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Fine structure of the pecten oculi of the barred owl (*Strix varia*)

B.J. Smith[1], S.A. Smith[1] and C.R. Braekevelt[2]

[1]Department of Biomedical Sciences and Pathobiology, Virginia-Maryland Regional College of Veterinary Medicine, Blacksburg, Virgnia, United States and [2]Department of Anatomy, The University of Manitoba, Winnipeg, Manitoba, Canada

Summary. The pecten oculi of the barred owl (*Strix varia*) has been examined by light and transmission electron microscopy. The pecten in this species is of the pleated type and is small in comparison to the size of the ocular globe. The pecten consists of 8-10 accordion-like folds that are linked apically by a pigmented tissue bridge. Each fold contains numerous capillaries, larger supply and drainage vessels, and abundant pleomorphic melanocytes. Most of these capillaries are extremely specialized vessels that possess plentiful microfolds on both the luminal and abluminal surfaces. Some capillaries however display only a few microfolds. The endothelial cell bodies are extremely attenuated, with most organelles located near the nucleus. All capillaries are surrounded by a very thick fibrillar basal lamina, which is thought to provide structural support to these small vessels. Pericytes are commonly found within these thickened basal laminae. Numerous melanocytes are also present, with processes that form an incomplete sheath around the capillaries. These processes are also presumed to provide structural support for the capillaries. As in other avian species, the morphology of the barred owl pecten is indicative of extensive involvement in substance transport. When compared to the pecten of more visually-oriented species, this pecten is smaller, has fewer folds, and displays a reduced number of microfolds within the capillaries. In these and other features, the barred owl pecten is similar to the pecten of the great horned owl (*Bubo virginianus*).

Key words: Pecten, Barred owl, Ultrastructure, Eye, *Strix varia*

Introduction

In the vertebrate eye, two separate vascular systems supply specific regions of the retina. The choriocapillaris, consisting of large-diameter fenestrated capillaries, supplies the outer retina (photoreceptors and retinal pigment epithelium). A second vascular supply, termed a supplemental nutritive device (SND) (Walls, 1942) or supplementary retinal circulation (Rodieck, 1973) supplies the inner retina. This supplemental supply takes various forms in different vertebrate groups, appearing in birds as the pecten oculi. The pecten is a highly pigmented and vascular organ devoid of muscle or nervous tissue which projects as a fan-like structure from the optic disc into the vitreous chamber (Walls, 1942; Michaelson, 1954; Prince, 1956).

The function of the pecten has been debated for many years, with numerous activities having been ascribed to this structure. However, the only function well supported by scientific studies is its role as a nutritive source for the inner region of the avascular avian retina (Walls, 1942; O'Rahilly and Meyer, 1961; Wingstrand and Munk, 1965; Bawa and YashRoy, 1972). Light and electron microscopic studies have demonstrated the pecten's capillaries to be extremely specialized for substantial involvement in transport, supporting its role as a nutritive organ (O'Rahilly and Meyer, 1961; Raviola and Raviola, 1967; Fielding, 1972; Dieterich et al., 1973; Braekevelt, 1984, 1986, 1988, 1990, 1991a,b, 1993).

As part of an ongoing comparative morphological study of the pecten oculi, this report describes the fine structure of the pecten of the barred owl (*Strix varia*) and compares and contrasts these findings with observations in the great horned owl (*Bubo virginianus*) and other avian species.

Materials and methods

Eyes were obtained from three adult, light-adapted barred owls with normal vision that were destined for euthanasia for injuries unrelated to the eye or head. With the bird under deep anesthesia, the eyes were rapidly enucleated, incised at the equator, and fixed for 5 h in 5% gltuaraldehyde buffered to pH 7.3 with 0.1M Sorenson's phosphate buffer. The region of the eye posterior to the scleral ring was then removed and washed in 5% sucrose in 0.1M Sorenson's buffer (pH

Offprint requests to: Dr. B.J. Smith, Department of Biomedical Sciences and Pathobiology, Virginia-Maryland Regional College of Veterinary Medicine, Blacksburg, VA, USA 24061-0442

7.3), and the pecten and underlying retinal tissue carefully dissected free. The pecten of one eye from each bird was left intact for purposes of gross measurements. The other pectens were cut into pieces approximately 1 mm^2, and post-fixed for 2 h in 1% osmium tetroxide in the same phosphate buffer (pH 7.3). The tissues were then dehydrated though a series of graded ethanols to methanol and then to propylene oxide, and embedded in Araldite.

