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Inhalt:

I. Wissenschaftliche Mitteilungen.

1. On a New Mode of Persistence of the Posterior Cardinal Vein in the Frog (Rana temporaria): With a Suggestion as to the Phylogenetic Origin of the Post-Caval Vein.

By W. Woodland, University College, London.

(With 5 figures.)

eingeg. 23. Februar 1905.

Part I.

The abnormality referred to in the above heading was found in a male frog which was undergoing dissection during class-work at the London Hospital Medical College. It is of more than usual interest since only three similar variations have hitherto been described, from all of which it differs considerably, and moreover it is perhaps of some importance since, essentially consisting as it does of the disappearance of the post-caval vein and its replacement by a persistent right posterior cardinal, it possesses on this account a phylogenetic significance.

The persistent posterior cardinal, which forms the most conspicuous feature in the abnormality, is, as shown in the accompanying figure, a trunk of considerable size — at least twice the calibre of an ordinary large vein such as the femoral — and runs more or less parallel[1] to the vertebral column. Anteriorly, it communicates with the very much swollen bladder-like base of the subscapulo-jugular vein (which in consequence possesses three confluent tributaries, the opening of the posterior cardinal being situated between those of the quite normal internal jugular and subscapular veins when viewed from above or below) opening on its dorsal side; posteriorly, the posterior cardinal is in line and continuous with the also large right renal-portal. This right renal-portal,

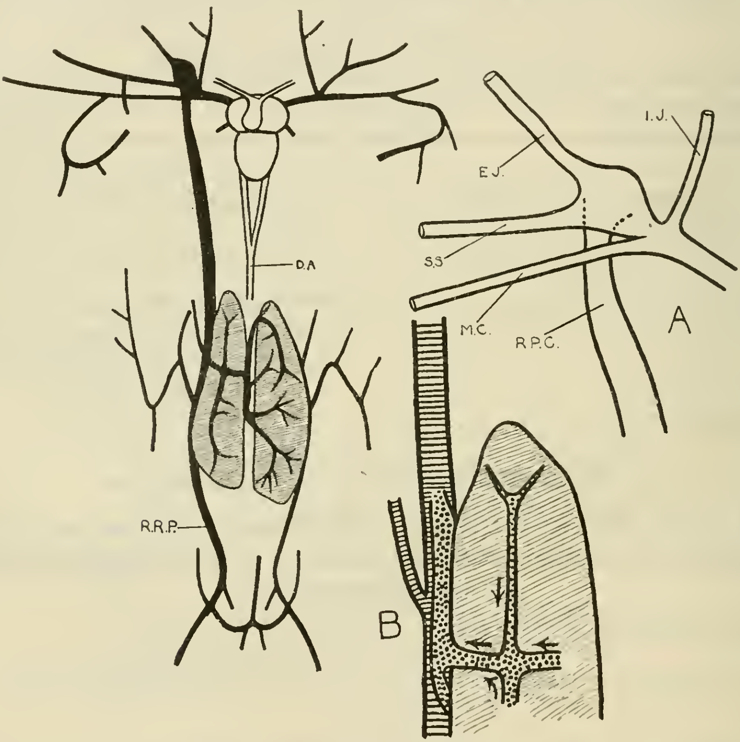

Fig. 1. The abnormally persistent right posterior cardinal vein. *A*. The dorsal junction of this posterior cardinal to the swollen base of the subscapulo-jugular. *B*. Veins entering the right renal-portal vein from the right kidney. *I.J*, internal jugular; *E.J*, external jugular; *S.S*, Subscapular; *M.C*, Subclavian; *R.P.C*, right posterior cardinal; *D.A*, dorsal Aorta; *R.R.P*, right renal-portal.

it is important to notice, possesses no venae renales advehentes, i.e. sends no branches into the substance of the right kidney, as is the case with the quite normal left renal-portal, though, where continuous with the posterior cardinal in the anterior third of the kidney, it receives at right

[1] It approaches the median line half-way down the trunk. See Part II.

angles a large transverse tributary lying on the ventral side of the right kidney (from which it receives in its turn two longitudinally-disposed factors, one anterior, the other posterior) which proceeds from the large inter-renal vein, and also a smaller one just posterior to this which is derived from the kidney capillaries.

