

Renal Microvasculature of the Rainbow Trout, *Salmo gairdneri*: Scanning Electron Microscopy of Corrosion Casts of Glomeruli

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ABSTRACT Scanning electron microscopy of corrosion casts of blood vessels permits detailed and accurate study of the microcirculation. The present study examined the renal microvasculature of the rainbow trout, *Salmo gairdneri*. The conventional picture of a glomerulus with one afferent arteriole was common, but glomeruli were often supplied by two afferent arterioles. In the majority of these, the intrarenal artery gave rise to a single afferent arteriole that branched to form two smaller vessels before reaching the glomerulus. Glomeruli with two afferent arterioles that arose independently from the intrarenal artery also occurred. The majority of glomeruli had a single efferent arteriole, but a proportion of glomeruli had two efferent arterioles. Efferent arterioles were smaller in diameter than the afferent arterioles. The glomerular capillaries were arranged in lobules, with few anastomoses between lobules, so that, for glomeruli with two afferent or two efferent arterioles, vascular perfusion and thus filtration within discrete lobules is probable.

The renal vasculature of the rainbow trout has already been examined by preparation of vascular casts for scanning electron microscopy, and the sequence of vessels from the dorsal aorta to the afferent arterioles and anastomosing glomerular capillaries was described (Anderson and Anderson, 1976).

Euryhaline teleosts are known to vary the number of perfused glomeruli to regulate overall glomerular filtration rates (Brown et al., 1980; Gray and Brown, 1985). In seawater, low filtration rates are associated with a small number of filtering glomeruli compared with a much larger population of filtering glomeruli in fish adapted to freshwater. Double afferent or double efferent arterioles would provide pathways for partial perfusion of glomeruli which could add a further level of control of glomerular activity. Since double afferent and efferent arterioles do occur in mammals (Murakami et al., 1971; Murakami, 1976), the vascular pathways associated with the trout glomerulus have been re-examined.

MATERIALS AND METHODS

Animals

Rainbow trout, *Salmo gairdneri*, weighing 200 to 400 gm (1½ to 2 years old) were obtained from local commercial fisheries, and kept in aerated, dechlorinated tapwater (dissolved O₂ 11–13 ppm; unionized ammonia, 0.010–0.015 ppm; pH 7.6–7.8) at 10–12°C, and fed on pelleted trout diet (Mainstream, BP). They were starved for at least 1 week before experimental study since anaesthesia of starved animals is more predictable than anaesthesia of fed animals.

Surgical Preparation

Seven trout were anaesthetised by immersion in a 0.003% (wt/vol) solution of MS222 (Sandoz Ltd), and the dorsal aorta was catheterised (Brown et al., 1978). Blood was flushed from the vasculature by perfusion of 20 to 25 ml 1% Lignocaine in Ringer's solution (Brown et al., 1983), draining off excess fluid at the heart. Perfusion was carried out at a rate of approximately 0.2 ml min⁻¹ using a hand-controlled syringe. No attempt was made to record the perfusion pressure.

Preparation of Vascular Casts

Vascular casts were prepared by intra-aortic injection of the low viscosity methacrylate resin, Mercor (Japan Vilene Co. Ltd., Tokyo). In most preparations Mercor was diluted with methyl methacrylate (12.5 gm Mercor: 5 gm methyl methacrylate) before addition of 150 mg catalyst. This produced a resin with a lower viscosity and a working time of 20 to 30 min as compared to 5 min of working time with Mercor. Individual animals were injected with between 2 and 4 ml of resin, at 0.2 to 0.4 ml min⁻¹.

The cadavers were left at room temperature, for 1 hr after Mercor injection, and overnight after injection of methacrylate-diluted Mercor, to allow polymerisation of the resin. The whole kidneys were dissected out and digested at room temperature, by immersion in a 20% (wt/vol) solution of potassium hydroxide, until clean casts were obtained. In six animals the kidney was divided into three equal parts—caudal, mid, and anterior kidney before digestion.

Received April 26, 1983; accepted June 26, 1985.

Casts were taken from the potassium hydroxide at random and transferred to distilled water for examination under a binocular dissecting microscope. Polymerised resin was very brittle and was therefore handled carefully. Pieces of vasculature and the associated glomeruli were transferred to a dish of absolute alcohol, which softened the resin (Murakami et al., 1971) and permitted detailed examination of the casts. Softened specimens were returned to distilled water to harden the cast and then dried and mounted on adhesive tape-coated stubs. Casts, coated with gold (SEM prep 2, Nanotech Sputter Coater), were examined in a Cambridge Stereoscan 600. Glomeruli were tilted and rotated and where necessary photographed several times to permit detailed examination of the afferent and efferent arterioles.

Vascular Dimensions

Measurements of vascular dimensions were made on scanning electron micrographs using an Apple II microcomputer and digitising tablet. The mean of triplicate measurements was taken. Glomerular size was measured only where there was filling of the entire network of glomerular capillaries, and the complete glomerulus was visible. Measurements were taken on two axes: first, from the vascular to the urinary pole of the glomerulus; and second, on the axis perpendicular to the first measurement.

