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Origin and Early Evolution of Echinoderms

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Abstract

Echinoderms are a major group (phylum) of invertebrate animals with a rich fossil record stretching back to the Cambrian period, approximately 518 million years ago. While all modern species are characterized by pentaradial (i.e., fivefold) symmetry, Cambrian echinoderms also include taxa with different types of symmetry (e.g., bilateral symmetry). These distinct forms were present from very early in the phylum's history, demonstrating that the initial diversification of echinoderm body plans was extremely rapid. The phylogenetic relationships of Cambrian echinoderms have long been debated, hindering efforts to reconstruct the evolution of the phylum, but recent analyses have consistently recovered bilaterally symmetrical forms as the earliest-diverging echinoderms. This reveals the sequence of character acquisition in echinoderm evolution, indicating that radial symmetry is a derived character of the group, which evolved after the acquisition of a mineralized skeleton. Cambrian echinoderms were adapted to diverse modes of life, with ecology an important factor shaping their early evolution. However, the reasons why echinoderms evolved their unique pentaradial body plan remain unclear.

- The Cambrian fossil record provides valuable insights into the origin and early evolution of echinoderms over half a billion years ago.
- Cambrian echinoderms were morphologically diverse, with several extinct groups exhibiting character combinations that distinguish them from living species.

- Phylogenetic analyses of bilateral, asymmetrical, triradial, and pentaradial fossils have allowed us to decipher the assembly of the modern echinoderm body plan.
- Echinoderms became ecologically diverse early in their history, with varied modes of feeding, locomotion, and attachment.

1. INTRODUCTION

Echinoderms are a taxonomically, morphologically, and ecologically diverse phylum of invertebrates with a very distinctive body plan that differentiates them from other animals (Peterson et al. 2000, Mooi & David 2008, Smith 2008) (**Figure 1**). They are almost exclusively marine and can be found in all Earth's oceans in habitats ranging from intertidal to deep sea. Modern forms are characterized by pentaradial (i.e., fivefold) symmetry as adults (**Figure 1*b***), which differs markedly from the bilateral symmetry exhibited by their closest living relatives, the hemichordates. They also possess a high-magnesium calcite endoskeleton, typically with a mesh-like microstructure termed stereom (**Figure 1*d***), a feature that can be recognized in some of the oldest echinoderms from the Cambrian period (e.g., Donovan & Paul 1982, Berg-Madsen 1986, Clausen & Smith 2005, Kouchinsky et al. 2015) (**Figure 1*g***). The presence of a mineralized skeleton from early in the phylum's history means that echinoderms have a rich fossil record, making them an ideal group with which to examine macroevolutionary patterns and processes, ranging from the emergence of morphological diversity (e.g., Foote 1992, Deline et al. 2020) to evolutionary change in response to ecological and environmental pressures (e.g., Gorzelak et al. 2012, Hopkins & Smith 2015, Wright 2017). Owing to their experimental accessibility, echinoderms are also a focus of investigation in developmental biology, with certain species model organisms for studying the cellular, molecular, and genetic mechanisms of embryogenesis (McClay 2011, Ettensohn 2017) and regeneration (Candia Carnevali 2006, García-Arrarás & Dolmatov 2010). Furthermore, genomic and transcriptomic data are becoming increasingly available (e.g., Janies et al. 2016, Arshinoff et al. 2021), facilitating comparisons with other animal phyla. Together, this makes echinoderms an excellent system for exploring body plan evolution.

The fossil record of echinoderms consists of more than 15,000 named species (Mooi 2016). It includes abundant isolated plates, as well as articulated and partially articulated specimens that are rich in morphological characters (Foote 1992, Deline et al. 2020). Although rarely preserved in fossils, soft tissues can sometimes be inferred from skeletal morphologies; elements of the water vascular system such as tube feet and radial canals may be reconstructed based on holes, depressions, and grooves in ambulacral plates (e.g., Nichols 1972, Paul & Smith 1984, Dean 1999) (**Figure 1*e***), while stereom microstructure (**Figure 1*d*,*g***) can inform on the nature of the soft parts originally in contact with the skeleton (e.g., Roux 1975, Smith 1980, Clausen & Smith 2005, Gorzelak & Zamora 2013, Gorzelak 2021). Fossil echinoderms are thus a valuable source of anatomical information that can directly inform on evolutionary change in deep time.

In this review, we outline how the study of fossil echinoderms can help uncover the origin and early evolution of the phylum. We begin by summarizing the phylogenetic context and key characteristics of echinoderms as a guide for interpreting their fossil record. We then discuss the earliest fossil evidence for echinoderms, synthesizing current knowledge and recent discoveries related to the origin, diversity, phylogeny, and ecology of the group. This provides a more complete picture of echinoderm evolutionary history stretching back over half a billion years ago and allows us to identify several outstanding questions that would benefit from further research.

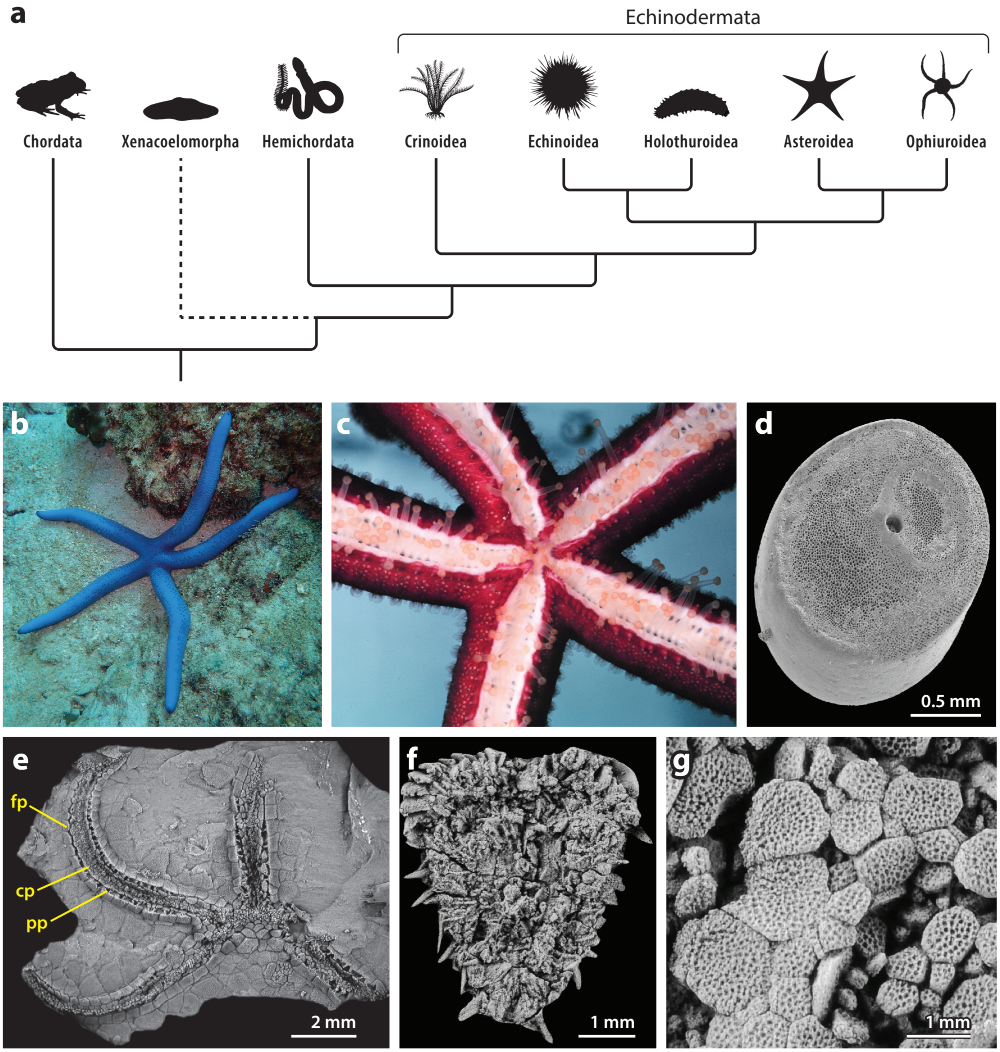

Figure 1

Phylogenetic context and key characteristics of echinoderms. (*a*) Deuterostome phylogeny. The dashed line signifies that the phylogenetic position of Xenacoelomorpha is uncertain. Silhouettes from PhyloPic (public domain). (*b*) The modern asteroid *Linckia laevigata* showing pentaradial symmetry. Photograph of original specimen provided by Hugh Carter. (*c*) A modern asteroid showing tube feet. Photograph of original specimen by James McVey, NOAA Sea Grant Program (public domain). (*d*) An isolated plate of a modern echinoderm showing stereom microstructure. Scanning electron microscope image of original specimen provided by Przemysław Gorzelak. (*e*) The Cambrian echinoderm *Kailidiscus chinensis* showing pentaradial symmetry and ambulacral plating (in a 2-1-2 pattern). Photograph of latex cast whitened with NH_4Cl sublimate provided by Colin Sumrall. (*f*) A Cambrian echinoderm showing bilateral symmetry. Photograph of latex cast whitened with NH_4Cl sublimate. (*g*) Plates of a Cambrian echinoderm showing stereom microstructure. Photograph of latex cast whitened with NH_4Cl sublimate. Abbreviations: cp, cover plate; fp, flooring plate; pp, podial pore.

