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Worms and gills, plates and spines: the evolutionary origins and incredible disparity of deuterostomes revealed by fossils, genes, and development

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ABSTRACT

Deuterostomes are the major division of animal life which includes sea stars, acorn worms, and humans, among a wide variety of ecologically and morphologically disparate taxa. However, their early evolution is poorly understood, due in part to their disparity, which makes identifying commonalities difficult, as well as their relatively poor early fossil record. Here, we review the available morphological, palaeontological, developmental, and molecular data to establish a framework for exploring the origins of this important and enigmatic group. Recent fossil discoveries strongly support a vermiform ancestor to the group Hemichordata, and a fusiform active swimmer as ancestor to Chordata. The diverse and anatomically bewildering variety of forms among the early echinoderms show evidence of both bilateral and radial symmetry. We consider four characteristics most critical for understanding the form and function of the last common ancestor to Deuterostomia: Hox gene expression patterns, larval morphology, the capacity for biomineralization, and the morphology of the pharyngeal region. We posit a deuterostome last common ancestor with a similar antero-posterior gene regulatory system to that found in modern acorn worms and cephalochordates, a simple planktonic larval form, which was later elaborated in the ambulacrarian lineage, the ability to secrete calcium minerals in a limited fashion, and a pharyngeal respiratory region composed of simple pores. This animal was likely to be motile in adult form, as opposed to the sessile origins that have been historically suggested. Recent debates regarding deuterostome monophyly as well as the wide array of deuterostome-affiliated problematica further suggest the possibility that those features were not only present in the last common ancestor of Deuterostomia, but potentially in the ur-bilaterian. The morphology and development of the early deuterostomes, therefore, underpin some of the most significant questions in the study of metazoan evolution.

Key words: Cambrian Explosion, macroevolution, Deuterostomia, Hemichordata, Chordata, Echinodermata, biomineralization, larval evolution.

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I. INTRODUCTION

Deuterostomia, one of the major divisions of animal life, is comprised of three phyla. Chordata includes familiar animals such as fish, reptiles, birds and mammals (including ourselves). Echinodermata, named as such for their generally spiny skin, includes sea cucumbers, sea stars, sea urchins, brittle stars, and sea lilies. Hemichordata includes the acorn worms and their miniaturized relatives with feathery arms known as pterobranchs. Surveying the adult morphology of such different animals, it can be difficult to visualize how these groups share a close evolutionary history. However, developmental characters, such as the pattern of radial cleavage of embryonic cells and the formation of the mesoderm through enterocoely have historically been used to unite the deuterostomes in contrast to their sister group the protostomes [i.e. arthropods, molluscs, annelids, etc. (Swalla & Smith, 2008; Peterson & Eernisse, 2016)], and the presence of pharyngeal openings remains an important unifying morphological character (although they have subsequently been lost in modern echinoderms).

The early evolutionary history of the three deuterostome phyla, however, has been contentious, due principally to two factors. The first is the high degree of morphological and ecological disparity amongst its constituent taxa. While not a common focal point in discussions of metazoan eco-morphological disparity, non-vertebrate deuterostomes display examples of most major ecological modes and evolutionary transitions, including: transitions from bilateral to radial symmetry; miniaturization of body plans; multiple independent acquisitions of coloniality; complete and partial metamorphosis; and multiple switches between sessile and motile lifestyles across major clades. Although these characteristics make the deuterostomes significant, and fascinating, for the study of ecology and evolutionary biology, they have also made teasing apart the details of deuterostome interrelationships fraught with difficulty. For example, even the now widespread consensus of the sister-taxon relationship between Hemichordata and Echinodermata was only achieved relatively recently, with alternative topologies being presented through the mid 1990s (Turbeville, Schulz & Raff, 1994). Another pertinent example are the many phyla which have historically been considered part of Deuterostomia, such as phoronids and chaetognaths, but which are now placed outside this superphylum (Dunn *et al.*, 2008; Marlétaz *et al.*, 2019). This list of animal groups with debated deuterostome affinity includes the problematic and still controversial xenoturbellids. Previously thought to belong to Platyhelminthes (Smith, Teyler & Rieger, 1986; Peterson & Eernisse, 2001), the phylum Xenacoelomorpha (xenoturbellid and acoel worms) was only recently recognized (Philippe *et al.*, 2011) and since then, independent data sets have resulted in conflicting phylogenetic affinities. Despite being a group of relatively featureless worms, they have recently received attention for being the possible sister group to the rest of Bilateria (Cannon *et al.*, 2016; Rouse *et al.*, 2016) or nested deeply within it as close relatives of the hemichordates and echinoderms (Marlétaz *et al.*, 2019; Philippe *et al.*, 2019; Kapli & Telford, 2020).

A combination of morphological, developmental, and molecular data was necessary to arrive at the currently most accepted framework of the Ambulacraria (Hemichordata + Echinodermata) as sister group to Chordata, yet even the monophyly of this group has recently been questioned, with some researchers pointing out that many of the supposed characters uniting them are more phylogenetically widespread than once believed (Kapli *et al.*, 2021). While only a minority of studies thus far have pointed to a lack of support for Deuterostomia, the continued debate regarding the phylogenetic status of such a major branch of animal life highlights the difficulty in studying early deuterostome evolution.

The second factor confounding a clear view of deuterostome origins is the depauperate early fossil record of the chordates and hemichordates, particularly compared to most protostome groups. Molecular clock estimates place the divergence of ambulacrarians from chordates between the Cryogenian and the Ediacaran [~660–570 million years ago (Ma) (Erwin *et al.*, 2011; Simakov *et al.*, 2015; Delsuc *et al.*, 2018)], but the oldest unequivocal fossils of any of the three constituent phyla are from the Cambrian (Shu *et al.*, 1999; Maletz, 2014*a*; Zamora & Rahman, 2014). By this time each major lineage had already diversified significantly, and, while retaining some plesiomorphic characters, they had diverged quite considerably from the deuterostome last common ancestor (LCA). Equally confounding is the plethora of characteristics that early fossil deuterostomes possessed with no clear extant analogue, as well as combinations of modern features that have not been seen for over half a billion years. From spirally symmetrical echinoderms, to chimeric hemichordates, to a wide array of enigmatic fusiform chordates, we can reasonably extend Hyman's (1955, p. vi) famous salutation of the echinoderms as a 'noble group especially designed to puzzle the zoologist' to their entire superphylum.

The purpose of this review is to synthesize a number of insights into deuterostome origins that have been made possible from the description of early Paleozoic fossils over recent years. These fossils represent a wellspring of new data, but have yet to be put into a unified framework for discussion (Fig. 1; Table 1). We begin by summarizing some of the active debates regarding these fossils on a group-by-group basis, drawing together significant but currently disparate studies. Because the deuterostome phyla have had strikingly different eco-evolutionary trajectories, each section is tailored to major challenges in each phylum. For example, inferring the LCA of the crown group Hemichordata has been a major challenge, therefore, we give more detail on each class and their recently expanding soft-tissue fossil record. On the other hand, while we have a relatively good understanding of the crown group Echinodermata, inferring major morphological transformations within its morphologically disparate stem group remains controversial. Therefore, the echinoderm section is focused on our understanding of homologies and the wealth of stem lineages described to date. We then provide a broader picture of early deuterostome ecology and evolution, as revealed by a holistic consideration of the fossil record, developmental biology of extant deuterostomes, and molecular phylogenies. Finally, we describe current gaps in knowledge, comment briefly on several outstanding problematic taxa, and outline potential future avenues of research for this group, particularly with regards to understanding the morphology of both the ambulacrarian and deuterostome LCAs.

II. PHYLUM HEMICHORDATA

The phylum Hemichordata consists of two classes: the Pterobranchia and the Enteropneusta. The morphological differences between these two groups in their adult forms are vast. Enteropneusts are vermiform animals with a muscular proboscis at the anterior end, which facilitates their creeping and burrowing lifestyles (Fig. 2A). By contrast, pterobranchs are miniaturized animals with feathery feeding appendages, which cohabit collagenous tubes that they build co-operatively (Fig. 2B). These apparent differences are reconciled by developmental data and the maintenance of a basic tri-coelomic body plan in both classes, and their close relationship is further supported by all recent molecular analyses (Cameron, 2005; Osborn *et al.*, 2012; Cannon *et al.*, 2014). Debate still exists regarding whether the pterobranchs are derived from within the Enteropneusta or whether these groups are sister taxa (Merker, Gruhl & Stach, 2014). However, the majority of recent analyses support the latter conclusion, and we will proceed with that framework herein. Arguably, the hemichordates have the worst fossil record of any of the three constituent deuterostome phyla, although this paucity of fossil data manifests differently between the two classes. The pterobranchs, in the form of graptolites, have an exceptional record in some regards (Fig. 2C,D), with their ecological significance over tens of millions of years resulting in a wide spatiotemporal breadth from the mid-Cambrian to mid-Carboniferous (approximately 510–320 Ma) (Xu *et al.*, 2005; Maletz, 2014*b*). However, among the hundreds of graptolite species described, all are known from their recalcitrant, secreted homes known as tubaria; no convincing evidence of a pterobranch zooid exists in the fossil record. By contrast, fossil enteropneusts with soft tissues are known, but are exceedingly rare, and many of the younger representatives are relatively data poor with regards to the characters preserved. This picture has begun to change recently, as enteropneusts are now found to be a significant

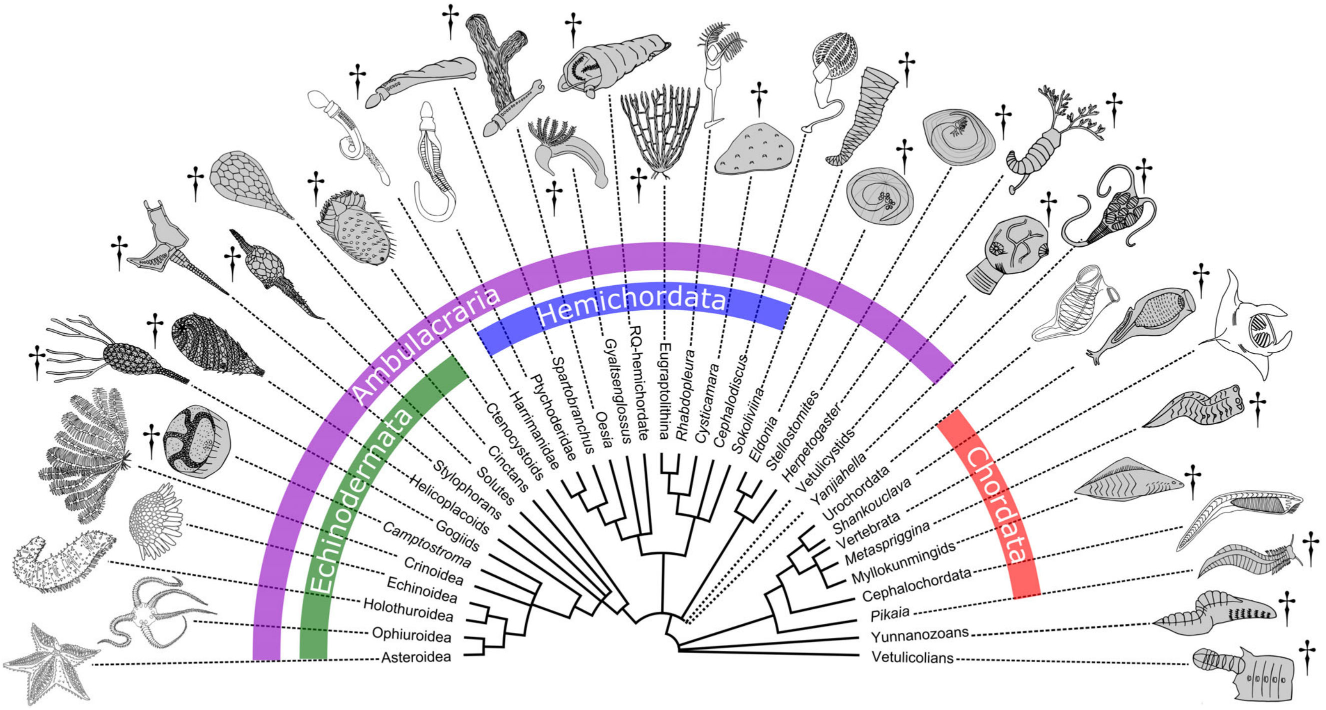

Fig. 1. A simplified phylogenetic tree describing the breadth of taxa considered in this study. Taxa in grey with daggers are extinct, taxa in white are extant. The dashed lines leading to *Yanjiahella* and the vetulicystids represent their controversial affinities with their respective parts of the tree topology. The vast majority of the species displayed date back to the middle Cambrian, and represent body plans that provide unique insights into the origins of Deuterostomia.

but unrecognized component of many Cambrian ecosystems (Nanglu *et al.*, 2016; Nanglu, Caron & Gaines, 2020*b*).

(1) Class Pterobranchia

Extant pterobranchs are microscopic, tentaculate filter feeders (Fig. 2B). They live in colonies, either facilitated by a system of attachment organs known as the stolon in the Rhabdopleuridae, or in a more loose arrangement without obligate attachment as in the Cephalodiscidae (Cameron, 2005). This latter condition has led to the cephalodiscids sometimes being described as pseudo-colonial (Maletz, 2014*b*). In both families, the zooids produce a collagenous dwelling known as a tubarium, which can take a variety of forms from a series of columnar tubes to a bramble of collagenous spines (Maletz, 2017). The abundant and morphologically diverse tubaria of the extinct graptolites constitute the vast majority of the hemichordate fossil record (Fig. 2C). Through this record, we know that pterobranchs were a significant part of marine ecosystems for large periods during the Paleozoic, particularly in the form of planktonic graptolites (Xu *et al.*, 2005; Servais *et al.*, 2010). This current review is focused principally on the earliest origins of Deuterostomia and its constituent groups, and so a comprehensive review of pterobranch evolutionary and ecological dynamics across their entire history is beyond our scope [for further reading, see Sheets *et al.* (2016) and Maletz (2017)]. However, one particular study merits particular consideration here. A phylogenetic analysis of both extant and extinct pterobranch tubes found that the extant genus *Rhabdopleura* nested within what is classically referred to as Graptolithina (Mitchell *et al.*, 2013). This study then concluded that *Rhabdopleura* represents a living graptolite; therefore, the typical narrative that the graptolites went extinct during the Carboniferous may not be strictly true. Whatever the exact placement of *Rhabdopleura*, however, it can still be said that the halcyon days of hemichordate diversity had ended by the Carboniferous, following the extinctions of the planktonic graptolites, and that in the subsequent 300 million years they have made little mark in the geological record.

The earliest known fossil pterobranch is either a putatively identified fragment of tube periderm from the middle Cambrian Kaili biota (Harvey *et al.*, 2011) or the 'problematic' tubular fossil *Sokoloviina costata* from the Fortunian Stage of the Cambrian (541–529 Ma), which has recently been suggested to be a pterobranch tube (Maletz, 2019). These fossils introduce one of the cardinal difficulties in graptolite palaeobiology – no pterobranch in the entire fossil record preserves convincing soft-tissue data on the zooids (see Sennikov, 2016 for one possible exception). This is not surprising when the microscopic, fragile nature of the zooids is considered in comparison with their relatively recalcitrant collagenous tubes. This conclusion finds empirical support from an

Table 1. A list of taxa key to understanding the origins of Deuterostomia and its constituent phyla. While not comprehensive of every relevant fossil, this table includes those discussed in detail in this review. Ages and references are also included for these taxa, as well as an indication of their broader affinities, both for reference within this study as well for those looking to date their own studies by the first appearances of major groups. Asterisks indicate non-monophyletic taxa and question marks indicate uncertain taxonomic placement. Ma, million years ago.

Taxon	Broader affinity	~Age (Ma)	Stratigraphic age	Reference
Arkarua adami	Uncertain	558–550	Ediacaran	Cracknell *et al.* (2021)
Tribrachidium heraldicum	Uncertain	558–550	Ediacaran	Cracknell *et al.* (2021)
Yuyuanozoon magnificissimi	Stem-group Deuterostomia	518	Cambrian, Age 3	Li *et al.* (2018)
Vetulicola cuneata	Vetulocolia, stem-group Deuterostomia	518	Cambrian, Age 3	Xian-Guang *et al.* (2017)
Banffia constricta	Vetulocolia, stem-group Deuterostomia	506	Cambrian, Age 5	Conway Morris *et al.* (2015)
Xidazoon stephanus	Vetulocolia, stem-group Deuterostomia	518	Cambrian, Age 3	Shu *et al.* (1999)
Didazoon haoae	Vetulocolia, stem-group Deuterostomia	518	Cambrian, Age 3	Shu *et al.* (2001)
Metaspriggina walcotti	Stem-group Chordata	506	Cambrian, Age 5	Conway Morris & Caron (2014)
Pikaia gracilens	Stem-group Chordata	506	Cambrian, Age 5	Conway Morris & Caron (2012)
Cathaymyrus haikouensis	Stem-group Chordata	518	Cambrian, Age 3	Shu *et al.* (1996); Xian-Guang *et al.* (2017)
Myllokunmingia fengjiaoa	Myllokunmingids, stem-group Chordata	518	Cambrian, Age 3	Shu *et al.* (1999); Xian-Guang *et al.* (2017)
Haikouichthys ercaicunensis	Myllokunmingids, stem-group Chordata	518	Cambrian, Age 3	Shu *et al.* (1999)
Zhongjianichthys sp.	Myllokunmingids, stem-group Chordata	518	Cambrian, Age 3	Zhao *et al.* (2019*a*)
Shankouclava anningense	Stem-group Urochordata (?), Chordata	518	Cambrian, Age 3	Xian-Guang *et al.* (2017)
Herpetogaster collinsi	Cambroernids, stem-group Ambulacrarian (?)	506	Cambrian, Age 5	Caron *et al.* (2010); Yang *et al.* (2020)
Herpetogaster haiyanensis	Cambroernids, stem-group Ambulacrarian (?)	518	Cambrian, Age 3	Yang *et al.* (2020)
Eldonia ludwigi	Cambroernids, stem-group Ambulacrarian (?)	506	Cambrian, Age 5	Zhu *et al.* (2002)
Eldonia eumorpha	Cambroernids, stem-group Ambulacrarian (?)	518	Cambrian, Age 3	Xian-Guang *et al.* (2017)
Stellostomites eumorphus	Eldonioids, Cambroernids, stem-group Ambulacraria	518	Cambrian, Age 3	Zhu *et al.* (2002)
Rotadiscus grandis	Eldonioids, Cambroernids, stem-group Ambulacraria	518	Cambrian, Age 3	Zhu *et al.* (2002); Xian-Guang *et al.* (2017)
Pararotadiscus guizhouensis	Eldonioids, Cambroernids, stem-group Ambulacraria	518	Cambrian, Age 3	Zhu *et al.* (2002)
Vetulocystis catenata	Vetulicystids, stem-group Ambulacraria	518	Cambrian, Age 3	Shu *et al.* (2004); Xian-Guang *et al.* (2017)
Dianchicystis jianshanensis	Vetulicystids, stem-group Ambulacraria	518	Cambrian, Age 3	Shu *et al.* (2004)
Thylacocercus ignota	Vetulicystids, stem-group Ambulacraria	504	Cambrian, Drumian	Conway Morris *et al.* (2015)
Yanjiahella biscarpa	Stem-group Ambulacraria	518	Cambrian, Age 3	Guo *et al.* (2012)
Sokoliviina costata	Stem-group Pterobranchia, Hemichordata	535	Cambrian, Fortunian	Maletz (2019)
Cysticamara	Stem-group Pterobranchia, Hemichordata	480	Cambrian, Age 10	Maletz (2019)
Unnamed Burgess Shale hemichordate	Stem-group Enteropneusta	506	Cambrian, Age 5	Nanglu & Caron (2021)
Gyaltsenglossus senis	Stem-group Enteropneusta, Hemichordata	506	Cambrian, Age 5	Nanglu *et al.* (2020*a*)
Oesia disjuncta	Stem-group Enteropneusta, Hemichordata	506	Cambrian, Age 5	Nanglu *et al.* (2016)
Spartobranchus tenuis	Stem-group Enteropneusta, Hemichordata	506	Cambrian, Age 5	Caron *et al.* (2013)
Yuknessia	Hemichordata	506	Cambrian, Age 5	LoDuca *et al.* (2015)
Megaderaion callovianum	Ptychoderidae, Enteropneusta, Hemichordata	166	Jurassic	Alessandrello *et al.* (2004)
Mazoglossus ramsdelli	Harrimanidae, Enteropneusta, Hemichordata	309	Carboniferous	Bardack (1997)
Helicocystis moroccoensis	Helicocystitidae, stem-group Echinodermata	514–508	Cambrian, Age 4–5	Smith & Zamora (2013)
Camptostroma roddyi		516–513	Cambrian, Age 4	Durham (1966)

