CHAPTER XV

THE EYES OF MAMMALS

The portrait of GEORGE LINDSAY JOHNSON (1853–1943) (Fig. 535) seems to be a suitable introduction to this chapter on the mammalian eye. He was one of those extraordinary people whose life was full of interest and odd happenings. Born in England, in Manchester, he received much of his early education in Germany and for that purpose was in Strasbourg when it was taken by the Germans in 1870. Thereafter he completed his medical studies and ophthalmic training in London, leaving in 1911 for South Africa where he died at the age of 90. In London he spent most of his spare time in the Zoological Gardens where he studied intensively the comparative anatomy of the eye, making contributions to the Royal Society on the eyes of Reptiles, Amphibians and Mammals. This interest he maintained to the end. So enthusiastic, indeed, was he that at an advanced age, determined to observe the fundus of the whale in life, he joined a whaling expedition, had a special crane built on the deck of the ship and had himself lowered over the back of the animal so that he could sketch its fundus. His *Pocket Atlas of the Fundus Oculi* is well known ; and his extraordinary versatility is exemplified in the many optical instruments which he devised as well as his pioneer work in colour photography, a subject in which he maintained an interest to the end of his life.

MAMMALIA, the highest class of the Vertebrates, have evolved from primitive Reptiles on diverging lines from the Birds[1]; both classes show high adaptations, and if the Birds possess the air, Mammals possess the earth although a few have taken to the air and more to the trees, while others have become amphibious or aquatic. The Mammals, however, have two distinctive peculiarities—the elaboration of the brain and the intimate organic connection between mother and offspring. They possess in common several characteristic features—a covering of hair, a diaphragm and a four-chambered heart, three auditory ossicles and a three-chambered ear, a single jaw-bone, and—a circumstance peculiar to Mammals—the young are nourished by milk secreted from the female mammary gland. The eyes are not so fully developed as those of Birds, but their comparative anatomical simplicity is more than compensated functionally by the efficiency of the central nervous organization of vision.

From the ocular point of view—and from practically every other point of view—the extant members of the class are divided into three subclasses, which, it should be remembered, are not linearly derived the one from the other :

(1) The PROTOTHERIA or MONOTREMES which are oviparous, the young being hatched from eggs outside the body.

(2) The METATHERIA or MARSUPIALS, in which the young are born in an immature state and are (generally but not invariably) nourished and protected for some time in an external pouch (or marsupium).

(3) The EUTHERIA or PLACENTALS, in which the young are nourished within the uterus through the placenta until development is far advanced. It is among the Placentals that cerebral advancement begins to be marked.

[1] p. 234.

Sept. 17/1930

Yours most sincerely
Geo Lindsay Johnson

FIG. 535.—GEORGE LINDSAY JOHNSON (1853–1943).

Fig. 536.—The Platypus, *Ornithorhynchus* (from Burton's *Story of Animal
Life*, Elsevier Pub. Co.).

Fig. 537.—The Echidna, *Tachyglossus* (from Burton's *Story of Animal
Life*, Elsevier Pub. Co.).

The eyes of these three types differ considerably, those of the first two, particularly the Monotremes, exhibiting many features characteristic of their reptilian ancestors adapted for nocturnality.

THE MONOTREME EYE

THE MONOTREMES are the most primitive of Mammals and include two types (Figs. 536–7) : the duck-mole or duck-billed platypus (*Ornithorhynchus*), found in the rivers and lakes of Australia and Tasmania, a shy creature with an enormous flat bill, which spends most of its time grubbing for small animals in the muddy bottoms ; and the spiny ant-eaters (the echidna, *Tachyglossus*, found in Australia, New Zealand and New Guinea, and its near relative, *Zaglossus*, found only in New Guinea), nocturnal ant-eating creatures burrowing in rocky regions. Neither relies primarily on vision ; the platypus relies largely on hearing, the eyes being closed when submerged, but the vision appears to be acute during
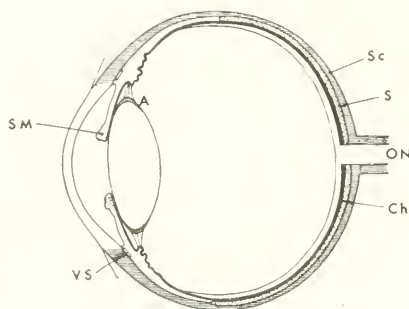

FIG. 538.—DIAGRAM OF A MONOTREME EYE.

A, small annular pad ; Ch, choroid ; ON, optic nerve ; S, scleral cartilage; Se, sclera ; SM, sphincter muscle ; VS, ciliary venous sinus.

the twilight hours. Vision can be only of secondary importance to the nocturnal ant-eater with its keratinized cornea.

The monotreme eye has many affinities with the eyes of Reptiles which it resembles much more than the typical eye of Mammals ; the eye, indeed, is that of a reptile in a mammal. There are only two outstanding differences between it and the reptilian eye. The first concerns the intra- and extra-ocular musculature, the former being confined to a sphincter of smooth fibres, the latter including a superior oblique muscle arising from the apex of the orbit. In the second place, the (otherwise typically reptilian) retina is completely avascular without any cone-like structure nor any participation of a hyaloid system in its nutriment. There has, however, been comparatively little work devoted to the subject—Marcus Gunn (1884) (the specimen sent from Australia to London preserved in Scotch whisky), O'Day (1938–52) and Newell (1953) on *Ornithorhynchus*, and Owen (1868) (macro-
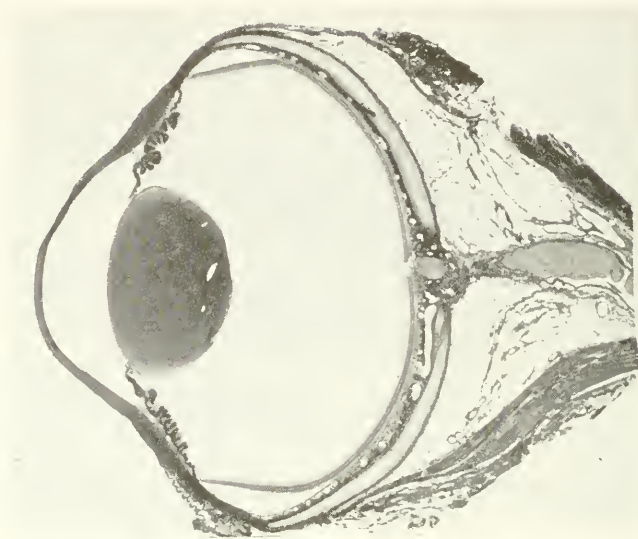
FIG. 539.—THE EYE OF THE PLATYPUS, *ORNITHORHYNCHUS* (× 11) (O'Day).
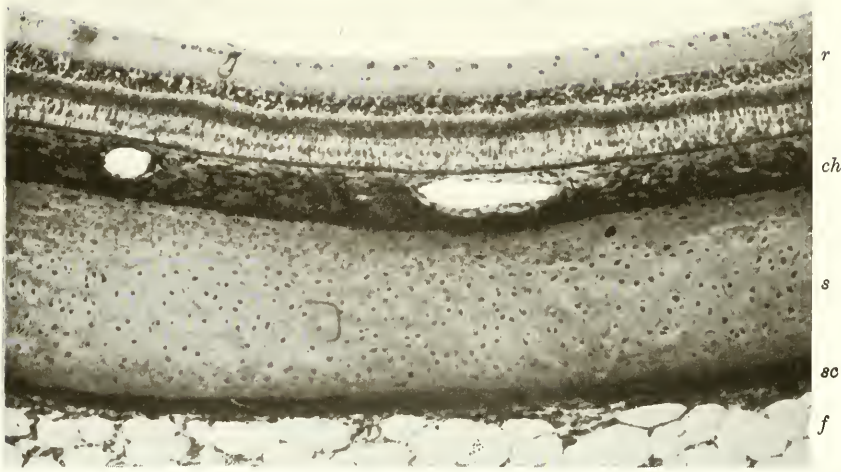

540.—THE EYE OF THE ECHIDNA, *TACHYGLOSSUS* (× 7) (O'Day).

FIG. 541.—THE POSTERIOR SEGMENT OF THE GLOBE OF THE PLATYPUS.
ch, choroid ; f, orbital fat ; r, retina ; s, scleral cartilage ; sc, fibrous sclera (× 126) (O'Day).

scopic examination), Kolmer (1925–36), Franz (1934), Gresser and Noback (1935) and O'Day (1938–52) on the echidna (Figs. 538 to 540).

THE GLOBE OF THE EYE is roughly spherical, the sclera, as in most Reptiles, having a well-formed cartilaginous cup extending forwards to a little behind (*Tachyglossus*) or to the level of the ora (*Zaglossus*) or to the level of the ciliary processes (*Ornithorhynchus*) ; it is perforated to allow the transmission of the optic nerve, and the intra-ocular vessels and nerves (Fig. 541). This is the only instance of a scleral cartilage among the Mammals.[1] The corneal epithelium of the echidna is heavily keratinized like that of other ant-eaters (the armadillo, *Xnarthia*, and the aard-vark, *Orycteropus*), possibly as a protection against the formic acid with which ants defend themselves. As in aquatic Vertebrates generally, the corneal epithelium of the platypus is thick and Bowman's membrane is absent. The anterior ends of the ciliary processes are connected by a shelf-like structure running circumferentially around the globe (the *Sims* of Virchow, 1886 ; the
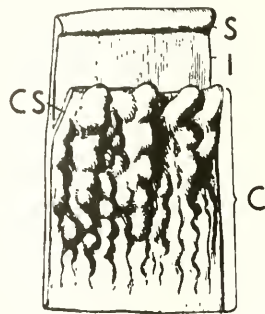

FIG. 542.—THE CILIARY PROCESSES OF ECHIDNA
C, ciliary body ; CS, ciliary shelf ; I, iris ; S, sphincter muscle (after Franz, 1911).

[1] With the exception of the cartilaginous nodules in *Notoryctes*, p. 438.

FIGS. 543 AND 544.—THE CILIARY BODY OF MONOTREMES.

FIG. 543.—The ciliary body of the platypus.
Note the large ciliary venous sinus in the connective tissue filling the angle of the anterior chamber. The small annular pad in the lens is seen to the right (O'Day).

FIG. 544.—The ciliary body of the echidna.
The ciliary venous sinus is much smaller (O'Day).

ciliary web of Walls, 1942)—a mammalian characteristic (Fig. 542). As in Sauropsida generally, the connective tissue of the ciliary region runs forwards to be inserted into Descemet's membrane and embedded in this lies the ciliary venous sinus, a structure more pronounced in Placentals [1] (Fig. 543). The brown *iris* is tenuous, consisting merely of
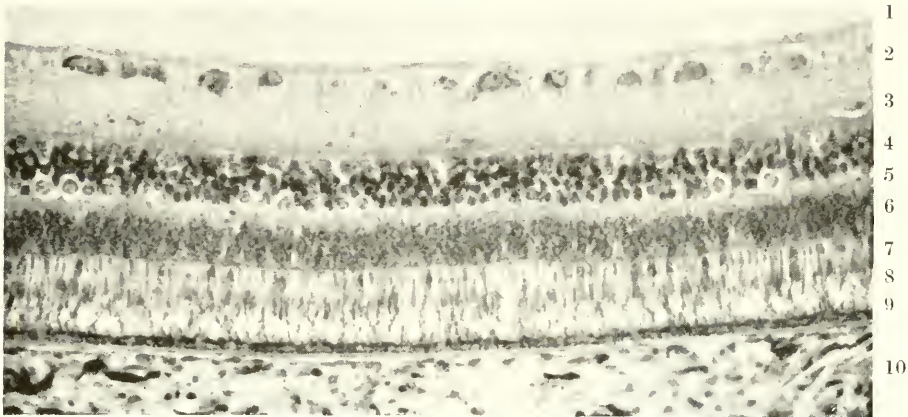

FIG. 545.—THE RETINA OF THE PLATYPUS.

1, optic nerve fibre layer ; 2, ganglion cells ; 3, inner plexiform layer ; 4, inner nuclear layer ; 5, outer plexiform layer ; 6, outer nuclear layer ; 7, external limiting membrane ; 8, visual cells ; 9, pigmentary epithelium ; 10, choroid (O'Day).
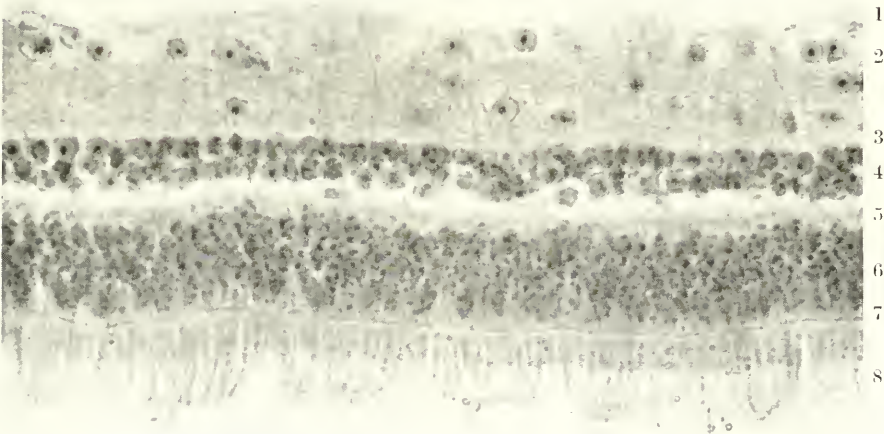

FIG. 546.—THE RETINA OF THE ECHIDNA.

1, optic nerve fibre layer ; 2, ganglion cells ; 3, inner plexiform layer ; 4, inner nuclear layer ; 5, outer plexiform layer ; 6, outer nuclear layer ; 7, external limiting membrane ; 8, visual cells (O'Day).

[1] p. 472.

the two epithelial layers and some radial blood vessels lying in loose connective tissue. The sphincter muscle, comprised of the unstriated fibres characteristic of Mammals, is massive ; it constitutes the only intra-ocular muscle for a dilatator or ciliary musculature is absent, nor is any accommodative mechanism present.[1]

Except in the aquatic platypus, the *lens* is relatively small and flat and the zonular fibres, arising from the coronal zone of the ciliary body, are inserted into its equator. In this region the subcapsular epithelium is tall, twice as tall as at the anterior pole, to form a miniature annular pad, a characteristic of Reptiles (Fig. 543).

The *retina* is entirely avascular, dependent on the choroid for nutriment. Ophthalmoscopically the fundus of the echidna is of a
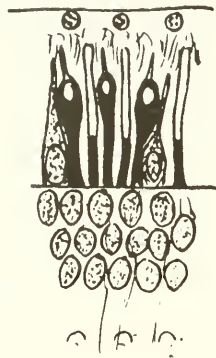

FIG. 547.—THE VISUAL ELEMENTS OF THE PLATYPUS.

Showing double and single cones (the latter in the centre) and the long slender rods (O'Day).

FIG. 548.—A VISUAL ELEMENT FROM THE PURE-ROD RETINA OF THE ECHIDNA (O'Day).

uniform brownish colour with a chalky-white oval optic disc from which nerve fibres radiate ; it thus closely resembles a common sauropsidan type (Johnson, 1901) (Plate XIII, Fig. 1). The visual elements are sauropsidan in character : the platypus has a duplex retina, the rods and cones being in approximately equal numbers. The cones are both single and double with oil-droplets in the former and in the chief member of the latter, but with no paraboloids ; the echidna has a pure-rod retina with no oil-droplets (Figs. 545 to 548). In neither genus is there evidence of an area centralis or a fovea. In the *optic nerves* of the platypus there are some 32,000 fibres (Bruesch and Arey, 1942).

THE OCULAR ADNEXA are sauropsidan apart from the extra-ocular muscles. The lids are thick and well-formed ; the echidna has a

[1] A dilatator is also absent in Crocodilians and Marsupials.

PLATE XIII

THE FUNDI OF MONOTREMES AND MARSUPIALS
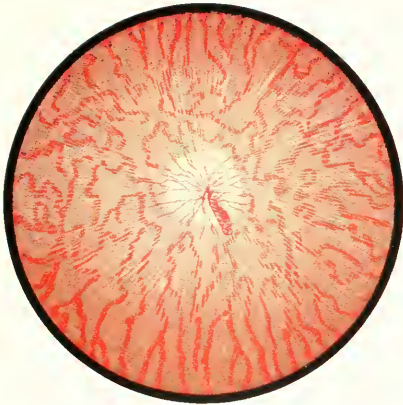
(Lindsay Johnson)

FIG. 1. —The Echidna.

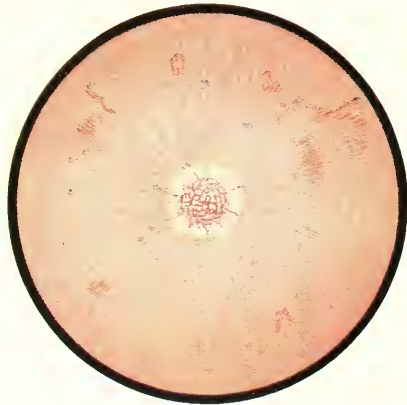

FIG. 2.—The rufous rat-kangaroo,
Hypsiprymnus rufescens.

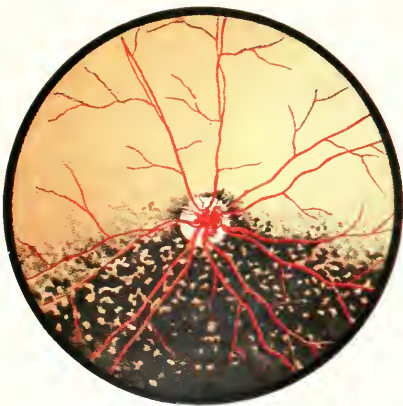FIG. 3. —The squirrel-like phalanger,
Belideus sciurus.

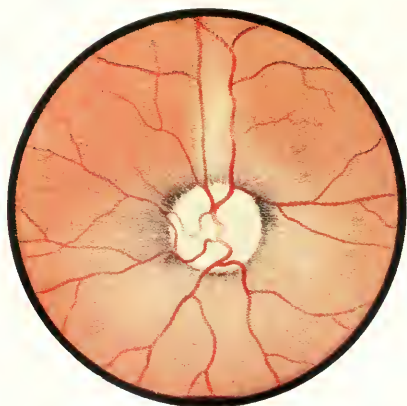

FIG. 4. The Virginian opossum,
Didelphys virginiana.

FIG. 5.- The Tasmanian devil, *Sarcophilus
ursinus.*

tarsus in the lower lid only ; the platypus in neither (Newell, 1953). Lacrimal and harderian glands are said to be present in both. The platypus has a well-formed and quite opaque nictitating membrane ; the ant-eater has none. The eye of the echidna, however, has a habit of rolling inwards and retracting into the socket rhythmically, an action aided by squeezing the lids (Johnson, 1901) ; the same protective phenomenon is seen in Edentates, the bandicoot and the porcupine. Both have the usual six extra-ocular muscles in addition to a retractor bulbi muscle ; but the superior oblique muscle is essentially mammalian in type. It will be remembered that in Vertebrates below Mammals the recti take origin from the apex of the orbit, the obliques from its anterior part[1]; in Monotremes the superior oblique arises close to the origin of the recti and is threaded through a pulley in the supero-medial aspect of the anterior part of the orbit so that it runs sharply backwards towards the temporal aspect of the globe. This typically mammalian form is supplemented in the echidna by a second muscular slip running to the globe directly from the anterior nasal orbital wall, a relic of the sub-mammalian arrangement.

The orbit in the platypus is merely a shallow depression at the cephalic extremity of the combined temporo-orbital fossa, provided only with dorsal and median walls and without an interorbital septum —a non-mammalian configuration (Watson, 1916 ; Kesteven and Furst, 1929 ; de Beer and Fell, 1936). There is no optic foramen, for the optic and other cranial nerves leave the skull through a large pseudo-optic foramen (Watson, 1916 ; Hines, 1929).

THE MARSUPIAL EYE

The MARSUPIALS (METATHERIA)—in the Eocene period a large and widespread group—are today found only in Australasia with the exception of the American opossums (Didelphyidæ),[2] arboreal, rat-like animals found in Central and South America, and the Selvas (Cænolestes), a primitive family until recently believed extinct, found in South America. In Australasia, however, where competition from the higher carnivorous Mammals has not occurred, there are many forms—(a) the cat-like dasyures (Dasyuridæ) (including the squirrel-like banded ant-eater, Myrmecobius, and the Tasmanian devil, Sarcophilus); (b) the burrowing, mole-like Notoryctidæ [3] ; (c) the burrowing, rabbit- or rat-like bandicoots (Peramelidæ) ; (d) the squirrel-like arboreal Phalangeridæ, including the flying phalangers, Petaurus and Acrobates (Phalangerinæ), the bear-like wombats (Phascolomyinæ), and the koala (Phascolarctinæ) ; and (e) the unique kangaroos and wallabies (Macropodidæ).

Banded ant-eater, Myrmecobius

Marsupial mole, Notoryctes

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[1] p. 277, Fig. 293.

[2] Incidentally, among the American opossums, the pouch is generally absent, and the young are carried on the back of the mother, their tails coiled round hers.

[3] Notoryctes typhlops, the marsupial mole, has vestigial eyes, less than 1 mm. in diameter, which lack lens, vitreous and visual cells, p. 733.
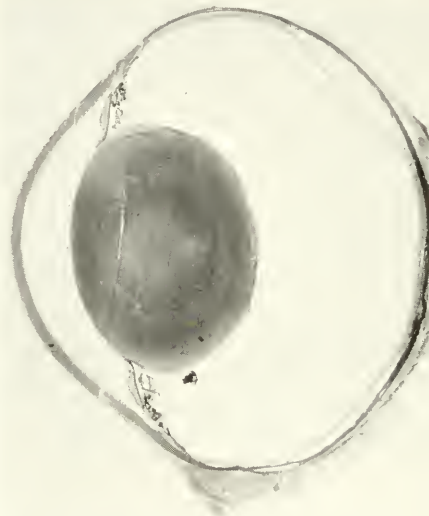
The eyes of Marsupials represent a transition between the wholly reptilian-like eyes of Monotremes and the mammalian-like eyes of Placentals. The globe is spherical and the sclera fibrous like that of snakes, the ciliary musculature shows a reptilian ancestry but the structures accessory to reptilian accommodation have all been lost, the retina may have a vascularization either of the reptilian or mammalian type, a retinal tapetum as occurs in some Reptiles may be present, and the visual elements, closely resembling those of Monotremes, are typically reptilian.

Spotted cuscus,
*Phalanger
maculatus*

Fig. 549.—The Eye of the Wallaby (× 5) (O'Day).

Dasyure,
Dasyurus

Tasmanian devil,
Sarcophilus

THE GLOBE OF THE EYE is spherical or almost spherical, with a large cornea and a fibrous sclera without cartilaginous or osseous supports ; the marsupial mole, *Notoryctes*, has cartilaginous nodules in the sclera. There is no Bowman's membrane but a thick Descemet's membrane. The choroid is of the mammalian type with, in a few species, a tapetum fibrosum (the flying phalanger, *Petaurus*, and some of the Dasyuridæ—the cat-like *Dasyurus*, the Tasmanian wolf, *Thylacinus*, the Tasmanian devil, *Sarcophilus*). In *Dasyurus* this extends over the entire fundus but is functional only in the upper half where the retinal epithelium is devoid of pigment. The ciliary body is well formed and provided with processes, and a ciliary musculature is always present despite the fact that no accommodation has yet been demonstrated in any member of the group (Figs. 550–1). Sometimes it is disposed as in Reptiles, comprised of a meridional muscle (of
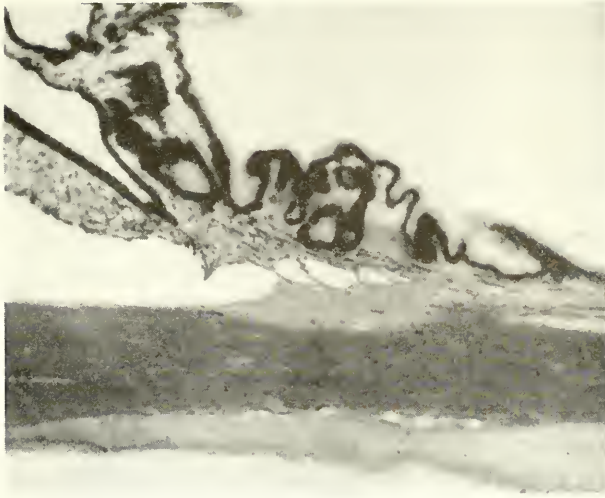
FIG. 550.—THE CILIARY REGION OF THE WALLABY.

