



The role of Cnidaria in evolution and ecology

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ABSTRACT

The recent setting of specific features of the Cnidaria into evolutionary and ecological frameworks suggests the centrality of this phylum in many fields of the life sciences. From an evolutionary point of view, the Cnidaria, with their diploblastic planulae, might represent the ancestral state of higher Metazoa in the light of a peramorphic origin of animal complexity from a simple, individual organism. Medusan development in the Hydroidomedusae via a medusary nodule, furthermore, implies the formation of a third tissue layer (the muscle layer lining the subumbrellar cavity). Cnidarian polyps are diploblastic, whereas at least some of their medusae are triploblastic: the evolutionary enigma of the passage from a diplo- to a triploblastic organisation takes place every time hydrozoan polyps bud medusae! Cnidarian polyps have also the premises of the skeletal architecture of higher animals: their chitinous or carbonatic skeletons are similar to those of arthropods and vertebrates respectively. From an ecological point of view, the coelenterates probably play roles that are much more important than usually perceived. Both Cnidaria and Ctenophora feed on the eggs and larvae of most benthic, planktonic and nektonic organisms and might be crucial (with a keystone role?) in maintaining biodiversity high, by feeding on potentially monopolising species. The efficiency of gelatinous predators becomes evident during periodic outbreaks of their populations, with serious implications even on fisheries yields, demonstrating that their impact can be higher than ours!

KEY WORDS: Cnidaria - Metazoan evolution - Triploblasty - Keystone role - Gelatinous plankton.

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THE CNIDARIAN CROSSROAD

Metazoan evolution is usually described as being marked by a series of capital events: the origins of animal multicellularity, of tissues, of triploblasty, of coelomic cavities and of bilateral symmetry (see Valentine, 2004 for a recent review). Besides these landmarks, the rest of Metazoa evolution is a series of increases in complexity or of variations on some basic themes. Many changes in the way we look at metazoan relationships changed in recent years (see Valentine, 2004), but the base of the tree remains unchanged: sponges, cnidarians and ctenophores are always at their place, the stem of the whole tree.

Sponges are the living proof of how a protozoan colony can become a metazoan, without reaching a level of organisation involving a recognisable body form, real tissues and a nervous system. The Cnidaria are the first animals with tissue layers, muscles, and sense organs. They lie at the base of the tree because they are diploblastic, have a radial symmetry, and do not have a real brain. Furthermore, they are present in the fossil record since the Precambrian, when the other animals similar to the present ones were absent. The strange creatures of the Precambrian, besides cnidarians, apparently did not pose the foundations of future metazoan organisations, whereas these are evident in the Cnidaria. The Cnidaria are good candidates as the crossroad of metazoan evolution.

Bilateral symmetry

Cnidaria, if considered throughout their life cycle and not as adults only, are not completely radial. They are bilateral, even at the start of their life. The planula has an anterior and a posterior pole and, sometimes, also an up and a down surface, as the tail of some hydrozoan larvae is actively moved along a left and a right axis (Piraino, unpublished observation). Molecular evidence of bilaterality in cnidarians is already available. A localized, asymmetric expression of a dorsalizing gene (*dpp/BMP2/4*) was observed in embryos of the coral *Acropora millepora* (Hayward *et al.*, 2002). More recently, Finnerty (2003) and Finnerty *et al.* (2004) showed that, in the sea anemone *Nematostella vectensis*, *Hox* genes are expressed in a staggered anterior-posterior pattern, and two TGF β genes involved in the dorso-ventral axis formation of Bilateria, *dpp* and *GDF5*-like, also exhibit asymmetric expression along a secondary (dorso-ventral) body axis.

