A simple visual system without neurons in jellyfish larvae

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Earlier detailed studies of cnidarian planula larvae have revealed a simple nervous system but no eyes or identifiable light sensing structures. Here, we describe the planula of a box jellyfish, *Tripedalia cystophora*, and report that these larvae have an extremely simple organization with no nervous system at all. Their only advanced feature is the presence of 10–15 pigment-cup ocelli, evenly spaced across the posterior half of the larval ectoderm. The ocelli are single cell structures containing a cup of screening pigment filled with presumably photosensory microvilli. These rhabdomeric photoreceptors have no neural connections to any other cells, but each has a well-developed motor-cilium, appearing to be the only means by which light can control the behaviour of the larva. The ocelli are thus self-contained sensory–motor entities, making a nervous system superfluous.

1. INTRODUCTION

Cnidarians are simple, radially symmetrical invertebrates most classes of which have a metamorphic life cycle including a swimming larva, a stationary polyp and a free-swimming medusa (Müller & Leitz 2002). Cnidarian larvae are of the planula type. The early development has been described morphologically and molecularly in great detail (Okada 1927; Hayward *et al.* 2001, 2002). After fertilization of the egg and several cell divisions, a flattened blastula is formed, resembling a shallow bowl. The upper and lower ectoderm separate centrally, and after gastrulation a second tissue layer, the endoderm (or gastroderm) appears. After the formation of cilia the free-swimming planula is complete within 24–72 h, for most species (Martin 2000; Gröger & Schmid 2001; Hayward *et al.* 2001). The larvae are simple with a surface epithelium containing motor cilia and microvilli, and occasional sensory neurons and nematocytes (Müller & Leitz 2002). After some time spent swimming, the planulae settle with the anterior pole to the substrate to form polyps, which can propagate asexually through fission, or form medusae through strobilation, metamorphosis or budding. The medusae can subsequently reproduce sexually to form new larvae (Müller & Leitz 2002). The medusae of some species release the gametes directly into the water, whereas others retain the embryos until the planulae are mature (Berrill 1949). Our present investigation of cubozoan larvae reveals a simpler organization than in most other cnidarian larvae, and the body plan is radially symmetrical.

Two types of photoreceptor are found in animals: the rhabdomeric type, where microvilli constitute the photoreceptive part of the cell, and the ciliary type, where one or more modified cilia form the photoreceptive structure (Salvini-Plawen & Mayr 1977). Rhabdomeric photoreceptors are found in invertebrate groups such as arthropods and cephalopods, whereas ciliary photoreceptors are typically found in vertebrate eyes. It has long been known that some cnidarian medusae have eyes of a surprisingly elaborate type, and the most complex examples are found in cubozoans (see Pearse & Pearse 1978; Laska & Hündgen 1982). Cnidarian photoreceptors are of the ciliary type (Bouillon & Nielsen 1974; Singla 1974; Martin 2002). It has also been reported that cnidarian larvae respond to light stimuli (Cargo 1979), but photosensory structures have remained unknown. We here report that the planula larvae of cubomedusae have prominent photoreceptors and that they break the rule by having rhabdomeric photoreceptors. Our ultrastructural study further reveals that there is no nervous system to which the ocelli can pass visual information.

2. MATERIAL AND METHODS

(a) *Animals*

Gravid females of *Tripedalia cystophora* were collected in mangrove swamps near La Parguera, Puerto Rico. Larvae were excised in seawater and transferred to fixative. For comparison we used cubozoan planulae of a second family, namely *Chiropsalmus* sp. and *Chironex fleckerii* collected at the north beaches of Cairns, Queensland, Australia. Unfortunately, the state of preservation (in formalin) was not good enough for a detailed ultrastructural study of larvae of the last two species.

(b) *Histology*

For transmission electron microscopy (TEM), larvae were fixed in 2.5% glutaraldehyde and 2.5% paraformaldehyde in cacodylate buffer for at least 2 h. They were then rinsed in cacodylate buffer, stained in 1% OsO_4 for 1 h, dehydrated in an ethanol series, embedded in Epon resin and polymerized. Sections were cut with a diamond knife and stained with lead citrate and uranyl acetate in an LKB ultrastainer. The sections were examined in a JEOL 1200 EX transmission electron microscope.

