are connected.

Three further branches (3, 4, 5) that cross to the left lung, bifurcate at some distance from their origin, and both the resulting arteries send ramifications to the left lung. The fifth branch (6) to cross sends ramifications (L) to the ventral wall of the left lung only. The last branch that crosses (7) curves posteriorly on reaching the left lung; one of its rami is connected to a branch of the left pulmonary artery by an anastomosis (A).

Python molurus molurus (L.) (Pl. III figs. *c, d*)

An anastomosis was found in only two out of the four specimens examined. The two specimens in which no anastomosis was found were in a rather poor state of preservation, and it is possible that the connecting vessel has been overlooked.

In one of the specimens with an anastomosis ten branches of the right pulmonary artery cross to the left lung. The first branch and its ramifications are shown in Pl. III fig. *d*. In its course across the ventral surface of the right lung, this branch (1) gives off several small arteries to the ventral wall of the right lung. On reaching the mesial border of the right lung the branch curves posteriorly. At the curve an artery (VL) is given off to the left lung; this artery bifurcates: one branch with its ramifications (V) remains on the ventral surface of the left lung; the other branch goes dorsad, passing between the trachea and the left lung; on the dorsal surface it sends collaterals (DR, DL) to both lungs. The main branch of the right pulmonary artery goes caudad over a short distance, lying between the mesial walls of the lungs. In this part of its course it sends ramifications (RV, LV) to the ventral walls of both lungs. It then curves dorsad passing between the lungs, and it gives off arteries (MR, ML, N) to the mesial walls of the lungs. Arriving at the dorsal side of the lungs, the branch bifurcates; one of the resulting arteries (RD) ramifies in the dorsal wall of the right lung, the other (LD) going to the dorsal wall of the left lung.

The second to ninth branches all give off collaterals to the ventral wall of the left lung, while the branches themselves curve dorsad between the lungs. In this part of their course they send arteries to the mesial walls of both lungs. The branches end by ramifications in the dorsal walls of the lungs.

The ramifications of the tenth branch are shown in Pl. III fig. *c*. After giving off some small arteries (VR) to the ventral wall of the right lung, the branch bifurcates into a dorsal ramus (D) and a more ventral ramus (LA). The dorsal ramus (D) divides into two arteries: one (DM) that runs caudad along the dorso-mesial surface of the right lung, and one (DL) that goes to the dorsal wall of the left lung. The ventral ramus (LA) gives off an artery that ramifies (VL) in the ventral wall of the left lung; it then curves caudad to pursue its course along the mesial and dorso-mesial surface of the left lung. From this ramus arise arteries to the ventral (V) and mesial (M) walls; one of these rami (B) unites with a branch (C) of the left pulmonary artery.

In another specimen two such connexions were found between the ramus of the right pulmonary artery and branches of the left pulmonary artery.

Python molurus bivittatus Kuhl (Pl. I fig. *c*)

The situation as found in one of the specimens examined by me is shown in Pl. I fig. *c*. Ten branches cross to the left lung. The tenth branch (10) is a very strong artery; it curves caudad and runs posteriorly parallel to the left pulmonary artery. To the latter it is connected by a short but wide anastomosis (A). The fifth branch (5) that crosses to the left lung gives off a ramus that goes posteriorly and dorsad between the lungs; this ramus extends caudad to the level of the sixth branch (6) of the right pulmonary. In the second specimen an anastomosis is present too, but the branch of the right pulmonary and the left pulmonary artery are farther apart; the connecting vessel is longer and narrower than in the first specimen.

Python sebae (Gmel.) (Pl. II figs. *a, b*)

Three specimens have been examined. The course of the major branches of the right pulmonary artery of one of these specimens is shown in Pl. II fig. *b*. At a short distance craniad of the right lung the pulmonary artery gives off a branch (C) that goes to the anterior lobe of the right lung. This branch bifurcates; one ramus (T) turns craniad and passes along the ventral surface of the trachea; the other ramus (VR) ramifies in the anterior lobe of the right lung. Seven branches cross to the left lung. Of these the fifth and sixth bifurcate close to their origin, and each of the resulting arteries sends ramifications to the ventral wall (V) of the left lung, as well as to the mesial (M) and dorsal (D) walls. The seventh branch (7) curves posteriorly, and it (ML) pursues its course along the mesial surface of the left lung. The left pulmonary artery gives off a narrow branch (A) that unites with the branch (ML) of the right pulmonary artery. The seventh branch gives off a ramus (RD) to the dorsal surface of the right lung.

In a second specimen the branch of the right pulmonary artery comes closer to the left pulmonary artery, and the two are connected by a short vessel (Pl. II fig. *a*: A).

Acrantophis madagascariensis (Dum. & Bibr.) (Pl. V fig. *c*)

Hoffmann (1886, pl. CXXXV fig. 1: *Pelophilus madagascariensis*) figures the arterial system of *Acrantophis madagascariensis* (Dum. & Bibr.) from drawings made by Gadow. The common pulmonary trunk is shown to divide into the right and left pulmonary arteries, each of which shows a single row of branches. The situation shown in Hoffmann's plate does not agree with that found in a specimen that I examined in the Amsterdam Zoological Museum.

On its mesial side the pulmonary artery first gives off two small branches to the anterior lobe of the right lung, and then a very strong branch (Pl. V fig. *c*: 1). This branch goes obliquely caudad to the mesial surface of the lung. On reaching the line of contact between the lungs, the branch passes dorsad between the lungs, but it does not quite reach the dorsal surface of the lungs. In its course across the ventral surface of the right lung, the branch gives off an artery that ramifies (AR) in the anterior lobe of the right lung, as well as in the anterior lobe of the left lung (AL). The branch further gives off small arteries to the ventral (V), mesial (M) and dorsal (D) surfaces of both lungs. Eventually the branch bifurcates: one artery (MR) goes caudad along the dorso-mesial surface of the right lung, the other (ML) along the dorso-mesial surface of the left lung. The latter artery (ML) is connected to the left pulmonary by an anastomosis (A).

Eryx jaculus jaculus (L.) (Pl. VI figs. *d, e, f*)

Two specimens have been examined.

I. The first specimen shows only one branch crossing to the left lung

(Pl. VI fig. *e*). When still on the ventral surface of the right lung, this branch bifurcates: one artery (AA) goes obliquely anteriorly, the other (PA) runs obliquely posteriorly. The anterior artery (AA) gives off a ramus (VR) that returns to the right lung. The posterior artery (PA) is connected to the left pulmonary artery by a short oblique vessel (A).

II. In the second specimen two branches (Pl. VI fig. *f*: 1, 2) of the right pulmonary artery cross to the left lung. The first of these sends a ramus (VR) back to the right lung. The second branch (2) has a ramus (ML) that passes caudad along the mesial surfaces of the left lung; no anastomosis could be found. A remarkable feature in this specimen is that the left pulmonary artery abruptly becomes much narrower at a short distance from its origin (Pl. VI fig. *d*: LP). Indian ink injected into the common pulmonary trunk filled the wide basal part of the left pulmonary artery, and penetrated over a short distance into the narrow part, but it would not flow farther caudad. The left pulmonary artery in this specimen must have had a very limited function.

III. Species and subspecies that possess a direct connexion between the right and left pulmonary artery.

Liasis amethistinus amethistinus (Schn.) (Pl. I fig. *a*)

An anastomosis between the right and left pulmonary arteries is present in all three specimens that have been examined by me.

The following notes refer to a specimen that was examined in more detail. Eight branches of the right pulmonary artery cross to the left lung (Pl. I fig. *a*); the eighth branch forms the anastomosis with the left artery (A). At a short distance from its origin this branch (8) gives off a relatively wide artery (B) that runs caudad along the mesial surface of the right lung, parallel to the right pulmonary artery; this artery sends ramifications to the ventral (V) and mesial (M) walls of the right lung. The eighth branch further gives off a ramus that passes dorsad between the lungs (not indicated in the figure); it ramifies in the dorsal walls of both lungs. The main stem of the branch (A) joins the left pulmonary artery.

The left pulmonary artery is much narrower than the right pulmonary, and in its course it gradually diminishes in diameter. At the point where it is joined by the anastomosing branch, the diameter of the left pulmonary is about half that of the branch, and about one fourth that of the right pulmonary. Caudad of the anastomosis the left pulmonary is wider again. In fact it looks as if the artery that goes caudad from the junction is the branch of the right pulmonary rather than the continuation of the left pulmonary artery.

Liasis amethistinus kinghorni Stull

A single specimen has been examined. An anastomosis is present. The specimen did not show any important differences from those of *Liasis amethistinus amethistinus* (Schn.).

Liasis fuscus albertisii Ptrs. & Doria

Six branches of the right pulmonary artery cross to the left lung. The sixth branch joins the left pulmonary artery. Unlike the situation in most other forms, the anastomosis passes ventrad of the pulmonary vein.

Liasis mackloti mackloti Dum. & Bibr. (Pl. I fig. *d*)

Three specimens were examined. In one of these, two anastomoses (Pl. I fig. *d*: A1, A2) are present, while the other specimens show only one anastomosis. In one of these latter specimens five branches of the right pulmonary artery, the fifth of which forms the anastomosis, cross to the left lung.

Liasis olivaceus papuanus Ptrs. & Doria

In the single specimen examined one anastomosis is present.

Python reticulatus (Schn.) (Pl. IV fig. *a*)

Four specimens of this species have been examined; in all four an anastomosis is present.