It is not by chance that one of the theories on the origin of the Metazoa is known as "the Planula theory" (von Salvini Plawen, 1978). Moreover, even Haeckel, in his Gastrea theory, imagined an ancestor to the Bilateria that looks much like a planula. Hadzi's (1963) theory of the Plathyhelminth identified in acoelous turbellarians the first representatives of the Metazoa. Nevertheless,

why not bilateral organisms that, by peramorphosis, became either sponges, or polyps or medusae? In his treatise on "Ontogeny and Phylogeny", Gould (1977) invoked pedomorphosis as the motor of evolution, while giving little attention to peramorphosis (the term is not even in the glossary at the end of the book). Maybe, if ontogeny recapitulates phylogeny, the first Metazoa were just planulae (something like the Placozoa of today). By peramorphosis, then, these simple bilateral planula-like organisms might have developed aploblastic (sponges) or diploblastic (cnidarian polyps) organisations, being confined at playing a larval role. Then, by pedomorphosis, the bilateral organisation of these larvae became an adult feature again, and the bilaterian saga began.

Phylogenetic analysis of myosin heavy chain type II (Ruiz-Trillo *et al.*, 2002) supported the basal position of acoels as the extant earliest bilaterians, and it draws renewed attention to the cnidarian planula as a model for the precursor of the Bilateria, which gave rise to an acoel-like organism by progenesis. All theories on the start of Metazoa evolution might well be reconciled while looking at the larvae of the stem groups of the Metazoa. The results of planula development (either as polyp or medusa) are around since more time than any other body organisation in the animal kingdom. Is this because they are primitive or because they are extremely successful? Simplicity is often the secret of success.

Triploblastic Diploblasts

"As a working hypothesis, I suggest that most of the crucial evolutionary ideas, both structural and biochemical, were evolved very early, and, once realized, have, by a sort of "principle of genetic parsimony", never really been discarded even though we may lack, at our present stage of knowledge, either morphological or physiological evidence of a certain features in the life cycle of a given organism today. What has primarily happened is that, where a basic attribute is not expressed, genetic information has been merely shuffled about and put to other use, but remains in the genome of the organism and, under appropriate situations, is ready for utilization -given time to be genetically mobilized, of course." (Dougherty, 1963, p. 2).

The subumbrellar cavity of the hydromedusae is lined by striated muscle. Striated muscle is mesodermic in all organisms. In traditional textbooks, cnidarians have "simple" epithelio-muscular cells, and striated muscle cells are seldom mentioned. Why is this passed under silence? Maybe because this is against the traditional dogma that wants Cnidaria as "simple" animals. Furthermore, textbooks say that the Scyphozoa medusae originate by strobilation, those of the Cubozoa by metamorphosis, and those of the Hydrozoa by budding. The budding of most Hydrozoan medusae, however, is not a form of asexual reproduction in which a morph produces another morph with its same architecture, as the

budding in all other animals. In the Hydroidomedusae (see Bouillon & Boero, 2000), medusae are produced by a process that falls within the domain of embryology, since it implies the formation of a whole set of features that were not present in the former stage.

Coloniality blurs this phenomenon since not all the polyp material transforms into a medusa, but this is an irrelevant detail. In between ectoderm and endoderm a nodule is formed, the medusary nodule (Fig. 1). "In between" means that it is in the middle, between ectoderm and endoderm: it is mesodermic. This third layer cavitates and its wall becomes lined by striated muscle cells. At the end of medusan ontogeny the cavity becomes open and is the propulsory organ of the medusa: the subumbrellar cavity. However, at the beginning of development it is closed. In addition, it remains closed in the species that have fixed gonophores, to become open only during spawning. A third layer that becomes hollow, in other animals, is called a mesoderm that by schizocoely acquires a coelom. Boero *et al.* (1998) proposed this view of cnidarian morphology and, soon, other researchers started to find molecular evidence supporting it, revealing that mesoderm-coding genes in "higher" Metazoa are present also in the Cnidaria (Spring *et al.*, 2000).

Polyps are diploblastic, but medusae are triploblastic! And coelomate, at least during ontogeny. One of the mysteries of Metazoan evolution (the passage from diploblasts to triploblasts) is solved every time a hydro-polyp buds a medusa!