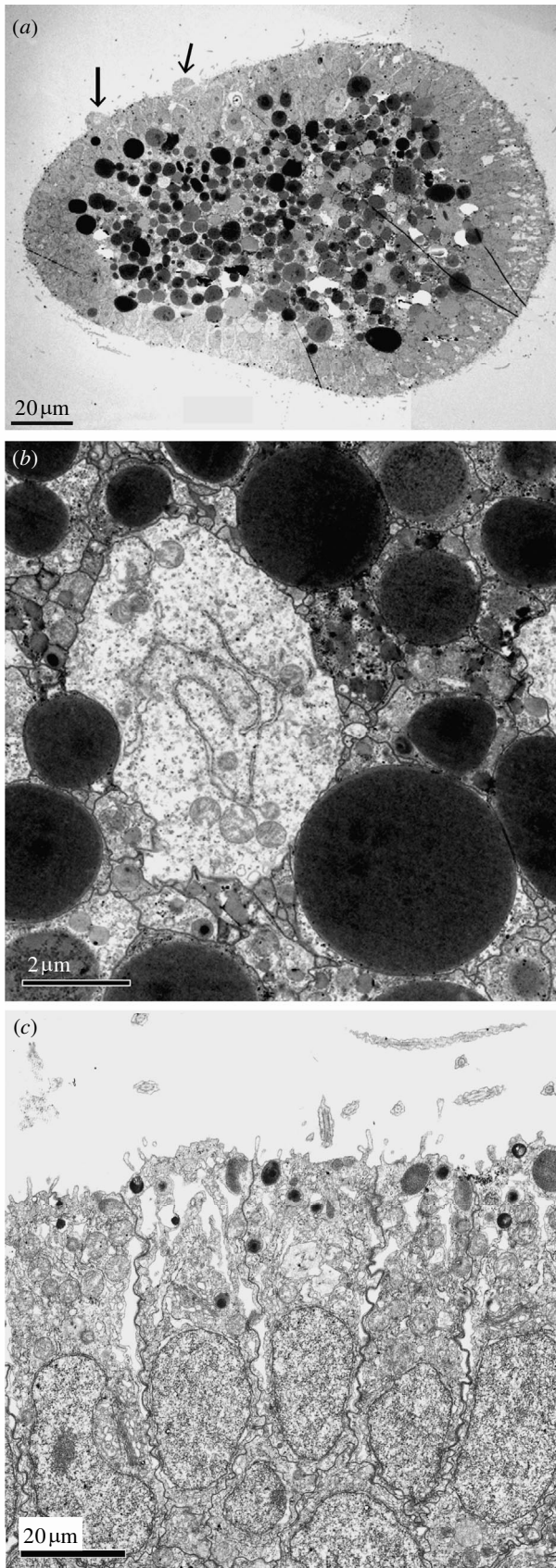*Author for correspondence (dan-e.nilsson@cob.lu.se).

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2349

(*a*)

20 μm

(*b*)

2 μm

(*c*)

20 μm

Figure 1. (*a*) Longitudinal cross-section through the larva of *Tripedalia cystophora*, showing the general appearance of the animal. The anterior pole is broader (to the right in the picture) and protruding ocelli (arrows) are found only in the posterior half of the larva. The dermal cell layer encases the gastrodermal cell mass. There is no mesogloea or basal membrane between the two tissue layers. (*b*) A close-up of the gastroderm showing a lightly stained interstitial-like cell with densely packed ribosomes, but few other organelles. The remaining gastrodermal cells are darker stained and have a more complex morphology. The electron-dense granules within the darker cells have a diameter of up to 4 mm. (*c*) This shows the appearance of the epidermal layer with its columnar organization. The cell nuclei are located close to the gastroderm. The epidermal cells are monociliated and covered with surface microvilli. There is a high abundance of lysosomes and ribosomes in the cytoplasm of these cells. The apical borders of neighbouring cells are joined with desmosomes.

larvae are rounded but of a similar size. They have a single-layer ectoderm covering a more amorphous endoderm/gastroderm. There are two morphologically distinct cell types in the gastroderm (figure 1*b*). One type stains lightly in TEM and resembles interstitial cells with ribosomes and a few other organelles (Martin & Chia 1982). The more common type is the yolk cell, which stains darker and contains electron-dense 'yolk' granules. These granules are large (up to 4 μm in diameter) and alter the cell shape accordingly.