The conformation of the "renal-portal system" in this frog is also interesting. The only venous blood which is supplied to the two kidneys is, as just implied, derived from the venae renales advehentes of the left renal-portal vein which "capillarize" in the left kidney and then communicate by four main branches with the large inter-renal. From this inter-renal the venous blood flows by way of the transverse tributary already mentioned direct into the junction of the right renal-portal and posterior cardinal, so that there exists no "renal-portal system" in the substance of the right kidney. The colour of the blood in the several veins confirms this since blood entering the posterior cardinal by the transverse tributary (derived both from the left renal-portal and subsidiary veins and from the renal arteries) is distinctly reddish-purple in hue, whereas the blood contained in the large right renal-portal is of a deep blue, this difference of colour clearly showing that none of the more deeply coloured blood enters the kidney substance. This difference in blood-colour is diagrammatically indicated in the above figure (*B*) by means of the dotted and striped appearances given to the respective veins.

It remains to be mentioned that all the veins arising from the left pre-caval are normal, the abnormality only affecting the right side of the animal. The considerable size of the persistent right posterior cardinal, right renal-portal and right pre-caval veins is of course due to the fact that the whole of the venous blood derived from the posterior portions of the body is returned to the heart by these veins.

Though the above abnormality is new as regards the particular mode of persistence of the frog's posterior cardinal, yet, as before stated, it is not the first example of a persistent posterior cardinal having been found in this animal; three such have previously been described, brief accounts of which I will here give for comparison.

In 1888, Howes (1) described the persistence in a female frog of a left posterior cardinal. This, as in my specimen, was posteriorly continuous with the renal-portal of the same side, but, unlike my specimen, was also joined by a transverse branch at the anterior end of the kidney to the post-caval, which vein was present though it was of smaller size than usual; anteriorly, the posterior cardinal joined the pre-caval in the usual manner. This abnormality is represented diagrammatically in fig. 2.

In 1889, W. N. Parker (2) described another instance of the persistence of a left posterior cardinal in a male frog. This posterior cardinal was continuous posteriorly, not with a renal-portal but directly with the inter-renal vein, and thus in this region was equivalent to, and doubtless homologous with, a true post-caval; anteriorly, the posterior cardinal entered the left pre-caval, as indicated in fig. 3 — this mode of termination of the anterior extremity of the vein alone indicating its posterior cardinal nature. According to Parker, Howes found another example of a variation identical with that which he before described, save that the left persistent posterior cardinal opened into the left subclavian instead of into the left pre-caval — which statement I presume

Fig. 2.

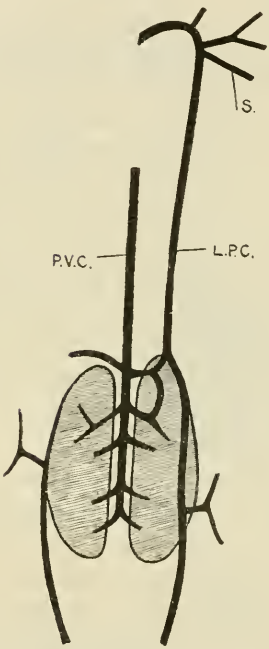

Fig. 3.

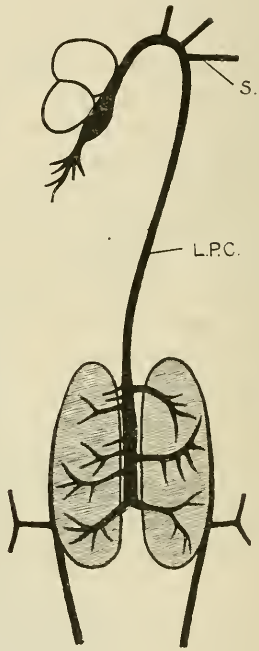

Fig. 2. Persistence of a left posterior cardinal vein in a frog. Post-caval vein also present. (Modified after Howes.)

Fig. 3. Similar abnormality in a frog. Post-caval vein absent, except as an inter-renal vein. (Modified after W. N. Parker.) *S*, subclavian; *P.V.C*, posterior vena cava; *L.P.C*, left posterior cardinal.

merely means that the junction of the posterior cardinal was situated further to the left of the heart than usual.

Part II.

A Suggestion as to the Phylogenetic Origin of the Posterier Vena Cava.

