The A/P axis in echinoderm ontogeny and evolution:
evidence from fossils and molecules

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SUMMARY Even though echinoderms are members of the Bilateria, the location of their anterior/posterior axis has remained enigmatic. Here we propose a novel solution to the problem employing three lines of evidence: the expression of a posterior class *Hox* gene in the coeloms of the nascent adult body plan within the larva; the anatomy of certain early fossil echinoderms; and finally the relation between endoskeletal plate morphology and the associated coelomic tissues. All three lines of evidence converge on the same answer, namely that the location of the adult mouth is anterior, and the anterior/posterior axis runs from the mouth through the adult coelomic compartments. This axis then orients the animal such that there is but a single plane of symmetry dividing the animal into left and right halves. We tentatively hypothesize that this plane of symmetry is positioned along the dorsal/ventral axis. These axis identifications lead to the conclusion that the five ambulacra are not primary body axes, but instead are outgrowths from the central anterior/posterior axis. These identifications also shed insight into several other evolutionary mysteries of various echinoderm clades such as the independent evolution of bilateral symmetry in irregular echinoids, but do not elucidate the underlying mechanisms of the adult coelomic architecture.

INTRODUCTION

Except for sponges, cnidarians, and their allies, almost all animals have conspicuous anterior/posterior (A/P), dorsal/ventral (D/V), and left/right (L/R) axes. These axes are defining characters of the Bilateria, and because the bilaterians are monophyletic (Adoutte et al. 1999), bilateral symmetry must have emerged during the initial evolution of this great clade of animals (Peterson et al. 2000). Within the Bilateria, the echinoderms secondarily evolved radially symmetric body plans. Their radial symmetry confounded early attempts to classify echinoderms, and they were often allied with cnidarians as "Radialia," although their larval forms are clearly bilaterally symmetrical (see Hyman 1955; Winsor 1976 for historical discussions). It is now clear that echinoderms are the sister taxon of the hemichordates, and these together constitute the sister taxon of the chordates, the three taxa together comprising the deuterostomes. This phylogenetic topology is supported by mitochondrial DNA (Castresana et al. 1998a, 1998b), 18S rRNA (Turbeville et al. 1994; Wada and Satoh 1994), and cladistic morphological analyses (Peterson and Eernisse, unpublished data). Because both hemichordates and chordates are clearly bilaterally symmetrical, it follows that the radial symmetry of echinoderms cannot be homologous to the radial symmetry of cnidarians. Instead radial symmetry in echinoderms is an apomorphy of at least the crown-group members of the phylum, and presumably, of some of its stem lineages as well.

Although this much is well accepted, one of the many aspects of echinoderm anatomy "designed to puzzle the zoologist" (Hyman 1955), is the location in the adult echinoderm body plan of primary axes homologous to those of hemichordates, chordates, and other bilaterians. This difficulty stems in part from the lack of a clearly defined head region, and the absence of a brain or other concentration of neurons and sensory structures. Moreover, although axes of bilateral symmetry appear in some groups of echinoderms, their homology is equivocal, because key landmarks such as the position of the anus or hydropore vary in position among them (Hotchkiss 1998). As we show in this paper, the apparent planes of bilateral symmetry in some of these forms are of no relevance to the problem of identifying fundamental morphological relationships of the echinoderm body plan. We propose here a new interpretation of axial homologies in echinoderms, based on three separate kinds of evidence: the pattern of expression of a posterior class *Hox* gene in the coeloms of the nascent adult body within a sea urchin larva; the anatomy of certain early fossil echinoderms; and the relation between

endoskeletal plate morphology and the associated coelomic tissues, as analyzed by Mooi and David (1997, 1998). A plausible pathway for evolution of the radially symmetric echinoderm body plan from a bilaterally symmetric ancestor can thus be derived. These ideas also illuminate some of the enigmatic aspects of echinoderm anatomy, and as we show, they provide a useful framework for interpretation of gene expression patterns during the ontogeny of the adult echinoderm body plan.

EXPRESSION OF THE *Hox11/13b* GENE IN AN ECHINOID LARVA

A cluster of ten *Hox* genes has recently been isolated from the genome of *Strongylocentrotus purpuratus* (Martinez et al. 1999; see also Popodi et al. 1996 for the *Hox* cluster of *Heliocidaris erythrogramma*). This cluster includes paralogs of almost all vertebrate *Hox* genes. Quantitative measurements of transcript concentration, using probes specific to each *Hox* gene, have shown that most of these genes are not expressed at all during embryogenesis, but that they are transcribed copiously once adult body plan formation is initiated in the feeding larva (Arenas-Mena et al. 1998). Thus, as in all Bilateria, the *Hox* gene complex would appear to be utilized in the development of the phylotypic echinoderm body plan. Where they are utilized is a particularly interesting question, given their radially symmetric character (Raff and Popodi 1996). Here we consider the locus of expression of the most posterior gene of the cluster examined, *Hox11/13b* (as indicated by its name, the homeobox of this gene displays diagnostic features shared specifically with vertebrate *Hox11*, *12*, and *13* genes; Martinez et al. 1999). Expression of *Hox* genes of this class at the posterior end of the anterior/posterior axis is a bilaterian synapomorphy. In the following argument we use the pattern of expression of the *Hox11/13b* gene early in adult body plan development as a marker of posterior homology, with respect to the body plans of other deuterostomes.

