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Vascular Anatomy of the Fish Gill

KENNETH R. OLSON
Indiana University School of Medicine, South Bend Center for Medical Education, University of Notre Dame, Notre Dame, Indiana 46556

ABSTRACT The fish gill is the most physiologically diversified vertebrate organ, and its vasculature the most intricate. Application of vascular corrosion techniques that couple high-fidelity resins, such as methyl methacrylate, with scanning electron microscopy yields three-dimensional replicas of the microcirculation that have fostered a better appreciate gill perfusion pathways. This is the focus of the present review. Three vascular networks can be identified within the gill filament. The arterioarterial (respiratory) pathway consists of the lamellae and afferent and efferent segments of the branchial and filamental arteries and lamellar arterioles. The body of the filament contains two post-lamellar pathways: the interlamellar and nutrient. The interlamellar system is an extensive ladder-like network of thin-walled, highly distensible vessels that traverses the filament between, and parallel to, the lamellae and continues around the afferent and efferent borders of the filament. Interlamellar vessels are supplied by short, narrow-bore feeder vessels from the medial wall of the efferent filamental artery. A myriad of narrow-bore, tortuous arterioles arise from the basal efferent filamental artery and efferent branchial artery and anastomose to form the nutrient circulation of the arch and filament. In the filament body, nutrient capillaries and interlamellar vessels are often closely associated, and the former may ultimately drain into the latter. Many of the anatomical characteristics of interlamellar vessels are strikingly similar to those of mammalian lymphatic capillaries, with the exception that interlamellar vessels are directly fed by arteriovenous-like anastomoses. It is likely that gill interlamellar and mammalian lymphatics are physiologically, if not embryologically, equivalent. *J. Exp. Zool. 293:214–231, 2002.*

As indicated throughout this volume, fish gills are the primary, if not sole organ of respiration, osmoregulation, and nitrogen excretion; they are also major contributors to acid–base balance and hormone metabolism. Diverse regulatory functions often require a variety of anatomical specializations and nowhere may this be more evident, yet under-appreciated, than in the angio-architecture of the fish gill, arguably the most complex circulation found in any vertebrate organ. This review takes on the relatively straightforward task of summarizing the vascular networks within the gill arch. Hopefully, this will revive the more arduous work remaining, namely, that of associating form with function. This may well be one of the most intellectually challenging and mechanistically enlightening venues in comparative physiology.

HISTORICAL PERSPECTIVE

Early work on gill vascular anatomy in the 1800s (reviewed by: Laurent and Dunel, '76; Hughes, '84; Laurent, '84; Olson, '91) fairly accurately described the respiratory circulation but there were disparate views of the non-respiratory pathways, some of which remain to the present day. Müller (1839) identified two filamental pathways, the respiratory (arterioarterial) pathway and an arteriovenous pathway, which originated from the efferent filamental artery (EFA) and formed a venous network in the filament body. Riess (1881), on the other hand, felt that the filament had arterial, venous, and lymphatic pathways, the latter occupying the bulk of the vasculature in the filament core. It was his opinion that the arterial circulation directly supplied nutrient vessels, and because it was closely associated with the lymphatic vessels, allowed red cells to enter it as well. Steen and Kruysse ('64) employed light microscopy and observed red cell movements when filaments were compressed under glass cover slips and concluded that, in addition to the arterioarterial pathway,

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*Correspondence to: Dr. K.R. Olson, SBCME, B-19 Haggar Hall, University of Notre Dame, Notre Dame, Indiana 46556. E-mail: olson.1@nd.edu
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blood could directly bypass the lamellae via the central filamental vasculature. This observation was corroborated in histological sections of gills injected with India ink by Richards and Fromm ('69). Transmission electron microscopic studies of Newstead ('67) and Morgan and Tovell ('73) complimented the often overlooked work of Dornesco and Miscalenco ('63, '67, '68a,b, '69) and showed that vessels in the filament core were not a lamellar bypass. This became even more evident when Gannon et al. ('73) revolutionized the field by applying the technique of vascular corrosion replication to the study of gill vessels. With this method, the vasculature is injected with a liquid methyl methacrylate that upon polymerizing in the vessels, forms a rigid three-dimensional replica of the vascular lumen. Once freed of tissue by alkali maceration, the replica can be examined by light or scanning electron microscopy (Gannon, '78). Laurent and Dunel ('76) provided the first comprehensive view of teleost gill vessels using silicone vascular casts. This study (Laurent and Dunel, '76) and a later comprehensive review (Laurent, '84) described the standard arterioarterial respiratory pathway and identified a cavernous, vasculature in the core of the filament that was predominantly perfused via post-lamellar vessels.

Work in the 1980s and 1990s primarily utilized methyl methacrylate, which offers several advantages over silicone in vascular replication. First, the interfacial tension between methyl methacrylate and water (or plasma) is considerably lower than that between silicone and water. Thus the methacrylate front deforms easier and it more readily enters capillary-size vessels. Second, methyl methacrylate is less viscous. Third, methacrylate replicas are rigid and support themselves in air and under an electron beam, thereby enabling an accurate three-dimensional examination. These factors combine to produce an accurate replication of vascular luminal topography, even down to the level of individual endothelial cells. We have used methacrylate corrosion replicas to perform a detailed examination of gill vessels in a variety of fish. I have chosen to rely heavily on these replicas in the present discussion because they allow easily visualization of vascular pathways, and with the higher resolution attainable, two vascular pathways in the filament become evident. At the risk of oversimplification, but in the interest of space, a number of more the subtle vagaries in perfusion pathways in different fish have been omitted.