2. PHYLOGENETIC CONTEXT AND KEY CHARACTERISTICS

Modern molecular (e.g., Bourlat et al. 2006; Dunn et al. 2008; Philippe et al. 2011, 2019; Simakov et al. 2015; Cannon et al. 2016) and morphological (e.g., Peterson & Eernisse 2001, Cameron 2005) phylogenies consistently recover echinoderms as the sister group to hemichordates (**Figure 1*a***). This clade, termed Ambulacraria, is characterized by the presence of a body arranged into three sets of coelomic compartments (axocoel/protocoel, hydrocoel/mesocoel, and somatocoel/metacoel) (Peterson & Eernisse 2001, 2016; Cameron 2005). Ambulacraria is sometimes allied with *Xenoturbella* and acoelomorphs (Xenacoelomorpha) in the group Xenambulacraria (Bourlat et al. 2006; Philippe et al. 2011, 2019). An alternative hypothesis places Xenacoelomorpha as sister to Nephrozoa, a major clade of bilaterians that includes protostomes (e.g., annelids, arthropods, and mollusks) and deuterostomes (e.g., chordates, echinoderms, and hemichordates) (Cannon et al. 2016, Rouse et al. 2016). Ambulacraria (or Xenambulacraria) is generally regarded as the sister group to chordates within Deuterostomia (e.g., Peterson & Eernisse 2001, Cameron 2005, Bourlat et al. 2006, Dunn et al. 2008, Simakov et al. 2015, Cannon et al. 2016, Rouse et al. 2016), although some recent analyses have challenged the monophyly of this superphylum (e.g., Philippe et al. 2019, Kapli et al. 2021). This may reflect the fact that there are very few characters shared by all deuterostomes, with developmental features that were previously used to define the group, such as deuterostomy and radial cleavage, found in several nondeuterostome bilaterians (e.g., Martín-Durán et al. 2012, 2017). Pharyngeal openings (ciliated perforations of the pharyngeal wall that occur as either simple pores or dorsoventrally elongated slits) are the only widely accepted morphological synapomorphy (i.e., shared derived character) of the group (Cameron et al. 2000, Cameron 2005, Ruppert 2005, Gillis et al. 2012, Lowe et al. 2015; although see Kapli et al. 2021). They are present in chordates and hemichordates and are thought to have been secondarily lost in echinoderms (Smith 2005, 2008; Swalla & Smith 2008; Peterson & Eernisse 2016). Putative pharyngeal gill slits have been described in certain nonradial fossil echinoderms (e.g., Jefferies 1986, Dominguez et al. 2002, Smith 2005, Álvarez-Armada et al. 2022), but this is disputed by some (e.g., Lefebvre & Vizcaino 1999, Lefebvre 2003).

There are five extant classes of echinoderms: asteroids, crinoids, echinoids, holothuroids, and ophiuroids. Asteroids, echinoids, holothuroids, and ophiuroids together form the subphylum Eleutherozoa, with crinoids the sister group to this clade (Smith et al. 2004) (**Figure 1*a***). Within Eleutherozoa, the current consensus based on molecular data is that asteroids plus ophiuroids (Asterozoa) are sister to echinoids plus holothuroids (Echinozoa) (e.g., Cannon et al. 2014, Telford et al. 2014, Reich et al. 2015, Simakov et al. 2015). Extant echinoderms differ from other deuterostomes in having a pentaradial adult body plan (**Figure 1*b***), which develops from an initially bilaterally symmetrical larva (Smith 2008). They are also characterized by a water vascular system, comprising a network of fluid-filled canals and tubular outgrowths (i.e., tube feet) (**Figure 1*c***) derived from the left hydrocoel (the second coelomic compartment in echinoderms) (Peterson et al. 2000; Cameron 2005; Smith 2005, 2008). However, one or both of these traits are apparently absent or highly modified in some fossil groups (Sumrall & Wray 2007, Zamora & Rahman 2014) (**Figure 1*f***). Mutable collagenous tissue, connective tissue that can very rapidly alter its mechanical properties under nervous control, is another feature of living echinoderms believed to be unique to the phylum (Wilkie et al. 2021), but there is no direct evidence of this in extinct forms. The sole derived character unambiguously shared by all known extinct and extant echinoderms is the stereom endoskeleton. Stereom microstructure (**Figure 1*d***) is recognized in all major living groups and can be preserved in fossil material (**Figure 1*g***), including isolated plates and articulated specimens from the Cambrian (e.g., Donovan & Paul 1982, Berg-Madsen 1986, Clausen & Smith 2005, Gorzelak & Zamora 2013, Kouchinsky et al. 2015, Zamora et al. 2020). Moreover, the development of the skeleton in extant echinoderms is governed by a unique combination of genes and proteins (Bottjer et al. 2006, Gao et al. 2015, Dylus et al. 2018) that are hypothesized to have been present in the earliest fossil taxa (Bottjer et al. 2006). Modern enteropneust hemichordates (i.e., acorn worms) can also possess biomineralized ossicles composed of different polymorphs of calcium carbonate (Cameron & Bishop 2012, Larouche-Bilodeau & Cameron 2022), but these do not exhibit stereom microstructure. Thus, stereom is almost certainly a derived trait of echinoderms that evolved after their divergence from hemichordates.

3. ORIGIN

Recognizing the oldest evidence for echinoderms in the fossil record is key for deciphering the phylum's origin. Most recent molecular clock analyses suggest that echinoderms originated ~590–560 Ma, during the late Ediacaran (Erwin et al. 2011, Simakov et al. 2015, Dohrmann & Wörheide 2017), with the living classes diverging slightly later, in the Cambrian or Ordovician (Erwin et al. 2011, Pisani et al. 2012, Simakov et al. 2015). The Ediacaran–Cambrian fossil record could therefore provide a window into the earliest evolution of echinoderms. However, defining a search image for early echinoderms is difficult because, as highlighted in the previous section, some or all of the diagnostic characteristics of extant forms might be absent.

The oldest putative fossil echinoderms come from the late Ediacaran (~558–550 Ma) White Sea assemblage. These are two taxa characterized by radial symmetry, *Tribrachidium heraldicum* and *Arkarua adami*. *Tribrachidium* has a hemispherical body with three curved ridges that meet at the apex and spiral toward the margin (**Figure 2*a***). The body and main ridges are sometimes covered

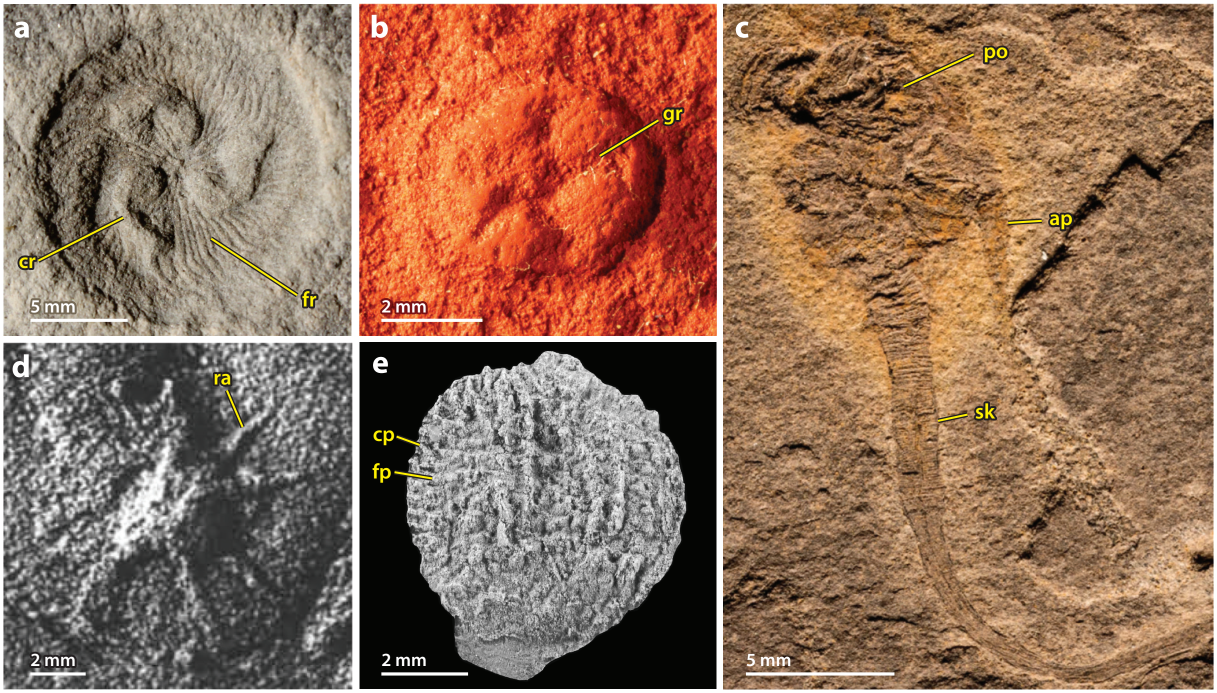

Figure 2

Oldest putative fossil evidence for echinoderms. (*a*) *Tribrachidium heraldicum* from the Ediacaran of Russia. Photograph of original specimen adapted from Rahman et al. (2015a) (CC BY-NC 4.0). (*b*) *Arkarua adami* from the Ediacaran of Australia. Photograph of cast adapted from Cracknell et al. (2021) (CC BY 4.0). (*c*) *Yanjiahella biscarpa* from the Fortunian of China. Photograph of original specimen adapted from Topper et al. (2019) (CC BY 4.0). (*d*) *Asteriacites* from the Fortunian of China. Photograph of original specimen adapted from Crimes & Jiang (1986). (*e*) *Sprinkleoglobus extenuatus* from the Cambrian Stage 3 of China. Photograph of latex cast whitened with NH_4Cl sublimate adapted from Zhao et al. (2022) (CC BY 4.0). Abbreviations: ap, appendage; cp, cover plate; cr, curved ridge; fp, flooring plate; fr, fine ridge; gr, groove; po, plate-like ossicle, ra, ray; sk, stalk.

