Characteristics of the eye of the Indian mongoose (*Herpestes auropunctatus*)

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The refractive state, optical structure, and intraocular muscles of the eye of the Indian mongoose, *Herpestes auropunctatus*, were examined using a variety of refractive and anatomical techniques. Additional observations concern the structure and function of the tapetum lucidum and the diurnal activity levels. The mongoose eye is emmetropic (zero refractive error), or nearly so, a surprising finding in view of the small (8.0 mm diameter) size of the eye and the fact that the small-eyed mammals seem to show varying degrees of apparent hyperopia. The optical media, particularly the size, shape, and relative location of the ocular lens, are those of a diurnal species. Accommodation, induced pharmacologically, is of a magnitude (11–13.5 diopters) normally associated with primates. The ciliary muscle consists of large and well-developed fascicles of longitudinal fibres. The iris muscles, especially the sphincter, are much larger, on a relative basis, than those of the human iris. The mongoose eye is characterized by the existence of an obvious bright green tapetum cellulosum located in the choroid. The spectral quality of the tapetal reflection matches spectral radiometric measures made in grasses that the animal inhabits. Activity observations confirm the strict diurnality of the mongoose. Though a tapetum is normally associated with nocturnal vision, the mongoose tapetum may be of use in ensuring that the light reflected by the dense vegetation and incident to the eye stimulates cones with relatively high stimulus thresholds.

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La réfraction et l'anatomie, structure de l'oeil et des muscles intraoculaires, ont été étudiées chez la mangouste *Herpestes auropunctatus*. La structure et le rôle du tapetum, de même que l'intensité de l'activité le jour, ont fait l'objet d'observations additionnelles. L'oeil de la mangouste est emmétrope (sans anomalie de réfraction) ou presque, ce qui est assez surprenant dans le cas d'un oeil aussi petit (8,0 mm de diamètre) lorsqu'on sait que les mammifères à petits yeux montrent ordinairement des signes d'hypermétropie. Les milieux optiques, particulièrement la taille, la forme et la position relative du cristallin, sont ceux d'une espèce diurne. L'accommodation, provoquée par des méthodes pharmacologiques, s'est avérée d'une amplitude (11–13,5 dioptries) normalement associée aux primates. Le muscle ciliaire est constitué de gros faisceaux bien développés de fibres longitudinales. Les muscles de l'iris, particulièrement le sphincter, sont relativement beaucoup plus gros que ceux de l'iris humain. L'oeil de la mangouste se caractérise par la présence d'un tapetum cellulosum vert brillant, bien apparent, dans la choroïde. Le spectre de réflection du tapetum concorde avec les mesures radiométriques spectrales des herbes où vit l'animal. L'observation des activités de l'animal confirme la nature strictement diurne de la mangouste. Bien que le tapetum soit une structure normalement associée à une vision nocturne, celui de la mangouste sert probablement à assurer que la lumière reflétée par la végétation très dense et la lumière incidente directe stimulent les cônes à seuils de sensibilité relativement élevés.

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Introduction

The information available concerning the characteristics of the mammalian eye deals primarily with eyes of a relatively small number of species, mainly primates, as well as a number of domesticated and laboratory animals (Walls 1942; Hughes 1977; Sivak 1978). The viverrids, the largest family (81 species) of the order Carnivora, includes the civets, genets, and mongooses (Vaughn 1972). The subfamily Herpestinae, which includes the mongooses, consists of 41 species (Morris 1965). Compared with the eyes of diurnal primates, those of the mongooses are of particular interest because of the animals' diurnal lifestyle (Matthews 1971; Kavanau and Ramos 1975).

The Indian mongoose, *Herpestes auropunctatus*, is native to the shrubby grasslands of Asia and has been widely introduced in the Caribbean and Pacific regions. It is a vigorous and successful predator, opportunistically preying on most forms of animal life. The mongoose seems to hunt primarily by sight in diurnal light conditions. This point is highlighted by the retinal study of viverrids by Dücker (1959) and by the recent work of Hope *et al.* (1981), who report that the retina of *H. auropunctatus* is potentially useful for research requiring rod and cone populations numerically comparable to those of primates. This study describes the refractive properties and accommodative mechanism of the eye of the Indian mongoose. Additional observations deal with the structure and function of the tapetum lucidum and the diurnal activity levels.