The ectodermal epithelium is equally simple and contains only three distinguishable cell types. These are the monociliated epithelial cells (figure 1*c*), a few nematocytes, and 10–15 photoreceptor cells (described in detail below). The epithelium is organized as a columnar monolayer with the cell nuclei close to the epithelial base. The ectoderm is thicker in the anterior and posterior end of the larva. Each cell is *ca*. 2 μm wide and 12 μm tall, and its surface is covered with microvilli. The apical borders of neighbouring cells are joined with desmosomes. The epithelial cells contain many mitochondria, lysosomes and ribosomes (free, or as rough endoplasmic reticulum), which suggests a high metabolic rate. Otherwise they resemble typical epithelial cells, seen in a wide array of metazoans. There is no basal membrane or mesogloea between the two tissue layers.

We did not find any neurons or neuron-like structures in any part of the body. The *Tripedalia* larvae were collected directly from female medusae and may not have been fully mature. Despite this they swam freely after excision and stayed healthy and active for several hours in small containers of sea water. Our comparison of mature larvae of *Chiropsalmus* and *Chironex* also support the conclusion that cubozoan larvae do not possess a nervous system.

(b) *Ocellar structure*

There are *ca*. 10–15 ocelli in each larva. In *Tripedalia* these are located in the posterior end, compared with the direction of movement, and they are evenly spaced, forming a regular hexagonal pattern. Despite being located in the 'wrong' end, the ocelli face forward and stick out, as if struggling to see in the forward direction (figure 1*a*). In *Chiropsalmus* the ocelli are located around the middle

3. RESULTS

(a) *The structure of the larva*

Tripedalia planula larvae (figure 1*a*) have a pear-like shape with a maximum diameter of *ca*. 80 μm and a total length of 120 μm, while the *Chiropsalmus* and *Chironex*

and in *Chironex* in the anterior end. In neither do they protrude outside the epithelial surface as in *Tripedalia*.

Each *Tripedalia* ocellus is a single photoreceptor cell, similar to the other epithelial cells, but with fewer ribosomes (figure 2a). Each photoreceptor cell contains a large lysosome-like granular vesicle located close to the nucleus. The photoreceptor contains a cup of screening pigment, the cavity of which is filled with microvilli projecting from the inside of the cup at all sides of the cavity. Because these microvilli are located in the cup and represent the only large membrane area in the cell, we can convincingly argue that they must be the sites of photoreception. The pigment cup forms a 3 μm thick screen of pigment granules surrounded by plasma membranes. The opening of the cup has a diameter of *ca.* 2 μm, and is open to the environment. The pigment cup restricts the sensitivity angle such as to effectively form a directional light meter aiming laterally/forward. The swimming larvae are rotating at *ca.* 2 revolutions s^{-1} around their longitudinal axis. As a consequence, the ocelli are performing a continuous circular scanning of the forward direction.

The photoreceptor has a single cilium protruding from inside the pigment cup, but as this is practically identical to the cilia of the other epithelial cells (figure 2b,c), we interpret these as being non-photoreceptive. Photoreceptive cilia are usually heavily modified (Salvini-Plawen & Mayr 1977), but those of the larval ocelli are indistinguishable from regular motor cilia, complete with a distinct 9+2 filament structure, a basal body with a second perpendicularly arranged centriole and a striated rootlet. Judging from the structure and anchoring, the cilium must be assumed to be motile rather than sensory. We did a careful search for microvilli protruding from the cilia, only to find that all microvillar attachments on the numerous sections we analysed protrude directly from the membrane inside the pigment cup. The photoreceptor must thus be categorized as rhabdomeric, with a non-sensory motor-cilium.

