# Vascular Specialization in Fish, but No Evidence for Lymphatics

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Blood distribution in the systemic circulation of bony fishes is effected by a dualistic construction of the vasculature: A secondary arterial system originates from the well known (primary) arteries by multiple root-like shunt vessels. These secondary arteries and the vessels they supply should no longer be regarded as lymphatics. After an intensive search for unequivocally lymphatic vessels in fish, it appears doubtful whether there are any at all in this class of vertebrates.

In 1927/29 R. H. Burne described “fine” vessels around systemic arteries in teleostean fishes. These vessels seemed to embrace the main arteries with fingerlike projections and were found to join eventually the peripheral lymphatic system [1, 2]. Burne has shown that his “fine” vessels should histologically be classified as small arteries. In spite of careful studies, however, it was only in the gill region of the cod that he was able to find a narrow connection between the arterial system proper and the system of “fine” vessels. Consequently he regarded the “fine” vessels as afferent lymphatics. Giacomini [3] also described the secondary vessels as lymphatics which were fed by numerous “glomeruli vasali”. These earlier results seem to have been too unusual to be integrated into a consistent picture of the systemic circulation of fish. Interpretation of the secondary vessels as lymphatics may have been another reason why these vessels are no longer mentioned in recent reviews concerning the vascular system of fishes.

While examining vascular corrosion casts [4] of various holostean and teleostean fish (*Amia calva, Lepisosteus osseus, Salmo gairdneri, Tinca tinca, Osphronemus goramy*), Burne’s “fine” vessels have been rediscovered: In all species studied, one or two small arterial vessels regularly parallel the dorsal aorta, segmental arteries and arteries in the head, tail and fins. They have not been found in the brain or intestines. In addition, scanning electron microscopic inspection of the vascular casts and of the luminal surface of corresponding vessels in tissue blocks [5] revealed that the small accompanying vessels originate by multiple root-like shunts (arterio-arterial anastomoses) from all neighbouring primary arteries (Fig. 1 a, b). In effect they form a secondary vessel system which constitutes a considerable part of the blood vascular system in fish.

In our casts the diameter of the arterio-arterial shunt vessels is fairly constant (10–14 µm). Their origin on the luminal side of segmental arteries is marked by endothelial cells with large tentacular microvilli. These cells occupy the initial part of the shunt vessel as well as the adjacent wall of the segmental artery immediately upstream of the shunt’s origin (Fig. 1 b).

The endothelial microvilli (Fig. 1 c) may take up information on rheological, osmotic and/or chemical properties of the blood in the primary arterial system and elicit appropriate adjustments of the luminal diameter of the shunt vessels. But the microvilli could also be involved mechanically in plasma skimming at the origin of the shunts. Plasma skimming is to be expected here, at least in stress situations, as the secondary vessels are often devoid of red blood cells in histological preparations. On the other hand, white blood cells, travelling in the marginal stream of the primary arteries, might be trapped between the microvilli and guided preferentially into the secondary vessels. Such a mechanism could be most useful after infections or traumatic peripheral lesions. It remains to be studied which of the possible functions of the endothelial microvilli is effective under physiological conditions.

Arterio-arterial shunts with essentially the same pattern of endothelial specialization are also present in trout gills at the origin of the central filament arteries (Fromm’s arteries) [6]. Apparently a dualistic arterial system of ordinary (primary) arterial vessels and secondary arteries originating from the primary ones via multiple minute shunts is a general principle of the circulatory system of many if not all fish.

According to Burne’s observation [1, 2] the secondary vessels supply mainly the oral mucous membrane and the skin. Thus fish are probably able to

