REVIEW

Comparative morphology of the tapetum lucidum (among selected species)

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Abstract

Objectives The phenomenon of 'eye-shine' is seen in a variety of animal species, and is generally thought to be related to the presence of an intraocular reflecting structure, the tapetum lucidum. The tapetum lucidum is a biologic reflector system that is a common feature in the eyes of vertebrates. It normally functions to provide the light-sensitive retinal cells with a second opportunity for photon-photoreceptor stimulation, thereby enhancing visual sensitivity at low light levels. The tapetum lucidum is presented here according to a classification based on the location, as well as the composition, of this reflective layer. Finally, the physical and chemical properties, as well as the origins of the different tapeta lucida, are discussed and compared.

Methods The anatomic and biochemical aspects of the tapetum lucidum in various vertebrates are examined. Morphologic observations were made from paraffin and plastic embedded specimens. Specimens were treated with traditional stains and observed by light and transmission electron microscopy.

Results Some species (primates, squirrels, birds, red kangaroo and pig) do not have this structure and they usually are diurnal animals. In vertebrates, the tapetum lucidum exhibits diverse structure, organization and composition. Therefore, the retinal tapetum (teleosts, crocodilians, marsupials, fruit bat), the choroidal guanine tapetum (elasmobranchs), the choroidal tapetum cellulosum (carnivores, rodents, cetacea), and the choroidal tapetum fibrosum (cow, sheep, goat, horse) are described.

Conclusions The tapetum lucidum represents a remarkable example of neural cell and tissue specialization as an adaptation to a dim light environment and, despite these differences, all tapetal variants act to increase retinal sensitivity by reflecting light back through the photoreceptor layer. These variations regarding both its location and structure, as well as the choice of reflective material, may represent selective visual adaptations associated with their feeding behavior, in response to the use of specific wavelengths and amount of reflectance required.

Key Words: morphology, tapetum lucidum, vertebrates

INTRODUCTION

The visual senses include perceptions of light, color, form, space and movement. The light sense, by which light is perceived as such, and gradations in its intensity appreciated, is the most fundamental of the visual senses and it is highly developed in vertebrates.[1] The attainment of a high standard of light sensitivity involves certain structural specializations in the eye. The eyes of animals to which an acute perception of light is a necessity can be differentiated from animals which need excellent visual acuity. From this point of view vertebrates can be divided into three main classes: diurnal animals (adapted to bright light), nocturnal animals (adapted to near-darkness of night), and arrhythmic animals (adapted either to bright or dim illumination). The ocular microanatomy of a nocturnal and a diurnal eye are very different, with compromises needed in the arrhythmic eye. Anatomic differences in light gathering are found in the organization

of the retina and the optical system. The size of the eye and those of its different structures influence the amount of light gathered. The presence of a tapetum lucidum influences the light sensitivity capabilities of a species.

The phenomenon of 'eye-shine' is seen in a variety of animal species, and is generally thought to be related to the presence of an intraocular reflecting structure, the tapetum lucidum.[2,3] The tapetum lucidum is a biologic reflector system that is a common feature in the eyes of vertebrates. It normally functions at low light levels to provide the light-sensitive retinal cells with a second opportunity for photon-photoreceptor stimulation, thereby enhancing visual sensitivity (Fig. 1).[4,5] While increasing retinal sensitivity in dim illumination, the tapetum lucidum may harm visual acuity in bright illumination.[4]

Tapeta lucida in vertebrates exhibit diverse structure, organization and composition (Fig. 2). Despite these differences, all tapetal variants act to increase retinal sensitivity by reflecting light back through the photoreceptor layer. Tapeta lucida can be classified according to the location as well as the nature of the reflective materials that constitute them. The reflecting material may be located within the cytoplasm of the retinal epithelium (retinal tapetum lucidum) or in the choroid. The choroidal tapetum lucidum lies immediately adjacent to the choriocapillaris and external to the retinal epithelium (Fig. 1). The reflective material of the choroidal tapetum lucidum may be a guanine tapetum, an array of extracellular fibers (tapetum lucidum fibrosum), or a layer of cells (which compose the tapetum lucidum cellulosum) packed with organized, highly refractive material (tapetal rodlets) (Fig. 1).[3,5,6]

This paper is a review of the anatomic, histologic and biochemical aspects of the tapetum lucidum of various vertebrates. Three basic tapetal morphotypes of vertebrates are described and compared: the absence of tapetum, the retinal tapetum lucidum, and the choroidal tapetum lucidum.

ABSENCE OF TAPETUM

Animals without a tapetum lucidum (e.g. primates, squirrels, birds, red kangaroo and pig) generally have diurnal habits, and a red or orange to pale gray fundus reflection (Fig. 2, lane 1).[7,8] The red to orange background results from reflection of light from choroidal blood vessels.[2] Birds are apparently the only large group of animals in which the tapetum is consistently absent.[16]

RETINAL TAPETUM LUCIDUM

Retinal tapeta lucida are common in fish and some reptiles, but rarely occur in mammals.[3,6,9] In most of these species the retinal tapetum can be classified as either a lipid (in some teleosts, mammals) or guanine type (in some teleosts, reptiles) (Table 1).

Another differentiation can be made among the retinal tapeta lucida based on whether the tapetum is occlusible (found in most of teleosts), or nonocclusible (or static) (found in mammals). The variation in 'eye-shine' in occlusible tapeta

in teleosts is caused by the migration of black pigment (melanin) within the retinal pigment epithelium (RPE) and the choroidal cells. Melanin migrates towards the vitreous when the eye is illuminated and towards the sclera (backwards) in dim light or darkness (Fig. 1). The migration of melanin can mask or unmask the reflecting material depending upon the degree of environmental illumination.[10–12]

In certain species the tapetum is occlusible not because of a pigment migration within a cell, but because of a visual cell movement called the retinomotor movement, as well as the migration of the processes of the RPE cells between the cells and over the reflective material (elasmobranchs).[12,13]

It is thought that the function of the occlusible tapetum is related primarily to reduction of 'eye-shine' rather than modifying retinal sensitivity, as the tapetal reflection contributes only 30% of the light reaching the photoreceptors (70% of the light directly reaches the photoreceptors).[14,19]

Fish – teleosts

Two morphologic types of tapeta lucida can be observed in the eyes of fishes: one that lies in the choroid such as occurs in elasmobranchs (that will be discussed later); and the other that lies in the pigment epithelium of the retina such as occurs in teleosts.[1,11,14]

