

Biology of neglected groups: Cnidaria / Biologie des groupes négligés : Cnidaria

What's new in cnidarian biology?

G.O. Mackie

Abstract: This introduction to the following collection of eight review articles on aspects of cnidarian biology looks at reasons why people study these animals, their economic importance, and their conceptual interest as highlighted in the reviews.

Résumé : Dans notre présentation de huit articles de synthèse sur divers aspects de la biologie des cnidaires, nous examinons les raisons qui poussent certains chercheurs à étudier ces animaux et nous soulignons l'importance économique et l'intérêt conceptuel des cnidaires, tels que démontrés dans ces articles.

[Traduit par la Rédaction]

Why do people study Cnidaria? How do they get interested in them? There must be almost as many answers to these questions as there are workers in the field. In my own case for what it's worth I had four reasons for picking siphonophores for my doctoral thesis. (1) I needed a project on a marine animal in order to apply for a postgraduate scholarship to work at Naples. (2) I came across a statement by Libbie Hyman to the effect that she had seen *Halistemma* "dart about vigorously, often executing loop-the-loop curves" (Hyman 1940). How could a "colony" of dozens of different "persons" swim in a coordinated manner? (3) When, amazingly, I got the scholarship and went to Naples, I was smitten with the sheer, weird beauty of these extraordinary animals and (4) whether I recognized it then or not, I was influenced as a student by my contacts with A.C. Hardy. Hardy had invented the continuous plankton recorder. He was a kind and thoughtful man, but an unusual lecturer. It was hard at first to take him seriously. He got so excited it was almost impossible to follow what he was saying. He spluttered and pranced and gesticulated. We made fun of him, but the message came through that marine animals were fascinating and marine ecosystems important. His enthusiasm shines through in his books (e.g., Hardy 1956, 1967).

So there were all these separate strands, some of which may be reflected in the experience of other researchers: cnidarians are weird and beautiful creatures; they are important in the sea and relevant to human affairs; they present interesting conceptual problems, not least because of the key position they occupy in the evolutionary tree.

Beautiful, deadly predators

In his preface to the proceedings of the Fifth International Conference on Coelenterate Biology, R.B. Williams writes:

"it is impossible to separate aesthetic and scientific interests in these animals. They are among the most beautiful of any, rivalling all others in their graceful forms and often vivid colours" (Williams et al. 1991). When I started teaching about invertebrates in Alberta, I was almost at my wits' end trying to convey to the students some impression of what cnidarians really look like. I could show them Hardy's vivid water colours in *The Open Sea* or Carl Chun's lithographs of siphonophores from the Canary islands (e.g., Chun 1891), surely the best of any 19th century representations of marine plankton, or Ilona Richter's superb illustrations of medusae for the *Flora and Fauna of the Gulf of Naples* (Brinkmann-Voss 1970), but it was hard for the students to reconcile these images with the leathery and shrunken preserved objects that were the only hands-on material available to them.

Things are better now. There are many Web pages showing colour photographs of cnidarians as they really look. There are numerous TV documentaries on coral reefs and intertidal life. The public has discovered cnidarians. At the Monterey Bay Aquarium the moon jelly exhibit is one of the most popular of all the displays. The availability of manned submersibles and ROVs has brought a new awareness of the importance of gelatinous predators in the deep sea. The TV documentary *Ocean Drifters* (National Geographic Society, 1993), filmed by Edith Widder in the Gulf of Maine, is only one of many enthralling videos on marine plankton and it well deserved its Emmy award.

What makes these animals so interesting, however, is not just their aesthetic appeal but the fact that they are also deadly predators. Voronina (1964) called siphonophores "a living net stretched across the world's oceans". I only realized how true this was when I dived with Claudia Mills in the submersible *Pisces IV* in the waters around Vancouver Island and saw *Nanomia* and *Cordagalma* in their natural

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habitat. Bruce Robison's videos from Monterey Bay show the same thing: swarms of siphonophores with their extended tentillae almost touching one another. A single *Nanomia* may have as many as 5–7 million nematocysts deployed in batteries on fishing filaments having a combined length of 3–4 m (Mackie 1999). In the Gulf of Maine there can be up to 8 colonies/m³ (Rogers et al. 1978). Bad news for the local copepods!

Cnidaria and *Homo sapiens*

Of major concern at the present time is the deterioration of coral reefs around the world. Coral bleaching (loss of zooxanthellae) has been on the increase for some 20 years. In the nutrient-poor waters where they live, bleached corals eventually die if they fail to regain their symbionts. Human activities certainly play a part in reef decline, directly through overfishing, increased sedimentation, and nutrient overloading and probably indirectly through global warming. An increase of 1 or 2°C in water temperature can bring about bleaching. Increased solar irradiance in the ultraviolet (UV) range may also play a part.