(Continues on next page)

Table 1. *(Cont.)*

Taxon	Broader affinity	~Age (Ma)	Stratigraphic age	Reference
	Edrioasteroidea*, stem-group Echinodermata or stem-group Eleutherozoa			
Kailidiscus chinensis	Edrioasteroidea*, stem-group Echinodermata or stem-group Eleutherozoa (?)	509	Cambrian, Age 5	Van Roy *et al.* (2015)
Stromatocystites pentangularis	Edrioasteroidea*, stem-group Echinodermata or stem-group Eleutherozoa (?)	513–501	'middle' Cambrian	Zamora *et al.* (2015)
Ctenoimbricata spinosa	Stem-group Echinodermata	509–504	Cambrian, Age 5	Zamora *et al.* (2012)
Ctenocystis colodon	Ctenocystioidea, stem-group Echinodermata	513–498	'middle' Cambrian	Ubaghs & Robison (1988)
Protocinctus mansillaensis	Cincta, stem-group Echinodermata	513–501	'middle' Cambrian	Rahman & Zamora (2009)
Coleicarpus sprinklei	Soluta, stem-group Echinodermata	513–498	'middle' Cambrian	Daley (1996)
Castericystis vali	Soluta, stem-group Echinodermata	513–498	'middle' Cambrian	Ubaghs & Robison (1988)
Jaekelocarpus oklahomensis	Mitrata, Stylophora, stem-group (?) Echinodermata	318–314	Early Pennsylvanian	Kolata *et al.* (1991)
Lagynocystis pyramidalis	Mitrata, Stylophora, stem-group (?) Echinodermata	467–458	Middle Ordovician, Darriwilian	Parsley (2000)
Ceratocystis sp. indet.	Cornuta, Stylophora, stem-group (?) Echinodermata	516–513	Cambrian, Age 3	Clausen & Smith (2005)
Archaeocothurnus bifida	Cornuta, Stylophora, stem-group (?) Echinodermata	513–498	'middle' Cambrian	Ubaghs & Robison (1988); Sumrall *et al.* (1997)
Proscotiaecystis melchiori	Cornuta, Stylophora, stem-group (?) Echinodermata	478–470	Early Ordovician, Floian	Vizcaino & Lefebvre (1999)
Thoralicystis sp. indet.	Cornuta, Stylophora, stem-group (?) Echinodermata	485–478	Early Ordovician, Tremadocian	Lefebvre *et al.* (2019)
Reticulocarpos hanusi	Cornuta, Stylophora, stem-group (?) Echinodermata	467–458	Middle Ordovician, Darriwilian	Jefferies & Prokop (1972)
Phyllocystis crassimarginata	Cornuta, Stylophora, stem-group (?) Echinodermata	478–470	Early Ordovician, Floian	Vizcaino & Lefebvre (1999)
Gogia prolifica	Eocrinoidea*, stem-group Echinodermata or stem-group Crinoidea	513–505	'middle' Cambrian	Sprinkle (1973)
Helicoplacus sp.	Helicoplacoid, stem-group Echinodermata	521–514	Cambrian, Age 3	Durham (1993); Smith *et al.* (2013)

experimental decay study of the modern pterobranch *Rhabdopleura*, where the zooids disappeared entirely within 2–4 days, the stolon (for which there is preserved evidence in fossil graptolites) persisted for 61 days without any visible degradation, and the tubarium itself showed no signs of degradation for the entire length of the study (208 days; Beli, Piraino & Cameron, 2017). The one fossil suggested to represent the soft-tissue preservation of a pterobranch zooid itself, *Galeaplumosus* (Hou *et al.*, 2011), has subsequently been redescribed as one of the arms of the anemone-like animal *Xianguangia* (Ou *et al.*, 2017). *Xianguangia* itself, has since been debated as either a benthic ctenophore (Zhao *et al.*, 2019*b*) or cnidarian (Ou *et al.*, 2022); neither assignment is relevant to deuterostome origins, but the debate itself underscores the labile nature of both the tissues and phylogenetic placements of early Paleozoic problematica.

This lack of zooid preservation poses significant problems for reconstructing the early evolution of the pterobranchia. However, we can make inferences based on what is known of the earliest tubes. (*i*) Their construction is more similar to *Rhabdopleura* than to *Cephalodiscus*, which has led to the essentially unanimous reconstruction of graptolite zooids as *Rhabdopleura*-like (i.e. two feeding arms). (*ii*) The size of the earliest recognizable pterobranch tubes (Harvey *et al.*, 2011; Maletz, 2019), including a wide variety of benthic forms from the middle Cambrian (Ramírez-Guerrero & Cameron, 2021), suggests that the inhabitants themselves had already undergone miniaturization. (*iii*) Similarly, the

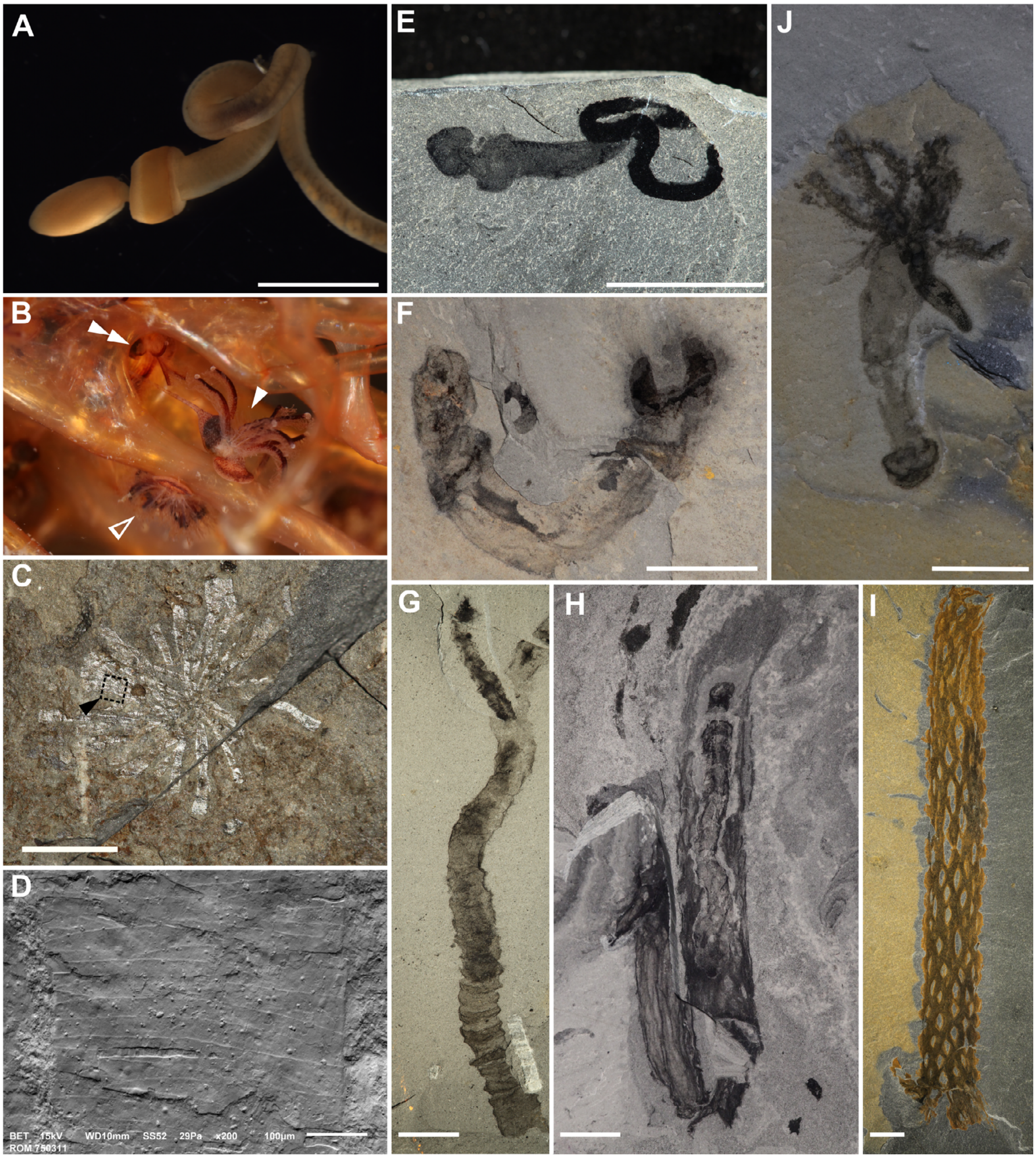

Fig. 2. Representatives of the phylum Hemichordata. (A) The extant harrimanid enteropneust *Harrimania planktophilus*, showing the characteristic tripartite division of proboscis (acorn-shaped structure), collar (rectangular area) and vermiform trunk. (B) Three specimens of the extant pterobranch *Cephalodiscus hodgsoni*, indicated by arrows, inside their coenicium. (C) The fossil pterobranch *Yuknessia stephenensis* (ROMIP 62918). (D) A closeup of the boxed section in C, showing fine-scale banded structures called fuselli, confirming that *Yuknessia* is a hemichordate and not an alga as previously believed. (E) The stem-enteropneust *Spartobranchus tenuis* (GSC-113051). (F) The stem-enteropneust *Oesia disjuncta* (ROMIP 63713). (G) The tube-shaped dwelling of *Spartobranchus tenuis*, with the worm preserved inside (USNM 509820). (H) *Oesia disjuncta* preserved inside a curved, branching tube (ROMIP 63715). (I) The tube of *Oesia disjuncta*, showing the characteristic, spirally arranged pores (ROMIP 63716). (J) The stem-hemichordate *Gyaltsenglossus senis* (ROMIP 65606). Scale bars: 1 cm (A, E–J), 5 mm (C), 100 μm (D). Approximate size of zooids in B: 2 mm. Photograph credits: Karma Nanglu (A), Kevin Kocot (B), Jean-Bernard Caron (C–J). GSC, Geological Survey of Canada; ROMIP, Royal Ontario Museum (Invertebrate Paleontology); USNM, Smithsonian National Museum of Natural History.

early tube record suggests that the initial diversification of the pterobranchs occurred along the benthos, with fully planktonic Graptoloidea exploding in diversity during the Ordovician (Sadler, Cooper & Melchin, 2011; Cooper *et al.*, 2014). (*iv*) Finally, the ubiquity of the stolon system in well-preserved Cambrian graptolites suggests that obligate colonial-living forms evolved early in the evolutionary history of this group (Ramírez-Guerrero & Cameron, 2021).

(2) Class Enteropneusta

Until recently, the fossil record has provided minimal insights into the early evolution of the enteropneusts. Enteropneust fossils are exceedingly rare and generally of poor quality, with the oldest dating back to the Carboniferous, roughly 150 million years after which many crown classes had already evolved (Arduini, Pinna & Terruzzi, 1981; Shabica & Hay, 1997; Bechly & Frickhinger, 1999; Alessandrello, Bracchi & Riou, 2004). The taphonomic concerns that plague the pterobranchs are also exacerbated for the enteropneusts. Despite enteropneusts being much larger than an individual pterobranch zooid (with the exception of meiofaunal taxa; Worsaae *et al.*, 2012), experimental evidence still shows rapid *post-mortem* loss due to decay (Nanglu, Caron & Cameron, 2015), and the apparent lack of a tubarium in extant forms seemed to make the overall preservation potential of enteropneusts abysmal.

A series of recent discoveries from the middle Cambrian Burgess Shale (∼506 Ma) have reversed that trend, providing a sudden abundance of morphological data pertinent to enteropneust origins (Fig. 2E–J). The first two were the redescriptions of *Spartobranchus tenuis* (Walcott, 1911*a*) and *Oesia disjuncta* as hemichordates (Fig. 2E–I). Both of these taxa were part of Walcott's original discoveries, but had eluded their correct phylogenetic placement for over 100 years. With additional material from localities such as Marble Canyon (Caron *et al.*, 2014) and imaging techniques (i.e. cross-polarization, higher resolution photography, scanning electron microscopy), it was found that both of these taxa possess a gross morphology highly reminiscent of extant enteropneusts. *Spartobranchus*, in particular, is very similar to a modern harrimanid (Fig. 2A, E; Caron, Conway Morris & Cameron, 2013), while *Oesia* possesses a set of unique features such as a hyper-extended pharynx which do not have a clear analogue among extant hemichordates (Nanglu *et al.*, 2016). Most notable, however, is the fact that both taxa are found dwelling inside organic tubes – a relatively smooth, corrugated tube in the case of *Spartobranchus* and a porous, filamentous tube in the case of *Oesia* (Fig. 2G–I). Together with the subsequent discovery of more vermiform enteropneusts living communally in enlarged tubular dwellings (Nanglu & Caron, 2021), these fossils strongly support the ability to secrete tubes in the LCA of Enteropneusta; when taken together with the ubiquitous tube building of the pterobranchs (except for the poorly known extant taxon *Atubaria*; Komai, 1949), tube building seems a likely plesiomorphic trait for crown-Hemichordata.

The recently described *Gyaltsenglossus senis* (Fig. 2J) provides an interesting counterpoint to the three preceding taxa (Nanglu, Caron & Cameron, 2020*a*). Like them, it has the vermiform, trimeric body plan of an enteropneust, with an elongate proboscis similar to the genus *Saccoglossus*. However, the mesosome has a crown of feeding arms arranged similarly to the cephalodiscid pterobranchs, and the worms are not found in association with any tubes. In the study describing this new genus, *Gyaltsenglossus* was found to be a stem-group hemichordate. However, while the inclusion of *Gyaltsenglossus* within total group Hemichordata had high support, its exact position in relation to the two reciprocally monophyletic classes had somewhat lower support. Thus, while the morphology of this new species may provide a window into the ancestral hemichordate body plan, we believe it is most conservative to discuss a number of alternative hypotheses for the functional morphology and ecology of the hemichordate LCA that synthesize the recently discovered wellspring of fossil data with both developmental and molecular data from their extant relatives.

(3) Synthesis

There are four central questions when discussing the morphology and ecology of the hemichordate LCA: (*i*) when did tube building emerge; (*ii*) when and how was a colonial lifestyle adopted; (*iii*) when did miniaturization occur; and (*iv*) what was the ancestral ecological mode of Hemichordata?

Cambrian pterobranch tubes and the stem-group enteropneusts from the Burgess Shale clearly indicate that tube-building behaviour was present by the middle Cambrian. Further, a wide variety of taxa currently recognized as algae or indeterminate burrows may in fact be unrecognized hemichordate tubes, as was the case for *Spartobranchus*, *Oesia*, and *Yuknessia* (Caron *et al.*, 2013; LoDuca *et al.*, 2015; Nanglu *et al.*, 2016); in essence, hemichordates and their tubular dwellings were not only present by the middle Cambrian, but may have been currently unrecognized major components of early benthic ecosystems. Tube building, therefore, appears plesiomorphic to the crown-group Hemichordata, making the tubes of *Spartobranchus* and *Oesia* homologous with those of the pterobranchs (including graptolites). As noted above, *Gyaltsenglossus* does not possess a tube, and phylogenetic analyses support its placement as a stem-group hemichordate. In this case, *Gyaltsenglossus* may have preceded the acquisition of tube building, or represent an early, independent loss of tube building. Within modern representatives, it has been further suggested that the modern deep sea enteropneusts of the family Torquaratoridae may form mucus tubes, indicating a close phylogenetic affinity with *Spartobranchus* (Halanych *et al.*, 2013). We view this as highly unlikely given the roughly half-a-billion year gulf between these taxa. If these structures are taken to be true permanent dwellings roughly equivalent in complexity to those of the Cambrian enteropneusts and the pterobranchs, the Torquaratoridae would therefore represent an independent re-acquisition of tube-building behaviour. However, these putative torquaratorid tubes lack any obvious form of substantive proteinaceous structure and dissipate after a few days. They appear more likely to be a function of the copious mucus secretions of the enteropneusts being maintained over prolonged periods due to the low temperature and minimal benthic disruption characteristic of the deep sea environments in which torquaratorids are found (Nanglu *et al.*, 2015).

Two related questions are the timing of coloniality and miniaturization within Hemichordata, and how these ecologically significant morphological steps were achieved. Minimally, we know that some middle Cambrian pterobranchs were already colonial, based on the preservation of the stolon system (Ramírez-Guerrero & Cameron, 2021), and miniaturized, based on micrometer-scale tubes (Harvey *et al.*, 2011; Maletz, 2019). The builders of these earliest pterobranch tube fragments are not preserved, but have been tentatively assigned a cephalodiscid rather than a rhabdopleurid affinity based on the tube morphology (Maletz, 2019). If so, it is logical to infer that they had either the pseudo-colonial arrangement of modern cephalodiscids, or were solitary animals. While the phylogenetic position of the communal hemichordate worms from Raymond Quarry remains unclear (i.e. the body fossil material was not of sufficient quality to perform a meaningful phylogenetic analysis; Nanglu & Caron, 2021), two possibilities seem likely: they are stem-group enteropneusts (based primarily on their harrimanid-like morphology), or stem-group pterobranchs (based on their pseudo-colonial living arrangement). Should the former be true, these hemichordates represent an independent acquisition of a colonial lifestyle outside of the pterobranchs. If the latter is true, they may be members of a clade representing the transition between a vermiform, tube-building hemichordate LCA towards the colonial and miniaturized form of the crown-group Pterobranchia. This conclusion would also increase the support for a vermiform hemichordate LCA, with the tentaculate form of the pterobranchs being a derived state. This hypothesis has found further support in a recently discovered vermiform enteropneust from Chengjiang pushing the earliest record of that group a further 10 million years older than previously known (Yang *et al.*, 2021).

The morphology and ecology of the hemichordate LCA has factored into debates regarding deuterostome origins for decades. A notable, well-known example is Romer's hypothesis of vertebrate origins postulating a sessile, tentaculate deuterostome LCA, similar in gross morphology to pterobranchs, giving rise to the hemichordates (from within which the chordates were derived) and the early arm-bearing echinoderms (Romer, 1967). Gill bars and gill slits have played a similarly important role, connecting the vermiform enteropneusts to the chordates (most obviously, the urochordates and cephalochordates), a conclusion supported by highly conserved pharyngeal transcription networks between hemichordates and cephalochordates (Gillis, Fritzenwanker & Lowe, 2012). We treat the deeper origins of these body plan characteristics at greater length in Section VI after reviewing the salient echinoderm, chordate and problematic fossils necessary for a superphylum-level discussion.

