

Microvasculature of the Retina, Ciliary Processes and Choroid in the North American Raccoon (*Procyon lotor*) Eye: A Scanning Electron Microscopic Study of Corrosion Casts

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ABSTRACT. We have studied the vasculature of the retina, ciliary processes and choroid in the North American raccoon (*Procyon lotor*), a nocturnal mammal, using light and scanning electron microscopic examination of corrosion casts. We carried out an identical study in the crab-eating macaque (*Macaca fascicularis*), which forages only during the daytime, in order to compare the ocular vasculature with that of nocturnal mammals. Our observations in raccoons demonstrated a photoreceptor layer associated with rich lymph and a poorly vascularized retina. The meridian region of the eye, which lies in the horizontal plane and pass around the optic disc, had a markedly sparse capillary network. This horizontal sparse vascular band may correspond to a visual streak. Ciliary process capillaries were delicate, and formed a well-developed and compact network. Choriocapillaries were quite thin and formed a coarse capillary network. This contrasted with the dense retinal and well-extended choroidal capillary networks noted in the macaques. Our findings suggest that the sparse retinal capillary network in raccoons is extremely beneficial for photon capture, thereby allowing the raccoon to see well at night, as the retinal vessels restrict the inflow of photons toward the photoreceptors. The well-developed lymph probably compensates for the sparse retinal capillaries and choriocapillaries and nourishes the retina in the nocturnal raccoon.

KEY WORDS: corrosion casts, eye, raccoon, SEM, vasculature.

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The North American raccoon (*Procyon lotor*) is a mammalian nocturnal omnivore that is found throughout most of the United States. Recently, they have also been found to be present throughout most of Japan. They were initially imported as pets but due to an increase in escaped or abandoned animals, their numbers have grown over the past decade, especially in urban and suburban areas. Raccoons cause a variety of problems, including feeding on dog or cat food, feeding on trash in garbage cans, establishing dens in attics or wall spaces, and/or causing damage to vegetable gardens. The raccoon is widely known for its habit of “washing” its food in water. The species name, *lotor*, actually means “the washer” in Latin. The animal has a very well-developed sense of touch, but its vision is not very good. The behavior in which they dunk their food in water looks like washing and is referred to as “dabbling”. However, this “washing” of food items more than likely helps to enhance their sense of touch and assist them in finding food underwater through the use of their sensitive paws and digits. This action also enables them to sort out items that are not edible. Another nocturnal animal, the vizcacha (*Lagotomus maximus maximus*) [11], has an avascular retina, and rabbits [23], guinea pigs [19] and horses [19] are known to have poorly vascularized retinas. However, information on the vascular system of the raccoon eye has not been previously reported. Our study presents the results of light and scanning electron microscopic examinations of corrosion casts of the microvasculature of the raccoon eye. Although their nocturnal habits imply a poorly developed visual system, this issue is relevant to our understanding of the retinal

structure and how it functions to enhance night vision. We also performed resin injections on the diurnal crab-eating macaque (*Macaca fascicularis*), which is a good model [2] in conjunction with the rhesus monkey (*Macaca mulatta*) [24] and marmoset (*Callithrix jacchus*) [7] for examination of possible differences between diurnal and nocturnal mammals. Therefore we compared the macaque results with those observed in the raccoon.

MATERIALS AND METHODS

In this study 16 eyes were taken from 8 male raccoons (3–6 kg in weight). The raccoons were captured in 2001 in Kamakura City (139° 29'E, 35° 21'N), in Kanagawa Prefecture, Japan, under a wildlife nuisance control program. The animals were anesthetized with sodium pentobarbital (20 mg/kg) injected peritoneally, and their pupils were dilated with instillation of 0.5% tropicamide and 0.5% phenylephrine eyedrops for fundus examination. The fundi were examined under an indirect ophthalmoscope, and photographed with a fundic camera (Kowa RC-II, Kowa Co., Ltd., Tokyo, Japan). In addition, in this study four adult male crab-eating macaques (5.2–5.7 kg in weight) were used for antibiotic toxicity tests and for necropsy and histological analyses, which did not involve the eyes or brains. Under deep anesthesia induced with barbiturates, the carotid artery was opened and bled in both types of animals. Additionally, the jugular vein was also opened. A catheter was inserted into the carotid artery and fixed with thread at the site. Physiological saline solution (room temperature) was

infused via this catheter until the saline solution emerging from the jugular vein was completely cleared of blood. Using a syringe under manual pressure of less than 120 mm Hg, a combination of methylmethacrylate monomer and Mercor (Dainippon Ink & Chemical Co., Ltd., Tokyo, Japan) (volume ratio=8:2) was then injected via the same catheter until the jugular vein was filled with the perfused resin. After polymerization, repeated baths in a 20% NaOH solution at 50°C for 2–3 days were used to macerate the eyes, and the resulting samples were then rinsed in running water. Under a dissecting microscope, each part of the eye was isolated, mounted on an aluminum stub, spattered with gold in an ion-coater (IB-3, Eiko Engineering, Co., Ltd., Ibaraki, Japan) and examined under a scanning electron microscope (SEM) (ABT-32, Topcon Co., Ltd., Tokyo, Japan). Vascular vessel diameters were measured on the SEM photographic prints taken at $\times 300$.