Hox11/13b is one of the two *Hox* genes expressed in the *S. purpuratus* embryo, where it is transcribed in many embryonic regions (Dobias et al. 1996; see also Ishii et al. 1999). However, the embryonic expression is likely to be irrelevant to adult body plan formation, because the transcripts are largely in embryonic and larval structures which are not included in the radially symmetric juvenile which emerges at metamorphosis. After about 2 weeks of feeding, the *Hox11/13b* gene is activated in the coelomic mesoderm of the rudiment from which the adult body plan derives. The pattern of expression is illustrated in the whole mount *in situ* hybridization shown in Fig. 1. This result is particularly revealing: *Hox11/13b* transcripts appear throughout the paired somatocoels; as diagrammed in Fig. 1B, at this stage these are thin

sacs which have grown down the sides of the stomach. The left somatocoel adjoins the rudiment which forms where the vestibule invaginates and makes contact with the left hydrocoel. Expression of *Hox11/13b* confirms that the somatocoels are the posterior coeloms. Note that there is no expression in the vestibule, the anlagen of the adult nervous system, nor in any other mesodermal cells, though the gene is also expressed in the larval anus (a detailed description of posterior *Hox* gene expression in larval development will appear elsewhere; Arenas-Mena et al. unpublished data). Because the mesodermal somatocoels are the primary sites of *Hox11/13b* expression in tissues that will give rise to the adult body parts, we rely on the architecture of the mesoderm to identify axial homologies, rather than on the adult nervous system, which has been used in the past to address this same question (e.g., Raff and Popodi 1996; Morris 1999).

HOMOLOGIES BETWEEN ECHINODERM AND HEMICHORDATE COELOMS

The disposition of the anlagen of the mesodermal components is a fundamental feature in both echinoderm and hemichordate development (Peterson et al. 1997, 1999a, 1999b). Figure 2 shows what we envision as the primitive arrangement of the coeloms in the common ancestor of these two sister phyla. There is an anterior coelom called the protocoel in hemichordates, and the axocoel in echinoderms that may or may not have been paired. An anterior coelom is usually connected to the exterior via the hydropore. The middle pair of coeloms, i.e., the mesocoel or hydrocoel, is found in both phyla, but the right hydrocoel is greatly reduced in echinoderms; its only contribution to the adult body plan is the madreporic vesicle. The most posterior pair of coeloms are the metacoels or somatocoels, that is the loci of *SpHox11/13b* expression in the sea urchin larva. Thus, the latest common ancestor of echinoderms and hemichordates can be presumed to have had at least five coeloms arranged in a clear anterior/posterior fashion with the protocoel(s)/axocoel(s) anterior, and the metacoels/somatocoels posterior.

Although the initial organization of these mesodermal anlagen is similar in the larvae of hemichordates and echinoderms, the final disposition of the coelomic sacs (or their derivatives) in the adult forms becomes markedly different. In the hemichordate, the mesoderm, because it is derived from the gut, forms in the apical/blastoporal axis, the primitive axis of symmetry among bilaterian larvae (Nielsen 1995). In the adult the anterior/posterior axis runs in the same plane as the apical/blastoporal axis of the embryo/larva such that the apical plate of the larva is found at the tip of the proboscis at metamorphosis, and the anus is terminal (Hadfield 1975; Peterson et al. 1999a). As in hemichordates, in larval echinoderms the coelomic sacs are also constructed along the api-
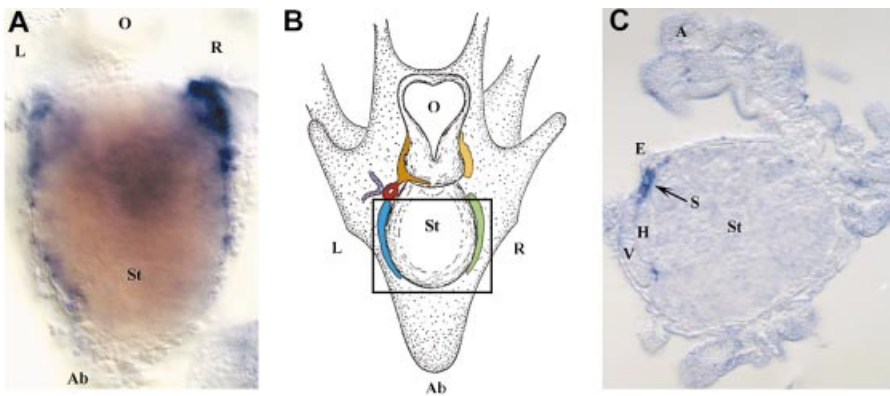
Fig. 1. In situ hybridization to *SpHox11/13b* mRNA in an *S. purpuratus* larva. (A) Nomarski optical view of a two-week-old larva hybridized with *SpHox11/13b* antisense probe. The gene is transcribed throughout the paired somatocoels with decreasing concentration of product toward the aboral side. (B) Diagram of a 2-week-old sea urchin larva color coded to show the different coelomic compartments: dark brown, left axocoel; light brown, right axohydrocoel; red, left hydrocoel; blue, left somatocoel; green, right somatocoel. The squared pink and purple tissue is the vestibule. The box indicates the area shown in focus in (A). (C) Oblique section near the area of maximum expression shown in (A). Specific staining is clearly restricted to the left somatocoel. No expression is found in the hydrocoel, vestibule, or endoderm. The right somatocoel is not shown. Abbreviations: A, larval arms; Ab, aboral; E, ectoderm; H, hydrocoel; L, left; O, oral; R, right; S, somatocoel; St, stomach; V, vestibule. B modified from Hyman (1955).

