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The Radiata and the evolutionary origins of the bilaterian body plan

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Abstract

The apparent conservation of cellular and molecular developmental mechanisms observed in a handful of bilaterian metazoans has spawned a “race” to reconstruct the bilaterian ancestor. Knowledge of this ancestor would permit us to reconstruct the evolutionary changes that have occurred along specific bilaterian lineages. However, comparisons among extant bilaterians provide an unnecessarily limited view of the ancestral bilaterian. Since the original bilaterians are believed by many to be derived from a radially symmetrical ancestor, additional evidence might be obtained by examining present-day radially symmetrical animals. We briefly review pertinent features of the body plans of the extant radial eumetazoan phyla, the Cnidaria, and Ctenophora, in the context of revealing potential evolutionary links to the bilaterians. © 2002 Elsevier Science (USA). All rights reserved.

1. Introduction

It is now well accepted that the Metazoa is a monophyletic group (Fig. 1) comprising all descendants of the last common ancestor of sponges and eumetazoans (Borchiellini et al., 1998; Christen et al., 1991; Collins, 1998; Medina et al., 2001; Müller, 1995, 1998; Müller et al., 1994; Wainright et al., 1993). The overwhelming majority of eumetazoan animals belong to the Bilateria, a clade whose common ancestor exhibited bilateral symmetry. Non-bilaterian eumetazoans include the Cnidaria (sea anemones, hydras, and jellyfishes) and the Ctenophora (comb jellies). These two phyla, collectively known as the Radiata, have been traditionally distinguished from the Bilateria on the basis of three major morphological criteria: body axes, symmetry, and germ layers (e.g., Hyman, 1940). The traditional distinctions between Bilateria and Radiata can be summarized as follows. Bilaterians are bilaterally symmetrical and triploblastic (consisting of endoderm, ectoderm, and mesoderm). They have two main axes of polarity, the anterior–posterior and the dorsal–ventral axes. Cnidarians and ctenophores are generally regarded as radially

symmetrical and diploblastic consisting of endoderm and ectoderm. They possess a single major axis of polarity, the oral–aboral axis.

With respect to body axes and germ layers, the Bilateria is commonly thought to possess the derived condition. Triploblasty is thought to be derived from diploblasty (e.g., Nielsen, 1985). Biaxial polarity (having two axes of polarity, e.g., anterior–posterior and dorsal–ventral) is thought to have evolved from monaxial polarity (having a single axis of polarity, e.g., oral–aboral). There is no consensus on the evolution of symmetry (reviewed in Willmer, 1990). Some authors hypothesize that the ancestral eumetazoan was radially symmetrical, perhaps resembling a cnidarian planula larva (e.g., Beklemishev, 1969; Hyman, 1940; von Salvini-Plawen, 1978) or of the “Gastrea-type” (Haeckel, 1874; Nielsen, 1998). Alternatively, the ancestral eumetazoan may have been bilaterally symmetrical (Hadzi, 1963; Jägersten, 1955). Furthermore, bilateral symmetry may have evolved once, or it may have evolved in multiple lineages (Ax, 1996).

Body axes, symmetry, and the number of germ layers are fundamental characteristics of animal body plans (reviewed in Arthur, 1997). These traits have profound consequences for animal ecology and evolution. For instance, in the pelagic environment, radial symmetry is associated with weak swimming or drifting, and bilateral