To provide a histological reference for our castings, 10% formalin (4°C) was injected through the carotid artery to fix the raccoons and primates. Eyes were then removed by dissection, dehydrated in ethanol and embedded in paraffin wax. Afterwards, 5 μ m sections were cut and stained with hematoxylin and eosin.

All animals were treated in accordance with the Azabu University Animal Care and Use Guidelines. The animal facility at Azabu University is accredited by the Office for Protection from Research Risks (OPRR) (#A5393-01), U.S.A. The handling and use of the raccoons was regulated under the authority of the Nature Preserving Center of Kanagawa Prefecture.

RESULTS

General topography and histology: Fundus examination revealed an oval optic disc, several retinal vessels and a horizontal avascular band passing around the optic disc, corresponding to the visual streak. A well-developed tapetum extended to most of the ocular fundus. The tapetum nigrum was observed around the optic nerve head and the nasal region of the optic disc (Fig. 1). Raccoons had typical eyes in nocturnal animals with large outstanding corneas, wide pupils and thick round lenses that occupy most of the eyeball (Fig. 2). Histological sections showed that the iris and ciliary body were associated with a distinct pigmentation pattern. The pigment epithelium contained few melanin granules. The choroidal pigmented cells formed a thick, continuous and dark layer. The photoreceptor layer in the retina was associated with distinct rich lymph and was mainly formed by rod-like outer segments (Fig. 3). This was in contrast to the macaque's retina, which had a relatively greater number of cones. The ganglion cell layer and the inner and outer nuclear layers exhibited a sparse cell population.

Microvascular anatomy: The eyeball receives most of its blood supply from the long posterior and short posterior ciliary arteries, which supply blood to the anterior segment of the eye and the choroid, respectively, and the central retinal

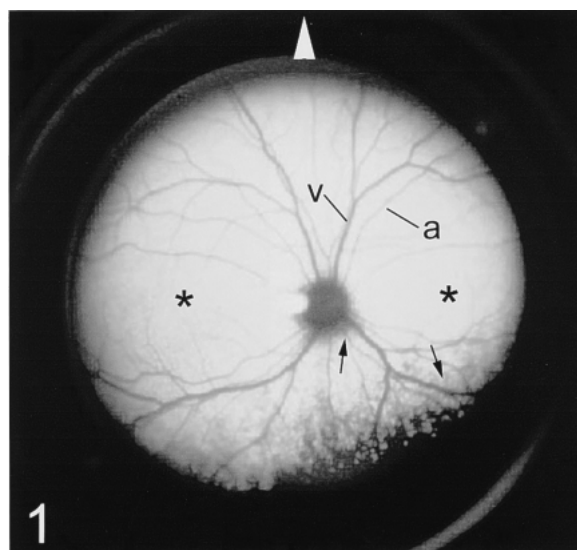


Fig. 1. Ophthalmic photograph of the right eye of an adult raccoon. The tapetum nigrum (arrows) is seen around the optic nerve head and nasal region of the optic disc. A horizontal sparse vascular band passing around the optic disc can be seen and corresponds to the visual streak (*). a: retinal artery, v: retinal vein. Arrowhead: 12 o'clock.

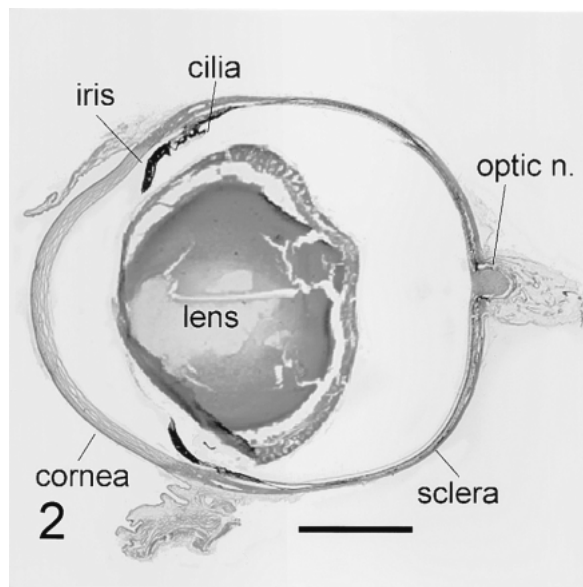


Fig. 2. Vertical section through a raccoon eye. H & E stain. Bar=4 mm.

artery, which supplies blood to the retina. Complete descriptions of the vasculature and histology of the monkey eye appear elsewhere [14, 16, 20].

