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The Anatomy and Histology of the Rudimentary Eye of Neurotrichus

Abstract

Fossorial insectivores are functionally adapted to relative darkness and show anatomical regression in eye morphology. *Scalops* has retained the vitreous body, and the retina has rods and cones. *Talpa* has embryonal lens cells. *Notoryctes*, a fossorial marsupial, has a rudimentary retina without rods and cones, and has lost the vitreous, lens, and pupil. *Neurotrichus* is a rare shrew-like mole with minute optic globes. These are unique in the presence of a pigmented extension of the retina, covering the anterior surface of the optic lens. The globe is collapsed upon the retina and the embryonal lens. Rod and cone cells are poorly defined. The vitreous is missing. There is no palpebral fissure, and the extraocular muscles do not have a proximal bony attachment. The central part of the iris is markedly proliferated. Behavioral studies indicated that *Neurotrichus* is blind, which raises a question about the possible function of the pigmented lenticular covering and the proliferated iris.

Loss of visual perception has occurred in several vertebrate groups, notably in the cave-dwelling fishes and salamanders. In the mammals, two families of the Insectivora (Talpidae, Chrysochloridae) and one family of Marsupalia (Notoryctidae) are of fossorial habit, and have accompanying diminution in visual function. In *Scalops*, Slonaker (1902) demonstrated that despite the rudimentary and presumably non-functional eye, the vitreous is retained in some individual specimens and rods and cones are present. In *Talpa,* another genus of moles, Kohl (1895) and Quilliam (1964) found that the vitreous and aqueous are retained in much the same eye structure as in sighted mammals. Ritter (1899) described in *Talpa* a nearly normal lens structure. Franz (1934) (after Sweet) described *Notoryctes typhlops* in which the vitreous, lens, and pupil are absent, the retina is rudimentary and without rods and cones, and the extraocular muscles are not striated. A comparison of these studies with *Neurotrichus*, a talpid in which the eye structure has not yet been examined, is noteworthy.

Neurotrichus is the smallest of the North American Talpidae, measuring about 100 mm in total length. This talpid is also the least fossorial of the moles, and in its hunting habits on the surface of the forest floor resembles the shrews. *Neurotrichus* is restricted to the humid coastal forests of British Columbia, Washington, Oregon, and Northern California. There is one species (*gibbsii*) and three subspecies (*hyacinthus, gibbsii,* and *minor*). The eye of *Neurotrichus* is subcutaneous and minute. Dalquest and Orcutt (1947) and Reed (1944) have studied *Neurotrichus* in the laboratory and concluded that the animal is blind. This paper describes the ocular anatomy of specimens of *Neurotrichus gibbsii minor* collected at Seattle, Washington.

Methods

Five adult specimens were fixed entire and decalcified. The head was then sectioned sagittally. Twenty adult specimens were dissected and the eyes removed with a block

of epidermis and surrounding tissue. Since the eyes are minute, no intrinsic optic axis could be discovered in specimens fixed in Bouin or Gibson solution. The blocks were sectioned, therefore, at several angles relative to the head. Slides were prepared by paraffin and celloidin block. Sections were stained with haemotoxylneosin, Verhoff, Weigert myelin, Mallory Triple, and Van Gieson. *Neurotrichus* is a rare animal. Few field naturalists have observed it, and no embryological material for sectioning was collected. No EM material has been obtained to date.

Gross Anatomy

There is no palpebral opening. The eye is completely covered by a densely furred integument and is not visible externally except by parting the guard hairs and undercoat. The pigmented globe is then visible through the skin. Directly external to the globe, the skin is hairless and thinner, and thrown into shallow peri-ocular folds. The skin is freely moveable over the eye. When the skin is removed, the eye remains imbedded in the subcuteaneous tissue and is connected, as is the cornea, to the corium by delicate strands of connective tissue.

The eye is a deeply pigmented sphere 0.7 to 1.0 mm in diameter. A thin opaque covering of connective tissue forms a delicate equatorial ring attached to the dermis. No pupil or iris is visible in gross fixed specimens. The extraocular muscles are large at the equatorial ring but rapidly attenuate as they pass posteriorly, close to the course of the optic nerve, to disappear in the subcutaneous tissue over the *M. masseter.* The eye is not contained in a bony orbit but is positioned on the lateral side of the rather conical head at the level of the fourth maxillary tooth. The eye of an embryo specimen (33 mm in total length, head 17 mm) photographed by Dalquest (1947) was deeply pigmented and easily visible through the almost hairless skin.

