Novel modification of the tetrapod cardiovascular system in the West African caecilian *Herpele squalostoma* (Amphibia: Gymnophiona: Caeciliaidae)

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(With 2 figures in the text)

Aspects of the cardiovascular system of *Herpele squalostoma* are described and compared to other caecilians. Novel modifications of the systemic arches, anterior vertebral arteries and vertebral structures associated with the systemic arches are identified. The evolution of aortic arch diversity in caecilians is considered from the perspective of efficiency of the cardiovascular system. A speculative hypothesis is advanced concerning the evolutionary history of the systemic arches in *H. squalostoma*. It is argued that modification of vertebral structures is the result of epigenetic interaction between the vertebral column and the evolving systemic arch.

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**Introduction**

Described by Stutchbury (1834), *Herpele squalostoma* was the first species of African caecilian known to Science. This species appears to be widespread in Tropical West Africa, in the region east of the Gulf of Guinea, and fairly large collections have been made suggesting that it may be locally abundant (Taylor, 1968). Despite the fact that *H. squalostoma* is fairly well represented in scientific collections, and that it has been known for over 150 years, knowledge of the morphology of this species is incomplete. Parker (1936) and Taylor (1969) provided figures and terse descriptions of the skull, and Nussbaum & Naylor (1982) included this species in a survey of the trunk muscles of caecilians.
The caecilian cardiovascular system shows considerable interspecific structural variation (Acolat, 1939; Ramaswami, 1944; Lawson, 1970), but surprisingly little attention has been paid to this diversity from either functional or systematic perspectives. As is true for most caecilian species, there are no reports of the cardiovascular system of _H. squalostoma_.

Recent dissection of the heart and aortic arches of _H. squalostoma_ has revealed an unusual modification in the passage of the systemic arches of this species which appears to be unique. Novel vertebral features that are clearly associated with the cardiovascular modification are also found.

**Materials and methods**

Observations were made using a binocular dissection microscope. The heart and aortic arches were exposed through midventral incisions in the body wall and pericardium. The heart and proximal aortic arches were removed from a single specimen to facilitate examination of their dorsal surfaces. Vessels were traced by careful dissection. No attempt was made to inject vessels owing to their small size and the presence of coagulated blood. Figures were prepared from camera lucida drawings.

Four ethanol preserved specimens (BMNH 1914.5.27.36, 1968.108, and 2 uncatalogued specimens) were dissected and one dry skeletal preparation (BMNH 1909.7.6.16) was examined. Comparative observations were made on a taxonomically diverse sample of caecilian species as part of a general survey of caecilian cardiovascular morphology.

**Results**

*The heart and truncus arteriosus*

The heart of _H. squalostoma_ lies enclosed within a tough, transparent pericardial sac at about one-third of the total length of the body behind the snout tip. It is elongate, and extends for about the length of two primary annuli, in the region of the 28th to 32nd primary annuli. As is typical of caecilians (Ramaswami, 1944; Lawson, 1966), the heart of _H. squalostoma_ is composed of a partially divided sinus venosus, left and right atria, a single, highly muscular and trabeculate ventricle, and a short and cylindrical conus arteriosus (Fig. 1a, b). There is a single row of three valves within the conus arteriosus. A network of coronary veins, as reported by Lawson (1966) in _Hypogeophis rostratus_, extends over the surface of the ventricle and conus arteriosus. The posterior apical end of the sub-conical ventricle is bound to the pericardium by a short and stout connective tissue bundle. Both these latter features appear to be common to all caecilians.

The conus arteriosus leads into an elongate truncus arteriosus which is subdivided by septa into separate chambers (Fig. 1c–e). Proximal to the conus arteriosus, the truncus is divided by a vertical septum into a smaller left and a larger right chamber. More distally, each of these chambers is subdivided by a further oblique septum into a ventromedial carotid chamber and a much larger dorsal common systemic-pulmonary chamber. As the truncus arteriosus passes through the anterior limit of the pericardium its internal chambers separate and the common systemic-pulmonary chambers become divided giving rise to the paired carotid pulmonary and systemic arches.

