

The Posterior Cardinal Veins and Kidneys of Fishes, with Notes on Their Phylogenetic Significance

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Abstract The variations of the relation and relative size of the posterior cardinal veins and the fusion of the left and right kidneys in some major fish groups are described. The morphological variations of these characters in the two systems are interpreted and hypotheses concerning the phylogenetic interrelationships of the fish groups are made. The neoposterior cardinal veins being equally long is treated as a plesiomorphic character state for actinopterygians. In the vast majority of these fishes the right neoposterior cardinal vein is much longer and larger in diameter than the left one. The left neoposterior cardinal vein of osteoglossomorphs (including hiodontids) is larger and longer than the right. This synapomorphic character state supports their monophyletic relationships. The presence of a connection between the hepatic and neoposterior cardinal vein in brachiopterygians suggests their affinity with other sarcopterygians. The presence of an anterior median sinus in chondrichthyans formed by the fused parts of the anterior neoposterior cardinal veins may be synapomorphic for gnathostomes and indicates the monophyly of chondrichthyans. Complete separation of the left and right kidneys which is here hypothesized as an apomorphic character state of the gnathostome kidney morphology has appeared at least three times in this fish group. This character state casts light on the monophyly of Brachiopterygii, Dipnoi, and Tetrapoda. Occurrence of similar character states in other gnathostomes is due to convergence.

While conducting a survey of gnathostome kidney morphology, I noticed some morphological variations in the posterior cardinal vein system and the fusion of the left and right kidneys (Mok, 1978). The phylogenetic significance of these diversities have not been sufficiently exploited. Therefore, I undertook a preliminary review of these two systems with special attention to the application of these morphological variations to reconstruct the phylogenetic history of gnathostomes.

Materials and methods

The specimens examined in the present study are from the Ichthyology Department, American Museum of Natural History (AMNH); personal collections of Dr. Peter Moller (PM) of the City University of New York, and Mr. Guido Dingerkus (GD) of the Ichthyology Department, American Museum of Natural History. One or more individuals of each species studied were examined. The viscera including the gastrointestinal tract and the swimbladder (if present) were removed.

After the removal of these organs, the kidney could be easily observed. The posterior cardinal veins are embedded on the surface of the left and right kidneys. The shape of the kidney, the size, length, and relation of the left and right posterior cardinal veins were recorded.

Specimens examined: Chimaeridae: *Chimaera phantasma*, AMNH uncat., 150 mm TL (total length). Dasyatidae: *Taeniura meyeni*, AMNH uncat., 150 mm TL. Squalidae: *Squalus acanthias*, AMNH 1023, 160 mm TL. Latimeriidae: *Latimeria chalumnae*, AMNH 36941, 1300 mm TL. Lepidosirenidae: *Lepidosiren paradoxa*, GD 7.068.1, 540 mm TL. Polypteridae: *Calamoichthys calabaricus*, AMNH uncat., 190 mm, 240 mm TL; *Polypterus ornatipinnis*, AMNH 6349, 108 mm TL; *Polypterus palmas*, AMNH 6300, 110 mm, 114 mm TL. Acipenseridae: *Acipenser stellatus*, AMNH 20694, 157 mm TL. Polyodontidae: *Polyodon spathula*, AMNH uncat., 288 mm TL. Lepisosteidae: *Lepisosteus oculatus*, AMNH 37370, 148 mm TL; *Lepisosteus platyrhincus*, AMNH

27734, 237 mm TL. Amiidae: *Amia calva*, AMNH uncat., 107 mm TL. Osteoglossidae: *Osteoglossum bicirrhosum*, AMNH uncat., 75 mm, 80 mm SL (standard length). Pantodontidae: *Pantodon buchholzi*, AMNH uncat., 75 mm SL. Hiodontidae: *Hiodon alosoides*, AMNH 23754, 60 mm, 67 mm SL. Notopteridae: *Notopterus* sp., AMNH uncat., 150 mm, 160 mm SL; *Xenomystus nigri*, AMNH uncat., 150 mm, 160 mm SL. Gymnarchidae: *Gymnarchus niloticus*, PM uncat., 312 mm TL. Mormyridae: *Gnathonemus* sp., AMNH 19671, 110 mm TL; *Mormyrops deliciosus*, AMNH 6892, 142 mm SL; *Petrocephalus* sp., AMNH 6885, 84 mm SL. Anguillidae: *Anguilla rostrata*, AMNH 36091, 283 mm TL.