The developing Cambrian fossil record provides as many questions as it does answers when it comes to the ecology of the early hemichordates, as nearly every conceivable character and character combination appears synchronously. *Oesia* has been interpreted as a pharyngeal filter feeder, as are some extant harrimanids (Cameron, 2002; Vo *et al.*, 2019), based on its protracted, gill bar-dense pharynx, which may be analogous to the pharyngeal baskets of tunicates (Cameron, 2005). *Spartobranchus* lacks similar specializations and was likely a deposit feeder (Caron *et al.*, 2013). Despite lacking direct evidence of the zooids, the rhabdopleurid affinities of the Cambrian graptolite tubes suggest that they were tentaculate suspension feeders (Maletz, 2017; Ramírez-Guerrero & Cameron, 2021). *Gyaltsenglossus* appears to have been able to employ a combination of both tentaculate filter feeding and deposit feeding moderated by its long, *Saccoglossus*-like proboscis (Nanglu *et al.*, 2020*a*). Moreover, the Cambrian hemichordates with soft-tissue preservation thus far appear to share a ubiquitous and morphologically distinct posterior structure, which may have been used for facultative attachment. Therefore, it seems that while the hemichordate LCA was most likely a vermiform and motile animal, a sessile mode of life facilitated by a benthic attachment structure cannot be completely ruled out.

Synthesizing the above insights, it is clear that recent fossil discoveries have provided an unexpected deluge of new data for investigating hemichordate origins. However, clear, conclusive statements regarding hemichordate ancestry and the detailed sequences of early character acquisition within this phylum remain somewhat elusive. When you consider the decades of lead time that researchers on groups such as Cambrian arthropods and molluscs have had, to say nothing of the relative abundance of material from younger periods, the enigmatic status of early hemichordate evolution is not only excusable, but to be expected. At the same time, it is comforting to see that the relatively recently discovered soft-tissue diversity of the Cambrian hemichordates appears to recapitulate what we already know from more diverse and readily fossilizable phyla: all character combinations appear possible, in addition to entirely new characters that defy straightforward homology with modern taxa. The final point to consider is that despite the beauty and scientific significance of Cambrian fossils (particularly those from localities such as the Burgess Shale and Chengjiang), they are only the best material we have available, rather than the ideal. To truly grasp the origins of phyla, we must necessarily have older fossils that begin to approach our best estimates for the divergence times of superphylum-level divisions. A call for broader fossil collecting and re-examinations of problematic specimens gathering dust in museum collections is particularly relevant for Hemichordata, as their morphology leaves them liable to being misidentified as burrows, algae, or the tubes of other taxa.

III. PHYLUM ECHINODERMATA

The phylum Echinodermata is a morphologically and taxonomically diverse group with five extant classes containing at least 7000 named species and a vast fossil record containing more than 13,000 named species (Wray, 1999). Phylogenetic relationships of the five extant classes are well understood and well supported by both molecular and morphological data (e.g. Smith *et al.*, 2004; Janies, Voight & Daly, 2011; Telford *et al.*, 2014; Reich *et al.*, 2015; Fig. 1). A sister-group relationship between echinoderms and hemichordates is also consistently recovered by molecular phylogenetics (Bromham & Degnan, 1999; Cannon *et al.*, 2014).

Echinoderms possess a high-magnesium calcite mesodermal endoskeleton that is covered by epidermis (Gorzelak, 2021). The skeleton may be constructed from large interconnected and/or rigidly sutured plates, such as in echinoids, or it may consist of smaller elements embedded in soft tissues, such as in holothuroids. At a microscopic scale, most skeletal elements of post-metamorphic echinoderms are composed of a porous, interconnected meshwork called stereom (Smith, 1990; Gorzelak, 2021). This stereom endoskeleton, composed of high-magnesium calcite, is the only synapomorphy shared by all known echinoderms (Zamora & Rahman, 2014; Zamora *et al.*, 2020). In extant echinoderms, stereom development is regulated by a suite of genes that are unique to echinoderms, and it is thought that the same genes were responsible for stereom formation in fossil taxa (Bottjer *et al.*, 2006; Gorzelak & Zamora, 2013; Thompson, 2022). The stereom plates are bound together and supported by muscles or ligaments, including a ligamentary mutable collagenous tissue that is capable of passively altering its mechanical properties. To date, mutable collagenous tissue has been found only in echinoderms and is present in all extant clades; as a result, mutable collagenous tissue represents a synapomorphy of at least crown-group echinoderms (Wilkie *et al.*, 2021). Relationships between stereom microstructure and overlying soft tissues have been used to investigate the possibility of mutable collagenous tissue occurring in stylophorans (e.g. Clausen & Smith, 2005; Gorzelak & Zamora, 2013, 2016), but it remains unclear whether this feature was a synapomorphy of all echinoderms (Baumiller, 2008). Other characters that are common to pentaradial echinoderms include the presence of an unpaired water vascular system derived from the left hydrocoel (mesocoel) and the loss of gill slits (but note that crown-group asteroids and ophiuroids have paired water vascular systems, which are interpreted to represent a derived condition). Within Metazoa, pentaradial symmetry is unique to echinoderms, and although it is recognized in extant and many extinct groups, it is absent from some early echinoderm lineages. Whether pentaradial symmetry is an echinoderm synapomorphy or a synapomorphy within its crown group depends on the interpretation of echinoderm homology and the phylogenetic position of extinct, non-pentaradial groups (David *et al.*, 2000; Smith, Zamora & Álvaro, 2013; Lefebvre *et al.*, 2019; Deline *et al.*, 2020).

Despite being prone to disarticulation, the fossil record of the phylum is of comparatively good quality as a result of its mineralized endoskeleton (Foote & Sepkoski, 1999). Although the total number of formally recognized classes has fluctuated over the years, more than 30 major clades of echinoderms have been identified spanning 21 nominal taxonomic classes (Sprinkle & Kier, 1987; Sumrall & Wray, 2007; Zamora & Rahman, 2014), although several of these classes are likely paraphyletic or polyphyletic. The oldest echinoderms are known from the Cambrian Stage 3 (~521 Ma), and most major groups had evolved by at least the Middle Ordovician (~470 Ma). While a rich fossil record may generally allow for robust inferences of evolutionary changes, difficulties in confidently identifying homologous characters among groups pose a major challenge to inferring the echinoderm LCA. This task is further complicated by high morphological and ecological disparity among echinoderm taxa that evolved within a relatively short span of time, including extreme variations on body plan symmetry (Zamora & Rahman, 2014; Deline *et al.*, 2020; Novack-Gottshall *et al.*, 2022; Fig. 3). As a result, the relationships among the stem lineages and between stem- and crown-group echinoderms remain somewhat controversial and phylogenetic interpretations have shifted repeatedly with the discovery of new fossils, descriptions of previously unrecognized morphological features, alternative homology schemes, and implementation of quantitative phylogenetic methods.

Here, we discuss our understanding of echinoderm homology, important evolutionary transitions in light of recent discoveries, and challenges that are central to understanding relationships within the Echinodermata. A comprehensive appraisal of the phylum is beyond the scope of this treatment given their extensive fossil record, so we here focus on major echinoderm groups and individual taxa that are central to the study of deuterostome origins and relationships. These include the oldest echinoderms known from the Cambrian with morphologies reflecting key evolutionary transitions in the echinoderm body plan (e.g. symmetry), and the extant classes that have informed our understanding of echinoderm development and genomics.

(1) Homology: integrating fossils, phylogenetics, and development to understand early echinoderm evolution

Phylogenetic analyses of early, anatomically enigmatic stem-group taxa are key to understanding the evolutionary transition from pre-radial to pentaradial symmetry in echinoderms. Thus, identifying homologous morphological characters among taxa with radically disparate body plans is critical to reconstructing phylogenetic relationships accurately, and continued refinement of homology concepts remains a central challenge in the study of early echinoderm evolution (e.g. Mooi, David & Marchand, 1994; David & Mooi, 1998; Sumrall & Waters, 2012; Kammer *et al.*, 2013). A major source of information concerning echinoderm homologies, especially for extinct lineages, comes from comparative analyses of developmental patterns and ontogenetic criteria in extant and fossil clades

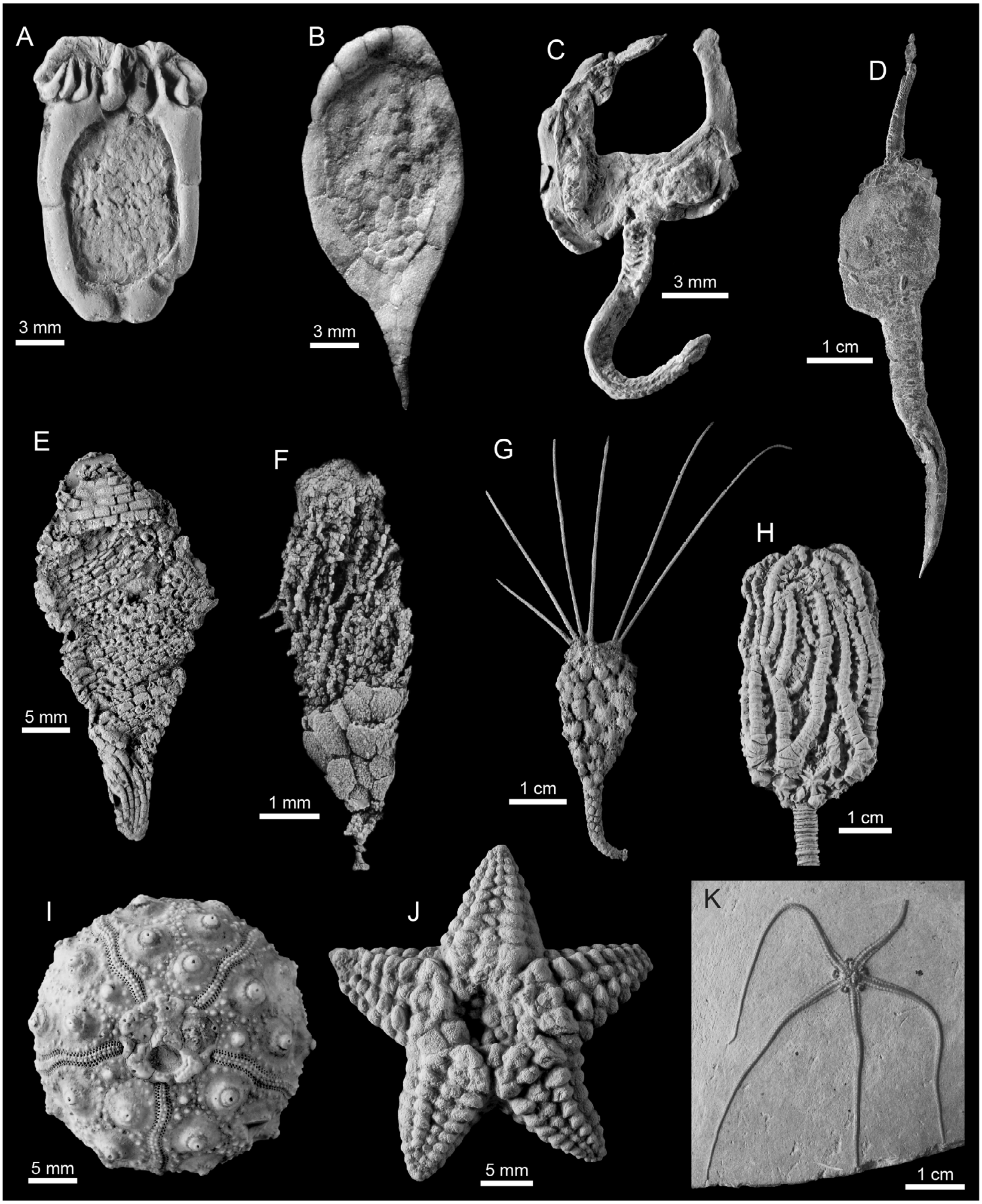

Fig. 3. Representative echinoderm taxa showing major variations in body plans, including (A, B) bilaterally symmetric forms, (C, D) asymmetric forms, and (E–K) radiate forms. (A) Ctenocystoid *Ctenocystis colodon* (USNM 423874) from the Middle Cambrian of Utah, USA; (B) cinctan *Protocinctus mansillaensis* (MPZ 2004/170) from the early Middle Cambrian of Spain (image courtesy of I. Rahman); (C) stylophoran *Archaeocothurnus bifida* (USNM 415804) from the Middle Cambrian of Utah, USA; (D) solute *Castericystis vali* (USNM 393391) from the Middle Cambrian of Utah, USA; (E) helicoplacoid *Helicoplacus* sp. (USNM S 10007) from the Early Cambrian of California, USA; (F) helicocystoid *Helicocystis moroccoensis* (NHM UK EE15375) from the Early Cambrian of Morocco (image courtesy of S. Zamora); (G) gogiid *Gogia prolifica* (USNM 64351) from the Middle Cambrian of British Columbia, Canada; (H) crinoid *Konieckicrinus josephi* (UMMP 74779) from the Late Ordovician of Ontario, Canada; (I) echinoid *Heterosalenia occidentalis* (USNM 442325) from the Late Cretaceous of Jamaica; (J) asteroid *Hudsonaster incomptus* (USNM 40882A) from the Late Ordovician of Ohio, USA; (K) ophiuroid *Geocoma* sp. (USNM 440935) from the Lower Jurassic of Germany. Institutional abbreviations: MPZ, Palaeontological Museum, Zaragoza University, Spain; NMH UK, Natural History Museum, London; UMMP, University of Michigan Museum of Paleontology; USNM, Smithsonian National Museum of Natural History.

(e.g. Mooi *et al.*, 1994; Sumrall & Wray, 2007; Swalla & Smith, 2008; Ausich *et al.*, 2020).

The bewildering morphological disparity exhibited among extant echinoderms seemingly presents a barrier to deciphering homologous skeletal features across classes. However, a body of interrelated hypotheses collectively called the Extraxial/Axial Theory (EAT) postulates that the skeletal architecture exhibited by different body wall regions during larval development provides insight into understanding the echinoderm body plan (Mooi *et al.*, 1994; David & Mooi, 1996, 1998; Mooi & David, 1997, 2008). In essence, the EAT proposes that differences in adult morphology among echinoderms can be explained by tracking the fate of two body-wall regions of larval tissues responsible for producing skeletal material, termed the axial and extraxial regions. Consequently, evolutionary differences among major lineages of echinoderms can be explained by changes to the retention, growth, or resorption of different skeletal regions during development. The axial skeletal region develops from the rudiment, comprising the hydrocoel and left somatocoel, and forms the basis for the plates associated with the ambulacral system, mouth, tube feet, and water vascular system, as well as the interambulacra in echinoids. The extraxial region comprises the non-rudiment larval body and makes up the remaining portions of adult echinoderm skeletons. The extraxial region can be separated into two types, the imperforate and perforate extraxial regions, depending on whether or not they are pierced by orifices in contact with ambient sea water (e.g. anus, genital pores, etc.).

The EAT model has been a highly successful and influential framework for understanding broad-scale echinoderm homologies, and has been applied to hypotheses regarding skeletal homologies among both extant clades and Cambrian stem groups (eg. David *et al.*, 2000). Interestingly, when interpretations of the EAT model are applied to the fossil record, it appears that the relative contribution of axial *versus* extraxial material in adult echinoderm skeletons has changed dramatically through time and varies widely among clades. For example, the skeletal material in Cambrian taxa is dominated by the extraxial skeleton, whereas in extant clades, such as echinoids, it is hypothesized to be composed almost entirely of axial tissue (Mooi & David, 1997; Peterson, Arenas-Mena & Davidson, 2000). Similarly, many extinct clades feature imperforate extraxial elements in their skeletons, whereas crinoids are the only crown-group clade to retain them in their stalks.

Another useful model for resolving skeletal homologies is called Universal Element Homology (UEH) (Sumrall, 2010, 2015, 2017; Sumrall & Waters, 2012; Kammer *et al.*, 2013). In contrast to EAT, which emphasizes the developmental origin and fate of axial *versus* extraxial skeletal regions, UEH focuses on the identification of individual skeletal elements associated with the mouth (peristome) and the ambulacral system (Sumrall, 2017). The UEH framework relies heavily on two methodological considerations: (*i*) detailed analysis of morphological features in fossil clades with respect to symmetry, plate relationships, and identifying changes in the presence/absence of individual homologous elements; and (*ii*) testing homology hypotheses among echinoderm lineages using character analysis (Patterson, 1988; Sumrall & Waters, 2012). As a consequence, UEH has significantly advanced understanding the anatomy and phylogeny of many extinct echinoderm lineages.

To reconstruct patterns of character evolution accurately among early echinoderms, we must rely on robust, well-supported phylogenetic frameworks that include extinct stem- and crown-group lineages. We emphasize that homology schemes provide a theoretical basis for empirical phylogenetic analyses. Because the EAT and UEH models have been hypothesized to make different predictions of phylogenetic relationships (*cf.* David *et al.*, 2000; Kammer *et al.*, 2013), they are sometimes contrasted as alternative homology schemes in the literature (e.g. Zamora & Rahman, 2014). However, we consider it unfruitful to position these approaches in competition with one another. Scientific models are valid only within the sphere of their explanatory domains. Because EAT and UEH emphasize different aspects of echinoderm morphology and skeletal evolution, they have overlapping but non-identical spheres of applicability across the echinoderm tree of life. For example, it is unclear how aspects of the EAT model can be fully applied to extant taxa that do not have larval skeletons, either because they are direct developers (e.g. crinoids) or otherwise lack larval skeletogenic cells (e.g. asteroids). Further, the fully bimodal division of embryological tissues into axial and extraxial elements has been argued to first appear in Cambrian taxa such as *Helicocystis* (Smith & Zamora, 2013) (Fig. 3F), which may be phylogenetically derived with respect to non-radial taxa. If Smith & Zamora's (2013) hypothesis is correct, it would imply the EAT model is non-applicable to pre-radial taxa, which often lack clear divisions between skeletal regions (e.g. ctenocystoids), and therefore interpreting the morphology of many stem-group lineages solely within the context of EAT (David *et al.*, 2000) may potentially be misleading. Similarly, the UEH model is not truly universal because it cannot be applied to taxa like echinoids, which lack the homologous skeletal characters emphasized by the model (i.e. oral characters useful for identifying homologies in blastozoan taxa are inapplicable to echinoids) and has also never been applied to non-radial taxa. Nevertheless, much of the data supporting the EAT and UEH models are not mutually exclusive, and the features emphasized by each model likely reflect how phylogenetic information can be nested at different hierarchical scales of body plan organization (Wright, 2015). For example, resolving phylogenetic relationships among fossil and extant echinoderms will require recognition of synapomorphies at both shallow and deep nodes in their evolutionary tree. Although convergences are difficult to rule out over vast evolutionary timescales (Erkenbrack & Thompson, 2019), the EAT model may be critical to identify homologous features at the broadest phylogenetic scales, and therefore help resolve echinoderm phylogeny at the deepest nodes. Similarly, UEH has been highly successful for inferring relationships among many extinct lineages, both within classes and among closely related major clades, thereby contributing to improved resolution in slightly shallower nodes in the echinoderm tree. Both EAT and UEH are based on morphological features and are amenable to quantitative phylogenetic analysis. To the best of our knowledge, a combined framework incorporating concepts from EAT and UEH has never been used to assemble a character matrix of fossil and extant echinoderms, but we believe a synthetic approach may be necessary to assemble a fully resolved echinoderm phylogeny because neither homology framework is universally applicable across the echinoderm tree of life. In the remaining sections and in Fig. 1, we present echinoderm relationships in the context of results from quantitative phylogenetic analyses that have been most recently applied to echinoderms, with references to other notable alternative hypotheses where appropriate.