Despite careful studies of numerous specimens and electron microscopy micrographs, we were unable to find anything that could possibly be interpreted as axons. Nor did we find any signs of synaptic or electrical (gap junction) connections between the photoreceptor cells or any other cell in the larvae. This is in agreement with the complete lack of a nervous system. There is thus no structural basis for believing that sensory information is in any way communicated between cells in the larva.

4. DISCUSSION

(a) *An extremely simple body plan*

We have demonstrated the amazing simplicity of cubozoan planula larvae, being composed of only five cell types (figure 3a). Such a simple larval organization is reminiscent more of that in Porifera than in other Cnidaria. Between the two tissue layers of anthozoan planulae, a basal membrane or mesogloea have been described for *Acropora millepora* (e.g. Hayward *et al.* 2001) or for *Pocillopora damicornis* (Vandermeulen 1974), but we found no sign of such structures in cubozoan larvae. Instead, the tissue layers are in direct contact with each other without supporting or separating structures in between.
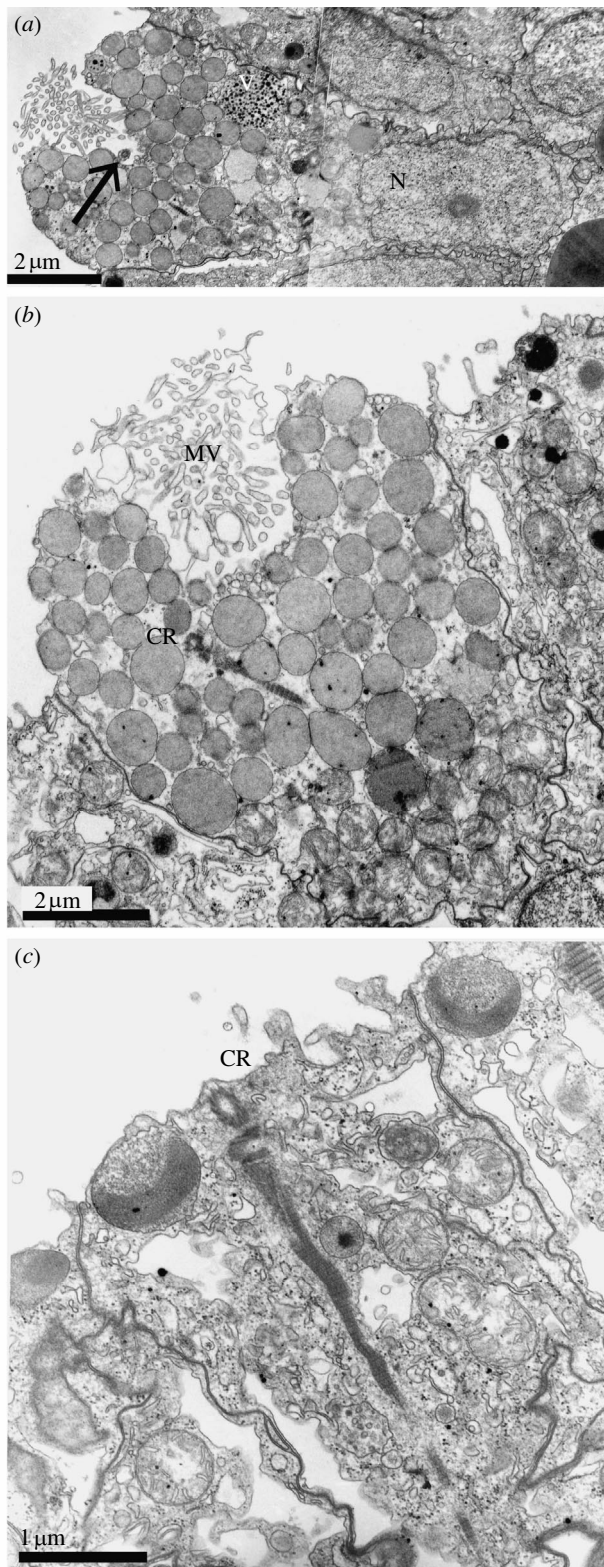