Whilst pursuing some enquiries into the subject of the "Renal Portal System", I was incidentally led to consider the possible reason for the replacement of the posterior cardinal veins by the post-caval which occurs in all animals above fishes — tetrapoda, as Credner calls them — and since I am not aware that the idea, though simple enough, has been expressed before, I gladly take the opportunity here provided of publishing my conclusions along with the description of an abnormality associated with the structure to which the conclusions refer.

As leading up to the subject proper, it will first be necessary to consider why the posterior cardinal veins of fishes assume a mid-dorsal position in the body-cavity. Taking the familiar illustration of a flexible lathe, it is an elementary truth that during flexion the substance situated at the sides of the lathe is more subject to pressure (due either to compression or distension according to the direction of flexion) than the substance situated near the median vertical plane (supposing the lathe to be placed edge-up) — the pressure attaining a maximum at the extreme periphery and a minimum midway between the two sides

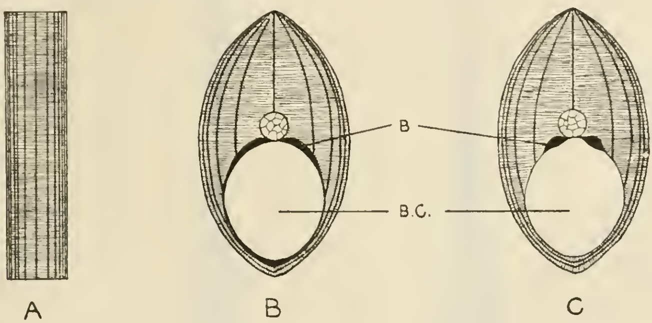

Fig. 4. *A*. lathe viewed in section. The degree of approximation of the lines indicates the intensity of pressure experienced by the substance of the lathe in any given region. The some remark applies to *B* and *C*, which diagrammatically represent transverse sections of a typical fish, illustrating the evolution of the posterior cardinal veins. In *B* is indicated a tendency on the part of the blood to flow either dorsally on ventrally on account of the lateral flexion of the body. In *C* is shown the mid-dorsal course which the blood actually pursues. *B*. blood in vascular space; *B.C.* body-cavity.

(fig. 4*A*). Now the fish-body, although ovate in transverse section and, in the region of the body-cavity, hollow, yet essentially resembles a lathe from the mechanical standpoint, and is therefore similarly affected by flexion such as that involved in swimming. Flexion of the fish-body, like that of the lathe, involves considerable alternate compression and distension of the substance at the sides but not of that in the median vertical plane; hence it follows that intercellular spaces situated in the lateral body-wall—such as vascular channels—will ultimately be obliterated (since, owing to the periodic obstruction offered, the blood will eventually cease to flow through them) and that those situated dorsally or ventrally to the body-cavity in the median vertical plane will persist, and not only persist but become well-developed, since the mass of the venous blood, prohibited from returning to the heart by way of the constricted lateral channels situated between the coelomic epithelium and the external muscles, will be diverted into channels that are permanently open (Fig. 4 *B* and *C*). Confirmatory of this explanation of the median situation of the vascular channels (both dorsal and ventral) in the vertebrata is the fact that the tendency of these vascular channels to assume a median position is strictly correlated with the degree of flexion experienced by the portion of the body containing them. For example, in fishes the dorsal posterior cardinals diverge anteriorly where flexion is smallest and converge posteriorly as flexion increases, finally fusing to form a single vessel in the tail where flexion is at a maximum.

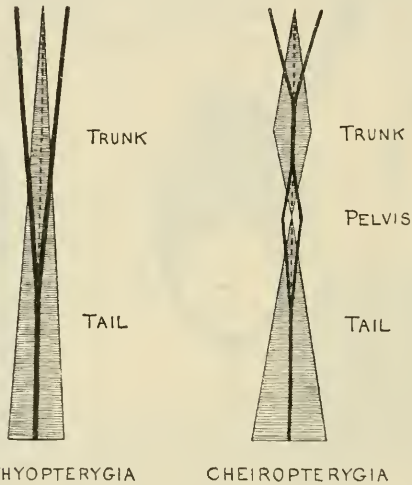

Fig. 5. The above diagrams roughly illustrate the direct relation existing between approximation of the veins to the median line and intensity of flexion in different parts of the body in *Ichthyopterygia* and *Cheiropterygia*. The veins are represented by the black lines; the intensity of flexion is roughly proportional to the width of the shading in any given region.