(2) Stem-group Echinodermata

Molecular phylogenies indicate crown-group echinoderms are defined as the most recent common ancestor of crinoids and eleutherozoans, and all of its descendants (Smith *et al*., 2004; Mallatt & Winchell, 2007; Janies *et al*., 2011; Reich *et al*., 2015). Thus, stem-group echinoderms comprise fossil taxa occupying phylogenetic positions outside the crown group but are more closely related to echinoderms than hemichordates. The fossil records of heterogeneous Cambrian stem groups provide direct evidence of early anatomical features and morphological transitions. As a result, they are critical for establishing early evolutionary relationships, ancestral morphologies, and patterns of character evolution.

Resolving relationships among stem-group echinoderms has proved challenging, but in recent years greater resolution has been achieved through a combination of phylogenetic analyses and the discovery of important new taxa. Although the earliest quantitative phylogenetic analyses recovered a range of conflicting relationships (Paul & Smith, 1984; Smith, 1984; Sumrall, 1997), rigorous phylogenetic treatments of Cambrian echinoderms have converged upon similar topologies. For example, the results of Topper *et al*. (2019) for echinoderm lineages are largely congruent with those of Smith & Zamora (2013) and Zamora & Rahman (2014) despite significant differences in the underlying character matrices. Notably, these analyses recover inconsistencies between phylogenetic positions and the first appearances in the fossil record of major groups. For example, helicoplacoids are one of the earliest groups of echinoderms known, yet are recovered as a relatively derived, radial clade in recent phylogenetic analyses (Smith & Zamora, 2013). These stratigraphic inconsistencies are not surprising given biases that affect sampling of the Cambrian echinoderm fossil record, including facies-dependent habitat and/or preservation of many groups, a poor rock record for key Cambrian intervals, geographical biases in sampling, and spatial heterogeneity of diversification (Zamora, 2010; Smith *et al*., 2013). In addition, it is now understood that the diversification of the echinoderm body plan was extremely rapid during the early evolutionary history of the group (Smith *et al*., 2013), at least among clades afforded class-level rank (Wright, Wagner & Wright, 2021).

Evolution of the pentaradial echinoderm body plan is perhaps the most relevant morphological feature for understanding hemichordate–echinoderm relationships and the ambulacrarian LCA. There are two competing hypotheses for the evolution of pentaradial symmetry. The first hypothesis, primarily based on phylogenetic evidence, postulates that the most primitive echinoderms were bilaterally symmetric forms (ctenocystoids and taxa like *Ctenoimbricata*) from which arose asymmetrical (cinctans and solutes), triradial (helicoplacoids), and finally (pseudo)pentaradial forms (e.g. helicocystoids, eocrinoids, and edrioasteroids) (Smith, 2005; Smith & Zamora, 2013; Zamora & Rahman, 2014; Fig. 1). The competing hypothesis, primarily based on the EAT model, postulates that pentaradial symmetry is a synapomorphy of the phylum and that non-pentaradial groups are secondarily derived in multiple lineages (David *et al*., 2000). Below, we provide an overview of some of the most important early echinoderm clades which have significant bearing on the morphology of the echinoderm LCA, particularly with regard to symmetry.

(*a*) *Non-radial stem-group echinoderms*

'Carpoids', which have also historically been referred to as homalozoans or calcichordates, are an extinct, morphologically heterogeneous, and non-monophyletic assemblage of early echinoderms that includes ctenocystoids, cinctans, solutes, and stylophorans (Rahman, 2009). Their fossil record ranges from the middle Cambrian to the Carboniferous. Although all 'carpoids' possess skeletal features like a stereom that unambiguously assign them to Echinodermata, they notably lack the radial symmetry that characterizes crown-group and other more derived echinoderm clades, and there is still debate as to whether all possessed water vascular systems (Clausen & Smith, 2005; Lefebvre *et al*., 2019). Although their unusual morphologies have made it challenging to interpret homologous characters and resolve relationships with other echinoderms and deuterostomes more broadly (David *et al*., 2000; Smith, 2005), carpoids have been recovered as early branching stem-group echinoderms in several recent studies. Thus, they may provide key insights into early patterns of echinoderm character evolution and the hypothetical transition from bilateral to pentaradial symmetry.

Ctenocystoids have a middle Cambrian–Ordovician fossil record and constitute one of the rarest groups of echinoderms (Zamora, 2010). Phylogenetic analyses have recovered them as the most basal group of echinoderms (Smith & Zamora, 2013; Zamora & Rahman, 2014). Ctenocystoids possess a bilaterally symmetric to weakly asymmetric theca composed of multiplated upper and lower integuments surrounded by a marginal ring of larger plates (Fig. 3A). Although ctenocystoids lack ambulacra, at least as typically expressed in echinoderms, they possess an anterior opening surrounded by moveable plates called the ctenidium or ctenoid apparatus (Rahman & Clausen, 2009), which some authors have tentatively viewed as being homologous with ambulacral grooves of other echinoderms (Robison & Sprinkle, 1969; David *et al*., 2000). Ctenocystoids lack stems or other appendages and openings like hydropores and goniopores, although they have a wide posterior periproct opening.

Cinctans (class Homostelea) are non-radiate echinoderms restricted to the middle Cambrian. They have a flattened theca that is weakly to strongly asymmetric. This theca consists of a rigid, marginal ring of large plates called the cinctus, which surrounds small, tessellated integument plates on the dorsal and ventral sides (Fig. 3B). An appendage called the stele projects from the posterior of the theca as a continuation of the cinctus. Cinctans possess two asymmetrically developed ambulacral grooves (or in some species, a single left feeding groove) that run along the marginal plates on the side of the theca. A small mouth opening is located on the right anterior side of the theca where the food grooves meet. A second, larger body opening is located on the ventral surface and is covered by a large plate called the operculum. Cinctans have been the focus of several detailed phylogenetic studies (Smith & Zamora, 2009; Zamora, Rahman & Smith, 2013*b*; Wright *et al*., 2021) and have also been included in analyses with other stem-group echinoderms that recovered them as one of the most basal group of echinoderms, after ctenocystoids (Smith & Zamora, 2013; Zamora *et al*., 2020).

Ctenoimbricata from the earliest middle Cambrian of Spain is morphologically intermediate between ctenocystoids and cinctans, and thus provides important insights into understanding homologies between the two groups (Zamora, Rahman & Smith, 2012). *Ctenoimbricata* has near-perfect bilateral symmetry, a clear anterior–posterior axis, a disc-like theca surrounded by a marginal ring of plates, and multiplated membranes on the upper and lower surfaces of the theca. Similar to ctenocystoids, *Ctenoimbricata* has a ctenidium that forms the feeding apparatus surrounding a large anterior opening. It has been interpreted as one of the most primitive echinoderms known, and is hypothesized to be either sister to Ctenocystoidea or sister to all echinoderms (Zamora *et al*., 2012). Interestingly, the phylogenetically basal position of *Ctenoimbricata* supports bilateral symmetry, rather than pentameral symmetry, as the ancestral condition for total-group Echinodermata (Zamora *et al*., 2012; Smith & Zamora, 2013; Zamora & Rahman, 2014). Note that palaeontological and developmental data corroborate one another on this issue, as the palaeontological evidence is consistent with the observation of bilaterally symmetric larvae in extant echinoderms.

Solutes (class Homoiostelea) range from the middle Cambrian to the Lower Devonian. They have a flattened, asymmetric, multiplated theca with two appendages that arise from either end of the body (Fig. 3D). The anterior appendage is shorter, flexible, offset laterally, and composed of two biserial rows of plates (floor plates and cover plates). There is broad consensus that the anterior appendage possesses a feeding ambulacrum, although it has been debated whether the anterior appendage is a true arm that possesses an extension of the coelom (Smith, 2005) or a brachiole that lacks a coelomic extension (Parsley, 1997; David *et al*., 2000). An opening near the base of the anterior appendage is typically interpreted as the mouth. The other appendage (stele) is longer and positioned centrally along the posterior margin of the theca. The stele has bipartite construction with a flexible, proximal section covered in imbricate plates and a stiff distal section. The plating and large central lumen that runs through the proximal portion of the stele suggests it was a muscular, moveable structure, unlike the stems of crown-group echinoderms, which lack muscles (Smith, 2008). A large anal opening covered in a multiplated cone is positioned near its base. Many solutes also have one or two additional openings positioned near the base of the anterior appendage. In solutes like *Coleicarpus* and *Castericystis*, a discoidal holdfast was present on the distal end of the stele (Daley, 1995, 1996), indicating the structure functioned as a stem in at least some taxa. This facultative attachment from the posterior end suggests body axes would have been maintained during development, thus indicating solutes were early, pre-torsion echinoderms (Smith, 2008).

Stylophorans are known from an abundant middle Cambrian–Carboniferous fossil record. Interpretations of stylophoran morphology have been contentious for decades, in part because of the potential bearing the group may have on understanding deuterostome phylogeny and character evolution. Stylophorans possess a flattened, weakly to strongly asymmetric theca that typically consists of a marginal series of elongated plates surrounding many smaller, internal plates (Fig. 3C). From the margin of the theca arises a single appendage, known as the aulacophore, which bears a medial lumen proximally and a groove distally. The function of this appendage has played a key role in the debate on stylophoran affinities and has led to several conflicting hypotheses. The two that currently retain the most traction are that the aulacophore was a moveable stem, where the median groove was filled with muscles for locomotion (Clausen & Smith, 2005; Rahman *et al*., 2009; Rozhnov & Parsley, 2017), or that it was a feeding arm, where the median groove represents an ambulacrum (Ubaghs, 1968; David *et al*., 2000; Lefebvre, 2003). Investigation of stereom microstructure in the aulacophore revealed the presence of galleried stereom, which is diagnostic of the presence of mutable collagen fibres and supports the interpretation of the appendage as a muscular stem (Clausen & Smith, 2005). More recently, however, exceptionally preserved specimens of *Thoralicystis* from the Lower Ordovician of Morocco were described that retain the first known traces of soft parts within the aulacophore (Lefebvre *et al*., 2019). These were interpreted as parts of the water vascular system, including tube feet and ambulacral canals, which would support the hypothesis of the stylophoran appendage as a feeding arm (Lefebvre *et al*., 2019). Based on this joint evidence, it has been argued that the aulacophore may have supported both functions of feeding and locomotion (Parsley, 1991; Ruta, 1999), and functional biomechanical investigations suggest stylophorans lived on the surface of the substrate and were capable of movement through lateral motions of the aulacophore (Clark *et al.*, 2020).

There are several openings in the stylophoran theca, all of which have been interpreted in a variety of ways: (*i*) an opening opposite the appendage, interpreted as either the mouth or anus depending on interpretation of the aulacophore; (*ii*) openings on or adjacent to the appendage, interpreted as the mouth or hydropore depending on interpretation of the first opening; and (*iii*) in some species, a series of slit-like openings on the surface of the theca, interpreted as gill slits or respiratory organs [e.g. David *et al.*, 2000; Lefebvre, 2003; Clausen & Smith, 2005; Smith, 2005; see Lefebvre *et al.* (2019: fig. 1) for a summary]. The interpretation of these openings as gill-slit homologues *versus* non-homologous respiratory structures is of particular importance in the context of deuterostome evolution, and is discussed further in Section VI.4.

Due to contention surrounding interpretations of stylophoran morphology, the phylogenetic position of stylophorans remains somewhat uncertain (Fig. 1). David *et al.* (2000) hypothesized that stylophorans might be closely related to crinoids based on application of the EAT hypothesis of homology to select portions of the skeleton, namely that the stylophoran appendage is homologous to the arm of a crinoid. However, their hypothesis was not investigated quantitatively and no evidence has since emerged to support it (Ausich *et al.*, 2015), even among studies explicitly stating they used the EAT model to construct phylogenetic character matrices (e.g. Hunter & Ortega-Hernández, 2021). Stylophorans were not included in the most recent phylogenetic investigations that spanned multiple Cambrian stem-group echinoderms (Smith & Zamora, 2013; Topper *et al.*, 2019; Zamora *et al.*, 2020), or in earlier studies of echinoderm phylogeny that placed 'carpoids' at the base of the echinoderm tree (Paul & Smith, 1984; Smith, 1984). The analysis of Sumrall (1997) recovered stylophorans in a clade with other 'carpoids' nested within blastozoans, although this blastozoan–carpoid relationship has not received subsequent support. This information, combined with results of more recent analyses (Smith & Zamora, 2013), suggests stylophorans might fall somewhere near the base of the echinoderm tree of life with other carpoid groups like solutes (Smith, 2008).

(*b*) *Radial stem-group echinoderms*

The development of radial symmetry in echinoderms was one of the most significant transitions in the group's evolutionary history. The earliest echinoderms known to have radial symmetry are the Early Cambrian helicoplacoids (Sprinkle, 1973). They possess a spindle- to pear-shaped theca with spirally arranged plates and triradiate ambulacra that arise from a laterally positioned mouth (Sprinkle & Wilbur, 2005; Fig. 3E). These ambulacra are structured like those of pentaradiate echinoderms, with paired flooring plates and cover plates. Unlike attached carpoids (e.g. some solutes), helicoplacoids attached to the substrate at their anterior end. This obligate anterior larval fixation resulted in the radial adult body plan of helicoplacoids (Smith, 2008), because anterior attachment would require torsion during development in order for the mouth to shift upwards. This pattern of larval development is still observed in the ontogeny of living crinoids (Nakano *et al.*, 2003). Thus, helicoplacoids document the early stages of the evolution of radial symmetry due to a shift from posterior to anterior larval attachment, although the reason for this change in attachment remains unknown (Smith, 2008).

A morphological and evolutionary gulf stretched between the triradiate helicoplacoids and pentaradial echinoderms until the discovery of *Helicocystis* from the Early Cambrian of Morocco (Smith & Zamora, 2013). *Helicocystis* has a spirally plated theca like that of helicoplacoids but possesses five ambulacra, rather than three (Fig. 3F). Thus, it represents an important transitional form that is intermediate between helicoplacoids and other pentaradial echinoderms. After *Helicocystis*, edrioasteroid-like taxa such as *Camptostroma* (from the early middle Cambrian of the eastern USA), *Stromatocystites* (known globally from the middle Cambrian; Zamora *et al.*, 2015), and *Kailidiscus* (from the early middle Cambrian Kaili Biota of China) are considered some of the most basal pentaradial echinoderms (Smith & Zamora, 2013; Zamora & Rahman, 2014). *Camptostroma* is clearly divided into a dorsal (aboral) portion, which is inferred to have remained buried in the sediment, and a ventral (oral) surface that has five raised ambulacra and a central mouth (Paul & Smith, 1984). *Stromatocystites* has a globular theca with a pad of fused plates on the aboral surface, that was presumably used for direct attachment to substrates (Zamora *et al.*, 2015). *Kailidiscus* possesses a discoidal theca that becomes inflated throughout ontogeny and has several features that are similar to those of isorophid edrioasteroids, such as a well-developed peripheral rim, elongated and curved ambulacra, and imbricate interambulacral plates (Zhao *et al.*, 2010). However, *Kailidiscus* also possesses numerous plesiomorphic features that resemble helicoplacoids or eocrinoids (Zhao *et al.*, 2010). Other early pentaradial echinoderms [e.g. gogiids (Fig. 3G), lepidocystids, eocrinoids, etc.] document a range of transitional morphologies. Within blastozoans, for example, evolutionary trends like increasing regularity of multiplated stalks, transitions from multiplated to holomeric stems, and shifts from imbricate to tesselate aboral plating occur within multiple groups (Sprinkle, 1973; Broadhead, 1982; Nardin *et al.*, 2017).

A number of enigmatic taxa have been assigned to Echinodermata over the years but remain problematica due to poor preservation, lack of diagnostic traits, and/or other morphological inconsistencies that preclude confident placement in the phylum. These include *Arkarua* (Gehling, 1987; Mooi & David, 1998) and *Tribrachidium* (Glaessner & Wade, 1966) from the Ediacaran of southern Australia, and *Yanjiahella*

(Topper *et al.*, 2019; Zamora *et al.*, 2020) from the Early Cambrian (Fortunian) of China. These taxa are discussed at greater length below in Section V. Other taxa originally identified as echinoderms have since been established as members of other phyla, such as the middle Cambrian *Echmatocrinus* (Sprinkle, 1973) from the Burgess Shale of Canada, which is now recognized as a cnidarian (Conway Morris, 1993; Ausich & Babcock, 1998, 2000).

(3) Crown-group Echinodermata

Crown-group Echinodermata, which consists of the five extant classes (Crinoidea, Asteroidea, Ophiuroidea, Echinoidea, and Holothuroidea) and their most recent common ancestor, represents a relatively derived portion of the echinoderm tree of life, limiting the degree to which they can directly inform the evolutionary history of early echinoderms and other deuterostomes. As a result, these relationships can only be fully deciphered through a detailed understanding of the morphology and phylogeny of extinct echinoderms, especially early taxa from the Cambrian. Instead, crown-group echinoderms have informed the question of deuterostome origins through an improved understanding of development, genetics, and phylogenetic relationships with hemichordates dated using molecular clocks.

(*a*) *Crown-group relationships*

Two major lineages are present in the crown group: the lineage that leads to the crinoids and the lineage that leads to the eleutherozoans, which include the classes Asteroidea, Ophiuroidea, Echinoidea, and Holothuroidea. The fossil records for all extant classes date back to Early and middle Ordovician rocks. Due to debates regarding the evolutionary origins of the extant classes, there is some uncertainty as to which extinct groups can be considered part of crown-group Echinodermata. Crinoids (Fig. 3H) are consistently recovered as sister to the other four extant classes that comprise the Eleutherozoa (e.g. Smith *et al.*, 2004; Mallatt & Winchell, 2007; Janies *et al.*, 2011; Reich *et al.*, 2015), and thus, the evolutionary origin of crinoids is key for identifying the crinoid–eleutherozoan split that defines crown-group echinoderms. While both stylophorans (David *et al.*, 2000) and edrioasteroids (Guensburg *et al.*, 2016) have been suggested to be the sister group to crinoids, most recent quantitative phylogenetic analyses have demonstrated that crinoids are nested within blastozoan clades (e.g. eocrinoids, diploporoids, glypocystitoids) as part of a monophyletic Pelmatozoa (Ausich *et al.*, 2015; Sumrall, 2015; Sheffield & Sumrall, 2019*a*,*b*). Thus, at least some blastozoans may also be considered part of the crown group. Similarly, edrioasteroid-grade echinoderms may (Smith, 1985) or may not (Guensburg *et al.*, 2016) be eleutherozoans, and the disparity of Cambrian forms has led some to question whether edrioasteroids are para- or polyphyletic (Zhao *et al.*, 2010; Zamora & Rahman, 2014). Consequently, additional phylogenetic analyses with broad taxonomic sampling of fossil taxa are needed to help decipher evolutionary relationships among eleutherozoans.

