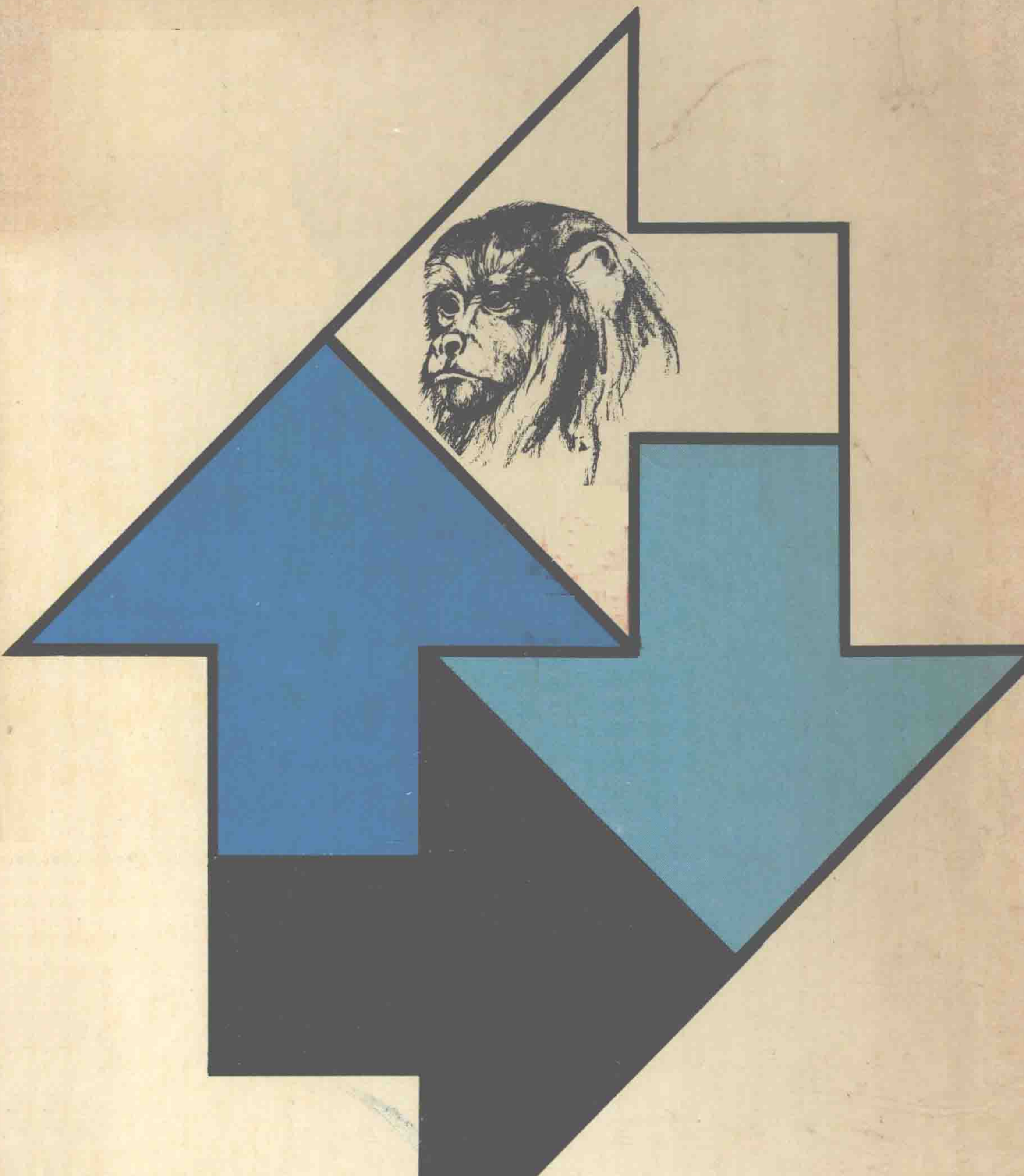
THE PRIMATE BRAIN

ADVANCES IN PRIMATOLOGY—VOL. 1



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ADVANCES IN PRIMATOLOGY
Volume 1