The choroid of teleosts is a connective tissue layer rich in blood vessels, and one or two choroidal glands. A choroidal tapetum of reflecting cells lying immediately outside the choriocapillaris is formed in a few primitive teleosts. More commonly, the tapetum lucidum is an integral part of the pigment epithelium in primitive teleosts (lying in the processes of the pigmented epithelial cells) (Fig. 3).[11,12] The reflective material is contained in spheres closely packed together in the apical processes of the pigment epithelial cells. It can vary in chemical nature (Table 1). The tapetum of the seatrout (*Sciaenidae*) contains highly refractive lipid (triglycerides) particles,[10,12] whereas the tapetum of gars (*Lepisosteidae*) is composed of a yellow phenolic compound.[11] The lipid tapetum observed in the seatrout has a white appearance, and reflects light diffusely, as the reflective material is not organized within spheres.[10,11] In contrast, the tapetum of gars possesses a yellow reflective material (yellow pigment) that occurs in regular array and is contained in a myriad of small spheres. The spheres are organized in parallel sheets with packing being hexagonal in the plane of the sheet.[11] The 'eye-shine' varies in color (from yellow to dark brown) depending on the retinomotor movement on the stage of light adaptation of the eye, and characterizes the tapetum of these teleosts as occlusible (Fig. 1).[10–12]

The stratum argenteum is a 'silvery' reflective layer in the outer choroid, adjacent to the sclera, frequently present in fish larvae but not as frequent in adults. In species known to have a stratum argenteum as adults, like the toadfish (*Toadfishes*), the tapetum lucidum is absent or vestigial and there is little choroidal melanin.[12]

The choroid of toad fish is thin and contains blood vessels, a choroidal gland, and a stratum argenteum. There is loose
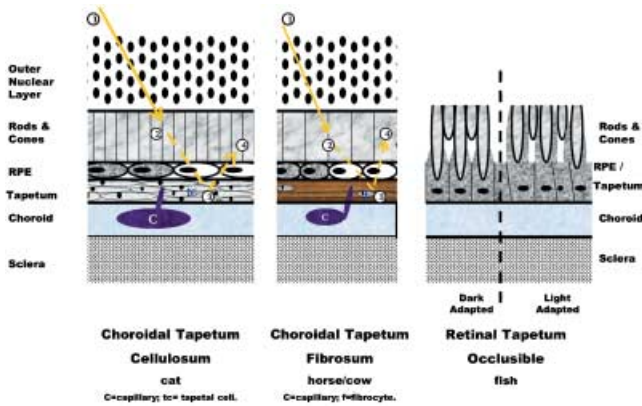
Figure 1. Diagram of the three types of the tapetum lucidum present among vertebrates. 1. Incoming light ray; 2. First stimulation on the rods and cones; 3. Reflection on the tapetum lucidum; 4. Second stimulation on the rods and cones.
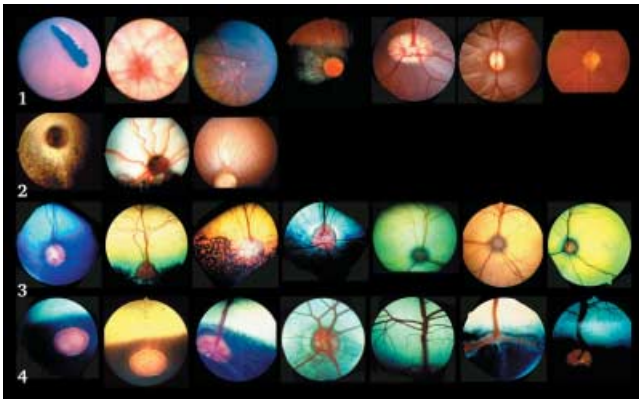

Figure 2. Ocular fundus of various species showing the absence or the presence a tapetum lucidum that can exhibit various colors. From right to left: lane 1: absence of tapetum: bird, albinos rat, hooded rat, red kangaroo, pig, rhesus monkey, human. Lane 2: retinal tapeta: alligator, possum, fruit bat. Lane 3: Choroidal tapeta cellulosa: puppy, dog (3), cat, jaguar, leopard. Lane 4: choroidal tapeta fibrosa: foal, horse, sheep, goat, cow, deer, mouflon.
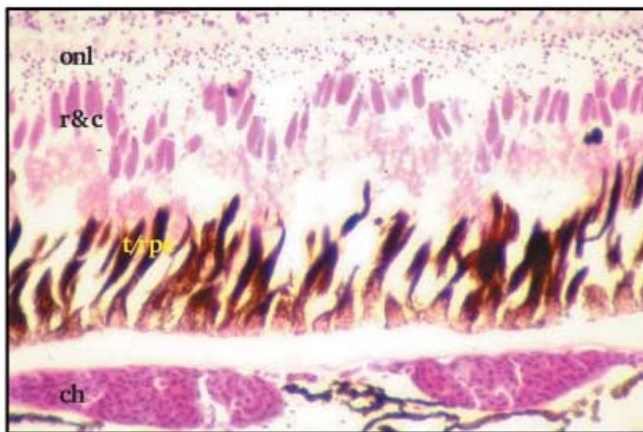

Figure 3. The retinal tapetum lucidum in fish (teleosts): oscar (*Astronotus oscellatus*). onl, outer nuclear layer; r & c, rods and cones; t/rp, tapetum/retinal pigment epithelium; ch, choroid. (H&E staining, original magnification ×400.)
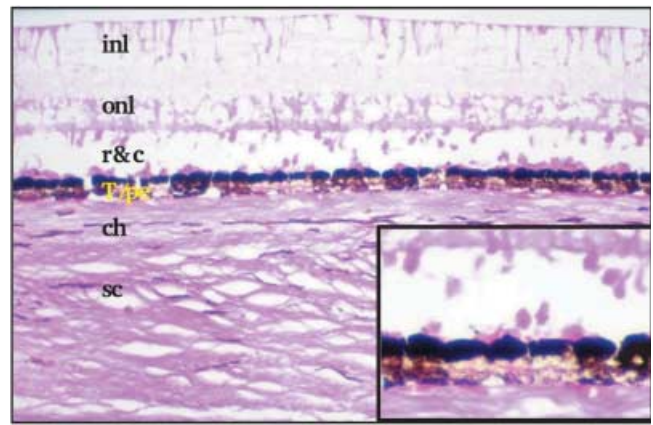

Figure 4. The retinal tapetum lucidum in alligator (*Alligator mississipiensis*). inl, inner nuclear layer; onl, outer nuclear layer; r & c, rods & cones; t/rpe, tapetum/retinal pigment epithelium; ch, choroid; sc, sclera. (H&E staining, original magnification ×200, insert ×400.)
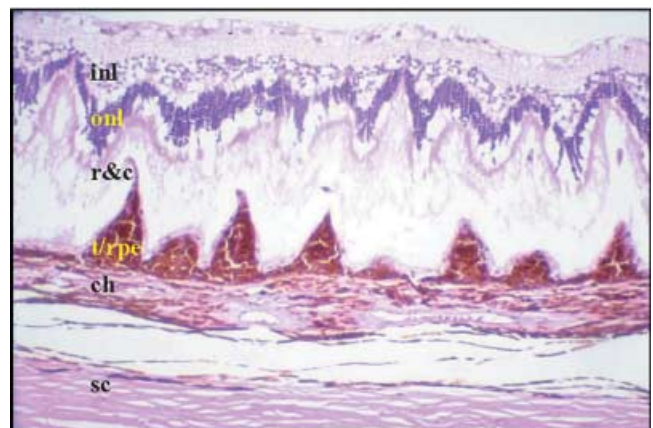