Pieces of plastic-embedded tissue were subsequently reoriented using a wax mount. Thick (0.5 µm) and thin (50-60 nm) sections were cut on an LKB ultramicrotome. Thick sections were stained with toluidine blue and examined by light microscopy. Thin sections were stained in aqueous uranyl acetate and lead citrate and examined and photographed in a Philips EM 201 transmission electron microscope.

Results

As in all avian species described to date, the pecten oculi of the barred owl is located over the ovoid optic disc, and projects freely into the vitreous body. The body of the pecten is comprised of a series of 8 to 10 pleats or accordion-like folds joined together apically by a pigmented bridge of tissue (pons pectinis). In the barred owl, the pecten is 5 mm long at the base, and tapers to a sloping crest about 4 mm long. The pecten projects into the vitreous body, with the bridge sloping from about 4 mm at its highest end to about 3 mm at the lowest part.

A fine basal lamina (vitreo-pectineal limiting membrane) continuous with the inner limiting membrane of the retina envelops the entire pecten (Figs. 1, 3, 7). Each pleat or fold measures 25-30 µm in width and is composed of abundant highly specialized capillaries, two or more larger blood vessels, and numerous melanocytes (Fig. 1). The pecteneal capillaries are extremely specialized vessels that most typically measure 10-12 µm in luminal diameter, while larger capillaries measuring 15-20 µm are also noted (Figs. 1, 4). A minimum of two, though more typically three or four, endothelial cells comprise the capillary wall (Fig. 1). The endothelial cells are joined by elaborate and often extensive occluding (tight) junctions (Figs. 4, 6, 7).

Most of the endothelial cell body of both large and small capillaries consists of an attenuated region from which abundant processes arise on the luminal (apical or internal) as well as abluminal (basal or external) surfaces (Figs. 1, 3, 4, 7). These processes are best classified as microfolds rather than microvilli, since branching of the folds occurs, and a range of widths is visible in various single planes of section (Figs. 6, 7). The folds on the luminal surface are generally longer and straighter, measuring about 1.0 µm in length (Figs. 6, 7). Abluminal folds, in contrast, are relatively short (0.7 µm) and tortuous, compressed between the external surface of the endothelial cell and the basal lamina (Figs. 6, 7). While the majority of capillaries possesses abundant microfolds, some capillaries possess only sparse projections on either surface (Figs. 1, 2, 4, 5).

The nuclear region of the capillary is the widest part of the endothelial cell with a large, vesicular nucleus that is normally seen as a flattened oval (Figs. 1, 2, 4, 7). Most cell organelles occupy the nuclear region, although small mitochondria, polysomes, microbodies, short profiles of rough endoplasmic reticulum (RER), and bundles of microfilaments also occur throughout the cell body (Figs. 4, 5).

The capillary basal lamina is also highly specialized. The outermost layer of the basal lamina is typical in form, but is distanced from the endothelial cell body by several concentric layers of fine fibrillar material that are separated from each other by an amorphous substance (Figs. 3, 4, 6, 7). The basal lamina is thus exceptionally thick, averaging about 1.0 µm in width.

Pericytes are commonly associated with the capillaries, lying enclosed within this thickened basal lamina (Figs. 1, 3, 4, 6). These undifferentiated cells possess a minimum of organelles and no microfolds. In the barred owl nearly all the pericytes are separated from the abluminal folds of the endothelial cells by a varying width of intervening basal lamina fibrillar material (Figs. 3, 4, 6).