THE PRIMATE BRAIN

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PREFACE

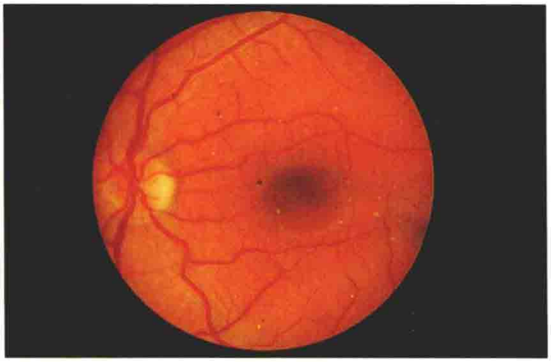
This is the first of a series of publications, each volume of which will contain the latest studies and critical appraisals on a specific topic in primatology and allied fields. The editors will make efforts to produce volumes that will be understandable and interesting to investigators in the field, graduate students, and others who may not share a professional interest in primatology. The articles will stress fundamental principles and, wherever possible, approach the subject from a phylogenetic or comparative point of view. The chapters will be more than exhaustive annotated bibliographies. Contributors have aimed at presenting factual material supplemented by discussions of the significant and provocative aspects of each topic. Other objectives of the series are to evaluate the concepts and to crystallize the guidelines in the field. In summary, the editors and the publisher hope that this series will provide an effective vehicle for communication among primatologists and those with allied interests.

In this initial volume several aspects of the nervous system of primates are presented. The authors of these chapters have established guidelines and standards for the future publications of the series. We thank them for their efforts and cooperation.

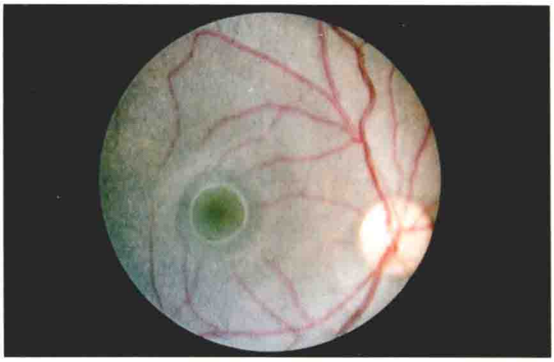
We wish to thank the publisher, especially Mr. Richard van Frank and Mr. William Belfer for their support, guidance, and professional assistance.

CHARLES R. NOBACK
WILLIAM MONTAGNA

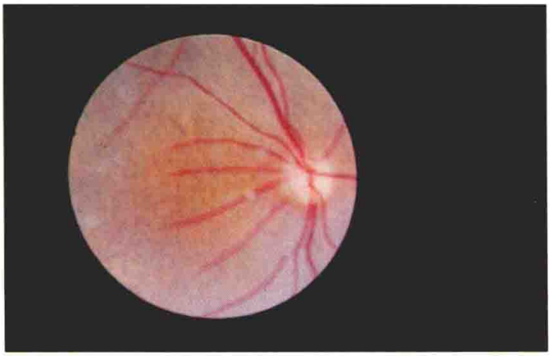
Plate I. Photographs of the fundus of a representative sample of primates.



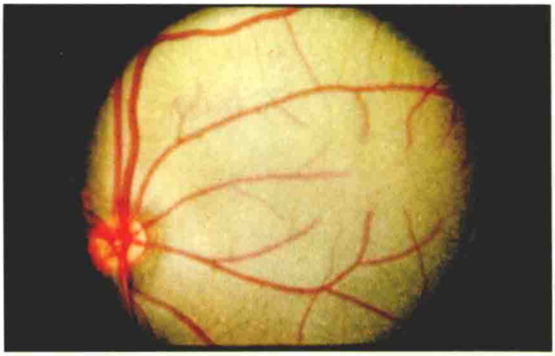
a. *Homo sapiens.* Lightly pigmented (blond) subject. Note light pigmentation of retina, large, round nerve head, large, slightly oval macula, smooth appearance of retinal surface, and termination of vessels outside fovea centralis.



b. *Colobus polykomos.* Characteristic higher primate retina. Note relatively lighter pigmentation which in part permitted photography of extremely well-defined macular ring reflex. Macular area is quite regular, and nerve head is round as in human.

