Review

COELENTERATE ORGANS

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Cnidaria and ctenophores, though of the 'tissue grade of construction', can form organs of considerable complexity, for example the prehensile tentilla of *Euplokamis*, the erupting nematocyst batteries of the siphonophores *Stephanophyes* and *Nanomia* and the complex eyes of cubomedusae such as *Carybdea* and *Tripedalia*. The polypoid and medusoid members of siphonophore colonies are functionally equivalent to organs and may be considered as 'zooid-derived organs'. There is no reason to regard the lack of a single, dominant nerve centre as a factor constraining organ development in coelenterates.

Keywords: Coelenterate; organs; construction; complexity; neural organisation

When I wrote to David Macmillan proposing 'coelenterate organs' as a subject for this article he told me he already gave his students a lecture on the topic. "The textbooks (he explained) make such a song and dance about the lack of 'organs' in tissue grade animals that I got sick of marking essays that told me cnidarians are limited because they don't have 'organs'." So that makes two of us. To be fair, teachers and textbook writers generally have to seize whatever weapons come readily to hand in trying to impose some sort of order on the invertebrates and while telling students that coelenterates lack organs they are probably well aware that this is something of an oversimplification. Hyman (1940) herself while describing coelenterates as "metazoa of the tissue grade of construction" states on p. 33 that "incipient organ systems" are present. Hyman's general point is that animals with only two primary body layers are severely limited when it comes to forming

organs compared with those that have a third layer, the mesoderm. The mesoderm "provides material and space for the development of many organs" (Hyman, 1951, p. 2), which sets the ecto- and endoderm free to specialize as covering and digestive layers. Many later writers, myself included, have followed this reasoning, and such is the elegant simplicity of the concept of the three grades of construction – cellular, tissue and organ grades – that, with various reservations and caveats, it continues to be expounded. My purpose in this article is not to question its pedagogical utility, merely to emphasize that coelenterates can and do form organs of considerable complexity.

The term 'organ' can be applied where "tissues of various kinds are closely associated to form one structure . . . adapted for the performance of some one function" (Buchsbaum et al., 1987). As with most definitions, one quickly runs into problems when moving from the general to the particular. It could be argued for instance that the tentacles of hydra are organs, as they consist of myoepithelial, neurosensory and nematogenic tissues united in the common task of food capture, but this seems to be pushing the idea too far as by that standard almost any part of a coelenterate could be called an organ. A good case can be made for complex sensory structures: eyes and balancing organs are often present in medusae, and statocysts are particularly well developed in ctenophores (Tamm, 1982). Various species have specialized body parts serving for attachment, swimming, floating, creeping and burrowing which approach the status of organs. In anthozoans, acontia, acrorhagi and prehensile mesenteric filaments could qualify. There is in fact a continuum of structures of varying degrees of complexity, and no simple criterion for deciding which of them deserve to be called organs. This however is true of animal life at all levels and need not stop us from identifying structures fully deserving of the designation. And what are we to do about the specialized, polymorphic members of siphonophore colonies? Are they organs or individual zooids, or both? I touch on this question below, but my main object here is simply to draw attention to certain structures that fully justify the connotation 'organ', demonstrating the elegance and complexity that can be achieved with only two primary body layers.