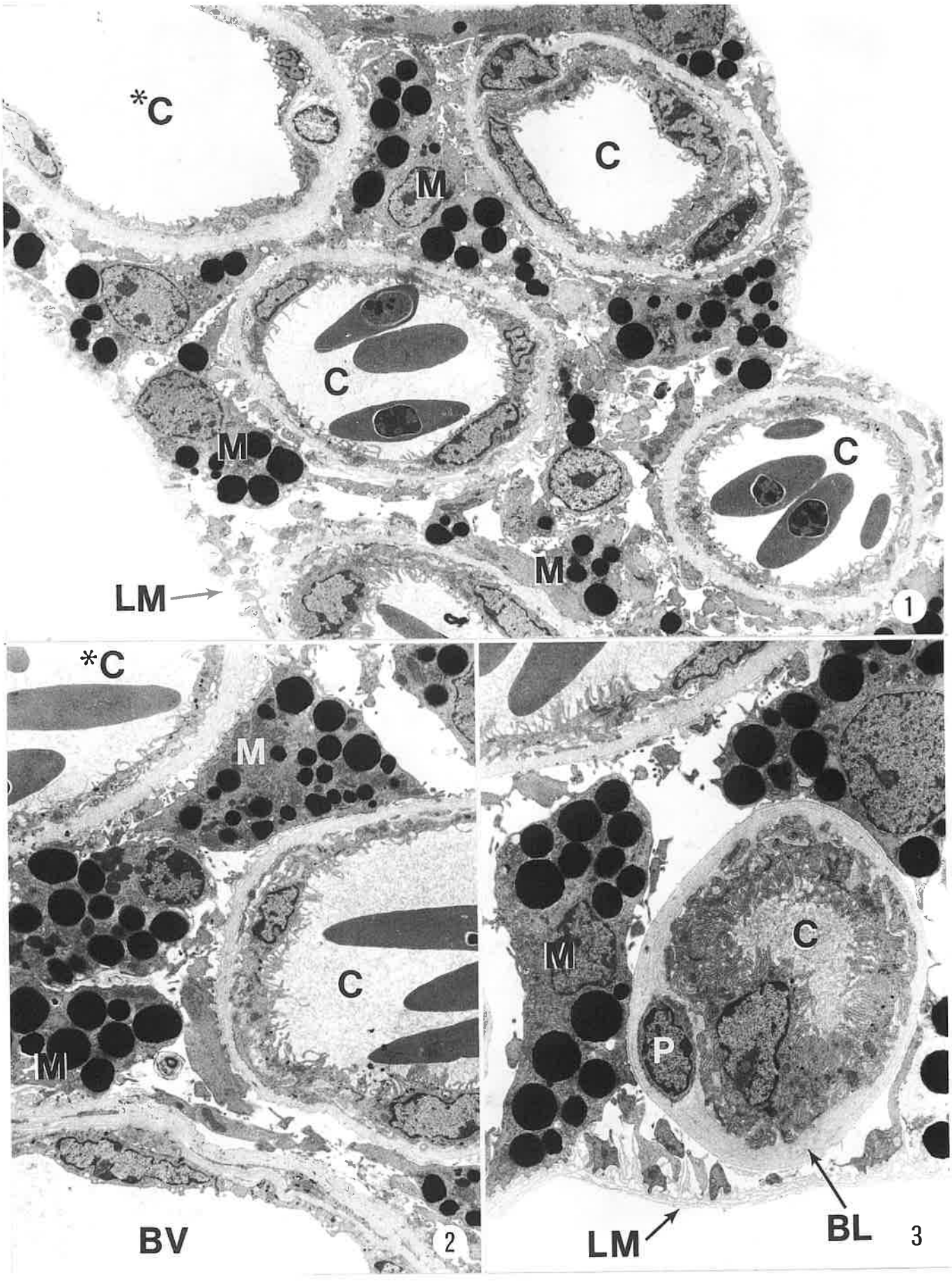
All pecteneal blood vessels larger than capillaries are difficult to distinguish as either arterioles or venules due to similarities in their mural structure (Fig. 2). Microfolds are absent from either surface of the non-fenestrated endothelium of these larger vessels (Fig. 2). In non-nuclear regions, the endothelial cells measure 0.5 µm or greater in thickness, although the cells are wider near the nucleus. The cytoplasm contains mitochondria, polysomes, microbodies, and short profiles of RER and tight junctions join the individual endothelial cells. A thickened basal lamina similar to that of the capillaries surrounds these vessels, and contains flattened cells similar in form to smooth muscle cells (Fig. 2).

Melanocytes are present among the capillaries and larger vessels throughout the structure of the pecten, but

Fig. 1. Electron micrograph of a single fold of the pecten of the barred owl. Capillaries (C) of varying sizes are indicated. *C indicates a capillary with relatively few microfolds. The pecteneal limiting membrane (LM) and melanocytes (M) are also indicated. x 4,000

Fig. 2. Electron micrograph to illustrate the variability in the number of capillary microfolds. One capillary (C) shows well-developed microfolds over most of its luminal surface, while the second (*C) exemplifies the capillary type with fewer folds. Melanocytes (M) are indicated as is a larger supply or drainage vessel (BV). x 5,000