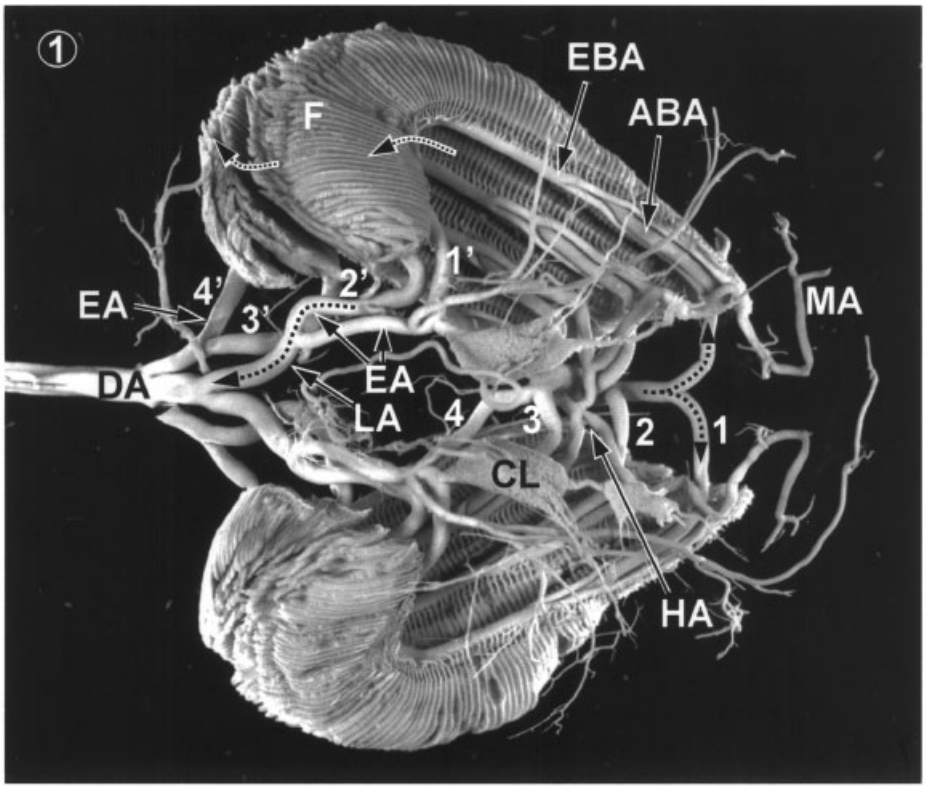
BRANCHIAL BASKET

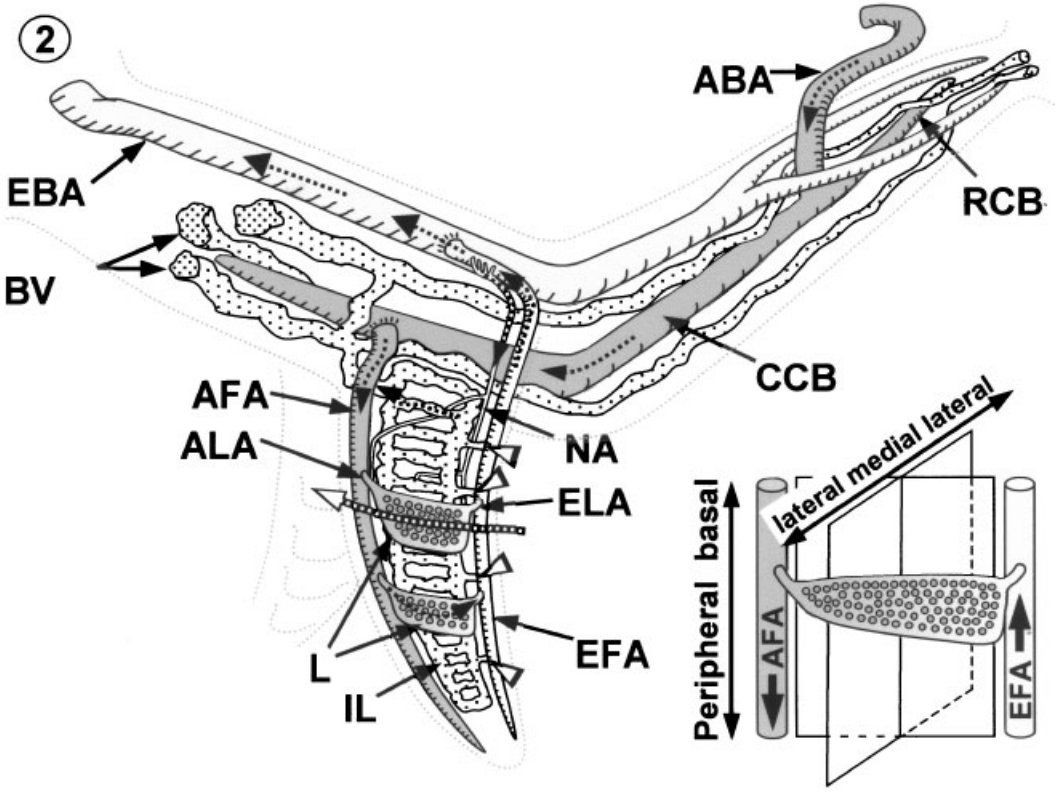
Figure 1 is a vascular replica of the four pairs of gill arches that line the buccal cavity in typical teleosts, and Figure 2 is a schematic of the major vessels in the arch and filament. In fish with an elongated buccal cavity the ventral aorta is a relatively straight vessel and the afferent branchial arteries arise in pairs to supply, in order, the fourth through first pair of arches. If the buccal cavity is relatively short, such as in the catfish in Figure 1, a dorsal branch from the ventral aorta supplies the third arch afferent branchials and then bifurcates into the afferent branchials of the fourth pair of arches. The other (ventral) branch of the ventral aorta proceeds anteriorly and gives rise to the second pair of afferent branchials and then often continues for some distance before

Fig. 1. Vascular corrosion replica of the branchial basket of the channel catfish, *Ictalurus punctatus*, viewed from the dorsal surface, anterior to right. Dotted arrows on vessels indicate direction of blood flow, dotted arrows on white arrow indicate water flow across filaments (F). Abbreviations: 1–4, afferent branchial arteries to gill arches; 1′–4′, efferent branchial arteries from gill arches; ABA, afferent branchial artery entering arch; EBA efferent branchial artery bifurcates to go anteriorly around ABA; DA, dorsal aorta; CL, carotid labyrinth, EA, epibranchial arteries; HA, hypobranchial arteries formed from confluence of anterioventral EA from 2nd and 3rd arches; LA lateral aorta; MA, mandibular artery from 1st arch EBA. Adapted from Olson ('91) with permission.

Fig. 2. Schematic of major vessels in the gill arch and filament. The afferent branchial artery (ABA) enters the arch and bifurcates into a recurrent branch (RCB) that proceeds anterioventrally and a concurrent branch (CCB) that continues posteriodorsally. The respiratory (arterioarterial) circulation in the filament consists of the afferent and efferent filamental arteries (AFA, EFA) and arterioles (ALA, ELA) and the lamellae (L). This is drained from the arch by the efferent branchial artery (EBA). Interlamellar vessels (IL) traverse the filament and are supplied by small feeder vessels (arrowheads) from the EFA or by nutrient vessels (N) that arise from the basal EFA and EBA. The IL system presumably is drained from the arch by the branchial veins (BV). Thin dotted arrows indicate direction of blood flow; large white-on-black dotted arrow indicates path of water flow across lamellae. (**Inset**) Descriptive orientation of the filament. The plane of the filament core is parallel to the AFA and EFA; afferent and efferent denote the filament edge closest to the respective arteries. Medial lies along the filamental plane, lateral extends away from this plane. Basal refers to filamental tissue nearest the arch support skeleton and peripheral proceeds toward the free end (tip) of the filament. Arrows indicate direction of blood flow. Redrawn after Olson ('91).

bifurcating into afferent branchials that supply the first pair of arches. The afferent branchial artery travels posteriorly along the ventral (hypobranchial) limb of the gill arch to the ceratobranchial area, and here it bifurcates into an anterior (recurrent) and posterior (concurrent) branch





(Fig. 2). Both branches terminate within the gill arch.

Efferent branchial arteries arise from the efferent filamental arteries and they may exit the arch from either the posteriodorsal or anterioventral aspect of the arch. The internal and external carotid and hyoidean arteries branch off the dorsal EBA shortly after leaving the first gill arch. This EBA continues posteriorly as the epibranchial artery and after anastomosing with the epibranchial artery from the second arch, forms the lateral aorta (Fig. 1). The two lateral aortae then anastomose to form the anterior aspect of the dorsal aorta. Epibranchial arteries from the third and fourth arches also anastomose and the resulting vessels join the dorsal aorta.

A single EBA is found in, and exits from, the posteriodorsal (epibranchial) arch. However, the anterioventral EBA bifurcates and continues anteriorly past the ABA as separate vessels (Figs. 1 and 2). The lateral-most branch from the first gill arch exits the arch and becomes the mandibular artery, and in some fish, the afferent pseudobranch artery (Fig. 1). Often medial branches from the second and third arch efferent branchial arteries anastomose with each other, and then with their equivalent contralateral arches to form the hypobranchial circulation. In some species, medial branches from the first or fourth arches may also be involved.

ARTERIO-ARTERIAL CIRCULATION

The arterioarterial (respiratory) circulation consists of the lamellae and afferent and efferent components of the branchial arteries, filamental arteries and lamellar arterioles. These vessels and their descriptive orientation are shown in Figure 2.

Afferent filamental arteries (AFA) arise from the afferent branchial artery slightly lateral to the central plane of the gill arch and they are offset from, and alternate with, AFA supplying filaments of the contralateral hemibranch (Figs. 2 and 3). There is a curious bellows-like dilation of the AFA in numerous fish such as channel catfish (Boland and Olson, ’79), carp (Dornesco and Miscalenco, ’63), perch (Laurent and Dunel, ’76), trout (Fromm, ’74; Laurent and Dunel, ’76), bowfin (Olson, ’81), and possibly even tuna (Olson et al., 2002). Generally ampullae are located near the peripheral margin of the interbranchial septum. In some fish (i.e., catfish, carp, bowfin), the ampullae are interconnected, suggesting that they may be evolutionary relics of the elasmobranch cavernous bodies (Laurent, ’84). Other plausible physiological attributes of the ampullae include a pulse-dampening function or even a pressure assist pump (Fromm, ’74; Laurent, ’84; Olson, ’91). The latter has been suggested on the basis of the close association of the ampulla with the filamental support cartilage and the marked

Fig. 3. Cross-section through the gill arch of the snakehead, *Channa punctata*, showing the relationship between the afferent and efferent branchial arteries (ABA and EBA) and a small branchial vein (arrowhead). Dotted arrows indicate direction of blood flow, lamellae (L). Adapted from Olson et al. (’94) with permission.

Fig. 4. Bellows-like ampullae (*) in the afferent filamental arteries of the rainbow trout, *Oncorhynchus mykiss*. Filaments from the near hemibranch have been removed. The afferent branchial artery (ABA) bends at the junction of the cerato- and epibranchial bones (left) and here the length of afferent filamental artery between the ABA and ampullae is reduced (Olson, unpublished).

Fig. 5. Lateral view of an ampulla (A) from the bowfin, *Amia calva*. Note also the long afferent lamellar arterioles (arrows) that supply several lamellae near the base of the filament. Arrowhead indicates nutrient vessels in the interbranchial septum. Adapted from Olson (’81) with permission.

Fig. 6. Vasculature of rainbow trout, *O. mykiss*, lamella. Holes in the lamellar replica, formed when the pillar cells were digested, give the impression that these cells are loosely aligned to form parallel channels traversing the lamella. The relationship between the inner margin of the lamella and the interlamellar (IL) and thin nutrient vessels is evident. Dotted arrow indicates direction of blood flow across lamella. The afferent lamellar arteriole passes through a space in the IL (solid arrow) and short efferent lamellar arterioles drain the lamella (right). From Olson (2000) with permission.

