In vivo Observations on a Specialized Microvasculature, the Primary and Secondary Vessels in Fishes

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Abstract


Microscopical observations have been made on the blood circulation of intact, unanaesthetized specimens of the transparent glass catfish. Along the segmental arteries of the trunk, groups of short, curled vessels of capillary dimensions (termed inter-arterial anastomoses) branch off and reunite to form large so-called secondary arteries running parallel to the main (primary) arteries. Secondary arteries give rise to capillaries in the median ventral fin membrane. Secondary capillaries are drained via separate secondary veins. When blood passes from primary to secondary arteries via the inter-arterial anastomoses a pronounced plasma skimming is observed. Hence, blood perfusing the secondary capillaries of the fin membrane contains very few red blood cells.

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Introduction

Numerous reports have appeared over a long span of years describing lymphatic vessels in teleost fish (Hewson 1769, Allen 1906, Burne 1927, Jakubowski 1960, Wardle 1971). An extensive review of the anatomical literature dealing with lymphatic vessels in fish, as well as other vertebrates, is given in Kampmeier (1969). Modern handbooks and reviews on microcirculation and lymphatic vessels deal only very briefly with lymphatics in fish and basically repeat the statements of the older literature (Yoffey and Courtice 1970, Kaley and Altura 1977, Casley-Smith 1980). Only a few electron microscopical studies have been carried out on the fine structure of potential lymphatic vessels in fish comparable to the studies which have elucidated the structure of terminal lymphatic vessels in mammals.

Recent anatomical studies on a number of fish species have, however, shown that vessels hitherto considered to be lymphatics are of an entirely different nature (Vogel et al. 1973, Vogel 1981, Vogel and Claviez 1981). Lymphatics originate from minute, blind-ended terminal vessels in the tissues and collect and return tissue fluid to the venous system. In contrast, the so-called lymphatics in fish are in open communication with the systemic arteries via a large number of anastomoses of capillary dimensions. Vogel (1981) has proposed the terms inter-arterial anastomoses and secondary vessel system for these anastomoses and the vessels originating from them.

The present paper is a report on in vivo observations of these inter-arterial anastomoses, as well as parts of the secondary vessel system, in a transparent fish, the glass catfish, Kryptopterus bicirrhis.

Material and Methods

The glass catfish, Kryptopterus bicirrhis (Teleostei, Siluridae), is an ideal animal for the purpose of microscopical observation on the microcirculation. The larger part of the body consists of the tail region, which is almost completely transparent except for the spinal column and small, scattered groups of pigment cells. A large anal fin runs along the ventral margin of the tail region. The viscera are confined to the anterior part of the fish. This region, as well as the gill region, are not transparent. Thus the present report is confined to a description of the circulation in the transparent tail region (Fig. 1, inset).

The fish (total length 5–7 cm) were purchased at a local aquarist store and were fed live Daphnia.
During microscopic observation the intact unanaesthetized fish was placed in a small amount of water in a Petri dish. The fish remained quiet for long periods of time, thus making clamping or restricting it unnecessary. Upon return to the holding aquarium, no signs of ill effects were observed, even after up to three hours of continuous observation on the same animal.

Observations were made using a Leitz Orthoplan microscope with normal or Leitz Uiltropak objectives, which can be immersed in water, and a combination of reflected and transmitted light. Magnifications varied from 25 to 690 times. The figures are based on 35 mm photographs and video recordings made with a Philips Observation Camera (VK 4900).

**Observations**

**Description of the Vascular System**

The overall layout of the vascular system of the ventral part of the tail region of the glass catfish is depicted in a semi-diagrammatic fashion in Fig. 1. The location of the two segments shown is indicated on the inserted sketch of the fish. The dorsal aorta (5) gives rise to segmental arteries (9), one in every second segment, which supply capillary networks of the skeletal muscle and skin of the trunk (not drawn in Fig. 1), as well as capillaries (11) supplying electoreceptors (12) and skin in the proximal part of the anal fin. These capillary networks are drained via segmental veins (14), alternating with the segmental arteries, into the caudal vein (6).