Fig. 3. Electron micrograph to indicate a typical pecteneal capillary (C) with luminal and abluminal processes. A pericyte (P) is indicated as is a melanocyte (M) and the thickened basal lamina (BL). The pecteneal limiting membrane (LM) is also labelled. x 6,000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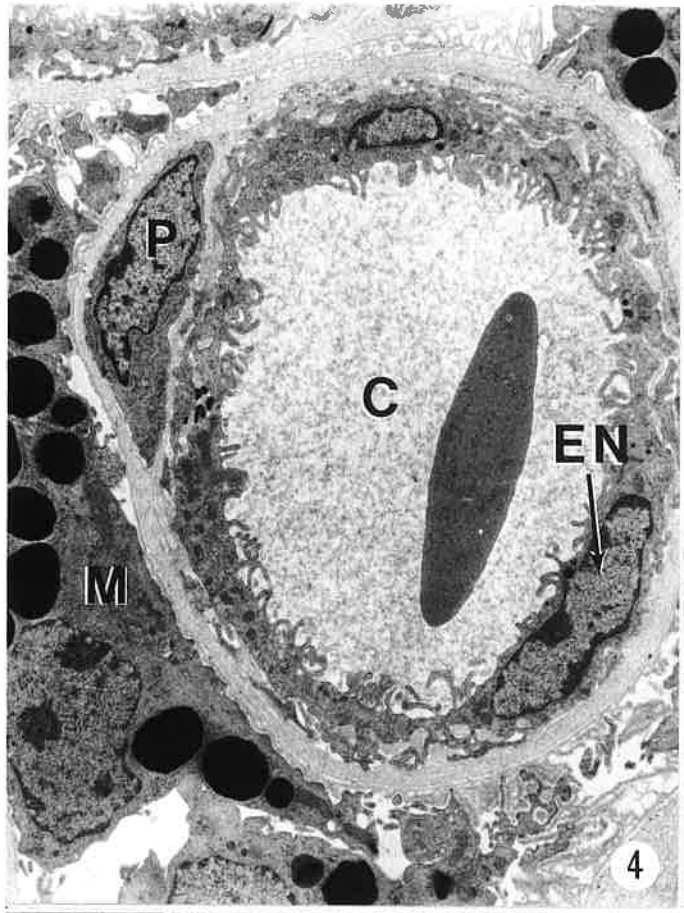
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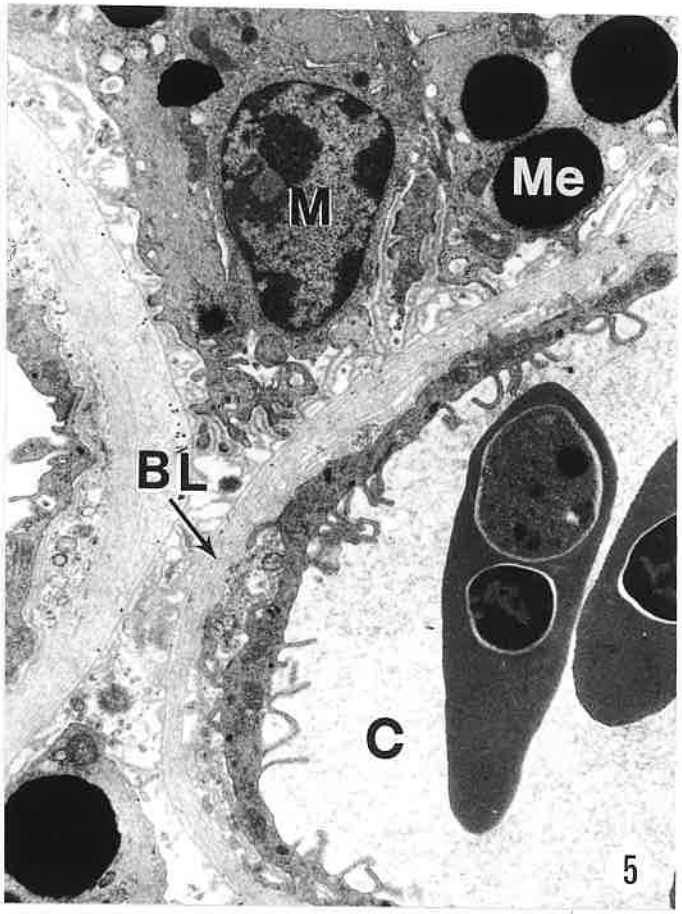
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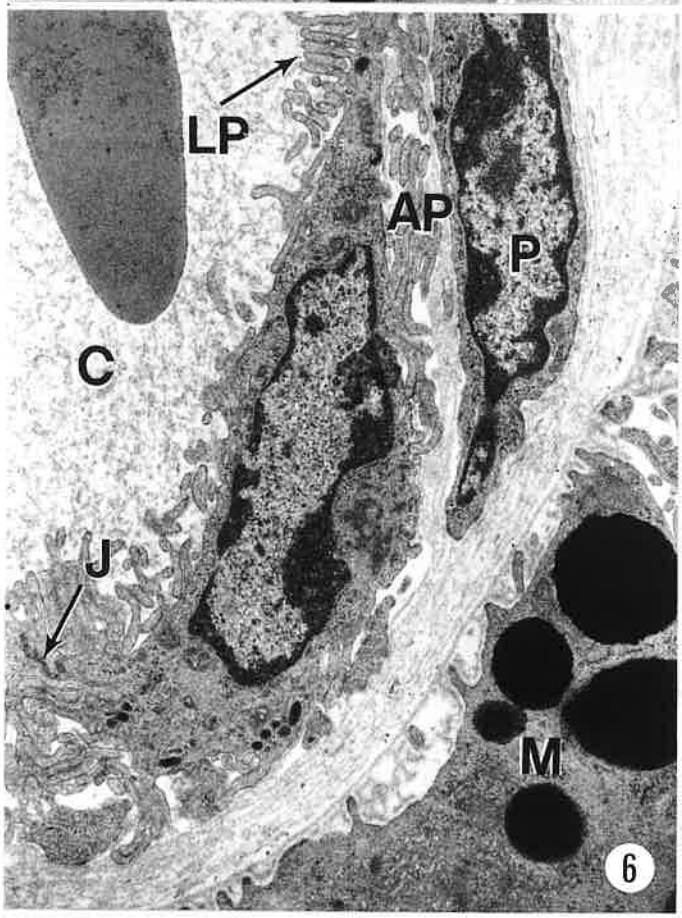
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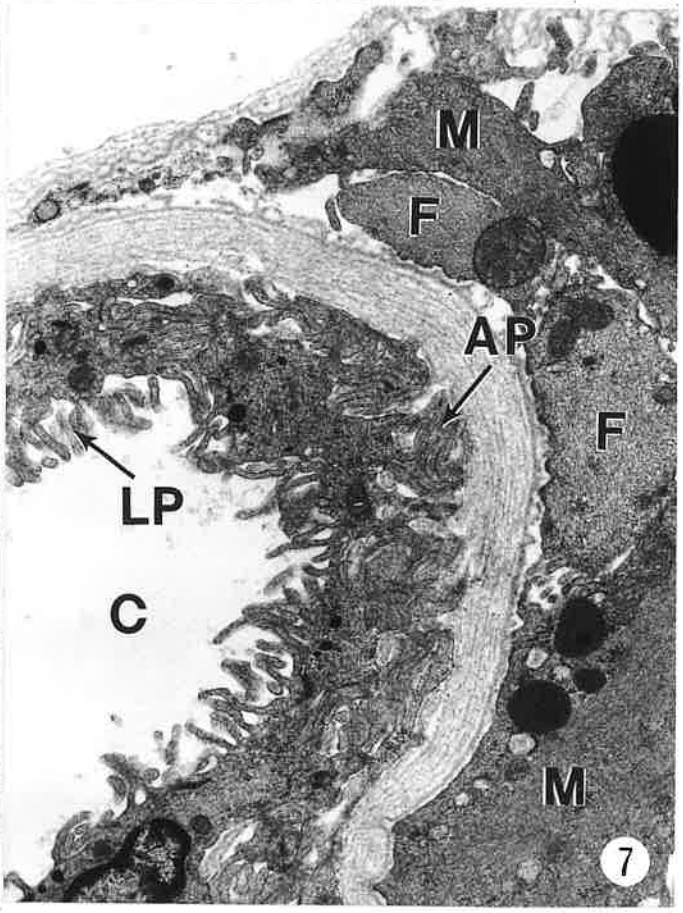
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Fig. 4. Electron micrograph of a pecteneal capillary (C) with a moderate number of luminal microfolds. An endothelial cell nucleus (EN) as well as prominent pericyte (P) and adjacent melanocyte (M) are also indicated. x 7,000