In one specimen the course of the arteries that pass dorsad, between the lungs, has been studied in some detail. The right pulmonary artery was injected with Indian ink, and this enabled me to trace the course of some (though not all) of the finer ramifications. It proved that the branches that ascend to the dorsal surface are connected to one another, as well as to branches of the right and left pulmonary arteries that curve round the lateral surfaces of the lungs. These connexions are shown in Pl. IV fig. *a*, in which the dorsal and lateral surfaces of the lungs have been drawn in one plane. The second branch (2) that crosses to the left lung passes dorsad between the lungs; on arriving at the dorsal surface it gives off one ramus (RD) to the right lung and one (LD) to the left lung; further a strong ramus goes caudad. This latter, posterior vessel joins an anterior ramus of the third branch that crosses to the left lung. In this way the second and third branches are connected by a strong longitudinal vessel (LA). From this longitudinal vessel ramifications go to the dorsal surfaces of the right and left lung. Some of these ramifications are connected to branches that arise from the right pulmonary artery (C) and to branches of the left pulmonary artery (D). Thus the ramifications of the right and left pulmonary arteries form an arterial network round both lungs. The ramifications of the third branch are connected to those of the fourth branch by a very narrow vessel (A) only. In a similar manner the following branches are connected to one another (e.g., the fourth to the fifth branch by artery B); they are also connected to the right and left pulmonary arteries by vessels (C, D) that curve round the lateral surfaces of the lungs. In this specimen only a few connexions could be traced, but I feel sure that many more of these connexions are present. Injection of fresh specimens may prove their existence.

Hopkinson & Pancoast (1837) in their plate XX fig. 1 give the impression that the common pulmonary trunk divides into the right and left pulmonary arteries close to the lungs. This is incorrect; the bifurcation is situated at the anterior level of the auricles.

Chondropython viridis (Schleg.) (Pl. VI figs. *a, c*)

Two specimens have been examined; the first has a length of head and body of 1190 mm; the other is a juvenile specimen with a length of head and body of 663 mm.

In the larger specimen (Pl. VI fig. *a*) eight branches cross to the left lung. The seventh branch joins the left pulmonary artery. Caudad of this anastomosis the eighth branch goes to the left lung. On reaching the line of contact between the lungs, this branch (8) curves posteriorly; it goes caudad between the two lungs giving off rami (M) to the mesial walls of both lungs; eventually the branch (ML) passes to the left lung to pursue its caudad course along this lung's mesial surface.

The juvenile specimen (Pl. VI fig. *c*) shows two anastomoses. The anterior of these (A1) passes ventrad of the pulmonary vein (PV), the posterior anastomosis (A2) passes dorsad of this vein. These anastomoses are formed by the fourth and fifth branches.

Morelia argus (L.) (Pl. III figs. *a, b*; Pl. IV fig. *b*; Pl. V fig. *a*)

Of this species seven specimens have been examined, two of which show the "*variegata*" colour pattern. As these specimens show variations in the number of anastomoses, the situation of the vessels may be described in some detail.

I. In the first specimen the following branches arise from the mesial side of the right pulmonary artery (Pl. IV fig. *b*) [1]).

1, 2, 3: Three small branches go to the anterior lobe of the right lung. Each of these branches divides into a ventral and a dorsal ramus, which supply the ventral and dorsal walls of the lobe.

4. At the level of the last tracheal rings, the right pulmonary gives off a strong branch that passes across the ventral surface of the right lung. After giving off some very small vessels to the ventral wall of the right lung and its anterior lobe, the branch passes ventrad over the cartilages of the very short right external bronchus. At this point a ramus originates that goes obliquely anteriorly and to the left; besides sending ramifications (LV) to the anterior lobe of the left lung, it sends a small artery (T) craniad on the ventral surface of the trachea. On reaching the line of contact between the two lungs the branch curves posteriorly; it passes dorsad between the two lungs. One major and two minor rami are sent to the ventral wall of the left lung, while another minor ramus passes to the ventral wall of the right lung. On its course between the lungs the branch gives off rami (M) to the mesial walls of both lungs. On reaching the dorsal side of the lungs the branch bifurcates: one artery (RD) ramifies in the dorsal wall of the right lung, the other (LD) ramifies in the dorsal wall of the left lung. These arteries may extend just to the dorso-lateral surfaces of the lungs.

5. This branch sends the majority of its ramifications to the ventral wall of the right lung, only two minor rami pass to the ventral surface of the left lung.

6. A small branch that remains on the ventral surface of the right lung.

7. A strong branch that passes over the ventral surface of the right lung, and that passes between the lungs to their dorsal side. In its course this branch gives off rami to the ventral and mesial walls of both lungs. On the dorsal surface it bifurcates into one artery to the right and one to the left lung.

8, 9. The ramifications of these branches are confined to the ventral wall of the right lung.

10. A very strong branch, a ramus of which joins the left pulmonary artery (first anastomosis: E). In its course across the ventral surface of the right lung this branch gives off rami to the ventral wall of this lung; a ramus that arises from its posterior side sends two small arteries to the

1) In the diagram only the more important ramifications have been indicated; most of the finer branches have been omitted.

ventral surface of the left lung. On reaching the mesial border of the right lung the branch divides into two arteries:

1°. A narrow artery (E) that passes across the ventral surface of the left lung, and that joins the left pulmonary artery. In its course it gives off some fine vessels to the ventral wall of the left lung.

2°. A much wider artery that passes dorsad between the lungs; in its course it sends ramifications to the mesial walls of both lungs. On arriving at the dorsal surface this artery bifurcates into an anterior and a posterior branch; each of these again bifurcates into a right and a left artery which ramify in the dorsal wall of the right and left lung respectively.

II. Another strong branch that is connected to the left pulmonary artery (second anastomosis: F). On reaching the mesial border of the right lung it divides into two arteries:

1°. A rather wide artery that passes across the ventral surface of the left lung; it curves caudad, and in this curve it is joined by the left pulmonary artery (second anastomosis: F).

2°. An artery that passes dorsad between the two lungs; on the dorsal surface it bifurcates into two rami. Each of these rami curves caudad, and pursues its course on the dorsal surface of the right (RD) and left (LD) lungs respectively. Their ramifications supply the dorsal walls of the two lungs.

Posteriorly of the second anastomosis the lungs draw apart, and no further branches cross from the right pulmonary artery to the left lung.

On its lateral (right) side the right pulmonary artery gives off branches (G) that ramify in the lateral wall of the right lung; in the diagram only two of these branches have been indicated.

The left pulmonary artery gives off small branches on its mesial (right) side that ramify in the ventral wall of the left lung, and which may perhaps send some capillaries to the mesial wall of this lung. On its lateral (left) side the left pulmonary artery gives off branches (H) that supply the left part of the ventral wall and the lateral wall of the left lung.

At the junction of the second anastomosing branch (F) with the left pulmonary artery, the latter is much the narrower of the two. In fact the situation strongly gives the impression, that the artery that proceeds caudad from this junction is the branch of the right pulmonary artery, rather than a continuation of the left pulmonary. Much of the blood supply of the left lung caudad of the anastomosis apparently derives from the right pulmonary artery.

II and III. Both these specimens agree with that described above in having two anastomoses. The anastomoses of one of these are shown in Pl.

III fig. *b* (A1, A2). In one specimen seven branches cross to the left lung craniad of the two anastomoses.

IV. In this specimen nine branches of the right pulmonary artery cross to the left lung (Pl. V fig. *a*). The first to fourth branches send ramifications to the ventral, mesial and dorsal walls of both lungs. The fifth branch (5) supplies the ventral walls of both lungs, but it does not pass to the dorsal surface. The sixth branch (6) forms the anastomosis with the left pulmonary artery. Caudad of this anastomosis the left pulmonary artery (B) soon peters out.

Caudad of this anastomosis the seventh, eighth, and ninth branches of the right pulmonary artery cross to the left lung. The eighth branch on reaching the left lung bends caudad; it continues its course (E) over the ventral surface of the lung. This branch gives off a ramus (D) that goes obliquely anteriorly, and that comes very close to a ramus (C) of the left pulmonary artery, but no connexion between the two was found. The caudal part (E) of the eighth branch has the position that in other specimens is occupied by the caudal part of the left pulmonary. At first I took the eighth branch to be a second anastomosis, but a careful examination showed that there is no connexion to the left pulmonary artery. The situation in this specimen may provide an argument for the supposition that (in other specimens) the artery supplying the left lung caudad of the anastomosis is the continuation of a branch of the right pulmonary artery, and not the continuation of the left pulmonary.

V. The fifth specimen, a female with the "*variegata*" colour pattern, shows one anastomosis. Craniad of this anastomosis six other branches cross to the left lung.

VI. One anastomosis was found in the sixth specimen. The soft parts were badly preserved, and a more elaborate examination was impossible.

VII. The seventh specimen is a juvenile of the "*variegata*" pattern. It shows three anastomoses (Pl. III fig. *a*). On its mesial side the right pulmonary artery gives off the following branches that cross to the left lung.

1. A strong branch that passes obliquely caudad across the ventral surface of the right lung. On reaching the adjoining borders of the lungs, it bends caudad, and it gradually ascends to the dorsal side, passing between the lungs. In its course this branch gives off rami to the ventral surface of the right lung, to the ventral surface of the left lung and its anterior lobe (LV), and to the mesial walls of both lungs; finally it divides into a right (RD) and left (LD) artery supplying the dorsal walls of the right and left lung respectively.

2. Another strong branch, resembling the one anterior to it, but its caudad course is not as long.

3. A narrow branch that ramifies in the ventral wall of the left lung.

4. A very strong branch. On reaching the mesial border of the right lung it gives off a narrow vessel that goes to the ventral surface of the left lung, where this vessel bifurcates; the anterior of the resulting arteries (A1) joins the left pulmonary artery, and forms the first anastomosis. The main stem of the branch curves dorsad between the lungs; it soon bifurcates into rami that both pass to the dorsal side; each of these rami divides into a right and a left artery.

5, 6. Two strong branches that pass dorsad between the lungs. They supply the ventral, mesial and dorsal walls of both lungs.

7. This strong branch goes obliquely posteriorly. In its course over the ventral surface of the right lung it gives off a ramus which bifurcates: one artery remains in the right lung, the other artery ramifies in the ventral wall of the left lung. The branch itself on reaching the left lung joins the left pulmonary artery (second anastomosis: A2).

8. A branch of the usual type. It curves posteriorly on reaching the left lung, and passes dorsad between the lungs.

9. This narrow branch sends one ramus to the ventral surface of the left lung, while the branch itself passes dorsad between the lungs.