cal/blastoporal plane, because they too are derived from the gut. However, this linear relationship is transient; later in development the coelomic sacs change positions with respect to their origins in the larva. This occurs by means of a series of complicated movements and torsions that bring the mesoderm out of register with the apical/blastoporal axis (Hyman 1955; Ubaghs 1967).

Fig. 2. The coelomic architecture of the common ancestor of hemichordates and echinoderms. On the left is a dorsal view, and the right a left view. There are five (or possibly six) coeloms: the anterior protocoel or axocoel, connected to the exterior via the hydropore; two middle coeloms, the mesocoels or hydrocoels; and two posterior coeloms, the metacoels or somatocoels. Abbreviations: A, anterior; D, dorsal; L, left; P, posterior; R, right; and V, ventral.

The angle between the axis formed by adult mesodermal components and the primary embryonic axis ranges from almost 180° in crinoids (i.e., where the future oral end of the adult is near the blastoporal site of invagination), to roughly 90° in echinoids and asteroids, and is close to 0° in some holothurians and ophiuroids (i.e., where the future oral end of the adult is near the position of the apical pole of the embryo/larva). The important point for our discussion is that since the apical/blastoporal axis of the larva may or may not be parallel to the anterior/posterior axis of the adult, it is of no significance whatsoever in considering either the homologies of the adult axes or the ontogenic processes by which these are generated. This problem is not unique to echinoderms, and larval axis designations (e.g., right, dorsal, etc.) are often not applicable to the adult. For example, on the one hand, the larval and adult axes are clearly parallel in annelids and enteropneusts, while on the other hand, in many indirectly developing nemerteans the primary axis of the juvenile is orthogonal to the apical/blastoporal axis of the embryo/larva (see Fig. 3 in Peterson et al. 1997). Axial differences between the structures of indirectly developing embryos/larvae and the body plans of adult forms arise directly from the utilization of set-aside cells, the progeny of which produce the adult body plan, and which are mounted within the embryo at various angles to the embryo/larval axis (Davidson et al. 1995; Peterson et al. 1997).
