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SHORT REVIEW

Building divergent body plans with similar genetic pathways

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Deuterostome animals exhibit widely divergent body plans. Echinoderms have either radial or bilateral symmetry, hemichordates include bilateral enteropneust worms and colonial pterobranchs, and chordates possess a defined dorsal–ventral axis imposed on their anterior–posterior axis. Tunicates are chordates only as larvae, following metamorphosis the adults acquire a body plan unique for the deuterostomes. This paper examines larval and adult body plans in the deuterostomes and discusses two distinct ways of evolving divergent body plans. First, echinoderms and hemichordates have similar feeding larvae, but build a new adult body within or around their larvae. In hemichordates and many direct-developing echinoderms, the adult is built onto the larva, with the larval axes becoming the adult axes and the larval mouth becoming the adult mouth. In contrast, indirect-developing echinoderms undergo radical metamorphosis where adult axes are not the same as larval axes. A second way of evolving a divergent body plan is to become colonial, as seen in hemichordates and tunicates. Early embryonic development and gastrulation are similar in all deuterostomes, but, in chordates, the anterior–posterior axis is established at right angles to the animal–vegetal axis, in contrast to hemichordates and indirect-developing echinoderms. *Hox* gene sequences and anterior–posterior expression patterns illuminate deuterostome phylogenetic relationships and the evolution of unique adult body plans within monophyletic groups. Many genes that are considered vertebrate 'mesodermal' genes, such as *nodal* and *brachyury T*, are likely to ancestrally have been involved in the formation of the mouth and anus, and later were evolutionarily co-opted into mesoderm during vertebrate development. *Heredity* (2006) **97,** 235–243. doi:10.1038/sj.hdy.6800872; published online 26 July 2006

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Deuterostome phylogenetic relationships

Deuterostome phylogenetic relationships have been reviewed extensively elsewhere (Schaeffer, 1987; Cameron *et al*, 2000; Bourlat *et al*, 2003; Smith *et al*, 2004; Blair and Hedges, 2005; Zeng and Swalla, 2005; Delsuc *et al*, 2006) so will be briefly discussed here. Deuterostomes are monophyletic, and include two great clades: Ambulacraria, which consists of Echinodermata and Hemichordata (Figure 1I; Cameron *et al*, 2000; Peterson, 2004; Smith *et al*, 2004), and Chordata, which consists of Tunicata, Cephalochordata (lancelets), and Vertebrata (Figure 1II; Cameron *et al*, 2000; Zeng and Swalla, 2005). Xenoturbellida, a potentially new phylum of the Deuterostomia that has been described, is thought to be related to the Ambulacraria, but the exact placement within the deuterostomes is not yet clear (Bourlat *et al*, 2003).

There is a plethora of evidence for echinoderms and hemichordates as sister groups (Peterson, 2004; Smith *et al*, 2004; Zeng and Swalla, 2005), so features that hemichordates share with chordates were likely to have been present in the deuterostome ancestor (Gerhart *et al*, 2005; Rychel *et al*, 2006). There is both molecular and morphological evidence that the Ambulacraria are monophyletic (Cameron *et al*, 2000; Peterson, 2004; Smith *et al*, 2004). Similarities in the larvae of echinoderms and hemichordates have been noted for years (Figure 2; Morgan, 1891; Dautov and Nezlin, 1992; Strathmann and Eernisse, 1994; Nielsen, 1997) and echinoderms and hemichordates have recently been shown to share motifs in three posterior *Hox* genes, *Hox 11/13a*, *11/13b* and *11/13c*, as discussed later (Peterson, 2004). This raises the interesting question of how the two phyla have such different adult body plans, when they have such similar larvae.

Conversely, within chordates, Tunicata is the only subphylum that is classified by larval, rather than adult characteristics (Zeng and Swalla, 2005). Tunicates are monophyletic (Swalla *et al*, 2000) and have a unique adult body plan, including the cellulose tunic, as discussed in Zeng and Swalla (2005). It is difficult to place tunicates reliably within the deuterostomes, due to the long branches found for most of their genes (Winchell *et al*, 2002; Blair and Hedges, 2005; Zeng and Swalla, 2005). Interestingly, new genome analyses suggest that tunicates are more related to vertebrates than cephalochordates, but these results could be an artifact of incomplete data from cephalochordates and hemichordates (Blair and Hedges, 2005; Philippe *et al*, 2005; Delsuc *et al*, 2006). Understanding the position of the tunicates