10. A moderate branch; on its anterior side it gives off two rami to the ventral surface of the left lung, on its posterior side it gives off a ramus that passes along the mesial wall of the left lung. The branch itself joins the left pulmonary artery (third anastomosis: A3).

Caudad of this third anastomosis no further branches cross to the left lung.

From the study of the specimens described above it becomes clear that the left pulmonary artery supplies blood to part of the left lung only, viz., to part of the ventral wall on the mesial side of the left pulmonary, to the ventral wall laterad of the left pulmonary, to the lateral wall except to its dorsal border, and perhaps to part of the mesial wall. This pertains to the anterior part of the left lung, where its mesial wall is in contact with the right lung. In this region the right pulmonary artery supplies blood to the whole of the right lung, to part of the ventral wall of the left lung, and to the latter's mesial and dorsal walls.

Epicrates cenchria cenchria (L.) (Pl. V fig. *b*)

Only three branches cross to the left lung. The first of these (1) is a narrow branch, which gives off a ramus to the ventral surface of the right lung, and one to the ventral surface of the left lung; the branch itself passes dorsad between the lungs to ramify in their dorsal walls.

The second branch (2) is much wider; it connects the right pulmonary artery to the left pulmonary.

Caudad of the anastomosis a third branch (3) sends ramifications to the left lung, while the branch (MR) itself goes caudad along the mesial surface of the right lung. One ramus (LV) goes obliquely anteriorly to the ventral surface of the left lung; a second ramus (ML) passes caudad along the mesial surface of the left lung, parallel to the left pulmonary artery.

Epicrates inornatus inornatus (Reinh.)

An anastomosis is present; it goes obliquely posteriorly from the right to the left pulmonary artery.

Boa canina L. (Pl. IX fig. *g*)

The first specimen examined by me had been preserved in alcohol for a long time, and the soft parts were not too well preserved; in this specimen I failed to find a connexion between the right and left pulmonary arteries.

From the Zoological Gardens "Blij-Dorp", Rotterdam, I received a fresh specimen that shows a distinct anastomosis. In this specimen the pulmonary vein is imbedded between the mesial walls of the two lungs, and the ventral walls of the lungs (in ventral view) partly overlap this vein.

The first branch of the right pulmonary artery (Pl. IX fig. *g*: 1) goes obliquely posteriorly; at some distance from its origin it gives off a ramus that bifurcates immediately after its origin. The arteries that result from this bifurcation pass dorsad between the lungs, and they ramify in the dorsal walls of both lungs (RD, LD). After these dorsal arteries have branched off, the main branch bifurcates; one artery (1 A) goes obliquely anteriorly and it passes into the left pulmonary artery (LP); the other artery (1 B) goes obliquely posteriorly and after some distance it curves caudad, to pursue its course along the ventral surface of the left lung. The left pulmonary artery gives off a branch (C) that goes caudad over a short distance; the artery (1 B) gives off a branch (D) that runs anteriorly. These arteries (C, D) approach one another closely, but they are not connected. It seems as if these two short vessels form part of the original course of the left pulmonary, but that the latter's course has been interrupted for some unknown reason, and that the main blood flow, therefore, passes through the arteries 1 A and 1 B.

The second branch of the right pulmonary (2) sends a ramus (DR) to the dorsal surface of the right lung and one (ML) to the mesial surface of the left lung; the latter gives off two arteries to the dorsal surface of the left lung (DL).

Boa enydris enydris L. (Pl. VI fig. *b*; Pl. IX figs. *e, f*)

Three specimens have been examined. They show considerable variation; in two specimens the right and left pulmonary arteries are connected, but in the third specimen no trace of an anastomosis was found.

I. In the first specimen (Pl. IX fig. *f*) two branches of the right pulmonary artery cross to the left lung. They both pass ventrad of the pulmonary vein. The first branch ramifies (V) in the ventral wall of the left lung. The second branch forms the anastomosis. The right pulmonary artery, the anastomosis, and the artery that goes caudad from the junction are completely filled with blood; the left pulmonary artery is filled with blood over a short distance craniad of the anastomosis, but the greater (anterior) part of the left pulmonary is empty. This seems to indicate that the blood supply of the caudal part of the left lung derives from the right pulmonary artery. The anastomosing branch sends ramifications (M) to the mesial walls as well as (RD, LD) to the dorsal walls of both lungs.

II. The situation in the second specimen (Pl. VI fig. *b*) is more complicated. A branch of the right pulmonary artery bifurcates at some distance from its origin; one ramus (AR) goes craniad, the other (PR) obliquely caudad. The anterior ramus sends two small arteries (L) to the left lung; these pass dorsad of the pulmonary vein (PV); the ramus itself ramifies in the ventral wall of the right lung. The caudal ramus (PR) curves to the left and it passes ventrad of the pulmonary vein; it (AL) then curves anteriorly, and it passes into the left pulmonary artery (LP). Before crossing the pulmonary vein this ramus gives off an artery (ML) that passes dorsad of the vein, and it curves posteriorly to pursue its course caudad along the mesial surface of the left lung. After the ramus (PR) has crossed the pulmonary vein, it gives off a further artery that bifurcates; one branch (RV) returns to the ventral surface of the right lung ventrad of the vein; the other branch (LV) ramifies in the ventral wall of the left lung.

III. The third specimen (Pl. IX fig. *e*) does not show an anastomosis. Two branches of the right pulmonary artery send ramifications to the left lung. The first branch (1) gives off an anterior artery (AA) that sends rami to the ventral (V) and mesial (M) walls of both lungs. A posterior artery (PA) also sends rami to the ventral (VR, VL) and mesial (M) walls of both lungs. The branch itself (1) passes dorsad between the lungs. The second branch (2) gives off rami to the ventral wall of the left lung

(LV), and to the mesial walls (M) of both lungs; finally it passes to the left lung, where it (ML) pursues its course caudad along the dorso-mesial surface.

Enygrus asper schmidti Stull (Pl. VII figs. *c, d, e, f*)

Two specimens have been examined. In one of these the ramifications of the pulmonary artery were completely filled with blood, and therefore many details could be studied. The situation in this specimen may be described in the first place.

I. The right pulmonary artery (Pl. VII figs. *c, d*) on its lateral side gives off a strong branch (DA) that curves dorsad around the lateral surface of the right lung. On the dorsal surface this branch goes obliquely posteriorly to the mesial border of the lung; in its further course the branch runs caudad (MA) along the mesial surface of the right lung. On the dorsal surface of the right lung this branch (Pl. VII fig. *d*: DA, MA) gives off numerous small arteries that freely anastomose amongst each other, and that are also connected to the right pulmonary artery itself. A strong ramus (Pl. VII fig. *d*: B) crosses to the dorsal surface of the left lung, where it ramifies; some of these ramifications (C) are connected to the left pulmonary artery. At the point where this ramus reaches the line of contact between the lungs, it gives off an artery (Pl. VII figs. *c, d*: D) that passes ventrad between the lungs. On the ventral side this artery bifurcates: one branch (E) goes to the ventral wall of the right lung, the other (F) passes caudad over the ventral surface of the left lung. This latter branch (F) anastomoses with the left pulmonary artery.

At the posterior level of the rather well marked right external bronchus the right pulmonary artery gives off a rather strong branch (Pl. VII fig. *c*: 1). This branch crosses to the left lung, where its ramifications are connected to branches (G) of the left pulmonary artery. More posteriorly numerous branches (H) arise from the mesial side of the right pulmonary artery. These branches ramify on the ventral and mesial surfaces of the right lung; their ramifications form a network, which consists of two longitudinal vessels (J, K) and numerous transverse vessels (N). By other transverse vessels (O) the network is connected to the branch (MA) of the right pulmonary artery that runs along the mesial surface of the right lung. Farther posteriorly the arterial network is present too, but it does not show the pattern of distinct longitudinal and transverse arteries (Pl. VII fig. *c*). An arterial network is also present on the dorsal surface of the right lung (Pl. VII fig. *e*).

In this specimen the right and left pulmonary arteries are connected by anastomoses both on the ventral and dorsal surfaces. Moreover, the lungs are surrounded by a complete arterial network.

II. In the second specimen (Pl. VII fig. *f*) I examined only the anastomosing branch on the ventral side. It is strongly developed, and it forms a direct connection between the two pulmonary arteries. One of the rami (T) passes craniad in the groove between the external bronchi.

Enygrus bibroni bibroni Hombr. & Jacq.

The two specimens examined by me were not so well preserved. It could be ascertained, however, that connexions between the right and left pulmonary arteries are present, both on the ventral and dorsal surfaces.

In the best preserved of the specimens several branches of the right pulmonary artery pass ventrad of the pulmonary vein. These branches are connected to branches of the left pulmonary artery, and besides they are connected by narrow longitudinal arteries. Thus, an arterial network is formed of branches of the right and left pulmonary arteries, together with longitudinal arteries; the remarkable feature is that part of this network is situated ventrad of the pulmonary vein.

Eunectes scytale (L.) (Pl. V fig. *d*)

Five specimens have been examined; four of these were foetuses which apparently were close to their time of birth. In all a distinct anastomosis between the right and left pulmonary arteries is present. The number of branches that cross is low; in two specimens I counted three of such branches, the third of which forms the anastomosis. In some specimens (Pl. V fig. *d*) the situation is such that it may be said that the branch of the right pulmonary artery continues its course caudad along the left lung, rather than that the artery of the caudal part of the left lung is the continuation of the left pulmonary artery.

Constrictor constrictor constrictor (L.) (Pl. VIII figs. *d, e, f*)

Five specimens have been examined. In all of these an anastomosis is present. Only two to four branches cross to the left lung; the last of these branches forms the anastomosis. The situation in three specimens is shown in Pl. VIII figs. *d, e, f*. In one of these specimens (Pl. VIII fig. *e*) the third and fourth branches are connected to each other by a narrow vessel (B). In another specimen only two branches cross to the left lung, but the second branch (Pl. VIII fig. *f*: 2) bifurcates, and both rami (AR, PR) send ramifications to the left lung. The posterior of these rami (PR) sends an artery (ML) to the ventro-mesial surface of the left lung, and this artery (ML) is connected to the left pulmonary artery by two anastomoses (A). This species should perhaps be placed with group II rather than with group III.

