

Did internal transport, rather than directed locomotion, favor the evolution of bilateral symmetry in animals?

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Summary

The standard explanation for the origin of bilateral symmetry is that it conferred an advantage over radial symmetry for directed locomotion. However, recent developmental and phylogenetic studies suggest that bilateral symmetry may have evolved in a sessile benthic animal, predating the origin of directed locomotion. An evolutionarily feasible alternative explanation is that bilateral symmetry evolved to improve the efficiency of internal circulation by affecting the compartmentalization of the gut and the location of major ciliary tracts. This functional design principle is illustrated best by the phylum Cnidaria where symmetry varies from radial to tetradial, biradial and bilateral. In the Cnidaria, bilateral symmetry is manifest most strongly in the internal anatomy and the disposition of ciliary tracts. Furthermore, the bilaterally symmetrical Cnidaria are typically sessile and, in those bilaterally symmetrical cnidarians that undergo directed locomotion, the secondary body axis does not bear a consistent orientation to the direction of locomotion as it typically does in Bilateria. Within the Cnidaria, the hypothesized advantage of bilateral symmetry for internal circulation can be tested by experimental analysis and computer modeling of fluid mechanics. The developmental evolution of symmetry within the Cnidaria can be further explored through comparative gene expression studies among species whose symmetry varies. *BioEssays* 27:1174–1180, 2005.

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Introduction

The evolution of bilateral symmetry has profoundly impacted animal evolution. The overwhelming majority of modern animals exhibit bilateral symmetry (>99%), and the appearance of widespread bilateral symmetry in the fossil record is coincident with the dramatic radiation of animal body plans known as the Cambrian explosion. Symmetry has an over-

riding effect on behavior and ecology.^(1,2) Animals that exhibit radial symmetry are typically either sessile bottom dwellers (e.g. hydras and sea anemones) or planktonic drifters (e.g. jellyfishes). Bilateral symmetry is associated with directed locomotion (swimming fishes, burrowing worms, crawling insects, etc.). The secondary loss of bilateral symmetry in the echinoderms is associated with the loss of directed locomotion. Thus, the maintenance of bilateral symmetry in so many independent animal lineages over the last 500 million years must have been driven, at least in part, by selection for directed locomotion. However, the origin of bilateral symmetry is a separate question. The contemporary selective advantage of a trait cannot always explain its origin. For example, recent studies suggest that insect wings may have evolved from ancestral gills.^(3–5)

It is widely held that the bilateral symmetry in the Metazoa evolved from radial symmetry due to selection for directed locomotion.^(1,2,6) Many workers have focused on the benthic environment as the likely venue for the transition from radial to bilateral symmetry. “The bilateral symmetry of the majority of the Metazoa has developed in connection with active progressive motion (creeping) on the surface of a solid substrate, which produces differentiation of dorsal and ventral sides.⁽⁶⁾” Whether in the pelagic environment or the benthic environment, the ability to move horizontally increases the likelihood of encountering food. Bilateral symmetry would have conferred a selective advantage over radial symmetry for such directed foraging.⁽¹⁾ Increasing polarization along the locomotory axis would have evolved as sensory and food-handling structures became concentrated at the anterior pole, leading to the elaboration of the anterior–posterior axis. Increasing polarization along the principal environmental gradient would lead to the elaboration of the dorsal–ventral axis. So, the typical Bilaterian animal swims or crawls in a consistent direction relative to its primary body axis (i.e. it travels “head first”), and it maintains its secondary body axis in a preferred orientation relative to the environmental gradient (i.e. dorsal side up). However, while the Bilateria support the strong association of bilateral symmetry with directed locomotion,

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DOI 10.1002/bies.20299
Published online in Wiley InterScience (www.interscience.wiley.com).

they cannot demonstrate that directed locomotion brought about the origin of bilateral symmetry because both of these traits are primitive within the Bilateria.

