The phylogeny, evolutionary developmental biology, and paleobiology of the Deuterostomia: 25 years of new techniques, new discoveries, and new ideas

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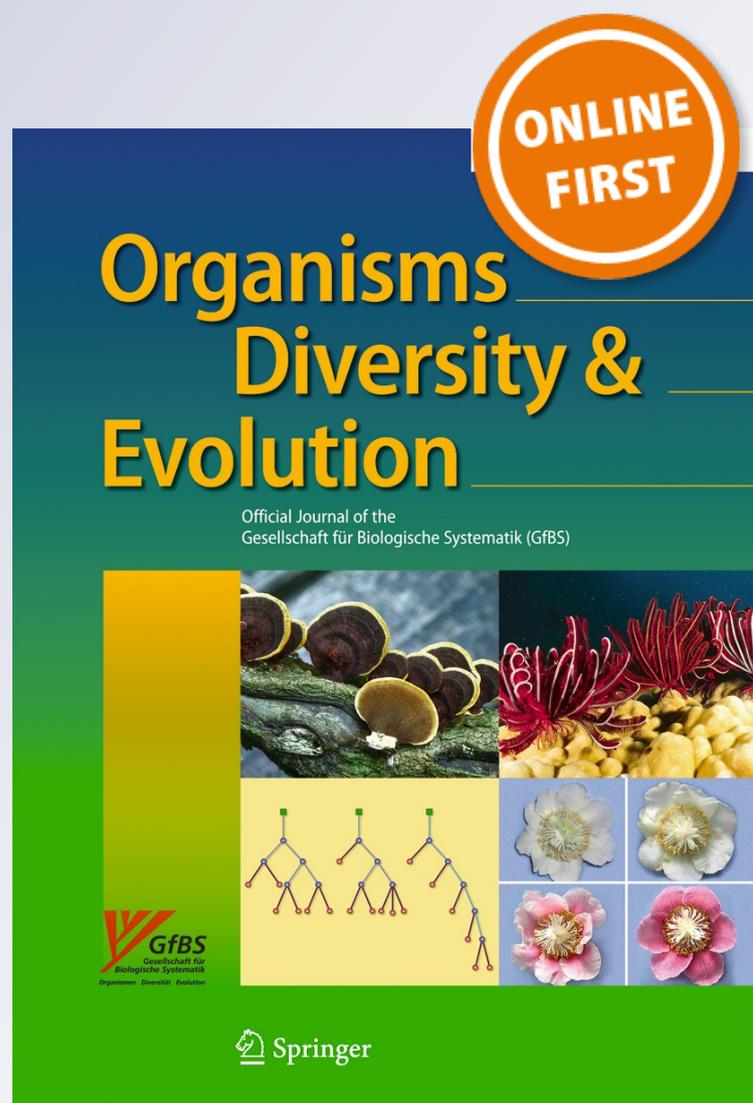
Kevin J. Peterson[1] · Douglas J. Eernisse[2]

Abstract Over the past 25 years, new techniques, new discoveries, and new ideas have profoundly impacted our understanding of deuterostome interrelationships and, ultimately, deuterostome evolution. During the late 1980s and early 1990s morphological cladistic analyses made predictions about both taxonomic history and homology, predictions that would be tested independent of the morphological characters themselves with the advent of molecular systematics, the rise of evolutionary developmental biology, and continued exploration of the fossil record. Thanks to these three areas of inquiry, we have gone from scenarios where animals like mobile enteropneust hemichordates and chordates were derived from sessile filter-feeding animals like modern lophophorates, echinoderms, and pterobranch hemichordates, to a new perspective where hemichordates are recognized as the nearest living relative of the echinoderms, and that vagile gill-bearing animals like Cambrian vetulicolians are seen—at least by some—as close to the deuterostome last common ancestor, with both sessility and filter-feeding convergent features of deuterostomes (e.g., echinoderm) and non-deuterostomes (e.g., lophophorates) alike. Although much of the backbone of the new deuterostome phylogeny is supported by multiple independent data sets, as are statements of homology of

several different morphological characters, in particular the homology of gill slits across Deuterostomia, nonetheless, the next quarter century of study on this remarkable group of animals promises to be as equally illuminating and exciting as the past quarter century.

"Although we have derived a biologically sound phylogenetic tree, or cladogram, of the better known metazoa, there is no doubt other hypotheses of relationships will continue to be proposed as more data and analyses become available."
Brusca and Brusca (1990, pg. 889)

And boy would there ever! These are the parting words of Brusca and Brusca to the reader to close their magisterial volume on the invertebrates. Brusca and Brusca (1990) were one of the very first workers (Jefferies 1986 might be the first) to apply cladistic reasoning to the problem of animal phylogeny, generating a hand-built cladogram of most of the major animal phyla. This use of cladistics would be revolutionary in terms of our understanding of the tree of life, but who could have known that a paper published just a few years before their volume would herald in a completely new way to approach animal evolution (Field et al. 1988), and would eventually lead to workers comparing hundreds of genes from dozens of taxa to infer a phylogeny (Delsuc et al. 2005, 2006; Dunn et al. 2008; Hejnol et al. 2009; Philippe et al. 2009, 2011). Or that just a few years prior a seemingly simple insight would allow for workers to work with virtually any

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gene of interest, as long as one knew or could guess a bit of the sequence (Saiki et al. 1988). Workers could now target specific genes for not only the elucidation of phylogeny (e.g., 18S rRNA, Holland et al. 1991) but because very similar genes seemed to underlie the development of animals as disparate as fruit flies and mice (Carroll et al. 2005), one could begin targeting genes underlying development in virtually any animal and begin to understand the evolution of body plans and to test centuries-old hypotheses of homology (Raff 2000). Or that new fossil finds, like the early Cambrian Chengjiang fauna discovered in the early 1980s (Xian-guang et al. 2004), coupled with fresh perspectives on old fossil finds (Gould 1989, 1991; Seilacher 1989, 1994), would lead to new interpretations of ancient morphology and would reveal character combinations in long-extinct animals not even remotely imagined given today's biota. Further, refinements to the absolute geological time scale (Bowring et al. 1993; Grotzinger et al. 1995) would reveal that, for the most part, the fossil record of animals begins spectacularly within a few tens of millions of years after the start of the Cambrian (Knoll and Carroll 1999; Erwin et al. 2011); this "Cambrian explosion" would become even more curious when viewed from the perspective of the molecular clock, which suggested (e.g., Runnegar 1982) and continues to suggest (Douzery et al. 2004; Peterson et al. 2008; Erwin et al. 2011) that animal divergence times preceded the Cambrian by possibly tens to hundreds of millions of years. Indeed, by 2015, we as a community have a rather solid understanding of the phylogenetic relationships, character distributions, and general timing to constrain ideas concerning the origins of our phylum—the Chordata—from the rest of the animal kingdom, supporting some earlier ideas, rejecting others, and, most importantly, raising new issues that will need to be addressed over the next 25 years. But in 1990, all of this was just around the corner.

