THE *TRUNCUS ARTERIOSUS* OF AMERICAN FROGS, *RANA SPHENOCEPHALA, PALUSTRIS, PIPIENS, CLAMITANS* AND *CATESBEIANA*, AS CONTRASTED TO EUROPEAN SPECIES[1)]

By

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(*With one plate and seventeen text-figures*)

Author's Abstract

The *Truncus arteriosus* of American *Rana* is essentially the same as in European *Rana*. Chief differences occur in *Rana catesbeiana* in which the anterior *Bulbus cordis* valves are seldom found in schematic order. Two constant variations from the European species are to be found, however, in all American species i.e. the *Septum medianum interpulmonale* continues further posteriorly in the *pulmo-cavum* and the *Canalis caroticus dexter* is smaller than the *Canalis caroticus sinister*.

India ink injection through the pulmonary vein shows that the Spiral valve of the *Bulbus cordis* together with the flexion of the arms of the *Truncus impar* and the contraction of the ventral bulbus wall on the edge of the Spiral valve, brings about a complete separation of the two types of blood.

The much used cut of the *Truncus arteriosus* of PARKER and HASWELL shows the *Truncus arteriosus* in erroneous aspect. GAUPP's figure or the figure shown in this paper is much to be preferred for general text-book representation.

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Contents

Introduction

Historical. The structure of the *Truncus arteriosus* of *Rana* was first investigated by BRÜCKE ('51), in which the details of its morphology were carefully worked out. However, his drawings and observations on several points were questionable and consequently were modified by FRITSCH ('69). Both BRÜCKE and FRITSCH were forerunners in the study and their works formed the background and basis for the classic investigations of SABATIER ('73) a few years later.

In 1882, BOAS published a comparative study of the *Truncus arteriosus* of Amphibia, which even today is standard in most respects. In part it offers the clearest description of the truncus of Amphibia that has ever been written. However, the truncus of *Rana* is not treated in so much detail as one would like, since BOAS is dealing more in comparisons with other forms rather than pure morphological descriptions.

It was with GAUPP ('96), that the most complete work on the *Truncus arteriosus* was carried out. His remarkable drawings and well organized descriptions give us the best idea of this complicated structure. The work that he carried out has formed a basis for comparison throughout this investigation. Even though GAUPP's descriptions are accurate anatomically speaking, for the European forms, this fact does not give us the authority to say that the American *Rana* are similar to the European, as one is often led to believe from reading

TABLE 1

Comparison of the number of valves and the location of the opening of the pulmo-cutaneus trunci as given by various authors

Author-Text-Species	Number of Posterior Bulbus valves	Number of Anterior Bulbus Cordis Valves	Position of Opening of Pulmo-cutaneous Arch
GAUPP, E. — "Anatomie des Frosches." 1896 (*Rana esculenta*)	3 semi-lunar	3 valves with one divided by a septum	"*Bulbus cordis*"
BOAS, J.E.V.—Über den Conus arteriosus der Amphibien." 1882 (*Rana platyrrhina*)	3 semi-lunar	3 valves with one divided by a septum	"*Bulbus cordis*"
SEDGWICK, A. — "Text Book of Zoology." 1905 (*Rana platyrrhina*)	3 semi-lunar	3 semi-lunar	"*Conus*" (same as Bulbus cordis)
HOLMES, S.J.—"Biology of the Frog." 1927 (*Rana temporaria*)	3 semi-lunar	Spiral valve "widens out at its anterior end into a cup-like valve. Two smaller valves at the same level."	"*Truncus arteriosus*" (same as Bulbus cordis)
PARKER and HASWELL—"Text-Book of Biology" 1897. (*R. temporaria*)	3 small semi-lunar	1 valve with end of Spiral valve free	"*Truncus arteriosus*" (same as Bulbus cordis)
MARSHALL, M.A.—"The Frog." 1896. (*Rana* —)	3 semi-lunar	3 semi-lunar	"*Synangium*" (same as Truncus impar)
LANGER, A.—"Evolution of the Bulbus cordis." 1894. (*R. mugiens*)	3 semi-lunar	3 semi-lunar	"*Bulbus cordis*"
BOURNE, G. C.—"Comp. Anatomy of Animals." 1900. (*R. mugiens*)	2 semi-lunar	3 to which one the spiral valve is fused	Opens "just to the middle of the three valves"
ROLLESTON, G.—"Forms of Animal Life." 1870 (*Rana* —)	3 semi-lunar	3 of which one is the spiral fold, the other two are dorsal and ventral	"*Bulbus cordis*"
PEELLE, M.—"The Truncus of *Rana sphenocephala*." 1931	3 semi-lunar	3 of which one is a continuation of the septum bulbi	"*Bulbus cordis*"

American texts in which the basis of the descriptions used are GAUPP's. How much the internal characteristics of the *Truncus arteriosus* of American forms are similar to the old world forms has been the problem of this research. As far as I can ascertain, the American *Rana* have not been studied in respect to the *Truncus arteriosus.* The European investigators have worked on the following species : *Rana platrryhina, esculenta, mugiens* and *temporaria.* To my knowledge the American species, *Rana pipiens, clamitans, palustris, catesbeiana,* and *sphenocephala* have not been carefully investigated.

Many authors have used different terminologies for the study of the *Truncus arteriosus,* thus causing considerable confusion. Reference to table I will show that BOAS and GAUPP, the two important investigators in the study of the *Truncus arteriosus* are in agreement.

Material and Methods

Rana sphenocephala, the Southern Leopard frog of the United States, was used for the main part of the investigation, since this species was accessible at the time. Being closely related to *Rana pipiens,* it was thought that it would show close affinity in structure to that species, which was later shown to be a correct hypothesis. *Rana palustris, pipiens, clamitans* and *catesbeiana* were also studied and compared with *R. sphenocephala* and the European species.

The chief means of making this study was by dissection of the posterior and the anterior portions, respectively of the truncus. This method of study served to show fairly well under the dissection microscope the principal parts of the truncus. To secure the valves in natural position it was found helpful to inject the heart with alcohol. The method that was used is as follows : A frog was bled by cutting a leg artery while the heart was still beating. The heart was then injected with 95% alcohol through the dorsal aorta. After complete distension, the heart and truncus were removed and fixed in BOUIN's solution. This procedure usually placed the truncus in excellent condition for general study with the low power dissection microscope.

Another method that was used both for dissection and serial sectioning was the BJELOUSSOW's gum arabic process. BJELOUSSOW's gum arabic mass was injected into the beating heart and truncus, through the ventricle. After distension of the heart and truncus, the whole animal was immersed in 95% alcohol. This was done in order to produce a decided reaction in the fluid itself. BJELOUSSOW's mass has the property of hardening and swelling to twice its natural volume when thrown into alcohol. When treated in this fashion the *Truncus arteriosus* greatly enlarged and gave the observer a better change to study its morphology. It was found almost impossible to fix the truncus satisfactorily in BOUIN's fluid without first injecting with BJELOUSSOW's mass.

It was the general procedure to make complete serial sections of the heart and truncus in various species of *Rana* and check them with each other. At least two complete serial series were made of each species studied and with *Rana sphenocephala,* on which the main part of this investigation was carried out, as many as ten series were made. After so doing, two wax model reconstructions were made at the same time, and the corresponding internal structures checked with each other.

In relation to the physiology of the *Truncus arteriosus,* several India ink injections were made through the pulmonary vein. These experiments will be described later under the physiology of the *Truncus arteriosus.*

General Description

Outwardly, the *Truncus arteriosus* of *Rana sphenocephala* is little different from any other common species of frog. It has (Fig. 1) its origin near the upper anterior portion of the ventricle, somewhat to the left of the extreme right margin of that structure. The course it takes across the auricles is more or less diagonal from right to left. As a whole, the *Truncus arteriosus* is divided into two portions, a *Truncus impar* region to the anterior and a *Bulbs cordis* region to the posterior. There is a medium pinching in near the anterior extremity of the *Bulbus cordis* which shows distinctly as a line between the two truncial areas. Though *Rana sphenocephala* shows this line quite clearly it not so apparent in *Rana clamitans* and *Rana catesbeiana.* The left fork of the *Truncus impar* continues in the same general direction as the *Bulbus cordis,* while the right arm bears off quite sharply in that direction.

We can easily distinguish the two main parts of the *Truncus arteriosus* by size and shape. The posterior region, or the *Bulbus cordis* is usually much larger in diameter than the anterior portion, or *Truncus impar.* The color of the two areas also differs, in that the *Bulbus cordis* is the darker. The size of the *Bulbus cordis* varies in relation to the portions we examine. The middle of the *Bulbus cordis* is usually swelled out, whereas its anterior and posterior extremities are pinched in. Its contour is bulged and uneven.