Showing the well-formed ciliary processes, the meridional muscle, and the well-formed fibres of the pectinate ligament traversing the deep ciliary cleft (× 60) (O'Day).

Brücke) arising from the cornea ; more often circular fibres are added anteriorly (*Dasyurus* ; the opossums, *Marmosa*, *Didelphys*, etc.). The iris is densely pigmented and richly vascularized with many vessels standing out from the anterior surface ; the pupil is round (in *Dasyurus viverrinus* the contracted pupil is a vertical slit) and a sphincter of unstriated muscle surrounds the pupillary margin but a dilatator is absent. In the bandicoot, *Perameles*, nipple-like cystic protrusions of the pigmented retinal layers form flocculi [1] around the pupillary margin. The angle of the anterior chamber and the circumferential ciliary venous sinus are of the mammalian type (Fig. 550).

The lens is comparatively large, flat in diurnal, round and almost filling the interior of the globe in the smaller nocturnal types ; there are often traces of the annular pad of Reptiles, but it never touches the ciliary processes as is characteristic of Sauropsida.

The type of retinal vascularization varies. Usually this structure is avascular, and, as if in compensation, the choroidal vessels are so large as to be easily seen ophthalmoscopically (except in some phalangers) ; frequently there

[1] p. 469.

Opossum, *Didelphys*

FIG. 551.—THE CILIARY PROCESSES OF THE KANGAROO, *MACROPUS AGILIS* (after Franz, 1911).

I, iris ; CS, ciliary shelf.

Wallaby,
Petrogale

are fine vessels on the optic disc, sometimes (as in the kangaroo and wallaby) projecting like a dome-shaped cushion above it resembling a vestigial reptilian cone.[1] In those species, however, wherein the choroid is under-developed (the flying-phalanger, *Petaurus*) or is insulated from the retina by an impermeable retinal tapetum, a mammalian-like retinal circulation exists, paired arteries and veins radiating from the disc in the inner layers of the retina, clothed in glial sheaths and protruding somewhat into the vitreous ; in the opossum, *Didelphys*, the capillaries penetrate through the entire thickness of the retina to the external limiting membrane (Plate XIII).
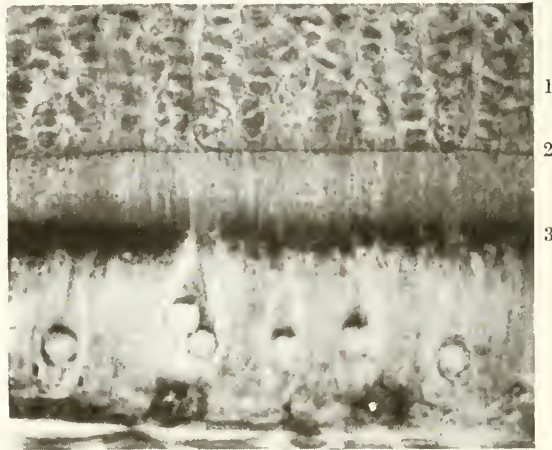

Fig. 552.—The Visual Cells of an Australian Marsupial.

The native cat, *Dasyurus viverrinus*. 1, outer nuclear layer ; 2, external limiting membrane ; 3, visual cells, showing the filamentous rods and the single and double cones with oil-droplets (in both members of the latter) (O'Day).

Koala,
Phascolarctus

In the Virginian opossum, *Didelphys virginiana*, a retinal tapetum exists, a unique phenomenon among Mammals apart from the fruit-bat, *Pteropus*. The tapetum is in the form of a semi-circle with its straight horizontal lower edge at the level of the disc ; in this area the epithelial cells are tall, devoid of pigment and packed with guanine-like crystals of unknown chemical nature. The visual cells are reptilian in type and resemble those of the monotreme eye (O'Day, 1936–39) ; the retina, in fact, is that of a Sauropsidan in the eye of a Mammal (Figs. 552–3). The rods are filamentous and outnumber the cones which are either single or double in type, lacking paraboloids but possessing oil-droplets. It is interesting that in all Australasian types so far examined double cones have oil-droplets in both members ; this is a rare

[1] p. 362. Compare also the Rodents, p. 481.

condition which occurs only exceptionally in American Marsupials and it is noteworthy that in American opossums some of the single cones lack oil-droplets. It is also interesting that among Mammals only the Monotremes and Marsupials have either double cones or oil-droplets.
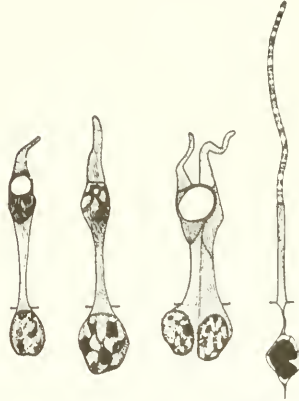

Wombat,
Phascolomys

FIG. 553.—THE VISUAL CELLS OF AN AMERICAN MARSUPIAL.

The American mouse-opossum, *Marmosa mexicana*, showing (from left to right) a single cone with oil-droplet, a single cone without oil-droplet, a double cone with an oil-droplet in one member, and a long filamentous rod (× 1,000) (Gordon Walls).

THE OCULAR ADNEXA have received little attention. A poorly developed nictitating membrane is present, a harderian and a lacrimal gland as well as a retractor bulbi muscle. The Virginian opossum, *Didelphys virginiana*, has no true nictitating membrane ; two folds of conjunctival tissue arising from either canthus close over the eye in the mid-line while the globe retracts into the socket. In other forms (the bandicoot, *Perameles*) when the eye is touched the globe rolls backwards and retracts as the nictitating membrane flashes over it, the lids sometimes closing over it at the same time.

Rabbit bandicoot,
Peragale

THE PLACENTAL EYE

The PLACENTALS (EUTHERIA) comprise the vast majority of Mammals and include a multitude of types. These can be arranged in 15 orders, the enumeration of which will facilitate understanding of the subsequent discussion.

(1) INSECTIVORA, the most primitive type of Placentals found widely in temperate and tropical lands except S. America and Australasia (where insectivorous opossums exist).

The most widely known representatives are the true shrews (Soricidæ), the true moles with vestigial eyes (Talpidæ) including the water-moles or desmans (*Myogale*), and the hedgehogs (Erinaceidæ). Further types are the otter-shrew of W. Africa (*Potamogale*), the oriental tree-shrews (Tupaiidæ) (sometimes classed among the Prosimians), the elephant-shrews (Macroscelidæ) of Africa with very

TYPICAL MAMMALS : 1

(Drawn not to scale but to a standard size)

INSECTIVORA

Hedgehog   Golden mole   Tree-shrew

CHIROPTERA   DERMOPTERA   PRIMATES

Flying fox   Flying lemur   Lemur   Tarsier
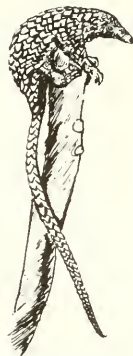
" EDENTATA "

Armadillo   Aard-vark

Pangolin

RODENTIA

Marmot   Beaver   Porcupine   Vizcacha

large eyes, and the golden mole of S. Africa (*Chrysochloris*), the eyes of which are small and hidden under the skin. There are two further and little known representatives extant—the tenrecs of Madagascar and *Solenodon* of Cuba and Haiti. Most are terrestrial, some are burrowers, some (the tree-shrews) arboreal, and a few aquatic (*Myogale*, *Potamogale*). Most feed on insects ; some arboreal forms eat leaves as well ; the moles eat worms ; and the otter-types, fish.

From the Insectivora three orders are directly derived—the Chiroptera, the Dermoptera and the Primates.

(2) CHIROPTERA (bats), the only Placentals capable of active flight ; the arms and the fingers, with the exception of the first, the hindlegs and (in the Microchiroptera) the tail, support a fold of skin which constitutes the wing.

Two sub-orders exist : (1) the large MEGACHIROPTERA—the huge flying foxes of Africa and the Pacific countries (*Pteropus*) with a wing-span of up to 5 feet and large eyes (Fig. 750), the giant bats of India (*Cynopterus*) and of the Egyptian pyramids (Xantharpyia) ; and (2) the small insectivorous MICROCHIROPTERA found all over the world—the British *Vespertilio*, the American blood-sucking vampire, *Desmodus*, etc.

(3) DERMOPTERA (flying lemurs), arboreal vegetarians which glide from tree to tree buoyed up by a fold of hairy skin connecting the fore and hind limbs. They inhabit Malaya and the Philippines (*Galeopithecus*).

(4) PRIMATES. An order derived from the primitive Insectivores ; they were primarily and still mainly remain arboreal. They comprise three sub-orders : the Lemuroidea, the Tarsioidea and the Anthropoidea, the first being the most primitive and the last the most advanced ; the first two are frequently known as Prosimians, the last constitutes the Simians.

(*a*) LEMUROIDEA, small nocturnal lemurs of Ethiopia and the East, have many primitive characters in common with the Tupaiidæ with which they seem to have had a common origin. They fall into two groups—true lemurs (Lemuridæ) confined to the island of Madagascar, and the Lorisidæ, never found in Madagascar—*Loris* and *Nycticebus* of the E. Indies, the potto, *Perodicticus* (Fig. 752), and the agwantibo, *Arctocebus*, of W. Africa, and the bush-baby, *Galago*, of Africa.

(*b*) TARSIOIDEA, of which there is only one survivor, the tarsier (*Tarsius*), differ from the lemurs among other things in having the orbit directed forwards and almost completely separated from the temporal fossa. They are generally looked upon as a separate line of evolution which branched off the Primate stock at an early period and eventually produced the Anthropoids.

(*c*) ANTHROPOIDEA, comprising 5 families of essentially diurnal species, distributed between the New World (Platyrrhini) and the Old (Catarrhini) :

(i) HAPALIDÆ—marmosets—the most primitive monkeys, small squirrel-like creatures, found in C. and S. America ;

(ii) CEBIDÆ—the American monkeys—including such species as the capuchins (*Cebus*) imported into Europe ; *Nyctipithecus* (*Aotes*), the only nocturnal monkey ; the bald-headed sakis (*Pithecia*) ; the long-limbed spider monkeys (*Ateles*) ; and the howling monkeys (*Alouatta*) ;

(iii) CERCOPITHECIDÆ—the Old World monkeys, including the African baboon (*Papio*), the mandrill (*Mandrillus*), the macaques (*Macaca*), etc. ;

(iv) SIMIIDÆ—the anthropoid apes, including the gibbon (*Hylobates*), the orang-utan (*Pongo*), the chimpanzee (*Pan*), and the gorilla (*Gorilla*) ;

TYPICAL MAMMALS : II

(Drawn not to scale but to a standard size)

CARNIVORA

Lynx	Hyæna	Raccoon	Coati
Civet cat	Polecat	Badger	Sea-lion

ARTIODACTYLA

Llama	Gazelle	Giraffe	Chevrotain

PERISSODACTYLA HYRACOIDEA

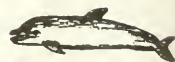|			
Zebra	Rhinoceros	Tapir	Hyrax

CETACEA

Blue	Hump-back whale	Sperm whale	Dolphin

(v) HOMINIDÆ, with several extinct genera (*Pithecanthropus*, etc.) and the single living genus, *Homo*.

(5) XENARTHRA—these comprise three distinct sub-orders :

(*a*) the solitary nocturnal, arboreal sloths (BRADYPODIDÆ) (3-toed *Bradypus*, or 2-toed *Cholœpus*) of S. and Central America, vegetarian in habit, which spend a sluggish life hanging from the branches of trees (Fig. 751) ;

(*b*) the terrestrial or arboreal ant-eaters (MYRMECOPHAGIDÆ) of neotropical distribution ;

(*c*) the omnivorous nocturnal armadillos (DASYPODIDÆ), mainly of S. America, with a dermal armature of bony scutes, which actively run and burrow.

(6) PHOLIDOTA. The small family of burrowing, termite-eating, scaly pangolins (*Manis*) of Ethiopia and the East.

(7) TUBULIDENTATA. The equally small family of shy, nocturnal, termite-eating aard-varks (*Orycteropus*) of Africa, living in burrows.

The Xenarthra, Pholidota and Tubulidentata used to be classed together as EDENTATA owing to the simplicity of their teeth or the lack of them.

(8) RODENTIA, the largest order of Mammals, comprising more than 4,000 species, mainly small, terrestrial and vegetarian, which gnaw their food in a characteristic way. They are represented by two sub-orders[1] according to their dentition :

(*a*) those provided with two pairs of upper incisors (LAGOMORPHA)—the rabbit (*Oryctolagus*), the hare (*Lepus*) and the pikas or calling hares (*Ochotona*) ;

(*b*) those provided with a single pair of upper incisors, which are conveniently divided into three groups :

> (i) the SCIUROMORPHA—the common squirrel (*Sciurus*), the souslik or ground squirrel (*Citellus*), the prairie-dog (*Cynomys*), the flying squirrel (*Pteromys*), the marmot (*Marmota*), the beaver (*Castor*) ;
>
> (ii) the MYOMORPHA—the rat (*Rattus*), the mouse (*Mus*), the vole (*Microtus*) ;
>
> (iii) the HYSTRICOMORPHA—the porcupine (*Hystrix*), the guinea-pig (*Cavia*), the chinchilla, the vizcacha (*Lagostomus*), the coypu (*Myocastor*), and others.

(9) CARNIVORA. A large amorphous order of active and fierce flesh-eaters of wide distribution and mostly terrestrial. It is comprised of 2 sub-orders :

(*a*) the terrestrial FISSIPEDIA, including 7 families : the cat-like Felidæ (cat, lion, tiger, leopard, cheetah, jaguar, lynx), the Viverridæ (civet cats, mongoose, etc.), the Hyænidæ (hyænas), the dog-like Canidæ (dog, wolf, jackal, fox, etc.), the bear-like Ursidæ, the Procyonidæ (Himalayan pandas, and the American raccoon and coati), and the Mustelidæ (otter, sea-otter, skunk, badger, marten, polecat, ferret and weasel, etc.) ;

(*b*) the aquatic PINNIPEDIA, marine fish-eating Carnivores, clumsy on land where they come for breeding purposes : Phocidæ (seals), Otariidæ (sea-lions or eared-seals), and Odobænidæ (walruses).

(10) ARTIODACTYLA. Even-toed hoofed animals, terrestrial and herbivorous in habit, wherein the hoof is formed by the third and fourth digits showing a cleft between. Of these there are four extant groups :

(*a*) the SUOIDEA (pigs and boars, Suidæ ; peccaries of America, Dicotylidæ ; and the African hippopotamus) ;

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[1] The Lagomorpha are now generally accepted as a separate order.

(*b*) the TYLOPODA (camel and dromedary of Africa and Asia, and the llama of S. America) ;

(*c*) the PECORA (Ruminants) (deer and giraffe, and the Bovidæ—ox, bison, sheep, goat, antelope, gazelle) ;

(*d*) the TRAGULINA, small chevrotains of the East and Africa.

(11) PERISSODACTYLA. Odd-toed hoofed animals wherein the foot is essentially formed by the enlarged third digit—Equidæ (horse, ass, zebra), Rhinocerotidæ (rhinoceros), Tapiridæ (tapir).

(12) HYRACOIDEA, the small rodent-like hyraxes (" coneys ") of Africa and Syria of arboreal habits.

(13) PROBOSCIDEA, the vegetarian elephants of Africa (*Loxodonta africana*) and the Orient (*Elephas maximus*).

The Artiodactyla, Perissodactyla, Hyracoidea, and the Proboscidea used conveniently to be classed in one heterogeneous group of UNGULATA (hoofed animals).

(14) SIRENIA.[1] The sluggish, vegetarian, and fully aquatic fish-like sea-cows, which crop grasses in shallow littoral waters—the manatee (*Manatus ; Trichechus*) of S. America and S. Africa, and the dugong (*Halicore*) of Oriental and Australian coasts.

(15) CETACEA. The carnivorous fish-like whales and dolphins, fully adapted for marine life. There are two distinct orders :

(*a*) the baleen whales (MYSTACOCETI) with baleen (or whale-bone) plates instead of teeth, which sound to great depths and feed blindly by trawling for plankton which they strain through the frayed margins of their plates (the right-whale, *Balæna* ; the hump-back, *Megaptera* ; the blue whale or rorqual, *Balænoptera*, etc.) ; the great rorquals (particularly the blue whale) are the largest animals in existence, over 100 feet in length and well over 100 tons in weight ;

(*b*) the toothed whales (ODONTOCETI), squid- and fish-eating animals which use their vision to catch their prey and are therefore adapted with more perfect eyes, some of them swimming in packs like wolves attacking the unwieldy whale-bone whales (the sperm-whale, *Physeter*; the killer whale, *Orca*; the narwhal, *Monodon* ; the porpoise, *Phocæna* ; the dolphin, *Delphinus*). There is a small family of fresh-water dolphins (the susu, *Platanista*) with rudimentary eyes.

Within the many orders of Placentals a considerable range of variations in the structure of the eye occurs, but throughout the entire class the similarity is great. It seems likely that the first representatives (Insectivora) were nocturnal in habit, and that, as occurs in snakes, the eye has evolved from this as a basis showing innumerable adaptive changes to suit the many environments (diurnal, arboreal, aquatic, etc.) to which the prolific class has suited itself. Only in a few instances among the Insectivores (moles) and Rodents has the burrowing habit led to the degeneration of the eyes.[2] The general characteristics of the placental eye may be summarized as follows (Figs. 554 to 563).

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[1] The legend of the mermaid is said to derive from sailors' fanciful descriptions of the manatee sitting on the rocks nursing its baby in its arms ; hence the generic name, Sirenia. It is to be remembered that a third species, *Rhytina* (Steller's sea-cow), growing to enormous dimensions (25 feet or more), was found in great herds by Bering in 1741 near the Asiatic coasts of the Bering sea. Sluggish and docile in habit it became extinct at the end of the 18th century owing to its wholesale massacre for food.
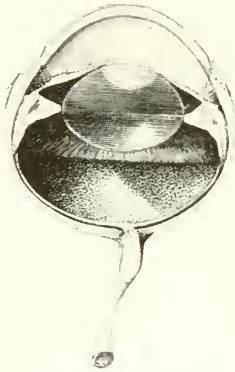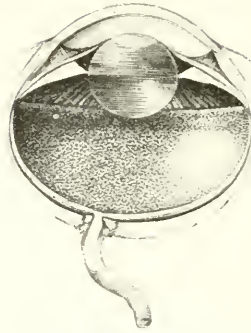
[2] p. 13.

Fig. 554.—The lynx.
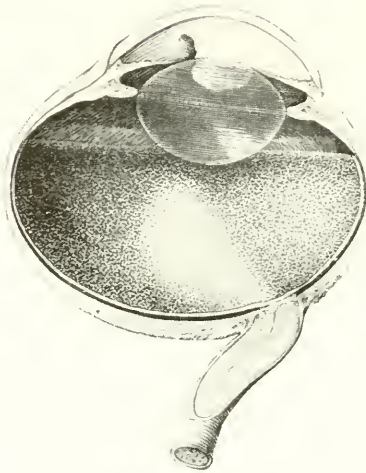*Felis lynx.*

Fig. 555.—The seal,
Phoca grœnlandica.

Fig. 556.—The marmot,
Marmota alpina.

Fig. 557.—The horse,
Equus caballus. Note
the flocculus in the
pupil.

Fig. 558.—The porcupine,
Hystrix cristata.

Fig. 559.—The wolf,
Canis lupus.
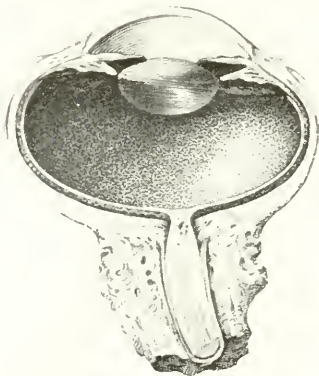
Fig. 560.—The elephant,
Elephas maximus.

Fig. 561.—The monkey,
Simia inuus.

A selection of Soemmerring's engravings illustrating in natural size the
lower half of the hemisected left eye in each case.

The lack of any scleral support, cartilaginous or bony, results in a spherical globe.

The choroid is of the standard vertebrate type, usually thinner than that of man, and may contain a tapetum. The ciliary body has a variable topography, but the ciliary muscle, often vestigial, is always composed of plain muscle fibres. A peculiarity is that the anterior surface of the iris is partially covered by a mesodermal leaf additional to that found in other Vertebrates. The angle of the anterior chamber is continued by a cleft of varying depth, extending into the ciliary region bridged across by delicate strands of uveal tissue.

The lens—usually lenticular in shape but round in aquatic species—is suspended freely from the ciliary processes by a well-developed zonule and is deformed in accommodation (when this function is present) by the elasticity of its capsule, being stretched or relaxed by the ciliary muscle.

The retina with few exceptions is duplex in type and of typical vertebrate architecture.

Most of these characteristics are seen in some form or another in other classes of Vertebrates : in only three features does the placental eye differ characteristically from all others :—

1. In the development and fate of the hyaloid system of vessels, the persisting remnants of which frequently supply an intra-retinal system of vascularization.

2. In the formation of a mesodermal layer of the iris superficial to the structures found in other Vertebrates.

3. In an accommodative mechanism depending on a relaxation of the tension normally maintained upon the capsule of the lens.

It is unnecessary in a volume of this type to describe the detailed morphology of the placental eye which conforms closely with that of man—to which an entire subsequent volume will be devoted. It will suffice to describe those features which show marked variations from the general scheme (Figs. 554 to 563).

The General Shape and Size of the Globe. In shape the placental eye is spherical, a necessity with its fibrous, unbuttressed sclera. As a rule the cornea continues the scleral curve, although sometimes there is a shallow corneo-scleral furrow with a protruding cornea having a smaller radius of curvature, as in man ; alternatively, while the peripheral zone of the cornea maintains the curve of the sclera, its apex may be more acutely curved, as is seen in Carnivores. In Cetaceans the shape of the globe is fish-like [1] with a short antero-posterior axis ; it is interesting that the Pinnipedes, less wholly adapted to an aquatic existence than the Cetaceans, have a spherical globe. In some nocturnal prosimian Primates such as the lemuroids (galago and *Nycticebus*) and *Tarsius* the shape is almost tubular (Fig. 743).
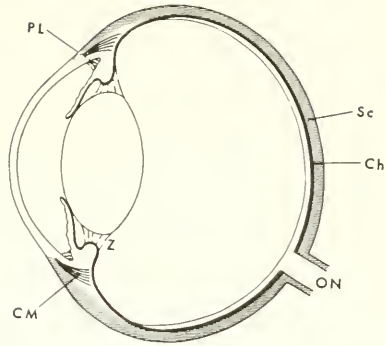
[1] p. 276.

Fig. 562.—Diagram of the Eye of a Placental.

