

Fig. 9. A pair of arteries arising from the beginning of the median dorsal aorta. The main course descends towards the sino-atrial junction. Ventro-anterior view. Bar=2 mm.

it passes laterally, making a curve of reverse arch, to join the anterior cardinal from below.

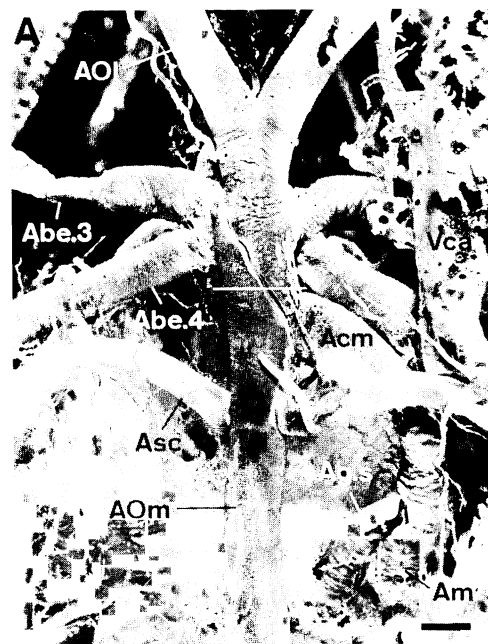
The facial vein runs up closely along the anterior aspect of the orbital artery and smoothly joins the anterior cardinal vein (Figs. 6, 8B). The largest of its tributaries is the infraorbital vein draining most of the face.

The anterior cardinal runs backward, adjacently along the median aspect of the orbital artery at the beginning, then over the efferent branchial arteries across, penetrating the head kidney. In front of the head kidney this venous trunk is equipped with a set of valves (Fig. 8B).

**4-3. Coeliac region.** The abdominal viscera enclosed by the peritoneal cavity, i.e. the spleen and the gut and its derivatives, are supplied by the unpaired coeliaco-mesenteric artery and drained ultimately by the hepatic veins. The excretory organs, which lie outside the parietal peritoneum, are not included in this circulatory region. The arterial supply to the gonads was not traced because none of the specimens was mature enough.

The coeliaco-mesenteric artery arises to the right from the median dorsal aorta just behind the junction with the posterior two pairs of efferent branchial arteries (Fig. 10). The coeliaco-mesenteric departure is preceded by baffle equipment within the aorta. From the aortic wall into the lumen projects a pair of dorso-ventral band-like baffles which traverse the aorta diagonally back to the posterior border of the coeliaco-mesenteric opening.

Just after arising the coeliaco-mesenteric artery splits into the coeliac artery and the mesenteric artery.



B

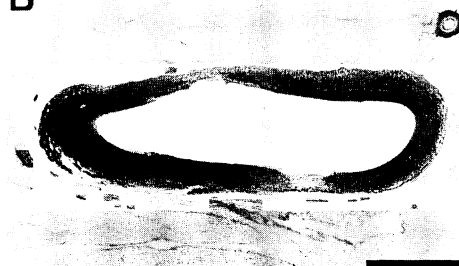


Fig. 10. Band-like baffles in the median dorsal aorta. Bar=1 mm(A), 0.5 mm(B). A: The baffle trace on a vascular cast. Dorsal view. B: The histological section through the dorsal aorta at the level of the line in (A), stained with resorcin-fuchsin and picro-fuchsin. Hardly any collagenous nor elastic fibers are included in baffles.

The coeliac artery supplies the pyloric area (Fig. 11C). It runs along the right side of the oesophagus and the stomach, curves around under the stomach, then gives off a branch which passes around the anterior margin of the pylorus. It then breaks up into numerous branches to supply the left lobe of the liver and the anterior halves of the pyloric caeca. Behind the pylorus the coeliac trunk also breaks up to supply the duodenum and the posterior halves of the pyloric caeca.