Investigators have given to the main divisions of the *Truncus arteriosus* various names. MARSHALL ('96), calls the *Bulbus cordis,* the "Pylangium," and the *Truncus impar,* the "Synangium." PARKER and HASWELL ('97), call the anterior portion of the truncus, the "Conus arteriosus" and the posterior region the "Truncus arteriosus." GAUPP ('96) whose terminology I follow uses the term "Truncus arteriosus" to indicate both the *Bulbus cordis* and the *Truncus impar.*

In the *Truncus arteriosus* we meet with numerous valves and septa. Standing at the entrance of the *Bulbus cordis* there are three small semi-lunar valves (Plate IV). Extending longitudinally through out the *Bulbus cordis* a long valve known as the Spiral valve or *Septum bulbi* divides the truncus lengthwise into two nearly equal divisions. Near the anterior end of the *Bulbus cordis* is located another set of three vavles, known as the anterior bulbus valves (Plate IV). Each of these valves assumes a complex fusion with the bulbus wall, but their identity is quite distinct and there is no difficulty in separating them from each other. The function of each valve is dependent on its location in the bulbus cavity. The valves may be said to assume two general positions in reference to the wall of the *Bulbus cordis,* i.e. a dorsal and ventral location; two valves having their origin from the bulbus wall totally and the other from the bulbus wall and the anterior margin of the Spiral valve. Of the two valves that originate from the bulbus wall, one arises from the ventral surface and one from the left dorsal area (Plate IV). The ventral structure is known as *Valve 3* and the dorsal one as *Valve 2*. The last named valve lies directly dorsal to *Valve 3* and stands guard to the entrance of the pulmonary trunk. It is for this reason known sometimes as the pulmonary valve. Its ventral companion, *Valve 3* assumes a different function in that it guards the entrance to the aortic trunks. The remaining valve is *Valve 1*. It has its origin as a continuation from the anterior portion of the Spiral valve. One might describe it as a cup with its bottom side fused to the anterior margin of that structure. The cup like cavity it forms is not single, but is bisected by a septum, *Septum principale* which comes back posteriorly from the *Truncus impar*. This partition in other words divides the valve into half valves, a dorsal portion and a ventral portion. This arrangement can be seen if we cut across transversaly the anterior portion of the *Bulbus cordis* and open up the left wall (Fig. 11).

The anterior portion of the *Truncus arteriosus* or that portion known as the *Truncus impar*, is made up of a short tabular section in the posterior extremity and a divided "Y" like section in the anterior division (Fig. 1). Internally, the *Truncus impar* is divided by a horizontal septum throughout its entire length, the *Septum principale* (Plate IV). Each of the parts thus formed is again divided by a septum at right angles to the *Septum principale*, the *Septum medianum interaorticum* (Fig. 2 and Plate IV). By this division the *Truncus impar* is divided into four parts, two dorsal portions which are pulmonary in function in contrast to the two ventral which are aortic.

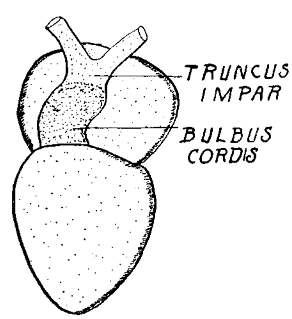


Fig. 1. Heart and *Truncus arteriosus* of *Rana sphenocephala*.

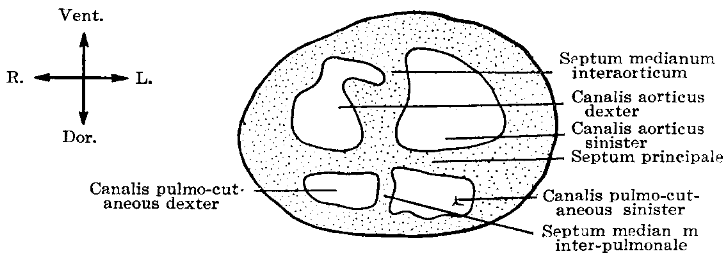


Fig. 2. Cross section through the *Truncus impar* of *Rana sphenocephala* at the beginning of the *Septum medianum interpulmonale.* (Level "L" of Plate IV.) ca. ×8.

The division of the *Truncus impar* into these four regions continues throughout the entire structure. Towards the head the aortic cavities are again bisected by a horizontal septum, the *Septum carotideum dexter* and *sinister* (Fig. 3). They receive their names in accordance to their location, i.e. whether they appear in the right or left truncus arm. Thus the carotideum septum in the left arm of the *Truncus impar* is known as the *Septum aortico-carotideum sinister* (Plate IV. and Fig. 3), and the septum in the right arm as the *Septum aortico-carotideum dexter* (Plate IV). The complete division of the structure into six parts does not occur in the lower part of the *Truncus impar* but takes place just before the bifurcation of the two truncial arms. Figure 2, represents the situation that we find in the posterior region of the *Truncus impar* (level L. Plate IV), whereas figure 3 (level M. Plate IV) is drawn to show the situation as we find it in the extreme

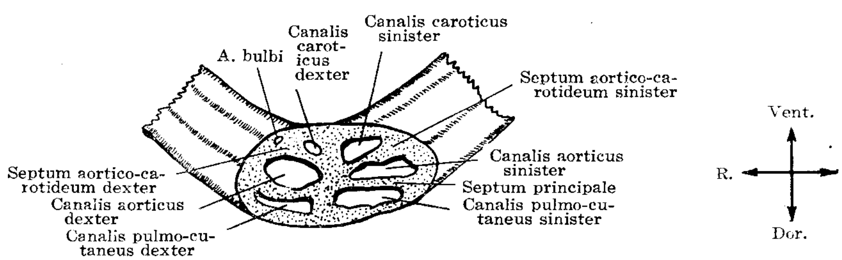


Fig. 3. Cross section through the *Truncus impar* immediately caudal from the bifurcation point. In this view we are looking towards the head with the direction of the blood flow. (Level "M" of Plate IV.) ca. ×8.

anterior portion of the undivided *Truncus impar*, immediately behind the bifurcation point.

The condition thus brought about by these horizontal and vertical septa is such that each arm of the *Truncus impar* as it goes in its respective direction, takes along with it three canales, that are extensions we might say of the three cavities formed on each side of the *Septum medianum interaorticum*. We, therefore, find in each arm of the *Truncus arteriosus* three canales, namely, the pulmonary, the systemic, and the carotid. Depending on which arm of the *Truncus arteriosus* we examine, these various canales are named as follows: In the right arm: the pulmonary canal, *Canalis pulmo-cutaneus dexter*; the systemic canal, *Canalis aorticus dexter*; the carotid canal, *Canalis caroticus dexter*. In the left arm: the pulmonary canal, *Canalis pulmo-cutaneus sinister*; the systemic canal, *Canalis aorticus sinister*; and the carotid canal, *Canalis caroticus sinister* (Plate VI).

The Posterior Valves of the Bulbus Cordis

The *Bulbus cordis* arises from the ventricle as a thick short tube. The opening into it from the ventricle is guarded by three small semilunar valves, which prevent the backward flow of blood into the ventricle during the second half of the contraction. The nature of these valves from a morphological viewpoint presented an interesting study, since GAUPP ('96) neglected to study them in detail. He gives their names only, as *Left Ventral Valve*, *Right Ventral Valve* and *Dorsal Valve* (Fig. 4). In the species studied in this investigation, *Rana sphenocephala*, *clamitans*, *palustris pipiens* and *catesbeiana*, these three valves have always been found well developed. Figures 5, 6 and 7 show typical arrangement in cross section.

The posterior *Bulbus cordis* valves (Fig. 4), take their respective names from the areas from which they have their origin. That is to say, the *Left Ventral Valve* arises from the left ventral wall of the *Bulbus cordis* and the *Right Ventral Valve* arises from the right ventral wall. This places the *Dorsal Valve* between the two larger *Left* and

Right Valves. Its base is, however, not in a line with the base of the two main structures. In serial cross sectioning it does not make its appearance until the upper most portions of the right and left valves are reached. This means, (Fig. 4), that the *Dorsal Valve* is located near the anterior margin of the *Right Ventral* and *Left Ventral* valves.

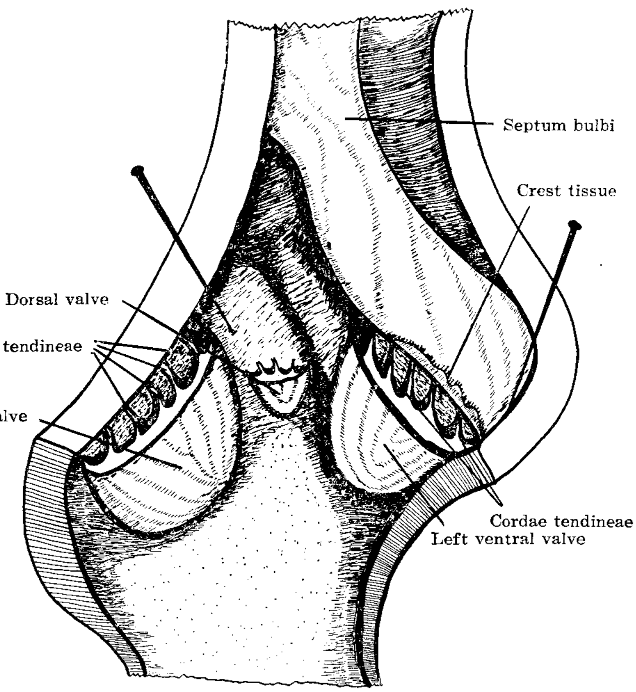


Fig. 4. Posterior portion of the *Bulbus cordis* opened from ventral side, showing the posterior *Bulbus cordis* valves. Somewhat modified after GRAHM KEER.