Figure 5. The retinal tapetum lucidum of a fruit bat (*Pteroptus giganteus*). inl, inner nuclear layer; onl, outer nuclear layer; r & c, rods & cones; t/rpe, tapetum/retinal pigment epithelium; ch, choroid; sc, sclera. (H&E staining, original magnification ×200.)

connective tissue between the choriocapillaris and the stratum argenteum. Melanocytes are absent except for a few near the globe equator. The outermost layer of the choroid is occupied by a thin stratum argenteum which lies adjacent to the sclera, is bilaminate, and becomes a layer of pentameric crystals and a layer of yellow birefringent granules. The inner surface of the stratum is shiny, has an orange metallic luster, and is mostly a specular reflector, reflecting much of the incident light. It consists of two or more cell layers (iridophores). The iridophores are polygonal in shape and loaded with packets of elongated thin pentagonal crystals that are oriented with their long axis parallel to the argenteal surface. The thin crystals are superposed over each other and form a good reflective system. The reflective material is uric acid (Table 1). The outer surface of the argenteum is covered by a thin yellow sheet that has a mat appearance. The yellow packets are in the form of 1-μm diameter small
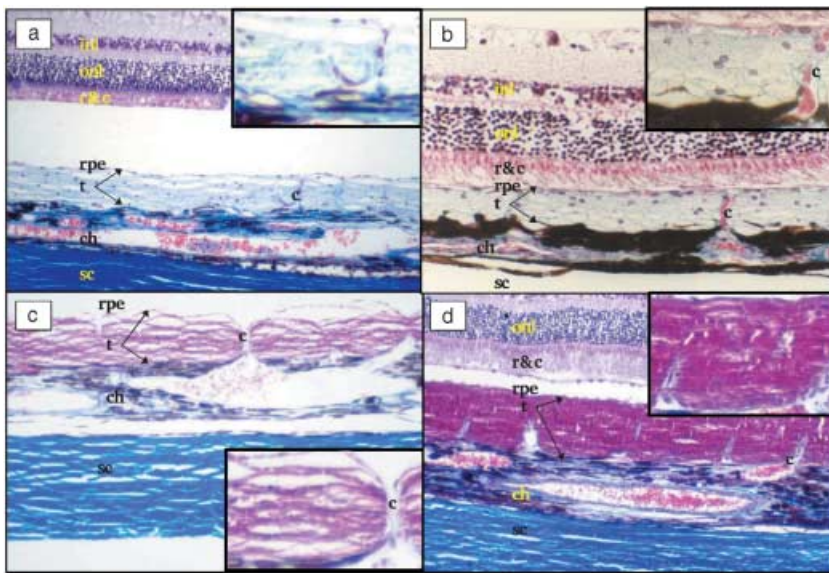
Figure 6. The tapetum lucidum cellulosum consists of layers tapetal cells regularly arranged. Tapetum cellulosum of the dog (a), the mink (b), the cat (c), and the cougar (d). inl, inner nuclear layer; onl, outer nuclear layer; r & c, rods & cones; t, tapetum; rpe, retinal pigment epithelium; ch, choroid; sc, sclera; c, capillary. (Trichrome staining, original magnification ×200, insert ×400.)
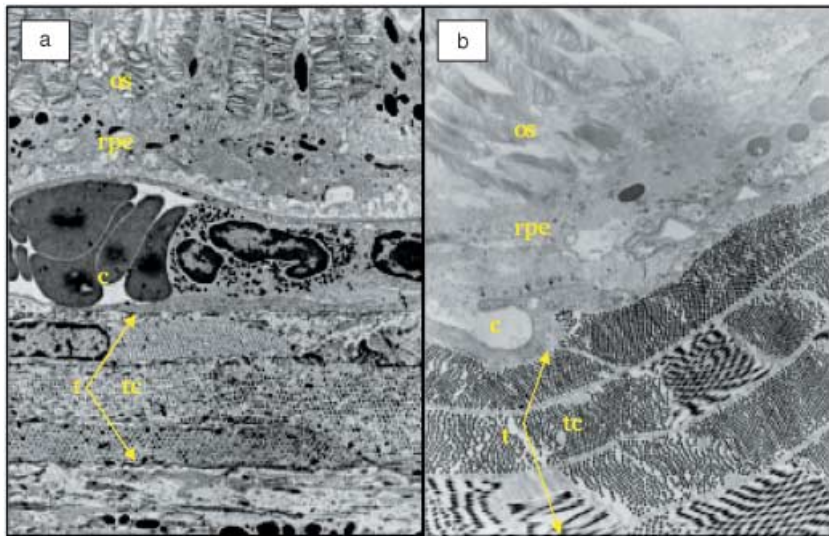

Figure 7. Electronic microscopy of the tapetal area in a dog (a) and a cat (b). The rodlets in the tapetal cells are more precisely oriented in the tapetum of the cat than in the tapetum of the dog. os, outer segment; rpe, retinal pigment epithelium; t, tapetum; tc, tapetal cell; c, capillary. (Original magnification ×4000.)

granules, appear to have a geometric form, and are packed closely in a continuous mass. By moving posteriorly or anteriorly within the cells, both the choroidal and the retinal pigment prevent the light from reaching the argenteum (Fig. 1) and retina. Therefore, the tapetum is occlusible in toadfish.[12]

Reptiles – crocodilians

In crocodilians, a semicircular area of the retinal epithelium in the superior fundus shows a fair sulfur yellow coloration and is specialized as a tapetum lucidum (Fig. 2, lane 2, #1).[9,15] Guanine crystals or calcium salts of guanine appear to be the most common reflective material in this tapetum lucidum (Table 1).[9,15,16] Nearly all of the epithelial cells contain membrane-bound tapetal crystals. The crystals measure 100–120 nm in thickness and up to 0.7 μm in length.[9,15] In the *Caiman crocodilus* the guanine crystals are highly organized at a cellular level, being perpendicular to the long axis of the retinal photoreceptors (e.g. to the path of light).[9] In contrast, no such regular orientation of the guanine has been seen in the spectacled caiman (*Caiman sclerops*).[15] In spectacled caiman, the reflecting material is much closer to the photoreceptors, which may allow dispersion of the reflected light to occur more readily. In the tapetal area, no melanosomes are formed indicating a nonocclusible tapetum in the *Caiman sclerops*.[15] At the edge of the tapetum, however, both guanine crystals and melanosomes are found within the epithelial cells.[15] In comparison, the dark coloration of the inferior part of the fundus in the *Caiman crocodilus* is caused by masking of tapetal crystals by melanosomes; therefore, the tapetum is an occlusible type. Outer segments of the retinal receptors are deeply inserted into broad, mainly crystal-containing processes of the pigment epithelial cells.[9] Other than the presence of guanine crystals, the fine structure of the retinal pigment epithelial cells of the crocodilians in general resembles that found in other vertebrates (Fig. 4).[15]