The mesenteric artery, on the other hand, takes

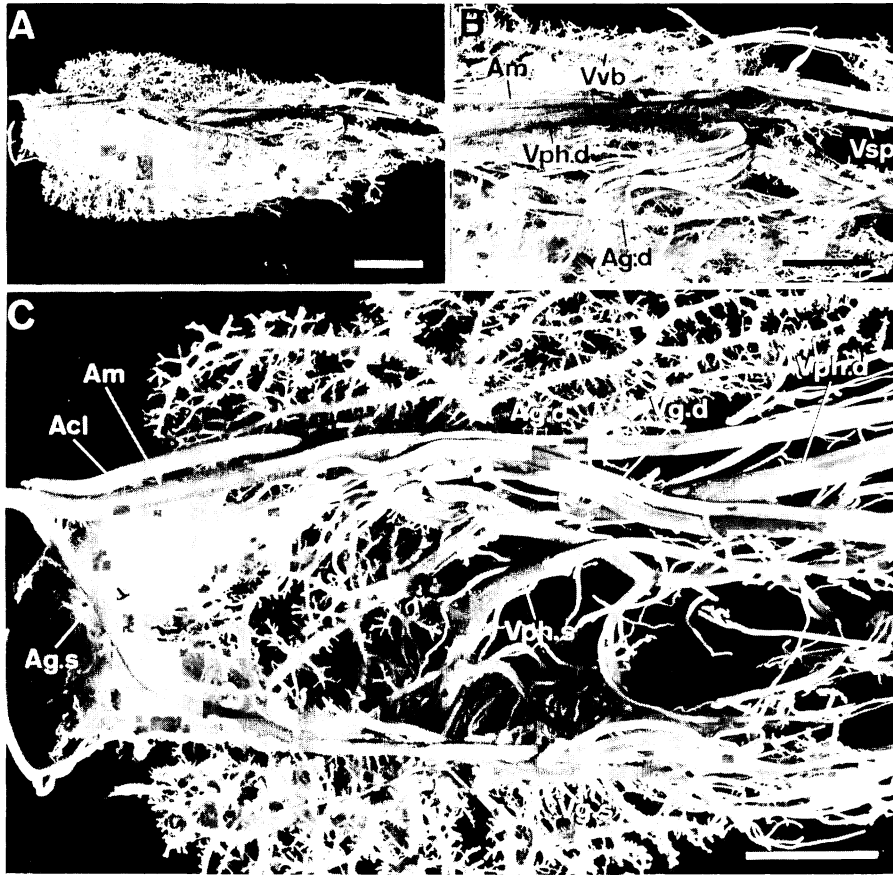


Fig. 11. Visceral vasculature. Bar=10 mm(A), 5 mm(B, C). A: General dorsal view. B: Enlargement of the posterior region. C: Enlargement of the anterior region after removal of gastric capillary bed.

care of the whole length of the abdominal space (Fig. 11B, C). The mesenteric trunk, giving off two gastric branches, runs backward along the mesentery on the right of the stomach up to the anterior border of the spleen, then breaks up into four backward branches which supply the spleen and the intestine.

The left gastric artery is given off from the very beginning of the mesenteric artery to the left side. This vessel traverses the dorsal aspect of the oesophagus along the anterior margin of the air bladder, then supplies the stomach as it passes backward along the left side of this organ.

The right gastric artery leaves the mesenteric trunk at some distance from the beginning of the latter. This artery nourishes the air bladder at first; it gives off upward a number of radial branches spreading on the ventral surface of the anterior half of the bladder. Then it supplies the stomach,

running backward along the right dorsal wall up to the posterior end of this organ.

The splenic artery, which enters into the spleen from its front, is the central one of the posterior four branches of the mesenteric artery. The other three branches are the intestinal arteries: they extend backward along the three sections of the intestine which makes turns at the posterior end and the center of the abdominal space so that the three longitudinal tubes sandwich the spleen. From near the arising point of the left one of these intestinal arteries, two posterior gastric arteries are given off towards the ventral wall of the posterior blind portion of the stomach. These arteries are folded up with the accompanying veins when the stomach is deflated (Fig. 11B).

Venous blood in this region is carried anteriorly into the liver by the hepatic portal system (Fig. 11B, C). The framework of this system is com-

posed of the right and left hepatic portal veins, which are the venous companions of the mesenteric and coeliac arteries, respectively. These veins empty into the liver-lobes of the respective sides, but their anterior branches join each other to empty into the ventral part of the liver from behind.

The right hepatic portal vein collects venous blood from the posterior half of the viscera except the gall-bladder. This portal trunk is formed, being adjacent to the breaking terminal of the mesenteric artery, by convergent union of three longitudinal intestinal veins from behind. Just prior to the union, the left and the middle veins are jointed by the posterior gastric veins and the splenic vein, respectively. The right portal trunk runs forward along the left ventral side of the mesenteric artery and bifurcates on the inner surface of the right lobe of the liver, so that its rightward branch enters the liver at once. The antero-leftward branch empties into the ventral part of the liver together with its associate coming from the left portal vein.