Deuterostome phylogeny: 25 years ago

Although numerous ideas have been proposed concerning the origins of the chordates from the rest of the animal stock, ranging from the somewhat probable (e.g., Garstang 1928; Romer 1967) to the utterly fanciful (e.g., Løvtrup 1977) (see Stach 2008 and Holland et al. 2015 for recent summaries, and Gee 1996 for an excellent extended review), we chose to use Brusca and Brusca's (1990) summary diagram as a jumping-off point to discuss the impact the "new animal phylogeny" had on our understanding of deuterostome interrelationships and character distributions (see Eernisse et al. 1992 though for a summary of many different ideas concerning the interrelationships of the major groups of animals including deuterostomes and deuterostome relatives). As mentioned above, Brusca and Brusca were one of the very first attempts to understand higher-level animal phylogeny using cladistic

reasoning, and their explicit use of characters allows us to examine the fate of these character choices, in addition to the entire phylogeny. Figure 1a summarizes the deuterostome portion of the Brusca and Brusca phylogeny. According to these authors, deuterostomes were comprised of five major groups, the chaetognaths, the echinoderms, the lophophorates (the brachiopods, the phoronids, and the bryozoans or ectoprocts), the hemichordates, and the chordates. Deuterostomes were largely recognized on the basis of shared embryological traits, including the namesake character, the fate of the blastopore (character 1), the tripartite division of the body plan with the three sets of coeloms derived from archenteric mesoderm (characters 2–4), and a largely diffuse, non-ventral nervous system. Lophophorates were hypothesized to be more closely related to chordates than to the echinoderms because of the presumed shared possession of feeding tentacles with pterobranch hemichordates (character 6), and hemichordates were hypothesized as the chordate sister group because of the shared possession of gill slits (character 8). The exact placement of chaetognaths remained nebulous (cf. Darwin 1844), and the authors hypothesized a basal position among deuterostomes given the absence of feeding tentacles and gill slits, similar to echinoderms. Chordates were presumed to have lost tentacles, and, although not highlighted, were implied to have lost or modified beyond recognition the presumed ancestral trimeric arrangement of the coeloms as well as the ancestral dipleurula larva found in some echinoderms, hemichordates, and lophophorates (Nielsen 1985, 1987). Chordates were united by the possession of the endostyle and notochord, and the muscular post-anal tail. Only the gill slits and (possibly) the dorsal hollow nervous system were to be found lower in the tree, specifically in the (enteropneust) hemichordates.

Soon after their text was published, Schram (1991) published a more explicit data matrix with presented results based on analysis with parsimony software (unlike Brusca and Brusca 1990) and with discussion of the importance of character choice and taxon selection as central to the support of a specific phylogenetic result. His tree (Fig. 1b), although not among the shortest trees for his data set (Eernisse et al. 1992), is somewhat similar to the one from Brusca and Brusca (1990), (Fig. 1a), but important differences are apparent. First, Schram correctly interpreted chaetognaths as not possessing trimeric coeloms (e.g., Kapp 2000), and thus in his tree, chaetognaths are actually nested within a paraphyletic "protostomia" (see also Eernisse et al. 1992). A paraphyletic "lophophorata" is at the base of Deuterostomia, united by the shared possession of non-spiralian developmental characters, the specific feeding mechanism of adults and larvae, and (except in ectoprocts, Nielsen 1985, 1987), trimery (= archimery), the trimeric arrangement of the body coeloms. Schram split the hemichordates into its two generally recognized constituent taxa, the pterobranchs and the enteropneusts,
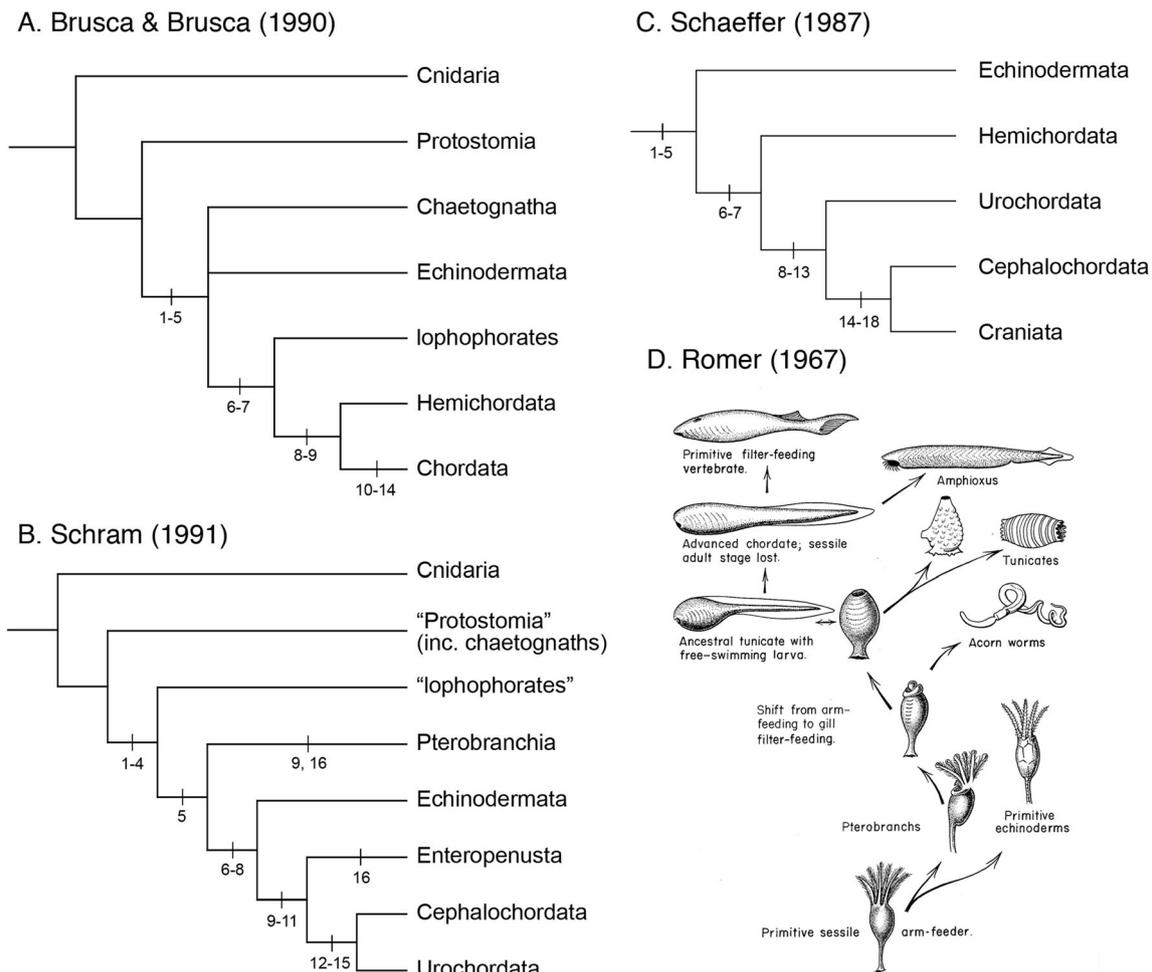
Fig. 1 Three early deuterostome cladograms and a consistent evolutionary scenario. **a** The cladogram of Brusca and Brusca (1990). Characters are as follows: *1* Complete gut with mouth not arising from blastopore. *2* Mesoderm derived directly from archenteron. *3* Body cavity (coelom) tripartite and derived by enterocoely. *4* Sheets of subepidermal muscles derived, at least in part, from archenteric mesoderm. *5* Longitudinal nerve cords not ladder-like in arrangement and not emphasized ventrally. *6* Ciliated feeding tentacles derived from mesosome and containing extensions of the mesocoel. *7* Circulatory system derived, at least in part, from mesodermal mesoderm (varies among taxa). *8* Pharyngeal gill slits. *9* Dorsal hollow nerve cord. *10* Loss of mesosomal tentacles. *11* Notochord. *12* Muscular, locomotor, postanal tail. *13* Endostyle. *14* Tadpole larva. **b** The cladogram of Schram (1991). Characters are as follows: *1* Loss of spiral quartet cleavage. *2* Loss of 4d mesoderm. *3* Upstream particle capture in adults. *4* Upstream particle capture in larvae. *5* Tornaria/bipinaria larva. *6* Loss of coiled/looped gut. *7* Loss of lophophore. *8* Loss of upstream particle capture in adults. *9* Pharyngeal slits. *10* Dorsal nerve cord from tube-like infolding of ectoderm. *11* Pharyngeal slits divided. *12* Loss of upstream particle capture in larvae. *13* Loss of archimeric (= trimeric) coelom. *14* Loss of tornaria/bipinaria larva. *15* Notochord. *16* Buccal diverticulum (= stomochord). **c** The cladogram of Schaeffer (1987). Characters are as follows: *1* Specific type of embryonic cleavage induction. *2* Enterocoelous development. *3* Blastopore becomes larval anus. *4* Similar sequence of intron positions. *5* Larva free-swimming with ciliated bands. *6* Ciliated pharyngeal slits resulting from fusion of endoderm and ectoderm. *7* Pharyngeal skeleton. *8* Embryonic fate map. *9* Mesodermal induction involving vegetal-animal axis signal. *10* Notochord and lateral muscle bands. *11* Neural induction via archenteron roof. *12* Endostyle. *13* Larva free-swimming and tailed. *14* Somites. *15* Dorsal hollow nerve cord. *16* Predominance of creatine phosphate. *17* Median fin. *18* Larva a miniature adult. **d** The evolutionary scenario of Romer (1967)