For measurements of afferent and efferent arterioles, care was taken to avoid any misidentification of these vessels. Afferent arterioles arose from intrarenal arteries with longitudinal endothelial folds, whereas the efferent arterioles and glomerular capillaries were smooth (Figs. 1–10). Afferent arteriole length was measured from the point of origin at the intrarenal artery, to the glomerulus (see Fig. 1). Efferent arteriole length was taken as the length from the glomerulus to the first division of the vessel (see Figs. 2, 3).

RESULTS

Penetration of the resin into the vasculature varied according to the volume injected; 4 ml of resin resulted in areas of the kidney with complete filling of the arterial and venous vasculature. In such areas examination of the glomerular microcirculation was difficult, and pieces of cast venous vasculature had to be broken away to expose glomeruli and their arterioles.

Microvascular Patterns

The dorsal aorta gave rise to a series of segmental arteries from which arose renal arteries. Additional renal arteries arose directly from the aorta. The renal arteries gave rise to intrarenal arteries from which the afferent arterioles arose to supply the glomeruli. The surface topography of cast arteries indicated deep longitudinal endothelial folds with intercellular bridges (Figs. 1–10).

Many glomeruli were supplied with a single afferent arteriole, but in some glomeruli the afferent arteriole branched so that two separate arterioles supplied an individual glomerulus. A small proportion of glomeruli were supplied by two afferent arterioles (double afferent arterioles) which arose completely separately from the intrarenal artery.