1. The Prehensile Tentilla of Euplokamis

Each of the two tentacles of this cydippid ctenophore carries a dozen or so food-catching side-branches, or tentilla (Mills, 1987), (Figs. 1 and 2A). The tentillum is normally kept coiled up, but on contact with prey, it is shot out rapidly, sticking to the prey object by colloblasts and holding it to the
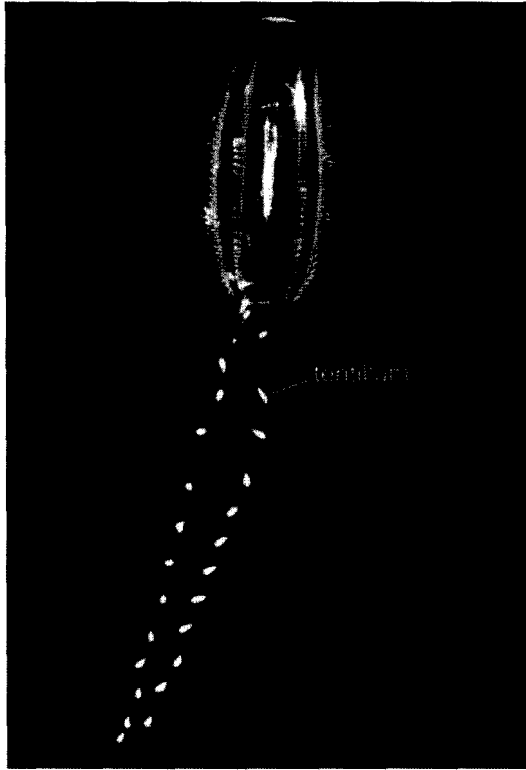
FIGURE 1 *Euplokamis dunlapae*, living specimen from Friday Harbor, Washington, USA (photo by Claudia Mills).

tentacle while it is hauled up struggling to the mouth to be ingested (Fig. 2B). The tentillum is about 1 mm long in the coiled state, 6 mm extended. It is truly prehensile in the sense implied by the dictionary definition *adapted for seizing or grasping, especially by wrapping around*. Uncoiling occurs so fast it is hard to see, recalling the flicking out of the sticky tongue in insectivorous toads (Ewert, 1980).

The main components of the tentillum are shown in Fig. 2C. Though the functional aspects have never been properly studied, one can make an educated guess about the way the whole thing works. Discharge is almost certainly due to contraction of the striated muscle bundles. These lie on the outer side of the coil and, as they shorten, will tend to straighten the structure out. Rows of fluid-filled boxes along the sides presumably resist compression and prevent buckling and kinking during striated muscle contraction. Return to the coiled state may be partly due to the transverse
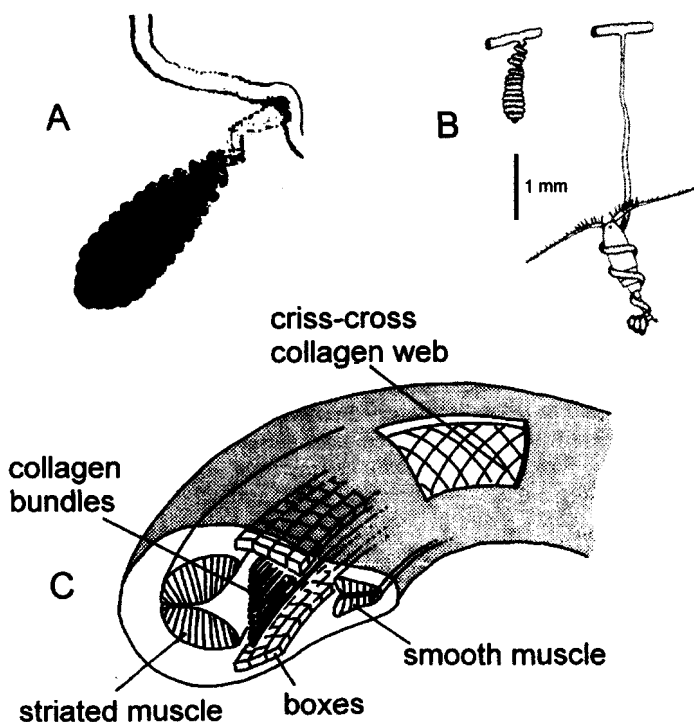
FIGURE 2 *Euplokamis* anatomy (from Mackie *et al.*, 1988): A. photo of tentillum prior to discharge; B. tentillum before discharge and after ensnaring a copepod; C. simplified model of a coiled, relaxed tentillum to show major histological components.

array of collagen bundles, which would store strain energy like a spring. There is also a criss-cross web of collagen fibres below the epidermis resembling similar collagen sheaths that serve for shape maintenance in other animals (Wainwright *et al.*, 1976). Longitudinal smooth muscles on the inner curve of the tentillum probably assist recoiling, and help to maintain the coiled state tonically. A second set of smooth muscle cells (not figured) that lie in the space between the two striated muscle blocs may antagonize the first (Mackie *et al.*, 1988).