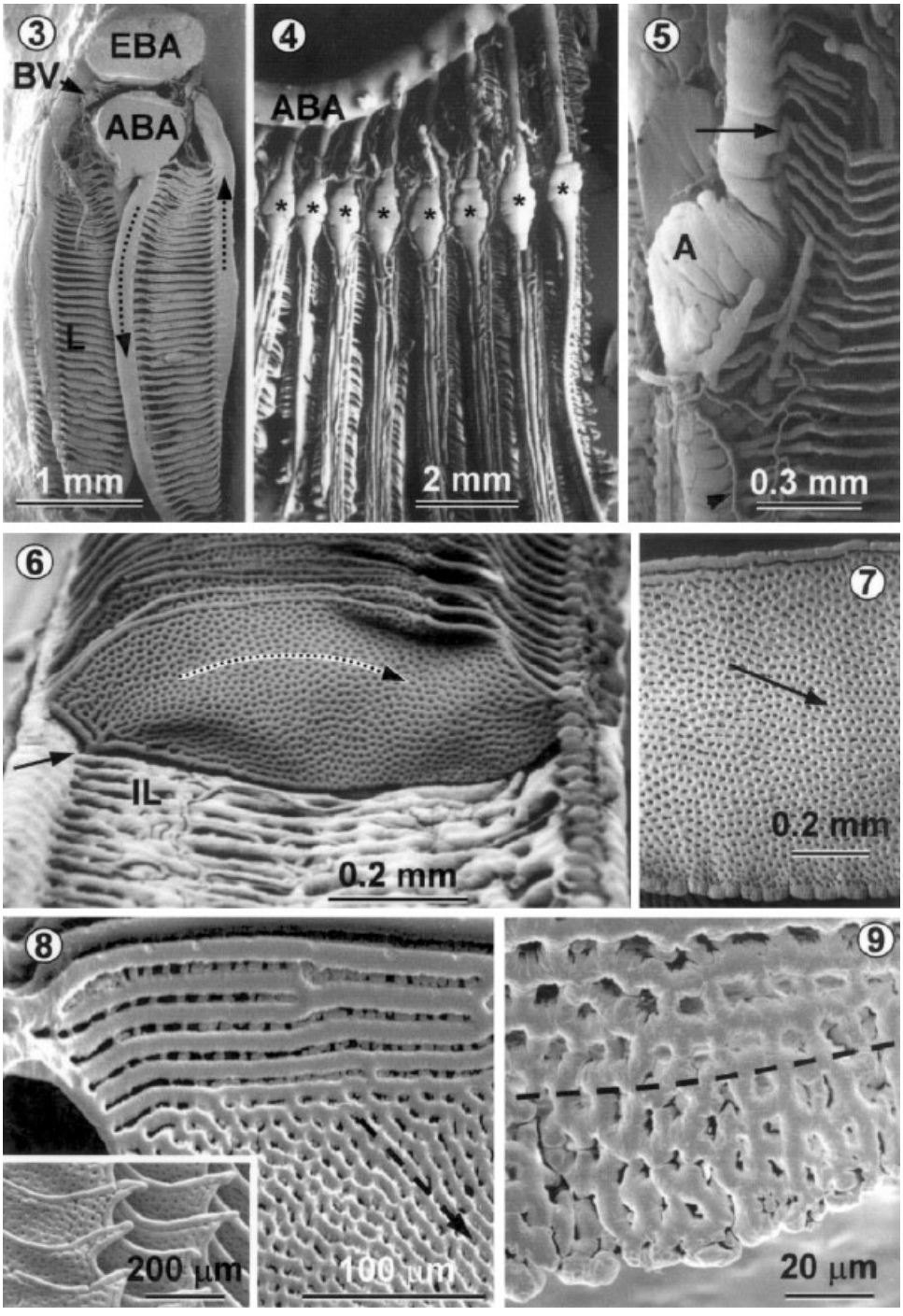
Fig. 7. Vascular sinusoid midway across the lamella of *Squalus acanthias* (afferent side on left). The somewhat dilated and smooth outer marginal channel (upper) contrasts with the irregular inner margin (lower). Alignment of pillar cells (dark holes) forms channels that run slightly diagonal to the long axis of the lamella (Olson and Kent, unpublished).

Fig. 8. Multiple outer marginal channels are present near afferent side of lamella (left) in skipjack tuna, *Katsuwonus pelamis*. Pillar cells in lamellar sinus are aligned to form diagonal channels across the lamella (dashed arrow). Adapted from Olson et al. (in press). (**Inset**) Multiple projections of outer marginal channel near efferent side of dogfish, *S. acanthias*, lamellae. Adapted from Olson and Kent (’80) with permission.

Fig. 9. Pillar cells in inner margin of singi, *Heteropneustes fossilis*, lamella are tightly spaced and a definitive inner channel is absent. Pillar cells spread out and form distinct channels at the point where the lamella emerges from the filament body (dashed line). Adapted from Olson et al. (’90) with permission.

reduction in the thickness of the vascular wall where it abuts up to the cartilage (Laurent, '84). Ampullae have not been found in eels (Laurent and Dunel, '76), smooth toadfish (Cook and Campbell, '80), lingcod (Farrell, '80a) striped bass (King and Hossler, '86), or in a variety of air-breathing fish (Fig. 3; see also Munshi et al., '90; Olson et al., '90, '94, '95). Peripheral to the ampulla, the AFA progressively tapers and ultimately ends in the tip of the filament. There is no bypass around the filament tip as was previously thought.

Numerous afferent lamellar arterioles (ALA) originate along the length of the AFA. ALA in the



basal filament are long, especially in fish with a prominent interbranchial septum, and often one ALA will branch to supply up to 4 or 5 lamella on the same side of the filament (Laurent, '84; Olson, '91). Tuna have unusually long ALA that feed 10 or more lamellae and are connected with each other to form a continuous vascular manifold in the basal filament (Olson et al., 2002). In the peripheral filament, ALA usually supply individual lamellae, or in some instances they may branch to supply two lamellae on either the same, or opposite sides of the filament. Rarely do ALA in the peripheral filament supply more than two lamellae. Vascular resistance in lingcod ALA is higher than that of any other segment in the arterioarterial pathway (Farrell, '80b).

The lamellae consist of a thin, flat vascular sinusoid sandwiched between parallel sheets of pillar cell flanges, basement membrane and a simple squamous pavement epithelium (Figs. 6–12). Pillar cells are spool-shaped cells (Figs. 10–12) with a trunk-like body that separates the epithelial layers. Cytoplasmic flanges of pillar cells spread out and attach to their neighbors. These flanges delimit the vascular space and prevent blood from contacting the thrombogenic basement membrane sheet that envelopes the lamella (Hughes, '84; Laurent, '84). Numerous thread-like strands of collagen connect the two apposed sheets of basement membrane (Hughes and Weibel, '72) and presumably provide structural support against the distending intravascular pressure. Collagen strands usually occur in circular clusters of four to ten and at first glance they appear to be just inside the pillar cell membrane. However, in cross section it is evident that the collagen strands do not penetrate the pillar cells but rather the pillar cell membrane has enveloped the strand much as a tree grows around a wire fence (Fig. 10; see also Hughes and Weibel, '72). Presumably this eliminates any thrombogenic response. (It is intuitively easy to visualize this in the middle of the pillar cell; however, the conundrum of how the collagen threads are enveloped by the pillar cell flanges has not been addressed.) Axially-oriented immuno-reactive myosin filaments have also been described in the pillar cell body (Smith and Chamley-Campbell, '81). These may provide structural support or possibly have contractile activity (Farrell et al., '80; Laurent and Dunel, '80). If contractile, pillar cells would be under endocrine or paracrine control as they are not innervated (Hughes and Wright, '70). Communicating (gap) junctions have been reported in pillar cells from the hagfish (Bartels and Decker, '85), but they have not yet been reported in teleosts. Autoradiographic and immunohistocytochemical studies have shown that pillar cells exert a variety of metabolic effects on plasma-borne substrates (Olson, '98; see also Olson, 2002, this volume). Perhaps one of the most significant questions that remains unanswered is whether or not pillar cells are active participants in regulating lamellar perfusion.

Endothelial cells replace pillar cells in the lateral wall of the outer marginal channel (Figs. 10 and 11), and this is the only area of the lamella that has a true endothelium. These endothelial cells are the only lamellar cells that exhibit classical Weibel-Palade bodies (Boyd et al., '80).