Pilato (1992, 2000) discussed embryonic and larval development and germ cell differentiation in early Metazoans and, following Dawydoff (1928) and Hyman (1940), he regarded the Cnidaria as triploblastic animals. According to his "theory of endoderm as secondary lay-

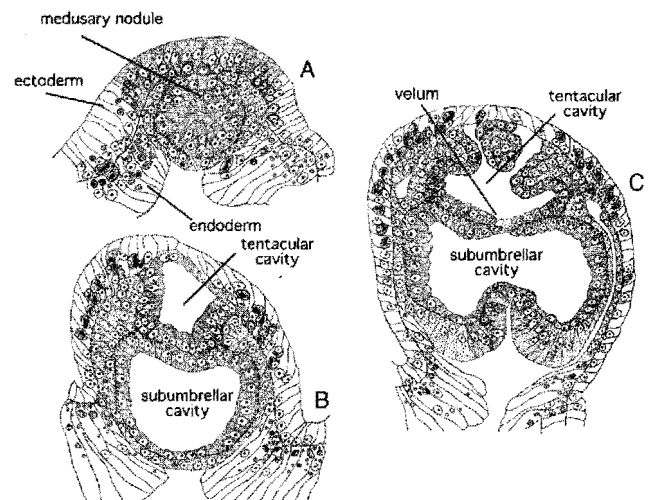


Fig. 1 - Development of a Hydroidomedusan medusa: a medusary nodule originates in between ectoderm and endoderm (A), the cavity of the subumbrella, lined by striated muscle, is formed below the tentacular cavity (B, C) (after Bouillon, 1957).

er" (Pilato, 1992), the endoderm layer is formed during the course of embryonic and larval development, including cnidarian planulae, by secondary differentiation from a true mesenchyme of ectodermal derivation, which migrated inward first to fill the blastula cavity.

From an evolutionary point of view, in the earliest diploblastic ancestor of Metazoans the ectomesenchyme originally played a supportive role to the embryo body wall, without digestive function. It is a fact that there is no sign of digestive cell differentiation within the inner planula layer. The planula has no true mouth, it will develop only after metamorphosis and primary polyp formation. Pilato (2000) suggested that a first group of inner cells differentiates from the internal mass to originate cnidoblasts and interstitial cells. Pilato (2000) also stated that the germ cells of Cnidaria derive from interstitial cells and, thus, cnidoblasts, i-cells and gametes should be considered as mesodermic derivatives. Indeed, early precursors of cnidoblasts in planula larvae develop within the inner mass of cells and their derivation can be hardly considered as ectodermic, even though the final destination of differentiated cnidocytes lies among epidermal cells. However, hydrozoan germ cells can be formed also by de-differentiation and re-differentiation of fully specialized cells of ectoderm, endoderm, or even isolated subumbrellar muscle cells (Schmid, 1992).

Recently, Martindale *et al.* (2004) found that the developmental expression of seven cnidarian genes, whose bilaterian homologs are implicated in mesoderm specification, is mostly located within the endodermal layer. Martindale *et al.* (2004) listed several examples of both developmental (e.g. Martindale & Henry, 1999; Henry *et al.*, 2000) and molecular data (Rodaway & Patient, 2001; Maduro & Rothman, 2002; Stainier, 2002) as additional support to their conclusion that mesoderm of triploblasts must have evolved from endodermal precursors. However, the overall homology of the mesoderm is still questionable. In fact, it is known that most spirals have two sources of mesoderm, ectomesoderm and endomesoderm (Boyer & Henry, 1998) and genes involved in mesoderm specification do not always show the same localization within bilateria: as an example, *twist* (a gene known to be involved in mesoderm formation in all triploblasts) is absent in the endomesoderm of *Patella vulgata*, being localized only in a subset of ectomesodermal cells (Nederbragt *et al.*, 2002).

Pilato (1992, 2000) regarded the cnidarians as triploblastic animals by a re-interpretation of planula development. Boero *et al.* (1998) reached the same conclusion by looking at medusa development and structure. Orthologs of vertebrate mesoderm-marker genes are now repeatedly detected in cnidarians, and their activation often shows a consistent pattern of expression with the formation of medusa structures. Investigations on developmental molecular genetics are going to solve doubts upon the functional homology of genes sharing high sequence similarities between cnidarians and vertebrates. However, the identification of a mesoderm-ho-

mologue layer in Medusozoa does not imply that the origin of triploblasty of Bilateria falls within the Cnidaria. Simply, it may demonstrate that the present representatives of the two taxa share a much closer common ancestor than previously thought.