Figure 8. The tapetum lucidum fibrosum consists of layers of collagen fibers regularly arranged. Tapetum fibrosum of the horse (a), the sheep (b), the dolphin (c), and the pilot whale (d). inl, inner nuclear layer; onl, outer nuclear layer; r & c, rods & cones; t, tapetum; rpe, retinal pigment epithelium; ch, choroid; sc, sclera; c, capillary. (Trichrome staining, original magnification ×200, insert ×400.)
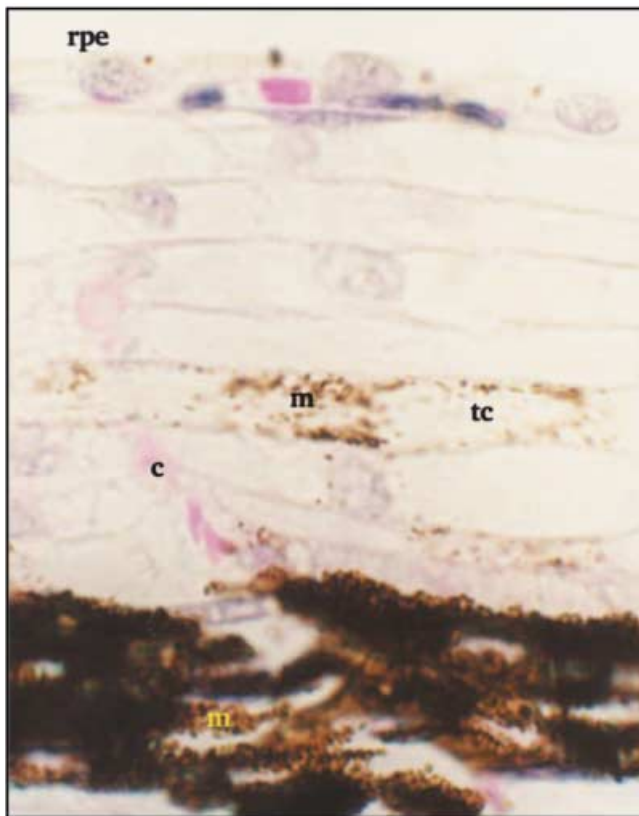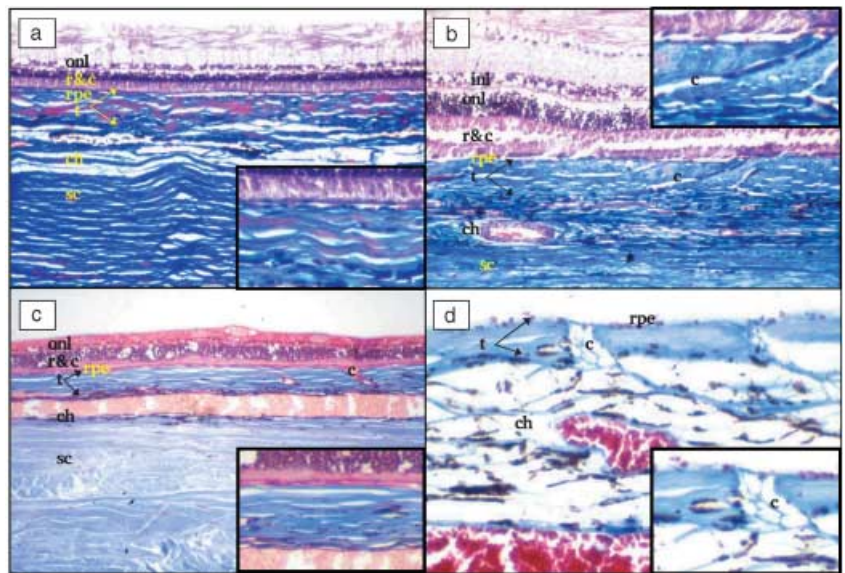

Figure 9. Melanocytes may be the progenitor cell of the tapetal cells. A tapetal cell in the tapetum cellulosum of the mink containing melanin granules (m). tc, tapetal cell; c, capillary; rpe, retinal pigment epithelium; m, melanin granules. (Trichrome staining, original magnification ×1000.)

Mammals – marsupials – opossum
A tapetum lucidum is present in a semicircular area of the superior retinal epithelium of the opossum (*Didelphis virginiana*) (Fig. 2, lane 2, #2). The reflecting material consists of a large quantity of lipoidal spheres scattered throughout the epithelial cells. The size and shape of the lipoidal spheres vary somewhat from cell to cell, but all of the spheres within the same epithelial cell are generally of a similar morphologic appearance.[1,16,17] The reflecting material contains cholesterol or cholesterol esters (Table 1).[16,17] Centrally in the tapetal area, very few or no melanosomes are found, indicating a nonocclusible tapetum. At the periphery, the epithelial cells contain both reflecting material and melanosomes. The choriocapillaris over the tapetal area is organized in a similar way to other mammals, as will be discussed later.[17]

Mammals – fruit bats
The tapetum lucidum in fruit bats (*Pteroptus giganteus*) appears white to yellow when isolated *in vitro* (Fig. 2, lane 2, #3), but the reflected color is red *in vivo*, probably due to retinal blood. The tapetal material lies at the base of the retinal cells (which are arranged in a zig-zag manner) on the inner side of the cones of pigment (Fig. 5). The reflecting material is believed to be contained in many spherules and to be phospholipid in composition (Table 1).[1,11,13,16,18]

CHOROIDAL TAPETUM LUCIDUM

Guanine tapetum
Fish – elasmobranchs Two morphologic types of tapetum lucidum can be observed in the eyes of fish: one in the choroid that occurs in elasmobranchs, and the other which occurs in teleosts and lies in the pigment epithelium of the retina.[1,11,14]

The elasmobranch tapetum in *Squalus* and *Scyliorhinus* consists of sheets of 12–13 superposed guanine crystals in the choroid. The thickness of the crystals ranges from 60 to 80 nm, which corresponds to the measured reflectance peaks around 470–520 nm (Table 2). This type of biologic photon reflector system approximates 'ideal' multilayer reflectors, although three features weaken its capability. The reflectance

Table 1. Retinal tapeta among the vertebrates

Classification	Type of tapetum	Reflective material (nature, shape, size)
Fishes		
Teleosts		
Seatrout[10,11]	Occlusible	Spherules triglycerides; diameter: 0.4 µm
Gars[11]	Occlusible	Spherules yellow pigment (Phenolic compound); diameter: 0.24 µm
Toadfish[12]	Argenteum stratum	Acid uric
	Occlusible	
Reptiles		
Crocodiles		
Alligator mississipiensis[13]		Spherules guanine
Caiman crocodilus[9]	Occlusible	Spherules guanine; diameter: 0.7 µm; length: 0.12 µm
Caiman sclerops[15]	Non-occlusible	Guanine
Marsupials		
Opossum[16,17]	Non-occlusible	Lipoidal spherules; cholesterol and esters˙
Placentals		
Bats		
Fruit bat (Eidelon)[13,16]		Spherules

peak is much too broad, the arrangement of the reflective surface is not always parallel to the retinal plane, and the presence of migrating retinal epithelial cells in *Squalus* (an occlusible tapetum) results in optical interference. The elasmobranchs that have a choroidal tapeta often have very elaborate occlusible tapeta lucida, as in some teleosts. The pigment in retinal epithelial cells overlying the tapetum of the *Squalus* can migrate between and over the reflective cells during illumination, and retreat during darkness to expose the reflectors (Fig. 1). Retinal epithelial pigment migration may also occur to limit exposure of an animal with 'eye-shine', as light in the sea is very directional, and 'eye-shine' might increase the chance of being caught by predators.

