

Gross Anatomy of the Vascular System and the Lateral Musculature of the Yellowtail *Seriola quinqueradiata* (Carangidae)

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Abstract A description is presented about the arrangement of the whole vascular system and the lateral musculature of the yellowtail. The sino-atrial valves are bilaterally continuous with the longitudinal bundles of atrial trabeculae, which keep the valves closed during atrial systole. The afferent filament arteries leave the afferent arch artery rather oppositely, far from the filament rows to interlock with the basal portions of the efferent filament arteries, then run down towards the filaments. The departure of the coeliaco-mesenteric artery is preceded by baffles equipped within the median dorsal aorta, so that the straight aortic flow is partially turned towards the coeliaco-mesenteric artery. The segmental vessels are completely double-tracked, *i.e.*, every unit consists of an artery and a vein closely coupling up to the distal end, instead of an artery or a vein alternating in a series. Such double tracking of the segmental vessels may represent a pre-adaptive modification that allowed tunas' ancestors to evolve the vascular heat exchangers. Each myomere is subsegmented into four "submyomeres" and as a result, the lateral musculature looks as if it were made up of a larger number of narrower myomeres.

Tunas and lamnid sharks are warm-bodied fish (Carey et al., 1971). They have developed an internal band of red muscle and retia mirabilia which act as counter-current heat-exchangers. The retia can be divided into four types: lateral subcutaneous rete nourishing the internalized red muscles, central rete just below the vertebral column, visceral rete associated with the liver, and carotid rete beneath the brain case. The subcutaneous rete, which is found in all members of the warm-bodied fish, communicates with longitudinal cutaneous vessels. The position of the lateral cutaneous vein in the porbeagle shark *Lamna nasus* suggests that it is homologous with the lateral cutaneous of other sharks (Burne, 1923). The cutaneous artery in tunas and lamnids, and the cutaneous vein in tunas, on the other hand, are new vessels in evolution.

How have the tunas and lamnids developed these specialized structures? The interpretation needs some transitional forms. Fossils hardly document soft anatomy, so the information should be derived from extant species closely related to them. However, there is little continuity in muscular and vascular design between the tunas and non-tuna scombrids.

The warm-bodied fish represents the most successful form among the pelagic, fast-swimming

fishes which vary in lineage and have been led to convergence in many external characters. It is hence likely that pelagic fast-swimmers other than the warm-bodied fish have modified their muscular and vascular arrangement in a similar direction to the warm-bodied fish. For example, the carotid rete, which is found in *Thunnus thynnus* (Linthicum and Carey, 1972), also occurs in billfishes, where the rete combines with a lump of brown tissue to form a brain heater (Carey, 1982). Furthermore, Burne (1923) was able to trace the progress of elongation and convolution of the carotid arteries in successive steps among some pelagic sharks belonging to different families of Lamniformes, and he placed the carotid rete of *L. nasus* as the final step.

The yellowtail is an active swimmer among the teleosts. The present study was designed to examine whether or not this fish has any modifications comparable with the muscular and vascular specializations in the warm-bodied fish. The vascular system was examined throughout the body by means of corrosion casting technique. This work revealed a feature shared with the tunas and, in addition, several features of general interest. A peculiarity was also found in the swimming musculature. Before discussing these findings, this paper describes the whole vascular system so as

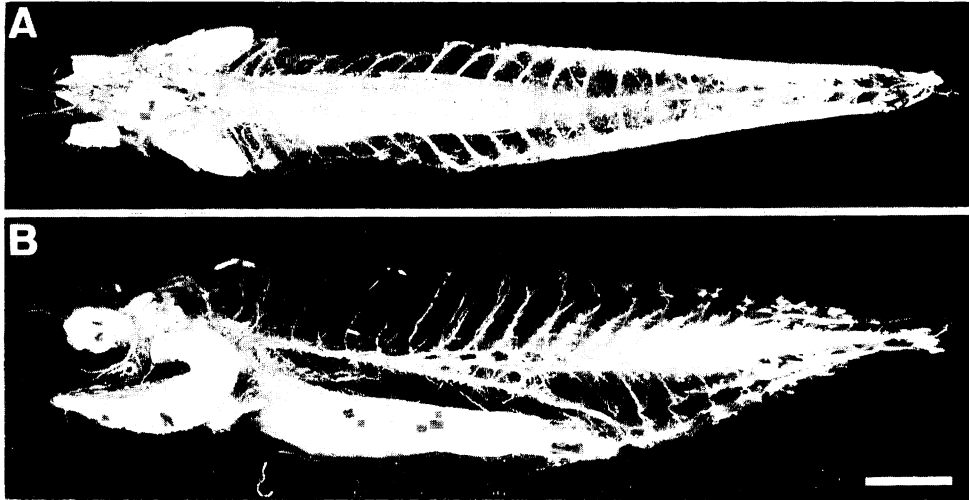


Fig. 1. A vascular cast seen from dorsal (A) and lateral (B) aspects. Bar=20 mm.

to serve for an easy understanding of the three-dimensional vascular anatomy of teleost.

Materials and methods

Twenty-one yellowtail, *Seriola quinqueradiata*, ranging from 260 to 360 mm in fork length and from 230 to 540 g in body weight, were provided by the Fishery Research Laboratory of Kyushu University. They were anaesthetized with quinaldine or benzocaine until respiratory movements ceased, then fixed or cannulated.