and found that echinoderms were more closely related to the enteropneust/chordate clade than were pterobranchs (echoing the calcichordate hypothesis of Jefferies 1986, see also Gee 1996) and making "hemichordata" polyphyletic with the buccal diverticulum (= stomochord) evolving twice independently. Also according to Schram's (1991) published hypothesis, pharyngeal gill slits evolved twice independently, with simple openings present in pterobranchs and more elaborated gill slits

with an underlying skeleton present in the last common ancestor of enteropneusts and chordates. Aside from the gain of the notochord, loss generally pervades the origin of chordates with the secondary loss of upstream capture in adults (i.e., loss of the lophophore) and larvae (i.e., loss of the dipleurula larval form itself) and the loss of trimery. Thus, taxon selection (e.g., the splitting of hemichordates and lophophorates into subtaxa in Schram vs. Brusca and Brusca), character choice (e.g., the

inclusion of larval characters in Schram's matrix), and character coding (e.g., Schram's coding of the absence of trimery in chaetognaths) necessarily result in a different hypothesis for deuterostome inclusion and interrelationships.

Despite these differences, both Brusca and Brusca and Schram saw the origins of the chordates near or within the hemichordates, with at least one of the chordate hallmark characters (gill slits) homologous to the gill slits of at least enteropneust hemichordates. This notion was consistent with earlier influential ideas of chordates origins, echoing one of the first cladistic analyses focused on deuterostome interrelationships (Fig. 1c, Schaeffer 1987; see also Maisey 1986 who found a very similar set of relationships). Further, characters found in echinoderms and hemichordates not found in living chordates were interpreted as having been lost then early in chordate evolution (Gee 1996). These characters would include the dipleurula larva and trimery or the presence of a body plan consisting of three sets of usually paired coeloms, with the first bearing a hydropore connected to the metanephridium (Balser and Ruppert 1990; Ruppert and Balser 1986), and the second bearing ciliated extensions into the feeding structures, whether this was the lophophore, the pterobranch tentacles, or the echinoderm water-vascular system. Therefore, these early phylogenetic analyses were consistent with ideas that envisioned the deuterostome ancestor as a sessile filter-feeding organism (e.g., Romer 1967, Fig. 1d) with a unique developmental mode and coelom arrangement as compared to protostomes.

25 Years hence—molecular phylogenetics

From the outset of metazoan molecular phylogenetics, it was clear that there were problems with this picture of deuterostome evolution and, in particular, envisioning chordate origins within sessile filter-feeding organisms. Specifically, a close affinity between lophophorates (the brachiopod *Lingula reevi*) and the deuterostomes (echinoderms and chordates) was not supported; instead Field et al. (1988; see also Patterson's 1989 and Lake's 1990 reanalysis of the Field et al. data) found the brachiopod closely related to the annelid/ mollusc portion of the tree, separate from the arthropods and, importantly upon reanalysis (Patterson 1989; Lake 1990), the deuterostomes. Although only a single partial sequence of 18S rRNA was used, the idea that lophophorates were not allied with the deuterostomes, but instead with a subgroup of protostomes, was supported by the shared possession of setae in brachiopods, polychaete annelids, pogonophorans, and echiurans (Gustus and Cloney 1972; Orrhage 1973; Ghiselin 1989; Lüter and Bartolomaeus 1997). Further, it was found with each additional molecular analysis starting with Halanych et al. (1995) (see also Halanych 1996a; Mackey et al. 1996) that all three lophophorate groups nested

near the annelid-mollusc group separate from the deuterostomes, a clade christened by Halanych et al. (1995) the Lophotrochozoa. This result continued to receive strong support from the first phylogenomic studies (e.g., Dunn et al. 2008; Helmkampf et al. 2008a, b), in addition to numerous other shared characters between "lophophorates" and the annelid/ mollusc group including specific *Hox* genes (de Rosa et al. 1999; Passamaneck and Halanych 2004) and sequence analyses of the mitochondrial genome (e.g., Stechmann and Schlegel 1999; Waeschenbach et al. 2006; Yokobori et al. 2008; Jang and Hwang 2009; Sun et al. 2011). Nonetheless, the monophyly and phylogenetic position of the lophophorates within the Lophotrochozoa remain outstanding questions still actively being addressed by ever larger and more taxonomically inclusive data sets (Hausdorf et al. 2010; Nesnidal et al. 2013; Laumer et al. 2015; Luo et al. 2015).

Chaetognaths were also pulled away from the deuterostomes at the outset of metazoan molecular phylogenetics (e.g., Telford and Holland 1993; Wada and Satoh 1994; Halanych 1996b), with all results consistent with a non-deuterostome affinity, but unable to strongly support an alternative placement. Most other types of data are consistent with a placement somewhere among or basal to the protostomes including additional molecular sequence analyses (e.g., Peterson and Eernisse 2001; Marlétaz et al. 2006; Matus et al. 2006; Dunn et al. 2008; Helmkampf et al. 2008a, b), mitochondrial genomics (Helfenbein et al. 2004; Helmkampf et al. 2008a; Sun et al. 2011), and large-scale transcriptomics (Marlétaz, et al 2008), although their exact phylogenetic placement continues to remain an outstanding problem (Edgecombe et al. 2011).

Although the first study to include representatives of all three major deuterostome groups (echinoderms, hemichordates and chordates) supported both the monophyly of Deuterostomia and the traditional relationship of Chordata + Hemichordata to the exclusion of the Echinodermata (Holland et al. 1991), increasing both the number of taxa and the number of nucleotides analyzed resulted in hemichordates sharing a more recent common ancestor with the echinoderms to the exclusion of the chordates (Wada and Satoh 1994; Turbeville et al. 1994; Halanych 1995). Thus, from the outset of molecular phylogenetics, the deuterostomes comprised three traditional phyla—the Echinodermata, Hemichordata, and Chordata—and that, within deuterostomes, hemichordates were more closely related to the echinoderms instead of the chordates. This was a most interesting result given the results of Brusca and Brusca (1990) and Schram (1991), and although a few scattered papers would continue to find support for Hemichordata (or at least Enteropneusta) + Chordata sister grouping (e.g., morphology, Peterson 1995; molecules, Winnepenninckx et al. 1995), virtually, every subsequent sequence-based phylogenetic analysis (e.g., Bromham and Degnan 1999; Cameron et al. 2000; Peterson and Eernisse