Vasculature of the retina: The blood supply of the retina issues from the central retinal artery. This artery divides into ten or twelve arteries and enters the retina at the periphery of the optic disc. In the retina the major arteries follow

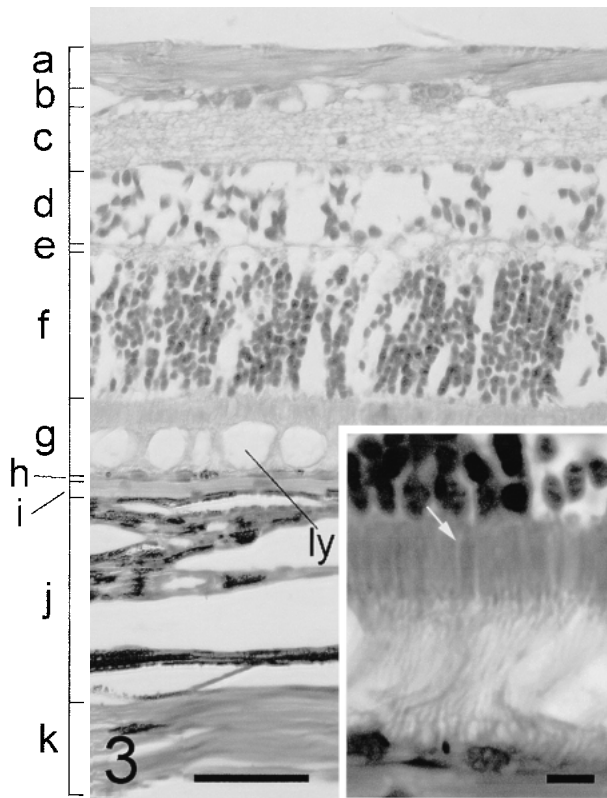


Fig. 3. Light micrographs of the raccoon retina. Note the photoreceptor layer, which consists of rod-like structure, is very thick and accommodates distinct lymph (ly). a: optic nerve layer, b: ganglion cell layer, c: inner plexiform layer, d: inner nuclear layer, e: outer plexiform layer, f: outer nuclear layer, g: photoreceptor layer, h: pigment epithelium, i: tapetum, j: vessel layer, k: suprachoroid layer. H & E stain. Bar = 50 μ m. Inset: The photoreceptor layer, but at a higher magnification. A shorter photoreceptor probably cone cell can be observed (arrow). Bar = 10 μ m.

a wavy course to the base of the ciliary body (Fig. 4). The major arteries, which have a luminal diameter up to 61–66 μ m, ramify into smaller arterioles by means of side branches, mostly at right angles to the parent artery. The arterioles (16–20 μ m in diameter) follow a relatively long course as precapillary arterioles and then ramify into capillaries (Figs. 5A, 5B). At their branching site, retinal precapillary arterioles show luminal constrictions, known as “intra-arterial cushions”, which might control blood flow at the branching sites (Fig. 5B). The retinal capillaries are quite thin and form a capillary net in the superficial region (vitreous side) of the retina. They drain into the postcapillary venules, which extend into a venous network just under the retinal capillary network. The venules then join with and drain into larger veins, which merge into the posterior ciliary vein via the retinal vein near the optic disc. The periarteriolar capillary-free zones noted in other animals were not present. Several of the retinal capillaries form a sparse network through which choriocapillaries can be easily

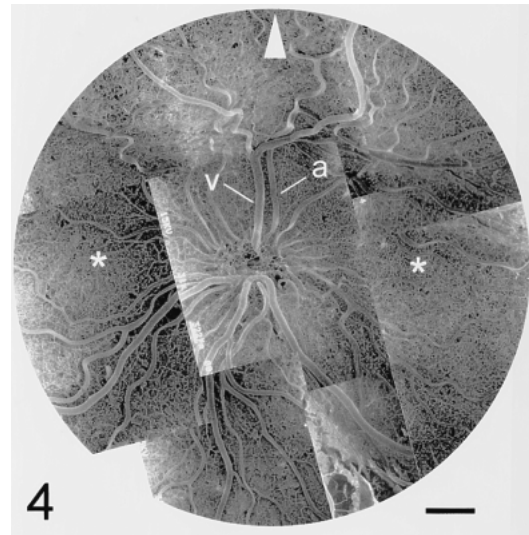


Fig. 4. Montage of scanning electron micrographs of the entire retinal vasculature of the left eye in the raccoon. Retinal arteries, veins and capillary networks are observed. Note the sparsely vascularized regions passing around the optic disc, which correspond to the visual streak (*). a: retinal artery, v: retinal vein. Arrowhead: 12 o'clock. Bar = 600 μ m.