The *Dorsal Valve* is too small to be seen plainly in gross dissection, but its presence can be ascertained by cross sectioning as shown in figures 5 to 7. Except in *Rana catesbeiana,* this valve is so minute that even in cross section it is hardly discernable. Any theory as to its rôle in circulation must, because of its small size be discarded. Theoretically, blood flowing backwards would push it ventrally into the cavity of the bulbus where it would interlock with the other two valves and help to further close the passage way.

Of the two valves, *Right Ventral* and *Left Ventral* each varies in size with different species. There is no apparent evidence that the variation is constant and what appears as variation may be faulty sectioning and preparation. Neither one of the valves is to any extent larger than the other. In certain sectioning though, the *Left Ventral Valve* lasted longer in the series than did the *Right Ventral* structure. This would indicate that it is to a slight extent the larger. In figure 4, however, I have drawn them of as nearly the same size as possible, believing that the variation that occurs in certain instances is not the typical condition.

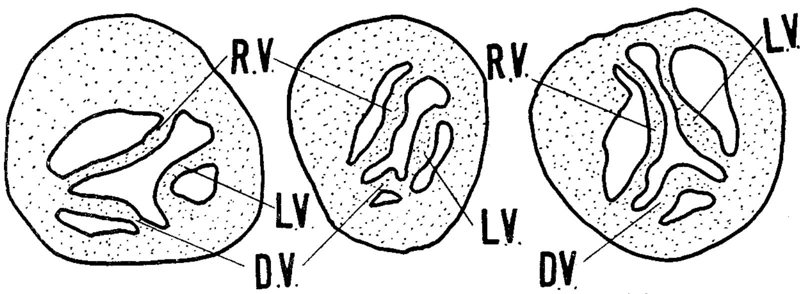


Fig. 5. Fig. 6. Fig. 7.

Figures 5 to 7. Cross sections through the posterior *Bulbus cordis* region in *Rana pipiens, sphenocephala* and *clamitans*. ca. ×8.

Fig. 5. *Rana pipiens*. R.V., right ventral valve.
Fig. 6. *Rana sphenocephala*. L.V., left ventral valve.
Fig. 7. *Rana clamitans*. D.V., dorsal valve.

The posterior bulbus valves turn their open mouths towards the cavity of the *Bulbus cordis*. Thus they prevent the backward flow of blood as it tends to rush into the ventricle during the latter part of the heart contraction. As BOURNE ('00) has pointed out the semi-lunar valves of the *Bulbus cordis* are tied to the inner bulbus wall by *Cordae tendineae*, as shown in figures 4 and 8, in a similar fashion as are the valves between the ventricle and auricles. The presence of *cordae tendineae* substantiates the hypothesis that the posterior *Bulbus cordis* valves act only as preventors against a return flow of blood during the heart contraction. I would judge from their location and minute size that they do not play a part in bringing about a separation of the venous and arterial blood, as does the Spiral valve of the *Bulbus cordis* proper. The *Dorsal Valve* being much weaker than the other two is only partly held in place by a cord along its anterior margin. The presence of *Cordae tendineae* is not seen in gross dissection because of the minuteness of the cords. In cross sectioning they are often torn because of their delicacy. However, if care is taken their arrangement can be seen as in *Rana sphenocephala* (Fig. 8). It will be noticed that they are

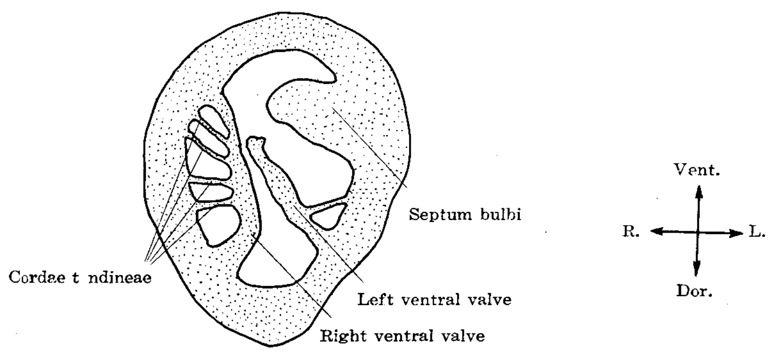


Fig. 8. Cross section through the *Bulbus cordis* of *Rana sphenocephala* showing the *Right* and *Left Ventral valves* with *Cordae tendineae* (At this point in the *Bulbus cordis* the *Dorsal Valve* does not show). Drawn with aid of Camera Lucida. ca. ×10.

stretched across from the anterior edge of the *Right Ventral Valve* to the *Bulbus cordis* wall. Only one cord in this section could be found intact between the *Left Valve* and the bulbus wall. This is not due to the lack of such, but because of the infirmity of the cords, which were torn in sectioning. In this area, the *Dorsal Valve* does not show. This is the logical situation, since the section was made anterior to the position of the dorsal structure.

The Septum Bulbi of the Bulbus Cordis

The most important structure in the *Truncus arteriosus* is the *Septum bulbi* or Spiral valve. In *Rana sphenocephala* and other common species of the United States, as BOAS ('82) pointed out for the European forms, the spiral shape is not so apparent as has been thought. Its basal direction is on the other hand more in the nature of a broad curve from left to right throughout the bulbus cavity. There is very little twisting to be seen.

The origin of the Spiral valve is in the lower part of the *Bulbus cordis*, where it developes from the left ventral wall in close connection with the *Left Ventral Valve* of that region (Fig. 4); the upper edge of the *Left Ventral Valve* striking against the origin of the *Septum bulbi*.

In the posterior portion of the middle region of the *Bulbus cordis* immediately in front of the junction of the *Septum bulbi* with the ventral bulbus wall, the basal portion of the Spiral valve swings about to the left 180 degrees, or we might say rotates from right to left on an arc of 150 degrees or more. This flexion of the basal portion carries the whole *Septum bulbi* around with it and places it on the dorsal bulbus wall. Thus the Spiral valve, which at its origin was fused to the ventral bulbus wall, soon in its course through the cavity comes to rest in a dorsal-ventral position in the bulbus cavity. The turning is abrupt and may be thought of as a quick spiral twisting (hence the name of the valve probably), though the space through which it turns is too short to be seen unless orientation of wax models is attempted.

After arriving in dorsal position, the Spiral valve swings across the cavity of the bulbus in a gradual curve from left to right. From a ventral cut through the bulbus wall, even this slight curve, which might have suggested the name for the valve is not impressive. On first observation, the *Septum bulbi* appears as a straight longitudinal partition in the bulbus cavity. However, if on close scrutiny and in preparation of wax models care is taken, the slight curve can be ascertained.

The *Septum bulbi* in the posterior region of the *Bulbus cordis* is in itself quite different from what it is throughout the cranial area. A condition is present in certain species of *Rana* in which this portion of the *Septum bulbi* has on its right ventral surface an attached crest of tissue (Plate IV). In *Rana catesbeiana* and *sphenocephala* this crest of tissue is strongly developed and forms a free flapping edge to the *Septum bulbi* (Plate IV and Fig. 9). The crested nature of the septum.

I have always found in *Rana sphenocephala* and *catesbeiana*. With *Rana catesbeiana* its development is quite marked, as it extends along the ventral edge of the Spiral valve for a distance of over three millimeters. In this comparatively long space, considering the length of the *Bulbus cordis* itself, the crest of tissue goes through alternations. Its edge in the posterior part of its course is straight, but in the middle and distal portion, it is twice dentate. Thus it appears ruffled and undulated (Fig. 4 and Plate IV).

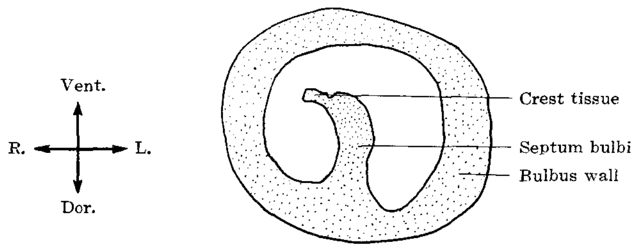


Fig. 9. Cross section through the posterior portion of the *Bulbus cordis* in *Rana sphenocephala* showing the crest of tissue of the *Septum bulbi*. ca. ×8.

Because of the delicacy and membranous character of the crest, cross sections made through the *Bulbus cordis* in this region usually result in the knife tearing them and producing poor results. Occasionally, however, a cross section as in figure 9 can be obtained which shows the crest in characteristic manner. This section was taken from *Rana sphenocephala* and drawn with aid of camera lucida. As yet I have not found such a crest in *Rana clamitans* or *palustris*. In *Rana catesbeiana* it is one of the most striking things about the *Septum bulbi* that appears in gross dissection. As far as can be ascertained this modification of the *Septum bulbi* does not occur in the European forms.

As the *Septum bulbi* leaves the posterior region of the *Bulbus cordis* cavity it divides that structure into two parts, a right cavum, the *Cavum aorticum* and a left cavum, the *Cavum pulmo-cutaneum* (Fig. 10 and Plate IV.) The division thus accomplished is of course understood to exist only when the ventral wall of the *Bulbus cordis* is contracted and pressing firmly against the free edge of the *Septum bulbi*. These same cava, namely the *Cavum aorticum* and the *Cavum pulmo-cutaneum* continue throughout the whole *Truncus arteriosus* including both the anterior and the posterior portions of *Bulbus cordis* and *Truncus impar*. In the continuation anteriorly they retain the same names given them in the lower part of the *Bulbus cordis*, namely the *Cavum aorticum* and *Cavum pulmo-cutaneum*.

