Evolutionary Significance of Fine Structure of Archiannelid Eyes

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Summary. The structure of the ocelli of representatives of four of the five families of archiannelids (Polychaeta: Annelida) was studied by light and electron microscopy. The apparent photoreceptoral organelle in each species is an array of microvilli (rhabdomere). Cilia were observed in the eyes of only a couple of specimens in one species of archiannelid (Nerilla antennata). They were unassociated with the rhabdomeres; we regard them as adventitious. Support is given by this study to the theory that the photoreceptoral organelle of the ancestral annelid was a rhabdomere. Other features of the ocelli are described and illustrated.

A. Introduction

One of us (RME) developed a theory of two lines of evolution of photoreceptors: ciliary and rhabdomorphic (Eakin, 1963, 1968). The former includes cnidarians, echino- phores, chaetognaths, echinoderms, and chordates; the latter, an offshoot of the ciliary lineage, includes platyhelminths, aschelminths, mollusks, annelids, and arthropods. However, there are exceptions, the fate of most theories, especially among annelids (see, e.g., Dhaunaut-Courtois, 1965, 1968; Krasne and Lawrence, 1966; Kernés, 1966; 1968, 1971, 1975; Whittle and Golding, 1974; Ermak and Eakin, 1976). Finally, Vanfleteren and Coomans (1976) concluded that because of the exceptions, in other taxa as well as in the Annelida, the type of photoreceptor, ciliary or rhabdomorphic, is not sufficiently ‘conservative’ to be useful in phylogenetic speculation at the phylum level, although helpful in showing relationships between subgroups within a phylum.

Although the archiannelids are a heterogeneous group and despite uncertainty regarding the primitiveness of their features, we undertook a study of the ocelli in

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representatives of four of the five presently recognized families of the order in the hope that the structure of their photoreceptors would throw some light on the probable nature of the light-sensitive organelle in the ancestral stock of the phylum.

Figs. 1–4. Diagrams of median sections through ocelli of Protobrulis (Fig. 1), Saccocirrus (Fig. 2), Dnephrus (Fig. 3), and Nerrila (Fig. 4). Inserts: dorsal view of head of each archiannelid, respectively, showing positions of ocelli. A axon; CC corneal cell; CI cilia; ER submicrovillar endoplasmic reticulum; L lens; M mitochondria; PC pigmented (supportive) cell; PCN pigmented cell nucleus; PCV pigmented cell microvilli; PG pigment granule; PL platelet; PLC platelet (supportive) cell; SC, SC1, SC2 sensory cells; SCN sensory cell nucleus; SCV sensory cell microvilli (thylakid); V vesicles
B. Materials and Methods

The four archiannelids used in this study were: Protodrilus (sp?), Saccocirrus sonomacus (Martin, 1977), Dinophilus gyrocielatus (Schmidt, 1857), and Nerilla antennata (Schmidt, 1848). The worms were collected by GGM from the intertidal zone at Shell Beach, north of Bodega Bay, California.

The heads of the annelids were severed and trimmed with a microknife. Several fixatives were used; that most often employed was 2% glutaraldehyde (diluted from 8% Polysciences product by seawater), in a 0.1 M cacodylate buffer, pH 7.2, for 15—60 min at room temperature. Following cold osmification (1% in cacodylate buffer) for 1 h, the specimens were dehydrated with ethanol, embedded in Epon, thick- and thin-sectioned, and studied by light and electron microscopy (RCA 3G). Despite many variations in procedure we could not achieve superior electron microscopy of these archiannelids. Among the fixatives tried was an 80% solution of osmium tetroxide in carbon tetrachloride (Huber and Kosin, 1976) to obtain a better preservation of Nerilla, the most troublesome of the genera studied. The results were unsatisfactory, although that fixative did yield a good picture of the reflecting platelets in the eyecup (Fig. 18). Electron microscopy of Protodrilus and Dinophilus was conducted by GGM, that of Saccocirrus and Nerilla by CTR.