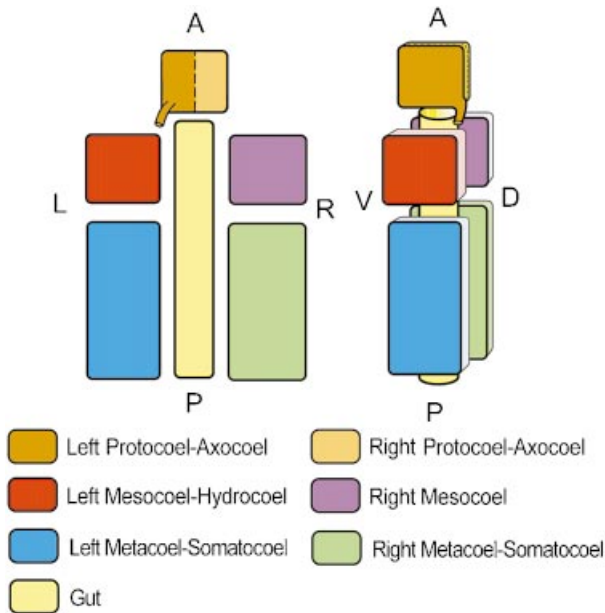
The outcome of the movements and torsions by which the coeloms are rearranged during echinoderm development is diagrammed in Fig. 3A. In the adult echinoderm, the derivatives of the left hydrocoel (most prominently, the water-vascular system) are stacked on top of the left somatocoelar derivatives. The left somatocoel is then stacked on top of the right somatocoel. A consistent way to describe this relationship is to say that the left hydrocoel is oral to the left somatocoel, which in turn is oral to the right somatocoel (see Fig.
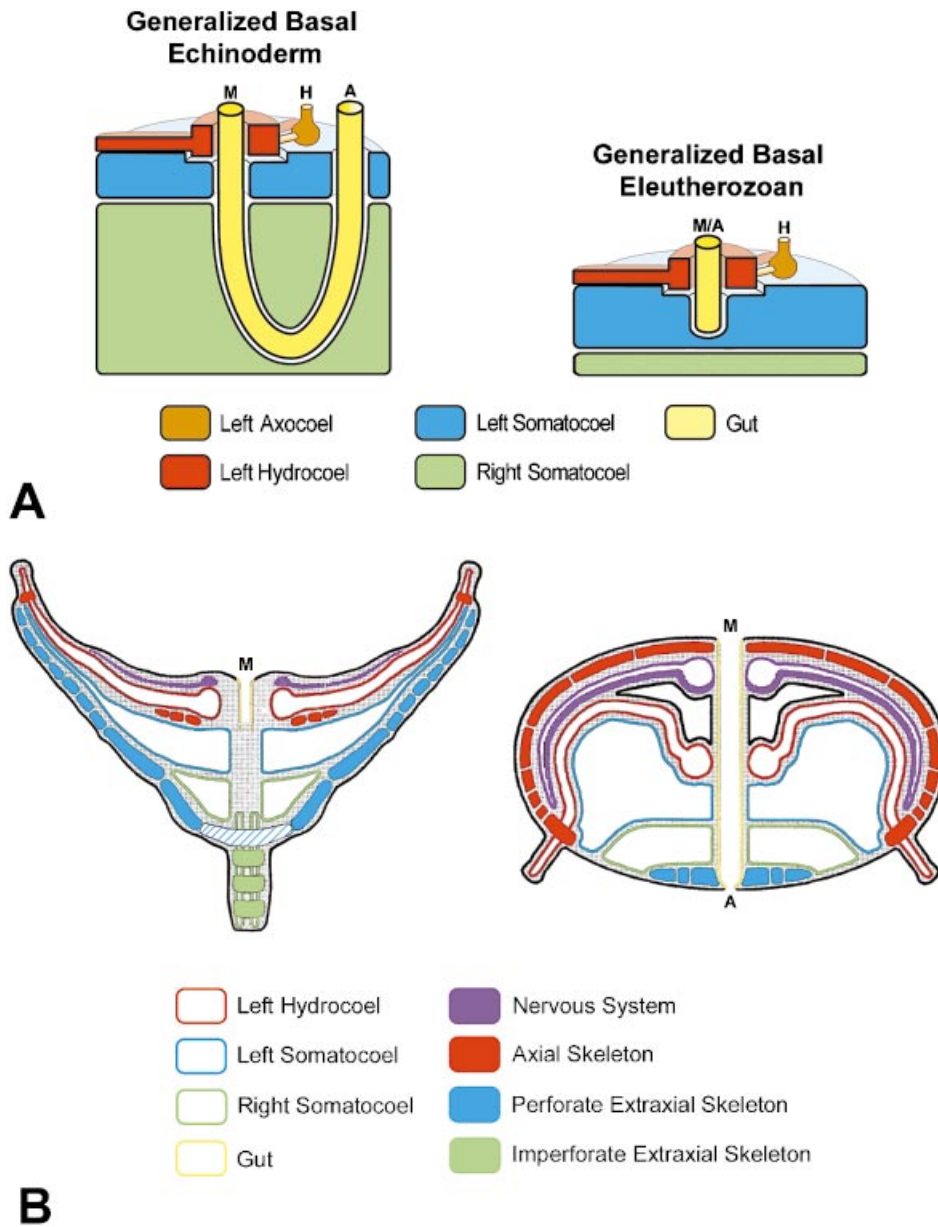
Fig. 3. The coelomic architecture of echinoderms, and the correspondence between the coeloms and the skeleton. (A) Highly diagrammatic cut-away views of a canonically organized early echinoderm (e.g., an edrioasteroid) and of an early eleutherozoan, displaying the "stacking" of the coeloms: the left hydrocoel (red) is oral with respect to the left somatocoel (blue), which in turn is oral to the right somatocoel (green). Notice that the gut (yellow) is U-shaped with the mouth and anus in the same plane. The axial sinus (brown), is connected to the water-vascular system via the stone canal (dark yellow), and the hydropore is placed asymmetrically with respect to the mouth and anus. In the early evolution of eleutherozoans, there is a dramatic decrease in the contribution of the right somatocoel, and the anus and posterior gut are lost as well. (B) Cross-sections of a crinoid (left) and sea urchin (right) showing the relation between the coeloms and the skeleton. Both are shown with the oral side upwards (and hence the sea urchin is upside down from its position in vivo). It is unclear if the plate indicated by blue hatching in the crinoid is part of the perforate or imperforate skeleton, although as an infrabasal it is most likely perforate extraxial, hence the blue coloring. The coelom in black in the sea urchin is the hyponeural sinus, a coelom derived from the left somatocoel. Abbreviations: A, anus; H, hydropore; M, mouth; M/A, mouth/anus (i.e., primitive mouth which also functions as the anus). (B) Modified from Mooi and David (1997).