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Methods

Refractive error was measured retinoscopically with trial lenses. In retinoscopy, a light source reflected by a mirror is moved across the pupil. The speed and direction of the resulting pupil reflection is used as an objective measure of refractive state (Grosvenor 1982). Measurements were carried out on anaesthetized (chloroform) and unanaesthetized animals by means of a conventional halogen-source retinoscope, as well as a retinoscope in which the source was limited to specific portions of the visible spectrum (red and blue). The latter was used to determine the axial chromatic aberration of the eye, i.e., the degree to which the eye's refractive error is wavelength dependent (Bobier and Sivak 1978).

Accommodative ability was studied by artificially inducing accommodative refractive error changes with drugs. Refractive measurements were made on animals anaesthetized with chloroform and compared with measurements made following the topical application (to the cornea) of a parasympathomimetic (10% pilocarpine hydrochloride). This procedure also permitted the size of the dilated and constricted pupil to be studied.

We employed two additional refractive techniques to measure refractive state in an unanaesthetized caged animal. Photorefraction (orthogonal and isotropic) has been used to measure refractive state in a variety of vertebrates (Howland *et al.* 1983; Sivak and Howland 1987). The method is based on photographically estimating the size of the point spread reflex and computing the defocus from pupil size. Photorefractions were performed at a distance of 1 m when the animal's attention was attracted to the camera.

Corneal curvature was measured in vivo photokeratoscopically. In this procedure the corneal reflections of a series of concentric illuminated rings are photographed. Radius of curvature is calculated from the minification produced by the cornea as a convex mirror (Sivak *et al.* 1977). Asymmetry in corneal curvature (astigmatism, ±2 diopters) would show up as elliptical reflections of the rings.

Intraocular dimensions and curvatures were measured by way of a rapid freezing and sectioning procedure after the eyes were enucleated from two animals that were sacrificed with an overdose of chloroform. Each eye was frozen in acetone and dry ice, placed on a freezing microtome, and sectioned. A photograph was taken of the remaining block of tissue as each section (25 μm) was removed. The photograph indicating greatest lens thickness was considered to represent a sagittal section of the eye through the geometric centre of the lens. Radii of curvature were measured and calculated in accordance with the formula

$$r = \frac{y^2}{2s} + \frac{s}{2}$$

where r is the radius, s is the sagittal depth of a chord, and y is 1/2 of that chord.

An anatomical study of the intraocular muscles (iris muscles and ciliary muscle) was carried out using standard procedures for light microscopy. Three animals were sacrificed with an overdose of sodium pentobarbitol. The eyes were enucleated and fixed in 10% formalin. The ciliary body and iris were dissected and embedded in paraffin, sectioned, and stained with Goldner's trichrome stain.

Additional ocular tissue, particularly the retina–choroid border, was prepared for electron microscopy in an effort to examine the location of the particularly obvious tapetal reflection of the eye of the Indian mongoose. In this case, the tissue was fixed in glutaraldehyde, infiltrated with osmium, dehydrogenated, embedded in plastic (Epon), and sectioned.

In an effort to characterize the spectral quality of the tapetal reflection, a series of fundus photographs were taken while an animal was anaesthetized with chloroform. The photographs were taken with a hand-held fundus camera (Nikon) and standard colour film (Kodachrome X).

An approximate measure of spectral reflectance of the tapetum was obtained by photographing the fundus reflex through a diffraction grating, using an isotropic photorefractor attachment and a tungsten source. The spectra were recorded on panchromatic Kodak recording film and scanned with a microdensitometer. Relative film density was measured across the visible spectrum. The spectral scale was calibrated using an artificial eye and interference filters.

A spectral radiometer (Spectron) was used to characterize the spectral quality of the grassy Caribbean environment inhabited by the Indian mongoose in the western hemisphere. Measurements were made with the light-sensitive probe pointing horizontally within vegetation. Comparative measurements were made for green verdant areas, grass that was turning brown, and a sheet of white paper. Light intensities were measured with a GE type 213 light meter.