Five of them were fixed intact in 10% formalin for general dissection; from one specimen several tissue blocks were cut for histological examination. The tissues were decalcified in Plank-Rychlo's fluid prior to embedding in celloidin. Sections were stained with Weigert's resorcin-fuchsin for elastic fibres, followed by Van Geison's picro-fuchsin for collagen.

Sixteen fish were subjected to intravascular injection of acrylic resin; three of them were fixed in 10% formalin and dissected, and the rest were corroded for making a vascular cast (Fig. 1). The casting procedures were fundamentally similar to those described by us (Iwamizu and Itazawa, 1986a).

Resin preparation. Acrylic resin was prepared by either one of the following ways:

1) Semipolymerized methyl methacrylate, the base of resin, was prepared by heating the monomer with 2,4-dichlorobenzoyl peroxide (Murakami,

1973). The base was weighed out by 20% of the fish weight estimated, added with 10% butylphthalate (Murakami, 1971), 0.5% Sudan III or IV, and 1% benzoyl peroxide in advance. The mixture was chilled until it was added with 0.5–1% N, N-dimethylaniline immediately prior to the injection.

2) Mercor CL (Dainippon Ink and Chemical Co., Tokyo) and methyl methacrylate monomer (inhibitor-free) were weighed out respectively by 12% and 8% of the fish weight estimated. Benzoyl peroxide was added to the latter by 1–2% of the total weight of the two liquids. Both liquids were chilled until they were mixed immediately prior to the injection.

Casting procedure. An anaesthetized fish was placed ventral side up on a trough, and the gills were continually irrigated with the anaesthetic water from a tube placed in the mouth until fixative perfusion. Heparin (ca. 400 unit) was injected into the ventricle, then the pericardium was opened through a midline incision. A polyethylene cannula connected with perfusate reservoirs was inserted into the bulbus arteriosus via a transverse incision in the ventricle, then ligatured. The posterior opening on the ventricular incision was kept free to permit the overflow of blood and perfusates.

The cannulated fish was perfused with 50 ml heparinized saline (20 units/ml) first, second with unheparinized saline for about 10 min, third with 20–50 ml fixative (2.5% glutaraldehyde in 100 mM

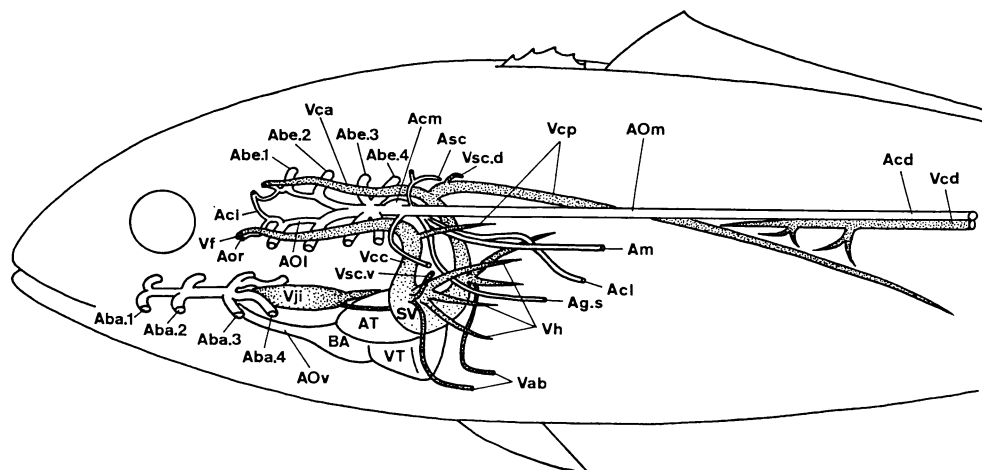


Fig. 2. Diagram of the main blood vessels as seen in dorso-lateral view. Veins are stippled.

phosphate buffer, pH 7.4), and finally with acrylic resin. All the perfusates were allowed to flow into the vascular system by a static head of 70 cm.

The fish, except that for dissection, was placed in 50°C water for a night, macerated in 20–30% HCl for one or two days, and washed in water. The cast sunk in water, as it was or after it was dried, was observed under a stereomicroscope.

Nomenclature. The nomenclature of blood vessels more or less follows Bertin (1958). The terms are symbolized in figures as follows.

Heart: SV, sinus venosus; AT, atrium; VT, ventricle; BA, bulbus arteriosus.

Aortae: AOv, ventral aorta; AOL, lateral dorsal aorta; AOm, median dorsal aorta.

Arteries: Aaa, afferent arch a.; Aae, efferent arch a.; Aba (.1–4), (1st–4th) afferent branchial a.; Abe (.1–4), (1st–4th) efferent branchial a.; Acc, coracoid a.; Acd, caudal a.; Aci, internal carotid a.; Acl, coeliac a.; Acm, coeliaco-mesenteric a.; Acr, coronary a.; Aen, encephalic a.; Afa, afferent filament a.; Afe, efferent filament a.; Ag (.d, s), (right, left) gastric a.; Ahb, median hypobranchial a.; Aic, intercostal a.; Aio, infraorbital a.; Ama, afferent mandibular a.; Am, mesenteric a.; An, nutrient a.; Aon, orbito-nasal a.; Aop, ophthalmic a.; Aor, orbital a.; Apbe, efferent pseudobranchial a.; Apba (.p, s), (primary, secondary) afferent pseudobranchial a.; Asc, subclavian a.; Aso, supraorbital a.