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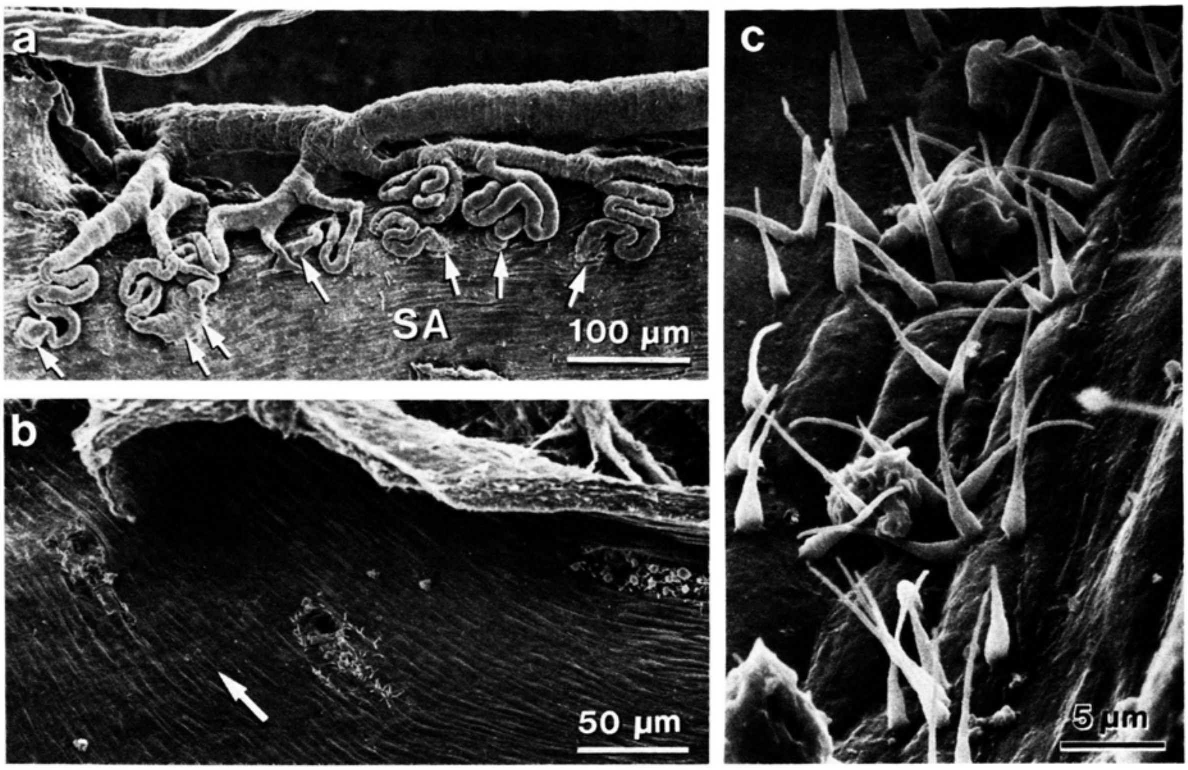

Fig. 1. Scanning electron micrographs of material from *Osphronemus goramy*. Similar results have been obtained in all fish studied. (a) Corrosion cast of a segmental artery (SA) from which several shunt vessels originate (arrows). The shunts unite to feed a small secondary artery. (b) Wall of a segmental artery from the luminal side. Origins of arterio-arterial shunts can be easily identified by the characteristic pattern of their specialized endothelial cells. Blood flow direction is indicated (arrow). (c) Endothelial cells at the entrance of an arterio-arterial shunt vessel. Tentacular microvilli, up to 10 µm long, are localized mainly on the marginal cell region. Often two or three microvilli share a common origin. Occasionally white blood cells seem to be trapped between them.

regulate blood flow in these areas independently of blood perfusion of muscles by their systemic arterio-arterial shunts. The secondary vascular system might therefore well be involved in immediate adaptive responses of euryhaline fish under osmotic stress. The degree of effective cutaneous respiration [7] might also be altered by active variation of skin perfusion. Finally, blood redistribution and plasma skimming at the origin of the secondary vascular system may contribute to changes in hematocrit reported during exercise [8].

The relative volume of the blood space attributed to the primary and to the secondary arterial system is not known. At any rate, when analysing various blood parameters in fish, the possibility should be kept in mind that a fairly large compartment of the vasculature could for some time be cut off from the main circulatory pathways.

In the gills the main function of the central filament arteries is to supply blood to the central venous sinus (CVS) of each gill filament. Interestingly, the CVS had for some time been regarded as a lymphatic vessel, too [9, 10]. In fact, its wall structure and also its irregular outline in many fish is quite similar to lymphatics in higher vertebrates. Furthermore, when examined histologically, the CVS is usually free of red blood cells. However, in view of direct shunts between filament arteries and the CVS in many fish and of blood supply to the CVS via central filament arteries, there can be no doubt that the CVS is to be classified as a venous vessel [11–13]. Absence of red blood cells in the CVS might also be due to plasma skimming. As in the systemic circulation, the degree of such skimming is probably regulated by the specialized endothelial cells governing the inflow into the shunt vessels.