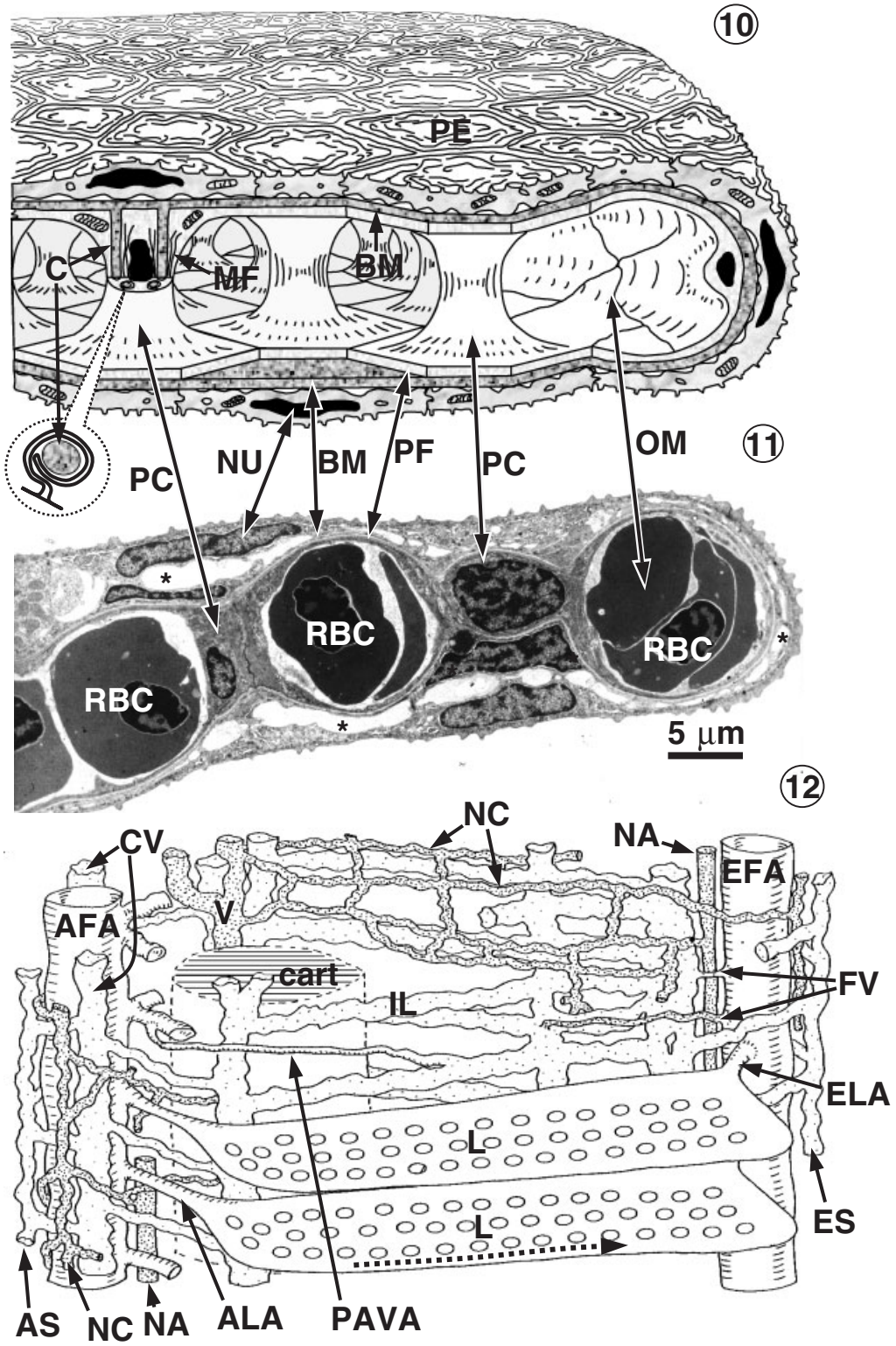
Three blood pathways have been described in the lamella, an outer and inner marginal channel and the lamellar sinusoid. The outer marginal channel is dilated and perhaps serves as a preferential pathway around the lamellar circumference (Figs. 6–8, 10, and 11). It has been observed in all fish examined to date. In many fish, the diameter of the outer channel is greatest near the afferent end of the lamella where it presumably helps distribute blood to the more

Fig. 10. Schematic cross-section through lamella near outer marginal channel (OM). Other abbreviations: BM, basement membrane; C, collagen strands; MF, microfilaments; NU, cell nucleus; PC, pillar cell; PE, pavement epithelial cell; PF, pillar cell flange; PM plasma membrane. Dotted inset shows pillar cell membrane enveloping collagen strand.

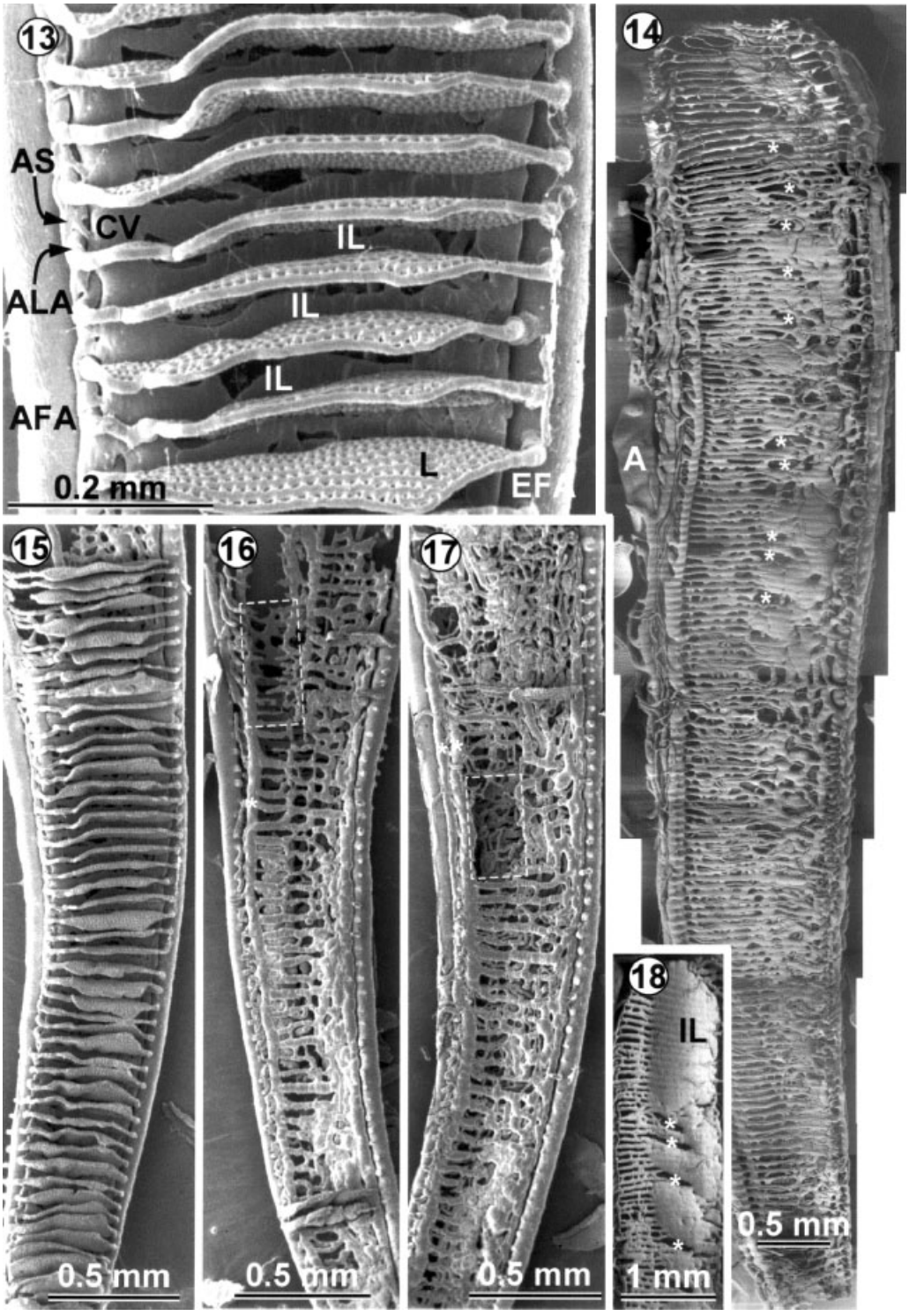
Fig. 11. Transmission electron micrograph of rainbow trout, *O. mykiss*, lamella. Subepithelial sinuses are evident (*). Abbreviations: RBC, red blood cell; other abbreviations as in Fig. 10. Micrograph courtesy of J. Mallatt and R. McCall.

Fig. 12. Schematic of a composite teleost filament showing relationships between respiratory, interlamellar, and nutrient circulations. Abbreviations: AFA, afferent filamental artery; ALA, afferent lamellar arteriole; AS, afferent sinus; cart, filamental cartilage; CV, collateral vessel; EFA efferent filamental artery; ELA, efferent lamellar arteriole; ES, efferent sinus; FV feeder vessels; IL, interlamellar system; L, lamella; NA, nutrient artery; NC nutrient capillary; PAVA, prelamellar arteriovenous anastomosis; V, vein. Dotted arrow indicates direction of blood flow. Redrawn from Olson ('91) with permission.

lateral lamellar sinusoids. The channel may narrow somewhat midway across the lamella, but becomes progressively dilated toward the efferent side in order to receive additional blood draining into it from the lamellar sinusoids (Fig. 6). This pathway clearly has the lowest resistance and in



cross-section often has more red cells (Fig. 11), which suggests that red cells may be preferentially shunted through it (Soivio and Tuurala, '81). One might expect that this takes advantage of the fact that the outer marginal channel has over 50% more surface area in contact with respiratory water, and it has the lowest unstirred boundary effects. There may be additional preferential pathways immediately medial to the outer channel (Fig. 7). These are formed by closely aligned pillar cells, thus they do not have an endothelial cell component. These pathways may assist in dis-



tributing blood across the lamellae or they may take advantage of the enhanced water flow.