In life, when the ctenophore is fishing for food with its tentacles extended, the tentilla can be seen to perform writhing movements, uncoiling slightly (revealing bright red pigmentation) and then recoiling, probably due to alternating contractions in the two sets of smooth muscle. The movements, which occur rhythmically, are rather like the wriggling of a small planktonic polychaete, and might have evolved as a lure attracting fish larvae into the vicinity of the tentacle ("aggressive mimicry": Purcell, 1980).

Considered as an organ, the tentillum is remarkable not just for the variety of tissues brought together and behaviourally integrated in the common task of food capture, but for the high state of differentiation of the tissues themselves. This is the only known example of striated muscle in a ctenophore. It must have evolved *de novo*, but the appearance and packing ratios of the thick and thin filaments are typical of the tissue as seen in other animals, as are the Z-disc specializations, large mitochondria and subsarcolemmal cisternal network. The enormous ($< 2.0\,\mu m$ diam) collagen bundles of the central lamina show a clear and regular 52 nm banding pattern, rarely if ever visible in natural collagen in other ctenophores. The nerve bundles supplying the striated muscles contain some exceptional large axons, presumably serving as fast conduction pathways and reducing response latency. As one of the most complex coelenterate organs, this tentillum surely merits closer investigation.

2. The Erupting Nematocyst Batteries of *Nanomia* and Other Siphonophores

All cnidarians have nematocysts which discharge threads into or around their prey, but in siphonophores, thousands of nematocysts of several different sorts are organized into batteries (Fig. 3A), complex organs that themselves erupt explosively during food capture. The batteries are attached to the tentacle by a muscular pedicel and have a retractile terminal filament equipped with its own arsenal of highly specialized nematocysts. In *Nanomia*, there is also a hood, or involucrum, partially covering the battery (Fig. 4A). The battery is constructed around a central axis containing a gastrovascular canal, longitudinal muscle band and associated nerves (Fig. 4B). Coiled around this is the cnidoband which bears some 4500 nematocysts – stenoteles, microbasic mastigophores and homotrichous anisorhizas (Purcell, 1984). The mesogloea is differentiated into a long, looped "elastic strand" whose ascending branch runs immediately beneath the cnidoband, to which it is firmly attached.

No nautigo?hor

Leuckart (1854) and Chun (1891) agree that prey must first be snagged by the terminal filament before the battery can be set off. The frantically struggling copepod is then pulled up by contraction of the terminal filament and brought into contact with the cnidoband, which triggers eruption of the battery. During eruption, the spongy, ectodermal tissue connecting the ascending portion of the elastic strand with the cnidoband tears, allowing the cnidoband to flick out sideways (Fig. 3B), whereupon the nematocysts
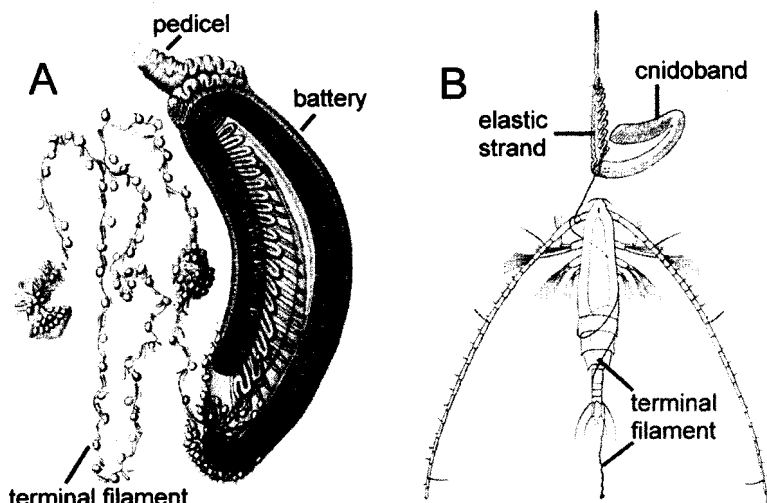
FIGURE 3 Nematocyst battery of *Stephanophyes* (after Chun, 1891): A. detail of undischarged battery; B. battery in process of eruption, with copepod ensnared in the terminal filament. The cnidoband has separated from the elastic strand but has not yet discharged its nematocysts.
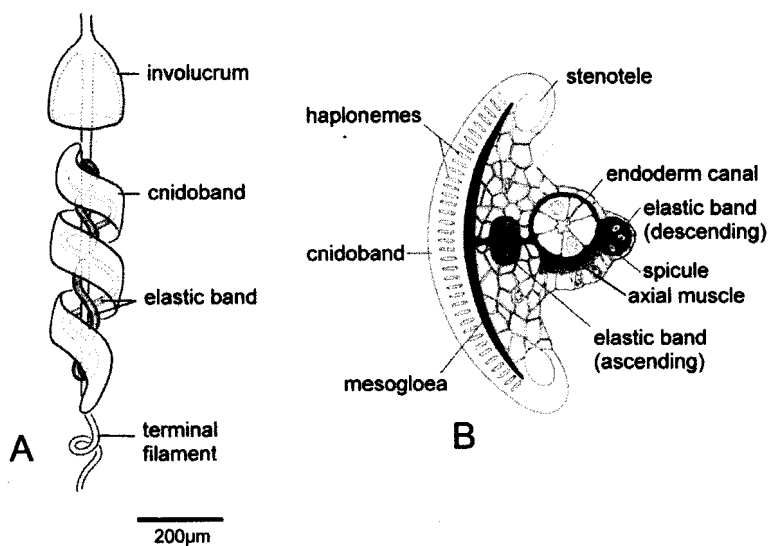