Loss of reef biodiversity is serious for many reasons, but one that should not be overlooked is the value of Cnidaria as potential sources of biopharmaceuticals. Many soft corals produce antifouling or antibiotic agents, some of which are of interest to drug companies. A Caribbean gorgonian produces a compound that reduces skin inflammation and is marketed for cosmetic purposes. Sea anemones produce a whole range of toxins, some of which have specific effects on neuronal sodium and potassium channels and are of considerable interest to neurobiologists. They also have therapeutic uses. One recent report describes the use of a compound (ShK) derived from the toxin of a Caribbean sea anemone that has potential for treatment of multiple sclerosis (Beeton et al. 2001).

Many jellyfish justly deserve their evil reputation as stingers. There have been roughly 100 deaths due to *Chironex fleckeri* stings during the past 100 years in North Australian waters. Disturbed by the increase in *Chrysaora* in Chesapeake Bay in the late 1960s, the United States Congress passed "The Jellyfish Act", aimed at regulating jellyfish populations. The resulting funding generated much new knowledge of jellyfish biology, even though the hoped-for control methods failed to materialize. A recent meeting on jellyfish blooms attracted 70 scientists from 13 different countries (Purcell et al. 2001).

There are many other areas where the activities of humans impact on Cnidaria, and vice versa. In some cases both sides suffer, as when the electricity grid in the northern Philippines collapsed on 8 December 1999. Jellyfish were apparently sucked into the water-cooling system of the central power station, closing it down and blacking out a huge area. Fifty truckloads of the offending cnidarians had to be removed from the clogged ducts. President Estrada went on TV to explain that the blackout (unlike previous power outages) was not due to a military coup and did not represent "an attempt to destabilize the government". According to press reports, the jellyfish congregated inshore because they sensed that an earthquake was imminent. The night after the

blackout there was indeed an earthquake measuring 6.8 on the Richter scale!

Conceptually interesting animals

The articles in this issue of the *Canadian Journal of Zoology* will go a long way toward satisfying the need for authoritative updates in several important areas of cnidarian biology. While the articles by no means cover the whole gamut of current research on the group, they have been selected for topicality and conceptual interest.

Nematocysts are the cnidarians' secret weapon. They have enabled the group to achieve enormous success as predators with little of the investment in elaborate sensory and morphological specialization that characterizes most predators. Thus, cnidarians have prevailed despite their exceedingly simple basic body plan. In a sense, they are "little more than a gut with tentacles" (Kass-Simon and Scappaticci 2002).

Nematocysts are probably the most complex secretion products of single cells to be found anywhere in the animal kingdom. Kass-Simon and Scappaticci (2002) touch briefly on their morphology, but focus chiefly on dynamic aspects of nematocyst biology where, despite major advances in recent years, much remains to be explained: how and when do nematocytes become programmed to produce specific nematocysts during their differentiation from interstitial (stem) cells? What triggers the extraordinary process whereby the future, dischargeable filament inverts and coils up inside the developing nematocyst capsule? What substrate cues guide migrating nematocytes to their destinations, and how do they co-assemble with other types into complex batteries? The mechanism of discharge and the chemical modulation of discharge thresholds continue to present challenging problems despite striking recent progress. It has become increasingly clear that some nematocytes are not independent effectors as was once supposed. Their discharge thresholds can clearly be affected by events in surrounding nervous and non-nervous cells. At the same time, certain nematocytes are found in places where there are no nerves or excitable epithelia, and they may be truly independent in the way that G.H. Parker originally proposed.

As the concept of cnidarians as loosely coordinated assemblages of semi-autonomous action systems and independent effectors has faded, the realization has grown that they are well-coordinated animals with surprisingly sophisticated, and often centralized, nervous systems. Swimming in jellyfish is long overdue for the type of comprehensive, comparative survey that Richard Satterlie provides (Satterlie 2002). It sometimes seems that workers in this field, like shipworms or bark beetles, are burrowing away into the same substrate, but their tunnels never meet. The deeper and more intricate the tunnels become, the harder they are for outsiders to penetrate. How does the saying go?—the *Polyorchis* people speak only to the *Aglantha* people, and the *Aglantha* people speak only to God. Here, thankfully, is a modern synthesis by someone who knows all three classes of medusae intimately and can compare and contrast them in terms of fundamental mechanisms. Satterlie (2002) makes very clear that cubomedusae, despite a superficial resemblance to hydromedusae, are neurologically speaking little more than aberrant scyphomedusae. This is bound to resurrect the old debate about

whether or not Cubozoa deserve to be placed in a separate class (Werner 1973). I am not convinced that they are more different from Scyphozoa than, for example, the Rhopalonematidae are from other Hydromedusae. Molecular genetics will give us some answers, probably sooner rather than later.