Some fish, such as tuna, may have multiple channels in the outer margin (Olson et al., 2002). Six of these are shown in Fig. 8. The most medial channels have the narrowest diameter and do not travel very far across the lamella. These are clearly distributing channels and they act as a manifold to efficiently aliquot blood along the outer border of the lamella. The inner margin of the tuna lamella becomes similarly complex at the efferent end to receive the blood.

A peculiar almost spiny projection (Fig. 8, inset) has been observed in the outer channel of such disparate fish as elasmobranchs (Cook, '80; Olson and Kent, '80), and the skipjack tuna (Olson et al., 2002). In elasmobranchs, the number of projections on a single lamella may range from zero to three, even in a single gill arch. The number of projections on each lamella does not appear randomly distributed, but appears to increase as the size of the lamella increases, although this has not been thoroughly examined. Skipjack lamellae either have a single projection or none at all. It is unclear if these projections offer any hemodynamic advantage although they obviously increase the length of the outer channel. Alternatively, they may be part of the lamellar structure that is important in directing respiratory water flow.

The lamellar sinus is flat vascular sheet usually no thicker than a single red blood cell (Hughes, '84). Pillar cells may be more or less randomly dispersed (Fig. 6) to let blood percolate across the lamella (see also Fig. 14 in Hughes, '84). Alternatively, they may be loosely arranged in rows to provide some direction to blood flow (Figs. 7 and 9), or closely aligned to form capillary-like vessels (Fig. 8). The latter case is most apparent in the tuna where blood is directed diagonally across the lamella (Muir and Brown, '71). It has been estimated that this reduces vascular resistance in the skipjack and bluefin tuna lamella 16- and 80-fold, respectively (Muir and Brown, '71).

The inner marginal channel has been described as a continuous dilated pathway around the medial border of the lamella (Newstead, '67; Morgan and Tovell, '73; King and Hossler, '86). A dilated inner channel is clearly evident at the afferent and efferent ends of the lamella where it undoubtedly assists in the distribution and collection of blood, respectively. However, most vascular replicas show that the channel does not continue uninterrupted across the lamella, and in fact, by midlamella the pillar cells are so tightly packed (Figs. 7 and 9) that they appear to impede flow, especially for cellular elements (Tuurala et al., '84). Hughes and Morgan ('73) and Zenker et al. ('87) have shown that lamellae develop from the proliferation of pillar cells along the medial border and a high pillar cell density in this area is to be expected. Furthermore, because as much as 10–30% of the medial margin of the lamella is usually imbedded in the body of the filament, gas exchange in this region is probably severely limited (Smith and Johnson, '77; Cook and Campbell, '80; Farrell et al., '80; Hughes and Mittal, '80; Olson, '81; Pärt et al., '84; Tuurala, et al., '84; Olson et al., '90). Plasma skimming into the non-respiratory portion of the lamella buried in the filament body may also be osmotically economical. In tuna, however, even the inner channel is relatively close to the surface and it is continuous (Olson et al., 2002). This may be an adaptation to the premium placed on gas exchange (although a complete inner channel has also been observed in striped bass lamellae; King and Hossler, '86).

Lamellae (especially the longer ones) of many fish are shaped like a right triangle with the inner channel as the side, the afferent and lateral

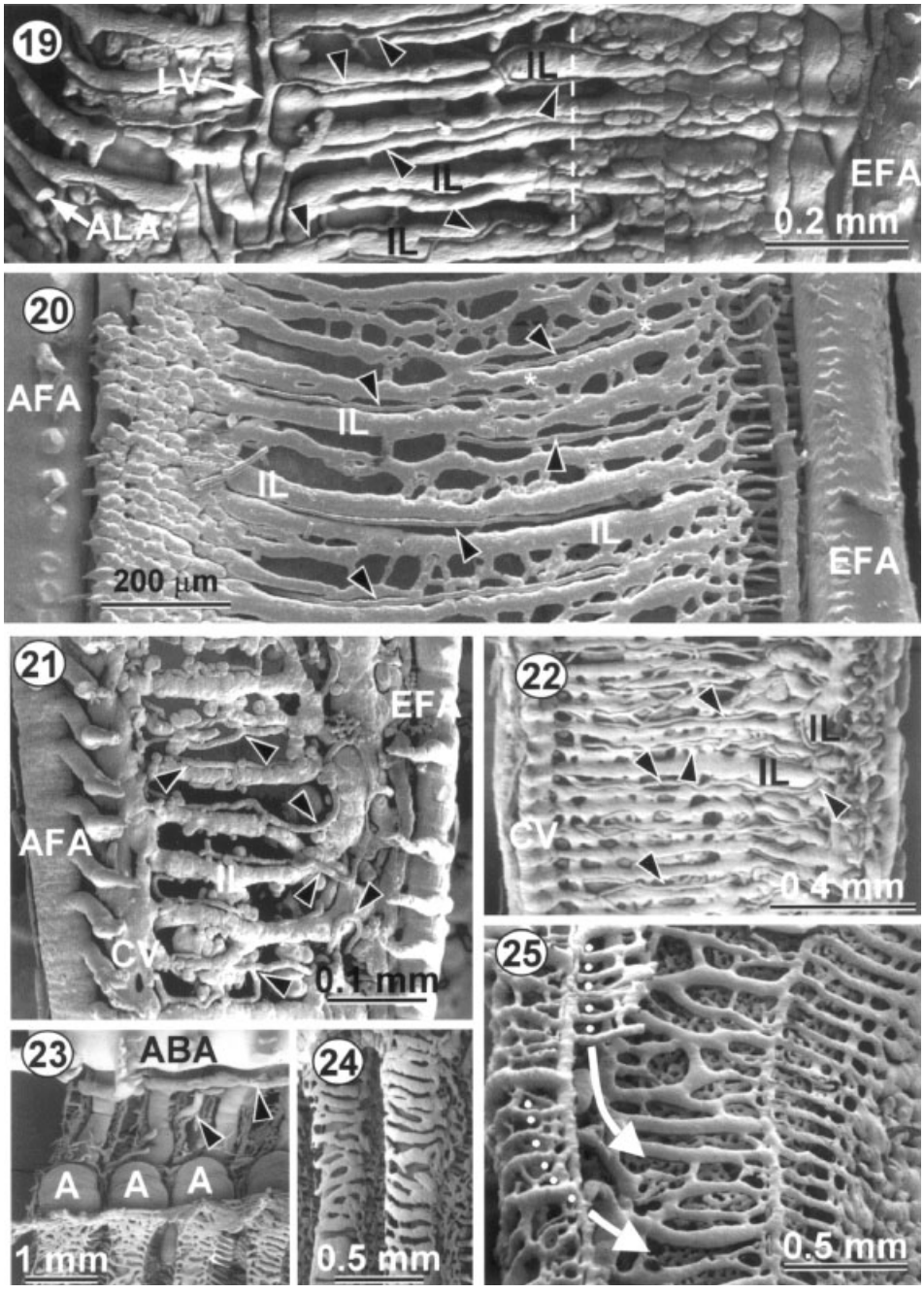
Fig. 13. Relationship between respiratory lamellae (L) and interlamellar system (IL) in the walking catfish, *Clarias batrachus*. Note parallel blood channels in lamella; afferent sinus envelops afferent lamellar arteriole (ALA). Other abbreviations as in Fig. 12. Adapted from Olson et al. ('95) with permission.

Fig. 14. Montage of interlamellar and nutrient vessels in rainbow trout, *O. mykiss* filament. Nutrient vessels to the adductor muscle are visible above the ampulla (A); *, space occupied by extensions of filamental cartilage rod (Olson, unpublished observation).

Figs. 15–17. Gill filaments of walking catfish, *C. batrachus* with lamellae intact (Fig. 15), with lamellae removed and interlamellar system filled (Fig. 16), and with lamellae removed and both interlamellar and nutrient vessels filled (Fig. 17). In Figs. 16 and 17 the interlamellar and nutrient vessels on the opposite side of the filament are exposed (dashed rectangles). ⁎, afferent collateral vessels. Adapted from Olson et al. ('95) with permission.