The anterior bifurcating point of the right hepatic portal trunk is joined by the right gastric vein, which accompanies the right gastric artery all along and drains the area supplied by the arterial companion. This vein makes a U-turn ventrally and posteriorly towards the junction with the portal trunk near the beginning of the arterial companion.

The left hepatic portal vein drains the pyloric area supplied by the coeliac artery. On the right side of the duodenum several veins from the pyloric caeca meet to start this portal trunk, which passes forward on the right side of the pylorus, curves to the left crossing the coeliac artery from above, and approaches the midline under the stomach. There it gives off the antero-rightward branch that empties into the ventral part of the liver together with its associate coming from the right portal. After that the left hepatic portal trunk passes left transversely on the dorso-posterior surface of the ventral part of the liver, giving off several branches towards the liver from behind, and also receiving a vein from the left-anterior bunch of the pyloric caeca. Finally this portal trunk empties into the left lobe of the liver from inside, together with the left gastric vein.

The left gastric vein lies along the arterial companion, but its anterior half is backward in blood

flow: on the midway this vein gives off ventrally a short draining stem, which at once bifurcates into a longitudinal vessel on the inner surface of the left lobe of the liver. The anterior tributary terminates in junction with the left hepatic portal trunk just before entering into the hepatic parenchyme.

The gall-bladder, which is slender and lies longitudinally on the right dorsal side of the folded intestine, is drained by the gall-bladder vein running along this organ (Fig. 11B). Anteriorly this vein empties into the posterior end of the right lobe of the liver by itself, but its branches within the liver have connections with those from the right portal vein.

The dendritical hepatic veins within the liver converge anteriorly into a right and a left short stem (Fig. 5). These stems penetrate the transverse septum to empty into the lateral wings of the sinus venosus from behind.

**4-4. Parietal region.** The parietal vessels are metamerically arranged in accord with muscular and skeletal arrangements. The kidney, which also receives metameric arterial supply, belongs to this circulatory region. All the parietal venous blood except that from the subclavian veins passes through the renal portal system.

The anteriormost set of parietal vessels that take care of the pectoral region are different in size and course from the proceeding series. A pair of large subclavian arteries arise in common from the ventro-right side of the median dorsal aorta just behind the origin of the coeliaco-mesenteric artery (Fig. 8C). The common opening for these arteries is equipped with a pair of longitudinal baffles on the inner wall of the aorta. On each side the subclavian artery runs laterally, then curves down along the pectoral girdle and terminates in ramification at the base of the pectoral fin. One of the terminal branches extends forward ventrally as the coracoid artery, close to the pericardium on the way, and finally anastomoses with the median hypobranchial (Fig. 5). Near its beginning the subclavian artery gives off a dorsal branch which turns forward to nourish the epaxial muscles in the occipital region.

The drainage of the pectoral region is assumed by two veins arising at the base of the pectoral fin on either side. The dorsal subclavian vein goes up along the pectoral girdle to empty medially into the posterior cardinal vein. The ventral