Insights into the Evolution of Animal Symmetry from the Cnidaria

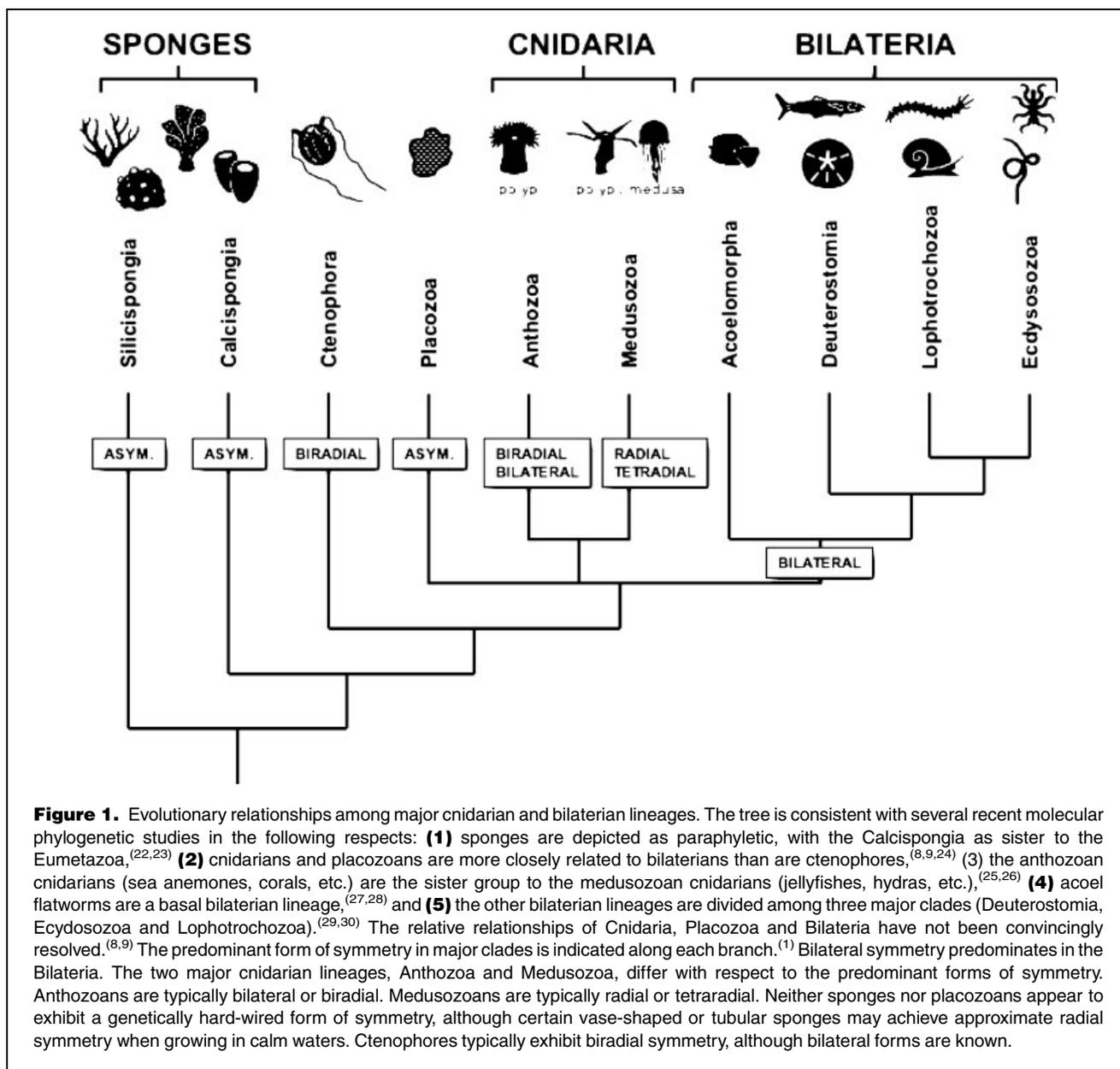
The phylum Cnidaria should be particularly informative about the early evolution of animal symmetry and the likely condition from which bilaterians evolved for four reasons. First, the Cnidaria is a closely related outgroup to the Bilateria, possibly the sister group to the Bilateria.^(7–9) Second, the major lineages within the phylum Cnidaria differ with respect to the predominant form of symmetry.⁽¹⁾ Radial symmetry and tetradial symmetry predominate in the Medusozoa, a clade that includes the true jellyfishes, sea wasps, hydras and hydromedusae (Fig. 1). Bilateral symmetry and biradial symmetry predominate in the Anthozoa, a clade that includes the corals, sea anemones and sea pens.⁽¹⁰⁾ Third, the body plans of modern Cnidaria (polyps, jellyfishes, and frond-like colonies) are reminiscent of the body plans found in Precambrian faunal assemblages that may represent early animals.⁽¹¹⁾ These extinct cnidarian-like organisms may represent crown-group cnidarians, stem-group cnidarians, or even stem-group Bilaterians. In other words, modern Cnidaria may resemble “a grade of late Precambrian organization from which Bilaterians evolved”.⁽¹²⁾ Fourth, recent molecular data from the starlet sea anemone, *Nematostella vectensis*, suggest that bilateral symmetry actually evolved prior to the evolutionary split between Cnidaria and Bilateria.⁽¹³⁾ *Nematostella* is one of many bilaterally symmetrical anthozoan cnidarians, and the expression of patterning genes along its primary and secondary body axes suggest possible homology with Bilateria. In both *Nematostella* and bilaterian animals, *Hox* genes are expressed in staggered domains along the primary body axis, and *dpp* is expressed in an asymmetric fashion about the secondary body axis.⁽¹³⁾ Asymmetric expression of *Dpp* appears at two different times during development. First, during gastrulation, *Dpp* is expressed asymmetrically about the blastopore. Later, as the pharynx materializes, *Dpp* is expressed in the ectoderm at one end of the long axis of the pharyngeal lumen. This axis, known as the directive axis⁽¹⁴⁾ (Fig. 2), is the animal's secondary body axis, analogous and perhaps homologous to the dorsal–ventral axis of Bilateria. Asymmetric expression of *Dpp* about the directive axis may reflect homology to the dorsal–ventral axis of Bilateria.^(13,15) Asymmetric expression of *Dpp* about the blastopore has also been reported for the coral *Acropora millepora*.⁽¹⁵⁾ However, at this time, *Hox* expression has not yet been characterized in *Acropora*, and *Dpp* expression has not been characterized during the development of the pharynx, when bilateral symmetry becomes apparent.