in numerous finer ridges. *Tribrachidium* was tentatively suggested to be an echinoderm based on the presence of triradial symmetry and interpretation of the finer ridges as tube feet (Glaessner & Wade 1966), but this has not been followed by most subsequent workers (e.g., Fedonkin 1985, Seilacher 1999, Dzik 2003). There is no evidence of a plated skeleton, and the supposed tube feet instead correspond to surface branching structures (Ivantsov & Zakrevskaya 2021). Helicoplacoids (a group of Cambrian echinoderms with spiral plating) are thought to exhibit triradial symmetry (Paul & Smith 1984, Sprinkle & Wilbur 2005) but are otherwise very different in morphology to *Tribrachidium*; closer similarities can be drawn to other triradial disc-shaped Ediacaran taxa (Fedonkin 1985, Erwin et al. 2011, Hall et al. 2020, Ivantsov & Zakrevskaya 2021). An echinoderm affinity can therefore be rejected for *Tribrachidium*.

Arkarua is discoidal to hemispherical with five straight grooves radiating from a central depression (**Figure 2*b***). Owing to the presence of pentaradial symmetry and general morphological similarities to some Cambrian echinoderms (e.g., *Cambraster*), it has been interpreted as an echinoderm, with the five grooves taken as homologous to ambulacra (Gehling 1987, Mooi & David 1998). Moreover, it was suggested that faint transverse divisions of the grooves could correspond to ambulacral pores (Gehling 1987). Like *Tribrachidium*, there is no evidence of a plated skeleton in *Arkarua*. The grooves show no close similarities to the ambulacra of Cambrian pentaradial echinoderms, which are composed of cover and flooring plates with podial pores (Zamora & Rahman 2014) (**Figure 1*e***), and the supposed transverse divisions noted by Gehling (1987) are not clear in any of the figured specimens. There is also no evidence of other typical echinoderm characteristics, such as a periproct (plated structure surrounding the anus). Lastly, the true fivefold symmetry exhibited by *Arkarua*, in which five grooves radiate from the central depression, is unlike the pseudo fivefold symmetry seen in the earliest pentaradial echinoderms from the Cambrian, where ambulacra are arranged around the mouth in a 2-1-2 pattern (Sprinkle 1973, Sumrall & Wray 2007, Zamora & Rahman 2014) (**Figure 1*e***). Together, this argues against the interpretation of *Arkarua* as an echinoderm. While echinoderms are unique among bilaterians in possessing a pentaradial body plan, some fossil cnidarians also exhibit this type of symmetry (Dzik et al. 2017, Xian et al. 2019), and thus it is not phylogenetically informative in the absence of any other diagnostic traits. The similar body plans of *Arkarua* and some early echinoderms most likely represent convergent adaptations for a common mode of life (i.e., suspension-feeding sediment attachers), rather than being indicative of a close relationship.

The bilaterally symmetrical fossil *Yanjiahella biscarpa* from the lowermost Cambrian (Fortunian, ∼539–535 Ma) of Hubei Province, China, is another candidate for the oldest known echinoderm. It has a globular body, a stalk divided into proximal and distal regions, and a pair of slender appendages (**Figure 2*c***). Originally described as a possible echinoderm (Guo et al. 2012), *Yanjiahella* was later interpreted as the earliest diverging stem-group echinoderm (Topper et al. 2019). Potential similarities to enteropneust hemichordates, such as bilateral symmetry and a muscular stalk with a postanal anchoring structure, were viewed as ambulacrarian symplesiomorphies. The body of *Yanjiahella* is made up of embedded plate-like ossicles, but there is no trace of stereom microstructure (cf. **Figure 1*d*,*g***) or any plate morphologies that are characteristic of an echinoderm-type endoskeleton (e.g., a periproct). Moreover, the paired appendages show no evidence of plating (i.e., cover and flooring plates), as has been described in all early echinoderms with erect feeding appendages (Zamora & Rahman 2014), and the construction of the stalk differs from anything previously reported in the phylum. Phylogenetic analyses provide very weak support for the placement of *Yanjiahella* as a stem echinoderm, with alternative positions as a stem hemichordate or stem ambulacrarian also possible (Topper et al. 2019, 2020; Zamora et al. 2020). We therefore consider there to be insufficient evidence to determine the phylogenetic position of *Yanjiahella* at this time.

The lowermost Cambrian trace fossil record also provides possible evidence for the existence of early echinoderms. Star-like traces, consisting of about 10 thin rays emerging from a central area (**Figure 2*d***), have been reported from the Fortunian of Yunnan Province, China (Crimes & Jiang 1986, Zhu 1997). These trace fossils were assigned to the ichnogenus *Asteriacites*, which is interpreted as an asterozoan resting trace when described from younger rocks (Knaust & Neumann 2016). The occurrence of *Asteriacites* in lowermost Cambrian rocks could therefore indicate the existence of an asterozoan-like echinoderm from this time interval (Crimes & Jiang 1986). However, the presence of 10 thin rays in these traces differentiates them from all other *Asteriacites*, which are characterized by five arms. Additionally, the general morphology does not closely resemble any known *Asteriacites* ichnospecies, in which the arms are either slender and distinctly set off from a central disc or grade from a central area and continuously taper distally (Knaust & Neumann 2016). These differences from younger *Asteriacites*, coupled with the absence of any asterozoan-like body fossils until the Lower Ordovician (Jell 2014, Blake & Guensburg 2015, Hunter & Ortega-Hernández 2021), raise substantial doubts over their interpretation as early echinoderm trace fossils.

Perhaps the earliest definitive echinoderm comes from the Chengjiang biota (Cambrian Series 2, Stage 3) of Yunnan Province, China. The Chengjiang Lagerstätte preserves some of the oldest evidence for diverse animal phyla, including annelids, chaetognaths, and chordates (Hou et al. 2017). Several fossils from this deposit have previously been interpreted as echinoderms, including *Cambrofengia yunnanensis* (Hou et al. 1999), *Cotyledion tylodes* (Chen et al. 1996), the eldonioids *Eldonia eumorpha* and *Rotadiscus grandis* (Friend 1995), and the vetulocystids *Vetulocystis catenata* and *Dianchicystis jianshanensis* (Shu et al. 2004), but these species lack any convincing echinoderm apomorphies (Paul & Smith 1984, Swalla & Smith 2008, Clausen et al. 2010) and are thus better placed in alternative positions in animal phylogeny: *Cambrofengia* as an arthropod (Hou et al. 2017), *Cotyledion* as a stem entoproct (Zhang et al. 2013), and eldonioids as stem ambulacrarians (Caron et al. 2010, Li et al. 2023) (the affinities of vetulocystids remain uncertain). However, the recently described taxon *Sprinkleoglobus extenuatus* has a plated skeleton comprising a globular theca with five recumbent ambulacra composed of cover and flooring plates with podial pores (**Figure 2*e***), characters that allow it to be unambiguously interpreted as an edrioasteroid echinoderm (Zhao et al. 2022). This provides a minimum age constraint for the phylum Echinodermata of ~518 Ma, corresponding to the most recent estimate for the depositional age of the Chengjiang biota (Yang et al. 2018).