Histology

Tenon's capsule is thin and cannot be traced anterior to the conjunctival angle. The sclera is composed of several layers of fibroblasts varying from seven to twelve. The cornea is poorly differentiated from the sclera. The cornea is slightly thinner, and the fibroblasts of the substantia propria have more widely separated nuclei. No Bowman's membrane is distinguishable. A few scattered epithelial cells may represent the corneal mesenchymal epithelium.

The choroid is a densely pigmented layer enveloping the globe of the eye except for the small pupillary aperture. At the ciliary body the choroid is much thickened, and here the pars ciliaris retinae separates from it to pass as an adherent pigmented layer across the entire anterior surface of the lens except at the pupil. The non-pigmented cells of this part of the ciliary epithelium, continuous with the neural retinal layer, are cuboidal with eosinophilic cytoplasm. Some of these cells are deflected onto the surface of the lens posterior to the equator, but most form a continuous layer in contact with the anterior capsular cells. The pigmented layer is visible to the pupillary margin.

From the ciliary body the choroid extends anteriorly, closely applied to the inner surface of the sclera and cornea. The choroid is much thickened at the pupil, with light-colored vascular and muscle cells relieving its usually dense pigmentation. There is a well developed pupillary margin. Nearby, in some sections, the pigmented cells of the

anterior surface of the lens are tenuously adherent to the posterior surface of the iris. Otherwise, there is much difficulty trying to distinguish any elements of the pars iridica retinae.

The outer surface of the iris has a one- to two-cell layer of epithelium reflected from the inner surface of the cornea. The entire iris is thick and heavily pigmented.

The ciliary body, composed in the main by the markedly thickened choroid, contains no recognizable muscle cells or fibers of a supensory ligament.

The retina and lens fill the eye. There is no vitreous. The inner limiting membrane is not seen in the section, but most of the remaining retinal layers are clearly demarcated. The optic nerve fibers and ganglion cells are prominent, and nerve fibers loop vertically through this layer. Cells with large nuclei containing a nucleolus and irregular dark-staining bodies in the nucleoplasm and with eosinophilic cytoplasm are present, along with axonic fibers. The inner plexiform layer is present, and a prominent inner nuclear layer is composed of cells with dark nuclei. The nuclear layer is about six cells in depth. There is a prominent outer plexiform layer. The outer nuclear layer is also about six cell layers in depth, the nuclei dark in color. The receptor layer is columnar in structure, but cell detail is faint and definite rods and cones cannot be distinguished. There is a thin outer layer of cells with deeply staining nuclei and pigmented cytoplasm.

The optic nerve can be traced from the optic papilla as it courses posteriorly from the globe to the optic foramen, accompanied by other nerve trunks. Some sections show the optic nerve in close proximity to the ciliary ganglion. The optic nerve penetrates the layers of the globe tangentially. Some fibers can be traced through the entire thickness of the retina as a path of cells entering the ganglion cell layer.

The lens is an ellipsoid structure with a smoothly curved posterior surface and a less smoothly curved anterior surface. The outline of the anterior curvature is modified by the enlarged pupillary rim of the iris. The lens is composed of polyhedral, elongate or columnar cells, each with a dark-staining nucleus. The capsular cells are smaller and flattened. There are numerous vacuoles in the lens substance, especially near the anterior surface.

The posterior chamber of the eye is almost as extensive as the width of the globe, extending from the ciliary bodies across the anterior surface of the lens to the minute pupil. The anterior chamber is all but eliminated by the adherence of the choroid and iris to the inner surface of the sclera and cornea. There is a broad conjunctival sac lined with epithelial cells. These are cuboidal and one- to three-cells thick on the interior surface of the integument, flattened over the cornea, and in thickened layers in the fornices. The conjuctival sac contains desquamated cells and amorphous material. The cells have dark cytoplasm and large oval or rounded, deeply staining nuclei. Some small masses of tubuloalveolar tissue are found adjacent to the conjunctiva, but they open onto the skin surface.