The morphological manifestations of bilateral symmetry in Cnidaria are far subtler than in Bilateria. For example,

Nematostella is roughly cylindrical, giving an outward appearance of radial symmetry (Fig. 2). This external semblance of radial symmetry is disrupted only by the slit-like mouth opening.⁽¹⁴⁾ In contrast to the outward appearance, the internal anatomy exhibits pronounced bilateral symmetry about the directive axis, which passes through the long axis of the pharyngeal lumen.⁽¹⁴⁾ In addition to the oblong cross section of the pharyngeal lumen, there are two other prominent structural manifestations of bilateral symmetry: the mesenteries and the siphonoglyph. The mesenteries are lamellae that extend from the pharynx to the body wall, thereby subdividing the internal body cavity (the coelenteron). The siphonoglyph is a ciliated groove in the wall of the pharynx that generates ciliary currents in the coelenteron.

Despite the fact that many anthozoan cnidarians exhibit bilateral symmetry, adult Anthozoa are generally sessile or sedentary animals that do not “engage in the active unidirectional movement seen in bilateral, cephalized creatures.”⁽¹⁾ Some Anthozoa do exhibit limited locomotory capability but their locomotion is random with respect to the directive axis.⁽¹⁾ For example, sea anemones such as *Metridium* and *Aiptasia* can locomote by gliding along the substrate on their flat pedal disc. The anemone *Liponema brevicornis* can assume a ball-like shape and roll across the sea floor in the direction of the bottom currents. The anemone *Stomphia* can eject itself off the sea floor by undulating its body column. These modes of locomotion are diverse and bear no consistent relationship to organismal symmetry. Furthermore, fossil evidence and phylogenetic inference based on extant taxa suggest that the common ancestor of the Anthozoa may have been a sessile benthic animal.⁽¹⁶⁾ Therefore, directed locomotion cannot explain the widespread occurrence of bilateral symmetry in adult Anthozoa. Neither can directed locomotion explain the bilateral symmetry exhibited by Cnidarian planula larvae. Many planulae are active swimmers but, while their locomotion is directed along the primary apicobasal axis, the directive axis does not exhibit a preferred orientation to the environmental gradient during locomotion the way that the dorsal–ventral axis of bilaterians does. For example, the planulae of *Nematostella* rotate continuously about their primary apicobasal axis as they swim in the apical direction.