C. Observations

The major features of the four types of eyes studied are shown diagrammatically in Figures 1—4, with the insert on each Figure indicating the position of the ocelli on the dorsum of the head of the respective animal. Nerilla (Fig. 4) possesses two pairs of eyes, the others one pair only.

1. Ocelli of Protodrilus and Saccocirrus

The simplest eyes are those of Protodrilus (Figs. 1 and 5—7) and of Saccocirrus (Figs. 2 and 8—12), each consisting of two cells: a cup-shaped, pigmented, supportive cell and a sensory cell. A major part of the latter projects into the cavity of the former, whereas the remainder (nucleated soma) of the sensory cell lies above and medial to the eyecup. The ocelli are approximately 12 μm in diameter.

The probable photosensitive organelles in the ocelli of the archiannelids studied are the rhabdomeres or arrays of microvilli, which project from the inner surface of the receptorial part of a sensory cell (i.e., away from light entering the eyecup), except in Dinophilus (see below) in which the villi are directed toward the light. The tips of the villi lie adjacent to the inner plasma membrane of the pigmented cell. Each villus measures 0.1 μm in diameter and about 1.4 μm in length (Protodrilus) or 3.2 μm (Saccocirrus).

Mitochondria are situated distally to the rhabdomere (i.e., toward the cuticle). In Protodrilus they are abundant, and many are arranged in a layer (Fig. 7) near the narrow connection between the receptorial and nucleated parts of a sensory cell (Fig. 5); in Saccocirrus they are scattered and not numerous. In the former species long profiles (Figs.
5 and 6) of submicrovillar endoplasmic reticulum (see Whittle, 1976) largely fill the region of the sensory cell between the short microvilli and the layer of mitochondria just mentioned. The submicrovillar ER is not prominent in *Saccocirrus*. Cilia or basal bodies were not observed. An axon leads from the soma of a sensory cell but in no instance were we able to follow its course to the nearby brain.

A supportive cell is characterized by its cup shape (Figs. 5 and 7–9) and by the possession of many spheroidal granules of black pigment (melanin?). The nucleus of a supportive cell is usually situated adjacent to the cell’s basal membrane. In *Saccocirrus* the margin of the pupil of the ocellus is ringed with an array of long (5.0 μm) microvilli, of uniform diameter (0.1 μm), which arise from the lips of the pigmented cell except where the sensory cell enters the eyecup (Figs. 2 and 9–11). The villi project over the receptive part of a sensory cell so that in places those from opposite sides almost touch one another (see Fig. 2). These villi, unlike the sensory microvilli, may arise from a common stalk (Fig. 11). Where the sensory cell enters the pigmented cup the lips of the cup (supportive cell) seem to be firmly attached to the neck of the receptive cell by prominent adhering zonules (Fig. 10).

A fringe benefit of our study of the eyes of *Saccocirrus* was an observation of its cuticle, a trilaminar structure through which microvilli (MV, Fig. 12) of the epidermal cells pass to project a short distance above the surface of the worm and end in small fuzzy-coated knobs. The three layers, from outside to inside, are: a narrow, dense, granular epicuticle; a slightly wider zone of less tightly packed granules; and a wide filamentous stratum. The innermost layer is separated from the surface of the epidermis by a space into which open large secretory vacuoles (SV) of the epidermal cells.

Because the cuticle will not be discussed later, we add here that the epidermal vacuoles, noted above, may bear precursors of the cuticle and that they are formed by fusion of vesicles that probably trace their origin to the Golgi apparatus. The structure of the cuticle in *Saccocirrus* is similar to that of other archiannelids, as described by Rieger and Rieger (1976). The reader will also find in the paper just cited a provocative hypothesis on the evolution of the cuticle in the vermiform Spiralia.