Other articulated specimens from the Cambrian Stage 3 that can be recognized as echinoderms owing to the presence of stereom microstructure and/or echinoderm-type plate morphologies are the helicoplacoids *Helicoplacus* (**Figure 3*e***), *Polyplacus*, and *Waucobella* from the Poleta Formation of the western United States (Durham 1967) and the eocrinoids *Alanisicystis andalusiae* from the Alanís beds in Spain (Ubaghs & Vizcaïno 1990) and *Alanisicystis* sp. and an indeterminate eocrinoid from the Issafen Formation of Morocco (Smith et al. 2013). Durham (1967) mentioned the existence of a single poorly preserved specimen of an indeterminate edrioasteroid from rocks correlated with the Poleta Formation, but to the best of our knowledge this specimen has never been figured. Isolated edrioasteroid and possible eocrinoid plates are also known from the Poleta Formation (Durham 1967, Sprinkle & Wilbur 2005), with eocrinoid ossicles reported from the Atdabanian of Germany (Elicki & Schneider 1992), Siberia (Kouchinsky et al. 2015), and the United Kingdom (McKie & Donovan 1992). Although international correlation can be difficult for the Cambrian, all this material is thought to be similar in age or slightly younger than *S. extenuatus* (Zhao et al. 2022), making it among the oldest evidence for echinoderms.

Together this points to the existence of diverse, widely distributed echinoderms from their initial appearance in the fossil record from the Cambrian Stage 3, suggesting a more ancient origin

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Figure 3 (*Figure appears on preceding page*)

Cambrian nonradial and radial echinoderms. (*a*) The solute *Coleicarpus sprinklei* from the Miaolingian of North America. (*b*) The cinctan *Gyrocystis testudiformis* from the Miaolingian of Spain. (*c*) The cinctan *Lignanicystis barriosensis* from the Miaolingian of Spain. (*d*) The stylophoran *Ceratocystis perneri* from the Miaolingian of Bohemia. (*e*) The helicoplacoid *Helicoplacus gilberti* from the Cambrian Series 2 of North America. (*f*) *Helicocystis moroccoensis* from the Cambrian Series 2 of Morocco. (*g*) The ctenocystoid *Courtessolea moncereti* from the Miaolingian of France. (*h*) The ctenocystoid *Ctenocystis utahensis* from the Miaolingian of North America. Panels *a–h* show photographs of latex casts whitened with NH_4Cl sublimate. (*i*) *Ctenoimbricata spinosa* from the Miaolingian of Spain. Virtual reconstruction. Abbreviations: am, ambulacra; an, anus; ct, ctenoid plate; cu, cup; dr, dorsal roof; mf, marginal frame; pa, posterior appendage; pm, plated membrane; sp, suroral plate; st, stem; th, theca.

for the group and implying that the earliest fossil record of echinoderms is incomplete (Smith et al. 2013, Zamora & Rahman 2014, Nanglu et al. 2023). This may be because a stereom endoskeleton did not evolve in echinoderms until the upper part of the Cambrian Stage 2, coincident with the origination of a high-magnesium calcite skeleton in several other clades (Kouchinsky et al. 2012, Wood & Zhuravlev 2012, Murdock 2020). Earlier echinoderms would presumably have been soft-bodied, with much lower preservation potential and few (if any) characters that would allow us to recognize them as belonging to the group. The mismatch between the oldest unambiguous fossil evidence for echinoderms (~518 Ma) and molecular clock estimates for their origin (~590–560 Ma) might therefore be explained as an artifact of the fossil record and the difficulty identifying the earliest stem representatives of the phylum, as inferred for animals more broadly (Cunningham et al. 2017).

4. CAMBRIAN DIVERSITY AND DISPARITY

In addition to preserving the oldest evidence for echinoderms in the fossil record, the Cambrian is important as it documents the phylum's initial taxonomic and morphological diversification (Foote 1992, Deline et al. 2020, Novack-Gottshall et al. 2022). More than 200 distinct forms have been reported from this period, including 132 named species, 95 named genera, and numerous unnamed or unidentified taxa (**Supplemental Table**). Eight formally recognized classes are known from the Cambrian, although some may be paraphyletic or polyphyletic (Paul & Smith 1984, Zamora & Rahman 2014). These include cinctans, ctenocystoids, edrioasteroids, eocrinoids, helicoplacoids, rhombiferans, solutes, and stylophorans, as well as two genera (*Ctenoimbricata* and *Helicocystis*) that have yet to be formally assigned to a new or existing class (**Figures 3** and **4**). Several of these groups extend into the Ordovician and beyond, but below we focus on their Cambrian occurrences, which inform on the earliest steps in their evolution.

Supplemental Material >

Cinctans were restricted to the middle Cambrian (Wuliuan and Drumian) of West Gondwana and Siberia, with a total of 17 genera and 26 species formally described (**Supplemental Table**). They have a flattened, weakly to strongly asymmetrical theca and a short posterior appendage (**Figure 3*b*,*c***). The theca consists of a uniserial ring of large marginal plates that surround dorsal and ventral membranes of small, thin plates. One or an asymmetrical pair of grooves run along the anterior margin of the theca, leading to the mouth in the anterior right of the marginal frame. These grooves are covered by multiple sets of small plates and are interpreted as food grooves housing a pterobranch-style tentacular system constructed from both the left and right hydrocoels (e.g., Smith 2005) or recumbent brachioles (e.g., David et al. 2000). Cinctans were short-lived compared to other groups of Cambrian echinoderms, exhibiting relatively low levels of diversity in the Wuliuan and reaching peak diversity in the Drumian (**Figure 5**), before going extinct close to the Drumian–Guzhangian boundary.

Ctenocystoids are known from the middle Cambrian (Cambrian Stage 4–Wuliuan boundary interval to Drumian) and Late Ordovician of Baltica, Gondwana, and Laurentia. Five genera and eight species have been named from the Cambrian (**Supplemental Table**). They have a

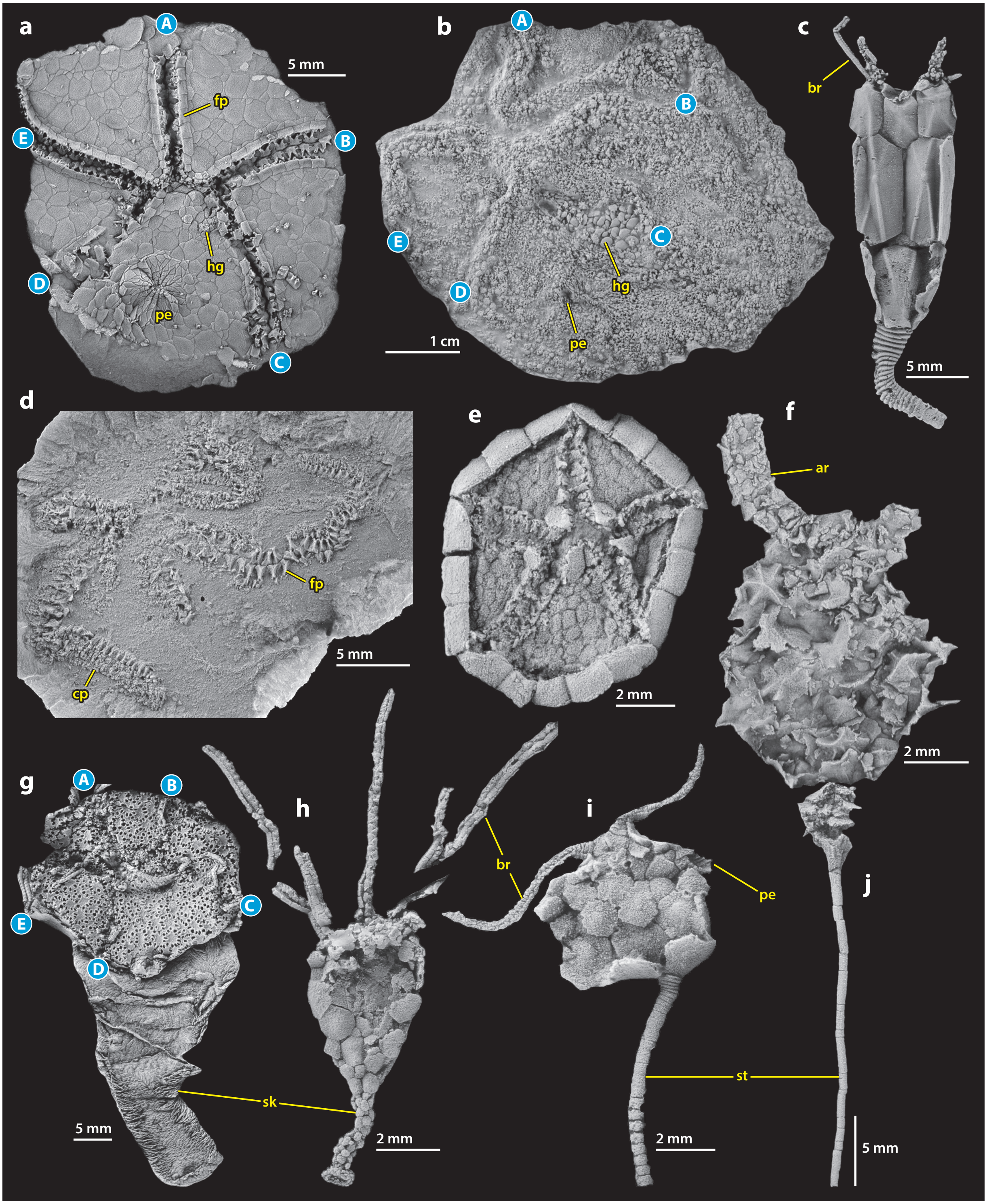

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Figure 4 (*Figure appears on preceding page*)