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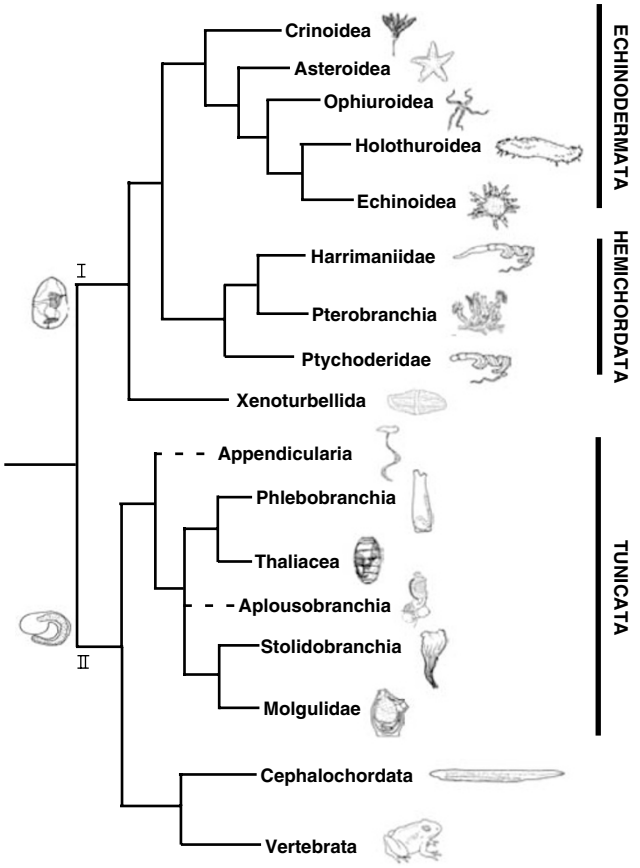

Figure 1 Current deuterostome phylogeny, with the three major invertebrate clades marked on the right: Echinodermata, Hemichordata and Tunicata. Vertebrates and Cephalochordata (lancelets) form a fourth clade, Chordata. Ciliated Ambulacraria larvae (I) and Tunicata tadpole larvae (II) are likely to have separate origins. Uncertainties in the Tunicata phylogeny are marked by dotted lines. Modified from Zeng and Swalla (2005).

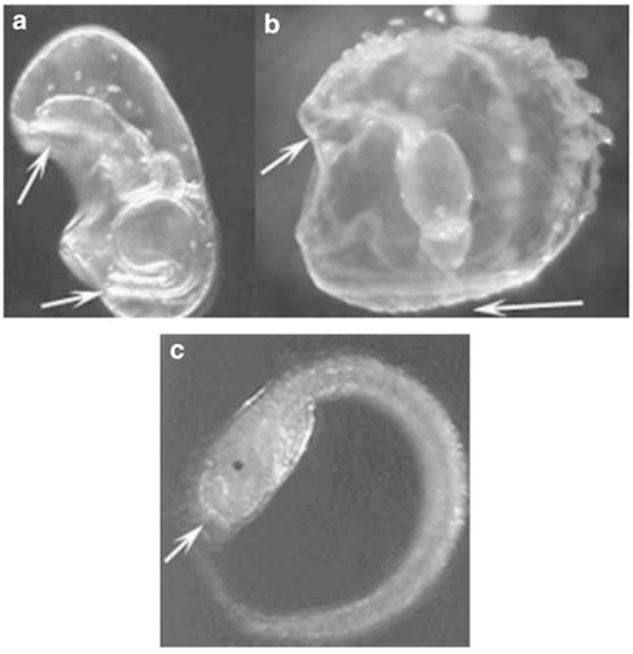

Figure 2 Deuterostome larvae, showing (**a**) a sea star echinoderm larvae, (**b**) a hemichordate tornaria larva and (**c**) a tunicate larva, all oriented with the mouth to the left and anus to the bottom. (**a**) Sea star larvae have an anterior (top left), which was the original animal pole of the egg. (**b**) Anterior in the hemichordate tornaria larva is the apical tuft (top of photo). (**a, b**) Both of these larvae feed with ciliary beating and have well-developed guts and coeloms. The mouth of the sea star and hemichordate larvae are seen to the left (arrow). The posterior anus forms at the former vegetal pole (arrows at bottom). In hemichordates, the larval mouth becomes the adult mouth and the proboscis develops anterior to the mouth. The gill slits and abdomen of the worm will develop posteriorly. (**c**) The tunicate larva is nonfeeding and lacks a heart, blood and gut, which will develop after metamorphosis. An arrow marks the anterior, where the mouth will form after metamorphosis, but is not yet open. There is no anus at this stage.

within the deuterostomes will require continued phylogenetic and genomic analyses, coupled with careful studies of evolutionary and developmental processes, including analyses of gene networks (Davidson and Erwin, 2006).

Early development in the deuterostomia

All deuterostomes gastrulate at the vegetal pole, thus the blastopore is formed at or near the vegetal pole, later becoming the anus (Chea *et al*, 2005). However, the chordate larvae of ascidians have completely different structures and functions than the larvae of echinoderms and hemichordates (Figure 2; Ettensohn *et al*, 2004). Many echinoderm and hemichordate species have feeding larvae that capture food by ciliary motion and can spend months feeding in the plankton (Figure 2; Dautov and Nezlin, 1992; Strathmann and Eernisse, 1994; Nielsen, 1997). On the other hand, chordate ascidian larvae are nonfeeding, and must metamorphose in order to be able to feed (Figure 2; Davidson *et al*, 2004). We believe that these larvae have independent evolutionary origins (Zeng and Swalla, 2005). Ascidian embryos and larvae share many genetic pathways with chordate embryos (Passamaneck and Di Gregario, 2005), while echinoderms and hemichordates share similar genetic pathways during the embryonic and larval stages (Shoguchi *et al*, 1999). In hemichordates and indirect-developing echinoderms, the animal–vegetal axis of the egg becomes the anterior–posterior axis of the larva, so a mouth is formed secondarily at the location where the archenteron contacts the ectoderm (Figures 2–4; Chea *et al*, 2005). In contrast, in chordates, gastrulation results in the movement of large amounts of mesoderm into the archenteron, in order to form the notochord and the surrounding muscular somites, so the anterior–posterior axis lies at a right angle to the animal–vegetal axis (Chea *et al*, 2005).