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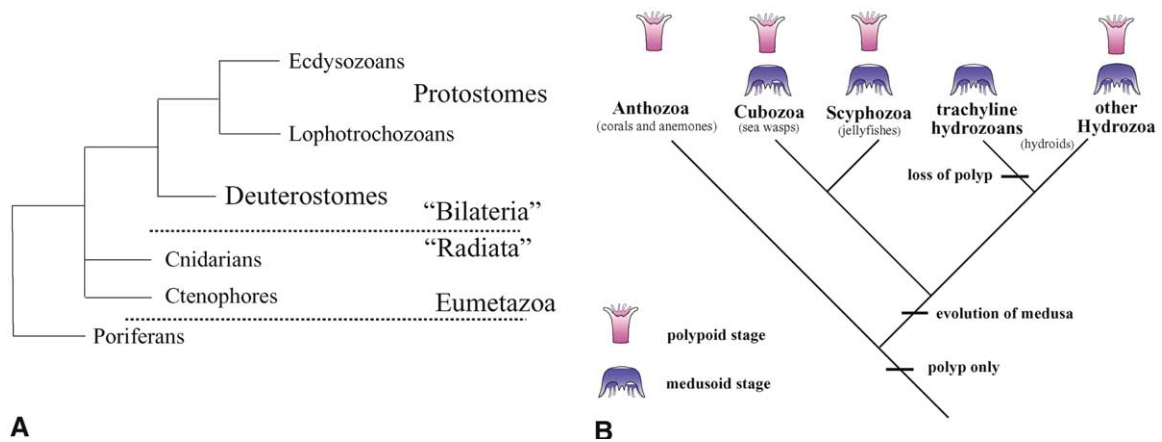


Fig. 1. Phylogenetic relationships of the major metazoan superphyla (A) and of the phylum Cnidaria (B). (A) The ctenophores and cnidarians are the two “diploblastic” eumetazoan members of the Radiata. Recent molecular evidence suggests that the cnidarians are more closely related to the bilaterians than are the ctenophores. (B) Anthozoans, with their simple “egg to embryo to adult polyp” life history are the basal group of cnidarians. The pelagic medusa represents an “invention” of the more derived cnidarians.

symmetry is associated with active swimming. The molecular and developmental changes that underlie such character state transitions are not well understood. If the Bilateria and Radiata are so dramatically and qualitatively different as the traditional distinctions suggest, then cnidarians and ctenophores might reveal very little about the origins of bilateral symmetry, dorsal–ventral polarity, and triploblasty in Bilateria. However, the differences between cnidarians, ctenophores, and bilaterians with regard to these characters are not so clear-cut. The Cnidaria and the Ctenophora differ from each other in interesting ways, and both phyla are more similar to the Bilateria than commonly held. For example, representatives of the “Radiata” may display radial symmetry, but they more often display bi-radial or even bilateral symmetry. The range of character states displayed by cnidarians and ctenophores may help reconstruct important intermediate states on the way to the evolution of bilateral symmetry and triploblasty and may call into question commonly held beliefs about the origins of these derived traits.

2. Symmetry: are the Radiata radially symmetrical?

2.1. Cnidarian symmetry properties

The human mind often imposes its preconceived notions of organismal complexity onto a phylogenetic framework. This was clearly the case for hypotheses on the evolution of the coelom and the phylogenetic position of the acoelomate flatworms (Adoutte et al., 2000; Balavoine, 1997). Likewise, it is easy to conceive of a phylogenetic series in which “simple” animals were constructed on a radially symmetrical platform (Fig. 2A) in which morphogenetic patterning signals (presently of unknown identity) simply diffused out from a

unified source (e.g., the blastopore or cells around the center of the oral–aboral axis) with definitive adult structures obeying some kind of polar coordinate patterning system (Fig. 2B). Cnidarians are supposed to represent this kind of radially symmetrical body plan that is centered around their oral–aboral axis. However, symmetry is a character that displays variation within the phylum Cnidaria. A careful look at the phylogenetic distribution of symmetry types within the phylum implies that radial symmetry was derived within Cnidaria. Therefore, the extant radially symmetrical cnidarians should not be viewed simply as a proxy for the hypothetical radial ancestors of the Bilateria.

Most cnidarians have a complex life cycle consisting of benthic polypoid and pelagic medusoid (jellyfish) stages. This biphasic life history (which may be solitary or colonial) has been exploited to various degrees by different forms, some spending the majority of their life either in one phase or the other. While the overt appearance of benthic hydroids and large elaborate medusae appear to be quite different, their body plans are actually extremely similar. Both are essentially “epithelial animals” consisting of an outer epidermis and an inner gastrodermis that are basically co-planar with one another. Separating these two layers is a largely acellular mesoglea, consisting of extracellular matrix materials with loose aggregations of interstitial stem cells. Both polyps and medusae have a blind gut, so that the mouth also serves as the anus.

