34
THE EYES OF HAGFISHES

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SUMMARY

Though probably functional light receptors, hagfish eyes are small, that of Myxine glutinosa only 500 μm diameter, and degenerate. Demonstrated extraocular photoreception may be more important for hagfish behaviour. Eptatretus species eyes are beneath an unpigmented skin patch, but Myxine glutinosa eyes are buried beneath muscle. All hagfishes have only an undifferentiated corneo-scleral layer, and extraocular muscles are absent. We found no lens in any hagfish examined. Eptatretus species have a vitreous cavity, with scattered collagen fibrils, some forming dense aggregates. Choroidal capillaries, but not pigment, occur in all species examined. Eptatretus retain a hollow optic cup, but at the margin epithelium and neuroretina are continuous, without extension to ciliary body or iris, both of which are absent. Developmental anomalies are common in peripheral retina in all. The Myxine optic cup has no lumen, the margins meeting at a fibrous plug. Eptatretus species retinas contain photoreceptors, with clear outer segments in the periphery, but few or none in the fundus. Myxine has few, degenerate outer segments, indenting the opposing epithelium. Receptor synapses are sessile. Synaptic bodies, like vertebrate ribbons, occur in Eptatretus, but only simple synapses in Myxine. Myxine optic nerve contains a few hundred thin axons only.

34.1 INTRODUCTION

Writing of the sense organs of hagfishes, Ross (1963) observed that the eye and ear, the most important sense organs of higher vertebrates, are small and simple in hagfishes. The olfactory organs, on the contrary, are well developed, and hagfishes are readily attracted to a bait by smell (Adams and Strahan, 1963). Few accounts of the vertebrate eye discuss the situation in hagfishes, for at least two good reasons. One is that hagfishes, though chordates, are not vertebrates, and the other is that their eyes are small and degenerate, and thus poorly suited to studies on vision. Even those of the most visually advanced species lack most components of an optical system, and those of Myxine are buried beneath muscle, with no trace of their existence visible from the surface. This is not to say that hagfishes are insensitive to light. Newth and Ross (1955) showed that destruction of Myxine glutinosa eyes had no effect on the light sensitivity, which was maximal in an area in front of the eyes. They studied the distribution of light-sensitive areas on the skin of Myxine, finding concentrations just behind the tentacles and in an area round the cloaca. Some light sensitivity was present over most of the rest of the animal. The reaction time of this dermal light sense was long, 2–3 min at threshold intensity, and about 10 s in maximal illumination. They found that removal of a portion of skin abolished the response, indicating that the sense organs
must reside in the skin. The animal’s reaction was abolished anterior to a transection of the spinal cord, but behind the cut, reflex movements continued, showing that the afferents go more or less directly to the spinal medulla, rather than via a nerve, as they do in lampreys, which also have a cutaneous light sense.

The discussion of hagfish eyes which follows is based on findings reported in the literature, with our observations on new material, mostly fixed with a view to resin embedding and possible electron microscopy. We follow Bo Fernholm (this volume) for nomenclature of the hagfishes we have studied, but give authors’ attributions, with Fernholm’s equivalent in parentheses, where these are different in the literature.

Holmberg (1970) used the terms supranuclear and subnuclear to identify the portions of the receptors towards the outside and inside of the eye respectively, but we prefer the terms vitread and sclerad, by analogy with better developed vertebrate eyes, even though vitreous and differentiated sclera are lacking in *M. glutinosa*.

The hagfish eye has been examined by a number of workers, from Krause (1886), Kohl (1892) and Retzius (1893) in the nineteenth century to a succession of work more recently (Allen, 1905; Stockard, 1907; Ducker, 1924; Kobayashi, 1964). The important papers of Holmberg and colleagues from Stockholm, quoted *in situ*, were the first to provide ultrastructural information on the retinal cells, and form an important basis for this chapter.

Fernholm and Holmberg (1975) compared the structure of the eyes in three species of hagfish, *Myxine garmani*, *Polistotrema (Eptatretus) stoutii* and *M. glutinosa*. Of these Holmberg (1970) had already examined the retinal cells of *M. glutinosa*, with the least developed eyes. The same author (1971) had also compared the retinal cells in *Myxine* and *Polistotrema (Eptatretus) stoutii*, using electron microscopy in both cases, and giving excellent diagrams summarizing the features of epithelial and receptor cells. Fernholm and Holmberg’s comparison showed that *M. garmani* had the most advanced structure, and that *P. stoutii* occupied an intermediate position. Holmberg (1971) quoted the results of Kobayashi (1964) on *M. garmani*, himself describing and illustrating the situation in *Polistotrema (E.) stoutii*.

### 34.2 EPTATRETUS STOUTII, E. ATAMI, E. BURGERI AND E. CIRRATUS

Allen (1905) examined the eyes of 19 adult *Bdellostoma (Eptatretus) stoutii* from series sections of paraffin-embedded hagfishes which had been fixed entire in Müller’s fluid. Material from the four species above, and from *Myxine glutinosa*, has been examined recently by the authors, and brief descriptions follow. The eyes of the *Eptatretus* species are all better developed than those of *Myxine glutinosa*, in that all have a vitreous cavity. None, however, has a lens. They are sufficiently similar that a single description will serve for all, with specific differences noted in context. Allen found that the eyes in his *E. stoutii* were variable in size between specimens, though these were all between 43 and 47 cm long, but were even more variable between right and left sides in a single individual. Approximately 1.3 mm diameter, the eyes were embedded in fat, just beneath a transparent patch in the skin on the side of the head; in some cases the eye abutted the surface tissues, when the external aspect of the eye was flattened, and in others it was wholly buried. He found no evidence of eye muscles, but did identify a slender optic nerve passing through the fat. His *Eptatretus* eyes had a thin and undifferentiated corneoscleral coat, in some cases fused with the deep surface of the overlying skin. The retinal portion of the eye was represented by an incompletely developed optic cup, of which the two layers remained separated and which enclosed a vitreous cavity. The outer layer of the optic cup was a simple single layer of