Veins: Vab, abdominal v.; Vb, branchial v.; Vca, anterior cardinal v.; Vcc, common cardinal

v.; Vcd, caudal v.; Vce, cerebral v.; Vcp (.d, s), (right, left) posterior cardinal v.; Vf, facial v.; Vg (.d, s), (right, left) gastric v.; Vh, hepatic v.; Vic, intercostal v.; Vin, interorbital v.; Vio, infraorbital v.; Vji (.d, s), (right, left) inferior jugular v.; Von, orbito-nasal v.; Voph, ophthalmic v.; Vph (.d, s), (right, left) hepatic portal v.; Vsc (.d, v), (dorsal, ventral) subclavian v.; Vsp, splenic v.; Vvb, gall bladder v.

Other organs: Ch, choroid; Cl, cleithrum; H, liver; Pb, pseudobranch; Ph, pharynx; T, thyroid.

Results

1. General survey of vascular system. The topography of the main vessels is diagrammatically shown in Fig. 2. The heart, which lies within the cardiac space beneath the pharynx, gives off a ventral aorta forward along the midsagittal plane (Figs. 3, 4). From this aortic trunk four pairs of afferent branchial arteries curve upward along the respective branchial arches. Each afferent vessel exhausts itself into discrete vascular beds of gill filaments and is re-formed into the efferent branchial artery along it. Dorsally the efferent branchials reach the dorsal aorta which distributes the arterial blood to most parts of the body.

Anteriorly the dorsal aorta forms itself into a pair of vessels below the skull; posteriorly they meet beneath the atlas to start a single median trunk extending all along the vertebral column. When mentioned in distinction from each other, the paired vessels and the median trunk are

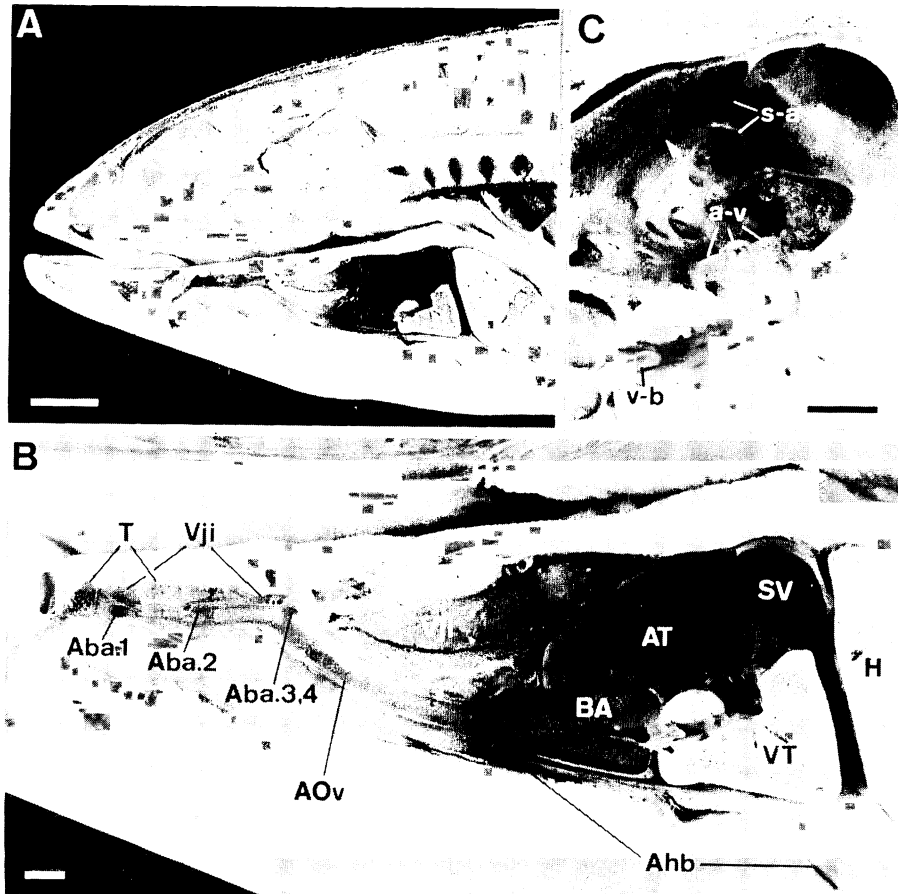


Fig. 3. Midsagittal section of the head. Bar=10 mm(A), 2 mm(B, C). A: The whole image. B: Enlargement to show the arrangement of the heart and the ventral aorta. The third and fourth afferent branchial arteries share the common stem (Aba. 3, 4). C: Enlargement to show the arrangement of sino-atrial (s-a), atrio-ventricular (a-v) and ventriculo-bulbar (v-b) valves. The arrow indicates the trabecular bundles continuous with the sino-atrial valves.

called lateral dorsal aortae and median dorsal aorta, respectively. The posterior portion of the median dorsal aorta is often called caudal artery because it passes through the haemal canal together with a caudal vein.