Recent evidence from morphology, ribosomal DNA sequence analysis, and mitochondrial gene order agrees that the class Anthozoa (the corals and sea anemones) is the sister group to a clade containing the other three classes (Hydrozoa, Scyphozoa, and Cubozoa; Bridge et al., 1992, 1995; Kim et al., 1999; Medina et al., 2001; Odorico and Miller, 1997; Fig. 1). The notable feature of the anthozoans is that they display only the polyp phase

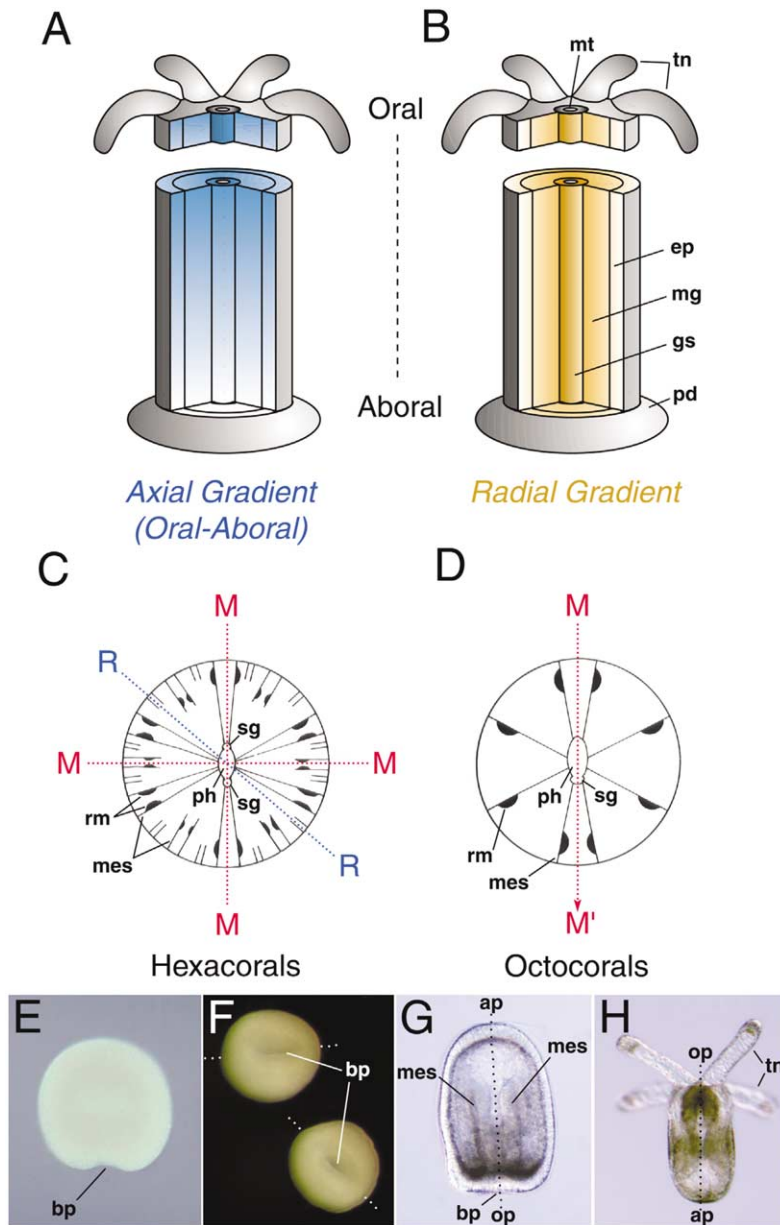


Fig. 2. Axial properties of a “radially” symmetrical metazoan. Patterning must occur in two orthogonal directions, along the longitudinal (oral–aboral) axis (A) and radially from this axis (B). Cross-sections through the body column of extant anthozoans (C) and (D) show that in addition to rotational planes of symmetry (R), both hexacorals (C) and octocorals (D) show either two or one plane of mirror symmetry (M). (E)–(H) Micrographs of the embryos of the anthozoan *Nematostella vectensis*. Lateral (E) and oral (F) views of gastrulating embryos (roughly 275 μm in diameter) showing a symmetry plane (dotted line) that runs through the slit-like blastopore (bp). (G) Lateral view of a late planula stage (swimming direction toward top of page) showing the two mesenteries (mes) on either side of the oral–aboral axis (375 μm in length). (H) Newly settled four tentacle (tn) stage polyp (oral–aboral length = 400 μm excluding tentacles) showing the planes of mirror symmetry through the oral–aboral axis. ap, aboral axis; ep, epidermis; gs, gastrodermis; mes, mesenteries; mg, mesoglea; mt, mouth; op, oral pole; pd, pedal disk; ph, pharynx; rm, retractor muscle; sg, siphonoglyph; tn, tentacles.