The numbers of glomeruli, for each fish, with single, branching, and double afferent arterioles are presented in Table 1. Sixty-three percent to 96% of the glomeruli examined in individual animals were supplied by a single afferent arteriole (Figs. 1–3, 9, 10).

In the majority of glomeruli with two afferent arterioles the intrarenal artery gave rise to a single arteriole that branched to form two vessels before reaching the glomerulus (Figs. 4–6). However, 5% of the total sample of glomeruli was supplied by two afferent arterioles that arose independently from the renal artery (Figs. 7, 8).

In approximately 60% of glomeruli the efferent drainage was also cast. Glomerular capillaries usually joined to form a single efferent arteriole (Figs. 1–3, 6–8), but in all animals glomeruli with two independent efferent arterioles occurred (Table 2, Figs. 4, 5, 9). Where the efferent arterioles were cast, the proportion of glomeruli with two efferent vessels varied from 3% to 41% for the individual animals. In the seven animals double afferent and/or efferent arterioles occurred in 40%, 12%, 31%, 20%, 35%, 12%, and 44% of glomeruli, respectively.

There were no noticeable differences in the frequency of the different vascular arrangements between the caudal, mid, and anterior kidney regions.

Vascular Dimensions

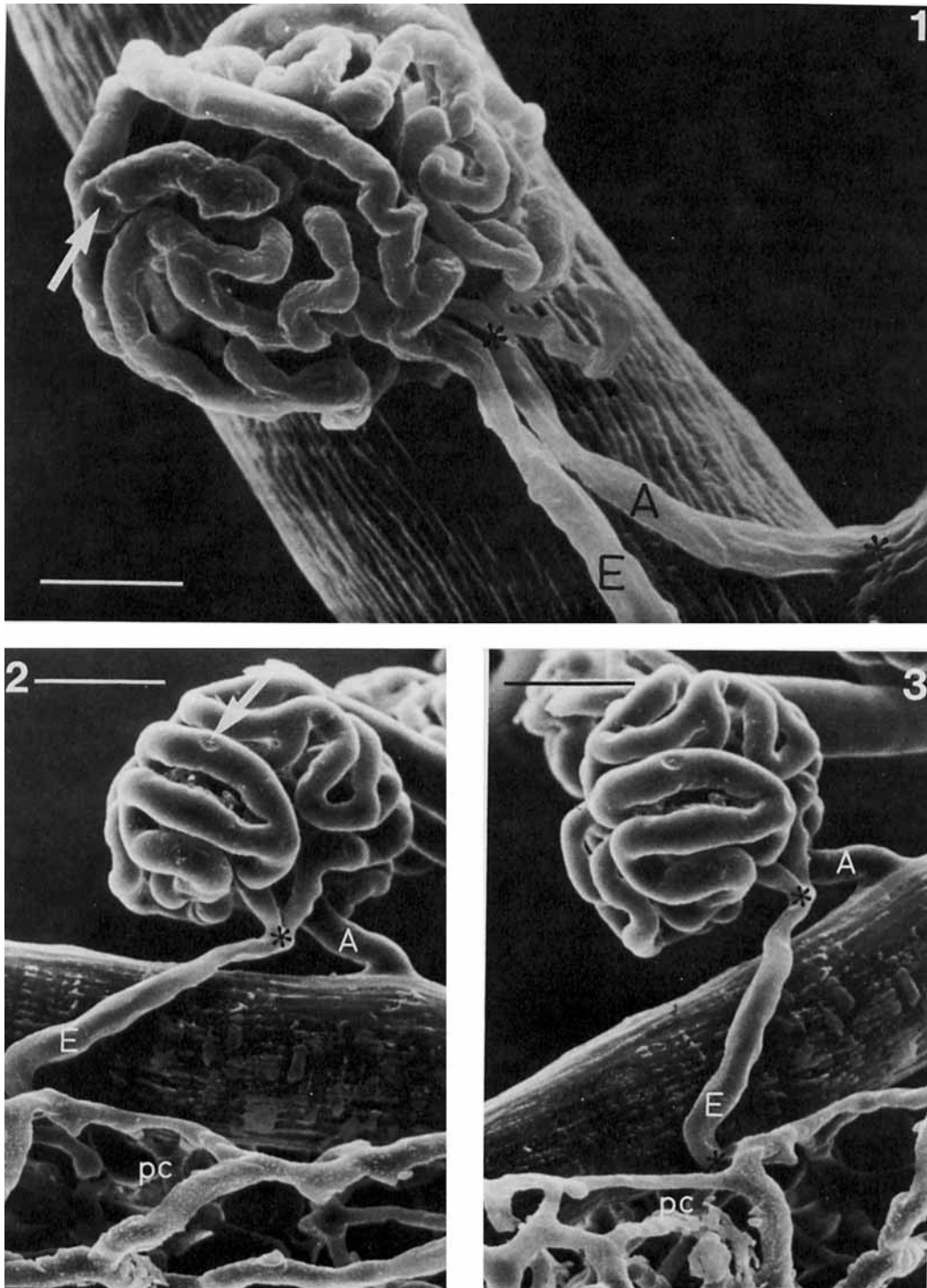
Table 3 presents data on the size of glomeruli in the seven experimental animals. There were no consistent differences of glomerular size between anterior, mid, and posterior kidney. Glomeruli were generally ovoid in shape with the axis between the vascular and urinary