Eleutherozoans can be further grouped into Asterozoa [Asteroidea (Fig. 3J) and Ophiuroidea (Fig. 3K)] and Echinozoa [Echinoidea (Fig. 3I) and Holothuroidea]. Recent analyses with molecular data overwhelmingly support the Asterozoa hypothesis, with ophiuroids being sister to asteroids and this clade being sister to the Echinozoa clade (Cannon *et al.*, 2014; Telford *et al.*, 2014; Reich *et al.*, 2015). The alternative Cryptosyringida hypothesis is mainly supported by morphological and larval data (Smith, 1984; Raff & Byrne, 2006). Our knowledge on the relationships within the eleutherozoan classes has progressed immensely in the last decade, especially with phylogenomic analyses of living groups. A recurring pattern found in nearly all groups is that homoplasy has played a major role in echinoderm evolution. The asterozoans are composed of four classes, two of these extinct and probably paraphyletic (i.e. somasteroids and stenuroids), and many fossil genera previously classified as asteroids and ophiuroids have been transferred to the extinct classes (Dean Shackleton, 2005; Blake, 2013; Hunter & Ortega-Hernández, 2021). Within the living groups, molecular and morphological analyses (Thuy & Stöhr, 2016; Linchangco *et al.*, 2017; O'Hara *et al.*, 2017) have greatly changed our understanding of the relationships among asterozoan higher taxa. The echinozoans are composed of three classes: Echinoidea, Holothuroidea and the extinct Ophiocistioidea. Understanding the relationship among these three classes has not been trivial because ophiocistioids have characteristics of both echinoids and holothuroids (Reich & Haude, 2004). Support for the close relationship between holothuroids and ophiocistioids has increased with the discovery of ophiocistioids with preserved soft tissues in the Herefordshire Lagerstätte (Rahman *et al.*, 2019), but the question remains if this class is truly monophyletic. Molecular studies with the living echinozoan classes have shown that pervasive homoplasy has obscured our understanding of relationships among major groups. Within the Echinoidea, for example, there is strong evidence clypeasteroids are actually not monophyletic (Mongiardino Koch *et al.*, 2018, 2022; Mongiardino Koch & Thompson, 2021) and the relationships among holothuroids remain largely unresolved (Miller *et al.*, 2017). For a review of research performed on asteroids and ophiuroids, see Mah & Blake (2012) and Stöhr, O'Hara & Thuy (2012), respectively.

(*b*) *Major transitions in light of developmental research*

Much research is needed before the genetic basis for the origin of pentamery can be fully understood, but substantial progress has been made in the last decade (Baughman *et al.*, 2014; Kikuchi *et al.*, 2015; Szabó & Ferrier, 2018). We have solid knowledge of the way in which Hox genes specify the axial identity in the early development of bilaterally symmetric taxa. The role that Hox genes play in specifying the pentaradial symmetry in echinoderms, however, remains a mystery. Developmental research has been addressing the transition from a bilateral larva to a pentaradial adult, but most studies (Hano *et al.*, 2001; Cameron *et al.*, 2006; Morris & Byrne, 2014; Tsuchimoto & Yamaguchi, 2014; Koop *et al.*, 2017; Li *et al.*, 2020) have focused on echinoids and for a long time, our inferences were based on their highly derived, apparently idiosyncratic Hox cluster organization. Research on other classes (Méndez *et al.*, 2000; Mito & Endo, 2000; Li, Stoeckert & Roos, 2003; Li *et al.*, 2020; Hara *et al.*, 2006; Baughman *et al.*, 2014; Kikuchi *et al.*, 2015) have shown that the ancestral Hox cluster in echinoderms is rather conserved and similar to that of hemichordates (Li *et al.*, 2020), which means that the modifications seen in echinoids (i.e. gene inversions and translocations) do not explain the evolution of pentaradial symmetry. The same has been observed with the ParaHox cluster (Annunziata, Martinez & Arnone, 2013; Arnone, Byrne & Martinez, 2015), but data are still limited. Changes in the Hox cluster within other echinoderm classes have also helped narrow down the number of genes possibly involved in body symmetry (Byrne, Martinez & Morris, 2016; Li *et al.*, 2020) and the evidence is pointing to the posterior part of the cluster, which has remained largely conserved. Also, two posterior Hox genes so far unique to echinoderms have been recently described. *hox11/13d* and *hox11/13e* are detached from the main Hox cluster and future studies should reveal whether they play a role in echinoderm development and in setting the echinoderm symmetry (Szabó & Ferrier, 2018). Another likely possibility is that Hox genes do not play a role in establishing pentaradial symmetry, but the evidence for this hypothesis (Kikuchi *et al.*, 2015) comes from a study in the paedomorphic holothuroids.

Research has focused on understanding the role of varied signalling pathways in establishing pentamery in the ontogeny of echinoderms [see Thompson (2022) for a thorough explanation of how cell to cell signalling works]. For example, the change in symmetry could have evolved from the left–right asymmetry widely recognized in the early development of deuterostomes (Jefferies, Brown & Daley, 1996; Kaul-Strehlow & Stach, 2013; Namigai, Kenny & Shimeld, 2014) and promoted by the Nodal and, possibly, the bone morphogenetic protein (BMP) signalling pathways (Duboc & Lepage, 2008; Grande *et al.*, 2014; Fresques & Wessel, 2018; Soukup & Kozmik, 2018). Hemichordates and echinoderms are both tricoelomate with a single anterior coelom followed by two paired coelom pouches (the mesocoel/hydrocoel and the somatocoel), a condition most likely present in the ambulacrarian LCA. Although the coelom pouches are bilaterally symmetric in adults of the enteropneust *Saccoglossus kowalevskii* (Agassiz, 1873), left–right asymmetry is noted in early developmental stages (Kaul-Strehlow & Stach, 2013), and minor deviations from bilateral symmetry in some enteropneusts is also noted (Larouche-Bilodeau, Guilbeault-Mayers & Cameron, 2020). An enhanced asymmetry is noted on echinoderm larvae. All extant echinoderms possess pentameral symmetry, and the larval development of these groups is unique among bilaterians as a result of this symmetry. Larvae begin as free-swimming, bilaterally symmetric forms, undergo an asymmetric developmental phase with the development of the rudiment, and ultimately metamorphose into pentaradial adults (Nakano *et al.*, 2003; Haesaerts, Jangoux & Flammang, 2006; Smith, 2008). The rudiment forms from the association between the left hydrocoel and the left somatocoel, and later develops into radial structures such as the ambulacra and the water vascular system (Peterson *et al.*, 2000). As it is derived mostly from one hydrocoel, the water vascular system in echinoderms is unpaired and likely homologous to the left hydrovascular tentacular system of hemichordates (Smith, 2005). Before metamorphosis, larvae undergo torsion that results in the rotation of the body axis and reduction/loss of the right hydrocoel. Torsion is thought to have evolved in the early evolution of echinoderms as a whole-body modification to facilitate substrate attachment *via* an adhesive pad in the anterior region of the larvae (Smith, 2008; Smith & Zamora, 2013). In some groups, obligate attachment of larvae occurs, which may be permanent (e.g. crinoids) or temporary (e.g. asteroids), while other groups remain unattached throughout development (e.g. echinoids). Because of conflicting interpretations of Cambrian fossils, the timing of the evolution of torsion remains controversial.

Two synthetic hypotheses have been proposed to explain the evolution of radial symmetry during development. The first hypothesis suggests that the coelom pouches are stacked during the development of the rudiment such that the oral–aboral axis in echinoderms corresponds to the anterior–posterior axis in the other deuterostomes (Peterson *et al.*, 2000; Mooi & David, 2008). Then, equal outgrowths (appendages) from the main axis would form ambulacra (Hotchkiss, 1998). The second hypothesis suggests that both axes are rather separate and that the echinoderm ambulacra follow the same pattern as the anterior–posterior axis of chordates (Raff & Popodi, 1996; Morris, 2012). Pentamery would have evolved from a five-fold duplication of this pattern (Morris & Byrne, 2014). Both hypotheses are plausibly supported by developmental data and the fossil record (Arnone *et al.*, 2015; Kikuchi *et al.*, 2015; Lapraz, Haillot & Lepage, 2015). However, understanding the early development of echinoderms has been challenging because rearing their larvae through metamorphosis, so that the relevant morphogenic genes can be assayed, is generally a long and costly process. A third hypothesis is that the change in axis after torsion disturbed gene expression in the rudiment such that adult morphogenesis is led by existing regulatory modules that have been co-opted (Smith, 2008; Tsuchimoto & Yamaguchi, 2014; Li *et al.*, 2020).

The co-option of gene regulatory networks may have actually been involved in major evolutionary steps in echinoderm development, for example, in the formation of the larval skeleton. A skeletonized larval stage – the pluteus larva – is recognized in echinoids and ophiuroids, and comparative research has shown that holothuroid larvae also form skeletogenic cells derived from the mesoderm (McCauley *et al.*, 2012), although they do not have pluteus larvae. The presence of pluteus larvae has been used to support the Cryptosyringida hypothesis. With increasing support for the Asterozoan hypothesis, however, this evolutionary transition was most likely the result of homoplasy. In this context, two equally parsimonious scenarios have been proposed: (*i*) the formation of skeletogenic cells evolved independently in echinozoans and ophiuroids; or (*ii*) the larvae of ancestral eleutherozoans formed skeletogenic cells and the lineage leading to the extant asteroids lost the gene expression to form them (Erkenbrack & Thompson, 2019). Because of the similarity in skeletal morphology and in gene expression, the genetic module to form the larval skeleton was probably co-opted from the adult gene regulatory network in the ancestral eleutherozoan and largely modified within and among the classes (McCauley *et al.*, 2012; Gao *et al.*, 2015; Dylus *et al.*, 2016; Morino, Koga & Wada, 2016; Cary & Hinman, 2017; Erkenbrack & Thompson, 2019). Inferring the evolution of the larval skeleton in other lineages is challenging because the fossil record of Paleozoic echinoderm larvae is non-existent (Reich, 2021). Also, most major lineages of crinoid higher taxa perished in the Permo-Triassic extinction and according to current data, the surviving lineages are direct developers. Therefore, in light of gene co-option, we cannot rule out the presence of skeletonized larval forms in crinoids or in extinct classes. The presence of a larval skeleton in the echinoderm LCA, however, is very unlikely.

(4) Synthesis

In light of difficulties in establishing homologies across echinoderm groups, high morphological disparity of early echinoderm forms, and the incomplete Cambrian record, reconstructing the echinoderm LCA is quite challenging. The available evidence broadly supports a sessile benthic organism that developed from a bilateral, planktonic, feeding dipleurula-like larva. Skeletons would only be present in the adult form, which would be covered by a polyplated theca. This theca was probably not flexible and the mutable collagenous tissue would have evolved later, after the specialization of different types of stereom that took place in the earliest middle Cambrian. This tissue would have provided flexibility, improving movement and body expansion. The water vascular system was probably present in the echinoderm LCA, in a paired (derived from both hydrocoels) or unpaired form depending on when torsion evolved. Finally, additional studies are needed to shed light on the timing of more controversial evolutionary steps. For example, did the echinoderm LCA have pharyngeal openings or did they re-evolve in stylophorans? Is the ctenocystoid ctenoid organ homologous to ambulacral grooves, thus suggesting that ambulacra were present in the echinoderm LCA? When did biomineralized and muscular appendages evolve and when was the post-anal tail lost? Was the echinoderm LCA bilateral or were nonradial groups secondarily derived from pentaradial ones? We expect the examination of known and new fossils under improved imaging, as well as the refinement of analytical approaches, will greatly advance our understanding of these evolutionary steps and how they inform the body symmetry, ecology and morphology of the echinoderm LCA.

IV. PHYLUM CHORDATA

The phylum Chordata is composed of three sub-phyla: Cephalochordata, Urochordata, and Vertebrata. The significant differences between these three clades have led some authors to argue that each should be raised to the phylum level (Satoh, Rokhsar & Nishikawa, 2014), an argument that would not change our interpretation of evolutionary events but that underscores the unique qualities of the chordate body plan and developmental modes. While it is out of the scope of this review to consider the higher relationships within each of these classes, a brief treatment is necessary to frame the acquisition of stem-lineage characters.

(1) The early record of the chordate classes

Vertebrata is the most diverse of the three chordate classes, and due to the presence of readily preservable structures such as bones and teeth, they have a rich fossil record. Two hypotheses exist for subdividing the vertebrates into two major clades. The first is that hagfish and lampreys form a reciprocally monophyletic group (cyclostomes) with the rest of the vertebrates (gnathostomes), based on the absence or presence of a jaw, respectively (Sansom, Gabbott & Purnell, 2011). This hypothesis is compatible with both morphological and molecular data. Less strongly supported is the alternative Craniate hypothesis, in which lampreys are grouped with the jawed vertebrates, with hagfish as a sister taxon to the rest of the Vertebrata (Miyashita *et al.*, 2019). In either scenario, the abundant early fish referred to as 'ostracoderms' likely represent a paraphyletic group, stem to both major lineages of modern vertebrates. Conodonts may also represent stem vertebrates, but due to the relatively sparse soft-tissue record of the group (Briggs, Clarkson & Aldridge, 1983), our understanding of their evolutionary position remains somewhat uncertain (Miyashita, 2016; Zhang *et al.*, 2017).

Cambrian Lagerstätte provide some insights into the form of the earliest stem vertebrates, with four taxa being most notable (Figs 1 and 4A, B). The first are the myllokunmingids from Chengjiang in China (~516 Ma), including *Myllokunmingia*, *Haikouichthys* and *Zhongjianichthys* (Shu *et al.*, 1999; Zhao, Li & Selden, 2019*a*). These taxa all possess a fusiform, fish-like body that can be divided into two broad regions. The body region contains features that we might expect to be plesiomorphic to Vertebrata, principally myomeres and a notochord, as well as a dorsal sail-like fin and a smaller ventral fin (Shu *et al.*, 2003). The head region contains branchial arches and gill pouches in the pharynx, a pair of anterior eyes, and a pair of smaller organs between them, which may represent part of an olfactory organ (Shu *et al.*, 2003). The younger *Metaspriggina* from the Burgess Shale in

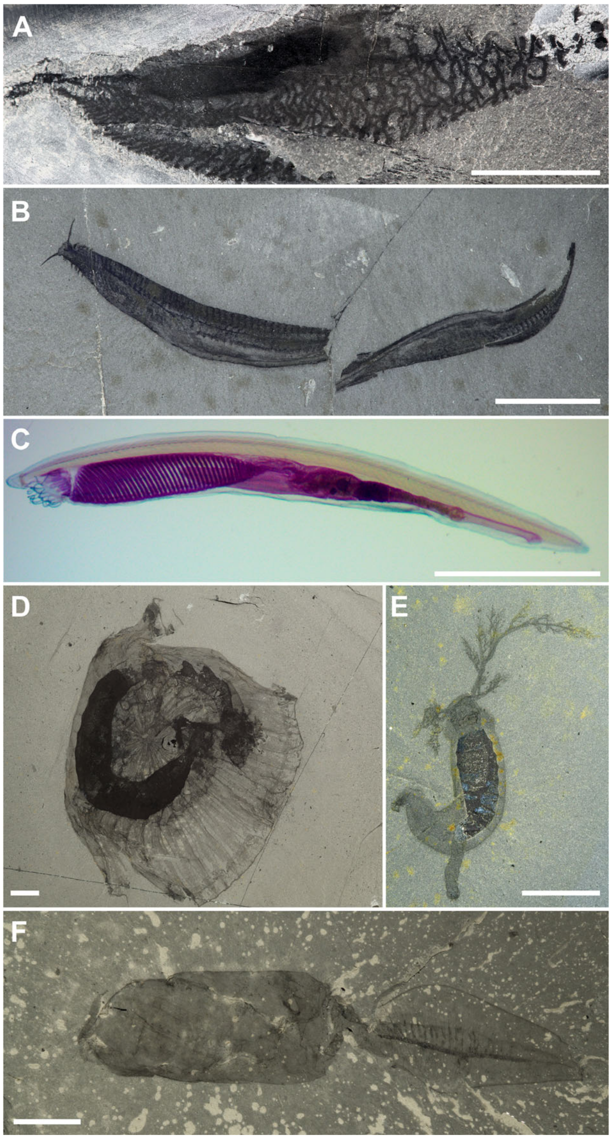

Fig. 4. Representatives of the phylum Chordata, and problematic fossils of deuterostome affinity. (A) The stem-vertebrate *Metaspriggina walcotti*, with paired eyes preserved on the right side of the image (ROMIP 62938). (B) The stem-chordate *Pikaia gracilens*, with anterior sensory structures and filamentous appendages preserved on the left side of the image (USNM 57826). (C) The modern cephalochordate *Branchiostoma lanceolatum*, which has been compared with many Cambrian chordates. (D) The fossil *Eldonia ludwigi*, a cambroernid related to Ambulacraria (ROMIP 59550). (E) The fossil *Herpetogaster collinsi*, a cambroernid related to Ambulacraria (ROMIP 58051). (F) The fossil *Banffia constricta*, a vetulicolian of enigmatic affinity (ROMIP 49914); vetulicolians may represent an early lineage of deuterostomes. Photograph credits: Jean-Bernard Caron (A, B, D–F); Donna Wheeler (C). Institutional abbreviations: ROMIP, Royal Ontario Museum (Invertebrate Paleontology); USNM, Smithsonian National Museum of Natural History. Scale bars: 1 cm.

Canada (~506 Ma; Fig. 4A) also possesses prominent myomeres and a notochord, but otherwise is significantly different from the other taxa (Conway Morris & Caron, 2014). It lacks any fins, although recent hydrodynamic experiments suggest that it was still capable of an active swimming lifestyle without them (Rival, Yang & Caron, 2021). Relative to total body size, its eyes are larger than those of the myllokunmingids, and are positioned more anteriorly. Finally, *Metaspriggina* possesses seven pairs of branchial bars, the posterior six of which have corresponding gills (the openings of which are unconfirmed, but inferred based on the presence of gill filaments). The first set of branchial bars lacks gills, and is thickened, which has been suggested as a form of proto-mandibular bar similar to the arrangement found in gnathostomes (Conway Morris & Caron, 2014). Other anatomical details of these taxa, such as the putative kidney of *Metaspriggina* or gut traces in the myllokunmingids are of limited relevance to deeper chordate relationships and are thus not considered here.

By comparison, the early records of both urochordates and cephalochordates are relatively sparse. Urochordata form the group Olfactores with Vertebrata, a relationship borne out by the tadpole-like juvenile form of ascidian tunicates as well as molecular phylogenies (Delsuc *et al.*, 2006; Swalla & Smith, 2008). Urochordate fossils are exceedingly rare, with the middle Cambrian *Shankouclava* remaining the most convincing fossil to date (Chen *et al.*, 2003). *Shankouclava* possesses many of the most distinctive features of a modern tunicate, including the eponymous tunic itself, a pharyngeal basket and an oral siphon (Chen *et al.*, 2003), suggesting that many components of the crown tunicate body plan were already well established by the middle Cambrian (Swalla & Smith, 2008). As a result, while this fossil helps us calibrate some expectations regarding the acquisition of tunicate characteristics (i.e. the atrial siphon may have been a later innovation), it is not particularly informative of the LCA to either Olfactores or Chordata broadly.

Two Cambrian fossils have previously been compared with cephalochordates (Fig. 4C), but have since moved to a stem-vertebrate position. The first is the iconic *Pikaia* from the Burgess Shale (Fig. 4B). The most easily recognized features in *Pikaia* are the myomeres whose segmental arrangement led Walcott to describe it initially as an annelid (Conway Morris & Caron, 2012). A thin dorsal fin and a putative notochord round out the general chordate suite of characters also seen in the early vertebrates above, but the anterior region of *Pikaia* differs significantly from the myllokunmingids. Notably, *Pikaia* lacks visible gills, has a bi-lobed head with a pair of presumably sensory tentacles, and a series of nine-paired, filamentous appendages. The older *Cathaymyrus* from Chengjiang is perhaps the most enigmatic of the early chordates considered herein, due to its exceptional rarity and incomplete preservation of the head region (Shu, Conway Morris & Zhang, 1996). Critically, a pharyngeal region with gill slits is preserved, in addition to both myomeres and a putative notochord.