Apart from the ordinary branching into smaller and smaller arteries, the main branches of the segmental arteries give rise to groups of short, curved vessels of capillary dimensions (8), which immediately unite to form new vessels (10) running parallel to and being almost as large as the segmental arteries.

Figure 2 shows a photograph of a segmental artery (9) surrounded by two groups of small, curved branches (8) opening into vessels (10) running parallel to the segmental artery.

In accordance with the terminology proposed by Vogel (1981), the small, curved branches of the segmental arteries are called inter-arterial anastomoses and the vessels to which they give rise are termed secondary arteries. Consequently, the vessels of the ordinary arterial system will be termed primary arteries.

Figure 3 shows two still pictures from a video recording of an inter-arterial anastomosis, as well as a line drawing based on the original video recording. A red blood cell is seen at two different stages of passage through the anastomosis. The anastomosis has the calibre of a capillary, i.e. the red blood cell fills the lumen of the anastomosis completely and is even somewhat deformed during passage. As shown in Fig. 1, the secondary arteries (10) proceed distally to run along the thin rays of the anal fin. After passing the proximal region of the anal fin, characterized by electoreceptors and capillaries of the primary vessel system, they divide into two secondary arterial vessels running along each side of the fin ray. They give rise to a number of long, straight secondary capillaries (13) in the distal part of the anal fin membrane (Fig. 4).

The secondary capillaries of the fin membrane unite into secondary venous vessels along the fin rays. In most cases these vessels merge into one at the base of the fin ray and open into a larger longitudinal secondary venous collecting vessel (16), as shown in the left half of Fig. 1 and Fig. 5. In some cases (right part of Fig. 1) the secondary veins from the fin ray do not merge. One opens into the large secondary vein (16) along the base of the anal fin. The other proceeds centrally to open into a similar but somewhat smaller secondary venous collecting vessel (7), the secondary subvertebral vein (Vogel 1984). This is situated just ventral to the main primary vessels along the spinal column. It represents the 'truncus lymphaticus subvertebralis' or 'cardinal lymphatic' of previous authors (cf. Kampmeier 1969). Flow in the longitudinal collecting vessels is towards the head.

Since the spinal column is not transparent, the presence or absence of inter-arterial anastomoses along the main aorta cannot be ascertained. The dorsal region of the fish is less transparent than the ventral parts, making a detailed description of the vessels impossible. The presence of a few inter-arterial anastomoses has, however, been observed, as well as secondary segmental veins draining into a longitudinal secondary venous vessel just dorsal to the spinal column.

**Blood Flow in the Secondary Vessel System**

As blood passes from the primary arteries through the inter-arterial anastomoses, a very pronounced plasma skimming occurs. Thus the cell volume or haematocrit in the secondary vessel system is quite low. The haematocrit of the secondary vessel blood has not been measured, but judging from a visual impression a fair guess would be 1% or less.

Although quantitative measurements of blood flow or velocity have not been made, it is safe to say on the basis of visual observation of the vessels that there is a substantial flow through the inter-arterial anastomoses and secondary vessel system.

Blood velocity is lower in the secondary seg-
mental arteries than in the primary segmental arteries. Flow is very sluggish in the longitudinal secondary venous collecting vessels, which are of a much larger calibre than even the largest primary arteries or veins.

Discussion

The existence of inter-arterial anastomoses and a secondary vessel system has been demonstrated in a number of fish species (Vogel 1981). From these studies it appears that the secondary vessel system gives rise to capillaries in the skin of the body surface, as well as in the fins. Usually the fins are at the same time supplied by ordinary capillaries of the primary vessel system. Thus the finding that the fin membrane is exclusively supplied by secondary capillaries, whereas the general body surface has only primary capillaries,
may be a specialized feature of the glass catfish. What the present study has added to the anatomical evidence is the observation that the inter-arterial anastomoses are fairly wide open in the live fish and carry a substantial blood flow.