In this species Jacquart (1864, Pl. XII: *Boa constrictor*) indicates a vessel that may be the anastomosis.

Constrictor constrictor imperator (Daud.) and **Constrictor constrictor occidentalis** (Phil.)

Of these subspecies one specimen of each has been examined. They agree with the typical subspecies.

IV. Species with two lungs, but with only one pulmonary artery

Calabaria reinhardtii (Schleg.) (Pl. IX fig. *d*)

Two specimens have been examined, and they both show the same remarkable situation.

Both lungs are well developed, but the left lung receives its blood supply from the right pulmonary artery only. The left pulmonary artery has disappeared, except for a small rudiment (Pl. IX fig. *d*: LP), that forms a diverticulum of the common pulmonary trunk (CP). This rudiment is connected to the left aortic arch (Ao) by strands of connective tissue, i.e., by a ligamentum arteriosum (LA).

One strong branch (1) of the right pulmonary artery crosses to the left lung; on reaching this lung the branch divides into a ventral (LV) and a dorsal (LD) ramus that supply the ventral and dorsal surfaces of the lung respectively.

ANILIDAE

The left lung is more reduced than in the Boidae. In *Cylindrophis rufus* (Laur.) the length of the left lung equals about 12% of that of the right lung; in *Anilius scytale* (L.) the length of the left lung equals only 3.5% of that of the right lung. Nevertheless, both pulmonary arteries are present.

Cylindrophis rufus (Laur.) (Pl. IX fig. *a*)

One specimen has been examined. On its mesial side the right pulmonary artery gives off two narrow arteries (Pl. IX fig. *a*: 1, 2) that ramify in the anterior lobe of the right lung; some collaterals (T) go to the ventral wall of the trachea.

Two branches (3, 4) cross to the left lung. The anterior of these (3) goes to the anterior half of the left lung; its ramifications form at least two anastomoses (A) with the left pulmonary artery. The posterior branch (4) goes to the posterior half of the lung.

Cylindrophis boulengeri Roux

In the single specimen examined, the situation is much the same as in *Cylindrophis rufus* (Laur.).

Cylindrophis maculatus (L.)

One specimen has been examined. The length of the left lung is only 6.7% of that of the right lung. The right pulmonary artery sends one branch to the left lung. Whether this branch forms an anastomosis with the left pulmonary artery could not be ascertained with absolute certainty.

Cylindrophis isolepis Blgr. (Pl. IX fig. *b*)

The length of the left lung is 11.7% of that of the right lung. One branch of the right pulmonary artery crosses to the left lung (Pl. IX fig. *b*: 1). This branch passes ventrad of the trachea; it reaches the lung together with the very short left external bronchus. Just before reaching the left lung, the branch gives off a narrow ramus (RV) to the ventral surface of the right lung, which it reaches on the left side of the right bronchus. The branch divides into an anterior (AA) and a posterior (PA) artery. Connexions to the left pulmonary artery could not be found, but in these very small lungs they can be found only in very well preserved or in injected specimens.

Anilius scytale (L.) (Pl. IX fig. *c*)

Two specimens have been examined. The left lung is still more reduced than in the *Cylindrophis* species. In ventral view the left lung is completely covered by the ventricle of the heart.

The common pulmonary trunk (Pl. IX fig. *c*: CP) divides into the right (RP) and left (LP) pulmonary arteries. At its base the left pulmonary is only slightly narrower than the right. However, after a short distance the left pulmonary artery abruptly becomes much narrower; its diameter becomes reduced to about one fourth of that at its base. As a very narrow vessel the left pulmonary artery pursues its course to the left lung.

The right pulmonary artery gives off five narrow branches (1-5) to the ventral surface of the right lung and its anterior lobe. The anterior lobe of the right lung is dorso-ventrally flattened; caudad of the heart the right lung becomes compressed. The right pulmonary artery curves ventrad and medially along the right border of the ventricle; just caudad of the apex of the heart the pulmonary turns caudad again. At this point the right pulmonary artery gives off a relatively strong branch (6). This branch soon bifurcates; one artery (C) goes posteriorly and to the left, the other artery (B) goes anteriorly. The posterior artery (C) ramifies in the left and dorsal walls of the right lung. The anterior artery (B) gives off a ramus (DR) to the dorsal surface of the right lung. On reaching the posterior border of the left lung, the artery divides into two branches. One of these (A) goes to the left lung, it is confluent with the left pulmonary artery. The second branch (E) almost immediately divides into two vessels. One of these (VR) turns to the right over the ventral surface of the right lung; it gives off a collateral (VL) to the ventral surface of the left lung. The other vessel passes between the lungs, and it sends at least one collateral (DL) to the dorsal surface of the left lung.

XENOPELTIDAE

Xenopeltis unicolor (Reinw.) (Pl. VIII figs. *a, b*)

Four specimens have been examined. In all specimens branches of the right pulmonary artery cross to the left lung, and one of these branches forms the anastomosis with the left pulmonary. The number of branches that pass to the left lung is 3 (2 specimens) or 4 (2 specimens). In three specimens the last branch to cross forms the anastomosis (Pl. VIII fig. *b*: 3); in one specimen the second branch (Pl. VIII fig. *a*: 2) joins the left pulmonary artery. In this latter specimen the anastomosis is followed by another branch (Pl. VIII fig. *a*: 3) that sends ramifications to the left lung. The branches also send rami (Pl. VIII fig. *b*: D) to the dorsal surface of both lungs.

The anastomosing branch often is distinctly wider than the left pulmonary artery (Pl. VIII fig. *a*: 2), and the way in which it is joined by the latter suggests that it is this branch that goes to the caudal part of the left lung, rather than a continuation of the left pulmonary.

Thompson (1913, p. 418) mentions two pulmonary veins in *Xenopeltis*. One of these is formed "of two branches that arise along the mesial side of each lung"; these two branches join, and from this junction a single vein goes anteriorly to the heart. This is indeed the situation such as it is found in *Xenopeltis*, and also in Boidae with two lungs. Thompson's statement that *Xenopeltis* possesses a second pulmonary vein, that "courses along the angular ventral border of the right lung and enters the anterior inferior corner of the auricle", and that has frequent anastomoses with the right branch of the other pulmonary vein, is certainly erroneous. The vessel described in this way by Thompson (l. c., p. 418: right [pulmonary vein]) is in fact the right pulmonary artery, and this of course does not enter the auricle, nor does it form anastomoses with the true pulmonary vein. The anastomoses mentioned by Thompson are the branches of the right pulmonary artery that pass dorsad of the vein, and/or the branches of the pulmonary vein that pass dorsad of the artery.

In none of the specimens examined did I find the posterior perforation that affords communication between the lungs, such as this is mentioned by Thompson (l. c., p. 418). The anterior perforation mentioned by that author apparently is the orifice through which the lungs communicate with the trachea.

COLUBRIDAE

Elaphe radiata (Schleg.) (Pl. IX fig. *h*)

The left pulmonary (Pl. IX fig. *h*: LP) has become reduced to a diverticulum of the common pulmonary trunk; it is connected to the left aortic arch (Ao) by a ligamentum arteriosum. One branch of the right pulmonary artery sends ramifications to the left lung. This branch passes ventrad of the pulmonary vein (PV).

Elaphe flavolineata (Schleg.)

In this species the conditions are the same as in *Elaphe radiata* (Schleg.).

ELAPIDAE

Bungarus candidus (L.) and **Bungarus fasciatus** (Shaw)

The situation resembles that in the *Elaphe* species. One branch of the right pulmonary artery sends ramifications to the rudimentary left lung.

VIPERIDAE

Crotalus durissus L. (Pl. VIII fig. *c*)

In this species a rudimentary left lung is present. Moreover, a tracheal lung has developed. As I have described in a previous paper (Brongersma, 1949), the pulmonary artery (P) divides into two branches. One of these passes dorsad and to the right; it divides into a ramus (A) that goes craniad along the dorsal side of the tracheal lung, and a ramus (B) that goes caudad to the true lung. The other branch (C) goes craniad along the ventral surface of the tracheal lung. From this branch arises an artery (D) that sends a ramus (E) caudad along the left side of the trachea. This ramus (E) gives off vessels to the tracheal lung and one artery (F) to the rudimentary left lung.

Thus, in this species the rudimentary left lung does not receive a branch directly from the right pulmonary, but from a newly acquired ramus (C) of the pulmonary artery. Another explanation would be to consider the arteries C-D-E-F as representing the left pulmonary artery of the snakes with two well developed lungs, but to me this explanation appears to be far-fetched.

Trimeresurus wagleri (Boie)

The rudimentary left lung in this species receives a branch of the posterior ramus of the right pulmonary artery (dorsal branch of the pulmonary artery of Brongersma, 1949, p. 62). In this species the ramus of the pulmonary artery that goes craniad along the ventral surface of the tracheal lung is absent.

Summary and Conclusion

The present paper must be considered to be of a more or less preliminary nature. It has been written to draw the attention to some remarkable features of the pulmonary arteries in snakes with two well developed lungs.

In all Boidae and Anilidae with two lungs, and in *Xenopeltis unicolor* (Reinw.), one or more branches of the right pulmonary artery go to the left lung. In the majority of the species and subspecies examined an anastomosis connects the systems of the right and left pulmonary arteries. In the few species of which a number of specimens have been examined (e. g., *Morelia argus* (L.), *Boa enydris enydris* L., etc.) it proved that a considerable amount of variation occurs. In *Morelia argus* (L.) the number of anastomoses varies from one to three; in *Boa enydris enydris* L. some specimens show an anastomosis, while in others it is apparently absent. It is hoped that more specimens of these and other species will become available to study the variation. Especially important will be studies on the ontogenetic development of the pulmonary arteries. How do the anastomoses arise? Does a branch of the right pulmonary artery grow out till it reaches and joins the left pulmonary, or is the branch of the right pulmonary already present in the left lung at a time when the left pulmonary artery does not yet reach so far caudad? In some specimens the branch of the right pulmonary curves caudad, and it gives the impression that it is this branch that poceeds caudad along the left lung, while the left pulmonary artery is only a narrow vessel that links up with this branch.