Fig. 5. Electron micrograph to illustrate a capillary (C) with very few luminal microfolds. A melanocyte (M), large melanosome (Me) and the thickened capillary basal lamina (BL) are also indicated. x 9,000

Fig. 6. Electron micrograph of the nuclear region of a typical pecteneal capillary (C). Luminal (LP) and abluminal processes (AP) are labelled as are a pericyte (P) and a melanocyte (M). A cell junction (J) is also labelled. x 13,200

Fig. 7. Electron micrograph of a pecteneal capillary (C) and adjacent melanocytes (M). The capillary shows abundant luminal (LP) and abluminal (AP) processes, while the melanocyte processes are particularly well supplied with bundles of microfilaments (F). x 13,200

are most common at its periphery and at the bridge or apex. Pecteneal melanocytes are large, pleomorphic cells possessing numerous long processes of varying size. The processes enfold both the capillaries and larger blood vessels in an incomplete covering, and semi-isolate the capillaries from each other (Figs. 1, 2). The body of many melanocytes makes direct contact with the basal lamina of the capillaries (Figs. 2-4). Melanocytes share certain features with endothelial cells, including large and vesicular nuclei and the positioning of most organelles in the perinuclear region (Figs. 3-5). The melanosomes within these cells are typically round and very electron-dense averaging 2.0 µm in diameter (Figs. 2-5). Premelanosomes were not observed. Melanosomes are typically absent from the melanocyte processes that are smaller than 2.0 µm. However, these smaller cellular processes often display abundant microfilaments (Figs. 5, 7).