FIGURE 4 Nematocyst battery of *Nanomia* (after Mackie and Marx, 1988): A. battery stretched out slightly to show internal structure; B. diagrammatic cross-section through an intact battery, based on electron microscopy.

discharge into the prey. It is not known precisely where the force for eruption comes from but eruption is rapid, violent and irreversible and the prey ends up harpooned or lassooed by hundreds of nematocysts with little hope of escape. The process as described in *Nanomia* agrees in most respects with Chun's account for *Stephanophyes*, but in *Nanomia* the cnidoband is coiled around the axis prior to eruption, uncoiling during discharge, and the ascending arm of the elastic strand tends to separate from its attachment point under the involucrum instead of staying attached (Mackie and Marx, 1988). In either case, the elasticity of the strand evidently provides some slack in the system and reduces the chances of the prey jerking itself loose. A final touch is provided by a row of spicules with hooks that project from the surface of the elastic strand and hold it directly to the prey's bristles following eruption.

Here then, we have an organ built up of nerves, muscles, friable ectoderm, specialized, elastic, extracellular matrix components, hooked spicules, three sorts of cnidocytes and their nematocysts all arranged around a central axis and designed to explode on appropriate stimulation.

The fishing behaviour of *Nanomia bijuga* has been observed from a ROV in Monterey Bay by Bruce Robison (personal communication). The siphonophore swims for a certain distance then stops, using the momentum from swimming to extend its tentacles. After a while, the tentacular net starts to collapse under its own weight and if no prey are caught the siphonophore pulls in its tentacles and batteries and moves off, swimming for 5–10 min before deploying them again. Even a small *Nanomia* 15 cm long would have about 10 tentacles, each with some 12 nematocyst batteries, giving it a total of about 120 batteries. Large specimens of *Nanomia cara* observed from a submersible in the Gulf of Maine had up to 80 tentacles (Marsh Youngbluth, personal communication). Assuming 15–20 batteries per tentacle (Purcell, 1984) we arrive at a figure of 1200–1600 batteries with a total of 5–7 million nematocysts per siphonophore. Fully deployed, the batteries would be spread out on all sides around the axis of the siphonophore by fishing filaments having a combined length of 3–4 m. Given that *N. cara* can occur at high densities in these waters, up to 8 colonies per cubic metre (Rogers *et al.*, 1978), it would be lucky *Calanus finmarchicus* (the preferred food) that escaped capture. The importance of physonectid siphonophores in marine ecosystems has yet to be properly assessed but it is clear that they are major midwater predators, "a living net stretched across the worlds oceans" (Voronina, 1964). Several groups of workers using submersibles and ROVs are currently attempting to determine their ecological significance more precisely.