Fig. 18. Interlamellar system (IL) of rainbow trout, *O. mykiss*, distended by excessive filling pressure (compare with Fig. 14). ⁎, space occupied by extensions of filamental cartilage. Adapted from Olson ('83) with permission.

outer channel as the hypotenuse and the outer channel at the efferent end as the base (see Fig. 14 in Hughes, '84, and Fig. 5 in Farrell, '80a). The latter is also the entry side for inhalant water and it is often refereed to as the ''leading edge''. It is generally accepted, that this shape ''ensures that blood in the marginal channels at the [water] inlet side will come into contact with water containing the highest P_{O_2}'' (Hughes, '84). This shape may confer other advantages, if we can assume that the largest blood/water P_{O_2} gradient is on the afferent (systemic venous blood inlet, water outlet) side of the lamella and the smallest P_{O_2} gradient is near the efferent (blood outlet, water inlet) side. First, with the widest portion of the lamella near the efferent end, blood flow velocity will be the lowest. This increases the opportunity for blood P_{O_2} to approach that of inhalant water (this is also where water P_{O_2} is maximal). Second, slow blood velocity and



maximal contact area may not be as important on the afferent side of the lamella because gas exchange is favored by the high blood/water P_{O_2} gradient. However, by reducing the lamellar width at the afferent end there will be less resistance to water flow (a right triangle has half the surface of a rectangle of equal length and width). This could reduce respiratory work without compromising gas transfer. Clearly future modeling of gill gas transfer will need to examine the contribution of lamellar shape.

Efferent lamellar arterioles are typically short (Fig. 6). In most fish they drain individual lamellae into the lateral wall of the efferent filamental artery, although several lamellae draining into a single efferent lamellar arteriole have been observed in striped bass (King and Hossler, '86). Generally the efferent lamellar arterioles drain into the mediolateral or lateral walls of the efferent filamental artery. As the efferent filamental artery approaches the base of the filament it turns to anastomose with the efferent branchial artery. A well-innervated, muscular, sphincter has been observed in this area that may affect gill perfusion (see Sundin and Nilsson, 2002, and Olson, 2002, this volume). The efferent filamental artery also gives rise to two types of vessels: one that directly enters the interlamellar system and another that forms nutrient vessels of the secondary circulation.

ARTERIOVENOUS CIRCULATION: INTERLAMELLAR SYSTEM

The arteriovenous circulation, in all but a few fish, is derived exclusively from post-lamellar vessels and functionally it is a systemic circuit. It has been described as a single network in most descriptions of gill vessels (cf. Laurent, '84). This interpretation is still equivocal, and I feel that there is enough evidence to support further division of this system into two pathways: the interlamellar and the nutrient. This approach is taken in the following two sections.

The interlamellar system arises from post-lamellar vessels and forms an extensive, and in many fish highly ordered, vascular network in the gill filament (Figs. 12, 14, and 16–22). This system is unique in its relationship to other vessels and gill tissues, in its structure, and in the vessels that feed it. The volume of the interlamellar system is second only to that of the lamellae.

The interlamellar system derives its name from the observation that much of this circulation consists of a repetitive, ladder-like series of vessels that traverse the filament body between the lamellae (Figs. 12 and 13). These vessels are found on both sides of the afferent side of the filament, just lateral to the filamental cartilage (Fig. 12). On the efferent side of the cartilage, interlamellar vessels from the opposite sides of the filament approach each other and may continue toward the efferent filamental artery as a sheet of parallel interdigitating vessels as seen in the catfish (Fig. 19; Boland and Olson, '79). (Interlamellar vessels on opposite sides of the filament are 90 degrees out of phase, as are the lamellae.) Alternatively, interlamellar vessels may remain paired as in the walking catfish (Fig. 27; Olson et al., '95), or skipjack where they are separated by the broad filamental cartilage (Olson et al., 2002). In many replicas, the interlamellar vessels along the efferent side are even less organized and take on a sack-like look (Laurent, 1884; King and Hossler, '86). It is not yet clear whether this is an accurate representation of the vessel or if it is an artifact produced during tissue preparation. As shown in the trout (cf. Figs. 14 and 18; Olson, '83) and toadfish (Cook and Campbell, '80), moderate

Figs. 19–22. Interlamellar (IL) and nutrient capillaries (arrowheads) in the channel catfish, *I. punctatus* (Fig. 19), skipjack tuna, *K. pelamis* (Fig. 20), singi, *H. fossilis* (Fig. 21), and rainbow trout, *O. mykiss* (Fig. 22). Nutrient capillaries drain into longitudinal filamental veins (LV) in the channel catfish; AFA, afferent filamental artery; CV, afferent collateral vessel; EFA, efferent filamental artery. IL vessels from opposite sides of filament interdigitate to right of dashed line in Fig. 19. In Fig. 20, the asterisk (*) shows nutrients from afferent side anastomosing with IL vessels on efferent side of filament. Adapted from Boland and Olson ('79), Olson et al. ('90, in press), and Olson, unpublished observation, all with permission.

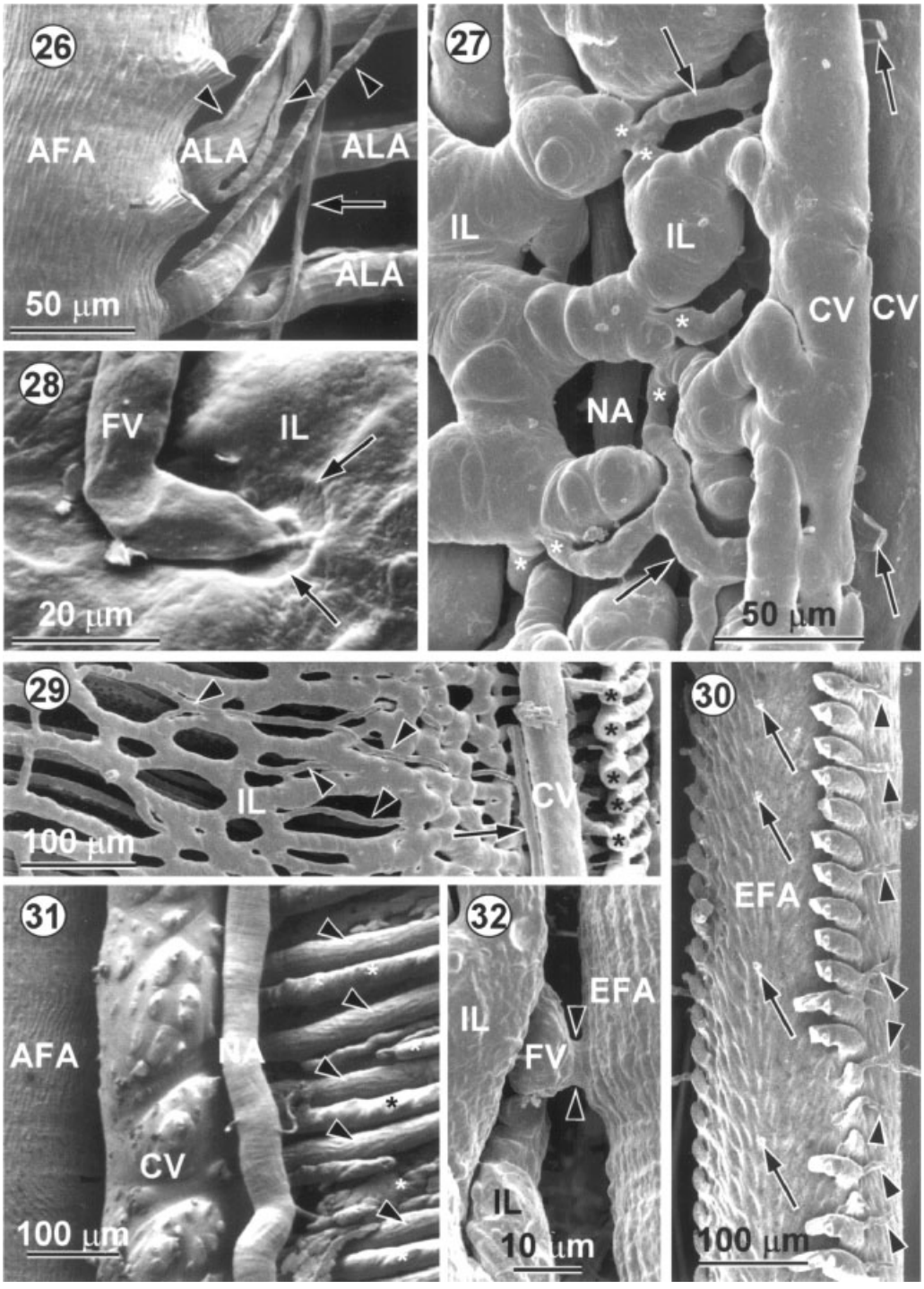
Fig. 23. Filaments of near hemibranch have been removed from afferent branchial artery (ABA) exposing afferent sinus (bottom of micrograph) surrounding filamental artery distal to ampullae (A) and arch nutrient vessels (arrowheads) in the bowfin, *A. calva*. Adapted from Olson ('81) with permission.

Fig. 24. Afferent sinus surrounding two filamental arteries in the bowfin, *A. calva*. Adapted from Olson ('81) with permission.

Fig. 25. Afferent sinus extends between filaments and envelops water channel (arrows) in dogfish shark, *S. acanthias*. Adapted from Olson and Kent ('80) with permission.

increases in perfusion pressure can greatly distort the appearance of interlamellar vessels.