TABLE 1. Distribution of afferent arteriole types in the rainbow trout kidney

Animal No.	No. of glomeruli examined	Single afferent arteriole	Branching afferent arteriole	Double afferent arterioles
1	38	24	10	4
2	91	87	2	2
3	62	44	12	6
4	59	53	3	3
5	34	25	5	4
6	49	46	3	0
7	28	22	6	0
Total	361	301	41	19

TABLE 2. Distribution of single and double efferent arterioles in the rainbow trout kidney

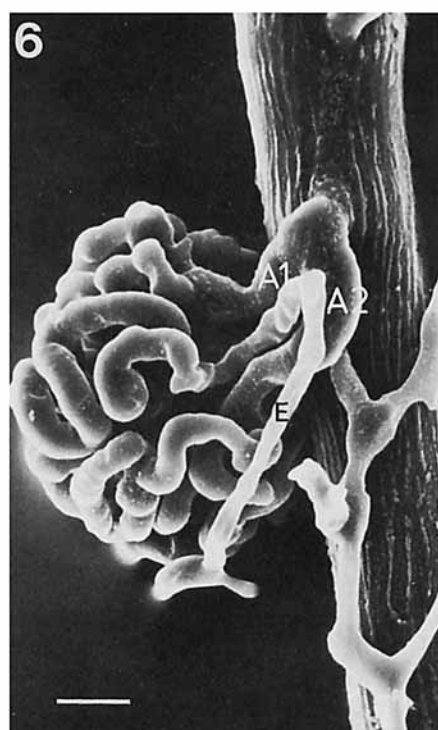
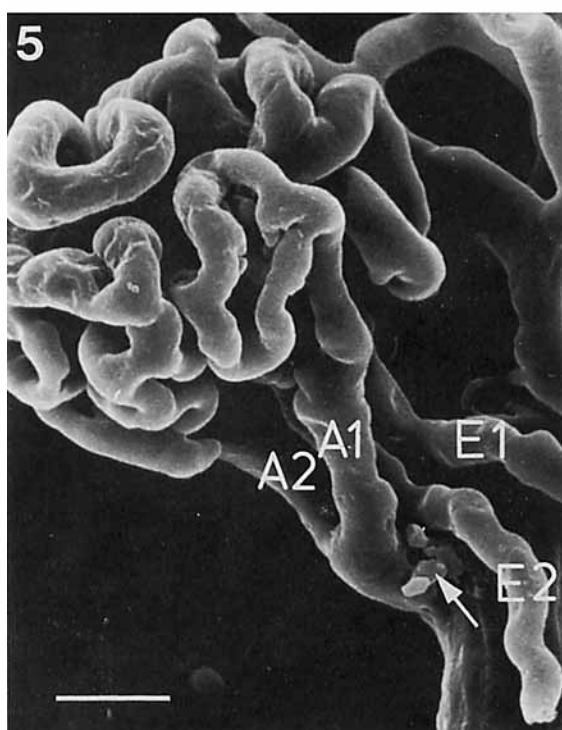
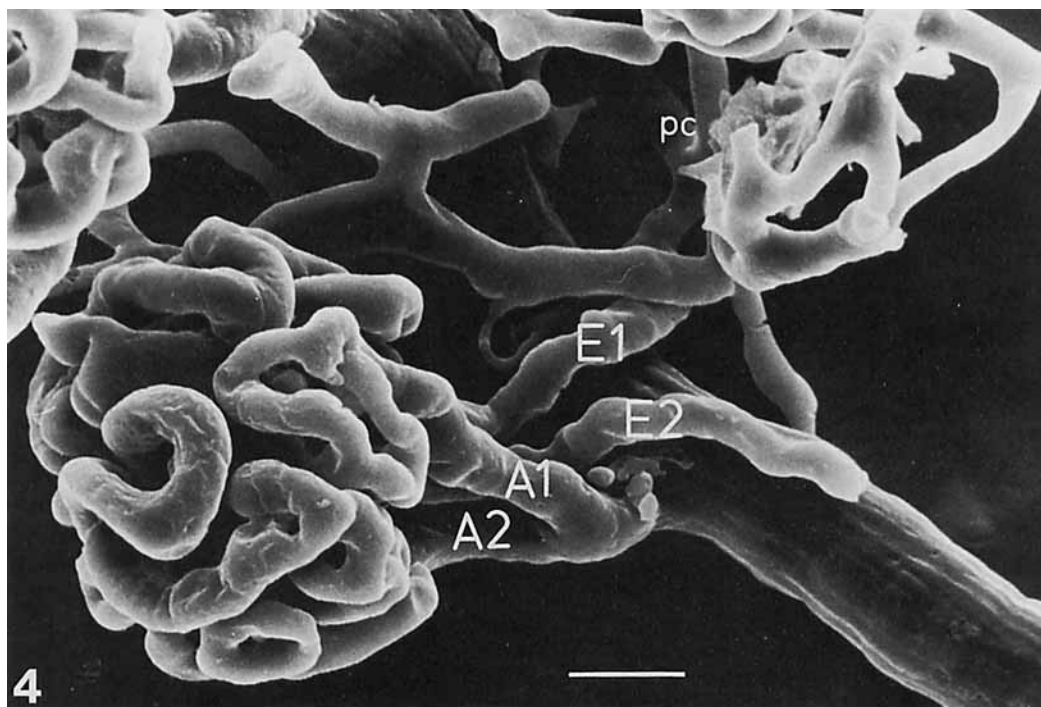
Animal No.	No. of glomeruli examined	Single efferent arteriole	Double efferent arterioles
1	38	18	4
2	91	46	8
3	62	34	1
4	59	33	6
5	34	21	4
6	49	32	3
7	28	10	7
Total	361	194	33



Figs. 1-3. Corrosion casts of glomeruli with single afferent (A) and efferent (E) arterioles. Arrows indicate endothelial cell indentations. Intrarenal arteries showing longitudinal folds give rise to afferent arterioles.

Fig. 1. Asterisks show positions of origin and end of afferent arteriole used to measure the length of the vessel. Bar = 20 μ m.

Figs. 2, 3. Photomicrographs of the same glomerulus at different angles of rotation. pc = peritubular capillaries. Efferents from separate lobules form a single vessel (a rare occurrence). Asterisks show beginning of the single efferent arteriole and the first division into peritubular capillaries, used to measure the efferent arteriole length. Bar = 40 μ m.