of the life cycle. Anthozoan polyps, which may be dioecious or hermaphroditic, produce gametes and generate embryos that develop into a ciliated free-swimming non-feeding planula larvae. The planula generates tentacles at its posterior pole and metamorphoses directly into a benthic adult polyp. In almost all other cnidarians (save two groups of hydrozoans, the trachyline hydromedusae, and the siphonophores), the

polyp buds a free swimming medusae. The medusa represents the sexual phase of the life cycle and generates gametes that form planula larvae, which give rise to benthic polyps. In agreement with recent phylogenetic analyses, it is thought that the ancestral life cycle of cnidarians was entirely polypoid, and that the medusa was an “invention” to facilitate dispersal in the ancestor of the “Medusozoa” (Hydrozoa, Scyphozoa plus

Cubozoa). Thus, studying the anthozoans and the embryonic formation of the polypoid adult is most relevant to the discussion of bilaterian origins.

If one takes a close look at a cross-section through the body column of the anthozoans, they display either one (hexacorals) or at most two (octocorals) distinct planes of mirror symmetry (see Willmer, 1990 for review). Furthermore, since the basic adult symmetry properties of virtually all animals are generated during the embryonic period, one should look at early gastrula and post gastrula stages of development of anthozoans such as the starlet sea anemone *Nematostella vectensis*. These embryos display two clear planes of mirror symmetry. This kind of biradial mirror symmetry represents a special case of bilateral symmetry. The “radial” symmetry of medusae is an adaptation for pelagic life that permits multidirectional locomotion in a three-dimensional environment without continuous reorientation of the body plan. Pelagic medusoid forms (e.g., jellyfish) show the strongest tendencies toward true radial symmetry. However, since the medusa itself is believed to be derived within the phylum, the body plan of the medusa may be irrelevant to the symmetry properties of the ancestral eumetazoan or the ancestral bilaterian.

2.2. Ctenophore symmetry properties

The argument for radial symmetry is even more difficult to make for ctenophores. Ctenophores are a group of pelagic animals (save a group of derived benthic forms, the platyctenes) that bear only superficial similarities to cnidarian medusae. Ctenophores “glide” through the water column via eight longitudinal rows of comb plates (rather than the “pumping” action of cnidarian medusae). Each comb plate is composed of parallel arrays of cilia that serve as “paddles.” The beating of each comb row is controlled in part by the apical organ, a gravity sensing, synapse rich, statocyst located at the aboral pole (Fig. 3). Their primary longitudinal body axis can be described as an oral–aboral axis, and there are two apparent planes of symmetry that include this axis in all ctenophores thus far examined. These two planes (the esophageal or “sagittal” and the tentacular planes) divide the animal into four nearly identical quadrants (Fig. 3). However, these planes of symmetry are not planes of *mirror* symmetry, but planes of *rotational* symmetry. This is due to the presence of two anal canals located on either side of the apical organ at the aboral pole in diametrically opposed quadrants. These structures link the lumen of the gut to the external environment via the anal pores. The embryological origin of these structures is well known (Martindale and Henry, 1995, 1999), and their presence in only two of the four quadrants does not appear to result from simple truncation or loss their of development in the other two quadrants. There are significant differences in the generation of other distinct cell types between the