*The carotid and pulmonary arches*

The carotid arches run cephalad, along the lateral margins of the trachea. They bend laterally and lose their association with the trachea as the oesophagus widens into the pharynx, and here
FIG. 1. The heart of *Herpele squalostoma* (BMNH 1914.5.27.36) in ventral (a) and dorsal (b) views, with cross-sections of the truncus arteriosus (c–e); showing internal septation at the three levels indicated in (a), a = atria, ca = carotid arteries, co = conus arteriosus, lpa = left pulmonary artery, lpa = left lateral vertebral artery, llva = left medial vertebral artery, lsa = left systemic arch, ml = anterior limit of the pericardium, pa = right pulmonary artery, rpa = right pulmonary artery, rna = right medial vertebral artery, rlva = right lateral vertebral artery, rmva = right lateral vertebral artery, rs = right systemic arch, svs = sinus venosus sinistra, ta = truncus arteriosus, v = ventricle.
they give rise to external and internal carotid arteries, which form the major arterial supply to the head. The left common carotid and its anterior derivatives are slightly smaller than the corresponding vessels of the right side.

The pulmonary arches of each side bend dorsolaterally as they pass through the pericardium. The arteries then extend posteriorly close to the dorsal wall of the coelom to supply each lung. The left pulmonary artery is less massive than the right and this difference in size correlates with the asymmetric development of the lungs in this species. The elongate right lung is about 30% of the total body length, whereas the left lung is essentially rudimentary and is less than 5% of the length of the right.

**The systemic arches**

The systemic arches also bend dorsolaterally, just anterior to the pulmonary arches, after penetrating the pericardium. They then extend a little posteriorly, before curving anterodorsally again and running cephalad to a position about the length of one trunk myomere anterior to the pericardium. At this point they pass through a small perforation in the musculus subvertebralis pars ventralis together with the ventral ramus of a spinal nerve. The arch and nerve of each side continue to extend dorsally, passing through the main mass of the musculus subvertebralis, and eventually reaching the ribs of the corresponding vertebra. For a description of the subvertebral muscle units referred to here see Naylor & Nussbaum (1980). The systemic arches and associated nerve extend slightly anteriorly across the ventral surface of the capitulum, and then bend dorsally to lie in front of the rib-vertebral articulation. The nerve then bends medially and runs to the central nervous system through the intervertebral space, which is expanded by emargination of the anterior and posterior lateral margins of the neural arches of the adjacent vertebrae (Fig. 2).

The systemic arches of each side separate from the nerve. They bend posteriorly and pass through the aperture delimited by the vertebral body, capitulum and tuberculum. The arches then run posterovertrnally and medially along a slight groove in the ventral surface of the vertebral centrum. The two arches extend to the midline and emerge, separately but in contact, from the vertebral musculature at a position just anterior and dorsal to the pericardium. Upon re-entry to the coelomic cavity, the paired arches fuse, forming a single dorsal aorta which continues posteriad and provides the arterial supply posterior to the heart. In the specimens examined, there is minor variation in the position of the heart relative to the vertebral column, and corresponding variation in the particular vertebra with which the systemic arches are associated.

**The anterior vertebral arteries**

Proximal to the truncus arteriosus, the systemic arches give rise to a pair of vertebral arteries, a medial, and a more laterally originating vessel, on each side. These vessels run anteriorly and slightly dorsally, lateral to the trachea and oesophagus, before they also bend more strongly dorsally and penetrate the pars ventralis of the musculus subvertebralis. The more lateral vertebral arteries enter the vertebral musculature one or two vertebral segments anterior to the systemic arches. The somewhat larger, medial vertebral arteries extend a further two or three vertebral segments anterior to the lateral vessels. Both intraspecific and intra-individual minor variation is seen in the vertebral segment with which the vertebral vessels become associated, the latter being due to asymmetry in the bilateral development of the paired vessels. As with the systemic arches, these vessels penetrate the deeper main body of the musculus subvertebralis. In contrast, however,
Fig. 2. Vertebrae and ribs of *Herpele squalostoma* (BMNH 1909.7.6.16): (a) the vertebra and right rib associated with the systemic arch (the 31st) in lateral view; (b) in dorsal view; (c) a typical trunk vertebra and left rib (the 42nd) in lateral view; (d) in dorsal view. vc = centrum; cp = capitulum; tb = tuberculum; na = neural arch; vk = ventral keel; r = rib; ps = parapophysis; zs = zygosphene; pz = prezygapophysis; dp = diapophysis.
at the anterior margin of the corresponding rib, each vessel divides into anterior and posterior branches. These branches are difficult to trace because of their small size, but the posterior branch passes through the aperture at the rib vertebral articulation, and both appear to remain closely associated with the lateral surface of the vertebra. The branches from both of the vertebral arteries of the same side of the body probably form an interconnected network of vertebral arteries that supply the anterior trunk (see below). Unlike the systemic arches, they do not appear to re-emerge into the coelom.