Ch, choroid ; CM, ciliary muscle ; ON, optic nerve ; PL, pectinate
ligament bridging the ciliary cleft ; Sc, sclera ; Z, zonule. Note the relative
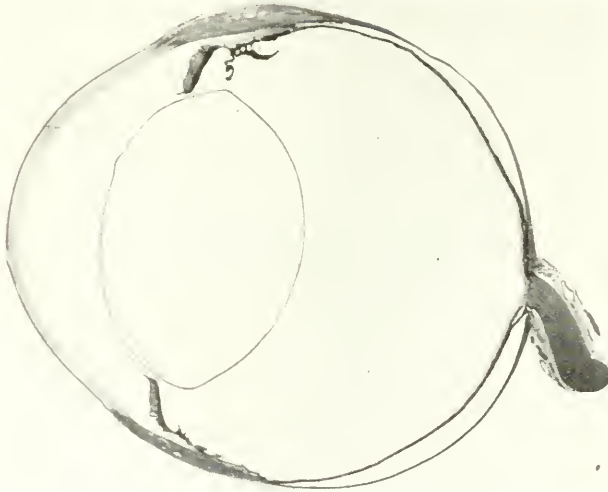simplicity of the eye.

Fig. 563.—Section of the Eye of the Cat ($\times$ 3·25) (Norman Ashton).

The size of the globe varies within wide limits ; neglecting the
minute degenerate eyes of the mole (0·8 mm. diam.) and one or two
species of burrowing rodents,[1] it ranges from 1 to 2 mm. in diam.
in the shrews and bats to the enormous eyes of some whales (145 $\times$
129 $\times$ 107 mm. in the great blue whale, *Balænoptera musculus*) (Pütter,
1903). In comparison with the size of the body, however, that of the
eye is more uniform : while the former varies as 1 : 60 among
terrestrial Placentals, the latter only varies as 1 : 30. The eye of
the seal (internal antero-posterior diam., 52 mm.) is comparatively

[1] p. 733.

much larger than that of the whale, which, in fact, measures only 1/250 to 1/600th of its gigantic body (Figs. 555, 564) ; that of the elephant (axis 35 mm.) or rhinoceros (axis 23 mm.) is correspondingly small (Fig. 560), and the minute eye of the vole (axis 1·75 mm.) is relatively greater in comparison with the length of its body (10 cm.) than is the eye of man. Although as a general rule Haller's ratio [1]— that the size of the eye varies inversely as the size of the body[2]—holds good, marked variations occur with the visual habits of the animal. In the lower orders of nocturnal habits which depend little on vision (Insectivores, Chiroptera, Edentates and some Rodents) the eyes are small relatively and absolutely ; in the more highly developed and visually alive types they are larger. Among these it varies generally with the visual efficiency and swiftness of movement, and is generally larger in nocturnal species. Thus the eye of the nimble horse (axis 45 mm.) is larger than that of the lethargic elephant (axis 35 mm.) (Fig. 557), while the small (usually nocturnal) Primates have comparatively larger eyes than the large diurnal species (with the conspicuous exception of the Hapalidæ—marmosets and tamarins) (Ashley-Montague, 1943–44) (Figs. 752 and 753).

Measurements of the various placental eyes are found in Emmert (1886), Pütter (1903), Hotta (1906), Kolmer (1910), Franz (1912), Linsenmeyer (1912), Guist (1923), Wolfrum (1926), Rochon-Duvigneaud (1943) and Steindorff (1947) ; their weight and volume in Liebig (1874), Koschel (1883), Emmert (1886), Welcker (1903), Schleich (1922), Vitello (1931), Steindorff (1947) and Henderson (1950).

The *corneo-scleral envelope* corresponds with that of man with the exception of the aquatic Placentals, apart from the generalization that the eye of a relatively large animal tends to have an unusually thick sclera—elephant, rhinoceros, etc. The envelope is entirely fibrous without any supporting skeletal structures.[3] Among the Cetaceans particularly the sclera is enormously thick, a feature described by Bennett (1836) ; indeed, the sclera at the posterior pole may be 3/4 the length

[1] p. 401.
[2] Magnitudo oculorum est fere in ratione inversa animalium. Balænæ, Rhinoceroti, Elephanto parvi sunt oculi. Haller, *Et. Phys.* IV–XVI (1768).
[3] A fibrous sclera is also found in Cyclostomes, pearl-fishes and some eels, adult Urodeles (excluding *Triton* and *Hynobius*, and degenerative limicoline types), some tree frogs, snakes and Marsupials (excluding *Notoryctes*).
    cartilage is found (a) in the form of a posterior cup in Fishes (except Teleosteans), adult Anurans (except some tree frogs), larval Urodeles, Reptiles (excluding snakes and the chameleon), Birds and Monotremes ; (b) in the form of a ring in Teleosteans ; (c) as islands in elephant fishes, *Triton* and *Hynobius*, limicoline Urodeles (enormously large), the chameleon (at the fovea) and *Notoryctes* ; (d) calcified in some Selachians and some Teleosteans.
    bone is found (a) as anterior ossicles in most Teleosts, Chondrosteans, Cœlacanths, Reptiles (excluding snakes and Crocodilians) and Birds ; (b) in the form of a ring in *Xiphias* and *Thunnus* (anteriorly), *Hypopachus*, and many Birds (posteriorly as the os opt.

of the antero-posterior axis of the globe. In the hump-back whale, *Megaptera*, for example, the antero-posterior diameter of the eye is 40 mm., the thickness of the sclera at the posterior pole is 30 mm., while its thickness at the limbus is only 3 mm. (Rochon-Duvigneaud, 1943) (Fig. 564). The cornea of this species is correspondingly thin (1·5 mm. at the periphery ; 0·5 mm. at the apex). In addition, the whale has an immensely thickened accessory optic nerve sheath composed of connective-fatty tissue lying outside the dural sheath

FIG. 564.—The EYE OF THE WHALE.

A hemisection to show the enormous thickening of the sclera and the accessory optic nerve sheath. Note that the relatively small lens is kept in place artificially by a glass strut (specimen from A. Arruga ; Museum, Institute of Ophthalmology).

encased in a thick aponeurotic-like capsule. Set on this massive stalk, the globe, of course, is immobile. A similarly thick accessory sheath surrounds the optic nerve of the elephant and the hippopotamus (Rochon-Duvigneaud, 1943) : in both of these the sclera is very thick and the eyes are capable of little movement.

The phenomenal thickness of the sclera in the whale is often said to be necessary to resist the enormous pressures involved when the animal sounds to great depths. It is to be remembered, however, that the cornea is thin and that abyssal fish do not share this characteristic ; the sclera of the deeply diving shark, *Etmopterus*, is microscopically thin and that of the Chimæras discontinuous.[1] It is probable, indeed, that reinforcement in this sense is un-

[1] p. 290.

Figs. 565 to 572.—The Corneal Epithelium of Mammals.
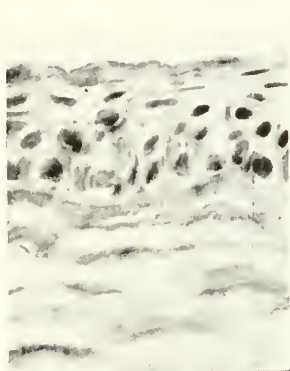

Fig. 565.—Rabbit.

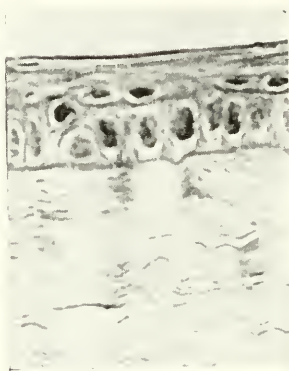Fig. 566.—Dog.

Fig. 567.—Guinea-pig.
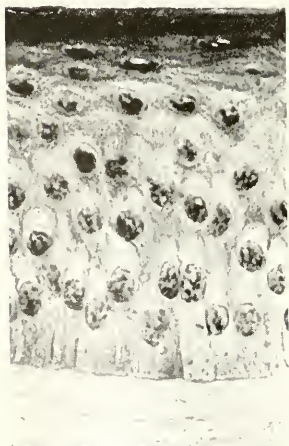

Fig. 568.—Rat.

Fig. 569.—Pig.
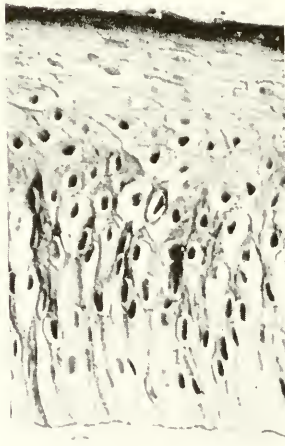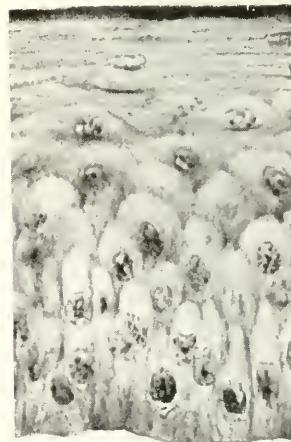

Fig. 570.—Horse.

Fig. 571.—Ass.

Fig. 572.—Ox.

565.—Periodic acid Schiff's stain (Norman Ashton).
566 to 572.—Masson's trichrome stain (Cahnettes, Déodati, Planel and Bec).

neccssary for the pressure on the surface is equally transmitted to all the fluid contents of the body including the inner eye. It is more likely that the rein-forcement of the posterior region of the sclera is necessary to maintain the non-spherical shape in the huge cetacean globe rendered mechanically weak by its great size, thus taking over the supportive function of the scleral cartilage in fishes with similarly shaped eyes.

The *cornea* of Placentals is usually circular or almost so, but in Cetaceans and in a great number of the Ungulates (Equidæ, Ruminants and the hippopotamus) it is horizontally oval corresponding to the configuration of the pupil. In many, a pigmented ring encircles the limbus spreading a considerable distance into the corneal tissue ; sometimes this is confined to epidermal pigment (Rodents such as rabbit, hare, guinea-pig, rat, marmot, etc. ; the horse and the gorilla) (Fig. 607) ; sometimes to this is added pigment in the deep interstitial tissues (Carnivores such as the cat, dog, fox, lion ; Ruminants such as
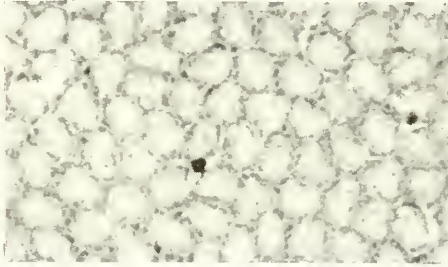

Fig. 573.—The Endothelium of the Cornea of the Rabbit.

Showing a sheet of corneal endothelium lining the anterior chamber which has been stripped away from Descemet's membrane. No nerve fibres are seen but there are a few circular blobs of stain lying between the cells ($\times$ 400) (Zander and Weddell).

the ox and deer ; the porpoise, the dolphin, the whale and the chimpanzee). In the rhinoceros the pigmented region of the cornea is vascularized. The pigmentation may be an anti-glare device for it is absent in crepuscular or nocturnal animals.

The histological structure of the cornea is built on the typical vertebrate plan seen in man except that most species have no Bowman's membrane ; Descemet's membrane with its endothelium, however, is always present and is often very substantial. Although Bowman's membrane is a relative rarity, the basal membrane of the epithelium seems always to be present (Calmettes *et al.*, 1956 ; Sheldon, 1956). The thickness of the epithelium varies considerably (Figs. 565 to 572)[1]; that of the endothelium is constant (Fig. 573). Blood vessels some-times invade the cornea proper from the limbus, whereas in Primates

[1] 20 layers of cells in the horse ; 10-12, pig ; 9-11, ox; 8-10, dog ; 6-8, rabbit ; 5-6, guinea-pig, rat (Virchow, 1910 ; Calmettes *et al.*, 1956).

FIG. 574.—A diagrammatic representation of the arrangement of the nerve bundles which enter the periphery of the cornea in different planes (methylene blue).

Upper left quadrant : the nerve bundles entering the cornea from the episcleral plane. Upper right quadrant : entering from the subconjunctival plane. The lower half shows the manner in which the plexiform pattern of nerve fibres arises from these bundles. It is to be noted that they are not by any means all radially disposed and that some fibres pass from limbus to limbus across the centre of the cornea.

FIG. 575.

FIG. 576.

FIG. 575.—Terminals in the substantia propria arising from a nerve bundle (methylene blue) (× 350).
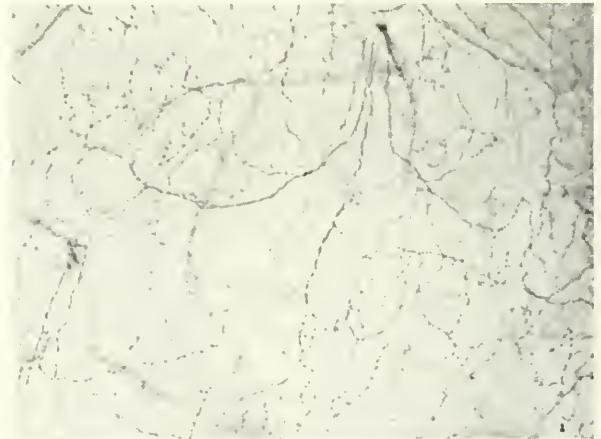
FIG. 576.—Nerve terminals in the epithelium showing the axons piercing Bowman's membrane, multiplying and passing in all directions in the epithelium. The stromal plexus is out of focus (methylene blue) (× 130).

they are found only in fœtal life ; in some animals they persist much longer (*e.g.*, cat), while in others they may be permanent (ox, sheep, Gerlach, 1848). In most Mammals the nerve plexus is more complicated than in man.

Since the early observations of Schlemm (1831) who demonstrated nervefibres entering the cornea in stags and oxen, a considerable amount of work has been done on this problem. Most of the early work [1] is unconvincing, but Cohnheim (1866–67), by introducing the gold chloride impregnation technique, demonstrated their presence and complexity in the cornea of rabbits and guineapigs, as well as in frogs and birds. This advance was followed by a large number
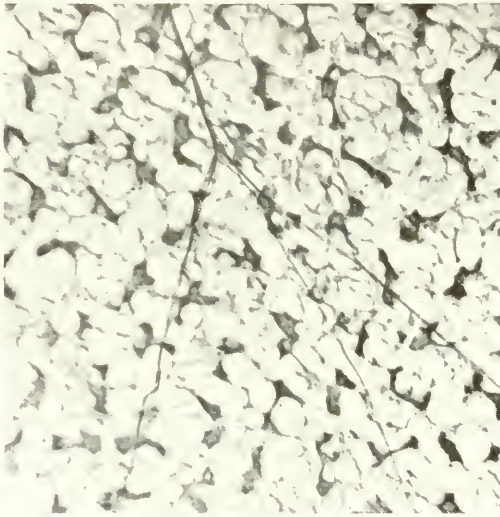

FIG. 577.—THE NERVES IN THE CORNEAL ENDOTHELIUM IN THE RABBIT.
Flat section, fixed in bromformalin, stained with del Rio Hortega's " panoptic silver carbonate technique " (J. R. Wolter).

of contributions which were assessed in the important papers of Waldeyer and Izquierdo (1880) and Ranvier (1881) wherein the innervation of the cornea of Fish, Amphibians, Reptiles and Birds as well as Mammals was assessed. The introduction of the methylene blue method of staining nerve fibres stimulated a classical paper by Dogiel (1891) dealing with the monkey and man, while a considerable number of Mammals was studied using the silver technique by Crevatin (1903), Bielschowsky and Pollak (1904) and Cajal (1909). This work was consolidated chiefly on Mammals by Virchow (1910), Agababow (1912) and particularly Attias (1912). More recent studies using a variety of techniques including polarization and phase-contrast microscopy are those of Boeke and Heringa (1924) (monkey), Nakajima (1930) (rabbit), Egorow (1934) (guineapig), Boeke (1935) (monkey), Reiser (1935–37) (pig and guinea-pig), Borr (1939) (rat), Peris (1947–49) (bull, sheep, rabbit, pig, cat, etc.), Rodger (1950)

[1] Bochdalek (1837–39) (larger Mammals), Pappenheim (1839–40) (oxen), Purkinje (1845) (different Mammals), Kölliker (1848–66) (rabbits), Luschka (1850) (rabbits), Ciaccio (1863–81) (mice).

(rabbit), Zander and Weddell (1951) (rat, guinea-pig, rabbit, monkey and man, as well as the dogfish, *Scyllium*, and the frog, *Rana*), Rexed and Rexed (1951) (rabbit), Itahashi (1952) (rabbit), Bell *et al.* (1952) (cat), Palumbi (1953) (rabbit, rat, cow, horse, and man), and Wolter (1955–56) (rabbit).

Branches of the ciliary nerves derived from the ophthalmic division of the trigeminal enter the cornea at the limbus. After supplying a perilimbal plexus, they lose their myelin sheaths and run radially into the corneal stroma in some 70 to 80 nerve-trunks (Fig. 574). As these branch they form a plexiform arrangement at all levels in the stroma, more dense, however, in the superficial layers. Some of the branches terminate in the stroma in bead-like thickenings (Fig. 575); many of them terminate in the corneal epithelium penetrating Bowman's membrane when this structure is present. In this layer the nerve fibres shed their sheaths of Schwann and the naked axons subdivide to form a delicate
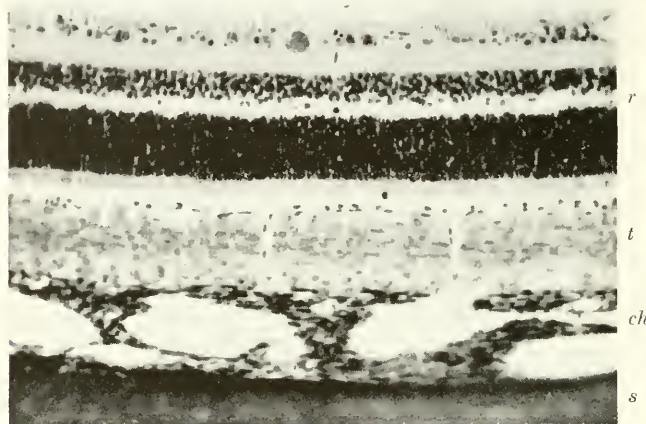

Fig. 578.—The Posterior Segment of the Eye of the Kitten.
ch, pigmented vascular choroid; *r*, retina; *s*, fibrous sclera; *t*, tapetum
($\times$ 150) (Norman Ashton).

plexus terminating in beaded formations in all layers of the epithelium. Although there appear to be histological differences between the fibres, the evidence suggests that these nerves are all of a sensory nature (Fig. 576).

A most interesting finding has been reported by Wolter (1957)—the presence of nerve fibres in the endothelium of the cornea in the rabbit (Fig. 577); their function is unknown, nor have they been observed in other Vertebrates.

An interesting peculiarity is the *keratinization of the corneal epithelium* seen in two types of Placentals. In some aquatic forms (seals, dolphins and particularly in whales) the epithelium is thick and keratinized as a protection against sea-water[1]; while in the ant-eating Placentals (Xenarthra, as the armadillo; Tubulidentata such as the aard-vark) a similar keratinization occurs, corresponding to that seen in the ant-eating Monotremes (the echidna), presumably a protection against the formic acid emitted in defence by the termites. The armadillo, *Dasypus*, is peculiar in that the cornea is vascularized to its apex, probably a necessary source of nutriment since the heavily cornified epithelium

[1] Compare the thick corneal epithelium of the platypus, *Ornithorhynchus* (p. 433).

is impervious to tears and presumably cannot mediate an adequate respiratory exchange.

The Choroid. The layers of the choroid in the placental eye correspond with those of man (Fig. 578),[1] the choriocapillaris being usually thin, exceptionally so in the Sciuridæ (squirrels) and Gliridæ (dormice) ; exceptions to this are aquatic types (Pinnipedes, Cetaceans) wherein the choroid is unusually thick. One interesting and variable feature. however, is the TAPETUM LUCIDUM,[2] an adaptation acquired by certain nocturnal animals to improve vision in dim illumination. Optically the tapetum acts as a mirror which, lying behind the rods and cones, reflects the incident light so that it traverses the visual elements twice, thus increasing differences in apparent brightness.

The tapetum of Placentals was first adequately described by Brücke (1845) and thereafter the subject has received much study ; its histological characteristics were fully elucidated by Sattler (1876) while its ophthalmoscopic variations were beautifully illustrated by Johnson (1901) (Plates XIV and XV). It lies in the upper posterior part of the fundus with a preference for the temporal side which is used for forward vision. Ophthalmoscopically it appears as a bright area in the fundus. usually of triangular shape with its base horizontal just above the optic disc, sometimes lying entirely above this structure (horse). sometimes including it (cat) ; it varies, however, considerably in extent, being unusually large in the Cetaceans (dolphins and whales), while in the Pinnipedes (seals) it occupies the entire posterior area of the fundus up to the equator and beyond on the temporal side. In the tapetal area pigment is lacking in the retinal epithelium to allow the transmission of light, and, lying between the choroidal layer of vessels and the choriocapillaris, it is traversed by small vessels to supply the latter, visible ophthalmoscopically as stellate dark dots on the bright background—the " stars " of Winslow. The tapetum does not appear ophthalmoscopically in the puppy until some weeks after birth (Usher, 1924).

Histologically two types of tapetum are found, both completely different in origin and structure—the tapetum fibrosum and the tapetum cellulosum (Figs. 579 and 580).

The TAPETUM FIBROSUM develops from the thin layer of elastic fibres found normally in the inner layer of small vessels of the choroid (Sattler, 1876). It is composed of dense fibrous tissue the fibres of which are closely woven together so that the entire structure glistens like a piece of fresh tendon. Among Placentals such a tapetum is typically found in the Ungulates. among which it is almost universal

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[1] The unique structure of the choroid of the larger bats will be noted subsequently, p. 459.

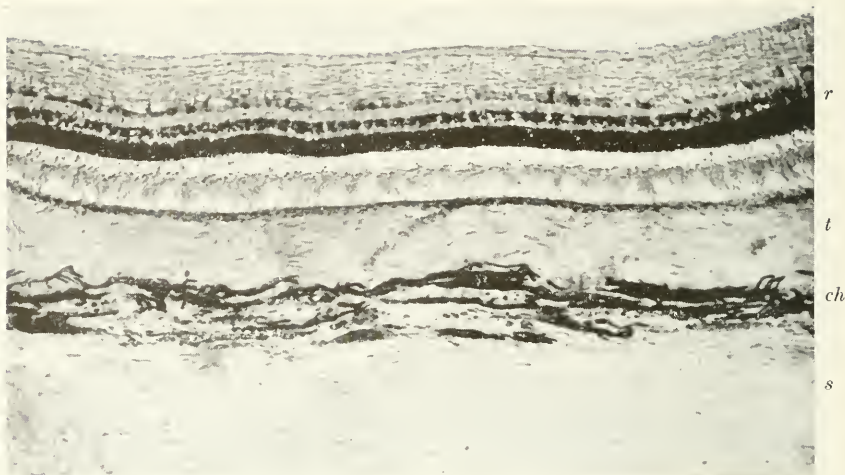[2] *Tapetum lucidum,* bright carpet.

FIG. 579.—THE TAPETUM FIBROSUM OF THE HORSE.

Showing the dense closely-woven layer of fibrous tissue ; *ch*, choroid ; *r*, retina ; *s*, sclera ; *t*, tapetum (× 126) (Norman Ashton).
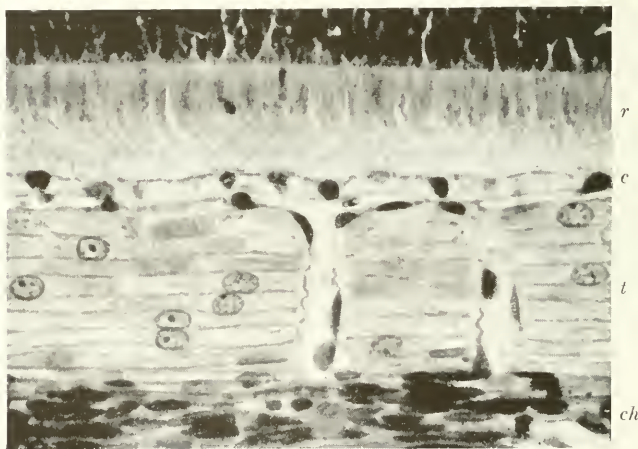

FIG. 580.—THE TAPETUM CELLULOSUM OF THE KITTEN.