On either side the lateral dorsal aorta extends forward as the stem of the carotid system supplying most of the head. The median dorsal aorta gives off, at its base, a large coeliaco-mesenteric artery nourishing the whole viscera within the peritoneal cavity, and then the somatic branches metamerically all along its course. The majority of the arterial supply is hence derived from the dorsal aorta. However, some ventral part of the head is supplied by several arteries which arise individually from the ventral ends of the efferent

branchial arteries.

The framework of the somatic drainage is constructed by the paired cardinal veins situated on either side of the dorsal aorta. The anterior cardinals collect veins in the head to run back in courses above and lateral to the lateral dorsal aortae. The posterior cardinal veins, paired but reduced in the left, run forward on the ventral surface of the elongated kidney as the drainage of this organ. Because almost all the somatic veins in the trunk and tail are the constituents of the renal portal system, the posterior cardinals represent the final drainage of parietal circulation. The anterior and posterior cardinals on either side meet to start the common cardinal vein or ductus Cuvieri, which passes down around the

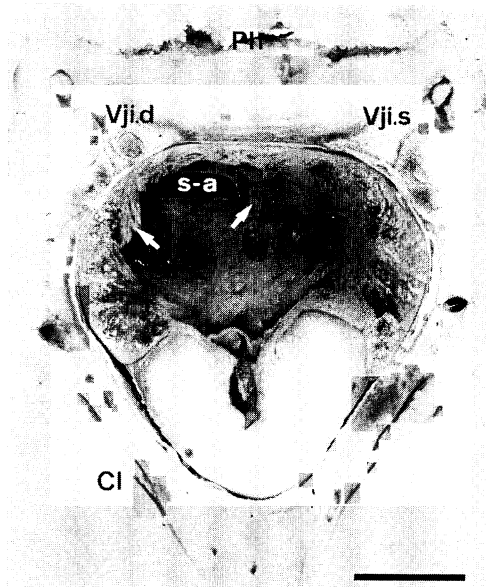


Fig. 4. Cross section through the atrio-ventricular orifice of the heart, showing the location of the sino-atrial orifice (s-a) and the trabecular bundles (arrows) continuous with the sino-atrial valves. Bar=5 mm.

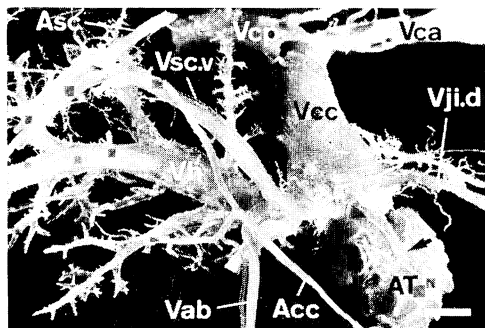


Fig. 5. Vasculature around the sinus venosus as seen in ventro-lateral view. Only in this figure the fish faces to the right. The partial cast of the atrial lumen (AT) bears the trace of trabecular bundles (arrow) continuous with the sino-atrial valves. Bar=2 mm.

oesophagus to joint the sinus venosus. This junction is so smooth that it makes itself the lateral wing of the sinus where other veins arrive (Fig. 5).

Four pairs of veins join the lateral wings of the sinus venosus: the inferior jugular vein from the front of the heart; the ventral subclavian vein, abdominal vein and hepatic vein from behind. The inferior jugulars, paired but reduced in the left, drain the ventral part of the head. The

ventral subclavian and abdominal veins collect some part of the parietal venous blood, while the most part is led to the renal portal system. On either side these two veins enter the sinus through a common stem just lateral to the hepatic vein. The hepatic vein represents the final drainage of the visceral circulation because the liver receives a hepatic portal system from behind.

2. Heart. The heart consists of four consecutive compartments, sinus venosus, atrium, ventricle and bulbus arteriosus from back to front (Fig. 3). They fold back ventrally in an S-shape along the midsagittal plane so as to make up a compact structure as a whole. The atrium extends laterally to cover the upper halves of the ventricle and the bulbus. The ventricle is triangular and pyramidal in shape, and has a thick compact layer in its wall. The bulbus is long and smoothly tapers down into the ventral aorta. In spite of the symmetrical outline of the heart, the sino-atrial orifice deviates to the left from the midline (Fig. 4).

Each orifice between the cardiac compartments is furnished with a set of valves (Fig. 3C). The sino-atrial valves are a dorso-ventral pair of flaps projecting into the atrial lumen. They extend laterally and continue to the longitudinal bundles of atrial trabeculae on both sides (Figs. 4, 5). The atrio-ventricular valves consist of four inverted cups: the larger antero-posterior pair is accompanied with the smaller bilateral pair. The distal part of each valve breaks up into vertical strips which connect with the ventricular trabeculae. The ventriculo-bulbar valves are a bilateral pair of tough, semilunar ones.

The heart is enclosed in a lubricating space, the pericardial cavity. This cavity is completely separated from the peritoneal cavity by the transverse septum, to which the liver attaches from behind. The serous lining of this cavity, the pericardium, is reflected inwards at the anterior and dorso-posterior ends of the heart to envelop this organ loosely as the epicardium. There is no connecting strand between these parietal and visceral pericardial membranes.