Finally, daily activity patterns of captive Indian mongooses were determined with a deep-red light beam and photocell. Interruption of the light beam activated an electronic counter which summed and printed hourly results. In captive studies, six mongooses were maintained separately in cages exposed to natural lighting and weather conditions on St. Croix, U.S. Virgin Islands. The light beam bisected the living space of the mongooses. The activity of a wild population of about 20 animals habituated to visiting a feeder was recorded by installing the photocell apparatus across the feeder entrance (Nellis and Everard 1983).

Results

Refraction and accommodation

The refractive and accommodative findings of this study vary substantially from the measurements expected for small mammals. Measurements of refractive state made on four anaesthetized animals show emmetropia (no refractive error) or slight amounts of myopia and hyperopia. Values for seven eyes range from +0.50 to −1.50 diopters, the average being −0.14 diopters. A bright green tapetal reflection from the fundus made viewing of the retinoscopic reflex difficult. The reflex was easier to see when the retinoscopy was performed through colored filters. Measurements with red and blue (Kodak Wratten filters Nos. 25 and 47, with dominant wavelengths of 617 and 470 nm, respectively) indicate that the axial chromatic aberration of the mongoose eye amounts to approximately 2 diopters, the eye being emmetropic for a point in between.

Photorefractive results on the four unanaesthetized animals show a refractive state range of +2.00 to −2.00 diopters. This range is similar to that found by retinoscopy performed on two unanaesthetized mongooses.

The topical application of pilocarpine resulted in iris constriction as well as marked accommodative changes in refractive state. For the three eyes studied, these changes indicated accommodative abilities ranging from 11.0 to 13.5 diopters. Control measurements made with a 2.0-mm artificial pupil before the application of pilocarpine show that the pupil size does not significantly affect refractive measurements and therefore spherical aberration is not significant. In two cases the changes induced by pilocarpine were unilateral, whereas in one mongoose the refractive change was bilateral and equal, although pupil constriction was only noted in the eye to which pilocarpine was applied. Retinoscopy performed on an unanaesthetized and unrestrained mongoose indicated emmetropia or slight myopia for distances from the eye varying from 6 in. (1 in. = 25.4 mm) to 4 ft, a shift equivalent to about 6.5 diopters of accommodation.

The change in size and shape of the pupil is described as follows. The dilated pupil is approximately 3.80 mm in diameter and slightly oval, the long axis being horizontal. The visible onset of constriction occurs 5 min after application of the drug.

Full constriction takes place in 20 min. The constricted pupil is teardrop-shaped, with horizontal and vertical dimensions of 2.5 and 1.1 mm, respectively, the narrow end of the aperture being the nasal end.

Structure of the eye

The gross anatomy of the mongoose eye fits the description of a typical diurnal mammal given by Walls (1942). In contrast to a nocturnal eye such as that of the rat, in the mongoose eye the cornea occupies a relatively small proportion of the circumference of the ocular globe, and the crystalline lens is markedly nonspherical in shape (Fig. 1). Average values from frozen sections of four eyes indicate an axial diameter of the globe of 9.0 mm (8.8−9.1 mm). The cornea has a diameter of about 6.0 mm with a radius of curvature of approximately 3.5 mm. Corneal radius from photokeratoscopy (of three eyes) is 3.75 mm. Anterior and posterior lens radii are 3.40 (3.28−3.62) and 2.40 (2.18−2.55) mm, respectively.

Light-microscope sections of the ciliary body demonstrate the existence of a large ciliary muscle made up of fascicles of longitudinally oriented (iris root to choroid and ora serrata) smooth muscle cells (Fig. 2). This may be contrasted with the eye of a small nocturnal mammal, such as the rat, in which the ciliary muscle is virtually nonexistent (Walls 1942; Hughes 1977).