Analogy or homology?

The coelom, being formed by several developmental patterns, is a polyphyletic structure; this is accepted by almost everybody. But what about mesoderm? And what about striated muscle? Can we think that striated muscle has been invented several times? And, furthermore, what about the coding for these structures? Is it possible that, by chance, body parts with similar structures are independently evolved while being coded by gene sets of similar structure? Recent data have been interpreted to suggest that photoreception might have arisen only once in animal evolution: cnidarian *PaxB* and especially *PaxC* orthologue genes can induce ectopic eyes when expressed in *Drosophila* imaginal discs (see Ball *et al.*, 2004 for a review on the origins of developmental mechanisms). What looks analogous at a morphological level might prove homologous at a molecular level, as suggested by Dougherty (1963).

The evolutionary samba

If the evolution of the Metazoa is a sequence of peramorphosis (two steps ahead), paedomorphosis (one step back) and peramorphosis (two steps ahead), then the evolutionary samba is a sequence of co-options of structures and functions that might be used temporarily in one line and become permanent in other lines, just like a closed body cavity lined by striated muscle. This continuous back and forth blurs the actual relationships among body organisations, and the advent of molecular techniques is a nice way to test even the craziest ideas. Like that of Cnidaria as bilateral and individual in the planula stage, diploblastic and colonial in the polyp stage, and triploblastic and coelomate in the medusa stage. They have all the conditions occurring in "higher" animals. They did not "choose" one; they developed them all.

Bony cnidarians

Cnidaria are often gelatinous and soft. This is true for jellyfish and sea anemones. However, both antho- and hydrozoans have species with carbonatic skeletons. In addition, the Hydrozoa and Scyphozoa (and some Anthozoa) have chitin, just like insects: the perisarc of their polyps is a chitinous exoskeleton. They do not have to moult because, with coloniality, growth occurs by addition of zooids and not by increase in size of individual organisms. However, some species undergo hydrothecal renovation, with "moult" of the chitin that wraps the renewed hydranth. Some species, furthermore, have skeletons with basal joints that resemble ar-

tenticulations even though they are not governed by muscles. The spicules of gorgonaceans and alcyonaceans are an internal skeleton. Moreover, the calcium-based corallite of madreporarians is similar in structure to our skeleton. Skeletal architectures, in the Cnidaria, have the premises of all "higher" skeletal organisations, both as materials and as position. Maybe, in the future, molecular approaches will show that these resemblances might well be homologies, being controlled by the same set of genes that can be found in higher animals.

The cnidarian big bang

The following heretic view is the natural consequence of all the above: the Cnidaria might be considered as the group from which all the other metazoan "great" body plans arose, when the Cambrian explosion occurred. The Cambrian explosion is almost like the Big Bang. If one asks a physicist "what was there before the Big Bang?" the answer is that this is an ill-posed question ("we do not know" is not part of the physicists lexicon). But if one asks a palaeontologist "what was there before the Cambrian explosion and is still around now?" the answer is "the Cnidaria". There were also other creatures, but we do not see in them the foundations of future metazoan organisations, whereas these are evident in the Cnidaria, from bilateral symmetry, to coelomic cavities, to mesoderm, to skeletal organizations.

Ancestors

Cladism does not admit that something can derive from something else: there are only common ancestors and present-day organisations cannot derive one from the other. However, a new body plan can reasonably originate from a modification of a representative of an ancestral body plan whose other representatives remain unmodified and coexist with the new one.