observed (Fig. 5A). As shown by fundus examination, the retinal vessel corrosion casts also exhibited a specialized region spanning most of the eye's diameter, appearing as a horizontal band passing around the optic disc. This region of the retina consisted of only a sparse capillary net, which corresponded to the visual streak (Figs. 1, 4). In the crab-eating macaque, retinal capillaries exhibit a similar but much denser network, with a large number of capillaries in all retinal regions. Distinct periarteriolar capillary-free zones are present (Fig. 6). The horizontal band of a sparse network was not observed.

Vasculature of the ciliary body: Ciliary processes of the raccoon eye are well developed and pigmented by melanocytes, as compared to those of the crab-eating macaque. The ciliary processes are supplied by the iridociliary ring artery, which originates from the long posterior ciliary arteries. The iridociliary artery travels about halfway between the iris and the lateral border of the eyeball, where it branches into the ciliary arterioles and capillary beds. Microvessels in the ciliary processes form closely packed plates of vessels, and are radially arranged (Figs. 7A, 7B). The ciliary arterioles of both raccoons and monkeys had ringlike circular constrictions that may represent the action of precapillary “sphincters”, which control regional blood flow to functionally critical areas. Each ciliary process is supplied by a single arteriole, which originates from the ciliary arteriole at the iris root. Each arteriole enters the anterior margin of its ciliary process and then extends the entire process. The thin (9–11 μ m in diameter) capillaries form broad, flat, complex and densely packed capillary beds when they reach the cili-

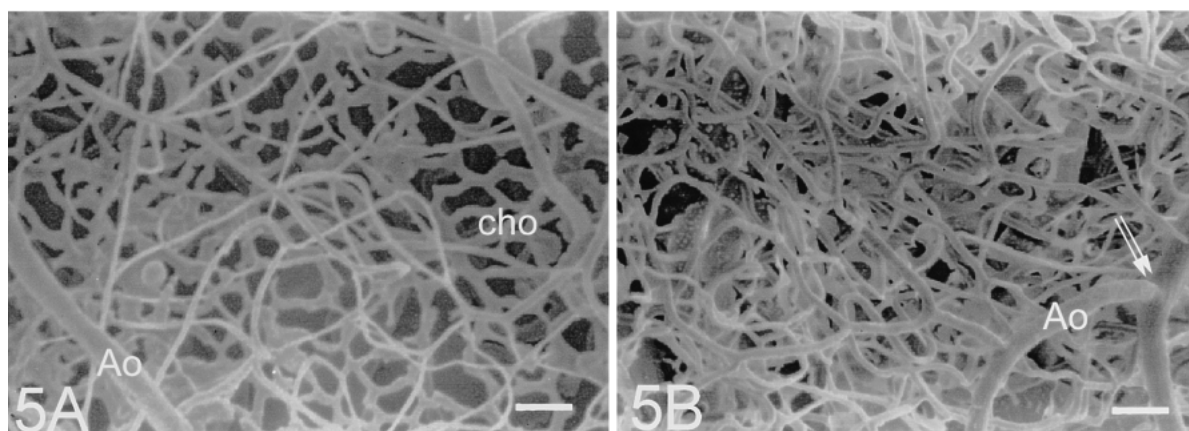


Fig. 5. Vasculature of the raccoon retina. A. In the visual streak, the retina consists only of a sparse capillary net. The choriocapillaries (cho) can be seen through the retinal vessels. Ao: arteriole. Bar=33.3 μ m. B. In the remaining regions, capillaries form a relatively dense network, as compared to those in the visual streak. An intra-arterial cushion is seen (double arrow). Ao: arteriole. Bar = 33.3 μ m.