Results

Posterior cardinal vein system. The posterior cardinal vein system of primitive gnathostomes consists of (1) the paired renal portal veins representing the posterior part of the protoposterior cardinal veins, present in chondrichthyan embryonic stage and in adult cyclostomes (see below), (2) the medial unpaired caudal vein joining the renal portal vein at its anterior end, and (3) the paired neoposterior cardinal vein which is a composite of the subcardinal vein and the anterior section of the protoposterior cardinal vein (Smith, 1960).

In elasmobranchs such as *Squalus*, a connection between the anterior section of the protoposterior cardinal vein and the subcardinal vein on each side is formed early in ontogeny (Walker, 1956: fig. 1A). The left and right subcardinal veins communicate medially by some short cross anastomoses at their posterior sections and have no connection to the posterior sections of the protoposterior cardinal veins. These anastomoses may be absent in the adult, e.g., *Squalus acanthias*, *S. sucklii* (O'Donoghue and Abbott, 1928), and *Scyllium canicula* (O'Donoghue, 1914). A medial interrenal vein is present posteriorly in *S. canicula* (O'Donoghue and Abbott, 1928: fig. 1B). This vein is composed of the fused posterior (or the subcardinal) sections of the neoposterior cardinals or of one of these veins when the other has lost its posterior section. O'Donoghue and Abbott (1928: 873) wrote about the interrenal vein,

"We have no evidence to show whether this single interrenal posterior cardinal vein in *Squalus* is formed by the fusion of the two limbs of the loop (loop of Jacobson), or whether only one of them persists, as for example in *Mustelus antarcticus* and *Noto-rhynchus maculatus*."

Besides the posterior fusion of neoposterior cardinal veins, a spacious medial sinus may be frequently formed by the fused anterior portion of the neoposterior cardinal veins in chondrichthyans, such as *Squalus acanthias*, *S. sucklii*, *Scyllium canicula* (O'Donoghue, 1914; O'Donoghue and Abbott, 1928: fig. 1B), *Raja nasuta* (Parker, 1881), and *Hydrolagus collii* (Stahl, 1967). This anterior sinus is insignificant in *Mustelus antarcticus* (Parker, 1886: pl. 34). The time of its appearance is variable. It develops in late embryonic stages in *Scyllium canicula* (O'Donoghue and Abbott, 1928), but does not appear until maturation in *Squalus* (Walker, 1956).

There are resemblances between the posterior cardinal vein system of holocephalian fish (*Hydrolagus collii*) and the elasmobranchs. In the former, there are numerous, sizable communications between the left and right neoposterior cardinal veins, and posteriorly at the origin of the trunk between the kidneys, there is a single median vein, the interrenal vein (Stahl, 1967). Stahl made no mention of the composition of the interrenal vein.

There are some generalized characters of the chondrichthyan posterior cardinal vein system: (1) the left and right neoposterior cardinal veins are recognizable and equal in length; (2) the posterior parts of these veins are connected by anastomoses; (3) a median anterior sinus is present; (4) the extreme anterior sections of these veins (or the neoposterior cardinal sinuses) tend to increase in diameter. The primitive nature of the first character state is indicated by the presence of neoposterior cardinal veins of equal length in both embryonic and adult stages of some elasmobranchs (e.g., Walker, 1956). Reduction in length of either one of these veins, or longitudinal fusion of their posterior sections, has also been observed in chondrichthyans. The left neoposterior cardinal vein is shortened in *Mustelus antarcticus*; the short left neo-