The iris muscles are also of an unusual size for a mammal. For example, in contrast to the sphincter muscle of the human iris, which is restricted to a region close to the pupil margin, that of the mongoose extends from the edge of the pupil to a position close to the root of the iris (Fig. 2). The dilator muscle is easily seen although portions are obscured by the cells of the pigmented epithelium of the iris. It has been shown that the large iris sphincter muscle of certain birds can assist the ciliary muscle in deforming the lens during accommodation (Levy and Sivak 1980). A similar mechanism has been suggested as a means of producing large accommodative changes in the eye of the otter to help compensate for the refractive loss of the cornea when the eye is in water (Walls 1942; Schusterman and Barrett 1973). Though the mongoose would not need the extensive refractive changes required by an aquatic mammal, it may have an accommodative mechanism superior to that normally described for mammals (Walls 1942).

An examination of the fundus of the Indian mongoose reveals the existence of a bright green tapetal reflection concentrated on the upper (dorsal) portion of the eye (Fig. 3). From a distance, the entire ocular reflex appears bright green. Electron microscopy demonstrates the existence of a multilayered tapetum cellulosum (Duke-Elder 1958) located in the choroid between the choriocapillaris and the rest of the choroidal vasculature (Fig. 4).

Relation between visual environment and tapetum

Radiometric measurements of grassy mongoose habitats show a broad spectral maximum at about 550 nm (Fig. 5). This measurement may be contrasted with a broader function for grass that is turning brown (roughly 550−650 nm) and for a sheet of white paper (roughly 450−650 nm). The fundus reflectance data show a broad spectral curve with a shallow peak at about 570 nm (Fig. 5). Light intensity at midday at the top of the grass canopy is over 60 hlx, whereas at the level of mongoose trails through the vegetation the light level at midday is 1−2 hlx.

Activity measures indicate that captive Indian mongooses are diurnal, but that they can become active at night for short periods if disturbed. Captive mongooses are late risers and are often found in a sleeping posture as late as 1 h after sunrise. Wild mongooses are strictly diurnal. The first feeder visits in the morning began when ambient light levels reached 0.5 hlx, and final visits in the afternoon occurred at about the same light level. Hundreds of hours of searching fields at night with powerful spotlights during other projects have never revealed an active mongoose after dark (Nellis and Everard 1983).

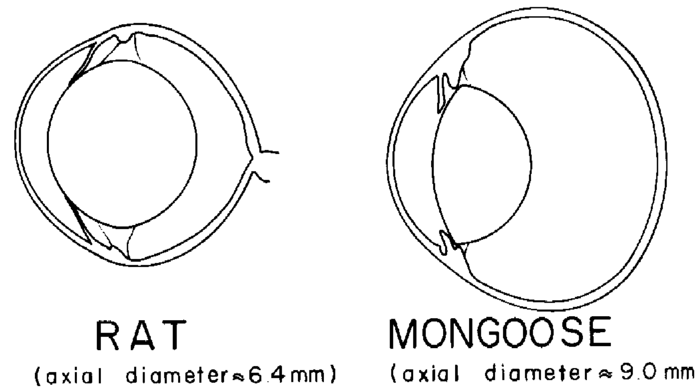

FIG. 1. A schematic comparison of the gross structure of the eye of the rat (a small nocturnal mammal) with that of the mongoose (a small diurnal mammal). The cross section of the rat eye is modified after Walls (1942).

Discussion

The results contrast strongly with common descriptions of mammalian ocular optics. For example, it is widely stated that with the exception of primates (and perhaps squirrels), mammals have little or no accommodative ability (Walls 1942; Duke-Elder 1958; Glickstein and Millodot 1970; Hughes 1977). Walls (1942) refers to the nocturnality of ancestral and lower-order mammals and the consequent emphasis on visual sensitivity at the expense of resolution ability. Diurnal groups such as the primates and the sciurids have had to be content with an indirect accommodative mechanism which is inferior to that of the majority of reptiles and birds. The findings presented in this paper indicate that this view may be an overgeneralized one. The possibility of accommodation of avian magnitudes in amphibious mammals such as the otter (Schusterman and Barrett 1973; Ballard 1987; Murphy *et al.* 1988), and in the mongoose, suggests that the mammalian accommodative mechanism is not uniform.