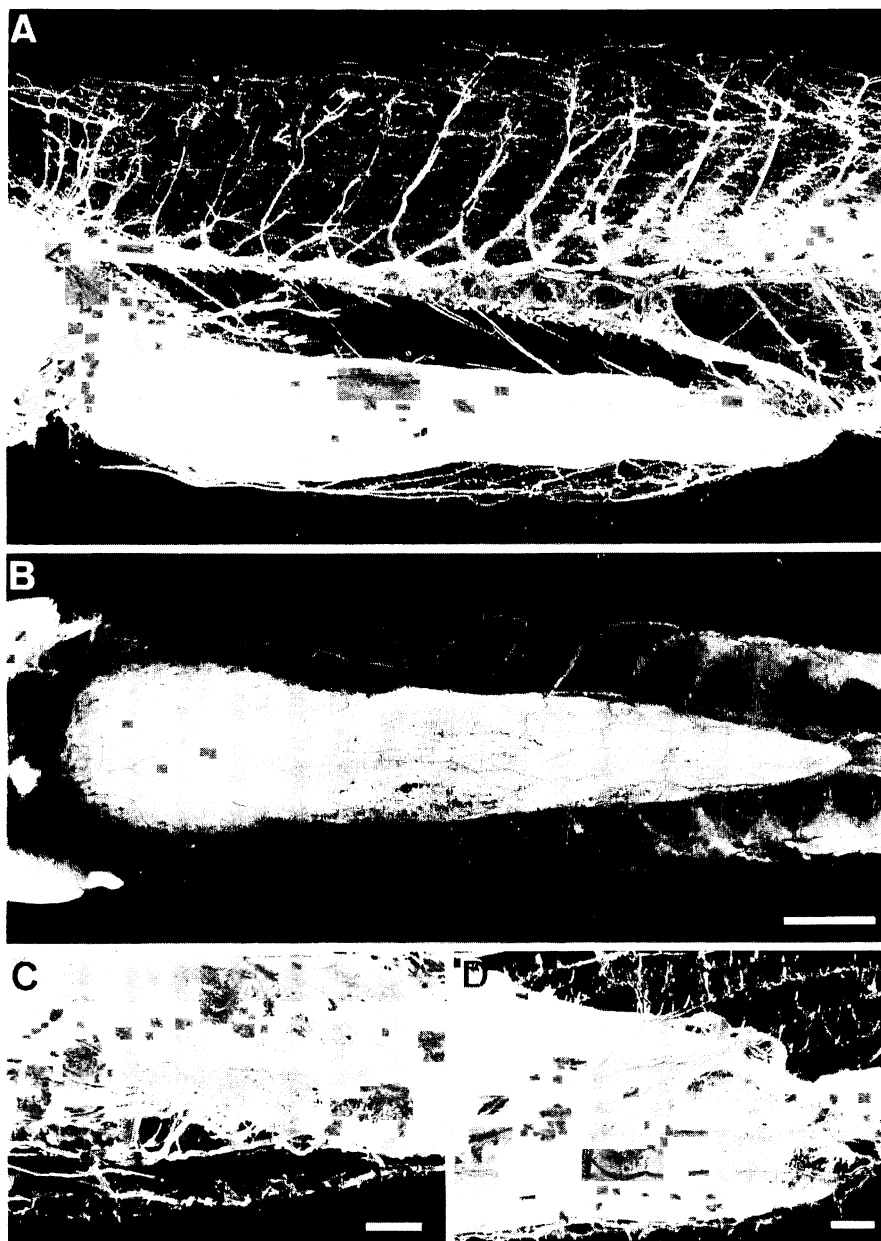


Fig. 12. Parietal vasculature in trunk. Bar=10 mm(B), 2 mm(C, D). A: Lateral view after removal of the left side row of lateral segmental vessels. B: Ventral view. At a posterior point (asterisked) the ventral vascular network makes a connection with the visceral vasculature. C: Ventro-lateral view of the parietal-visceral connection in (B). D: Ventral view of the connection in another specimen.

subclavian vein goes forward to join the lateral wing of the sinus venosus together with the abdominal vein (Fig. 5).

There are no iliac vessels. The pelvic girdle locates just behind the heart and has arterial supply from the hypobranchial artery.

Behind the subclavian vessels are arranged basically similar units of artery and vein in a series (Fig. 12A). They are called segmental vessels. The segmental arteries arise at intervals from the median dorsal aorta. The segmental veins in the tail join the caudal vein; those in the posterior

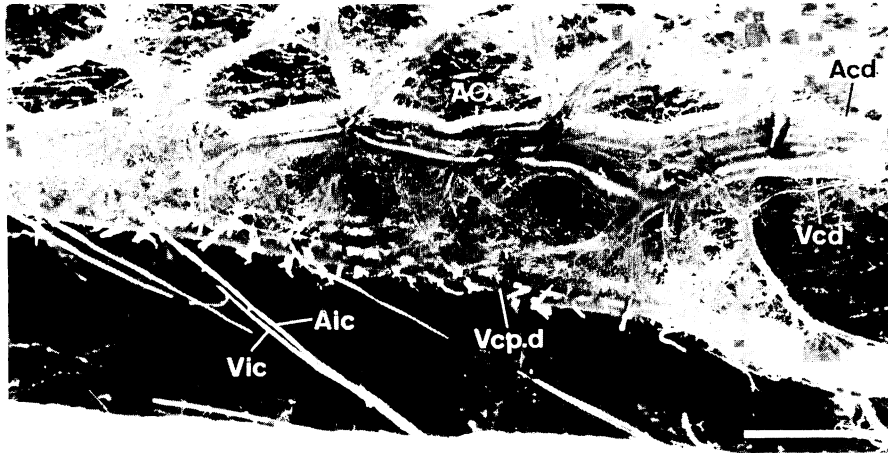


Fig. 13. Lateral view of the renal portal system. Bar=5 mm.

half of the trunk join the renal portal trunk, the anterior prolongation of the caudal vein within the kidney (Fig. 13); those in the anterior half of the trunk empty into the kidney individually, but some of the neighbouring veins are connected with each other by a longitudinal vessel within the kidney.