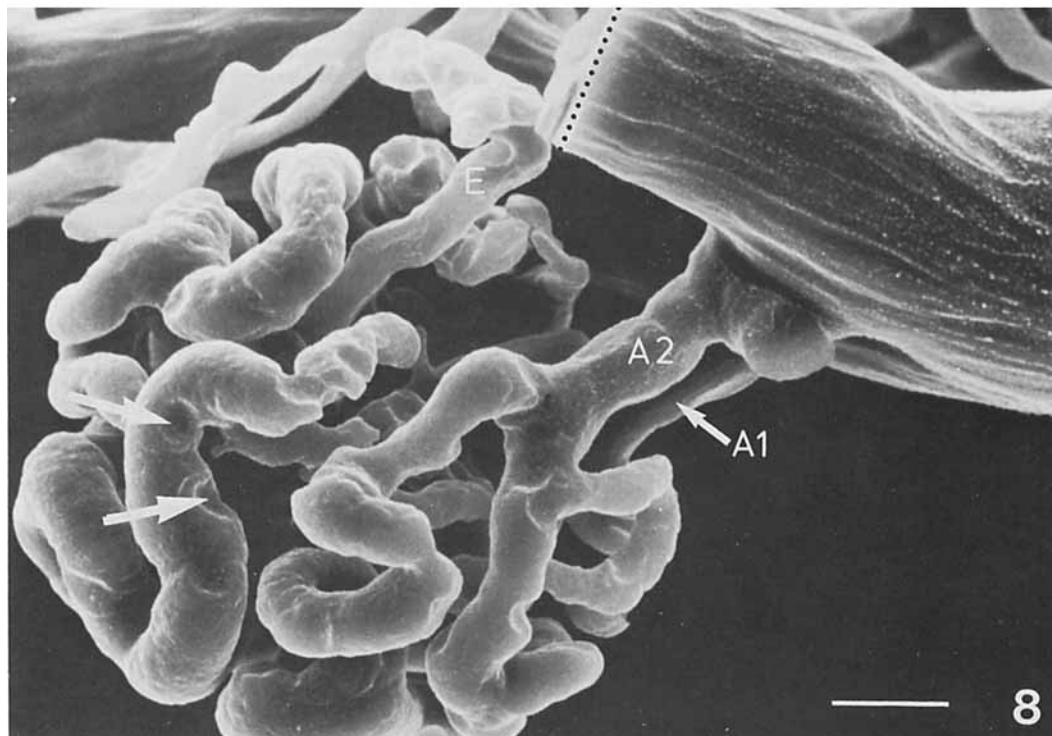
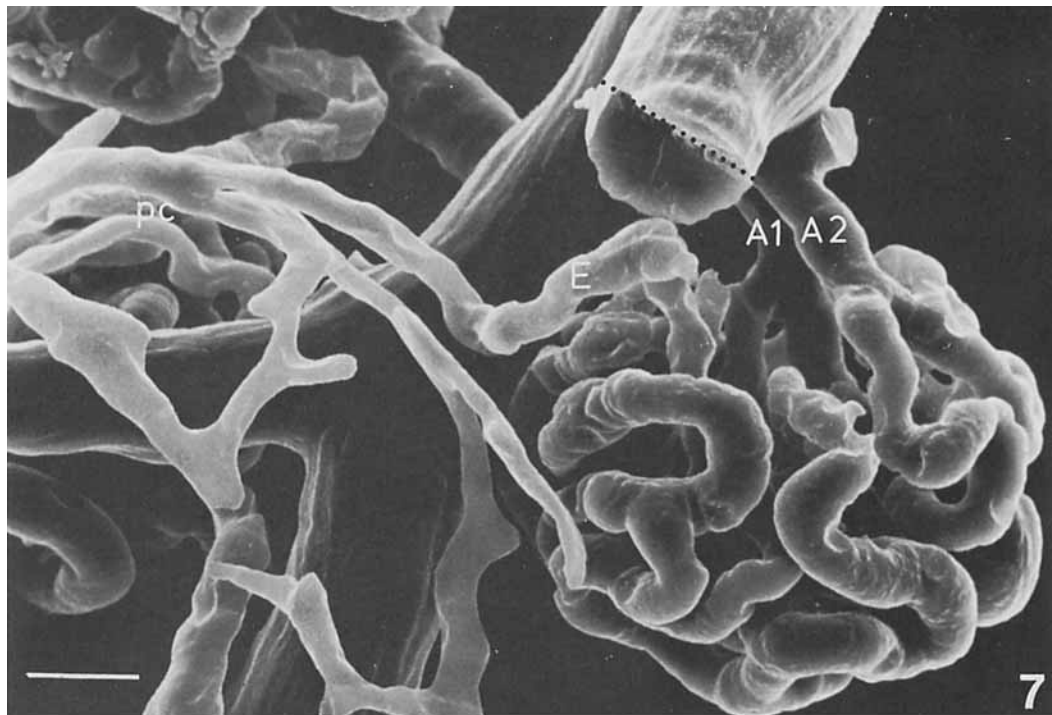


Figs. 4-6. Corrosion casts of glomeruli with afferent arterioles that branch to form two independent arterioles A1 and A2, supplying separate lobules of the glomerulus. Bar = 20 μ m.

Figs. 4, 5. Photomicrographs of the same glomerulus at different angles of tilt and rotation, two efferent arterioles (E1, E2). One efferent

arteriole enters the peritubular capillary network (pc). Arrow indicates undigested material.

Fig. 6. Single efferent arteriole (E).



Figs. 7, 8. Glomerulus photographed at different angles of tilt and rotation, with two separate afferent arterioles (A1, A2) and a single efferent arteriole (E). The intrarenal artery was cut to expose the glomerulus (dotted lines). Arrows indicate endothelial cell indentations. pc = peritubular capillaries. Bar = 20 μ m.