Nothing is known about the way in which these structures function, but in this respect a specimen of *Boa enydris enydris* L. is interesting. As described on p. 25 the greater part of the left pulmonary artery is empty, while the right pulmonary, the anastomosis, and the artery caudad of the junction are completely filled with blood. This situation gives the impression that the caudal part of the left lung receives its main supply of blood through the anastomosis. It is possible, of course, that the anastomosis brings blood to the left lung only under special (as yet unknown) circumstances. Until the function of the anastomosis has been elucidated, it remains difficult to explain why it is present in some specimens, while it is absent in others of the same species. It may well be that the whole problem of these arterial connexions is one to be solved by the study of hydrodynamics rather than by anatomy or embryology.

Common opinion has it that the left pulmonary artery becomes reduced, and finally disappears as a sequence of the reduction of the left lung. In species with a much reduced left lung (e. g., *Anilius scytale* (L.)) the left pulmonary is only a very narrow vessel, although it is still present. *Calabaria reinhardtii* (Schleg.) shows a remarkable situation in this respect. The left lung is still well developed, but the left pulmonary artery has become reduced to a mere rudiment, and it has lost contact with the left lung.

Among the Boidae the groups I to IV form a series in so far as the importance of the right pulmonary artery in being the vessel that transports blood to the left lung increases. The process culminates in *Calabaria* (group IV) where the right pulmonary artery is the only vessel that brings blood to the left lung. In many species the left pulmonary artery has become more reduced than seems rational with regard to the size of the lung, and the right pulmonary artery with its crossing branches has taken over part of the function of the left pulmonary. It might be that this situation precedes the reduction of the left pulmonary, rather than being a sequence of it.

On p. 9 I have mentioned that the groups I to III (into which I divided the Boidae for the sake of convenience) do not form taxonomic units. With group IV, represented only by *Calabaria reinhardtii* (Schleg.), the case is slightly different. This species differs from the other Boidae in more characters, e. g., in the absence of palatine teeth. Whether this species can be retained in the subfamily Pythoninae will have to be shown by further studies on its anatomy.

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EXPLANATION OF THE PLATES

All figures are diagrams. With a few exceptions (indicated below) the figures show part of the lungs and arteries in ventral view. In the figures RP stands for right pulmonary artery, LP for left pulmonary artery, and PV for pulmonary vein. References to the other abbreviations are given in the descriptions, and therefore they are not repeated here. A broken line has been used to indicate the outline of the lungs. Branches of the right pulmonary artery have been indicated by numerals; except in Plate IV fig. *b*, only branches that cross to the left lung have been numbered.

Plate I

Fig. *a*, *Liasis amethistinus amethistinus* (Schn.).
Fig. *b*, *Python regius* (Shaw).
Fig. *c*, *Python molurus bivittatus* Kuhl.
Fig. *d*, *Liasis mackloti mackloti* Dum. & Bibr.
Fig. *e*, *Charina bottae bottae* (Blainv.).

Plate II

Figs. *a*, *b*, *Python sebae* (Gmel.).
Fig. *c*, *Python curtus curtus* Schleg.

Plate III

Figs. *a*, *b*, *Morelia argus* (L.), specimens VII, II.
Figs. *c*, *d*, *Python molurus molurus* (L.).

Plate IV

Fig. *a*, *Python reticulatus* (Schn.), dorsal and lateral surfaces of lungs drawn in one plane.
Fig. *b*, *Morelia argus* (L.), specimen I.

Plate V

Fig. *a*, *Morelia argus* (L.), specimen IV.
Fig. *b*, *Epicrates cenchria cenchria* (L.).
Fig. *c*, *Acrantophis madagascariensis* (Dum. & Bibr.).
Fig. *d*, *Eunectes scytale* (L.).

Plate VI

Figs. *a, c, Chondropython viridis* (Schleg.); *a,* adult, *c,* juvenile.
Fig. *b, Boa enydris enydris* L., specimen II.
Figs. *d-f, Eryx jaculus jaculus* (L.); *d, f,* specimen II; *e,* specimen I.

Plate VII

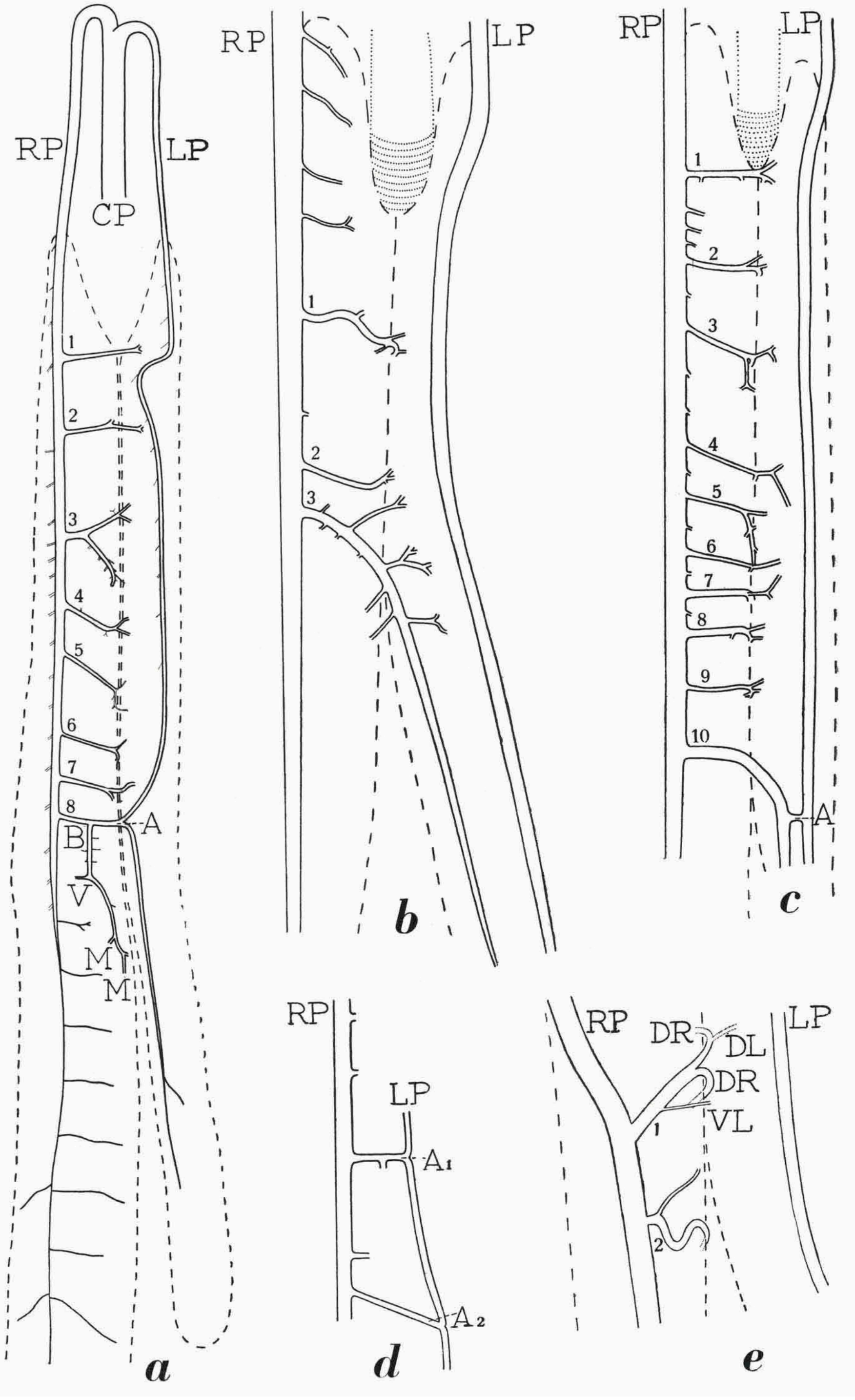
Figs. *a, b, Enygrus carinatus* (Schn.); in fig. *b* the dorsal view is shown.
Figs. *c-f, Enygrus asper schmidti* Stull; figs. *c-e,* specimen I; fig. *f,* specimen II. Fig. *d* shows the dorsal view; fig. *e,* dorsal view of a more caudal part of the right lung.

Plate VIII

Figs. *a, b, Xenopeltis unicolor* (Reinw.).
Fig. *c, Crotalus durissus* L.
Figs. *d-f, Constrictor constrictor constrictor* (L.); the situation in three different specimens is shown; in fig. *f* only the anastomosing branch is drawn.