(2) The chordate context of deuterostome origins

While admittedly somewhat sparse, we can say with some confidence that palaeontological data provide direct support for myomeres and the notochord as being plesiomorphic to Chordata. The former are ubiquitous among the unambiguous Cambrian chordates, with the exception of *Shankouclava*, which already displays the highly specialized adult tunicate morphology and which we may reasonably speculate had myomeres in its larval form. The notochord is similarly unsurprising as a chordate morphological synapomorphy supported by fossil data, however, it is slightly less confidently resolved than myomeres. Given the nature of Burgess Shale-type preservation, entailing two-dimensional carbonaceous compressions, a dark, axial structure may alternatively be interpreted as a notochord, gut, or other characters depending on the observer. This effect is compounded by all manner of taphonomic effects, such as incomplete preservation, or the angle of preservation causing the positioning of the structure to be different than anticipated (Donoghue & Purnell, 2009). While the only salient taxa in which a notochord is debatable are *Pikaia* and *Cathaymyrus*, as potential stem-group chordates, this should be noted. On a similar note, incomplete preservation of the gut is one factor that makes identifying the anus difficult, which in turn leads to some equivocacy in identifying a postanal tail, one of the other major features typically listed as a chordate synapomorphy. *Metaspriggina* appears to have had a postanal tail, while it is unclear in the myllokunmingids. It is similarly somewhat unclear in *Pikaia*, although the anus may have been terminal, and while an alimentary canal has been identified in *Cathaymyrus*, the full extent of this canal and the anus are unclear. The effect of variable interpretations of phylogenetically critical characters such as the notochord and postanal tail will come into sharper relief below (Section V) during the discussion of enigmatic fossils of possible deuterostome affinity, such as the yunnanozoans.

Of the remaining characters typically listed as chordate synapomorphies, gill slits are the most important when considering the form and life history of the deuterostome LCA, and palaeontological data strongly support their inclusion. All of the well-known Cambrian chordates possess a pharyngeal region with gills, with the exception of *Pikaia* whose unique, cephalochordate-like body plan may already show significant deviations from the chordate LCA (Mallatt & Holland, 2013), and in which the anterior appendages might have served a respiratory role in conjunction with small pores (Conway Morris & Caron, 2012). Our picture of the chordate LCA, therefore, appears to be a relatively small, fusiform, animal that was an active swimmer (as evidenced by well-developed myomeres) and that may have had a filter-feeding lifestyle facilitated by gill pores in the pharyngeal region. The pharynx, in particular putative homologues among problematic taxa with implied deuterostome affinity, will become a central point of discussion below.

V. PROBLEMATIC TAXA

When considering groups at the superphylum level, identifying consistent synapomorphies can become fraught with difficulty. The deuterostomes (and protostomes for that matter) are classically defined by developmental characters that are unlikely to fossilize, and we know that many of these characteristics are found outside of Deuterostomia as well (Kapli *et al*., 2021). Compared with the protostomes, deuterostomes also seem to be a less-abundant group in early Paleozoic oceans, and their body plans may have been less prone to fossilization than protostomes overall, giving us far less data to work with (i.e. early hemichordates and chordates lacking skeletonizing elements, some echinoderms being prone to disarticulation). We might also consider that Protostomia includes roughly 24 phyla, compared to the three within Deuterostomia. As a result, speculating on the successive ancestral forms to superphyla within protostomes in a grading fashion provides a scaffold of hypotheses to build upon sequentially. For example, consider the rich field of hypotheses for lophotrochozoan evolution and origins derived from taxa such as the halwaxiids (Conway Morris & Caron, 2007), halkierids (Vinther & Nielsen, 2005) and *Pelagiella* (Landing *et al*., 2021). By contrast, the three deuterostome groups have few obvious morphological ties that we might expect to find in a fossil. In this way, diversity, disparity and taphonomy all work together in concert to produce the enigma of deuterostome origins.

Thus, identifying problematica as having some type of 'deuterostome affinity' hinges largely on the taxonomic expertise and perspective of the observer in question. Further compounding this problem is the general lack of quantitative phylogenetic frameworks for most of the fossils we consider below. On the one hand, this often leads to phylogenetic placement based on a debate regarding which characters are 'important' using logical inference rather than easily repeatable analysis. On the other hand, dismissing the conclusions of these studies because most have not been placed into a true phylogeny drastically underestimates the difficulty of homologizing any structures in these taxa at all. To that end, we summarize what we believe to be the enigmatic taxa most relevant to a comprehensive understanding of the current status of deuterostome origins without commenting at length on the relative arguments for or against the placement of these taxa. The strength of the characters used to arrive at these placements will be investigated on a case-by-case basis as relevant in Section VI.

In the Ediacaran, two fossils are sometimes referred to as potential echinoderms, *Tribrachidium* (Glaessner & Wade, 1966) and *Arkarua* (Gehling, 1987; Mooi & David, 1998), based principally on their unusual, radially symmetrical body plans. In *Tribrachidium*, this takes the form of spirally arranged, triradial symmetry, while *Arkarua* is pentaradially symmetrical with straight grooves. As previously discussed, however, taxa that have more recently been confidently assigned to Echinodermata support pentaradial symmetry to be a derived, rather than an ancestral trait [i.e. *Ctenoimbricata* (Zamora *et al.*, 2012)]. Additionally, as is the case with most Ediacaran taxa, establishing confident placement within Metazoa, let alone any echinoderm synapomorphies, is controversial. *Arkarua*'s affinity with Echinodermata is debated due to the lack of stereom or any kind of mineralized skeleton, and due to poor preservation, features such as body openings and internal structures are entirely unknown (Zamora & Rahman, 2014). *Tribrachidium* has also been hypothesized to belong to groups as disparate as Porifera (Seilacher, Grazhdankin & Legouta, 2003; Grazhdankin, 2014) and Ctenophora (Tang *et al.*, 2011; Budd & Jensen, 2017). Considering their Precambrian age, we should not be surprised that easy affiliation with any modern phylum is unclear. However, considering this substantial uncertainty, we will not discuss these particular taxa any further with respect to ambulacrarian or deuterostome origins.

The cambroernids are a group proposed by Caron, Conway Morris & Shu (2010), comprising two distinct body plans. The first is represented by a group of discoidal fossils including *Eldonia* (Fig. 4D) from the Burgess Shale (Caron *et al.*, 2010), and presumably other discoidal taxa typically referred to as eldonids or eldonioids. These include *Stellostomites*, *Rotadiscus* and *Pararotadiscus* from Chengjiang (Zhu, Zhao & Chen, 2002), Ordovician forms such as *Discophyllum mirabile* (Friend, 1995) and the Devonian *Discophyllum cryptophya* (Friend, 1995). Their gross morphology generally resembles a flattened disc, which may be subdivided by a series of mesenteries and, in *Stellostomites*, has concentric rings on the dorsal surface (Zhu *et al.*, 2002). Aside from the discoidal external morphology, the most characteristic features of this group are the coiled coelomic sac and the dendritic feeding tentacles. The other morphology found among the cambroernids is that of *Herpetogaster* (Fig. 4E), known from the Burgess Shale (Caron *et al.*, 2010), the Pioche formation of Nevada (Kimmig, Meyer & Lieberman, 2019) and Chengjiang (Yang *et al.*, 2020). *Herpetogaster* has dendritic tentacles similar to those of the eldonids, and also has a recurved body similar to the coiled coelomic sac of their discoidal relatives. However, it lacks both dorsal and ventral disc coverings. Instead, it has a pedunculate morphology, presumably oriented perpendicular to the benthos by its stalk and holdfast (Caron *et al.*, 2010). In brief, *Herpetogaster* is reminiscent of an eldonid without its disc, with a stalk, and shifted 90° relative to the sediment–water interface.

An ambulacrarian affinity for the cambroernids relies on relatively broad morphological comparisons. These began with Walcott's original comparisons between *Eldonia* and the pelagic holothurian *Pelagothuria*, which have since been mostly acknowledged as superficial (Walcott, 1911*b*). Caron *et al.* (2010) drew comparisons between *Herpetogaster* and the hypothetical morphology of the ambulacrarian LCA when placing the cambroernids as putative stem-group ambulacrarians. However, as the authors themselves pointed out, homologizing structures definitively is non-trivial with such a distinct body plan. The feeding arms, for example, bear some similarity to pterobranchs or what might be expected in a stem-group echinoderm. However, they differ in their morphological arrangement from modern pterobranchs, and many of the earliest echinoderms apparently lack a feeding appendage. A broader issue is recognizing a clearly trimeric division of the body for comparison with hemichordates, or any echinoderm synapomorphy such as the stereom (or even individual ossicles). Further, the mesenteric division of the eldonids and the external segmentation of *Herpetogaster* lack clear analogues among the ambulacrarians, although they may find some homology in the segmented bodies of early chordates (Fig. 4). These features in particular also draw comparisons with other major divisions of animal life – the cnidarians and the protostomes, respectively. If the LCA to Bilateria was broadly deuterostome-like in its morphology and genetic potentiality, this combination of characters may be less problematic than originally envisioned. However, it is further worth considering that if the Cambroernids represent stem-group ambulacrarians, they may not possess many of the features which we might initially assume to be present in an early representative of that clade. The absence of a stereom may not be problematic in this context. Additionally, defining morphological features may have appeared drastically different half-a-billion years in the past, such that recognizing a homologous arrangement may be difficult. For example, the apparently terminal feeding arms of *Herpetogaster* may, in spite of appearances, be mesosomal in origin. This would establish a clearer homology with the tentacular arms of pterobranchs and echinoderms, which is difficult to validate with fossils in the absence of developmental data.

The clade Vetulicolia was erected in 2001 based primarily on material from Chengjiang (Shu *et al.*, 2001), and includes taxa such as *Vetulicola*, *Banffia*, *Xidazoon* and *Didazoon*. The vetulicolians share one of the most outwardly puzzling body plans among any fossil group. Their body is bipartite in gross morphology and there are significant morphological differences between the respective regions. The anterior region is the larger of the two and ranges in shape from subrectangular to roughly barrel shaped. The anterior-most point has a distinctive mouth, but is otherwise lacking in features indicating any high degree of cephalization. The anterior region has clear segments in some taxa such as *Didazoon* but these are less clear in others. This is in contrast to the tail region, which is unambiguously segmented in all known vetulicolians. Combined with the overall cuticularized body, the vetulicolians appear to have a great deal in common with the arthropods. However, the series of lateral openings on the anterior region have been interpreted as homologous with the gill pores of deuterostomes, resulting in a perplexing, chimeric group of animals (Shu *et al.*, 2010). In depth study of the morphology of these openings defies any clear comparison with respiratory structures in arthropods (Ou *et al.*, 2012). Instead, based on the apparent ability of the pores to open and close through muscular contractions, a filter-feeding lifestyle through ingesting then expelling large amounts of sea water is inferred. With some recent analyses finding a relative lack of support for deuterostome monophyly (Marlétaz *et al.*, 2019; Kapli *et al.*, 2021), the significance of the vetulicolian body plan as a mixture of classic deuterostome and protostome features has undergone renewed attention. The recognition of possible pharyngeal structures is further complicated when you consider morphological variation among the vetulicolians. In particular, the banffozoans do not appear to have gill pores as in *Vetulicolia* (Fig. 4F); whether this represents an early secondary loss or supports a protostome affinity for the vetulicolians over all is still debatable. We treat the topic of gill slit homology and vetulicolians further in Section VI.4.

Vetulocystids, including *Vetulocystis catenata* Shu *et al.* 2014 and *Dianchicystis jianshanensis* Shu *et al.* 2014 from Chengjiang (Shu *et al.*, 2004) and *Thylacocercus* from the Wheeler Formation (Conway Morris *et al.*, 2015), are an enigmatic group of animals that have been proposed as stem-group echinoderms with a bipartite body plan. The first part is a globose structure identified as a theca. The second is a structure described as a 'tail', which is shaped like a cone with a wide base in *Vetulocystis* and *Thylacocercus*, and a thinner, elongate stalk in *Dianchicystis*. This bipartite division was cited as a potential unifying character with the homalozoan echinoderms (and a potential link to the vetulicolians), as well as putative homology between the thecal openings of both groups (including a mouth, respiratory structures, and an anus; Shu *et al.*, 2004). However, there is a fundamental lack of any clear synapomorphies tying the vetulocystids to Echinodermata, or to the deuterostomes at all for that matter. Currently proposed connections are relatively tenuous, and the lack of key features such as the stereom poses substantial difficulty for placing vetulocystids among the echinoderms with any confidence. At the moment, they remain one of many intriguing possible deuterostome affiliates, but their nebulous phylogenetic position gives them little weight when considering early deuterostome evolution.

The identification of a stereom is also relevant to classify *Yanjiahella biscarpa* (Guo *et al.*, 2012), recently referred to as a stem-group echinoderm (Topper *et al.*, 2019). *Yanjiahella* is an unusual taxon with a semi-rigid tail and a pair of flexible feeding arms. A globular theca is covered in loosely organized plates, which do not always directly about their nearest adjacent plate. The long stalk is divided into a stiffened proximal stalk (adjacent to the theca) and a more flexible distal stalk. The posterior-most area of the distal stalk, occurring after the end of the intestine and therefore presumably the anus, is interpreted as a postanal anchoring structure, which may be homologous with those found in the hemichordates and chordates (Cameron, 2005; Nanglu *et al.*, 2020*a*). However, the exact placement of this taxon is under debate. Zamora *et al.* (2020) raised the issue that no definitive stereom was identified in *Yanjiahella*. They further pointed out that upon re-analysis of the character matrix in Topper *et al.* (2019), the only character found uniting *Yanjiahella* with the echinoderms was the identification of plate-like ossicles, and that they were unable to recover identical topologies as were initially reported. In response, Topper *et al.* (2020) pointed out that features used to define Echinodermata in Zamora *et al.*'s (2020) critique may only be useful to recognize crown-group echinoderms and their closest stem groups unambiguously. Therefore, the bilateral symmetry, muscular stalk, and linear digestive tract may represent features retained from the ambulacrarian LCA; presumably, the plate-like ossicles in loose arrangement on the theca may represent a form of intermediary condition between the non-biomineralizing ambulacrarian LCA and the comprehensive stereom already present in middle Cambrian echinoderms. Clearly, this fossil and related taxa merit further investigation and, as both groups of authors pointed out, may have important ramifications for understanding ambulacrarian evolution even if its exact placement is not yet certain. The question of biomineralization across deuterostomes is addressed in greater detail in Section VI.3.

The yunnanozoans from Chengjiang have had one of the most torturous phylogenetic histories. Originally described as enigmatic protostomes based on their segmented body plans, the recognition of repeated, filamentous gill-like structures have led many researchers to favour a deuterostome affinity (Shu *et al.*, 2010). In fact, the yunnanozoans have been placed in almost every conceivable deuterostome position, save the echinoderms. As this topic has been treated comprehensively relatively recently (Cong *et al.*, 2014), we will restrict this consideration to a description of their general morphology, which illustrates how such wide-ranging hypotheses are possible. The overall body plan appears chordate-like – elongate (if not necessarily fusiform), with a prominent dorsal fin, and a series of filamentous gills. Sac-like structures are exterior to the gills, and openings to the external environment lie between them. There are both dorsal and ventral rods in the anterior half of the animal, but many of the signs of cephalization found in even the earliest chordates, such as sensory structures, are not in evidence. Fundamentally, each component of the yunnanozoan body plan defies confident placement due to potential for reasonable alternative hypotheses. Do the repeated, block-like units represent segmentation or myomeres? Are the gills homologous with those of the hemichordates and chordates, or do they represent convergence towards a similar ecological mode? Does the dorsal axial structure represent a nerve cord or a notochord? The ubiquity of questions of this nature when considering the yunnanozoans has led to their phylogenetic placement remaining a point of contention that has no clear end.

VI. MAJOR FEATURES UNITING THE DEUTEROSTOMES

When considering the diversity described here, as well as the enigmatica of somewhat nebulous affinity, it can be difficult to isolate a concrete set of synapomorphies uniting the deuterostomes. Developmental characteristics such as the fate of the blastopore and radial cleavage are typically cited. However, some of these characteristics are found outside of Deuterostomia as well (Martín-Durán *et al.*, 2017; Kapli *et al.*, 2021), and are in any case unlikely to preserve in macrofossils (outside of Doushantuo-style embryo preservation). We therefore constrain the discussion of possible deuterostome-wide characters to the conserved Hox cluster and to what we view as the three features most likely to be recognized in the fossil record – larval development, biomineralized skeletons and the pharyngeal gill slits, with the caveat that while larval forms have been known to fossilize, their appearance in the fossil record is far less likely than either biomineralized or pharyngeal structures.

(1) Hox gene evolution

The Hox cluster of deuterostomes is mostly conserved, especially among ambulacrarians and cephalochordates, and generally composed of nine genes – four anterior genes, four central genes and one posterior gene cluster (Pascual-Anaya *et al.*, 2013). Homology among the anterior and central Hox genes has been relatively easy to identify. Gene duplications, modifications, and cluster splitting among the posterior part of the cluster (*hox9* to *hox15*), however, have made identifying homology among deuterostome genes a challenging task. The most supported hypothesis (Fig. 5) suggests that *hox9/10* was present in the deuterostome LCA and this gene was the precursor for the other posterior genes as follows: in ambulacrarians, *hox9/10* would have duplicated and ultimately formed three *hox11/13* paralogous genes, *hox11/13a-b-c*; in chordates, *hox9/10* would have duplicated and formed *hox11/12* and *hox13/14*, and these genes would have independently formed varied combinations of posterior genes within the chordate classes (Pascual-Anaya *et al.*, 2013; Sekigami *et al.*, 2017). Testing this hypothesis and inferring a thorough ancestral-state reconstruction at each major divergence event will require data from additional taxa within each deuterostome class.

Extensive modifications are found in the Hox cluster of three deuterostome lineages and major phenotypic changes may have been the result of gene reorganizations (Hajirnis & Mishra, 2021). The echinoid cluster of two camarodont echinoids includes the translocation of anterior genes (*hox1* to *hox3*) to the 5′ end of the cluster (Szabó & Ferrier, 2018; Li *et al.*, 2020). A broader sampling with representatives of different orders is needed to test whether this modification could be present in the LCA of crown Echinoidea [data have been published for the sand dollar *Peronella japonica*, but the organization of its cluster is still unknown (Tsuchimoto & Yamaguchi, 2014)]. Vertebrates generally have an organized cluster, but this has been quadrupled and further modified in various lineages. Finally, although the urochordate LCA most likely had a conserved cluster organization with only a couple of gene losses, gene dispersion and reorganization occurred independently in several lineages (Sekigami *et al.*, 2017).

(2) Larval morphology and biphasic lifestyles

Before molecular phylogenies were available to support unambiguously the sister-taxon relationship between hemichordates and echinoderms, similarities in larval morphology and subsequent development provided a crucial link between these disparate phyla. Hemichordates and echinoderms are both tricoelomate, although the vast modifications throughout development of the left hydrocoel in echinoderms to form the unpaired water vascular system makes this difficult to recognize in adults (Cameron, 2005). The larva of the indirect developing ptychoderid enteropneusts (called tornaria) possesses similarities to those found among the echinoderms, principally the structure of the apical organ, the organization of ciliated feeding bands and the way in which they use these bands to suspension feed (Strathmann & Bonar, 1976; Lacalli & Gilmour, 2001; Byrne *et al.*, 2007). Given these similarities, in addition to the presence of planktonic larvae among the pterobranchs, it has often been assumed that an indirect developing habit mediated through a planktonic larva is ancestral to Hemichordata, and Ambulacraria by extension (Nielsen, 2001; Röttinger & Lowe, 2012). While no fossil larvae have been found among the early echinoderms, it is reasonable to assume they were also indirect developers based on the ubiquity of this life-history strategy among extant and Mesozoic forms (Giese, Pearse & Pearse, 1991; Reich, 2021). It is also unsurprising that none have yet been recovered, given the need for Burgess Shale-type or Orsten-type preservation for embryos or larvae to be preserved (Maas *et al.*, 2006). Thus, fossilized deuterostome larvae (or better still, entirely fossilized developmental series) may be key to unlocking some of the deepest homologies between these groups, but they remain far less likely to be found than more macroscopic features such as pharyngeal characteristics.