Discussion

The eye of *Neurotrichus* presents comparative anatomists with a unique anatomical feature—i.e., the pigmented covering of the anterior surface of the lens. This pigmented tissue is an exterior layer of the pars ciliaris retinae. No other known vertebrate has taken this evolutionary route. Walls (1943) and Wolff (1949), in their reviews of the comparative anatomy of the vertebrate eye, describe no lenticular pigment layer

comparable to that found in *Neurotrichus*. Of further note in *Neurotrichus* are the markedly proliferated tissue of the central part of the iris, the loss of the vitreous body with collapse of the globe upon the lens and retina, the embryonal structure of the lens, the loss of rods and cones, the loss of any proximal bony attachment of the extra-ocular muscles, and the absence of a palpebral aperture.

The circadian rhythms of rest and activity in *Neurotrichus* are not known. Presumably it maintains a high level of searching and ingestion like the shrews (Sorex and others), with even less dependence on incident light. Its efficient non-visual sensory apparatus allows it to inhabit the dimly lit floor of heavy forests, in and beneath abundant surface vegetation and detritus, where visual acuity is relatively superfluous. Shrews, in similar habitats, have functional eyes. Comparative anatomical and behavioral studies of the microhabitat, which might allow evolutionary discussions, are so far sparse, and a correlation of *Neurotrichus'* peculiar visual anatomy with its adaptive skills can only be conjectural. The moles, more fossorial in habit, show even more anatomical regression in eye structures.

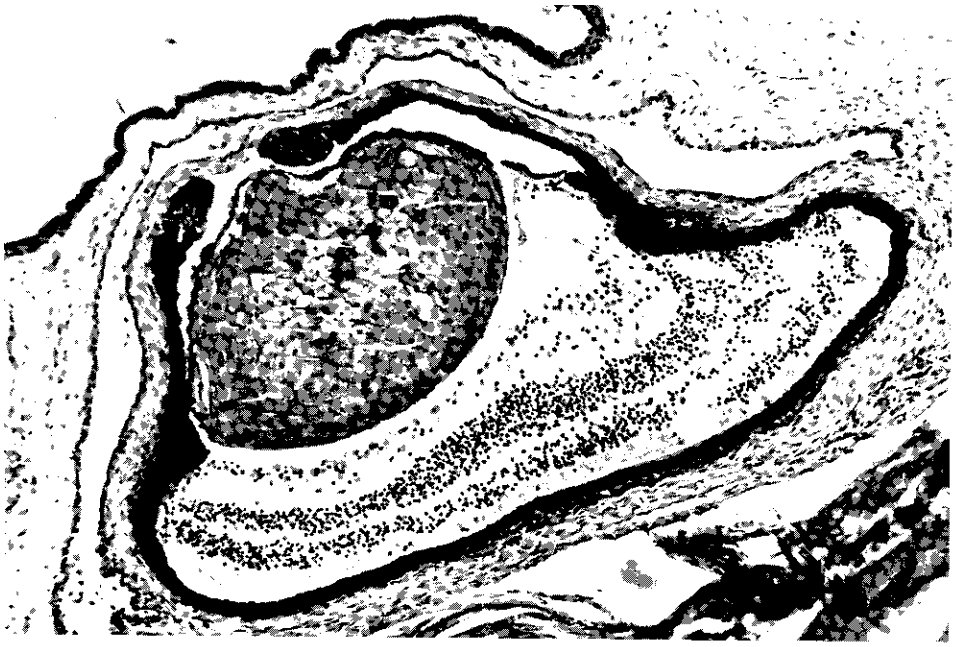

Figure 1. Subcutaneous eye of *Neurotrichus*. Layers of the retina, choroid and sclera, and the lens, iris, pupil, and conjunctival space are visible.

Figure 2. The sclera and pigmented choroid lie to the right of the poorly defined rods and cones.

Figure 3. From the right, epidermis, dermis, conjunctival space, cornea-sclera, pupillary margins, posterior chamber, and pigmented pars iridica retinalis.

Figure 4. The lens contains cuboidal and elongate cells. The ciliary body (center) lies at the equator of the lens. Anterior to the ciliary body the lens is covered by the pigmented pars iridica retinalis.

Figure 5. The layers of the retina are to the left. At the ciliary body (center) the continuation of the retina separates from the choroid and passes in front of the lens (top).