In spite of a vast amount of literature on lymphatics in fish [14, 15] some doubt concerning their very existence has always lingered [16, 17]. This applies even to intestinal lymphatics [18] which have been claimed to be proved in teleosts [19]. The large longitudinal vessels below the median fins as well as the large lateral subcutaneous vessels, traditionally regarded as typical lymphatics in fish [20] are also occasionally filled in our casts. Therefore they too may be venous vessels rather than lymphatics.

Unfortunately, histological and ultrastructural features useful to discriminate lymphatics from venous vessels in higher vertebrates [21] are also found in venous vessels of teleosts [22]. Similarly, due to a high capillary permeability in fish [23], uptake of coloured substances injected into the interstitial space will not allow to differentiate reliably between blood capillaries or venous blood sinus and potential lymphatics in fish. Thus only the immediate origin of a vessel in the tissue, without any connection to the arterial system, may be accepted as proof for its lymphatic nature. So far we have not been able to find any such vessel in teleosts.

In the evolution of vertebrates, lymphatics may have developed later than assumed so far. Perhaps in amphibia they originally functioned in fluid absorption in the intestines and the skin during early adaptation for land life. But only when circulatory systems with high blood pressure developed, lymphatics became indispensable as an additionsl draining device for tissue fluids.

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[1] R. H. Burne, Phil. Trans. **B 215,** 1 (1927).
[2] R. H. Burne, Phil. Trans. **B 217,** 335 (1929).
[3] E. Giacomini, Rend. R. Acad. Sci. Bologna N. S. **26,** 188 (1922).
[4] Casting methods according to T. Murakami, Arch. Histol. Jap. **38,** 151 (1975).
[5] For preparative methods see: W. Vogel, V. Vogel, and M. Pfautsch, Cell Tiss. Res. **167,** 373 (1976).
[6] W. Vogel, Z. mikrosk.-anat. Forsch. **92,** 565 (1978).
[7] G. Nonnotte and R. Kirsch, Resp. Physiol. **35,** 111 (1978).
[8] D. R. Jones and D. J. Randall, in: Fish Physiology (W. S. Hoar and D. J. Randall, eds.) p. 425, **Vol. VII,** Academic Press, New York 1978.
[9] J. A. Riess, Arch. Naturgesch. **47,** 518 (1881).
[10] M. Morgan and P. W. A. Tovell, Z. Zellforsch. **142,** 147 (1973).
[11] B. J. Gannon, G. Campbell, and D. J. Randall, 31st Ann. Proc. Elect. Micros. Soc. Amer. **31,** 442 (1973).
[12] W. Vogel, V. Vogel, and H. Kremers, Z. Zellforsch. **144,** 573 (1973).
[13] P. Laurent and S. Dunel, Acta Zool. (Stockh.) **57,** 189 (1976).
[14] F. Weidenreich, H. Baum, and A. Trautmann, in: Handb. vgl. Anat. Wirbeltiere **VI,** (L. Bolk, E. Göppert, E. Kallius, and W. Lubosch, eds.) p. 745, Urban und Schwarzenberg, Berlin 1933.
[15] H. Hoyer, in: Bronns Klassen und Ordnungen des Tierreichs **VI/1,** Echte Fische, Teil 2, (Z. Grodzinski und H. Hoyer, eds.) p. 78, Akad. Verlagsges., Leipzig 1938.
[16] B. Mozejko, Anat. Anz. **45,** 102 (1914).
[17] P. Mayer, Jena. Z. Naturw. **55** (N. F. **48**), 125 (1917/19).
[18] J. S. Robinson and J. F. Mead, Canad. J. Biochem. **51,** 1050 (1973).
[19] G. Glaser, Z. Anat. Entwickl.-Gesch. **100,** 433 (1933).
[20] O. F. Kampmeier, Evolution and Comparative Morphology of the Lymphatic System, Ch. C. Thomas, Springfield 1969.
[21] J. R. Casley-Smith, in: Microcirculation (G. Kaley and B. M. Altura, eds.) p. 423, **Vol. I,** Univ. Park Press, Baltimore 1977.
[22] W. Vogel, V. Vogel, and W. Schlote, Cell Tiss. Res. **155,** 491 (1974).
[23] A. R. Hargens, R. W. Millard, and K. Johansen, Comp. Biochem. Physiol. **48 A,** 675 (1974).