The similarities between these larval forms are so great that they are often described under the umbrella term of ‘dipleurula-type larva’, which the ambulacrarian LCA presumably would have possessed (Nezlin, 2000; Röttinger & Lowe, 2012; Cannon *et al.*, 2014; Strathmann, 2020; Lowe, 2021). The dipleurula-type larva was most likely a feeding planktonic larva with bilateral symmetry. The adult form of this hypothetical animal is unclear, although in classic formulations of a dipleurula-type origin for Ambulacraria, it was a sessile animal akin to pterobranchs (Garstang, 1928; Berrill, 1955; Romer, 1967). While this latter component of the hypothesis has not held up over the years (Lowe, 2021), it is still worth considering the possibility that the ambulacrarian LCA may have had a dipleurula-type larval form paired with a motile, vermiform adult morphology. The shift of tunicates from the earliest branching chordate lineage to vertebrate sister group also weakens the argument for a biphasic lifestyle in the deuterostome LCA. Therefore, the emerging picture of deuterostome developmental origins is as follows.

Based on the highly conserved antero-posterior patterning of gene expression between hemichordates and chordates (Gerhart, 2006), in particular amphioxus (Simakov *et al.*, 2015), the adult form of the deuterostome LCA was most likely a motile, vermiform or fusiform animal. The larval morphology of the LCA was likely simple (as in

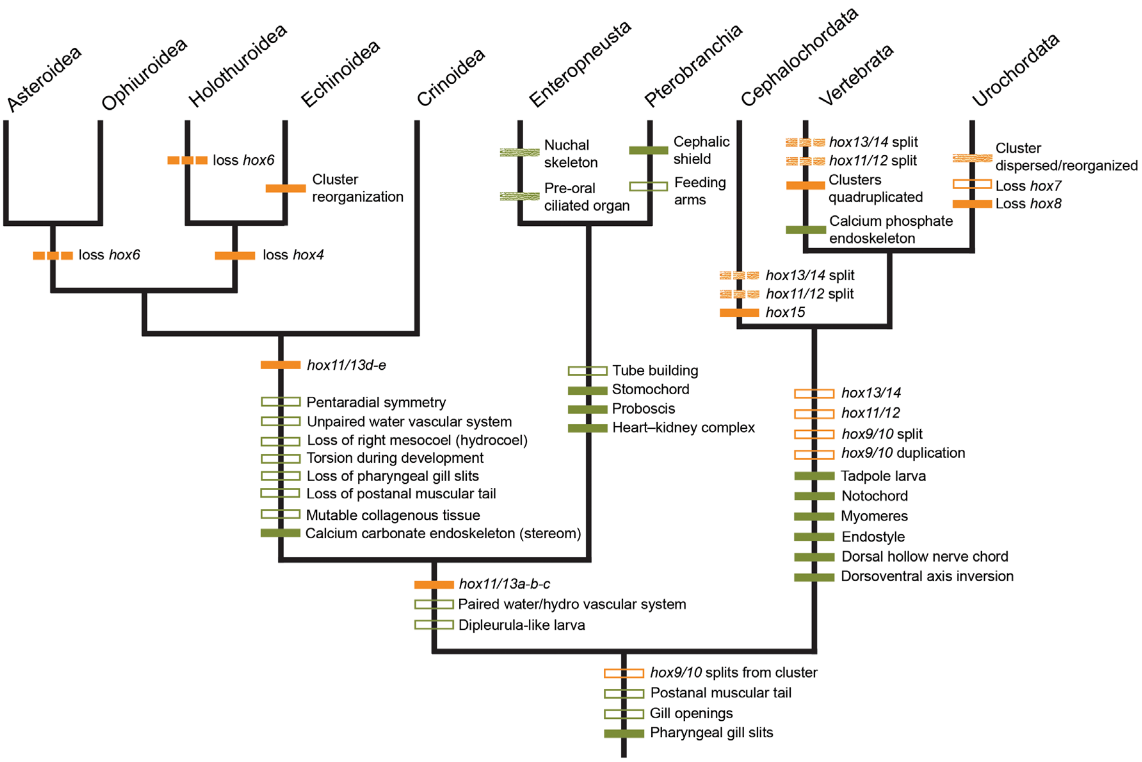

Fig. 5. Cladogram of crown-group deuterostome classes with inferred apomorphies. Orange bars refer to Hox genes (modified from David & Mooi, 2014) and green bars refer to other types of characters. Textured bars are changes that happened within the stem lineages, dashed bars are homoplasies and hollow bars are uncertain changes. Initial data indicated that *hox7* was lost in the Urochordata, but Aronowicz & Lowe (2006) suggested that this gene (or part of it) merged with *hox5* and *hox6*. See Section VI.1 for uncertainties regarding modifications in the posterior *Hox* cluster.

cephalochordates) or involved direct development, with the complex biphasic lifestyle of the urochordates being a later, independent acquisition. The acquisition of the dipleurula-type larva defines the ambulacraria crown group. In Echinodermata, this larval morphology was the substrate for the wide variety of larval types present in extant taxa, including the dipleurula-type larvae of crinoids (auricularia and non-feeding doliolaria), asteroids (bipinnaria) and holothurians (auricularia), which most resemble hemichordate tornaria, and the pluteus larvae of echinoids and ophiuroids. In Hemichordata, the ptychoderid larval form is attained through truncation of the antero-posterior transcription axis (Gonzalez, Uhlinger & Lowe, 2017), while in pterobranchs, the larva has become relatively simple, more visually akin to a planula-type larva than to a dipleurula-type larva (Lester, 1988; Dilly, 2014).

(3) Biomineralization across Deuterostomia

All three deuterostome phyla produce biominerals, albeit in different ways with vastly different expression with respect to their body plans and clade-specific minerals. This is most obvious in echinoderms, whose calcitic stereom is their most obvious synapomorphy, and chordates, which use calcium phosphate to produce four skeletal tissues. By contrast, the biomineralizing potential of hemichordates has only been recognized recently. Aragonitic ossicles have been found in the trunks of *Saccoglossus bromophenolosus* King *et al.* 1994 and of *Ptychodera flava* Eschscholtz, 1825 from Galapagos (Cameron & Bishop, 2012), none of which resemble the various types of echinoderm ossicles.

The precipitation of calcium phosphate by vertebrates has been inferred to be related to their high-energy, predatory lifestyle (Wagner & Aspenberg, 2011; Wood & Zhuravlev, 2012). On the other hand, preference for the two forms of calcium carbonate is directly related to the availability of magnesium and calcium in sea water, which are key constituents of calcite and aragonite, the polymorphs of calcium carbonate, and each clades' skeletal mineralogy typically matches the seawater chemistry that was present during the *de novo* acquisition of biomineralization (Porter, 2010; Balthasar & Cusack, 2015; Quattrini *et al.*, 2020). Although the Ediacaran was dominated by aragonite seas, Cambrian oceans went through oscillations in mineral concentration, favouring the precipitation of aragonitic and high-magnesium calcitic skeletons at times and low-magnesium calcitic skeletons at other times (Neilson, Brasier & North, 2016). Although echinoderms produce calcite skeletons, this calcite is high in magnesium and thus favours precipitation in aragonite seas (Stanley &

Hardie, 1999; Wood & Zhuravlev, 2012). As a result, it would be expected that the *de novo* acquisition of the echinoderm mineralized skeleton occurred during an aragonite sea interval. Instead, the oldest echinoderms found – unidentified dissociated ossicles and two radially symmetric groups, helicoplacoids and 'eocrinoids' – lived in predominantly calcite seas of Cambrian Stage 3 (Kouchinsky *et al.*, 2012; Zamora *et al.*, 2013*a*). However, molecular clock estimates indicate that echinoderms originated in the Ediacaran, around 590–560 Ma (Erwin *et al.*, 2011; Simakov *et al.*, 2015). Ocean chemistry prior to Stage 3 was predominantly aragonitic, so an origin of echinoderm biomineralization during this interval is consistent with molecular clock estimates. Similarly, a number of non-deuterostome clades with aragonitic or high-magnesium calcite skeletons originated in early Cambrian aragonitic seas, such as sponges, cnidarians and sessile lophotrochozoans, for example (Kouchinsky *et al.*, 2012; Wood & Zhuravlev, 2012; Murdock, 2020).

Although the most recent echinoderm phylogeny suggests that radial symmetry is derived, bilateral and asymmetric echinoderms do not appear in the fossil record until the middle of Stage 4 (Smith *et al.*, 2013), after another aragonite–calcite oscillation. This reversed Cambrian record might suggest that biomineralization could have evolved independently in multiple lineages, with radially symmetric echinoderms biomineralizing the skeleton first. However, although skeleton biomineralization occurred independently throughout the metazoan tree as a result of reutilization of developmental networks (Erwin *et al.*, 2011; Morgulis *et al.*, 2019; Murdock, 2020), the intricate nature of the echinoderm stereom strongly supports a single origination. As a result, a unique evolution of echinoderm biomineralization prior to Stage 3 suggests that echinoderms would have exhibited extremely high rates of morphological evolution (Smith *et al.*, 2013), which means that radially symmetric echinoderms (not only helicoplacoids, but also the pentaradial 'eocrinoids') would have evolved within 10–15 million years after the origin of the phylum. Within this timeframe, the evolution of varied stereom architectures, the loss of the right hydrocoel during development and change in symmetry, and other radical changes (Fig. 5) would have already taken place. Finally, if the rates of morphological evolution are not realistic, given the complexity exhibited by early echinoderms, we cannot rule out that the phylum could have originated tens of millions of years earlier than estimated.

Biomineralization generally results in relatively good preservation, but all scenarios above indicate that there may be a huge gap in the Cambrian record of the Echinodermata, challenging our understanding of its origin and early evolution. This gap may be explained by conditions in onshore Cambrian environments that were unfavourable to the preservation of articulated specimens (Zamora *et al.*, 2013*a*); although helicoplacoids were apparently well distributed, their preservation possibly owes to exceptional taphonomic conditions in offshore environments (Dornbos & Bottjer, 2001). In addition to distribution and varying taphonomic conditions, we must also investigate how biomineralization (i.e. the transition from no skeleton to a fully formed stereom as found in the plated theca of early-diverging taxa) evolved. Echinoderms are currently diagnosed by their stereom, but what lies between the ambulacrarian LCA and the first echinoderm?

Regardless of these scenarios, the ambulacrarian LCA probably lived in aragonite seas prior to Stage 3 and had a flexible biomineralization toolkit wired for different skeletal types. While using different minerals, five proteins identified from echinoid skeletal proteomes have putative homologues in the genome of the hemichordate *Saccoglossus kowalevskii* (Cameron & Bishop, 2012), including *msp130* genes known to be involved in echinoderm biomineralization (Piovani *et al.*, 2021; Thompson *et al.*, 2021). To date, *msp130* genes have been found in several prokaryotes, a couple of green algae, and a few metazoan lineages – deuterostomes, molluscs, and an annelid (Ettensohn, 2014; Szabó & Ferrier, 2015). Their absence in non-bilaterians prompted the hypothesis that *msp130* genes were introduced into selected bilaterian lineages *via* horizontal gene transfer and in the case of the deuterostomes, lost in the lineage leading to vertebrates and urochordates (Ettensohn, 2014). An alternative hypothesis is that these genes were already present in the ancestral bilaterian (Szabó & Ferrier, 2015). Data are still limited and as more genomes become available, we will be in a better position to evaluate the evolution of *msp130* genes in metazoans. An additional question that remains is whether these genes also have a biomineralizing function in hemichordates or whether they have been co-opted for other functions.

The earliest mineralized elements in chordates are the jaws of conodonts, for example *Proconodontus* (Murdock *et al.*, 2013). Similar to echinoderms, biomineralization in chordates includes the secretion of calcium-based minerals within an extracellular space by mesenchymal cells (Livingston *et al.*, 2006). Although specific biomineralization genes have been found in both echinoderms and vertebrates, several genes play a role in skeleton formation in these groups. These include at least nine genes [*alx1*, *erg*, *ets1/2*, *gataC*, *jun*, *rreb*, *snail*, *soxE* and *twist* (or their vertebrate orthologs)] that encode transcription factors that specify the identity of skeletogenic cells and six genes [*alpha-collagen*, *c-lectin*, *cara7la*, *mt14/mmpl7*, *scl4a10* and *tetraspanin* (or their vertebrate orthologs)] that activate terminal-differentiation genes (Piovani *et al.*, 2021). At most then, the deuterostome LCA may have had the basic genetic toolkit required for the formation and precipitation of biominerals, but this may have either been unexpressed or expressed in a limited fashion more akin to hemichordates than their sister phyla. This possibility may be most plausible if the LCA was a tricoelomate, motile, vermiform animal as we hypothesize in Section VIII.

However, it is difficult to find an actual direct example of this type of morphology in the fossil record. Perhaps the closest example is previously mentioned *Yanjiahella*, in which a true stereom may not be present, but the presence of a loosely organized, multi-plated morphology may align with the emerging picture of the ambulacrarian LCA. In this way, *Yanjiahella* may represent a stem-group echinoderm (as originally proposed by Topper *et al.*, 2019) from a lineage that pre-dates several of the characters whose absence or configuration Zamora *et al.* (2020) found problematic (i.e. stereom, food grooves, the position of the mouth). An alternative could be that *Yanjiahella* is a stem-group ambulacrarian which has developed a method for widespread biomineralization of plates across its body that is independent from that of the echinoderms. One possible affinity in this area of the deuterostome tree of life is with the cambroernids, as they share many features, namely: paired feeding arms around a presumed mouth and a stalked morphology in the case of *Herpetogaster* (Caron *et al.*, 2010). It is worth noting that the radial (presumably cambroernid) taxa, *Stellostomites eumorphus* Sun & Hou, 1987 and *Rotadiscus grandis* Sun & Hou, 1987, have regularly spaced, rounded structures as features of their external disc (Friend, 1995; Zhu *et al.*, 2002). While these have been interpreted as pores (Friend, 1995) and pustules (Zhu *et al.*, 2002), one possibility is that they represent biomineralized structures, as they appear to be structurally rigid, repeating, and evenly spaced. If such a relationship were to be validated, then the early cambroernids may have adopted extensive ectodermal biomineralization early in their history, and subsequently lost it in the roughly 10 million years separating Chengjiang from the Burgess Shale.

(4) The form of the pharynx and respiratory structures

Gill slits are one of the classically cited deuterostome homologies and, as the most macroscopically observable of these characters, of particular importance to viewing deuterostome origins through fossils. As reviewed above, both the chordate and hemichordate Cambrian fossil records support gill slits as being plesiomorphic to their respective phyla. While the gill slits themselves are not readily visible in either taxon, the hemichordates *Spartobranchus* (Caron *et al.*, 2013) and *Oesia* (Nanglu *et al.*, 2016) both preserve their gill bars in minute detail. Presumably, the gill slits would have been present as well based on their function, but may not have been fossilized due to their high decay susceptibility (Nanglu *et al.*, 2015). As noted in Section IV.2, *Pikaia* is the only Cambrian chordate without clear gill slit or gill bar homologues, suggesting gill slits to be plesiomorphic for Chordata as well. Most crucially, the gene regulatory network responsible for the creation of pharyngeal endoderm outpockets, the precursors to the gills in both hemichordates and chordates, is highly conserved across both phyla (Gillis *et al.*, 2012). The most problematic area to consider, therefore, is the identification of gill slit homologues in both the echinoderms and the various problematic taxa of uncertain deuterostome affinity.

The stylophoran echinoderms have structures that may be homologous with gill slits, which have been variously called gill pores, gill slits, cothurnopores, lamellipores, branchial slits and more. They appear as oblong perforations in the stereom of the animal which lead into the interior. Among the stylophoran group Cornuta, examples of these structures are clear in *Ceratocystis* (Ubaghs, 1967; Clausen & Smith, 2005), *Phyllocystis* (Lefebvre & Vizcaino, 1999; Smith, 2008), *Proscotiaecystis* (Lefebvre & Vizcaino, 1999), *Thoralicystis* (Lefebvre & Vizcaino, 1999), and *Reticulocarpus* (Jefferies & Prokop, 1972). Typically, they are clustered on the left side of the asymmetrical fossils towards the base of their single stalk/appendage. They can be organized into a line as in *Archaeocothurnus* and *Phyllocystis*, a recurved line between adjacent plates as in *Ceratocystis*, or a more irregular cluster as in *Reticulocarpus*. Establishing homology between these structures and gill slits is non-trivial, however, we can say from a functional perspective that they appear designed to serve a respiratory function (Lefebvre, 2003), given their morphology, position on the dorsal side of the theca, and connectivity between the internal and external environments. In *Phyllocystis* and *Thoralicystis*, these structures seem to be further specialized to have either two rows of grape-like structures (in the former) or lamellate folds (in the latter; Lefebvre & Vizcaino, 1999). Presumably, structures such as these might afford more surface area for gas exchange or reactivity, as is the case in many other branchial structures. Among the stylophoran mitrates, two taxa merit special consideration. *Jaekelocarpus oklahomensis* Kolata *et al.*, 1991 has a bilaterally symmetrical calcitic skeleton, with a prominent oral spine anteriorly and a three-part stalk/appendage posteriorly (Dominguez, Jacobson & Jefferies, 2002). Internally, it has three pairs of bilaterally arranged gill slit-like structures, which have been inferred to perform a cilia-mediated filter-feeding function. *Lagynocystis pyramidalis* has an atrium at the posterior end of the theca filled with an extensive row of branchial bars (Jefferies, 1973) which, similar to *Jaekelocarpus*, may have borne cilia to facilitate filter feeding. What is notable about these examples is twofold: (*i*) the branchial structures within the atrium constitute actual bars rather than just pores; and (*ii*) that these structures are part of the internal anatomy of the fossils rather than existing solely on the exterior surface. A recent study on the morphological characteristics of these structures (i.e. length, width, spacing), including these two taxa, found further evidence to support their homology with the gill bars of extant cephalochordates and hemichordates (Álvarez-Armada *et al.*, 2022). In a broader sense, there appears to be mounting evidence for pharyngeal gill slit homologues to be present in some early echinoderms. However, these may be restricted to relatively few stylophoran taxa, and the respiratory structures found in other fossil forms may represent independently evolved structures.

When the fossil record and data from comparative developmental biology are considered together, the typical conclusion is that gill slits are a deuterostome plesiomorphy, that echinoderms secondarily lost gill slits at least once, on the lineage leading to crown-group Echinodermata, and possibly more times depending on the phylogenetic placement of stylophorans (Fig. 3C) relative to bilaterally symmetrical taxa

(Fig. 1) such as the ctenocystoids (Fig. 3A). It is logical to infer, therefore, that the atrial openings of various echinoderm taxa appear to be modified gill pores, but this debate is far from settled. Indeed, even establishing that the stylophoran appendage is a feeding arm with tube feet rather than an elongate stalk is a relatively recent discovery, hinging on both new fossil discoveries and novel imaging techniques (Lefebvre *et al.*, 2019).