Cambrian pentaradial echinoderms. (*a*) The edrioasteroid *Kailidiscus chinensis* from the Miaolingian of China. (*b*) The edrioasteroid *Camptostroma roddyi* from the Cambrian Series 2 of North America. (*c*) The rhombiferan *Sanducystis sinensis* from the Furongian of China. (*d*) The edrioasteroid *Yorkicystis haefneri* from the Cambrian Series 2 of North America. (*e*) The edrioasteroid *Cambraster cannati* from the Miaolingian of Spain. (*f* and *j*) The rhombiferan *Dibrachicystis purujoensis* from the Miaolingian of Spain. (*g*) The eocrinoid *Kinzercystis durhami* from the Cambrian Series 2 of North America. (*h*) The eocrinoid *Gogia* sp. from the Miaolingian of North America. (*i*) The eocrinoid *Ubaghsicystis segurae* from the Miaolingian of Spain. Labels A–E indicate ambulacra. Abbreviations: ar, arm; br, brachiole; cp, cover plate; fp, flooring plate; hg, hydropore/gonopore; pe, periproct; sk, stalk; st, stem. Photographs of latex casts whitened with NH_4Cl sublimate.

weakly asymmetrical to bilaterally symmetrical theca, which is framed by a ring of marginal plates enclosing dorsal and ventral plated membranes (**Figure 3*g*,*h***). At the anterior of the theca, there is a specialized bilaterally symmetrical structure called the ctenidium, which is composed of a ring of small, blade-like ctenoid plates and a large central suroral plate. The ctenidium is thought to cover the mouth, and it is interpreted as a pair of recumbent brachioles (e.g., David et al. 2000) or a tentacular feeding apparatus (Rahman & Clausen 2009). An anus, comprising a pyramid of small plates, is located toward the posterior of the theca. Similar to cinctans, ctenocystoids were low in diversity in the Wuliuan and achieved their highest diversity in the Drumian (**Figure 5**).

Ctenoimbricata is represented by a single species (*Ctenoimbricata spinosa*) known only from the Murero Formation (Drumian) of North Spain (West Gondwana) (**Supplemental Table**). It has a flattened, bilaterally symmetrical theca composed of an anterior ctenidium, a uniserial ring of marginal plates, a dorsal partially calcified surface, and a ventral membrane of polygonal plates (**Figure 3*i***). The anterior ctenidium consists of a suroral plate and a ventral row of spine-like elements, which are covered by a dorsal roof of thin imbricate plates. *Ctenoimbricata*

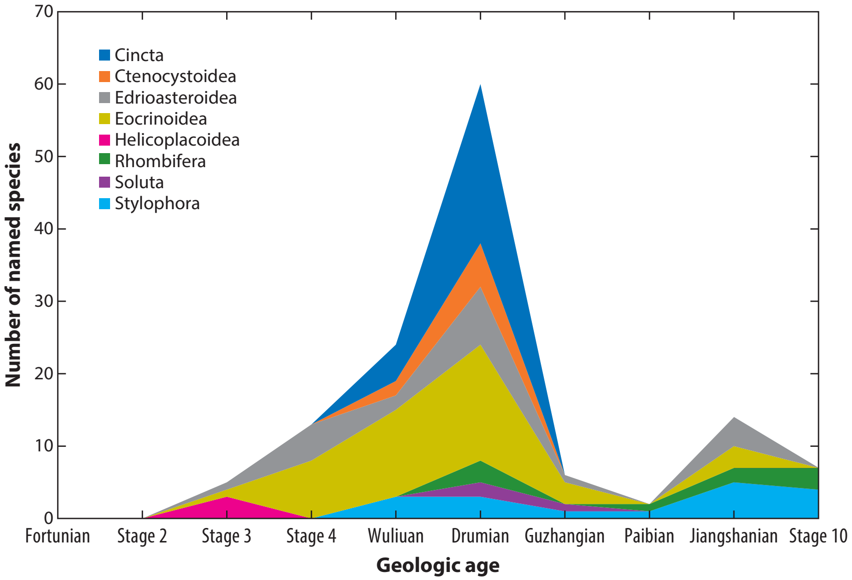

Figure 5

Diversity of named Cambrian echinoderm species grouped into eight formally recognized extinct classes (Cincta, Ctenocystoidea, Edrioasteroidea, Eocrinoidea, Helicoplacoidea, Rhombifera, Soluta, and Stylophora). Data from **Supplemental Table**.

Supplemental Material >

shares characters with cinctans (e.g., uniserial marginal ring) and ctenocystoids (e.g., ctenidium) (Zamora et al. 2012), but it has not been formally assigned to either class.

Supplemental Material >

Edrioasteroids ranged from the Cambrian to the Permian. Within the Cambrian, they have been reported from the Stage 3 to the Jiangshanian of Baltica, Gondwana, and Laurentia, with 15 named genera and 21 named species (**Supplemental Table**). They have a discoidal to globular theca with five recumbent ambulacra composed of cover plates and flooring plates (**Figure 4*a*,*b*,*d*,*e***). Ambulacra are arranged in a 2-1-2 pattern [A, shared BC, and shared DE, with ambulacra identified according to the Carpenter system (Carpenter 1884)] around the central mouth. Where it is known, the periproct is always situated on the oral surface between the C and D ambulacra, together with the hydropore and gonopore (Kammer et al. 2013). The aboral surface may be unplated or plated, sometimes with an attachment disk/structure or a polyplated stem terminating in a distal holdfast. Following their appearance in the Cambrian Stage 3, edrioasteroids fluctuated in diversity through the rest of the Cambrian, reaching their highest diversity in the Drumian (**Figure 5**).

Eocrinoids lived from the Cambrian to the Silurian; 27 genera and 43 species have been formally described from the Cambrian (Stage 3 to Stage 10) of Baltica, Gondwana, Laurentia, and Siberia (**Supplemental Table**). They have a globular to conical theca, multiple erect feeding appendages (brachioles), and typically an aboral stalk or stem (**Figure 4*g–i***). Small openings called epispires often occur at the sutures between adjacent thecal plates, and these are regarded as simple respiratory structures (Sprinkle 1973, Sheffield et al. 2022). The brachioles, consisting of brachiolar flooring plates and cover plates, arise from the oral surface of the theca and are usually associated with five ambulacra arranged in a 2-1-2 pattern. The periproct, hydropore, and gonopore are located in the CD interambulacral area (Sprinkle 1973, Kammer et al. 2013). The aboral appendage can be absent or greatly reduced, a stalk with irregularly arranged plates, or a stem with cylindrical columnals. A distal attachment structure is sometimes present. Eocrinoids steadily increased in diversity from the Cambrian Stage 3 to the Drumian, before undergoing a major reduction in diversity in the Guzhangian (**Figure 5**).

Helicoplacoids are known solely from the Cambrian Stage 3 of Laurentia, with only three monospecific genera formally recognized (**Supplemental Table**). They have a fusiform to pyriform theca with spiral plating (**Figure 3*e***). They are generally interpreted as possessing three recumbent ambulacra (e.g., Paul & Smith 1984, Sprinkle & Wilbur 2005, Smith & Zamora 2013), although Durham (1967, 1993) suggested that only a single branching ambulacrum was present. The ambulacra spiral around the theca in an anticlockwise direction. The mouth is thought to have been located on the side of the theca where the ambulacra converge (e.g., Sprinkle & Wilbur 2005) or at the upper pole (e.g., Durham 1993). At the lower pole, the theca is constructed of multiple small plates that form a holdfast-type structure (Zamora et al. 2017a).

Helicocystis moroccoensis was described from the Jbel Wawrmast Formation (Cambrian Stage 4–Wuliuan) of Morocco (West Gondwana) (**Supplemental Table**). It has a fusiform theca consisting of a spiral-plated part with five recumbent ambulacra, a basal cup, and a short polyplated stem (**Figure 3*f***). The ambulacra run spirally around the theca in a clockwise direction, converging toward the mouth at the upper pole. A conical periproct opens on the side of the spiral-plated part of the theca. *Helicocystis* shows similarities to both helicoplacoids (e.g., spiral plating) and early pentaradial echinoderms (e.g., ambulacra arranged around the mouth in a 2-1-2 pattern) (Smith & Zamora 2013), and hence probably represents a distinct class.

Rhombiferans existed from the Cambrian to the Devonian. In the Cambrian they have been recovered from the Drumian to the Stage 10 of Baltica, Gondwana, and Siberia, with eight genera and nine species named from this period (**Supplemental Table**). They have a globular to subcylindrical theca, erect feeding appendages, and a long, distally tapering stem (**Figure 4*c*,*f*,*j***).

There are typically five ambulacra in a 2-1-2 arrangement on the oral surface, associated with erect feeding appendages that take the form of brachioles without a direct connection to the theca or arms with a large lumen leading into the main body cavity. A periproct is located within the oral area in the CD interray or on the side of the theca. The stem is divided into a short proximal part constructed of cylindrical columnals or several rings of plates and a long distal part composed of narrow, elongate columnals. Rhombiferans appeared in the Drumian, later in the Cambrian than other echinoderm groups, with relatively steady diversity levels until the end of this period (**Figure 5**).