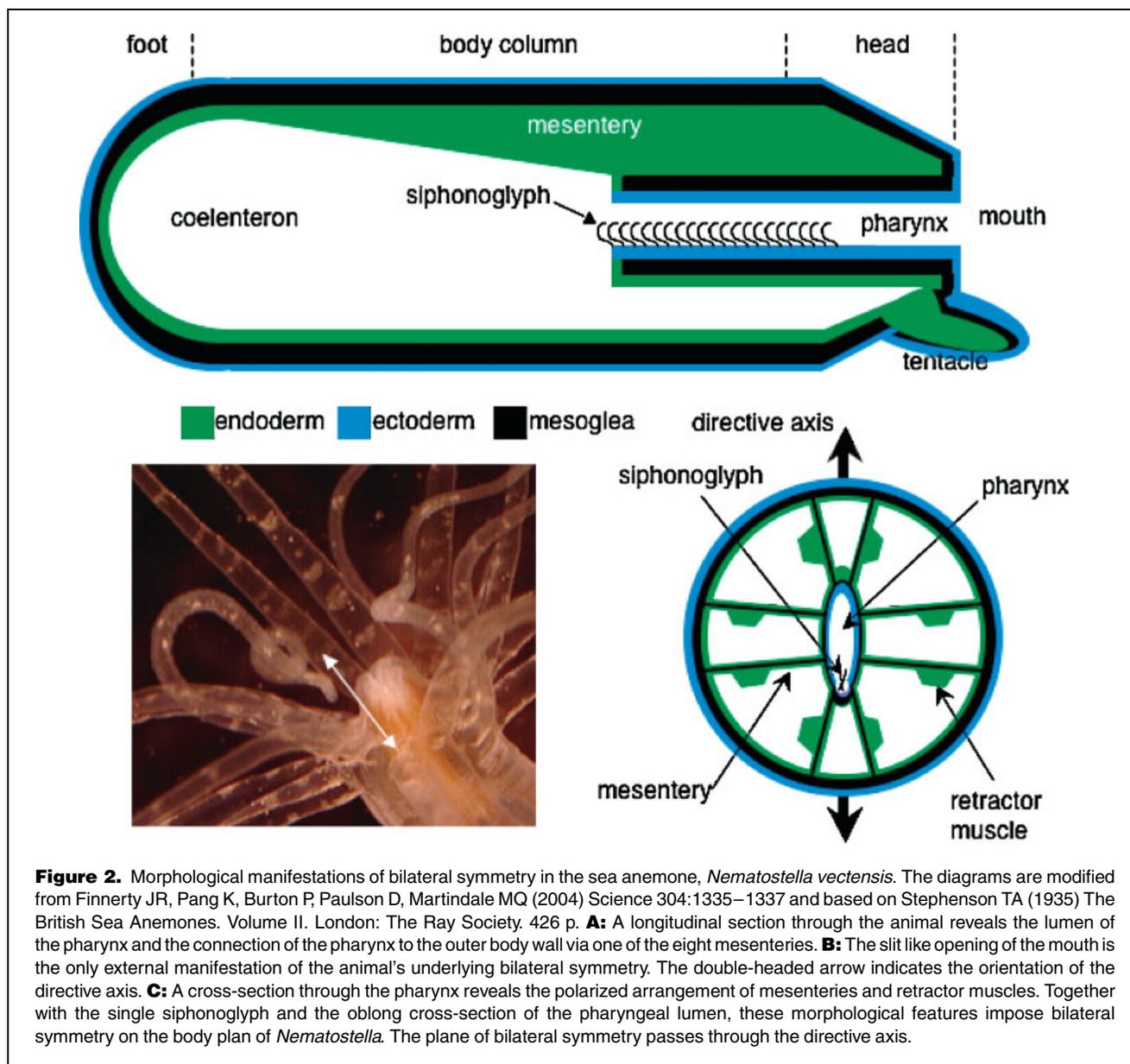
Why then do many anthozoans exhibit bilateral symmetry when their sessile or sedentary habits would seem to dictate radial symmetry? Since bilateral symmetry is most strongly manifest in the internal anatomy, particularly in the location of ciliary tracts, the selective advantage likely pertains to the efficiency of ciliary currents within the pharynx and the coelenteron. Internal ciliary currents have not been directly studied in *Nematostella*, but they have been studied in other anthozoans that exhibit bilateral symmetry. In the polyps of soft corals (Alcyonaria), the single siphonoglyph drives water currents from the pharynx into the coelenteron, while cilia on the opposing asulcal septa direct the water back out



again, creating an efficient, continuous, unidirectional flow (Fig. 3).⁽¹⁷⁾ Such an arrangement would be particularly beneficial in an organism with a blind gut, where the single opening must serve as both the mouth and anus.