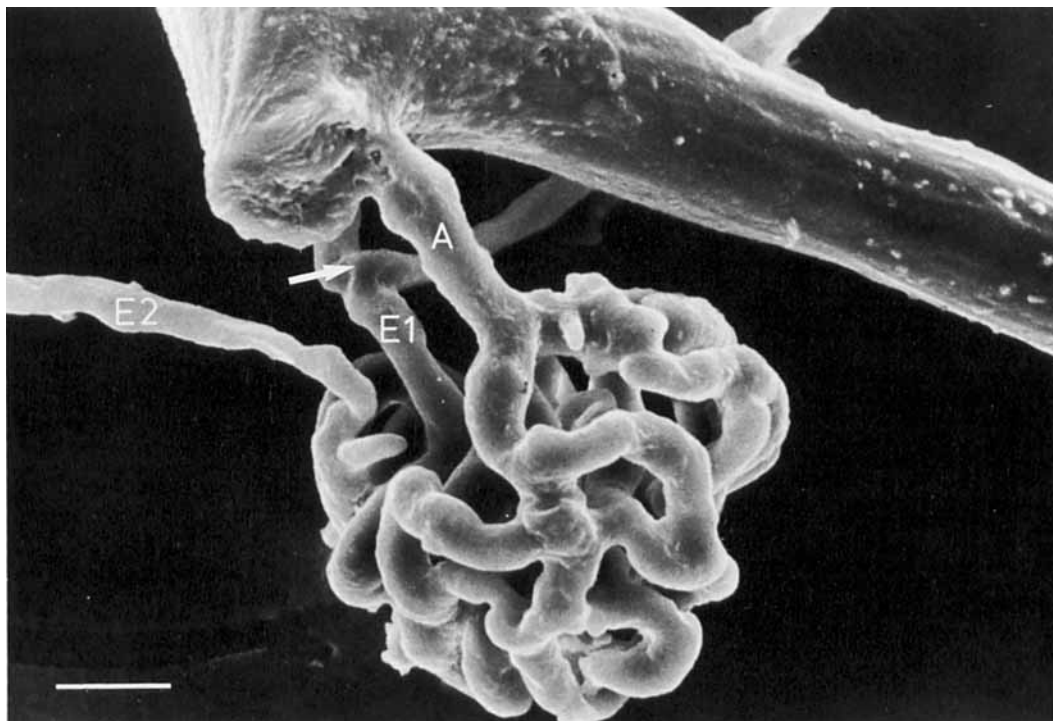


Fig. 9. Glomerulus with single afferent arteriole (A) and two independent efferent arterioles (E1, E2). The intrarenal artery was cut just beyond the origin of the afferent arteriole to expose the glomerulus. One efferent arteriole branches close to the glomerulus (arrow). Bar = 20 μm .

TABLE 3. Size of glomeruli of the rainbow trout¹

Fish	No. of glomeruli measured	Vascular to urinary pole axis (μm)	Axis perpendicular to vascular to urinary pole axis (μm)
1	26	54.7 \pm 2.8	64.1 \pm 2.7
2	65	47.3 \pm 1.7	64.7 \pm 2.1
3	51	60.1 \pm 1.9	78.5 \pm 1.8
4	46	44.0 \pm 1.7	60.1 \pm 1.8
5	30	53.4 \pm 1.9	73.0 \pm 2.2
6	38	44.9 \pm 2.4	63.9 \pm 2.3
7	24	53.0 \pm 2.3	72.8 \pm 2.2
Overall mean		51.1 \pm 2.2	68.2 \pm 2.5

¹Measurements are mean \pm SE.

poles being significantly smaller than that at right angles (Table 3; paired t-test, $p < 0.001$). Overall size varied considerably (20 to 103 μm along the vascular to urinary pole axis; 32 to 115 μm along the axis perpendicular to the vascular to urinary pole axis). Small glomeruli consisted of a few capillary loops forming a single lobule (Fig. 10). The complexity of the capillary loops increased as glomerular size increased, and large glomeruli appeared to consist of about three lobules (Figs. 1-9).

Afferent arterioles varied considerably in length (Table 4). Single afferent arterioles ranged from 9 to 224 μm . The mean length of single afferents was significantly longer than that of double afferents (Table 4; Student's t-test, $p < 0.001$). There were two separate populations of branching afferent arterioles; those of a similar length to double afferents arose as a single vessel but branched almost immediately (Fig. 6), while other longer afferents branched at some distance from their origin. Afferent arterioles that branched were significantly larger in diameter than both single afferent arterioles (Student's t-test, $p < 0.05$) and the subafferent arterioles that they formed (paired t-test, $p < 0.001$).

Efferent arterioles were significantly smaller in diameter than any type of afferent arteriole (Student's t-test, $p < 0.001$). The length from the origin of the efferent arteriole to the first division of the vessel varied from 5 to 338 μm with a mean distance of 60.8 μm .