Different adult body plans built from similar larvae

Hemichordate tornaria larvae are similar morphologically to the bipinnaria larvae of sea stars and the auricularia larvae of sea cucumbers (Figures 2–4; Dautov and Nezlin, 1992; Strathmann and Eernisse, 1994; Urata and Yamaguchi, 2004). This type of larva, with a distinct gut and three coeloms has been called collectively a dipleurulid larva (Nielsen, 1997). Development of a

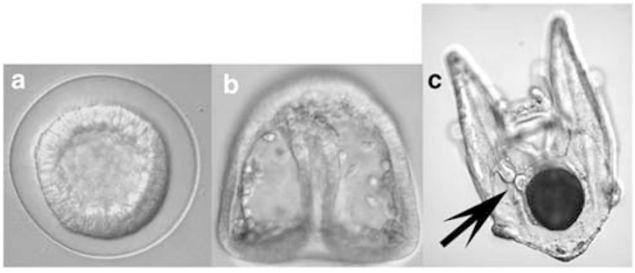

Figure 3 Echinoid development (**a**). Early blastula shows a thickening at the vegetal pole (bottom of the photo), where gastrulation will begin. (**b**) The archenteron invaginates at the vegetal pole (bottom of the photo), which will become the anus, and the mouth is formed to the left side in this photo, where the archenteron touches the ectoderm. This is also the site of *nodal* and *brachyury* expression in sea urchins (Duboc *et al*, 2004; Peterson *et al*, 1999b). (**c**) Later, the adult rudiment is formed where the ectoderm touches the larval coelom on the left side of the larva (arrow). This is opposite the second site of *nodal* expression in sea urchin larvae (Duboc *et al*, 2005).

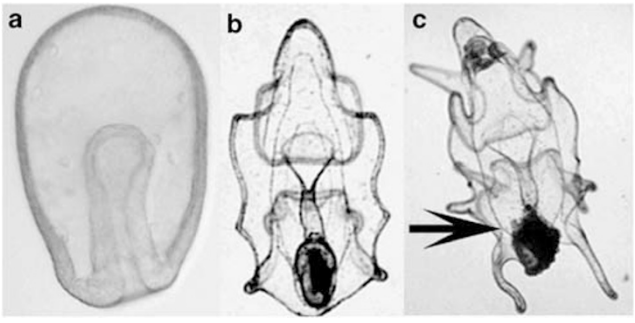

Figure 4 Sea star development (**a**). Sea stars gastrulate similarly to sand dollars, with the vegetal pole the site of archenteron formation (bottom of the photo), although the mouth is formed more at the midpoint of the larva. (**b**) Later, in the bipinnaria larva, the adult rudiment is seen as new pigmentation, forming in the posterior of the larva. (**c**) The advanced brachiolaria larva shows the anterior–posterior larval organization, while the radial adult is formed at the posterior of the animal (arrow). After metamorphosis, the tiny new radial sea star will engulf the rest of the bilateral larva.

hemichordate planktonic larvae and its complete metamorphosis into an enteropneust worm, *Balanoglossus misakiensis*, has recently been published (Urata and Yamaguchi, 2004). This study documents larval and adult structures throughout early development and metamorphosis in an enteropneust worm with tornaria larvae (Urata and Yamaguchi, 2004). The authors show that the hemichordate adult body plan is elaborated onto the larval body plan (Urata and Yamaguchi, 2004), as suggested by earlier studies (Morgan, 1891; Hadfield, 1975). *Balanoglossus misakiensis* embryos gastrulates at the vegetal pole and the blastopore at the vegetal pole becomes the anus (Urata and Yamaguchi, 2004; Chea *et al*, 2005). The mouth is formed secondarily to the side when the archenteron touches the ectoderm, similarly to echinoderm embryos (Figures 3 and 4). An apical tuft is formed at the anterior, where the animal pole was located in the fertilized egg (Figure 2; Hadfield, 1975). After metamorphosis, the nerves of the apical tuft degenerate and the proboscis coelom is formed, developing a proboscis at the very anterior of the animal (Figure 2; Urata and Yamaguchi, 2004). The larval mouth becomes the adult mouth of the worm, located in the collar region, while the posterior of the enteropneust worm is elaborated by growth posterior to the neck region (Urata and Yamaguchi, 2004). In summary, in enteropneust hemichordates, the adult body plan is dramatically different inmorphology from the larval body plan, but the adult retains the same anterior–posterior and oral–aboral axes.