The cardiac space is protected by some skeletal elements: the right and left cleithra bracket it on its ventro-lateral borders (Fig. 4), and the anterior end of the pelvic girdle comes in contact with its ventral border.

3. Branchial circulation. All the venous blood

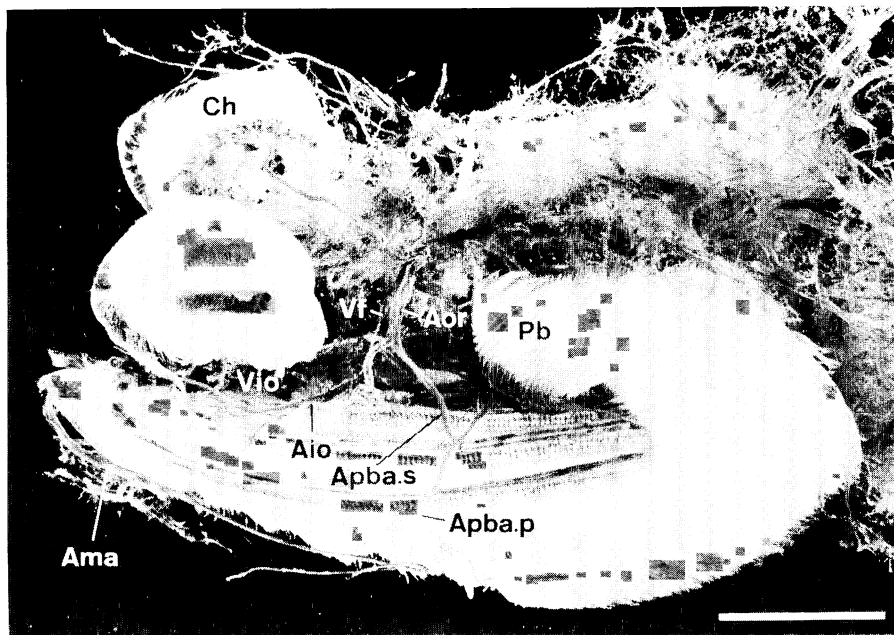


Fig. 6. Dorso-lateral view of the head vasculature. The pseudobranch has a dual afferent source. Bar = 10 mm.

pumped from the heart passes through the gills for exchange of gases and ions. The ceratotrichial part of each gill arch develops anteriorly and bears the greater part of the gill filaments (Fig. 6). The pseudobranch, which is a hemibranch with free filaments facing those of the first gill arch, is supplied with arterial blood and is hence different in function from the gills.

To clarify the description of the branchial arteries in this paper, their portions where the filament arteries come in and out are called, "arch arteries" according to Farrell (1980). The connecting portion of the efferent branchial artery between the efferent arch artery and the dorsal aorta corresponds to the epibranchial artery in selachians (Parker, 1886; O'Donoghue and Abbott, 1928), although this name has often been used improperly in teleosts, so as to designate a part of the lateral dorsal aorta and the common stem of the third and fourth efferent branchial arteries.

The ventral aorta curves upward to approach the posterior end of the last basibranchial, then goes straight forward until it terminates in lateral bifurcation into the first pair of afferent branchial arteries (Figs. 3B, 7C). The second pair of afferent branchials leave the aorta in the

middle of its straight course, penetrating their dorso-anterior walls into the aortic lumen to form a ridge-like baffle. On either side, the third and fourth afferent branchial arteries arise from a common stem, which is given off dorsally backward from the aorta at the point just in front of the ventral process of the last basibranchial.

Each afferent branchial artery curves back to enter the arch not at the ventro-anterior tip but at a point of some distance from the tip (Fig. 7C). Then it makes a slightly ventral turn and immediately bifurcates into anterior recurrent and posterior main branches, both of which taper off towards the respective ends of the arch to form the full length of the afferent arch artery. Each efferent arch artery runs along an inner lane parallel to the afferent arch artery. At both ends the efferent arch artery forms itself into hemibranchial pairs: the ventral fork grasps the terminal turning of the afferent branchial artery between them; the dorsal pair joins the unpaired trunk at the point where the latter just leaves the branchial arch as the efferent branchial or epibranchial artery (Fig. 8D).

The efferent branchial arteries make their ways in the pharyngeal roof medially towards the dorsal aorta (Fig. 8C). The anterior two pairs indi-

vidually meet the lateral dorsal aortae of the respective sides, whereas the posterior two pairs join the base of the median dorsal aorta in a convergent manner.

The neighbouring afferent and efferent filament arteries interlock each other in their proximal portions (Fig. 7F). The afferent filament arteries leave the afferent arch artery rather oppositely far from the filament rows, then run down around the afferent arch artery to reach the inner edge of each filament (Fig. 7E). In the most distal part of the septal area, each afferent filament artery enlarges slightly to form a small bleb (Fig. 7D). The efferent filament arteries, after running up along the outer edge of each filament, bend inward toward the afferent arch artery to fit into the inter-spaces between the basal portions of the afferent filament arteries, then bend outward to empty into the efferent arch artery.