Note the beautifully arranged tiers of endothelial cells traversed by small vessels running from the choroid to supply the choriocapillaris. *c*, chorio-capillaris ; *ch*, choroid ; *r*, retina ; *t*, tapetum (× 375) (Norman Ashton).

Peccary

(including the elephants) with the exception of the Suoidea (pig, peccary, hippopotamus) and the Tylopoda (camels, llama) ; it also occurs in the Cetaceans (whales and dolphins), in two Rodents, the spotted cavy, *Cuniculus*, and the flying squirrel, *Pteromys magnificus*, and in the only nocturnal Anthropoid (the night monkey, *Nyctipithecus*, in which it is extremely brilliant).

The TAPETUM CELLULOSUM, on the other hand, develops from the almost continuous layer of endothelial cells which separates the elastic layer from the choriocapillaris (Sattler, 1876). It is formed of several closely set layers[1] of thin, flat endothelial cells arranged in tiers with mason-like regularity resembling plant tissue rather than animal, each cell being packed with rod-like, doubly refracting crystals of an unknown chemical composition (? lipoid) (the *iridocytes* of Bruni, 1922) (Mürr, 1925–27). Such a tapetum occurs in all Carnivores (except two Viverrines, *Cynictis* and *Suricata*) including the Pinnipedes, and also in Prosimians—the lemuroids, *Loris, Nycticebus, Galago* and *Lemur catta*.
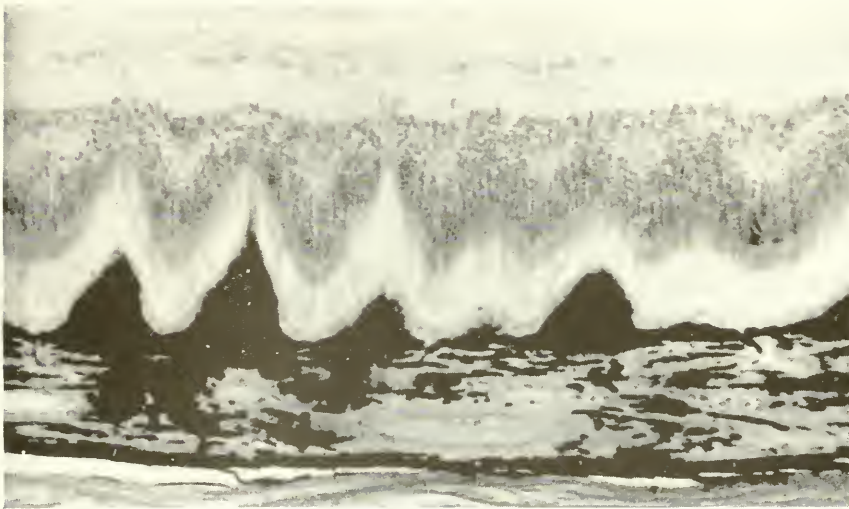
Suricate

FIG. 581.—THE PAPILLATED CHOROID OF THE FRUIT-BAT (FLYING FOX), *PTEROPUS POLIOCEPHALUS* (O'Day).

It is interesting that the pigment epithelium of the retina in Mammals is rarely densely pigmented nor is the pigment migratory. It may contain reflecting material : this in some fruit-bats (*Pteropus*) serves as a RETINAL TAPETUM in the upper part of the fundus, and in the dog is said to augment the effect of the choroidal tapetum.

VASCULAR CHOROIDAL PAPILLÆ are a unique phenomenon in the animal world found among the Megachiroptera—fruit-bats or flying foxes (*Pteropus, Epomophorus*) Kolmer, 1910–24; Fritsch, 1911; Gérard and Rochon-Duvigneaud, 1930) (Fig. 581). These structures which stud the fundus from the ora to the optic disc, form conical mesodermal papillæ each with a vascular core, and on this irregular surface the visual cells of the retina are arranged like trees on a range of hills. Although the retina is entirely avascular all its layers are thus

Flying fox

[1] 4 in the wolverine ; 8–10 in the lion ; 10 in the dog ; up to 35 and of a very large size in the seals.

intimately supplied with choroidal capillaries ; to a certain extent, also, the irregular arrangement of the visual cells in the hills and craters may act as an accommodative device.[1]

It is interesting that Rohen (1954) found in the dog thick longitudinal muscular layers in the walls of the posterior ciliary arteries and in the arteries of the posterior part of the choroid which he interpreted as a vascular shunt-apparatus regulating the flow of blood into the choroid. Such a mechanism he failed to find in the cat, rabbit, rat or guinea-pig, or in man.

The Ciliary Region. The size and topography of the ciliary region in Placentals vary considerably, the dominating factor being the presence or absence of an accommodative mechanism. Derived from nocturnal ancestors few Placentals, particularly of the lower species, have any marked degree of accommodative activity ; this, indeed, is found
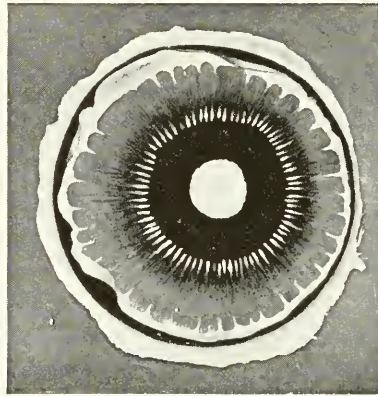

Fig. 582.—The Ciliary Body of Primates.

The inner aspect of the anterior part of the eye showing the ora serrata, the pars plana, ciliary processes and posterior surface of the iris.

only in the squirrels (Sciuridæ), the large Carnivores and the Primates. On this essentially depend the size of the ciliary body, its muscular development, the prominence of the ciliary processes, and the configuration of the angle of the anterior chamber. In most small-eyed primitive types with comparatively large lenses (Insectivores, Rodents, etc.) the ciliary body is small and narrow with miniature processes ; in the shrews it is a simple roll without processes, as in snakes.[2] In large-eyed Placentals, it assumes the prominent triangular shape with well-developed processes such as are seen in man. It is noteworthy, however, that from the aspect of pure anatomy, in many species a considerable degree of asymmetry exists ; thus in animals with an ovoid cornea (and pupil) the circular ciliary body encroaches far into the iris nasally and temporally, rendering the horizontal segment of

[1] p. 643.   [2] p. 386.

the pupil relatively immobile, while in many species (Ungulates and Carnivores) the tendency towards nasal asymmetry of the globe in the interests of binocular vision results in a curtailment of the ciliary region and the practical disappearance of the orbicular zone on the nasal side (Fig. 582).

The main determinant in the configuration of this region is the degree of development of the ciliary muscle[1] (Figs. 583–90). Anteriorly the ciliary body splits into two leaves ; one, the outer or scleral part, essentially muscular in structure, hugs the sclera as it runs to the corneo-scleral junction ; the other, sometimes fibrous, sometimes muscular,

FIGS. 583 TO 586.—THE CILIARY REGION IN MAMMALS.
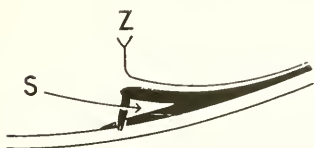

FIG. 583.—Rabbit.   FIG. 584.—Pig.
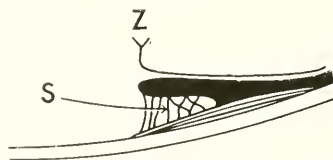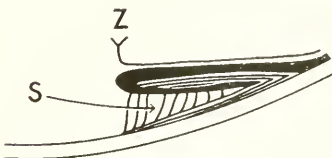
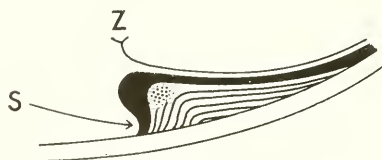FIG. 585.—Dog.   FIG. 586.—Ape.

S, the ciliary cleft (or sinus) ; Z, zonular ligament. The ciliary muscle where present is indicated by linear shading.

forming the base-plate of the ciliary body, runs inwards towards the root of the iris (Lauber, 1901) ; between these two leaves lies a triangular cleft of varying depth, the CILIARY CLEFT,[2] an extension of the anterior chamber which runs backwards deeply into the ciliary region. In the small-eyed and more primitive Placentals (Rodents, etc.) the ciliary muscle is either lacking or very rudimentary and probably functionless ; when present it consists of a few slender fascicules lying in much connective tissue in the outer leaf of the ciliary body (Lauber, 1901 ; Collins, 1921 ; Davis, 1929) (Figs. 583, 587). In these animals the ciliary cleft is small. In Ungulates the muscle is also confined to meridional fibres running close to the sclera, prolonged to find attachment to the inner layers of the cornea by the corneo-scleral trabeculæ (the cribriform ligament of Henderson, 1921) ; the inner leaf of the

[1] For the innervation, see Pines and Pinsky (1932), Boeke (1933), Warwick (1952).
[2] This formation is often known as the *ciliary sinus* ; I am using the term *ciliary cleft* to distinguish it from the *ciliary venous sinus*.

ciliary body is merely a simple fibrous base-plate of connective tissue (Zimmermann, 1932 ; Bonfanti, 1949) (Figs. 584, 588). In Carnivores the muscle is more fully developed ; both leaves of the ciliary body are provided with meridional muscular fibres, while the inner is provided with radial fibres (Figs. 585, 589). In both of these two classes

FIGS. 587 AND 588.—THE CILIARY BODY OF RODENTS AND UNGULATES (J. Rohen).
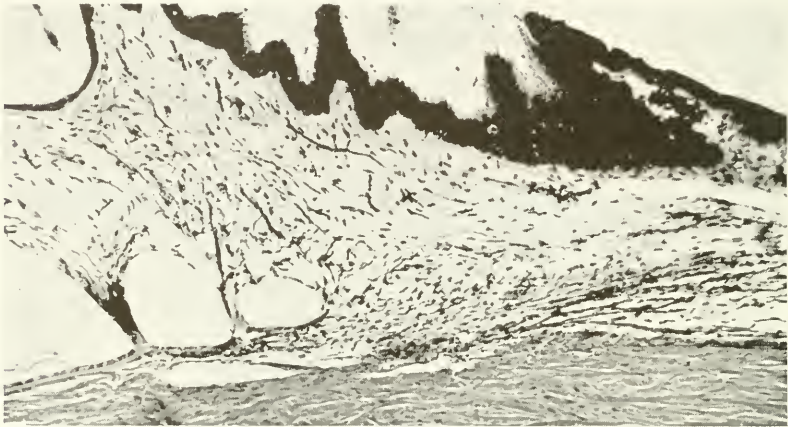
FIG. 587.—Rabbit ($\times$ 92).
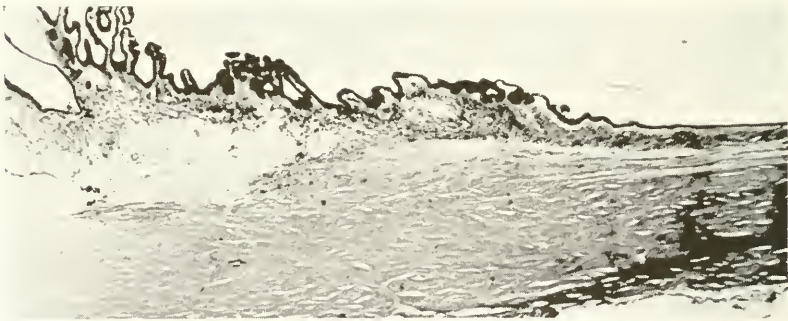
FIG. 588.—Pig (21).

the cleft is wide and deep ; but in Primates the muscle has developed to such an extent that its meridional and oblique fibres occupy the entire ciliary body ; moreover, its massive anterior attachment to the scleral spur (and through it by the scleral trabeculæ to the deeper layer of the cornea) has almost entirely obliterated the cleft leaving only remnant of it at the angle of the anterior chamber (Figs. 586,

In the lower Placentals the anterior gap between the two leaves
of the ciliary body forming the ciliary cleft deprives the root of the
iris of its support and consequently, to serve as anchorage, a series of
strands runs from the iris and the base-plate of the ciliary body towards
the limbal portion of the cornea where they pierce Descemet's membrane

FIGS. 589 AND 590.—THE CILIARY BODY OF CARNIVORES AND PRIMATES
(J. Rohen).

FIG. 589.—Dog (× 20).
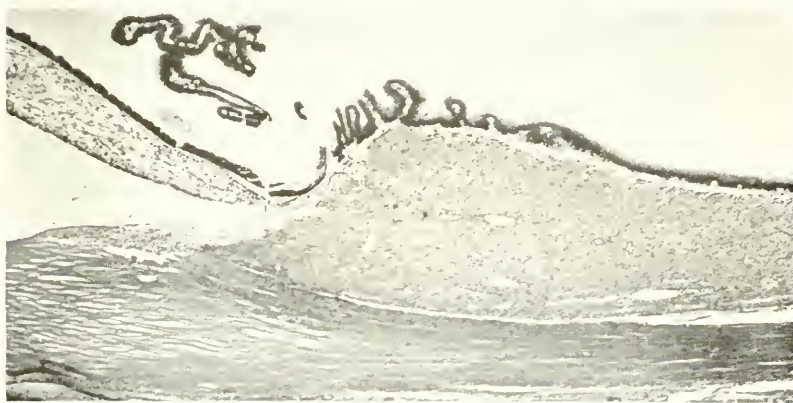
FIG. 590.—Ape (× 36).

and blend with the deeper layers of the substantia propria (Fig. 596).
These strands of connective tissue covered with endothelium, bridging
over the cleft, constitute the PECTINATE LIGAMENT, which gives support
to the root of the iris, the base-plate of the ciliary body and therefore
ultimately to the lens. In the lower Placentals wherein the cleft is
rudimentary and accommodative strain is lacking and in Primates
wherein the cleft is replaced by solid tissue, the pectinate ligament is

rudimentary or vestigial. In Rodents this ligament is made up of innumerable short fibres at the opening of the cleft, which itself is empty (Figs. 583, 591, 596) ; in Ungulates (such as the horse, ox, pig and sheep) the strands over the opening of the cleft are stout and well developed, like the girders of a bridge spanning the ciliary cleft, while the body of the cleft is filled by a close irregular meshwork of fine fibres appearing as spongy tissue (Figs. 584, 592) ; in Carnivora (such as the dog and cat) the more anterior strands supporting the root of the iris are thin and delicate like the cables of a suspension bridge, while the depth of the cleft is filled with fine threads running a fan-like course with no resemblance to spongy tissue (Figs. 585, 593, 597) ;

FIGS. 591 TO 594.—THE ANGLE OF THE ANTERIOR CHAMBER OF PLACENTALS.

As seen gonioscopically, showing the configuration of the pectinate ligament (from drawings from Troncoso).
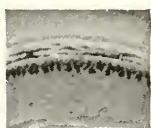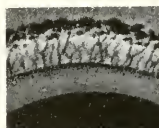

FIG. 591.—Rabbit.   FIG. 592.—Pig.   FIG. 593.—Dog.   FIG. 594.—Ape.

in the Pinnipedes (seals) the anterior strands are particularly stout. In the Primates (man) the pectinate ligament is discernible until the 6th month of fœtal life (Collins, 1899 ; Seefelder, 1910), but owing to its subsequent atrophy it can hardly be said to exist in the adult, the support of the lens being more adequately undertaken by the dense muscular and trabecular tissue of the ciliary body (Figs. 586, 594).

This interesting and important region has received a considerable amount of attention. The first to give an adequate description with illustrations was Murray (1780) at Uppsala who called the cleft at the angle of the anterior chamber of the ox the *ciliary canal*. In the following year, Felix Fontana (1781), the anatomist of Pisa and Florence, gave a description of the same region and since then the extensions of the anterior chamber into the ciliary region of Mammals have variously been called *Fontana's spaces* or *canals*. Shortly thereafter Kieser (1804) of Göttingen pointed out that such structures did not exist in man. Subsequently Hueck (1839) of Dorpat, studying the cow's eye, described the teeth-like structures stretching over Fontana's spaces from the root of the iris to the sclero-corneal junction as the *pectinate ligament* (*pecten*, a comb), an appropriately descriptive term ; since then it has been called by many names— the *suspensory ligament of the iris*, the *iris pillars*, and so on (Fig. 595).

Over the last century and a half much study has been given to the ciliary region of the mammalian eye—most of it histological.[1] More recently a better perspective has been put on the anatomical arrangements by the gonioscopic

[1] Flemming (1868), Iwanoff and Rollett (1869), Angelucci (1881), Dostoiewsky (1886), Virchow (1886–1910), Rochon-Duvigneaud (1892–93), Collins (1899), Asayama (1901), Huber (1901), Seefelder and Wolfrum (1906), Henderson (1908–50), Rohen (1953) and de Toledo Piza (1955).
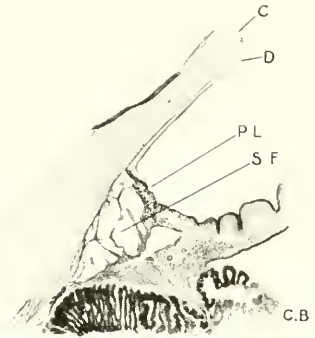
Fig. 595.—Diagram of the Angle of the Anterior Chamber of the Horse.

C, cornea ; CB, ciliary body ; D, Descemet's membrane ; I, iris ; PL, pectinate ligament ; SF, spaces of Fontana.
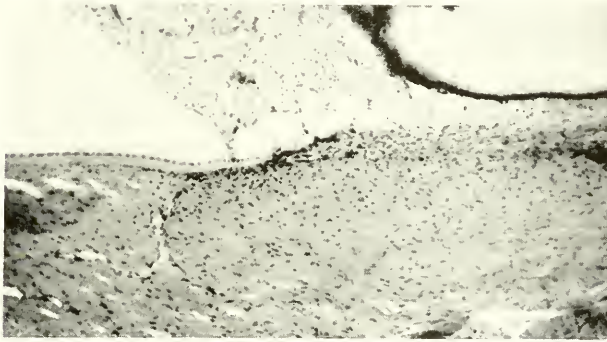
Fig. 596.—Section of the Anterior Chamber of the Rabbit.

Note the stout fibre of the pectinate ligament bridging over the entrance of the ciliary cleft and piercing Descemet's membrane ($\times$ 60) (Norman Ashton).

Fig. 597.—Section of the Anterior Chamber of the Cat.

Note the delicate strands of the pectinate ligament filling the ciliary cleft ($\times$ 60) (Norman Ashton).

and micro-anatomical methods applied by Troncoso and Castroviejo (1936) and Troncoso (1937). Troncoso called the cleft the *cilio-scleral sinus*, but since it does not separate the ciliary body and the sclera but extends into the ciliary body itself, *ciliary cleft* (or *sinus*) would seem a more appropriate name.

The *ciliary processes* vary considerably in their form, depending on the number and arrangement of the zonular fibres, the development

FIGS. 598 AND 599.—THE CILIARY PROCESSES OF PLACENTALS
(after Franz, 1911).
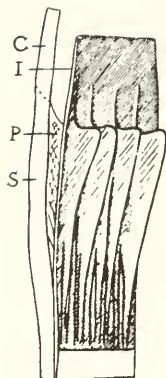
FIG. 598.—*Felis libyca.*
C cornea; *I*, iris; *P*, pectinate liga-
ment; *S*, sclera.
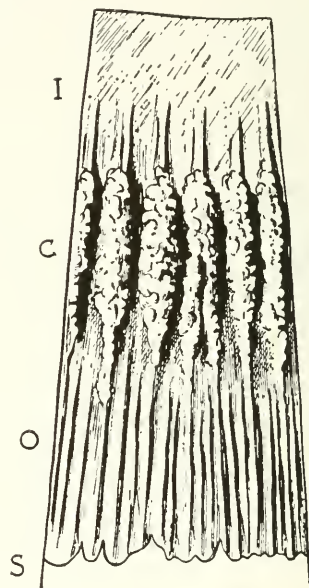
FIG. 599.—*Elephas maximus.*
C, ciliary processes; *I*, iris; *O*, orbi-
culus ciliaris; *S*, ora serrata.

of which depends on accommodative activity.[1] Three general types exist (Figs. 598 and 599).

1. In the lower orders as exemplified in the Rodents (rabbit), the processes are thin and blade-like with deep valleys between ; many of them extend far into the iris as is seen in the human embryo, touching the lens anterior to the equator, so that the corona ciliaris is in large part an iridic structure. The posterior chamber is thus exceedingly small.

2. In the Ungulates as exemplified in sheep, pigs and cattle, the processes are thick and club-like with shallow valleys and are confined

r the comparative anatomy see Würdinger (1886), Bayer (1892), Lauber (1901 Virchow (1910), Franz (1912), Hess (1913), Beauvieux and Dupas (1926), Tronce 42), Wislocki (1952), Rohen (1953).

to the ciliary region ; their anterior ends form a solid wall not encroaching upon the iris so that the posterior chamber is deep. The apices of the processes, however, touch the lens.

3. In Carnivora, as exemplified in the cat, dog, and lion, the ciliary processes are of two types—knife-like, tall, major processes between every pair of which lies a small minor process ; none of them reaches the lens. In the Primates the general arrangement is similar but the main ciliary processes are stouter and more rounded and several stumpy minor folds (plicæ ciliares) lie between the main processes.
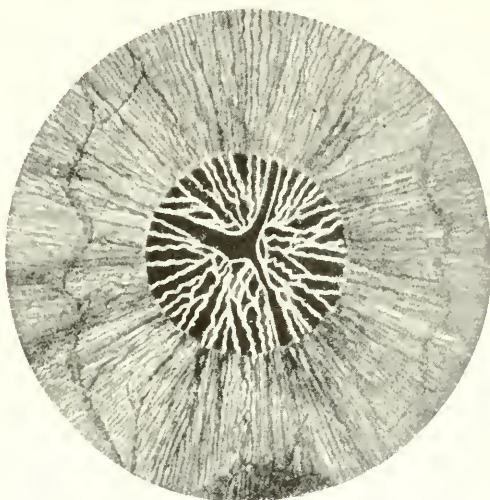
Fig. 600.—The Iris of the Fœtal Guinea-pig.

Note the circulus arteriosus iridis major faintly outlined in the nasal and temporal parts and the vessels of the pupillary membrane spanning the pupil (from a slit-lamp drawing by Ida Mann).

4. Finally, the ciliary processes are absent in the shrews (Soricidæ).[1]

Curious nervous structures have been described in the ciliary body of certain Cetaceans in the region of the angle of the anterior chamber which may perhaps be CILIARY RECEPTOR ORGANS. In the beaked whale, *Hyperoödon*, Pütter (1912) found elongated nervous structures which appeared to be associated with the ciliary nerves, and in the hump-back whale, *Megaptera*, Rochon-Duvigneaud (1943) described oval bodies isolated or lying in groups, resembling pacchionian corpuscles or the corpuscles of Herbst in the bill of the duck. Their function is enigmatic, but it has been suggested that they are sensory pressure-organs of value to the animal when it dives. This may be possible in view of the " corpuscles " described by Kurus (1955) in the ciliary body of man which conceivably may act as receptors to changes in the intra-ocular pressure.

[1] It will be remembered they are also absent in Fishes (except Selachians), *Sphenodon*, lizards and snakes.

The Iris. The deeper layers of the iris conform to the general vertebrate type. Both layers of the retinal epithelium are heavily pigmented except when a dilatator pupillæ muscle is present in which case the anterior layer lacks its pigment except near the pupillary border. The pupillary muscles are non-striated ; a sphincter is always present, massed particularly near the pupillary margin, but sometimes (in aquatic Placentals such as the otter, the Pinnipedes and the Cetaceans, and in the pig) extending peripherally throughout the entire width of the iris ; the dilatator is absent in the nocturnal representatives of the lower species.