Erupting batteries occur in many shapes and forms in other siphono-
phores, one of the most intriguing variations being seen in *Lynchnagalma*
utricularia, which has flotational bladders at the tips of the batteries (Claus,
1879). Together, the bladders buoy up the whole tentacle (Fig. 5), letting it
float out laterally instead of sinking slowly, as happens with *Nanomia*. It
would be interesting to know if *Lynchnagalma* swims as frequently as
Nanomia when fishing. Theoretically it could stay suspended in one spot
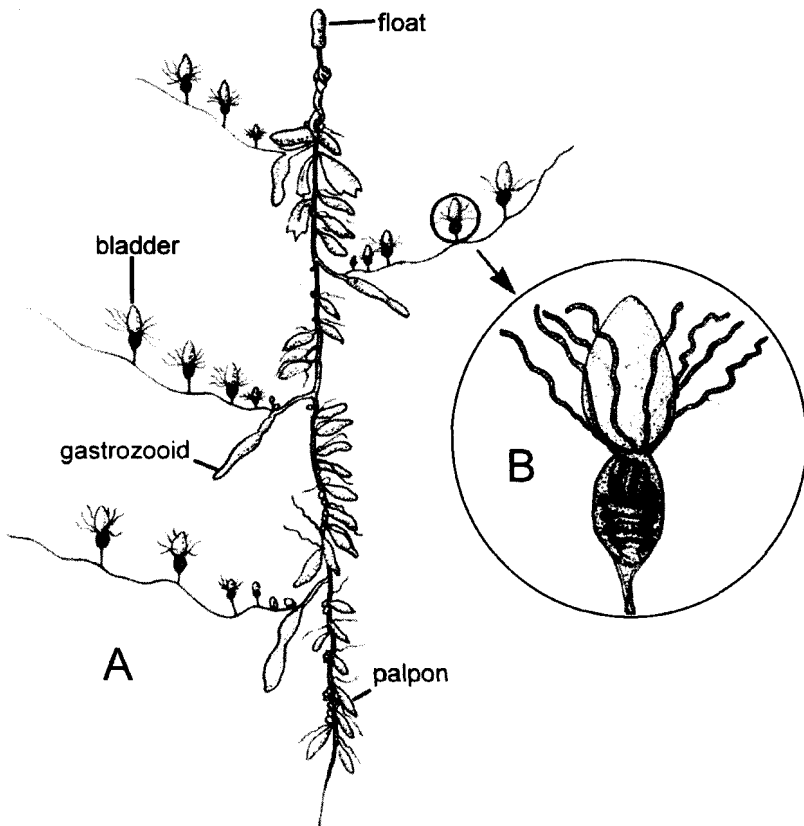indefinitely.

FIGURE 5   *Lynchnagalma (Agalmopsis) utricularia* (from Claus, 1879): A. Top part of the
colony showing the tentacles supported by flotational bladders associated with the nematocyst
batteries. The specimen has lost its nectophores, which should form a double column below
the float; B. battery enlarged.