Near the anterior end of the *Bulbus cordis*, the *Septum bulbi* broadens ventrally with a corresponding thickening of its basal portion (Plate IV). Its right and left margins, however, differ from each other in certain respects. A portion of the left edge goes over to the left bulbus wall and fuses with it. By this I have reference to the section or portion of the *Septum bulbi* located at the letter " Z " in Plate IV. This fusion was constant in all species investigated, except *Rana catesbeiana* which in a few instances lacked it.

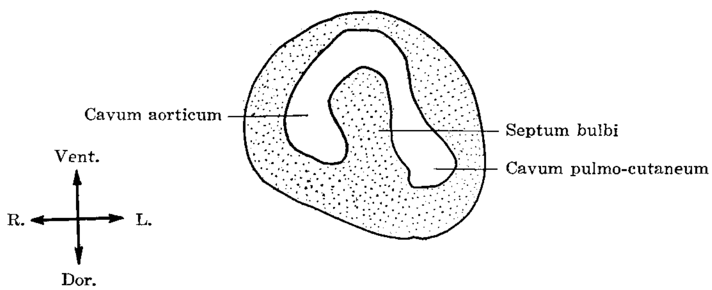


Fig. 10. Cross section through the exact middle portion of the *Bulbus cordis*, of *Rana sphenocephala* ca. ×8.

The central region of the anterior end of the *Septum bulbi* (located in Plate IV at letter " X ") is carried forward and forms a crown or roof over the floor of the aortic cavum. It thus produces a pocket or cup-like cavity, which open towards the head.

The tissue that makes up this arrangement is known as *Valve 1A* (Fig. 11). It constitutes just half of the whole valve however, a dorsal portion known as *Valve 1B*. continues down into the interior of the bulbus cavity. The two halves are together known as *Valve 1*. The division of these two parts of *Valve 1* is accomplished by a septum,

Septum principale (Fig. 11), which comes back from the *Truncus impar* and bisects in through its central portion.

It can be seen that the right edge of the Spiral valve (location at letter " Y " in Plate IV) fuses more or less broadly with the right dorsal wall. The exact situation referred to can be seen in cross section (Figs. 12—15). In these cuts, the *Bulbus cordis* in as near a location as possible to letter " Y " has been sectioned in various species of *Rana*. Here we find the typical number of anterior *Bulbus cordis* valves, namely, *Valves 1, 2* and *3*. *Valve 1* presents the most complicated situation in that it is composed of two parts, a dorsal and ventral portion. *Valve 1A* in these cuts can be orientated at location " X " in Plate IV, without difficulty. However, the morphological relationship is

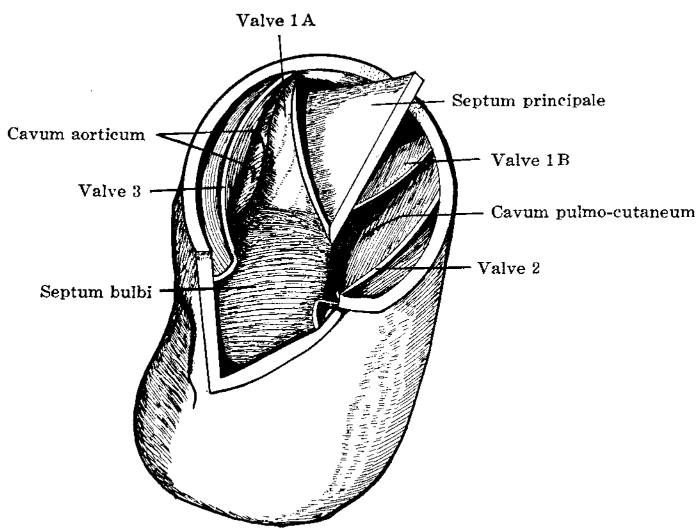


Fig. 11. Anterior portion of the *Bulbus cordis* opened along the left side. Anterior end cut transversely on an angle of about 10 degrees. Left edge of *Valve 1A* has also been cut and freed from left ventral wall. The whole *Bulbus cordis* has been turned somewhat to the right. (Drawn after GAUPP).

liable to be confusing from these two cuts alone. The situation is helped considerably by cutting across this area in gross dissection as has been done in figure 11. Here the *Bulbus cordis* is transversely cut on a slight angle and the left lateral wall opened by a V shaped incision.

The bulbus has been turned towards the right, that is the frog's right, so the orientation of the Spiral Valve and *Valve 3* is somewhat modified. We can see in this figure that the two half valves *V1A* and *V1B*, are separated from each other by a horizontal partition septum, the *Septum principale* which comes back in a horizontal plane from the *Truncus impar*.

The complexity of this region is not made clear in GAUPP's "Anatomie des Frosches" in the text descriptions, though his figure (similar to figure 15) is quite accurate. He describes the whole situation somewhat as follows: (translation)—"the end of the *Septum bulbi* extends to the right becoming as it does so, much thicker and forming a large valve, *Valve 1......*" He goes on to say that this valve is the largest in the anterior bulbus region. I must draw sort of distinction here for I find that *Valve 1* is comparatively weak in relation to the other two valves, namely *Valves 2* and *3*. If GAUPP has reference to *Valve 1* as a part of the anterior portion of the *Septum bulbi* his distinction is correct. If the valves are taken separately and compared, *Valve 1* is about second in size, *Valve 3* being the largest. Whatever may be the condition GAUPP referred to, *Valve 1*, if considered apart from the anterior portion of the *Septum bulbi*, is not very large. It can be seen from figures 12 to 15 that the cavity formed between the dorsal edge of *Valve 1A* and the *Septum principale* is rather small, and in some species like *Rana pipiens* (Fig. 15) is hardly discernible even in its greatest development as this figure has been selected to show.

The *Septum principale* may be thought of as a sort of partition that goes down into the middle of the cup-like depression formed by *Valve 1*, more or less completely dividing it into the two afore mentioned parts, *1A* and *1B*. BOAS ('82), has in a few instances observed that this septum does not always reach as far back as pictured in figure 11, that is resting completely on the bottom of *Valve 1*, but ends abruptly to the anterior. I have found this to be the condition in one species *Rana catesbeiana*. In all other species investigated the situation met with simulates what is normal in European forms.

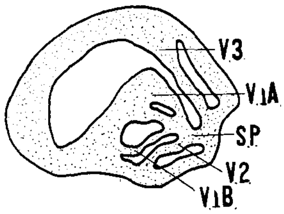


Fig. 12.
Rana Sphenocephala.

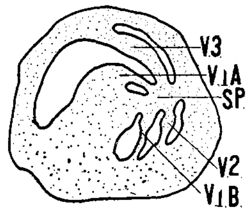
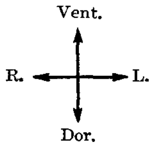


Fig. 13.
Rana Clamitans.



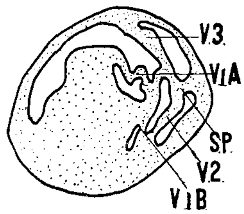


Fig. 14.
Rana Palustris.

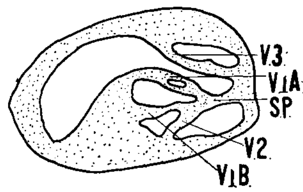


Fig. 15.
Rana Pipiens.

Figs. 12 to 15. Cross sections through the anterior *Bulbus cordis* valves. ca. ×8.

V. 1B., valve 1B V. 2., valve 2 S. P., septum principale
V. 1A., valve 1A V. 3., valve 3

However, in *Rana catesbeiana*, in a few instances, the condition met with is similar to figure 16. If this species were normal it should show in this area conditions similar to figures 12 to 15. As it is, there are in *Rana catasbeiana* several modifications. The edge of *Valve 1A* does not reach over to the left and fuse with the wall of the bulbus, but turns dorsally and fuses there. This variation is not constant, however, even in *Rana catesbeiana*, the normal situation that should be found having appeared in certain serial cuts. It is also apparent that the *Septum principale* has not made its appearance in this cut (Fig. 16). In other words, the septum ends anterior to this region.

Two other valves, besides *Valves 1A* and *B*, demand our attention. These are *Valves 2* and *3*. *Valve 3* is the largest of all the anterior bulbus structures. Whereas *Valves 1B* and *2* stand guard over the opening to the pulmo-cutaneus trunk, (refer to table 2), this valve, *Valve 3*, has the important function of guarding the entrance to the

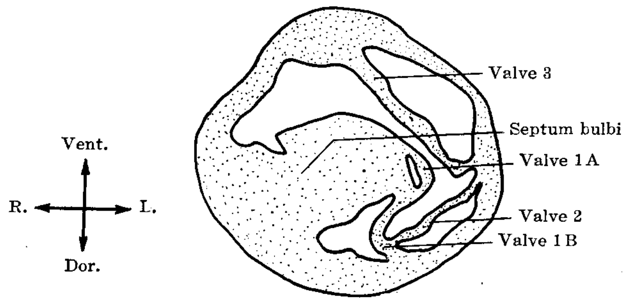


Fig. 16. Cross section through the anterior region of the *Bulbus cordis* of *Rana catesbeiana*. Drawn with aid of camera lucida. ca. ×8.

aortic cavum. Because of this very important function, the valve is well developed and firmly fused along the bulbus wall to give it greater rigidity.

TABLE 2

Function of the anterior Bulbus cordis valves.