In contrast, indirect-developing echinoderms exhibit a radical metamorphosis, where the axes of the adult body plan do not necessarily correspond to the larval body axes (Figures 3 and 4). For example, in echinoids, the touching of invaginating ectoderm and coelom will mark where the adult rudiment forms inside of the pluteus larva (Figure 3). The same pattern is seen in sea stars as shown in Figure 4. The adult sea star, with fivefold symmetry, emerges from a bilateral larva. The larval anterior was the original animal pole of the fertilized egg, and the posterior is the anus, where the blastopore was formed (Figure 4). Smith *et al* (2004) discuss how it is likely that the echinoderm ancestor was a bilateral adult and that the prevalence of pentaradial symmetry in extant forms involved a mass extinction of many clades of echinoderms.

In summary, if the Ambulacraria were classified on larval morphology, they would be considered one phylum. Instead, they are divided into separate phyla, echinoderms and hemichordates, based on adult morphology. The echinoderms have a derived body plan, many groups show pentaradial adult symmetry, and all extant echinoderms lack gill slits (Smith *et al*, 2004). It has been noted that hemichordates share gill slits with the chordates, so the deuterostome ancestor was likely a benthic worm-like creature with gill slits (Cameron *et al*, 2000; Bourlat *et al*, 2003; Peterson, 2004; Gerhart *et al*, 2005; Zeng and Swalla, 2005; Rychel *et al*, 2006). When one examines chordate features, hemichordates share at least three of these morphological characters: the gill slits, an endostyle and a postanal tail (Gerhart *et al*, 2005; Rychel *et al*, 2006). The simplest interpretation of these results is the chordate ancestor was worm-like, with an endostyle, a postanal tail and gill slits. The key chordate innovation, then, was the evolution of a notochord and a dorsal neural ectoderm with the resulting loss of an ectodermal nerve net in the adult (Swalla, 2006).

Coloniality is a fast track to new body plans

In both hemichordates and tunicates, very different body plans evolved by switching from a solitary to a colonial life history and perhaps even vice versa, from colonial to a solitary mode (Cameron *et al*, 2000; Zeng and Swalla, 2005; Zeng *et al*, 2006). Hemichordate phylogenies have shown that the colonial pterobranchs may be more closely related to the Harrimaniids, which have direct developing larvae, than to the Ptychoderids (Figure 1; Halanych, 1995; Cameron *et al*, 2000). Tunicate phylogenies show that the evolution of coloniality has occurred several times independently in tunicates (Swalla *et al*, 2000) and within ascidians (Wada *et al*, 1992; Zeng *et al*, 2006; Yokobori *et al*, 2006).

There are several consequences of evolving a colonial lifestyle from a solitary one, which affect adult axes and mode of reproduction (Figure 5; Davidson *et al*, 2004).

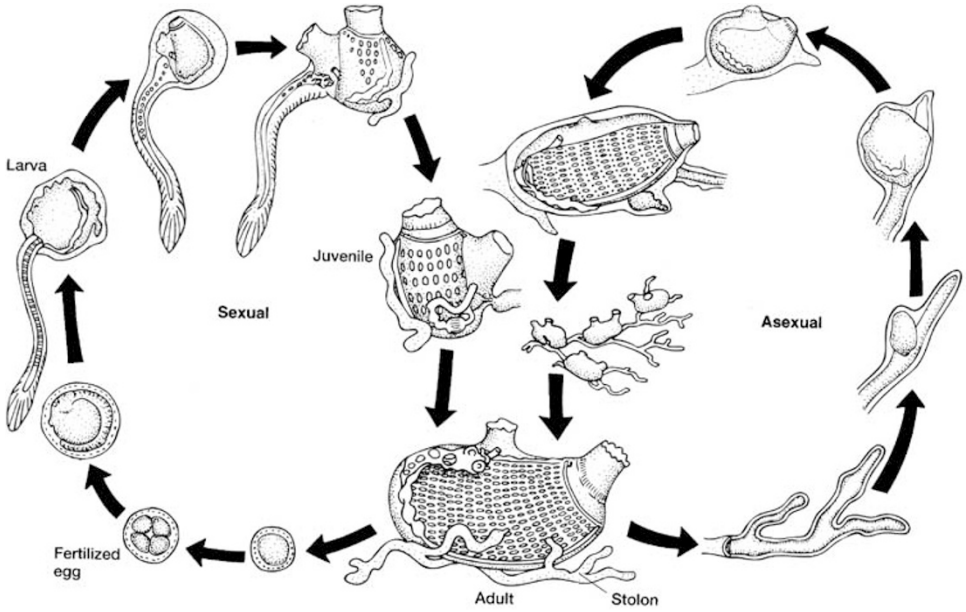

Figure 5 Coloniality in tunicates – a schematic diagram of the development of colonial ascidians. On the left is shown embryonic development into a tadpole larva, going through metamorphosis. On the right is a colonial ascidian in the process of budding. An exact replica of the adult can be formed either by a tadpole or by budding in colonial species. Used with permission from Kardong (2006).