3A). This is a general statement which is true irrespective of the amount of torsion involved (Hyman 1955). It is true whether the oral surface is directed away from the sea bottom, as in crinoids, or directed toward the sea bottom, as in echinoids.

RELATION BETWEEN ADULT SKELETAL AND COELOMIC ARCHITECTURE

Figure 3B shows that the arrangement of the adult coeloms is reflected in the skeletal anatomy (reviewed by Mooi and David 1997, 1998). Mooi and David have recognized two different types of skeleton in all echinoderms thus far examined, namely the axial skeleton and the extraxial skeleton. For our purposes the primary difference between these two types of skeleton is that the axial skeleton is associated with the water vascular system, which is derived from the left hydrocoel. The extraxial skeleton is not associated with the water-vascular system, and it is associated with somatocoelar skeletogenic tissues (there are other differences between these two types of skeletal plates extending beyond this discussion, which will not be reviewed here). The extraxial skeleton can be further subdivided into a perforate and an imperforate extraxial skeleton: the former includes the anus, hydropore, gonopore, and other pores such as epispires,

rhombs, etc., whereas the latter never contains any openings. Furthermore, the perforate and imperforate extraxial skeletons may be associated with the left and right somatocoels, respectively. Thus the linear arrangement of the adult derivatives of the coeloms (i.e., the hydrocoelar derivatives oral to the somatocoelar derivatives) is correlated directly with the position of the axial and extraxial skeletons. This relationship is shown by the color coding in Fig. 3B, for a crinoid (left) and an echinoid (right).

Mooi and David have shown that axial, and perforate and imperforate extraxial skeletal elements can be recognized throughout the phylum, even in bizarre early Paleozoic forms. Figure 4 shows three fossil taxa, an edrioasteroid (Fig. 4A), which is most likely a stem-group echinoderm (i.e., edrioasteroids arose before the latest common ancestor of the living forms; Paul and Smith 1984; Mooi and David, 1997); a solute (Fig. 4B), which is either another stem-group form (e.g., Littlewood et al. 1997) or a stem-group pelmatozoan (i.e., related to modern crinoids; see Sumrall 1997); and an early eleutherozoan (Fig. 4C) (see Dean 1999 for initial phylogenetic analysis). In all three forms the arrangement of axial and extraxial skeletons is apparent. Coelomic stacking appears to be a basic feature of echinoderm anatomy, seen in both living and extinct forms.

EVOLUTIONARY ORIGIN OF THE ECHINODERM ANTERIOR/POSTERIOR AXIS

The evidence we have reviewed so far yields the following statements. First, the transient mesodermal coeloms of echinoderm larvae have a clear anterior/posterior polarity, with the axocoel anterior and the somatocoels posterior. The polarity is certified by the patterns of expression of the *Hox11/13b* gene of *S. purpuratus* larvae, where it is transcribed in the mesoderm of the somatocoels, thus confirming that these indeed lie at the posterior end of the anterior/posterior axis. Second, the same polarity, here morphologically obvious, obtains in both larval and adult hemichordates, which are the sister group of the echinoderms. Third, the stacked coelomic architecture of modern echinoderms is the result of developmental changes which in echinoderms alter the original linear arrangement. Fourth, as Mooi and David showed, the morphology of the skeletal plates reflects the coelomic association of their skeletogenic tissues, and hence it would appear that stacking of coelomic derivatives has been part of the echinoderm body plan since at least the Early Cambrian.

Figure 5 shows our interpretation of the body axes of a canonical adult echinoderm. We use the edrioasteroid as a template, but the proposal is equally valid for all pentamerous echinoderms (and possibly non-pentamerous ones as well, e.g., helicoplacoids; see Fig. 6). The animal is shown in standard anatomical notation, with anterior to the left and dorsal to the top (note that this is not the normal position of edrio-

asteroids, which lived with the oral or anterior surface upward away from the sea floor, as in Fig. 4A). We propose that the stacking of coeloms follows the anterior/posterior axis such that the mouth is anterior, and the right somatocoel is posterior. As with other bilaterians (Brusca and Brusca 1990), the anterior/posterior axis orients the animal such that there is but a single plane of symmetry (the midsagittal plane) which divides the animal into left and right halves. This plane is positioned along the dorsal/ventral axis, and because it divides the animal into left and right halves it cannot be the anterior/posterior axis as proposed by Morris (1999). The midsagittal plane of symmetry is equivalent to the Carpenter plane of symmetry (see Hyman 1955; Moore and Fell 1966; Hotchkiss 1998) and as such defines the A ambulacrum, and the remainder of the ambulacra are lettered clockwise from A, viewed orally. The Carpenter ambulacral designations are shown in red letters in Fig. 5. Contrary to Hotchkiss (1998), we tentatively hypothesize that the area between the C and D ambulacra is dorsal because this is likely to be the primitive location of the hydropore in echinoderms. That is, the hydropore is dorsal in hemichordates, the outgroup for comparison. Note also that as in most hemichordates, the placement of the hydropore is to the right or to the left of the midline, and hence is the most conspicuous external asymmetry in both body plans. Although many earlier authors used the location of the anus (or periproct) to identify posterior (e.g., Moore and Fell 1966) it appears clear that the anus is not posterior, but is rather anterior and dorsal. This arrangement is not unprecedented: the anus in the adult sipunculid is also anterior and dorsal, but, of course, arose independently from that of the echinoderm.