Valve 1A	Guards the opening to the right aorta, left carotid and right carotid artery.
Valve 3	Guards the opening to the left aorta.
Valve 1B	Guards the opening to the pulmo-cutaneum trunks.
Valve 2	Guards the opening to the pulmo-cutaneum trunks.

Valve 2 (Plate IV), is rather small, but can be seen clearly in cross section and in a careful dissection. It lies dorsal on the *Bulbus cordis* wall immediately in front of the opening to the pulmonary arch. In all species investigated it has been found. There is little variation as its shape, size or position in the common forms of *Rana*.

The number of valves in the *Bulbus cordis* has been in dispute among various authors. Reference again to table 1, points out some of these differences. In general, it is agreed that the number of posterior and anterior valves is three. It will be noticed also that the location of the opening of the pulmonary arch, figured as "P" in Plate IV, is in dispute. BOURNE ('00) though mistaking the number of valves in the posterior region of the *Bulbus cordis* gives us the clearest description of the location of the opening of the pulmonary arch by saying it "opens just to the middle of the three valves," or in other words between *Valve 1B* and *Valve 2* as shown in figures 12 to 15. He has, however, in his drawing of the *Truncus arteriosus* made the pulmonary opening to appear in the *Truncus impar* (synangium) and the openings of the carotid arches to appear in the lower portion of the *Bulbus cordis*! Even a casual observation will tend to show that the carotid arteries do not open in the *Bulbus cordis.* In all probability BOURNE confused the opening of the pulmonary arch with the openings of carotid arches and labeled his drawing in exact reverse of the actual situation.

In opening the *Bulbus cordis* by a ventral cut as in Plate IV, only the ventral parts of the valves come to view. We can by this means easily see the large *Valve 3*, the smaller dorsal *Valve 2* and the ventral surface of *Valve 1A*. However, the dorsal portion of *Valve 1*, which is underneath the *Septum principale* cannot be discerned in such a view. It does show in cross section of various *Rana* as drawn in figures 12 to 15, which were taken through the exact middle portion of the anterior *Bulbus cordis* valves (position "X" in Plate IV). Even with careful pinning back of the *Bulbus cordis* walls, the small structure (*Valve 1B*) cannot be seen. In a cross section series it only lasts for a short distance and is easily overlooked. With *Rana palustris* (Fig. 14), it is of such a minute size that any theory as to its function in the role of circulation must be discarded. Its pocket forming portion is, however, distinct, but very small. Often times *Valve 1B* is supported by thread-like tissues developed between it and the *Septum bulbi*. This condition I have observed in only one species of frog, *Rana sphenocephala*.

Truncus Impar

It must be remembered that the two regions of the *Truncus arteriosus* are in continuation with each other and one cannot dogmatically say where the *Truncus impar* begins and the *Bulbus cordis* ends.

Oliver ('10), in describing Australian *Hyla* and the marked differences that appear between the *Truncus impar* and the *Bulbus cordis*, defines the *Truncus impar* (synangium) as that part of the *Truncus arteriosus* anterior to the Spiral valve. This definition is not good in relation to *Rana*, except in a general sence, since for a considerable distance the Spiral valve carries forward into the *Truncus impar* proper, as a fine thread of tissue. By this I have reference to the thin anterior marginal edge of *Valve 1* which is more or less the Spiral valve modified and carried forward into the cavity of the aortic arches, (location in Plate IV at "X." As far as this investigation is concerned the *Truncus impar* begins in the region where the *Septum principale* becomes firm and definitely divides the truncus cavity into two parts, a dorsal and a ventral region.

The *Septum principale* stretches across the cavity of the *Truncus impar* from the right to the left truncus wall. It forms a partition throughout the entire length of the structure and continues also into each arm, where it forms the dorsal floors for the systemic canales in each, and ventral roofs for the pulmonary arteries.

It is helpful to think of the *Truncus impar* beginning immediately anterior to the region from which sections figured in figures 12–15 were taken. This region in Plate IV is located by a dotted line "H." It is more or less a transitional zone between the *Bulbus cordis* and the *Truncus impar* proper. At this point the *Septum principale* has gone completely across the truncus cavity as a floor, separating a ventral portion, the aortic cavum from a dorsal portion, the pulmonary cavum. Thus two main cavities are formed in the *Truncus impar* in its posterior portion, known as the *Cavum aorticum* and the *Cavum pulmo-cutaneum*. As can be noticed these cava receive similar names to the cava in the *Bulbus cordis*. That is to say, the *Cavum aorticum* in the *Bulbus cordis* is continued into the *Truncus impar* under the same terminology, though its morphological nature is somewhat modified. The same can be said in reference to the *Cavum pulmo-cutanuem* in both these regions. At this point we do not have any vertical septa (level "H", Plate IV). The situation is relatively simple just posterior to area "H" in Plate IV, in that the *Septum medianum interaorticum* has not yet developed. In other words, we find only two cava, the *Cavum aorticum* and the *Cavum pulmo-cutaneum* in this transitional zone.

These cavities, the *Cavum aorticum* and the *Cavum pulmo-cutaneum* are single for only a short distance and are soon bisected by a vertical septum, *Septum medianum interaorticum* as they leave the transitional zone of the *Truncus arteriosus*. However, both are not divided at the same place, that is to say, each is divided into two parts at different levels of the *Truncus impar*. The pulmonary arch remains single for a considerable distance towards the head. The aortic cavum is almost immediately divided by the *Septum medianum interaorticum* (hence its name), into a right and left canal. The left cavum is known as the *Cavum aorticum sinister* or *Canalis aorticum sinister*. The right portion formed by the *Septum medianum interaorticum* receives a similar denotation, except in respect to the name denoting its location, being known as the *Canalis* (*Cavum*) *aorticus dexter*. The left canal, *Canalis aorticus sinister* (Plate IV) lies in the same general plane as the *Bulbus cordis*. The right branch, *Canalis aorticus dexter* is, however, flexed in an angle of nearly 50 degrees from the direction assumed by the left truncus arch. This flexion is important, as it is one of the contributing factors in bringing about a complete separation of the blood streams leaving the ventricle.

In Plate IV a dotted line "K" denotes an area in the *Truncus impar* from which figure 17 was drawn. In this portion of the *Truncus impar*, *Canalis aorticus dexter* and *Canalis aorticus sinister* show plainly. The *Canalis aorticus sinister* is slightly the larger. Hereto the *Cavum pulmo-cutaneum* is still a single undivided cavity, since it is a direct continuation of the *Cavum pulmo-cutaneum* of the *Bulbus cordis*. However, it differs from the *Cavum pulmo-cutaneum* of the *Bulbus cordis* in that it is much smaller in diameter. Its boundaries might be said to be made up of two portions of the *Truncus impar*, the *Septum principale* on the ventral, and the truncus wall on the dorsal side.

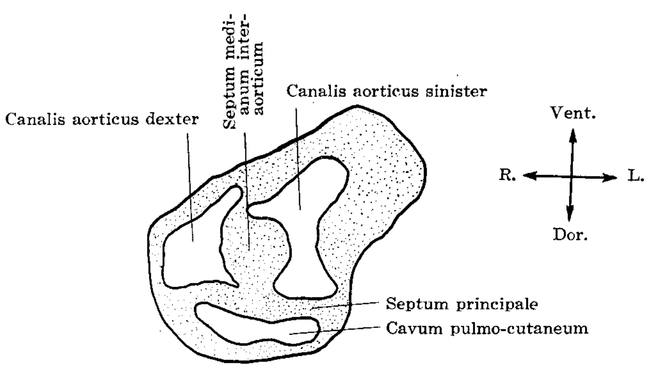


Fig. 17. Cross section through the *Truncus impar* of *Rana sphenocephala* taken at the point where the *Septum medianum interaorticum* divides the aortic cavum. The pulmonary cavum is still single. (Level "K" of Plate IV). ca. ×8.

The *Cavum pulmo-cutaneum* remains single until the *Septum medianum interaorticum* begins in the ventral portion of the *Truncus impar* to develope dorsally to the *Septum principale*. That is to say, this cavity remains single until the *Septum medianum interaorticum* becomes well established in the aortic cavum and sends out a dorsal undergrowth into the pulmonary portion. The partition that it sends down into the pulmonary area is known as the *Septum medianum interpulmonale* since it is a part of the *Septum medianum* that developed in the pulmonary tract. The condition that we now see in the *Truncus impar*, if it is taken in cross section, is as in figure 2. This section was taken at the level "L" of Plate IV. It will be noticed in figure 2 that the *Septum medianum inter-pulmonale*, forms a partition that makes the pulmonary trunk a double structure. Each half thus formed receives a name in accordance with the direction it takes. Thus the left portion which goes into the left truncus arm is known as the *Cavum* (*Canalis*) *pulmo-cutaneum sinister*, and the right portion which goes into the right truncus arm becomes the *Cavum* (*Canalis*) *pulmo-cutaneum dexter*. The *Canalis pulmo-cutaneum dexter* as it continues into the truncus arm becomes the right pulmonary artery in like manner to the *Canalis pulmo-cutaneum sinister* which becomes the left pulmonary artery.