(See fig. 5. *Ichthyopterygia*.) Now in vertebrates above fishes, though flexion of the trunk and tail still occurs, yet it is most important to notice that the flexions of these two portions of the body in these higher vertebrata are distinct from each other: the trunk and tail do not bend to and fro as one body, as in fishes, but act independently, with a nodal region, or region of no flexion, separating them — the pelvic region. Flexion of the trunk and tail originates from one centre so long as the limbs are not locomotor in function or but little so, but when, as in terrestial animals, the limbs exchange their balancing function for a locomotor one, then the trunk, becoming more important, acquires a flexion of its own distinct from that of the tail, which latter organ often quickly becomes of minor importance and diminishes in bulk. In this distinction between *Cheiropterygia* and *Ichthyopterygia* lies the explanation of the production of the post-caval vein. So long as the trunk and the tail constitute one continuous locomotor body, so long is there little chance of the two posterior cardinals approaching the median line and completely fusing at a point midway in the length of the trunk, since this point is necessarily anterior as regards the body as a whole, and anteriorly, flexion is of small degree [2]. But on the development of locomotor limbs, which act as fulcra in the movements of the body, flexion of the trunk portion of the animal body becomes altered in character and, instead of merely being, as it were a faint reflection of the violent movements of the tail, becomes strongly accentuated and also acquires a new stribution. In thedi trunk of a mammal [3] e. g. observation of the animal's movements shows us that flexion of the trunk is greatest about midway in its length, and decreases posteriorly towards the pelvis where flexion altogether ceases, as shown by vertebral fusion. This being the case, the primitive posterior cardinals are subject to a new distribution of forces, and, tending as in fishes to converge in the region of greatest flexion, in consequence are replaced midway in the length of the trunk by a median vein—the post-caval.

At the same time, owing to the decrease of flexion towards the anus (shown by the fusion of the sacral vertebrae) the posterior cardinals are more at liberty to maintain their initial separate condition posteriorly, and, as a matter of fact, persist as the renal-portal veins in the majority of Amniota, converging again, however, immediately behind the

[2] The posterior cardinals do to some extent meet and fuse anteriorly in the trunk ot Elasmobranchs and so anteriorly as to form a cardinal sinus between the gonads. But then the extreme activity and flexibility of these fishes must be borne in mind, also the fact that the veins are large sinuses. It is significant that in these fishes thus characterized, an anastomosis is formed between the cardinal sinus (or post-caval) and the right hepatic sinus. See further in text.

[3] The occurrence of lateral flexion of the trunk in higher vertebrata. besides being obvious from actual observation, is also evidenced by the structure of the trunk — by the separate condition of the vertebrae. the existence of ribs and the arrangement of the trunk muscles, etc. Moreover. the existence of this flexion is evidenced by its effect on internal organs like the liver. which, as Owen says. "is. as a rule, divided into a greater number of lobes in the present [Mammalia] than in the preceding classes. the body being more flexuous at the seat of this viscus. In the stiff-trunked whales and erectly-moving man the organ is more compact. and it is least sub-divided in the purely herbivorous Ungulates, where a minor degree of hydrocarbonates has to be elimintated", this organ being here very small. When flexion of the vertebral column does not occur. as e.g. in the sacral region of most vertebrates above fishes, and in the region of the carapace of Chelonians, then fusion of the constituents takes place. In anurous Amphibia the tadpole larval stage doubtless also forms a factor in the adult disposition of the vascular channels, and it is of course possible that the median disposition found in all higher vertebrata is in part a heritage from piscine ancestors.

anus, i. e. at the base of the tail where the effects of caudal flexion are most potent, to form the caudal vein (fig. 5 *Cheiropterygia*).

This replacement may theoretically either result 1) from the actual fusion of the posterior cardinals in the median line, or 2) from the persistence of one of them in the median line, or 3) from their replacement by a third and therefore new median channel. Actually, it is probable that processes 1) and 3) occur in all cases of ontogeny, process 1) occurring medianly and 3) anteriorly; however, according to Hochstetter, the post-caval of birds entirely results from process 3), and the post-caval of mammals, according to Gegenbaur, from processes 2) posteriorly and 3) anteriorly. Whether the method of replacement of the posterior cardinals by the post-caval which occurs in ontogeny truly represents the phylogenetic process (which was probably that indicated above for ontogeny — 1) medianly and 3) anteriorly) is an open question, but however this may be, it can hardly be doubted I think but that the primitive cause of the replacement was that which I have indicated and which is necessarily correlated with the evolution of locomotor limbs.