Solutes are known from the Cambrian to the Devonian. A total of four genera and three species are formally recognized from the Cambrian (Stage 4 to Stage 10) of East Gondwana and Laurentia (**Supplemental Table**). They have an ovoid to pyriform theca with a single anterior feeding appendage (ambulacrum) and a posterior stalk (**Figure 3*a***). The ambulacrum is short and consists of cover plates and flooring plates. It is interpreted as an arm housing coelomic extensions of the main body cavity (e.g., Smith 2005) or as a brachiole without a coelomic extension (e.g., David et al. 2000). The mouth is thought to have been located at the base of the ambulacrum (Smith 2005, Noailles et al. 2014). The anus, which is surrounded by a cone of plates, is situated at the opposing end of the theca. The stalk is long and either composed of irregular rings of small plates or divided into a cylindrical proximal region and a flattened distal part. Solutes were low in diversity throughout the Cambrian (**Figure 5**).

Supplemental Material >

Stylophorans ranged from the Cambrian to the Carboniferous. Cambrian forms include 14 named genera and 17 named species from the Stage 4 to the Stage 10 of Baltica, Gondwana, Laurentia, and Siberia (**Supplemental Table**). They have a flattened, weakly to strongly asymmetrical theca and a single tripartite appendage (**Figure 3*d***). The appendage is composed of a wide proximal part, a funnel-shaped median element, and a narrow distal part consisting of a single series of stout ossicles and two opposing sets of small cover plates. The discovery of an Ordovician stylophoran with soft tissues preserved in the appendage (Lefebvre et al. 2019) strongly suggests that this is an ambulacrum (marking this as the anterior of the animal), with the mouth situated toward the proximal end. At the posterior of the theca, there is an opening typically surrounded by multiple tooth-like plates, which is best interpreted as an anus (e.g., David et al. 2000). Although relatively low in diversity for much of the Cambrian, stylophorans were the most diverse group of echinoderms during the Furongian (**Figure 5**).

Following their first appearance in the fossil record in the Cambrian Stage 3 (represented by edrioasteroids, eocrinoids, and helicoplacoids), the overall diversity of Cambrian echinoderms increased until the Drumian, with cinctans and eocrinoids especially diverse during this period. Diversity levels then declined sharply in the Guzhangian, before recovering somewhat in the Jiangshanian and the Cambrian Stage 10, at which time rhombiferans and stylophorans were most diverse (**Figure 5**). This pattern differs somewhat from the global diversity of Cambrian marine animals, which peaked in the Cambrian Stage 3 (Na & Kiessling 2015). The extent to which Cambrian echinoderm diversity reflects a true biological signal as opposed to an artifact of preservation and sampling biases is unclear. Furongian paleoenvironments are thought to have been less conducive to the preservation of fossil echinoderms than other parts of the Cambrian, and so the apparent drop in diversity at the start of this series might partly reflect taphonomic bias (Smith 1988, Nardin & Lefebvre 2010, Zamora et al. 2013a). However, analysis of the mean number of species recorded per formation (i.e., alpha diversity) shows a similar trend to raw diversity (Zamora et al. 2013a), indicating that there was a genuine rise in echinoderm diversity through the Cambrian.

The disparity of Cambrian echinoderms is relatively high compared to their diversity (Foote 1992). Although the number of species described for the Ordovician (Lefebvre et al. 2013) is

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around ten times higher than for the Cambrian (**Supplemental Table**), the distinctiveness of echinoderm body plans is evident from their first appearance in the fossil record, with asymmetrical, bilateral, and radial forms all present by the end of the Cambrian Stage 4 (Smith et al. 2013). Echinoderm morphological diversity increased through the Cambrian, with variance peaking in the Furongian to Early Ordovician (Deline et al. 2020). This implies that echinoderms underwent an initial burst of morphological innovation during the Cambrian explosion that outpaced their taxonomic diversification, similar to other animal phyla (Jablonski 2017, Erwin 2021).

5. PHYLOGENY

Determining the phylogenetic relationships of Cambrian echinoderms is essential for understanding the early evolution of the phylum but has long proved controversial. This is largely because of the high disparity exhibited by the earliest fossil taxa (Foote 1992, Deline et al. 2020), which makes it very difficult to securely identify homologous characters across major groups (Zamora & Rahman 2014, Nanglu et al. 2023). Although a wide range of ideas have been proposed over the past century (e.g., Jaekel 1918, Bather 1930, Fell 1962, Ubaghs 1975, Haugh & Bell 1980, Paul & Smith 1984, Jefferies 1986, Sumrall 1997), there are currently two main competing hypotheses for early echinoderm phylogeny.

The first hypothesis (e.g., Mooi & David 1998, David & Mooi 1999, David et al. 2000) tentatively places the Ediacaran fossil *Arkarua* as the earliest stem echinoderm, followed by a polytomy of edrioasteroids, helicoplacoids, and a clade of all other echinoderms, which is in turn divided into blastozoans and crown-group echinoderms. Blastozoans comprise cinctans, ctenocystoids, eocrinoids, rhombiferans, and solutes, as well as several pentaradial groups that appeared after the Cambrian (e.g., blastoids). Crown-group echinoderms include the five extant classes plus stylophorans, which are placed as the sister group to crinoids. This model is informed by the extraxial-axial theory, a homology scheme that divides the echinoderm body into axial (i.e., parts of the skeleton associated with the water vascular system) and extraxial (i.e., the rest of the skeleton) regions differentiated by their mode of growth (e.g., Mooi et al. 1994, 2005; Mooi & David 2008). Distinct axial and extraxial regions are inferred to be present in all known echinoderms, including radial and nonradial fossils, with pentaradial symmetry taken as plesiomorphic (e.g., Mooi & David 1998, David & Mooi 1999, David et al. 2000).

The second hypothesis (e.g., Smith 2005, Zamora et al. 2012, Smith & Zamora 2013) has *Ctenoimbricata* and ctenocystoids at the base of the tree. The next branches are represented by cinctans, stylophorans, and solutes, followed by helicoplacoids and then *Helicocystis* as sister to all other echinoderms with pentaradial symmetry. The exact relationships between the main groups of extinct pentaradial echinoderms (e.g., edrioasteroids and eocrinoids) and the extant classes are ambiguous. This model relies on comparative analyses of the anatomy, development, and phylogeny of extant deuterostomes to establish character polarity in echinoderms, which suggests, for example, that bilateral symmetry and pharyngeal openings are plesiomorphic (e.g., Smith 2005, 2008; Swalla & Smith 2008).