Almost all body plans have been conserved since the very beginning of the history of life. If a new group originates and it is monophyletic, this means that the origin is single. This means that one event in one lineage led to the innovation, singling out a portion of that lineage. What about the rest of the lineage? It remained unmodified or became little modified, not acquiring a new body plan. Therefore, the ancestral lineage remains along with the new one. Just like Monera coexist with the Eucarya, and Protistans coexist with Fungi, Planta and Animalia. Extinctions are common for species, but they are very uncommon for body plans, at least after the Cambrian explosion, when a diversity plateau was abruptly reached (Valentine, 2004). Each novelty (i.e. new body plan) did not wipe out the preceding body plan, so most steps of evolution simply coexist. The evolutionary mechanism leading to new body plans has been suggested by Arthur (1997) with the proposal of the inverted cone (Fig. 2). The idea is simple and is similar to that of Goldschmidt's hopeful mon-

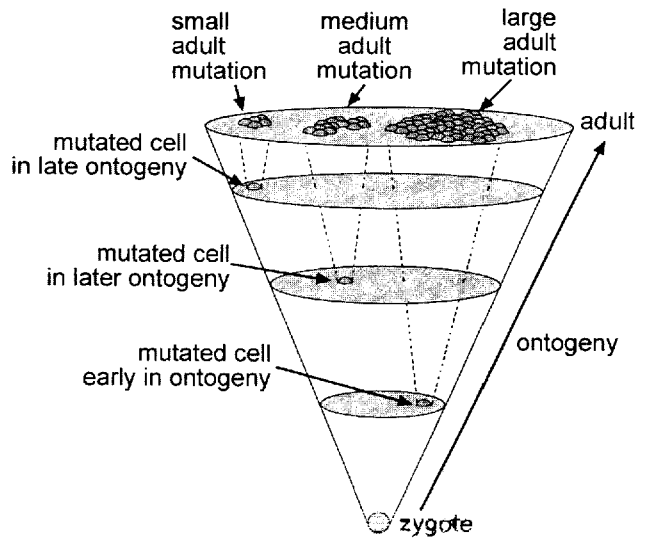


Fig. 2 - The inverted cone (redrawn after Arthur, 1997).

sters. A new species is the result of a mutation that is very near to the end of ontogeny, so near to the top of the inverted cone, Arthur's metaphor of ontogeny.

Such a change is little and the new species is very similar to the ancestral one. A change near the basis of the inverted cone, even a single mutation of a developmental gene, should have a deep effect on the resulting organism, so leading to a possibly new body plan. The nearer to the base of the inverted cone, the more "revolutionary" is the change. Of course, small changes are more easily successful, explaining why species are more abundant than higher taxa. On the contrary, a big change is often leading to unviable monsters, and this explains why phyla are so few, since the change required for their origin are unavoidably extremely "risky" (Fig. 3). Species within the same genus originate by gradual evolution, whereas higher taxa are the result of saltational evolution, as suggested by Boero (1996).

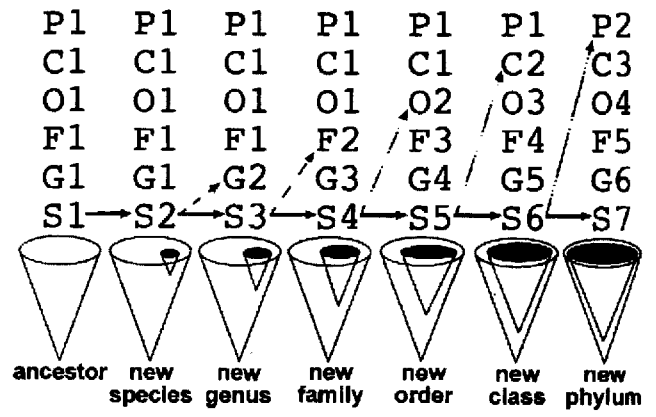


Fig. 3 - "New" higher taxa are the result of speciation events of differential magnitude (above) (after Boero, 1996). A single mutation can have different impacts on the resulting body plan, according to the moment of action of the mutated gene during ontogeny, as suggested by Arthur's (1997) inverted cone model (below).