Associated vertebra and ribs

The association of one of the trunk vertebra and its ribs with the novel passage of the systemic arches is reflected in corresponding modifications of these structures. The distinctiveness of the vertebra and ribs associated with the extra-coelomic passage of the systemic arch, as seen in dissection, is sufficient to allow the recognition of the modified vertebra in a dry skeletal preparation of this species (Fig. 2a, b). Compared with other trunk vertebrae (Fig. 2c, d), the associated vertebra is unique in a number of respects. The parasphenes are more robust and project a little further anteriorly from the centrum, the ventral keel (which is continuous with the zygosphene) is strongly emarginated just posterior to the parasphene, and the diapophyses are larger and project more strongly from the lateral surface of the prezygapophyses. Each rib has a relatively long capitulum and a massive tuberculum, and the body of the rib between the two heads is strongly emarginated.

Discussion

Some general considerations

Considerable interspecific variation in the cardiovascular system of caecilians was reported by Ramaswami (1944). Much of this variation concerns the extent of development of, and pathways taken by, the aortic arches. The aortic arches may be paired, with various degrees of bilateral size asymmetry, or either both or just one of the pulmonary and systemic arches may be single. In addition, the pulmonary and systemic arches may run cephalad to the pharynx before bending back upon themselves to supply the lungs and trunk, or they may curve posteriorly much closer to their points of origin from the truncus arteriosus, without looping into the pharyngeal region.

This variation may be largely understandable in terms of the evolving efficiency of the circulatory system in lineages that have undergone dramatic elongation of the body during their evolutionary history. Heritable modifications of the cardiovascular system that enhance its efficiency, in terms of the costs of development and maintenance of structure, and the energy expended in propelling the blood would, ceteris paribus, enhance fitness and be selected. With elongation of the body, the heart and arterial system is required to generate and sustain vascular momentum over an increased distance and this can be expected to generate an increased selection pressure for efficiency enhancing modifications.

Where vessels run in parallel and carry blood of a similar composition, then, all other things being equal, the efficiency of the circulatory system may be enhanced by fusion of the vessels, or by the elaboration of one of the vessels and reduction or loss of the other. Such modification has a two-fold advantage. First, resistance to fluid flow is inversely proportional to the diameter of the vessel, so that it is more efficient to propel like fluids along a common course through a single vessel than through separate vessels of lesser diameter. Secondly, less material and energy expenditure is
required in the development and maintenance of a single larger vessel than of multiple smaller ones carrying an equivalent volume of fluid. Thus functional considerations suggest that natural selection would favour the transition from paired to single arches, with the potential benefit of such a change increasing with elongation of the body and the extent of separate but redundant vascular pathways. This is not meant to imply that a morphologically ‘primitive’ circulation is less efficient than a ‘derived’ circulation. Functional considerations simply allow us to identify particular character states that are more likely to be derived than primitive because of their hypothesized efficiency enhancing effect. Primitively, caecilian aortic arches would be expected to be paired, as in fishes and other amphibians, so that outgroup and functional criteria suggest the same evolutionary polarity, i.e. that within the Gymnophiona paired systemic and pulmonary arches are primitive conditions and single arches are derived.

Similarly, the efficiency of the cardiovascular system may be enhanced, all other things being equal, by maximal reduction of the path lengths occupied by vessels within the functional constraint imposed by the requirement of a comprehensive circulation. A purely theoretical approach to the problem of optimization of the circulatory network for maximal efficiency provides an analogy to the construction of minimum length networks connecting taxonomic units in systemic studies. Of course, in the context of real organisms, such a theoretical analysis is impractical because of the complexity of structure. It would also be unlikely to provide complete insight into cardiovascular design because of phylogenetic and developmental constraints. However, the principle may be a useful guide in interpreting certain aspects of cardiovascular evolution. Thus, within caecilians, systemic and pulmonary arches that run cephalad to the pharyngeal region and then double back on themselves without giving rise to major anterior vessels appear less efficient than the posterior bending of these arches proximal to the heart. Natural selection would be expected to favour the shortening and elimination of the systemic and pulmonary arch loops that extend without major issue to the pharyngeal region. In fishes, and the larvae of other amphibians, the aortic arches do extend to the pharyngeal region where they vascularize the gills. Once again, the outgroup criterion therefore agrees with the above functional considerations in suggesting that, within the Gymnophiona, aortic arches extending in a loop to the pharyngeal region are primitive and shorter arches derived.