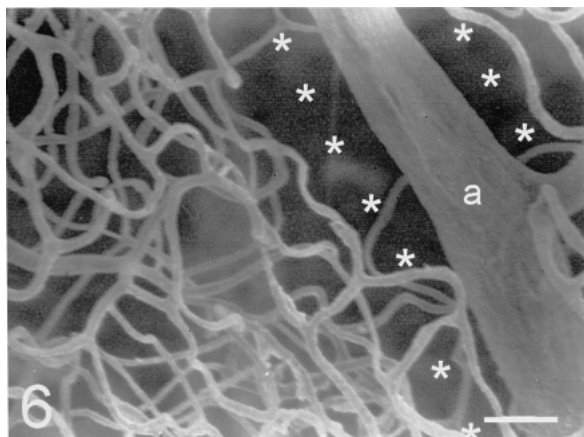


Fig. 6. Capillary bed of the crab-eating macaque retina. Note the dense retinal capillary net, as is also seen in other diurnal mammals. Asterisks denote the capillary-free zone. a: retinal artery. Bar = 33.3 μ m.

ary process margins. These capillaries drain into the collecting venules, which exhibit a less undulatory form and a smaller diameter (7–12 μ m). Compared to the ciliary process length, the relative length of the pars plana in the raccoon is extremely short and indistinct. As found in other mammals, the pars plana venules collect blood from the iris and ciliary processes, and then run posteriorly toward the vorticosae veins, where they empty together with the choroidal veins.

Crab-eating macaque ciliary processes exhibit a simpler microvasculature with small number of capillaries (Fig. 8A). Capillaries running along the anterior margin of the ciliary processes are large in diameter (23–28 μ m) and exhibit irregular indentations alternating with expansions (Fig. 8B). They connect the ciliary process arterioles directly to the collecting venules, forming a 'thoroughfare channel'. The ciliary collecting venules empty into the pars

plana venules, which are concentrically arranged. They then run posteriorly, forming a well-developed venous plexus at the anterior border of the choroidal veins. The vasculature of the pars plana was well developed and quite distinct as compared to that of the raccoon eye. The pars plana venules are long and arranged in parallel formation.

Vasculature of the choroid: The short posterior ciliary arteries form branches called the choroidal arteries, which run toward the anterior eye segment and supply the entire choroid. All choroidal arteries run in parallel arrays toward the choriocapillaries, so as to interdigitate with the choroidal veins draining this region (Fig. 9A). The arteries ramify two or three times into precapillary arterioles. The choroidal precapillary arterioles are large in diameter (21–27 μ m) and are characterized by a very short course to the choriocapillaries (Figs. 9A, 9B), which is contrary to the course taken by the arterioles in the retina. After branching off from the choroidal arteries, the precapillary arterioles pierce the tapetum at mostly right angles to the suprachoroida, and extend as far as the choriocapillaries. Intra-arterial cushions were frequently observed in the precapillary arterioles in the choroid, as well as in the retina. The choriocapillaries are small in diameter (10–14 μ m) and display a coarse choroidal network, suggesting poor blood flow for nourishing the retina (Fig. 10A). As the choroidal capillary bed continues anteriorly along the inner wall of the eyeball, it becomes increasingly less dense, and finally joins with vessels of the ciliary body at the ora serrata. As noted in the retinal arterioles, the venules gathering the choriocapillaries also show a very short course. Venous blood from the entire choroid drains into the vorticosae veins, and venules from the iris, ciliary body, and bulbar conjunctiva also converge into the vorticosae veins. In the crab-eating macaque, choriocapillaries are broad, somewhat flattened, sinusoid-like and large in diameter (17–39 μ m), and form a well-developed and freely inter-connecting capillary network, which drains enough rich blood to supply nutrition and oxygen to the retina (Fig.