The segmental vascular system consists of dorsal vessels along the anterior aspect of the neural spines, ventral ones along the anterior aspect of the haemal spines, and lateral ones along the intersections of the horizontal septa and the myosepta (Fig. 14). In the trunk region, the intercostal vessels are arranged directly beneath the peritoneum instead of the ventral segmental vessels (Fig. 12A). Every dorsal vessel, which goes up around the vertebral column either on the right or the left at random, shares a common stem with the lateral vessel of the same side (Fig. 14D). The ventral vessels individually come into and out of the longitudinal trunks.

The dorsal vessels and the ventral vessels have a distal branching pattern in common. Each vessel gives off a pair of lateral branches that often anastomose with the distal end of the intersegmental vessel (Fig. 14D). After that the vertical trunk divides into one or two pairs of branches which sandwich the muscles of the median fin. At the base of the median fin each one of these branches splits into an anterior and a posterior branch on either side.

Each lateral vessel splits into two main branches, the intersegmental or interfascial vessels, which run up and down along the intersection of the

myoseptum and the inner margin of the red muscle or the lateralis superficialis (Fig. 14A, B). From near the junction of the dorsal and ventral intersegmentals is given off a branch which penetrates the red muscles and splits antero-posteriorly to form a longitudinal vessel just beneath the skin (Fig. 14E). This vessel gives off inward branches along the intersections of the horizontal septum and the "submyosepta" mentioned below.

The arrangement of the segmental vessels shows a completely doubling pattern. All the tracks of all the series of these metameric vessels are laid with a set of vessels instead of an artery or a vein. Such a segmental vascular unit usually consists of an artery and a vein closely parallel up to the distal end. Sometimes the unit contains two veins sandwiching an artery all along between them.

The bottom of the abdominal wall is furnished with a vascular network which is continuous with the intercostal vessels (Fig. 12A, B). The anterior portion of this network is also supplied by the median hypobranchial artery, and is also drained by a pair of abdominal veins which open directly into the lateral wings of the sinus venosus from below. This network has a connection with the coeliac vascular system by some anastomoses (Fig. 12C, D).

**5. Lateral musculature.** The peripheral region of each myomere is subsegmented into four muscular sheets by three tendinous septa which fold parallel to the true myosepta (Fig. 15). The middle one of the three subsegmenting septa extends more deeply than the others, but never