Throughout the phylum Cnidaria, in both polyps and medusae, symmetry is more closely correlated with internal circulatory currents than locomotion. For example, those anthozoans that exhibit biradial symmetry typically possess dual siphonoglyphs, one at each end of the directive axis.⁽¹⁴⁾ The tetramerous symmetry of scyphozoan polyps is manifest

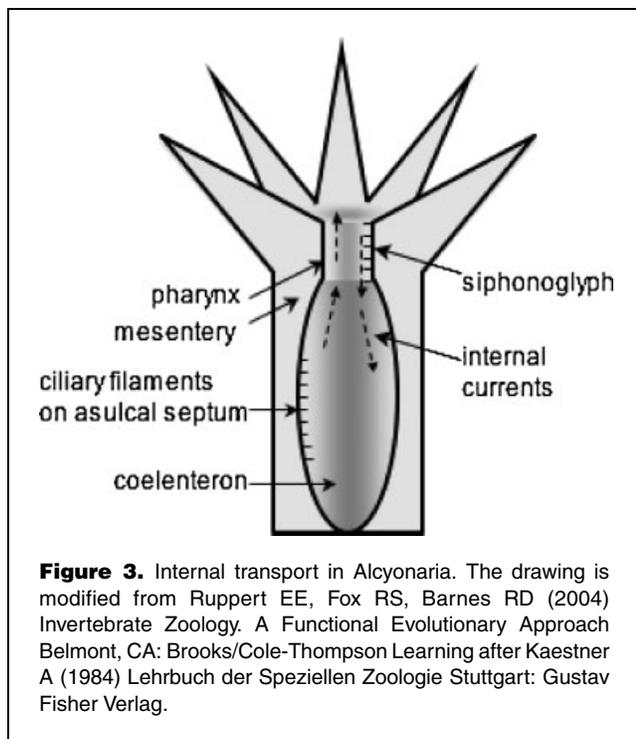
in the four equidistant gastrodermal septa that subdivide the coelenteron.⁽¹⁾ These septa directly affect circulation within the coelenteron and, additionally, each septum bears a septal funnel that communicates with the seawater via openings on the oral disc. Scyphozoan medusae, such as the moon jellyfish *Aurelia*, likewise exhibit tetradial symmetry, and this symmetry is manifest in the gastric circulation. There are four equivalent gastric sectors in the animal, each with an identical ciliary circulation driven by the cilia lining the septal funnel and the radial canals.



A new scenario for the evolution of animal symmetry

Clearly, selection for improved internal transport is much more plausible than selection for directed locomotion as an explanation for the maintenance of bilateral symmetry in anthozoan cnidarians. This suggests a question of deeper phylogenetic significance: could internal transport have favored the origin of bilateral symmetry in the Metazoa? A recent phylogenetic analysis of morphological characters suggests that the most recent common ancestor of the Cnidaria and Bilateria was a sessile benthic animal.⁽¹⁶⁾ Furthermore, recent molecular and developmental data