3. Cubomedusan Eyes and the Existence of God

Cubomedusae have four rhopalia each containing a statolith and one or more eyes or ocelli (Mayer, 1910). Species of *Tripedalia* and *Carybdea* used in recent anatomical studies have six eyes per rhopalium, four simple ocelli and two complex eyes. The larger of these faces inward, which might lead one to think that it has no role in sensing the environment outside the jellyfish, but Hartwick (1991) points out that the rhopalial stalk is muscular and can direct the rhopalium outwards as well as inwards. The complex eyes resemble the camera eyes of vertebrates and squid (Nilsson, 1990) having a cornea, a lens and a retina (Fig. 6A and B). There appears to be no vitreous body and the lens lies directly against the retina, separated from it only by a narrow, acellular layer ("capsule"). The lens resembles that of vertebrates in being a biconvex, cellular structure with little extracellular space and few cytoplasmic organelles. The lens proteins (crystallins) are very different from those of vertebrates or squid (Piatigorsky *et al.*, 1989), a finding consistent with the idea that these eyes had an independent evolutionary origin. There are roughly 11,000 cells in the retina (Berger, 1900; Pearse and Pearse, 1978) falling into three types, all of them ciliated, primary photoreceptors (Laska and Hündgen, 1982); one of these (Type I) presumably corresponds to the cell type whose pigment-containing outer segment abuts on the lens capsule (Fig. 6B). The distribution of pigment is reported to vary according to whether the eye is fixed in the dark or in the light, suggesting an ability to
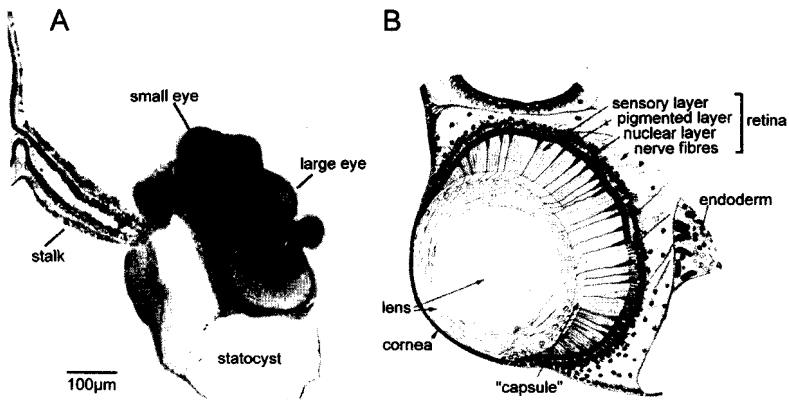

FIGURE 6   Cubomedusan eye structure: A. Histological section through a rhopalium of *Tripedalia cystophora* showing the two complex eyes (after Piatigorsky *et al.* 1989); B. drawing of the eye in section. Part of the pigmented zone is drawn without pigment to show the bases of the processes that extend through the retina up to the edge of the lens (after Berger (1900) from Pearse and Pearse (1978)).

adapt to ambient light intensity (Berger, 1900). Though proof is lacking, it seems probable that the eye is optically capable of forming an image. The lens is a type of Matthiessen lens, having a high refractive index in the centre, falling off towards the periphery (Page, 1997). This would give it a short focal length (a necessary feature, in view of the proximity of the lens to the retina) without excessive spherical aberration (Land, 1990).

Matsumoto (1995) reviews available evidence on the visual capabilities of various cubomedusae. The animals show a clear ability to distinguish light and dark objects. *Carybdea rastonii* will swim toward white objects 1 cm wide and away from dark ones (Matsumoto, 1995). *Chironex fleckeri* can reliably distinguish objects 1 cm wide up to 50 cm away, and some individuals appear able to resolve objects 0.5 cm wide (Hamner *et al.*, 1995). Viewing various sized grids directly through the isolated lens suggests an ability to resolve down to 0.1 mm (G.I. Matsumoto and D.-E. Nilsson, personal communication). *C. sivickisi*, which has attachment pads on its exumbrellar surface, appears to use vision in selecting objects to attach to (Hartwick, 1991). Barnes (1966) found that cubomedusae could detect a lighted match five feet away at night, and turn toward it, which raises the possibility that the medusae may use their eyes to detect bioluminescent objects in the dark (Pearse and Pearse, 1978; Page, 1997). Passano (1982) writes "In my experience *Tripedalia* is almost as elusive as a fish or shrimp when you attempt to catch it with a hand net which casts a shadow or creates turbulence in the water".

An eye would make little sense on its own without the neural circuitry needed to process visual data, and some authors have questioned whether cubomedusae have sufficiently advanced nervous systems to make proper use of the input from their relatively sophisticated eyes (Nilsson and Pelger, 1994; Gerhart and Kirschner, 1997). In a review of the latter work, Slack (1997) writes: "*Tripedalia*, apparently, has image-forming eyes but no central nervous system to process or interpret the image. Creationists used to tell us that the image-forming eye could not possibly have evolved by chance because of all the coordinated changes that would simultaneously have been required in the brain. So I am left unsure whether *Tripedalia* represents real evidence against the existence of God ...".