2001; Furlong and Holland 2002; Winchell et al. 2002; Blair and Hedges 2005; Bourlat et al. 2006; Mallatt and Winchell 2007; Dunn et al. 2008; Philippe et al. 2011; Cannon et al. 2014; Simakov et al. 2015) would find moderate to strong support for the resurrected taxon Ambulacraria (Metschnikoff 1881), the name given to the clade consisting of the last common ancestor of echinoderms and hemichordates and all descendants of that last common ancestor living or extinct (Halanych 1995) (Fig. 2). Some examples of other types of data supporting the monophyly of Ambulacraria include cladistic analyses of morphological matrices (Peterson and Eernisse 2001; Cameron 2005), mitochondrial codon usage (Castresana et al. 1998a, b; Perseke et al. 2011; 2013), a specific set of "posterior" *Hox* genes (Peterson 2004; Freeman et al. 2012), and uniquely shared microRNAs (Peterson et al. 2013; Tarver et al. 2013). Therefore, there is now considerable agreement that Hemichordata + Echinodermata is a natural grouping of animals, comprising (along with possibly *Xenoturbella* and acoelomorphs, see below) the sister group to the Chordata. In summary then, of the groups of animals considered by Brusca and Brusca (1990) and Schram (1991), Deuterostomia comprises just three major taxa, Chordata, Echinodermata, and Hemichordata, with echinoderms and hemichordates sister taxa (Fig. 2), a fundamentally radical revision of what not only constitutes Deuterostomia but also how they are related (and potentially classified, Satoh et al. 2014a) to one another (cf. Figs. 1 and 2) (Smith et al. 2004; Swalla and Smith 2008; Lowe et al. 2015).

As discussed above, molecular phylogenetics removed two groups from the Deuterostomia, the chaetognaths and the lophophorates. However, some recent results have also suggested that two other groups are deuterostomes, *Xenoturbella* and the acoelomorphs (termed the xenacoelomorphs by Philippe et al. 2011). Morphological and developmental considerations had already hinted at a relationship between acoelomorphs (acoel + nemertodermatid worms) and *Xenoturbella* (e.g., Nakano et al. 2013; reviewed in Nielsen 2010; Ach

atz et al. 2013), and molecular data have supported this affinity (Philippe et al. 2011). However, where the Xenoacoelomorpha lies within the broader context of animal evolution has been contentious with the two most strongly supported results being that xenacoelomorphs are either basal bilaterians (Hejnol et al. 2009) or, alternatively, as deuterostomes, possibly as the sister group of the ambulacrarians (Philippe et al. 2011) (recently reviewed in Ruiz-Trillo and Paps 2015; see also Simakov et al. 2015). An affinity between xenacoelomorphs and deuterostomes is supported by the possession of the gene *GNE*, present in all deuterostomes, acoelomorphs, and *Xenoturbella* but absent in protostomes and non-bilaterians (Mendoza & Ruiz-Trillo 2011). Nonetheless, irrespective of their final resting place, it is clear that xenacoelomorphs have undergone dramatic secondary reduction, not only in terms of gene content (e.g., Fritzsch et al. 2008), but also in morphology (Bourlat et al. 2009; Achatz et al. 2013), and thus likely have little to contribute to our understanding of character evolution within the deuterostomes (cf. Fig. 3).
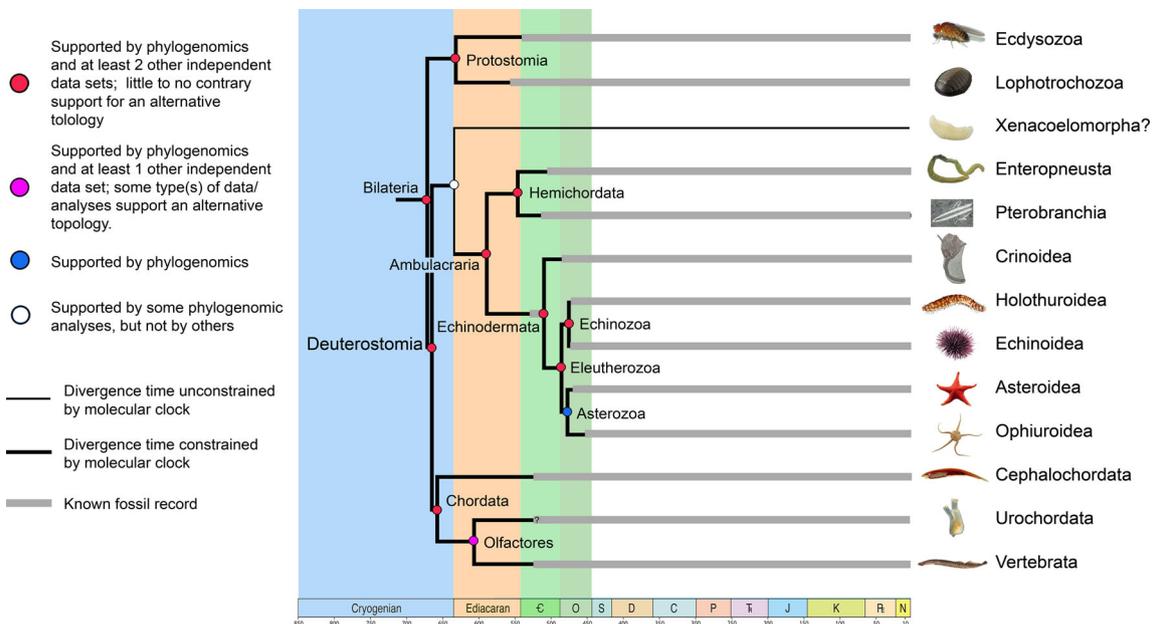
Fig. 2 The phylogeny and divergence times of the major deuterostome taxa. Shown is the consensus tree discussed in the text with each node labeled according to its relative support (see key). Most nodes are supported by abundant types of independent data (see text), but a few (e.g., Asterozoa), although supported by phylogenomics, are only weakly or not supported by other types of data. Also shown is the known fossil record of each group (*thick gray bar*) and the estimated divergence time (*thick black line*) for each group; taxa for which there are no molecular estimates of clade age are shown in *thin black lines*. See the text for references and details. Time line is from Erwin et al. (2011)

A

B

C

Even though the interrelationships of the classic deuterostome phyla appear to be resolved (Fig. 2), the intra-relationships within each of these three classically defined phyla have been troublesome, and only recently has each reached some modicum of stability and consistency. For hemichordates, although many early morphological cladistic studies found support for a para- or even polyphyletic Hemichordata (reviewed in Smith et al. 2004), they have been supported as monophyletic from the outset of molecular phylogenetics (Halanych 1995; Cameron et al. 2000; Peterson and Eernisse 2001; Smith et al. 2004). Further, these early studies also found support for a paraphyletic "Enteropneusta" as pterobranchs consistently were more closely related to harrimaniid enteropneusts than either was to ptychoderid enteropneusts (see also Cannon et al. 2009), a result supported by Peterson and Eernisse's (2001) morphological cladistic analysis. Further, like harrimaniids, pterobranchs do not possess a dipleurula-type larva but instead show direct development without an intervening feeding larval phase (Sato et al. 2008; Stach 2013). Nonetheless, a more extensive morphological cladistic analysis (Cameron 2005), as well as molecular phylogenies derived from considerations of 28S rDNA (Winchell et al. 2002), found enteropneusts monophyletic relative to pterobranchs. More recent data from both phylogenomics (Cannon et al. 2014; Simakov et al. 2015) and microRNAs (Peterson et al. 2013) fully support enteropneust monophyly (Fig. 2), and thus the morphological similarities between pterobranchs and harrimaniid enteropneusts are either convergent features in each of these body plans or retained plesiomorphies lost or modified in the other groups of enteropneusts (discussed further below).