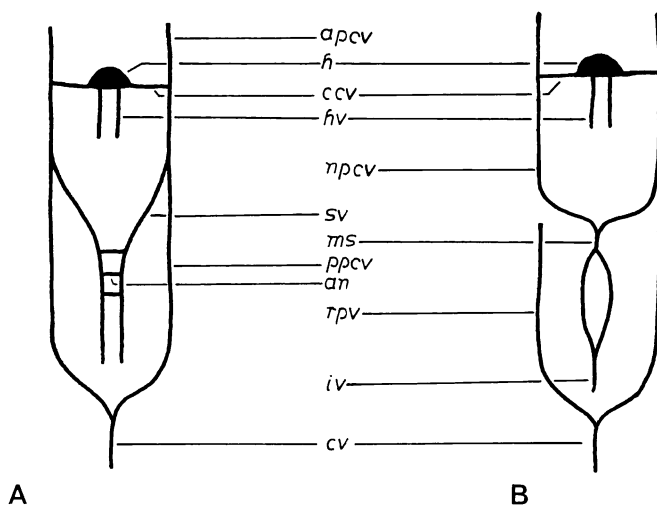


Fig. 1. Simplified diagram of the posterior cardinal vein system in (A) *Squalus* sp. (late embryonic stage; after Walker, 1956) and (B) *Scyllium canicula* (after O'Donoghue and Abbott, 1928). an, anastomosis; apcv, anterior protoposterior cardinal vein; ccv, common cardinal vein; cv, caudal vein; h, heart; hv, hepatic vein; iv, interrenal vein; ms, medial sinus of the fused neoposterior cardinal veins; npcv, neoposterior cardinal vein; ppvcv, posterior protoposterior cardinal vein; rpvcv, renal portal vein; sv, subcardinal vein.

posterior cardinal vein has short transverse anastomoses joining the long right one, which is also larger in diameter (Parker, 1886). Burne (1923:246) observed a reduction in neoposterior cardinal length in *Lamna nasus* and wrote, "It is clear that the posterior cardinal vein system has to all intents and purposes been eliminated, so far as the trunk circulation is concerned and its place taken by the subrenal rete and lower lateral cutaneous vein." In order to decide the nature (advancement or primitiveness) of the chondrichthyan interrenal vein, more studies have to be made. The possession of the interrenal vein might be apomorphic since it is absent not only from the embryonic stage (e.g. *Squalus*; Walker, 1956), but also from the adult stage (e.g., *Raja nasuta*; Parker, 1881) of some elasmobranchs. However, because of its presence in holocephalians, outgroup comparison provides a conflicting view to the above interpretation.

Medial fusion of the rear neoposterior cardinal veins also took place in the evolution of the postcava in tetrapods. Therefore, the nature of the interrenal in chondrichthyans is obscure. During the evolution of the

protopostcava which exists in all living tetrapods (except mammals), dipnoans, polypterids, and coelacanth (also see below), the subcardinal (or the posterior) portions of the neoposterior cardinal veins tend to fuse medially giving rise to a medial vein (Smith, 1960), which joins the right hepatic vein forming the protopostcava. Except for modern urodeles, the anterior sections of the neoposterior cardinal veins are separate from the protopostcava. In modern urodeles, these sections of the neoposterior cardinal veins retain their connections with the protopostcava only in its early developmental stage. Unlike chondrichthyans, this anterior fused area of the neoposterior cardinal veins in modern urodeles does not enlarge to form a sinus. As such, the presence of an anterior median sinus may be apomorphic for vertebrates, supporting the monophyly of chondrichthyans. There is no fusion of the subcardinal portions of the neoposterior cardinal veins in dipnoans, polypterids, and coelacanth. It seems that fusion of the neoposterior cardinal veins has developed twice in vertebrates (chondrichthyans and tetrapods). There is not enough information at the present time to determine