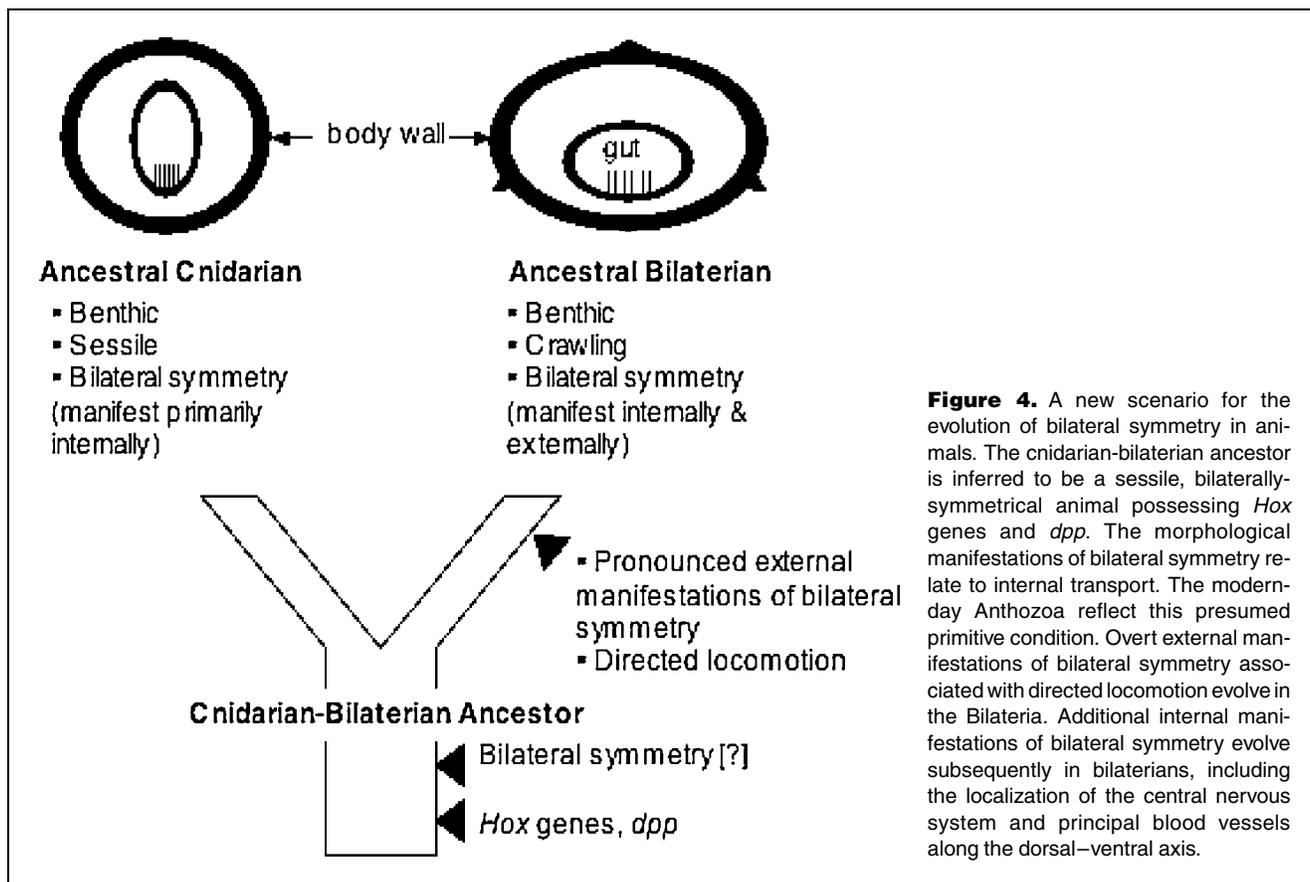
suggest that bilateral symmetry evolved in this ancestor.⁽¹³⁾ If bilateral symmetry evolved in the cnidarian–bilaterian ancestor, while directed locomotion evolved later, in the ancestral bilaterian, then the origin of this trait cannot be attributed to selection for directed locomotion. However, the origin of bilateral symmetry in the cnidarian–bilaterian ancestor could plausibly be explained by selection for improved internal circulation (Fig. 4). Subsequently, the bilaterian lineage would have evolved more overt external manifestations of bilateral symmetry under selection for directed locomotion. This conclusion is bolstered by the fact that many bilaterian animals have internal ciliary tracts that are distributed asymmetrically



about the dorsal–ventral axis, such as the endostyle of chordates, a ciliated, mucus-secreting groove in the ventral pharynx.

Future directions

This hypothesis predicts that bilaterally symmetrical arrangements of ciliary tracts can result in more efficient ciliary ventilation through the gut cavity than radially symmetrical arrangements. However, the optimum arrangement of ciliary tracts will vary with organismal size and shape as well as feeding ecology. For example, suspension feeding commonly relies on ciliary transport of prey items through the alimentary canal, where predation relies on muscular transport. Even among those suspension feeders that rely on ciliary transport, at very small sizes, it may be unnecessary to concentrate the cilia into a tract to achieve sufficient ventilation. At intermediate sizes, a single continuous ventilatory stream may be ideal (Fig. 3). At larger body sizes, it may be necessary to employ multiple independent ventilatory streams, as in the tetra-radially symmetrical jellyfishes. Within classes of Cnidaria, size exerts a pronounced influence on the internal anatomy of polyps. With increasing size comes increasing compartmentalization of the coelenteronic cavity, which can have the effect,



in Hydrozoa, of transforming radial symmetry into biradial symmetry. Considering the size-related developmental plasticity of cnidarian internal anatomy,⁽¹⁾ it is feasible that the ancestral cnidarian was plastic with respect to symmetry. This ancestor, and by extension, the cnidarian–bilaterian ancestor, may have possessed the genetic capacity to develop either bilateral or radial symmetry depending on organismal size.