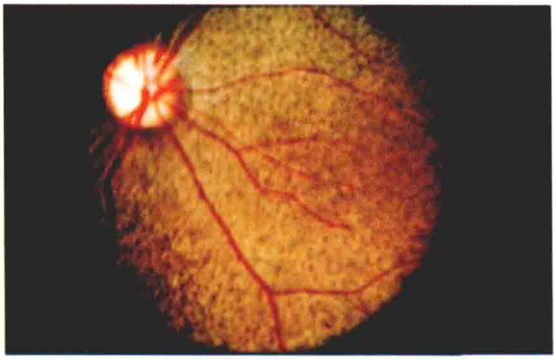


c. *Aotes trivirgatus.* This is the first nocturnal species represented, but it is more closely related to *Cebus* and *Saimiri* than to other nocturnal species. No macula or fovea can be visualized on a funduscopic examination, though a "foveal" area has been described in histological sections. Note spotted appearance of retina, which is found in most nocturnal species.

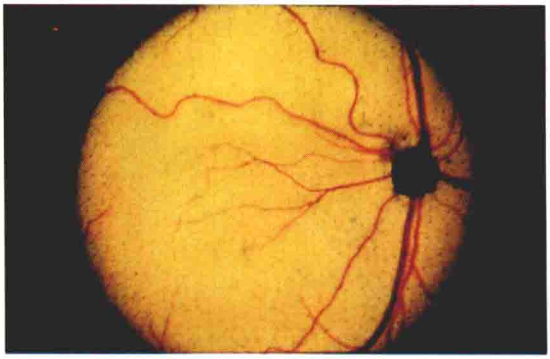


d. *Tarsius syrichta.* Highest of the prosimians represented here. This eye is unique among nocturnal species in revealing a macular ring reflex and foveal spot (the photograph barely does justice to these features, which are most distinctly seen with an ophthalmoscope). Note the relatively small nerve head and complex intertwining of vessels as they emerge. The beginning of dense peripheral deposits of pigment can be seen in the temporal and inferior portions of the photograph.

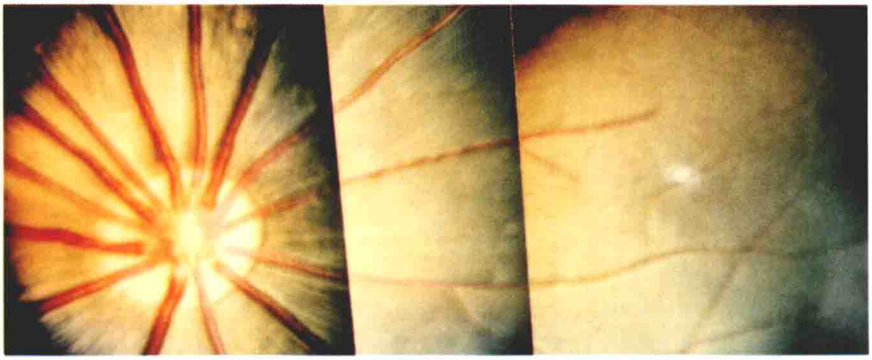
Plate I. (con't). Photographs of the fundus of a representative sample of primates.



e. *Lemur fulvis.* One of the more darkly pigmented retinas among the nocturnal species, this retina has an extremely mottled appearance. Dense accumulation of pigment may be noted just below the nerve head. The periphery of this retina (not shown in Plate) is almost black due to the density of the pigment.



f. *Nycticebus coucang.* This is the most highly reflective of the primate retinas shown. Use of neutral density filters in order to photograph the major portion of the retina produced blacking out of the optic nerve head. Note small size of nerve head and relatively large distance between nerve head and central retinal area (as defined by terminal pattern of blood vessels).



g. *Tupaia glis.* Composite photograph from the nasal to temporal portions of the fundus. Note the spoke-like radiation of the vessels from the optic nerve head. The central retinal area is located temporarily (upper right corner) in this species.