A very important implication of this model is that the five ambulacra are not primary body axes (see Raff and Popodi 1996), but instead are analogous to arthropod and vertebrate limbs because like these appendages, they are outgrowths from a central axis. This is entirely consistent with Hotchkiss' (1998) "rays-as-appendages" model except that ray A is not left but lies along the dorsal/ventral plane (and in our scheme would then be ventral). Also consistent with the interpretation of ambulacra as analogs of appendages is the expression of *Distalless* gene at the tips of the growing arms (Panganiban et al. 1997; Lowe and Wray 1997). Note also that our scheme is inconsistent with two ideas considered previously, namely that the radial nerve ring is an anterior/posterior axis joined head-to-tail, or that it is a bifurcation of a linear central nervous system to produce radial forms (Raff and Popodi 1996). Because our interpretation of echinoderm body axes is applicable to all echinoderms, living and extinct, it also indicates the morphological changes required during evolution to generate echinoderm body organization from that of a conventional bilaterally organized deuterostome ancestor. The developmental program elements that are specifically responsible for this aspect of the echinoderm body plan are those which execute coelomic stacking.
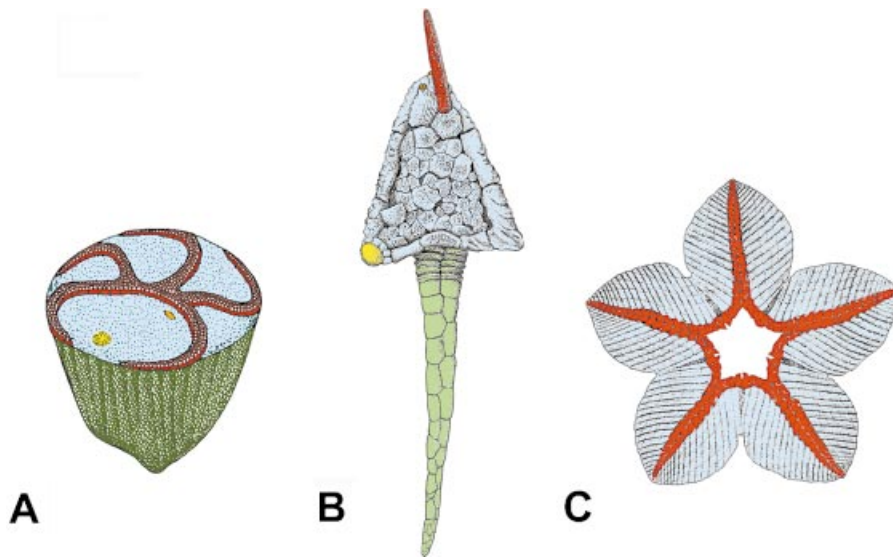
Fig. 4. Early Paleozoic echinoderms and the tripartite skeleton. (A) *Camptostroma roddyi*, an edrioasteroid from the Early Cambrian of Pennsylvania. The axial skeleton is in red, the perforate extraxial skeleton is in blue, and the imperforate skeleton is in green. The periproct (anus) is indicated in yellow, and the hydropore in brown. Skeletal designations are from Mooi and David (1998). (B) *Iowacystis sagittaria*, a solute (= homoiostelean homalozoan) from the Late Ordovician of Iowa. The color scheme is the same as for the edrioasteroid, but skeletal designations are our own interpretations following Mooi and David (1998). (C) *Vellebrunaster thorali*, an Early Ordovician asterozoan from France. This is an oral view of the animal, but there is no imperforate extraxial skeleton, nor is there a periproct. Again, skeletal designations are our own interpretations following Mooi and David (1998). (A) is from Paul and Smith (1984); (B) is from Caster (1967); (C) is from Spencer (1951).