2. Ocelli of Dinophilus

An eye (about 7.5 μm in diameter) of *Dinophilus gyrobellatus* is smaller and more complicated than those of the species just considered (Figs. 3 and 13–15). It consists of two sensory cells and one pigmented supportive cell. The latter encloses the receptive parts of the former (see Fig. 3) except basally where the receptive parts of the sensory cells connect by narrow stalks to their somas. As in *Protodrilus* and *Saccocirrus*, the sensory cell somas lie outside the eyecup, in this instance one on each side of the ocellus. But unlike *Protodrilus* and *Saccocirrus*, the microvilli (rhabdomere) in *Dinophilus* project from the distal ends of the sensory cells (i.e., toward the cuticle and in-

Fig. 5. Electron micrograph (EM) of median section through ocellus of *Protodrilus*. ER submicrovillar endoplasmic reticulum; M mitochondria; PC pigmented cell; PG pigment granule; SC sensory cell; SCN sensory cell nucleus; SCV sensory cell microvilli. X 13,400

Fig. 6. Higher magnification of submicrovillar ER in *Protodrilus*. X 71,500
Fig 7. EM of an oblique section through ocellus of Protodrilus showing distinct bands of mitochondria (M), submicrovillar endoplasmic reticulum (ER), and sensory cell microvilli (SCV). EP epidermis. X 12,700
Fig. 8. EM of median section through ocellus of *Saccocirrus*. ICV interstitial cell vacuoles; M mitochondria; PC pigmented cell; SCN sensory cell nucleus; SCV sensory cell microvilli. X 13,000
Fig. 9. EM of lateral section through ocellus of *Saccocirrus*. C cuticle above eye; EPN epidermal cell nucleus; IC interstitial cell; NC neurosecretory cell; PCN pigmented cell nucleus; PCV pigmented cell microvilli; SCV sensory cell microvilli. Rectangle: area seen in Figure 10. X 9,000

Fig. 10. An enlargement of marked area in Figure 9. ZA adhering zonules. X 29,000
Fig. 11. Higher magnification of villi of pigmented cell (PCV) and of sensory cell microvilli (SCV) of *Saccocirrus*. PG pigment granules. X 24,000

Fig. 12. EM of epidermis (EP) and cuticle (C) above ocellus in *Saccocirrus*. EC epicuticle; G Golgi apparatus; MV microvillus of epidermal cell; SV secretory vacuole of epidermis. X 19,000
coming light). The villi are parallel, straight, long (2.8 μm), and narrow (0.05 μm). Long profiles of submicrovillar ER lie below the villi, also a few mitochondria, some of which are unusually large. The supportive cell contains many black (melanin?) granules of various sizes. The nucleus is situated basally in that part of the cell lying between the somas of the two sensory cells. The median distal part of the cell is slightly swollen forming a biconvex, lens-like body containing membrane-bounded globules of finely granular, osmiophilic material (Figs. 13 and 14).

Returning to the microvilli, the presumed photoreceptor organelles, we note that they are relatively electron-lucent internally (Fig. 16). Close inspection of micrographs taken with a Siemens 102 electron microscope at higher magnification (insert, Fig. 16) reveals granules in the villar membranes that exhibit a regular periodicity. The particles may be molecules of the photopigment.

3. Ocelli of Nerilla

The four ocelli (each about 7 μm in diameter) of Nerilla antennata are the most complex of the eyes studied (Figs. 4, 17, and 18). Each consists of six cells: two sensory, two supportive, and two corneal. The soma of a sensory cell lies outside the eyecup, as in the other species, and connects with the receptorial part of the cell by a narrow stalk that enters the cavity of the ocellus (see Fig. 4) between supportive or corneal cells to which it is bound by adhering zonules. The rhabdomeres of the two sensory cells oppose and interdigitate with each other. Their central microvilli are straighter and shorter (1.7 μm) than the lateral curved ones, which are longer (3 μm). A sparse submicrovillar ER and many mitochondria lie beneath each rhabdomere. In one of the sensory cells in two of several specimens examined we observed a pair of short cilia and associated basal bodies situated near the shafts of the cells. The cilia were unrelated, insofar as we could observe, to the microvilli. An axon-like process leads from each sensory cell toward the brain, but we were unable to trace one very far.