As arguably the most distinctive of the "phyla," the monophyly of the living echinoderms has never been seriously questioned, and all data sets fully support a monophyletic

◀ **Fig. 3** Thinking and exploring outside of the box. **a** Shown inside of the *gray box* is the summary figure and the first line of the figure legend of Romer's 1967 seminal article on vertebrate evolution. Romer, like many of his contemporaries, saw chordate origins within the hemichordates, such that sessile tentaculate taxa like pterobranchs were ultimately our deuterostome ancestors (see Fig. 1d). Shown outside the box is our current understanding of deuterostome interrelationships and divergence times based on molecular phylogenetics (see Fig. 2). Along each of the branches are shown representative characters supporting the monophyly of each of the groups, highlighting the different types of methodologies and data types that have been used to attack the problem of chordate origins and deuterostome interrelationships. For example, gill slits, which express the transcription factor *Pax1/9* (1), resolve as an apomorphy for Deuterostomia (D); the notochord, which expresses the transcription factor *Brachyury* (2), resolves as an apomorphy of Chordata (C), whereas the stomochord (3), which does not express *Branchyury* (*arrow*) and instead expresses a different suite of genes (Satoh et al. 2014b), resolves as an apomorphy of Hemichordata (H). Recent and fossil echinoderms (i.e., the total-group Echinodermata, *e*) are recognized by the shared possession of stereom (4), whereas the recent echinoderm groups (i.e., the crown-group Echinodermata, E) all share coelomic torsion and stacking (5). Character types can also be molecular in nature and here include, for example, the clustering of the pharyngeal genes *PAX1*, *NKX2.1*, *NKX2.8*, and *FOXA1* on chromosome 14 in human (with their paralogous genes clustered on human chromosome 20), a clustering conserved across Deuterostomia, but not found in protostomes (6, Simakov et al. 2015). Other examples include the shared possession of genes across Deuterostomia for the use of endogenous sialic acids (7, Peterson and Eernisse 2001; Simakov et al. 2015), as well as two molecular characters supporting the monophyly of Ambulacraria, the shared possession of specific *Hox* genes, one of which (*Hox11/13b*) is expressed in the posterior gut of both echinoderms and hemichordates (8, Aronowicz and Lowe 2006; Peter and Davidson 2010), as well as specific microRNAs, in particular mir-2012, a miRNA found in both echinoderms and hemichordates (9). Finally, fossils can reveal morphologies lost or modified in the modern forms. For example, some stem-group echinoderms appear to possess gill slits (*10, arrow*, seen from the back of the cornute *Archaeocothurnus bifida*), in addition to showing an anterior theca and a posterior appendage. The divergence times are taken from molecular clock analyses (see Fig. 2) against an accurate and precise geological time scale (Bowring and Erwin 1998; Walker et al. 2013). The placements of character acquisitions along the respective branches are not to temporal scale. **b** The vetulicolian *Yuyuanozoon magnifiscissimi* from the early Cambrian of China (Ou et al. 2012) showing the clear bipartite division of the body into an anterior theca bearing gill slits (G1–G5, G2 indicated with *box*) and the posterior appendage. **c** The somato-visceral animal of Romer (1970). Images *1* and *7*, courtesy of Prof. Chris Lowe; image *2*, courtesy of Prof. Anna Di Gregorio; images *3*, *5*, and *9* from KJP's collection; image *4* from Bottjer et al. (2006); all remaining images from Wiki commons

Echinodermata (Smith et al. 2004). Further, all data sets support a fundamental division of extant echinoderms into the primitively stalked and sessile crinoids (Pelmatozoa) and the other four living monophyletic "classes" of free-living echinoderms, the echinoids, holothurians, asteroids, and the ophiuroids, collectively known as the Eleutherozoa (Fig. 2) (Smith et al. 2004). Within the eleutherozoans, virtually, all recent analyses agree that holothurians are the sister taxon to the echinoids with respect to asteroids (the Echinozoa, see Smith et al. 2004), but elucidating how ophiuroids are related to this taxonomic triumvirate has proven to be a perennial

problem in echinoderm systematics. Both morphological and molecular studies have given equally contradictory results with some (e.g., Littlewood et al. 1997; Smith et al. 2004) suggesting that ophiuroids are more closely related to echinozoans than to asteroids (the cryptosyringid hypothesis) whereas others (e.g., Mooi and David 2000; Janies 2001; Mallat & Winchell 2007) have suggested that ophiuroids are more closely related to asteroids than to the echinozoans (the asterozoan hypothesis) (reviewed in Smith et al. 2004). More recent analyses have made it clear that any particular result of analyses of echinoderm-wide multi-locus data sets is very sensitive to the choice of alignment, data partitioning, and tree search parameters (Janies et al. 2011; Pisani et al. 2012). Nonetheless, the most recent phylogenomic studies all strongly support the monophyly of Asterozoa (Cannon et al. 2014; O'Hara et al. 2014; Telford et al. 2014; Reich et al. 2015; Simakov et al. 2015). Therefore, our best estimate of echinoderm intra-relationships supports the topology shown in Fig. 2, but how this topology affects our understanding of morphological and larval evolution within the Echinodermata remains to be seen as understanding the evolution of these character types requires more extensive data from evo-devo types of studies (Telford et al. 2014).

Probably the biggest surprise though for deuterostome "phylum" level intra-relationships occurred within the Chordata. Traditional scenarios for the origin of vertebrates usually had a tunicate-like ancestor giving rise to the clade consisting of cephalochordates and vertebrates (e.g., Romer 1967, Fig. 1d) based largely on the observation that cephalochordates and vertebrates showed myomery (the repeated units of segmented musculature), a character lacking in urochordates and all other deuterostome taxa (Ruppert 2005; Stach 2008). In contrast, Jefferies (1986) posited a sister grouping between urochordates and vertebrates, a clade he christened the "Olfactores." But because the ancestors of all three chordate subgroups in Jefferies scheme were traditionally classified as echinoderms as these animals possessed a stereom skeleton that had to be lost independently in each chordate subgroup, Jefferies' hypothesis received little support. Because urochordates tended to be an unstable long-branched taxon, the earliest molecular phylogenies rarely recovered chordate monophyly (Halanych 1995; Turbeville et al. 1994; Wada and Satoh 1994). Only the study of Turbeville et al. (1994), based on a combined ribosomal plus morphological data matrix, was able to recover a monophyletic Chordata with cephalochordates and vertebrates as sister taxa (variously named the Euchordata or the Notochordata). Subsequent studies would usually continue to find the monophyly of Euchordata, albeit weakly (e.g., Cameron et al. 2000; Winchell et al. 2002; Mallatt and Winchell 2007).

A notable exception to these studies is Zrzavy et al. (1998) (see also Giribet et al. 2000) who recovered a monophyletic Olfactores based on both morphological and a combined

morphological+molecular analysis. Nonetheless, urochordates are notable in having both a simplified morphology and a reduced genome in comparison to euchordates (Dehal et al. 2002; Rowe 2004; Hughes and Friedman 2005; Berná and Alvarez-Valin 2014). This, along with an enhanced rate of molecular evolution (Winchell et al. 2002; Blair and Hedges 2005; Putnam et al. 2008; Tsagkogeorga et al. 2010; Berná and Alvarez-Valin 2014), has obfuscated the intra-relationships of the chordates. More recent phylogenetic studies specifically designed to reduce the amount of stochastic error associated with early, usually single-gene studies, robustly supported the monophyly of Olfactores (Blair and Hedges 2005; Philippe et al. 2005, 2011; Bourlat et al. 2006; Delsuc et al. 2006; Dunn et al. 2008; Putnam et al. 2008; Singh et al. 2009; Tsagkogeorga et al. 2010; Simakov et al. 2015). This result is supported by several other data sets including a consideration of morphological characters (Ruppert 2005, but see Cameron 2005 and Stach 2008 for an alternative view), microRNAs (Peterson et al. 2013), and the fact that migratory neural crest (Abitua et al. 2012) and epidermal placodes (Abitua et al. 2015), both long considered vertebrate hallmarks (Gans and Northcutt 1983), are present in urochordates but not in cephalochordates. And although Delsuc et al. (2006) tentatively hypothesized that cephalochordates were more closely related to the echinoderms than to the Olfactores, the inclusion of additional taxa, in particular a hemichordate, showed that this result was likely due to systemic error (Bourlat et al. 2006; see also Putnam et al. 2008; Philippe et al. 2011; Simakov et al. 2015). Therefore, given all of the different types of data currently available, our best estimate of chordate intra-relationships is that chordates are monophyletic and that vertebrates share a last common ancestor with urochordates to the exclusion of cephalochordates (Fig. 2).