Exceptions and rules

One supposed law of biology says that if one morph is lost, then it cannot be regained. The Cnidaria offer a sticking exception to this rule, or law. The paradigmatic hydrozoan jellyfish, *Obelia*, is flat, it does not have a velum, it has chordal tentacles and a “strange” striated muscle, and it buds like a hydranth, even though its budding starts with a medusary nodule. All other Hydroidomedusae are concave, have a velum, do not have chordal tentacles and are originated by a medusary nodule! If it were not for its hydroid, showing undeniable campanulariid affinities, the morphology of such a medusa would require a new class at least. Many specialists, from F. S. Russell, to K. W. Petersen, to J. Bouillon, and others thought that *Obelia* might well have been a re-invented medusa, but never published their opinions. Boero *et al.* (1996, 1997) argued that an explanation for *Obelia* origin might be that the coding for the medusa has been inhibited; the unexpressed genes have changed without any selective pressure and then they have been liberated again. A morph (the medusa) has been suppressed and then it has been reexpressed. The result is a mosaic of polyp and medusa, with an original body plan: a saltational event that is linked to gradual change at the level of the hydroid. The paradox is that this weird architecture is taken as the paradigm of hydromedusae in almost all textbooks that, however, depict it as concave and with velum, increasing the confusion of the students. The reasons for this choice are two: *Obelia* is common throughout the world and, furthermore, its medusa is the only one that can be squeezed in a microscopic slide while retaining most of its features! The exception becomes the rule! The rule (the medusary nodule) is forgotten.

FROM EVOLUTION TO ECOLOGY

The above considerations suggest that the role of Cnidaria in explaining the premises of metazoan evolution is paramount. Are they “important” also from other points of view? Maybe the Placozoa are important from an evolutionary point of view, but, with all probabilities, they are not crucial for ecosystem functioning. What about the Cnidaria?

It is part of textbook knowledge that coral reefs have a similar ecological importance to tropical rain forests, and this does not need to be stressed any longer. Passing from the benthos of coral reefs to the water column, jellyfish and ctenophores can be considered as the top predators of the plankton, together with Chaetognatha. A top predator cannot be as abundant as intermediate-level organisms, but its role is crucial. Top predators are rightly praised for their ecological role and, just for this, they are often protected. All conservation biologists call for the protection of key species (see Piraino *et al.*, 2002), like keystone species, i.e. predators that, in spite of not being very abundant, can keep biodiversity high

by preventing the monopolisation of biomass by extremely successful competitors. Keystone species are recognised with field experiments in which community composition is manipulated by removing the putative keystone. The absence of the keystone should lead to a decrease in biodiversity, with the monopoly of one or few species (a state that some ecologists call climax, but this is another story). While it is easy to remove limpets and starfish from the intertidal or to cage out sea urchins from the shallow subtidal, the removal of jellyfish from plankton communities is practically impossible. Jellies are usually rare, but then, suddenly, they can become very abundant. Sometimes they are so abundant to deplete resources completely, as it happened with *Mnemiopsis* in the Black Sea (C.I.E.S.M., 2001), but most of the times their blooms are just a population strategy to take advantage of resource pulses. These soft-bodied animals are implacable predators. They feed on crustaceans, but also on fish eggs and larvae. They presumably feed upon the first developmental stages (or on their food) of the species that produced more eggs and larvae than any others: the possible monopolisers!

Keystone jellies?

It is extremely difficult to demonstrate a keystone role for gelatinous predators: they are almost intractable with the tools of experimental ecology. That's why these animals are neglected by ecologists. They are difficult to catch, they are difficult to preserve, they are difficult to identify. Their elusive role becomes evident when they produce outbreaks that cannot pass unnoticed, otherwise they go back into oblivion, being discarded by plankton nets when they are too big, and being overlooked during sorting operations, because they are unrecognizable blobs and are overwhelmed in number by crustaceans. Due to the difficulty of field experimentation on these elusive animals, therefore, we probably will never test a possible keystone role for gelatinous predators. Purcell *et al.* (2001), among others, showed how important these animals are as predators of fish eggs and larvae. Probably it is their fault if the predictions of most models of fisheries fail. Possibly, gelatinous predators mix the cards that determine what will be the fish species that, at every season, will win the game of producing more offspring than its own competitors produce. They stand as a challenge to all modellers: try to model jellyfish blooms and outbreaks, predicting their occurrence and their impact. It is easier to simply ignore them. The side effect of this simplification is that the predictions fail (Boero *et al.*, 2004). Real life is much more complicated than in elegant mathematical models: a respectable model should respect the importance of jellyfish blooms and outbreaks!