Plate IX

Fig. *a, Cylindrophis rufus* (Laur.).
Fig. *b, Cylindrophis isolepis* Blgr.
Fig. *c, Anilius scytale* (L.).
Fig. *d, Calabaria reinhardtii* (Schleg.).
Figs. *e-f, Boa enydris enydris* L.; fig. *e,* specimen III; fig. *f,* specimen I.
Fig. *g, Boa canina* L.
Fig. *h, Elaphe radiata* (Schleg.).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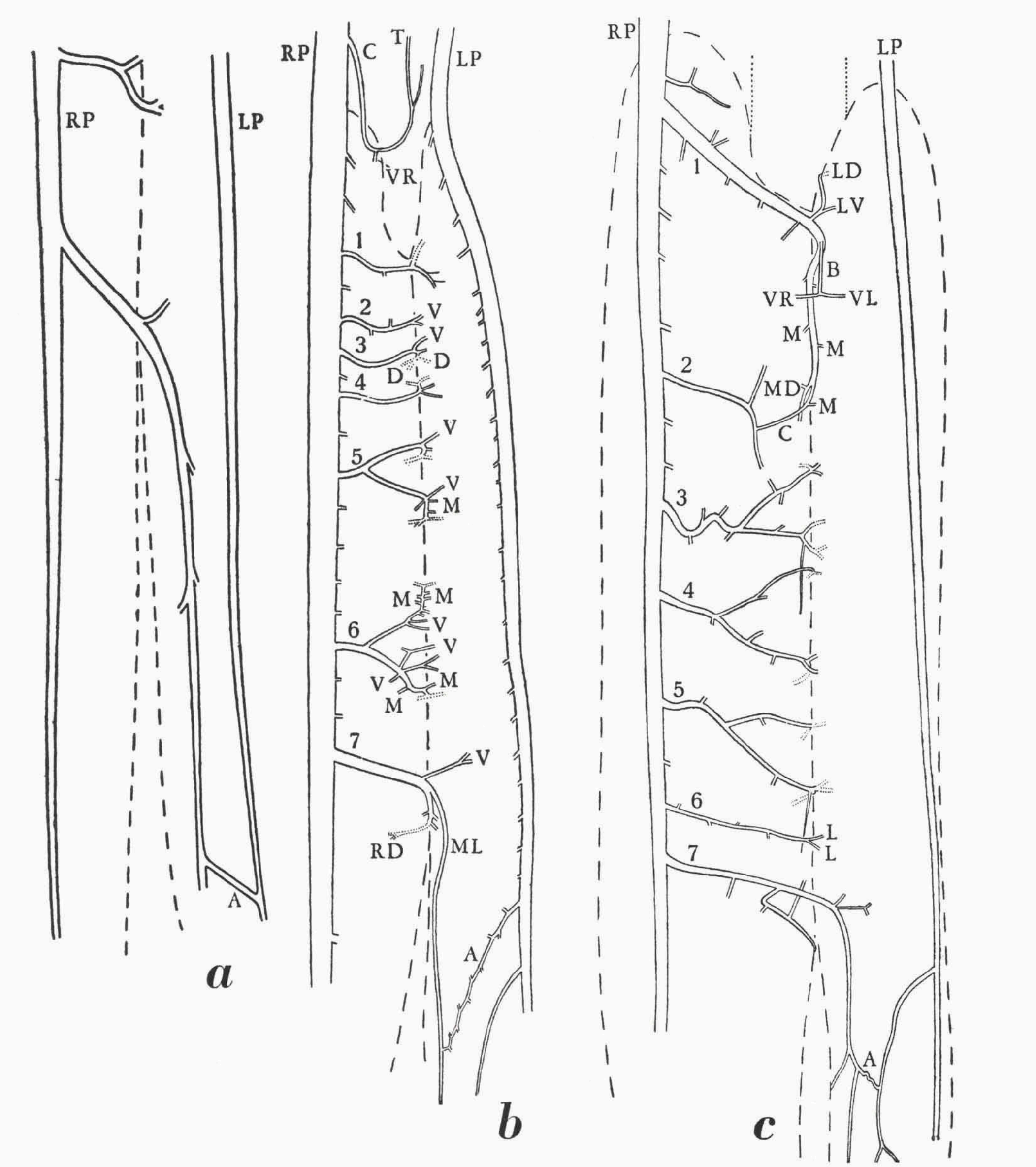