The supportive cells of an ocellus of Nerilla contain several layers of flat platelets that appear rectangular in section (Fig. 18). The platelets usually seem empty in our electron micrographs, probably because their contents were dissolved by ethanol during dehydration. The silvery appearance of the ocelli in the living animals is due to these platelets that probably contain some reflecting substance such as guanine. It is noteworthy that in the preparation of the specimens for microscopy the sheen of the eyes is lost during dehydration.

The two corneal cells of an ocellus lie beneath the epidermis of the head and, together with the two supportive cells, they form the wall of the ocellus. The former have large nuclei, sparse cytoplasmic organelles, but no platelets. Their surfaces facing the lumen of the eyecup bear stubby microvilli that are embedded in a layer of finely granular material.

Fig. 13. EM of lateral section through ocellus of Dinophilus, showing lens (L) composed of granular, membrane-bounded bodies derived from lips of pigmented cell (PC). C cuticle; SC sensory cell; SCV sensory cell microvilli. X 15,200. Micrograph retouched, especially fractured pigment granules

Fig. 14. Higher magnification of subunits of lens of Dinophilus. X 135,000
Fig. 15. EM of median section through ocellus of Dinophilus, showing the two sensory cells (SC₁ and SC₂). PC pigmented cell; PCN pigmented cell nucleus; SCN nucleus of a sensory cell; SCV sensory cell microvilli. X 22,900. Micrograph retouched, especially fractured pigment granules.

Fig. 16. Higher magnification of sensory cell microvilli of Dinophilus. X 141,700. Insert: still higher magnification of two adjacent villar membranes. X 302,700.
Fig. 17. EM of oblique section through ocellus of *Nerilla* showing two sensory cells (*SC*₁ and *SC*₂) and their interdigitating median (*SCVM*) and lateral (*SCVL*) microvilli. *BB* two basal bodies; *C* cuticle; *CCV* corneal cell microvilli; *EPN* epidermal cell nucleus; *PLC* platelet cell; *PLCN* platelet cell nucleus. X 12,500

Fig. 18. Higher magnification of platelets (*PL*) in ocellus of *Nerilla* fixed in 80% OsO₄. X 20,000
Finally, we observed many cells near the ocelli of *Nerilla* that contain numerous cored vesicles, resembling those in neurosecretory cells (not illustrated).

D. Discussion

1. Ciliary versus Rhabdomeric Photoreceptors

Eakin (1963, 1968) proposed a theory that there are two basic kinds of photoreceptors: ciliary and rhabdomeric. In the former the photopigment is incorporated in the membranes of villi (e.g., a hydromedusan) or lamellae (e.g., an ascidian) or internal tubules (e.g., a chaetognath) or disks (e.g., a vertebrate) — all derived from ciliary membranes — or in even an unelaborated ciliary membrane (e.g., a bryozoan) (see Eakin, 1972, for references). In the rhabdomeric type the photopigment lies in the membranes of villi (e.g., insect or snail or annelid) or lamellae (e.g., a rotifer), which arise directly from the plasmalemma of the receptorial cell. Rhabdomeres are unrelated developmentally or functionally to any cilia that may be present. Moreover, Eakin (1963, 1968) suggested that the types of photoreceptorial organelles have evolutionary significance and that they may be useful in determining phylogenetic relationships, even between phyla. He proposed that photoreceptors of the deuterostomes are characteristically ciliary, those of protostomes typically rhabdomeric.