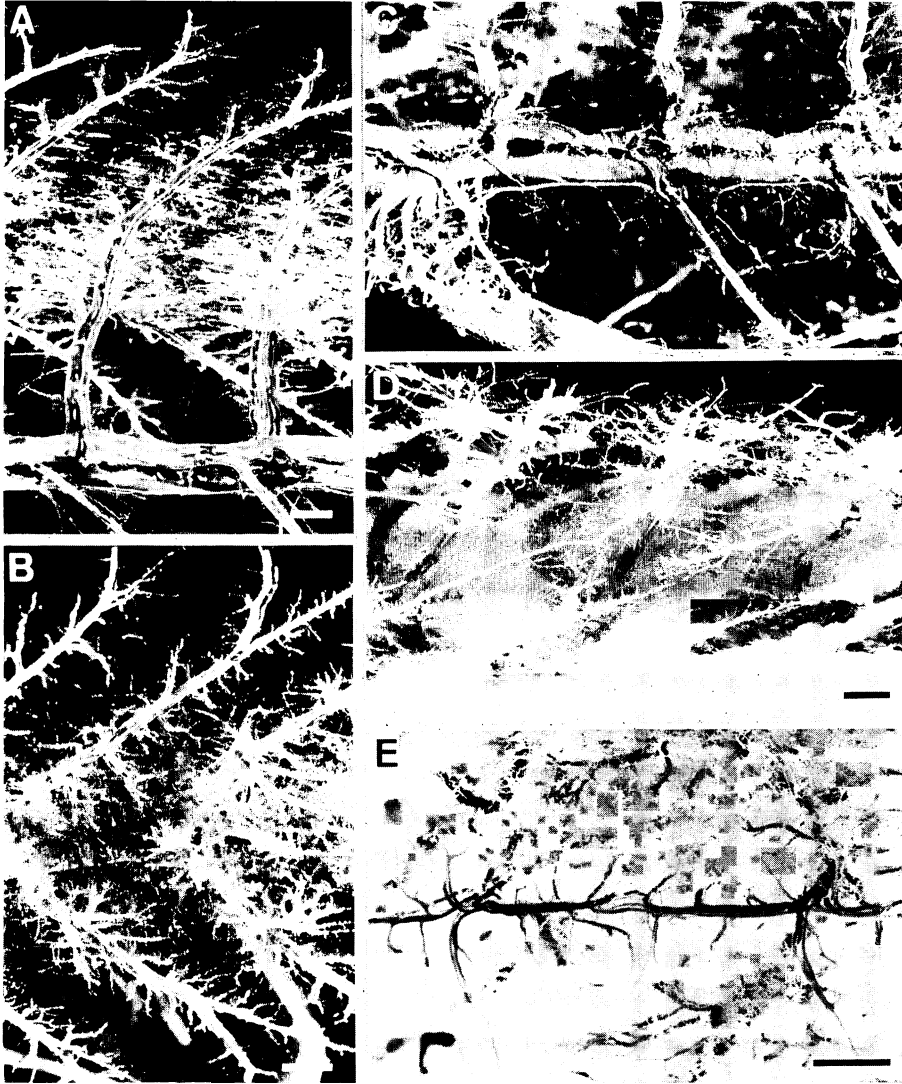


Fig. 14. Lateral or dorso-lateral views of the segmental vessels. Bar=2 mm in each. A: The right lateral segmentals and their branches viewed through the fish after removal of the dorsal and the left lateral segmentals. B: The left intersegmentals viewed from outside. C: Basal portions of the dorsal and ventral segmentals just behind the kidney after removal of the left lateral segmentals. D: Distal branches of the dorsal segmentals. The lateral branches are sometimes continuous with the dorsal extremities of the intersegmental vessels as in this figure. E: Subcutaneous vessels along the horizontal septum. They are derived from the lateral segmentals and give off inward branches.

reaches the vertebral column. The subsegmentations give an appearance to the lateral musculature as if it were made up of a larger number of narrower myomeres. The authors propose to designate the muscular subsegment and the subsegmenting septum as "submyomere" and "submyoseptum", respectively.

#### Discussion

The lateral musculature of the yellowtail is peculiarly modified in construction and vascular supply, i.e., the myomeres are subsegmented and the segmental vessels are double-tracked. Both modifications bring about an increase of the functional units of the lateral musculature which



Fig. 15. A cross section just anterior to the anus to show the subsegmentation in the myomeres. Between the true myosepta (asterisked) exist three "submyosepta", one of almost full depth and two of half depth. Bar=10 mm.

provides propulsive force. They are perhaps characters related to the swimming ability.

The myomere subsegmentation in the yellowtail can be recognized even with the naked eyes. The amberjack or kanpachi *Seriola dumerili* and the rainbow runner or tsumuburi *Elagatis bipinnulata*, rather cosmopolitan species of the same sub-family as the yellowtail, also share the same feature. Nevertheless, no description of this feature has so far been found in literature except a preliminary report of our own (Iwamizu and Itazawa, 1986b). The subsegmentation probably develops during very late stages in ontogeny, because such a character should come into sight when an investigator of fishes of early stages counts myomeres as routine work.

The segmental vessels have only rarely been studied in detail (Górkiewicz, 1947, Pollak, 1960,

1961; Mosse, 1980), and yet several works (Silvester, 1904; Allen, 1905; Kishinouye, 1923; Iwamizu and Itazawa, 1986a; Itazawa and Iwamizu, 1987) also allow us to know that these vessels are arranged more or less regularly in an alternating pattern of artery and vein in many teleosts. Even the irregular arrangement of the segmental vessels in *Clarias* (Nawar, 1955) does not seem to deviate very much from this type of vascular pattern. The alternating pattern is probably the basic arrangement of the segmental vessels, not only in the teleosts but also in some groups of Anamnia. It is common in Anamnia that the first step in the development of the segmental vessels is the construction of a ladder-like system stepped with an artery and a vein alternatively (Grodziński, 1959).