lineages of cells in the other two quadrants. The 2M macromeres in the quadrants that do not generate the anal canals make longitudinal and circumpharyngeal muscle cells, while the 2M macromeres that form anal canals make neither longitudinal nor circumpharyngeal muscles. The anal canals and differential formation of these muscle cell fates disrupt the “simple” embryonic and adult mirror symmetry of ctenophores. Furthermore, the anal canals serve to eliminate wastes and complete the formation of a “through-gut.” A through-gut was present in the ancestral bilaterian, but is not found in any cnidarian. The anal pores in extant ctenophores are admittedly quite small, and the majority of fecal material is expelled via the mouth. However their presence cannot be simply dismissed (as suggested by Hyman, 1940) when evaluating the origins of the bilaterian digestive tract and symmetry properties. The presence of anal pores may still reflect an intermediate stage in the evolution of the bilaterian through gut if the ancestral eumetazoan had such pores with the loss of these pores in the Cnidaria. Ctenophores therefore remain an enigma. The presence of anal canals and pores might represent vestiges of a through-gut, yet their presence breaks an otherwise good example of a bilaterally symmetrical organism.

3. Germ layers: are members of the Radiata really diploblasts?

Another fundamental feature that has been used to separate the Radiata from the Bilateria is the presence of definitive mesoderm. The evolutionary origin of a discrete mesodermal cell layer is unclear. The developmental derivation of muscle cells in Cnidaria, Ctenophora, and Bilateria is potentially informative. In bilaterians, muscle derives from mesoderm, along with the linings of the circulatory system and coelomic spaces and other connective tissues. Cnidarians are characterized by the presence of myoepithelial muscle cells. These cells combine a contractile process with a cell body residing in an epithelium. The cell body may be part of the outer epidermis or the inner gastrodermis. The contractile process project between the epidermal or gastrodermal epithelial sheets and their respective basal laminae, or they may cross the mesoglea.

Ctenophores on the other hand, have a relatively wide variety of distinctly different muscle cells that reside in different regions of the body (Hernandez-Nicaise, 1991; Martindale and Henry, 1999). Many, but not all, of these muscle cells reside within the mesoglea that separates the epidermis from the gastrodermis. Some of the muscle cells, the so-called parietal muscles, reside on the same side of the basal lamina as the respective epithelial sheets similar to what is seen in cnidarians, yet their cell bodies lie clearly outside the epithelium (Hernandez-Nicaise, 1991). Cell lineage studies in one species of ctenophore