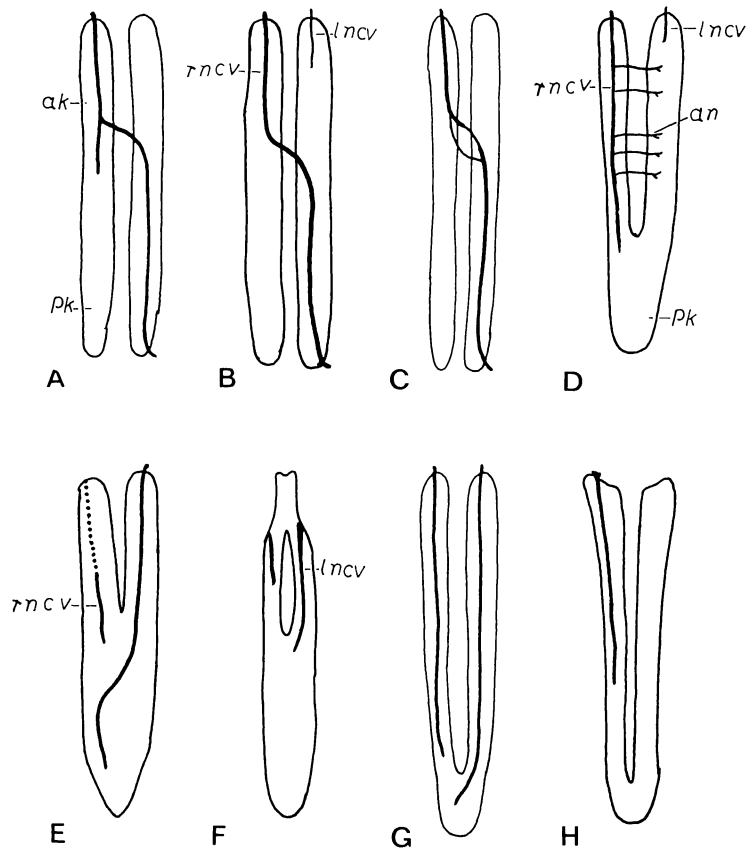


Fig. 2. Arrangement of posterior cardinal veins on the kidneys which are shown in the ventral view. A: *Polypterus ornatipinnis*. B: *P. palmas*. C: *Calamoichthys calabaricus*. D: *Anguilla rostrata*. E: *Acipenser stellatus*. F: *Polyodon spathula*. G: *Lepisosteus oculatus*. H: *Amia calva*. ak, anterior kidney; an, anastomose; lncv, left neoposterior cardinal vein; pk, posterior kidney; rncv, right neoposterior cardinal vein.

whether it represents a plesiomorphic character state of gnathostomes.

In dipnoans, e.g., *Protopterus annectens*, the large protopostcava, which is a composite of the right hepatic vein and the subcardinal portion of the right neoposterior cardinal vein, is connected to the left neoposterior cardinal vein by several transverse anastomoses (Parker, 1892). Both veins of this species are equally long. A vein homologous to the dipnoan protopostcava has been reported by Robineau and Anthony (1971) in *Latimeria chalumnae*. This species is slightly different from *Protopterus annectens* in that the left neoposterior cardinal vein drains directly into the posterior section of the protopostcava, without anastomoses (Robineau and Anthony, 1971), whereas the

left neoposterior cardinal vein and the protopostcava of *Protopterus annectens* and *Lepisosteus paradoxus* are connected by several cross anastomoses along their length.

The neoposterior cardinal veins of *Polypterus* spp. and *Calamoichthys calabaricus* are asymmetrical in diameter and length. The left vein was not observed in *Polypterus ornatipinnis* and *C. calabaricus*. In the former species, the right neoposterior cardinal vein branches into two at the mid-section of the right kidney; the left branch crosses to the left kidney and runs to the posterior end of the peritoneal cavity, where it connects to the distal end of the hepatic vein (Fig. 2A). In *P. palmas* and *C. calabaricus*, the right neoposterior cardinal vein crosses to the left

kidney at the mid-section of the right kidney and extends posteriorly to the rear end of the left kidney where it connects to the hepatic vein. The left neoposterior cardinal vein is present in *P. palmas*. It is short and does not drain into the distal end of the right neoposterior cardinal vein which is also in the left kidney (Fig. 2B, C). Kerr (1910) seems to be the only worker who reported the same observation. He (1910: 104) stated, "The hepatic vein is of great size and the main trunk of it traverses the liver right to its posterior end, and then runs free for a considerable distance through the splanchnocoele along the right side of the right lung till it joins the interrenal vein which I have described as a true primitive posterior vena cava of the same type as that in lungfishes and peculiar only in the fact its communication with the interrenal (posterior cardinal) vein is further back than usual."