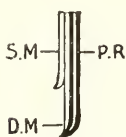The main (deeper) mesodermal layer of the iris corresponds with that of other Vertebrates, being supplied by a circular artery (the circulus arteriosus iridis major) derived from the anastomosis of each of the two long posterior ciliary arteries. This arterial circle is usually hidden behind the limbus but can sometimes be seen on the anterior surface of the iris, as in the guinea-pig (Fig. 600) ; from it radial vessels are given off to supply the sphincteric and subsphincteric plexuses, the blood being drained away by a radial system of veins. Superficially to this, however, lies a layer unique to Mammals—*the anterior mesodermal layer*. In embryonic life this layer grows in from the periphery in advance of the deeper layer of mesoderm and the retinal epithelium, carrying with it a rich vascular supply to constitute the anterior portion of the tunica vasculosa lentis. The central (pupillary) portion of this layer is diaphanous and almost acellular and as development proceeds it gradually atrophies, receding to a sinuous scalloped line peripheral to the pupillary margin where the superficial radial vessels anastomose to form a very imperfect circular arcade, the circulus arteriosus iridis minor. The site of the lesser circle which marks the limits of the superficial mesodermal layer is fortuitous, sometimes being close to the pupil, sometimes far away ; it varies in different species, between individuals of the same species, and in different parts of the iris in the same individual, but the general plan of vascularization remains the same (Mann, 1931) (Fig. 601). In most Placentals this layer is compact and covered by a continuous layer of endothelium ; in some Rodents (rabbit) and the higher Primates (*Macacus*, the gorilla and man) it tends to atrophy so that an incomplete layer is formed with the development of open crypts (Wolfrum, 1926 ; Vrabec, 1952). As we have seen, from its periphery are given off strands of endothelial-lined connective tissue which traverse the angle of the anterior chamber

Fig. 601.—Structure of the Iris of Placentals.

S.M, D.M, superficial and deep mesodermal layers. *P.R,* the two posterior retinal layers containing between them the potential cavity of the optic vesicle.

to find anchorage in the limbal region of the sclera (the pectinate ligament) ; these are of varying development in different species and are only vestigial in man.

The *pigmentation of the iris* is much more drab and uniform than in many other classes of Vertebrates. Except in albinotic individuals it is derived merely from melanin-containing chromatophores, and depending on their number and the density of pigment within them, the iris is a varying shade of brown, tending to yellow when the pigment is scarce and blue (as often in man) for reasons of optical transmission when the stromal pigment is sufficiently sparse. As a rule the pigment is plentiful and the eye dark brown or almost black, and since the chromatophores lie superficial to and between the vessels, the latter are usually completely obscured ; only in albino types can the vascular pattern be made

FIGS. 602 TO 606.—PUPILLARY APPENDAGES IN PLACENTALS.

FIG. 602.—The horse.   FIG. 603.—The gazelle.

FIG. 604.—The goat.   FIG. 605.—The camel.   FIG. 606.—The hyrax.

out. Occasionally and very rarely this simple pigmentary scheme is complicated by the presence of other pigments and iridocytes, a circumstance which gives rise to the green lustre of the eyes of some Carnivores, such as the cat, and some Prosimians. In animals provided with a choroidal tapetum, representative elements of this structure are found in the iris—fibrous elements in Herbivora, cellular in Carnivora (Wolfrum, 1926).

The pupillary margin is occasionally marked by special appendages the purpose of which is presumably to diminish glare. These may be of two types.[1] The first, the CORPORA NIGRA (grape-seed bodies or FLOCCULI of Kieser, 1803), are immobile and are formed by a proliferation of the pigmented epithelium as highly vascularized cystic protrusions of the marginal sinus.[2] They occur among the higher Ungulates (Figs. 602 to 605). In the Equidæ (horse, etc.) they are relatively simple, being confined to the upper edge of the pupil (Fig. 557) ; in

[1] For literature, see Bayer and Fröhner (1900), Johnson (1901), Lange (1901), Stein (1902), Zietzschmann (1905), Richter (1909–11), Schneider (1930), Rohen (1951–52).
[2] The embryonic persistence of the primary optic vesicle between the two layers of epithelium at the pupillary margin.

some Ruminants they are more fully developed, as in the gazelle where they are found both on the upper and lower margins of the pupil, or in the sheep where there are as many as 20, or in the wild goat, *Capra dorcas*, where the mesodermal portion of the iris, beautifully striped, participates in the projection ; in the Tylopoda (camel, llama) they reach their fullest development, forming a series of ridges and hollows on the upper and lower margins of the pupil which interlock on miosis (Zannini, 1932).

The second type of structure, called the UMBRACULUM by Lindsay Johnson (1901), is somewhat reminiscent of the operculum of some rays [1] (Fig. 606). In the coneys (hyraxes) it is a flap-like fibro-cellular structure, protruding from the mesodermal portion of the iris 2 mm. from its free edge. It is provided with a fan-like arrangement of (muscular ?) fibres and is remarkably contractile ; apparently without regard to the amount of light and perhaps under voluntary control, it can be retracted out of the pupillary aperture, extended so as to touch the lower margin of the pupil and almost totally occlude it, or protruded, flap-like, to touch the posterior surface of the cornea. An expansile operculum is also seen in some Cetaceans.

The *pupil* in most Placentals is round, both in dilatation and contraction. A slit-shape on contraction is achieved, however, in some Carnivora either as a protective or an optical device. The slit- or oval-shape is maintained by the arrangement of the fibres of the sphincter, two bundles of which cross above and below the pupil and are continued out to the periphery of the iris, a scissor-like action which compresses the pupillary aperture laterally (Michel, 1881 ; Eversbusch, 1885 ; Raselli, 1923 ; Theiler, 1950 ; Rickenbacker, 1953) (Figs. 608– 10). In the smaller Felidæ and Viverridæ and in some Hyænidæ and Rodentia, as is well seen in the cat or the chinchilla, the slit-like contracted pupil affords protection to an essentially nocturnal animal against excessive light when basking in the sun. In some of the hyænas (*Hyæna striata, H. brunnea*) the contracted slit has a constriction in the middle giving the impression of two pupils (K. M. Schneider, 1930). Among the Pinnipedes, in the seals and sea-lions the pupil is dilated and circular under water, but contracts to a vertical slit in the air (except in the bearded seal, *Phoca barbata*, wherein the slit is horizontal) ; this is almost certainly an adaptation for aerial vision which will be discussed at a later stage (Johnson, 1901).[2] The walrus, on the other hand, which feeds on land, has a broad, horizontally oval pupil (Franz, 1934).

While round pupils are the rule among Placentals, oval pupils are found in a considerable number of species—usually horizontally oval among Herbivora and vertically oval among Carnivora, a circumstance
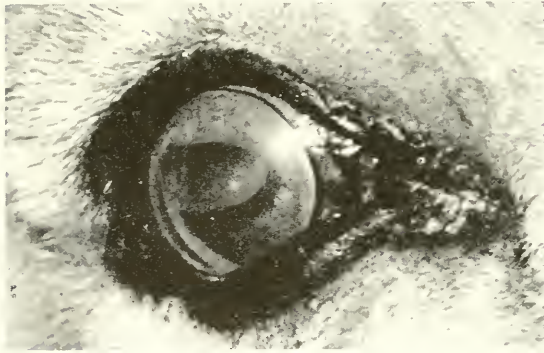
FIG. 607.—The Eye of a Pony.
Showing the typically horizontally oval pupil of an Ungulate
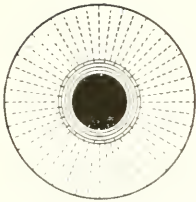(photograph by Michael Soley).
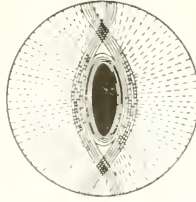

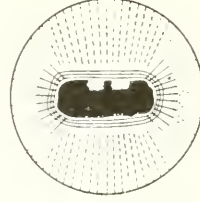FIG. 608.—Primate.   FIG. 609.—Cat.   FIG. 610.—Horse.

The round pupil is characteristic of diurnal and strictly nocturnal types.
The vertically oval pupil is characteristic of nocturnal types which bask in the
sun. The horizontally oval pupil is characteristic of Ungulates and several
other types (see text).

In the round pupil the sphincter muscle (solid lines) and the dilatator
muscle (broken lines) are symmetrically arranged. In the vertically oval pupil
part of the sphincter muscle surrounds the pupil but criss-crossing fibres
extend above and below to the periphery of the iris. In the horizontally
oval pupil most of the sphincter fibres encircle the pupillary aperture but other
fibres are orientated radially on each side to be anchored in connective tissue
(shown stippled in Fig. 610) in the nasal and temporal parts of the iris ;
these areas are devoid of dilatator fibres (from drawings by Eversbusch and
Gordon Walls).

depending not on diet but on habit, an adaptation in the first case to
suit diurnal, shade-loving animals, in the second, crepuscular or
nocturnal animals requiring protection from glare during daylight
(Figs. 607–10).

The following have vertically oval pupils :
Many Carnivora—the larger Felidæ (lion, tiger, leopard, jaguar) ; Canidæ
(dog, fox, etc.) ; most hyænas, and Viverridæ ; among the Procyonidæ, the
panda ; some Ursidæ (the arctic white bear, *Thalassarctos maritimus*, and
Melursus (Fig. 609)).

Few Rodents—the varying hare (*Lepus timidus*), the nutria-bearing coypu

Vizcacha

Mongoose

Weasel

Coati

Aard-vark

(*Myocastor coypus*), the S. American vizcacha (*Lagostomus trichodactylus*), the Patagonian cavy (*Dolichotis patagonica*), the chinchilla, and the American capybara (*Hydrochœrus capybara*).

Few Prosimians—*Nycticebus* and the galago of Zanzibar (*Galago zanzibaricus*).

The following Placentals have horizontally oval pupils :

Among the Ungulates, all Artiodactyls (Suoidea, Tylopoda and Ruminants), all Perissodactyls (Equidæ, Rhinocerotidæ) except the Tapiridæ (Figs. 607, 610).

All Cetaceans (whales) and Sirenians (sea-cows) except *Manatus inunguis*.

Among the Carnivora—a few Viverridæ (the mongoose, *Herpestes* ; *Cynictis* and *Suricata*) ; a number of Mustelidæ (the ferret, *Putorius furo*, the weasel, *Mustela nivalis*, the ermine, *M. erminea*, the mink, *Lutreola*, the wolverine, *Gulo*) ; among the Procyonidæ, the coati (*Nasua*). Among the Pinnipedes, the bearded seal (*Phoca barbata*).

Among the Rodents, the common squirrel (*Sciurus vulgaris*), the African squirrel (*Xerus*), the American chipmunk (*Tamias*), the prairie-dog (*Cynomys*), the marmot (*Marmota*).

Among the Tubulidentata, the aard-vark (*Orycteropus*).

The direct *pupillary reaction* to light is generally present (Hertel, 1907 ; K. M. Schneider, 1930 ; Kahmann, 1930–32 ; Rochon-Duvigneaud, 1933 ; Studnitz, 1934 ; Nordmann, 1947) ; a consensual reaction has been noted in many species (cat, dog, ox, horse, sheep, etc.) (Steinach, 1890–92 ; Schleich, 1922). Dilatation to stimuli such as pain or attention occurs in such species as the cat, the dog and monkeys (*Macacus*) (Levinsohn, 1902 ; Amsler, 1924 ; ten Cate, 1934), reactions particularly evident in the hyæna (Schneider, 1930). The pupils of Ungulates are remarkably insensitive to all stimuli in comparison with those of other Mammals, but the pupils of all Placentals react to atropine (Johnson, 1901).

The channels draining the aqueous humour from the angle of the anterior chamber are relatively simple in most Placentals.[1] Associated with the outer wall of the ciliary cleft there is a rich network of veins and venous capillaries which combine to form an intrascleral plexus, the main part of which lies about the level of the middle of the cleft ; this drains outwards by some 5–6 wide scleral veins to the subconjunctival veins (Fig. 611). Originally described by Hovius (1716) in the dog, and often called the CIRCLE OF HOVIUS, this plexus varies considerably in richness and complexity in different animals, being relatively sparse in Ungulates and elaborate in Carnivores. That these vessels are the essential exit-channels of the aqueous humour has been shown by the injection experiments of Nuel and Benoit (1900), Seidel (1923–24) and Kiss (1942–49), and when they reach the subconjunctival plane some of them may contain pure aqueous undiluted with blood (in the rabbit, Schmerl, 1947 ; Weekers and Prijot, 1950 ; Greaves and Perkins, 1951 ; Wegner and Intlekofer, 1952 ; Binder and Binder, 1). According to Rohen (1956) in the dog this plexus anastomoses

[1] For literature, see Lauber (1901), Maggiore (1917), Troncoso and Castroviejo (19), Troncoso (1937–42).

with branches of the anterior ciliary arteries with shunt-like vessels which can be opened or closed by large epithelioid cells. In the Primates, as we have seen, the ciliary cleft is obliterated by the great development of the ciliary muscle, thus cutting off the possibility of the drainage of aqueous by this route ; to maintain connections with the anterior chamber a special sinus, the CANAL OF SCHLEMM, is thus developed as a diverticulum from the intrascleral venous plexus,

FIGS. 611 AND 612.—THE DRAINAGE CHANNELS FROM THE ANGLE OF THE ANTERIOR CHAMBER IN PLACENTALS.
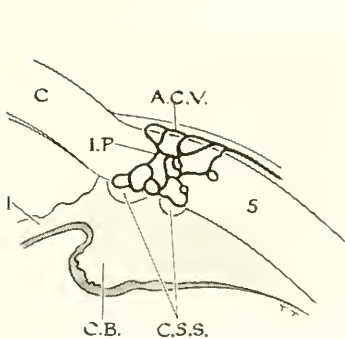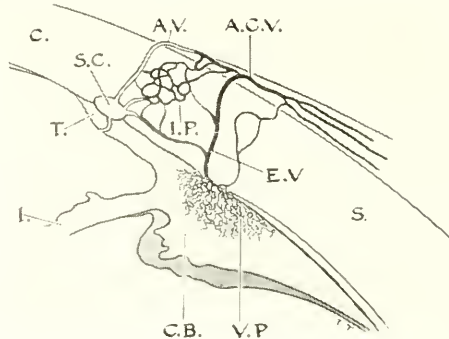

FIG. 611.—A lower Placental (rabbit).   FIG. 612.—A higher Placental (Primate).

ACV, anterior ciliary veins ; *AV*, aqueous vein ; *C*, cornea ; *CB*, ciliary body ; *CSS*, ciliary cleft ; *EV*, efferent ciliary veins ; *I*, iris ; *IP*, intrascleral ciliary plexus ; *S*, sclera ; *SC*, canal of Schlemm ; *T*, trabeculæ traversed by a canal of Sondermann ; *VP*, ciliary venous plexus.

In Fig. 611 the essential drainage is from the anterior chamber into the ciliary cleft, thence through the intrascleral plexus of veins into the anterior ciliary veins. In Fig. 612 the older channels are represented as in Fig. 611 draining from the ciliary venous plexus, but superimposed on this is a new drainage system represented by Sondermann's canals, the canal of Schlemm, an anterior extension of the intrascleral venous plexus, together with the intrascleral and aqueous veins emptying directly into the anterior ciliary veins.

placed anteriorly at the corneo-scleral junction at which level the angle of the anterior chamber is now closed (Fig. 612). This structure, which may branch to have more than one lumen and is lined by a single layer of endothelium, runs circumferentially around the globe separated from the anterior chamber by the corneo-scleral trabeculæ through which pass minute channels, the canals of Sondermann (1933), and is connected to the intrascleral venous plexus by numerous efferent channels, some of which reach the subconjunctival region directly as aqueous veins. This system, added to the intrascleral venous plexus to compensate for the closure of the ciliary cleft, plays the major part in the drainage of the aqueous humour in the eyes of Primates.

The *lens*, suspended freely from the ciliary processes, is usually relatively small and lenticular in shape in diurnal species, the anterior surface being usually the more convex in Carnivora, the posterior in Herbivora and Primates (Figs. 613 to 616) ; it approaches rotundity and is larger in nocturnal species, especially in the small-eyed lower forms, and is round in aquatic species such as the Cetaceans and Pinnipedes. Among Sirenians (sea-cows such as the manatee and dugong) the lens is lenticular in shape but, to suit the optics of an

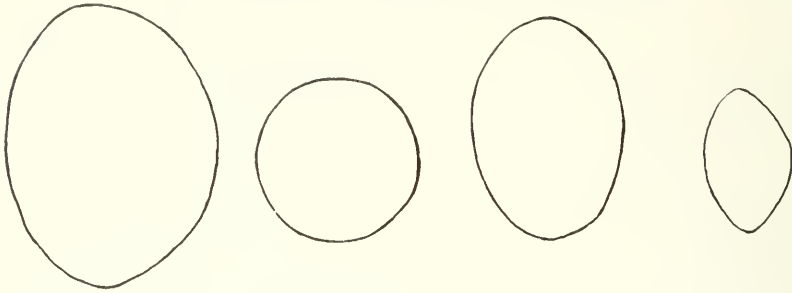Figs. 613 to 616.—The Lenses of Placentals.

Fig. 613.—Pig.　　Fig. 614.—Seal.　　Fig. 615.—Dog.　　Fig. 616.—Primate.

aquatic environment, approximated closely to the cornea so that the anterior chamber is very shallow. In the tree-shrew, *Tupaia*, and in most squirrels (Sciuridæ, except the nocturnal flying squirrels), the lens is tinted yellow (Merker, 1928 ; Walls, 1931). With regard to its structure, the same general plan of a series of radial lamellæ is apparent throughout the whole vertebrate phylum, with only minor modifications (Rabl, 1899) (Fig. 617). The sutural arrangements are usually simpler than in man, being made up of two lines having a vertical direction anteriorly and a horizontal posteriorly (*e.g.*, rabbit). This forms a transient stage in the development of the lens of Primates but eventually in these the lines branch into a tri-radiate form resembling the letter Y standing in the erect position anteriorly and the inverted position posteriorly (Figs. 618 to 620). In all adult Mammals, the subcapsular epithelium ends at the equator, but in many of the lower species it extends farther back. The *capsule* is always present and in some animals it is very thick. showing definite striations into layers ; thus in the horse at the anterior pole it is about 0·5 mm. thick and is made up of 26 layers. The local variations in thickness are not uniform :

Fig. 617.—The Radial Lamellæ of the Lens of the Chick (after Rabl).

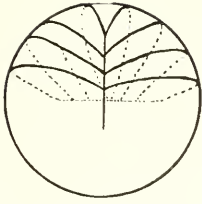Figs. 618 to 620.—Sutural Arrangements of the Lens in Placentals.

Fig. 618.—The sutural arrangements in a lower Mammal (a rabbit), forming a transient stage in the development of the lens of Primates.
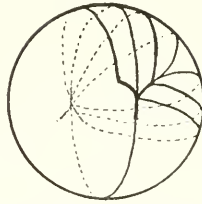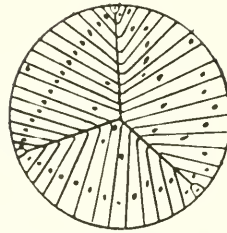
Fig. 619.—The general sutural arrangements in Primates.

Fig. 620.—The anterior surface of the lens in Primates.

in general, among Sauropsida the maximum thickness is at the equator ; in Mammalia the general scheme of the human capsule is followed. but the thinning at the anterior pole which seems to be associated with the formation of an anterior lenticonus during accommodation is peculiar to the Primates (Fincham. 1929) (Figs. 787 to 790).

The differences in configuration in the ciliary body necessitate variations in the arrangement of the *zonular fibres* (Figs. 621–3).[1] In Rodents with ciliary processes prolonged onto the iris the zonular fibres arise from their posterior halves only ; in Ungulates they arise from the posterior two-thirds of the processes but hug them anteriorly to their apex. In both cases they run along the floors of each valley and the sides of the adjoining processes to proceed in discrete bands towards the equator of the lens. In Carnivora, however, with their greater

Figs. 621 to 623.—The Zonular Fibres of Placentals.
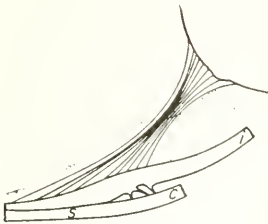
Fig. 621.—An Ungulate (pig).
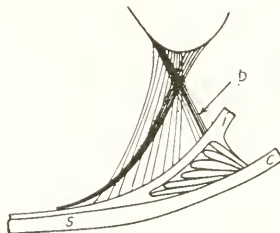
Fig. 622.—A Carnivore (cat).
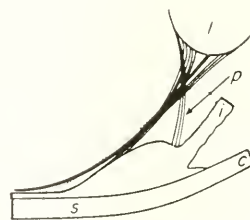
Fig. 623.—A Primate (monkey).

The zonular fibres are outlined in continuous lines, the major ciliary processes in dotted lines. *c*, cornea ; *i*, iris ; *l*, lens ; *s*, sclera. *p* indicates the smaller perpendicular bundles of fibres associated with the minor ciliary processes (from Kahmann and Walls).

[1] For the comparative anatomy of the zonule, see particularly Aeby (1882), Kahmann (1930), Teulières and Beauvieux (1931), Troncoso (1942), Wislocki (1952), Fukamachi (1953).

accommodation, the pattern of the zonule becomes more complex as it traverses the space between the ciliary body and the lens (Fig. 622). Bundles of fibres arise posteriorly from the orbicular portion of the ciliary body, run along the valleys hugging the sides of the major processes and find insertion into the lens anterior to the equator. Other fibres arising more anteriorly pass backwards to find insertion behind the equator, while the space between the two major systems is filled with fibres arising mainly from the minor processes and running perpendicularly to find insertion mainly into the posterior part of the attachment zone of the lens. In the Primates, on the other hand, fibres arising posteriorly in the orbicular region are inserted into the anterior lens capsule, while those arising more anteriorly are inserted into the posterior capsule, the latter being reinforced by perpendicular fibres arising far anteriorly ; between these two main systems of fibres a space (the " canal " of Hannover, 1852) exists which is traversed by a few of the fibres of the posterior system finding attachment to the equator itself (Fig. 623).

The *vitreous gel* is constituted as in man, the electron microscope showing a system of fibrils (ox, calf, sheep, pig, rabbit—Schwarz and Schuchardt, 1950 ; Schwarz, 1951).

FIGS. 624 TO 626.—TYPES OF HYALOID VESSEL (Ida Mann).

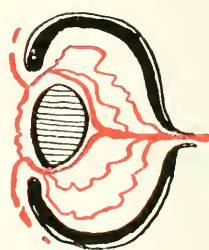FIG. 624.—Fishes.   FIG. 625.—Anurans.   FIG. 626.—Mammals.

FIGS. 627 TO 630.—TYPES OF RETINAL BLOOD SUPPLY IN VERTEBRATES
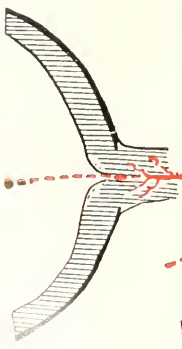(excluding the falciform process of Teleosts).

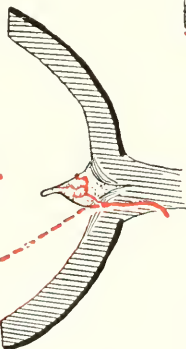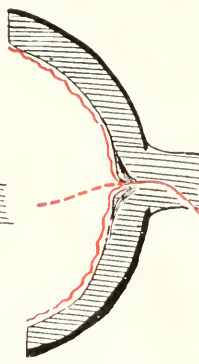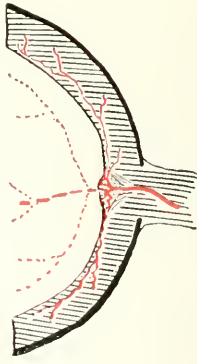FIG. 627.—The avascular retina.   FIG. 628.—The pecten or conus.   FIG. 629.—The membrana vasculosa retinæ.   FIG. 630.—The arteria centralis retinæ.