VARIATIONS ON THE MORPHOLOGICAL THEME

One conspicuous difference between the echinoderm body plan and other bilaterian body plans is that early echinoderms "sat" on or were attached to trilobite skeletal debris on the sea floor (see Daley 1996). Their posterior ends were downward, and their anterior ends faced upward, their ambulacra extending radially out from the anterior/posterior axis. Subsequent evolution within the phylum, especially within the eleutherozoans, has modified this primitive body plan extensively. First, as Mooi and David (1998) recognized, eleutherozoans have entirely lost the imperforate extraxial skeleton (e.g., the stalk or stem found in pelmatozoans and early stem-group forms). This loss is probably associated with their "mobile" existence, and must have occurred early in their evolutionary history. Primitive eleutherozoans also lacked an anus (Paul and Smith 1984), and the anus evolved anew, independently, in the ancestors of holothurians and echinoids, and in some asteroids. Finally, one notable group of eleutherozoans, the irregular echinoids, independently evolved a new plane of bilateral symmetry. This is shown in Fig. 6. Here recent echinoderms (except ophiuroids) are indicated in oral perspective with the hypothesized dorsal surface toward the top (as in Fig. 5). Each ambulacrum is assigned a Carpenter plane designation following the scheme of Hotchkiss (1998) who based the assignment of homologous rays on the particular sequence in which the ambulacral plates are laid down (Lovèn's Law); thus all are shown in presumed homologous orientation. In each view the anterior/posterior axis is compressed so that the orifices on the aboral side are visible. Notice that the plane of bilateral symmetry in crinoids (representative of most if not all pentamerous pelmatozoans), in asteroids, and in holothurians is homologous to the primitive plane of symmetry in edrioasteroids (see Fig. 5). However, in irregular echinoids, the new plane of symmetry is roughly perpendicular to the original plane of symmetry.
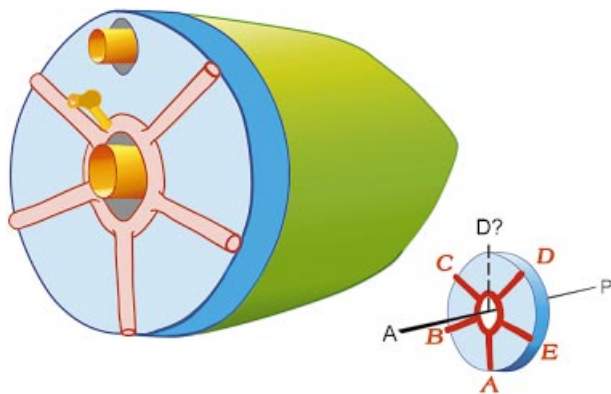

Fig. 5. Proposed interpretation of axial relations in a primitive echinoderm. Shown in standard anatomical position is an edrioasteroid-like echinoderm with its anterior end to the left and the dorsal side to the top. The hydrocoel (as the water-vascular system) is shown in red, the left somatocoel in blue and the right somatocoel in green. The U-shaped gut is in orange and the axial sinus is in brown. The red letters on the axis designation diagram are Carpenter letters identifying each ambulacrum. The designation of dorsal is equivocal and hence is indicated with a question mark. Note that there is an axis of bilateral symmetry orthogonal to the proposed anterior/posterior and dorsal/ventral planes, i.e., the left/right axis. Abbreviations: A, anterior; P, posterior; D, dorsal; R, right; L, left.

Extreme modifications to this basic architecture are not limited to eleutherozoans. Helicoplacoids, also included in Fig. 6, are a bizarre group of Early Cambrian echinoderms, also distinguished by their absence of pentamery; they have three instead of five ambulacra (Paul and Smith 1984; Durham 1993). Paul and Smith (1984) hypothesized that the single ray is homologous to ray A of pentamerous echinoderms; the next two rays are homologous to the B + C, and the D + E rays (thus in the evolution of pentamery each lateral ray split in two generating the five rays of modern echinoderms). Helicoplacoids were spiral in shape, and they lived embedded in soft mud with the long axis of the animal perpendicular to the sea floor. When oriented similarly to the other echinoderms in Fig. 6 (i.e., ray A toward the bottom of the page), it is evident that the long axis of the helicoplacoid lies roughly in the original left/right axis. This requires, however, that the predicted positions of the mouth, anus, and hydropore are as indicated in Fig. 6 (which is not known). Alternatively, were Durham's (1993) identification of the mouth at the upper tip of the body correct, then the long spiral axis of the helicoplacoid would be the anterior/posterior axis of pentamerous echinoderms.