It is one thing to doubt the existence of God, quite another to doubt the efficiency of the cnidarian nervous system. Such doubts stem from misconceptions about the nervous architecture in these animals. Unlike bilaterally symmetrical animals which have a head containing the major sense organs and brain, jellyfish have a radial symmetry and their sense organs and nerve centres are distributed symmetrically around the periphery.

Cubomedusae have four major rhopalial nerve centres interconnected by marginal nerve bundles containing hundreds of units of several sorts (Satterlie, 1979; Laska and Hündgen, 1982). Such a system is no less centralized than that of a worm and the fact that there is not one dominant centre but four is simply "a reflection of the evolutionary constraints imposed on animals having radial symmetry" (Satterlie and Spencer, 1987).

Details of the neural architecture are reviewed by Passano (1982). In addition to the four rhopalial ganglia, where swimming patterns are generated, there are pedal ganglia located at the bases of the four pedalia, from which nerves run to the tentacles. The tentacles and pedalia all around the margin show coordinated contractions. Nerves run radially from the rhopalial ganglia up toward the manubrium and down into the rhopalia. A network of large motor neurons spreads swimming impulses across the subumbrellar muscle sheet and circularly around the nerve ring, coordinating the four swimming centres. Components of this action system have been investigated electrophysiologically, showing that at the cellular level cubomedusae function in a conventional manner, with all-or-none action potentials in the neurons, graded, facilitating muscle responses and excitatory synaptic transmission (Satterlie and Spencer, 1979; 1987; Satterlie, 1979).

Recordings from the rhopalia show not only the motor impulses associated with swimming but another type of impulse sometimes associated with tentacle movements and sometimes occurring without any correlated behaviour (Passano, 1982). Both pulse types are affected by photic stimulation. It seems probable that there are at least three distinct nervous sub-systems in Cubomedusae: the large-fibre system coordinating swimming, a fine-fibre system running in the nerve ring that coordinates the pedalia and tentacles and a diffuse system of fine fibres analogous to the diffuse nerve net of scyphomedusae. Of these, it is the second system that receives input from the rhopalial sensory organs and is used "for the finer control of orientation and behaviour which seems to set the Cubozoa apart from other coelenterates" (Passano, 1982).

As with many cnidarians, the technical difficulty of recording from the very small units comprising the bulk of the neuronal population has frustrated attempts to analyse complex behaviour in terms of the underlying circuitry, and the ganglia of cubomedusae remain something of a 'black box'. In other medusae however, where it has been possible to explore the circuitry in more detail, studies have shown beyond any doubt that cnidarian nervous systems can be exceedingly complex. In *Aglantha* for example, some nine discrete, closely interacting, neuronal sub-systems are involved in

control of swimming and associated tentacle movements (Mackie and Meech, 1995; and unpublished). Yet this animal has no ganglia at all, merely bundles of neurons running circularly in the nerve ring with branches running radially up the subumbrella and down the tentacles! The cubomedusan nervous system may be a 'black box' at present but sooner or later (God willing) it will surely be found to have all the circuitry needed to process the information coming in from those beady little eyes.