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1

Morphology of the Primate Retina

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Introduction

The study of the central nervous system has tended more and more in recent years to focus on primates. The structure and function of the nervous system of humans are more similar to those of primates than to those of any other experimental animal. This same observation applies to the visual system in general and to its most peripheral representation, the retina. If we wish to generalize from experimental animals to humans, obviously we must use subjects for which such generalizations have some validity. In neuroanatomical, neurophysiological, neuropsychological, and biochemical investigations, primates are certainly the experimental subjects of choice.

The primates are predominantly visual animals. Although the other senses are well developed and quite acute, visual guidance of behavior is dominant under ordinary circumstances. Since the visual system and brain of higher primates closely resemble that of man, studies of vision in primates have increased tremendously in recent years. By far the majority of these studies have dealt with psychophysical and electrophysiological problems. Studies of the anatomy of the primate visual system, and the eye in particular, have been relatively sparse.

Among recent investigations of the primate eye, especially the retina, a large proportion have been electron microscopic studies, even though there is a dearth of light microscopic and gross morphological studies of the primate retina.

This review attempts to cover the comparative work done on the primate retina. We feel that it is reasonably comprehensive, particularly with respect to recent investigations, but is not exhaustive, since we have had to rely on secondary sources to some extent, particularly in relation to the very early investigations.

In researching studies of retinal structure, the names of a few investigators continually recur. These we believe represent the better, more detailed, and most comprehensive studies done. Where a given species has been studied by several investigators, we have attempted to present a consistent description of that retina. We have also tried to present some historical perspective in the investigation of various species and, where possible, have included the major areas of agreement and disagreement with respect to the characteristics of retinal structure.

Unfortunately there are a number of problems which are not easily resolved. Species designations are not always clear, and the work of earlier investigators, using different species designations, is sometimes impossible to correlate with later investigations. Where it has been possible to identify a species with surety, we have designated it according to current taxonomy (Hill, 1953, 1955, 1957, 1960, 1962, 1966; Walker et al., 1964; Buettner-Janusch, 1966; Napier and Napier, 1967). Often the material on which some reports are based consisted of old or poorly fixed eyes, and the interpretation of findings involved a very large element of judgement on the part of the investigator. We have evaluated these findings and attempted to present as accurate a picture of the retina as possible.

In addition to reviewing the work on retinal histology, we have included funduscopic studies of the retinas of various primates. This provides another useful and informative approach to the study of the primate retina.

Finally, we will discuss individual features of the primate retina, summarizing what is known and what remains unknown and indicating special problems requiring further study.

Comparative Anatomical Studies of Primate Retinas

PROSIMII

Tupaiiformes. Most authors agree that the retina of *Tupaia* is a diurnal type predominantly cone retina (Castenholz, 1965; Rohen, 1962; Rohen and Castenholz, 1967; Samorajski et al., 1966; Woollard, 1926).

The most detailed description of the retina of *Tupaia glis* is provided by Castenholz and is supported in its various details by other investigators.

The pigment epithelium is a single layer of cells throughout the retina and is uniformly heavily pigmented. In conformity with the cone structure of this retina, no tapetum lucidum is to be found.

The receptors are short thick cones that appear quite uniform across the retinal expanse. There is an increased density of receptors per unit area in the temporal retina (20 to 22 per 100 μ as contrasted with the nasal side (16 per 100 μ). The inner segments of the cones are longer (by 1.5 to 2 times) than are the outer segments. Among the prosimians, only *Lemur fulvis* shows such a proportion between inner and outer segments. In the other species studied, either the two segments tend to be approximately equal, or the outer segment exceeds the inner segment in length.