Discussion

Three morphologically distinct forms of the avian pecten oculi are classically described: the 1) conical, 2) vaned, and 3) pleated pecten. The distribution of the first two forms is relatively limited, with the pleated pecten being distributed most widely among the orders of Class Aves.

The conical pecten is a relatively simple, finger-like structure resembling the conus papillaris, the typical SND of the reptilian eye. To date, the conical pecten has been reported only in the kiwi (*Apternyx mantelli*) (Meyer, 1977). The vaned form of the pecten consist of a central flattened pillar giving rise to vertically-oriented vanes. This type of pecten is reported from some larger ratites, specifically, the ostrich and rhea (Walls, 1942; Meyer, 1977). The pleated pecten consists of a varying number of accordion-like folds arranged in a fan-like configuration. This pleated form has been reported from numerous taxonomic orders and species of birds (Dieterich et al., 1973; Bawa and YashRoy, 1974; Meyer, 1977; Braekevelt, 1984, 1986, 1988, 1990, 1991a,b, 1993) and, with variations, is likely found in all other birds. The barred owl, like the great horned owl, possesses a pleated pecten.

Considerable variation occurs in gross features of the pecten such as shape, size, and number of folds or pleats, as well as in ultrastructural features such as number of microfolds on the capillary endothelial cells and the thickness of the capillary basal lamina (Meyer, 1977; Braekevelt, 1984, 1986, 1988, 1990, 1991a,b, 1993). Further, these variations seem to correlate positively with the diurnal activity and/or visual requirement of the species. Visually-oriented birds thus have a relatively larger pecten than less visually-oriented species. Though owls in general are characterized by eyes of particularly large gross size, the pectens of the two described owl species are relatively as well as absolutely smaller (5-6 mm in the great horned owl, 5 mm in the barred owl) than the pecten found in some birds with grossly smaller eyes but greater visual activity, such as the great blue heron (8-10 mm) (Braekevelt, 1991a, 1993). Further, the complexity of the pecten also shows such a correlation, being more elaborate (increased numbers of gross folds and of microfolds) in birds utilizing vision to a greater degree (Walls, 1942; Meyer, 1977). The smaller size and fewer folds of the crepuscular nighthawk (4-5 folds) and nocturnal great horned (7-8 folds) and barred owls (8-10 folds), as compared to the intermediate number of folds in the mallard duck (12-14 folds), the great blue heron (14-15 folds), the common loon (14-15 folds), the visually acute pigeon (15-17 folds) and the particularly visually-oriented red-tailed hawk (17-18 folds) and American crow (22-25 folds) support this generalization (Braekevelt, 1984, 1986, 1988, 1990, 1991a,b, 1993, 1994).

The barred owl is the second species of owl in which pecteneal structure has been extensively described. The barred owl's pecten is slightly smaller in overall dimensions than the pecten of the great horned owl (Braekevelt, 1993), befitting a bird of slightly smaller body and eye size. The pectens of these two nocturnal species are otherwise highly similar, including certain of the features of the great horned owl's pecten that are distinct from other non-strigiform birds. The pectens of both owls are similar in overall size and number of pleats, as well as in the number, size, and distribution of pecteneal vessels. The occurrence of some pecteneal capillaries with very few microfolds first described in the great horned owl (Braekevelt, 1993) also occurs in the barred owl.

The positioning of the barred owl's pecten over the optic disk corresponds to that of all other birds described to date. Placement of a SND over the blind spot of the

retina probably offers the functional advantage of central placement within the eye as well as architectural and optical advantages of interfering to the least degree possible with vision. The enclosure of the entire pecten within a simple basal lamina (vitreopecteneal limiting membrane) continuous with the retina's inner limiting membrane is also conventional among birds (Dieterich et al., 1973; Braekevelt, 1986, 1990, 1993). No hyalocytes were observed in association with this membrane in this species, similar to most other species that have been described (Braekevelt, 1984, 1986, 1988, 1991a,b, 1993). Such cells have been reported as adherent to the membrane's outer surface in relatively few species (Semba, 1962; Braekevelt, 1990).