In addition to the respiratory vessels mentioned above, some non-respiratory vessels larger than an arteriole or venule are distributed in the gills. The efferent filament artery usually gives off, at its basal portion, a nutrient artery towards the outer edge or the septal area of the filament (Fig. 7E). The afferent and efferent arch arteries in each gill arch are accompanied by some indistinct branchial veins, one of which is a distinct vessel running along an outer lane of the afferent arch artery. This branchial vein leaves the arch along both the afferent branchial artery (Fig. 7C) and the efferent branchial artery (Fig. 8D) towards the inferior jugular vein and the anterior cardinal vein, respectively. The connection between each branchial vein and the anterior cardinal vein is quite indistinct because of its appearance like a lymph sinus.

4. Systemic circulation. The systemic circulation forms itself into a parallel circuit, the component circuits of which are represented by more or less distinct body regions. Each region is taken care of by a set of specific arteries and veins.

4-1. Hypobranchial region. The lower jaws and the neighbouring structures make up a unique region that does not derive the arterial supply from the dorsal aorta. The arteries in this region arise discretely from the ventral ends of the efferent arch arteries, characteristically from the outer or anterior hemibranchial vessels of the ventral forks (Fig. 7C).

On either side the ventral extremity of the first

efferent arch artery continues forward and makes a lateral U-turn penetrating the hypohyal, then follows the hyoid arch. There are many synonyms for this artery, and what is considered the most definite is the afferent mandibular artery based on the ontogeny (Allis, 1912). The main trunk of this artery supplies the pseudobranch as the primary afferent pseudobranchial artery (Fig. 6). Just before reaching the pseudobranch it anastomoses with a branch of the carotid system, the secondary afferent pseudobranchial artery.

From the second arch on either side an artery is given off medially along the anterior aspect of the afferent branchial artery (Fig. 7C). This vessel curves back ventrally and meets with the counterpart of the other side to form the median hypobranchial artery which runs backward along the ventral aspect of the ventral aorta (Fig. 7B). Posteriorly the main trunk of the median hypobranchial goes beneath and beyond the cardiac space (Fig. 3B) to reach the base of the pelvic fins. On the way it dorso-laterally gives off a pair of branches each of which joins the subclavian artery on either side. This interconnecting artery, termed coracoid artery (Silvester, 1904), is hence a branch of the subclavian artery as well (Fig. 5).

From the third arch on either side arise two medial arteries in front of the afferent branchial artery, having a common stem or an anastomosing vessel between their roots (Fig. 7C). The anterior vessel goes forward ventrally to join the median hypobranchial (Fig. 7B). The posterior one goes backward and meets with the counterpart of the other side to form the coronary artery. It runs backward along the dorsal aspect of the ventral aorta and the bulbus up to the ventriculobulbar junction, then ramifies.

From the fourth arch on either side arises an inward artery in front of the afferent branchial artery (Fig. 7A). The vessel from the right arch goes to the dorsal surface of the inferior jugular vein, then splits into a pair which runs backward together with the paired inferior jugular veins to reach the sino-atrial junction. The vessel from the left arch goes downward to supply the structures below the ventral aorta.

Some longitudinal vessels lying beneath the ventral aorta interconnect the radical part of the afferent mandibular and of the median hypobranchial (Fig. 7B, C). Their arrangement varies among individuals: in one specimen one of these vessels