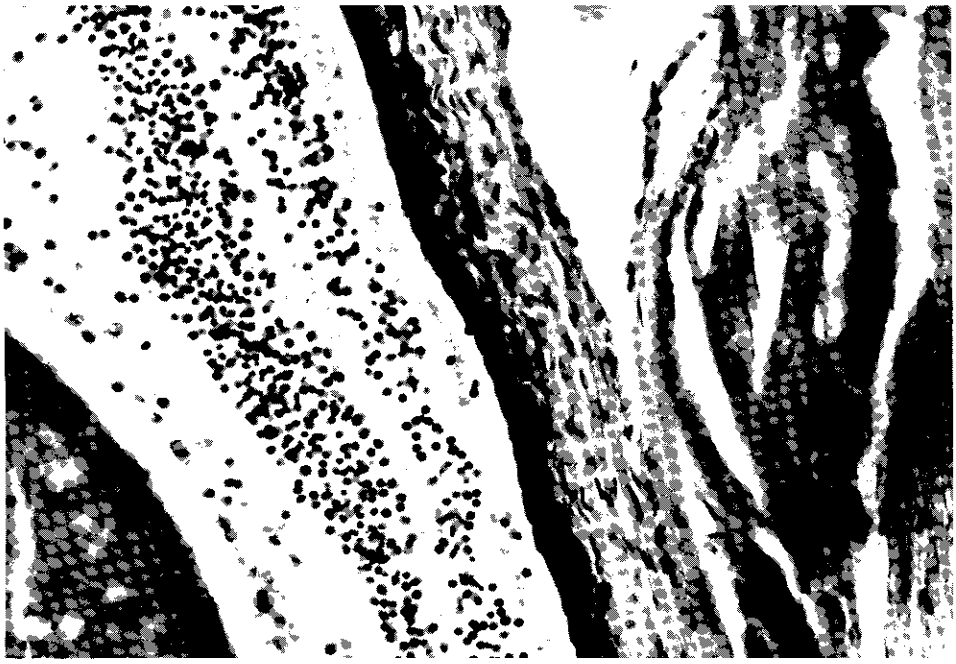

Figure 6. The sclera (center) and the pigmented choroid are external to the poorly defined receptor cells to the left.

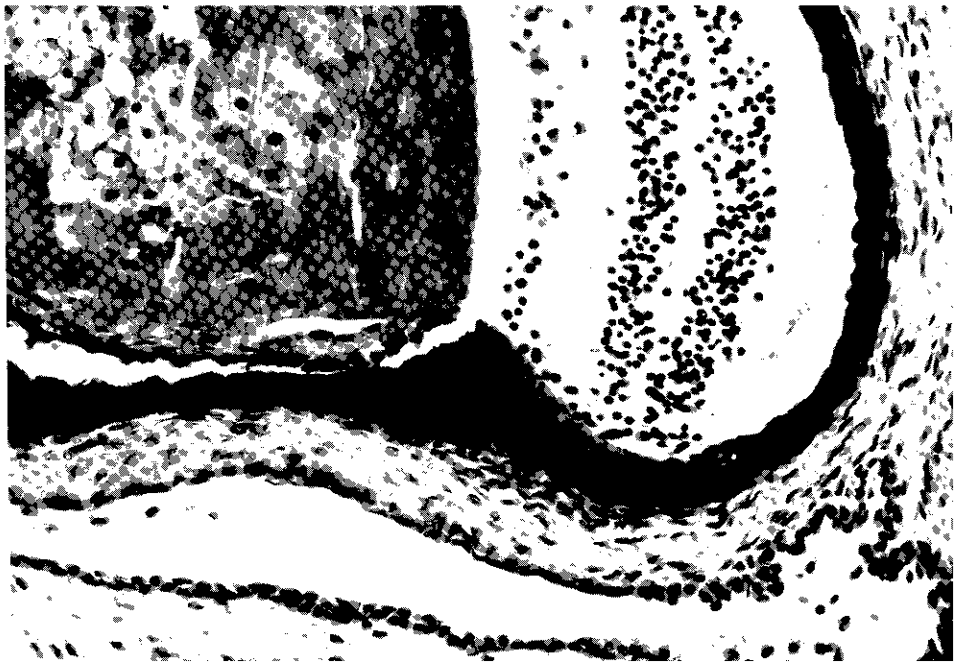

Figure 7. Amorphous receptor cell layer (right).

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