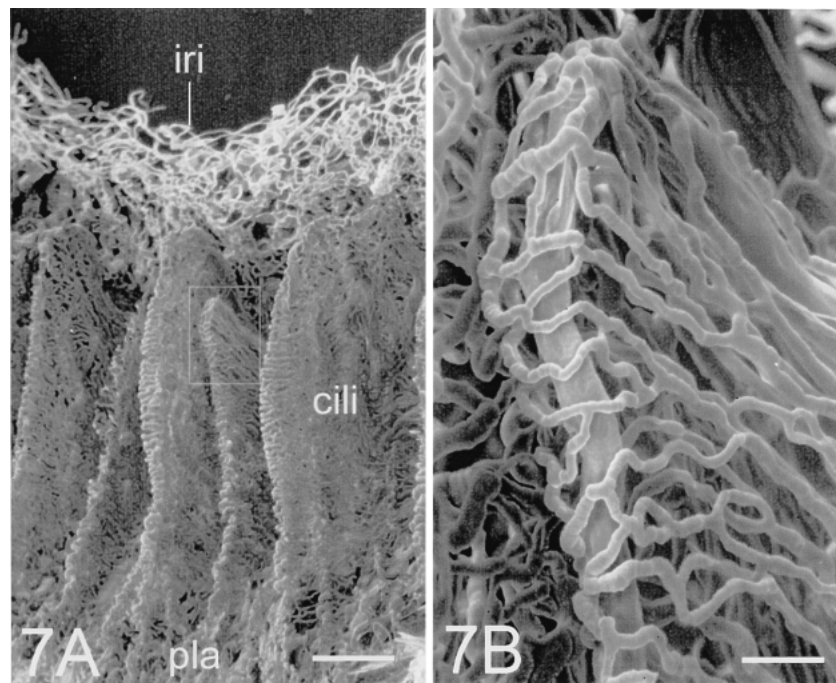


Fig. 7. Vasculature of the raccoon ciliary processes viewed from inside the eye. A. The ciliary processes are well developed and consist of fine capillaries. The thick marginal capillaries of the 'thoroughfare channel' are not seen. Bar=250 μ m. cili: ciliary process, iri: iris, pla: pars plana. B. Enlargement of area outlined showing thin capillaries that supply the ciliary process. Bar=33.3 μ m.

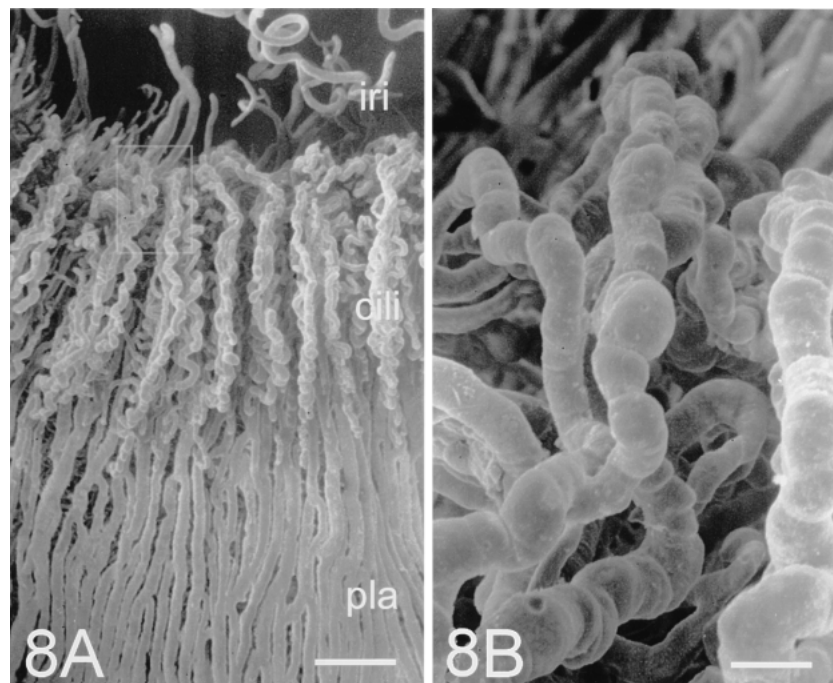


Fig. 8. Vasculature of the crab-eating macaque ciliary processes as viewed from the inside of the eye. A. The ciliary processes consist of thick marginal capillaries forming a 'thoroughfare channel' to the pars plana vessels. The pars plana venules are quite distinct. cili: ciliary process, iri: iris, pla: pars plana. Bar=250 μ m. B. Enlargement of area outlined showing thick marginal capillaries. Bar=33.3 μ m.