The choroidal tapetum of the Port Jackson shark (*Hetrodontus phillipi*) consists of a single layer of overlapping cells situated immediately external to the choriocapillaris, and is oriented at an angle of 30° to incoming light.[20,21] These tapetal cells alternate with, and are separated from one another by melanocytes that extend beyond the tapetal cells to intervene between the tapetal cells and the incoming light. The bulk of the tapetal cells are packed with evenly spaced guanine crystals. The size and spacing of these reflective crystals is commensurate with the principles of constructive interference. The crystals measure approximately 0.1 µm in width and 5.0–8.0 µm in length, and are separated by a space of 0.25 µm (Table 2). These values are very similar to those found in other elasmobranchs (short-tailed stingray and southern fiddler ray[20,22]). A typical tapetal cell will have 15–20 layers of these reflective crystals throughout the thickness of the cell. The retinal tapetum of the Port Jackson shark is an occlusible type.

Tapetum lucidum cellulosum

Mammals – carnivores

Common features Many mammalian carnivores have a choroidal tapetum of a cellular type (Table 2).[2] Histologically, the tapetum cellulosum is composed of layers of rectangular-shaped cells (Fig. 1). The choroidal stroma adjacent to the tapetum lucidum contains numerous small blood vessels that penetrate the tapetal layer to form a single-layered capillary network, known as the choriocapillaris, on the surface of the tapetum. The tapetum cellulosum is thus interposed between the large branching vessels in the choroid and the single layer of the choriocapillaris beneath the retinal epithelium. The thickness of the tapetum varies, being multilayered at its center, and thinning to a single cell (or lamella) at its periphery and adjacent to the optic nerve.[3,6,8,23–26]

The tapetal cells are gradually replaced by melanin-containing cells of the choroid at the outer edge of the tapetum (Fig. 1). At the periphery of the tapetum melanocytes often intermingle with tapetal cells, and it is not uncommon to observe cells which display morphologic characteristics of both tapetal cells and melanocytes.[5,25] The layers of melanocytes gradually increase toward the periphery of the tapetum.[8] Over the tapetal region, the retinal epithelium (RE) is nonpigmented to allow light to pass to and from the reflective tapetum. At the periphery of the tapetum the RE becomes pigmented. In nontapetal locations the RE is heavily pigmented to become the retinal pigment epithelium (RPE). Histologically, the tapetal melanocytes are as thoroughly dominated by a single type of cytoplasmic component (melanin granules) as the tapetal cells. The principal difference is in the high degree of order of the rods in the tapetal cells compared to the random packing of the melanin granules in the melanocytes.

The tapetum is supplied by branches of blood vessels of the pigmented choroid. These penetrating vessels run from the outer vascular layer of the choroid, pass through the tapetum lucidum at right angles and terminate in the extensive, anastomosing, capillary network: the choriocapillaris. These capillaries form a single layer which underlie all parts of the retina, are heavily fenestrated and are separated from the tapetum or pigment cells of the choroid by a narrow

Table 2. Choroidal tapeta among the vertebrates

Classification	Type of tapetum	Reflective material	Thickness; number of cell layers or crystals	Size of fibrils or Rodlet's dimensions
Fishes				
Elasmobranchs, Squalus[13,14,19]	Occlusible	Guanine crystals	60–80 µm	12–13 superposed crystals
Elasmobranchs, Port Jackson Shark[13,20,21]	Occlusible	Guanine	Length: 5–8 µm Width: 0.1 µm	15–20 superposed crystals
Placentals				
Carnivores				
Dog[8,27]	Cellulosum	Zinc cysteine	9–15 layers	Diameter: 4 µm Length: 0.14 µm Spacing: 0.20 µm
		Zinc cysteine	9–11 layers[26] 15–20 layers[3]	Diameter: 4 µm Length: 0.18 µm Spacing: 0.20 µm
			43 µm; 10–12 layers[41]	
Cat[5,18,25]	Cellulosum	Riboflavin	15–20 layers	Diameter: 4–6 µm Length: 0.10–0.12 µm Spacing: 0.15 µm
		Riboflavin, Zinc	16–20 layers[26] 30 layers[8] 18–30 layers[23]	Diameter: 8–10 µm Length: 0.15 µm Spacing: 0.08 µm
			6–10 layers[40]	Diameter: 5 µm Length: 0.23 µm Spacing: 0.40 µm
			35 layers[6]	
Ferret[26]	Cellulosum	Zinc cysteine	7–10 layers	
		Zinc cysteine	5–7 layers[30]	Diameter: 3–4 µm Length: 0.13–0.15 µm
			50 µm; 10–15 layers[27]	Diameter: 6 µm Length: 0.20 µm Spacing: 0.30 µm
Ranch Mink[31]	Cellulosum		30 µm; 2–3 layers	Non regular
Pinnipedes				
Seal (Grey Seal)[4]	Cellulosum	?	30–35 layers	Diameter: 5–6 µm Length: 0.10 µm Spacing: 0.15 µm
Ungulates				
Cow[36]	Fibrosum			Diameter: 0.15 µm Spacing: 0.20 µm Diameter: 0.20 µm[16]
Sheep[38]	Fibrosum	Collagen	100–200 µm	Diameter: 0.15 µm Spacing: 0.20 µm
			100–200 µm[23]	Diameter: 0.15 µm Spacing: 0.08 µm
			140 rows per layer: 9–16 layers[26]	Diameter: 0.15 µm Spacing: 0.18 µm
Lemurs				
Lemur (*Galago crassicaudatus*)[16]		Riboflavin		
Rodents				
Paca (*Cuniculus paca*)[32]	Fibrosum	?	12–15	Diameter: 8–10 µm Length: 0.2–0.25 µm Spacing: 0.15 µm
Primates				
Non human (*Aotus*)[16]	Fibrosum	Collagen		

layer of connective tissue that extends over the retinal surface. In the tapetal and peritapetal areas, the choriocapillaris is indented into the retinal epithelial layer leaving a flat inner surface to the reflecting tapetum, while in peripheral regions of the nontapetal fundus the RE is not indented by the choriocapillaris.[3,5,6,25–27]

The tapetum lucidum develops late in the eyes of some animals (e.g. dogs and cats), and is usually completely developed by 4 months of age (Fig. 2, lane 3, #1). Animals born with mature eyes have a well-developed tapetum although some tapetal maturation occurs after birth. The degree of pigmentation of the animal apparently has no effect on development of the tapetum, with the exception of individuals with partial or full albinism.