The cone nuclei of the outer nuclear layer form only one row throughout the retina, but again some differentiation between the nasal and temporal halves is found, the nuclei being elongated and oval on the temporal side and more rounded on the nasal side of the retina.

The outer plexiform layer is quite thin and shows no great differentiation between retinal areas.

The inner nuclear and inner plexiform layers are both well developed. The inner nuclear layer shows a differential nasal-temporal development. Temporally the bipolars form as many as eight rows of cells, while on the nasal side only six rows are found (Fig. 1).

The ganglion cell layer consists mostly of one row of cells, but there is a gradual increase in thickness temporally, and a fairly large area of the temporal retina contains four to five rows of ganglion cells.

The layer of nerve fibers increases in thickness nasally, reaching its greatest thickness around the nerve head.

Overall, the temporal retina is much thicker than the nasal half. A prominent area of about 2.5 mm in diameter located 3 to 4 mm temporal from the center of the papilla shows the greatest thickening. Castenholz (1965) describes this as a central "area-like" development, noting that no fovea-like depression is to be found.

This area centralis corresponds well to that which Wolin and Massopust (1967) described as a central retinal area of the fundus (Plate I, g).

Rohen and Castenholz (1967), by sectioning through the skull of *Tupaia*, including the eyes, have shown that the area-like retinal thickening is located in the relatively limited portion of the temporal retina which represents a binocular visual field. This provides additional anatomical support for the statements of Wolin and Massopust (1967) regarding the use of binocular vision by *Tupaia*.

The retinal vasculature shows a pattern unlike that of any of the other primates. The arteries and veins radiate out from the nerve head like the spokes of a wheel. Temporally in the fundus, however, there is a vascular free area which ophthalmoscopically looks much like a central visual area.

Rohen and Castenholz (1967) have also studied the retina of *Urogale everetti*. This retina is generally quite similar to that of *Tupaia glis* with the significant exception that no temporal specialized area equivalent to that of *Tupaia* was found.

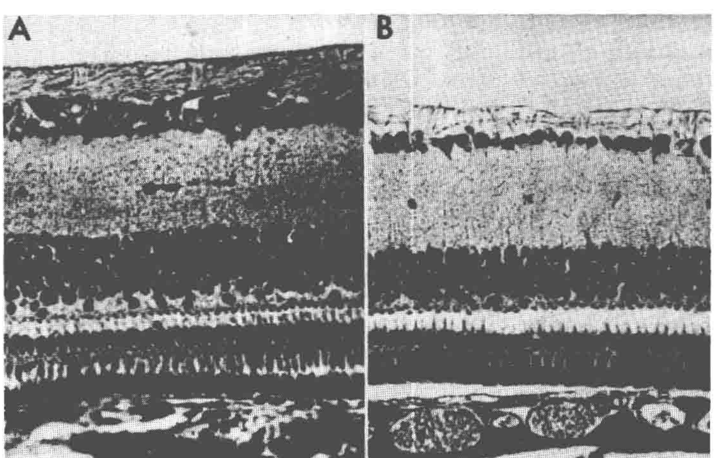

Figure 1. The retina of *Tupaia glis*. The temporal half (a) is thicker than the nasal half (b). From Castenholz, E. 1965. Z. Zellforsch., 65:646-661.

Lorisiformes. A variety of Lorisiformes are reported in the literature. These include *Loris tardigradus* (Rohen, 1962), *Nycticebus coucang* (Detwiler, 1943; Franz, 1911; Kolmer, 1930; Woollard, 1926), *Perodicticus potto* (Rohen, 1962), *Galago crassicaudatus* (Kolmer, 1930), *Galago "mala"* (Detwiler, 1939), *Galago demidovii* (Rohen, 1962), and *Galago senegalensis* (Castenholz, 1965; Rohen and Castenholz, 1967).