Viewed from a cladistic perspective, features of the cardiovascular system might provide useful characters for the estimation of evolutionary relationships. For example, the Ichthyophiidae is considered to be a relatively morphologically primitive family (Taylor, 1968; Nussbaum, 1979), and adult ichthyopilids have the primitive conditions of pulmonary and systemic arches that loop into the pharyngeal region. In ontogeny, these vessels supply the external gills (Ramaswami, 1944, pers. obs.) and their retention in adults, which cannot readily be explained in terms of adult function, may be due to a constraint of ontogenetic function. Variation in the structure of a number of internal features of the heart also provides a number of characters that, although not well understood functionally, may be readily polarized using outgroup criteria and may thus prove useful for future phylogenetic studies. A clear example is the number of rows of valves in the conus arteriosus. These valves are either single or paired in caecilians, with multiple rows typical of outgroup taxa (Goodrich, 1930) and therefore considered primitive within the Gymnophiona.

**Systemic arch evolution in Herpele**

In the context of *Herpele squalostoma*, the highly unusual modification of the systemic circulation may be partially illuminated by the above considerations. In this species the systemic
arches lack extensive anterior loops, and thus their evolution fits the above model of transitions to shorter, and hence more efficient, vascular networks. However, unlike other caecilians in which the systemic arches are shortened, those of *H. squalostoma* penetrate the vertebral musculature and have an extra-coelomic passage that is unique among tetrapods.

This feature shows some similarity to the pattern of the vertebral arteries in the South American typhlonectid caecilian, *Typhlonectes natans*. In this species, vertebral arteries arise from the single systemic arch and the dorsal aorta. They penetrate the vertebral musculature at the mid-line and extend dorsally to a central position relative to the ventral surface of the corresponding vertebral centrum. Generally, the vertebral arteries then bifurcate twice giving rise to left and right, anterior and posterior branches. The anterior branches run across the ventral surface of the vertebral centrum and pass through the aperture formed by the vertebral body and the heads of the ribs. Here the vessels of each side give off a lateral and a dorsal branch which supply the external muscular sheath and the deeper vertebral musculature, respectively. The posterior branches of the vertebral arteries unite with the anterior branches of the adjacent vertebral arteries to form a lateral arterial network that extends, with occasional and irregular interruptions, along the length of the vertebral column. The spacing of vertebral arteries is somewhat irregular with many vertebrae lacking a corresponding vertebral artery, and here supply is from other vertebral arteries via the extensive lateral networks (pers. obs.). Lawson (1970) did not describe posterior branches of the vertebral arteries in the caeciliid *Hypogeophis rostratus*, but did report many anastomoses between successive vertebral arteries, clearly suggesting that such vessels are present here also. In *H. squalostoma*, vertebral arteries that arise from the dorsal aorta posterior to the heart seem to follow the same pattern as the vessels in *T. natans*. Owing to their small size I have been unable to trace the vessels in detail but they clearly penetrate the vertebral musculature at the midline and bifurcate twice into anterior and posterior branches on each side. The similarity of what, at this stage, must be assumed to be a general caecilian pattern of vertebral arterial circulation to the novel passage of the systemic arches in *H. squalostoma* is suggestive of a possible evolutionary connection between the two patterns.

It is well known that the vascular system displays great developmental plasticity. The adult pattern of vessels is gradually established through processes of selective elaboration, fusion, confluence, retrogression, transformation and suppression of the numerous channels that develop as a diffuse plexus early in ontogeny (Richardson, 1937). Vessel development is probably epigenetic to a high degree, with the differential development of vessels being affected by haemodynamic factors such as the volume, direction and pressure of blood-flow through them, and by the respiratory and nutritional requirements of the tissues that they supply (Hughes, 1943). Even in adult animals, the circulatory system is capable of some epigenetic compensatory responses to damage to important vessels through the elaboration of parallel vessels of originally lesser importance.

An evolutionary transition in the systemic arches, from the ancestral condition with anterior loops to the pharyngeal region, to a more efficient system where these loops are shortened, could be achieved by the elaboration of pre-existing shorter channels at the expense of the longer ones. A multitude of such parallel channels is to be expected to occur transiently in development and to a lesser extent throughout ontogeny. In addition, many linkages between distinct vessels that occur early in ontogeny and which are subsequently lost may be available for evolutionary modification which could produce dramatic changes in the pattern of the circulation.