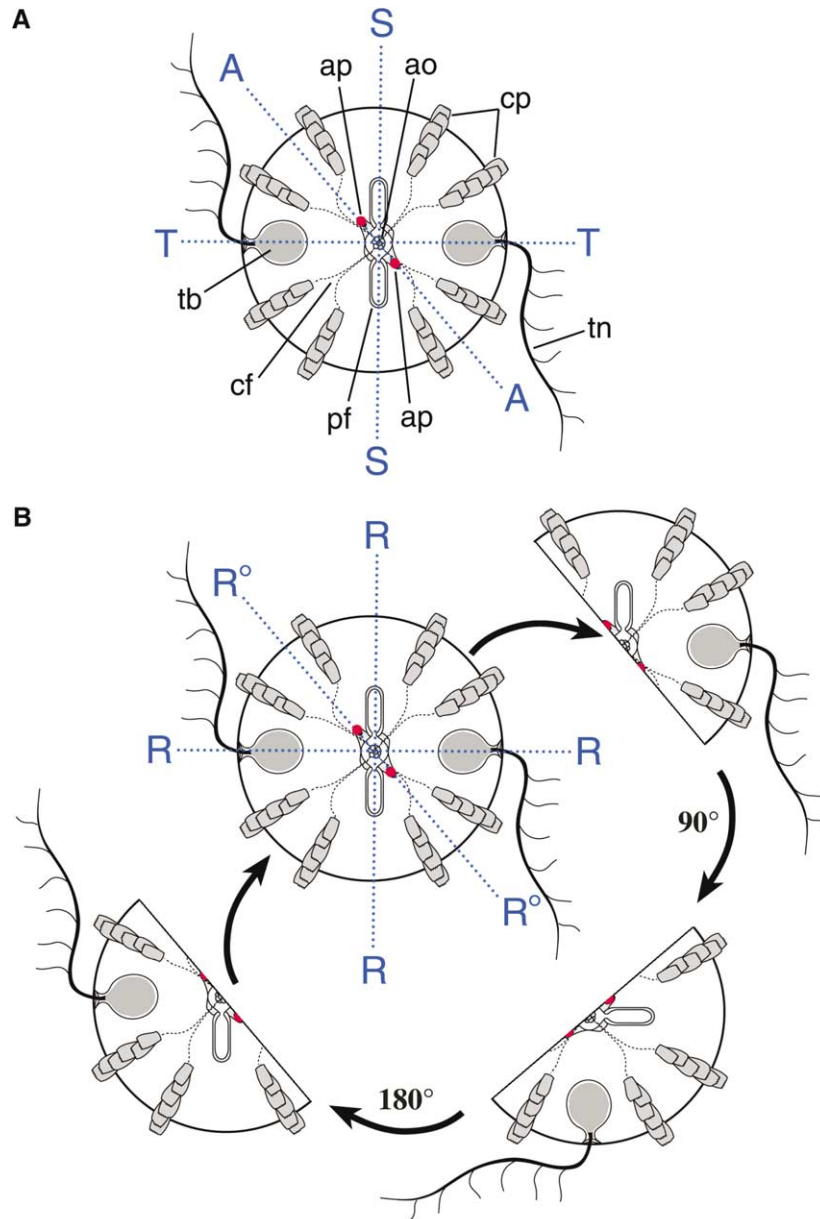


Fig. 3. Symmetry properties of ctenophores seen from the aboral pole. (A) Although ctenophores have been characterized as being biradially symmetrical through their sagittal (S) and tentacular (T) axes, neither of these are planes of simple mirror symmetry. (B) The presence of the anal pores (red) that connect the anal canals to the gut define the anal plane (A) and insure that every plane drawn through the oral–aboral axis is a plane of rotational symmetry (R) as illustrated by rotation through the plane of the anal axis (R^0). ao, apical organ; ap, anal pores; cf, ciliated furrows; cp, comb plates; pf, polar fields; tb, tentacle bulb; tn, tentacle.

have shown that all mesodermal cell types, including the parietal muscles, are generated from endomesodermal precursors (Martindale and Henry, 1995, 1999). This is of interest as these precursors must migrate across the basal laminae or move to their future location before the basal lamina on ectodermal derivatives is generated.

It has been assumed by positional arguments that epitheliomuscle cells of cnidarians are generated by the epithelial sheet they are located in, however, cell lineage studies have never been performed on these forms. Such studies are clearly important if one would like to under-

stand the evolutionary origins of muscle cells. All bilaterians that have been proposed to be basal triploblasts (including acoel flatworms; Ruiz-Trillo et al., 1999) generate muscle from endomesodermal lineages (Henry et al., 2000), while many also generate muscle from ectoderm, suggesting that muscle/mesoderm originated from endodermal precursors in metazoan evolution.

While muscle tends to be arranged differently in the Radiata relative to the Bilateria, this is not to say that cnidarians and ctenophores do not have sheets of contractile muscle cells as commonly occurs in bilaterians.

Sheets of striated muscle cells have been reported in the subumbrellar plate of some derived hydromedusae (Fautin and Mariscal, 1991; Schmid, 1974), and some ctenophores have been reported to have striated fibers (Hernandez-Nicaise, 1991). It is doubtful that these situations are homologous to the striated muscle seen in vertebrates, however, and raises questions as to the legacy of muscle cell evolution in the Metazoa. Did definitive muscle cells evolve more than once, and is striated muscle homoplastic? The situation in ctenophores appears distinct from cnidarians in the sense that their muscle cells are not part of an epithelial structure. Furthermore, it is true that neither ctenophores nor cnidarians have a true mesodermal sheet of cells at any stage of their development, unlike what is seen in bilaterians. Recent discoveries that cnidarians possess components of the bilaterian muscle cell developmental pathway (Spring et al., 2000; Finnerty et al., in preparation) argue that the eumetazoan ancestor had these genes available for use in a myogenic regulatory cascade.

4. What taxon is the sister group of the Bilateria?

The power and accuracy of phylogenetic inference in reconstructing the evolution of the Bilateria will depend on the accuracy of the phylogenetic hypothesis relating non-bilaterians to Bilateria. All three of the logical possibilities for the evolutionary relationships of Cnidaria, Ctenophora, and Bilateria have received support (reviewed in Collins, 1998): (1) Cnidaria as sister group to the Bilateria; (2) Ctenophora as sister-group to the Bilateria; (3) Cnidaria as sister group to the Ctenophora, composing a larger clade known as the Coelenterata. Unfortunately, the poor fossil record has provided little or no insight into this question due to the soft-bodied nature of cnidarians and ctenophores (Collins et al., 1983).