If by imagination, we can mentally picture this situation, an arrow bristle "P" (Plate IV) if it were passed into the opening of the *Truncus impar* from the *Cavum pulmo-cutaneum* of the *Bulbus cordis*, would divide into two parts, P′ and P′, both of which would emerge from the respective pulmonary arteries of the truncial arches. By this arrangement, it can be seen that the pulmonary blood finds exit at P′ and P′ in each truncial arm. This means that an even supply of blood is given to the right and left lungs.

The two canales, *Canalis pulmo-cutaneum dexter* and the *Canalis pulmo-cutaneum sinister* are separated from their ventral companions, the *Canalis aorticum dexter* and the *Canalis aortcum sinister* by a septum which extends horizontally out from the *Septum medianum interaorticum*. This septum is a continuation of the *Septum principale* which we met in the posterior portion of the *Truncus impar*. As it continues into each arm it forms the dorsal floor of the aortic arteries and the ventral roof for the pulmonary canales (Plate IV). The arteries, *Canalis aorticus dexter* and *Canalis pulmo-cutaneum dexter* are therefore one above the other, the aortic canal being ventral to the pulmonary. In like manner the same condition is simulated in the course of the *Canalis aorticus sinister* and *Canalis pulmo-cutaneum sinister* (Plate IV). These aortic canales present interesting morphological specializations, though the *Canalis aorticus sinister* is too simple to demand much description, other than to say that after it becomes clearly divided from the right canal it continues unmodified into the left truncial arm.

It is with the *Canalis aorticus dexter* that an extremely important modification occurs, in that the carotid arteries lead off from it before the truncial arms bifurcate (Plate IV). Immediately before the bifurcation point of the *Truncus arteriosus*, the carotid arteries open into the right systemic arch. They make their appearance in the vertical edge of the *Septum medianum interaorticum* as tiny little holes in that tissue. They can be seen in Plate IV, as "C" and "CS". Each canal that leads off from "C" and "CS" goes to an arm of the *Truncus* *impar.* "C" leads into the right carotid archway and "CS" leads into the corresponding similar canal on the left.

It is to be noticed in this connection that the left carotid artery or the *Canalis caroticus sinister* has its origin in the *Canalis aorticus dexter*, somewhat to the posterior of the opening to the *Canalis caroticus dexter*. By means of arrows, this situation can be seen in Plate IV, arrow C–C′ following the right carotid canal anteriorly to the arrow CS–C′S′. BOAS and GAUPP both pointed out that the carotid arteries arise at different levels. POHLMAN ('14) has tried to show that they arise by a common opening in the right aortic cavum. Evidence to support this view is rather shortcoming. The condition he contends exists, would make the *Truncus impar* in *Rana* in this respect, similar to the condition found normally in reptiles. His view-point, therefore, cannot be supported by homology, it seems to me, since the gap between Amphibians and Reptiles in respect to the Truncus it is quite marked.

The significance of having the carotid arteries open into the right aortic cavum is important in relation to the blood separation. It will be seen when the physiology of the *Truncus arteriosus* is discussed, that the flexion of the right truncial arm in a sharp angle to the left, causes it to receive the greater part of the pure blood stream. Hence, if the carotid arteries did not open into this half of the aortic cavum, they would not receive the vitalized blood, so essential to the head and brain.

The dorsal floor of the *Canalis caroticus dexter* and the *Canalis caroticus sinister* is formed by a continuation of the *Septum medianum interaorticum* in a left and right lateral direction. This horizontal septum extension of the *Septum medianum* divides the carotid arteries from the aortic canales (Plate IV). On the right hand side of the *Truncus impar*, the septum is known as the *Septum aortico-carotideum dexter*; on the left it has nearly the same term, except for the denotation of the direction assumed, being known as the *Septum aortico-carotideum sinister* (Plate IV).

At the point where the two main arms of the *Truncus arteriosus* divide, the bifurcation point as it is called, all the septa described above show in cross section (Fig. 3). This cut has been made just to the anterior of the openings of the carotid arteries, soon after they have become well established. This figure also shows the beginnings of a small artery, the *Artery bulbi,* a small blood vessel which feeds the wall of the *Truncus arteriosus.* It does not supply the walls of the heart proper, since they are nourished by the blood inside the organ itself.

TABLE 3

Parts of the *Bulbs cordis* (Pylangium)

VALVES	CAVA
Dorsal Valve	*Cavum pulmo-cutaneum*
Left Ventral Valve	*Cavum aorticum*
Right Ventral Valve	
Septum bulbi	
Valve 3	
Valve 2	
Valve 1A	
Valve 1B	
Valve 1	

Parts of the *Truncus impar* (Synangium)

SEPTA	VALVES
Septum aortico-carotideum dexter	*Valve 1A*
Septum aortico-carotideum sinister	*Valve 3*
Septum medianum interaorticum	
Septum medianum inter-pulmonale	
Septum principale	

CANALES

Canalis aorticus sinister or Vavum aorticum sinister
Canalis aorticus dexter or Cavum aorticum dexter
Canalis caroticus dexter
Canalis caroticus sinister
Canalis pulmo-cutaneus dexter
Canalis pulmo-cutaneus sinister

The various parts of the *Bulbus cordis* and the *Truncus impar,* that have been described can be listed as in table 3. It will be noted that in this compilation, there is some overlapping of structures as at their location. Thus, *Valve 3* and *Valve 1A* appear in both the *Truncus impar* and the *Bulbus cordis*. This is not to be confused with any error that might have crept in during the compilation of the table, since in actual reality these structures are found in both regions, though *Valve 3* is largely confined to the *Bulbus cordis* and *Valve 1A* more or less lies between the two regions in the transitional zone.

Variations

GAUPP in his "Anatomie des Frosches", Fig. 80 a, p. 280, represents the *Truncus impar* cut across at the point where the carotid arteries leave the *Cavum aorticum dexter* (similar to Fig. 3 in this paper). At this point he says the dorsal pulmo-cutaneum trunk is still a single tube, undivided by the vertical septum, *Septum medianum inter-pulmonale*. He has shown that the pulmo-trunk remains single for a considerable distance towards the head. I find, however, in *Rana sphenocephala* that at a corresponding level in the *Truncus impar*, an entirely different situation occurs, in that the *Cavum pulmo-cutaneum* is divided by the *Septum medianum inter-pulmonale* (Fig. 3). In other words, the *Septum medianum inter-pulmonale* goes further posteriorly in the pulmo-cavum than it does in the European species described by GAUPP. Sections made of the *Truncus impar*, even further towards the *Bulbus cordis* than shown in figure 3 show the *Septum medianum inter-pulmonale* to be quite firm, and dividing the pulmo-cavum into two parts, the *Cavum pulmo-cutaneum dexter* and *sinister*. I have observed this condition in every species studied and find it to be a constant variation from the European situation.

Another important difference between the American frogs and the European is in this same locality. GAUPP in Fig. 80 b, p. 280 represents the *Canalis caroticus dexter* as large and powerful, with the *Canalis caroticus sinister* rather small in diameter. With American forms, I find the exact reverse of this condition. The *Canalis caroticus dexter* is for some time much smaller than *Canalis caroticus sinister* (Fig. 3). This condition is not confined to *Rana sphenocephala* alone, but is constant in other *Rana* as well.

In *Rana sphenocephala* and *catesbeiana* the *Septum bulbi* has a strong crest. This is not apparent in the European species. *Rana sphenocephala* also differs from European species in that *Valve 1B* is supported by thread like tissue.

The *Truncus arteriosus* in *Rana* is not a highly variable structure, neither between various species or in the species itself. The most striking differences appear between *Rana catesbeiana* and other common forms. The variability of the *Truncus arteriosus* even in *Rana catesbeiana* is to be questioned in certain respects. With some individuals, of this species, the *Truncus arteriosus* seemed to be little different from the typical formation of *Rana sphenocephala*, while with some individuals variations seemed to appear. The most striking fluctuations are in reference to the anterior *Bulbus cordis* valves. These valves were seldom found in schematic arrangement. The *Septum principale* was also at variance, in that it sometimes failed to reach the bottom of *Valve 1*. BOAS has observed similar fluctuations in certain forms (*Rana platyrrhina*). Why such a variation should be confined to but one species of *Rana* in both American and European types is difficult to understand. There may be some cause to believe, if BOAS was right, that *Rana catesbeiana* and *platyrrhina* are closely related. Such a conclusion should not be drawn until *R. platyrrhina* is again carefully investigated.

The most striking phase of this investigation is the similarity that has been shown to exist between American and European *Rana* in respect to the *Truncus arteriosus*. Except in *Rana catesbeiana*, as pointed out before, there seems to be no outstanding differences between the old world forms and those confined to Eastern United States. Other than a few minor details, like the size of the carotid arteries in their early beginnings and the development of the *Septum medianum inter-pulmonale* further to the posterior in the *Truncus impar*, the European and American forms are identical. This is significant, since, in many respects, it indicates that the two forms of *Rana* are closely related.

Critical

The situation one meets in studying the *Truncus arteriosus* from various text-book diagrams is quite confusing. Obviously, one of the most important conceptions of this structure to be had by students, is from the much used cut of PARKER and HASWELL. From an anatomical standpoint, this drawing is far from perfect and in many ways inaccurate. PARKER and HASWELL picture the Spiral valve as a free flapping structure in the anterior portion of the *Bulbus cordis.* It is drawn to resemble a paddle that moves from left to right thereby closing the various openings to the pulmonary and aortic arches. However, there is nothing either in the European or the American forms of *Rana* to substantiate such a representation. As pointed out before, the *Septum bulbi* is broad and thick with a firm dorsal portion. Its anterior end is not free and has nothing of the ingenious paddle-spoon arrangement.