All of the Lorisiformes are basically nocturnal in habit, though some of them have been observed to be active in food seeking and other activities during the daytime (Hill, 1953; Walker et al., 1964).

The occurrence of a tapetum lucidum appears to be characteristic of the Lorisiformes. Both cellular and fibrous tapeta have been described. The distinction between the two types of tapeta, at least within the prosimians, may not, however, be as clear as is usually indicated. *Galago crassicaudatus* has a tapetum cellulosum (Kolmer, 1930; Rohen, 1962, also cites Luck, 1958, but gives no reference). *Perodicticus potto* is reported by Rohen (1962) to have a tapetum fibrosum. With respect to *Loris* and *Nycticebus,* however, the picture becomes less clear. Kolmer (1930) describes *Loris gracilis* (=*Loris tardigradus*) as having a small cellular tapetum, while Rohen (1962), in describing *Loris tardigradus,* reports a fibrous tapetum. Both Detwiler (1943) and Kolmer (1930) report studies of *Nycticebus coucang,* Detwiler designating the tapetum in this case as fibrous, while Kolmer classifies it as cellular.

Finally, with respect to *Galago senegalensis,* Rohen (1962) describes it as having a relatively thin tapetum cellulosum, as does Castenholz (1965). Rohen and Castenholz (1967, p. 113), however, list this same species as having a tapetum fibrosum.

We thus find agreement concerning the occurrence of a tapetum lucidum in all the Lorisiformes studied, but some lack of agreement regarding the structure of the tapetum in several species.

In the Lorisiformes the pigment epithelium is often differentially pigmented in the central fundus and in the periphery. The cells of the central portion of the pigment epithelium (where the tapetum is well developed) contain few if any pigment granules (Kolmer, 1930; Rohen, 1962; Detwiler, 1943), while in the periphery the cells are heavily pigmented.

Rarely does a definite report concerning the finding of cones in the retinas of any of these species appear. Kolmer (1930) reported apparently rudimentary, sparsely occurring small cones in the retina of *Nycticebus coucang* (Fig. 2). Rohen (1962) may also have seen some cone-like structures in the retina of *Loris tardigradus* but could not conclusively demonstrate them to be cones.

In all species reported, the outer nuclear layer is thicker than the inner layer. The differences between genera are not striking, the outer layer being reported as being 10 to 12 rows of cells and the inner nuclear layer 3 to 6 rows of cells in most species. Rohen (1962) reports 12 to 16 rows of cells in the outer nuclear layer of *Loris tardigradus.*

The inner reticular layer is characteristically thicker than the outer reticular layer in the genera reported. The differences between genera with respect to the thickness of these layers are more striking than is the case with reference to the nuclear layers. The extremes are *Galago crassicaudatus,* with an outer reticular layer 9 μ

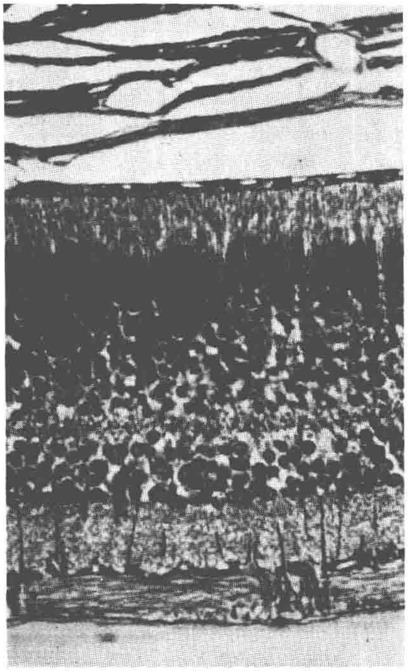

Figure 2. Retinal section from *Nycticebus coucang*. Note the thick outer nuclear layer, moderate inner nuclear layer, and sparse ganglion cells. From Kolmer, W. 1930. Z. Anat. Entwicklungsgesch., 93:679-722.

thick and inner reticular layer 20 μ thick (Rohen, 1962), and *Loris tardigradus*, with an outer reticular layer measuring 15 μ and an inner reticular layer of 40 μ.