Nervous centralization may be most obvious in medusan nerve rings, where as many as 14 physiologically distinct neuronal subsystems have been identified in one jellyfish (*Aglantha*), but it is also apparent in hydra, where there is a nerve ring around the hypostome. As noted in the article by Koizumi (2002), the perihypostomal ring contains at least four distinct neuronal subsets, distinguished by immunostaining. Whereas nerves and epithelial cells in other parts of hydra are constantly being displaced toward the extremities, the nerve ring and its surrounding ectoderm are virtually stationary. Addition of new neurons to the nerve ring is much slower than in other regions, foreshadowing the condition in higher animals, where the central nervous system, once formed, is largely static. Koizumi (2002) reviews the highly ingenious experiments devised by hydra workers to explore the factors controlling neural differentiation, such as the introduction of mutant nerve cell lines into hydras from which the original nerves have been removed. Such experiments show that neural differentiation is strongly influenced by peptides of epithelial origin as well as by neuropeptides.

Until fairly recently there was little solid information on cnidarian neurotransmitters, but work over the last 15 years carried out in the laboratories of Peter Anderson, Andrew Spencer, and, above all, Michel Anciaux has provided substantial evidence pointing to the presence and biological activity of taurine, dopamine, adrenalin, noradrenalin, serotonin, and melatonin in cnidarian nervous systems. In a few cases receptor sites have been localized and, using the polymerase chain reaction, genes coding for G protein-coupled aminergic receptors have now been cloned and sequenced in *Renilla* (Michel Anciaux, Université de Montréal, personal communication). Despite the paucity of information on “fast” transmitters, there is physiological evidence that they exist in *Aglantha*, where synaptic delays of as little as 0.7 ms have been recorded. In parallel with this work on amino acids and biogenic amines, impressive progress has been made on neuropeptides, reviewed here by Grimmelikhuijzen et al. (2002). Some 35 neuropeptides have been sequenced in cnidarians, some of which function as neurotransmitters or neuro-modulators, while others are neurohormones. They are synthesized as preprohormones sometimes in multiple copies, and processed by enzymes resembling those found in mammals. More than one peptide may be expressed in the same cell. Thus, the basic features of neuropeptide biology were presumably all well established in the stem group from which cnidarians and other metazoans evolved.

Moving from whole nervous systems to specific sense organs, the article by Vicki Martin provides the first comprehensive review of cnidarian photoreceptors (Martin 2002). Some readers will be surprised to see what a lot of research has been done on the subject. Martin gives special attention to cubomedusae such as *Carybdea*, which have “camera” eyes equipped with a cornea and lens and a retina containing some 11 000 cells. Some of the cells contain screening pigments that migrate in response to changing light conditions.

Immunostaining with antisera raised against various zebra fish opsins has allowed Martin and her co-workers to identify retinal photoreceptors in *Carybdea* that are presumably sensitive in the blue, green, and UV wavebands. Accounts of cubomedusan behaviour leave little doubt that these animals can “see” in the sense that they can form an image on their retinas and process it neurally, despite their lack of a single, dominant, ganglionic nerve centre. The presence of definitive visual organs in some medusae should not obscure the fact that many cnidarians that lack ocelli show behavioural or physiological evidence of being light-sensitive. Very little is known about the mechanisms involved, and new work is badly needed. Martin’s review usefully covers many of these cases of extraocular photoreceptivity.

The long-held belief, reiterated in innumerable grant applications, that cnidarians represent the ancestral state from which higher animals evolved has been fortified by the discovery of sets of genes in hydra that are homologous with those of bilateral metazoans. Most of the 80 genes so far isolated and characterized in hydra, including key developmental genes responsible for patterning, fall into this category. Faced with this evidence of conservation, Bosch and Khalturin (2002) raise an interesting question: is hydra just another fly? The work they review attempts to determine whether hydra has evolved its own unique set of control genes that have no homologies with those of higher animals. Unbiased searching has led to the identification of a number of genes essential for axial patterning and differentiation that are novel and unique to hydra. Thus, evolution has not been quite as “unadventurous” as is sometimes suggested. To the extent that hydra is “just another fly”, it may have to be seen as an upside-down fly, for expression of *Otx* and other genes strongly suggests that hydra attaches to the substrate by a region which corresponds to the head end in bilaterians, the “trunk” being represented in hydra by the hypostome (Meinhardt 2002).