Referring back to the case of the dorsal position of the posterior cardinals of fishes, the question as to why they are dorsally rather than ventrally situated in the median line is not a difficult one. As in the problem just considered, so here the answer is that the blood pursues this particular course because it is the path of least resistance. In the case of the posterior cardinals, the blood returned from the region of the tail passes forwards under and in close apposition to the vertebral column, in fact, in the haemal arch of each vertebra. Now in fishes the posterior extremity of the coelomic cavity is situated ventrally i. e. in the vicinity of the anus, and the dorsal side of the coelom gradually rises from this posterior ventral limit towards the dorsally-placed vertebral column; hence, owing to this conformation the dorsally-placed caudal vein must inevitably bifurcate into two vessels which continue to lie dorsal to the body-cavity, or, in other words, follow the course of the nearly straight vertebral column.

In vertebrates above fishes the tail region is often considerably reduced, but still in the vast majority of cases the channels returning the venous blood will continue to lie dorsally to the body-cavity, since this dorsal course is, as in fishes, more in line with the caudal vein than the ventral, and all animals, save the anurous Amphibia (which have a piscine larva however), possess tails of sufficient size to render the flow of blood in the caudal vein an important factor in determining this direction of flow. In mammals too, the upwardly-inclined iliac veins would tend to effect a junction with a dorsally-placed vein rather than with a sub-abdominal one, since the latter would be inclined in an opposite direction to them, *viz.* downwards, in the curve of the ventral body-wall.

However, this factor is not of much importance in animals like Reptilia in which the iliac veins lie approximately in a horizontal plane. For this reason then, viz., because the dorsal limit of the body-cavity is more in line with the caudal and iliac veins than the ventral, the posterior cardinals (post-caval) lie dorsally and therefore in close apposition to the vertebral column. Confirmatory of this explanation is the fact that when the dorsal limit of the coelom is not so much in line with the caudal and iliac veins as the ventral (as e. g. in *Chelonia*, where the extremely convex curvature of the vertebral column and the flat plastron conduce to this result) then the veins pursue the ventral course instead of the dorsal; likewise, because they are as much in line with the epigastrics as with the post-caval and nearer, the horizontal iliacs of Crocodilia (not the caudal, which is very large and quite in line with the dorsal post-posterior cardinals) are at liberty to open into the former instead of the latter, which they do; and it is also possible that the blood contained in the coccygeo-mesenteric of birds pursues a ventral course merely because such is, owing to the form and position of the trunk, as easy of passage as the dorsal, the reduced "renal portal system" not offering so great an obstruction to the flow of the blood in the avian post-caval as in that of lower vertebrata.

But now, granted that the post-caval has been formed midway down the dorsal side of the trunk, there has yet to be effected a direct communication with the heart in order to entirely replace the posterior cardinals in the anterior region. How easily this communication may be made is shown by the fact, stated by Hochstetter, that even in Elasmobranchs an anastomosis is formed between the hepatic sinus and the posterior cardinal veins, this anastomosis being, and very rightly, in Hochstetter's opinion, tantamount to the formation of a post-caval[4]. The Dipnoi also only differ from other fishes in that one of the posterior cardinals opens into the heart instead of into the Cuvierian duct. A similar anastomosis is formed during the ontogeny of *Cheiropterygia*, the post-caval becoming connected with the right hepatic vein, which, losing its connection with the liver, conducts the blood returned from the posterior portions of the body directly to the heart. Hence at the time of formation of this anastomosis the blood in the post-caval can return by three routes to the heart — directly by the median anastomosis, indirectly by the lateral persistent anterior portions of the posterior cardinals.

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[4] See footnote on previous page.