The findings of emmetropia or near emmetropia reported in this study is also unexpected. Small mammals are usually described as hyperopic (Walls 1942; Hughes 1977). The explanation accepted by some writers (Wisenfeld and Branchek 1976; Hughes 1977) was developed by Glickstein and Millodot (1970) and is based on the assumption that the reflected light used in retinoscopy emanates from the vitreous surface of the retina. The magnitude of the spurious hyperopia introduced would depend on the refractive importance of the separation between the receptor layer of the retina and its vitreous surface. As retinal thickness is relatively constant among mammals of varying sizes, the hyperopia introduced increases with decreasing eye size. On the basis of an 9.0-mm eye, the Indian mongoose should be hyperopic by 8 diopters.

An alternative explanation by Walls (1942) points out that the hyperopia is not spurious and is to be expected in nocturnal animals having eyes adapted for sensitivity (e.g., a large spherical lens in close proximity to the retina). However, the emmetropia found in this study may be due to the existence of

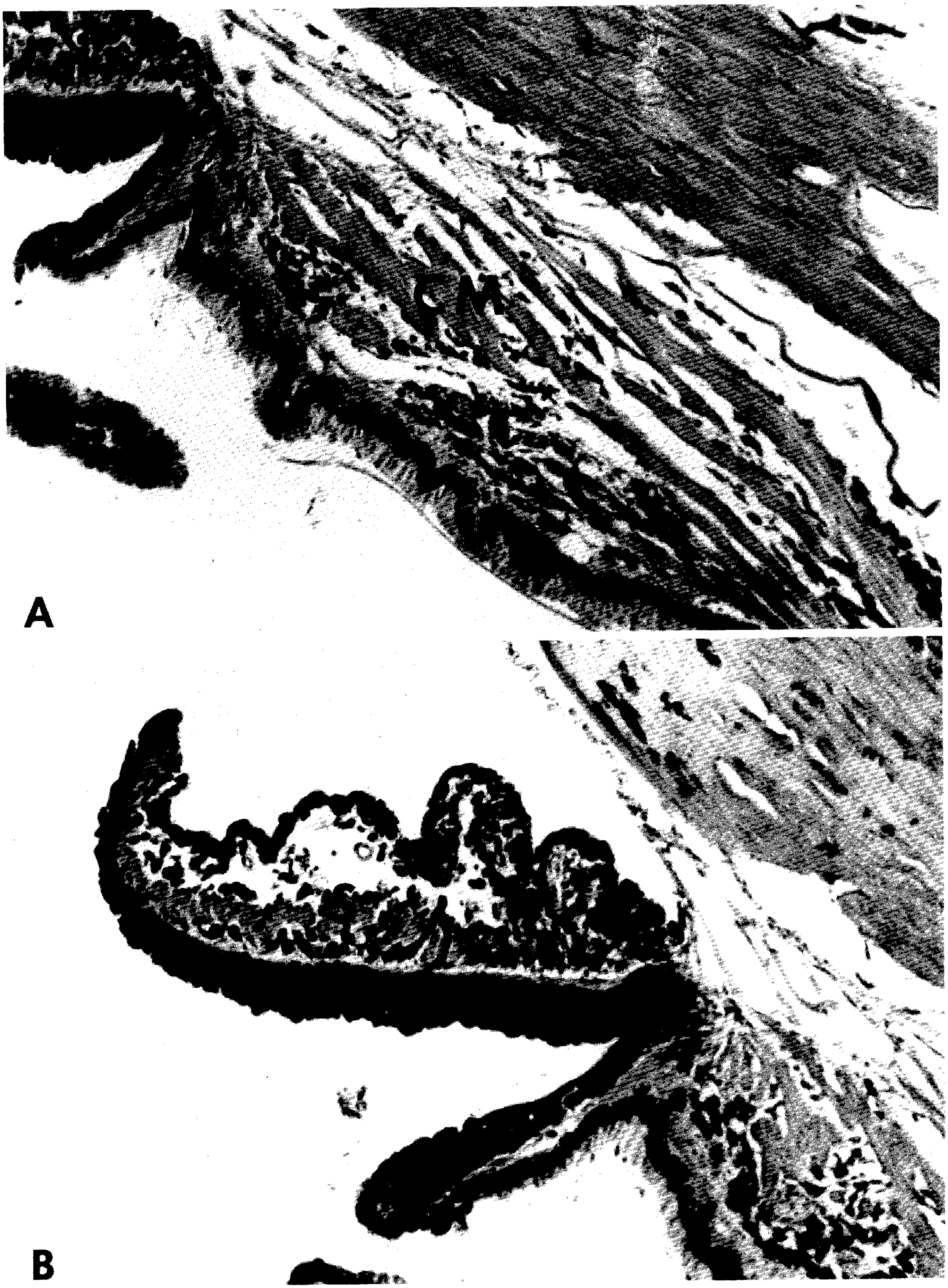

FIG. 2. Light microscope photographs of the ciliary body (A) and part of ciliary body with iris (B) of *Herpestes auropunctatus*. Note dense bundle of longitudinal muscle fibres (CM) below the ciliary epithelium and the large relative size of the sphincter muscle(s) of the iris. Approximately 100×.