Evolutionary developmental biology and comparative morphology

Twenty-five years of increasingly sophisticated molecular phylogenetic analyses, coupled with new types of data, and new looks at old data, have prompted a complete revision of our understanding of deuterostome inter-relationships and chordate origins. Indeed, we have gone from envisioning ancestral deuterostomes as sessile filter feeders similar to modern phoronids or pterobranchs (Fig. 1d) to a vagile and active worm-like animal, not too dissimilar from a modern enteropneust (e.g., Cameron et al. 2000; Peterson and Eernisse 2001; Lacalli 2002; Cameron 2005; Ruppert 2005; Zeng and Swalla 2005; Swalla and Smith 2008). However, a proper understanding of character evolution requires more than just a well-supported phylogeny: homology assessment consists of not only character congruence but also character similarity as well as character conjunction (Patterson 1982,

1988). Therefore, a more detailed examination of specific characters, in particular the evolutionary developmental biology and detailed ultrastructural morphology of those characters, is crucial to understanding character evolution and ultimately the evolution of the body plans themselves.

Romer's scenario for the origin of chordates (Fig. 1d) envisioned that pharyngeotremy—the possession of gill slits—evolved in the transition from stalked and armed ancestors similar to modern echinoderms and pterobranchs to the gill-bearing enteropneusts and chordates, a hypothesis fully supported by subsequent morphological cladistic analyses (Fig. 1a–c; see also Maisey 1986; Peterson 1995; Nielsen et al. 1996; Zrzavy et al 1998). Further, there was necessarily the loss of both the larval (the dipleurula, character 12 in Schram, Fig. 1b) and the tentaculated trimeric adult body plan (character 10, Brusca & Brusca, Fig. 1a; characters 13 and 14, Schram, Fig. 1b) at the origin of chordates with the evolution of a new tailed larva and acoelous adult. However, the new animal phylogeny posits a sister grouping between echinoderms and hemichordates (Fig. 2), and thus this taxonomic revision necessarily posits a revision of our understanding of these characters: characters shared between hemichordates (or at least enteropneusts) and chordates are either primitive characters for deuterostomes lost in the living echinoderms or arose convergently in hemichordates and chordates; characters shared between echinoderms and hemichordates to the exclusion of chordates no longer need to be considered losses in chordates but could now be synapomorphies for Ambulacraria. Further, the removal of lophophorates from Deuterostomia removes what appears to be a primary outgroup to polarize characters, in particular ciliated tentacles, highlighting the potential role convergence might be playing in at least some of these characters (Halanych 1996a).

With respect to gills, modern pterobranch hemichordates are polymorphic for this character, with *Cephalodiscus* having a pair of single-gill pores without a supporting skeleton, and *Rhabdopleura*—presumably because of its small size—lacking these pores altogether (Hyman 1959). Enteropneusts and chordates, in particular cephalochordates, have multiple gills with each gill supported by a collagenous skeleton and divided by tongue bars that grow from the dorsal wall to divide the simple pore into two gill slits. It might seem self evident that given their structural similarity (Gonzalez and Cameron 2009), gills are homologous across hemichordates and chordates, but because macrodasyid gastrotrichs have gill pores (= pharyngeal clefts, Ruppert 1982), and that optimization of characters by Schram (1991, Fig. 1b) hypothesized that gills arose independently between pterobranchs and enteropneusts+chordates (but see Eernisse et al. 1992), it is possible that gill pores, and in particular gill slits, arose independently in enteropneusts and chordates.

Two studies in particular (Ogasawara et al. 1999; Gillis et al. 2012; see also Simakov et al. 2015) have sought to

explore the developmental similarities between enteropneust and chordate gill slits, and both strongly supported homology (reviewed in Lowe et al. 2015). The transcription factors *Pax1* and *Pax9* are two paralogous genes that are expressed in the endodermally derived pharyngeal pouch epithelium of vertebrates, tissue that goes on to form the thymus and thyroid glands (Ogasawara 2000; Lang et al. 2007). In amphioxus, the single-gene orthologue *Pax1/9* is expressed in the pharyngeal endoderm starting at about the neurula stage and then downregulated where the gill slit primordium will form slightly later in the development (Holland and Holland 1995; Liu et al. 2014). Abrogation or reduction of Pax1/9 results in the malformation of the gill slits, presumably through changes to the expression of downstream targets of Pax1/9, including the transcription factor *Six1* (Liu et al. 2014). Ogasawara et al. (1999) were able to confirm expression of the *Pax1/9* orthologue in the epithelia of the differentiating gills of both urochordates and, importantly, the enteropneust hemichordate *Ptychodera flava.* More recently, Gillis et al. (2012) (see also Simakov et al. 2015) confirmed expression of *Pax1/9* in the endodermal gill pouches of the enteropneust *Saccoglossus kowalevskii* (see Fig. 3a, (1)) and further showed gill expression of *Six1*, in addition to other gill markers including *Eya.* Interestingly, Simakov et al. (2015) recently showed that in all deuterostomes (including the echinoderm *Acanthaster planci*, which lacks gill pores, and in human, which lacks gill slits), *Pax1/9* is genomically clustered with three other transcriptional factors that are expressed in the pharynx, and these genes are not clustered in available protostome genomes (Fig. 3a, (6)). Thus, there is a clear similarity at all levels of analysis between the endodermal gill pores of enteropneusts and chordates, including morphological structure, gene expression, and genomic clustering. Therefore, it seems clear that the last common ancestor (LCA) of hemichordates and chordates (i.e., the LCA of all living deuterostomes) had at least one simple endodermally derived gill pore connecting the pharyngeal lumen to the exterior of the animal (Fig. 3a, (1)) (Lowe et al. 2015; Simakov et al. 2015), a structure lost in the living echinoderms and amniotic chordates, and, assuming a deuterostome affinity (see above), in the xenacoelomorphs as well.

What about the other typical chordate characters? Many of the early morphological cladistic analyses supported the hypothesis that the dorsal hollow nerve cord, endostyle, and notochord, are chordate synapomorphies (Fig. 1a–c), and this still rings true today. With respect to the nervous system, there is a major disagreement among workers about the nature of the nervous system of the LCA of bilaterians, specifically whether this population possessed a relatively complex nervous system with some secondary reduction in complexity within the ambulacrarians (and, if relevant, the xenacoelomorphs) or whether this population possessed a relatively simple nervous system retained in the ambulacrarians and xenacoelomorphs and complex nervous systems arising

multiple times within the Bilateria including the chordates and several protostome groups (reviewed in Holland et al. 2015; Lowe et al. 2015). Nonetheless, when the chordate nervous system is considered as a *taxic* character (as opposed to a transformational character, see Patterson 1982; Carine and Scotland 1999), the dorsal and hollow nerve cord of chordates with a central and gelatinous canal filled with Reissner's fibers and connected to the archenteron at the posterior end via the neurenteric canal (Stach 2008) is a bona fide apomorphy restricted to this clade of bilaterian metazoans. The same is true for both the endostyle, which appears to have its origins in general pharyngeal tissue (Takacs et al. 2002; Ruppert 2005), as well as the notochord (Fig. 3a, (2)), another endoderm-derived organ (reviewed in Satoh et al. 2014b). In all three chordate subtaxa, the notochord has a distinct "stack-of-coins" morphology (Ruppert 2005; Stach 2008) and, thus, is not a taxic homologue of the hemichordate stomochord (Peterson et al. 1999; Ruppert 2005; Satoh et al. 2014b). Indeed, the stomochord resolves as a synapomorphy of hemichordates (Fig. 3a, (3)), where it serves to support the heart and glomerulus of the hemichordate, the homologue of the axial complex of echinoderms (Ruppert and Balser 1986; Balser and Ruppert 1990).