Cat (Felis catus) The tapetum lucidum in the cat covers nearly 50% of the fundus area, and is shaped roughly like a rounded equilateral triangle, with its apex upwards and its base passing horizontally just below the optic disc (Fig. 2, lane 3, #5). Tapetal development initially produces the immature feline tapetum that is pale blue in color (Fig. 2). Its predominant adult color varies from yellow to green between individuals (Fig. 2). Though the tapetum is undetectable grossly in the new-born, it becomes obvious in 3- to 4-week-old kittens, having essentially completed development at this time. Subsequent enlargement of the eye causes the relative extent of the tapetum to be reduced.[5,6,24,25]

Histologically, the feline tapetum consists of 15–20 layers of cells in its center, progressively thins and eventually disappears towards the periphery (Table 2, Fig. 6c).[5,6,8,23–25] Aging results in a loss of tapetal layers such that the adult cat tapetum has fewer layers than the kitten.[5,25,26]

In sagittal planes the individual feline tapetal cells appear rectangular, set in even brick-like rows, and show an orderly arrangement (Fig. 6c).[6] However, feline tapetal cells (located close to the retinal epithelial layer) are flattened (thickness of 3–4 μm), having the largest surface parallel to the retina. Only a small part of the tapetal cell is occupied by an ovoid and centrally located nucleus. The bulk of the cell is filled with numerous, electron-dense, membrane-bound rodlets of reflective riboflavin (Fig. 7b).[24,25,28] The rodlets are 4–6 μm in length and 0.1–0.12 μm in diameter, and are precisely arranged in a hexagonal lattice pattern with a space of 0.15 μm separating adjacent rodlets (Table 2).[25] These rodlets are grouped in bundles, which normally extend through the entire thickness of the cell. Within each bundle the centers of the rodlets are arranged parallel to the retinal surface with remarkable regularity (Fig. 7b).[24] At the border region of the tapetum, the feline tapetal cells sometimes contain melanin granules and, similarly, some tapetal cell-like melanocytes contain tapetal rodlets.[8,29]

Dog (Canis familiaris) The tapetum lucidum in the dog is a rounded equilateral triangle in shape, with the base oriented horizontally (excluding the optic disc in most of the breeds) and the apex directed upwards.[3,26] It covers an area of approximately 30% of the superior fundus. In fresh preparations the reflected color of the canine tapetum varies from yellow-green to green-blue with an irregular marginal area (Fig. 2, lane 3, #2–4). The tapetum in the center of the tapetal fundus of the dog consists of 18–20 layers of cells (Table 2), with each layer containing approximately 15–18 ranks of rodlets. The number of cell layers gradually thins towards the periphery where it ends.[3,26] Tapetal cells appear as polygonal plates arranged much like 'patio bricks' within each layer. Sagittally, the canine tapetum resembles a multiple layered 'brick wall' (Fig. 6a). Each cell is a rounded polygon, 40–48 μm in diameter and an average thickness of 3.28 μm. The cytoplasm is tightly packed with separate bundles of membrane-bound rodlets that displace other organelles and/or inclusions into the perinuclear or peripheral region (Fig. 7a).[3] Individual tapetal rodlets are fairly constant in their dimensions with a mean length of 4.0 μm and a diameter of 0.14 μm, and appear to contain a hard and apparently homogeneous core (Table 2). Within the bundle rodlets are primarily arranged into a compact regular hexagonal array, with a mean spacing of 0.2 μm (Table 2). In the dog, Bruch's membrane over tapetal areas is extremely attenuated, appearing as a single homogeneous layer (although it is bilaminate), with a mean thickness of 0.16 μm.

Ferret (Mustela putorius) The tapetum lucidum in the ferret is an iridescent triangular area in the rear pole of the eye above the optic disc. It is present in both the pigmented and albino eye.[27,30] A comparison of pigmented and albino ferrets revealed no morphologic differences of their cellular tapeta at both light microscopic and transmission electron microscopic levels.[30] The albino ferret lacks both retinal and choroidal pigmentation.[30] The ferret has a tapetum cellulosum situated in the superior choroid immediately external to the choriocapillaris.[27] It contains rodlets that have a diameter of 1.3–1.5 μm and a length of 3–4 μm (Table 2).[27] The ferret tapetum lucidum is 5–7 cell layers arranged as a brick-like structure (Table 2). Over the tapetum, the retinal epithelium is nonpigmented.[30] Several layers of pigmented melanocytes are present outside the tapetum lucidum in the choroid of pigmented ferret eyes. A high concentration of zinc cystein is found in the tapetal rodlets of ferrets.

Ranch mink (Mustela vison) All carnivores are believed to possess a well-developed choroidal tapetum cellulosum.[3,27] However, the tapetum present in the superior part of the fundus of the ranch mink seems to be degenerative. The presence of only 2–3 layers of apparently degenerative tapetal cells containing a haphazard arrangement of reflective material makes it very unlikely to function as an effective tapetum lucidum (Table 2). The few tapetal cells demonstrate a nonregular internal arrangement of membranes and apparently degenerative structures that differs greatly from the very regular, repeating pattern of reflective rodlets normally present within the cells of a developed tapetum cellulosum (Fig. 6b). The cause of this tapetal degeneration is

unknown but could be related to dietary insufficiencies in specific animals, or perhaps the genetics of inbreeding.[3]

Mammals – rodents

Paca (Cuniculus paca) A tapetum has only been reported in one rodent; the paca or spotted cavy (Table 2). The tapetum lucidum of the paca consists of several layers of ovoid-to-flattened cells within the superior choroid.[32,33] The electron-dense tapetal rodlets are typically uniform in diameter and highly organized in carnivores, but vary in size, shape, and orientation in the paca. Because the reflective material appears to be not highly ordered regarding size, orientation and spacing between the reflective units, the tapetum lucidum of the paca is unlikely to provide constructive interference and therefore produce a diffuse reflectance.[13]

Rat (Long Evans rat) A vestigial tapetum has been suggested in the hooded rat (*Long Evans rat*) for two reasons: this tapetum is localized in the superior hemisphere and the melanosone counts are very low in this dorsal area (Fig. 2, lane 1, #3).[34]

Mammals – cetacea

Grey seal (Halichoerus grypus) In the gray seal the tapetum lucidum is located in the choroid and overlays the entire effective fundus. It is composed of 30–35 layers of flattened polygonal cells at its thickest and is reduced to 15–20 layers of cells at the extreme periphery of the retina (Table 2). The thick tapetum and the fact that it overlays the entire fundus may be the result of the more three-dimensional environment in where this aquatic mammal resides. The tapetal cells show less reflective material within their cytoplasm at the scleral border of the tapetum, and are gradually replaced by melanin-containing choroidal cells. The bulk of the cytoplasm of the tapetal cells is filled with numerous membrane-bound rodlets of reflective material of unknown composition. These rodlets are 5–6 μm in length and 0.1 μm in width. They are arranged in an organized hexagonal-lattice pattern with a space of about 0.15 μm separating adjacent rodlets (Table 2).[4]