Ipsilateral interlamellar vessels are interconnected by several vessels that travel the length of the filament. Most notable among these are the afferent and efferent collateral vessels. The afferent collateral vessel, also called the companion vessels (Cook and Campbell, '80; Farrell, '80a), or collecting vessels (Olson, '81), are near the afferent filamental artery. They may be either lateral (Fig. 31) or medial (Figs. 20 and 21) to the lamellar arterioles, or as is most often the case,



there may be two interconnecting vessels on each side of the lamellar arterioles (Figs. 14 and 17). The interlamellar vessels, collateral vessels, and their anastomoses often completely encircle each afferent lamellar arteriole (Fig. 13; see also: Laurent and Dunel, '76; Boland and Olson, '79; Cook and Campbell, '80; Farrell, '80a; King and Hossler, '86). In the catfish, the medial vessel is shifted away from the afferent filamental artery toward the lateral margin of the filamental cartilage (Fig. 19; Boland and Olson, '79). The interlamellar system often continues as an irregular afferent sinus either part way or all the way (Figs. 21 and 22) around the afferent border of the filament. In elasmobranchs, where the filament is attached to septal tissue for most of its length, the afferent sinus forms an elaborate network lining the water canal and connecting adjacent filaments (Fig. 25; Olson and Kent, '80). Collateral vessels along the efferent side of the filament may be irregular in shape (Figs. 19, 21, and 22), or may be well defined vessels closely associated with their contralateral counterpart and adjacent to the medial wall of the efferent filamental artery (Fig. 27).

One of the least understood aspects of the interlamellar system is the origin of the vessels that feed it. Three sources have been described; prelamellar ''arteriovenous'' anastomoses (AVAs), postlamellar AVAs (feeder vessels), and filamental nutrient vessels. The term AVA is used by convention; there is no consensus on the true ''venous'' nature of the interlamellar system, or if some of the AVAs are more akin to capillaries (Laurent and Dunel, '76; Cook and Campbell, '80; Donald and Ellis, '83; Olson '91). Prelamellar AVAs most often originate from the afferent lamellar arterioles, less commonly from the afferent filamental artery, and rarely the inner margin of the lamella itself. They are most prevalent in eels (Laurent and Dunel, '76; Donald and Ellis, '83) where they may constitute a significant lamellar bypass (Hughes et al., '82). They are less prevalent but readily observed in catfish (Fig. 26; Boland and Olson, '79) and toadfish (Cook and Campbell, '80), and less common in tilapia (Vogel et al., '73, '74), icefish (Vogel and Kock, '81), and elasmobranchs (Cook, '80; Olson and Kent, '80; DeVries and DeJager, '84). They are very rare or non-existent in trout (Laurent and Dunel, '76), perch (Laurent and Dunel, '76), lingcod (Farrell, '80a) bowfin (Olson, '81), striped bass (King and Hossler, '86), and a variety of air-breathing teleosts (Olson et al., '86, '90, '94, '95).

Narrow-bore (typically 5–15 μm diameter) feeder vessels that connect directly from the medial wall of the efferent filamental artery to the interlamellar system (i.e., post-lamellar AVAs) have been observed in virtually all fish examined to date (Figs. 27, 30, and 32). These vessels hardly constitute a high-volume pathway as their density ranges from 1 feeder vessel per 2–4 pairs of lamellae in the eel (Donald and Ellis, '83) and striped bass (King and Hossler, '86) to 1 feeder per 10+ lamellae in tuna (Olson et al., 2002). Nevertheless, their universality is suggestive of their significance. Usually these vessels only travel a short distance into the filament body before branching several times prior to anastomosing

Fig. 26. Prelamellar arteriovenous anastomoses (arrowheads) in the channel catfish, *I. punctatus*; AFA, afferent filamental artery; ALA, afferent lamellar arterioles; arrow points to nutrient vessel. Relief of endothelial cells on large vessels is clearly visible (Olson, unpublished observation).

Fig. 27. Efferent filamental arteries have been removed to expose short feeder vessels (arrows) that pass between efferent collateral vessels (CV) and anastomose (*) with the interlamellar system (IL) in the walking catfish, *C. batrachus*. Compare irregular relief of IL with underlying nutrient artery (NA). Adapted from Olson et al. ('95) with permission.

Fig. 28. Anastomosis of feeder vessel (FV) with interlamellar system (IL) in the rainbow trout, *O. mykiss*, appears to be regulated by guard cells (arrows) (Olson, unpublished observation).

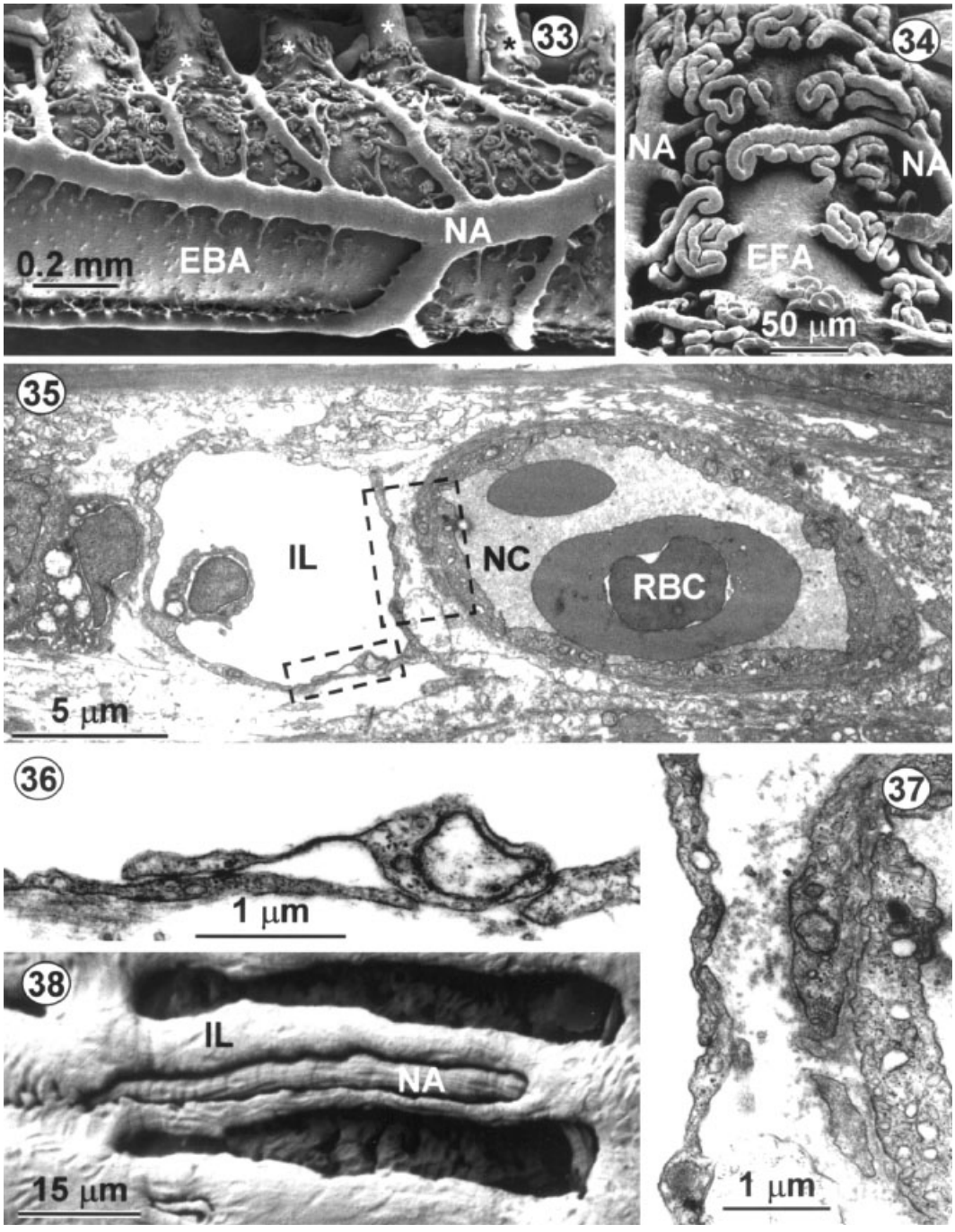
Fig. 29. Nutrient capillaries (arrowheads) from a single nutrient artery (arrow) traverse nearly halfway across a skipjack tuna, *K. pelamis*, filament and anastomose with IL vessels (IL); CV; efferent collateral vessel; ∗, broken lamellae. Inner marginal channels of lamellae on opposite of filament are visible on left beneath IL. Adapted from Olson et al. (in press).

Fig. 30. Origin of four feeder vessels (arrows) from efferent filamental artery (EFA) of skipjack, *K. pelamis*. Other vessels (arrowheads) arise from efferent lamellar arterioles and supply efferent sinus (broken away). Note endothelial impressions in replica. Adapted from Olson et al. (in press).

Fig. 31. Comparison of luminal surface of afferent filamental artery (AFA), afferent collateral vessel (CV), nutrient artery (NA), afferent lamellar arterioles (arrowheads), and interlamellar system (*) in the channel catfish, *I. punctatus* (Olson, unpublished observation).