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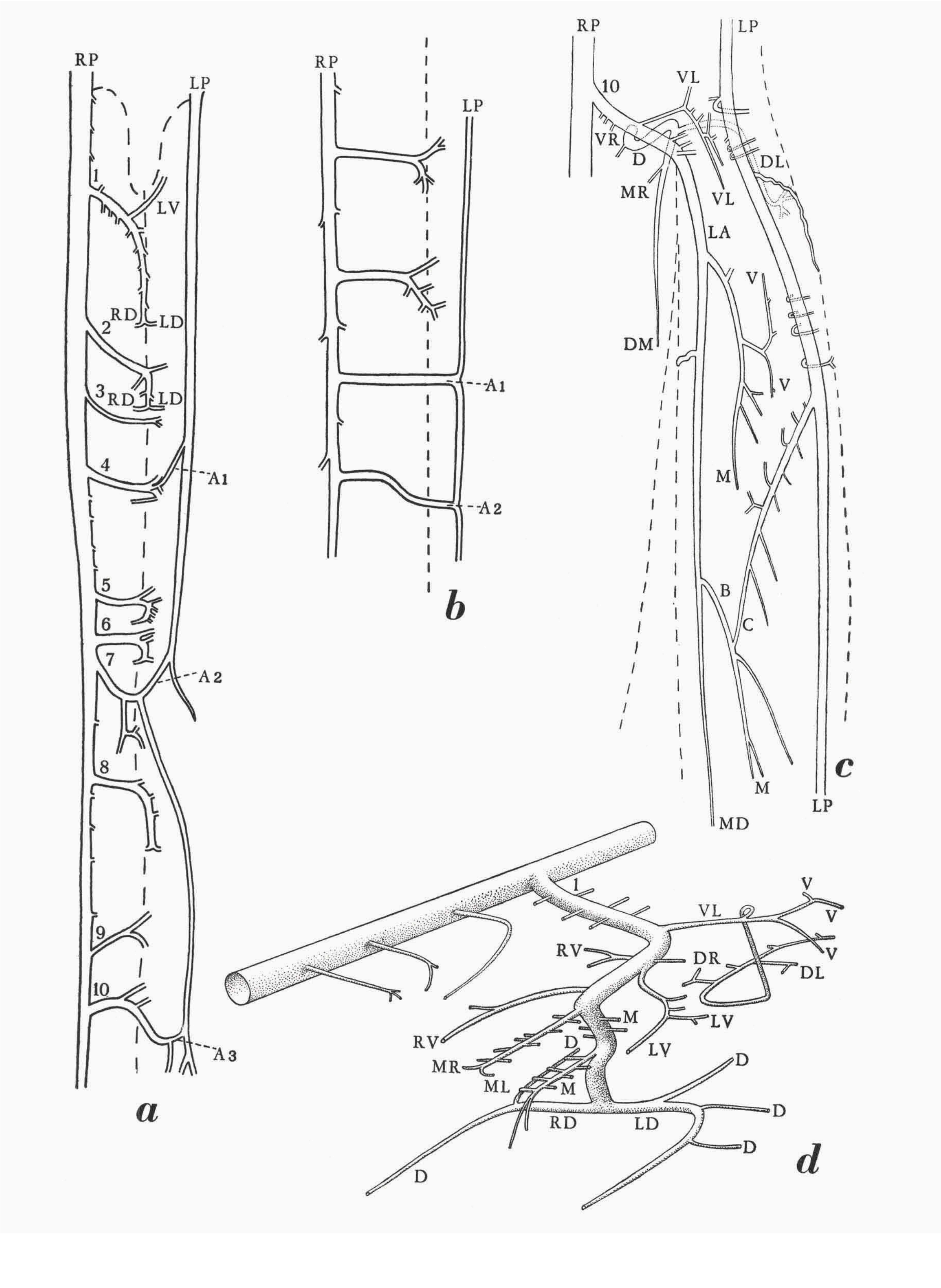
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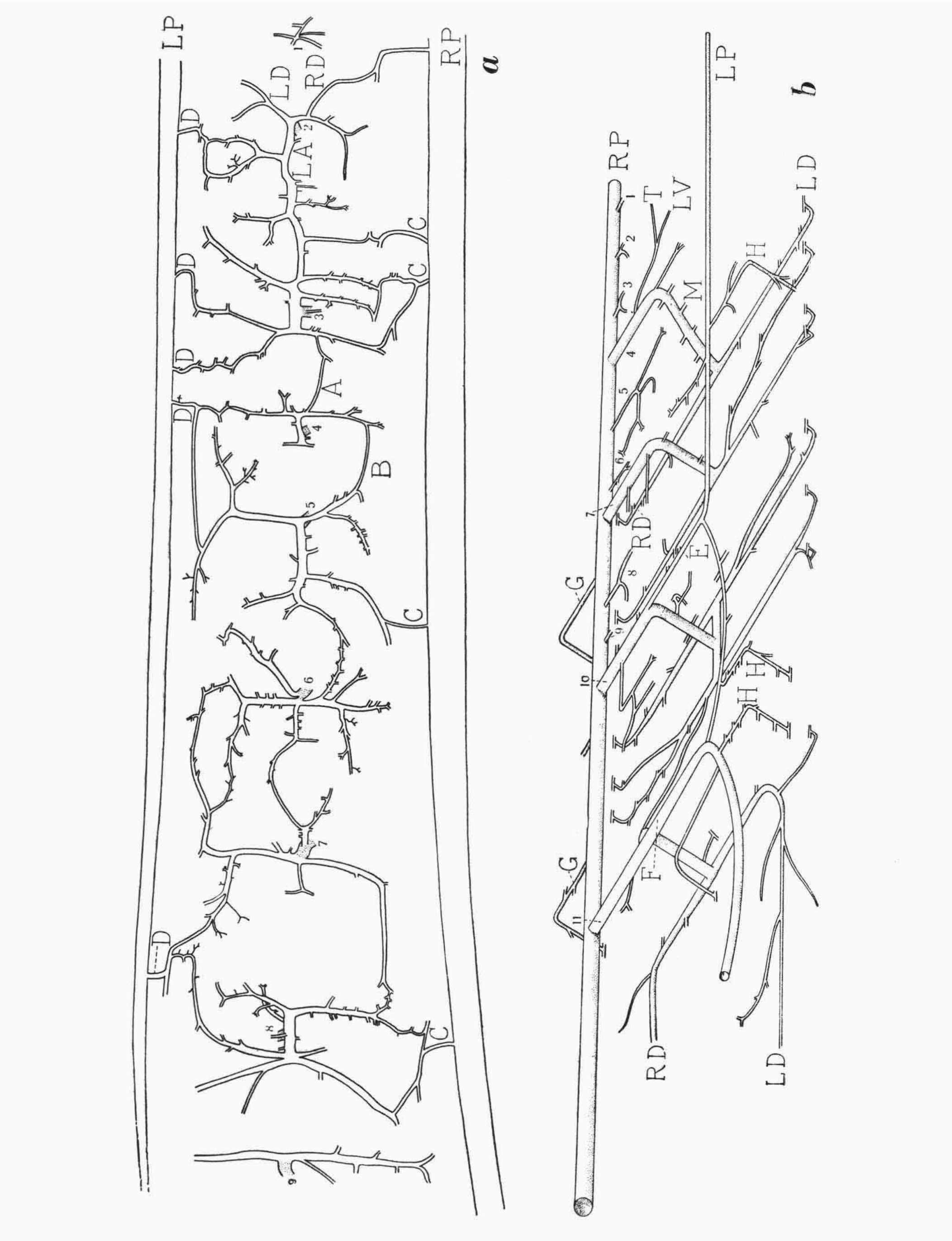
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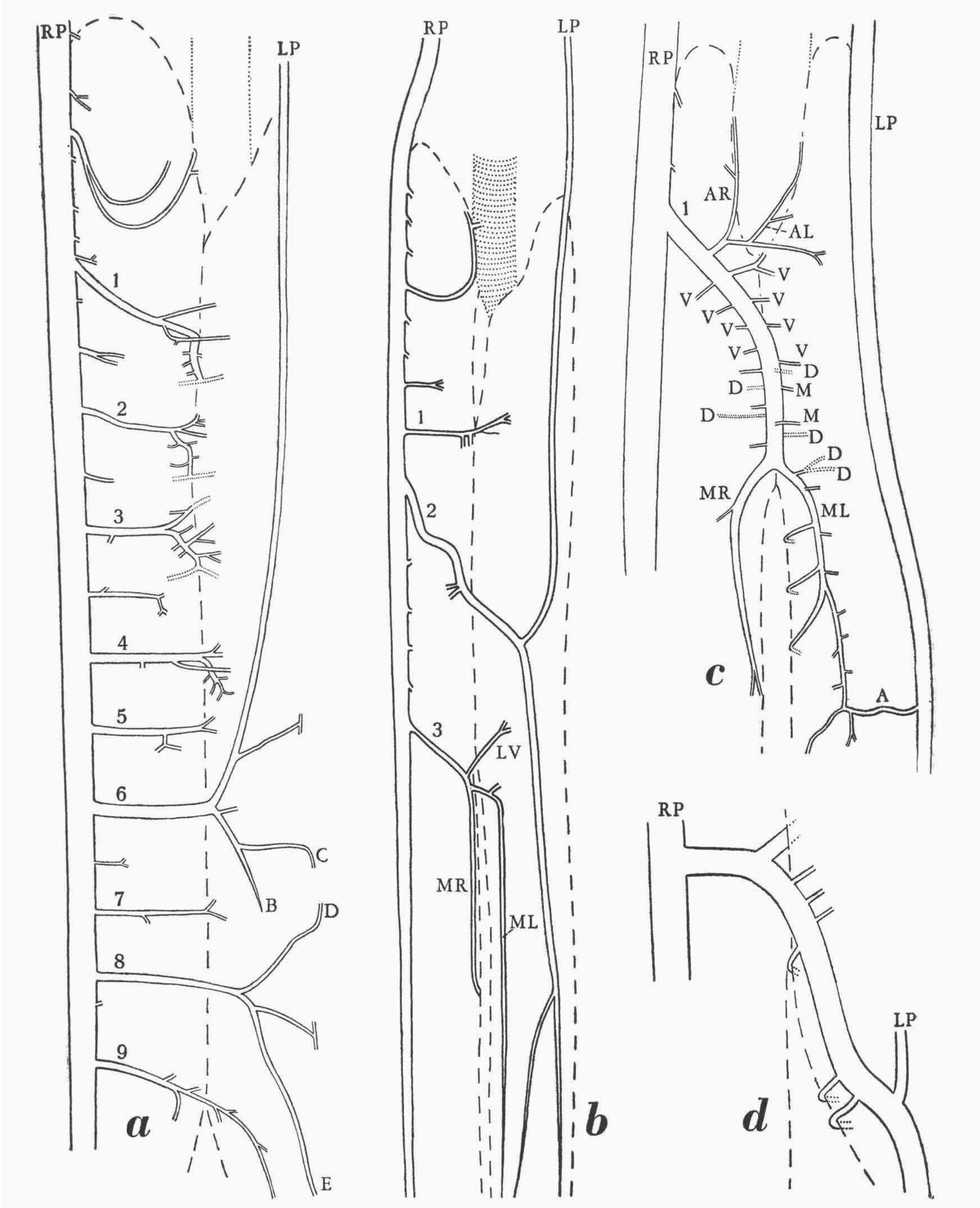
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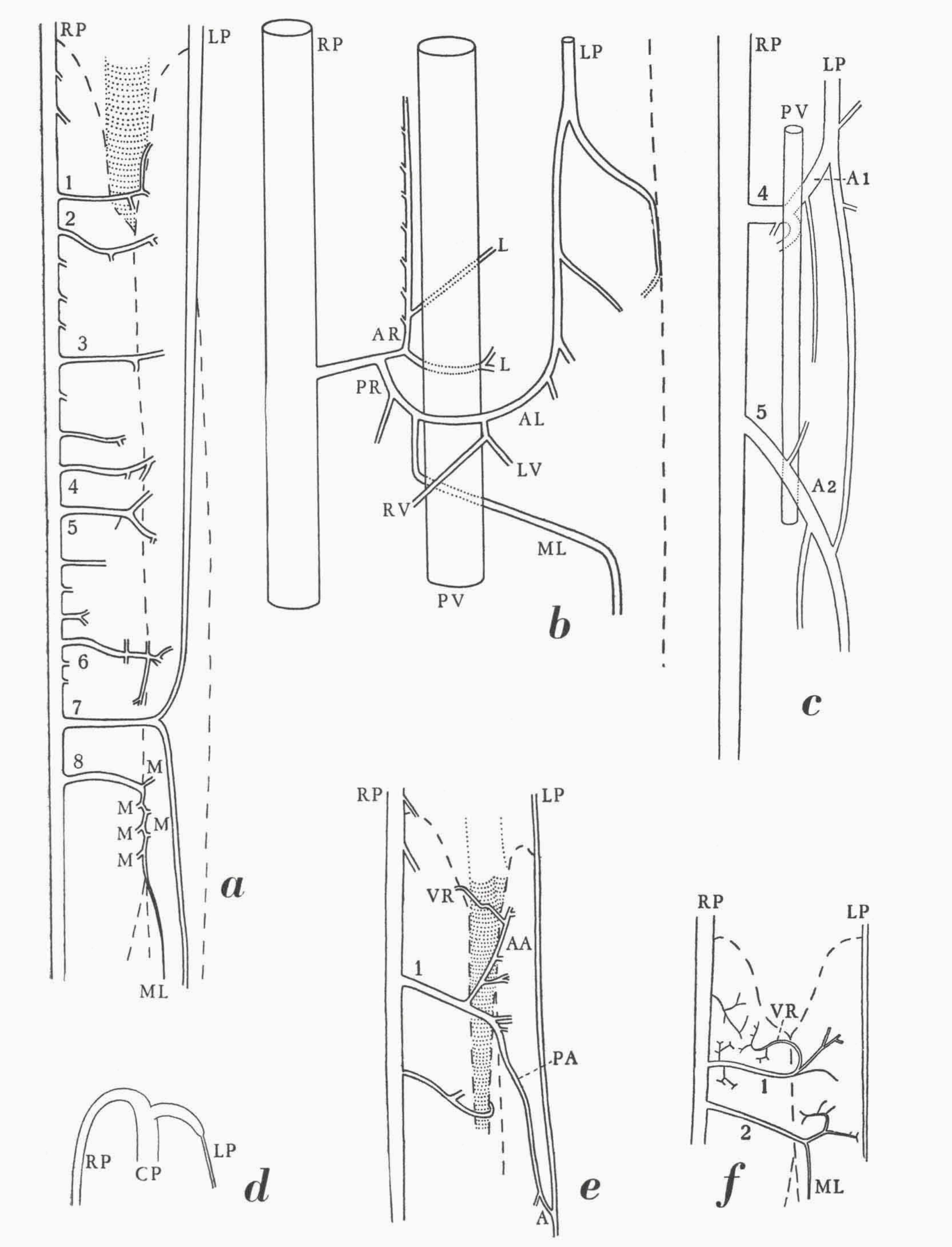