First, there is usually a miniaturization of the adult when comparing closely related solitary and colonial species (Kardong, 2006; Zeng *et al*, 2006). This is also normally accompanied by changes in polarity, as colonial species form a superstructure of individuals (Zeng *et al*, 2006). Finally, in colonial species, asexual reproduction goes on continuously by budding to form new individuals (Figure 5; Kardong, 2006). In contrast, solitary species reproduce solely by sexual reproduction (Figure 5; Davidson *et al*, 2004). Colonial species also brood their larvae, and spawn competent larvae that are ready to settle (Davidson *et al*, 2004; Zeng *et al*, 2006). These life history and body plan changes, miniaturization, budding, and brooding, are seen in the evolution of coloniality in both hemichordates (Cameron *et al*, 2000) and tunicates (Davidson *et al*, 2004).

There are no known extant deuterostome species that can switch from a solitary to colonial lifestyle. In extant deuterostomes, one sees closely related species that are colonial or solitary, and an intermediate social phenotype that may be an evolutionary step in becoming colonial (Zeng *et al*, 2006). However, in some aplousobranch colonial ascidians, reproduction continues asexually unless the possibility of outcrossing is detected through nonself sperm in the water (Bishop *et al*, 2000). As basal metazoans (cnidarians) have some solitary species, some colonial species and some species that are capable of switching life histories, it is possible that the deuterostome ancestor was capable of either a colonial lifestyle with asexual reproduction or a solitary lifestyle with sexual reproduction or a combination of both life histories (Davidson *et al*, 2004). In the evolution of echinoderms and chordates, especially in the cephalochordate/vertebrate lineage, the colonial lifestyle and asexual reproduction capacities were lost, after which all species became solitary and exclusively sexual.

In addition, it appears that echinoderm larvae have the ability to clone themselves when they are in the plankton for long periods of time (Eaves and Palmer, 2003; Knott *et al*, 2003). Under controlled laboratory conditions, the clones have been shown to be able to metamorphose and form normal juveniles (Eaves and Palmer, 2003; Knott *et al*, 2003). It is not yet known whether hemichordate tornaria larvae also have the ability to clone, but it would be an interesting finding. Solitary tunicate larvae and adults have not been reported to be able to clone, but colonial tunicates can form a new individual from single epidermal ampullae (Rabinowitz and Rinkevich, 2003). This capacity for cloning and regeneration in nonvertebrate deuterostomes has not received the attention and interest that it deserves. It is likely that the genetic programs involved in larval cloning and colonial budding will be similar to the programs necessary for regeneration and stem cell renewal (Laird *et al*, 2005). These processes will likely share genetic pathways across the deuterostomes, including vertebrates and humans.

Hox developmental gene expression in deuterostomes

One of the key innovations during the evolution of vertebrates was the duplication of developmental genes, including the clusters of homeobox gene transcription factors that are involved in anterior–posterior patterning in both protostomes and deuterostomes (Figure 6; Carroll, 1995). While ascidians (Di Gregorio *et al*, 1995; Spagnuolo *et al*, 2003) and lancelets (amphioxus) (Holland *et al*, 1994; Wada *et al*, 1999) have only a single *Hox* cluster, tetrapods have four clusters (Wada *et al*, 1999) and teleost fish have eight clusters (Figure 6; Amores *et al*, 1998; Meyer and Malaga-Trillo, 1999). In vertebrate embryos (Holland *et al*, 1994; Carroll, 1995), lancelet (Holland *et al*, 1994; Wada *et al*, 1999) and ascidian larvae (Di Gregorio *et al*, 1995; Spagnuolo *et al*, 2003) expression of the *Hox* genes proceeds in a collinear temporally and