Ciliary currents are amenable to direct observation and modeling, so their efficiency can be studied both empirically and theoretically.^(18–20) Additional work is needed to understand the physiological and ecological design constraints acting upon ciliary transport systems at different body sizes. The phylum Cnidaria should prove particularly useful for such studies since its members exhibit a wide range of natural variation in this trait. In addition, due to their extensive potential to survive injury and undergo regeneration, the size and internal anatomy of cnidarian polyps could be surgically manipulated, and ciliary flow can be monitored in animals with altered morphology, even as they regenerate their original form.

A second testable prediction of the hypothesis presented here is that the location of ciliary tracts in the alimentary canal of both Bilateria and Cnidaria will be under the control of the genes responsible for dorsal–ventral patterning in Bilateria. A recent study on the sea anemone *Nematostella* revealed pronounced asymmetric expression of several developmental regulatory genes about the directive axis.⁽¹³⁾ The *TGF-B* gene *dpp*, a gene known to be critical to the proper patterning of the dorsal–ventral axis of bilaterians, was expressed on one side of the pharyngeal ectoderm. A second *TGF-B* gene and three Hox genes were expressed on the opposing side of the coelenteron.⁽¹³⁾ As these expression data were obtained prior to the development of the siphonoglyph, it is not yet clear whether *dpp* is expressed in the side of the pharynx where this ciliary tract will form, or on the opposing side of the animal. Future research should focus on the correspondence of *dpp* expression with ciliary tract formation in a wide range of metazoans, including other cnidarians and bilaterians. For example, in those anthozoans possessing two siphonoglyphs, are there also two stripes of *dpp* expression in the pharyngeal ectoderm? Or alternately, has the asymmetrical *dpp* expression in the pharyngeal ectoderm been lost in biradial forms? If biradial symmetry evolved from bilateral symmetry, and not the other way around as generally supposed,⁽²¹⁾ then this may have been accomplished by the loss of a pattern element during development.

Of course, bilateral symmetry may have evolved independently in the Cnidaria and the Bilateria. If so, it may have originated under the same selection pressure or under different selection pressures in these two lineages. Paleontological evidence may ultimately prove decisive regarding the ecological explanation for the origin of bilateral symmetry. However, the extant Cnidaria are important because they

compel us to consider a novel explanation for the origin of this profoundly important trait.