Again this much-used picture represents the *Septum bulbi* as a thin partition lying in the truncus cavity like a letter "S." If the trouble to open the truncus is taken, a different situation appears. The valve is thick and firm, except for a narrow free edge that lies up against the ventral bulbus wall. This flap or crest tissue is, however, very minute and confined only to the posterior region of the *Bulbus cordis.* As a whole the valve is entirely different in appearance from the way it is pictured in the PARKER and HASWELL figure.

The relation of the openings of the carotid arches in the right aortic cavum is also very questionably represented. The situation is entirely diagramatic and misleading. The *Septum medianum inter-aorticum* is not shown at all. With its absence, any representation of how the carotid arteries arise is, of course, difficult to explain. However, the arrangement of the posterior *Bulbus cordis* valves is more or less accurate.

Because of these discrepancies in the PARKER and HASWELL figure, it is to be regretted that it has been used so frequently in standard zoological text books. The figure that appears in GAUPP's "Anatomie des

Frosches" is by far the best cut we have and should be used in preference to the PARKER-HASWELL figure. GRAHAM KERR'S figure in "Vergleichende Anatomie des Wirbeltiere" (p. 666) is also to be recommended as a good representation of the actual morphological conditions.

The Physiology of the *Truncus arteriosus* in *Rana*

As it is well known in *Rana*, the venous and arterial blood undergoes separation as it leaves the *Truncus arteriosus*. MAYER, as early as 1835, observed that when the ventricle was clipped near the tip, a dark and light colored type of blood emerged. It had been thought up to that time by competent observers that there was a mixing of the venous and arterial blood in the single ventricle, and that the spongy nature of that structure helped to make such a mixture possible and desirable.

In 1851 BRÜCKE made careful investigations as to the nature of the separation. He concluded that the *Septum bulbi* closed over the *Cavum pulmo-cutaneum* opening (location at "P" in Plate IV) and thereby brought about a separation of the venous and arterial blood during the second half of the contraction. This point was, however, severely criticized by SABATIER ('73), who placed more emphasis on the fact that the ventral wall of the bulbus contracted during the second half of the systole and thereby divided the *Truncus arteriosus* into a right and left compartment, preventing the pure blood from gaining entrance to the left pulmonary portion during the latter part of the contraction.

BOAS ('82) and GAUPP ('96), in their investigations have followed the last mentioned hypothesis. In this investigation, the main idea as formulated by SAVATIER has seemed the most logical to follow.

The two types of blood enter the single ventricle, the impure on the right from the right auricle, and the pure on the left from the left auricle. They are caught in the pocket-like formations of the ventricle and are thereby prevented from becoming mixed together to any great extent. As the heart contracts, the sinus venosus contracts first, to be followed by the right and left auricles in successive order. This forces the blood into the ventricle, the impure into the right side and the pure into the left. The next part of the contraction strikes the right half of the ventricle first and thereby drives the impure blood out into the *Bulbus cordis.* The wave of contraction then moves to the left across the ventricle and forces the pure blood in that region towards the opening of the *Bulbus cordis.* As it does so the *Bulbus cordis* itself contracts and forces the ventral wall of the bulbus against the Spiral valve, dividing the chamber into two compartments. Thus the impure blood going out first through the *Bulbus cordis* finds it in a relaxed condition and not divided into two separate cavities, whereas the pure blood that follows it, finds the bulbus contracted and in a different physiological condition.

The effects of this double phase contraction is to keep the blood streams from mixing as they leave the heart. The venous blood that leaves first through a relaxed bulbus finds easy access to the pulmonary arch (at "P" in Plate IV), since this arch has just been emptied in the previous half of the contraction and is offering a state of lower pressure. The impure blood, therefore, flows over the free edge of the *Septum bulbi* (Plate IV) towards the pulmonary opening "P". The gateways towards the carotid and aortic arches (location "X" in Plate IV) are still full of blood from the previous systole, and as the impure blood rushes out, this left-over blood prevents the impure blood from gaining entrance to the systemic and carotid arches. As the stream rushes into the pulmonary arch in its emptied condition, it forces the horizontal *Septum principale* upwards and thereby has the tendency to further hurry along the remaining pure blood that is still present in the aortic cavum.

As the contraction proceeds, the middle portion of the ventricle containing blood of somewhat a mixed sort is forced towards the opening of the *Bulbus cordis.* This blood as it is driven into the *Bulbus cordis* meets the early part of the *Bulbus cordis* contraction, the effect of it being to shut off the opening to the pulmonary arch, as explained before. However, the two truncus branches bear off in different angles, the left one in the same direction as the *Bulbus cordis* itself, and the right one bending sharply towards the dexter portion of the auricle. The result of this flexion is to offer easier access to the blood going towards the head in the left hand direction, since the blood pressure is logically lower where bends and sharp turns are obliterated. Thus it can be seen that the *Cavum aorticum sinister* (Plate IV) receives the mixed arterial blood which is flowing out of the *Cavum aorticum* of the *Bulbus cordis*. The significance of this condition is that the carotid arches which open into the right aortic cavum do not receive a mixed arterial blood supply. It further shows that the flexion of the right branch of the truncus in a sharp angle helps to prevent the mixed blood gaining access into the right aortic arch and consequently keeps the impure blood from going to the vital parts of the animal body.

As the *Cavum aorticum sinister* (Plate IV) fills up with the mixed arterial blood, there is evidently a small amount of blood of the same nature driven into the right aortic canal. This blood, though of less amount in all probability than what is received by the left aortic canal is pushed into the right systemic artery. It is soon followed by blood of a purer sort. The amount of impure blood that gains entrance to the visceral arch is very small.

The contraction in the ventricle now moves even further to the left, and forces the pure blood that has just entered the ventricle by the pulmonary vein into the *Bulbus cordis* region. Consequently, the timing of this operation has to be perfect or a mixing of the blood streams as they move from left to right across the ventricle will occur. As the pure blood from this region enters the *Bulbus cordis* it finds that organ still in a contracted condition. The pulmonary arch is, of course, still completely isolated from the aortic cavum by the vertical *Septum bulbi*. The left systemic arch is full of mixed blood and the right arch is just emptying itself of blood left over from the later part of the previous contraction. It has, of course, (speaking of the pure blood entering the *Truncus impar* from the *Cavum aorticum* of the

Bulbus cordis), no other way to go, except towards the right aortic arch, because the pressure is here much lower than in the left.

Thus the blood that comes last from the ventricle is more or less forced to go the way it does, by factors outlined above,—namely, the filling up of the left systemic and pulmonary arches with blood, and the consecutive contraction of the auricles, ventricle and truncus in precise physiological order.

To summarize the situation: the blood that leaves the ventricle first is venous in nature and goes to the pulmonary arteries along the arrows "P" and "P′" (Plate IV), where the pressure is less than in the carotid and systemic arches. The next blood to leave the heart comes from the middle portion of the ventricle and is more or less mixed. It, like the blood that follows, finds the pulmonary opening shut off from the aortic cavum by the Spiral valve, whereby it flows anteriorly and enters the most accessible tract, or the left systemic canal, since this canal lies in the same angle as the *Bulbus cordis*. The next blood that follows is of a high arterialized sort and finds its way towards the right aortic arch where the carotid canales receive it, directing it towards the head and other places that demand a pure type of blood. The two systemic arches thereby receive different types of blood. "The left arch receives mixed blood which is mainly sent to the viscera, the right arch receives purely arterial blood which is sent to the head and the posterior parts of the body...." (SEDGWICK pp. 287–288).

Much has been said of the physiological importance of the carotid gland. It is altogether probable that this organ assists in raising the pressure in the carotid arch. GAUPP has pointed out the fact that this gland, together with a valve located in the arc of the systemic arch (Valvula paradoxa), prevents the venous blood which enters the truncus in the first phase of the ventricle systole from passing into the systemic aortae. Just how much it brings about this physiological condition is impossible to ascertain. From the above description it is obvious that the Spiral valve of the *Bulbus cordis*, functions in the separation of the two kinds of blood. NOBLE ('25) has pointed out the fact that disuse of the lungs in Amphibia "conditions a complete loss of the Spiral valve." He further shows that all "Amphibia having well developed and frequently used lungs possess a functionally complete auricular septum and a Spiral valve." In these forms, if a small quantity of India ink is injected into the pulmonary vein, it can be seen to follow the path taken by the arterial blood as it leaves the truncus and passes into the carotid arteries.

BRUNER ('00) and POHLMAN ('14), both have denied that the Spiral valve is functional in the separation of the two types of blood. BRUNER has concluded that is acts only as a support for the ventral wall of the *Bulbus cordis.* Such a hypothesis is very questionable. Evidence to support the views of both these investigators is rather meager. NOBLE ('25), has confirmed the observations of OZORIO de ALMEDIA ('23), as to the actual separation of the blood, by means of India ink injections.