As referred to in Section V, a variety of problematica have been allied with the deuterostomes largely based on the recognition of putative gill slit homologues, notably including the vetulicolians and yunnanozoans, reinforcing the status of gill slit plesiomorphy as integral to our understanding of deuterostome evolution. However, the fossil taxa described in this section, to say nothing of their modern relatives, evidence a wide array of different morphologies and arrangements of possible gill slit homologues. We might further reasonably ask what the morphology and arrangements of the gill slits may have looked like in both the ambulacrarian and deuterostome LCA, and how informative any single extant pharynx-bearing taxon may be as a model.

First, we must recognize that the LCA to Deuterostomia may have had many of the components of the gene regulatory network responsible for producing a pharyngeal region in modern taxa, but that the morphological manifestation of the 'pharynx' may be drastically different than expected. This is particularly true when considering 'deep homologies' of groups that have diversified into morphologically disparate forms (Shubin, Tabin & Carroll, 2009; Tschoop & Tabin, 2017). We should, therefore, not put too much emphasis on any one specific subset of taxa as our model for the pharynx of the deuterostome LCA. As tempting as it may be to reconstruct such a hypothetical animal with a pharynx akin to a harrimanid enteropneust or a cephalochordate, it is perhaps better supported to envision only a vermiform animal with simple pores restricted to the anterior region of the body, but without a distinct pharynx or atrium arrangement.

Second, by definition our fossils post-date the actual divergence events leading to both Deuterostomia and Ambulacraria and, particularly in the case of the former, this discrepancy may be on the order of tens of millions of years. Therefore, the pharynges of fossils dating back even to the middle Cambrian may have already undergone significant specialization and, particularly in the case of radiate echinoderms, secondary loss. Another notable example are the pterobranchs, within which the cephalodiscids have undergone a reduction of gill pores to a single pair, and the rhabdopleurids have lost their gill slits entirely (Cameron, 2005). It has been hypothesized that too small a size imposes a functional constraint on gill pores as they become energetically inefficient at pumping water, which may have corresponded with a shift from pharyngeal to tentacular filter feeding (Vo *et al.*, 2019). The varying pore morphologies and arrangements among the early deuterostomes may, therefore, represent early specialization of a functionally important, ancestral character that is more labile than typically thought. Similarly, the absence of gill pores in taxa such as the eldonids is less surprising; the roughly 10–15 million years between the ambulacrarian LCA and the cambroernids may have been ample time to lose one of the most defining features of the early deuterostomes. Bearing this in mind, the pharyngeal disparity assembled through a comprehensive overview of the deuterostome fossil record is perhaps a better reflection of the functional advantages offered by a hybrid feeding and respiratory structure than it is of the exact form of the ancestral pharynx. In this context, it is important to remember that from the filamentous pores of the yunnanozoans, to the gill bars of the hemichordates and cephalochordates, to the stiffened internal gills of *Jaekelocarpus*, the shared homology is with that of the hypothetical simple pharynx of the deuterostome LCA rather than in any direct comparison between these half-a-billion-year-old fossils.

VII. WE'RE ALL DEUTEROSTOMES: MONOPHYLY, PROTOSTOMES AND XENACOELOMORPHA

We have so far focused on the three unambiguously deuterostome phyla; however, we cannot discuss common ancestors beyond the ambulacrarian LCA without reviewing the clade Xenacoelomorpha, which is composed of the xenoturbellids and acoel worms. Xenacoelomorphs are flattened worms abundant in coastal and deep water, including in hydrothermal vents (Nakano, 2015; Rouse *et al.*, 2016), but also found in fresh water and in symbiosis with other marine invertebrates (Sterrer, 1998; Achatz *et al.*, 2013; Børve & Hejnol, 2014). Since its recognition as a group on its own, Xenacoelomorpha has been placed in various branches within the bilaterian tree using extensive molecular data. After several studies in the last decade, relationships between the xenacoelomorphs and the other bilaterians are still contentious. Although some data support Xenacoelomorpha as monophyletic and sister to Nephrozoa (Hejnol *et al.*, 2009; Cannon *et al.*, 2016; Rouse *et al.*, 2016; Laumer *et al.*, 2019), there is also evidence that at least the Xenoturbellida may be sister to the Ambulacraria (Paps, Baguñ & Riutort, 2009; Philippe *et al.*, 2011, 2019; Delsuc *et al.*, 2018; Marlétaz *et al.*, 2019) forming the group Xenambulacraria. A third possible scenario is that deuterostomes are not monophyletic, with chordates being more closely related to the protostomes (Marlétaz *et al.*, 2019; Philippe *et al.*, 2019) than to Xenambulacraria. The reality is that a wealth of molecular data has failed to definitively resolve inter-phylum relationships in this part of the metazoan tree and heterogenous rates of evolution – bound to our inability to properly analyse such data – have been assumed to be the main challenge (Kapli *et al.*, 2021).

If they are indeed deuterostomes, the standing question is whether the xenacoelomorph lineage is secondarily simplified or whether the deuterostome LCA is much simpler than we think. The xenacoelomorph LCA (and especially the

Xenoturbellida) is thought to be simple both morphologically and from a genomic perspective. For example, only five Hox genes have been found in the Xenacoelomorpha to date – five in the Xenoturbellida (*hox1*, three central Hox genes and *hox9/10*) and three in the Acoelomorpha (*hox1*, *hox5*, *hox9/10*) (Cook *et al*., 2004; Jiménez-Guri *et al*., 2006; Fritzsch *et al*., 2008; Hejnol & Martindale, 2009; Moreno *et al*., 2009). Accordingly, if Xenacoelomorpha is sister to Ambulacraria, the deuterostome LCA would probably have its conserved cluster with nine genes and there would have been gene losses in the lineages leading to the Xenacoelomorpha and then to the Acoelomorpha. However, if Xenacoelomorpha is sister to the deuterostomes, the deuterostome LCA could have had a simplified cluster, with 5–6 genes – one anterior gene (or two if an ortholog of cnidarian *hox2* was maintained), three central genes and one posterior gene. In this scenario, 2–3 anterior genes and one central gene would have originated in the lineage leading to ambulacrarians and chordates, and 2–3 genes would have been lost in the lineage leading to the Acoelomorpha. Although a secondary simplification seems more parsimonious, it also challenges the assumption that complexity in free-living organisms increases over time. The answer to this conundrum might be paedomorphic evolution of soft-substrate burrowing, seen in Gastropoda (Brenzinger, Haszprunar & Schrödl, 2013; Martynov *et al*., 2020), Holothuroidea (Mooi & David, 1998), and likely to have occurred in other groups (but see Haszprunar, 2016).

A further challenge is inferring the relationship between deuterostomes and protostomes. The discovery that previously recognized deuterostome phyla (i.e. the three lophophorate phyla and Chaetognatha) are protostomes and that some deuterostome traits (i.e. deuterostomy, radial cleavage, enterocoely) may be plesiomorphic to Bilateria has prompted re-interpretations of the deuterostome and bilaterian LCAs (Kapli *et al*., 2021). Making homologous assessments among the three deuterostome phyla has been remarkably difficult. To make matters worse, traits shared by xenacoelomorphs and deuterostomes may rather be urbilaterian traits that were lost in the protostome lineage (Ruiz-Trillo & Paps, 2016). In this context, the distinction between the deuterostome and the bilaterian LCAs might be quite slim, especially because the branch from the urbilaterian to the deuterostome LCA is very short compared to the protostome branch (Kapli *et al*., 2021). A short branch suggests not only little recognizable morphological change, but also a short window of time that we must look for possible ancestors in the fossil record. The number of fossils retrieved from Lagerstätte suggests that we have many candidates, but the Problematica revisited here have brought more questions than answers and the recognition that early bilaterians were most likely worm-like animals that did not preserve phylogenetically important traits to tell the tale (or at least the traits that we have been focusing on). To have a solid understanding of the early evolution of bilaterians and deuterostomes, we must have a better idea of what we are looking for and hope that those traits have been well preserved in future findings. Also, the discovery of new species of Xenoturbellida in recent years (Rouse *et al*., 2016; Nakano *et al*., 2017), some of these from shallow water and more accessible for collection, should allow for exciting research in the near future.

These problems are compounded when you consider the wide range of divergence time estimates for the clades in question. For example, the deuterostome LCA may have lived as early as 660 Ma (Erwin *et al*., 2011) to as comparatively recent as 570 Ma (Simakov *et al*., 2015); Ambulacraria, by comparison, has been estimated to be 590–516 Ma (although the latter estimate is unlikely given putative ambulacrarians older than 515 Ma, Table 1; Erwin *et al*., 2011; dos Reis *et al*., 2015; Delsuc *et al*., 2018). Such estimates have been revised and should improve as new fossil evidence is found and as tree-calibration methods improve.

In essence, our hypotheses for the form of the deuterostome and ambulacrarian LCAs have to contend with three principal confounding factors: (*i*) the massive disparity among both extant and fossil forms within this superphylum; (*ii*) uncertainty in tree topology and the status of the xenacoelomorphs as deuterostome allies; and (*iii*) the gap in time between the origins of these taxa and their first known fossil representatives. With that in mind, we outline below three possible hypotheses for the early morphological evolution of the deuterostomes, given the considerable uncertainty surrounding the topic.

VIII. INFERRING THE LAST COMMON ANCESTORS

Swalla & Smith (2008) outlined three hypotheses for the form of the deuterostome LCA, which included modernizing many of the ideas proposed by Garstang, Berril, and Romer. The first hypothesis posited a simple, xenoturbellid-like animal as the deuterostome LCA. Even in 2008, several problems were noted with this hypothesis. First, it would suggest the independent acquisition of several morphological characters that we would otherwise interpret to be plesiomorphic, such as the gill slits and a muscular post-anal structure by chordates and ambulacrarians. Second, the plausibility of the hypothesis largely rested on what was assumed to be a 'basal' position of *Xenoturbella* to Ambulacraria, a relationship that is not borne out based on current data (Cannon *et al*., 2016; Rouse *et al*., 2016; Kapli *et al*., 2021). The other two hypotheses, which posit either an acorn worm-like or tentaculate deuterostome LCA, better withstand the scrutiny of modern data, and thus warrant more detailed consideration.

(1) What was shall be: the vermiform hypothesis revisited

The second deuterostome LCA hypothesis outlined by Swalla & Smith (2008) was a vermiform animal with superficial similarities to an enteropneust, discussed at greater length in Cameron, Garey & Swalla (2000). This animal would have had a simple nervous system with a gill-slit-laden pharynx. Since its formulation, several pieces of data have emerged supporting this hypothesis and overall, it seems to be the most strongly supported. The recent descriptions of several Cambrian hemichordates with soft tissues uniformly support a vermiform body plan being ancestral to the phylum. Further, the morphology of *Oesia disjuncta* demonstrates how a gill-slit-laden body plan may function without the necessity of being organized into distinct pharyngeal and digestive regions (Nanglu *et al*., 2016). Many of the defining features of the chordates, notably the notochord, myomeres and higher degree of cephalization, seem to be adaptations that work best in concert to facilitate a highly motile swimming lifestyle. In that context, they are likely innovations of that phylum rather than plesiomorphies of Deuterostomia. The crown-group echinoderm body plan is clearly highly derived within Bilateria, and is thus mostly uninformative for the form of the deuterostome LCA.

The form of the ambulacrarian LCA, therefore, would also appear to be vermiform, or at least elongate, with bilateral symmetry and a clear anterior–posterior axis. In addition to the gill slits, this hypothetical animal may have also had the ability to secrete biominerals in a rudimentary fashion. Early ossicles may have been diffuse throughout the trunk like in some enteropneusts, and then elaborated in the echinoderm lineage to form the stereom. But to consider the presence of a primordial skeleton in the ambulacrarian LCA, we need to also consider its mineral composition. Given the estimates of divergence time between hemichordates and echinoderms, the ambulacrarian LCA would have lived in aragonitic seas. Alternatively, the ambulacrarian LCA may not have been skeletonized at all, but rather had the underlying but unexpressed developmental capacity to form a skeleton. This worm may also have had a muscular postanal structure, akin to those seen in the Cambrian hemichordates and postanal tails of chordates, but this feature was subsequently lost in crown echinoderms.

In terms of body function and ecology, this benthic worm would be a filter feeder with a straight gut and posterior anus, and would locomote with a hydrostatic skeleton composed of circular and longitudinal muscles. This worm may also have been a broadcast spawner and developed through a dipleurula-like larva. It is also possible that a circulatory structure formed by the paired mesocoel was present.

Largely conserved in the protostome phyla, the nervous system of deuterostomes is remarkably varied and the possibility that xenacoelomorphs are deuterostomes only adds to this complexity. A reconstruction of nerve networks and Hox genes indicate that the urbilateria had a centralized nervous system (Holland *et al*., 2013). However, Xenoturbellida has a diffuse, ectodermal nerve net, and the nervous systems of echinoderms and hemichordates are a hybrid between this diffuse system and the chordate-like version with nerve cords (Gavilán, Perea-Atienza & Martínez, 2016; Formery *et al*., 2021). This variation suggests that the dorsoventral patterning system with a single medial nerve cord may have evolved three times in the Bilateria, although the molecular network was most likely established before the urbilaterian (Martín-Durán *et al*., 2018). The short branch leading the urbilaterian to the deuterostome LCA and the diversity of body plans and systems (e.g. early development, skeleton, nervous system) found in deuterostomes indicates that core developmental modules were well established in the deuterostome LCA and that tweaks drastically changed the overall body construction in its descending lineages.

(2) Going nowhere fast: the sessile origin hypothesis revisited

A sessile, tentaculate animal has also been hypothesized as a candidate for the deuterostome LCA. In its original formulation, this hypothesis relied on superficial similarities between stalked pterobranchs and their 'tentaculate' echinoderm relatives, as well as a possible connection between the indirect developing ambulacrarians and urochordates. While there is weaker direct evidence for this hypothesis than for a vermiform origin, we are still unable to rule it out definitively. The reciprocal monophyly of the pterobranchs and enteropneusts still permits some debate as to the ancestral hemichordate body plan. Despite recent discoveries such as *Gyaltsenglossus* supporting a vermiform hemichordate LCA, the absence of the miniaturized builders of early pterobranch tubes such as *Sokoloviina* does cast some ambiguity. It is conceivable, therefore, that the ambulacrarian LCA was a sessile tentaculate animal, with either a flexible muscular appendage for attachment to the benthos in a manner similar to *Yanjiahella* or *Herpetogaster*, or a wide stalk with a branchia-bearing 'theca' such as the vetulicystids. In such a scenario, it would be difficult to make any definitive claim regarding whether this body plan or a more active chordate-like body plan is the best candidate for the deuterostome LCA.

We feel compelled to point out, however, that supporting this theory hinges on ignoring what seems most probable in favour of what is merely possible. For one thing, we now know the urochordates to form the clade Olfactores with vertebrates, rather than being positioned as the earliest branching chordate lineage. Therefore, any support this theory may have once enjoyed stemming from the sessile nature of the tunicates or their indirect development style in comparison with those found among the ambulacrarians is now known to be convergence. Second, this scenario would affect our inference on the early evolution of echinoderms and possibly consider 'tentaculate' forms with a post-anal tail at the base. Finally, we might also expect convergence in stalk-like structures among a wide variety of early deuterostomes, reflecting a common and effective solution to the ecological problem of attachment to the benthos. Building support for this hypothesis based on some of the most enigmatic Cambrian taxa, therefore, is fraught with danger. Further, when we consider the probability that the LCAs of both the protostomes and Bilateria were motile animals, the likelihood of this hypothesis seems even more remote.

(3) Things fall apart: the bearing of non-monophyly on deuterostome origins

Finally, it bears considering how the possible non-monophyly of the deuterostomes may impact our understanding of their origins. It is perhaps better to frame this question in the opposite direction: how would a paraphyletic Deuterostomia impact our theories of bilaterian origins in general? If chordates find themselves allied with the protostomes, in what Kapli *et al.* (2021) suggested be described as the 'Centroneuralia', to the exclusion of the Xenambulacraria, then it would seem logical that many of the characteristics that previously defined deuterostomes are actually bilaterian synapomorphies. Developmental features such as deuterostomy and radial cleavage being ancestral would help reconcile earlier placements of lophophorates and chaetognaths among the deuterostomes, as these taxa would be interpreted as retaining the ancestral state rather than independently acquiring a suite of characteristics patterning the earliest stages of embryogenesis.

Kapli *et al.* (2021) also addressed one of the most intriguing possibilities with regard to what this might mean for the fossil record, namely, gill slits as a bilaterian plesiomorphy would make the chimeric body plan of the vetulicolians less alien. However, such a topology has ramifications for the entire suite of other problematica which are currently tied to the deuterostomes through features that might have been present in the bilaterian LCA. The yunnanozoans may share a similar phylogenetic position as the vetulicolians, with an interpretation of their body plan incorporating a cuticularized exoskeleton and segmentation with filamentous gill slit-like structures being a reflection of gill slit plesiomorphy within total-group Protostomia. The removal of the muscular, active swimming Chordata as sister group to Xenambulacraria might provide indirect support for a sessile origin to this phylum, incidentally making the position of the vetulicystids of more critical importance for considering xenambulacrarian origins. If a tricoelomate body plan is also ancestral to Bilateria, cambroernid affinities may lay closer to sessile, tentaculate taxa such as the lophophorates (Zhu *et al.*, 2002) than to the ambulacrarians (Caron *et al.*, 2010).

That being said, a lack of support for Deuterostomia has thus far only been demonstrated in a few recent studies, and so it may be premature to rewrite our understanding of bilaterian evolution just yet. However, even the most cursory speculation for what this result might mean for understanding animal origins underscores the widely disparate body plans of the deuterostomes, particularly when fossils are added to the mix. In many ways, despite hundreds of years of zoological effort and two decades since the publication of the new animal phylogeny (Halanych *et al.*, 1995; Aguinaldo *et al.*, 1997), we remain in an intellectual wild west with regard to deuterostome origins. No hypothesis, no matter how far-fetched it may seem, can be entirely discarded. No theory, no matter how enticingly logical, can claim to have emerged victorious among its competitors. The deuterostomes continue to elude a single, clean narrative to describe their early evolution, a state that is both fascinating and frustrating in equal measure.

IX. CONCLUSIONS

(1) The early evolutionary history of the deuterostomes remains enigmatic, but a clearer picture emerges when integrating fossils with molecular and developmental data. Holistic analyses using all three types of data are necessary for understanding deuterostome origins robustly.

(2) The three deuterostome phyla present unique challenges for inferring their ancestral conditions. Among hemichordates, disentangling the timing and sequence of events that led to the wide morphological disparity between pterobranchs and enteropneusts remains difficult. Establishing homologies and coming to a consensus on symmetry remains problematic for echinoderms. Chordates still suffer from a paucity of well-preserved material in the Cambrian.

(3) A wide variety of enigmatic fossil taxa are allied with the deuterostomes based on relatively few characters (i.e. gill pores, trimeric body arrangement), and thus may be liable to shifting their phylogenetic positions in coming years.

(4) With the available data, and through reviewing previous hypotheses for the form and function of the deuterostome LCA, we suggest that it was a motile, vermiform animal with simplified gill pores without much internal organization of the pharynx. It may have had the capacity to secrete calcium minerals, but in a highly limited fashion like modern acorn worms, rather than the more elaborate ossicles of echinoderms. This animal was likely to be a direct developer, or at most had a simple planktonic larval form less specialized than the hypothetical 'dipleurula'.

(5) To shed light more accurately on the early history of the deuterostomes, we need both to describe new fossil deuterostomes (whether through new field discoveries or revisiting existing museum collections), and to integrate them into a unified, quantifiable framework using the best phylogenetic methods available. This paired approach will lead to the most stable foundation from which to test new hypotheses for this significant division of animal life.

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