The double tracking of the segmental vessels has been known only in tunas, where this feature is put in the shade by the cutaneous vessels accompanied with heat-exchanging rete. On the other hand, non-tuna scombrids retain the usual, alternating pattern in segmental vascular arrangement (Kishinouye, 1923). Every pairing of an artery and a vein is a rudimentary heat exchanger, which once made may come to be improved under natural selection. The lack of continuity in vascular plan between tunas and non-tuna scombrids may suggest that the double tracking of the segmental vessels was the first, inevitable step toward further specialization.

The further steps in tunas' vascular specialization, i.e. the development of the cutaneous vessels and retia, may not be discussed separately from the internalization of red muscles, and yet the yellowtail with no trace of the latter shows a feature suggestive of the former, i.e. a rudimental subcutaneous system arising from each segment. In the yellowtail a line of the longitudinal branches derived from the lateral segmental vessels exists along the peripheral border of the horizontal septum. From these subcutaneous branches arise the inward branches penetrating the red muscles, and they are double-tracked up to the distal ends. Further, the neighbouring subcutaneous branches have a tendency to anastomose each other. Supposing that they anastomose in a series and lose the connections with the lateral segmental vessels except that on the anterior end, the result is the formation of a set of double-tracked cutaneous vessels accompanied with a coarse rete. These imaginary vessels, independent of the internaliza-

tion of the red muscles, disagree in location and yet may agree in formation with the real cutaneous vessels of tunas.

If the primitive cutaneous vessels were built up by the serial anastomosing of the longitudinal branches of intersegmental vessels, any lateral segmental vessels in anterior series could serve as the origin and the final drainage of the cutaneous vessels. In fact the origin of the cutaneous arteries varies in position within the genus *Thunnus* (Collette, 1978). What seems out of accord with this variation is the explanation by Takahasi (1926), who treated the rete formation so lightly that he regarded the tunas' cutaneous vessels as elongated segmental vessels.

The following features also deserve to be discussed here because of their seldom appearance in papers or books, although most of them are rather general aspects of the circulatory system of fish.

The sino-atrial valves are bilaterally continuous with the longitudinal bundles of atrial trabeculae in the yellowtail. This continuity is different in type from that seen in the cottid fish *Myoxocephalus scorpius*, where the sino-atrial valves do not have a completely free edge like caspid valves of higher vertebrates (Santer, 1985). In the bilateral continuity the trabecular tension must be transmitted to the valves during atrial systole. Such valves can be closed by the tension, possibly prior to the development of atrial pressure. The same structural condition occurs in the carp *Cyprinus carpio* and the red sea bream *Pagrus major* (Itazawa and Iwamizu, 1987). The connections of "muscle tails" in the cyprinid *Schizothorax curvifrons niger* (Saxena and Bakhshi, 1966) also seem to come under the same condition as those in the species mentioned above.

The ventral forking of the efferent arch artery is very common among teleosts (e.g. Silvester, 1904; Muir, 1970), and is unlikely to represent such a primitive arrangement as Goodrich (1930) diagrammed for lower teleostoms. What should rather be noticed is the presence of the recurrent afferent vessel accompanying the ventral forks of the efferent arch artery. These distal portions of both afferent and efferent vessels probably result from the ventral extensions of the embryonic branchial arteries as a late development of additional filament rows beyond the original ventral limit. This type of vascular development can be

seen in trout embryo where it occurs much later than the separation of the afferent and efferent branchial arteries (Morgan, 1974). The dorsal forking of the efferent arch artery, which is not a rarity among the teleosts (Silvester, 1904; Allen, 1905; Farrell, 1980; Itazawa and Iwamizu, 1987), may also reflect the dorsal additional development of filaments during later stages.

It is quite peculiar in gill vasculature that the afferent filament arteries arise being aimed away from the filament side. There is no structure to be avoided around. The interlocking of the afferent and efferent filament arteries is considered to have some physiological function.

The median hypobranchial artery of the yellowtail conforms, in derivation and extension, to the synonymic ventral artery of *Ophiodon* (Allen, 1905). In some cyprinids also, this vessel arises from the second and third pairs of efferent arch arteries (Mittra and Ghosh, 1932). However, such derivation appears to be unusual among other teleosts. In most cases the median hypobranchial has its source only from the second pair of efferent arch arteries. It is rather common that this artery reaches the base of the ventral fins, whereas it terminates in the sternohyoid muscles in teleosts where the ventral fins are absent or situated far back on the abdomen (Silvester, 1904).