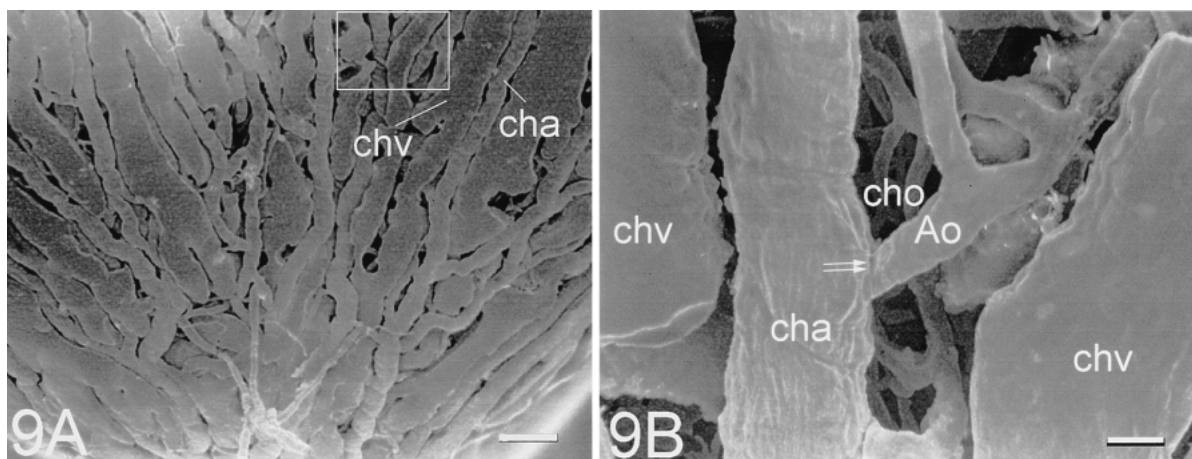


Fig. 9. Vasculature of the raccoon choroid (scleral view). A. Posterior part of the left eye, showing choroidal arteries (cha) and veins (chv), running parallel. Bar=300 μ m. B. Enlargement of outlined area, which shows a thick and short arteriole (Ao). An intra-arterial cushion is seen (double arrow). cha: choroidal artery, chv: choroidal vein, cho: choriocapillaries. Bar=33.3 μ m.

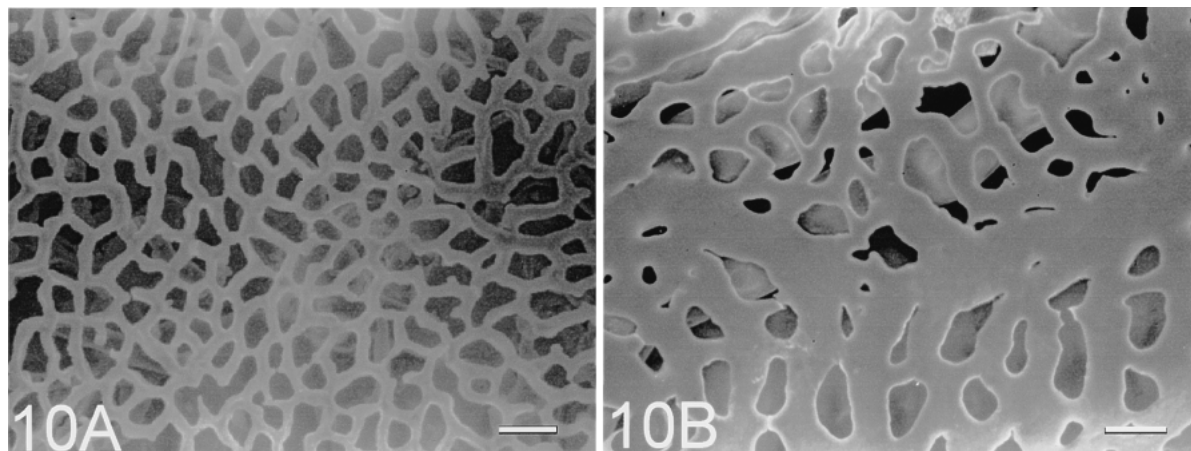


Fig. 10. Capillary bed of the choroid as viewed from the inside of the eye. Retinal vessels have been removed. A. Choriocapillaries of the raccoon. Note the poorly developed choroid with thin choriocapillaries. Bar=33.3 μ m. B. Choriocapillaries of the crab-eating macaque. Note the thick and sinusoid-like choriocapillaries. Bar=33.3 μ m.

10B).

DISCUSSION

Nocturnal animals, which need to see well at night, generally have eyes with wide pupils, large lens, rod-rich retinas and tapetum [11]. The vizcacha has an avascular retina [11] while the rabbit [23] and guinea pig [19] have a partially vascularized retina. This optical strategy plays a significant role in improving photon capture for greater night vision capabilities. Our observations of the eye of the raccoon were consistent with the general model for nocturnal mammals, and also demonstrated the presence of a sparse retinal capillary network, lymph-rich retina and a distinct ciliary process microvasculature. In addition, other structure-function relationships of the ocular microvasculature were well demonstrated by the corrosion casting technique.

The retinal arteries give rise to arterioles by means of side branches, mostly at right angles. The retinal capillaries are extremely thin in diameter (4–6 μ m), which results in red blood cells just barely being able to pass through the lumen. The ridges at the origins of the precapillary arterioles in the retinal and choroidal arteries represent intra-arterial cushions, which are sphincter-like thickenings of the intima, and play a significant role in regulating blood flow at the branching sites. Our observation of these cushions in the raccoon retinal vessels is consistent with previous corrosion cast studies of ophthalmic arteries in rats [1, 15], monkeys [14] and humans [10]. Plasma skimming is reported to occur in the retinal vessels [4, 12]. This phenomenon is characterized by blockages of the capillary entrances by red blood cells so that only plasma can pass through the capillary bed. The branching pattern consisting of right angles [18], intra-arterial cushions [3] and capillaries with extremely thin

diameters may be responsible for causing plasma skimming in the retinal capillary network. The retinal vascular network is an unrecognized contributor to the optical filtering properties of the eye. A photon has a 40–50% chance of encountering one or more capillaries before it reaches a photoreceptor [20]. Raccoons have a specialized sparse retinal capillary network in which the capillaries have thin diameters. This architecture results in red blood cells just barely being able to pass through the vessel, leading to plasma skimming, which as a net result, allows for the catching of more photons per unit area under darkness, and facilitates production of clear, sharp images.