The Retinal Vascularization

The hyaloid system of vessels is unique in its development in Mammals (Figs. 624–630). We have already seen in Fishes that this system of vessels runs along the ventral part of the globe in the open fœtal fissure, an arrangement seen in its most fully developed form in the falciform process of Teleosteans. In many Amphibians this arrangement is extended to constitute a superficial membrana vasculosa retinæ. In the Sauropsida the hyaloid vessel on entering the eye atrophies except for the formation of a conus or pecten at the disc itself. In Mammals the hyaloid artery in embryonic life runs directly to the posterior portion of the tunica vasculosa lentis, while a multitude of vessels ramifies in the vitreous. These vessels disappear in the later stages of embryonic life, the only visible remnant being a small residuum of glial tissue lying on the optic disc (Bergmeister's papilla). Sometimes this condition remains in the adult mammalian eye so that the retina itself is avascular ; more usually vessels grow out from the hyaloid trunk and invade to a greater or less degree the substance of the retina itself ; in this event the hyaloid trunk becomes the central retinal artery. With the exception of the eel and a colubrid snake,[1] it is only within the class of Mammals among all Vertebrates that a retina directly supplied by capillaries is found.

The mode of entrance of the central artery varies in different species. It is derived from the ciliary branch of the external ophthalmic, sometimes supplemented by anastomosis with the small internal ophthalmic artery.[2] In some species such as the rabbit a central artery accompanied by a central vein enters the optic nerve and runs upwards to reach the centre of the disc ; there, just before or just after emerging, it divides into nasal and temporal branches (Bruns, 1882 ; Henderson, 1903 ; Davis, 1929). In the cat the central retinal artery was found by Davis and Story (1943) to be invariably occluded and vestigial, the retina being supplied by the terminal posterior ciliary branches of the ciliary artery. In the dog, on the other hand, there is no central retinal artery but several posterior ciliary vessels pierce the sclera around the optic nerve-head where they give off retinal branches, appearing at the margin of the disc as cilio-retinal arteries. In this animal a central vein is sometimes present but even when it exists it immediately breaks up to leave the eye with the marginal arteries to enter the subarachnoid space (Wolff and Davies, 1931). Subendothelial cushions were described by Moffat (1952) in the ciliary arteries of the dog, the contraction of which might act by shutting off the choroidal blood supply and diverting it to the retina. In the Primates including man, the central retinal branch of the ophthalmic artery supplies the whole retina apart from small anastomoses from the posterior ciliary

[1] p. 390.   [2] p. 498.

arteries through the circle of Zinn (Wybar, 1956), but in the lower Mammals the tendency is for the posterior ciliary arteries to assume greater importance. It is to be remembered, however, that the appearance of arteries emerging from the optic nerve-head onto the retina in a marginal position around the disc, a formation suggestive of

FIGS. 631 TO 634.—TYPES OF PLACENTAL RETINAL VASCULARIZATION
(See also Plates XIV and XV.)

FIG. 631.—THE FUNDUS OF THE DOG.
The lightly coloured area is the tapetum. There is a venous circle at the disc.

FIG. 632.—THE FUNDUS OF THE CAT.
The lightly coloured area is the tapetum.

FIG. 633.—THE FUNDUS OF THE RABBIT.
The vessels are confined to the leashes of opaque nerve fibres.
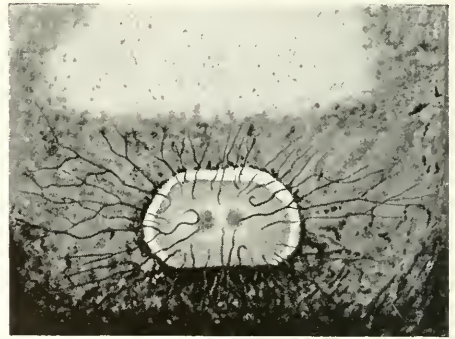
FIG. 634.—THE FUNDUS OF THE HORSE.
The lightly coloured area above the disc is the tapetum.

a ciliary origin, does not preclude their derivation from a central artery that has broken up into retinal branches in the substance of the nerve.

Among the Placentals almost every possible variety of retinal vascularization occurs, ranging from a complete absence of vessels, in which case the retina is nourished entirely from the choriocapillaris, to an elaborate system covering the entire retina in which the capillaries

may penetrate as far as the nuclei of the rods and cones.[1] Leber (1903) divided the retinæ of Placentals in this respect into 4 groups :—

(a) HOLANGIOTIC (ὅλος, all ; ἀγγεῖον, vessel) (Plates XIV, XV ; Figs. 631–2). The whole retina receives a direct blood supply either from a central artery or from cilio-retinal arteries which emerge either as a single trunk or as several branches from or around the optic disc. This type of vascularization occurs in some Insectivores (the hedgehog, *Erinaceus*, the mole, *Talpa*), some Rodents (mouse, squirrel, marmot),
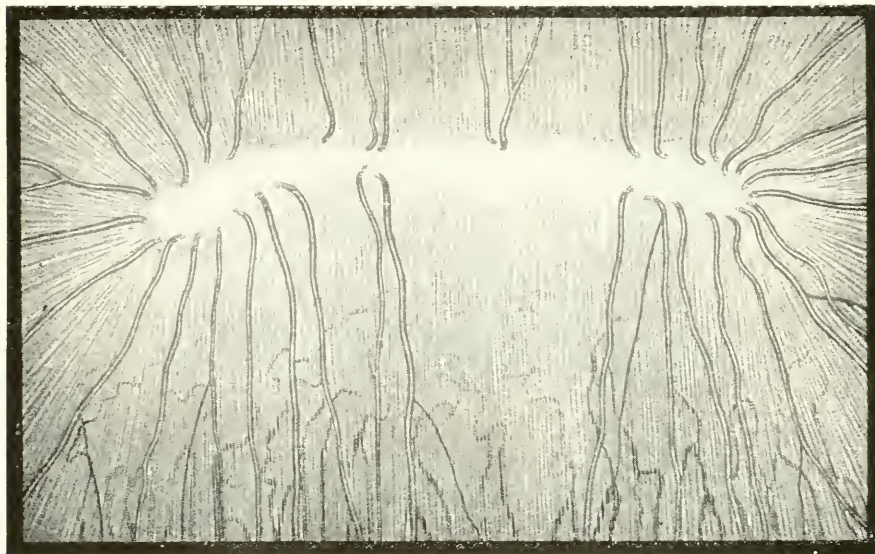
FIG. 635.—THE FUNDUS OF THE SQUIRREL, *SCIURUS VULGARIS*
(Lindsay Johnson).

some Carnivores (Felidæ, Canidæ, Ursidæ, some Viverridæ and the Pinnipedia), in a few Ungulates (pig, ox), and the Primates.[2]

In Primates the central artery emerges from the disc as a single vessel, but more usually several large arteries emanate therefrom ; in Carnivores a number of small arteries of the ciliary type emerge from the margin of the disc. In the squirrel and the marmot the disc is a long horizontal line from the entire length of which the vessels emerge (Fig. 635).

(b) MERANGIOTIC (μέρος, part) (Fig. 633). Part of the retina is supplied with vessels. This is only seen in the Lagomorpha (rabbit and hare), in which the vessels are limited to the horizontal expansions of medullated nerve fibres (Figs. 633, 637).

[1] For literature, see particularly H. Müller (1861), Sattler (1876), Leuckart (1876), His (1880), Bruns (1882), Barrett (1886), Schultze (1892), Johnson (1901), Leber (1903), Damel and Fortin (1937) (bat), Michaelson (1948–54), Rohen (1954) (rabbit).
[2] Compare also the Marsupials, *Didelphys* and *Petaurus*, p. 440.

(c) PAURANGIOTIC ($\pi\alpha\hat{\upsilon}\rho o s$, small) (Plate XV; Fig. 634). The vessels are very minute and extend only a short distance from the disc. This occurs in Perissodactyla (horse, tapir, rhinoceros which has only capillaries around the disc), the elephant, the Hyracoidea, the Sirenia (*Manatus, Halicore*) and among the Rodents in the guinea-pig (*Cavia porcinus*) (Fig. 636).

(d) ANANGIOTIC (*à*, privative) (Plate XV). The retina is without vessels. This group comprises the more primitive Mammals and includes most of the Chiroptera (bats), the Xenarthra (sloths and armadillos), and certain Rodents (the porcupine, *Hystrix*, the chinchilla, the beaver, *Castor*, and others). Many of these anangiotic
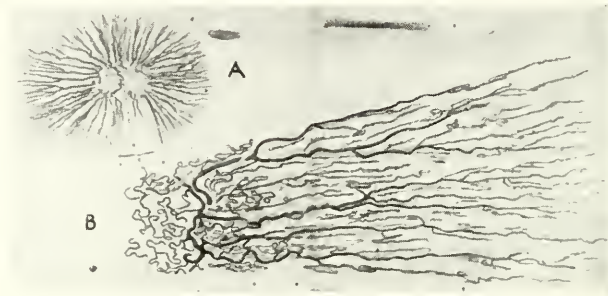
FIG. 636.—RETINAL VESSELS OF THE HORSE.

A, the general arrangement of the retinal vessels. *B*, a portion of the vascularized retina of the horse showing the peripheral loops, the T-shaped loops between the branches of the main vessel. There are many fine vessels in the optic nerve-head. Specimen injected with Indian ink (after L. Bruns).

FIG. 637.—RETINAL VESSELS OF THE YOUNG RABBIT.

Injected with Indian ink, mounted in glycerine ($\times$ 16) (I. C. Michaelson).

PLATES XIV AND XV

THE FUNDI OF PLACENTALS

PLATE XIV

The Fundi of Placentals   I

FIG. 1.—The toque monkey, *Macaca pileata*.   FIG. 2.—Monteiro's galago, *Galago monteiri*.

FIG. 3.—The raccoon, *Procyon*.

FIG. 4.—The common seal, *Phoca vitulina*.   FIG. 5.—The hog deer, *Cervus porcinus*

(Figs. 1 and 3. Arnold Sorsby ; Figs. 2, 4 and 5, Lindsay Johnson.)

PLATE XV

THE FUNDI OF PLACENTALS: II

(Lindsay Johnson)

FIG. 1. The Indian rhinoceros, *Rhinoceros unicornis*.
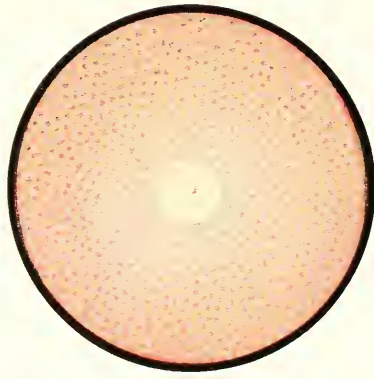
FIG. 2. The Australian fruit-bat, *Pteropus poliocephalus*.

FIG. 3. The common hedgehog, *Erinaceus europæus*.
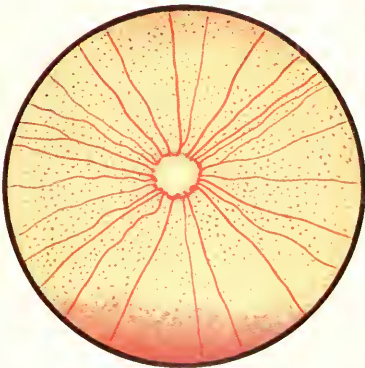
FIG. 4.—The flying squirrel, *Pteromys alborufus*.

FIG. 5. The Canadian beaver, *Castor canadensis*.

animals, particularly the Rodents, possess a capillary vascularization
on the optic nerve-head associated with a button-like projection
visible ophthalmoscopically, reminiscent of the papillary conus
of Reptiles.[1] A persistent hyaloid artery arising from the disc is
more common and is normal in a large number of Rodents and all
Ruminants.

The depth to which the vessels penetrate the retina varies con-
siderably. In some Insectivora (the hedgehog and the mole) the large
vessels lie superficially, each casting a shadow ophthalmoscopically
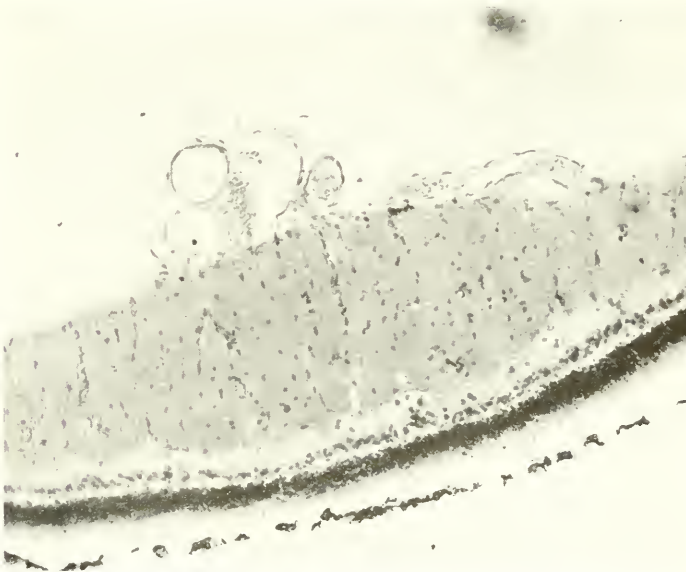
FIG. 638.—SECTION OF THE RETINA OF THE RABBIT.
Including the medullated nerve fibres. The large vessels are clearly pre-
retinal (I. C. Michaelson).

(Barrett, 1886) ; similarly in some Rodents (mouse, rabbit) they are
also very superficial and only partially embedded (Fig. 638). The
capillaries may not penetrate so deeply into the retinal tissues as in
man. In the horse and the rabbit they reach the nerve-fibre layer only ;
in the cat the ganglion layer ; but in most diurnal types with a
holangiotic retina the capillaries are reflected in the outer plexiform
layer as in man. In these the reticular capillary system is usually well
developed and consists of two main networks, an internal lying in the
nerve-fibre layer, and an external lying in the outer portion of the inner
nuclear layer, the meshes of the deeper net being smaller than the

[1] Compare the Marsupials, p. 440.

superficial. In most cases the superficial net is formed by the end-branches of the arterioles which do not reach the deeper net ; the two nets, however, intercommunicate freely by perpendicular or oblique capillary vessels, while the latter drains into the retinal veins and in all cases there is a zone free from capillaries around the arteries (His, 1880 ; Bruns, 1882). In some species of Rodents, however, members of the family Gliridæ (dormice) such as *Glis* and *Eliomys*, and the flying squirrel (*Pteromys*), the capillaries penetrate more deeply, reaching to the outer nuclear layer to supply the bodies of the visual cells and are not reflected until they approach the external limiting membrane (Kolmer, 1929 ; Rochon-Duvigneaud, 1943) ; in these animals it is interesting that the choroid is unusually thin.

It may be useful at this point to summarize the vascularization of the vertebrate retina. The *retina is avascular*, nourished indirectly from the choroid in Cyclostomes, Selachians, the cœlacanth, Chondrosteans, Urodeles, *Sphenodon*, Chelonians, Monotremes, Marsupials (except Macropodidæ, *Petaurus* and *Didelphys*), as well as anangiotic Placentals. This source may be supplemented by a specific structure—a falciform process in most Teleosts (except eels, Cyprinoids and goby-fish) and Holosteans ; a conus occurs in lizards and the kiwi (rudimentary in Crocodilians and the Macropodidæ) ; a pecten in Birds (except the kiwi).

Direct vascularization occurs by means of a membrana vasculosa retinæ in a few Teleosteans (certain eels, Cyprinoids and goby-fishes), Dipnoi, Polypterini, Anurans and Ophidians : in the eel and in *Tarbophis* the vessels penetrate into the retinal substance. Retinal vessels occur only in some Marsupials (*Petaurus* and *Didelphys*) and most Placentals.

The placental retina is of the ordinary vertebrate type with none of the specific peculiarities so frequently evident in other species (Fig. 639).[1] In its general architecture it does not show the same density or purity of lamination as is seen in Birds ; these features are most fully developed in some of the more active diurnal Rodents (the squirrel, *Sciurus* ; the prairie-dog, *Cynomys*). The visual elements in most species are duplex, the rods outnumbering the cones ; the cones are always single and are of simple construction, without oil-droplets or paraboloids (Figs. 266–7). In some of the lowest nocturnal forms rods alone are present (among Insectivores in the hedgehog and the shrew ; in the Chiroptera ; among Xenarthra in the armadillo ; and among Primates in the small nocturnal lemuroids, such as the galago and the loris, and in *Tarsius* and *Nyctipithecus*). The nocturnal Rodents have frequently been said to have a pure-rod retina,

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[1] For descriptive anatomy, see H. Müller (1856), Schultze (1866–71), Schiefferdecker (1886), Dogiel (1888), Chievitz (1891), Cajal (1894), Krause (1895), Greeff (1900), Zürn (1902), Detwiler (1924–49), Woollard (1925–27), Uyama (1934) (cat), Kolmer and Lauber (1936) (all classes), Parry (1953) (dog), Vonwiller (1954) (ox), and others. For the fine structure of the rods of the guinea-pig, see Sjöstrand (1949–53), of the rabbit, see de Robertis (1956), of the synapses of the visual cells see de Robertis and Franchi (1956).

but in the rat. the mouse (Schwarz, 1935), the dormouse (Vilter, 1953) and the guinea-pig (Kolmer and Lauber, 1936 ; O'Day, 1947 ; Vilter, 1949), cones are present although they are very few ; according to Detwiler (1949) they are absent in the chinchilla ; in the Cetacea (dolphins and whales) the cones are also few or non-existent. Only in the Sciuridæ (squirrels,[1] and particularly the marmot, the most
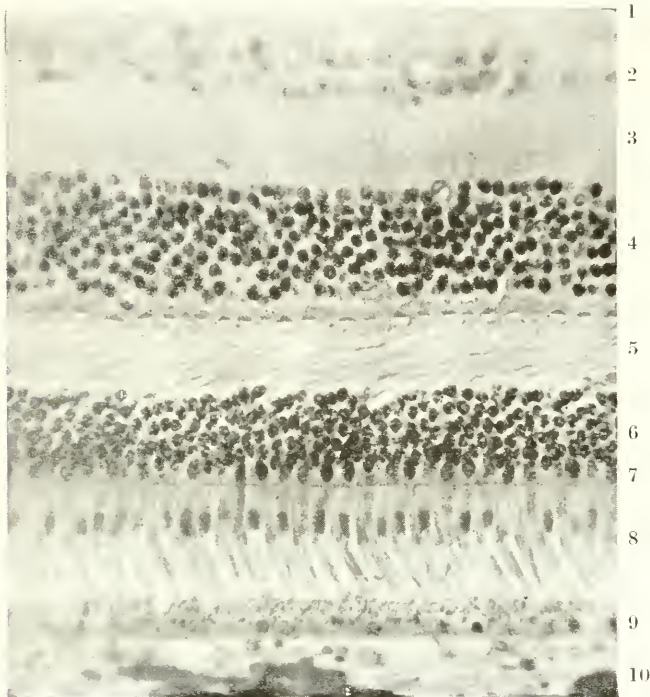
FIG. 639.—A MIXED ROD-AND-CONE PLACENTAL RETINA.

Section through the parafoveal part of the retina of the rhesus monkey (Mallory's triple stain, × 480) (Katharine Tansley).

1, optic nerve fibre layer ; 2, ganglion cell layer ; 3, inner plexiform layer ; 4, inner nuclear layer ; 5, outer plexiform layer ; 6, outer nuclear layer ; 7, external limiting membrane ; 8, visual cells ; 9, pigmentary epithelium ; 10, choroid.

diurnal of all Mammals which appears only during daylight) is a pure-cone retina known to exist (Rochon-Duvigneaud, 1929 ; Karli, 1951 ; Vilter. 1954).[2]

The contrast between the different types of retinal structure in Placentals is best brought out by a comparison between the rod-rich

[1] Except the nocturnal flying squirrel, *Pteromys*.
[2] For physiological evidence based on the spectral sensitivity, see Arden and Tansley, 1955 ; based on adaptation, see Tansley, 1957.
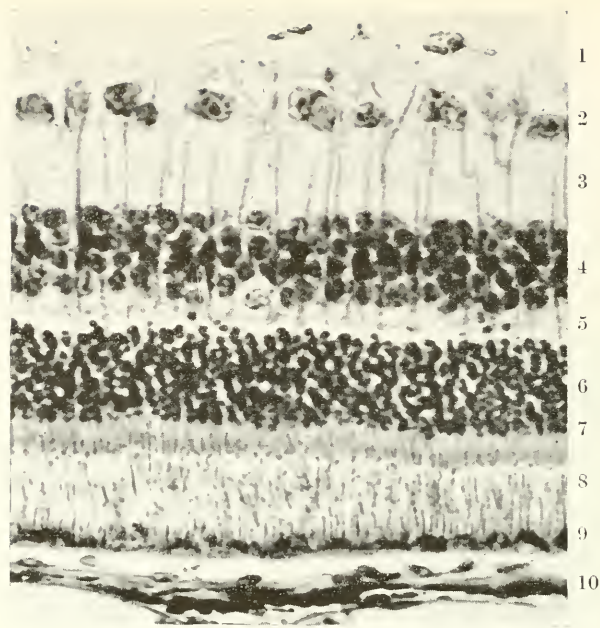
FIG. 640.—THE ROD-RICH PLACENTAL RETINA.
The retina of the rabbit (Katharine Tansley).
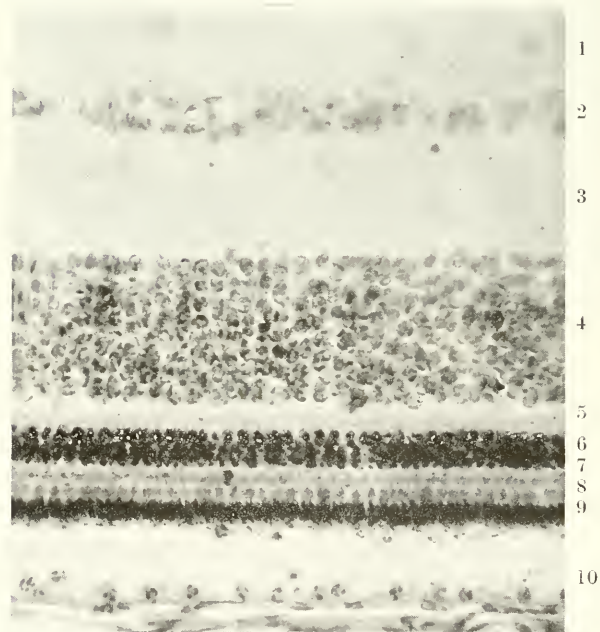
FIG. 641.—THE CONE-RICH PLACENTAL RETINA.
The retina of the squirrel (Katharine Tansley).

1, optic nerve fibre layer ; 2, ganglion cell layer ; 3, inner plexiform layer ;
 ... ner nuclear layer ; 5, outer plexiform layer ; 6, outer nuclear layer ;
7, ... rnal limiting membrane ; 8, visual cells ; 9, pigmentary epithelium ;
10 ... roid.

... e the few cells in the ganglion cell layer and outer nuclear layer in
Fig. ... in contrast to the larger numbers in Fig. 641. Compare Figs. 754
and ... In Fig. 641 note that the cones (8) are in two layers, one behind
the ot...

retina of the rabbit and the pure-cone (or virtually so) retina of the
squirrel (Figs. 640 and 641). In the rod-dominated retina the outer
limbs of the rods are long, the outer nuclear layer is thick, there are few
ganglion cells and few optic nerve fibres. In the retina of the squirrel,
on the other hand, the visual cells themselves are rather unusual and
somewhat atypical, being arranged in two layers, one outside the
other. Those of the inner layer have long striated outer limbs, while
in those of the outer layer this structure is shorter and buried in the
pigment epithelium. The inner nuclear layer is unusually thick as also
is the ganglion cell layer ; there are only 2 to 4 visual cells to each
ganglion cell and therefore to each optic nerve fibre, so that the latter
layer is again unusually prominent (Arden and Tansley, 1955).
According to Vilter (1954) the ratio of cone nuclei to ganglion cells in
the souslik, *Citellus*, is 200,000 : 90,000 for the whole retina.