The connection between the posterior ends of the right neoposterior cardinal vein and the hepatic vein at the posterior end of the peritoneal cavity and the degeneration of the left neoposterior cardinal vein distinguish polypterids from coelacanth and dipnoans. The connection between the hepatic and neoposterior cardinal veins is an advanced character relative to that of the actinopterygians and the chondrichthyans in which these veins remain separate. Two opposite views regarding the nature of the character of polypterids are proposed: either it is the plesiomorphic state of sarcopterygians under the assumption that the characters of polypterids and other sarcopterygians are homologous; or it is an autapomorphic character of vertebrates. Under the former hypothesis, coelacanth would appear more closely related to dipnoans and tetrapods than are polypterids; and these four taxa would appear to form a monophyletic group. The latter hypothesis is uninformative concerning the phylogenetic position of the polypterids, but it indicates the monophyly of coelacanth, dipnoans, and tetrapods. If information about the posterior cardinal vein systems of juvenile coelacanth, dipnoans, and polypterids were available, one would be able to decide between these two hypotheses. The second hypothesis seems more likely because the adult condition of

dipnoans and coelacanth, in which the hepatic vein connects to the anterior end of the posterior part of the right neoposterior cardinal vein, can hardly be derived from the condition of the polypterids, in which the posterior ends of these veins join.

The two neoposterior cardinal veins in chondrosteans and ginglymoids do not differ significantly in length. In *Acipenser stellatus* and *Polyodon spathula*, the left one is longer (Fig. 2E, F), whereas it is only slightly longer in *Lepisosteus oculatus* and *L. platyrhincus* (Fig. 2G). Anastomoses are absent from these groups.

Interestingly, *Amia calva* does not resemble the other lower actinopterygians mentioned. The long right neoposterior cardinal vein exists while the left one is absent (Fig. 2H). This character state is similar to higher neopterygians in that the right neoposterior cardinal vein is much longer than the left, of which only a short section drains the left extreme anterior kidney.

In the vast majority of teleostean kidneys, the right neoposterior cardinal vein is the major vein. The left one is much smaller, both in diameter and in length, and in some cases is absent (Ogawa, 1961; Mok, 1978). In most teleosts, there is no anastomosis between these veins, although in some cases, e.g., *Anguilla rostrata*, some small branches from the right neoposterior cardinal vein run transversely to the left kidney, but do not connect to the short left neoposterior cardinal vein (Fig. 2D). Jollie (1962), however, showed that in salmon two transverse anastomoses connect the large right and short left neoposterior cardinal veins.

In most osteoglossomorphs, the left neoposterior cardinal vein is much longer than the right (Fig. 3A~I). *Gymnarchus niloticus* is an exception in that a branch from the anterior section of the long right neoposterior cardinal vein runs transversely to the left kidney and continues to its posterior section (Fig. 2F). Although the osteoglossomorph condition is somewhat similar to that of the chondrosteans, I suggest that it has developed independently in these groups and that it is an advanced actinopterygian character state. The left side branch of *G. niloticus* is autapomorphic.