These ideas have been questioned several times when exceptions to the theory were discovered, such as ciliary photoreceptors in annelids (e.g., sabellids) and mollusks (e.g., a scallop) or a rhabdomeric photoreceptor in a chordate (e.g., a salp) (see Eakin, 1972, for references). The most recent challenge is that of Vanfleteren and Coomans (1976) who argue that, although the preceding concepts are helpful in considering relationships between taxa of lower rank, they are not applicable to phyla. These authors concluded that the cilium is the universal and primary photoreceptorial organelle because it is believed to be the organizer for not only true ciliary photoreceptors but also rhabdomeric ones. In some examples of rhabdomeres the cilium remains after inducing the microvilli (e.g., a sipunculid), often in vestigial form (e.g., in the onycophoran *Peripatus*), whereas in other instances it appears to disappear leaving only its basal body and striated rootlet (e.g., a nereid worm or a coccinellid beetle) and in still other forms the entire ciliary apparatus is absent (see Eakin, 1972; Vanfleteren and Coomans, 1976). The same idea was proposed by Röhlich et al. (1970).

We explain the exceptions to Eakin’s theory as secondary or coenogenetic structures. We shall here consider only the annelids. In earlier papers (e.g., Hermans and Eakin, 1969, 1970, 1974; Ermak and Eakin, 1976) it was held that most of the ciliary photoreceptors are integumentary structures, whereas in cerebral ocelli photoreceptors are rhabdomeric (see above citations for references). We believe that cerebral and integumentary ocelli are nonhomologous. The few scattered ciliated cells that have been noted in or near the brain of an annelid have not been shown to be photoreceptive, and they are not associated with a pigmented cup or a lens-like body or a tapetum — structures commonly found in eyes (again see above citations for references).

Second, if cilia or basal bodies are organizers of microvilli one would expect that in every instance of a rhabdomere or a brush border one would find evidence of ciliary
structures, in the embryo if not in the adult. Vanfleteren and Coomans (1976) cite the work of Home (1972), as well as other studies, in which centrioles and striated rootlets were observed near the rhabdometric microvilli of several species of beetles. However, similar discoveries have not been made on the many other arthropodan rhabdomeres that have been examined. True, few embryologic studies have been conducted. More are needed. Until better documentation is available, however, we do not think that it is safe to conclude that centrioles induce microvilli. To our knowledge ciliary structures are not associated with many brush borders, such as the arrays of villi on the epithelial cells of intestine, bile canaliculi, gall bladder, renal tubules, various glands, etc.

Third, photoreceptors are ectodermal in origin, and this germ layer is typically ciliated. It is not surprising, therefore, that ciliary structures are commonly seen in eyes. It can be argued, and we do, that cilia when present in association with arrays of photosensitive microvilli are adventitious, that is, in the sense of being incidental or, as Webster gives it, "lacking a relation to the intrinsic character of a thing". Moreover, cilia crop up in unexpected places, such as neurones (del Cerro and Snider, 1970; Chung and Keefe, 1976), pituitary (Wheatley, 1967), adrenal gland (Coupland, 1965), and pancreas islets (Boquist, 1968). In these instances they are adventitious in the sense of being sporadic and accidental. Whenever a centriole lies beneath a cytomembrane—not necessarily the cell membrane—there is the possibility of the induction of a cilium. We believe that the ubiquity of ciliary structures needs to be considered when drawing conclusions about the significance of those found in association with rhabdomeres.

2. Do the Archiannelids Possess Primitive Characteristics?

If our findings about the nature of the photoreceptor apparatus in the archiannelids that we studied is to have significance for the phylogenetic speculation to follow, we must first deal with this question. It should be said initially that the Archiannelida is a heterogeneous group of worms, the taxonomic status of which has varied with time. Hermans (1969) concluded that the Archiannelida should be considered not a separate class of the Annelida but an order within the class Polychaeta. At present five families are included in the order: Polygordiidae, Saccocirridae, Protodrilidae, Dinophilidae, Nerillidae (Hermans, 1969). We have sampled four of these families in this study. Unfortunately, we have not been able to obtain a specimen of Polygordius.