Tapetum lucidum fibrosum

All hoofed animals or ungulates, as well as whales (Fig. 8d), some marsupials, and one monkey (*Aotes*) are reported to possess a tapetum fibrosum.[13,35,36] In ungulates, closely and regularly arranged collagen fibers comprise the tapetum, which is often referred to as a fibrous tapetum (Fig. 1). The fibrous tapetum is basically acellular except for occasional fibrocytes (Fig. 2). The collagen fibrils are organized into well-ordered lamellae that branch and interconnect with adjacent lamellae at the same level, being parallel with the retinal surface.[2]

Cows The bovine tapetum fibrosum is situated in the choroid and restricted mainly to the superior fundus.[36] Over the central and mid-region of the tapetum the retinal epithelial layer is completely unpigmented, whereas over the peripheral tapetum, and certainly in the nontapetal periphery of the retina, the RE is moderately to heavily pigmented. The bovine tapetum appears blue in color (Fig. 2, lane 4, #4). The actual reflective material of the bovine tapetum is a large array of extracellular collagen fibrils arranged in lamellae of varying thickness. Fibrocytes are located at the borders of these lamellea. To date, collagen is the only fiber type reported in tapeta fibrosa. The collagen fibrils are arranged parallel to the surface of the tapetum, at a right angle to incoming light. The collagen fibrils display the typical cross-striations of native collagen at about 640 Å, and are fairly uniform in diameter at about 0.2 μm. They seem to be arranged in a flattened hexagonal array, with individual fibrils being separated by a center-to-center spacing of about 0.2 μm (Table 2). At the retinal edge of the tapetum, a rich vascularized lamella containing the choriocapillaris separates the tapetum from Bruch's membrane. Blood vessels from the pigmented outer region of the choroid penetrate the tapetum fibrosum to supply the choriocapillaris adjacent to Bruch's membrane. These penetrating blood vessels pass through the tapetal region parallel to the incoming light very close to a right angle. The bovine choriocapillaris, while abutting directly against Bruch's membrane, does not indent this membrane nor the retinal epithelial layer.[36]

Sheep and goat The sheep's tapetum reflects a greenish blue color in contrast to the adjoining regions of dense black pigmented choroid.[37] The tapetum is essentially a horizontal strip in shape, and its lower edge just touches the point of entry of the optic nerve (Fig. 2, lane 4, #2). The upper edge is a more complex shape, and is less clearly defined. The tapetum consists of a layer of collagen fibrils (100–200 μm in depth), in which a few fibroblats are present (Fig. 8b).[23] These collagen fibers are 150 nm in diameter and are regularly arranged with cross banding, in layers. Several hundred of the lamellae or layers (600–740 layers) are estimated to comprise the fibrous tapetum of the sheep.[37] Individual layers of fibrils all run in a longitudinal direction, and are arranged in a hexagonal pattern with the direction of light at right angles to a side of the hexagon. The layers of fibrils are frequently separated by cells which lie parallel to the retinal surface (pigment cells, fibroblasts, smooth cells). There is a maximum of 140 rows of collagen separated by 9–16 cellular layers. The fibrils within a row are separated from each other by a space of 67 nm, and the rows are separated from each other by a space of 80 nm[2,23,37] The spacing between the fibrils is 180 nm and does not seem to change with depth (Table 2). The spacing between the rows appears to be more constant than the diameter of the fibrils. In the nontapetal areas, melanosomes are numerous, whereas over the central tapetum fibrosum they are absent.[38]

The goat has a tapetum similar in shape to the sheep (Fig. 2, lane 4, #3). The penetrating blood vessels are less uniformly arranged than in the cow, and even less than those of the cat and dog tapetum.[23]

Horses The fibrous tapetum in the horse is composed of a layer of bundles of laminated areolar (loose) connective tissue with an iridescent surface. There are four or five layers of these fibers. The central tapetum of the horse is up to 30 microns thick (Fig. 8a). It extends horizontally from the surface of the optic disc almost to the equator, and to a comparable distance vertically above the optic disc to assume a rounded triangle or semicircle (Fig. 2, lane 4, #1 and 2). The choroidal capillaries penetrate the tapetum at right angles to the collagen lamellae and they are called 'Stars of Winslow' when observed end-on ophthalmoscopically.[39]

DISCUSSION

Tapetal color varies with species, breed, age, coat color and amount of pigmentation in the eye and skin (Fig. 2). Structure, organization and composition of the tapetum also vary from species to species (Tables 1 and 2). Despite these differences, however, all act to increase retinal sensitivity by reflecting light back through the photoreceptor layer.[2]

Physical properties of the tapetum lucidum: reflectivity
The high light reflectance of a tapetum is the result of thin-film interference. The tapetal structure consists of several alternative layers of high and low refractive index material whose thicknesses are compatible with the wavelength of light (one quarter of the wavelength of the light is the ideal thickness and it would give the best reflectivity). At each interface in such a structure, a certain proportion of the incident light is reflected and, depending on the thickness of the layers and the wavelength being considered, the contributions from each interface interfere either constructively or destructively.[19] The problem of producing efficient reflection in a biologic context is most often solved by arranging material with a higher refractive index in a medium with a lower refractive index. If the refractive material is randomly arranged, diffuse reflectance will occur. If, however, the higher refractive index material is of uniform size, orderly arranged, and separated by specific and precise spacing, the small number of reflectances will sum in a more constructive manner and a higher overall reflectance will be achieved.[36] Denton has indicated that in an ideal theoretical model of constructive interference, five layers of reflective material would give close to 75% reflection.[14] Land states that for most biologic systems the reflectance will approach 100% after 10–20 layers.[19] The difference between actual and ideal reflectance would seem to indicate that constructive interference in a biologic context is far from perfect. Structures such as bloods vessels, nuclei of cells, and imperfections in spacing and thickness of the reflective material probably all interfere with reflectance, and therefore more layers are presumably required to create an effective tapetum lucidum.[5,17]

From these different studies it appears that the extracellular structures in the tapetum fibrosum, and the endocellular ones in the tapetum cellulosum and retinal tapetum are identical in their spatial arrangement (Fig. 1). It therefore seems that tapetal types have the same general reflective mechanism regardless of their composition (Tables 1 and 2). It is interesting to note that the cellular rodlets present substantial chemical differences, compared to the collagen fibrils. The diverse chemical nature of the different tapeta may be responsible for determining different refractive indices. This factor may play a role in the utilization of different wavelengths of light by the animals according to their feeding behavior.

The hexagonal packing noted in the tapetum fibrosum and in the tapetum cellulosum seems to be the most efficient method to closely assemble cylindrical structures like collagen fibrils or rodlets of reflective material in order to achieve the best spatial arrangement. The relatively small differences recorded in diameter and spacing may indicate a small difference in the optimal wavelength of reflection between theses species, or might be due to the specimen fixation.