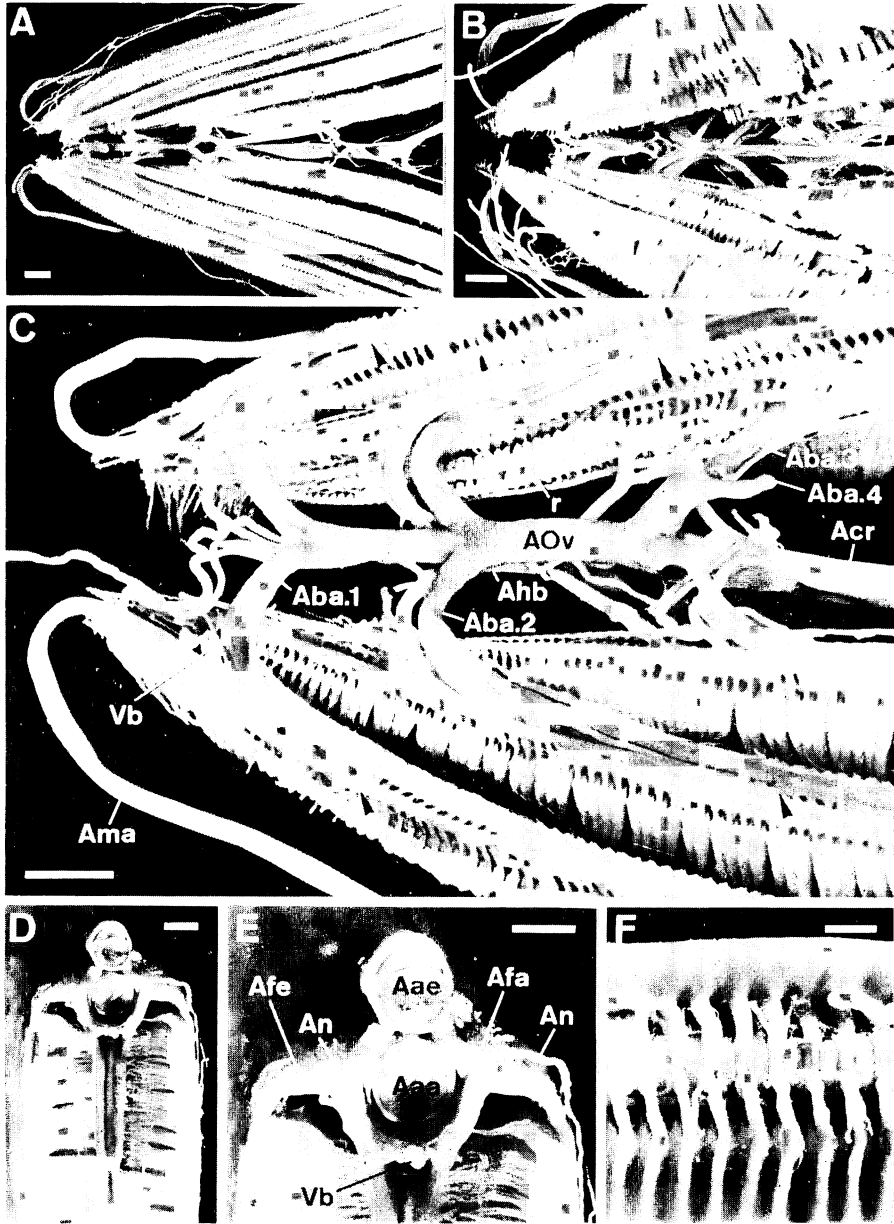


Fig. 7. Branchial and hypobranchial vasculature. Bar=2 mm (A-C), 0.5 mm (D-F). A: Dorsal view. B: Ventral view. C: Enlarged dorso-lateral view after removal of the inferior jugular vein and the fourth branchial arches. The third pair of afferent branchial arteries is partially broken. The recurrent afferent arch artery (r) is seen in the third arch. The junction of the forked efferent arch artery (arrows) is seen in the first and the second arches. D: Cross section through a gill arch at about the middle. E: Enlarged view of the upper half of (D). The junctions between arch and filament arteries are broken. F: Dorso-lateral view of the middle portion of a gill arch to show the interlocking arrangement of afferent and efferent filament arteries.

was large enough to be looked upon as an anterior portion of the median hypobranchial.

The inferior jugular veins, basically paired but partially fused, run backward beneath the pharynx to drain this region (Fig. 7A). Anteriorly these vessels originate as a single median vessel formed by union of paired hyoidean veins (Fig. 3B). Then it splits into a parallel pair running along the dorsal aspect of the ventral aorta. These veins anastomose each other in front of and behind the posterior lobe of the thyroid body, then fuse again just behind the ventral process of the last basibranchial to form a large sinus. This sinus extends posteriorly to border on the cardiac space over the atrium. Then it bifurcates into a pair of veins of which the left one is reduced. They run along the dorso-lateral edges of the cardiac space to empty into the lateral wings of the sinus venosus (Fig. 7A).

4-2. Head region. The greater part of the head is supplied by the carotid arterial system and drained by the anterior cardinal veins (Fig. 8). They are paired and bilaterally symmetric.

The carotid system consists of two main arteries on either side of the head: the internal carotid artery for deeper structures and the orbital artery for superficial structures. They both arise from a short, common stem that is formed by bifurcation of the first efferent branchial artery, rather than the prolongation of the lateral dorsal aorta (Fig. 8C, E).

The internal carotid artery supplies the brain and the olfactory and optic nerves. The main trunk of this vessel runs forward medially and anastomoses with the counterpart of the other side just in front of the pituitary to form a single encephalic artery passing upward into the braincase. As a result the internal carotids together with the lateral dorsal aortae make up an arterial circle below the skull, known as the "circulus cephalicus" (Ridewood, 1899). On about the midway the internal carotid trunk gives off the orbito-nasal artery anterolaterally. This artery soon makes a smooth medial curve to run forward along the olfactory nerve up to the olfactory organ. The optic artery, which follows the optic nerve to the retina, arises from the curve of the orbito-nasal.

The orbital artery takes over the supply to most of the face and to the pseudobranch. This vessel arises upward from the short carotid stem and turns forward laterally. On the way it gives off

the supraorbital artery which passes forward along the upper margin of the orbit. After that the main trunk turns downward to descend along the hind margin of the orbit, then bifurcates into the infraorbital artery and the secondary afferent pseudobranchial artery (Fig. 6): the former passes along the lower margin of the orbit; the latter runs ventro-posteriorly to anastomose with the primary afferent pseudobranchial artery which is the prolongation of the afferent mandibular artery.

The blood which has past through the pseudobranch is exclusively led to the choroidal body (Fig. 8C, E). The efferent pseudobranchial artery runs dorso-antero-medially crossing the orbito-nasal artery from beneath to enter the myodome. There it is connected with its counterpart of the opposite side by a cross-commissural vessel above the parasphenoid, then it turns forward laterally crossing the orbito-nasal from above to reach the choroid as the ophthalmic artery.