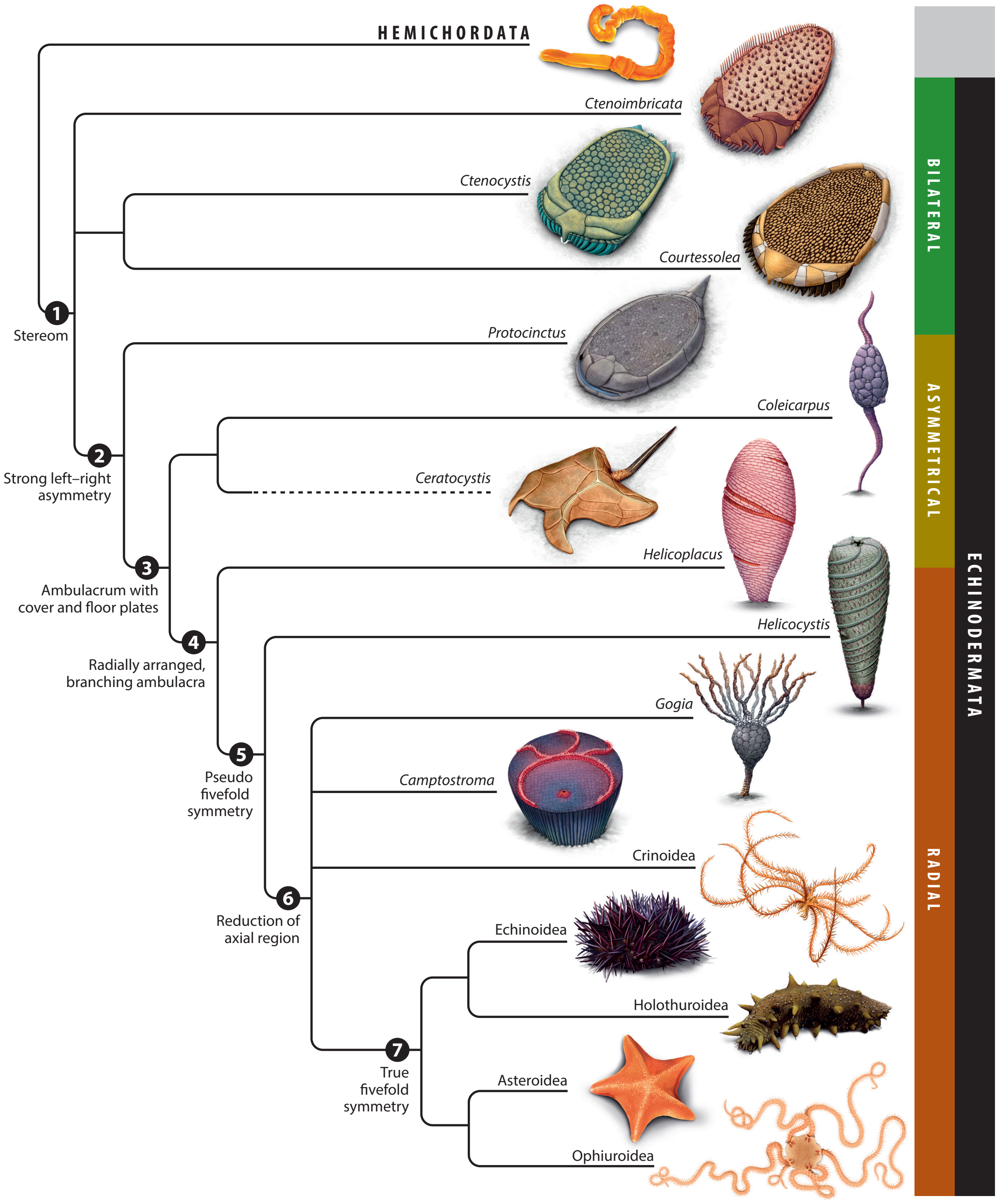
These two hypotheses differ most significantly in whether pentaradial symmetry is seen as plesiomorphic (e.g., Mooi & David 1998, David & Mooi 1999, David et al. 2000) or derived (e.g., Smith 2005, Zamora et al. 2012, Smith & Zamora 2013) for echinoderms. The stratigraphic ordering of fossils reveals that radial forms (i.e., edrioasteroids, eocrinoids, and helicoplacoids) were the first to appear (Durham 1967, Smith et al. 2013, Zhao et al. 2022) (**Figure 5** and **Supplemental Table**), and this has been taken as evidence supporting their placement as the earliest diverging echinoderms (David et al. 2000). However, stratigraphic congruence indices demonstrate that both phylogenetic hypotheses fit the known fossil record approximately equally well (Rahman et al. 2009). Moreover, as noted above, the Cambrian fossil record is likely incomplete and influenced by preservation and sampling biases (Smith et al. 2013, Zamora et al. 2013a, Zamora & Rahman 2014, Nanglu et al. 2023), strongly suggesting that the order of appearance of taxa in the fossil record should not be used to infer their position in phylogeny.

Quantitative phylogenetic analysis represents a more rigorous approach for resolving echinoderm phylogeny. Over the past decade, there have been multiple analyses focused on determining the relationships within clades of Cambrian echinoderms (e.g., Zamora et al. 2013b, 2023; Wright et al. 2021) or between early pentaradial forms (e.g., Zamora 2013; Nardin et al. 2017; Zamora et al. 2017b, 2022; Nohejlová et al. 2019; Hunter & Ortega-Hernández 2021) but comparatively few attempts to incorporate both radial and nonradial fossil taxa. However, several recent studies (i.e., Topper et al. 2019, Nanglu et al. 2020, Li et al. 2023), based on independently constructed matrices with large numbers of taxa and characters, obtained trees in which nonradial forms are early stem-group echinoderms. The alternative topology, with nonradial echinoderms derived, has not been recovered in recent quantitative analyses [although see Guensburg et al. (2023), who placed stylophorans as blastozoans but did not include any additional nonradial fossils]. This emerging consensus of early echinoderm phylogeny is presented in **Figure 6**.

This phylogenetic hypothesis allows us to propose a scenario for the stepwise evolution of the pentaradial echinoderm body plan from a bilaterally symmetrical ancestor (**Figure 6**). The stereom skeleton evolved in the stem lineage prior to the divergence of *Ctenoimbricata*, ctenocystoids, and all other echinoderms, with biomineralization likely involving a conserved toolkit of genes inherited from their most recent common ancestor (Thompson 2022, Nanglu et al. 2023). The bilateral symmetry of the ctenidium in *Ctenoimbricata* and ctenocystoids may indicate that it accommodated a tentacular feeding system constructed from both the left and right hydrocoels (Rahman & Clausen 2009), as seen in living pterobranchs and hypothesized for the ancestral ambulacrarian (Smith 2005). Next came the acquisition of strong left–right asymmetry, which is expressed in cinctans through the shape of the theca and the relative size of the left and right anterior food grooves. This was probably brought about by the onset of a markedly asymmetrical phase of development, which might have led to the suppression and/or complete loss of the right hydrocoel, giving rise to a tentacular feeding system constructed from the left hydrocoel only (as in extant echinoderms) (Smith 2005, Rahman & Zamora 2009). A single ambulacrum composed of cover and floor plates enclosing tube feet (presumably derived from just the left hydrocoel) evolved along the lineage leading to solutes, stylophorans, and all other echinoderms. This was followed by the acquisition of radially arranged, branching ambulacra along the lineage leading to helicoplacoids and all other echinoderms, taking the form of three ambulacra converging at a lateral mouth in helicoplacoids and five ambulacra arranged around an apical mouth in *Helicocystis* and all other echinoderms. The initiation of torsion (i.e., rotation of the internal organs) during development, perhaps associated with a shift from posterior facultative to anterior obligate larval attachment, may explain the emergence of a radial adult body plan (Smith 2008, Smith & Zamora 2013). Lastly, true fivefold symmetry, in which ambulacra are radially arranged around the mouth, evolved along the branch leading to eleutherozoans.

6. ECOLOGY

The Cambrian period was marked by major ecological innovation, including the diversification of biomineralized, burrowing, pelagic, and predatory animals (Marshall 2006, Erwin et al. 2011, Wood & Zhuravlev 2012, Budd & Jackson 2016). Similar to other phyla, early echinoderms were ecologically diverse, showing adaptations to a range of different lifestyles (Guensburg & Sprinkle 2000, Novack-Gottshall et al. 2022). Where several species co-occur, they are generally thought to



(*Caption appears on following page*)

Figure 6 (*Figure appears on preceding page*)

Echinoderm phylogeny including representatives of the major Cambrian groups (i.e., the ctenocystoids *Ctenocystis* and *Courtessolea*, the cinctan *Protocinctus*, the solute *Coleicarpus*, the stylophoran *Ceratocystis*, the helicoplacoid *Helicoplacus*, the eocrinoid *Gogia*, and the edrioasteroid *Camptostroma*) with key character changes marked. The dashed line signifies that the phylogenetic position of stylophorans is uncertain. Illustration created by Hugo Salais; modeled after phylogenies in Smith (2005), Zamora et al. (2012), and Smith & Zamora (2013).

have had different ecologies, indicating low levels of competition. Many Cambrian echinoderms are thought to have been sessile, living permanently attached to the substrate, as evidenced by the existence of fossil specimens preserved in direct association with skeletal fragments and/or the presence of specialized attachment structures (e.g., Sprinkle 1973, Daley 1996, Sprinkle & Wilbur 2005, Zamora & Smith 2010, Zamora et al. 2017a). These include eocrinoids, helicoplacoids, and *Helicocystis*, as well as some edrioasteroids, the solute *Coleicarpus*, and juveniles of the solute *Castericystis*. Most of these taxa are interpreted as hard substrate attachers, although edrioasteroids also include genera that attached directly to firm substrates stabilized by microbially induced sedimentary structures (**Figure 7*a***) or inserted the aboral part of the theca into the sediment (Dornbos 2006, Zamora et al. 2017a). All these forms are interpreted as passive suspension feeders, with particles captured using tube feet housed in recumbent ambulacra (edrioasteroids, helicoplacoids, and *Helicocystis*) or erect feeding appendages (eocrinoids, *Coleicarpus*, and juveniles of *Castericystis*) (Daley 1996, David et al. 2000, Smith & Zamora 2013, Zamora et al. 2017a). They were largely restricted to low tiering levels (i.e., less than 5 cm above the sediment–water interface), but the