As a model system for studying cellular differentiation, hydra has always led the field by an enormous margin. No other cnidarian comes close, yet many other species would probably serve as well, and typify the phylum better. In the area of metamorphosis, the hydroid *Hydractinia* provides an excellent model (Müller and Leitz 2002). Reviewers often have to decide how to reconcile the need for comprehensiveness with the need for focus in reasonable depth. Those authors solve this problem by providing interesting case studies, on settlement specificity for instance, drawing on work on medusae, hydroids, corals, and sea anemones, and then look at *Hydractinia* in particular detail. This approach allows good in-depth coverage of exciting new work on GLWamide neuropeptides, which, in *Hydractinia*, appear to be transported in the axons of sensory neurons located at the anterior pole as the “message” that triggers metamorphic changes in the posterior part of the larval body. The authors then take a look at alternative signalling mechanisms such as the propagated calcium transients discovered by Freeman and Ridgway (1990) in other hydrozoan species. The review includes a summary of work on allorecognition and elimination of competitors that stems from findings by W.A. Müller in the 1960s and has attracted considerable attention since. The costs and benefits of aggregation are analysed and here, too, the work on *Hydractinia* is of special importance.

In the area of reproductive biology and its evolutionary implications, sea anemones and corals are preeminent and Daphne Fautin's review focuses largely on them (Fautin 2002). Cnidarians reproduce both sexually and asexually, and the products of the two processes are not always easily distinguishable, such as when dealing with "planulae", which may be conventional or sexual larvae or vegetative propagules. Asexual reproduction can occur by transverse or longitudinal fission, fragmentation, pedal laceration, polyp bail-out in colonies, production of stolons, and possibly by amictic parthenogenesis, to name only some of the processes covered in this thoughtful review. We are dealing with animals "in which sexual reproduction may not be paramount, that during one lifetime may pass through two or more distinct phases differing radically in morphology and ecology, that may hybridize, that potentially are extremely long-lived, and that may transmit through both sexual and asexual reproduction mutations arising in somatic tissue" (Fautin 2002)

Not only is the border between sexual and asexual reproduction faint but it may not matter, in the sense that evolutionary diversification can proceed on the basis of either. Assumptions about the centrality of sexual reproduction in the evolution of this group, imported from studies on higher animals, need to be looked at very carefully; more precise, quantitative information on the occurrence of both sexual and asexual processes is needed.

Related themes are explored by Frank and Mokady (2002) in their review of coral biodiversity and evolution, a field that is being transformed by molecular approaches. How can we distinguish sibling species from morphotypes or incipient species? If there is evidence of reproductive isolation, how is it achieved and maintained? How can we distinguish clone mates from non-clone mates? If corals fuse, does this mean that they are clone mates, or merely immunocompatible? Biochemical and genetic techniques are increasingly being used in addressing such questions. Like Fautin (2002), these authors give special attention to hybridization. If two genetically different forms can hybridize, the Darwinian "tree of life" must have some anastomosing branches, giving it a reticular form. Reticulate evolution in corals (Veron 1995) is receiving increasing support. Simultaneous mass spawnings by many coral species in some reefs are well documented. Such episodes would tend to maximize opportunities for hybridization. Laboratory studies have shown that interspecific fertilization can take place. Here, too, molecular genetic techniques are proving crucial.

This is the third collection of reviews dedicated to particular invertebrate groups to be published in the *Canadian Journal of Zoology*. The others were on annelids (February 2001) and echinoderms (July 2001). The present collection maintains the high standard of interesting, scholarly work and the Editors are to be congratulated on their initiative and insight in putting it together.

Mass spawnings of papers

There have now been six International Conferences on Coelenterate Biology, starting in 1965. For a history of the earlier meetings, see my introductory note in Williams et al. (1991). The most recent conference in this series was held in the Netherlands in 1995 (den Hartog 1997). The next will be

held at the University of Kansas in July 2003 (<http://web.nhm.ukans.edu/inverts/iccb/index.html>).

For references to recent publications arising from the International Coral Reef Symposia and meetings of the Hydrozoan Society see the article by Fautin (2002). The next Hydrozoan Society workshop is scheduled for 2003 in Cape Town, South Africa. For news about these events and a general discussion of cnidarian topics see the Cnidaria internet list (<https://maillists.uci.edu/mailman/listinfo/cnidaria>).