Figure 2. In (a) a cross-section through a photoreceptor cell (ocellus) reveals the protruding pigment cup. A large lysosome-like vacuole (V) is located close to the nucleus (N), which is similar to those of other epithelial cells. Apart from microvilli, the pigment cup contains a single cilium (arrow). The close-up in (b) shows the microvillar mass (MV), an abundance of mitochondria, and the ciliary rootlet (CR). For comparison, the very similar ciliary rootlet (CR) of a monociliated epidermal cell is shown in (c).
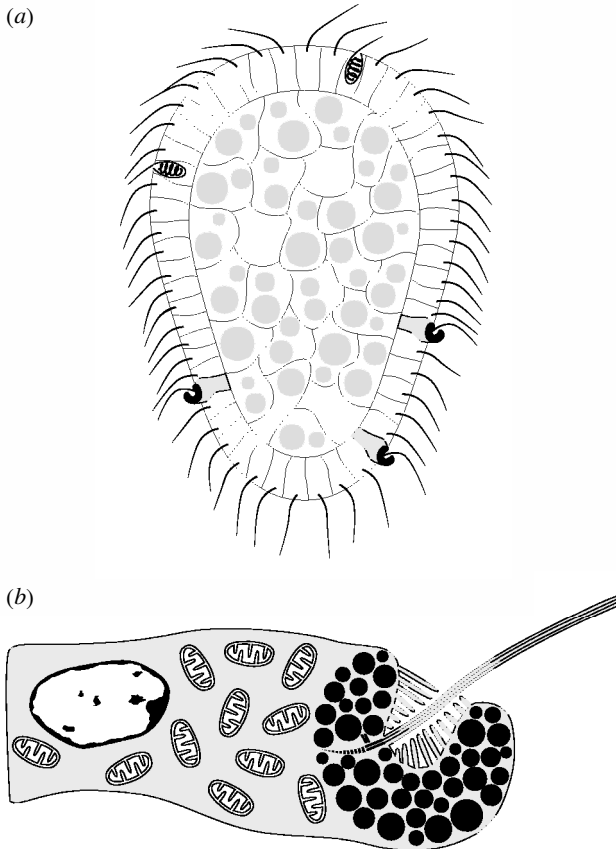
(a)

(b)

Figure 3. Schematic drawings of *(a)* the planula larva of *Tripedalia cystophora* and *(b)* a close-up of an ocellus. In *(a)* the two tissue layers and a total of only five different cell types reveal the extreme simplicity of the larval body. The epidermal cell types are, apart from the normal monociliated motor cells, the photoreceptors (ocelli) and nematocytes. The gastroderm is a homogeneous mass of two cell types: 'yolk' cells and lightly staining cells. The ocellus *(b)* has a fully developed kinocilium, photoreceptive microvilli and a pigment cup, all combined in the same cell. Also indicated in the ocellus are the striated ciliary rootlet, the nucleus and mitochondria. Ocellar morphology, together with the absence of a nervous system, indicate that each ocellus operates as an independent sensory–motor unit.

The cubozoan gastroderm is filled with electron-dense large granules, presumably containing proteins and lipids. These may add to the larva's buoyancy, and aid in long-term survival, or serve as nutrition during the metamorphosis to a polyp. In *Acropora* the larval gastroderm is extremely rich in lipids, which assures a survival time of up to months (Müller & Leitz 2002), and similar-looking granules of *Pocillopora* larvae have been identified as lipid-containing (Vandermeulen 1974). The nutritious content of the planula gastroderm has illustratively been called yolk, and when the larvae get older the granules have been shown to get vacuolized as the contents are metabolized (Widersten 1968).

Acropora larvae have an oral pore opening into a gastric cavity (Hayward *et al.* 2002), but we found no such structure in the larvae of *Tripedalia*, *Chironex* or *Chiropsalmus*. Scyphozoan larvae (*Aurelia aurita* and *Cyanea capillata*) also lack a gastric cavity (Widersten 1968). Interestingly, in the swimming *Acropora* planula, the oral opening is posteriorly compared with the direction of movement

(Hayward *et al.* 2002). The anterior–posterior polarity of a planula is defined not only by the direction of swimming, but also by the expression pattern of transcription factors and the formation of nerve cells (Gröger & Schmid 2001). The development of the *Podocoryne carnea* larvae shows similarities to Bilateria (Gröger & Schmid 2001), whereas the *Tripedalia* larvae described here have a pure radial symmetry also with respect to ocellar positions.