The recognition of the taxon Ambulacraria, and the repositioning of the lophophorates within the lophotrochozoans, dramatically reduces the number of supposed losses in the stem lineage leading to extant chordates. This is best seen in the cladogram of Schram (1991), (Fig. 1b), where he hypothesizes the loss of the upstream collection system in both the larvae (i.e., the dipleurula larva, see Lowe et al. 2015 for a recent overview) and the adult (the lophophore or equivalent), as well as the loss of trimery. However, the recognition that trimery is not present in any lophophorate taxon, in particular phoronids (Bartolomaeus 2001), polarizes the presence of trimery to just the two ambulacrarian taxa, with a dramatic reorganization of trimery in echinoderms (Peterson et al. 2000; Smith 2005, 2008). Further, the recognition that trimery is not present in lophophorates removes an architectural argument for homology between the lophophore and the tentacles of deuterostomes: ciliated extensions of the mesocoel now only apply to deuterostomes and do not apply to the lophophorates, further undermining homology between the two organs (Halanych 1996a). The homology between the arms of the crinoid and the tentacles of the pterobranch, although supported by this line of reasoning, is not supported when the fossil record is taken into account (see below).

The removal of the dipleurula larva from the ancestry of the chordates necessarily undermines one of the stalwart ideas behind chordate origins—that of Garstang (1928) (recently reviewed in Gee 1996; see also Holland et al. 2015 and Lowe et al. 2015). Garstang famously saw the origins of the chordate nervous system in the ciliated bands of the dipleurula larva (a nice example of a transformational homology, see above), but

the recognition that the dipleurula is restricted to the monophyletic ambulacrarians no longer requires that this larval type was present in the chordate lineage and was lost (or converted into the chordate tadpole larva). Further, this result is consistent with the nervous system of the chordate derived from an *adult* nervous system of an ancestor, whether simple or complex (see above). It is possible though that feeding dipleurula itself arose at least twice within the ambulacrarians as neither crinoids within the echinoderms (Nakano et al. 2003; Amemiya et al. 2015) nor pterobranchs or harrimaniid enteropneusts (the basal clade, see Cannon et al. 2014) within the hemichordates (Sato et al. 2008; Röttinger and Lowe 2012; Stach 2013) possess planktonic feeding larval stages. Indeed, considerations of the fossil record suggests that feeding larvae evolved multiple times within multiple lineages starting in the later Cambrian (Peterson 2005), long after the ambulacrarian LCA (Fig. 2). Nonetheless, testing hypotheses of larval gain and loss using gene expression data (c.f. Fig. 3) is not trivial given the confounding affects of homology of adult structures (e.g., mouth, foregut etc.), especially when coupled with relatively minor shifts in developmental timing, and the confounding affects of homology of cell types versus the similarity of organs housing homologous cell types(Dunn et al. 2007).

Paleobiology

The last 25 years of paleontological research into the evolution of deuterostome metazoans has revealed spectacular new finds, deeper insights into the morphology of older finds, and the rise of a new way to mine the fossil record of life, that of the organismal genome (Runnegar 1986; Peterson et al. 2007). Indeed, the coupling of the geologic fossil record with the genomic fossil record has revealed fundamental insights into the timing and pattern of divergence times, estimates that can then be compared and contrasted with Earth history to gain deeper insights into the history of life (e.g., Sperling et al. 2013).

With Zuckerkandl and Paulings's (1965) insight that the amount of observable change in two orthologous amino acid sequences is approximately proportional to the amount of evolutionary time passed since they last shared a common ancestral sequence, the molecular "clock" was born (Kumar 2005) and would greatly supplement the geological understanding of the history of life (e.g., Smith and Peterson 2002; Benton and Ayala 2003; Donoghue and Benton 2007; Peterson et al. 2007). Runnegar (1982) was one of the first workers to use this insight to test hypotheses about the origin of animals and concluded that the last common ancestor of deuterostomes lived ~900–1000 Ma ago, an estimate supported by more recent inquiries including Wray et al. (1996). However, with the development of better methodologies (Ho and Duchene 2014), in addition to the use of better calibration points (Benton and Donoghue 2007), this estimate has been revised downwards such that the latest estimate of the age of

the deuterostome LCA is about 660 Ma ago or late Cryogenian in age (Erwin et al. 2011) (Fig. 2), likely an accurate but imprecise estimate (dos Reis et al. 2015). Chordates split from the ambulacrarians and began diversifying almost immediately after this LCA such that the chordate LCA is as old if not older than the last common ancestor of protostomes (Douzery et al. 2004; Erwin et al. 2011). Ambulacrarians diversified slightly later in time, most likely during the middle Ediacaran, and the ambulacrian LCA is approximately the same age as the Olfactores LCA. Further, the analyses of Erwin et al. (2011) (see also Pisani et al. 2012; O'Hara et al. 2014; Simakov et al. 2015) suggest that the echinoderm LCA was early Cambrian and that the eleutherozoan origination and diversification occurred in the late Cambrian through early Ordovician, consistent with the known fossil record, unlike some earlier attempts at dating deuterostome origination times (Blair and Hedges 2005). Simakov et al. (2015) also provide the first molecular evidence for age of the hemichordate LCA, which they estimate to the very latest Ediacaran (~546 Ma) in age (Fig. 2), consistent with the known fossil record as pterobranch fossils are described from the early Cambrian of China (Hou et al. 2011).

However, the molecular estimate for the age for the LCA of enteropneusts by both Erwin et al. (2011) and Simakov et al. (2015) at sometime between 450 and 375 Ma seriously underestimates the paleontological estimate as fossils of what appears to be torquaratorid enteropneusts (Halanych et al. 2013), a recently described tube-bearing group of enteropneusts (Holland et al. 2005; Osborn et al. 2012) that are nested well within the enteropneust crown group and the likely sister group of the ptychoderids (Cannon et al. 2009; Osborn et al. 2012; Halanych et al. 2013; Cannon et al. 2014), are now described from Middle Cambrian Burgess Shale deposits (Caron et al. 2013). Either the fossils are mis-diagnosed and are representative of a more basal (i.e., stem group) enteropneust taxon, with the retention of tubes in torquaratorids a plesiomorphy (or, alternatively, a parallelism), or that the molecular estimate for the age of the enteropneust LCA is a serious underestimate of the true age of the enteropneust crown group.

Although the genetic fossil record can give estimates of divergence times of living taxa, only the geologic record provides snapshots of morphologies long extinct and the ability then to potentially reconstruct the evolution of the living form (e.g., Budd and Jensen 2000; Peterson et al. 2007; Raff 2007; Smith 2012; Janvier 2015). With the continued description of early to middle Cambrian fossil Lagerstätten, it is now clear that the hemichordate fossil record extends to at least the middle Cambrian (Harvey et al. 2012; Caron et al. 2013; Maletz 2014; Maletz and Steiner 2015) with the fossil records of both the echinoderms (Bottjer et al. 2006; Smith et al. 2013; Zamora and Rahman 2014) and the chordates (Shu et al. 2010; Donoghue and Keating 2014; Janvier 2015; see also

Conway Morris and Caron 2012, 2014) extending into early Cambrian deposits. Other putative deuterostome forms including the cambroernids (Caron et al. 2010, but see Maletz 2014) and the yunnanozoans (see below) do not extend deeper in time than the early Cambrian either, and thus the entirely of the known fossil record of deuterostomes (similar to most metazoan higher taxa) is restricted to the Phanerozoic (Erwin et al. 2011).