References

- Beeton, C., Wulff, H., Barbaria, J., Clot-Faybesse, O., Pennington, M., Bernard, D., Cahalan, M.D., Chandy, K.G., and Béraud, E. 2001. Selective blockade of T lymphocyte K⁺ channels ameliorates experimental autoimmune encephalomyelitis: a model for multiple sclerosis. *Proc. Natl. Acad. Sci. U.S.A.*, **98**: 13942–13947.
- Bosch, T.C.G., and Khalturin, K. 2002. Patterning and cell differentiation in *Hydra*: novel genes and the limits to conservation. *Can. J. Zool.* **80**: 1670–1677.
- Brinkmann-Voss, A. 1970. Anthomedusae/Athecata (Hydrozoa, Cnidaria) of the Mediterranean. Part I. Capitata. *Fauna Flora Golf. Neapel*, **39**: 1–96.
- Chun, C. 1891. Die canarischen Siphonophoren. *Abh. Senckenb. Naturforsch. Ges.* **26**: 553–627.
- den Hartog, J.C. (Editor). 1997. Proceedings of the 6th International Conference on Coelenterate Biology, The Leeuwenhorst, Nordwijkerhout, the Netherlands, 16–21 July 1995. Nationaal Natuurhistorisch Museum, Leiden, the Netherlands.
- Fautin, D. 2002. Reproduction in Cnidaria. *Can. J. Zool.* **80**: 1735–1754.
- Frank, U., and Mokady, O. 2002. Coral biodiversity and evolution: recent molecular contributions. *Can. J. Zool.* **80**: 1723–1734.
- Freeman, G., and Ridgway, E.B. 1990. Cellular and intracellular pathways mediating the metamorphic stimulus in hydrozoan planulae. *Roux's Arch. Dev. Biol.* **199**: 63–79.
- Grimmelikhuijzen, J.P., Williamson, M., and Hansen, G.N. 2002. Neuropeptides in cnidarians. *Can. J. Zool.* **80**: 1690–1702.
- Hardy, A.C. 1956. The open sea: the world of plankton. Collins, London.
- Hardy, A.C. 1967. Great waters. Collins, London.
- Hyman, L.H. 1940. The invertebrates: Protozoa through Ctenophora. McGraw Hill, New York.
- Kass-Simon, G., and Scappaticci, A.A. 2002. The behavioral and developmental physiology of nematocysts. *Can. J. Zool.* **80**: 1772–1794.
- Koizumi, O. 2002. Developmental neurobiology of cnidarians (especially *Hydra*). *Can. J. Zool.* **80**: 1678–1689.
- Mackie, G.O. 1999. Coelenterate organs. *Mar. Freshw. Behav. Physiol.* **32**: 113–127.
- Martin, V.J. 2002. Photoreceptors of cnidarians. *Can. J. Zool.* **80**: 1703–1722.
- Meinhardt, H. 2002. The radial-symmetric hydra and the evolution of the bilateral body plan: an old body became a young brain. *BioEssays*, **24**: 185–191.
- Müller, W.A., and Leitz, T. 2002. Metamorphosis in Cnidaria. *Can. J. Zool.* **80**: 1755–1771.
- Purcell, J.E., Graham, W.M., and Dumont, H.J. (Editors). 2001. Jellyfish blooms: ecological and societal importance. Kluwer Academic Publishers, Dordrecht, the Netherlands.
- Rogers, C.A., Biggs, D.C., and Cooper, R.A. 1978. Aggregation of the siphonophore *Nanomia cara* in the Gulf of Maine: observations from a submersible. *Fish. Bull.* **76**: 281–284.

- Satterlie, R.A. 2002. Neuronal control of swimming in jellyfish: a comparative story. *Can. J. Zool.* **80**: 1654–1669.
- Veron, J.E.N. 1995. Corals in space and time. University of New South Wales Press, Sydney.
- Voronina, N.M. 1964. Macroplankton distribution in the waters of the equatorial currents of the Pacific. *Oceanology*, **4**: 884–895.
- Werner, B. 1973. New investigations on the systematics and evolution of the class Scyphozoa and the phylum Cnidaria. *Publ. Seto Mar. Biol. Lab.* **20**: 35–61.
- Williams, R.B., Cornelius, P.F.S, Hughes, R.G., and Robson, E.A. (Editors). 1991. *Coelenterate biology: recent research on Cnidaria and Ctenophora*. Kluwer Academic Publishers, Dordrecht, the Netherlands.