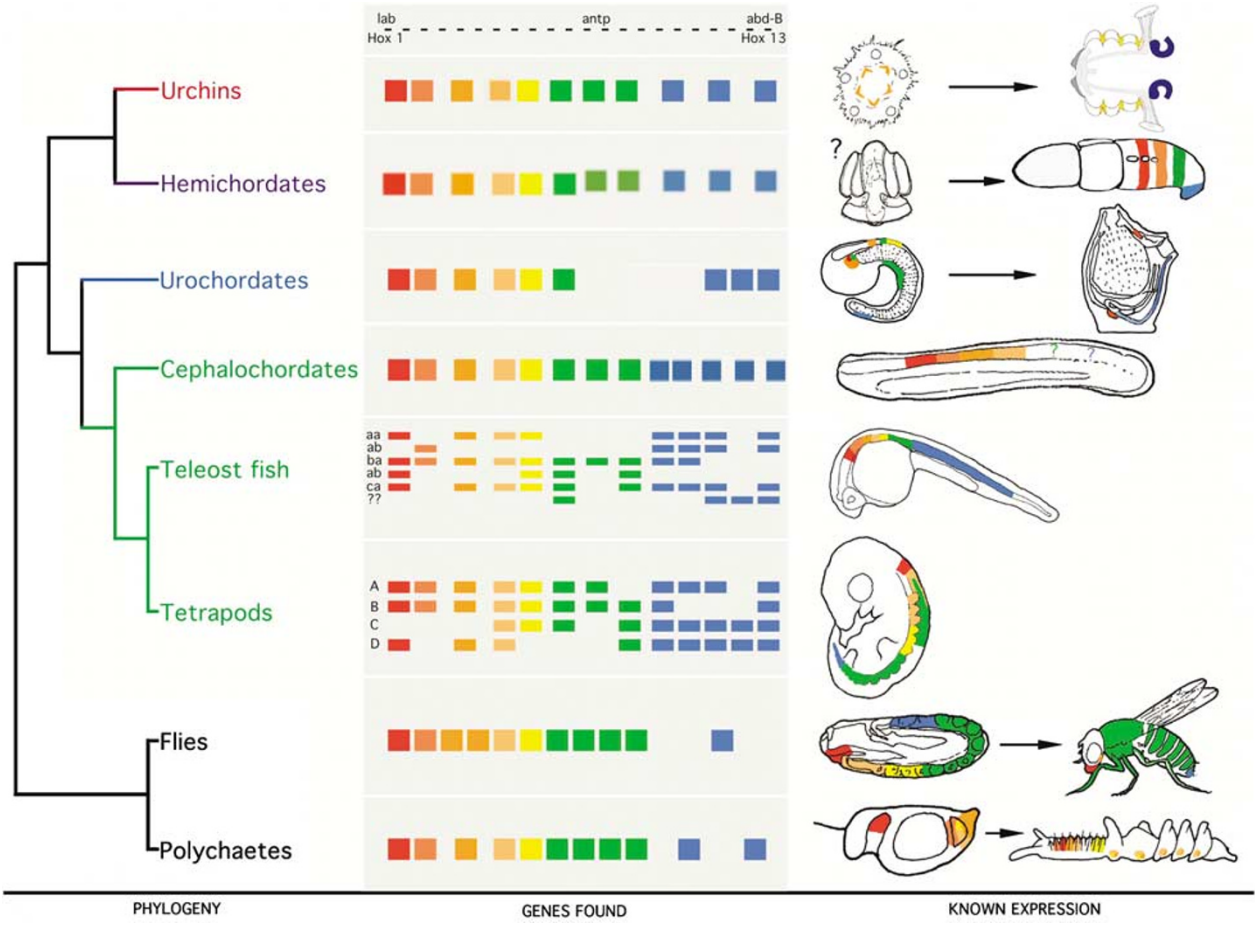

Figure 6 Expression of *Hox* genes in deuterostomes – the *Hox* gene cluster is duplicated in vertebrates. There are eight *Hox* gene clusters in teleost fishes, showing an additional duplication from the four *Hox* gene clusters found in the tetrapod vertebrates. In contrast, the invertebrate deuterostomes each have a single cluster. Ascidians lack some of the middle *Hox* genes, and the cluster is broken up onto two chromosomes. Echinoderms and hemichordates share an independent duplication of the posterior genes, called *Hox 11/13a*, *Hox 11/13b* and *Hox 11/13c*. Hemichordates show anterior to posterior expression in the ectoderm, which will produce a nerve net later in development. Echinoderms show adult expression in the nerve ring with the oral side corresponding to anterior in chordates and hemichordates.

spatially defined pattern from anterior to posterior (Figure 6). In all of the invertebrate deuterostomes there is a single *Hox* cluster. In echinoderm and hemichordate *Hox* clusters (Martinez *et al*, 1999; Long *et al*, 2003), the posterior *Hox* genes share motifs, suggesting that they diverged independently from the posterior *Hox* genes in the chordates (Peterson, 2004; Figure 6). In hemichordates, the expression of the *Hox* genes is in an anterior to posterior manner, with the anterior genes being expressed in the proboscis, and the posterior genes expressed in the postanal tail (Lowe *et al*, 2003; Figure 6). The expression of *Hox* genes in sea urchins initially did not appear to proceed in a colinear manner during embryonic development (Popodi *et al*, 1996; Arenas-Mena *et al*, 1998; Martinez *et al*, 1999). However, recent studies in a direct developing sea urchin suggest that the oral–aboral axis of echinoid echinoderms is similar to the anterior–posterior axis of hemichordates and chordates (Morris and Byrne, 2005). Furthermore, most of the *Hox* genes in the cluster are expressed only during the development of the adult, and so far only two show any early larval expression (Arenas-Mena *et al*, 1998; Martinez *et al*, 1999; Morris and Byrne, 2005). For *Hox* cluster members 6–11/13, expression is detected during late larval development in nested domains of the posterior coeloms; cluster member six is expressed in the anterior part and 11/13 in the posterior part with the intervening genes exhibiting overlapping domains (Martinez *et al*, 1999). These results suggest that the larvae of echinoderms and hemichordates may have evolved secondarily in the Ambulacraria clade of the deutero stomes. It is interesting that *Hox 1*, the most anterior *Hox* gene, is expressed just after the first gill slit forms in hemichordates and in vertebrates, suggesting that the positioning of the gill slits along the anterior–posterior axis is homologous (Lowe *et al*, 2003; Gerhart *et al*, 2005; Rychel *et al*, 2006; Figure 6).