There can be little doubt that the main venous vessels of the secondary vessel system are identical to what has previously been described as the main trunks of a lymphatic system in fish (Vogel 1984). This is particularly evident for the large calibre longitudinal collecting vessels. The demonstration that a certain kind of vessels are not lymphatics, but carry a flow of blood originating from open connections with the arterial system, is not proof that lymphatics do not exist. However, neither previous anatomical investigations (Vogel 1981) nor the present observations on the live glass catfish have resulted in any evidence in favour of the existence of lymphatics in this class of vertebrates. Having dismissed the possibility that bony fishes possess a lymphatic system, we are still faced with the existence of the secondary vascular system and the question as to what functional significance this system may have. Two facts concerning the nature of the secondary vessel system must be stressed. Firstly, we are dealing with a vessel system which, at least under the prevailing conditions, carries blood with very little haemoglobin. Secondly, the capillary beds of the secondary vessel system are situated primarily in the skin.

The low haemoglobin content of the blood in the secondary vessels suggests that it is not particularly involved in gas transport. Of interest in this context is the finding that fish may show a considerable cutaneous oxygen uptake which is largely consumed by the skin itself. Thus the skin is not a gas exchanger for the benefit of the rest of the animal (Kirsch and Nonnotte 1977, Nonnotte and Kirsch 1978, Steffensen and Lomholt, 1985). Even though the skin is supplied with oxygen by diffusion from the outside, it must still be supplied with nutrients and this function could well be fulfilled by capillaries of the secondary system.

Recently, evidence has been presented to show

Fig. 3. Two photographs from a video recording showing a red cell at two different stages of passage through an inter-arterial anastomosis. The line drawing is based on the original video recording. Blood flow direction is indicated by arrows.
Fig. 4. Distal part of the anal fin containing only vessels of the secondary system. Bar 250 μm.

Fig. 5. Low magnification photograph of the ventral part of the trunk and the proximal part of the anal fin. Bar 250 μm.
that fish skin plays an important role in active salt transport processes involved in osmoregulation (Nonnotte et al. 1979). The secondary system could be involved in this.

Both the proposed functions of the secondary capillaries in the skin could equally well be served by capillaries of the primary vessel system. One may ask if there are situations in which it may be of functional significance to perfuse the skin with blood of a very low haematocrit.

When exposed to hypoxic water we have observed the glass catfish to rise and breathe at the surface. Aquatic surface breathing is known to occur in a number of tropical freshwater fishes, including the glass catfish (Kramer and McClure 1982). This enables the fish to utilize the very top layer of the water, which will always have a high oxygen content. It represents a functional analogy to the habit of air breathing which is widespread among larger tropical fresh water fishes. Aquatic surface breathing as well as air breathing fishes exposed to very hypoxic water come into a situation where the oxygen obtained at the surface may be lost to the oxygen deficient ambient water if they have an intense blood perfusion of the skin. By perfusing the skin with blood of a very low haemoglobin content from the secondary vessel system, such a loss might be avoided, while still maintaining the supply of nutrients carried in the blood plasma. This requires that the oxygen demand of the skin can be met by diffusion from the ambient water at even very low oxygen tensions. Interestingly, Kirsch and Nonnotte (1977) found that excised pieces of fish skin can maintain a constant oxygen uptake in spite of oxygen tensions as low as 10 torr in the bathing medium.

The observations reported above on this hitherto unrecognized category of vessels certainly call for further physiological speculation, as well as experimentation. We hope that the demonstration of the extraordinary qualities of the glass catfish for observing the secondary vessel system in vivo will open up possibilities for studies of the function of this system.

Numbering for Figures

1 Vertebra
2 Heamal arch and ventral spinal process
3 Fin supporting bone (radial)
4 Fin ray
5 Dorsal aorta
6 Caudal vein
7 Longitudinal secondary venous collecting vessel along ventral aspect of spinal column (secondary subvertebral vein)

8 Group of inter-arterial anastomoses
9 Primary segmental artery
10 Secondary segmental artery
11 Capillary of primary vessel system
12 Electroreceptor
13 Capillary of secondary vessel system
14 Primary vein
15 Secondary vein along fin ray
16 Secondary venous collecting vessel along base of anal fin
17 Distal margin of anal fin membrane

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References


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