In *Tripedalia* planulae we could only identify two gastrodermal and three ectodermal cell types (figure 3*a*). Other cnidarian larvae are generally more complex in their cell composition (Widersten 1968; Müller & Leitz 2002). Larvae of the scyphozoan *Cassiopeia xamachana* are the only exception; they have only two ectodermal and two gastrodermal cell types (Martin & Chia 1982). Five ectodermal cell types have been described in hydra and anthozoan larvae: epitheliomuscular cells with a motor-cilium, gland cells, anteriorly located neurosensory cells, ganglionic nerve cells and nematocysts (Vandermeulen 1974; Müller & Leitz 2002), but the *Tripedalia* larvae have only two of these. Because larvae of another cubozoan, *Carybdea*, is similarly reported to have a simple epidermis (Okada 1927), this simplicity can be assumed to be general for cubozoan larvae. Pigmented spots on *Carybdea rastonii* and *C. alata* planulae have been reported earlier (Okada 1927; Arneson & Cutress 1976), but have not been identified as photoreceptors. As a result of the present investigation, it is likely that the larval pigment spots of *Carybdea* are indeed photoreceptor cells, and that this condition is general for cubozoan larvae.

Surprisingly, we could find no nerve cells in the larvae, although a simple nervous system is known from planulae of other cnidarian groups. In hydrozoan (Martin 2000) and anthozoan (Hayward *et al.* 2001) larvae there is a nerve net located between the gastroderm and the ectoderm. Two nerve cell types are found in the hydrozoan *Pennaria tiarella* larval ectoderm: sensory nerve cells with a broad base and a narrow neck projecting to the surface, and ganglionic nerve cells located between the gastroderm and ectoderm (Martin 2000). Similarly, in the *Acropora* larva, Arg-Phe-amide (RFamide)-positive neurons are located as a nerve net along the basal membrane, with projections towards the surface (Hayward *et al.* 2001). Sensory RFamide-positive cells first appear in 24–30-hour-old hydrozoan *Podocoryne* larvae, and later a different subset of tubulin-positive nerve cells appear from the anterior part (Gröger & Schmid 2001). The only reported cases of cnidarian larvae without a nervous system are the previously mentioned *Carybdea* and *Cassiopeia* (Okada 1927; Martin & Chia 1982), where the degree of cellular differentiation resembles that of *Tripedalia*.

(b) *A uniquely simple visual system*

The photoreceptor of the *Tripedalia* planula has a pigment cup contained within the cell (figure 3*b*). Larval eyes of similar optical simplicity have been described in the ciliated larva of the polychaete *Platynereis dumerilii*, but as in most such examples, its pigment cup is formed by a separate pigment cell (Arendt *et al.* 2002). Unicellular photoreceptors, and presumed photoreceptors without axons, are indeed known to exist in the animal kingdom (Salvini-Plawen & Mayr 1977; Blumer *et al.* 1995), but these simple traits are not combined in the same species, nor do

they exist in animals without a nervous system. The unicellular photoreceptors of *Tripedalia* are unique in their simplicity, yet they are highly specialized for photoreception.

Simple eye cups were probably the only existing eye type before the Cambrian explosion (Nilsson 1996; Fernald 2000), and despite being a simple optical solution it could clearly provide useful visual information to the animal. Simple omni-directional photosensitivity provides information on general luminance conditions, which are functions of depth in the water and time of day. Directional photoreceptors, such as those reported here, can be used to guide the animal to brighter or dimmer parts of the environment. By the motion of the animal itself it provides the simplest form of spatial vision which, although coarse, may be enough to seek out suitable habitats.

The photoreceptor of *Tripedalia* larvae has both microvilli and a cilium. We believe the microvilli to be the site of photoreception because the single cilium lacks membrane extensions for housing large quantities of photopigment, and is indistinguishable from conventional motor-cilia (figure 2). The evolutionary origin of photoreceptors has been suggested to be a general epithelial cell with a cilium and many microvilli, which subsequently gave rise to all the possible photoreceptors seen today (Salvini-Plawen & Mayr 1977). The photoreceptor described here (figure 3b) is close to such an origin. It also shows some similarity to the simple photoreceptor of the adult hydromedusa *Leuckartia octona*, claimed to be ciliary (Singla 1974).