DISCUSSION

The glomeruli of the rainbow trout varied considerably in size and complexity. Overall glomerular sizes measured from casts were higher than those previously reported (Brown et al., 1983), but the present measurements are likely to be more realistic as previous measurements were made from scanning electron micrographs of dehydrated and critical-point-dried tissue slices. Teleosts show renal growth and glomerulogenesis as body weight increases (Nash, 1931; Ford, 1958), and hence small simple glomeruli are likely to be recently

TABLE 4. Afferent and efferent arteriolar dimensions¹

	Mean \pm SE
Afferent arteriole	
Length	
Single afferent	42.5 \pm 2.1 (209)
Double afferents	29.9 \pm 1.9 (14)
Immediately branching afferent	31.1 \pm 2.9 (9)
Branching afferent, not immediately branching	69.0 \pm 6.6 (26)
Diameter	
Single afferent	10.8 \pm 0.1 (238)
Double afferents	8.9 \pm 0.4 (18)
Branching afferent	12.3 \pm 0.7 (24)
(i) Parent Vessel	
(ii) Subafferents	8.8 \pm 0.5 (24)
Efferent arteriole	
Length	60.8 \pm 4.6 (95)
Diameter	5.6 \pm 0.1 (237)

¹Values in μm are means from the seven animals. Numbers in parentheses are numbers of measurements. For lengths and diameter of double afferents and branching afferents a mean value per glomerulus was used.

formed, while the larger more complex glomeruli of three or four lobules are fully developed. A similar pattern of development has been noted in postmetamorphous and adult bullfrog kidney (Naito, 1984); and in the neonatal rat, during the first few days after birth, glomeruli increase in complexity and the number of lobules (Kazimierczak, 1980).

In this study the major concern was the microvasculature associated with the glomeruli. The occurrence of glomerular bypass shunts was noted but will be described separately. The conventional picture of a glomerulus with one afferent arteriole, anastomosing capillaries, and a single efferent arteriole was common in the trout kidney, but there was a noticeable occurrence of other vascular patterns (double and branching afferent arterioles and double efferent arterioles). There was, however, no evidence of any relationship between glomerular development and the type of afferent or efferent arteriole arrangement. Previous studies of the rainbow trout kidney (Anderson and Anderson, 1976) failed to note these unusual arrangements, and it seems likely that too few glomeruli were examined in adequate detail.

The branching of afferent arterioles before reaching the glomerulus has not previously been described in any other vertebrate kidney, and both double afferent and double efferent arterioles appear to be much more common in the trout than in most other species which have been studied (Murakami, 1971, 1976). Models of rat glomeruli have suggested that double afferent arterioles

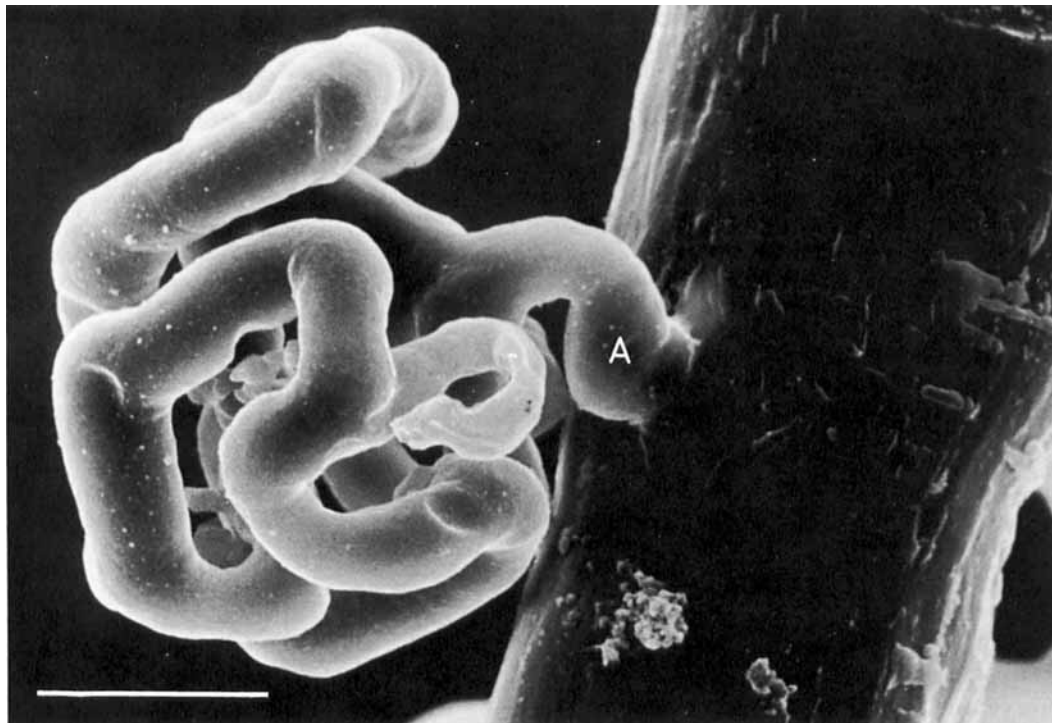


Fig. 10. Corrosion casts of a small and simple glomerulus consisting of a single lobule of a few capillary loops. A = afferent arteriole. Bar = 20 μm .

may be more common in mammals than previously suspected (Yang and Morrison, 1980), but a more recent examination of empty Bowman's capsules in kidney slices (Frank and Kriz, 1982) confirmed the low occurrence of double efferent arterioles in mammalian kidneys. In trout, double efferent arterioles arose separately from the glomerular capillary knot, rather than as a single vessel dividing close to the glomerulus. There is therefore little possibility that misinterpretation of the position of Bowman's capsule led to overestimation of the occurrence of double efferent arterioles.