The receptors are generally long (42 to 64 μ) and thin (1 to 1.5 μ), with the outer segments measuring approximately twice the length of the inner segments.

The ganglion cell layer contains only one row of cells in *Nycticebus coucang* (Rohen, 1962; Woollard, 1926) and in *Loris tardigradus* (Rohen, 1962), whereas in *Galago senegalensis* Rohen and Castenholz (1967) report a single row of ganglion cells peripherally, but three rows in the central area.

Lemuriformes. The lemurs are an unusual, varied, and little understood group of primates. The few species which survive well in captivity have aroused considerable interest and have been extensively studied. The remaining members of this infraorder are little known, some species being designated on the basis of observation by a few individuals. Only recently have the eyes of some of the lesser known species been subject to study (Rohen and Castenholz, 1967).

The Lemuriformes represented in the literature on the retina include *Lemur catta* (Castenholz, 1965; Kolmer, 1930; Rohen, 1962; Rohen and Castenholz, 1967), *Lemur fulvis* (Castenholz, 1965; Rohen, 1962; Rohen and Castenholz, 1967), *Lemur macaco* (Rohen, 1962), *Lemur rufifrons* (Kolmer, 1930), *Lemur variegatus* (Rohen, 1962; Rohen and Castenholz, 1967), *Lemur "niger"* (Woollard, 1927), Cheirogaleinae (Kolmer, 1930; Rohen and Castenholz, 1967), *Microcebus murinus, Indri indri, Avahi laniger*, and *Propithecus verreauxi* (Rohen and Castenholz, 1967).

Lemur catta is diurnal in habit (Walker et al., 1964). Nevertheless it has in many respects a retina well adapted to nocturnal life. It has a tapetum cellulosum in the central fundus, and the pigment epithelium contains little pigment except in the periphery beyond the boundaries of the tapetum (Kolmer, 1930; Rohen and Castenholz, 1967).

The receptors include rods and cones (Kolmer, 1930) with a ratio of about five rods to one cone (Fig. 3). Castenholz (1965) describes some cone-like structures in *Lemur catta* but does not regard them as true cones. Kolmer (1930) bases his judgment on both the receptor structure and the synaptic endings in the outer plexiform layer. He notes that the differentiation between the two types of receptors is not as obvious in the area centralis as it is more peripherally.

In support of Kolmer's report of cone receptors in this species, it should be noted that Bierens de Haan and Frima (1930) found evidence for some color perception in both *Lemur catta* and *Lemur mongoz*. The area centralis is well defined in this species, forming a dome-shaped thickening of the retina (Rohen and Castenholz, 1967). The receptors are longer in this region (40 μ), and the outer nuclear layer increases to 12 rows of nuclei. The other retinal layers also show an increase in thickness, and the ganglion cell layer which contains only 1 row of nuclei through the rest of the retina develops to 4 rows in this area. The overall increase in retinal thickness from the vicinity of the ora to the central area is about 65 percent.

Lemur fulvis is described by Rohen and Castenholz (1967) as having the largest eye of all the prosimians they investigated. It has an equatorial diameter of 18 mm. There is a central thickening of the retina produced by some thickening of all the respective layers. The ganglion cell layer, which consists of a single row of nuclei throughout, shows an increase in density of nuclei from 2 per 100 μ peripherally to 11 per 100 μ centrally. There are apparently some cone-like receptors, but there is doubt that these are true cones (Rohen, 1962; Rohen and Castenholz, 1967).