The capillary endothelium had been reported as a syncytium in some of the earlier fine structural studies of pecteneal capillaries (Seaman and Storm, 1963; Seaman, 1966; Fielding, 1972). However, improved fixation has demonstrated the endothelial cells to be distinct from one another, and joined by often very elaborate tight junctions (Raviola and Raviola, 1967; Dieterich et al., 1973; Meyer, 1977; Braekevelt, 1988, 1990, 1991a,b, 1993).

The pecteneal capillaries are extremely specialized vessels, morphologically without parallel in vertebrate vascularization (Fielding, 1972; Welsch, 1972; Hanzely et al., 1975; Meyer, 1977; Braekevelt, 1984, 1986, 1988, 1990, 1991a,b, 1993). The abundant long processes on both the luminal and abluminal surfaces is their most salient and singular feature. Most ultrastructural studies have referred to these processes as microfolds (Dieterich et al., 1973; Meyer, 1977; Braekevelt, 1984, 1986, 1988, 1990, 1991a,b, 1993) rather than microvilli (Nguyen et al., 1967), both because they branch, and because they lack the finger-like shape associated with the term of microvilli.

The barred owl's pecteneal capillaries in overall view are abundantly supplied with both luminal and abluminal folds. However, the distribution of microfolds among the pecteneal capillaries is not altogether even, in that some pecteneal capillaries display almost no microfolds. Such capillaries resemble the capillaries of the conus papillaris of reptiles (Nguyen, 1970, 1974; Braekevelt, 1989). Thus, relatively fewer microfolds characterize the pecten of the barred owl in comparison with other species described to date (Braekevelt, 1986, 1988, 1990, 1991a,b). In this respect, the barred owl's pecten is similar to that of the great horned owl (Braekevelt, 1993).

Though these two species of owls are indisputably nocturnal birds, the reduced numbers of microfolds characteristic of owl eyes apparently relates to factors other than simply a nocturnal nature. The pecten of the nighthawk (*Chordeiles minor*), another night-flying bird, is not characterized by reduced numbers of microfolds (Braekevelt, 1984). Thus, reduced microfolds in these pecteneal capillaries is not explained by the bird's normal activities taking place during times of very low light. This reduction seems more likely related to the degree to which owls rely on their sense of hearing. Though owl eyes are highly adapted to utilizing all available light, owls nonetheless rely extensively on their auditory sense to localize prey. Structural and functional specialization of owl's ears is so acute that many species are able to hunt successfully when blind, provided that their hearing is intact (Konishi, 1973, 1983). The suggestion is therefore made that the reduced numbers of microfolds of these owl's eyes is more likely related to owl's specialized and extensive use of hearing than to their nocturnal pattern of behavior.

The unusual thickness of the basal lamina of the pecteneal capillaries is a constant feature of all species described to date (Meyer, 1977; Braekevelt, 1984, 1986, 1988, 1990, 1991a,b, 1993). Such a feature might appear to be inconsistent with capillaries heavily involved with transport. However, being comprised of fibrillar material that is not densely or closely packed, the overall structural nature of the basal lamina likely presents no serious barrier to movement of materials. A plausible and perhaps essential role can be ascribed to the thickened basal lamina considering other structural features of the capillaries. Bundles of microtubules within the attenuated capillary cell body represent the sole form of structural support intrinsic to the capillaries. Such meagre provision is unlikely adequate to support the vast numbers of elaborate (and in the case of the luminal processes, also elongate) microfolds. The thickened basal lamina of the pecteneal capillaries very likely provides such support. Such a hypothesis is supported by noting a positive correlation between the thickness of this basal lamina and the size of the pecten itself among the species. Though greatly thickened in all species, this basal lamina is relatively thinner in species with grossly smaller pectens such as the nighthawk (0.5 µm), intermediate in thickness in species with pectens intermediate in size (0.75 µm in the mallard duck, 1.0 µm in the great horned and barred owls), and exceptionally thick (1.0-2.0 µm) in birds with the largest pectens, such as the great blue heron and common loon (Braekevelt, 1984, 1986, 1990, 1991a, 1993).

Pericytes, which are a common and constant feature of the wall of both retinal and hyaloid capillaries (Ashton and de Oliveira, 1966; Braekevelt and Hollenberg, 1970; Jack, 1972), are also present in the wall of pecteneal capillaries of this and other species (Braekevelt, 1984, 1986, 1988, 1990, 1991a,b, 1993). The function of these undifferentiated cells is uncertain. They may be supportive or contractile in nature, or perhaps represent reserve cells that could develop into endothelial cells as required. Melanosomes, which have been reported as occasionally occurring in the pecteneal pericytes of the great blue heron (Braekevelt, 1991a), were not observed in the pericytes of the barred or great horned owl (Braekevelt, 1993).