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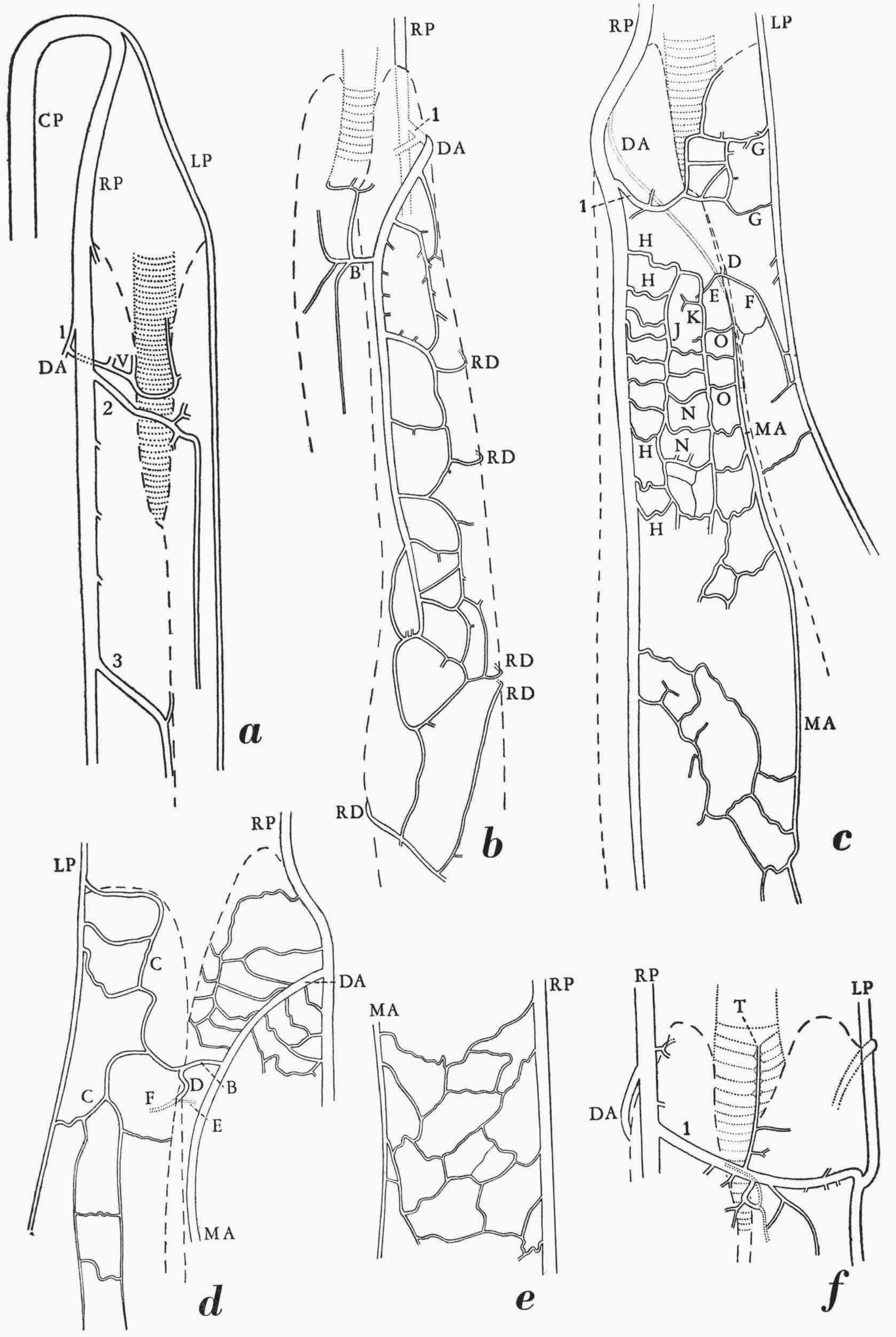
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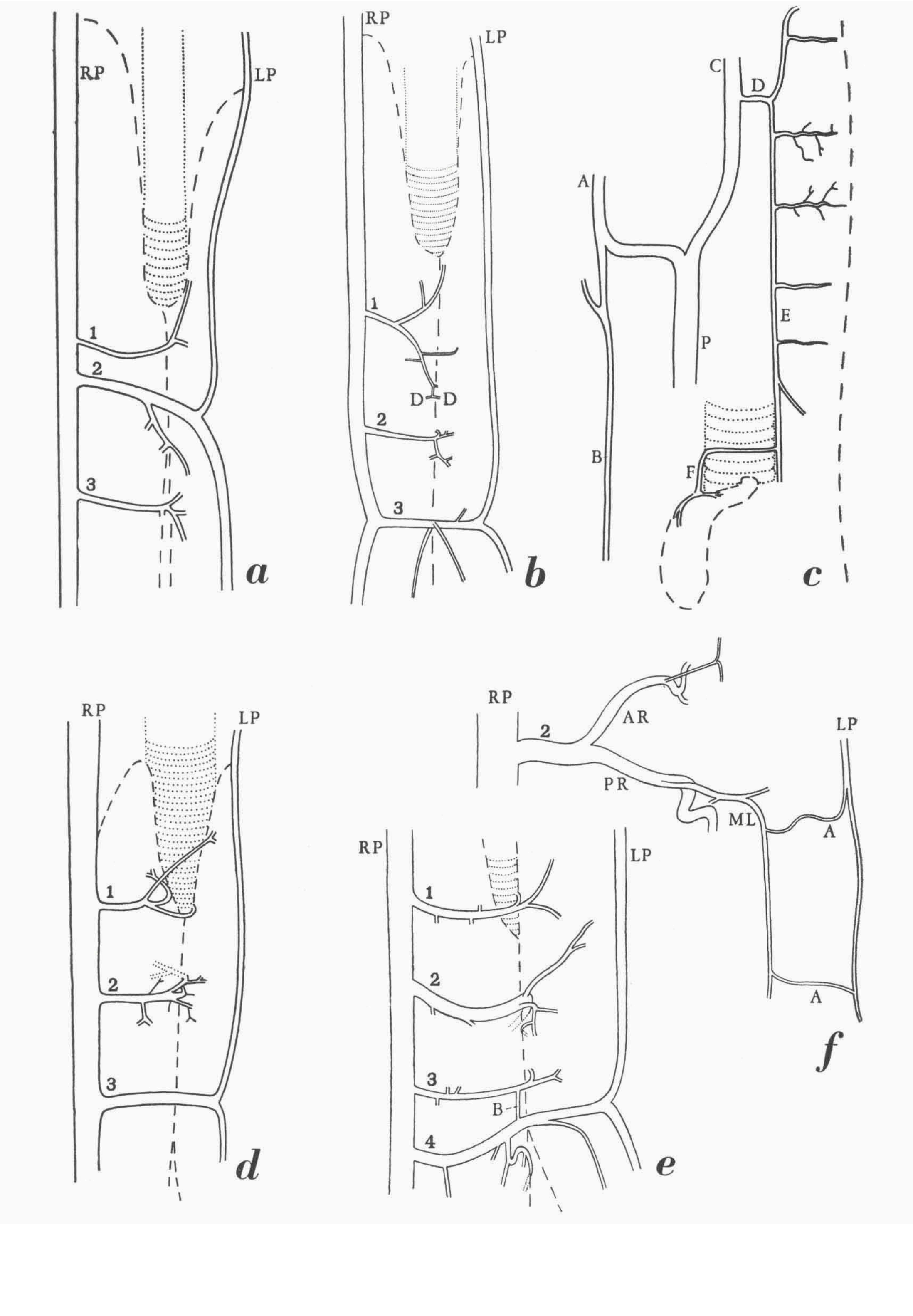
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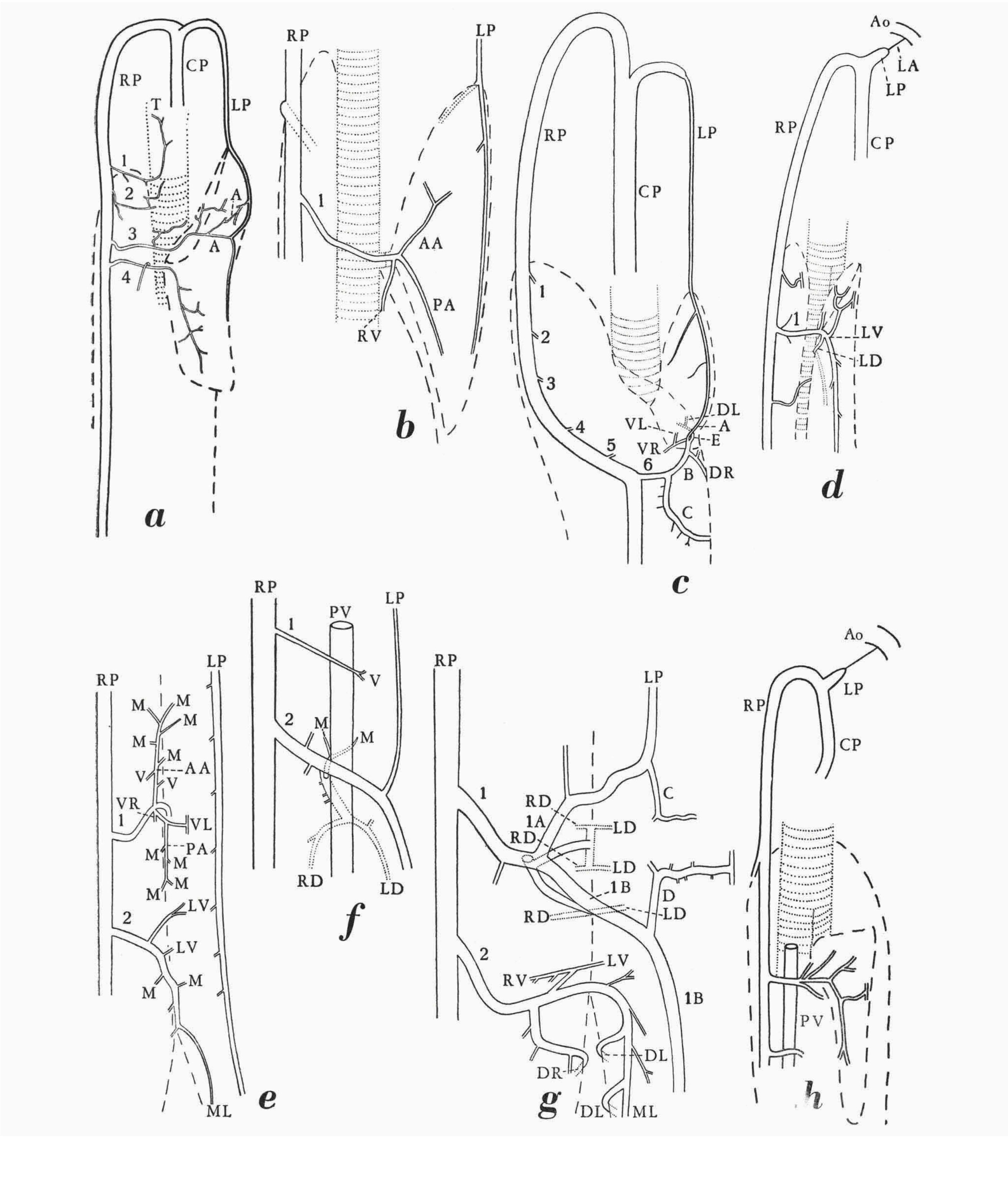

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