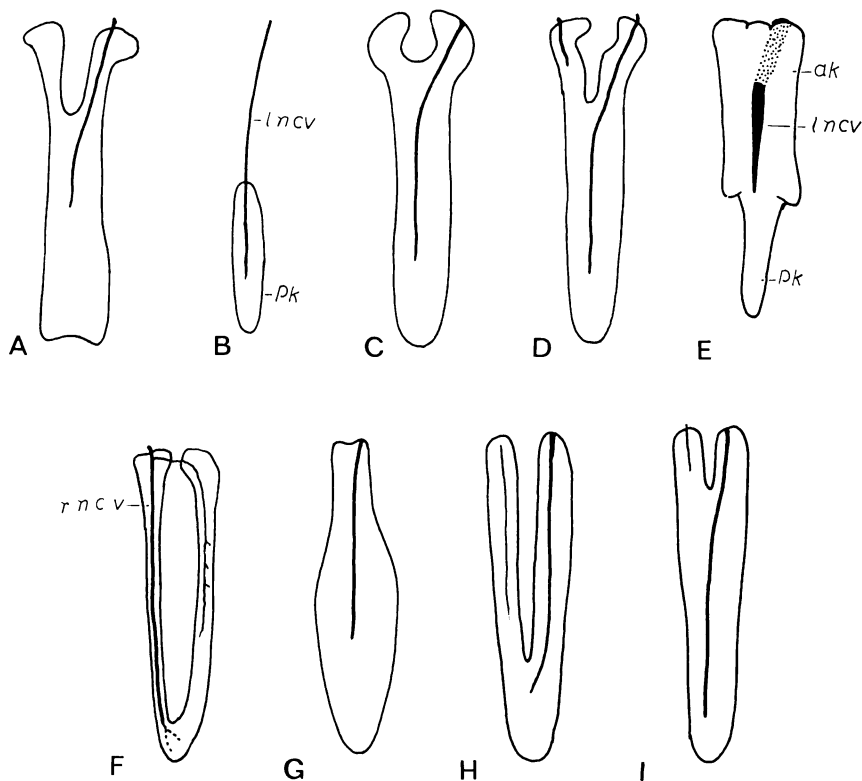


Fig. 3. Arrangement of posterior cardinal veins on the osteoglossomorph kidneys which are shown in the ventral view. A: *Osteoglossum bicirrhosum*. B: *Pantodon buchholzi*. C: *Hiodon alosoides*. D: *Notopterus* sp. E: *Xenomystus nigri*. F: *Gymnarchus niloticus*. G: *Gnathonemus* sp. H: *Mormyrops deliciosus*. I: *Petrocephalus* sp. ak, anterior kidney; lncv, left neoposterior cardinal vein; pk, posterior kidney; rncv, right neoposterior cardinal vein.

However, its long right neoposterior cardinal branch reflects its similarity to other teleostean patterns.

Cyclostomes lack subcardinal veins (Smith, 1960). Hagfishes, such as *Myxine glutinosa* and *Bdellostoma dombeiyi*, resemble each other in their posterior cardinal system in that (1) the left protoposterior cardinal vein is considerably larger than the right; (2) they are joined by a large number of short transverse commissural vessels located along their length; (3) the common protoposterior cardinal vein (the anterior section of the left protoposterior cardinal vein) passes forward to the left side and empties into the posterior end of the sinus venosus; (4) the anterior section of the right protoposterior cardinal vein is much

reduced in size or may even be absent as in *B. dombeiyi*; (5) a connection between the caudal vein and the protoposterior cardinal veins is present (equivalent to the connection of the caudal vein and the renal portal veins of gnathostomes; Jackson, 1901; Johansen, 1963). Lampreys are different in some aspects from the hagfishes: (1) the right protoposterior cardinal is larger than the left; (2) the left protoposterior cardinal vein joins the right just posterior to the level of the heart and both cardinals drain into the sinus venosus through the right duct of Cuvier (Jollie, 1962). Cyclostomes in general are characterized by (1) the absence of subcardinals, (2) the presence of anastomoses, and (3) asymmetrical development of the two protoposterior cardinals