Ciliary and rhabdomeric photoreceptors have been assigned various degrees of evolutionary significance (Salvini-Plawen & Mayr 1977; Nilsson 1994; Fernald 2000), but one should recall that the two types can sometimes coexist within the same species, and in rare cases even within the same eye (Eakin & Brandenberger 1981). Both types appear to have evolved independently several times (Salvini-Plawen & Mayr 1977; Nilsson 1994). The standard $9+2$ pattern of microtubules is usually heavily modified in ciliary photoreceptors (Salvini-Plawen & Mayr 1977), a modification that receptors in *Tripedalia* larvae do not share. Typical cnidarian photoreceptors, including those in the eyes of *Tripedalia* medusae, have ciliary photoreceptors with microvilli projecting from the ciliary membrane. It appears that cubozoan planulae are the first example of cnidarians with rhabdomeric receptors.

Discrete photosensory structures of planulae have not been described before. The negative phototaxis of the scyphozoan *Cyanea* larva has been attributed to an anteriorly located apical tuft of sensory neurons (Svane & Dolmer 1995). However, the apical tuft is generally believed to be mechanosensitive (Widersten 1968; Müller & Leitz 2002). The cubozoan planulae investigated here have no apical tuft.

Photoreceptors with a normal motor-cilium, and the absence of neural or electrical (gap junction) contact to other epithelial cells, are unusual features which may explain the functional principle of cubozoan larvae. If the ocelli are autonomous sensory–motor units, they may control the swimming direction of the larva by acting as independent rudders. The ocellar cilia need not propel the larva, as this is done by the normal epidermal cells. By simply flexing and stretching the ocellar cilia in response to light, the ocelli may steer the larva towards particular luminance conditions. This hypothesis is supported by several observations. The fact that the ocelli do not contain more mitochondria than other epidermal cells suggests that propulsion is not a part of ocellar function. Because photoreception is highly energy-consuming, the ocelli would need more mitochondria than epithelial cells to support both systems. Neither is there any indication of a direct involvement of ocellar cilia in photoreception, because the cell has many microvilli for this purpose. This only leaves a steering role for the ocellar cilia. The anchoring of cilia with stout rootlets further points to an effector function of the cilia. The lack of a nervous system, and the even spacing and distribution of ocelli, are strong indicators of ocelli operating as independent units with both sensory and effector properties.

It is particularly interesting to note that the ocelli are spread exclusively across the posterior half of the larva, but still pointing more or less in the anterior direction. Cubozoan planulae, and indeed cnidarian planulae in general (Widersten 1968), rotate around their long axis during swimming. In *Tripedalia* this rotation occurs with a rate of *ca.* 2 revolutions s^{-1}. The outward–forward pointing ocelli will thus continuously scan the envelope of a cone in the forward direction. If the ocellar cilia stretch or relax in response to light, they will consistently cause more drag during a part of the spinning cycle, and consequently be able to steer the larva. The only reason for having forward-pointing ocelli in a posterior location would be that this is a good place for the effector function of ocelli in this species. If this is correct, the behaviour of cubozoan larvae will depend crucially on the positioning of the ocelli. Our comparative material from *Chironex fleckerii* and *Chiropsalmus* sp. reveals different positions for the ocelli, and it also appears that the ocelli are more flush with the epidermal surface in these species. In yet another cubozoan genus, *Carybdea*, Okada (1927) reports pigment spots in a central band around the larva. It is tempting to believe that ocellar placement and morphology is tuned for finding different settling habitats in different species.

The unparalleled simplicity makes cubozoan larval ocelli attractive model organisms for studies of genetic control networks and how these can be modified to result in different morphologies and behaviours. With only two tissue layers, five cell types and no nervous system (figure 3a), cubozoan larvae are among the most simply organized animal life-forms. Although conspicuous, their ocelli (figure 3b) represent the simplest visual system yet described.

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