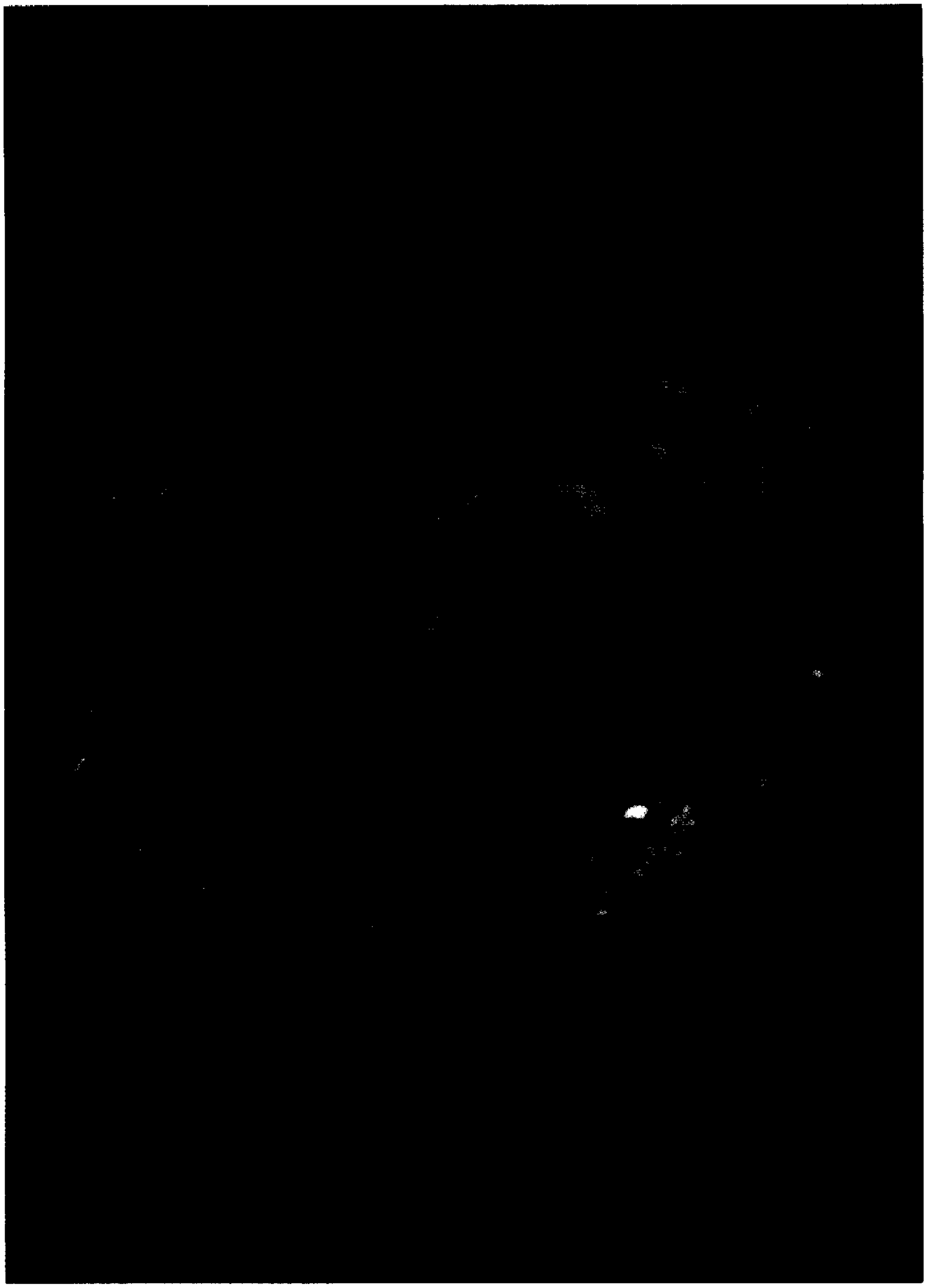

FIG. 3. Fundus photograph showing the bright green tapetal reflection.

a tapetum. Because the tapetum may be the source of the light used in retinoscopy and because it is located close to the retinal pigment epithelium and the retinal receptor layer, any spurious hyperopia is unlikely. The tapetal effect on retinoscopy might be explored in future work by comparing measures from varying portions of the retina in species in which the tapetum is restricted to a specific retinal region.

The activity observations confirm and complement the detailed experimental work of Kavanau and Ramos (1975), who found captive mongooses to be most active from 10:00 to 16:00. The total activity of the animals was over 99% diurnal, the balance taking place at twilight. No activity was recorded at night. This diurnal orientation is also demonstrated by the existence of a duplex retina in related species (Dücker 1959) and in *Herpestes auropunctatus*, in which 25–40% of the photoreceptors are cones, as in higher primates (Hope *et al.* 1981).

The presence of a well-developed tapetum lucidum may appear to be surprising for a diurnal animal because such structures are normally associated with nocturnal vision (Walls 1942; Duke-Elder 1958). However, the tapetum and the well-developed accommodative apparatus may be complementary factors related to chasing small, active prey (e.g., Orthoptera) in thick vegetation. The tapetum may be expected to enhance the photon density of the light reaching the retina from the grassy habitat, to stimulate cones with relatively high stimulus thresholds. The accommodative ability of the mongoose may be needed to allow continuous visual tracking of a target in a high-speed chase in a congested habitat. Thus, the mongoose eye appears to be well suited to the visual needs of the animal.