Additionally, the raccoon's more numerous rods allow them to catch more photons per unit area under darkness, while the low cone number indicates that the animal has poor color vision.

In the macaque, the ciliary microvasculature consists of capillaries with irregular and thick indentations that form thoroughfare channels as described by Funk [5] and Morrison *et al.* [13]. The thick marginal capillaries may be responsible for the very high blood flow values that are seen as compared to the choroid, kidney cortex and cardiac muscle, and the blood flow velocities of the ciliary process [6]. This bypass of the capillaries may allow for a large amount of arteriovenous shunt volume, in which the blood in the pars plana venules is not truly venous blood, but rather highly oxygenated blood. It is still unclear if this vascular feature is able to provide enough oxygen for nutrition of the peripheral retina. On the other hand, the arrangement of the ciliary body microvasculature in the raccoon was complex and well developed. It consisted of fine capillaries and the pars plana was extremely short as compared to the ciliary process length. This may contribute to several mechanisms for modulation of the ciliary process blood flow that involve producing aqueous humor in large quantities.

The blood supply to the choroid is via short arterioles of comparatively large diameters (21–27 μm) and compactly arranged thick capillaries, whereas the blood supply to the retina is via long arterioles with narrow diameters (16–20 μm) and extremely thin capillaries, which form a relatively sparse network. The anatomical differences between the two vessels may indicate a difference in the velocity of blood flowing to the choroid and retina, and may be the reason for the relatively high values seen for the choroidal blood flows [3]. Indeed, upon angiographic inspection, the filling pattern for fluorescein angiography in the eye was successively observed first at the choroidal phase, which is characterized by the filling of the choriocapillaries, and then in the retinal arterial phase, characterized by the hyperfluorescence of the retinal arteries. Again, the rich blood supply to the choriocapillaries, with its high oxygen pressure and high vascular permeability, would be anticipated based on its role in the diffusion of oxygen and nutrients through the choriocapillaries for nourishment of the photoreceptors, retinal pigment epithelium, and the other cells of the outer retina [3]. Animals whose retinal vasculature is less vascularized might be expected to be more dependent on the

choriocapillaries for nourishment and oxygen. However in raccoons, the choroidal capillary networks together with the retinal microvasculature are less well vascularized, and therefore the raccoon's retina might be expected to be more dependent on other circulating systems for nourishment and oxygen. Gruntzig *et al.* [8] first recognized a lymphatic flow that was present in the perivascular space around the retinal vessels, the vitreous body, the interstice between the glia cells of the papilla, and in the pial tissue and subarachnoid sheath of the optic nerve. Thus the well-developed lymphatic pathway in the photoreceptor layer in raccoons may compensate for this anatomical specialization of the retina in conjunction with the choroidal microvasculature. Additionally, in diurnal mammals, the choroidal circulation plays a significant role in dissipating heat generated by the focusing of light at the macula, suggesting that this function may be the primary reason for the relatively high values for the choroidal blood flow. The numerous, flattened, parallel veins in the choroid layer of the anterior and lateral surfaces of the eyeball could provide a large surface area for such cooling and would be consistent with this function.

The broad, horizontal band that lies on each side on the meridian consists of a sparsely vascularized network that may correspond to a visual streak. This horizontal band is found in many mammals and birds and functions as a hypersensitive retinal region [11]. This visual streak, which represents the field of best vision, probably serves the same purpose as the fovea in the human eye. Visual streaks along a straight horizontal line in a dorsal position to the optic disc, have been observed in vizcachas [11], cows [10], pigs [9], sheep [9], oxen [9], horses [9] and dogs [9], and are probably adaptations in these animals for use in searching for food or predators at ground level. Visual streaks inferior to the optic disc in the lower retina have been reported in rabbits [23], elephants [21], bats [17] and several birds including penguins [22], and are viewed as an adaptational feature that allows these animals to search for airborne predators, or the provision of a clear view of the underwater horizon. Thus, the positioning of the visual streak that extends in a horizontal line and passes around the optic disc in raccoons could be related to their habit of finding much of their food through the use of their sensitive front paws, and subsequent grasping of food for the purpose of closely inspecting it. Additionally, raccoons may be able to use this hypersensitive retinal region to extend their period of visual activity well into crepuscular or nocturnal periods.

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