The immortal jellyfish

Important discoveries sometimes occur by chance. A badly done experiment might lead to unexpected re-

sults and carelessness can become a standard procedure to particular experimentation. Several newly released medusae of the species *Turritopsis nutricula* have been forgotten for a few days, with no food and in water that gradually increased in both salinity and temperature. When looked at again, little polyps were found in their place, on the bottom of the rearing jars. The young medusae, stressed by improper environmental conditions, went back to a polyp stage. Bavestrello *et al.* (1992) reported this result at one of the workshops of the Hydrozoan Society, shaking our certainties about cnidarian ontogeny, and about ontogeny in general. The amazing phenomenon has been carefully described later (Piraino *et al.*, 1996; Boero, 1998). Polyps and medusae have much different cells and tissues and, usually, the path in their life cycles goes unvariably from polyp to medusa to planula. In this case, however, the cells of the medusa dedifferentiate, form a ball of tissue, and then redifferentiate into a stolon that then buds polyps that, in their turn, produce new medusae. It is as if a butterfly were able to rearrange its cells and revert to a state of caterpillar, inverting its ontogeny. The media from all over the world baptised this species as “the immortal jellyfish”, suggesting that this species might become a new experimental animal to study aging and, possibly, rejuvenation. Kubota (unpublished) at Kyoto University repeated the observations of Bavestrello and Piraino with Japanese *Turritopsis* medusae and found that they can go back to polyp at least three times, each time producing new medusae that go back to polyp. Evidently, in the field, the little medusae die for some reason; otherwise, the whole ocean would be full of them. The phenomenon, however, is of some interest and induces to consider that limiting experimental biology to a few model animals might restrict the possibility of finding unexpected results.

Taxonomy and the grinding frenzy

In the era of biodiversity, all of a sudden, funding agencies discovered that the people who can give names to living beings are becoming rare. Naming things is our way to understand the world and transmit our knowledge! We take creatures, we pass them through our machines to uncover their secrets, but if we want to take them back, in the field, and be sure about what we are inspecting, we have to know them and to give them names. This paradoxical situation led the National Science Foundation of the US to launch the PEET project (Boero, 2001). In the past, taxonomists usually became specialists by chance; they were not programmed. These future specialists are programmed. This means that we are facing a crisis, and we cannot wait for things to happen by chance. The Cnidaria are very special objects for taxonomists, especially the Hydrozoa. Hennig was an entomologist, but he proposed the Hydrozoa as a test of cladism: “in the Hydrozoa the classification of the medusae is still rather independent

of that of the polyps. For entire families of medusae we still do not know to which polyp families they belong as alternation of generation forms. This group presents an opportunity to test the efficacy of the methods of phylogenetic systematics by using them in all strictness first to produce independent classifications of the medusa and polyp generations. Then the incongruence between the two classifications would have to be tested according to the viewpoints sketched above” (Hennig, 1966). This protocol does not work: *Obelia* hydroids and medusae are the most powerful falsification of the general value of this procedure. The task of future taxonomists is to clean up synonymies by producing genus and family revisions, by using all the tools of both traditional and modern taxonomy, from the comparison of structures to the comparison of genetic sequences.

A FUTURE FOR CNIDARIA

The usual view of Cnidaria in phylogenetic studies is that they are basic to the Metazoan tree but that they are a dead end of evolution, the same is valid for jellyfish in ecology: important sometimes but usually negligible. This marginal role is also the result of lack of generalisation of results by those who study cnidarians. Cnidariologists have many arguments to show that they have the privilege of studying animals that are among the most interesting ones in the whole biosphere. Cnidaria are important in evolutionary and developmental biology, ecology and morphology. All these disciplines, when tackled at the cnidarian level, reveal basic issues, not blurred by the specializations that make all other animals “too advanced” to be treated as paradigms of general issues.

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