Squirrel

An *area centralis* specifically elaborated for acute vision is found
among Placentals, but not commonly (Chievitz, 1891 ; Slonaker,
1897 ; Zürn, 1902) : most require no specific differentiation for their
panoramic vision. When it does occur it may take one of two forms
—a band stretching across the posterior part of the fundus or a cir-
cular area lying temporal to the optic disc ; occasionally both are
combined.

A *band-shaped area* is seen in Rodents, most pronounced in the temporal
region ; in the rabbit it is a broad streak 3–4 mm. wide in its central part running
just underneath the optic disc, and throughout its extent the retina is thicker
than elsewhere particularly in its rod-and-cone layers and in the layer of ganglion
cells (Chievitz, 1891). According to Krause (1895) the content of visual purple
is greater within this area than elsewhere ; and external to it the choroid is
thickened (Davis, 1929). The squirrel has a similar (pure-cone) band but less
well defined. Among the Ungulates, some Artiodactyls (Ruminants such as
the ox) have a similar band-shaped area running horizontally above the disc
and the lower part of the tapetum, associated with a round area centralis in
the temporal region.

Such a *temporal round area* is common in Ungulates (sheep, goat, horse, etc.) ;
it is also typical of the Carnivores, particularly the Felidæ, lying lateral to the
optic disc. In this family, particularly in the cat, the tiger and the lion, the
area centralis becomes highly differentiated ; the visual elements (cones,
according to Thieulin, 1927) are closely packed and ganglion cells are accumulated
in several layers, while there is an external depression (an " external fovea ") on
the choroidal aspect (Borysiekiewiez, 1887, tiger ; Zürn, 1902, cat ; Brückner,
1949, lion).[1] In the dog also there are said to be no rods in the central area
(Zürn, 1902). Among the Primates a central area is present in the Prosimians
(*Lemur catta*, *L. macaco*, etc.) and among the Simians in the nocturnal
Nyctipithecus. In *Tarsius*, one of the Prosimians, the macular region shows a
sudden increase in the number of percipient elements : the number of bipolar
and ganglion cells also increases, showing that the elements, although still
retaining the morphological characteristics of rods, are assuming the physiological

Tarsier

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[1] According to Wölfflin (1947), who examined a hypnotized lion, the macula is not
ophthalmoscopically visible.

characteristics of cones. There is, however, no displacement of the bipolar cells or nerve fibres and no true fovea.

A *fovea* occurs only in the Primates, appearing first in *Tarsius* ; it and *Nyctipithecus* have a pure-rod fovea (Polyak, 1957). All the Anthropoidea except *Nyctipithecus* have a central area and a well-formed pure-cone fovea of the same type as man, which the retinal vessels approach and encircle but do not invade (Fig. 642) (Woollard, 1926).[1]

The *optic disc* in the majority of Placentals is circular as in man, but in some Carnivores (Canidæ, as the wolf, jackal, fox) it is kidney-shaped and in many Ungulates and all Equidæ it is horizontally oval.

Primate
(squirrel monkey)

Fig. 642.—The Fovea of a Primate.
Macaca rhesus (× 114) (Katharine Tansley).

In most Sciuridæ this is exaggerated to form a unique type—a long, thin, tape-like structure stretching horizontally across the fundus above the axis of vision—which reaches its greatest development in the marmot (Fig. 635) ; this arrangement gives excellent upward vision for the arboreal family of squirrels. The optic disc lies on the level of the surface of the retina except in Carnivores and the flying squirrel, *Pteromys*, wherein it is sunk to form a deep pit. It varies considerably in colour ; usually white or pink, it is red in the Equidæ, bright red in the hedgehog and mole, pink surrounded by a green ring in the seal.

The *optic nerve* is of the standard type seen in man, the only exceptional feature being the enormously thick accessory sheath

[1] Blumenbach (1805), Albers (1808), and Soemmerring (1818) in several of the Simians ; Slonaker (1897) in the gorilla ; Wolfrum (1908) in *Macacus* ; Franz (1912) in *Halobates* ; Woollard (1925–27) in several of the Anthropoidea ; Detwiler (1943) in marmoset and the rhesus monkey.

already noted [1] to be present in whales, the hippopotamus and the elephant ; some of the fibres are non-myelinated (Bruesch and Arey, 1942). A minute subdivision of the fibres into fasciculi is common only among Mammals, and there is evidence that the complexity of the glial framework increases in proportion to the visual development of the animal in the evolutionary scale (Deyl, 1895).

The inner architecture and septal system of the optic nerve throughout the Vertebrates is interesting in this respect. As occurs ontogenetically in man, Cyclostomes show merely a central column of ependymal cells which have become invaginated within the developing nerve, and from them processes radiate outwards towards the periphery. The same arrangement is seen in the Dipnoan, *Protopterus*. In some Selachians and other Dipnoans and in snakes this simple arrangement is reduplicated and the nerve is broken up into a number of bundles each of which has a similar core of cells. In the remainder of the Vertebrates the pattern is altered : oligodendroglial cells (derived from the original ependymal cells) are scattered throughout the nerve. As the visual functions become more highly developed in the higher Vertebrates and man, the fasciculation becomes progressively less obvious, the number of fibre-bundles increasing and the original ependymal system becoming more uniformly dispersed throughout the whole structure.

It is interesting that the *lamina cribrosa* at the optic nerve-head shows wide variations. In general it may be said that in those Mammals which have good day-vision this structure is well developed with many collagenous fibres (squirrel, cat, monkey), while in species with a poor visual capacity (Rodents such as the rat, mouse and rabbit) the lamina is absent and the retina may even herniate in folds into the optic nerve sheath (Tansley, 1956) (Figs. 643–6).

In all Vertebrates below Mammalia the *decussation of the optic nerve fibres* at the chiasma is complete (or practically so in some Reptiles[2]) so that each eye is connected solely with the opposite side of the brain (Harris, 1904 ; Kappers, 1921) ; in all Placentals it is incomplete, but the crossed fibres always remain the more numerous. In Vertebrates below Mammals the fibres remain in distinct and separate fasciculi as they cross : in Placentals they become intimately intertwined and interlaced (Cajal, 1898 ; Bossalino, 1909). In general the number of uncrossed fibres varies with the degree of frontality of the eyes (Newton, 1704 ; J. Müller, 1826 ; Gudden, 1879) [3] ; in animals with laterally directed eyes they are relatively few [4] ; they number about 1/6 of the total in the horse,[5] 1/4 to 1/3 in the dog [6] and cat,[7] about 1/3 in the higher Primates, and about 1/2 in Man.[8] This arrangement whereby corresponding half-fields of each retina are connected to

[1] p. 451.   [2] Snakes, p. 392.
[3] A relationship sometimes referred to as the Law of Newton-Müller-Gudden.
[4] Rodents such as the rat and rabbit, Bellonci (1884), Singer and Münzer (1888), Pick and Herrenheiser (1895), Brauwer and Zeeman (1925), Overbosch (1926).
[5] Dexler (1897).
[6] Vitzou (1888).
[7] Nicati (1878), Brauwer and Zeeman (1925), Overbosch (1926).
[8] Brauwer and Zeeman (1925).

Figs. 643 to 645.—The Optic Nerve-head of Placentals.
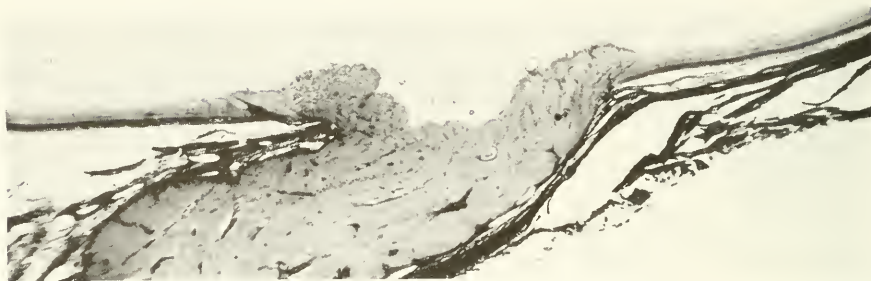
Fig. 643.—The Optic Nerve-head of the Rabbit.

Note the absence of collagen fibres at the site of the lamina cribrosa (Kolmer's fixative ; Azan ; × 27) (Katharine Tansley).

Fig. 644.—The Optic Nerve-head of the Mouse.

Note the band of evenly arranged oval nuclei running across the nerve (Kolmer's fixative ; Feulgen ; × 369) (Katharine Tansley).
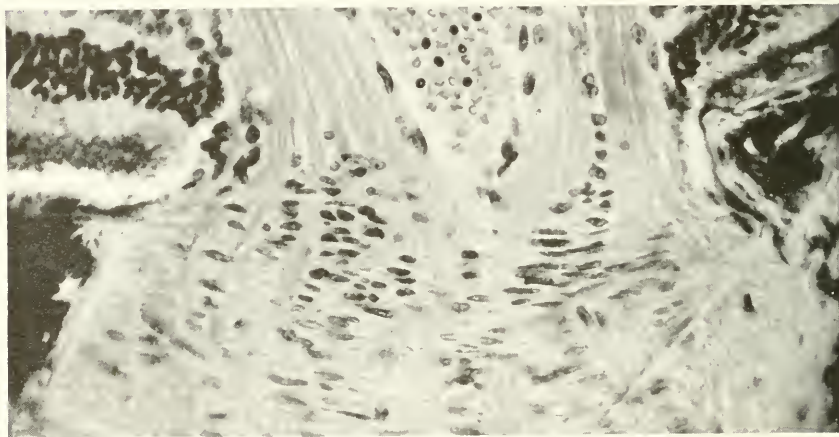

Fig. 645.—The Optic Nerve-head of the Cat.

Note the well-developed collagenous fibres at the lamina cribrosa (Kolmer's fixative ; Azan ; × 50) (Katharine Tansley).

the same side of the brain lays the foundation for full coordination, visual and motorial, between the two eyes.[1]

The semi-decussation of fibres results in great alterations in the finer structure of the lateral geniculate body, the relay station between the optic nerve fibres and the cerebral cortex. It will be seen[2] that in the lower Vertebrates this structure is insignificant but that in Mammals in which visual projections on a considerable scale are first relayed to the cortex it becomes much more complex, particularly the dorsal nucleus to which this function is assigned. In the lower Mammals this structure is relatively simple and it

FIG. 646.—THE LAMINA CRIBROSA OF THE KITTEN.
Twenty-four hours before birth (Wilder's stain ;   × 160) (Katharine Tansley).

would seem that each optic nerve fibre connects with several cells in the geniculate body which itself shows no ordered lamination. In the Australian opossum, *Trichosurus vulpecula*, an agile arboreal animal, however, the dorsal nucleus shows a four-layered structure (Packer, 1941), while in Carnivores and Primates, six layers appear (Le Gros Clark, 1941–42). This system of lamination is associated with the partial decussation of optic nerve fibres in the chiasma—a characteristic of Mammalia : in the opossum crossed fibres terminate in the 1st and 3rd layers, uncrossed in the 2nd and 4th : in the Primates crossed fibres terminate in the 1st, 4th and 6th layers, uncrossed in the 2nd, 3rd and 5th layers (Figs. 647 and 648). In the Primates also each retinal cell is projected onto the geniculate body in a point-to-point manner. The reception unit for each of a pair of retinal corresponding points is thus a band of cells involving three laminæ, while the projection unit onto the visual cortex is a band of cells involving all six layers.

[1] See further, p. 697.
[2] p. 541.

Figs. 647 and 648.—The Representation of the Retina on the External
Geniculate Body.
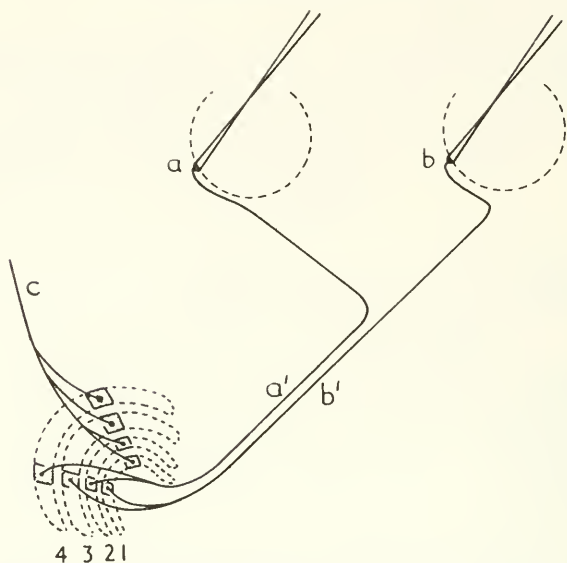
Fig. 647.—In the Australian Opossum (after Packer).
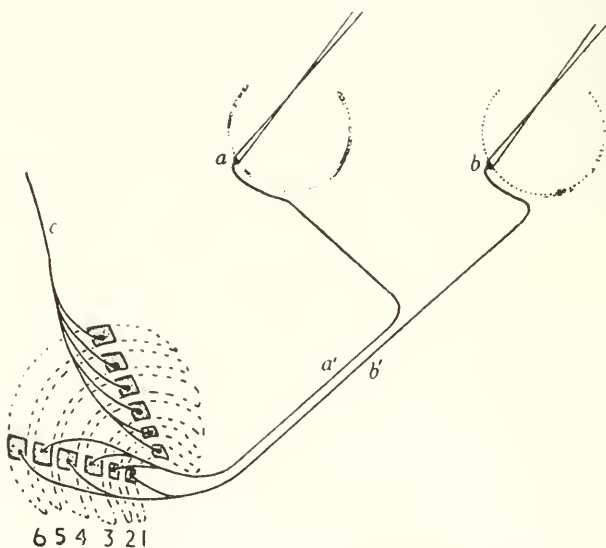
Fig. 648.—In the Primate (after Le Gros Clark).

Impulses from corresponding points (a, b) in the two retinæ pass up the optic
tract. Uncrossed impulses (a') terminate in laminæ 2 and 4 in the opossum,
and 2, 3 and 5 in the Primate. Crossed impulses (b') terminate in laminæ 1 and
3 in the opossum and 1, 4 and 6 in the Primate. These fibres terminate in a
reception unit in the lateral geniculate body which forms a band of cells
radiating from the hilum of the nucleus. The projection unit from the
lateral geniculate body (c) to the visual cortex forms a band of cells involving
all the laminæ in each case.

THE OCULAR ADNEXA

The *conjunctivæ* of many Mammals show large papillæ (horse) or follicles (ox, dog, pig, rabbit) which are not present in the physiological state in man (Bruch, 1853 ; Morano, 1873 ; Miimi, 1935). There is usually an accumulation of pigment, especially near the limbus, but frequently continued into the cornea, contained in branched contractile cells. The transition from the conjunctival to the corneal epithelium is usually gradual, but in some animals (horse) it is abrupt (Zietzschmann, 1904). Variations occur in the conjunctival glands ; thus sweat glands are seen in the bulbar conjunctiva of the pig, the goat and the ox. Small diverticuli filled with epithelial cells somewhat resembling epithelial cell-nests forming tubular depressions near the limbus were first described in the pig as the *glands of Manz* (Manz, 1859 ; Stromeyer, 1859), vestigial traces of which may be seen in man. Their function is uncertain : according to Aurell and Kornerup (1949) they are the remnants of accessory lacrimal glands which develop in the pig in embryonic life, sometimes persisting in the form of epithelial buds and sometimes as tubules with poorly developed lumina.

In the typical Placental, three *eyelids* are present—an upper, a lower, and a nictitating membrane (or third eyelid) ; the aquatic Placentals, however, form an exception.[1] Of the three, the upper lid, as in Selachians, is the more fully developed and with few exceptions (elephant, deer, hippopotamus, mouse) descends more than the lower ascends—a reverse of the action seen in most lower Vertebrates wherein the lower lid is the more mobile.[2]

It is interesting that Mammalia is the only class wherein spontaneous shutting and opening of the lids or blinking is highly developed ; although sometimes slow, particularly in primitive forms, the blink-movements are usually very rapid, and except in types with completely lateral eyes, the blink reflexes of both eyes respond when one is threatened or touched.

The upper lid always has a stiffening tarsal plate, the lower sometimes; it is usually comprised of dense fibrous tissue but is occasionally cartilaginous (in the hedgehog, bat and leopard, Anelli, 1936). Embedded in the tarsi and opening on the lid-margin are tarsal (meibomian) glands providing an oily secretion ; in view of the fact that they evolve from the glands of hair-follicles it is understandable that they are found only in Mammals. In Mammals the tarsal glands are usually smaller than in man : they are absent in aquatic types, replaced by Zeis's glands in the elephant, and by sebaceous glands on the caruncle in the camel (Richiardi, 1877). At the external angle they

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[1] p. 501.
[2] The lower lid is the more mobile in Amphibians, Reptiles (except *Anolis alligator* wherein both are equally mobile, and ? Crocodilians) and, with few exceptions, Birds.

are large and modified in some Rodents (Loewenthal, 1931). Glands
of Moll are present in many Ungulates (ox, pig), Carnivores (dog, cat),
and Primates (apes, man) ; but in Rodents they are absent (rabbit,
guinea-pig, rat, mouse) (Ikeda, 1953). Most Mammals have cilia
(Zietzschmann, 1904), the whale, elephant and hippopotamus being
exceptions (Matthiessen, 1893) ; among domestic animals those of
the lower lid are rudimentary, while localized absences occur, such as in
the mid-region of the upper lid of the horse (F. Smith, 1922). Eyebrows
are specialized in many Placentals (particularly the cat) into long
tactile vibrissæ ; the camel has a somewhat similar formation on its
lower lid.

The movements of the two main lids are elaborately controlled by
muscles. In terrestrial Placentals they are closed by the con-
traction of the annular orbicularis oculi muscle with a sphincter-like
interlacing system of fibres (Zietzschmann, 1904 ; Meinertz, 1932–42 ;
Rohen, 1953–54). All are provided with a levator palpebræ superioris,
except the aquatic Cetaceans which have a dilatator rimæ palpebrarum
distributed round the lids (Stannius, 1846, in dolphins ; Virchow, 1910,
in whales). The elephant has a depressor palpebræ inferioris similar
to the levator of the upper lid (Virchow, 1910), and in Herbivores the
external malar muscle serves as a depressor of the former.

The palpebral muscles of Müller are more fully developed in lower Mammals
than in man : in aquatic Mammals the fibres are striated, in terrestrial Mammals
they are plain. According to Groyer (1903) they are developed in association
with the superior and inferior recti : these divide into two parts, one of which
is striated and is inserted into the eyeball, the other is inserted into the lids.
Owing to the great development of the upper lid, the muscle running to it
divides again into two, forming a large levator muscle anteriorly, and a small
palpebral muscle posteriorly. In those cases wherein the palpebral muscles are
composed of plain fibres, they are supplied by the sympathetic nerve, but where
they are striated they are supplied by the nerves to the recti.

The *third eyelid* in Placentals is characteristically rudimentary ;
although often reinforced by a plate of hyaline cartilage it lacks a
specific musculature as is found in so many lower Vertebrates.
Entirely passive in its movements, it is rarely functional, slipping
over the eye when the globe is retracted. Occasionally, as in the bear
and the rhinoceros, it drifts partly across the cornea when the animal
becomes sleepy. The mechanism of its movement is much less specialized
than in lower Vertebrates, for any muscular elements it contains are
merely vestigial. It seems to be forced out from the canthus across
the cornea by the propulsive action of the retractor bulbi muscle as it
pulls the eyeball inwards : while the return of the membrane, although
probably largely due to its own elasticity, may be helped by the opposite
action of the orbital muscle of Müller. It is most rudimentary in the

lower forms (Insectivora, Chiroptera, Edentata and Rodentia) and in Primates ; in these with few exceptions it is immobile (Law, 1905 ; Anelli, 1935). In one monkey (*Macacus speciosus*) it is capable of slight movement (Johnson, 1901), and in the aard-vark, *Orycteropus*, it is freely motile over the keratinized cornea, probably acting as an added protection against the formic acid ejected by the ants on which it feeds. In the Carnivora, apart from the Mustelidæ, it is more fully developed, but in the skunk, with its proptosed eyes, it is altogether lacking. In a few Carnivores it is larger (cat, giant panda, bear, deer), while in Ungulates it is most highly differentiated ; in these it is sufficiently large to be swept passively but rapidly right across the cornea when the globe is retracted and it is probable that it serves a valuable function in these animals by giving protection to the eyes from long grasses when they graze.

Among Placentals the nictitating membrane has a basis of hyaline cartilage in most domestic animals (horse, donkey, ox, dog, wolf, pig, goat, cat, hare, etc.) ; in the rabbit (as in Birds) its basis is merely cellular parenchymatous tissue (Naglieri, 1932). Acinous glands resembling the lacrimal gland in structure are also present (Anelli, 1935) ; muscular fibres are vestigial.

Most Placentals possess two orbital glands. A *lacrimal gland* secreting a watery fluid is situated in the upper temporal quadrant ; as is usually the case among Vertebrates it is associated with the more mobile lid, in this class, the upper. We have seen that in terrestrial Amphibians in which the gland first appears in order to maintain the watery environment of their ancestors for the protection of the cornea, it is situated at the medial canthus in association with the lower lid; in Reptiles and Birds it migrates to the outer canthus still maintaining the same association with the lower lid ; in Mammals it appears at the lateral angle beneath the upper lid (Lor, 1898) (Fig. 649). The structure of the gland varies : it is tubular in man, but is alveolar in some Mammals (horse, pig, ox ; Mobilio, 1912–13) ; in some animals it empties by a single duct (Rodents). Sirenians,[1] the pronghorn, *Antilocapra americana*, and the mouse family are said to lack a lacrimal gland[2] ; in the pig its secretion is mucoid rather than watery, and in Cetaceans it is oily.[3]
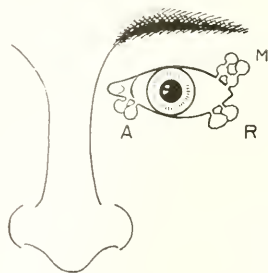

Fig. 649.—The Migration of the Lacrimal Gland in Phylogenetic Development.

A, position in Amphibians; *R*, position in Reptiles and Birds ; *M*, position in Mammals (after Wiedershein).

[1] p. 502.
[2] A lacrimal gland is also lacking in Cyclostomes, Fishes, aquatic Amphibians, *Sphenodon*, Ophidians, penguins and owls.
[3] p. 502.

The tears are drained away by the *lacrimal passages*. Since the lacrimal gland was originally situated at the nasal end of the lower lid, the lacrimal passages are always located in this region. These passages are built on the same general plan throughout the Vertebrates and only minor modifications exist (Walzberg, 1876 ; Lichal, 1915 ; Rochat and Benjamins, 1916 ; Sundwall, 1916). The puncta usually open on the inner surface of the lid, not on the margin as in man. The rabbit has one (inferior) canaliculus (Monesi, 1906 ; Rochat and Benjamins, 1916 ; Zaboj-Bruckner, 1924). The sac is rudimentary or lacking in most domestic animals. In some (such as the rat) the naso-lacrimal duct is small and inconspicuous. In others (such as the guinea-pig) it is wide with a well-developed ciliated epithelium and surrounded by a rich venous plexus ; in others again (such as the horse) it is relatively narrow (1 to 2 mm.) with several dilatations (1 to 2 cm.) throughout its length (Kelemen, 1950 ; and others). The passages are completely lacking in aquatic types (the Pinnipedes, the Mustelidæ, the hippopotamus, and the Cetaceans) and the elephant (Sardemann, 1884).