Opinions about the phylogenetic position of the archiannelids have varied. Polygordius, Protodrilus, Saccocirrus, and Dinophilus have been considered primitive (Hatschek, 1878). Dinophilus was regarded as neotenous (Nachtsheim, 1919); and the archiannelids in general were thought to be secondarily reduced (Remane, 1932). Hermans (1969) argued that the evolutionary position of the archiannelids cannot be discerned at this time and that their presumed primitive and advanced features (see Hatschek, 1893) are best explained as adaptations to the interstitial habitat. Swedmark (1964) concluded that an interstitial fauna is characterized by small body size, slender body form, abundant ciliation for locomotion, and slender tactile structures (absent in Dinophilus), to list a few traits. We suggest that the ancestral polychaete or ancestor to the polychaetes could have been a small, slender, highly ciliated interstitial form with a pair of two-celled ocelli similar to those of Protodrilus or Saccocirrus.
3. A Speculative Conclusion

Assuming that the ocelli studied by us are representative of the eyes of archiannelids, it follows that the rhabdome is the characteristic photoreceptor of cerebral ocelli in this order of polychaetes. Since the rhabdome is the only type of photoreceptor thus far found in cerebral ocelli of polychaetes, we conclude that it was probably the photoreceptor organelle of cerebral ocelli in the earliest annelids, regardless of whether the archiannelids represent an ancestral stock or whether they are secondarily simplified, interstitial polychaetes. In only one of the four archiannelids examined by us (Nerilla) did we find any evidence of cilia in the photoreceptors, and in this instance they were short, rudimentary, deeply embedded in the sensory cell, and unrelated to the microvilli.

It is conceivable that the archiannelids arose from some platyhelminth or nemertean. It is certainly worthy of note that there is a similarity in the ocelli of flatworms and nemerteans and those of the archiannelids here described. The eyes of the first two groups are simple, outwardly directed, pigmented cups, formed by one cell into which project the receptoral parts of one or two photosensory cells. The presumed light-sensitive apparatus is an array of microvilli, the rhabdome. In some instances, such as the ocellus of a rhabdocoele examined by Eakin and Westfall (Eakin, 1968), and that of Planaria vitta (Hesse, 1897), the ocellus is composed of only two cells — one sensory, the other pigmented and supportive — as in the eyes of Protagrillus and Saccocirrus. In other flatworms the pigmented one-celled eyecup encloses two photoreceptoral cells (e.g., the freshwater rhabdocoele Dalycella viridis, Bedini et al., 1973; or the miracidium of the tematode Fasciola hepatica, Kümmler, 1960). In still others (e.g., Planaria torva) there are three sensory cells (Hesse, 1897) and so on to examples of ocelli with multiple pigmented cells forming the cup and many sensory cells (e.g., Dugesia lugubris, Röhlisch and Török, 1961).

We postulate that from a two-celled ocellus more elaborate cerebral eyes evolved, in the archiannelids and in other groups of polychaetes. The eyes of Dinophilus and Nerilla are more complicated than those of Protagrillus and Saccocirrus not only in respect to number of cells (3 in the former and 6 in the latter) but also with regard to specialized structures, such as a lens-like body in Dinophilus and reflecting platelets in Nerilla. In the higher polychaetes further advances and specializations occurred. The somas of the sensory cells became incorporated into the eyecup so that a retina was created consisting of an intermingling of receptoral and supportive cells (see Hermans and Cloney, 1966). The ancestral inverted position of the rhabdome (i.e., with microvilli directed away from the light) was reversed, the microvilli projecting toward the light (converse type). Additionally and secondarily, integumentary ocelli have evolved, such as the branchial eyes of Branchionemma vesiculosum (Krasne and Lawrence, 1966) and Dasyphus bombynnus (Kernéis, 1968), to mention only two studies, and the pygidial ocelli of Chone ecandata (Ermak and Eakin, 1976).
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