Fig. 32. Origin of feeder vessel (FV) from efferent filamental artery (EFA) is constricted (arrowheads) in singi, *H. fossilis*. IL, interlamellar vessels. Adapted from Olson et al. ('90) with permission.

with the interlamellar system (Fig. 27); they do not appear to anastomose with the efferent collateral vessel, even though collateral vessels are closer to the efferent filamental artery than the interlamellar vessels are (Fig. 27). A sphincter-like constriction has been observed at the origin of some feeder vessels (Fig. 32) and also at the anastomoses of feeders with interlamellar vessels (Fig. 28). Entrance into feeder vessels (or into some prelamellar AVAs) may be guarded by endothelial cells with microvillous projections that extend into the lumen of the filamental artery (Vogel et al., '76, '78a,b; Donald and Ellis, '83), or the orifice may have a smooth endothelium (Cook and Campbell, '80). Extremely narrow-bore feeder-like vessels formed by cuboidal endothelial cells with numerous microvilli and large intracellular whorls have been reported in tilapia by



Vogel et al. ('74), but these have not been reported in other fish. Typically the endothelial topography observed in replicas of feeder vessels resembles that of the interlamellar system (Figs. 27 and 28). The fine structure of interlamellar and nutrient endothelial cells is described in a later section.

In many fish, the interlamellar system extends around the efferent filamental artery as the efferent sinus. In the bowfin (Olson, '81), eel (Donald and Ellis, '83), and tuna (Olson et al., 2002) this sinus also receives blood from narrow-bore vessels originating from the efferent lamellar arterioles.

ARTERIOVENOUS CIRCULATION: NUTRIENT SYSTEM

The nutrient circulation is formed from post-lamellar vessels and supplies the gill arch support tissue, the filamental adductor and abductor muscles and the core of the filament. Nutrient vessels may arise from the efferent branchial artery as relatively large-diameter vessels, as in the smooth toadfish (Cook and Campbell, '80) and icefish (Vogel and Kock, '81); however, more often nutrient vessels are formed from the condensation of a myriad of narrow-bore, tortuous arterioles emanating from the walls of the basal portion of the efferent filamental arteries and from the efferent branchial artery. Because of the similarity of this arrangement with other vascular networks in the skin, fins, oral and peritoneal cavities, and heater vessels in tuna, the gill nutrient and interlamellar vessels have been considered to be part of the secondary circulation (Laurent, '84; Vogel, '85; Steffensen and Lomholt, '92; Olson, '96). In retrospect, this classification may have been too inclusive and additional studies are needed to clarify the relationships between gill interlamellar and nutrient systems. In the present discussion, the nutrient vasculature is treated as a separate network with the understanding that this is still an arbitrary distinction.

The tortuous arterioles forming the gill nutrient circulation are shown in Figs. 33 and 34. Typically, the origin of these vessels is somewhat dilated and this is followed by a narrow (usually <15 μm), very convoluted segment that may be well over 100–200 μm long. Because of these convolutions, the linear transit of the tortuous vessels is generally less than a third of their axial length. Vogel ('78a,b) has shown in the trout that the endothelial cells guarding the opening of the arterioles have numerous microvilli, but this is not a universal finding (Cook and Campbell, '80). Through repeated anastomoses, the tortuous vessels form progressively larger nutrient arteries, such as those in Fig. 33. The location of nutrient arteries in the arch tissue varies from fish to fish; most commonly they are found between the afferent and efferent branchial arteries, peripheral to the afferent branchial artery and between the afferent filamental arteries (Fig. 23), or in the peripheral margin of the interbranchial septum. These arteries are supplied from both the efferent filamental and branchial arteries.

The filamental nutrient circulation in most fish is supplied locally from the base of the efferent filamental artery. Usually a pair of arteries form on the lateral wall of the efferent filamental artery and as they travel peripherally, they turn medially and anastomose into a single vessel. This vessel then bifurcates, one branch going toward the afferent filamental artery, the other follows the efferent filamental artery (Figs. 2, 12, 27, and 29). Sometimes an additional branch travels up the

Fig. 33. Numerous small tortuous vessels arise from the efferent branchial (EBA) and efferent filamental (*) arteries and anastomose to form nutrient arteries (NA) in the climbing perch, *Anabas testudineus*. Adapted from Olson et al. ('86) with permission.

Fig. 34. Higher magnification of tortuous vessels from efferent filamental artery (EFA) that anastomose to form nutrient arteries (NA) in climbing perch, *A. testudineus*. Adapted from Olson et al. ('86) with permission.

Fig. 35. Transmission electron micrograph of interlamellar (IL) and nutrient capillary (NC) in the filament of rainbow trout, *O. mykiss*. Dashed rectangles are enlarged in Figs. 37 and 38; RBC, red blood cell [from Olson and Kingsley, adapted from Olson ('96)].

Fig. 36. Magnification of Fig. 35 showing overlapping endothelial cell junctions in interlamellar vessels of rainbow trout, *O. mykiss* [from Olson and Kingsley, adapted from Olson ('96)].

Fig. 37. Magnification of Fig. 35 comparing thin interlamellar and thick nutrient capillary endothelia in rainbow trout, *O. mykiss*, filament [from Olson and Kingsley, adapted from Olson ('96)].

Fig. 38. Distension of interlamellar vessels (IL) appears to envelop nutrient arteriole (NA) in dogfish shark, *S. acanthias*, filament. Adapted from Olson and Kent ('80) with permission.

center of the filament. The nutrient artery near the afferent side of the filament supplies the filament adductor muscle (Fig. 14), and it may bifurcate and continue to the tip of the filament as paired vessels in the notches between the afferent filamental artery and the filamental cartilage. Vogel ('78b) named these vessels ''Fromm's arteries.'' Occasionally they have been confused with the collateral vessels of the interlamellar system (Cook and Campbell, '80), although vascular replicas clearly allow this distinction (Fig. 31). In many fish there is only a single nutrient vessel near the efferent filamental artery (Figs. 27 and 29).

Nutrient arterioles and/or capillaries in the core of the filament are closely associated with interlamellar vessels and the two often travel considerable distance across the filament together (Figs. 19–22, 35, and 38). This suggests that the two networks have distinct functions. Other anatomical differences are also apparent in cross sections (Figs. 35 and 37). Nutrient capillaries have a more regular circumference, they frequently contain red cells and an electron dense plasma, and their endothelium is thicker. Interlamellar vessels have few or no red cells, a less electron dense plasma and a thin endothelium. Margins of adjacent endothelial cells in interlamellar vessels often overlap (Figs. 36 and 37). Interlamellar vessels appear very distensible. When deflated, their endothelial cell nuclei bulge into the lumen (Fig. 35). When distended, they form a capacious network that may nearly completely envelop the nutrient vessel (Figs. 19 and 38), or at even higher pressure, they may appear to fill the filament core (Fig. 18). Many of these characteristics of interlamellar vessels are similar to those of mammalian lymphatic capillaries with the exception that the former are also connected to the vasculature. Both the interlamellar and nutrient systems are medial to the filamental basement membrane and may be as far, or farther, from the interlamellar epithelium as the basal channels of the lamellae.

Nutrient vessels may be drained from the filament by a separate venous system (Fig. 19), or they may anastomose with the interlamellar system. In the latter instance, most anastomoses are two-thirds of the way across the filament, closer to the efferent side (Fig. 20). Whether together or separately, the interlamellar and nutrient networks drain from the base of the filament into the branchial veins and from there the effluent is returned to the heart (Fig. 2).

FUTURE DIRECTIONS

An understanding of the physiological functions of the gill vasculature is predicated upon the resolution of a number of factors. (i) All vessels and their connections must be identified. There is still uncertainty about the nature and extent of input into the interlamellar system. The morphological characteristics of interlamellar and nutrient vessels needs to be examined in greater detail and circumstances that might affect the vessel's volume (filling pressure, environmental salinity, etc.) will give valuable insight. (ii) Flow patterns and direction of flow must be resolved. Flow between and within lamellae has often been offered as a mechanism of altering gas exchange. To date, the theoretical and experimental basis for these possibilities has only received cursory attention. The direction of flow within the interlamellar system is not known. There are multiple countercurrent and concurrent possibilities between lamellar, interlamellar, nutrient and water flow that could have substantial on physiological function. (iii) Mechanisms of perfusion regulation have to be identified and flow distribution quantified. It goes with out saying that understanding how alterations in perfusion impact function is a primary objective of gill physiology. Other information on specific vasoactive stimuli will also improve our understanding of the overall integration of homeostatic systems. (iv) Tissue adjacencies (and the specific functions of these tissues) must be determined. Are chloride cells or are subepithelial interstitial spaces functionally closer to inner marginal lamellar channels, interlamellar vessels, or nutrient vessels? Characterization of molecular commerce between the environment and these pathways is one of the ultimate objectives in discerning their function. These are the same challenges that have been faced by mammalian renal physiologists. Although our task seems more daunting, we can learn much from their methods and approach.

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