The arterial supply to the pharyngeal roof is independent from the carotid system. The anterior half is taken care of by two branches given off forward and backward from the second efferent branchial artery on either side. The posterior half is taken care of by a pair of arteries arising from the ventral surface of the median dorsal aorta just in front of the junction with the third and fourth efferent branchials (Fig. 9). On either side the main trunk of this artery runs posterolaterally and passes down along the anterior aspect of the common cardinal vein to reach the sino-atrial junction.

The anterior cardinal vein begins just behind the orbit by union of two principal veins, the interorbital and the facial vein (Silvester, 1904), which drain the respective areas supplied by the internal carotid and the orbital artery. These veins correspond to Allen's (1905) internal and external jugular veins, respectively.

The interorbital vein is a transverse vessel connecting the right and left anterior cardinals (Fig. 8C, E). At the midline it receives the cerebral vein which comes down nearly enclosing the encephalic artery, then extends forward bilaterally. The interorbital trunk curves back along the anterior aspect of the efferent pseudo-branchial commissure to cross the orbito-nasal artery from beneath on either side. There it is joined by the orbito-nasal vein and the ophthalmic vein, then

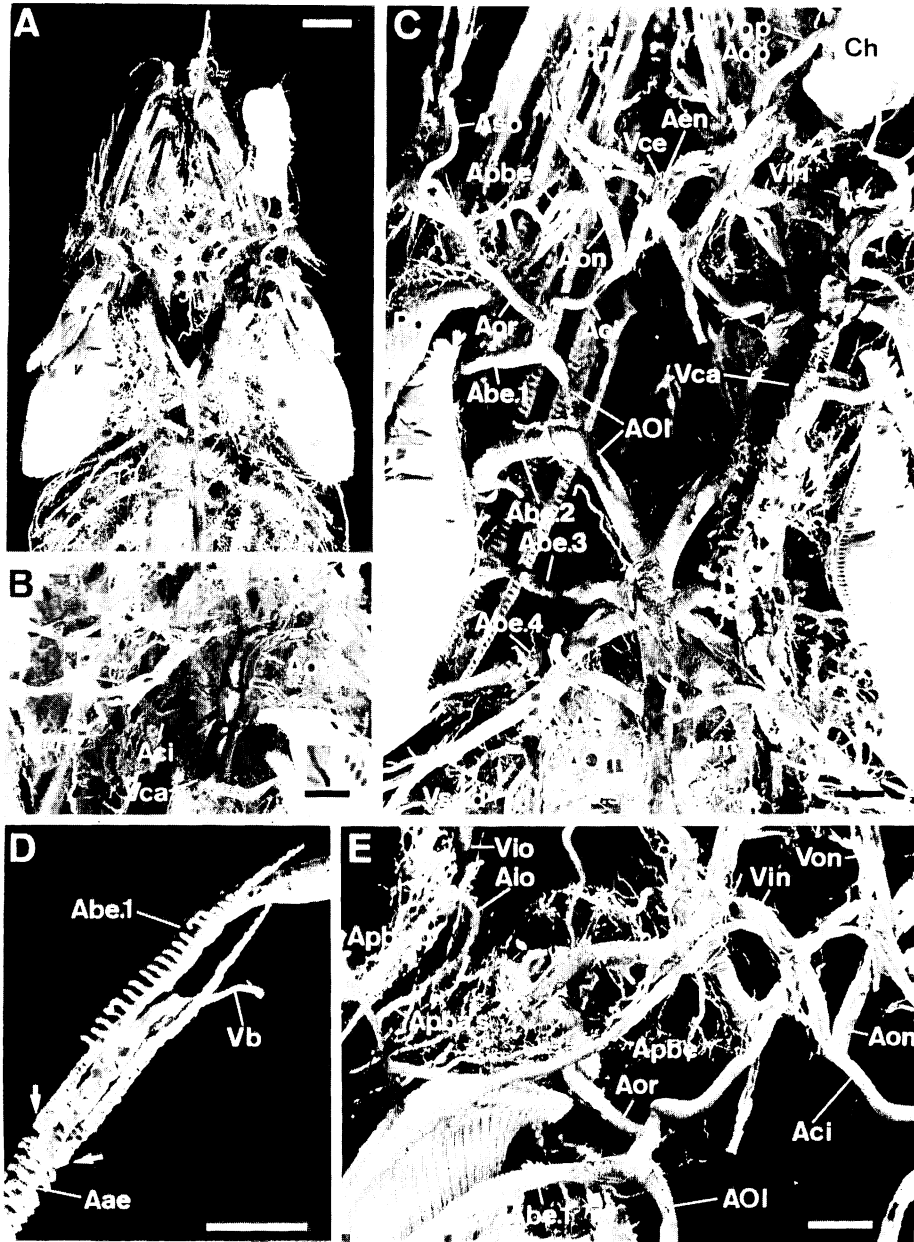


Fig. 8. Head vasculature. Bar=5 mm(A), 2 mm(B-E). A: General dorsal view. Cerebral capillaries have been removed. B: Enlargement from (A) to show the cerebral vasculature and the trace of the valves (arrow) in the anterior cardinal vein. C: Dorsal view around the "circulus cephalicus". Cerebral vascular bed and the left anterior cardinal vein have been removed. D: Dorsal view of the first branchial arch. Afferent arch artery and filament rows have been removed to show the dorsal forking of the efferent arch artery. Arrows indicate the junctions. E: Ventral view of the crossroads of the head vasculature.