Specifically, the observed dimensions and spacing of the collagen fibrils found in the bovine tapetum are commensurate with the principles of constructive interference. The dimensions and spacing observed for the collagen fibrils in the bovine eye are similar to those noted in the sheep and goat. The dimensions and spacing of collagen fibrils in the tapetum fibrosum are largely similar to the dimensions and spacing of the reflective rodlets in the tapetum cellulosum of the cat, ferret and dog.[3,36]

Nevertheless, spatial variations exist. In the cat, the tapetal cells contain more precisely packed rodlets than those in the ferret and dog (Fig. 7). The fact that the cat has a relatively high number of layers (15–20) coupled with a great efficiency of packing may explain the very great reflectance of the feline tapetum cellulosum.[5] Rodieck has indicated that the cat's eye reflects about 130 times more light than the human eye.[40] The dog tapetum, besides reflecting light of a different wavelength, does so less efficiently. While the reflecting rodlets of the dog are similar in dimensions to those of the cat (Table 2), they appear to be more closely packed, resulting in a unique value for the wavelength of maximal reflectance. In addition, the canine tapetal rodlets are less precisely oriented than those of the cat, which may result in a less efficient reflectance from the dog tapetum (Fig. 7). How much more light the feline tapetum reflects than the canine tapetum is not known.

The thickness of the tapetum cellulosum varies also from species to species, as described earlier (Table 2). The relatively small differences in rodlet diameter and spacing may indicate a small difference in the optimal wavelengths of reflection between these species. While species differences certainly exist with regard to tapetal thickness and rodlet composition and organization, the intraspecific differences that have been observed are probably due to breed variance, sampling of different areas and indeed to developmental stages.

In all species with a choroidal tapetum (either cellulosum or fibrosum), the retinal epithelium overlying at least the central region of the tapetum is nonpigmented (Fig. 1). This occurrence obviously allows for free passage of light to

and from the tapetum. Pigment in this location would be counterproductive to the function of a tapetum.

Among the vertebrates reported with a retinal tapetum are a number of teleosts, crocodilians, the fruit bat, and the opossum (Fig. 1). For these species, the tapetal material is located within the retinal epithelium itself, hence positioning the reflecting material closer to the photoreceptor cells.

Origin of the tapetal cells in tapeta cellulosa

The origin of the tapetal cells is still unknown. Some authors believe the cells come from differentiation of connective tissue cells[41,42] and some think they are modified melanocytes.[29,43] Some investigators have proposed that tapetal cells and choroidal melanocytes have a common origin from the cells of the mesoderm which invade the primitive optic cup. One piece of evidence to support this theory is that tapetal cells adjacent to the choroid frequently contain both rods characteristic of the tapetum and the pigment granules common to the choroidal melanocytes (Fig. 9). There is therefore coexistence of the tapetal rodlets and melanin granules in the same cells.[6,8,43]

Cytochemical data have shown that the rodlets observed in the cat are composed of melanin, and their development follows a similar course to that described in other melanogenic systems. The rodlet formation involves similar enzymatic mechanisms to those concerned in the construction of melanosomes.[29] There are striking morphologic resemblances between the structural features of the specific inclusions in the tapetal cells and those of developing melanosomes in melanocytes. However, the tapetal cells exhibit a new melanogenic system in which the melaninic structures have a constant diameter and a regular pattern. Tapetal cells represent uniquely differentiated and highly specialized choroidal melanocytes. It is interesting to note that, by the combination of structural and compositional modifications of the melanosomes and their arrangement in the tapetal cells, these highly specialized melanocytes have adopted the capacity to reflect light instead of absorbing it.[6,43]

Chemical properties of the tapetum lucidum

The reflective material varies widely in chemical composition from species to species. The collagen is the reflective compound in tapeta fibrosa. It has been evaluated that collagen constituted 65% of the dry weight of the sheep tapetum, with a significant amount of amino acids such as proline, hydroxyproline, lysine and hydroxylysine.[37] Among the reflective materials noted in tapeta cellulosa are guanine, cholesterol, zinc cysteine, riboflavin, pteridine, and a variety of lipids (Table 2). A high level of zinc (i.e. zinc cysteine) is present in the tapetal cells of both the dog and ferret tapeta, whereas the tapetal cells contain abundant riboflavin in the cat and the lemur[26,28] and abundant sulfur in the paca.[26] Riboflavin absorbs light at a low wavelength and fluoresces at 520 nm, which is approximately the maximum absorption of the rhodospin (500 nm). Thus, the cat and lemur tapeta appear to not only reflect light but amplify it into a more useful range by fluorescence.[5]

The diverse chemical nature of the different tapeta may be responsible for determining different refractive indices. This factor may play a role in the utilization of different wavelengths of light by carnivores and herbivores. In fact, it is well known that carnivores spend most of their active life at night (crespucular), while herbivores lead a more diurnal life (arrhythmic).[1,17]

Vascularization of the tapetum lucidum and related structures

The choriocapillaris consists of a single layer of large-caliber capillaries which are heavily fenestrated. The choriocapillaris noted in various species with a tapetum cellulosum is deeply indented into the RPE layer over the tapetal area. As the choriocapillaris is not indented into the RPE of species with a tapetum fibrosum, it is thought that this indenting of the choriocapillaris into the RPE over a tapetum cellulosum is mainly due to the rigidity of the reflective material within the tapetal cells.[3,5,25] This may indicate that the choriocapillaris is also involved in the metabolic support of the tapetum which is relatively poorly vascularized.[4,36] The radial alignment of the tapetal penetrating capillaries appears to be the best way to connect the choriocapillaris to both its supplying and draining systems, because this results in the least interference with tapetal reflectivity.[13] The 'Stars of Winslow' specifically describe the choroidal capillaries that penetrate the tapetum at right angles to the collagen lamellae and that can be observed ophthalmoscopically in horses. There are also choroidal capillaries that penetrate the tapetum at right angles to the long axes of the tapetal cells in carnivores. They can occasionally been ophthalmoscopically observed in cats, but rarely in dogs because of the brightness of the fundus and the lack of magnification with conventional ophthalmoscopes.

In most vertebrates Bruch's membrane is reported as a pentalaminate structure: the basal lamina of the choriocapillaris, the basal lamina of the retinal epithelium, and an inner and outer collagen layer with a central discontinuous elastic layer. In some species with a choroidal tapetum, Bruch's membrane may be reduced to only the two basal laminae. In teleosts Bruch's membrane is normally trilaminate (basal lamina of the choroid, basal lamina of the epithelium and a thick central collagenous layer).[27]

CONCLUSION

The tapetum lucidum represents a remarkable example of neural cell and tissue specialization as an adaptation to a dim light environment. This adaptation appears to have evolved on a number of separate occasions, and it is therefore not too surprising that both its location and structure, as well as the choice of reflective material are varied.[13]

Among mammals, variations are greatest within the carnivore family. These variations, which are entirely cellular in nature, may represent selective visual adaptations associated with their feeding behavior. These adaptations are probably in response to the use of specific wavelengths and amount of

reflectance required. Herbivores, on the other hand, appear to have evolved less remarkably with regard to the tapetum, having variations primarily directed to the amount of reflectance.

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