These considerations lead to the speculative hypothesis that, in the evolution of *H. squalostoma*, a developmental connection between the systemic arches and one of the vertebral artery systems
began elaborated at the expense of the primitive pattern of the systemic arch circulation. This hypothesis would account for the novel association of the systemic circulation with the vertebral column and the observed correspondence between the systemic arches of *H. squalostoma* and the general pattern of caecilian vertebral arteries. In particular, that part of the systemic arch of *H. squalostoma* that passes through the aperture at the vertebral-rib articulation, and extends across the ventral surface of the vertebral centrum to the midline, corresponds well with the anterior branch of a typical vertebral artery. To a lesser degree, there is some correspondence between the lateral branch of an anterior vertebral artery and that part of the systemic arch of *H. squalostoma* that extends through the musculus subvertebralis.

**Blood flow in vertebral arteries** is from the centre to the periphery. In contrast, the flow of blood in the corresponding sections of the systemic arches of *H. squalostoma* is from the periphery towards the centre. An interesting consequence of the hypothesis advanced here, is that there would have been an evolutionary reversal in the direction of blood in vessels that were originally vertebral but which have become incorporated into the systemic arches.

The hypothesis does not account directly for the novel form of the anterior vertebral arteries of *H. squalostoma* that do not penetrate the vertebral musculature along the midline, but which parallel the peripheral to central passage of the systemic arteries. Two alternatives may be suggested here. First, the modification of these vessels may have been correlated with the modification of the systemic arches, either as pleiotropic consequences of genetic and proximate causes responsible for the latter, or through the direct involvement of these vessels as transitional stages in the process of shortening of the systemic pathway. Secondly, it may be that the vertebral arteries of *H. squalostoma* were modified for some other reason, and that such a modification may have itself facilitated a subsequent modification of the systemic arches.

**Vertebral evolution**

The majority of the modifications of the ribs and vertebrae associated with the systemic arches are clearly ones that facilitate the passage of the systemic vessels, mainly through the enlargement of the aperture at the rib-vertebral articulation. The reduction of the ventral keel, where the systemic arches of each side meet, reflects a reduction in muscle attachment and in muscle mass in this region that might otherwise constrict the systemic arch. Modifications such as these may well be induced epigenetically by the presence of enlarged vessels. Their evolution more probably reflects a developmental response to changes in the systemic circulation, rather than the result of selection of genetic mutations primarily effecting vertebral structure.

**Conclusion**

The above scenario, as it concerns unrepeatable historical events, is mostly not directly testable and is necessarily highly speculative. The proposed explanation of vertebral modification in *Herpele squalostoma* by epigenetic interaction could potentially be tested by experimental manipulation of the developing circulatory system. For example, if it were possible artificially to enlarge selected posterior vertebral arteries during ontogenetic development, the epigenetic hypothesis would predict a remodelling of the rib-vertebral articulations in associated vertebrae, so as to enlarge the aperture between the capitulum, tuberculum and vertebral body. A possibly simpler but less direct test would be to use the natural variation in the sizes of the vertebral arteries...
along the trunk of caecilians and search for correlations between measures of this variation and of associated vertebral features. The epigenetic model predicts that such correlations will be found. The peculiarities of the cardiovascular system of *H. squalostoma* emphasizes the extent of interspecific variation in the caecilian cardiovascular system and the need for a more comprehensive documentation of this variation. The evolutionary polarity of the transitions between some of the conditions observed may be readily interpreted through the application of the outgroup criterion and through functional considerations. Lawson (1970) suggested that the caecilians comprised Old World and New World lineages, and that the reduction of aortic arches from paired to single had occurred independently in each of these groups. The fact that there are caecilians with the derived conditions of single arches within both geographical groups suggests that the dichotomous geographical grouping of caecilian taxa does not reflect phylogeny. This conclusion receives support from the limited attempts at cladistic analysis of the phylogenetic relationships within the Gymnophiona using characters from other morphological systems (Nussbaum, 1977, 1979; Duellman & Trueb, 1986). Generally, the phylogeny of caecilians is poorly understood (Nussbaum & Wilkinson, 1989) and study of the cardiovascular system may be anticipated to provide characters that help to improve this understanding.

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