The relatively high proportion of trout glomeruli with double efferent arterioles would suggest some functional role. Double efferent arterioles may be a primitive feature as the glomeruli of the agnathan hagfish each have two to four efferent arterioles (Heath-Eves and McMillan, 1974). The physiological significance of the agnathan multiple efferent arterioles is, as yet, unknown, but some influence on glomerular haemodynamics would be expected.

Corrosion of Bowman's capsule may, in the trout, have led to misinterpretation of the position of branching of the afferent arteriole. Branching within the capsule would represent the first formation of glomerular capillaries. However, branching of the afferent arteriole generally occurred at a considerable distance from the glomerulus ($31.6 \pm 2.1 \mu\text{m}$, $n = 34$), and it therefore seems likely that branching occurred outside Bowman's capsule.

Anderson and Anderson (1976) suggested that, in the trout, the afferent and efferent arterioles were of similar diameters, although in each of their micrographs the efferent arteriole would appear to be slightly narrower in bore than the afferent arteriole. In the present study, efferent arterioles were significantly narrower in bore than the afferent arterioles, a relationship which occurs in other vertebrates (Murakami et al., 1971; Morris and Campbell, 1978). Injection of resin may not, however, give an accurate representation of the size of vessels in vivo (Moffat and Fourman, 1963; Bielke et al., 1976); vascular pressures during injection, and resin shrinkage on polymerisation will influence cast dimensions. Vascular pressures during injection were not measured, but there was no apparent vascular damage that might have occurred with high injection pressures, and dilated vessels such as those shown using Cementex at high injection pressures (Bielke et al., 1976) were rare. Mercor shrinkage during polymerisation has been reported to be as high as 30–40% (Morris and Campbell, 1978), but in our tests resin polymerised in fine capillary tubing showed only 10% shrinkage in diameter, and no shrinkage in length.

In trout, as in other species, the glomerular capillaries tend to form lobules. Inter- and intralobular anastomoses between capillary loops of the glomerulus have been described (Rouiller, 1969; Shea, 1979; Kazimierzczak, 1980; Naito, 1984), and there is now evidence that the glomerular capillary network is nonplanar (Wahl et al., 1984). Microdissection and repeated SEM of glomerular casts at various stages of dissection (Murakami et al., 1971; Murakami, 1971), and glomerular reconstructions (Yang and Morrison, 1980) do, however, suggest that in the rat, glomerular lobules are more or less functionally independent. In trout, numerous interlobular connections were mentioned by Anderson and An-

derson (1976), but in the present study few interlobular capillary connections were noted, suggesting that glomeruli were made up of separate capillary lobules. The occurrence of double afferent or double efferent arterioles would seem to be more common in the trout than in other previously examined species. In glomeruli with two afferent or efferent arterioles regulation of blood flow to the separate capillary lobules is a possibility. Preglomerular sphincters have been noted at the origin of the afferent arteriole, and dense adrenergic innervation of terminal arteries and the afferent arteriole (Elger et al., 1984) indicates that neural control of afferent arteriolar tone is probable. The simultaneous occurrence of open and closed sphincters along a terminal artery suggests selective vasoconstriction is possible (Elger et al., 1984), which could include selective vasoconstriction of the two afferent arterioles supplying some glomeruli. Innervation of the efferent arteriole was not noted by these workers, but a close association between the efferent arteriole and the richly innervated muscular sheath of the collecting duct could give potential control of efferent vascular tone (Elger et al., 1984).

The rainbow trout is known to regulate urine output primarily by regulation of the number of filtering glomeruli (Brown et al., 1980). This is an important renal response to modification of environmental salinity, and probably occurs in many euryhaline teleosts (Lahlou, 1970; Henderson and Wales, 1974). Endocrine control of perfusion of the population of glomeruli also occurs (Brown et al., 1980; Brown and Oliver, 1985). The casts of the renal vasculature of the trout suggest that current concepts of the regulation of blood flow to individual glomeruli to control the filtering surface area should be extended to include regulation of blood flow to the separate lobules of glomeruli which have two afferent or two efferent arterioles. These glomerular types occurred in all experimental trout, but two animals had only a small proportion of double efferent arterioles, and two animals had a low proportion of double and branching afferent arterioles. However, at least 12% (12–41%) of glomeruli from all animals showed a vascular pathway for partial perfusion of glomeruli. A reduction of the filtering surface area is particularly associated with adaptation to increased environmental salinities so that similar investigation of the renal microvasculature of one or more stenohaline marine glomerular teleosts may be worthwhile.

ACKNOWLEDGMENTS

I am indebted to Dr. Walter Vogel, University of Tübingen, for his advice and stimulating discussion of the casting technique. I am also grateful to Mr. A. Sinclair, Ms. J. Mundy, Mr. R. Wheeler Osman, and Miss S.M. Taylor for their technical and photographic assistance.

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