The arrangement of the coronary artery in the yellowtail may be characterized by its arising from the third pair of efferent branchial arteries and its main course being along the dorsal aspect of the ventral aorta. This condition is basically similar to that of the dorsal coronary artery in *Lopholatilus* (Silvester, 1904) and *Ophiodon* (Allen, 1905), in which what is a little different from the yellowtail is that the dorsal coronary artery arises from either the right or left one of the third arches. According to Grant and Regnier (1926), the typical coronary supply to the fish heart is from a single artery arising from the fourth visceral (=second branchial) arch and reaching the heart along the ventral aspect of the ventral aorta, i.e. through the median hypobranchial artery. This seems true of fishes except for the acanthopterygian and paracanthopterygian teleosts, in which the median hypobranchial reaches the ventral fin base.

The band-like baffles within the median dorsal aorta for the coeliaco-mesenteric opening are remarkable in scale, i.e. the dorso-ventral pair



diagonally traverse the aortic lumen. They may act to turn the straight flow partially towards the coeliaco-mesenteric artery. However, equipment of baffles seems to be rather usual at arterial ramification. The orifice leading to the subclavian arteries is bracketed by a longitudinal pair of band-like baffles. The segmental arteries also take their origin from the raised funnels which project into the aortic lumen. Many teleosts are equipped with such funnel-like baffles (Satchell, 1971). The inner ridge formed by the ramification of the coeliac and the mesenteric arteries projects into the arterial lumen. This baffle may correspond to the semilunar valves reported in the striped bass *Morone saxatilis* (Groman, 1982). Arterial baffles may generally disturb axial accumulation of blood cells to ensure an inflow with normal haematocrit for the arterial branch (Satchell, 1971).

The paired arteries leaving the median dorsal aorta in front of the junction with the posterior two pairs of efferent branchial arteries are left confused in nomenclature. These arteries make their ways postero-laterally in the pharyngeal roof as they give off several branches backward and forward, then descend to form a pair of arches in front of the pectoral girdles. A similar artery is also reported in some teleosts by Vasisht and Kapoor (1965). These authors designated it as either occipital artery or first subclavian artery in different species. The difference between the occipital and the first subclavian is not clear. According to Ridewood (1899) the existence of two pairs of subclavian arteries, one of which arises in front of the common trunks of the last two efferent branchial vessels, is not a rarity among teleosts. In the yellowtail, however, the extremity of the artery in question reaches the sino-atrial junction of the heart. This artery may hence be called the posterior coronary artery (Foxon, 1955), if its poor development is ignored.

Although the most venous blood from the body wall collects in the renal portal system, some anterior part of the abdominal floor is drained by the abdominal veins, which open directly into the sinus venosus. The abdominal vein has been believed to be almost confined to Elasmobranchii (Harder, 1975); however, the ventral veins in the scorpaenoid fishes (Allen, 1905) and the vein numbered 7 of the tile-fish *Lopholatilus chamaeleonticeps* (Silvester, 1904) are probably its corre-

spondents. In the yellowtail the abdominal vein takes part in the formation of the vascular network in the abdominal floor. This parietal vascular system is connected with visceral vessels by some anastomoses. A similar network is known in the rainbow trout *Salmo gairdneri* (Górkiewicz, 1947).

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## ブリの血管系構築と筋節内分節

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ブリの全身血管系と体側筋の構築を記載した。心臓の洞房弁は両端が心房の心筋束と連続しており、心房収縮時には筋収縮により両側に引かれて閉じると考えられる。入鰓弁動脈は鰓弁列とは反対方向に入鰓動脈から分出し、出鰓弁動脈の基部と噛み合った後、入鰓動脈を迂回して鰓弁に達する。正中背大動脈の前端付近の管内には、後方への血流を部分的に斜めにさえぎる形の上下1対の帯状の突起が内壁から突出し、そこから分出する腹腔一腸間膜動脈への血液の分流を助けるものと思われる。体節血管はすべて末梢まで動・静脈が密接に並走する複線配列を示す。この型の体節血管の複線化を経て、マダロ類の祖先は皮膚血管と熱交換性奇網を発達させたものと考え、各筋節は深部を除き筋隔と平行な隔壁によって4分節されており、そのため体側筋が4倍数の筋節で構成されているように見える。

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