4. T.H. Huxley and the Polyorgan Debate

Siphonophores, like other animal colonies, can be viewed either as assemblages of individual 'members' (the polyperson theory) or as individual organisms in their own right whose parts are, functionally speaking, equivalent to organs (the polyorgan theory). T.H. Huxley was an early advocate of the polyorgan concept, defining an individual as the sum of the products of a single ovum. In an essay "Upon Animal Individuality" (cited by Reid, 1997) he wrote "A whole tree of Sertularia, a Pennatula, a Pyrosoma, a mass of Botrylli, must no longer be considered as an aggregation of individuals, but as an individual developed into many zooids". The fact that the zooids sometimes detach and lead a free life did not alter Huxley's belief in the transcendancy of the egg-individual. Today we use the term 'clone' for the separated products of a single ovum and 'colony' for cases where the products stay attached. For many ecologists the primary object of interest, as the unit upon which selection works, is the clone or colony rather than the 'individual' zooid. Botanists distinguish the 'genet' (genetic individual) from asexually budded 'ramets'. Thus, a mountain valley may contain hundreds of poplar trees which are all ramets belonging to a single genet. Likewise, the zooids in animal clones and colonies are merely expressions of an iterative growth process, the modules by which the genet expands in time and space. In highly developed polymorphic colonies like siphonophores the zooids not only remain attached but form parts of a linear organism with a front and a back end and a high degree of determinacy of form. Production of new zooids is restricted to specific budding zones. Nerves interconnect the zooids, and certain activities are coordinated on a colony-wide basis. The zooids themselves are specialized in a number of ways, e.g. for locomotion, feeding or sexual reproduction acting, in effect, as organs belonging to a single individual (reviewed by Mackie, 1986; Mackie et al., 1987).

While some parts of siphonophores are of uncertain derivation, others are clearly zooids of either polypoid or medusoid origin. Nectophores

for example, show typically medusan development and retain obvious medusan features: gelatinous mesogloea, marginal nerve rings, striated muscle arranged circularly in the subumbrella, radial and circular gastro-vascular canals etc., but they have no mouth or gonads and do not feed or produce sex cells. They are fed through canals connecting them to the stem of the colony and their swimming provides the propulsive force for the whole colony. Some siphonophores can even switch from swimming forwards to swimming backwards by simultaneously adjusting the angle at which the water jets are emitted from the velar openings of the necto-phores. Clearly, despite their phylogenetic derivation from medusae, necto-phores are functionally the locomotory organs of a single, well-integrated individual.

Other parts of the siphonophore like the float ("pneumatophore") are of less obvious derivation. The float develops from an invagination of the body wall but there the resemblance to medusogenesis ends, for there is nothing in later development or in the adult structure to suggest a medusoid derivation. It seems best to regard it as a neomorphic structure, a component of the primary individual derived from the egg, produced early in larval develop-ment for purposes of flotation. As such it clearly qualifies for organ status. Its contains a gas gland that secretes carbon monoxide. The gas is stored in a chitin-lined inner compartment. In forms like *Nanomia*, a valve at the tip of the float serves for emission of excess gas, expelled by peristaltic move-ments of the muscular outer wall of the float (Jacobs, 1937). In the surface-living *Physalia* the float is enormous, and carries an erectile crest which serves as a sail in windy conditions. The float then qualifies as an organ in the narrow classical sense, while nectophores and other secondarily budded, highly specialized zooids, should be called something else, perhaps 'zooid-derived organs'.

The various parts of a siphonophore can now be categorized as (a) the persistent, elongated body of the primary egg-individual (the central stem of the colony with its budding zones for secondary zooids) (b) secondary zooids budded from the stem of which the gonophores and nectophores are of medusoid origin, and the gastrozooids, palpons and bracts of polypoid origin (Totton, 1965). Tentacles in siphonophores are best regarded not as separate zooids ("dactylozooids") but as parts of either gastrozooids or palpons, just as the tentacles of hydra are parts of the hydra. Organs can develop anywhere within this assemblage. The float is an organ developed in the primary egg-individual, while nematocyst batteries are organs developed within secondary zooids which may themselves (in the functional sense) be considered as organs of zooid derivation.

CONCLUSIONS

Coelenterates have two ways of making organs: creating them as parts of individuals, and converting whole zooids into organs in colonies, as seen most strikingly among the Siphonophora. Organs frequently function in relation to feeding, digestion, locomotion and sensory perception. The lack of a true mesoderm may restrict the ability to make organs but certainly does not preclude it, and remarkably complex organs have evolved in some diploblastic animals. There is no reason to suppose that the alleged simplicity or primitiveness of the coelenterate nervous system was ever a limiting factor in organ evolution. The presence of multiple, distributed nerve centres rather than a single brain in medusae is compatible with advanced neural circuitry.

Acknowledgements

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