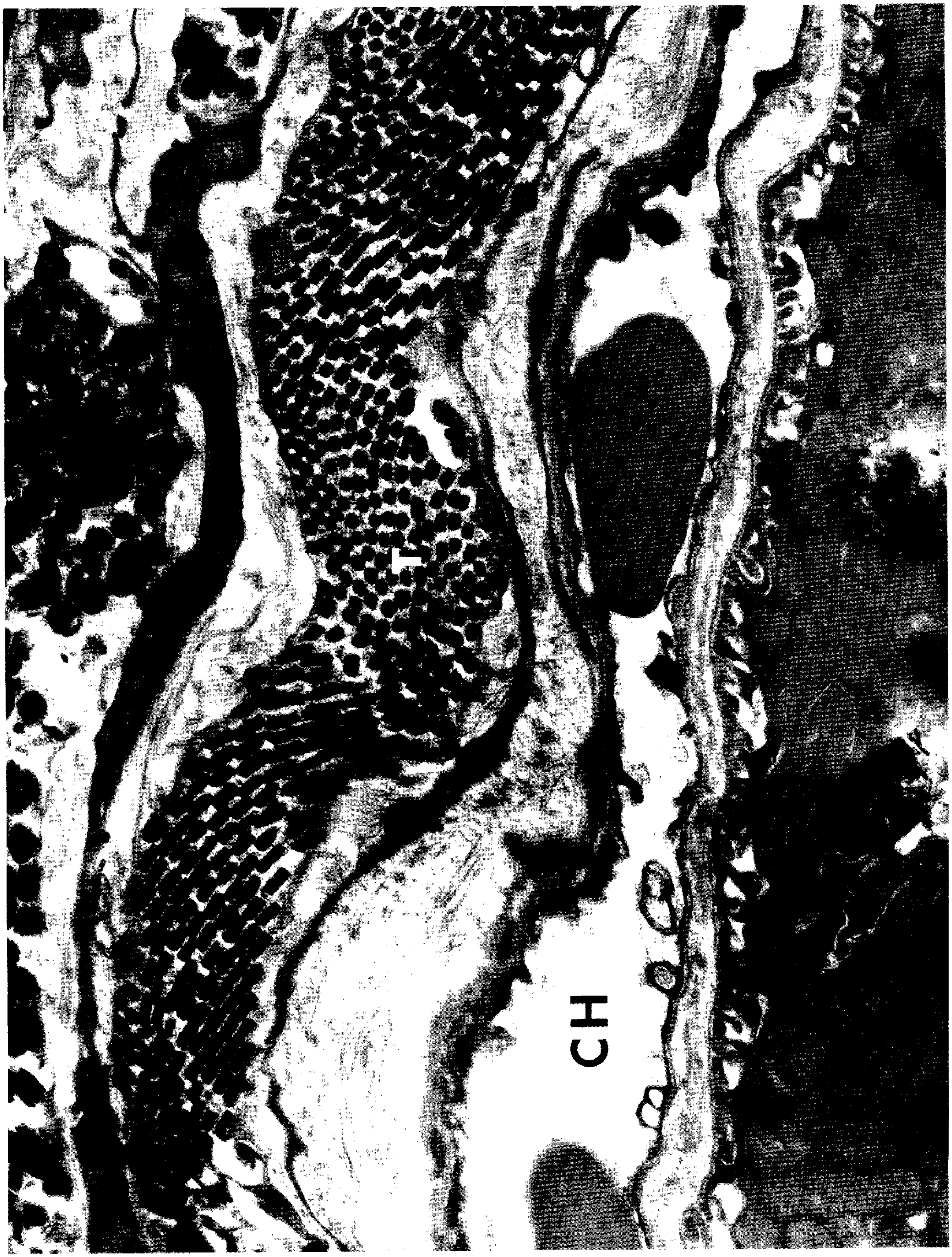

FIG. 4. Electron microscope photograph of choroidal retinal border, showing multilayered tapetal organization. T, tapetum; RPE, retinal pigment epithelium; CH, choriocapillaris. Approximately 17 000 ×.

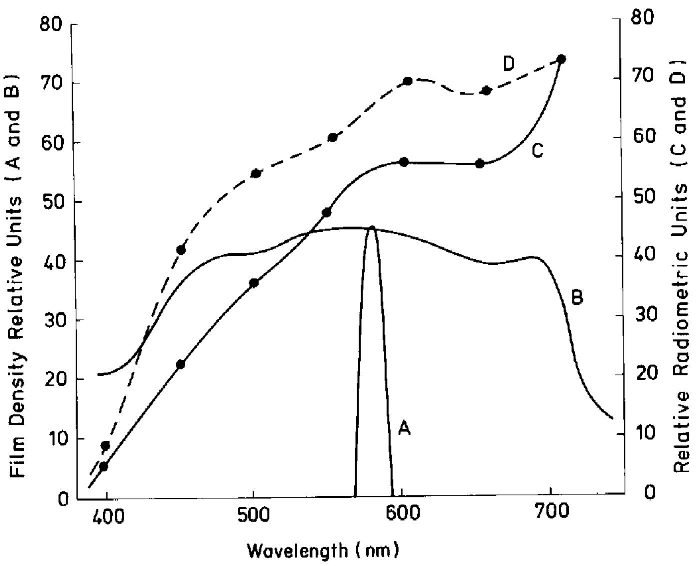

FIG. 5. Mongoose tapetal reflectance measures and spectral radiometric measurements of mongoose habitat: A, 577 nm calibrating interference filter for curve B; B, densitometric measurements of photograph of fundus reflex taken through diffraction grating. Because the film is panchromatic this curve approximates the relative spectral reflectance of the tapetum. C, relative spectral radiometric measurements of grassy mongoose habitat. D, relative spectral radiometric measurements from daylight reflected by a sheet of white paper. Curves C and D were normalized at 700 nm by dividing D by 25.

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