Rohen (1962) says that the existence of a tapetum cannot be definitely established in this species but that there is a lamellar layer of the choroid which could presumably be a tapetum. The pigment layer of the retina is relatively lacking in pigment in parts of the central area. Castenholz (1965) reports a multilayered tapetum cellulosum and a considerable reduction of pigmentation of the pigment layer in the central area. Rohen and Castenholz (1967), however, do not report the presence of a

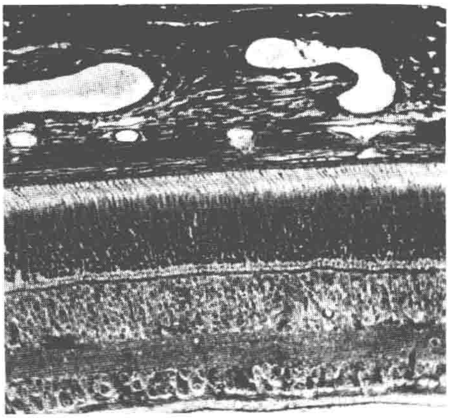

Figure 3. Retinal section from *Lemur catta*, taken near the central area. From Kolmer, W. 1930. Z. Anat. Entwicklungsgesch., 93: 679-722.

tapetum in *Lemur fulvis*, and they note that the periphery of the retina is lightly pigmented while the midfundus is unpigmented.

Kolmer (1930) describes the retina of *Lemur rufifrons* as a mixed rod and cone retina with numerous small cones interspersed between the rods, "resembling those seen in dogs and cats." The cones are more numerous in the central fundus and sparse in the peripheral retina. He finds no clear evidence of a specialized central area and no indication of a macula or fovea. Both deeply pigmented and weakly pigmented portions of the retina are described, but unfortunately he fails to specify their location. He also finds no evidence of tapetum in this species.

Kolmer (1930) describes the ganglion cell layer as being particularly poorly developed, with small sparsely located ganglion cells. He also notes the nerve fiber layer to be unusually thin and the Müllers cells to be well developed. In commenting on these findings, Rohen (1962) suggests that Kolmer may have been studying an eye(s) which showed the beginning of a retinal degeneration, such as he himself has occasionally found in other primates.

Woollard (1927) describes the retina of *Lemur niger*, which we are unable to place in current taxonomy. He describes it as "generally thin and without differentiation" and containing only rods in the receptor layer. The rods in the middle portion of the retina are much shorter than those of the periphery, but become elongated in the central portion. The outer nuclear layer consists of 10 rows centrally and 3 rows peripherally. The outer plexiform layer is so poorly developed that the inner and outer nuclear layers are almost in contact. The inner nuclear layer contains 5 or 6 rows of nuclei centrally but only 1 or 2 rows peripherally. The ganglion cell layer is 1 row throughout the retina, but the cells are closer together toward the center. Woollard finds no evidence of a macula or fovea and does not mention the occurrence of any tapetum, but he does comment on the moderate pigmentation of the pigment layer.

Kolmer (1930) describes the retina of *Lemur macaco* as a mixed rod and cone retina. Differences in size and staining of the receptor elements and well-differentiated synaptic endings in the outer plexiform layer provide the basis of this distinction. The pigment layer contains pigment throughout, and there is no evidence of a specialized central area or of any tapetum. Rohen (1962) gives essentially the same description of this retina.

Lemur variegatus is described by Rohen and Castenholz (1967). In general this retina is similar to that of *Lemur fulvis*. The presence of cones could not be determined with certainty although there is an area centralis which shows an increase in ganglion cells. The thickness of this part of the retina is only 7 percent greater than the surrounding area.

The retina has been described in two species of Cheirogaleinae. Kolmer (1930) describes the retina of *Cheirogaleus* (species undesignated) as being comprised predominantly of rods, small cones being seen only in the ratio of 1 to 1,000 rods. The outer nuclear layer is thicker than the inner, and the inner reticular layer is much better developed than the outer. From his illustration of this retina, the ganglion cells appear relatively sparse. The fundus is unpigmented, while a tapetum cellulosum composed of many layers of large flat cells is found, similar to that seen in the carnivores.