The richness and informativeness of the echinoderm fossil record deserve special attention as numerous finds of putative stem group forms has shed light on the early evolution of the echinoderm body plan (reviewed in Smith 2005, 2008; Bottjer et al. 2006; Zamora and Rahman 2014). Indeed, one of the most remarkable insights is that of Jefferies (1986; see also Dominguez et al. 2002) who discovered that superficially bilaterally symmetrical (the Mitrata) to asymmetrical forms (the Cornuta, see Fig. 3a, (10)) have no apparent water-vascular system, but instead have a series of pores that he homologized with the gill slits of hemichordates and chordates (see also Smith 2005; Smith 2008). Although this idea received little more than scorn for most of Jefferies' career (op. cit.), the realization that echinoderms and hemichordates are sister taxa, and that gill slits are homologous between hemichordates and chordates, predicts the existence of gill slits in early echinoderm ancestors (Cameron 2002; Smith et al. 2004), without having these taxa necessarily being chordates, as insisted upon by Jefferies (1986). Further, no putative stem-group form with a clear water-vascular system shows any structures that could even potentially be homologous with gill slits (Bottjer et al. 2006; Smith 2008), and thus these two characters (gills slits and water-vascular system) appear to be mutually exclusive as the evolution of the water-vascular system seemed to necessitate the loss of the gill slits. The early fossil record of echinoderms also strongly suggests that the arms of the crinoid are not homologous to the tentacles of the pterobranch because these primitively bilaterally symmetrical to asymmetrical stem group echinoderms show adaptations for deposit feeding (Zamora et al. 2012; Rahman et al. 2015), similar to modern enteropneusts (Cameron 2002), which are now known to lack tentacles across the entire group (Holland et al. 2005). Therefore, it appears that crinoid arms, pterobranch tentacles, and lophophores are all convergent adaptations for suspension feeding that arose at least three (if not more) times independently (Rahman et al. 2015).

Cambrian taxa also shed light into another interesting aspect of the echinoderm body plan, namely their extreme asymmetry relative to the other deuterostome groups, and the eventual acquisition of pentameral symmetry of the adult form. Aside from tunicates (Smith 2008), all other deuterostome taxa show a simple relationship between the larval axes (when present) and the adult axes such that the A/P and D/V axes correspond. Echinoderms though show a dramatic torsion event with the adult axes (whose precise identity still remain obscure, but see Peterson et al. 2000) bearing no direct relationship with the clearly identifiable axes of the larva (reviewed in Smith 2008) (Fig. 3a, (5)). Early fossil echinoderms show intermediate stages in the acquisition of both torsion and pentamery (Smith 2005; Zamora et al. 2012; Zamora and Rahman 2014), with carpoids like the cornute shown in Fig. 3a (image 10) having a clearly defined anterior-posterior axis, a highly asymmetrical head-like theca bearing gill slits on only the left side (Fig. 3a, (10, arrow)) and a bilaterally symmetrical posterior appendage. Other potentially basal forms show near perfect bilateral symmetry with a clear A/P axis and are interpreted as pharyngeal basket feeders (Zamora et al. 2012; Zamora and Rahman 2014; Rahman et al. 2015), but lack obvious external pharyngeal openings, and most also lack a clearly defined posterior appendage. Solutes though—the next crown-ward clade (Bottjer et al. 2006; Smith 2008; Zamora and Rahman 2014)—have a clear ambulacrum and hydropore on the left side of the body, no apparent gill openings, and a posterior appendage similar to that of the carpoid, but unlike cornutes and mitrates, was used—at least in some taxa—for attachment. More crown-ward echinoderm clades including the helicoplacoids show evidence of coelomic torsion and at least three ambulacra (Smith 2008; Zamora and Rahman 2014) and crown-group echioderms then having the characteristic pentameral (or $2 + 1 + 2$) ambulacran arrangment (see Peterson et al. 2000).

Jefferies long argued (summarized in 1986; see also Dominguez et al. 2002) that stylophoran echinoderms (the cornutes and mitrates mentioned above) were bipartitely organized animals, consisting of a head and tail with the head housing the pharyngeal apparatus and the tail a locomotory (as opposed to an attachment, see discussion in Smith 2008) organ. What is so fascinating in this light is the morphology of an extremely puzzling animal, the vetulicolian (Fig. 3b). Although various interpretations abound concerning the anatomy of these enigmatic fossils (e.g., Shu et al. 2001, 2010; Lacalli 2002; Briggs et al. 2005; Aldridge et al. 2007; Vinther et al. 2011; Ou et al. 2012; García-Bellido et al. 2014), all of these authors seem to agree on two things: (1) the animal consisted of an anterior head bearing five bilaterally symmetrical and laterally placed gill pores and (2) the animal had a posteriorly orientated (and strangely arthropod-like) locomotory tail (reviewed in Smith 2012). The fact that the animal has no other unambiguous features allying it to one of the three major deuterostome total groups (echinoderms, hemichordates or chordates) has led several of these authors to propose (or at least highlight) a potential stem- (or at least a total, see Smith 2012) group deuterostome affinity for vetulicolians because of the shared possession of gill pores. What is interesting then is that some chordates, some stem-group echinoderms, and vetulicolians

(as well as other potential stem-group deuterostome forms like yunnanozoans, see Shu et al. 2003, 2010) all have a clear bipartite organization with an anterior "head"-like structure usually bearing gill slits and a posterior locomotory tail. As Gee (2001) noted, the similarities—albeit somewhat superficial—are nevertheless striking between the overall bipartite morphology of a cornute (Fig. 3a, (10)), an ascidian tadpole (Fig. 3a, (2)), a vetulicolian (Fig. 3b), and Romer's (1970, 1972) somato-visceral animal (Fig. 3c). Of course, one needs to be cautious about such interpretations (see e.g., Janvier 2015), but this similarity of a bipartite constructional pattern across several different groups of deuterostomes and presumed deuterostomes might suggest that rather than looking into living enteropneusts as models for the deuterostome LCA (see above), vetulicolians might actually be close (at least in terms of its gross morphology) to this most interesting and important of animalian ancestors.

Conclusions

Progress in science "depends on the interplay of techniques, discoveries, and new ideas, probably in that order…."
Sydney Brenner (2002)

As a community, we have been blessed with the good fortune to work in a time when fundamental insights have been gained into unraveling the evolutionary history of not just deuterostomes but life in general. The last 25 years have been transformative in evolutionary biology like no other time in history, with progress obtained by exactly what Brenner (2002) prescribed: we have seen the development of new techniques, like phylogenomics, coupled with new discoveries, like the Chengjiang fauna, and with new ideas, ranging from a surprisingly simple idea like PCR to the wealth of new ideas that goes into sequencing and utilizing a complete animalian genome. Thanks to all of these developments, we now have a solid understanding of the phylogenetic backbone of deuterostome evolution, with well-constrained hypotheses of the timing of these divergences, in addition to unraveling the developmental underpinnings of important characters that were acquired in early in deuterostome evolution and how the acquisition of these characters impacted the ecology and morphology of these long-extinct animals. But of course, there is so much more that needs to be done, and the next 25 years promises to bring even more new techniques, new discoveries, and new ideas that will significantly impact our understanding of our time and place in the history of life.

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