References

- Ruppert EE, Fox RS, Barnes RD. 2004. Invertebrate Zoology. A Functional Evolutionary Approach. Belmont, CA: Brooks/Cole-Thompson Learning.
- Willmer P. 1990. Invertebrate Relationships. Patterns in Animal Evolution. Cambridge: Cambridge University Press. 400 p.
- Jockusch EL, Nagy LM. 1997. Insect evolution: how did insect wings originate? *Curr Biol* 7:R358–361.
- Averof M, Cohen SM. 1997. Evolutionary origin of insect wings from ancestral gills. *Nature* 385:627–630.
- Damen WG, Saridaki T, Averof M. 2002. Diverse adaptations of an ancestral gill: a common evolutionary origin for wings, breathing organs, and spinnerets. *Curr Biol* 12:1711–1716.
- Beklemishev WN. 1969. Principles of Comparative Anatomy of Invertebrates. Chicago: The University of Chicago Press.
- Collins AG. 1998. Evaluating multiple alternative hypotheses for the origin of Bilateria: an analysis of 18S rRNA molecular evidence. *Proc Natl Acad Sci USA* 95:15458–15463.
- Medina M, Collins AG, Silberman JD, Sogin ML. 2001. Evaluating hypotheses of basal animal phylogeny using complete sequences of large and small subunit rRNA. *Proc Natl Acad Sci USA* 98:9707–9712.
- Kim J, Kim W, Cunningham CW. 1999. A new perspective on lower metazoan relationships from 18S rDNA sequences. *Mol Biol Evol* 16:423–427.
- Bourne GC. 1900. The Anthozoa. In: Lankester ER, editor. A Treatise on Zoology. Part II. The Porifera and Coelenterata. London: Adam and Charles Black. p 1–84.
- Glaessner MF, Wade M. 1966. The late Precambrian fossils from Ediacara, South Australia. *Paleontology* 9:599–628.
- Budd GE, Jensen S. 2000. A critical reappraisal of the fossil record of the bilaterian phyla. *Biol Rev* 75:253–295.
- Finnerty JR, Pang K, Burton P, Paulson D, Martindale MQ. 2004. Origins of bilateral symmetry: Hox and dpp expression in a sea anemone. *Science* 304:1335–1337.
- Stephenson TA. 1935. The British Sea Anemones. Volume II. London: The Ray Society. 426 p.
- Hayward DC, Samuel G, Pontynen PC, Catmull J, Saint R, et al. 2002. Localized expression of a dpp/BMP2/4 ortholog in a coral embryo. *Proc Natl Acad Sci USA* 99:8106–8111.
- Marques AC, Collins AG. 2004. Cladistic analysis of Medusozoa and cnidarian evolution. *Invertebrate Biology* 123:23–42.
- Kaestner A. 1984. Lehrbuch der Speziellen Zoologie. Stuttgart: Gustav Fisher Verlag. 621 p.
- Warwick WJ. 1983. Mechanisms of mucous transport. *Eur J Respir Dis Suppl* 127:162–167.
- Southward AJ. 1955. Observations on the ciliary currents of the jellyfish *Aurelia aurita*. *J Mar Biol Assoc UK* 34:201–216.
- Cameron CB. 2002. Particle retention and flow in the pharynx of the enteropneust worm *Harrimania planktophilus*: the filter-feeding pharynx may have evolved before the chordates. *Biol Bull* 202:192–200.
- Martindale MQ, Finnerty JR, Henry JQ. 2002. The Radiata and the evolutionary origins of the bilaterian body plan. *Mol Phylogenet Evol* 24:358–365.
- Kruse M, Leys SP, Muller IM, Muller WE. 1998. Phylogenetic position of the Hexactinellida within the phylum Porifera based on the amino acid sequence of the protein kinase C from *Rhabdocalypus dawsoni*. *J Mol Evol* 46:721–728.
- Borchiellini C, Manuel M, Alivon E, Boury-Esnault N, Vacelet J, et al. 2001. Sponge paraphyly and the origin of the Metazoa. *J Evol Biol* 14:171–179.
- Podar M, Haddock SH, Sogin ML, Harbison GR. 2001. A molecular phylogenetic framework for the phylum Ctenophora using 18S rRNA genes. *Mol Phylogenet Evol* 21:218–230.

Hypotheses

25. Bridge D, Cunningham CW, DeSalle R, Buss LW. 1995. Class-level relationships in the phylum Cnidaria: molecular and morphological evidence. *Mol Biol Evol* 12:679–689.
26. Odorico DM, Miller DJ. 1997. Internal and external relationships of the Cnidaria: implications of primary and predicted secondary structure of the 5'-end of the 23S-like rDNA. *Proc Biol Sci* 264:77–82.
27. Ruiz-Trillo I, Paps J, Loukota M, Ribera C, Jondelius U, et al. 2002. A phylogenetic analysis of myosin heavy chain type II sequences corroborates that Acoela and Nemertodermatida are basal bilaterians. *Proc Natl Acad Sci USA* 99:11246–11251.
28. Telford MJ, Lockyer AE, Cartwright-Finch C, Littlewood DT. 2003. Combined large and small subunit ribosomal RNA phylogenies support a basal position of the acelomorph flatworms. *Proc Biol Sci* 270:1077–1083.
29. Aguinaldo AM, Turbeville JM, Linford LS, Rivera MC, Garey JR, et al. 1997. Evidence for a clade of nematodes, arthropods and other moulting animals. *Nature* 387:489–493.
30. Halanych KM, Bacheller JD, Aguinaldo AM, Liva SM, Hillis DM, et al. 1995. Evidence from 18S ribosomal DNA that the lophophorates are protostome animals. *Science* 267:1641–1643.