I have thought it advisable to repeat the experiments of these two investigators, using *Rana sphenocephala* and *Rana catesbeiana* in place of lower Amphibians. A Knower injection apparatus was set up and India ink forced into the pulmonary vein, while the heart was beating very slowly. The course of the dye was observed through the *Bulbus cordis* and thence through the *Truncus impar* and into the truncial arms. As with NOBLE's experiments, the blood turned black first of all in the carotid and then in the systemic arches. It never gained entrance to the pulmonary arch. This showed beyond a doubt, in a very simple fashion, that the dye was carried on the pure blood stream, unmixed with pulmonary blood, to the carotid and systemic veins. Further, it showed in reference to NOBLE's data that the Spiral valve brought about this condition. He found that in injecting the ink in a similar way into the pulmonary vein of Amphibians that lacked a Spiral valve, the ink was carried to all the truncial arches!

A similar separation could be observed if the ink was carefully injected into the tip of the left side of the ventricle, though with less degree of satisfaction. Care had to be maintained not to disturb the systole. The injection of the ink had to be made immediately after contraction of the heart and no ink allowed to flow from the needle until after the second or third beat. If ink escaped from the needle immediately after the injection, all three aortic arches colored up at once with the dye, proving beyond a doubt that the systole had been disturbed and that the Spiral valve had been thrown out of harmony. OZORIO de ALMEDIA ('23), has also shown this to occur in experiments with *Leptodactylus*, in which he interfered with the movements of the heart chambers by means of ice and thereby produced a mixing of the two blood streams. The fact that there was more or less a complete separation of the two kinds of blood when the India ink was injected into the tip of the ventricle tends to show that there is some justification in believing that the pocket-like formation of that chamber hinders the mixing of the blood.

If there had been a mixing of the venous and arterial streams, while the blood was in the ventricle, the ink would not have kept its identity with the arterial blood as it left through the *Truncus impar*. If a large degree of mixing had taken place, the pulmonary arch would have colored up nearly simultaneously with the darkening of the carotid and systemic arches. This, however, was not the result obtained, the carotic arches always received the dye first, providing the heart was not interfered with by mechanical touch.

NOBLE ('25), has definitely shown by experiments of this sort that Amphibians lacking a Spiral valve always have a mixing of the arterial and venous blood, the ink being evenly distributed to the pulmonary, systematic and carotid arches. Evidently, the Spiral valve in *Rana* is of major importance.

Summary

1. In *Rana sphenocephala, clamitans, palustris, pipiens* and *catesbeiana* there are three posterior *Bulbus cordis* valves. The two ventral valves are largest. The small dorsal valve is probably not functional.

2. The *Septum bulbi* is large and powerful throughout the whole of the *Bulbus cordis* and divides it into two cava, the *Cava pulmocutaneum* and the *Cavum aorticum*.

3. The posterior portion of the *Septum bulbi* (Spiral valve) in *Rana catesbeiana* and *sphenocephala* has a marked modification in a crest of tissue arising from the right ventral surface. No suggestion has been made in work of the European investigators, or others, of such a modification in old world forms of *Rana*. It is probably typical for certain species only.

4. The anterior *Bulbus cordis* valves in American *Rana* are of essentially the same form as in the European *Rana*. All three valves, *1, 2* and *3* are present, *Valve 3* being the largest. In *Rana sphenocephala* the *Septum principale* reaches back to the bottom of *Valve 1*. In *Rana catesbeiana* there is occasionally a failure of this septum to do so.

5. In *Rana catesbeiana,* the left portion of *Valve 1* does not fuse with the lateral bulbus wall, but turns dorsaly and fuses near the base of *Valve 2*.

6. In American *Rana,* the pulmonary trunk is divided almost immediately after its origin, by the *Septum medianum inter-pulmonale.* This is somewhat a variation to the situation found in European *Rana*.

7. The carotid arteries have separate origins, the right one further to the anterior than the left. The *Canalis caroticus sinister* is the largest of the two carotid canales—exactly opposite to the condition in the European *Rana*.

8. Frequent occurrence of the PARKER and HASWELL diagram of the *Truncus arteriosus* of *Rana* in zoological text-books, gives an entirely wrong conception of the actual morphology. GAUPP's figure in his "Anatomie des Frosches" is much more accurate for text-book reproduction.

9. Injection of India ink into the pulmonary vein shows that there is a complete separation of the two kinds of blood in *Rana,* and that the Spiral valve is functionally important.

10. No variation within the species itself was apparent except in *Rana catesbeiana* where occasionally the *Septum principale* failed to come all the way down into the bottom of *Valve 1*.

11. The fact that the *Truncus arteriosus* in American *Rana* is similar to the *Truncus arteriosus* of European *Rana* in most respects seems to indicate that there is a close relationship between the two forms.

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Since studying the American *Rana*, the author has found opportunity to investigate certain Japanese *Rana*. It is hoped that a comparison study can be made in the future of these forms with the American species. At this time the author wishes to express his deep gratitude to the Faculty of Science of the Hokkaido Imperial University for assuming the publication of this paper. In this connection I wish to thank Drs. OGUMA and INUKAI under whose direction this research have been completed and revised.

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Plate IV

Explanations of Plate IV

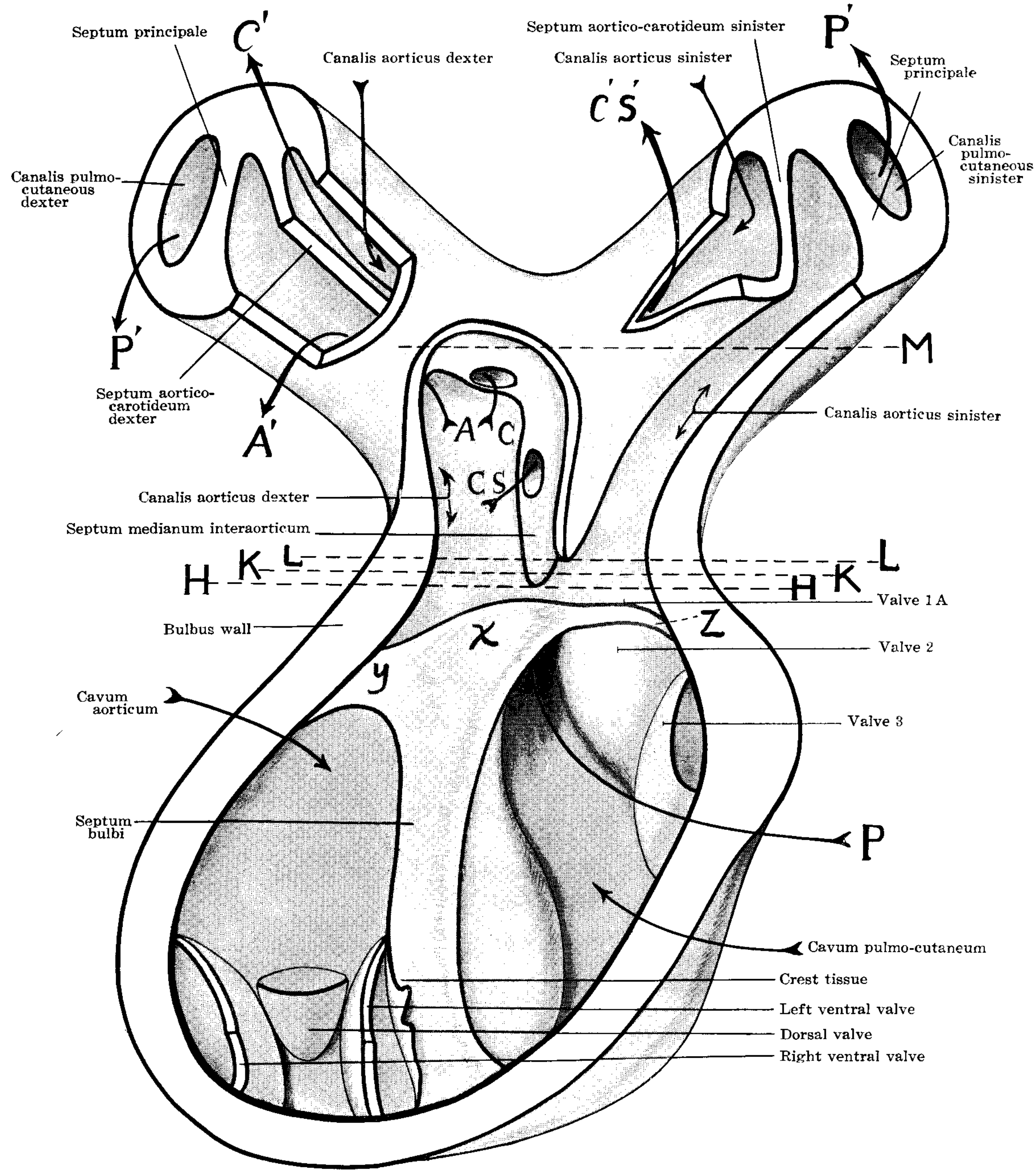
Truncus arteriosus of *Rana sphenocephala* opened along the ventral side.

A-A′., arrow bristle passed through the right systemic canal;

C-C′., arrow bristle passed through the right carotid canal;

CS-C′S′., arrow bristle passed through the left carotid canal;

H., level H; K., level K; L., level L; M., level M; P., arrow bristle passed through the pulmonary canal; P′., arrow bristle passed through the pulmonary canal; X., middle anterior edge of the spiral valve, area from which figure 11 is drawn; Y., right anterior edge of the spiral valve, also area from which figures 12–15 are drawn; Z., left anterior edge of the spiral valve.



M. L. Peelle: The Truncus Arteriosus of American Frogs, Rana Sphenocephala