On morphological and embryological grounds, arguments have been made for a closer relationship between the ctenophores and the bilaterians (Lang, 1881). Several characteristics including: the presence of definitive muscle cells, multiciliated cells (cells possessing multiple cilia that virtually all bilaterians-except cnidarians-possess; Ax, 1996; Nielsen, 1987; Rieger, 1976), their more complex behavior mediated by an apical, neural sense organ, a simplified through-gut, and presence of a highly stereotyped cleavage program (Martindale and Henry, 1997) suggest that ctenophores may represent the sister taxon to the Bilateria.

However, recent molecular phylogenies based on 18S rDNA support the notion the Cnidaria are more closely related to bilaterians than ctenophores (Kim et al., 1999; Medina et al., 2001; Podar et al., 2001; Wainright et al., 1993). Interestingly, ctenophores apparently have the least amount of genetic divergence than any other animal phylum sampled (Podar et al., 2001), perhaps due to

the fact that virtually all species of ctenophore, unlike cnidarians, are self-fertile hermaphrodites.

Data from developmental regulatory genes also support a close affinity between Cnidaria and Bilateria: the presence of definitive Hox genes (Finnerty, 1998; Finnerty and Martindale, 1997; Martinez et al., 1998) and ParaHox genes (Finnerty, 1998; Finnerty and Martindale, 1999), the genomic linkage of a Hox gene to an even-skipped ortholog (Finnerty, 2001), and the expression of Hox genes in a manner colinear to their genomic organization (Finnerty and Martindale, in preparation). Although cnidarians do not appear to possess central or paralog 3 class Hox or paraHox genes (Finnerty, 1998, 2001; Finnerty and Martindale, 1997; Martinez et al., 1998), there are reasons to believe that they might have lost them (Kourakis and Martindale, 2000). This conclusion is based on the fact that anthozoans possess anterior and posterior class Hox and ParaHox genes (Finnerty and Martindale, 1999), but phylogenetic reconstruction arguments suggest that the ancestral protoHox cluster possessed four genes prior to the duplication that gave rise to the definitive Hox and ParaHox clusters. Hence, both central and paralog three gene families may have been lost in cnidarians (Kourakis and Martindale, 2000). Whether this potential loss in Hox/ParaHox genes was accompanied by modifications in the adult plan, as appears to be the case for soil nematodes, remains to be seen. Ctenophores are still being surveyed for the presence of Hox genes. However, there appear to be far fewer, if any, authentic Hox genes in this phylum.

5. Conclusions

The data reviewed here suggest that cnidarians, and perhaps ctenophores, should be regarded as primitively bilaterally symmetrical animals and that bilateral symmetry might have evolved prior to origins of the Bilateria. Bilateral symmetry, therefore, should not be regarded as a defining feature (shared derived character state) of the Bilateria. If bilateral symmetry is truly homologous among Radiata and Bilateria, then dorsal-ventral polarity is likely to be a homologous trait as well. Bilateral symmetry requires polarity along an axis through the single plane of mirror symmetry. A cross-section through a bilaterally symmetrical anthozoan (a hexacoral) reveals such axial polarity. This axis of polarity might be homologous to the dorsal-ventral axis of Bilateria. We are currently looking for molecular and morphological indications of dorso-ventral polarity during the development of both ctenophores and cnidarians to determine whether all eumetazoans were once built on a bilaterally symmetrical platform. The presence of definitive mesoderm may also fail to distinguish the Bilateria from the Radiata. If the muscle cells of ctenophores constitute a mesodermal derivative,

then triploblasty is not a defining feature of the Bilateria. Only one major morphological character remains as an unambiguous defining trait of the Bilateria: the coelom. If acoel flatworms are derived platyhelminthes (and not basal triploblasts, Ruiz-Trillo et al., 1999), then the possession of a coelom can be regarded as the primitive condition for the Bilateria. Neither cnidarians nor ctenophores display a coelom at any stage of development.

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