The two lacrimal puncta separate a portion of the lower lid to form the caruncle. Since it is isolated from the margin of the lower lid by the development of the canaliculus, the caruncle is absent in those animals which have no lacrimal apparatus (Bromann and Ask, 1910). Frequently its cutaneous origin is emphasized by its continuity with the lid-margin (calf and dog) ; it may be deeply pigmented (Fey, 1914), and contains tubular mucous glands (Caprino, 1955).

Harder's gland (1694), an acino-tubular gland the primary function of which is to lubricate the nictitating membrane, lies on the nasal side of the orbit ; sometimes it is very large extending to a variable extent over the posterior aspect of the globe (particularly in the mouse). According to Miessner (1900) it is absent in the deer, among the lower monkeys it is rudimentary (Giacomini, 1887), and in the Anthropoids and man it is represented only by a transitory fœtal structure in the infero-lateral fornix (Loewenthal, 1910).[1] The gland of Harder secretes a sebaceous (Wendt, 1877) or a mucous material (pig, dog, sheep ; Virchow, 1910) which it pours into the conjunctival sac by two ducts.

The *extra-ocular muscles* comprise four recti, two obliques and (usually) a retractor bulbi muscle. The recti are arranged as in man ; the mammalian superior oblique differs from that of lower Vertebrates in the migration of its origin to the apex of the orbit, the reflected tendon being designed to retain the original direction of action (Poole, 1905) (Fig. 203). This mode of development is emphasized in some animals

[1] Harder's gland is also absent in Cyclostomes, Fishes and aquatic Amphibians.

(ass) by the presence of accessory muscles accompanying the reflected tendon ; these represent the direction of the original muscle, while the trochlea is situated at the origin of the primitive muscle from the orbital wall (Zimmerl, 1906 ; Mobilio, 1912). In man similar super-numerary fasciculi have been found as an anomaly, or the more primitive arrangement has persisted (Ledouble, 1897). The insertions of the obliques vary. In man and the chimpanzee the superior oblique is crossed over by the superior rectus, while the inferior crosses the inferior rectus (Fig. 650). In the majority of Mammals both obliques are crossed by the recti (Fig. 651) ; in the tiger the recti pierce the obliques (Fig. 652), and in the lion (as in the tortoise) the superior rectus

Figs. 650 to 653.—The Relation of the Oblique Muscles to the Recti.
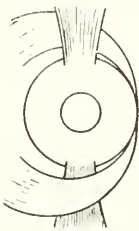
Fig. 650.—
Man and
chimpanzee.

Fig. 651.—
The majority
of Mammals.
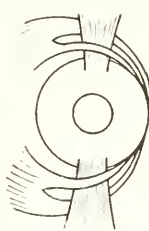
Fig. 652. —
The tiger.

Fig. 653. —
The lion.

pierces the superior oblique, and the inferior oblique pierces the inferior rectus (Fig. 653) (Ottley, 1879 ; Ovio, 1925).

A *retractor bulbi muscle* (*choanoid muscle*, Motais, 1887) occurs in most Mammals; it is particularly developed in Rodents, Ungulates and Sirenians, but is present only in a vestigial form in some monkeys (*Macacus*) and is absent in some of the higher Primates (F. Smith, 1922 ; Bradley, 1933 ; Winckler, 1933 ; Key-Aberg, 1934).[1] The muscle arises from the apex of the orbit, and, running within the muscle-cone, envelops the optic nerve and the posterior part of the globe to be inserted into the sclera behind the recti (Fig. 654). The insertion shows many variations. It may be continuous like the gamopetalous corolla of a flower, or discontinuous with the same general arrangement but in many separate bundles varying in indivi-duals of the same species or even between the two eyes of the same individual, or it may be divided into diverging slips (6 in the sloth-bear, *Melursus labiatus* ; 4 in the cat and dog ; 2 in the whale, etc.) (Fig. 655). It is supplied by nerve VI (Hopkins, 1916), and is usually regarded as a derivative of the lateral rectus (Johnson, 1901 ; Corning,

[1] The muscle is also absent in Cyclostomes, Fishes, Ophidians and Birds.

1900). Its action is probably to pull back the eye, a function eminently required in Herbivora which feed with the head lowered and also in Sirenians which graze at the water's edge ; in man this action is taken over by the tonicity of the recti themselves (Grimsdale, 1921). In the rhinoceros and at least one species of the Ursidæ (*Melursus labiatus*) a simultaneous contraction of the retractor and lateral rectus muscles flicks the eye quickly to the temporal side and at the same time retracts it—a substitute for blinking movements of the lids. A similar movement is seen occurring about once in each minute in the okapi, and as
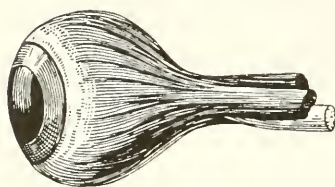
Fig. 654.—The Retractor Bulbi Muscle of a Sheep (Bland-Sutton).
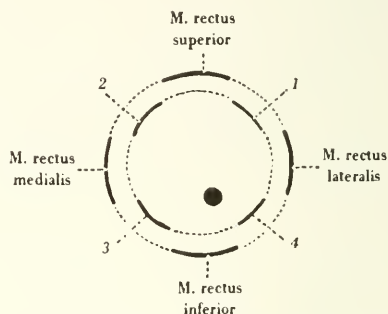
Fig. 655.—The Scleral Insertion of the Orbital Muscles of the Dog.

View from behind. 1–4, the insertions of the 4 heads of the retractor muscle which alternate with and are closer to the posterior pole than the recti (after O. C. Bradley).

the eye retracts the nictitating membrane, well developed as in most Ungulates, sweeps across the globe (Brückner, 1950). As a secondary action it helps to thrust out the nictitating membrane by pressure from behind. Watrous and Olmsted (1941) reported that after excision of all the other extrinsic muscles in the dog, the retractor bulbi was eventually capable of moving the eyeball in all directions.

In the higher Primates the retractor muscle is vestigial or absent. In *Macacus*, the remnant lies above the lateral rectus, and in this region vestigial muscular fibres have been found in man (Nussbaum, 1893 ; Ledouble, 1897 ; Fleischer, 1907). Indeed, according to Lewitsky (1910), there is always a well-marked connective tissue strand in this position in man, running from the back of the fascia bulbi to the apex of the orbit. Whitnall (1911) has reported a case wherein a well-developed muscle of four strands existed (Fig. 656).

The orbital muscle of Müller is found in many Vertebrates (Amphibians, Reptiles, Birds) as a well-developed striated muscle mass ; in Mammals it retrogresses and its fibres become plain. According to

Burkard (1902) it is a derivative of the maxillary musculature, which enters the orbit through the inferior orbital fissure and compensates for the deficiencies of a lateral wall. It is possible that in those animals in which it is well developed it may act as a protrudor muscle by pulling forwards the fascia occupying the fissure and thrusting the eye outwards.

It is curious that despite the elaborate provision of extra-ocular muscles and their comparative size, the ocular movements of most terrestrial Vertebrates are restricted.[1] The eye of the elephant, for example, is almost immobile despite the fact that the size of its extra-ocular muscles is " stupefying " (Soemmerring, 1818), corresponding to the size of the animal rather than to its eye which is relatively small and compares in bulk with that of the ox.[2]

COMMON TENDON OF ORIGIN OF MUSC. RETR. BULBI.

LAT. RECTUS VI NERVE
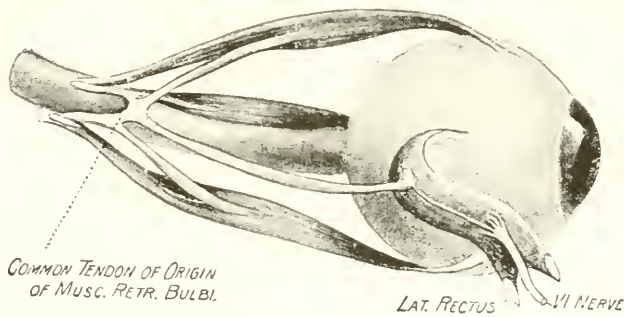
FIG. 656.—AN ABNORMAL RETRACTOR BULBI MUSCLE IN MAN.

Four muscular bundles run forwards towards the globe, each fusing with a rectus before reaching it. One bundle is innervated by nerve VI (indicated in the figure), and the others by nerve III (Whitnall, 1911).

We have seen that among Amphibians the *orbit* opens freely into the cavity of the pharynx ; and among most of the lower Vertebrates the postero-lateral wall remains membranous, opening into the temporal fossa, a communication which persists in the higher Mammals and man as the inferior orbital fissure, the anterior end of which (in man) may exceptionally encroach upon the lateral wall to form a " spheno-zygomatic fissure " (Tanzi, 1892 ; Duckworth, 1904). The completeness of the orbital bony walls varies considerably owing to irregularities in the constituent bones ; the frontal and sphenoid are always present, the ethmoid and the palatine usually do not participate, and accessory ossicles are common (Maggi, 1898). Among the Rodents the orbit is always open, particularly so in the rabbit ; in this animal the floor of the orbit is largely muscular (Davis, 1929). In the elephant and some of the Artiodactyls the orbit is also open and is particularly so among the Carnivores, an adaptation resembling that seen in lizards and snakes

[1] p. 692 *et seq.*   [2] p. 450.

to allow ample scope for a wide gape of the jaws. On the other hand, among many Ungulates, particularly the horse and all horned animals, the orbit is enclosed and heavily reinforced, as if for protection against the severe injuries caused by horns, and also for strengthening the skull for combat. Among the Prosimians the orbit is incompletely closed, maintaining continuity with the temporal fossa ; among the Anthropoidea it is completely enclosed. A lining periorbita is invariably present, associated with muscular elements (Burkard, 1902 ; Ashley-Montague, 1931). The orbits vary much in position depending on whether the eyes look frontally or laterally (Koschel, 1883) [1] ; their capacity compared with the size of the globe also varies within wide limits (pig, 2·2 : 1 ; sheep, 1·6 : 1 ; horse, 3 : 1 ; ox, 6 : 1 ; man, 4·5 : 1, Dexler, 1893). Even among the Primates themselves the size of the orbit varies only very loosely with that of the globe, large Primates having a relatively small orbital capacity (Imai, 1934–36 ; Schultz, 1940 ; Chamberlain, 1954).

The vascular system is extremely variable throughout the vertebrate phylum. In man, the entire intra-ocular blood supply and most of the orbital blood supply is derived from the internal carotid artery ; in the lower Mammals, the external carotid takes the larger share and sometimes is the sole source of supply. In Rodents such as the rat and the rabbit the arrangements are relatively simple (Fig. 657). The main blood supply to the globe and the orbit is derived from the internal maxillary branch of the external carotid. The external ophthalmic divides into several branches which supply the muscles and tissues of the orbit, as well as the long and short ciliaries which enter the globe. A second artery of supply, the internal ophthalmic artery, is small. It is derived from the circle of Willis and ultimately from the internal carotid ; it runs through the optic foramen into the orbit, sends an anastomotic branch to the nasal long ciliary artery and enters the optic nerve near the globe to supply the retina as a central retinal artery (Krause, 1868 ; Henderson, 1903 ; Davis, 1929 ; Daniel *et al.*, 1953 ; Janes and Bounds, 1955).

Among the Carnivores, the dog and cat may be taken as typical. In the dog the arrangement is not very different from that in the rabbit (Fig. 658). Again, the main blood supply to the orbit and globe is by way of the external ophthalmic branch of the internal maxillary artery which is ultimately derived from the external carotid. In the same way an internal ophthalmic artery derived from the circle of Willis (that is, ultimately from the internal carotid) also enters the orbit to anastomose with the ciliary branch of the external ophthalmic. There is, however, a large anastomotic branch (the arteria anastomotica) between the internal carotid and the external ophthalmic arteries, so

[1] p. 672.

FIGS. 657 TO 662.—THE CAROTID CIRCULATION IN MAMMALS
(after Daniel *et al.*, 1953).
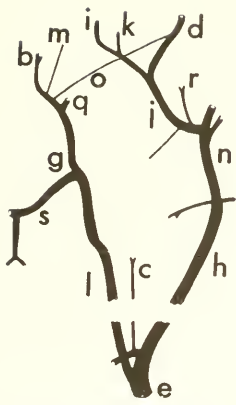
FIG. 657.—The rabbit.
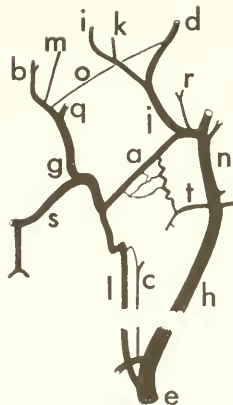
FIG. 658.—The dog.
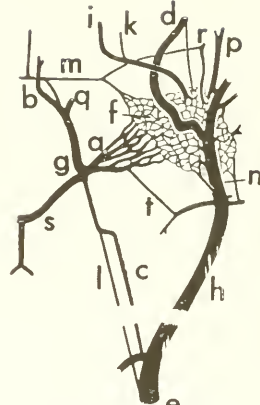
FIG. 659.—The cat.
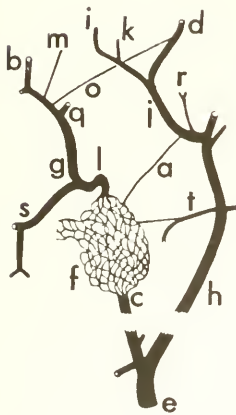
FIG. 660.—The pig.
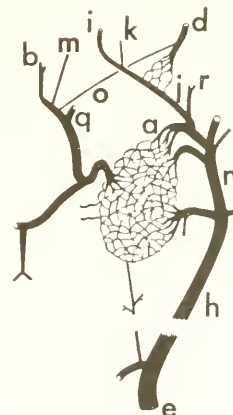
FIG. 661.—The sheep.

FIG. 662.—The ox.

a, arteria anastomotica ; *b*, anterior cerebral artery ; *c*, ascending pharyngeal artery ; *d*, ciliary artery ; *e*, common carotid artery ; *f*, carotid rete ; *g*, circle of Willis ; *h*, external carotid artery ; *i*, external ethmoidal artery ; *j*, external ophthalmic artery ; *k*, frontal artery ; *l*, internal carotid artery ; *m*, internal ethmoidal artery ; *n*, internal maxillary artery ; *o*, internal ophthalmic artery ; *p*, lacrimal artery ; *q*, middle cerebral artery ; *r*, arteries of extrinsic ocular muscles ; *s*, posterior communicating artery and proximal part of posterior cerebral artery ; *t*, ramus anastomoticus.

large that the intra-ocular circulation can be maintained unimpaired either by the external or internal ophthalmic arteries (Ellenberger and Baum, 1891 ; Henderson, 1903 ; Parsons, 1903 ; Jewell, 1952 ; Daniel *et al.*, 1953). It is interesting that in association with this anastomotic vessel there is a relatively simple arterial network (the

rete of Hürlimann, 1912) situated intracranially in the cavernous sinus.

In the cat the circulation is unique in that the internal carotid in the adult is vestigial, being reduced to imperforate connective tissue strands (Fig. 659). The external carotid, on the other hand, is well developed and its large internal maxillary branch provides the basis of an elaborate anastomotic network (the carotid rete) which is situated extracranially near the apex of the orbit. From this rete large anastomotic vessels supply the circle of Willis by way of the orbital fissure. Also from this rete seven independent trunks (corresponding to the ophthalmic circulation of human anatomy) supply the orbital tissues and the globe. The largest branch of the internal maxillary—the ciliary artery—reaches the optic nerve where it breaks up into its numerous terminal ciliary branches which enter the eyeball ; there is no central artery of the retina (Tandler, 1899–1906 ; Hürlimann, 1912 ; Daniel *et al.*, 1953 ; etc.). Davis and Story (1943) found that from the circle of Willis a tenuous ophthalmic artery sometimes entered the orbit to anastomose with the ciliary artery ; but even when it occurs it is small and incidental. The whole of the orbit and eye is therefore supplied from the external carotid as well as the greater part of the circulation of the brain.

Among Ungulates, in the pig the circulation resembles that of the dog, but a well-formed rete is present supplied proximally by the ascending pharyngeal artery; it empties into a large trunk which is the only persistent portion of the internal carotid artery and contributes to the circle of Willis (Fig. 660). Arising from this last vessel there is a tenuous internal ophthalmic artery which anastomoses with the ciliary (Versari, 1900 ; Daniel *et al.*, 1953). In the sheep, goat, ox and horse, the external ophthalmic artery may arise directly from the internal maxillary, as it does in the dog, or from one of the group of vessels which form anastomotic channels through the carotid rete with the circle of Willis. As in the dog, a tenuous internal ophthalmic artery is present in the sheep and the goat but not in the ox. In the sheep and goat the rete is supplied wholly from the external carotid and, as occurs in the pig, the internal carotid only exists as an afferent vessel from this arterial network to the circle of Willis. In the ox and horse, however, an internal carotid vessel is present (Figs. 661–2) (Zietzschmann, 1913 ; Daniel *et al.*, 1953).

The orbital veins have not been fully worked out but in a general way they correspond with the arterial supply. In man, the greater part of the venous system returns into the intracranial system ; in the lower Mammals the return is more and more to the extracranial system. In the rabbit the veins from the globe and orbit empty into an extensive ORBITAL SINUS which ramifies throughout the apex of the orbit,

enveloping the muscles and extending forwards to the level of the equator of the globe : its main exit channels are into the posterior and deep facial veins, the external and internal maxillary veins, and the vertebral vein (Davis, 1929).

The *orbital nerves* throughout the Placentals conform to the same general plan. The branches of the first division of the trigeminal serve as the sensory supply ; the sympathetic is vasomotor and innervates the smooth orbital muscle ; while the muscles are supplied by the IIIrd, IVth and VIth cranial nerves as in man except that the last nerve supplies the retractor bulbi muscle and the muscles controlling the nictitating membrane when these are present.

The CILIARY (ORBITAL) GANGLION is of interest. It is variable in nature but is always primarily associated with the IIIrd nerve. In the lower Fishes (Selachians, etc.) it is represented by groups of cells scattered along this nerve (H. Schneider, 1881 ; Pitzorno, 1913) ; in Teleosteans, Amphibians and Reptiles the ganglion becomes a specific entity associated with this nerve, usually without connection with the Vth or sympathetic (Schwalbe, 1879). In Birds it has a short root from the IIIrd nerve and a slender long root from the trigeminal (Lenhossék, 1911 ; Carpenter, 1911). Langendorff (1900) and Lodato (1900) were unable to confirm the nicotine reaction for the motor fibres in Birds ; it thus appears that physiologically as well as anatomically the cells in these animals are cerebro-spinal in type. It will be remembered that the ciliary muscle of Birds is striated. In Mammals, although it is small in Equidæ (Mobilio, 1912), the ciliary ganglion is always present, and in them the connection with the IIIrd nerve is always retained (Schwalbe, 1879 ; Peschel, 1893 ; Apolant, 1896). In many of them the root from the Vth nerve is absent, and frequently, when it is present, it conducts fibres of passage which are not relayed (Antonelli, 1890 ; Michel, 1894). The sympathetic root is more frequently absent ; and both of these roots may be absent in man. Among Mammals the ciliary ganglion is often represented by more than one group of cells.[1] It is probable that in many cases some of these different colonies of cells represent outgrowths of III and others outgrowths of V. When the ganglion is painted with nicotine the motor path is blocked, showing that this is mediated by cell-stations of the autonomic type (Langley and Anderson, 1892), while the sensitivity of the cornea remains unimpaired, showing that the sensory fibres are relayed in cell-stations which (if present) are of the cerebro-spinal type.

The ocular adnexa of aquatic Placentals deserve a special note. Some are only partially adapted to this medium. In the hippopotamus the orbits (like the nose) are elevated so that the eyes are readily kept above the water-level, the lids form a ring rather than a slit-shaped palpebral aperture, the lashes are sparse, and naso-lacrimal canals are lacking. In the Pinnipedes (seals and walruses) the orbits are also directed somewhat upwards, there are no tarsal glands, the lacrimal glands (although large in the fœtus) are small in the adult and the harderian glands are enormously developed, secreting an abundance of

[1] Ox, Muck (1815) ; rabbit, d'Erchia (1895), Mobilio (1912) ; pig, Antonelli (1890).

an oily substance to protect the keratinized cornea against the sea-water ;
in the absence of naso-lacrimal canals, this secretion pours copiously
over the face when the animal is on land (Fig. 663).   In Sirenians
(sea-cows) the lashes are extremely scanty but the lids freely mobile,
closing completely over the small eye when it is pulled backwards by
the well-developed retractor muscle.   There is no lacrimal gland but
the harderian gland is well developed, as in Pinnipedes, secreting a
copious thick mucoid secretion like egg-white (Fig. 664).

The Cetaceans (whales and dolphins) are completely adapted to
aquatic life : the lids are small, without tarsal plates or tarsal glands ;

FIGS. 663 AND 664.—AQUATIC PLACENTALS.
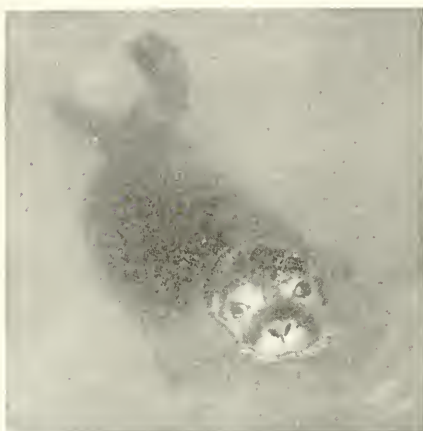
FIG. 663.—The Common Seal, *Phoca
vitulina*.

Showing the upwardly directed eyes,
as an adaptation for swimming (Zool.
Soc., London).
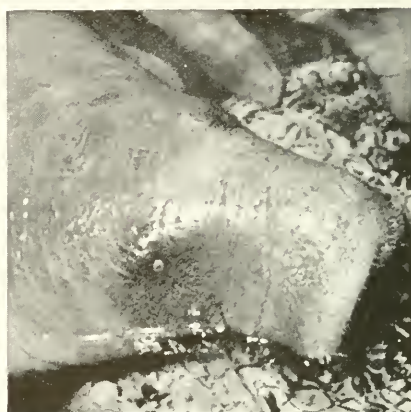
FIG. 664.—The Head of the Manatee,
Trichechus manatus.

Showing the small retractable eyes
(photograph by Michael Soley).

lashes are lacking ; a " lacrimal " gland is present but secretes not
tears but a fatty water-repellant secretion, and the same hypertrophy
of the harderian gland is seen, the oily secretion of which is augmented
by that of numerous oil-glands distributed over the palpebral conjunc-
tiva.   The naso-lacrimal conducting mechanism is absent as also is
the nictitating membrane.   The extra-ocular muscles are, however,
enormous, more in keeping with the size of the animal than that
of the small eye ; each rectus is comparable to the biceps of man.
In the whale this seems curious in view of the immobility of the
downward-looking eye fixed firmly on its immensely rigid accessory
optic nerve sheath and situated low down on a level with the
angle of the mouth about one-third of the length of the huge animal
away from its anterior extremity.   It has been said that the enormous

muscles might be of value in keeping the eye warm by their tonic contraction in deep diving into the icy-cold ocean depths since here the thick layer of oily fat which insulates the rest of the body is absent ; but such a function is questionable. It would seem rather that, as in the elephant, the muscles have retained a size compatible with that of the animal while the globe has not.

For monographs on the study of the eyes of particular species, see :

Rodents—rabbit, Davis (1929) ; chinchilla, Detwiler (1949) ; mouse, Schwarz (1935) ;

Ungulates—okapi, Brückner (1950) ;

Carnivores—dog, Arey *et al.* (1942) ;

Primates—*Nycticebus, Nyctipithecus,* Detwiler (1939–41); apes, Hotta (1906).

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