Larger afferent and efferent vessels lie among the folds of the pecten in addition to the specialized capillaries. In the chicken (Dieterich et al., 1973) and in the pigeon (Raviola and Raviola, 1967), these vessels are

distinguishable as arterioles and venules. However, in other described species (Braekevelt, 1984, 1986, 1988, 1990, 1991a,b, 1993), such a distinction is seldom if ever possible. This similarity of structure between most supply and drainage vessels within the pecteneal body implies a lowered blood pressure within the pecten, which would facilitate transport functions.

Large numbers of pigmented cells are common to the pecten of all species described to date (Walls, 1942; Fischischweiger and O'Rahilly, 1966; Fielding, 1972; Bawa and YashRoy, 1974; Meyer, 1977; Braekevelt, 1984, 1986, 1988, 1990, 1991a,b, 1993). These melanocytes likely fulfil multiple purposes in the pecten. Since no other cell types are present within the pecten to act as supportive elements, the melanocytes probably contribute to the structural support of the organ. The numerous melanocyte processes, their disposition surrounding capillaries, and the abundant microtubules and microfilaments within their processes all corroborate such a function. Though statistical significance has not yet been investigated, a trend of an increasing quantity of microfilaments and microtubules with increasing size of the pecten has been observed (Braekevelt, 1986, 1988, 1990, 1991a,b, 1993). In addition to a structural role, pecteneal melanocytes may contribute to a higher metabolic rate within the pecten. Absorption of light by melanosomes should increase the pecteneal temperature, thereby increasing the rate of metabolic processes such as transport (Bawa and YashRoy, 1974). Melanocytes distributed throughout the pecten likely contribute to this effect. Interestingly, the concentrations of melanocytes present in the bridge and peripheral regions are strategically placed to receive light first and in the greatest intensity.

Several structural features of the pecten clearly imply a function involving transport. The tremendous surface area supplied by the capillaries' abundant microfolds, the reduction of the endothelial cell body outside of the nuclear area (exclusive of the microfolds) to a narrow strip, and the concentration of the majority of cellular organelles in the perinuclear region are all suggestive of transporting activity (Raviola and Raviola, 1967; Meyer, 1977). Lowered blood pressure as implied by lack of morphological distinction between afferent and efferent vessels would facilitate such a function. Additionally, alkaline phosphatase, an enzyme required for active transport of materials across cell membranes, is present at high levels in the pecten (Welsch, 1972). The endothelial cell's extensive microfolds may also be present to subserve the alkaline phosphatase system. Thus, the pecten is heavily implicated in both the passive diffusion and the active transport of materials (Wingstrand and Munk, 1965; Bawa and YashRoy, 1972; Welsch, 1972; Meyer, 1977).

A number of sometimes highly imaginative functions has been ascribed to the avian pecten. These have included conceptualizations such as a magnetic field detector used in migration, a sunshade, an ocular thermoregulation device, an intraocular pressure regulation device, a dark mirror, and provision of a fixed point for a navigational aid (reviewed in King and McLelland, 1984). However, structural and functional studies to date best support the concept of a supplemental nutritive device (Walls, 1942; Wingstrand and Munk, 1965; Rodieck, 1973). As such, the pecten is comparable to the falciform process of some teleost fish, the conus papillaris of reptiles, the supraretinal or vitreal vessels of amphibians and some teleost fish, and the intraretinal vessels of mammals (Walls, 1942; Michaelson, 1954; Duke-Elder, 1958; Nguyen, 1974; Braekevelt, 1988, 1989, 1990, 1991a,b, 1993). Structural features directly suggesting a nutritive function include the more numerous, longer and more elaborate microfolds on the luminal surface of the capillaries as compared to the abluminal surface. As with the brush border in renal proximal tubular cells, this suggests that the direction of transport is out of the lumen. In the case of the pecten, nutrients would then diffuse through the vitreous body to reach the avascular region of the retina. The suggested role of the abundant melanosomes on increasing pecteneal temperature and hence rate of transport functions has already been discussed. The increase in the pecten's alkaline phosphatase on light adaptation (Bawa and YashRoy, 1971, 1972), i.e., when the retinal light-sensitive cells are active and have greater metabolic demands, further supports the hypothesis that the pecten is involved in a nutritive role.

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