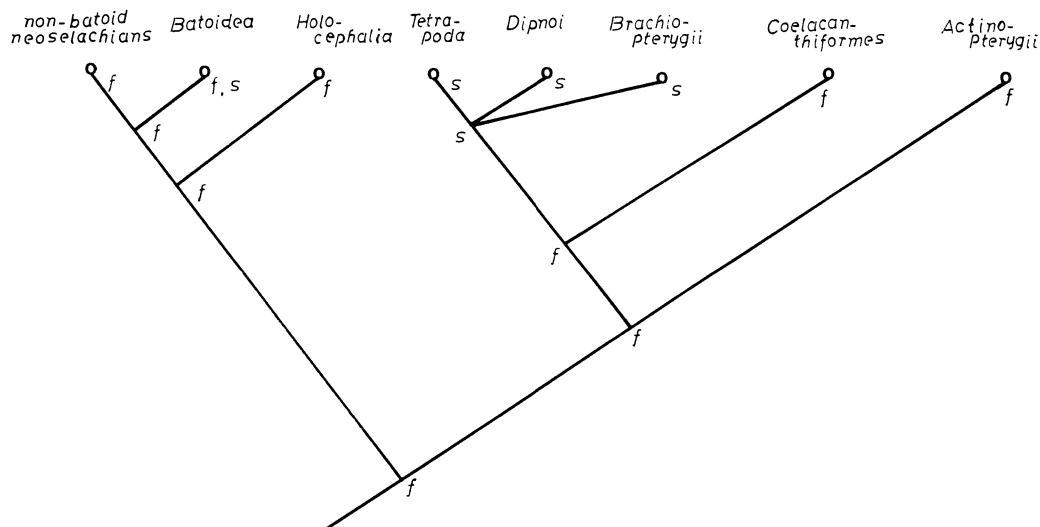


Fig. 4. Cladogram of the major groups of vertebrates on the basis of the kidney morphology and other characters studied by previous workers. Distribution of the two character states of the connection between the left and right kidneys (f: fused; s: separate) in living groups (○) and hypothetical ancestors are listed.

and the extreme anterior end of these veins.

Smith (1960) suggested that the absence of subcardinals in cyclostomes is secondary. In the lack of ontogenetic evidence, it would seem reasonable to say that the nature of this character (absence of these veins) is still obscure.

Fusion of the left and right kidneys. Complete separation of the left and right kidneys occurs in some batoids (e.g., *Taeniura meyeni*, AMNH uncat., 150 mm TL, personal observation), dipnoans, such as *Protopterus annectens* (Parker, 1892: pl. 5), *Lepidosiren paradoxa* (Kerr, 1901; personal observation was made on a 540 mm TL specimen, GD 7.068.1), polypterids (both *Polypterus* spp. and *Calamoichthys calabaricus*) and some euteleosts (Budgett, 1901; Mok, 1978). Whether all dipnoans have the same kidney morphology, namely, complete separation of the left and right components of the kidney, is not certain. Ballantyne (1928) wrote about this organ in *Neoceratodus forsteri*: "Two kidneys are fused for a short distance at the level where the most anterior vasa efferentia open into the kidney tissue." Since there is no illustration in his paper, the exact position of fusion is not known. Whether the kidneys are really fused in this species is doubtful to me. It might

be the same condition that occurs in *Protopterus annectens*, wherein the posterior parts of the kidneys near the urinary bladder are "fused" superficially. They are, in fact, separate and are only connected by the lymphadenoid tissue that coats these organs (Parker, 1892).

For the other living gnathostomes (including chimaeras, non-batoid neoselachians, some batoids, coelacanthiforms, actinopterygians), the posterior kidneys or the extreme posterior kidneys are fused to various degrees. The kidney of *Latimeria chalumnae* is specialized in that only the extreme posterior parts (or the extreme posterior kidneys) are present (personal observation, AMNH 36941, 1300 mm TL; Millot and Anthony, 1973). They are fused medially, placed on the floor at the posterior end of the peritoneal cavity. For cyclostomes, the kidney structure is strikingly different from that of gnathostomes (Fänge, 1963). Therefore, comparison between the cyclostome and gnathostome kidneys at the gross structural level provides no information for determining the nature of the two character states (complete separation versus partly fusion) of gnathostome kidneys.

With regard to the distribution of these

character states (fusion and separation of the kidneys) among gnathostomes, a hypothesis concerning the sarcopterygian interrelationships can be reached. This hypothesis is the most parsimonious one involving a minimum number of kidney character state reversals (Fig. 4). The Coelacanthiformes are considered as the plesiomorphic sister-group of a monophyletic assemblage that includes the Dipnoi, Brachiopterygii, and Tetrapoda. In the latter group monophyly is indicated by the complete separation of the kidneys. I suggest that kidney separation in some batoids has evolved independently.