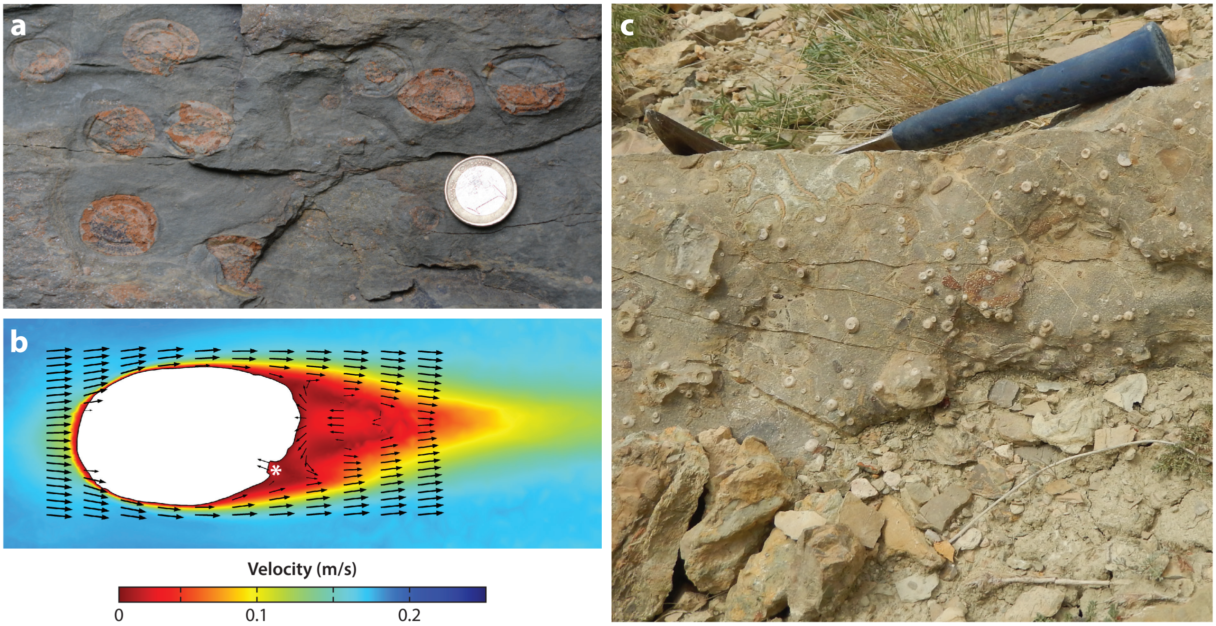


Figure 7

Cambrian echinoderm ecology. (*a*) Slab from the Furongian of Spain with specimens of the edrioasteroid *Cambraster* attached to a clayey substrate stabilized by underlying microbially induced sedimentary structures. (*b*) Horizontal cross section of flow velocity from computer simulation of water flow around the cinctan *Protocinctus mansillaensis* orientated with the mouth down current and assuming active feeding. Arrows indicate the direction and magnitude of flow. The white asterisk indicates the position of the mouth. Panel adapted from Rahman et al. (2015b). (*c*) Hardground from the Furongian of North America encrusted with discoidal pelmatozoan holdfasts.

development of stalks and stems in eocrinoids allowed them to reach greater heights above the seafloor (Sprinkle 1973, Guensburg & Sprinkle 2000, Dornbos 2008).

Other Cambrian echinoderms lack attachment structures and are therefore seen as free-living deposit or low-level suspension feeders. This includes some solutes (e.g., *Pahvanticystis* and adults of *Castericystis*), which were likely moderately mobile, moving over the sediment using the flexible proximal part of the posterior stalk and feeding on particles at or just above the sediment–water interface with their single anterior ambulacrum (Daley 1995, Noailles et al. 2014, Lefebvre & Lerosey-Aubril 2018). Stylophorans were also moderately mobile, using the ambulacrum for both feeding and locomotion (Lefebvre et al. 2019, Clark et al. 2020). Cambrian rhombiferans either rested on the seafloor or introduced the distal part of the stem into the sediment to enhance stability (Dornbos 2006, Zamora et al. 2017a). Similar to solutes, they used their erect feeding appendages for deposit or suspension feeding and the stem for locomotion (Guensburg & Sprinkle 2000). Lastly, cinctans, ctenocystoids, and *Ctenoimbricata* were either immobile or very slow moving, feeding on particles suspended in water close to the seafloor (Smith 2005, Rahman & Clausen 2009, Zamora et al. 2012). Computer simulations of fluid flow suggest that at least some cinctan species relied on actively generated feeding currents (Rahman et al. 2015b, 2020) (**Figure 7*b***), and the same may have been true for ctenocystoids and *Ctenoimbricata* (Rahman & Clausen 2009, Zamora et al. 2012).

Echinoderm ecological diversity increased steadily during the Cambrian as new groups emerged and diversified (Guensburg & Sprinkle 2000, Novack-Gottshall et al. 2022). The earliest echinoderms known from the Cambrian Stage 3 (i.e., edrioasteroids, eocrinoids, and helicoplacoids) were sessile suspension feeders, most of which attached directly to hard substrates, demonstrating that the supposed transition from mat-stabilized sediments to unconsolidated soft substrates (i.e., the Cambrian substrate revolution) was not a necessary precursor to the evolution of this mode of attachment (Zamora et al. 2017a, Zhao et al. 2022). Free-living and mobile suspension feeders (i.e., ctenocystoids and stylophorans) first appeared in the Cambrian Stage 4, with deposit feeders (i.e., some solutes and rhombiferans) emerging in the Wuliuan or Drumian. Early hard substrate attachers were absent from microbial reef cores and were instead more common in reef flanks (Álvaro et al. 2013). They were largely restricted to relatively low-energy, offshore environments (Dornbos 2006, Zamora et al. 2010), but the evolution of specialized attachment structures such as well-developed marginal rings in some edrioasteroids (Zamora & Smith 2010) and discoidal holdfasts in pelmatozoans (Zamora et al. 2010, Peel 2017) allowed them to colonize more energetic nearshore environments, including carbonate hardgrounds (**Figure 7*c***), from the Miaolingian (Peel 2017). There was a progressive increase in tiering height through the Cambrian, driven by the development of stems and stable attachment surfaces, which enabled some eocrinoids to feed at intermediate or high levels by the Furongian (Sprinkle 1973, Guensburg & Sprinkle 2000, Dornbos 2008). This trend of slowly increasing ecological diversity through the Cambrian contrasts with echinoderm morphological diversity, which increased at a much faster rate (Foote 1992, Deline et al. 2020, Novack-Gottshall et al. 2022). This supports the idea that morphological novelty preceded ecological innovation in early echinoderms (Novack-Gottshall et al. 2022).

It has been hypothesized that ecology was a key factor shaping the evolution of echinoderm body plans, with pentaradial symmetry an adaptation for a suspension-feeding mode of life (Stephenson 1967, 1974). However, as noted above, most Cambrian echinoderms, including both radial (e.g., edrioasteroids, eocrinoids, and helicoplacoids) and nonradial (e.g., cinctans, ctenocystoids, and stylophorans) forms, were likely suspension feeders. Furthermore, extant echinoderms with pentaradial symmetry exhibit a wide range of feeding modes, including deposit feeders, grazers, predators, scavengers, and suspension feeders. Together, this undermines the suggested link between pentaradial symmetry and efficient suspension feeding (Stephenson 1967, 1974), and thus the reasons why a pentaradial body plan arose in echinoderms remain unclear (Smith 2008).

7. CONCLUSIONS

The Cambrian fossil record provides valuable insights into the origin and early evolution of echinoderms. Over the past decade, our understanding of this crucial interval has increased substantially, with important new fossils described that help bridge the morphological gulf between disparate echinoderm body plans (e.g., Zamora et al. 2012, Smith & Zamora 2013, Zamora & Rahman 2014). Moreover, the implementation of rigorous quantitative methods is allowing us to tackle outstanding questions, from the phylogenetic relationships of different groups of early echinoderms (e.g., Topper et al. 2019, Nanglu et al. 2020, Li et al. 2023) to how morphological and ecological diversity changed during the phylum's initial radiation (e.g., Deline et al. 2020, Novack-Gottshall et al. 2022). Nevertheless, there remain important gaps in our knowledge of echinoderm evolution, such as how and why key characters like stereom and pentaradial symmetry first evolved, and the discovery of new fossils may be key for addressing these. Coupled with recent advances in the developmental genetics of modern species (e.g., Formery et al. 2023), this will serve to cement the status of echinoderms as an ideal model system for studying evolution through deep time.

SUMMARY POINTS

1. Stereom is the only derived character shared by all known echinoderms.
2. Echinoderms first appear in the fossil record in the Cambrian Stage 3, ~518 Ma, but probably had a cryptic history stretching back to the Ediacaran.
3. Echinoderms were widespread and morphologically diverse from their earliest appearance in the fossil record, with distinct asymmetrical, bilateral, and radial body plans.
4. Phylogenetic analyses suggest that echinoderms evolved through successive bilateral, asymmetrical, triradial, and pentaradial stages.
5. Morphological innovation allowed early echinoderms to explore new ecological niches and may have played an important role in driving their evolutionary radiation.

FUTURE ISSUES

1. Further work is needed to establish the international correlation of formations preserving the oldest fossil echinoderms from East Gondwana, West Gondwana, and Laurentia, and thereby accurately constrain the age of the first echinoderms.
2. The affinities of several fossils previously interpreted as early echinoderms, such as the Ediacaran forms *Tribrachidium* and *Arkarua* and the Cambrian taxa *Yanjiahella* and vetulocystids, remain ambiguous.
3. Molecular clock analyses indicate that the extant echinoderm classes diverged during the Cambrian, but there is no clear fossil evidence of their presence until the Ordovician.

4. Broader sampling of Cambrian fossil taxa is needed to fully resolve the phylogenetic relationships of early echinoderms.
5. Understanding how and why the pentaradial echinoderm body plan arose will require the integration of molecular, developmental, and paleontological data.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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