EVOLUTIONARY MYSTERIES

Many aspects of the ontogeny and architecture of the adult echinoderm body plan remain mysterious. An important question, since in it lies a key to echinoderm evolution, is how in development the left somatocoel becomes stacked on top of (or, more properly, anterior of) the right somatocoel. Because *Hox* genes such as *SpHox11/13b* are initially expressed in the mesodermal anlagen while they are still bilaterally symmetrical, stacking of the coeloms evidently follows *Hox* gene expression. A second and possibly related mystery is the reduction of the right hydrocoel. How this occurs and what its functional significance is remains obscure. Peterson et al. (1999b) showed that the mesoderm of both hydrocoels of the echinoderm express *brachyury*, as does the mesoderm of both mesocoels of the hemichordate (Peterson et al. 1999a). Hence a left and right hydrocoel are primitively part of the echinoderm body plan, just as are a left and right somatocoel, by similar arguments. An interesting possibility is that in crinoids the right hydrocoel is in fact not reduced, but gives rise to the pentamerally organized chambered organ. Even though both ontogenetic evidence (summarized in Hyman 1955), and the extraxial character of the skeletal plates on the crinoid stalk (Mooi and David 1998) weaken this suggestion, it could be tested. Were the chambered organ in fact a right hydrocoelar derivative, it should share patterning mechanisms with the left hydrocoel and the mesocoels of hemichordates (e.g., expression of *Brachyury*). However, if the chambered organ is in fact a right somato-
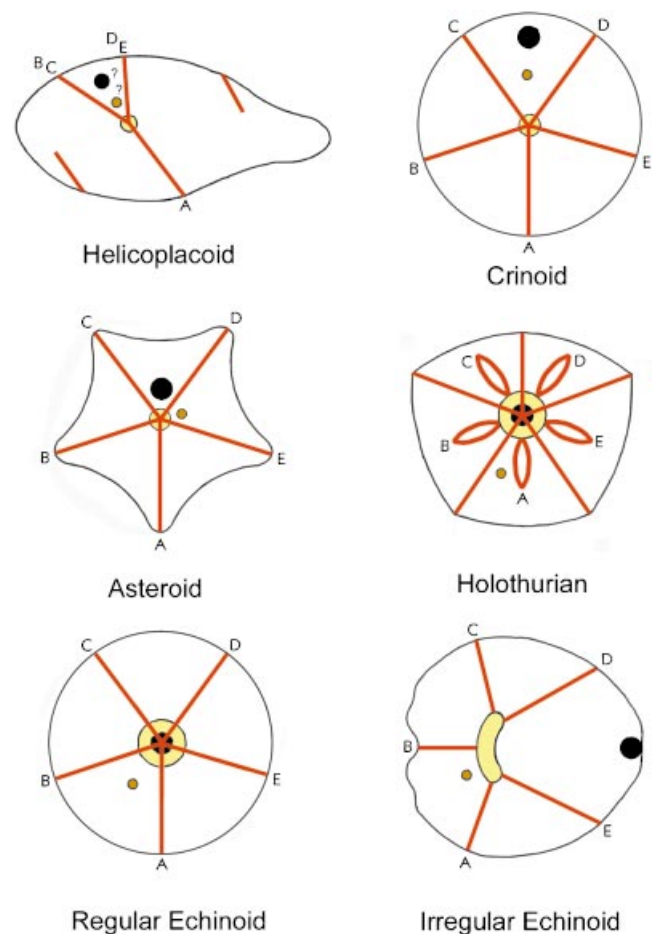

Fig. 6. Ambulacral maps in oral view of recent echinoderms, and of the extinct helicoplacoid. The anterior/posterior axis is perpendicular to the plane of the figure. The dorsal side is toward the top, and ventral at the bottom. Stylized ambulacra are shown in red, with Carpenter letters indicating proposed homologous rays in each echinoderm taxon (data from Hotchkiss 1998). Note that in holothurians, it is the tentacles around the mouth and not the tube feet along the body which are homologous to the ambulacra in other echinoderms (see Mooi and David 1997, 1998 for discussion). The mouth is shown as a yellow oval, the anus as a black oval, and the hydropore as a brown oval. The maps are drawn such that they are compressed in two dimensions so that for example, the anus of the echinoid, even though it is located aborally, is visible in the diagram. The question marks in the helicoplacoid indicate that the anus (periproct) and hydropore have not been located. Ray designations in the helicoplacoid are from Paul and Smith (1984). The axes of symmetry in the crinoid (crinoidal plane), asteroid (asteroid plane), and holothurian (holothurian plane) are the same as in the edrioasteroid and hence are the primitive midsagittal plane. The position of the anus in the asteroid is analogous to its position in the crinoid only because after the anus was lost in the asteroid stem-lineage (see Paul and Smith 1984), it evolved anew in the same interambulacral position (CD) as in the crinoid and other primitive echinoderms (Hotchkiss 1998). The symmetry plane in irregular echinoids (Lovèn plane), however, is not homologous to the original midsagittal plane of symmetry. The plane designations and design of the figure are modified from Ubaghs (1967).

coelar derivative, it should express the crinoid ortholog of *SpHox11/13b*.

CONCLUSIONS

In this paper, we present a new interpretation of axial relations in the radially symmetrical echinoid body plan and a theory for its derivation from a bilaterally organized common ancestor. The key to echinoderm anatomical organization is the stacking of the coelomic mesoderm derivatives. These begin in ontogeny as paired coelomic sacs arranged bilaterally along the axis found by the mouth, the foregut, and the midgut, but then undergo a series of rearrangements that result in a stack of coelomic derivatives in the juvenile. The result is an architecture in which the mouth at the primitively anterior pole of the anterior/posterior axis overlies the left hydrocoelar derivatives, which in turn overlie the derivatives of the primitively posterior somatocoels, first the left, and below it the right somatocoelar derivatives. Coelomic stacking is general for all echinoderms, both crown and stem-group forms. The developmental program that directs this ontogenic process is thus a genetic synapomorphy of the echinoderms. The Precambrian installation of this program in a branch of the deuterostomes is to be regarded as among the fundamental evolutionary steps leading toward the echinoderm body plan.

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