In animals which are not very active and in which in consequence there is not a very great flow of blood to render a median channel of much greater advantage than lateral channels, nor flexion of the trunk to cause tensions in these laterally situated veins[5] and thereby to render still more advantageous the adoption of a median channel, these lateral channels persist, but in all active animals they disappear, at any rate in the capacity of affording alternative courses for the return to the heart of the blood contained in the post-caval. Thus, to give the few examples which are obtainable, though the Salamanders are thoroughly terrestrial yet they are extremely inactive in their movements and correlated with this inactivity. "Hochstetter states that the hepatic portion of the post-caval remains undeveloped exceptionally in the Salamander, in which case either one or the other cardinal becomes correspondingly enlarged" (Howes). Speaking more generally, "the anterior part of both posterior cardinals persists in Urodeles [not in some of the more active species] and in *Bombinator*, as the paired azygos vein, and this may exceptionally be present on one or both sides in other Anurans" (Wiedersheim). In the two specimens of *Bombinator* (described by Boulenger [3] as being "thoroughly aquatic during its periods of activity" and as only "proceeding by small leaps on land") examined by Howes, the azygos veins as just stated, joined the posterior cardinals (post-caval); Howes also found this fairly frequently to be the case in *Alytes obstetricans* (in one specimen out of five), which "is nocturnal and slow in its movements . . . and progresses mostly crawling, but sometimes by short leaps" (Boulenger), and once in *Discoglossus*, which however "resembles the true frogs in the quickness of its movements . . . and is found in or about water" (Boulenger). Howes concludes that "the character is fairly distinctive of the Discoglossidae", which, as a group, contains the most primitive and inactive of Anura. On the other hand, no azygos veins are to be found in *Hyla*, which is a "powerful jumper and expert acrobat" (Gadow [4]), nor in

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[5] These flexions of the trunk which are involved, however slightly, in the ordinary activity of the animal inevitably cause any line situated at right angles to the median straight longitudinal axis of the animal to become inclined to that axis. How taking the junctions of the posterior cardinals to the Cuvierian ducts as two points, situated one on either side of the median line, it is evident that the line joining these constitutes such a transverse line as that just mentioned. Hence it follows that on the occurrence of flexion of the trunk to say the left, a vein attached anteriorly to the base of the right subclavian and posteriorly at the level of the kidneys to the median post-caval must undergo tension and therefore offer obstruction to the passage of blood; i.e. lead to the enlargement of the median continuation of the post-caval. It is pretty evident I think that in the course of many generations activity of the animal would, in the manner just indicated, lead to the sole persistance of this anterior median channel.

Pipa nor *Dactylethra*, both of which, though "entirely aquatic", yet "swim actively" (Gadow), nor in *Pelodytes*, which is a "good climber" and "jumps in the manner of the true frogs" (Boulenger), nor in *Pelobates* which "hops along, frog-like", nor finally in the exceedingly active terrestrial frogs and toads.

Despite the scantiness of the evidence to hand, I feel certain that an extended investigation into the facts would conclusively prove a correlation to exist between activity of the animal and the disappearance of those azygos veins which form indirect communications between the post-caval vein and the heart.

With regard to the posterior sections of the posterior cardinals, which, as we have seen, persist in all Chiropterygia save Mammalia and to which persistance indeed, as hope to show in a subsequent paper, is chiefly attributable the existence of the renal cardinal meshwork, their replacement by the single median posterior section of the post-caval in Mammalia seems to be due in some manner to the growing importance of the hind limbs. For in Apteryx, a purely terrestrial bird which, like Mammalia, possesses large perpendicular hind-limbs and at the same time has no renal cardinal meshwork, the two post-posterior cardinals are, as before described, closely apposed in the median line and in fact resemble a single vessel longitudinally slit.

As I have before said, so far as I am aware from ordinary reading, the above is the first attempt to rationally account for the replacement of the posterior cardinals by the post-caval; it is true that a "rule that all air-breathing animals (Amphibia and Amniota) possess a post-caval" has been vaguely laid down, but no definite reason has yet been assigned to show why the possession of pulmonary organs necessarily implies the presence of a post-caval. Owen, in my opinion, approaches nearer to the truth when he says that "the cardinal veins, essentially those which return the blood from the osseous and muscular segments of the trunk, are largest in the Perennibranchs, and decrease, as the hind limbs acquire more size and power, in the Newts and Land-Salamanders, until, in the tail-less and long-legged Frogs and Toads, the primitive venous trunk of the body is reduced to the condition of the 'azygos' vein in Mammals", implying that increase of limb-power is one cause of the disappearence of the posterior cardinal veins.

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