Discussion

The interrelationships of sarcopterygians have been widely discussed, but are not agreed upon. Dipnoans, for example, are of uncertain relationships (Moy-Thomas and Miles, 1971); it has been hypothesized that they are closely related to the Crossopterygii (e.g., Westoll, 1949; McAllister, 1968; and Gardiner, 1973); to the Actinopterygii (Bertmer, 1966), to choanates (Miles, 1977), or that they are a separate group related to the common stock of crossopterygians and actinopterygians. As for the systematic position of crossopterygians, Bjerring (1973) argued against the monophyly of the crossopterygians and suggested that coelacanthiforms are not members of this group on the basis of the differences in their cranial subdivisions. However, he did not make further suggestions concerning the relationship of coelacanthiforms. The systematic position of polypterids is also equivocal. Pehrson (1947), Stensiö (1947), DeBont and Paulus (1964), McAllister (1968), and Gardiner (1973) agreed upon the actinopterygian affinity of polypterids. Nelson (1969, 1973), on the other hand, placed them in the subclass Sarcopterygii on the basis of the evidence of gill arch and jaw structures. Jessen (1973) remarked that the shoulder girdle and pectoral fin of *Polypterus* show no similarities at all with those of actinopterygians, which are clearly distinguishable from polypterids and occupy a position of their own among fishes in general.

I suggest that the presence of a connection between the hepatic and neoposterior cardinal vein in coelacanth, polypterids, dipnoans, and

tetrapods is synapomorphic, indicating the monophyly of these groups. However, the difference in the manner of connection between the hepatic and neoposterior cardinal vein of polypterids and the other aforementioned groups raises questions concerning the homology of these structures. Data about the development of this connection in polypterids would be helpful in answering these questions.

The monophyly of tetrapods, dipnoans, and polypterids, indicated by kidney fusion, fits with the evidence of Miles (1977). With regard to the two hypotheses of the hepatic and neoposterior cardinal veins connection, the hypothesis that the polypterid character state is plesiomorphic in sarcopterygians (see above) conflicts with the evidence of kidney fusion. If the polypterid character is autapomorphic, this particular venous character and kidney fusion do not conflict. On the basis of the present data, I favor the latter hypothesis that the polypterid character is autapomorphic.

Neoposterior cardinal veins being equally long is plesiomorphic for actinopterygians. Halecostomes (including halecomorphs and teleosts) seem to be a monophyletic group, because they share the apomorphic character state that the right neoposterior cardinal vein is much longer than the left. A similar state in some elasmobranchs seem to be convergence.

The transverse connection between the neoposterior cardinal veins by anastomoses is plesiomorphic for gnathostomes. The loss of this connection in most actinopterygians would seem to be apomorphic at certain levels within this group.

There has been conflict of opinion concerning the phylogenetic relationship of the Hiodontidae. McAllister (1968) erected a new suborder for this family, separated it from the group that includes the Osteoglossidae, Pantodontidae, Notopteridae, Mormyridae, and Gymnarchidae, and considered it to be a relative of the elopoids, albuloids, or clupeoids by the shared character of the otophysic connection of the swimbladder diverticuli. In contrast, Ridewood (1904, 1905), Regan (1929), Berg (1940), Gosline (1960), and Greenwood (1963) have agreed that the Hiodontidae forms part of a single group that includes the above mentioned families. Greenwood et al.

(1966) have called it the Osteoglossomorpha. McAllister's hypothesis has recently been contested by Nelson (1972) on the basis of a gut character shared by these families, including the Hiodontidae: the anterior section of the intestine passes posteriorly to the left rather than the right of the esophagus and stomach. This evidence led Nelson (1972) to the conclusion that the Osteoglossomorpha are a monophyletic group. The posterior cardinal vein system supports the osteoglossomorph affinity of the Hiodontidae. The left neoposterior cardinal vein being larger or longer than the right, a character shared by the osteoglossomorphs including hiodontids, is apomorphic within halecostomes and suggests the osteoglossomorph affinity of the Hiodontidae.

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魚類の後主静脈と腎臓の形態，ならびにその系統学的意義

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魚類の主な分類群における後主静脈の分布，サイズと左右の腎臓の癒合の変異について記載し，これらの諸形質をもとに魚類の系統について若干の考察を行った。軟骨魚綱の板鰓類と全頭類の後主静脈系は類似している。硬骨魚綱全骨類のアミアにおける形状は軟骨類（チョウザメ，ヘラチョウザメ）や他の全骨類（レビズステウス）とは異なっており，むしろ真骨類の形状と類似している。シーラカンズ類，ポリプテルス類，ハイギョ類，四肢動物では肝静脈と新後主静脈が連絡しており，単系統的と考えられるが，ポリプテルス類のものは他の群のものととの相同関係に疑問が残る。