Nodal gene expression and left–right asymmetry

Nodal is a member of the TGFβ superfamily of signaling molecules found in all phyla of deuterostomes, but *nodal* has not yet been reported in the Ecdysozoa or Lophotrochozoa (Chea *et al*, 2005). *Nodal* and the entire *nodal* signaling cascade of genes is expressed early during gastrulation during the formation of mesoderm in

vertebrates and lancelets as reviewed in Chea *et al* (2005). Later, *nodal* is expressed on the left side of chordate embryos and is necessary for left–right asymmetry (Chea *et al*, 2005). In light of these results, the expression and function of *nodal* in echinoderms and hemichordates is very interesting.

Nodal expression has been reported in sea urchins at the site where the mouth forms during gastrulation, and has been shown to pattern the oral–aboral axes in the developing embryo and pluteus larvae (Duboc *et al*, 2004; Flowers *et al*, 2004; Figures 2–4). Later, *nodal* is also expressed opposite the site of the adult rudiment formation in larval urchins, which normally forms on the left side of the larvae (Duboc *et al*, 2005; Figures 2–4). It is intriguing that *nodal* serves multiple functions during deuterostome development, a theme that is fundamental to the evolution of developmental processes (Davidson and Erwin, 2006). *Nodal* expression is found in the developing mouth in the direct-developing hemichordate, *Saccoglossus kowalevskii*, similar to the early echinoderm expression (Christopher J. Lowe, personal communication). Later expression of *nodal* in hemichordates might be interesting and informative as to how the hemichordate left–right axes correspond to chordate axes (Chea *et al*, 2005; Gerhart *et al*, 2005).

Brachyury gene expression

A novel tissue, the notochord, unites the chordates as a monophyletic group (Figures 1 and 7). Notochord is necessary as a developmental signaling tissue during neural tube formation and also remains as a structural tail tissue in ascidian larvae and cephalochordates (Smith and Schoenwolf, 1989). One transcription factor known to be necessary for notochord development in chordate embryos is the T-box transcription factor *brachyury T* (Holland *et al*, 1995). *Brachyury T* is expressed in developing notochord cells in vertebrates (Wilkinson *et al*, 1990), lancelets (Holland *et al*, 1995), ascidians (Yasuo and Satoh, 1993, 1994) and larvaceans (Bassham and Postlethwait, 2000) (Figure 7). In lancelet and vertebrate embryos, *brachyury T* is expressed early in presumptive mesoderm, and later in the notochord and posterior mesoderm (Holland *et al*, 1995; Figure 7). However, in ascidians, *brachyury T* expression was seen only in the notochord, at the time of cell fate restriction (Yasuo and Satoh, 1993, 1994). As *brachyury T* is expressed exclusively in the ascidian notochord (Yasuo and Satoh, 1993, 1994), it was believed that the expression of *brachyury T* in echinoderms (Shoguchi *et al*, 1999; Peterson *et al*, 1999b) and hemichordates (Tagawa *et al*, 1998; Peterson *et al*, 1999a) might allow clues from which tissues the notochord evolved (Figure 7). However, the results of *brachyury T* gene expression underscore the differences in morphology between nonfeeding ascidian tadpole larvae and feeding larvae of indirect-developing hemichordates and echinoderms (Figure 2).

Brachyury T expression in sea urchins was found early in the vegetal plate at the mesenchyme blastula stage, later in secondary mesenchyme after gastrulation and was absent in sea urchin larvae (Peterson *et al*, 1999b). As metamorphosis began, expression was seen in the mesoderm of the left and right hydrocoels in the developing adult urchin (Figure 7; Peterson *et al*, 1999b). In contrast, the pattern of *Brachyury T* expression

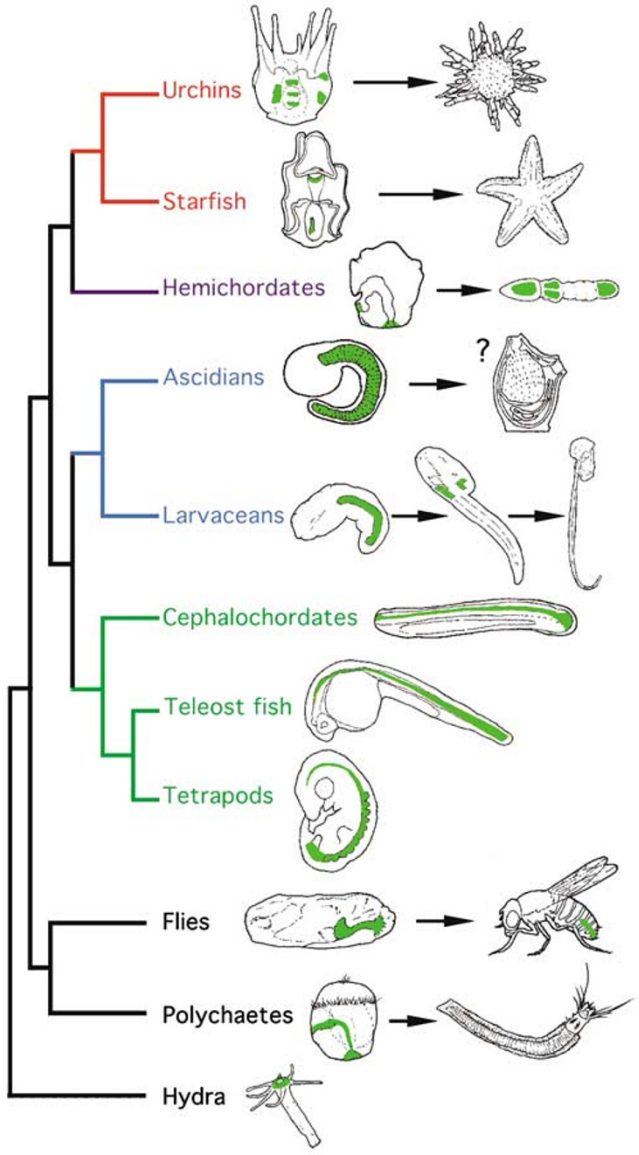

Figure 7 Expression of *Brachyury (T)* in animals. *Brachyury* is expressed in the hindgut in flies and in the gut during larval development in polychaete worms. In echinoderms and hemichordates, *brachyury* is expressed in the anus during gastrulation, then later where the mouth is formed. *Brachyury* was co-opted into the notochord in chordates, but in larvaceans, it is expressed in notochord and later in the mouth and anus after metamorphosis.

in sea star larvae (Shoguchi *et al*, 1999) was similar to expression in hemichordate larvae (Tagawa *et al*, 1998; Peterson *et al*, 1999a; Figure 7). In hemichordate embryos, expression of *brachyury T* was first seen in the vegetal plate early in gastrulation (Tagawa *et al*, 1998). High expression continues at the vegetal plate and finally is still expressed during development of the larval anus (Figure 7; Tagawa *et al*, 1998; Peterson *et al*, 1999a). Expression is also seen in the larval mouth from the time of induction by the archenteron (Peterson *et al*, 1999a). Later, after metamorphosis, expression is high in the adult proboscis, collar, and the posterior region of the trunk and gut (Figure 8; Peterson *et al*, 1999a). Therefore, the expression of *brachyury T* in posterior gut is seen in all

deuterostomes: chordates, echinoderms and hemichordates (Figure 7). In contrast, notochord expression is restricted entirely to the chordates (Figure 7). This separation of expression patterns in tunicates is documented nicely in expression results of *brachyury T* in larvaceans (Bassham and Postlethwait, 2000). In larvaceans, a pelagic tunicate, expression is first seen only in the larval notochord (Figure 7; Bassham and Postlethwait, 2000). However, after metamorphosis and the development of the gut in the adult, expression is seen in the oral and anal mesoderm (Bassham and Postlethwait, 2000; Figure 7). These results suggest that if *brachyury T* expression were examined in ascidians after metamorphosis, then there would be expression in the posterior gut. In summary, *brachyury T* expression patterns suggest that deuterostomes may share a common mesodermal transcription factor for development of the mouth and anus, but no light is shed on the evolutionary origin of the notochord. A screen for genes that are downstream of *brachyury T* in ascidians has yielded a number of candidates that will be interesting to clone and characterize in hemichordate and echinoderm embryos (Hotta *et al*, 2000). *Brachyury T* is also expressed in the hindgut of flies (Lengyel and Iwaki, 2002) and in the mouth and anus of polychaete larvae (Arendt *et al*, 2001). One idea is that *brachyury T* is a general transcription factor for a suite of genes that can be activated to allow cell movement, or convergence and extension (Lengyel and Iwaki, 2002). The other possibility is that *brachyury T* was originally important for ectodermal–endodermal interactions during the formation of the gut and anus (Technau and Scholz, 2003). Later, in chordates, the continued expression of *brachyury T* on one side of the blastopore may have induced many more cells to ingress opposite of the endoderm, allowing the evolution of the notochord and somites (Chea *et al*, 2005). An experiment to test this hypothesis would be to over-express *brachyury T* in hemichordate larvae on one side of the blastopore and determine whether the body axes of the worm are altered as a result of induced expression.

Summary

Deuterostomes show widely divergent adult body plans in extant taxa. The evolution of these divergent body plans has occurred through different developmental scenarios. Echinoderms and hemichordates share similar larvae, but in hemichordates the adult body plan is built onto the larval body plan, whereas in echinoderms a radical metamorphosis results in dramatically different adults. Coloniality has evolved several times repeatedly in the tunicates and has also evolved in hemichordates. The evolution of coloniality changes a suite of characteristics in larval and adult features in ways not well understood. Tunicate larvae probably evolved independently and may not represent the 'ancestral' chordate. *Hox* genes specify anterior–posterior polarity in the deuterostomes, but the cluster has evolved independently in the Ambulacraria, Tunicata and Chordata (lancelets and vertebrates). Vertebrates have increased mesoderm and may have co-opted *brachyury T* and *nodal* into mesoderm for increased cell movement into the blastopore during gastrulation. Further inquiry into the evolution of developmental processes may give us a better understanding of the evolution of divergent deuterostome body plans.

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Recommended resources

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